Plant breeding perspectives

Centennial publication of
Koninklijk Kweekbedrijf en Zaadhandel
D. J. van der Have

1879-1979

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Centre for Agricultural Publishing and Documentation
Wageningen
1979

ISBN 90 220 0697 2

Design: Pudoc, Wageningen
Printed in the Netherlands

Under the Gracious Patronage of
H.R.H. the Prince of the Netherlands

This book was written and produced
between 1975 and 1979
to mark the occasion of
the 100th anniversary of
Koninklijk Kweekbedrijf en Zaadhandel
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Kapelle, the Netherlands

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Soestdijk Palace, January 1979.

> "And he gave it for his opinion, that whoever could make two ears of corn or two blades of grass to grow upon a spot of ground where only one grew before, would deserve better of mankind, and do more essential service to his country than the whole race of politicians put together".
>
> Jonathan Swift
> "Gullivers Travels" 1726

Four years ago I was invited to become patron of the project, which, with the appearance of this volume, has now reached completion. In producing the book, the purpose of D.J. VAN DER HAVE Co., Royal Seed Producers and Merchants was to make a significant contribution to solving the grave problems presented by a rapidly expanding world population.

Their principal aim was to demonstrate the potentialities of plant breeding as an essential starting point for improving world food production. The outcome is the publication that now lies before the reader, Plant Breeding Perspectives.

The MIT report entitled Limits to Growth, published for the Club of Rome's project in 1972, shocked the world. But since that time, a gradual change has become apparent in the approach to the complex problems posed in it. One of the views to emerge is that, given a balanced world economic structure, this planet of ours, with the fundamental assistance of the plant breeder, is capable of providing food in sufficient quantities for all our needs in the coming decades. It is clear that for this purpose the role not only of plant breeding but of all scientific methods of agriculture will be of the utmost importance.

It is a matter of great satisfaction that the VAN DER HAVE Centennial Committee, in close collaboration with FAO, have been able to draw upon the intelligence, energy and time of such eminent plant breeders as those who, from all over the world, have contributed the chapters which follow. Their contributions are evidence that they have taken to heart the far-sighted words of Jonathan Swift, written two and a half centuries ago. I congratulate the D.J. van der Have Co. on the publication of this book and on the effort that has been put into it by all concerned.

Bernhard

The Prince of the Netherlands.

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Foreword

The decision to produce this book was taken in 1974. At that time, public attention was beginning to focus on the world food problem, partly owing to the interest aroused by the so-called 'green revolution' and the award of the Nobel Peace Prize of 1970 to the plant breeder Dr. Norman E. Borlaug, and partly also in response to the publications of the Club of Rome. As a contribution to the continuing discussions on this important subject, the management of the D.J. van der Have company felt that a broad survey of the role and potentialities of plant breeding in the production of food crops, prepared by a panel of plant breeders from both developing and developed countries, would be a valuable and worthwhile undertaking.

The breeders invited to take part in the project were:

Dr. W.L. Brown (USA)
Dr. T.T. Chang (Philippines)
Prof. K. Gotoh (Japan)
Prof. D.E. McCloud (USA)
Dr. B.R. Murty (India)
Prof. R. Riley (UK)
Dr. Yu. M. Sivolap (USSR)
Prof. J. Sneep (Netherlands)
Dr. H.G. Strube (Federal Republic of Germany)
Dr. M.S. Swaminathan (India)

The preparation of the book has occupied five years and has involved many panel meetings, excursions and discussions in France, India, Iran, Japan, Kenya, the Philippines, Romania, Taiwan, the United Kingdom, the USA and the USSR, as well as the Netherlands. These included a special meeting of nutritionists held at Evian for the preparation of Chapter 1. In compiling the remaining chapters, the panel was also able to enlist the aid of specialists in other fields.

The company is much indebted to the members of the Honorary Committee for their encouragement and support. It also acknowledges with gratitude the time and energy devoted to the project by the members of the panel and all other contributors. In particular, our special thanks go to Prof. J. Sneep who, in collaboration with A.J.T. Hendriksen, undertook the heavy task of collating and editing the contributions of the individual authors, and to Miss. O. Holbek who, as coeditor, revised the English text. The company is grateful to the Commonwealth Agricultural Bureaux for making Miss Holbek available for this work. Thanks are also due to the many members of the company who by personal effort and the sacrifice of spare time have made it possible to bring the book to completion. It is hoped that this centenary publication will not only encourage the company's employees in their future activities but will also, on a wider scale, prompt further constructive thinking towards a better world.

June, 1979

D.J. van der Have

A. Dirkzwager

A.J.T. Hendriksen

Preface

'Plant breeding perspectives' is intended for rather a wide circle of readers. Primarily it is designed to give practical plant breeders and students of plant breeding a panoramic view of the total subject and its main implications, especially those aspects that have a bearing on food production and the relative priority to be accorded to breeding for yield, quality and stability. It should also be of use in providing guidelines for those concerned with plant breeding strategy on a broad scale, including administrators responsible for recommending or authorizing plant breeding projects, members of bodies dealing with regulations on seed and planting materials, and agricultural consultants advising on aid to developing countries. At the same time, it is hoped that agronomists, plant protectionists and nutritionists will find matters of interest to them in the more detailed sections on special topics. The volume should not, however, be regarded as a textbook or handbook. Our aim has been, rather, to describe, by means of selected examples, important features in the practice of plant breeding, and to examine how these can be put to use in the future.

The book has many authors, the different chapters being written in part by members of the panel and in part by specialists in various fields. Every chapter is, however, the outcome of full discussions within the panel and of consultations with breeders and other workers in Europe, the USA, Japan and several countries in the developing world. The reader will have little difficulty in detecting a diversity of style and approach corresponding to the diversity of authorship. This variation is deliberate: the editors feel that by avoiding the imposition of a rigidly uniform pattern for all the papers, it has been possible to retain a certain liveliness and immediacy.

The opinion has been expressed that breeders can furnish at least a quarter of the increase in food production that is still required for the future well-being of mankind. In part this is a question of reducing not only the gap between experimental yields and those which are biologically possible, but also the gap between actual on-farm yields and experimental yields, which is due to such constraints as pests, diseases and drought. Equally important, however, are improved methods of cultivation, better water management, land reclamation and further increases in soil fertility. Socio-economic patterns and ways of reducing postharvest losses and improving the distribution of agricultural produce are also important factors. All these considerations and their relation to plant breeding are the concern of this book.

The first three chapters deal with basic matters: the present world food situation, some of the physiological constraints that the plant breeder has to work with, and the genetic resources upon which much future breeding will depend. The longest and most detailed chapter, on current breeding methods, includes specific examples of current work in crop breeding. Problems of adaptation, resistance to pests and diseases, and questions having special relevance to developing countries form the subject matter of the next few chapters and are followed by a survey of methods likely to come into greater use in the future. The final link in the chain that runs from geneticist and breeder to the farmer who ultimately grows the crop is provided by a chapter on seed production and distribution. As the title indicates and as will be clear from the perusal of the chapters already mentioned, the scope of the book includes not merely past and current work but also future potentialities. The final chapter takes up this latter theme and examines trends which are likely to be of importance in the remaining years of the century.

It was felt that a subject index would be of limited value for a book in which the breadth of treatment varies so greatly from chapter to chapter. Instead we supply a detailed list of contents which, together with the summaries of the principle themes and conclusion presented at the head of each chapter, should duly guide the reader to those aspects of the subject which particularly interest him.

J. Sneep and A.J.T. Hendriksen (Editors)
O. Holbek (Coeditor)

1 Food supplies, nutrition and plant breeding

In spite of increases in world food production, the food intake of large numbers of people, and especially of children below the age of five, is too low for health. Among major reasons for this are the high growth rate of the world population, inadequacies in the distribution of food, and postharvest losses. Cereals are the most important staple food for most of the world, providing about half of the total protein and energy intake, and more than half in many developing countries. Since World War II, the increase in total food production has been more rapid than the increase in world population. In some developing countries, however, the increase in output has been overtaken by population growth. Before 1940, Asia, Africa and Latin America were net exporters of cereals; they are now importers. In the late 1960s, grain stocks in the developed countries reached a peak and prices of wheat and rice fell. Sufficient food for the world's needs seemed to be assured and the Green Revolution gave promise of more to come. But in 1972 a reversal took place: the Peruvian anchovy catch, the world's main source of fishmeal protein, fell dramatically and as a consequence soya bean stocks were depleted. Cereal stocks also dwindled, as a result of crop failures which had led to a drop in total cereal production of about 3%. The USSR, previously self sufficient, began to purchase wheat from the USA, and India and China were also forced to import wheat. The food crisis was rapidly followed by a marked rise in prices of fuel and fertilizers. The causes of undernourishment in developing countries are complex, involving not merely food production but also socioeconomic barriers such as distribution, purchasing power and eating habits; the existence of inadequate farming systems; the difficulty of combining high yields with resistance to adverse biotic and abiotic factors; and lack of food storage facilities. Improving the stability of food supplies by international food security systems would help to insure against incidental shortages. But responsibility for such systems is still a problem in the field of international cooperation. Most of the undernutrition in the developing world is simply due to an inadequate intake of energy, usually as a result of poverty. Where energy intake is sufficient, most protein requirements are also met adequately. The first goal of any food policy should be to cover the energy requirements of a population. Changing the aminoacid pattern of cereals or other crops by breeding is probably less important than increasing yield and yield stability. Food quality can sometimes be improved by breeding. Among the main objectives by which plant breeding can contribute to the prevention of undernourishment are:

- *the improvement of yield potential and stability of yield in cereals,*
- *the improvement of yield in grain legumes,*
- *the maintenance of food quality in crops bred for improved yield.*

Introduction

Since the world food crisis of the early 1970s, interest in world nutrition problems has been growing steadily. The crisis drew attention to the interdependence of food production, trade, stocks and prices and to how seriously unprepared the world was, both for vagaries of weather and for man-related environmental factors, including civil strife. Although the accuracy of objective measurements of the world food situation is a matter of argument, present indications are favourable, and the sense of crisis which prevailed at the World Food Conference in Rome in November 1974 has abated. Since cereals are the basic foodstuff in much of the developing world and are the only major foodstuff transported in large quantities in international trade, quantitative appraisals of the world food situation are now commonly based primarily on the prevailing cereal situation. Half of the protein and energy consumed by humans comes from cereals: wheat, rice, maize, millet, sorghum, rye and barley. In the poorer countries these may even provide 60-70% of the total energy consumption. When cassava, sweet potato, potato, yams, banana, common bean, soya bean and groundnut are added to the cereals, about 90% of all food requirements in the developing countries are covered. In many cases the last-mentioned crops are also of growing importance as sources of farm income and foreign exchange. The changes in world cereal production during the period 1975-1977/1978 have been markedly more favourable than in the previous three years. Many governments in both developing and developed countries are now concerned with maintaining farm prices at levels necessary to provide production incentives to farmers.

In spite of increased food production, which usually increases per caput food availability, and in spite of lower prices and the accumulation of stocks in the major wheat-exporting countries, the food intake of large numbers of people in the developing world is by almost any standard too low. There are two main reasons: firstly, a substantial part of any increase in food production is absorbed by current population growth; and secondly, the per caput gains in production do not necessarily result in equivalent increases in available food or in an adequate distribution of food.

The adequacy of the food supplies (in terms mainly of dietary energy rather than protein) can be evaluated against a scale of requirements. On this basis, the most deficient regions are the tropics of Africa and Asia. From the latest FAO data (1977f) on per caput dietary energy supplies it is seen that whereas in 1970 and 1971 92% of Africa's nutritional requirements were met, in 1974 the figure was 91%. For tropical Asia the figures were 94% and 95% respectively in 1970 and 1971, and only 93% in 1974. In Latin America and the Near East there was a very modest increase, from 105 to 107% and from 98 to 100% respectively. Since actual requirements, real per caput food availability and real food consumption are all uncertain, the World Health Organization (WHO) is rather cautious in indicating absolute numbers of undernourished people. On the other hand, FAO estimates that, although their relative number has decreased, the total number has risen from 400 million (in 1970) to 450 million at present. These figures are based upon food balance sheet data collected annually by FAO from 1970 onwards. FAO also estimates that about 40% of the children under five years of age in the developing world may be inadequately nourished, a fact which accounts directly or indirectly for half of the high death rate in this age group. The damaging effects of undernutrition, especially during the early years of growth, can be irreversible with respect to physical and mental function. Consequently, a portion of the survivors can suffer handicaps of learning and work capacity.

International organizations are very much aware of the situation. Although some action started soon after World War II, it is mainly in the last few years that several important conferences sponsored by the United Nations have attracted world attention. In the early 1970s the Consultative Group for International Agricultural Research (CGIAR) began to support the research of several major international research centres, mainly aiming at increasing food production. In 1974, the third World Food Conference was held in Rome, and in 1977 both the WHO Assembly (Geneva) and the World Food Council (Manila) studied the problems involved and formulated useful recommendations.

In 1978 the most recent proposals for action were made by the UN Administrative Committee on Coordination (ACC) in Rome. These included:

– Appraisal of current information on the state of nutrition and on the impact of current policies and programmes and the opportunities for action.

– Supplementary action in the area of food production, storage and marketing. This could involve: nutritional considerations in agricultural planning; encouragement of production of food legumes; study of the role of women in food production, home processing and marketing; and reduction of postharvest losses.

– Nutrition intervention aimed at groups at risk, for example, iodization of salt for the prevention of endemic goitre.

– Involvement of the family and community in nutritional improvement.

1979 is the United Nations International Year of the Child. It is infants and preschool children who are the principal victims of malnutrition.

The rest of this chapter gives an analysis of the world food situation and the effects of agricultural development on food supplies, followed by a diagnosis of important problems of world nutrition, with notes on several deficiency diseases, and finally a survey of the nutritional value of the main food crops, with suggestions as to how plant breeding can help to improve human nutrition.

However, it should not be forgotten that the question is not solely one of greater inputs into agriculture, resulting in more employment, higher purchasing power, increased per caput food availability etc. If food production in the developing countries is to keep pace with the growing population in the Third World, there will also have to be a restructuring of distribution systems and attitudes. Changes in attitude will be necessary not only in developing countries but also in the developed world.

World food situation: past, present and future

FOOD SUPPLIES SINCE WORLD WAR II

Before 1940, Asia, Africa and Latin America were net exporters of wheat, rice, maize and other cereals to the more industrialized nations. By the end of World War II, however, they had lost their surplus, increases in demand exceeded production increases, and the net flow was reversed. Their net exports of cereals averaged 5 to 10 million t per year in the period 1934-1938 and their net imports of cereals from the developed world rose from an average of 4 million t a year in 1948 to some 25 million t in 1964, and a 35 million t average for the period 1974-1976, despite severe import restrictions due to foreign exchange deficits. Fig. 1.1 shows some details of trade in grain. (Note: according to FAO terminology, 'cereals' include wheat, rice, maize, barley, oats, rye, millets and sorghum; 'grains' are cereals excluding rice; 'coarse grains' are cereals excluding rice and wheat. It is not always clear in which sense 'grain' is used in the literature).

According to FAO projections, the cereal deficit in the developing countries will be 71 million t by 1985, compared with 47 million in 1977, an amount that has already caused severe difficulties.

Throughout the postwar years, world food production rose more rapidly than population growth. Surprisingly, indexes of agricultural production show that farm production has been growing at about the same rate in both developed and less developed areas during the past two decades, that is by 2.8% annually. In the developing countries this increase has been steady, but the increase in population growth rate has been rather explosive, from 2.1% in 1950 to 2.7% at present.

Consequently, the increase per annum in per caput food availability is lower today than in the early 1950s. In addition to population growth, there has been a slight but steady growth in average annual income since 1960, and the two factors together result in an increase in food demand of about 3.5%. During the period when production has been increasing less rapidly, wheat imports have filled much of the gap. Fig. 1.2 shows total and per caput food production indices for high-income countries and the poorest countries in the period 1961-1965. These global figures, however, conceal many facts, such as the unequal distribution of production increases among countries and of food among different economic and social groups within countries. As the World Food Conference Assessment says: 'In such widely dispersed countries as Brazil, India and Tunisia, the 20% of the population with lowest income has half the per capita energy intake of the top 10%.' Thus the degree of undernutrition is much worse than the national averages suggest. Also hidden is the fact that in the poorest countries agricultural production has often not kept pace with population growth and that there has been no increase in per caput food supplies at all; in Africa actual decreases have been observed.

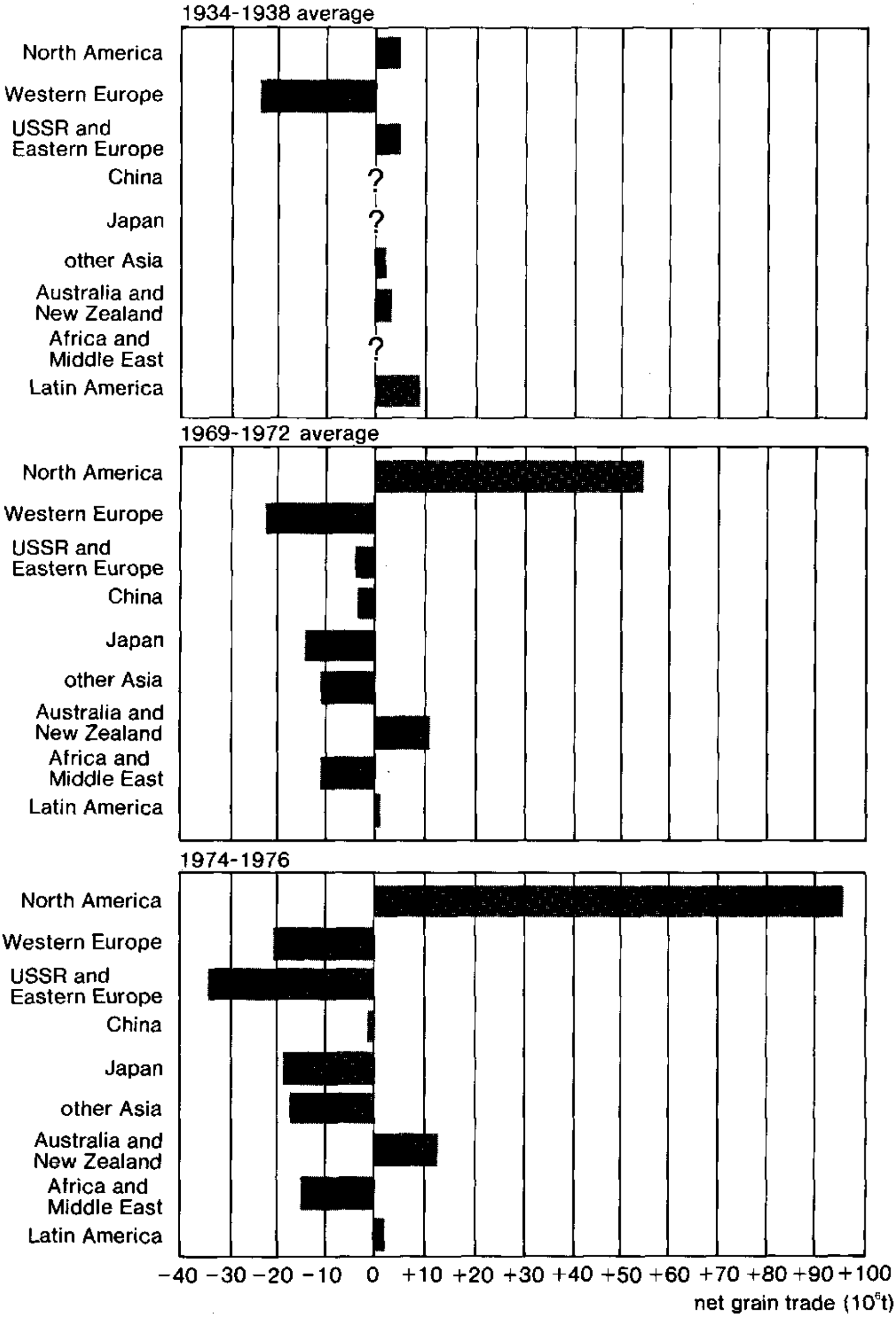

Fig. 1.1. Changes in grain trade between 1934/38 and 1974/76 (from: Brown, in Wortman, 1976).

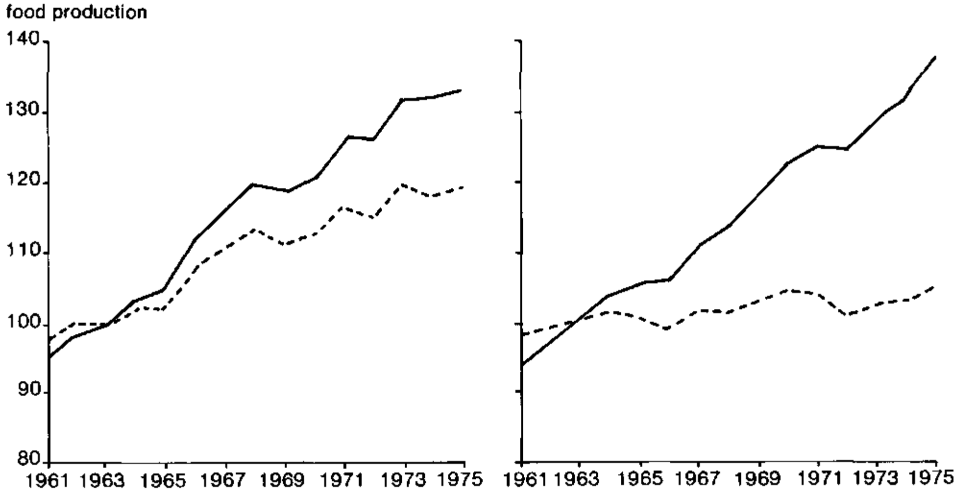

Fig. 1.2. Food production in developed (left) and developing (right) countries. Continuous line: total food production. Broken line: food production per caput (from: FAO, 1977f).

ORIGINS OF THE FOOD CRISIS

During the 1950s and 1960s the trends in agricultural production were overshadowed by the existence of substantial stocks of farm products, especially of cereals.

These stocks (which were expensive to maintain) made it possible to undertake food aid programmes and even encouraged those countries where apparent surpluses existed to reduce production, particularly North America and Australia. The main problems of reserves are always who should hold them and who should pay for them. However, the existence of the stocks gave the world a sense of security, though a closer analysis would have revealed that there was little justification for such complacency. In fact, the developing countries were able to meet the disparity between domestic production and demand only through imports from the overproducing parts of the world. The widespread fear of an approaching world food famine in the mid-1960s had been allayed by the late 1960s. World grain stocks reached a peak, and subsequently wheat and rice prices fell (Fig. 1.3).

Although there had been at least two earlier waves of pessimism regarding world food supplies since the end of World War II, by the early 1970s abundant food supplies seemed to be assured, thanks to the so-called Green Revolution (which began in 1968-69) and also to the harvest from the seas, which at that time was still rising. The prospect was so rosy that in 1969 FAO suggested that the food problems of the future might be those of surplus rather than shortage! Then world wheat production began to fall, while consumption continued to rise, and by 1971 world grain stocks had dropped sharply.

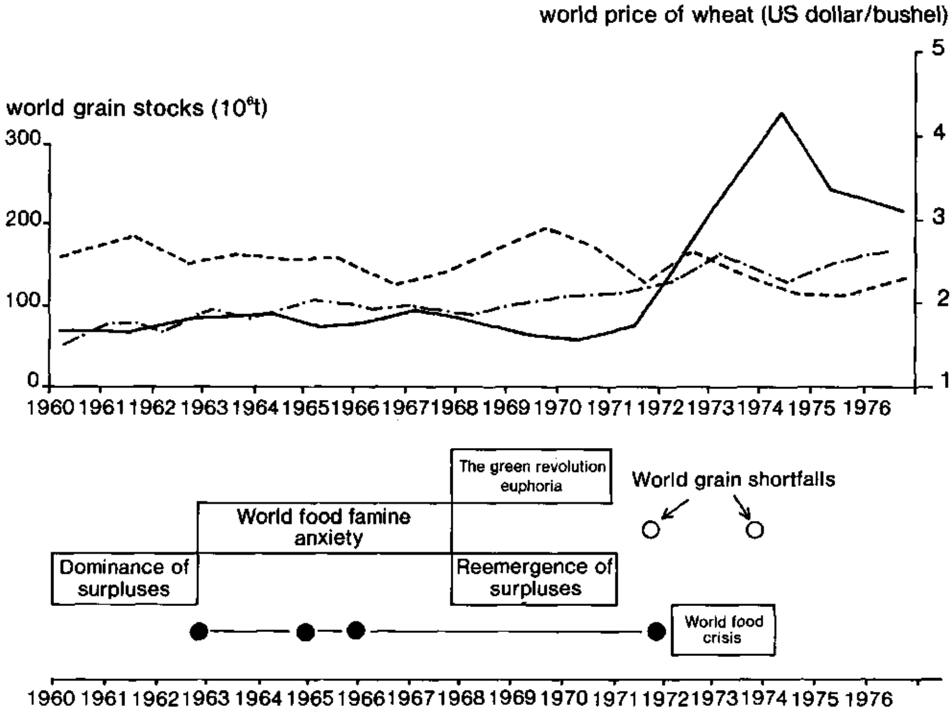

Fig. 1.3. Changes in world grain exports -·-, stocks --- and price —, 1960-1976 (adapted from: USDA, 1974).

Similar, though less pronounced, downward trends occurred for stocks of other important staple foods such as coarse grains, soya beans and sugar. Thus, almost unnoticed, the world slipped into a situation where supplies were insecure and highly vulnerable to unforeseen contingencies.

In due course the shocks came, not one at a time, but several together:

– Although the total catch of the fishing industry, an important source of protein for many poor nations, remained steady in 1970 and 1971, in 1972 the Peruvian anchovy catch, one of the world's principal sources of fishmeal protein for animal feed, failed almost totally. The demand for soya beans, the other main alternative protein source, was reinforced: soya prices quadrupled within a few months and stocks of soya beans fell rapidly.

– In 1972, for the first time for more than two decades, overall world food production of cereals actually fell, by about 3%. The first crop failure was in the USSR: 30% less winter wheat. Massive purchases of wheat by the USSR followed, eliminated American reserves and caused the international prices of wheat, maize and rice to rise sharply (Fig. 1.3). In addition, India and China, normally nearly self sufficient in cereals, had to import wheat. As these countries account for almost half the world population and half the wheat consumption, even relatively small fluctuations in their production will exert a magnified effect on world import demand. There were also droughts in other areas of the world, for instance in the Sahel countries in Africa, and war and floods in Bangladesh, all in 1972. Existing stocks of cereals were insufficient to bridge the shortfall between production and demand. In 1973 prices for most staple agricultural products rose to unprecedented levels.

– Owing to the oil crisis of 1973, fertilizer prices rose almost as sharply as grain prices. The increase in oil and fertilizer prices made it difficult for farmers in parts of the developing world to profit from the Green Revolution. The increased oil prices also dislocated the economies of the wealthy nations, reducing their contributions to international aid.

Further absolute reductions in stocks took place, although, because of the steepening world economic recession, the demand also fell.

In spite of a considerable improvement in the world cereal harvest in 1973/1974 – with record productions in some cases – the increases failed to match the new demands, and stocks were far below the 18% of annual world consumption which FAO considers to be the minimum ratio necessary to ensure world food security. The USSR, self sufficient before 1972, has since then continued to purchase wheat from the USA, right up to the present.

For sugar, the most dramatic developments did not occur until 1974/75. Consumption had by then outstripped the yearly increases in production. Carryover stocks had been reduced by three years of deficit. The 5% rise in world production in 1973/1974, compared with the year before, was insufficient to compensate the world deficit and this, combined with other factors, caused the world price to double: consumers faced rapid price increases, which were, however, followed again by a drop.

Summarizing, we may note that the real world food crisis, which first became apparent towards the end of 1972, developed with disturbing suddenness, through a combination of long-term problems and temporary setbacks caused by adverse climatic conditions. Shortages developed as a result of continuing population increases, crop failures, a sharp rise in oil prices and consequent reductions in food aid shipments, resulting in the starvation of many thousands of people. Nevertheless, major studies carried out in 1974 to investigate the causes and nature of present world food problems, revealed little anxiety for the future.

POPULATION GROWTH

The world's population is believed to have remained essentially stable from biblical times to about 1750. The current explosion, of which some 80% is taking place in the less developed countries, is however not unique, for similar bursts have accompanied earlier technological breakthroughs. But as such bursts were always followed by contraction, the overall picture is of a fairly stable population. The nature of the forces that ultimately caused a levelling-off is not quite clear. Such factors as food supplies, territory and water, which today are regarded as limiting to population growth, cannot have been of importance in palaeolithic times, the era of the first population burst followed by a contraction.

Although concern at the population explosion only became world-wide in the 1950s – the first 'brainstorm' meeting was held in 1954 in Rome, the second in 1965 in Belgrade, followed by the first UN World Population Conference in 1975 in Bucharest – it was as early as 1798 that Thomas Malthus, in his *Essay on the Principle of Population*, wrote 'I think I may fairly make two postulata. First, that food is necessary to the existence of man. Second, that the passion between the sexes is necessary, and will remain nearly in its present state. Assuming then, my postulata as granted, I say, that the power of population is indefinitely greater than the power in the earth to produce subsistence for man. Population, when unchecked, increases in a geometrical ratio. Subsistence, increases only in an arithmetical ratio. . . By that law of our nature which makes food necessary to the life of man, the effects of these two unequal powers must be kept equal. . . I see no way by which man can escape from the weight of this law which pervades all animated nature. . . '

That the resulting misery and vice described by Malthus have so far been held at bay is of course not due to population control – man's numbers have increased roughly four and a half times since 1798 – but to increased food supplies. The 19th century witnessed great agricultural changes. Vast new acreages were brought under the plough in all continents except Europe, in some cases together with improved irrigation. This period of expansion was immediately followed by a series of technological breakthroughs. By the 1930s, Malthus and his gloomy forecasts had been pretty well forgotten.

Advanced countries were concerned not so much with overpopulation as with underpopulation. European governments in particular pursued programmes of population encouragement in order to enhance their political and military power. On the agricultural side, superabundance, not shortage, seemed the key problem, with most industrial states adopting tariffs and other restrictive measures.

Whereas the world population in 1930 was 2000 million, it reached 3000 million in 1960, stands at 4000 million today and is heading for 6000 million by the end of the century, assuming that the annual rate of increase in the developing market economies will gradually decline from 2.7% today to 2.2% by the year 2000. About 90% of the additional 2000 million will be in those countries.

World War II can be regarded as a turning point in many respects, certainly from the point of view considered in this chapter. With the decline of Europe a new set of superpowers emerged, together with a Third World of former colonies harbouring the bulk of the world's population. The emergence of the latter took a number of forms, including political independence and the introduction of public health measures allowing a rapid reduction in death rate – without a simultaneous reduction in birth rate. These are the underlying causes of the third great population increase in history, in addition to the industrial and scientific revolution. The rapid population growth characterizing the Third World today was to be seen in the industrialized countries a century or more ago (Fig. 1.4). The initial stability of population growth

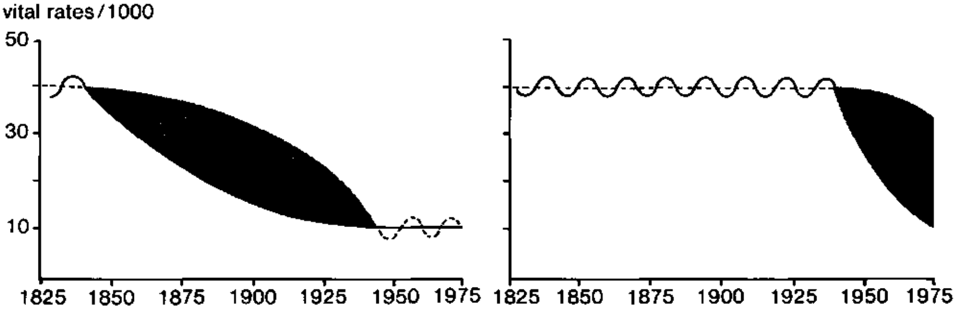

Fig. 1.4. Population growth in developed (left) and less developed (right) countries, 1825-1975 (schematic). Birth rate ---, death rate ——. (from: Poleman, 1975).

is characterized by both high birth and death rates. Then, as public health measures are introduced, the death rate drops. Birth rate, however, remains at its old level and a period of population 'explosion' sets in. Then the birth rate falls in its turn and population growth again approaches stability, but at a much lower level. Most of the industrialized countries have passed through this transition and have reached, if not precisely zero population growth, the condition immediately preceding it. For them the transition time averaged between 50 and 100 years.

Virtually all of the less developed countries have passed through the stage of declining death rates and are in the interval of maximum population growth. The world increase in population, recently estimated at 80 million people per year, is most rapid in the areas that are experiencing the greatest nutritional difficulties. Today, however, there is a tendency towards slightly declining birth rates, especially in some 15 or more of the smaller countries of the Third World, notably South Korea, Cape Verde, Mauritius and Sri Lanka. The life expectancy, infant mortality, and death and birth rates in these countries are such as are usually only achieved in societies with much higher incomes. If other low-income countries had similar death and birth rates, world population growth would not be so alarmingly high.

These heartening results seem to be associated with a wide range of programmes for food distribution, education, health services and land tenure, and other labour-intensive rural programmes, but far too little is yet known of the specific relationships and the different circumstances involved. More research is needed to introduce more appropriate birth control systems adapted not only to national but also to nutritional situations. However, for family planning to be rapidly introduced, parents must realize that two live births are no longer necessary to ensure that one child will reach maturity.

FACTORS CAUSING FAMINE, CHRONIC UNDERNUTRITION AND HUNGER

The history of man is punctuated by frequent famines. Practically every year since the end of World War II there has been a serious famine somewhere, particularly in Asia and since 1958 in Africa. Almost all recorded famines have resulted from widespread crop failure, caused by drought, flood or earthquake, crop diseases or pests, or sometimes by the impact of war. There is a sharp difference between a famine and a state of chronic undernutrition, such as is endemic in some populations. Both situations, however, cause hunger, and may be followed by death. For those who survive a critical famine, health is usually restored after food has been supplied, whereas people in a state of chronic starvation may be mentally and physically crippled as long as they live. Among the long-term consequences of many famines is the destruction of seed for future crops, which makes it difficult for farming to return to normal when the famine is over.

Famine can be attacked directly if it occurs in a definable area and has a finite duration. As long as food is available somewhere, relief agencies can deal with the crisis. Undernutrition, on the other hand, which afflicts a far larger proportion of mankind, is harder to define and to attack. It is often a chronic condition and to many observers it seems to be getting worse in certain areas. Owing to its chronic character it mainly affects children in the lowest-income groups and can lead to irreversible damage to their physical and mental condition.

The reasons for hunger and undernutrition in developing countries are many and complex and include such interdependent factors as personal income levels, employment and purchasing power, levels of food production, place where the food is produced and how it is distributed, rate of population increase, national and international income levels and their rates of change, the quality of the available food, and eating habits. Behind these factors lie the institutional policies, and the technological factors that affect how resources are used in a particular physical and social environment. And underlying everything is the political will, or lack of it, to combine these factors more effectively.

The immediate cause of hunger in an individual family is often poverty, and poverty means insufficient and poor-quality food. This interacts with infection, poor social conditions and other typical elements of a poverty environment.

The extent of world hunger is increased by instabilities in food supplies, particularly in the short term, resulting mainly from (a) the inability of farming systems in much of the world to combine high yields with resistance to weather aberrations and pests, (b) inadequate food storage facilities on the farm and elsewhere along the distribution chain and (c) restraints on the movement of food from areas of surplus to areas of deficit. These factors can all be improved.

World malnutrition is sometimes seen solely or primarily as a distributional problem. This is often true: national and international food distribution is indeed much in need of improvement, particularly distribution to pockets of especially severe undernutrition and starvation.

FAO has shown that in 1975 the average world food supply per caput – the food availability – was about 10,750 kJ per day, and about 13,860 kJ for developed countries. FAO places the average nutritional requirement for countries with a developing market economy in the 9240-10,080 kJ range, and the *average* per caput energy production in these countries now falls within this range. Nevertheless, there is still much undernutrition and no foreseeable prospect of improvement, because technical and other difficulties prevent a near-equal distribution. Improved distributional policies alone might alleviate the most pressing needs and they may, in time, come close to eliminating undernutrition and starvation as major global problems. Possibly a better way of solving the problem is to increase purchasing power by stimulating employment in rural areas, as has been done, for instance, in the 'food for work' programmes in India. This may lead finally to a sufficient per caput consumption and not only a sufficient average per caput availability.

SOCIOECONOMIC FACTORS AND FOOD AVAILABILITY

Until recently, discussions about food supplies and population have tended to treat the world as one unit (compare the first in contrast to recent reports of the Club of Rome). With regard to food availability, the nations of the world are now frequently divided into five groups:

1 The industrialized nations, where food is plentiful but pockets of poverty persist. Here governments could act through assistance to the poor and nutrition-education programmes. The chief members of this group are the USA, Canada, the nations of Western Europe, Australia, New Zealand, Japan, Israel and South Africa, which total less than 800 million people. Their gross national product (GNP) per caput in 1975 was on average $4500. Their greatest nutrition problems are the result of poor-quality diets and over-eating.

2 The nations with centrally planned economies, where, irrespective of economic philosophy, an egalitarian pattern of income distribution together with government control of food supplies and distribution have seemed in the past few years to insure their populations against undernutrition. In this category are mainland China, Mongolia, some Southeast Asian countries, Eastern Europe and the Soviet Union with a total population of some 1300 million. Their GNP per caput is probably in the lower range of the middle-income developing countries.

3 The nations of the Organization of Petroleum Exporting Countries (OPEC), whose overall wealth is undeniable but whose pattern of income distribution does not ensure that this wealth will benefit the poor.

4 A group of countries in Asia, the Near East and Latin America, which at present are virtually self sufficient in food. The demand, however, is limited by the uneven distribution of income, as reflected in the undernutrition of large sections of the population. In Brazil, for example, with the highest economic growth rate in the world, malnutrition is rampant in the northeast and in the shanty towns surrounding the large cities.

(The third and fourth groups of nations are the middle-income developing countries, which include about 600 million people with a GNP per caput in 1975 of about $950. This group of countries has the highest rate of population growth (about 2.8% annually) because their death rates have dropped far more rapidly than their birth rates).

5 The nations designated by the United Nations as 'least developed', which are spread across tropical Asia and the middle of Africa, include about 1300 million people. They have too few economic resources to provide for the people in the lowest-income groups. Their GNP per caput is under $200. Many of these countries are exposed to recurring droughts, floods or cyclones; some have recently been ravaged by civil strife; and they are all poor in natural resources and investment capital, many of them also in arable land. These are the countries that suffer the severest hunger and undernutrition, provide the least amount of food per person, and have no capabilities for increasing production per person or for financing imports. A handicap for many developing countries is their small size; in about 70 of them the population is less than five million, and in half of these it is less than one million (based on the 1975 FAO statistics). Such nations, many of them newly independent, cannot expect to develop for themselves the full range of scientific and other professional services required in fields that are important to development; they must rely on external resources. Of the 44 countries listed by the United Nations as being 'least developed' or as being 'most seriously affected', 36 have become independent since 1945, 29 of them only since 1960. The departure of the colonial powers left many of them without the skills needed to improve food crop production, with weak institutions and in many cases without the reliable market outlets or the sources of supply that had existed when they were part of a colonial system. Therefore it is not surprising that undernutrition is widespread in these countries.

It is estimated that 94% of the people who receive insufficient energy and protein live in developing countries. According to FAO (1977f), out of 128 developing countries, approximately 70 had a deficit in food energy supplies in 1974. Africa has the largest number of such countries, nearly half, followed by Latin America, the Far East and the Near East. In the Far East and Africa nearly 30% of the population probably suffers from significant undernutrition; in the Near East and Latin America the figure is 15%. Relevant information from the Asian centrally planned economies is incomplete.

Even after independence, the attention of government and industry has tended to remain centred on cash crops that can generate foreign exchange, often at the cost of food crops. There has been little concern with providing research and training or establishing the marketing systems that characterized former successes with export crops.

Developing countries are agrarian, with 50 to 80% of their population in rural areas, often far from centres of government. The magnitude of the task in agriculture is colossal. Every published study shows that a near doubling of food production is required if these nations are to break their dependence on food aid, reach minimum levels of food production and achieve higher rates of economic growth.

The recent introduction of a more intensive cropping system, which takes into account agricultural resources, population density, food preferences, nutritive needs and the state of technology, is beginning to have an adjusting effect upon food supplies. In some countries, potatoes and rice produce almost twice as much energy per unit of surface as wheat (Table 1.1). If the population presses heavily on the food

Table 1.1. 1976 Crops of important foodstuffs in yield, energy and production (from: FAO, 1977b).

Foodstuff	Yields (t/ha)				Energy (10^6 kJ/ha)				Production (10^6 t)			
	S. Am.	Afr.	Asia	Eur.	S. Am.	Afr.	Asia	Eur.	S. Am.	Afr.	Asia	Eur.
Potato	8.9	8.2	10.8	17.7	30.0	28.6	37.7	62.0	9.2	4.0	59.1	109.7
Cassava	12.3	6.9	10.7	–	77.5	43.5	67.3	–	32.1	41.9	30.0	–
Sweet potato	9.5	6.0	9.3	12.4	44.4	28.2	43.9	58.0	2.7	5.1	126.2	0.1
Pulses	0.5	0.4	0.7	0.7	7.6	6.0	9.7	9.5	2.7	5.1	28.4	2.5
Rice	1.8	1.7	2.5	4.8	24.5	24.4	34.4	66.6	13.6	8.0	312.5	1.8
Maize	1.7	1.2	1.9	3.8	24.8	18.0	29.1	57.0	27.3	23.7	55.1	44.5
Wheat	1.3	1.2	1.4	3.2	17.0	15.7	18.5	41.5	16.1	10.8	110.7	85.2
Soya bean	1.7	0.9	0.5	1.5	27.7	13.7	7.7	23.4	12.3	0.1	13.8	0.4

S. Am. = South America; Afr. = Africa; Eur. = Europe.

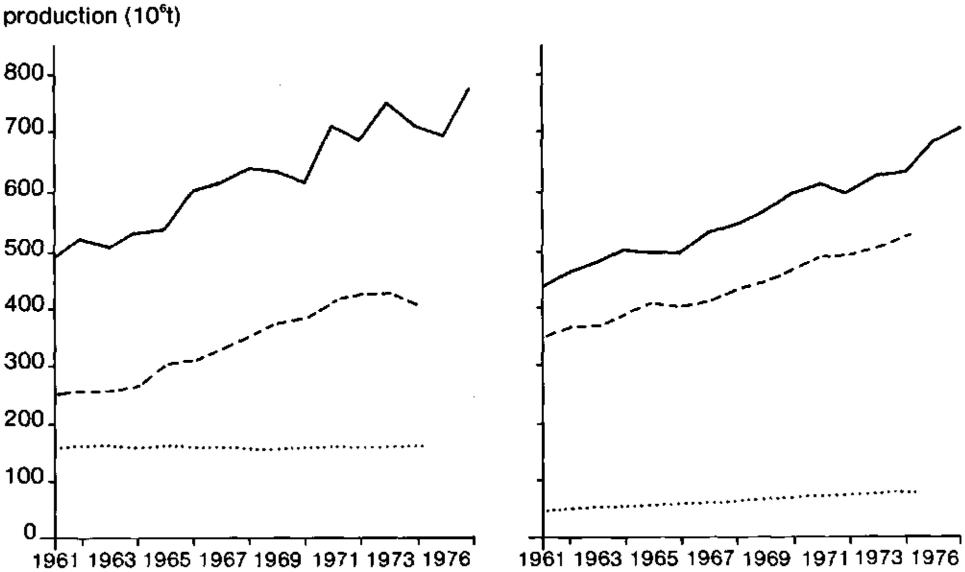

Fig. 1.5. Production and use of cereals for food and feed in developed (left) and developing (right) countries, 1961-1976, in 10^6 t. Production —, feed ---, Food . . . (from: FAO, 1977).

supplies, the production of such crops becomes more intensive: witness the high percentage of land under maize and potatoes in the Sierra region of Peru. In countries which live close the margin of want, the livestock population is also very small. It appears to be historically inevitable that as wealth increases the consumption of animal products also increases (cf. Fig. 1.7). This means that more of the basic foodstuffs (mainly cereals, but also legumes and even fish) are fed to domestic animals such as cattle and poultry. The efficiency of the conversion of plant food into animal food varies with the animal, and also with the type of animal product, but is in most cases rather low. However, here it should be taken into consideration that 70-80% of what is used as feed is unsuitable for human consumption. Moreover, the nutritional value – particularly the protein value – of animal food is often much higher than that of plant food. Fig. 1.5 shows the use of cereals for food and feed in the developed and developing countries in 1961-1976.

The degree of economic development and level of income have important implications for the types of food which can be produced to fill human needs. In Fig. 1.6 the dietary patterns, expressed in energy, show clear shifts in the consumption of

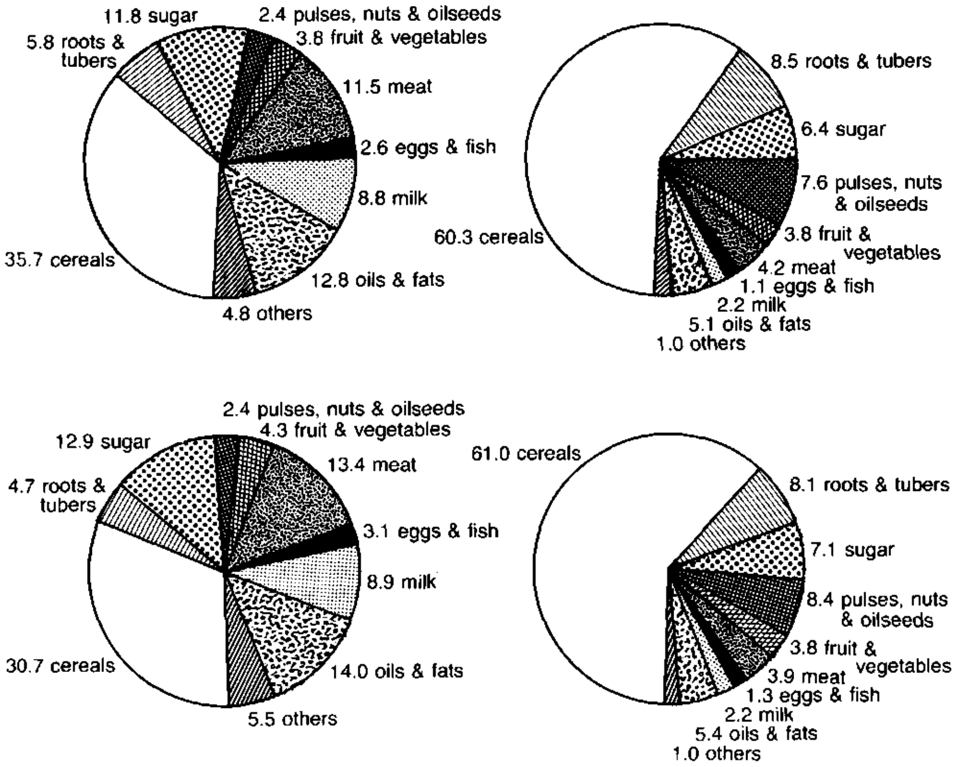

Fig. 1.6. Dietary patterns in developed (left) and developing (right) countries, 1961/63 (top) and 1972/74 (bottom), in percentage share of food groups in per caput energy supply (from: FAO, 1977f).

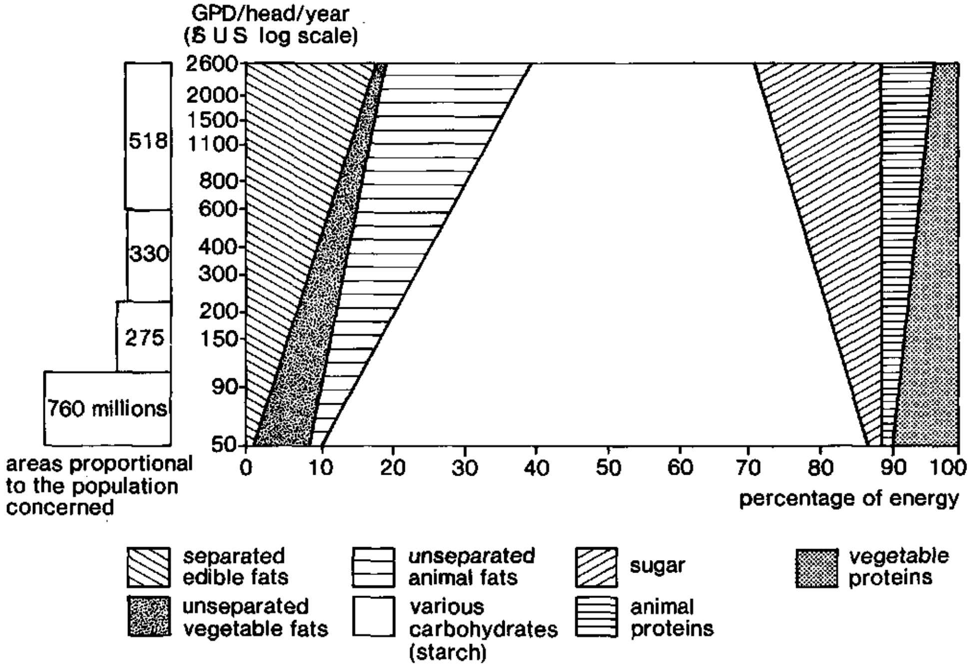

Fig. 1.7. Relation between income (gross domestic products/head/year) and dietary energy source. Correlation based on 85 countries (from: Périssé et al., 1969).

cereals, sugar, meat, fats, and roots and tubers in the developed countries between 1961-1963 and 1972-1974. In the developing countries little change is noted, except for an increased consumption of sugar and a decrease in pulses, nuts and oilseeds. Fig. 1.7 shows that the shift from plant to animal food is correlated with increase in income, expressed as the value of gross domestic products per head. Remarkably, it also shows that in all countries, rich and poor alike, protein provides about 10% of the dietary energy, which appears to be the balance spontaneously reached by human beings. However, *it is the proportion of protein of animal origin which rises with income.* We must also remember that downward adjustments in the diet will be strenuously resisted. Habit is strong and acquired tastes are powerful.

FOOD BALANCE SHEETS AND FOOD AVAILABILITY

Nutritional assessments can be made by constructing a 'food balance sheet', in which agricultural output, stocks and purchases are balanced against the food used for seed for the next year's crop, animal feed and wastage and an estimate is derived of the food available for human consumption. That amount can then be matched against the FAO's tables of nutritional requirements to obtain an estimate of the adequacy of the national diet.

The method has a number of drawbacks. For several reasons it tends to result in underestimates. One is the difficulty of obtaining estimates of agricultural production: the smaller the crop, the less tax or rent the farmer has to pay. Second, the foods included in the balance sheets tend to be the items that figure prominently in channels of trade: cereals, soya beans and heavy livestock. Other farm products – eggs, small animals, fruit and vegetables – vital to a good diet but grown for family consumption or sold locally, are almost impossible to count, and are therefore estimated indirectly.

On the other hand, in some respects the method tends to overestimate. For example, it is extremely difficult to estimate postharvest losses due to pests and microorganisms. Such losses are close to 10% for the USA wheat crop and probably higher for other crops, even with the advanced technology available. In tropical countries the losses can easily amount to 50%. In short: there is a tendency to underestimate on the supply side and to overestimate on the utilization side. Actual food availability

Table 1.2. Average daily energy and protein supply per caput. The figures relate to protein and energy content of food available at the retail level after allowance for storage and marketing losses and waste. (adapted from: FAO, 1977b).

Region	Energy (10^3 kJ)			Protein (g)			Energy as percentage of requirement		
	1961	69/71	72/74	1961	69/71	72/74	1961	69/71	72/74
Developed market economies	13.1	13.7	14.0	90	94	95	123	129	131
Western Europe	13.4	13.9	14.2	88	92	93	125	130	132
North America	13.9	14.6	14.8	101	104	104	126	133	134
Oceania	13.8	13.9	14.1	98	100	101	124	125	127
Other developed market economies	10.7	11.5	11.9	74	82	85	109	117	121
Eastern Europe and USSR	13.5	14.3	14.5	95	101	103	126	133	135
Total developed countries	13.3	13.9	14.1	91	97	98	124	132	132
Developing market economies	8.8	9.2	9.1	53	55	54	92	96	95
Africa	8.7	9.0	8.8	52	54	53	89	92	91
Far East	8.4	8.7	8.5	49	50	49	91	94	92
Latin America	10.0	10.6	10.6	64	66	65	101	106	107
Near East	9.6	10.1	10.2	63	65	65	93	98	100
Asian centrally planned economies	8.2	9.3	9.6	54	61	63	83	94	97
Total developing countries	8.6	9.2	9.2	53	57	57	89	95	96
World	10.1	10.6	10.7	65	68	69	101	106	107

will thus typically be underreported. For this reason, figures on food supplies do not provide a particularly accurate index either of the amount of food or of the types of food actually consumed. Finally, the main drawback is that the food balance sheets conceal inequalities of food consumption within countries, as for example between various socioeconomic groups. Nevertheless, data from these sheets permit the average per caput availability of food to be calculated.

Table 1.2 shows the per caput availability of energy and protein and the energy as percentage of the requirement for some regions for 1961, 1969-1971 and 1972-1974. Protein is not indicated as a percentage of the requirement, as the result could be very misleading in view of the fact that protein is not utilized adequately as protein if the energy intake is insufficient. From column 2 it appears that protein supplies are well in excess of national requirements; however, as energy supplies are not adequate in several regions, the surplus of protein availability is more apparent than real.

Table 1.3. Number of countries with surplus and deficit of energy supplies by region, in 1961, 1969/71 and 1972/74. The data in this last period refer to 109 developing countries (from: Cambell, pers.comm.), in both previous periods to 96 (adapted from: FAO, 1975a).

	1961				1969/71 average				1972/74 average			
	surplus		deficit		surplus		deficit		surplus		deficit	
	more than 10%	less than 10%	less than 10%	more than 10%	more than 10%	less than 10%	less than 10%	more than 10%	more than 10%	less than 10%	less than 10%	more than 10%
Developed regions												
Western Europe	14	5	–	–	17	2	–	–	19	–	–	–
North America	2	–	–	–	2	–	–	–	2	–	–	–
Oceania	2	–	–	–	2	–	–	–	2	–	–	–
Eastern Europe and USSR	4	3	1	–	7	–	1	–	7	1	–	–
Other developed countries[1]	1	2	–	–	2	1	–	–	3	–	–	–
Total	23	10	1	–	30	3	1	–	33	1	–	–
Developing regions												
Latin America	5	4	8	8	8	6	7	4	9	9	9	5
Far East	–	4	5	7	4	4	5	3	6	1	6	5
Near East	1	1	2	10	1	3	6	4	3	2	2	4
Africa	–	5	14	18	3	8	14	12	2	8	14	18
Asian centrally planned economies	–	2	–	2	1	1	1	1	2	2	2	–
Total	6	16	29	45	17	22	33	24	22	22	33	32
World	29	26	30	45	47	25	34	24	55	23	33	32

1. Japan, Israel and South Africa.

With regard to energy, it is generally considered that supplies in the developing regions should be at least 10% above aggregate requirements, thus allowing for maldistribution. In 1961, only six developing countries had this surplus; however, the number rose to 17 by 1969-1971 and to 22 in 1972-1974, as Table 1.3 shows. The number of countries with supplies below the basic requirements decreased from 75 in 1961 to 58 in 1969-1971, but increased to 65 in 1972-1974 owing to the food crisis. In 1961, 45 countries failed to reach the 90% of requirement, and in 1969-1971 the figure was 24 (12 in Africa), whereas in 1972-1974 the figure was 32 (18 in Africa). Fig. 1.8 shows the energy supplies of several regions in 1972-1974.

If, on the one hand, the total amount of available food calculated from the balance sheets is rather uncertain, on the other hand the values for nutritional requirements have rather a wide range and are dependent on several factors such as weight, sex, age, activity and physiological state. The quantities recommended are obtained from studies with healthy individuals, engaged in occupations involving moderate activity, and must, therefore, be treated with considerable caution when used for all types of population groups. These variations make it difficult to generate precise values for

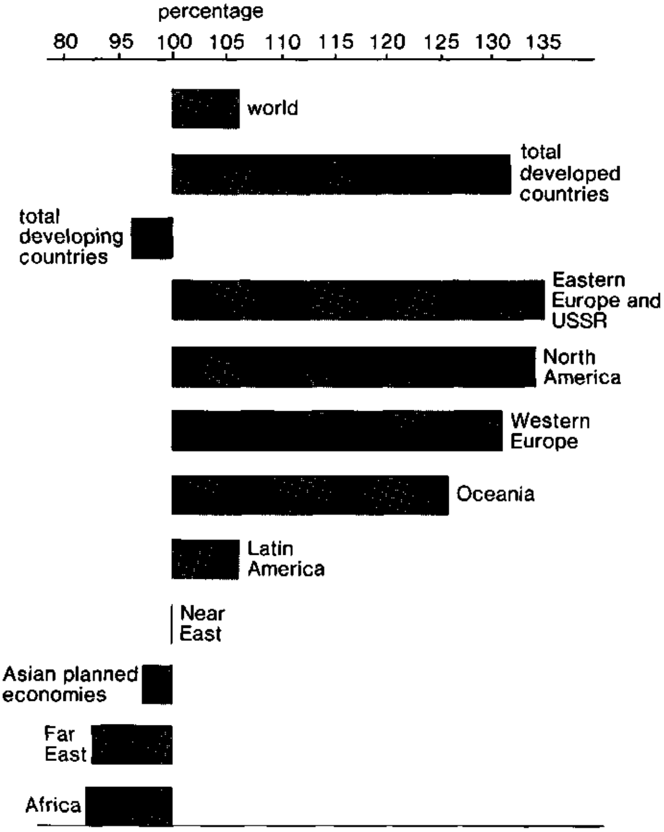

Fig. 1.8. Energy supply as percentage of requirements 1972/74 (from; FAO, 1975a)

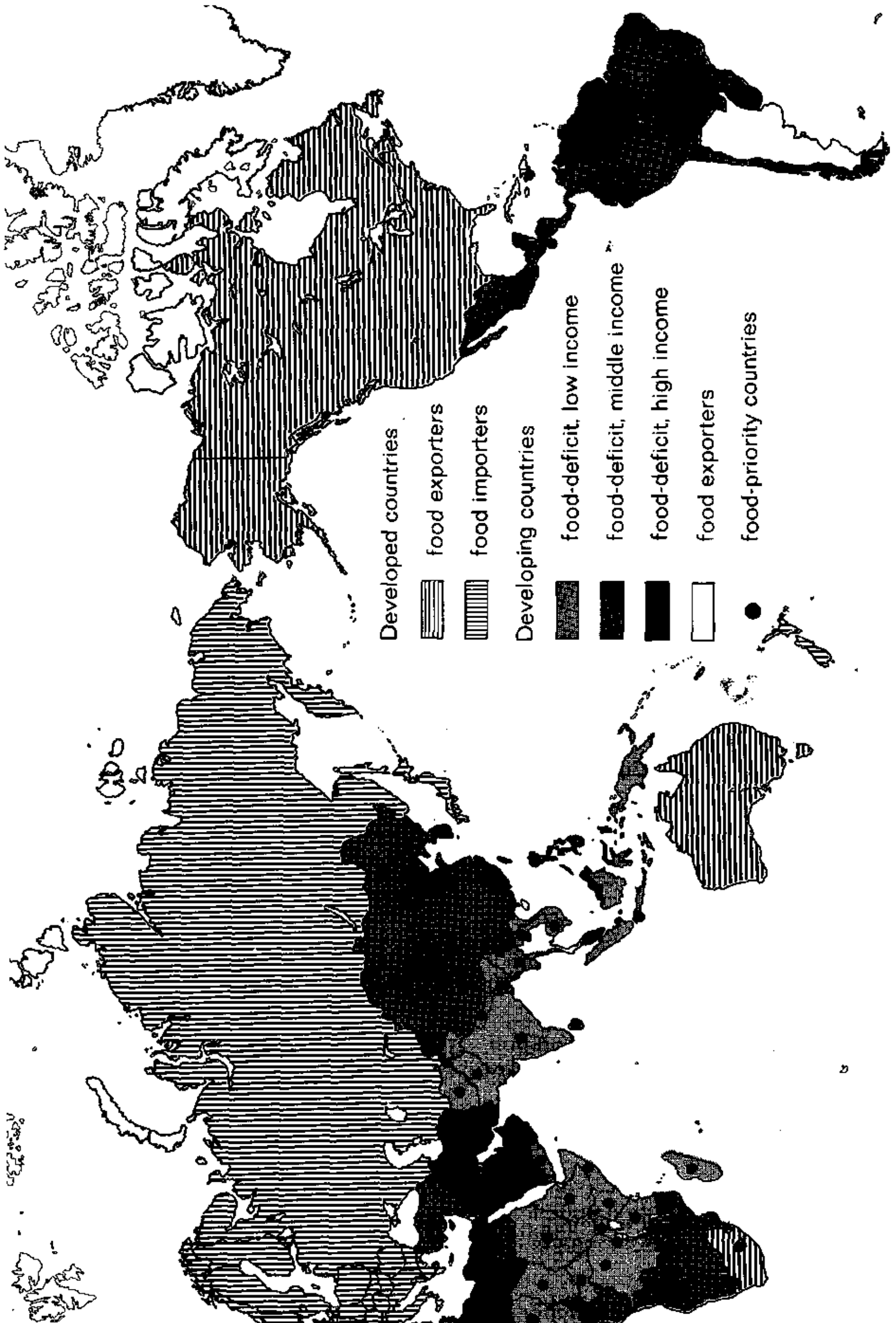

Fig. 1.9. Distribution of countries with a surplus or deficit in food production in the developed world (exporters and importers) and the developing world (exporters and food-deficit countries) (from: Wortman, 1976).

nutrient requirements in either individuals or population groups. However, it is necessary for policy-making bodies to have figures from which to derive safe levels of intake.

In developing countries, where a large fraction of the population is likely to be suffering from diseases, children are often greatly underweight and below normal in height owing to the combined effects of repeated infections and undernutrition. As a result, the body size of adults is also small. For such cases the age-specific nutritional figures derived from well-nourished populations may be unnecessarily high, and estimated energy requirements may also be excessive. If, however, average per caput availability falls below the estimated per caput requirement, the people of the country or region risk being inadequately nourished.

As a consequence of these excessive estimates of requirements the numbers of undernourished people may be overestimated. In order to assign really reliable figures to the degree of hunger and undernutrition in the world today we would need large-scale surveys that include both clinical examinations based on an established definition of undernutrition and individual consumption surveys that determine the amount and types of food eaten and the distribution of food within each family unit.

Even if the figures obtained are doubtful and not based on actual known nutritional requirements, the situation they reflect is clear enough: although nobody can really tell how many people are suffering from undernutrition, it is certain that the number is great and also that many would benefit from a more varied diet. The largest concentration of undernourished people is in South and Southeast Asia and sub-Saharan Africa, as may be seen from Fig. 1.9.

THE CONTRIBUTION OF HIGH-YIELDING VARIETIES TO WORLD FOOD PRODUCTION

As mentioned above, several factors such as population growth and the increased food demand associated with an increased GNP per caput was beginning to press hard on the global food situation. It is possible that an actual decline in food availability was prevented only by the introduction in the latter half of the 1960s of the high-yielding varieties (HYVs) of wheat and rice associated with the Green Revolution (cf. Fig. 1.3).

The breeding research that led to the development of the high-yielding varieties had started before the mid-1960s, when the world first became really aware of the food crisis. In India, the monsoon failed two years running and the USA began shipping 20% of its wheat into the subcontinent. HYVs of grains were introduced on a commercial scale in India in 1966-1967. Greatly increased production, especially of wheat, followed. Two years later, 30% of the area sown to wheat was under HYVs. By 1972-1973 HYVs accounted for more than half of the area sown and nearly 75% of total production. At the same time the area sown to wheat increased by nearly 50%. New HYVs of rice were introduced commercially in 1966-1967, and rapidly adopted, although not so rapidly as wheat. Following these applications in South Asia, we see a rising tide of agricultural success. New maize varieties have had some success in other areas, for instance in Kenya.

One of the consequences of the increased areas sown to HYVs has been – particularly in India – a decline in the planting of legumes such as pulses. The cultivation of HYVs needs more fertilizers and, what is more important, it leads to unbalance in what traditionally had been a satisfactory diet. Biological assays have shown that mixed diets of cereals and legumes are better in quality, especially protein quality, owing to the mutual complementation of their essential aminoacids. This is indicated in Fig. 1.10, where the X-axis gives the beans/maize ratio in the diet, and the Y-axis the relative protein quality. It shows that the nutritional benefits are optimal for a 50:50 mixture.

Legumes are also a very important complementary food in regions where root crops such as cassava are the staple food. In a diet based on cassava nearly all the protein consumed is derived from legumes, as cassava itself contains only very little protein. This subject deserves more attention, for populations which are mainly dependent on root crops and plaintain are nutritionally very vulnerable.

Although the term 'Green Revolution' suggests more upheaval than it really caused, nevertheless, there have been modest increases in per caput production in the less developed areas as a result, notwithstanding the rapid increase of population. Rice and wheat, two historically basic crops, have broken traditional yield limits, particularly in South and Southeast Asia and China. The new HYVs of wheat have doubled and even tripled traditional yields. Cereal prices were an important incentive in making their cultivation extremely profitable. These semidwarf varieties have a

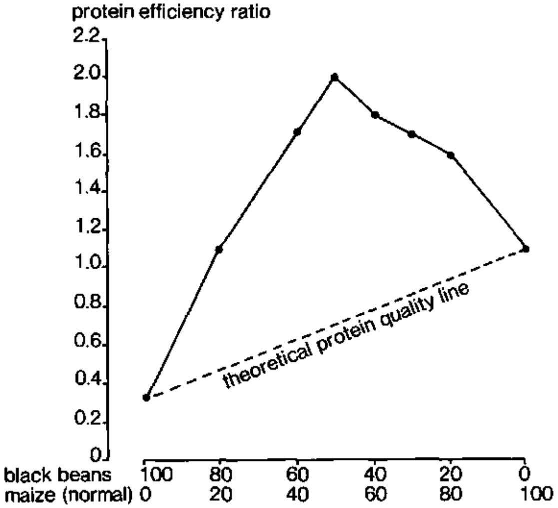

Fig. 1.10. Effects of different ratios of beans and maize on the protein quality of the mixture (INCAP).

short, sturdy stem which is able to support a large, full head of grain even when battered by wind and rain. Compared with their predecessors, they are able to convert larger amounts of fertilizer into grain without lodging and their responsiveness to fertilizers is much higher. Their impact on production goes beyond their immediate effect on yields: they clearly represent a new departure in agricultural technology, of which the final effect is incalculable.

New varieties have also been bred which have a shorter growing period. A Philippines-bred rice has cut the growing time in the field from 120 to 90 days, whereas traditional rice varieties may need as many as 180 days. Such developments allow extra crops to be grown each year. However, even with good irrigation systems, multiple cropping requires a high level not only of managerial skill to coordinate a series of complex activities, but also of technological skills to cope with irrigation, fertilization, new seeds, mechanization, pesticides, and crop handling and storage equipment. In short, food supplies can be increased, but only if the developing nations can take the necessary steps.

Although technology rather than agriculture has generally been thought to be the originator of change, the Green Revolution did touch off a series of changes that stimulated industry: fertilizer, machinery, fuel, transportation and processing. An important question is whether the farming technology required for the innovations in cultivation is equally available to the poor farmer and the better endowed farmer. When the poor farmer is able to adopt the new system he will grow as much as the rich farmer. So far, however, the Green Revolution in rice has touched the life of only one in four of the world's rice farmers.

Enhanced agricultural productivity of both food and cash crops is the best lever for economic development and social progress in the developing world. The crucial question is whether governments will have the power to act. However, it should be borne in mind that there is no 'scientific' solution for political inadequacies. In western countries such changes required 50 or 75 years, in the developing world they will have to be accomplished within 10 or 15 years; these countries have no time to lose.

PROSPECTS

It seems likely that the world food balance in the next decade will be rather precarious. The margin between surplus and shortage is very narrow and the increasing import requirements of the developing countries, coupled with the periodic entry into world markets of large-scale purchasers such as the USSR, is likely to ensure that world prices remain relatively high.

The overall outlook is one of continuing uncertainty and instability; attempts have to be made to rebuild depleted stocks where necessary but, until some type of international food security system, such as that recommended by the World Food Conference in 1974 and even as early as the late 1940s by leading members of the FAO, has come into existence, the world will remain at the mercy of each year's harvests.

The challenge that the developing world faces is not the same in all regions and countries. It is projected that the developing countries with market economies will be experiencing an average annual population growth rate of 2.7%, as against a growth rate of food production of 2.6%. The gap between the two is much wider in Africa, Asia and the Far East; thus the situation in these regions is more critical. In Latin America and in the Near East, on the other hand, the production growth rates are expected to be a little higher than the population growth rates, as the figures in Table 1.4 show.

The centrally planned economies are in a more favourable situation in this respect because their expected population growth rate is substantially lower than the extrapolated food production growth rate. If the other developing countries had a similar low population growth rate, the recent trends in food production would give less cause for concern.

There can be no doubt that the outlook calls for greater efforts to produce more food in the developing countries themselves. Even in Africa, where problems in the short and medium term are the most serious, the cereal production rate in the 1980s could be accelerated, if programmes for the development of idle land and other resources were undertaken with a sense of urgency. But the disadvantages of such a procedure should also be taken into account (cf. Chapter 2, pp. 52-53).

Broadly speaking, it has been suggested that the developing countries need to increase their food production by about 3-4% per year up to the end of the century.

Table 1.4. Food demand and production: projections and extrapolations to 1985 (adapted from: FAO, 1975a).

Regions	Volume growth rates (1970-85) compound rate per year			Population growth rate
	demand		extra-polated food production	
	high-income group	modal-income group		
Developed countries	–	1.5	2.8	0.9
Market economies	–	1.4	2.4	0.9
Eastern Europe and USSR	–	1.7	3.5	0.9
Developing market economies	4.0	3.6	2.6	2.7
Africa	4.1	3.8	2.5	3.0
Asia and Far East	4.0	3.4	2.4	2.6
Latin America	3.8	3.6	2.9	2.8
Near East	4.2	4.0	3.1	2.9
Asian centrally planned economies	3.5	3.1	2.6	1.5
All developing countries	3.8	3.4	2.6	2.3
World	(2.7)	2.4	2.7	2.0

This estimate is based on:

- about 2.5% for annual population increases, if these stay at present levels;
- about 1% for average annual increases in per caput food consumption, which seems a minimum goal given present levels of undernutrition, and which takes into account the greater palatability demanded when economic conditions improve (cf. Fig. 1.7).
- Maintaining roughly the current proportion of their food supply that comes from net cereal imports (about 15% of cereal consumption in recent years for the importing countries), on the assumption that they probably cannot import more over long periods because of balance-of-payments problems.

The 3-4% estimate allows for considerable differences in these three factors among countries and over time; some countries may need to attain higher rates of growth of food production. This increase can only be obtained from an expanded crop area and/or from higher production per hectare per year. Annual increases in crop area will probably not exceed an average of 1% per year over the next 25 years and may be appreciably less. In the developing countries, these increases averaged 1.4% in the 1960s, declining over the decade and increasing slightly over the 1970s. In addition to this, it should be noted that not only does a high population growth require a high growth in agricultural production but it also usually entails the sacrifice of arable areas for additional housing.

Although costly programmes for settling large new areas in Latin America and elsewhere are being planned or implemented, higher returns can usually be realized from investment in existing farmland. High costs and other typical difficulties are likely to continue to slow down the development of new land. Thus adequate food supplies for the low-income areas of the world will depend on substantial increases in production per hectare, averaging about 2.5% per year over the next 20 to 25 years. Areas that are experiencing rapid population growth but lack land reserves may require increases in yield of 3-5% a year.

The estimates given above are based on data obtained from surveys in 71 countries, of which 30 had by 1975 achieved or exceeded the 3-4% rate of production increase needed for the future.

However, most of the poorest countries are only beginning to develop the capabilities needed to support a rising rate of productivity. They lack the capital, skills and organization necessary. Because of their greater poverty and undernutrition, they need proportionately larger annual increases in per caput food supplies than the middle-income developing countries, and they can least afford continuing large-scale imports to supplement their own production.

Unprecedented rates of agricultural development are unlikely to occur without special programmes being organized. These must be built around higher-yielding farming systems, supported by adequate price incentives for greater production. Provision must be made for adequate supplies of water, fertilizer, quality seed of approved varieties, energy and other inputs, and for marketing. Land tenure needs changing in many countries. Credit and other services must be provided. Large numbers of people must be trained and extension services strengthened. Research capabilities must be greatly intensified. Price, trade, budget and other policies must support an integrated development effort. All this is a formidable undertaking for a developing country.

All countries depend on one another to serve as export markets or sources of imports or both: for food products, for the above-mentioned supplies or services needed to produce food, or, further back in the food production chain, for petroleum, steel or technical education. The policies that individual countries or groups of countries pursue to secure markets or sources of supply affect the trade of other countries and the stability of their food supplies and prices. Large-scale changes in population growth and in diet in some parts of the world affect food availability and markets in the other parts. International cooperation can reduce the instability of national food supplies that is due to weather and pests, and can improve national access to the world's technology and to natural resources used for food production. In view of all these considerations, few countries can be self sufficient in meeting their food and nutrition needs. Some may come close to autonomy, but at high cost.

Besides increased production growth rates, there are other major objectives to be considered:

- an equitable and efficient distribution of food, particularly among the poorer sections of the population;
- increasing employment in agriculture and related sectors;
- increasing the share of developing countries in expanded trade in agricultural products.

Local, national and international measures are needed to prevent sudden sharp drops in food supplies and to prevent severe market gluts that discourage production. Improved technology can reduce losses of crops and livestock caused by weather, pests and postharvest losses. Production research must emphasize not only increases in yield but also stability of yield. Farmers would benefit substantially from improved weather prediction. Better food preservation and storage methods are needed in the developing countries both at the farm level and beyond. These should be supplemented by improved international storage and emergency transport arrangements.

It is important that action be taken to reduce cycles of glut and shortage and also to prevent these from distorting perspectives on the more serious longer-term problem. A few consecutive years of good harvests should not be allowed to divert attention from the action needed.

Thus there are two components to the solution of the nutrition problem: increased production of food, primarily in the developing countries, and widespread increases in family income to obtain adequate purchasing power, particularly among the poor. The higher incomes will have to come primarily from full employment and increased agricultural productivity, and secondarily from the development of industry and public and other works that will be in demand as rural areas become more prosperous. The bulk of the food supplies of most agrarian countries is provided by individual farmers with tiny family-operated holdings. Improvement of the productivity and income of these will require the introduction of new high-yielding varieties, and science-based crop and animal production technologies tailored to the unique combination of soil, climate, biological, ecological and economic conditions of individual localities in every nation.

CONCLUSION

The most important grounds for optimism are the increasing ability of many developing countries to tackle their own food problems. While progress over the past decade has been uneven and many difficulties remain, the present situation necessitates recommendations such as:

- larger numbers of trained, experienced technical and managerial persons in institutions serving agriculture and marketing;
- clearer perceptions on the part of policy makers and officials of what is needed to improve food systems and accelerate development;
- greater availability of fertilizers, quality seed, water, farm capital and supporting services, including research;
- labour supplies to facilitate the intensive farming practices that can result in high yields per hectare with relatively small capital inputs;
- availability of a wide array of external assistance;
- greater agreement among the nations and organizations of the world on the nature of the problems;
- establishment of national and international food security systems.

Unfortunately, the national and international policies and activities that affect the nutritional status of world populations are seldom examined systematically to identify their effects on nutrition. Even programmes designed to improve nutrition are rarely evaluated for their effectiveness. Research is needed not only on the extent and functional significance of undernutrition but also on the merits of present and future policies affecting food systems. Research in these areas could prevent a significant proportion of diseases presently attributed to undernutrition and its associated cost, and could improve the quality of human life and performance.

To eliminate widespread undernutrition, the developing countries must roughly double food production by the end of the century, provide the poorest people with adequate access to food supplies, enhance the power of buying nutritionally high-quality food, and learn how to provide a healthier diet for all their people. These are difficult but attainable goals. Only then can the aim of the 1974 World Food Conference, of 'removing hunger and undernourishment as a major scourge by the end of this century', be fulfilled.

Diagnosis of current world nutrition problems

INTRODUCTION

For a better understanding of the human nutritional problems it is first necessary to summarize some physiological background information. Human beings lack the biochemical machinery to manufacture a variety of compounds which are essential for the formation and maintenance of tissues and for the metabolic reactions that sustain life. To this group of about 50 essential nutrients, which must be obtained preformed from the environment, belong all the vitamins and many minerals, besides a number of protein building units (the aminoacids) and some fatty acids. As long as the overall diet supplies all the essential nutrients and there are no disturbances in the functions of digestion, absorption or transportation, the cells and tissues of the body are usually capable of synthesizing the many thousands of additional compounds required for life.

If the intake of one or more nutrients is too low to meet the normal needs of cells, adaptive changes occur within cells and tissues to conserve the limited supply. If the intake continues to be inadequate, these metabolic adaptations break down and deficiency disease rises above the 'clinical horizon', with characteristic symptoms that can lead to disability and death. In addition to the essential nutrients the body needs a supply of energy.

The assessment of the quantitative requirements for energy and essential nutrients is far more difficult than is generally realized. In animal husbandry the minimum needs of the animal for individual nutrients can be judged in relation to certain productive functions such as growth and milk yield. The nutrient requirements of the human organism cannot be defined so readily because its well-being is far more difficult to measure. What are the appropriate yardsticks?

Some nutrients or their breakdown products are excreted daily, mainly through respiration and in the urine, faeces and sweat. For the healthy adult body to remain in metabolic equilibrium the total intake of a nutrient in food must equal the total loss. The same holds for the total energy intake and total energy expenditure. The metabolic balance approach can be used for measuring the requirements for some nutrients, but the figures are rather uncertain, as such studies can only be of short duration and it is therefore rather doubtful whether the results can be extrapolated to long-term nutritional and health significance. Furthermore, it is arguable whether they are valid for large population groups all over the world, as the experiments have usually involved only few subjects, usually young and privileged persons. For instance in developing countries, where protein availability is low, its physiological utilization is better than in countries with a surplus of protein. Also, nutrient requirements depend on a variety of environmental factors which may be physical and biological. Diseases, too, may directly upset the mechanisms controlling the metabolism of essential nutrients, thereby altering dietary nutrient requirements. Knowledge of nutrient requirements in infants and in young children is also on uncertain ground. There is a tendency to regard such individuals as small adults, and, with some allowance for growth, to extrapolate their requirements proportionately by weight from studies of older individuals. This approach does not take into account changes in the metabolic activities of cells and in the rates of nutrient turnover with age.

Man's inability to manufacture the essential nutrient compounds has exposed him to deficiency diseases. In this part, we will survey some of the main nutritional diseases, first in the developing countries and next in the developed world.

Malnutrition may arise in one of four ways:

1 There is simply not enough food available and the consequence is undernutrition (marasmus and kwashiorkor).

2 The diet may lack one essential nutrient or more, giving rise to deficiency diseases such as xerophthalmia (due to deficiency of vitamin A), beriberi (vitamin B_1), pellagra (nicotinic acid), scurvy (vitamin C), rickets and osteomalacia (vitamin D), goitre (iodine) and several kinds of anaemia (iron, folic acid).

3 A person may have a condition or an illness, either genetic or environmental (e.g. infectious) in origin, that prevents him from digesting food properly or from absorbing some of its constituents; this is called secondary malnutrition.

4 Too many calories or an excess of one or more components of a reasonable diet are consumed; this condition is overnutrition.

In areas where the food supply is limited, two or more of the first three causes of malnutrition are often found in combination. Another nutritional disease should also be mentioned here, which is susceptible of control by plant breeding. It has only fairly recently been recognized that moulds in foods and feeds can have serious effects on man and animals, both in the developed and in the developing world. Mycotoxins, present in certain food contaminated by moulds, particularly groundnuts, have been shown to cause disease, e.g. liver cancer, and death. Animal experiments have shown that, although at lower levels mycotoxins may not cause overt signs of illness, they may reduce growth rate, feed efficiency and resistance to infectious diseases.

DEVELOPING COUNTRIES

According to such international organizations as WHO and FAO, the most important diseases due to nutritional deficiencies in developing countries, against which specific action is needed, are:

- protein-energy malnutrition;
- nutritional anaemias;
- night blindness, xerophthalmia and keratomalacia;
- goitre.

Other less important deficiency diseases are rickets and osteomalacia, scurvy, pellagra and beriberi. All of these diseases could be corrected by an adequate diet; however, this should now be regarded as a long-term solution. Short-term solutions are available in some cases, such as iodization of salt against goitre. Protein-energy malnutrition, on the other hand, can only be prevented by an adequate diet: there is no short cut. The causes and consequences of the above-mentioned nutritional deficiency diseases will be discussed below in more detail.

Protein-energy malnutrition

Protein-energy malnutrition remains the major nutritional problem among certain population groups, young children being the most vulnerable. It is the result primarily of an inadequate intake of energy or protein or both over a period of time and can be manifested in many different ways, depending on factors such as age, physiological condition, presence of concomitant infections and vitamin deficiencies. Apathy, incapacity for physical work, weight loss and low birth weight are among the most frequent symptoms, and in the youngest group can range from the slight impairment of growth or thinness seen in mildly undernourished children to the gross alterations shown by those suffering from kwashiorkor or marasmus.

Marasmus and kwashiorkor are the extremes. Marasmus means wasting and is due to a continued restriction of both dietary energy and protein, as well as other nutrients. Kwashiorkor is due to a quantitative and qualitative protein deficiency, but energy intake may be adequate. Besides these, there are many intermediate and less well defined forms, which provide the vast majority of the cases. In a community where there is much malnutrition, 40% of children may be malnourished, perhaps 2% may have marasmus and perhaps only 1% kwashiorkor.

The child receiving insufficient protein and/or energy fails to thrive, and he becomes underweight. He readily falls ill and dies (e.g. of measles). Figures from some hundreds of surveys of young children, carried out in various regions, testify to the magnitude of the problem: up to 40, 50 and in some countries even 60% of the children studied showed moderate protein-energy malnutrition. Nutritional status is known to be very closely linked with other ecological, sociological and economic conditions. It is in fact most often a manifestation of a broader deprivation. However, little real information is available on who is malnourished or why. That poor people often are is a matter of general knowledge.

It is now widely accepted that most malnutrition in the developing world is due simply to inadequate intake of energy. In the light of the most recent recommendations on protein needs (FAO/WHO Expert Committee on Nutrition 1973), it seems improbable that a dietary intake sufficient to cover energy requirements will be insufficient to meet protein requirements. This means that protein deficiency is unlikely to occur in the absence of energy deficiency, a possible exception being in populations that subsist on cassava, plantains, yams or breadfruit, all of which are extremely low in protein content. Until recently, the protein problem has been overemphasized and too much stress laid on protein deficiencies. The first goal of a food policy should be to satisfy the energy needs of a population.

In most populations where the staple food is a cereal such as rice, wheat, maize or millet, serious protein deficiencies seldom occur except where there is also an energy or overall food deficiency. Most cereals contain 8-12% protein and are often consumed with moderate quantities of legumes and vegetables. If energy requirements are met, protein deficiencies, if present, are certainly confined to young children.

Important lessons are to be learnt from the past. The production of relatively expensive protein-rich foods, the aminoacid fortification of cereal grains, the production of single-cell protein etc. are no panacea for the world's nutrition problem for they can only reduce protein-energy malnutrition to a very small degree. Similarly, changing the aminoacid pattern of cereals or other food crops by breeding is in all probability much less important than increasing the yields per hectare of such crops.

There is also the question of how to feed young children. During the first few months of life breast feeding ensures an adequate diet. Weaning foods, however, generally depend mainly on the local staple food, and it is at weaning that growth deprivation can start. The composition and quantity of the weaning foods, are therefore of utmost importance. Although it is difficult to give general rules, one aim should be a more diversified diet, for example by increasing the cereal, legume and/or vegetable consumption. The daily quantity needs attention because the diets made up of local foodstuffs (often tubers) have a low energy density and are consequently too bulky to allow daily energy requirements to be met. A main determinant of the energy density is the fat content, and increasing the energy density of infant diets by the addition of fat should be beneficial. This should be done especially in combination with control of infectious diseases, for the environment usually presents constant infection hazards.

In conclusion we may say the following regarding protein-energy malnutrition:

- It affects the quality of life of several hundred million people, especially children.
- Primary causes are diets in which dietary protein and/or energy are restricted; however, lack of dietary energy is more important than lack of dietary protein.

Nutritional anaemias

The most important causes of anaemia are those caused by nutritional deficiencies, mainly of iron and folic acid. Any significant degree of anaemia is always associated with an inability to make sustained physical effort. It is not directly dangerous to life but leads to a loss of efficiency and impaired general health.

The anaemia due to iron deficiency is the most common throughout the world, affecting mainly women of reproductive age, infants and children. In tropical areas, both parasitic infestations and the poor availability of dietary iron contribute to its high prevalence. In men, prevalences of between 20 and 40% have been found; in women these are even higher and the cases are more severe. Iron anaemia is also frequent in early life.

The most valuable sources of iron are meat and liver; they should preferably be eaten regularly. Examples of less expensive sources are soya beans and nuts. Green vegetables and certain fruits, especially dried apricots, peaches, prunes and raisins, are useful sources, but in general fresh fruits and vegetables are of greater value because of their ascorbic acid content, which facilitates the absorption of iron. Cereals cannot be relied upon to contribute greatly to iron intake, since the phytates and phosphates present reduce its absorption. Generally it can be said that iron absorption is better from foods of animal origin than from foods of vegetable origin. The level of iron absorption in some of these foods is shown in Fig. 1.11.

The second important nutritional anaemia is that due to folic acid deficiency, which in any community is undoubtedly most commonly observed during pregnancy and lactation. The present evidence suggests that the high prevalence in pregnancy is a universal phenomenon and not associated simply with the economically underprivileged. In general milk and fruits are poor sources, whereas liver in particular and green vegetables are richer sources.

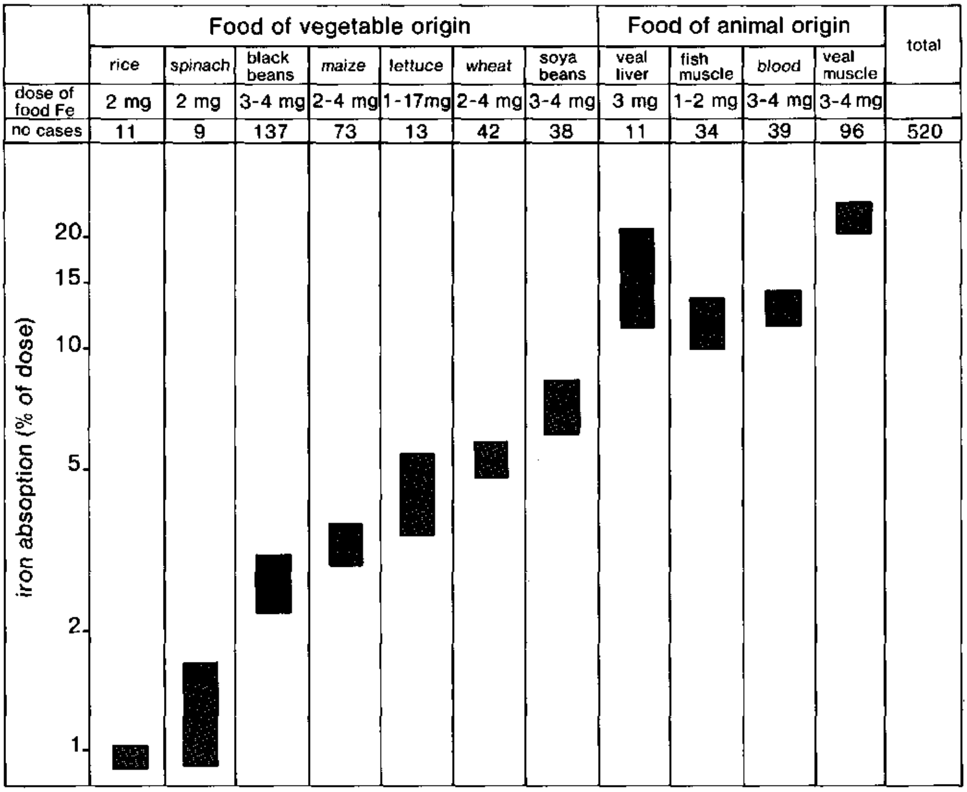

Fig. 1.11. Iron absorption from food (from: WHO Group of Experts, 1972).

Other deficiency diseases

Vitamin A deficiency is a major cause of blindness in many countries, such as India, Indonesia, Bangladesh, the Philippines, north-east Brazil and El Salvador. Moreover, it should be regarded as a major problem in view of its socioeconomic consequences. WHO estimates that on a global basis some 50,000 to 100,000 children become blind each year because of vitamin A deficiency. The first symptom is night blindness, followed by xerophthalmia. A more serious stage is keratomalacia, which is closely associated with protein-energy malnutrition. The peak age, when blindness is most likely to occur, is between 2 and 5 years, when kwashiorkor is so common.

Vitamin A activity is vested in several related compounds. The two most important of these are vitamin A as such, present only in animal foods (milk, butter, cheese, egg yolk, liver, some fatty fish) and certain plant pigments, chiefly β-carotene, which in fact is present in both animal and vegetable foods, but mainly in plants. Some of the β-carotene provided by food is converted into vitamin A and therefore it is called provitamin A. The total vitamin A value, obtained from both vitamin A (retinol) itself and the converted carotene, is referred to as vitamin A activity.

In many parts of the world where animal foods are seldom eaten, as in most developing countries, almost all the vitamin A activity comes from vegetable sources, e.g. green leaves and carrots (β-carotene) and red palm oil (α-carotene); all other vegetable oils are devoid of vitamin A activity. It should be mentioned that carotene absorption depends in part on the quantity and quality of the dietary fat. There is no good reason why blindness due to vitamin A deficiency should not be almost totally eliminated in the next 10 years. Much attention is given today to programmes for the vitamin A fortification of foods, such as sugar, tea and cereal products, and for providing young children regularly with capsules containing vitamin A. Vitamin A is a very cheap nutrient, and the major costs involved are in the delivery system.

The long-term solution of this problem is undoubtedly an agricultural one. Suitable varieties of carotene-rich vegetables and fruits, which are acceptable to the food habits of the people and which may readily be cultivated in a given region (for example in small family gardens), should be developed. It is a tragedy that in communities with a high prevalence of vitamin A deficiency carotene-rich vegetables are often readily available but not eaten because of ingrained food habits and food preferences.

Goitre is the name given to enlargement of the thyroid gland. Iodine deficiency is the prime cause of endemic goitre. It occurs in areas where soils are low in iodine, and can only be eliminated by raising the iodine intake of the population. It is estimated that 200 million people are affected. Where endemic goitre is severe, in a few isolated areas in Nepal, the Andes, Zaire and New Guinea, cretinism may affect as many as 1% to 5% of the population. Usually 90% of the iodine is consumed in the food; the remainder is provided by the water. The addition of iodine to salt for instance has had nothing but beneficial consequences.

(In recent years international organizations like WHO and FAO and also IUNS (International Union of Nutritional Sciences) have stressed the need to eradicate the above-mentioned florid forms of malnutrition by the end of the century. Technically this should be possible, but whether it is so politically remains questionable.)

Rickets is a disease of the growing skeleton in children; the term osteomalacia is applied to the same disease occurring after the skeleton has completed its growth. The cause is vitamin D deficiency. This vitamin can be synthesized in the skin under the influence of the ultraviolet rays in sunlight. Rickets is likely to occur where local habits or circumstances prevent exposure to sunlight. It has been suggested, though not established, that low calcium intake and possibly the reduction of the bioavailability of dietary calcium by such factors as phytic acid in cereals may be a contributory cause. Rickets, owing to a combination of poor child-rearing habits and inadequate diets, continues to affect some 30-50% of very young children, at least to a mild degree, in some areas, e.g. in the eastern Mediterrean region and in Ethiopia.

Scurvy, caused by an inadequate intake of vitamin C (ascorbic acid), is at present rare, although in countries where maternal and child health services are inadequate, infantile scurvy may be more common than reports indicate, particularly in prematurely weaned infants. Sources of vitamin C are citrus fruits, soft fruits, green vegetables and potatoes (cf. Table 1.6).

Pellagra is associated with an inadequate intake of niacin (nicotinic acid). The body is capable of transforming the essential aminoacid tryptophan to niacin. Pellagra is therefore also associated with low intakes of tryptophan, and hence in many parts of the world with the consumption of maize diets. Niacin is present in many foods, especially meat, eggs, milk and cereals (despite their low tryptophan content). The disease still occurs in mild chronic seasonal forms in endemic foci (Middle East), usually in rural areas, where it continues to be a public health problem. Diversification of the diet is an important means of prevention. In addition, improvement of the nutritional value of maize and of maize processing may be effective.

Beriberi, which is caused by thiamine (vitamin B_1) deficiency, was once a major and widespread disease problem but its prevalence has been greatly reduced although it remains endemic in a moderate or mild form in certain areas, and periodic outbreaks are reported in times of crisis. Infantile beriberi especially has been a major problem in some areas of the world, with a high mortality rate.

Beriberi is associated particularly with the consumption of polished rice. In areas where the rice is either 'parboiled' or 'undermilled', it is rarely seen, owing to the high thiamine content of the aleurone layer of the rice grain, which is not removed by either of these processes. Beriberi tends to disappear as economic conditions improve and diets become more varied. Important sources of thiamine are cereal germ, nuts, peas, beans and other pulses and in addition yeast. All green vegetables, roots, fruits, meat foods and dairy produce (except butter) contain moderate amounts of thiamine. Prevention should be directed towards a diversification of the diet and the encouragement of the use of parboiled or undermilled rice.

DEVELOPED COUNTRIES

In the developed countries the deficiency diseases discussed above are rather uncommon, at least in their severe forms. The diets in the developed world are diets of affluence (cf. Fig. 1.7) and are characterized by an increase in total fats and a reduction in total carbohydrates and hence in the so-called dietary fibre. The related western public health problems include ischaemic heart disease, obesity, diabetes, hypertension and dental caries.

In the developing countries there is evidence that in the lowest-income groups, with dietary fat comprising about 10% of the energy intake, an increase to 15-20% of fat, with due regard to the essential fatty acids, would have beneficial effects. In the developed countries, although many physically inactive people seem to tolerate diets containing more than 40% of dietary fat without apparent health problems, sizable fractions of the population are affected by various degenerative diseases such as ischaemic heart disease. The high fat consumption in these countries has automatically increased the consumption of saturated fats and consequently the cholesterol level in the blood. There is substantial evidence that in these populations a decrease in the dietary fat content to 30-35% of the energy intake, and an increase in the ratio of polyunsaturated to saturated dietary fatty acids to 1 : 1, would be beneficial.

The essential fatty acids, the most important of which is linoleic acid, a polyunsaturated fatty acid, are required for the normal growth and function of all tissues and should be included in the diet. Edible oils and fats of animal origin include tallow, lard and the oils from marine mammals and fish; the major vegetable oils traditionally consumed in many countries are those from groundnut, coconut, rapeseed, mustard, oil palm, olive and sesame. Most of the vegetable oils used are relatively rich in polyunsaturated fatty acids, primarily linoleic acid. Rapeseed oil has received much attention in recent years; reports from the 1940s onwards have revealed that feeding large amounts of rapeseed oil, which in traditional rapeseed varieties has a high concentration (around 40%) of erucic acid, causes growth retardation and changes in the heart, adrenals and liver of laboratory animals. By means of breeding the content has been lowered to nearly zero in some varieties; notwithstanding, when oil from these varieties is used to feed laboratory animals, lesions are still observed.

As a consequence of dietary recommendations regarding polyunsaturated fatty acids (especially linoleic acid), the demand for these fatty acids has greatly increased. This has resulted in much breeding work to improve oil yield and composition genetically, an example being the above-mentioned rapeseed strains.

Space does not permit us to deal with the increased sugar consumption in the western world or the role of dietary fibre in present-day western diets.

Nutritional objectives for plant breeders

INTRODUCTION

So far we have discussed the world food situation and the main problems of world nutrition. Although food production and even food production per head have improved, according to FAO data (cf. Fig. 1.2), it is clear that hunger and malnutrition are still the fate of large numbers of people. There is growing evidence that both the quality and the quantity of diets play a significant role in health problems of all countries. It is generally believed that if widespread malnutrition is to be eliminated, developing countries should attempt to double their food production by the end of the century. Eight food sources – rice, wheat, maize, sugar, sorghum, millet, cassava and animal products – provide most of the nutrients for people in developing countries. They account for about three-quarters of the energy intake and two-thirds of the protein consumed, and in the case of the poorest populations may account for as much as 85-90% of the energy and protein. The importance of many other foods consumed in the developing countries must also be recognized. Potatoes, yams and sweet potatoes, peas and beans, nuts, fruits and vegetables, are important sources of energy and essential nutrients.

This section of our chapter is concerned with the protein values of food crops, the use of mixed diets (e.g. beans and maize, Fig. 1.10) and the percentage of energy derived from protein in food crops.

In food composition tables, protein content may be expressed either as g/100 g of food, or as the proportion of the energy in the foods provided by protein. In Table 1.5 the latter mode of expression is used. This table enables foods which are poor, adequate or good sources of protein as far as energy content is concerned to be distinguished. In most satisfactory human diets 10-12% of the energy is obtained from the protein.

With regard to recommended intakes, a useful guideline is an intake of 1 g of protein/kg body weight/day. Another way of expressing the requirement is that dietary protein should provide up to 10% of the energy intake – this being a safe target especially for children – with a minimum of about 8% for healthy adults. This takes into account the lower mean biological value of the dietary proteins in the developing countries.

A committee of the US National Research Council has recently formulated 22 priority research areas belonging to four categories: nutrition, food production, food marketing, and policies and organizations. Within the category of food production, plant breeding is one of the priorities, and our aim is to suggest some guidelines for research in this area.

Generally speaking, there are two ways of arriving at an adequate nutritional standard for diets in developing countries. One approach is to put the main effort into improving the intrinsic quality of a basic food crop, for example by trying to increase a certain limiting aminoacid. This approach involves difficulties. The

Table 1.5. Protein content of various foods, expressed as their contribution (%) to the energy provided by each food (adapted from: Brock & Autret, 1952).

Foods arranged according to protein content	Proportion of energy provided by protein (%)
Poor protein sources	
Cassava	3
Cooked bananas (plantains)	4
Sweet potatoes (*Ipomoea batatas*)	4
Taros	7
Adequate protein sources	
Potatoes	8
Rice (home-pounded)	8
Maize (whole-meal)	10
Millet (*Setaria italica*)	12
Sorghum (*Sorghum vulgare*)	12
Wheat flour (medium extraction)	13
Millet (*Pennisetum glaucum*)	14
Good protein sources	
Groundnuts	19
Cow's milk (3.5% fat)	22
Beans and peas	26
Beef (lean)	38
Cow's milk, skimmed	40
Soya bean	45
Fish, fatty	46
Fish, dried	62

second and easier method is to set up nutritional goals within the basic food crop in relation to existing local or regional eating patterns. Before we go on to define such nutritional goals, it must be made clear that present knowledge regarding recommended intakes is limited and is moreover liable to confusing shifts of opinion, so that all recommendations must be regarded as provisional.

GENERAL NUTRITIONAL GOALS

On the basis of the information supplied in the earlier parts of this chapter we may suggest the following general nutritional goals for plant breeders.

1 Because cereals are an important source of basic energy and protein, efforts should be concentrated on improving their yield, in terms of both yielding capacity and yield stability.

2 The yield of food legumes should be improved, thus making their cultivation more attractive. Fig. 1.12 shows yield increases for various crops in the USA, based on data obtained from USDA (1962, 1977) agricultural statistics for 1961 and 1977.

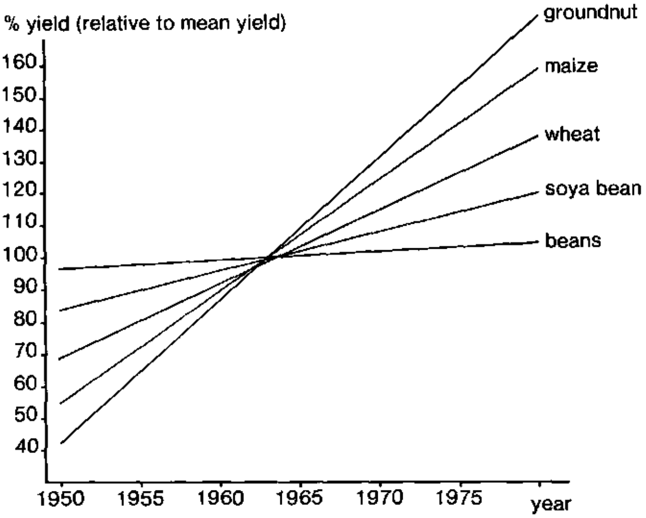

Fig. 1.12. Mean yield increases 1950-1977, relative to the means for the entire period. 100% corresponds to 1732 kg/ha for groundnuts, 4086 kg/ha for maize, 1734 kg/ha for wheat, 1626 kg/ha for soya beans and 1379 kg/ha for beans (based on: USDA 1962, 1977).

The yields are expressed in percentages of the mean yield of each crop over the period 1951-1976. For beans, the increase is only 2.6% per year.

3 People will probably accept new foods when they add to the palatability of the diet, especially in countries with a favourable economic development. Adequate diversification of the crops grown may help to improve palatability and thus facilitate adequate energy intake.

4 In general the attention paid to protein yield should be secondary to that given to energy yield; the nutritional quality of a diet is best improved by improving its composition.

5 On the other hand, care should be taken that breeding for higher yields does not result in varieties with a poorer nutritional value than those they are going to replace.

6 There is still wide genetic variation in the content of some important nutrients in food crops. Where possible this should be exploited to improve the nutritional value of a given diet.

7 Because malnutrition often occurs in unfavourable ecological conditions, breeders should pay special attention to varieties giving reasonable yields under such conditions.

8 In breeding new varieties, consumer and/or user quality should be maintained, as noticeable changes in taste or appearance are not readily accepted.

9 Breeders should realize that food habits, local food processing and food preparation practices are often firmly linked to traditional cultural patterns; new varieties,

even when they are obviously better in nutritional quality, are not accepted as a matter of course.

10 The energy density of certain staple foods should be improved, for instance by increasing fat content, in order to limit their bulkiness (see pp. 30-31).

11 In all cases where information is available, attention should be paid to toxic substances and substances affecting digestibility. However, results can only be obtained if methods of analysis suitable for large numbers of samples of breeding materials are available.

12 More attention should be paid to differences in susceptibility to storage diseases and other storage losses (see p. 29).

SPECIFIC NUTRITIONAL GOALS

Before discussing the various foods separately, it will be useful to demonstrate the large differences in crop yields (kg/ha), energy yields (kJ/ha) and production (1000 t) to be found among a number of important foodstuffs in South America, Africa, Asia and Europe (Table 1.1). Table 1.6 lists the nutritional value of a number of these foodstuffs. Such information is of use in formulating priorities and evaluating breeding programmes. Crop-specific goals for the breeder are given below.

Rice Table 1.5 shows that in rice the proportion of energy from protein is about 8%. This means that in diets based on a high percentage of rice the proportion of energy from protein can be too low, especially in populations suffering from malnutrition, infectious diseases etc. In such situations the recommended protein-energy ratio in the diet should be 10% rather than the minimum of 8%, particularly for the growing child. Raising the protein content by 1 or 2% could thus be very effective. It may be noted that rice protein is of high nutritional quality and digestibility. Another character which could be of importance here is the improvement of the energy density (cf. point 10 above) by the development of varieties which take up less water during cooking.

Wheat The major goal for wheat, next to higher and more stable yields, is consumer or user quality. For bread wheat this means that milling and baking quality should receive attention. However, it would then be necessary to ensure that the grower receives adequate remuneration for growing high-quality varieties or to take other measures which favour the use of such varieties. Unless this is done the farmer will choose varieties for their agricultural value only.

Maize and sorghum Quality improvement in maize illustrates the complexity of quality problems. For example, protein content can be increased significantly by selecting for this character. This results in populations with an increase in zein, which has no nutritive value for human and non-ruminant animals. Therefore hybrids derived from high-zein lines are no better nutritionally than normal maize and yields of such

Table 1.6. Comparison of nutritive value of a number of foodstuffs per 100 g edible portion (based on: Platt, 1965, and Burton, 1974).

Foodstuffs	Energy (kJ)	Energy sources (g)			Minerals (mg)		Vitamins (mg)				
		protein	fat	carbohydrates	Ca	Fe	carotene	B_1	B_2	nicotinic acid	C
Potato	350	2	0.1	16	15	1	–	0.1	0.03	1	25
Cassava (fresh)	630	0.7	0.3	34	30	1	–	0.06	0.03	0.6	35
Sweet potato	470	2	0.3	26	25	1	–	0.1	0.04	0.7	30
Yam	430	2.4	0.2	23	20	0.8	–	0.09	0.06	0.4	10
Pulses	1400	20	2	60	150	2-8	12-120	0.4	0.2	2	–
Rice (brown)	1400	8	2	76	10	2	–	0.2	0.1	2	–
Maize	1500	10	4.5	70	12	5	500	0.31	0.1	2	–
Wheat	1300	10	2.4	62	30	4	–	0.40	0.15	6	–
Green leafy vegetables:											
highest value	200	4	–	12	250	25	6000	0.08	0.25	1.0	200
lowest value	40	1	–	1	50	1	600	0.03	0.03	0.2	10
Fruits:											
highest value	300	2.0	–	20	40	1.0	1800	–	–	1.0	300
lowest value	80	0.2	–	2	5	0.1	0	–	–	0.2	0

hybrids are lower than normal. A second example concerns the introduction of opaque-2 maize, which has improved lysine content. When used for human consumption opaque-2 varieties have been less acceptable than normal varieties, owing to differences in taste, texture and appearance and also the greater susceptibility to kernel moulds. Furthermore, high-lysine hybrids yield approximately 10% less than their normal counterparts which, for economic reasons, has prevented their use in animal feeds. Breeders should therefore concentrate on improving protein quantity and quality without losses in total yield and consumer quality. High-lysine mutants are also available in sorghum, but like those of maize they show reduced yields and consequently have yet to be of practical importance.

Millets The various millets are cultivated in the drier regions of Asia and Africa and often serve as a major energy and protein source. The grain of pearl millet can contain up to 20% protein but lysine is often seriously deficient. New varieties are now available in India which have a protein content of 18-20% combined with sufficient lysine and good yields.

Cassava Fresh cassava roots contain 50-75% of water and less than 1% of protein, the remainder being mostly starch. Only about 3% of the energy is derived from protein: this is less than half of the proportion of energy derived from protein in potatoes, yams and taro and only about one-third of the safe target for the protein energy content of a diet (cf. Table 1.5). Thus it is not surprising that protein-energy malnutrition is common in all communities dependent on cassava. An additional problem of cassava is the presence of a glyceride, linamarin, from which hydrogen cyanide is released by enzymic action. The latter is toxic and associated with prevalence of neuropathies. Breeders should determine whether the protein content of cassava could be improved – any improvement would be beneficial – but the possible unfavourable effect on yield (cf. Chapter 2 pp. 66-67) should not be overlooked. The possibility of reducing the toxic constituents should also be investigated.

Potatoes Fresh potato tubers contain approximately 75% water and 25% dry matter, of which 20% is starch, 1.5-2% is protein and only 0.1% is fat; there are also valuable amounts of vitamin C and vitamins of the B group. Of the average energy yield of 350 kJ/100 g, 7.6% is derived from protein. In comparison with other foodstuffs (Table 1.6), its energy value is very low – a disadvantage if it is to become staple food in countries with marginal energy supplies – and so is the protein content. However, the biological value of the protein is higher than that of any other plant protein (Kofrányi, 1967). In addition, potato crops produce the highest yields of energy and protein per hectare per day. Consequently, this crop can be an important supplement in the frequently one-sided diets of the tropics and subtropics. In most European countries the potato is the people's cheap food *par excellence.* In most tropical and subtropical countries however, it is still only of minor importance in the daily diet (exceptions being the countries of the Andes and Argentina) and is regarded as a luxury product. By increasing not only the acreage but more especially the yield per hectare, and by improving disease and insect resistance, total potato production could be raised considerably. This, together with a reduction in price, would enable the potato to reach a much greater proportion of the population than is the case at present, and could thus make a notable contribution to the improvement of the food situation. To ensure steady supplies, storage facilities in tropical countries need drastic improvement.

Vegetables Much use is made of vegetables in western societies, the quantities used varying from 150 to 300 g/person/day, but the consumption in developing countries is very irregular and usually limited to some tens of grammes. Especially in the humid tropics better nutritional advantage should be taken of the abundant leaf production. The energy content of leaves is very low, about 80 kJ/100 g, but leaf vegetables are an important source of β-carotene, ascorbic acid and folic acid; cereals and pulses are in general totally devoid of the last two of these. It is impossible to overemphasize the improvement in health that could result in many developing countries from even a small intake of vegetables; for example, the β-carotene contributed to the diet by green vegetables has a far-reaching importance (see p. 33).

Further, green leafy vegetables have a protein content of about 2 to 5 g/100 g, which is especially important when food intake is marginal. The iron content of leafy vegetables is fairly high, ranging from 1.5 to 5 mg/100 g. Even though much of the iron present in vegetables may not be absorbed, their relatively high content of ascorbic acid may promote its absorption.

The amount of calcium is probably also physiologically significant. Many green vegetables are rich in calcium (range 25-300 mg/100 g) and could be an important calcium source for the less privileged, for whom the main dietary sources of calcium – milk and dairy products – are often luxury foods and not readily available. Finally, certain B vitamins, such as thiamine, riboflavin and niacin, are present in leaf vegetables. There can be drawbacks to the consumption of leaves – for example, cassava leaves contain hydrogen cyanide and amaranth contains oxalates – but when the drawbacks are known, appropriate methods of domestic food preparation can be devised and the quantities eaten restricted. In breeding vegetables an important objective is improvement of consumer and user quality. Another objective is iron availability and absorption. For lettuce the wide variation in iron content reported allows ample scope for improvement by breeding.

Oil-bearing seeds and fruits The breeding of oil-bearing seeds, fruits and nuts should have two objectives:

– the ratio of polyunsaturated fatty acids to saturated fatty acids in western diets should be increased;

– the energy density of diets in developing societies with marginal food energy supplies should be increased.

Some vegetable oils, like those of rapeseed, sunflower, soya beans and cottonseed, contain substances toxic both to laboratory animals and to man. Plant breeding programmes have been successful in removing many of these substances; however, as a consequence, adequate yields have been difficult to achieve, for example in cotton, which is more susceptible to insect attack when the toxic substance gossypol has been removed.

Legumes These need little or no N fertilization and their cultivation is therefore of great economic importance. Their yield level is still low. There has been little development either in the breeding of high-yielding varieties of grain legumes or in the application of agricultural technology to legumes. Indeed even land that used to grow pulses has shifted to wheat in winter and to rice or maize in summer. This development must be regarded as very unfavourable, for in the developing countries legumes, like cereals, are among the staple foods supplying not only basic energy and protein needs, but also vitamins and minerals (iron and calcium) (cf. Table 1.6).

Certain difficulties are associated with the digestion of grain legumes or pulses. The factors responsible are not really known, and this makes it difficult to suggest methods for improvement. It is sometimes stated that the digestive problems are the reason for the rather low consumption of pulses. Antiphysiological compounds present in legumes, such as trypsin inhibitors, amylase inhibitors and haemagglutinins are sometimes held responsible for the low protein digestibility. However, these substances are largely or completely destroyed by heat treatment during food preparation and it is worth noting that the method of cooking and its duration can influence the digestibility of beans significantly.

Flatulence is a notorious result of the consumption of pulse foods. The gas-producing factor is to be found in the carbohydrate fractions of low molecular weight, which include sucrose, stachyose and raffinose. However, the specific factor or factors responsible have not yet been identified. Stimulation of the consumption of grain legumes in societies where symptoms like flatulence are not tolerated could give rise to problems in normal social relations. This probably applies to most societies and could have an unfavourable influence on the introduction of legumes into eating patterns. The subject needs further study.

High-yielding legume varieties should also receive attention. Such varieties could be of importance for legume consumption in developing countries where today the local varieties with their low yields have little to attract the small marginal farmer. High-yielding varieties would provide economic incentives to grow grain legumes. Most plant breeding effort is directed to such common legume species as soya beans, groundnuts, peas, beans, broad beans, lentils, chickpeas, pigeon peas and cowpeas. Other species with the potential to become an important crop, like the winged bean, are, however, also worthy of attention. In this respect valuable work has been done by the Asian Vegetable Research and Development Center in Taiwan.

Finally, it is worth stressing that improving the aminoacid profile of legumes by breeding should not be regarded as a matter of priority, especially when funds and trained personnel are limited.

Plant breeders should, however, make every effort to contribute to a steady food energy supply; they should give special attention to improving local food crop yields by breeding for resistance to stresses such as drought, pests and diseases. Finally, they should be aware of the relationship between agricultural production and nutritional needs, especially in ecologically unfavourable regions.

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Acknowledgement

The authors wish to express their sincere appreciation to Hans K. Henderickx (Agricultural Faculty of the University of Gent) and to Paul Lunven (FAO, Food Policy and Nutrition Division, Rome) for their valuable help in supplying recent data and their constructive comments on the manuscript. Their contributions and support are gratefully acknowledged.

A stimulating 2-day workshop on the subject, specially organized in August 1977 at Evian (France), provided further information and we are grateful to those who participated, namely: F. Aylward † (Oxford, UK), E. M. DeMayer (Geneva, Switzerland), J. J. Gottenbos (Vlaardingen, Netherlands), M. Jul (Copenhagen, Denmark), P. Lunven (Rome, Italy), J. Mauron (Vevey, Switzerland), O. Mellander (Göteborg, Sweden) and D. Miller (London, UK). A. J. T. Hendriksen (D. J. van der Have B.V., Rilland, Netherlands) and F. de Koning (Wageningen, Netherlands) were responsible for the technical organization of the workshop.

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2 Physiological potential of crop production

The possibilities of increasing world food production, both by increasing yields and by expanding the area under cultivation, are considerable. Efforts to meet food demands through agricultural development should be directed rather to the former than to the latter. The potential production rate of C_3 plants is in general around 200 kg and of C_4 plants 200-400 kg dry matter ha^{-1} day^{-1}, depending on the weather. The rate has so far not been increased by breeding and the prospects for doing so do not seem very bright. Differences in the total biomass production of crop species depend mainly on the length of the total growing period, and differences in the seed production of small grains mainly on the length of the growing period after anthesis. Both depend on temperature and day length and may be manipulated by breeding. However, breeding has had little effect on the relative length of the postanthesis period in rice or on the date of anthesis in wheat, and breeding successes with small grains are mainly attributable to control of diseases and lodging, permitting optimal N fertilization and resulting in delay of leaf senescence. Plants such as maize and Brussels sprouts, in which axillary buds form the economic yield, do not tolerate dense planting, as this leads to a monopolization of the flow of assimilates by the main growing point. Here breeding should aim at large, uniform single plants; in the case of cross-pollinated species this may be facilitated by hybridization.

Grain number in cereals and supply of photosynthates in general have to be increased simultaneously which limits the possibility of breeding. To prevent self destruction of the plant by translocation of nitrogen and minerals from the vegetative mass to the seeds, it may be worthwhile to breed for a high vegetative mass at the onset of anthesis, together with a low assimilation rate. Nitrogen uptake depends little on root density, and the utilization of nitrogen by the plant, once it has been taken up, can only be improved by sacrificing protein content. Hence most efforts to improve efficiency of N use by breeding are ill directed. Varietal mixtures or multilines have little advantage, since the relative yield of a mixture is equal to one. Breeding to produce C_3 plants with features of the assimilation system of C_4 plants has had little success. The CO_2 concentration in the intercellular air spaces of leaves can be regulated to some extent during assimilation, depending on growing conditions, species and possibly variety. In breeding for economic utilization of water by the plant, full regulation should be aimed at, whereas in breeding for high assimilation rates and suitability for CO_2 fertilization the aim should be absence of regulation.

Aspects of world food production

There can be no doubt that a precarious balance exists between food supply and demand in many regions of the world. Considerable discussion, however, centres on the extent to which food production is and will be determined by socioeconomic constraints and lack of knowledge and incentives at the farmer's level or simply by the physical impossibility of increasing productivity.

Buringh et al. (1975) calculated the potential world food production, under the assumption that fertilizers and adequate varieties are available and that pests and diseases are absent. For each continent 30 to 50 broad soil regions were distinguished. For each region, the following calculations were made.

The length of the growing season was determined on the basis of the temperature and the potential grain production (wheat, rice) calculated from radiation data (cf. pp. 70-77). Water was assumed to be optimally available, though this is often not the case. To estimate the water requirement under optimal conditions, the potential evapotranspiration was calculated according to Penman's method (1948). This estimate was compared with the availability of water from rain and irrigation, taking into account the storage capacity of the soil. To allow for soil evaporation, the figure for available water was reduced by 15% of the potential evapotranspiration. The potential yield was then reduced in proportion to the relative availability of water.

Apart from the availability of water, many soils are either not or only marginally suitable for agriculture. Some are very poor, stony, steep or shallow or already used for urban or other nonagricultural purposes. Others again cannot be reclaimed by present-day techniques, so that only part of the potential agricultural land can be used for crop production. Even where there is sufficient water, the yield in such areas may be less than the potential because they cannot be worked, because they have mineral deficiencies that cannot be overcome etc. The resulting reduction factor for potential yield was estimated. Either this factor or the reduction factor for water was applied, whichever appeared to be the smaller. Of course, considerable guesswork was involved, but comparison with actual yield data on experimental farms showed that the computed yields are certainly not too high.

The result of the exercise is presented in Fig. 2.1 for the six continents. Within each broad soil region, the area potentially available for cultivation is given by the shaded areas. The type of shading designates the yield level that can be achieved. For instance the potential agricultural area in Africa is 23% of the total land area. The 6% cultivated at present is very small compared to the potential, as is the actual yield of 1000 kg ha^{-1} in comparison with the average maximum yield of over 10,000 kg ha^{-1}. Hence there are considerable possibilities for increased food production. In Asia, 16% of the continent is already under cultivation, whereas 20% can be regarded as potential agricultural land. The average yield for Asia, exclusive of China, is 1500 kg ha^{-1}, again with an average maximum yield over 10,000 kg ha^{-1}. Hence in this continent it is difficult to increase food production substantially without a transition to intensive modern agriculture with a high per area yield. The present world average for grain production is 1800 kg ha^{-1} and the total grain production is 1.36×10^{12} kg. This amount is grown on 65% of the cultivated land area. If 65% of the potential agricultural land were to be used to grow cereal crops, the maximum grain equivalent production would be 32.4×10^{12} kg, or 24 times the present production. Table 2.1 shows a survey of land use and productivity of several world regions for the year 1965, at

Table 2.1. Actual and potentially suitable agricultural land and actual and maximum production (from: de Hoogh et al., 1976).

Region	Arable land			Agricultural production			Maximum yield/ha 10^3 grain equivalents
	in use in 1965 10^6 ha	potentially suitable 10^6 ha	used in %	in 1965 10^9 grain equivalents	maximum 10^9 grain equivalents	produced in %	
North America	220	546	40	316	5695	5.5	10.4
Western Europe	129	147	88	180	1695	10.6	11.5
Japan	6	8	75	30	114	26.3	14.3
Australia etc.	59	284	21	73	3167	2.3	11.2
Eastern Europe (incl. USSR)	288	522	55	252	4737	5.3	9.1
Industrial economies	702	1507	47	851	15408	5.5	10.2
Latin America	122	695	18	150	12610	1.2	18.1
Middle East	52	111	47	28	832	3.4	7.5
Tropical Africa	174	643	27	74	9474	0.8	14.7
Southern Asia	266	382	70	261	7895	3.3	20.7
China	111	349	32	242	3611	6.7	10.3
Developing countries	725	2180	33	755	34422	2.2	15.8
World	1427	3687	39	1606	49830	3.2	13.5

which date the maximum productivity was about 30 times the actual production.

Although there are small areas where the present food production reaches more than 50% of its potential value, it may be concluded that for the world as a whole the actual production is still very much lower than the potential production.

Obviously the problem is not so much yield potential as the economic and social constraints on the rate of increase of food production. In Fig. 2.2 (de Wit & van Heemst, 1976), the average grain yields in kg per hectare for the various continents from 1954 to 1973 are arranged along a continuous scale. Below a yield level of 1700 kg ha^{-1}, the rate of yield increase is only 17 kg ha^{-1} year^{-1}, but above this yield level, the rate jumps to 78 kg ha^{-1} year^{-1}. Presumably, this break point represents the yield

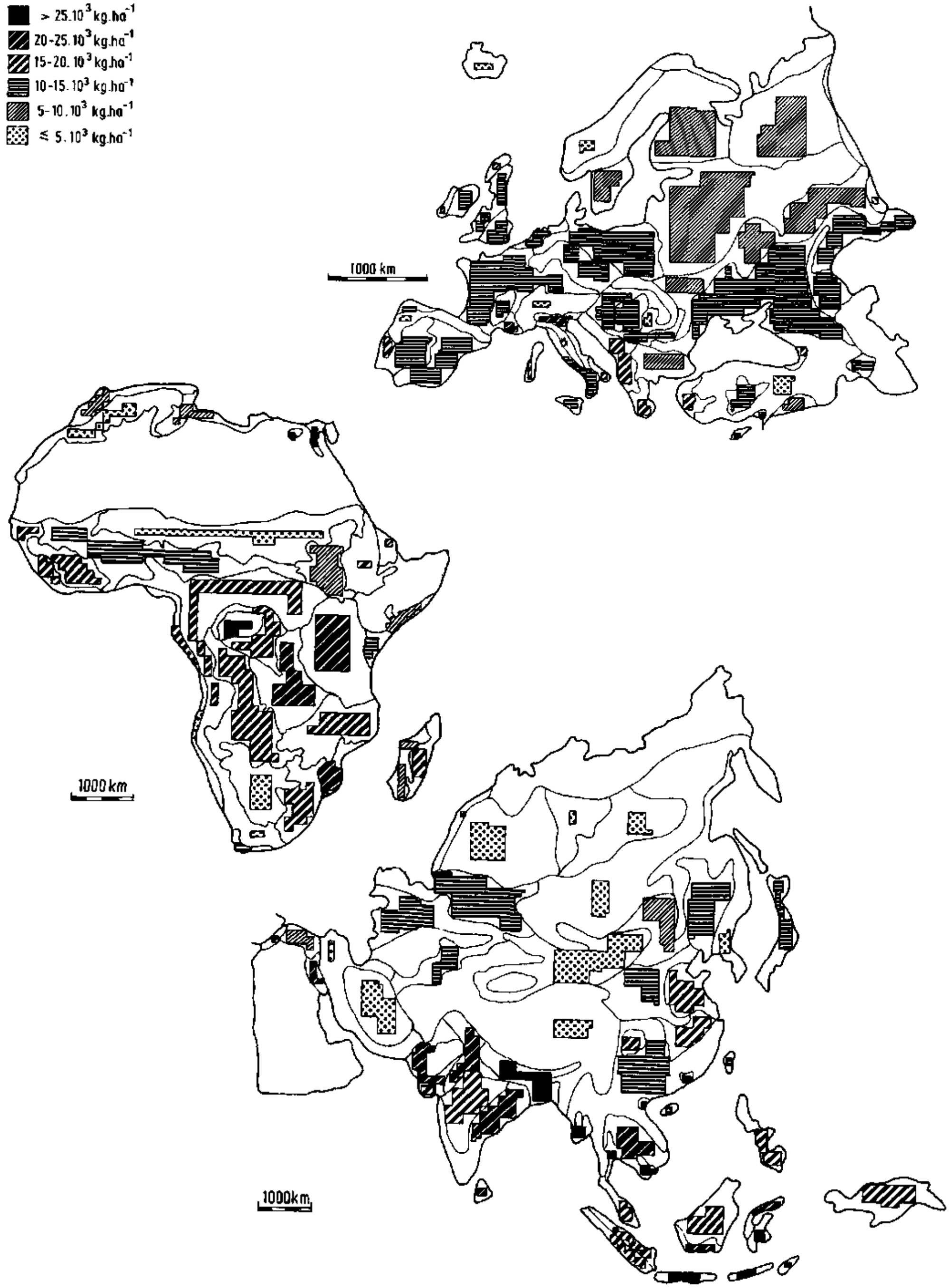
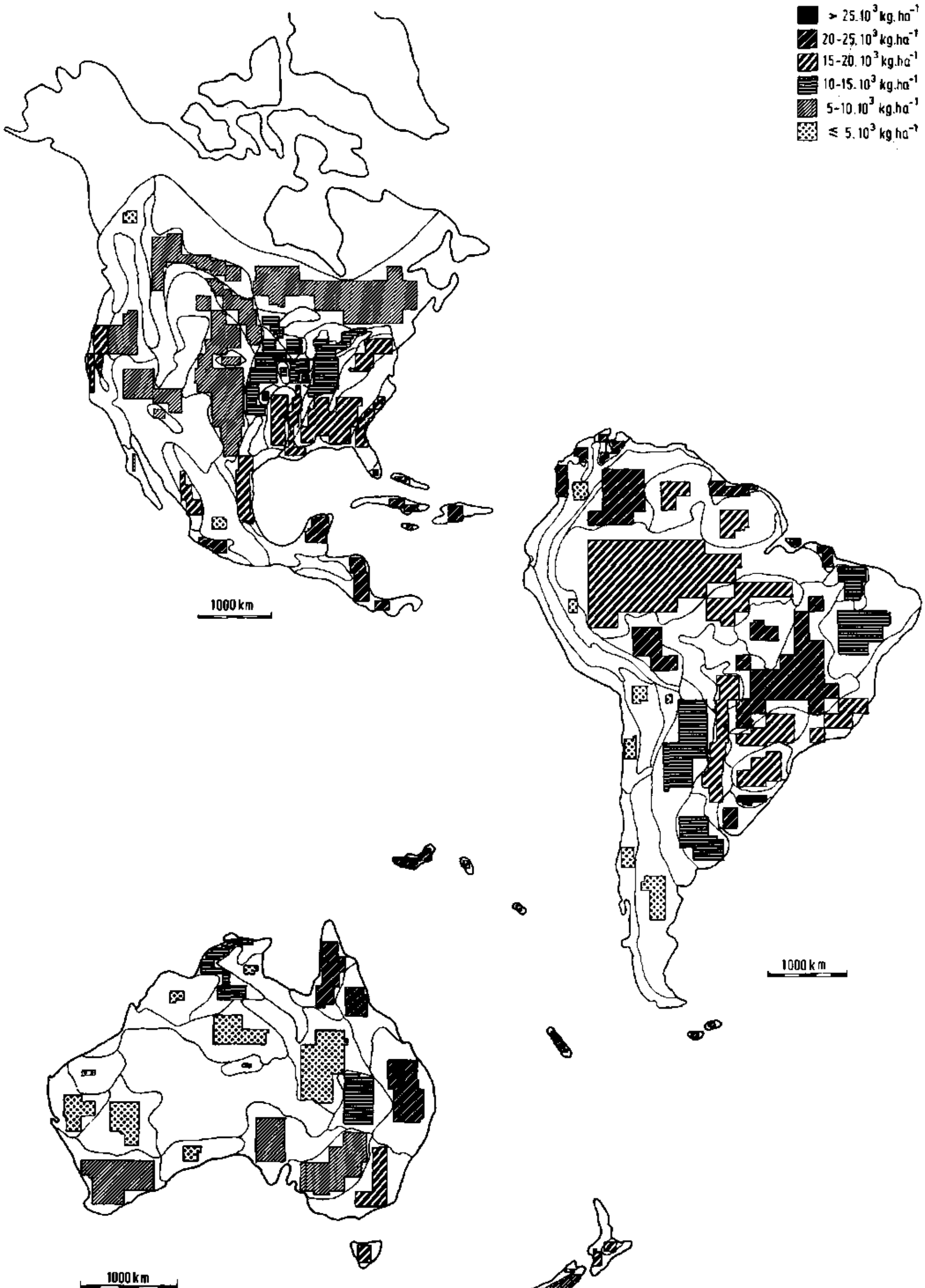


Fig. 2.1. Broad soil regions with their area of potentially arable land marked by the shaded area per region and its average potential yield, in kg grain eq. ha^{-1} $year^{-1}$ indicated by the type of shading. Water and soil constraints are taken into account (from: Buringh et al., 1975).


$> 25.10^3$ kg.ha^{-1}
$20-25.10^3$ kg.ha^{-1}
$15-20.10^3$ kg.ha^{-1}
$10-15.10^3$ kg.ha^{-1}
$5-10.10^3$ kg.ha^{-1}
$\leq 5.10^3$ kg.ha^{-1}
1000 km
1000 km
1000 km

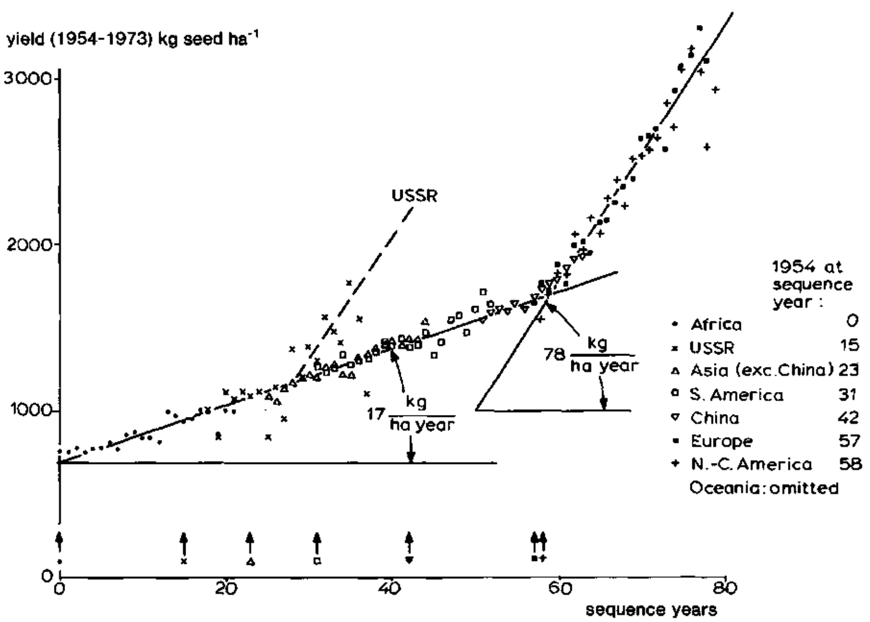


Fig. 2.2. Yields from 1954 to 1973 in the main regions distinguished by FAO, ordered along a continuous yearly time scale. The position of the year 1954 is marked by an arrow for each region. Oceania, with an average yield of 1200 kg ha^{-1}, is omitted because of the erratic fluctuations in the reported yield data (from: de Wit & van Heemst, 1976).

level at which the transition occurs from traditional agriculture with little outside input to modern agriculture with considerable input of outside resources. Just below this yield level, the relative yearly increase is only 1%, and this is far too low to keep up with the population increase. Where this is the case, emphasis tends to be put on increasing the acreage of land under cultivation to prevent hunger. Just above the break point, the relative yearly increase is 4.5%, which is larger than the population increase in the countries concerned; emphasis then shifts to taking marginal land out of production, to converting primary into secondary products and to producing luxury goods.

The transition from the more traditional situation to modern high-input agriculture has been attempted at a yield level of 1100 kg ha^{-1} in the USSR, but not too successfully, as appears from the scattering of the yield data. China has just passed the break point of 1700 kg ha^{-1}, so that the intended emphasis on mechanization and increased use of fertilizers in the present 5-year plan seems appropriate.

Ecologically this course of development is most alarming. It suggests that in countries with a yield level just below 1700 kg ha^{-1}, the demand for food is met by taking more and more land into agricultural production, destroying the natural ecosystem in the process. After one or two generations, however, the transition to agricultural systems that permit yearly yield increases in excess of population increase is likely to be made, whereupon this land is again left uncultivated, in the often vain hope that a favourable ecosystem will be restored by natural processes.

Clearly, the main concern of governments, ecologists, agriculturists and planners should be to meet food demands by exploiting the large production potential of land already in use and to avoid indiscriminate and probably only temporary further reclamation of natural reserves.

Potential production of biomass and seed

Considerable attention has been paid in plant physiology and crop science to the fundamental aspects of gross and net CO_2 assimilation of leaves and crop surfaces. The most important of these are discussed below (cf. pp. 70-77).

The potential production rate of a crop is defined as the growth rate of a closed, green crop surface, optimally supplied with water and nutrients, in a disease and weed-free environment under the prevailing weather conditions. This potential production rate differs in the so-called C_3 and C_4 plants (the name refers to the length of the C-skeleton of the first product of assimilation). In C_4 plants (maize, sorghum, sugar cane, tropical grasses), it varies from about 350 kg dry matter ha^{-1} day^{-1} in warm and sunny climates to about 200 kg dry matter ha^{-1} day^{-1} in temperate, humid climates as in the Netherlands. For C_3 plants (species from temperate regions and rice), the potential growth rate appears to be about 200 kg dry matter ha^{-1} day^{-1}, the main cause of variation being the availability of light. These data apply for the growing season, that is, roughly, under situations where the average daily temperature is above 10 °C for C_3 and 15 °C for C_4 plants.

The maximum net assimilation rate of leaves (F_m) may vary considerably, but there are several reasons why these differences are hardly reflected in the potential production rate of crop surfaces. Only part of the total leaf surface of a crop is operating at the light saturation level, so that any relative increase in crop assimilation is only about half of the relative increase in F_m. Moreover an increase in F_m is often associated with increased leaf thickness, increased light absorption and decreased availability of light for the lower leaves. It should also be taken into account that the presence of so-called physiological sinks (storage organs such as seeds etc.) may result in a higher F_m, but that on the other hand the presence of sinks depends on the crop assimilation rate at earlier growth stages (cf. pp. 59-63). This tends to reduce fluctuations.

The experimental evidence for the absence of significant differences in potential growth rates among species and within species is considerable. For instance, the potential growth curves of the main agricultural crops in the Netherlands all appear to exhibit practically the same slope, as illustrated in Fig. 2.3 (Sibma, 1968; de Wit, 1968). The C_4 crop maize shows the same slope, but this is because it is here grown at the limit of its temperature range. However, it should be taken into account that the determination of growth rates under field conditions is subject to relatively large experimental error, so that it is in any case difficult to establish differences (de Wit et

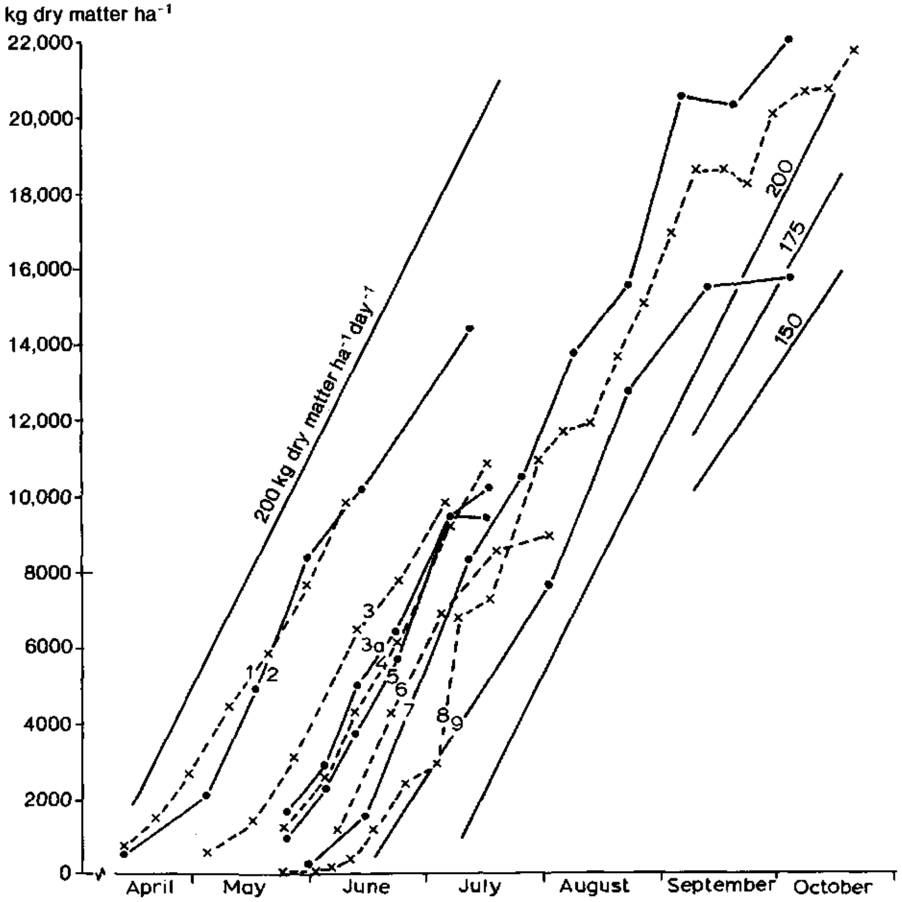


Fig. 2.3. The growth rates of the main agricultural crops in the Netherlands under (near-)optimal growth conditions; compared to the curves corresponding to 200, 175 and 150 kg ha^{-1} day^{-1}. 1. Grass (Alberda, 1960). 2. Wheat (de Vos, 1965). 3. Oats + barley (de Wit, 1960). 3.a. Oats + peas (de Wit, 1964). 4. Oats (de Wit, 1964). 5. Peas (de Wit, 1964). 6. Barley (de Wit, 1966). 7. Potatoes (Bodlaender, 1965). 8. Sugar beets (Bakermans, 1965). 9. Maize (Meyers, 1973). (In brackets: author, year of measurement.)

al., 1978).

It also appears that the potential growth rate for natural grassland in Israel near Beersheva is the same as for wheat, if both are optimally supplied with nutrients and as long as water is available, as may be seen in Fig. 2.4 (van Keulen, 1975). That wheat continued to grow for a longer period in this case is due to the fallow in the previous year, which led to a larger amount of available water. The growth rate in both cases is about 160 kg dry matter ha^{-1} day^{-1} and is in accordance with calculations made on the basis of the radiation conditions (cf. pp. 70-77).

The potential production of perennial ryegrass in the Netherlands appears to be about 20,000 kg dry matter ha^{-1}, taking into account the periods of reestablishment

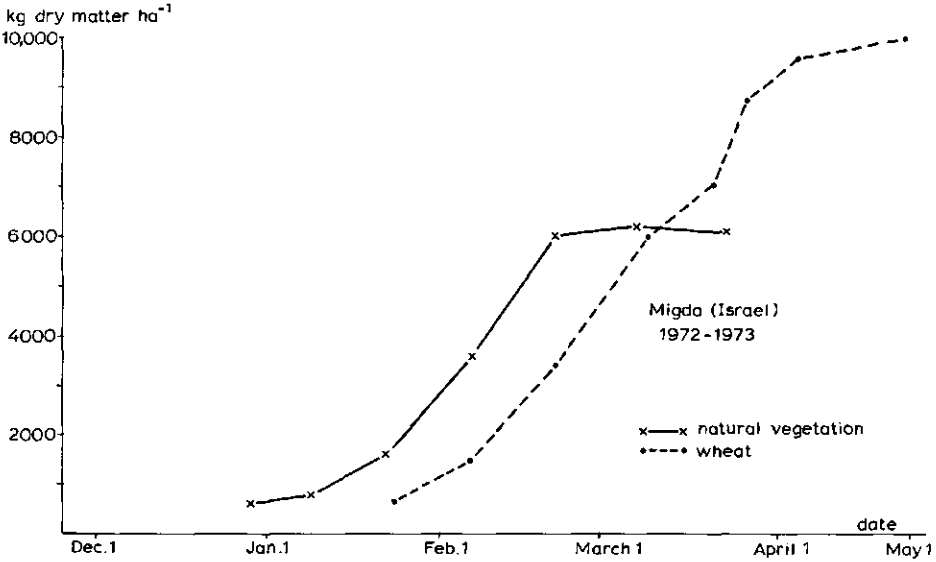


Fig. 2.4. The growth of wheat and natural grassland in Migda (Israel) under (near-)optimal water and nutrient supply (from: van Keulen, 1975).

of the closed crop surface after cutting (Alberda & Sibma, 1968). Dickinson (1847) obtained the same amount 120 years earlier with Italian ryegrass, kept well supplied with water and with the urine of horses, servants and maids by means of a London water cart. Similarly, field measurements of CO_2 assimilation showed no difference between the wheat variety Staring introduced in 1940 and the variety Lely introduced in 1970, as shown in Fig. 2.5.

It must be concluded that, whatever its importance in other respects, plant breeding has not resulted in any increase in potential growth rate, in spite of the relatively large variations in maximum leaf assimilation rates observed under laboratory conditions. Apparently the overall process is very much limited by physical constraints of light and CO_2 availability and by complicated feedbacks between assimilation on the one hand and growth and development on the other. Knowledge of these interrelations is still so limited that any breakthrough in the near future seems doubtful (cf. pp. 70-77). The optimism which is often expressed by biochemists who study basic processes without taking into account the integrated system in which these operate, would not seem to rest on a very firm basis.

The obvious way to increase total biomass production under optimal supplies of water and nutrients is to extend the growing season, either by lengthening the growth period of the species concerned or by shortening the growth period and growing more than one crop within the season. In this respect especially attention has been given to breeding for better growth at low temperatures, but complications related to vernalization effects and lack of frost hardiness may occur. To evaluate the

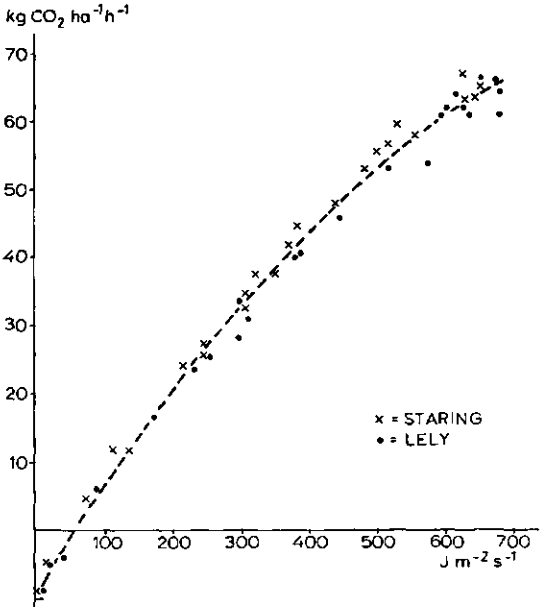


Fig. 2.5. Net CO_2 assimilation as a function of light intensity, as measured under field conditions for Staring and Lely, two wheat varieties from 1940 and 1970, respectively.

potential of this approach, Sibma (1977) promoted early growth of maize by means of plastic covers. By choosing suitable varieties so as to avoid earlier ripening, he did indeed obtain an early yield increase that was maintained throughout the season (Fig. 2.6).

The high yield potential of C_4 plants in the tropics is confirmed by yield studies of tropical grasses and maize (Dayan & Dovrat, 1977) and is especially marked for sugar cane, which also has an extremely long growing period. Growth rates of 300 kg dry matter ha^{-1} day^{-1} may be maintained over a full year, resulting in yields of over 100,000 kg ha^{-1} $year^{-1}$. If fossil fuel becomes scarce, there may be a possibility of covering energy requirements to some extent by energy farming in countries with large areas of good, potential agricultural land per caput and a not too ecology-conscious government. Sugar cane would then be an obvious candidate, the more so because its husbandry is well understood and the necessary breeding work has already been done.

It is generally accepted that the carbohydrate stored in cereal grains is mainly derived from current photosynthesis during the grain-filling phase. The amount of nonstructural carbohydrates present at the onset of flowering is around 1500 kg ha^{-1} (Table 2.2). Taking respiration during translocation into account, the contribution of such carbohydrates to the total seed weight can hardly exceed 1000 kg ha^{-1}. Bidinger et al. (1977) observed a preanthesis contribution of 13% for wheat and 12%

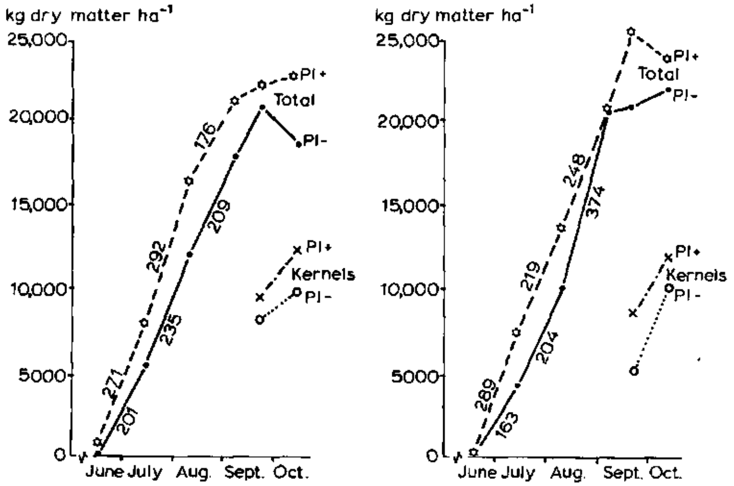


Fig. 2.6. Dry matter yields of two maize varieties, Capella (left) and Pioneer hybrid 3853 (right), grown from 25 April (sowing) to 20 May under plastic (Pl+) and control (Pl—). Numerals upon the growth curves indicate crop growth rate in kg dry matter ha^{-1} day^{-1} for the period concerned (from: Sibma, 1977).

for barley, relative to seed weight, amounting to about 650 kg dry matter ha^{-1}.

Hence yield depends mainly on rate and duration of photosynthesis after anthesis. Experimental data on the course of photosynthesis in cereals are given by Puckridge (1968), Biscoe et al. (1975) and Moss (1976). They all show a rapid decline after flowering, but the data pertain to experiments with moisture stress during this phase. De Vos (1975) presents results of an experiment under conditions closer to the optimum. In this case the level of photosynthesis remained high for about 30 days after flowering, after which there was a linear decline over the next 20 days. Assuming a potential seed production of 210 kg ha^{-1} day^{-1} at 16% moisture, this amounts to 210 × 40 = 8400 kg seed ha^{-1} plus another 1200 kg seed from translocated nonstructural carbohydrates. The calculated total is then close to the yields of 10,000 kg ha^{-1}

Table 2.2. Nonstructural carbohydrates in kg per ha present at the onset of grain filling (A) and at ripening (B) in winter wheat for three consecutive years.

	A	B
1974	1520	320
1975	1680	220
1976	1240	180

observed by de Vos.

Maximum rates of assimilation are in general observed around flowering (Puckridge, 1968; Fukai et al., 1976) and appeared to be about 65 kg CO_2 ha^{-1} h^{-1} around noon on clear days in de Vos's experiment. Extremely high values of 100 kg CO_2 ha^{-1} h^{-1} were reported by Moss (1976) for both barley and wheat. It is tempting to attribute these to experimental error, but it may be that in the conditions of the experiments no stomatal regulation occurred, which would lead to assimilation rates reminiscent of those for C_4 plants (cf. pp. 70-77).

The duration of the seed-filling stage is reduced by increasing temperature, at least under controlled conditions (cf. pp. 59-63; Sofield et al., 1974; Spiertz, 1974). Under natural conditions this effect of higher temperatures will be more or less compensated by higher radiation, thus enabling the crop to reach a similar yield level. This is demonstrated in Fig. 2.7, where the course of grain growth is given for two contrasting years, 1974 with rather low temperatures and 1976 with extremely high temperatures but also high radiation.

Record farm yields of 10,000 kg per hectare and over are reported to have been obtained with various wheat varieties (Austin & Jones, 1975; Briggle & Vogel, 1968). For the variety Gaines, the yield has even reached 14,000 kg in Washington State, USA. According to Hageman (1977), in this last case the crop was sown in

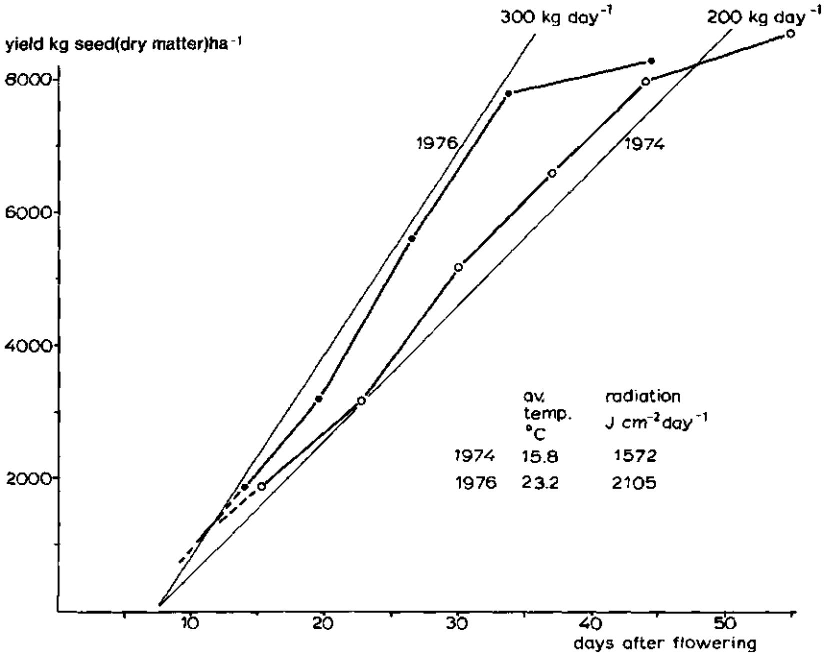


Fig. 2.7. Course of grain growth during two seasons with an extreme difference in weather conditions (wheat).

October but harvested in early September, indicating an extremely long postanthesis period.

Whether a further real increase in yield, of say 25%, can be achieved and what properties would have to be improved in order to achieve it, is a crucial question. Enhanced photosynthesis could make a contribution and full elimination of stomatal control (cf. pp. 70-77) may afford some increase, but in general the prospects are not bright. Another effective means might be to increase the duration of grain growth, and at the same time to prolong the active period of assimilating plant parts. Probably this trait has already been used by breeders unintentionally, in the normal course of selection, but its possibilities have not been exploited systematically.

Growth studies under favourable, disease-free conditions often show that the ear may ripen more rapidly than the leaves senesce, so that kernel growth in itself may be more limiting than leaf activity (Jenner & Rathjen, 1975). A further trait, often associated with yield improvement, is the sink capacity. Kernel number per ground area is often positively correlated with yield (Fischer, 1975; Gallagher et al., 1975). The latter author showed that increased kernel number, achieved by crowding or CO_2 feeding during ear formation, resulted in increased yields. But by and large, kernel number and photosynthesis have to be increased simultaneously to achieve increases in yield potential.

Growth and development interactions

As pointed out in the previous sections one of the main determinants of the total biomass production of crops optimally supplied with water and nutrients is the length of the growth period. The length of this period is mainly determined by temperature and photoperiodism and can to a large extent be influenced by plant breeding. The possibilities of growing wheat at lower latitudes, maize at higher latitudes and soya bean at both have been extended by the introduction of plant types showing a low response to day length. The differences within species are large, as illustrated in Fig. 2.8.

For small grains the seed/total weight ratio is an important indicator of economic yield. This ratio increases with the ratio of the length of the growth period after anthesis to the total growth period, possibly as a result of a shift towards relatively earlier anthesis. However, this is not the case for the new semidwarf rice varieties, which need only 100 days on the field so that it is actually possible to grow three crops. Here the shortening of the growing period has influenced all the developmental phases of the plant in approximately the same way, as is illustrated in Fig. 2.9 for IR8, a medium-duration variety from IRRI, and B9C, a short-duration breeding line from Bogor, Indonesia.

There are, however, differences in this respect. On the rain-fed paddy-fields of countries like Burma with a pronounced monsoon climate, a long vegetative period is necessary. Planting has to be done around the 1st of June, harvesting cannot be done before the end of November and early anthesis would suffer too much from the

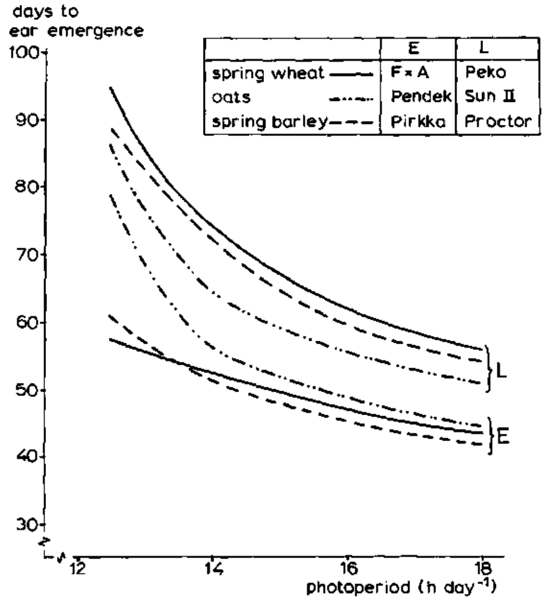


Fig. 2.8. Photoperiod response curves for some early (E) and late (L) varieties of cereals (from: de Vos, 1971).

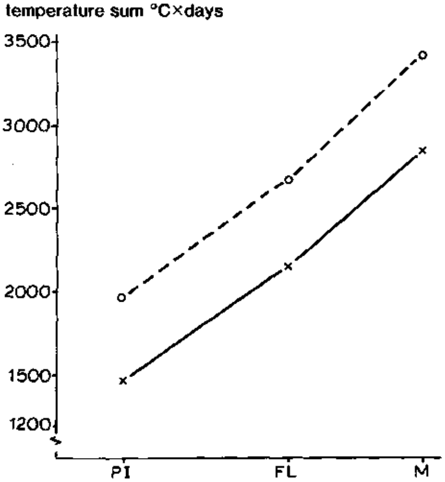


Fig. 2.9. Temperature sum required for panicle initiation (PI), flowering (FL) and maturity (M) for two rice varieties, IR8 (o --- o) and B9C-Md-3-3 (x —— x) grown in Indonesia (Paransih Isbagijo, personal communication).

heavy midmonsoon rains. Breeding rice varieties for these conditions is still a challenge.

An impressive breeding achievement has been the prevention of lodging and the maintainance of a reasonable harvest index, in spite of huge biomass increases made possible by fertilization. Roberts (1847) reported seed/total weight ratios ranging from 0.38 to a maximum of 0.46 for wheat and in this connection was especially impressed by the variety Piper's Thickset. In the course of time the seed/total weight ratio has increased to slightly over 0.5. But in the Netherlands, this seems not due to earlier anthesis or later ripening of the ear, since present phenological data are comparable with those of Staring (1860). The most important cause of increase of the seed/total weight ratio is the delay in leaf senescence, brought about by the higher nutritional status and better control of ripening diseases. The role of plant breeding in the latter, although important, will not be discussed here.

Whatever future developments may be, the small grains with their aerial seed organs will always give relatively low economic yields. The potato, with its heavy underground tubers, and stems which need only carry the light leaves, seems much better designed in this respect; in this species, the tuber/total weight ratio may be maintained at 0.8.

A conspicuous characteristic of rice, as compared with wheat or barley, is that the 1000-kernel weight of a given variety is always the same, owing to the rigidity of the hull around the seed. However, the constancy of the kernel weight is associated with great flexibility of the plant. An increased supply of carbohydrates in the early stages of growth leads to a proportionate increase in the initiation and development of new tillers. The proportion of these tillers that becomes reproductive is a function of the carbohydrate supply per tiller during the period of panicle initiation. The number of spikelets per surviving panicle is likewise determined by the availability of carbohydrates per panicle, and finally, the number of filled grains is determined by the flow of photosynthates per spikelet. Hence a period of low light during tillering and high light during ear formation results in a small number of ears relative to the number of tillers, whereas in the reverse situation this number is relatively large. Eventually, therefore, the plant always ends up with the number of kernels that can be completely filled for the existing combinations of weather and crop conditions. Yield is often broken down into components with spurious multiplication strings, such as:

weight/ha = ears/ha × seeds/ear × weight/seed

It is, however, clear from the foregoing that a high value of one of the terms excludes high values of the others, irrespective of the heritability of the individual components.

An interesting observation by Yoshida (personal communication) is that there is an approximately linear relation between the 1000-kernel weight of a rice variety and the length of its growing period. This also suggests that, irrespective of variety, a certain carbohydrate supply per day is needed by an individual kernel during initiation if it is not to abort. This behaviour of the rice plant shows that in many cases the discussion as to whether it is the source (assimilate supply) or the sink (storage capacity) that is limiting for grain yield, is a trivial one, as the plant has a regulating mechanism for both.

As illustrated in Fig. 2.10, for barley, maize and Brussels sprouts, the density of sowing or planting hardly effects total dry matter yield over a wide range, but with respect to economic yield there may be a narrow optimum for some species, but not

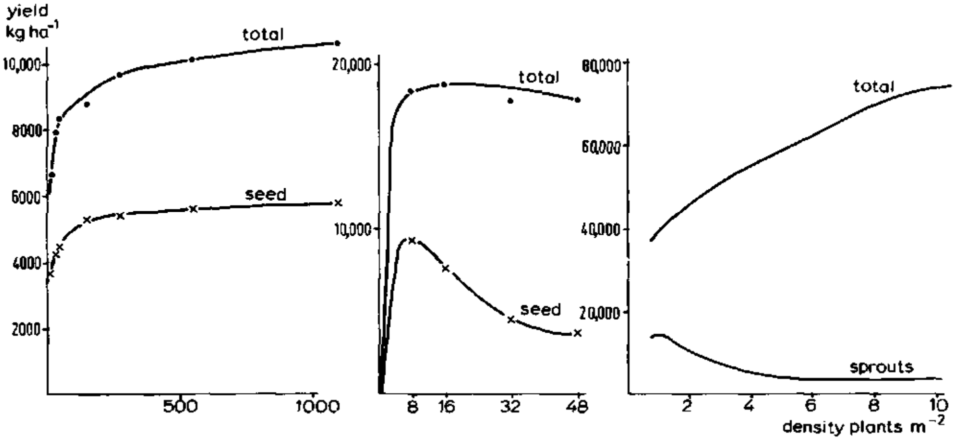


Fig. 2.10. Relation between plant density and yield (total and economic) for barley (left), maize (centre) and Brussels sprouts (right).

for others.

In Brussels sprouts (Nieuwhof, 1962) the main growing point remains vegetative and the economic yield is formed by axillary, leafy buds of appropriate size. Taking into account that, for a closed surface, crop assimilation rate is independent of density of planting, the flow of photosynthates per plant decreases with increasing plant density. Beyond a certain density, this flow is completely monopolized by the main vegetative growing points, so that no buds or only small, nonmarketable buds are formed. This occurs at a planting density which is still too low to achieve maximum dry matter production.

The ears of maize also originate from axillary buds, whereas the main growing point terminates in the male inflorescence. The ear primordia also abort as soon as the flow of photosynthates becomes so small that it can be monopolized by the emerging male tassel. This leads to barren plants and thus to yield losses which cannot be compensated by neighbouring plants. Maize is therefore grown at densities that are suboptimal with respect to total biomass yield. This is true even for maize grown for silage, for here, too, quality depends on the relative quantity of kernels.

However, in the case of plants with a determinate growing point, of which barley is an example, the optimum density range for seed yield is wide. Whether the tiller is large or small, its growing point always terminates in an ear with correspondingly larger or smaller numbers of kernels. In other words, such species will tolerate miniaturization and nonuniformity.

This difference in response between indeterminate and determinate species throws light on some aspects of hybridization. In indeterminate plants, there is a premium on uniformity and plant size. Brussels sprouts and maize are indeterminate and cross pollinating and their uniformity and size, in so far as these are genetically determined, are most conveniently controlled by hybridization. Plants like peas and beans are indeterminate and self pollinating; varieties of these species are therefore genetically uniform and hybridization does not contribute further to their uniformity.

Small grains are determinate and, whether self pollinating or not, there is no premium on uniformity or size. This led de Wit (1968) to conclude that the prospects offered by hybridization programmes in wheat and rice are limited. Sunflower is also determinate, with a seed/total weight ratio little affected by plant density, and this, too, raises doubts as to the usefulness of hybridization. This does not imply that sunflower hybridization programmes have not been successful, but only that their necessity is doubted. It would be more sensible to direct breeding efforts towards developing normal varieties.

Utilization and translocation of nitrogen

For plants to be able to express their physiologically determined yield potential, an adequate supply of nutrients at all stages of growth is a prerequisite, and varieties that can stand adequate nitrogen fertilization without lodging are one of the main achievements of plant breeding. To achieve higher yields by means of fertilizer application the element applied must be taken up by the crop and after uptake be utilized to produce economically useful plant material. A convenient way of distinguishing between these two processes is to present the results of fertilizer experiments in the way illustrated in Fig. 2.11 (de Wit, 1953; van Keulen, 1977) for a rice crop. Fig. 2.11a gives the relation between grain yield and the total amount of nitrogen taken up in both grain and straw. Fig. 2.11b gives the relation between the amount of fertilizer applied and the amount taken up, while Fig. 2.11c, constructed from the previous two through the elimination of the uptake, shows the relation between fertilizer application and grain yield. We confine our discussion of this scheme to nitrogen, because this is one of the most important fertilizers, and to irrigated rice, because in this crop all complications due to water stress are absent.

The uptake yield curve presented in Fig. 2.11a passes through the origin, obviously, because at zero uptake no yield is obtained. At low values of N uptake the relation between yield and uptake is linear. This means that under limited supply, each unit of nitrogen taken up results in an equal amount of grain being produced, because the seed/straw ratio is little affected by N shortage. The nitrogen in the tissue is thus diluted to the same minimum level in all cases. An extensive analysis of yield uptake curves for nitrogen in rice (van Keulen, 1977) showed that with irrigated rice this initial efficiency of nitrogen is constant and amounts to about 70 kg grain per kg nitrogen taken up. This value reflects a grain/straw ratio of about 1, a minimum nitrogen concentration in the grain of about 1% and a minimum concentration of about 0.4% nitrogen in the straw, which cannot be remobilized and translocated to the grain. The same value of 70 kg grain per kg nitrogen taken up also holds for other small grains under normal conditions.

At higher levels of uptake the curve deviates from the straight line, reflecting

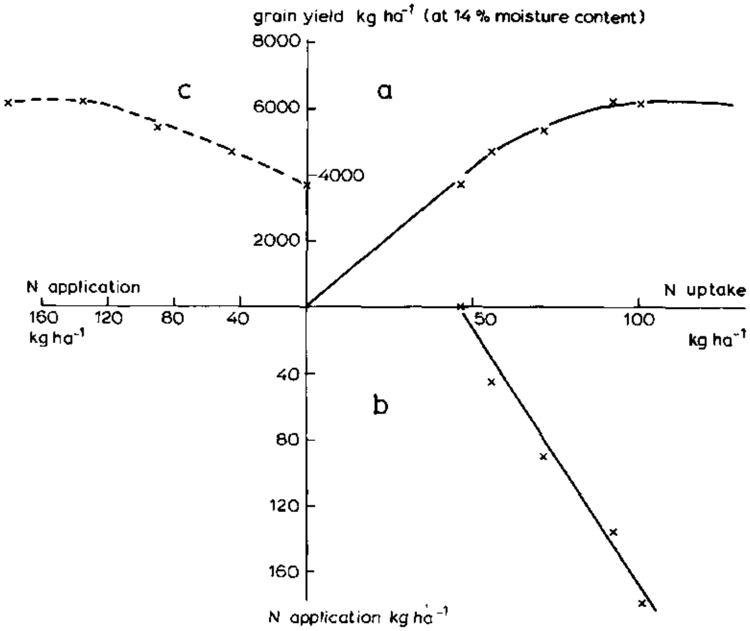


Fig. 2.11. Relation between N uptake and grain yields (a), between N application and N uptake (b), and between N application and grain yield (c) for IR5 rice grown in Muara, Indonesia, dry season 1971 (from: van Keulen, 1977).

increasing concentrations of nitrogen in the harvested material. Finally a plateau is reached, where increased N uptake does not result in higher grain yields. The level of this plateau is determined by whatever growth factor is in short supply. Under optimum supply of other nutrients and in the absence of pests and diseases the level of the plateau for irrigated, semidwarf rice varieties is determined by the available radiant energy (van Keulen, 1976).

A higher efficiency of nitrogen, once taken up, can only be achieved by increasing the grain/straw ratio or by breeding for varieties having a lower minimum N level, especially in the grain. It is questionable whether lower N levels would be an improvement. Undoubtedly a greater weight of grain could then be produced for the same amount of nitrogen, but at the expense of a lower protein content of the seed.

There is much more scope for improving the efficiency of nitrogen utilization in the relation between fertilizer application and uptake by the plant. The relation given in Fig. 2.11b is representative of the results of the majority of nitrogen fertilizer experiments on rice: a linear relation between application and uptake over the full range of applications. The intercept with the horizontal axis represents the uptake without fertilizer and is mainly determined by the quantity and quality of the organic material in the soil and the N-fixing activity of blue-green algae.

The slope with respect to the vertical represents the fraction recovered of the applied fertilizer. This recovery appears to be low under normal husbandry practices, that is, broadcast application of ammoniacal nitrogen in three split doses, at transplanting, at active tillering and at panicle initiation. Part of the ammonium volatilizes directly into the atmosphere, and part is converted into nitrates. These nitrates may end up in the reduced soil layer, either by mass flow or diffusion, where they are subject to denitrification. This nitrogen is then lost within a very short time in gaseous form (van Keulen, 1977).

A major improvement in recovery can often be made by adopting a different system of application. Placement of ammonium nitrogen directly into the reduced soil layer prevents the conversion into nitrates and hence the subsequent denitrification. Recovery percentages are then often at least doubled (van Keulen, 1977). This method, in which all the fertilizer may be applied at transplanting, could considerably increase fertilizer efficiency.

Uptake by the canopy competes with denitrification and leaching processes, so that higher recoveries are found for nitrogen applied at later stages of crop growth, when the rate of uptake by the plants is higher. It would be advantageous if plants could accumulate larger amounts of nitrogen in the vegetative tissues at early stages of development. Much attention has been given to the N-reductase level in plants, but there is no indication at all that nitrogen, once taken up in otherwise well-fertilized plants, is not utilized rapidly (Hageman, 1977).

During the reproductive stage of growth, most of the available photosynthesis products are transferred to the seeds or to storage organs. The amount of seed formed per unit of photosynthate depends to a large extent on the composition of the seed in terms of carbohydrates, proteins and lipids and may be estimated on the basis of growth requirement data (cf. pp. 70-77). The result of such an estimation (Sinclair & de Wit, 1975) is given in Fig. 2.12 for 24 species, on the basis of a supply of 250 kg photosynthate per ha per day. The seed growth rate of barley is estimated at 188 kg ha^{-1} day^{-1} and of groundnuts at 108 kg ha^{-1} day^{-1}. The difference is due to the higher protein content and much higher oil content of the groundnuts.

The seed also needs minerals and nitrogen for its growth. The nitrogen uptake by the seed is one-sixth of the protein growth rate and varies from 6 kg N ha^{-1} day^{-1} for soya bean to 2 kg N ha^{-1} day^{-1} for barley. The position of the points in relation to the vertical axis of Fig. 2.12 marks these rates for the 24 crop species.

These are very high uptake rates and there are many situations where the supply from the root system during seed formation cannot keep up with the demand. The stock of inorganic nitrogen (NH_4^+, NO_3^-) in the soil may be exhausted, as may the stock of organic material that is rapidly mineralized. Also the nitrogen may be located in the dry topsoil and not in the deeper soil layers that still contain water (Rehatta et al., 1979). It may also happen that the activity of the root system is reduced, for example by aging, this being reflected in the *Rhizobium* activity in the case of leguminous crops. In all cases where the requirements of the seed cannot be met by supplies from the root, the remaining nitrogen is extracted from the vegeta-

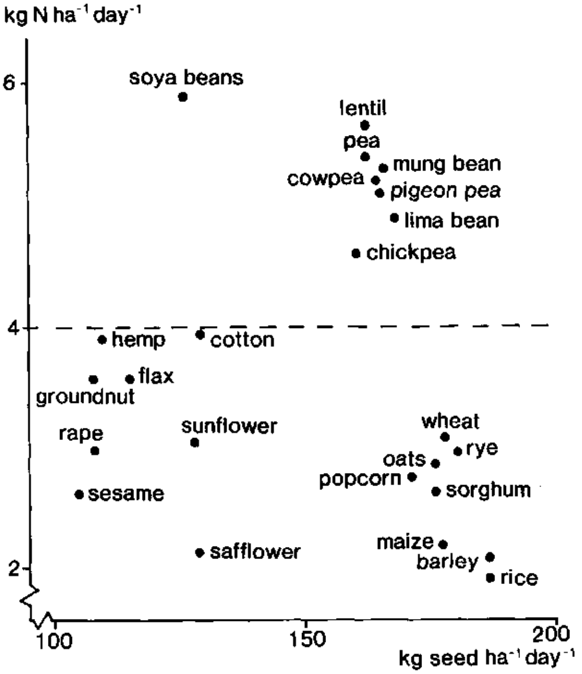


Fig. 2.12. Seed production rate and nitrogen requirement of the seed, both in kg ha^{-1} day^{-1}, for 24 crop species with an assumed available photosynthate of 250 kg ha^{-1} day^{-1} (from: Sinclair & de Wit, 1975).

tive parts of the plants, especially the leaves; this in turn reduces the supply of photosynthates. In this way, the goose that lays the golden eggs is killed.

The self-destructive property of plants described above has been analysed in more detail by Sinclair & de Wit (1976) for soya beans with a protein content of about 38%. The analysis was made under the assumption of proportionality between assimilation and nitrogen fixation by *Rhizobium*, with a reference fixation rate of 3 kg N ha^{-1} day^{-1} at potential assimilation. The result is presented in Fig. 2.13 in terms of changes in active leaf area at N uptake rates from the soil of 2 and 4 kg N ha^{-1} day^{-1}. The latter uptake rate is high if taken in conjunction with the assumed fixation rate by *Rhizobium*. It appears that the plant destroys itself within a period of 22-30 days, depending on the uptake rate. The normal length of the seed-filling stage for soya bean is explained by this self-destructive process. The simulated yield varies from 2550 to 3550 kg ha^{-1}. Its relatively low value is due to self destruction in connection with the high protein and oil content of the seed.

Even wheat has to be managed carefully to meet the seed requirement of 3 kg N ha^{-1} day^{-1}: breeding for a prolonged root activity may be helpful. On the other hand the nitrogen content of the storage roots of cassava is less than 0.5% on a dry matter basis, so that this plant is truly not self destructive. It therefore yields well in terms of

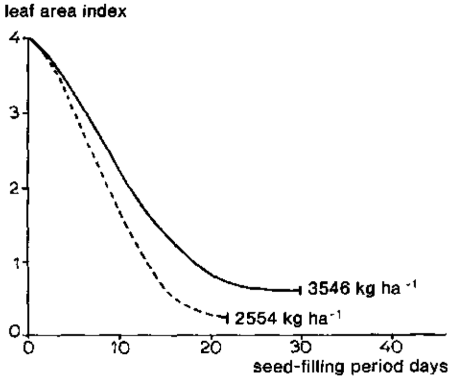


Fig. 2.13. Simulated changes in leaf area indices with time for soya bean crops with an initial leaf area index of 4, and two rates of root nitrogen supply (4 kg N ha^{-1} day^{-1} —— and 2 kg N ha^{-1} day^{-1} ---). Final seed yields in kg ha^{1} are presented in lower, righthand portion of figure (from: Sinclair & de Wit, 1976).

energy production on African soils poor in nitrogen. Breeding cassava for a higher nitrogen content will clearly be self defeating.

There is some tendency among breeders to breed for low vegetative mass. It is in fact possible to go quite far in this direction before the leaf area at the time of flowering is so much reduced that the potential assimilation cannot be reached. However, breeding for reduced vegetative mass involves breeding for small storage capacity for nitrogen and minerals, and since many crops are grown in situations where self destruction is the rule rather than the exception, rapid loss of photosynthetic capacity and low yields are the result.

In the case of soya beans with low *Rhizobium* activity during the reproductive phase, it may be worthwhile to breed for plants with an extended period of vegetative growth. It may even be worthwhile to breed for plants with low photosynthesis or a low utilization of assimilates by the grain. In such plants, self destruction is delayed, so that the seed-filling stage and the duration of N uptake and fixation are extended.

Mixtures

Among crop scientists and plant breeders there is continued interest in mixed cropping and the use of multilines. The most straightforward means of analysing this is by replacement and diallel experiments. In a replacement series, the two crops are sown in different proportions, including the monocultures, in such a way that the total density remains the same. In most diallel experiments, the crops are sown in rows as monocultures and also in alternate rows, again maintaining the overall density at the same level.

Two typical results are schematically presented in Fig. 2.14, with the relative seed frequency of two species, cultivars or lines along the horizontal axis. In Fig. 2.14a the yield curve for the higher-yielding species A is convex and for the lower-yielding species B concave, the former being obviously the stronger competitor. In Fig. 2.14b

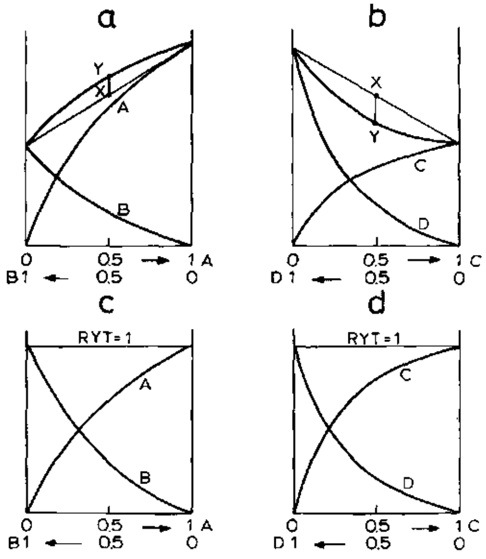


Fig. 2.14. Two typical replacement diagrams with a relative yield total (RYT) equal to one, in absolute (above) and relative (below) terms. The difference Y−X is the competitive ability.

the yield curve for the lower-yielding species C is convex and for the higher-yielding species D concave. The phenomenon that the lower-yielding is the stronger competitor is not at all uncommon and is called the Montgomery effect (Montgomery, 1912; de Wit, 1960).

In both cases, when the yields of the species are presented as a fraction of their monoculture yields, the convexity and concavity of the yield curves is the same (Fig. 2.14c and 2.14d). The sum of these relative yields, the relative yield total (RYT), is equal to one, as given by the horizontal lines in the figures (de Wit, 1960; de Wit & van den Bergh, 1965). It is then said that the species exclude each other or compete for the same niche. Trenbath (1976) analysed the results of over 500 replacement experiments, mainly among small grains and grasses. Excluding legume/nonlegume combinations, the results are presented in the distribution diagram of Fig. 2.15. The average RYT proved to be very close to one and the standard deviation appeared to be small, as is also the case in diallel experiments with cultivars or lines among small grains (Spitters, in preparation).

The agronomic importance of this observation is that the same yields of both components may be obtained from the same total area by sowing the species separately. The area fractions are obviously equal to the relative yields. In the situation presented in Fig. 2.14a and 2.14c, the yields of the 1:1 or diallel mixture are reproduced by sowing 0.67 of the area with the stronger competitor A and 0.33 of the area with the weaker competitor B, both in monoculture, whereas in the situation presented in Fig. 2.14b and 2.14d, it would be necessary to sow 0.8 of the area with the stronger and 0.2 of the area with the weaker competitor. The only consequence of mixing in situations where RYT is equal to one is that for a 1:1 mixture more seed of

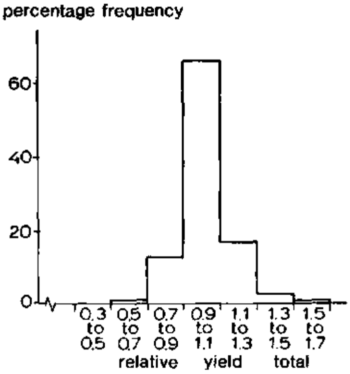


Fig. 2.15. Distribution of values of relative yield total (RYT), excluding legume/nonlegume combinations (from: Trenbath, 1976).

the weak competitor is necessary and less of the strong competitor, compared with a combination of monocultures giving the same yield. However, the highest yield is in any case obtained by growing the more productive monoculture.

In plant breeding and genetics, diallel yields are often compared with the so-called midparent yield. This comparison is illustrated in Fig. 2.14a and 2.14b, where the curved lines that join the two monoculture yields represent the sum of the yield of the two species. The straight line that joins the two monoculture yields is the sum of the monoculture yields when the species are sown in monoculture on an area proportional to the relative frequencies along the horizontal axis. The point X then represents the midparent yield and the point Y the total observed diallel yield. The difference Y—X may be called the combining ability in mixture, but great diversity in terminology exists. This ability is positive when the higher-yielding cultivar is the stronger competitor (Fig. 2.14a) and negative when the lower-yielding cultivar is the stronger competitor (Fig. 2.14b). It becomes zero when the monoculture yields are the same or the two cultivars are equally competitive, i.e. when the yield curves are straight.

But whatever the combining ability, in none of these cases is there any advantage or disadvantage in creating mixtures, since the RYT is equal to one. This fact is very often not appreciated among plant breeders and this is the reason for much unjustified optimism regarding the usefulness of multiline mixtures. The time for abandoning the calculation and analysis of such combining abilities is long overdue.

There are some situations, however, where the RYT is higher than one and in such cases a greater surface area is needed to obtain the same yields from monoculture, so that mixing has a real advantage. This mixed-cropping advantage is often expressed when the growth periods of the two species or cultivars are only partly overlapping, as is clearly shown by Schepers & Sibma (1976) for mixtures of early and late potatoes planted at different times. RYTs larger than one may occur also in multilines or variety mixtures, if the lines or varieties have different resistances to different diseases or physiological races of the same disease. However, most examples are spurious, because they are based on calculations like those mentioned above for combining ability. RYTs larger than one may also occur in mixtures of legumes and nonlegumes, if time is allowed for the transfer of the nitrogen to the nonleguminous species in the mixture. This is generally the case for perennial grass-legume mixtures, but is less often so for mixtures of annuals (de Wit et al., 1966). The popularity of mixtures of maize or sorghum with beans or soya beans in many tropical regions is therefore hardly related to this phenomenon.

In the last-mentioned type of mixture, the relationships are much more subtle. In a maize mixture, maize is the taller species and is therefore less shaded than in monoculture, and may thus be able to form relatively more seeds (cf. pp. 59-63); the beans or soya beans, on the other hand, are more shaded than in the monoculture so that their self-destructive property, as described above (pp. 63-67), is less manifest. The relatively better performance of both species in the mixture then leads to a RYT greater than one and an advantage for mixed cropping.

Present goals in plant breeding and crop husbandry in this connection are, or should be, the further elimination of the adverse effect of dense planting on seed production in maize and the mitigation of the self-destructive properties of plants. Exploiting the subtler advantages of mixtures by plant breeding involves the exploitation and consolidation of undesirable traits and is in the long term counterproductive.

CO_2 assimilation of leaves and crop surfaces

Whatever the complications of the process of agricultural production, potential biomass production is one of the main determinants and considerable attention has therefore been given over the years to the rate of CO_2 assimilation of leaves and crop surfaces. Curves showing the characteristic dependence of leaf assimilation rate on the absorbed photosynthetically active irradiance in the wavelength range of 400-700 nm are presented in Fig. 2.16 for leaves of plant species of the C_3 and C_4 type. The main parameters that govern the curves are the maximum net assimilation rate at high irradiance, F_m, the respiration rate in the dark, F_d, and the initial slope of the curve or initial light use efficiency, ε . The parameter with the greatest variation is F_m: its range is about 30-90 kg CO_2 ha^{-1} h^{-1} for C_4 plants and about 15-50 kg CO_2 ha^{-1} h^{-1} for C_3 plants.

Maize, sorghum, millet, sugar cane and many tropical grasses are of the C_4 type and small grains, including rice, temperate grasses and many dicotyledonous crops, are of the C_3 type. As mentioned earlier, the name refers to the length of the C-skeleton of the first product of assimilation, but there are other important differences between these two plant types (Gifford, 1974).

The main carboxylating enzyme in C_4 plants has an affinity to CO_2 which is about twice as great as that of the carboxylating enzyme in C_3 plants (Sinclair et al., 1977). Moreover, in C_3 plants a respiratory process occurs during photosynthesis, which results in a dependence of assimilation on the oxygen concentration in the air. This photorespiratory process is absent in C_4 plants. However, the energy requirement for

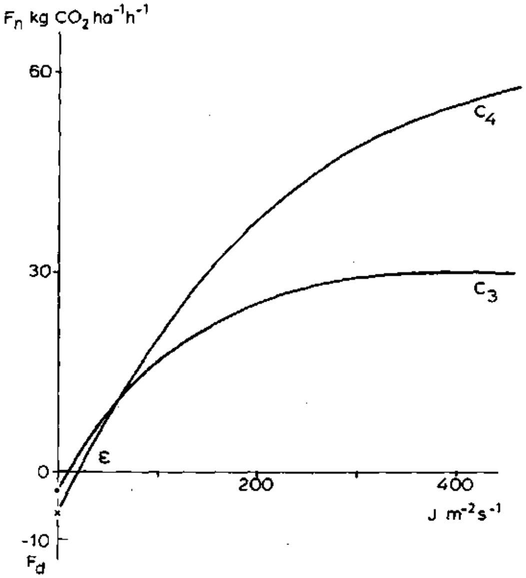


Fig. 2.16. Characteristic net CO_2 assimilation functions (F_n) of individual leaves for C_3 and C_4 plants.

assimilation in C_4 plants is inherently higher (Björkman & Ehleringer, 1975; Ehleringer & Björkman, 1976), so that the initial light use efficiency for C_4 plants is nevertheless equal to or only slightly higher than the 14 ng CO_2 per Joule absorbed light in the 400-700 nm range observed for C_3 plants. Up to now, selection for C_3 species with C_4 traits has had little success.

Under some conditions, certainly not all, CO_2 concentration in the intercellular air spaces is regulated over a wide range of CO_2 concentrations and light intensities through adaptation of the stomatal openings. The regulatory level is about 210 vppm for C_3 and 120 vppm for C_4 (Raschke, 1975; Troughton, 1975; Goudriaan & van Laar, 1978a; de Wit et al., 1978). The consequence of this difference is that at normal CO_2 concentrations of 330 vppm and at lower light levels net assimilation is the same, but stomatal conductivity and consequently the transpiration rate is about half as great in C_4 plants as in C_3 plants. At high light intensities, the net assimilation of C_4 plants is twice that of C_3 plants but the stomatal conductivity and consequently the transpiration rates are about the same. Assimilation rate and transpiration rate are the main determinants of the transpiration coefficient, which is consequently roughly twice as great for C_3 as for C_4 plants, irrespective of light intensity (de Wit, 1958).

Actual and simulated experiments show that transpiration coefficients of 100 and 200 kg water per kg dry matter are possible for C_4 and C_3 plants respectively, if the internal regulation of the CO_2 concentration is fully manifested (de Wit et al., 1978).

However, regulation of internal CO_2 concentration does not always occur. Sometimes, in both C_3 and C_4 plants, the stomata remain fully open, and this leads to relatively high transpiration rates at low light intensities and increased assimilation with increasing CO_2 concentration in the air. It also permits very high maximum net assimilation rates, which for C_3 plants are reminiscent of those of C_4 plants (El-Sharkawy & Hesketh, 1965; Warren Wilson, 1966). This lack of stomatal response was reported for sunflower (Goudriaan & van Laar, 1978a) and cucumber (Challa, 1976) and may possibly be brought about by absence of water stress (Raschke, 1975), but heritable plant properties may also be of importance. Under dry conditions, CO_2 regulation is clearly a desirable property (de Wit et al., 1978), but under greenhouse conditions absence of regulation permits CO_2 fertilization (Challa, 1976).

Leaf senescence often results in a decline in net assimilation, accompanied by increased stomatal resistance (Davis & McCree, 1978). Where there is nitrogen shortage, decreased assimilation is sometimes accompanied by stomatal closure and sometimes not (van Keulen, 1975; unpublished results).

Mesophyll resistance comprises diffusion resistance for CO_2 in the aqueous phase, transport resistance across membranes and carboxylation resistance in the initial stages of CO_2 assimilation. At a given intercellular CO_2 concentration and at high light intensity, CO_2 assimilation is inversely proportional to this resistance (Chartier et al., 1970; Jones & Slatyer, 1972; Sinclair et al., 1977). The maximum net assimilation, F_m, is often positively correlated with the content of carboxylating enzyme per leaf area (Wareing et al., 1968) and is uncorrelated with the concentration of chlorophyll, which is usually present in abundance (Gabrielsen, 1960). The presence of sinks may cause the enzyme content to rise and thus increase net assimilation. The main component of enzyme content per leaf area is leaf thickness, rather than enzyme concentration (Louwerse & van der Zweerde, 1977). Breeding for high F_m may therefore result in breeding for thicker leaves, the advantage of which may then be offset by a lower leaf area. Such effects may explain the poor relation between F_m and yield for cultivars of wheat, as found by Dantuma (1973).

The dark respiration, F_d, at normal temperatures is roughly one-ninth of F_m (Tooming, 1967). Here, too, leaf thickness and enzyme content are probably the main components. For horticultural crops grown in the greenhouse, a low F_d is especially important because leaf respiration is relatively important under low light conditions. Varietal differences in this respect are not well documented.

The maximum assimilation rate F_m and the dark respiration rate F_d depend much more on temperature than does the initial efficiency, ε . The CO_2 assimilation of C_4 plants is negligible below 12 °C, but C_3 plants may still show considerable assimilation at 0 °C. The temperature sensitivity of leaves of young plants grown under controlled conditions is much greater than that of leaves of somewhat older plants grown in the field. Because adaptation to changes in temperature has been little studied and is not well understood (de Wit et al., 1978), it is difficult to extrapolate from controlled conditions to the field.

In view of the large environmental effects, it is not surprising that it is extremely difficult to determine the genetic contribution towards variation in F_m. However, carefully executed experiments with leaves from plants at the same developmental

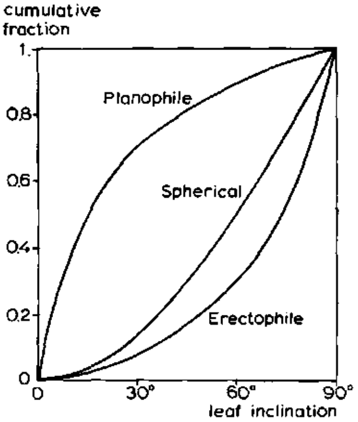


Fig. 2.17. The cumulative distribution of the inclination of leaves for three types of leaf angle distribution (from: de Wit, 1965).

stage and with optimal nutrition show the existence of genetic differences, even among modern varieties (Stoy, 1965; Khan & Tsunoda, 1970c; Dantuma, 1973). Surprisingly enough, it also appears that F_m in wild *Triticum* species is higher than in the cultivated types (Evans & Dunstone, 1970; Khan & Tsunoda, 1970a, 1970b).

The rate of CO_2 assimilation of a crop depends on incoming visible radiation in the same way as does that of an individual leaf. In fact, the initial light use efficiency for absorbed photosynthetically active radiation is exactly the same. The maximum CO_2 assimilation per ground area is the sum of the maximum rates of the individual leaves above the ground area under consideration. In the idealized situation, where all leaves have the same maximum assimilation rate, F_m, the maximum canopy assimilation is given by $F_m \times$ LAI, LAI being the leaf area index (ratio of leaf area to area of soil). But even in this idealized situation, the calculation of crop assimilation is complicated because of the varying illumination intensities of the different leaves. For this reason computer models have been widely used to deal with the problem (de Wit, 1965; Duncan et al., 1967; Goudriaan, 1977; de Wit et al., 1978). In these models the leaf angle distributions (Fig. 2.17), leaf reflection and transmission coefficient, leaf assimilation function etc. can all be varied to allow their effects to be studied. The incoming photosynthetically active radiation (PAR) under a clear sky depends on solar height and can be used in the model to find the assimilation rate at each moment of the day. Integration of the rate of CO_2 assimilation yields the daily total amount. In Table 2.3 daily total gross CO_2 assimilations are listed for a closed crop surface (LAI = 5) with a random leaf angle distribution and an assimilation light-response curve as given in Fig. 2.16. Two situations are considered: $F_m = 30$ kg CO_2 (ha leaf)$^{-1}$ h^{-1} (typical for a C_3 plant) and $F_m = 60$ kg CO_2 (ha leaf)$^{-1}$ h^{-1} (typical for a C_4 plant). The dark respiration (F_d) is assumed to be zero, so that the result refers to the gross assimilation rate. The model used for these calculations (Goudriaan & van Laar, 1978b) is more concise than the one used by de Wit (1965). There are some other differences, which result in lower values for overcast skies and higher

Table 2.3. Calculated gross CO_2 assimilation in kg CO_2 ha^{-1} day^{-1} of a closed canopy with a spherical leaf angle distribution, on a clear (PC) and an overcast (PO) day, for two maximum assimilation rates of individual leaves (F_m).

Northern latitude		$F_m = 30$ kg CO_2 (ha leaf)$^{-1}$ h^{-1}						$F_m = 60$ kg CO_2 (ha leaf)$^{-1}$ h^{-1}					
		15 Jan.	15 March	15 May	15 July	15 Sept.	15 Nov.	15 Jan.	15 March	15 May	15 July	15 Sept.	15 Nov.
0	PC	623	654	630	622	654	629	894	946	906	892	947	904
	PO	293	312	297	292	312	297	321	345	327	321	345	326
20	PC	486	610	699	707	637	503	680	873	1010	1021	915	707
	PO	217	286	334	338	301	227	234	314	369	373	332	245
40	PC	294	507	721	747	562	321	389	707	1033	1071	790	427
	PO	117	225	339	352	254	130	122	242	372	387	275	137
60	PC	66	333	704	756	417	98	71	437	980	1057	558	107
	PO	15	130	312	338	170	25	15	135	336	365	180	25

values for clear skies. In the calculations, the incident radiation under a clear sky is 5 times that under an overcast sky. Because the upper leaves are saturated with light, the gross CO_2 assimilation under a clear sky is only 2-3 times higher.

A crop property widely discussed among crop scientists and plant breeders is the leaf angle distribution (Fig. 2.17). Under an overcast sky there is hardly any difference in daily total CO_2 assimilation between more horizontal (planophile) and more erect (erectophile) leaf angle distributions. Under a clear sky in the tropics and in summer in latitudes up to about 50 °C the more erectophile leaf angle distributions give an advantage of approximately 30 kg CO_2 ha^{-1} day^{-1} at most, compared to the more planophile ones: the consequences of the effect of the leaf angle on light distribution are not impressive. This conclusion was also drawn by de Wit (1965), in spite of many references in the literature to the opposite. However, literature data do exist that show a marked effect of leaf angle upon crop yield. These results can only be explained by a correlation of leaf angle with other crop properties or with the occurrence of diseases.

In order to calculate potential productivity the daily totals of the gross CO_2 assimilation are required. Data of this kind can be drawn from a table such as Table 2.3, or can be calculated by means of simple equations as given by Goudriaan & van Laar (1978b), who also give a simple procedure to account for incomplete soil cover. The net accumulation can be found from the daily gross CO_2 assimilation after subtraction of the quantity lost in respiration.

Respiratory losses can roughly be divided into maintenance and growth respiration. Growth respiration is best expressed by means of a conversion efficiency. The overall weight ratio between substrate and end product depends entirely on the chemical composition of the latter. Table 2.4 gives the conversion efficiencies, calculated by Penning de Vries (1975) on the basis of the biochemical pathways. A higher temperature increases the rate of the conversion process (or rate of growth) but its efficiency remains unaltered. Among the chemical components of plants, lipids are the most expensive to manufacture, in terms of efficiency of conversion. It is therefore not surprising that oil crops tend to yield less than other crops. As far as growth respiration is concerned, the only scope for plant breeding would seem to be in

Table 2.4. Efficiency of conversion of substrate (glucose) into plant constituents (From: Penning de Vries, 1975).

Compounds		Production value (g material/g glucose)
Carbohydrates		0.826
Nitrogenous compounds (normal mix of aminoacids,	from NO_3^-	0.404
proteins and nucleic acids)	from NH_3	0.616
Organic acids		1.104
Lignin		0.465
Lipids		0.330

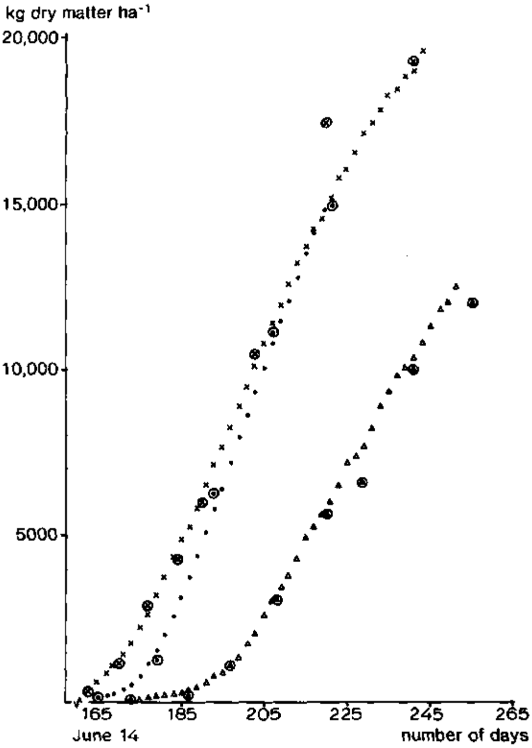


Fig. 2.18. Simulated and measured (circled) dry matter production of maize in Ames (Iowa, USA, 1963), Davis (California, USA, 1968) and Flevoland (Netherlands, 1972) at a plant density of 10 plants m^{-2}. Ames ×, Davis ● and Flevoland Δ.

changing the chemical composition of the end product.

For maintenance respiration the outlook is probably different. Maintenance is necessary because proteins more or less spontaneously decay and have to be rebuilt. Increase of temperature enhances the decay process, and hence the rate of maintenance respiration. An average figure for the rate of maintenance respiration is about 1.5% loss of dry weight per day, at a protein content of 20%, but there is variation among species and varieties (Penning de Vries, 1975). The background of this variation is not clear as yet, but it may be amenable to plant breeding. Reduction of maintenance respiration is a goal worth considering, and could be profitable particularly for the later stages of crop growth and for horticultural crops grown under poor light conditions. Under these circumstances the maintenance respiration may consume 50% or more of the daily gross gain in dry matter production.

The net daily gain in dry matter may be estimated by

$$P_n = 0.7 \times (P_g - 0.015 \times W),$$

where P_g is the daily gross assimilation, 0.7 represents an average value for the conversion efficiency and 0.015 an average for the maintenance respiration. W is the

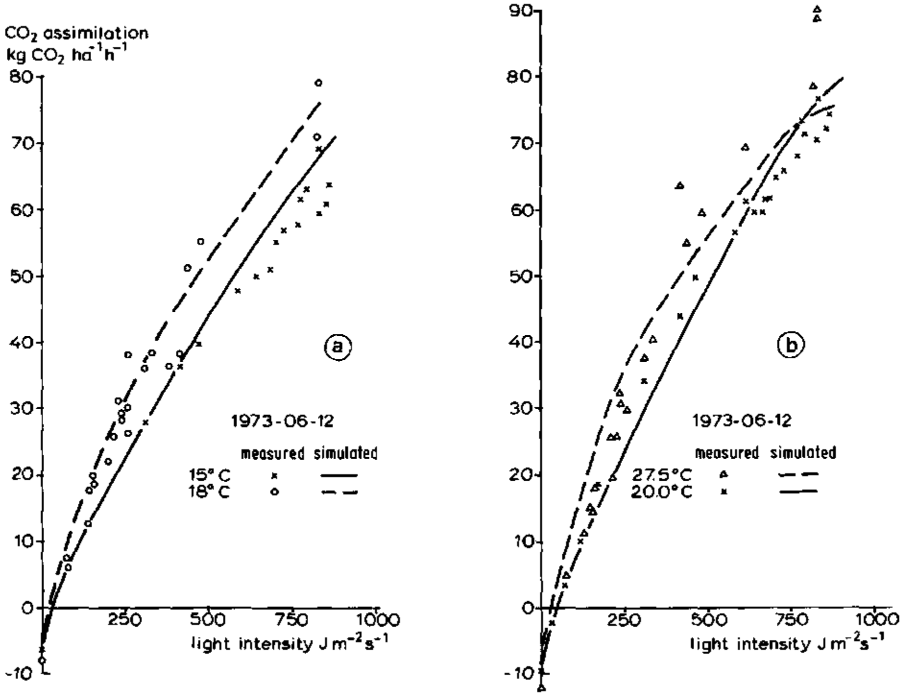


Fig. 2.19. CO_2 assimilation at four temperatures as a function of light. Species: *Zea mays* cv. Caldera 535; density: 3 × 3 cm (a), 4 × 4 cm (b); sowing date: 1973-06-01; measuring date: 1973-06-12; location Droevendaal, Wageningen; LAI: 17.5 m^2m^{-2} (a), 14.7 m^2m^{-2} (b); dry weight shoot: 3708 kg ha^{-1} (a), 3297 kg ha^{-1} (b) (from: van Laar et al., 1977).

standing dry matter, equal to the accumulated value of the net daily gain P_n. Such equations can be employed for the calculation of potential production (van Keulen, 1976; van Heemst et al., 1978; McCree & Kresovich, 1978; McCree & Silsbury, 1978). More sophisticated calculation methods will also account for the influence of water stress, temperature fluctuations or changes in chemical composition. In such cases the use of a computer simulation model is indispensible.

Some results of a simulation of the standing dry matter of a maize crop in California, Iowa and the Netherlands, together with the results of periodic harvests, are given in Fig. 2.18 (de Wit et al., 1978). Measured values for leaf area index and chemical composition of the plant were used, so that only the simulation of assimilation, respiration and transpiration can be evaluated. The results were obtained without adaptation of plant parameters. The same model was used to simulate the daily course of the net CO_2 assimilation and the transpiration rate. An example of a measured and a simulated light-response curve for a canopy is given in Fig. 2.19. The equipment described by Louwerse & Eikhoudt (1975) for the measurement of crop photosynthesis and transpiration under field conditions is shown in Fig. 2.20.

It is the good overall agreement between calculated and measured net assimilation rates under a wide range of conditions that justifies the estimation of potential production presented at the beginning of this chapter.

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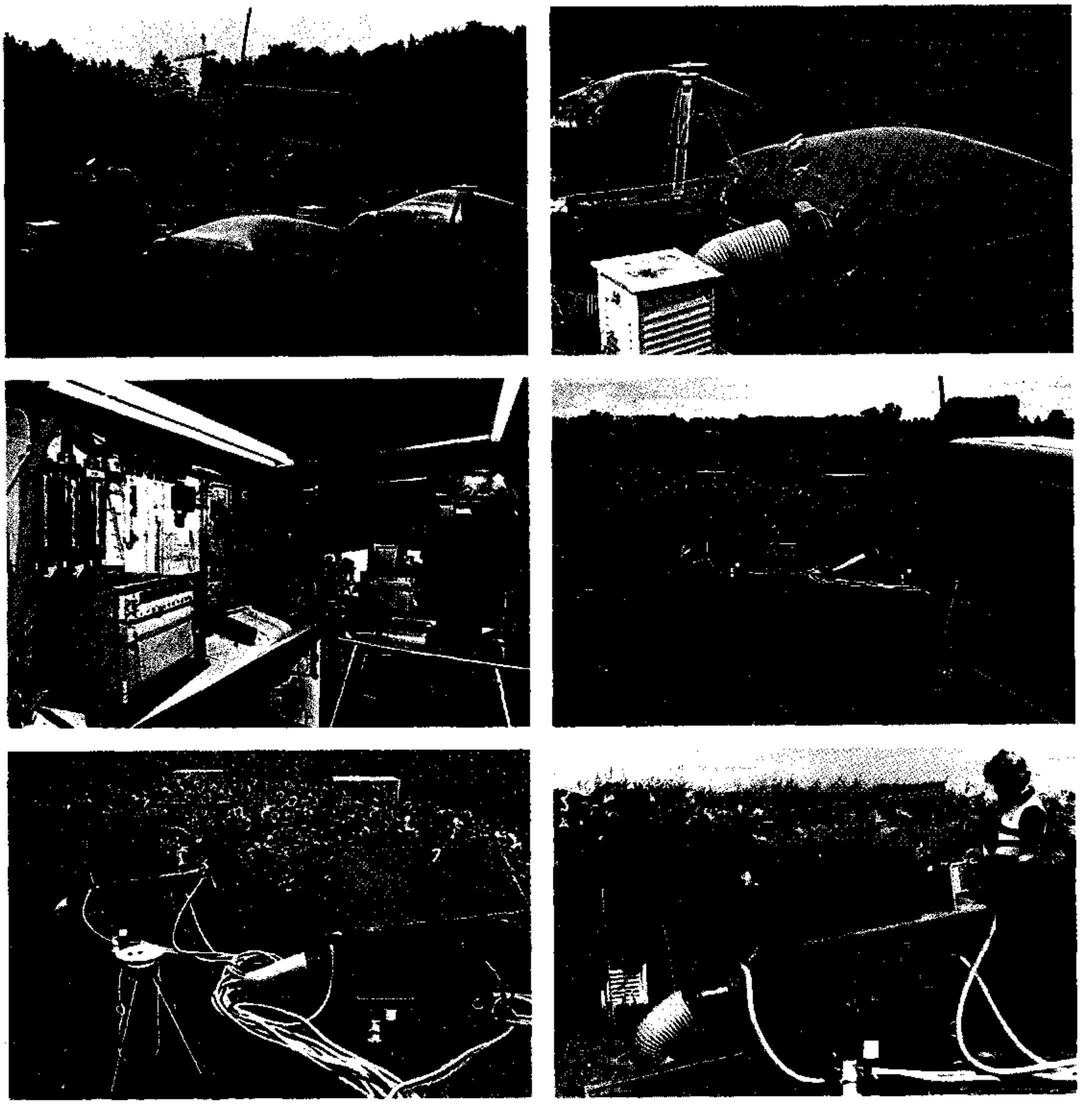

Fig. 2.20.
Top left – The mobile equipment ('photomobile') for measuring photosynthesis, respiration and transpiration in the field. Plant chambers as used for a grass crop.
Top right – Plant chambers of photomobile as used for grass. In the foreground a Stephenson hut (for recording temperature) and a Kipp solarimeter.
Centre left – Measuring and recording equipment installed inside the van.
Centre right – General view of measuring equipment in a sunflower crop.
Bottom left – Air conditioning units and plant chambers of photomobile, as used for sunflower. In the foreground Kipp solarimeter for measuring radiation intensity.
Bottom richt – Detail of air conditioning unit of photomobile. In the background a plant chamber for sunflower measurement.
(Photographs: Office of Joint Services (BGD)).

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3 Crop genetic resources

Modern breeding work is in urgent need of gene pools from which new genes can be introduced into existing cultigens in order to improve their yield stability and their resistance to diseases and adverse conditions. This necessitates searching for new sources of favourable genes in wild relatives of crop species and preserving the genetic wealth of known centres of diversity. Such centres are in jeopardy as a result of the extension of modern agricultural techniques, which is leading to the rapid replacement of primitive crop populations and of genetically heterogeneous land races by uniform, internationally grown varieties. Varietal uniformity entails the additional danger of genetic vulnerability to epidemics. It is therefore important to conserve the valuable genes still to be found in unimproved varieties, old varieties, breeding stocks etc. Genetic conservation is a complex process involving collection, storage (seed storage, cold storage of vegetative parts and, to some extent, storage of tissue cultures) and also, where possible, the preservation of natural habitats of genetic diversity. Problems of conservation include contamination, genetic drift in small populations, and exposure to undesirable selection pressures. Systematic evaluation is costly and time consuming but is a prerequisite for the effective utilization of germplasm collections, as is the recording of accessions and the development of suitable documentation systems. Vigorous action should be taken to develop an adequate global network for collection, conservation, evaluation, utilization and information exchange.

Importance and urgency of genetic conservation

As every plant breeder is aware, diverse gene pools are the foundation of an effective crop improvement programme. Not only do new gene pools provide the necessary building blocks for further varietal improvement, but genetic diversity is essential if high levels of productivity are to be sustained. For with the intensive cultivation of a few major varieties within a crop species, and with the continuous monoculture frequently practised in the tropics, the danger of serious crop losses from outbreaks of pests is continually increasing. Furthermore, past breeding efforts have largely been based on relatively small samples of locally adapted cultivars, with the result that, as the state of varietal improvement has advanced, the genetic base of the crop has become narrower. Only in recent years has it become apparent that plant breeding programmes with a broad genetic base can help to prevent the rapid and extensive spread of pests and diseases and thus sustain high crop yields. In any crop, in order to meet the growing needs of varietal improvement, and to ensure the effectiveness of breeding, it is essential to assemble, preserve and develop the entire array of existing germplasm, as far as this is available.

For several decades it was taken for granted that diverse germplasm was readily available in the native habitats of crop plants, as reported in earlier literature. While the development and diffusion of improved cultivars was often publicized, the gradual but widespread disappearance of the diverse and less productive indigenous varieties (land races) by replacement went on unnoticed. Developments in hydroelectric or irrigation projects, highways, industrial sites, housing areas and commercial agriculture aggravated the loss of the wild and weed races of crop plants. In the Middle East, especially Turkey and Iraq, the disappearance of unimproved wheats (einkorn, durum and common) and barley cultivars took place at an alarming rate within less than two decades (Kuckuck, 1956; Kjellqvist, 1973). Numerous wild and weed races of other crop species have likewise disappeared from their known habitats in other areas. Such sources of unimproved germplasm are truly irreplaceable, for many of them are potentially useful genotypes consisting of gene complexes that have become coadapted to specific environments through long periods of natural selection and are not readily reconstituted by modern plant breeding techniques.

An example of the urgent need to conserve the entire range of crop germplasm is provided by the rapid replacement of earlier varieties of wheat and rice by high-yielding semidwarfs: in less than a decade the planted areas of the latter in Asia, Africa and Latin America (excluding the Communist countries) have reached totals of 29.39 and 25.27 million hectares respectively (Dalrymple, 1978). The situation is similar but less acute for cotton, potato, maize, sugar beet, rice and soya bean cultivars in the USA; hybrid sorghums in many parts of the world; and wheat cultivars in Australia and Canada (National Academy of Sciences, 1972). The best-known example of genetic vulnerability due to varietal uniformity is provided by the epidemics of southern corn leaf blight (*Cochliobolus heterostrophus*) during 1970-71 on maize hybrids that have the T-type cytoplasm conferring male sterility.

Although much has been written about the urgency of conserving dwindling crop genetic resources, systematic and intensive efforts in collecting the threatened land races, wild taxa and weed races have been rather few and limited in scope. Time is now running out, especially in the many areas of the world where agricultural technology has made rapid advances since the beginning of scientific plant breeding. The conservation of endangered germplasm is the joint responsibility, both professionally and socially, of all biologists, and it may be hoped that, with the establishment of the International Board for Plant Genetic Resources (IBPGR) under the Consultative Group on International Agricultural Research (CGIAR) in 1974, vigorous action in assembling existing crop germplasm will be taken.

Sources of germplasm

Fig. 3.1 shows the different kinds of sources from which the entire range of germplasm for any major crop can be assembled. Gene pools may be indigenous, introduced or locally developed.

The various resources that need to be conserved may be categorized as follows:

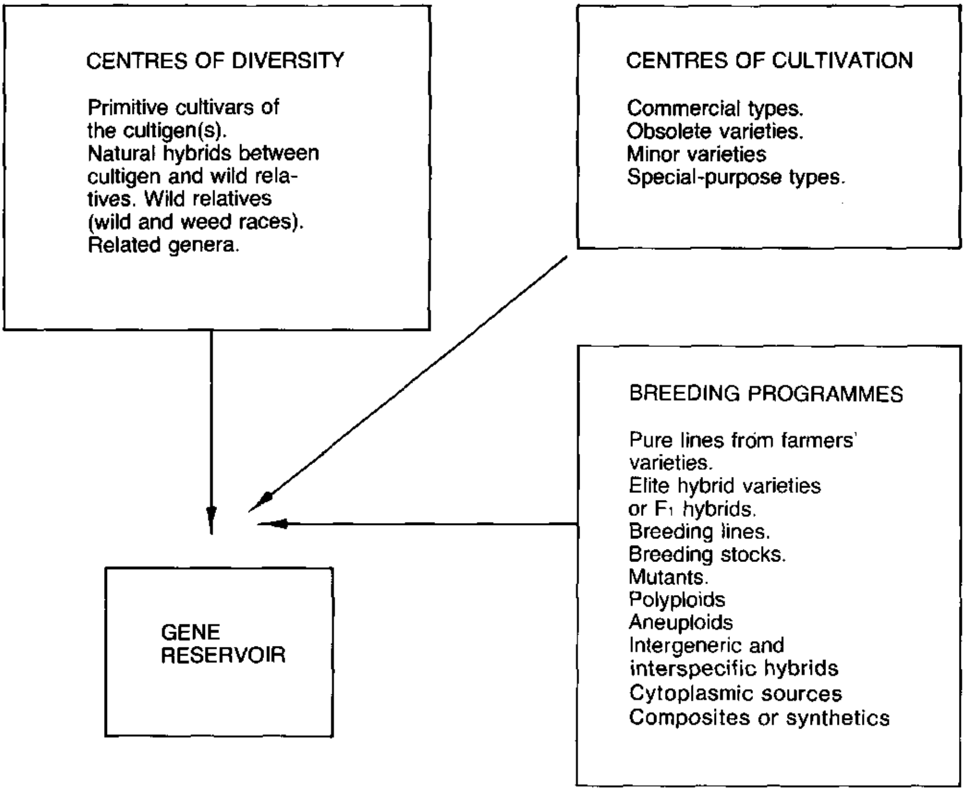

Fig. 3.1. The full spectrum of germplasm in a crop species (cultigen) and its sources.

1 modern elite cultivars or high-yielding varieties;
2 the principal commercial varieties;
3 special-purpose types;
4 obsolete types;
5 breeding stocks (elite germplasm);
6 mutants, genetic testers, polyploids and aneuploids;
7 land races (unimproved or primitive types);
8 useful cytoplasmic sources of variability;
9 weed races;
10 wild species;
11 man-created intergeneric or interspecific hybrids;
12 related genera.

The genetic composition, variation, agronomic value and genetic potential of each of the above categories are discussed by Chang (1976).

Survey and collection of germplasm

A comprehensive and objectives-orientated survey of crop germplasm is a prerequisite for effective field collection. Such work received considerable stimulus from the classic investigations of N.I. Vavilov and his coworkers on the centres of origin and diversity of crops (Vavilov, 1926, 1951), though the initial efforts of these workers were primarily aimed at increasing our total knowledge of crop plants. Collection-orientated surveys were later proposed and partially implemented by the International Biological Programme (IBP) in about 1964, the 1967 FAO/IBP Technical Conference on Plant Exploration and Conservation (Frankel & Bennett, 1970), various FAO meetings and surveys (Frankel, 1975), several meetings of the Germplasm Group of The Rockefeller Foundation (Anon., 1971), the National Research Council Agricultural Board survey (National Academy of Sciences, 1972), and the 1973 FAO/IBP Conference on Crop Genetic Resources (Frankel & Hawkes, 1975a). Additional surveys on specific crops may be found in publications by Chang (1970, 1975), Frankel (1973), Yen (1974), Varnell & McCloud (1975), Zeven & Zhukovsky (1975), Grubben (1977) and the International Rice Research Institute (IRRI, 1978b).

Priorities in collecting various crops have been reviewed and enumerated by the International Board for Plant Genetic Resources (IBPGR), high priority being assigned to wild relatives and land races (IBPGR, 1976a). Such priorities are being updated by the crop advisory committees of the IBPGR and other regional bodies interested in genetic conservation (IBPGR/PCARR, 1977; IBPGR/NBPGR, 1978).

Procedures for collecting germplasm in the field are described by Bennett (1970), Chang et al. (1972) and Hawkes (1976). The *modus operandi* of organizing international and interinstitutional field collection programmes for rice germplasm is described by Chang & Perez (1975). Appropriate sampling methods and adequate sample sizes are essential and are discussed by Oka (1969), Allard (1970), Chang et al. (1972), Marshall & Brown (1975), Qualset (1975) and Hawkes (1976).

Preservation and information exchange

Collected samples or populations should be preserved by one or more of the following methods:

– Long-term storage of seeds: most economical and convenient for sexually reproduced crops and for vegetatively propagated crops when seeds can be obtained; rather bulky for large-seeded crops or large numbers of seed stocks; poorly suited to unorthodox (recalcitrant) seeds.

– Cold storage of vegetative parts: necessary for vegetatively propagated crops; longevity of stored stocks restricted to a few years at most.

– Long-term storage of meristems or other plant tissues: suitable for long-term storage of large numbers of disease-free stocks, but techniques for certain species and their regeneration need to be improved; genetic stability during storage is also uncertain for some crops.

– Establishment of mass reservoirs of composite or naturally mixed populations: useful for certain breeding programmes where natural forces could favour selection, but adverse environments, competition and outcrossing may not be controllable.

– Establishment of genetic reserves (or ecosystem conservation): best suited to industrial, medicinal or other plantation crops and also wild races, but rather difficult to maintain or manage.

The pros and cons of each method have been discussed by Harlan et al. (1940), Frankel (1950), Borlaug (1959), Jensen (1962), Simmonds (1962) and in several chapters of *Crop genetic resources for today and tomorrow* (Frankel & Hawkes, 1976).

In order that conserved stocks should not alter their genetic composition during rejuvenation, seed used for multiplication or rejuvenation should be obtained from sufficiently large samples. Moreover, no subjective selection should be made against variants in the population – inherently variable samples are best maintained in bulk or as different subsamples. It is also desirable to grow land races and wild species at sites which are representative of their original habitats. Reidentification before and after harvesting is essential (Chang, 1976).

With regard to seed stocks in working collections, most plant breeders use short or medium-term storage to extend the life span of their stocks and to minimize the need for frequent seed rejuvenation. Repeated seed rejuvenation has the disadvantages of giving rise to:

- errors and mechanical mixtures;
- loss of unadapted or susceptible accessions;
- changes in genetic composition, especially when population size is small;
- increased work loads and field and storage-space requirements (Chang, 1976).

For the storage and preservation of base collections of the world's major crops, the International Board for Plant Genetic Resources (IBPGR, 1977) has proposed a network of international and regional institutions; minimum requirements for such collections are put forward by FAO (1975). Harrington (1972) and Roberts (1972) discuss methods for seed storage, and IBPGR (1976b) recommends the construction of medium and long-term storage facilities. It is suggested that seeds of base collections be preserved at a minimum of two sites and that seed for preservation be separated from seed for distribution.

Although many listings of germplasm collections maintained at different agricultural research centres are available (*Plant Introduction Newsletter* and *Plant Genetic Resources Newsletter* of FAO, 1970-76; Anon., 1975; Reitz, 1976), few details are known of the individual accessions in each collection or of the availability of viable seed for distribution, and even less is known of their geographical origin, taxonomic or genetic history or morphological and agronomic characteristics. Detailed catalogues and computer print-outs, but in limited numbers only, are in existence for the major collections of the US Department of Agriculture, the Indian Council for Agricultural Research, the Vavilov Institute of Plant Industry in the USSR, the National

Institute of Agricultural Sciences of Japan, the International Rice Research Institute (IRRI) in the Philippines, the Institut für Pflanzenbau und Saatgutforschung der FAL in West Germany, and (for peas) the John Innes Institute in the UK.

This is one crucial area that needs development. The genetic resources centres must evolve appropriate documentation systems that will allow improved exchange and distribution of the stocks and related information kept in the centres and elsewhere. The IBPGR (1977) has directed much of its effort towards the development of such systems. During the 1960s, the International Atomic Energy Agency (IAEA) and the FAO also devoted much effort to standardizing the recording and processing of crop research data (Konzak & Dietz, 1969). The decimal coding systems used for the growth stages of cereals (Zadoks et al., 1974) illustrate the advantages of uniform recording systems for similar crops. Working groups and Crop Advisory Committees of the IBPGR have recently developed uniform descriptions and descriptor states for the cultivated potato, wheat and *Aegilops,* rice and sorghum.

Systematic evaluation and utilization

The conservation and use of genetic resources are two inseparable components of varietal improvement. Without the systematic evaluation of existing resources the valuable gene pools in the germplasm collections cannot be utilized to the full. It is unfortunate that for many crops these different facets of germplasm work – conservation, evaluation and utilization – have not been fully integrated at the principal national research centres. Coordination and consolidation in this area could lead to more effective use of the often limited facilities and technical manpower available.

The most promising sources of genes controlling resistance to pests or tolerance of adverse physical environments are likely to be found in minor varieties, special-purpose types or primitive cultivars (land races). Fortunately, the spread of high-yielding varieties has been slow in areas where such types are most likely to be found and portions of these potentially valuable gene pools are therefore still available for collection and use by breeders. In evaluating genetic materials of this kind introduced from a foreign source, appropriate plant quarantine measures should be applied to the initial plantings. Where new introductions may carry seed-borne diseases or dangerous pests, it is best that they be tested in a site isolated from the production areas.

Systematic evaluation for any trait is a costly and time-consuming process. For this reason, goals should be clearly defined and procedures properly designed before testing begins, and colleagues in related disciplines should be consulted during the planning and testing stages. Testing at 'hot spots' where the relevant production problems are present is a convenient and inexpensive means of evaluating large numbers of accessions. In a discussion of the methodology of systematic evaluation, Chang (1976) reviews three common ways of evaluating collected samples: descriptive recording, systematic characterization, and empirical testing. A flow chart

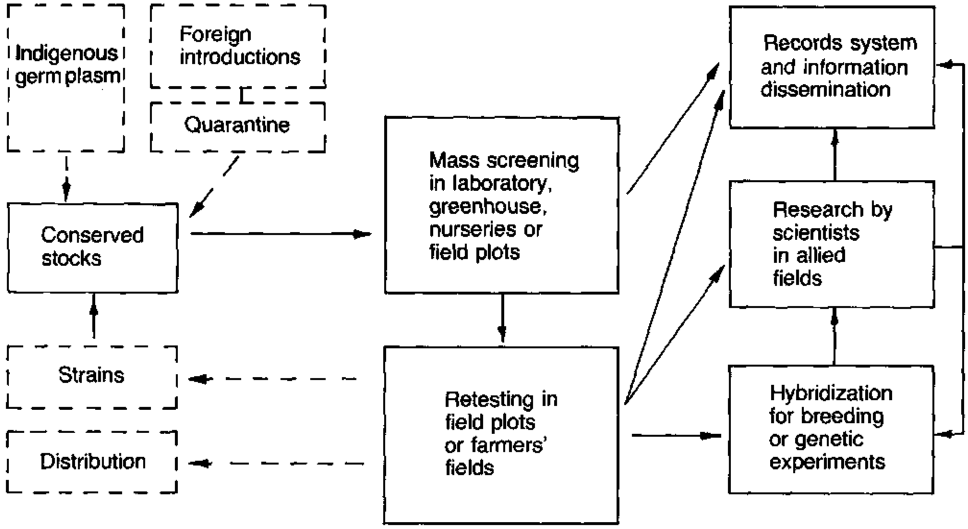

Fig. 3.2. Flow chart outlining the necessary steps in the evaluation and utilization of rice germplasm in relation to conservation and dissemination. Operations indicated by solid lines and arrows are directly related to evaluation, utilization, and information storage and retrieval. Dotted lines and arrows indicate indirect activities.

outlining the necessary steps in systematic evaluation and utilization at a national crop research centre is given in Fig. 3.2.

An instructive example of objectives-orientated and multidisciplinary efforts in evaluating germplasm is provided by the Genetic Evaluation and Utilization (GEU) programme of the International Rice Research Institute (IRRI), in which plant breeders are teamed up with 'problem area' scientists such as entomologists, plant pathologists, soil scientists and plant physiologists in tackling complex traits that require specialized knowledge. This multidisciplinary approach has proved both effective and efficient in screening germplasm, in identifying many valuable sources of resistance or tolerance and in utilizing the newly identified gene complexes for the development of genotypes giving high and stable yields. The wide array of elite germplasm of rice thus developed is being extensively tested for suitability for various biotic, edaphic or climatic niches in the major rice-producing areas and for improving grain quality and nutritional or cooking characteristics. The problem areas covered by the GEU programme are: resistance to insects, resistance to diseases, resistance to drought, improved protein content, tolerance to toxic or nutrient-deficient soils, tolerance to deep water or flooding and tolerance to low temperatures. Combined resistance or tolerance to several stresses is an ultimate objective (IRRI, 1974).

Relatively advanced lines from the GEU programme as well as resistant parents in IRRI's germplasm bank are channelled into the International Rice Testing Program (IRTP), which also incorporates nationally developed or identified selections into a world-wide testing network (IRRI, 1977). In this way, rice breeders all over the world can both contribute and share elite germplasm from diverse breeding programmes.

Similarly, the Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT) has been coordinating international and regional uniform nurseries of wheat and maize for yield performance or disease resistance for more than two decades (CIMMYT, 1976). More recently other international institutes have also initiated multilocation testing programmes.

Among countries conducting national research programmes, the USA has the longest history and the best-developed programmes of conserving, evaluating and utilizing crop germplasm (Burgess, 1971; Creech & Reitz, 1971; Reitz, 1976). Benefits from such programmes have recently been reviewed by Oldfield (1976). The US National Seed Storage Laboratory at Fort Collins, Colorado, has also served as a depository for a part of the maize collection of CIMMYT and the rice collection of IRRI.

A number of wild relatives have furnished valuable genes towards the improvement of cultigens. Notable examples are the leaf rust resistance genes for common wheat from *Agropyron elongatum*, resistance to tobacco mosaic virus from *Nicotiana glutinosa*, resistance to the grassy stunt virus of rice from *Oryza nivara*, and resistance to sugar cane mosaic virus from *Saccharum spontaneum*. Many other examples may be found in the vegetable crops.

Need for genetic diversity in major crops

Recent advances in plant breeding and the rapid diffusion of improved varieties have within a short period of time reduced the number of principal cultivars in the major crops of several countries to such a small group that the cultivars are not only uniform in respect of many agronomic and quality traits but are also genetically related or similar. This alarming reduction of genetic diversity and the consequent increase in genetic vulnerability to serious disease and insect ravages have been studied and publicized in several articles, of which *Genetic vulnerability of major crops* (National Academy of Sciences, 1972) provides the most comprehensive and detailed review. A similar review, focusing on the rapid spread of semidwarf wheats and rices since 1966-67 and the consequent reduction in the genetic base of two of the major food crops in tropical and subtropical areas, was recently prepared by Chang (1979).

Selected examples of crops in which uniformity for single traits is present are given in Table 3.1. High levels of uniformity are demanded by growers, processors, consumers, agricultural engineers and governments, but as most of the desired traits are controlled by a single gene or a few major genes, it is obvious that growing such uniform cultivars over vast areas is potentially dangerous.

Examples of the devastating effects of epidemics during the last 150 years as a result of the diminishing genetic base may be cited to focus on the importance of

Table 3.1. Examples of crop uniformity for single traits.

Crop	Trait
Beans	stringlessness
Maize	Texas cytoplasmic male sterility high lysine content (opaque-2)
Rice	semidwarfism photoperiod insensitivity
Sorghum	milo source of cytoplasmic male sterility
Wheat	semidwarfism photoperiod insensitivity cytoplasmic male sterility from *Triticum timopheevi*

maintaining genetic diversity in major crops:

- The Irish famine of the 1840s due to the potato late blight epidemic (*Phytophthora infestans*).
- The wheatless days of 1917 in the USA, due to stem rust epidemics (*Puccinia graminis*).
- The great Bengal famine of India in 1943 associated with the brown spot disease of rice (*Cochliobolus miyabeanus*).
- The complete elimination in the mid-1940s of all oats derived from the variety Victoria in the USA, due to the Victoria blight disease (*Cochliobolus victoriae*).
- The southern corn leaf blight epidemic (*Cochliobolus heterostrophus*) of 1970-71 on all US maize hybrids carrying T-type cytoplasmic male sterility.
- The rapid shift from the rice brown planthopper (*Nilaparvata lugens*) biotype 1 to biotype 2 during 1974-76, when large areas in the Philippines and in Indonesia were planted to a few semidwarf rices.

Whereas uniformity within a crop leads to genetic vulnerability, reinstatement of genetic diversity is one of the most effective means of protection against such vulnerability. On the other hand, the sequential release of varieties with vertical resistance based on major genes can only lead to 'boom and bust' cycles as described by Robinson (1976). Where the choice of pesticides is limited, integrated pest control measures and community efforts in cultural management should be adopted to supplement genetic resistance (Chang, 1979).

In subtropical and tropical areas where continuous planting of a single crop such as rice is practised, broadly based diversity within the crop is particularly desirable in order to (a) slow down genetic changes in major pests, (b) prevent minor pests from evolving into major pests, (c) counterbalance the epidemic-prone situation associated with continuous monoculture and (d) provide the potential for further genetic improvement (Chang, 1976). In this connection, increasing attention is being given to the sources of semidwarfism and cytoplasm used in breeding (IRRI, 1978a).

Global network for genetic conservation and utilization

When the urgency of conservation, the massive efforts needed, and the painstaking nature of preservation are jointly considered, it becomes obvious that a cooperative network is needed to implement and coordinate the necessary activities on a global basis. Meetings sponsored by FAO and the Consultative Group on International Agricultural Research (CGIAR) led to the establishment of the International Board for Plant Genetic Resources (IBPGR) in 1974. The IBPGR has assumed responsibility for identifying needs in exploration and collection, promoting and assisting field collection, improving and safeguarding storage of collected samples, training genetic resources workers, promoting information exchange, improving data storage and retrieval systems relating to genetic conservation, advising on financial needs in new or deficient areas of activity (IBPGR, 1975) and for disseminating information on plant genetic resources (Hawkes et al., 1976; Williams, 1976).

At the crop level, it is essential that there should be a network of international, regional, national and state research centres as well as seed banks concerned with the conservation, distribution and utilization of germplasm. In a network scheme proposed for rice, a conserved stock would be preserved at two or more sites; similar schemes may be suitable for other crops (Chang, 1976; IRRI, 1978b). Although networks of this kind have been fairly well developed for the major food crops (wheat, maize, rice, barley, sorghums, millets, potato, yams and several grain legumes) in recent years, there is still room for similar attempts in many other crops. With the establishment of the IBPGR there is hope that progress in such endeavours will be more rapid than hitherto. Meanwhile, it is gratifying to note the interest of crop specialists and regional bodies in initiating work on genetic conservation and evaluation (Varnell & McCloud, 1975; IBPGR/PCARR, 1977; SABRAO, 1977; IBPGR/NBPGR, 1978; IRRI, 1978b). Such work way be expected to expand as the returns from genetic projects resources become increasingly manifest.

Examples

RICE

The history of scientific rice breeding is so recent (dating from around 1906 in Japan) that until one or two decades ago the full spectrum of genetic diversity in the two cultigens (*Oryza sativa* and *O. glaberrima*) was still available for collection, preservation and utilization. Shortly before and after World War II, a number of national research centres made collections in the principal production areas; the national collections also included pure-line selections, improved varieties of hybrid origin and foreign introductions. In India and Japan, the International Rice Commission of the

FAO helped set up major collections for the three ecogeographic races, Indica, Japonica (Sinica or Keng) and Javanica. The two largest varietal collections that include substantial numbers of foreign introductions are held by the Central Rice Research Institute of India and the Agricultural Research Service of the US Department of Agriculture.

Shortly after World War II the research centres of Bangladesh, India, Malaysia, Pakistan, the Philippines and Thailand made fairly comprehensive collections of indigenous germplasm from lowland areas. A critical study (Chang, 1972a) of the different national collections in 1970-71 showed them to share a number of features:

- the principal commercial varieties and major or improved varieties from indigenous sources and from neighbouring countries were well represented;
- the numbers of minor varieties and special-purpose types were small;
- there were few or no mutants, wild relatives or wild species.

When the International Rice Research Institute (IRRI) was being established (1960-61), different national centres were encouraged to deposit their collections with IRRI, with the gratifying result that by the end of 1971 IRRI's total holdings amounted to 14,000 accessions (Chang, 1972b). Intensive field collection began in 1972, with 13 countries in South and Southeast Asia participating in the systematic collection scheme. By the end of 1978, 9480 samples had been collected directly by IRRI and collaborating national centres and another 12,560 samples by local extension workers. Most of the collections were made in remote areas in order to obtain minor unimproved varieties or special-purpose types; about 5000 samples were of the latter types. During 1976-78, several national and state centres systematically donated their collections to IRRI. At the end of 1978, the IRRI Germplasm Bank had more than 50,000 accessions of *O. sativa*, 1500 accessions of *O. glaberrima*, 860 populations of wild taxa and 640 genetic testers and mutants. Other material donated included wild and weed races collected by Japanese workers in South and Southeast Asia and in Africa, and African taxa collected by the Institut de Recherches Agronomiques Tropicales et des Cultures Vivrières (Paris) and the International Institute of Tropical Agriculture (Ibadan) in West Africa.

In evaluating and utilizing germplasm, IRRI has played a leading role both in demonstrating the effectiveness of screening for pest resistance (Chang et al., 1975a), tolerance to adverse soil factors (Ponnamperuma, 1977), resistance to drought (Chang et al., 1974) and other production-limiting factors and in supplying seed for such tests to workers all over the world (IRRI, 1978a). Many national centres have contributed breeding materials to different nurseries of the International Testing Program. More recently several collaborative research projects on yield-constraining problems (IRRI, 1978a) have been instituted by IRRI and national centres in connection with the Genetic Evaluation and Utilization programme. The international uniform rice observation nurseries include a diverse array of promising parents and have thus served as a working collection for new breeding programmes. IRRI also supplies F_1 and F_2 seed as well as bulk populations to workers in different countries. Thus the volume of international exchange of seed and seed-related information among rice workers has risen sharply in recent years.

This outline of the intense activity in progress in rice work throughout the world illustrates not only the means by which an international institute dealing with a specific crop can effectively assist and strengthen national programmes but also the unique role that a genetic resources centre can play (Chang et al., 1975b; IRRI, 1978b).

MAIZE

The first coordinated effort to collect, classify and preserve germplasm of maize (*Zea mays*) on a hemisphere basis was initiated in 1951 within the National Academy of Sciences/National Research Council (NAS/NRC). Operating under the Agricultural Board of NAS/NRC, a Committee on the Preservation of Indigenous Strains of Maize, working in close cooperation with The Rockefeller Foundation and several Latin American governments, directed and coordinated comprehensive maize collecting throughout South America, Central America and the major islands of the Caribbean. Financial support for the programme was provided by the US Department of State and funds were administered through the Office of Foreign Agricultural Relations of the USDA and the Institute of Inter-American Affairs.

During the years in which this programme was operative some 18,000 collections were made and deposited at three storage centres, (1) Chapingo, Mexico, (2) Medellín, Colombia, and (3) Piracicaba, Brazil. Also during this period the collections were grown, studied, described and classified according to race (Committee on Preservation of Indigenous Strains of Maize, 1954, 1955).

These studies resulted in the publication by the NAS/NRC of ten monographs which described the maizes of Cuba, Colombia, Central America, Brazil and other eastern South American countries, Bolivia, the West Indies, Chile, Peru, Ecuador and Venezuela. These publications, along with the previously published *Races of maize of Mexico* (Wellhausen et al., 1952), provide an excellent summary of the range of variation of the indigenous maize of the western hemisphere excluding North America.

While the work just described was the first attempt to conserve maize genetic resources throughout one hemisphere, maize was also included among those crop species acquired by various agencies of the US government beginning in the early 1800s. In 1819 American consuls abroad were requested to obtain plants and seeds of plants thought to be useful in the USA. Plant exploration was formally initiated with the establishment of the US Department of Agriculture in 1862, and in 1898 a Section on Seed and Plant Introduction was organized in the USDA.

In the 1920s N.I. Vavilov and his associates made extensive collections of maize in Mexico, Guatemala, Panama, Cuba and Colombia which were deposited at the USSR Institute of Plant Industry (Kuleshov, 1929, 1930). These collections, however, were not widely distributed outside the Soviet Union.

In the USA federal funds were made available to several states for the purpose of collecting open-pollinated varieties of maize when it became apparent in the 1940s that these were being rapidly replaced by more productive hybrids. Although many varieties had disappeared by that time, most of those still in existence in the mid-1940s were salvaged. The bulk of these are now being maintained by the North Central Regional Plant Introduction Station at Ames, Iowa.

Maize conservation was an important part of The Rockefeller Foundation-Mexican Government Agricultural Program initiated in Mexico in 1943. A similar programme of maize improvement was started in Colombia in cooperation with the Colombian government in the early 1950s in which maize collection, evaluation and conservation received major attention. More recently the Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT) has continued and expanded the work in maize germplasm conservation as a part of its global maize improvement programme.

The establishment of the International Board for Plant Genetic Resources (IBPGR) in 1974 has led to renewed interest in crop genetic resources including maize. A Maize Advisory Committee organized by IBPGR has:

- analysed the current status of maize germplasm in the various seed storage banks,
- identified the major gaps existing within and among collections,
- identified the geographical areas in which additional exploration and collecting are needed,
- established priorities for additional collecting,
- developed a minimal list of descriptors for collections,
- worked with the Information Sciences/Genetic Resources Program of the University of Colorado in the development of a comprehensive maize data base and documentation system for all existing collections.

Despite the loss of some accessions, most of the maize germplasm assembled during the NAS/NRC program of the 1950s still exists in viable form. The bulk of this is stored at CIMMYT, Mexico, the Instituto Colombiano Agropecuario (ICA), Colombia, and the Instituto Nacional de Investigaciones Agrícolas (INIA), Mexico.

The Spanish collection (Sanchez-Monge, 1962) is apparently lost but additional collecting sponsored by IBPGR will, it is hoped, replace most of that material.

Additional exploration in parts of Peru, Bolivia, Brazil, Argentina, Paraguay and Uruguay now in progress or in the advanced planning stages should go a long way towards filling the gaps in existing South American collections. Another geographical area that should receive more attention in the near future is the eastern Himalayas, including Bhutan, Assam and Sikkim of India and Nepal and south-west China. The maize from this area apparently includes some unique types of germplasm not duplicated elsewhere in the world, but their range of variation and geographical distribution is unknown because of the limited collecting that has been done in the area.

When considered in total, a vast amount of maize germplasm is now in storage around the world, but the use that has been made of these materials has been rather disappointing. One reason for this is the lack of knowledge among breeders and geneticists as to what is available and where it is located. Each seed depository maintains its own inventory but a comprehensive data base including all accessions of all banks has yet to be developed. It is for this reason that high priority needs be given to the joint Information Science/Genetic Resources USDA-IBPGR programme designed to fill this need.

FORAGE GRASSES

Domestication of the grasses is of relatively recent date. In tropical grasses the process began only a few decades ago. The evolutionary and domestication processes are still continuing over many areas of the world.

The distribution of the world's 10,000 species of grasses reflects primarily their climatic adaptation. The common habitats and mode of reproduction of some important forage grasses are summarized in Table 3.2.

Enormous variation exists within any one grass species and frequently exceeds the mean difference between related species. Much of the intraspecific variation is the result of human selection superimposed upon natural selection due to climatic and edaphic factors.

Varietal improvement work on forage grasses has largely relied on the ecogenotypic variation present in existing populations. Some grass species, such as molasses grass (*Melinis minutiflora*), have become more important in new environments where they are better adapted than in their original habitats. As a result, secondary diversification has rapidly taken place in new areas of cultivation.

Further improvement will hinge largely on the breeder's ability to detect and use the myriad ecogenetic variants in naturally occurring or cultivated populations. Hence grass breeders will have to play a greater role in the exploration, introduction, evaluation, utilization and conservation of the germplasm than hitherto.

MAN-MADE SPECIES AND ANEUPLOIDS

Wide crosses are often used in breeding in order to transfer certain traits (especially resistance to diseases and pests) into cultivated species (e.g. potato, wheat and rice). They have also been used for introducing cytoplasmic male sterility into crops (e.g. wheat, sorghum and rice).

Certain crops are amphidiploids and it has proved possible to resynthesize many of these and sometimes to improve them by adding new properties. The genus *Brassica* provides some well-known examples. The so-called man-made 'species' mostly arise spontaneously, albeit in low frequencies and accompanied by disturbances in fertility. Examples of these are triticale (*Triticum* × *Secale*) and × *Festulolium* (*Lolium* × *Festuca*).

The first wheat × rye crosses ever described are mentioned in a report of Wilson (1876). The hybrids were sterile. In 1888/1891 the first spontaneous amphidiploid

Table 3.2. Some important cultivated grasses.

Climate	Rainfall	Species	Common name	Origin	Mode of reproduction	Multiplication
1. Temperate	Extended	*Lolium perenne*	perennial ryegrass	Med.	cross	seed
		Lolium multiflorum	Italian ryegrass	Med.	cross	seed
		Dactylis glomerata	cocksfoot	Med.	cross	seed
		Phleum pratense	timothy	Med.	cross	seed
	Winter rainfall/ Med.	*Festuca arundinacea*	tall fescue	Med.	cross	seed
		Dactylis glomerata	cocksfoot	Med.	cross	seed
		Phleum pratense	timothy	Med.	cross	seed
		Phalaris tuberosa		Med.	cross	seed
	Summer rainfall/ semiarid	*Agropyron cristatum*	wheatgrass	CEAS	cross	seed
		Bromus inermis	brome grass	CEAS	cross	seed
2. Subtrop. and tropical	Extended rainfall	*Brachiaria decumbens*	signal grass	EAFR	apom.	seed
		Chloris gayana	Rhodes grass	EAFR	cross	seed
		Cynodon spp.	Bermuda/star grass	EAFR	cross	veg.
		Digitaria decumbens	Pangola grass	SAFR	—	veg.
		Panicum maximum	Guinea grass	EAFR	apom.	seed
		Pennisetum purpureum	elephant grass	EAFR	cross	veg.
		Pennisetum clandestinum	Kikuyu grass	EAFR	apom.	seed & veg.
		Setaria sphacelata	setaria	EAFR	cross	seed
	Seasonal rainfall/ semiarid	*Andropogon gayanus*	Gamba grass	TAFR	cross	seed
		Bouteloua gracilis	blue gama grass	NOAM	cross	seed
		Cenchrus ciliaris	buffel grass	EAFR	apom.	seed
		Eragrostis curvula	love grass	SAFR	apom.	seed
		Panicum maximum	Guinea grass	EAFR	apom.	seed
		Chloris gayana	Rhodes grass	EAFR	apom.	seed

Med. = Mediterranean; CEAS = Central Asia; EUAS = Europe/Asia; EAFR = East African; SAFR = South African; TAFR = Tropical Africa; NOAM = North America; cross = cross-pollinating; apom. = apomictic; veg. = vegetative was discovered. However, in spite of all later research, 8*x* triticale has never been a success. Since 1950, triticales based on allotetraploid wheat × rye crosses have been receiving attention. These seem to offer better possibilities.

In × *Festulolium* it has been possible to restore fertility through changes at the genome level. As a herbage grass, × *Festulolium* is apparently able to combine certain favourable properties of the parents. However, if it is to compete with existing grass species that have become adapted during the course of evolution, its fertility and stability will have to be improved.

The man-made forms may carry latent new properties, but they often also have the disadvantage of a lack of affinity both between the genomes themselves and between genomes and cytoplasm. This is in many instances detrimental to their stability and fertility. In addition, it should not be forgotten that selection by the hand of man for a few decades can never be a substitute for successful adaptive selection over long periods of evolution. Synthetic amphiploids (alloploids) of which one or both parents are crop species, or relatives of crop species, have been generated in the course of basic research and in plant breeding programmes. Examples may be found in the Triticinae and in cruciferous crops. Here, too, sterility often raises problems in seed propagation.

The long-term potential of this material for crop improvement and development cannot be predicted. But it is desirable that such synthetic species be conserved. The same is true for aneuploids, both spontaneous and induced. No system for doing so has yet been established, though the question of the conservation of genetic materials resulting from distant hybridization was raised at the International Wheat Symposium held at New Delhi in 1978. It is a matter of urgency that a solution to this question be sought by the relevant bodies.

Institutions engaged in the conservation of crop genetic resources

The following listing provides a reasonably complete tally of major institutions that are actively involved in the genetic conservation of crop genetic resources.

NATIONAL ORGANIZATIONS

Australia: Commonwealth Scientific and Industrial Research Organization (CSIRO). New South Wales Department of Agriculture.

Brazil: Centro Nacional de Recursos Geneticos (CENARGEN).

France: Institut de Recherches Agronomiques Tropicales et de Cultures Vivrières (IRAT). Institut National de Recherche Agronomique (INRA). Office de la Recherche Scientifique et Technique de l'Outre-Mer (ORSTOM).

German Democratic Republic: Zentralinstitut für Genetik und Kulturpflanzenforschung.

Germany, Federal Republic of: Institut für Pflanzenbau und Saatgutforschung.

India: National Bureau of Plant Genetic Resources. Also various crop-specific

Central Research Institutes or Coordinated Projects under the Indian Council for Agricultural Research.
Indonesia: National Biological Institute, Bogor.
Italy: Laboratorio del Germoplasma, University of Bari.
Japan: National Institute of Agricultural Sciences. Kyoto University.
Mexico: Instituto Nacional de Investigaciones Agrícolas.
Netherlands: A coordinated genetic resources programme between the Foundation for Agricultural Plant Breeding, Institute for Horticultural Plant Breeding, Institute for Plant Breeding, Gouvernement Institute for Research on Varieties of Cultivated Plants and Seed Testing Station, all at Wageningen.
Sweden: A coordinated Scandinavian gene bank at the Swedish Seed Testing and Certification Station near Lund.
UK: Royal Botanic Gardens (wild relatives of legumes, cereals and grasses). John Innes Institute. Scottish Plant Breeding Station. Plant Breeding Institute.
USA: Agricultural Research Service, US Department of Agriculture.
USSR: Vavilov All-Union Institute of Plant Industry (VIR). Also crop-specific All-Union Research Institutes.

Among various geographical regions, Europe has the largest number of gene banks operated by government institutions. Each of the following countries has one or more gene banks: Austria, Bulgaria, Czechoslovakia, France, Federal Republic of Germany, German Democratic Republic, Hungary, Italy, the Netherlands, Poland, Portugal, Romania, Spain, Sweden, Switzerland, the United Kingdom, the USSR, Turkey and Yugoslavia. Countries in both East and West Europe participate in the Gene Bank Committee of Eucarpia (the European Plant Breeders Association). Since 1975 the UN Development Programme (UNDP) and FAO have joined the meetings of the Committee and proposed the establishment of a European Cooperative Program (ECP). The Committee is working with the IBPGR on field collection. The major gene banks in West Europe are located at Lund (Sweden – at planning stage), Braunschweig (Federal Republic of Germany) and Bari (Italy). The Bari centre will be collaborating with the Aegean Regional Agricultural Research Institute (ARARI) in Turkey. The largest gene bank in East Europe is the Vavilov All-Union Institute of Plant Industry (VIR) at Leningrad, USSR, with huge modern storage facilities at Krasnodar.

INTERNATIONAL AND REGIONAL CENTRES

Colombia: Centro Internacional de Agricultura Tropical (CIAT), Cali.
Costa Rica: Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Turrialba. Instituto Interamericano de Ciencias Agrícolos (IICA), Turrialba.
Germany, Federal Republic of: Dutch/German Potato Gene Bank, Braunschweig.
India: International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad.

Mexico: Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT), El Batán.
Nigeria: International Institute of Tropical Agriculture (IITA), Ibadan.
Peru: International Potato Center (IPC), Lima.
Philippines: International Rice Research Institute (IRRI), Los Baños.
Sweden: Nordic Gene Bank, Lund.
Syria: International Center for Agricultural Research in the Dry Areas (ICARDA), Aleppo.
Taiwan: Asian Vegetable Research and Development Center (AVRDC), Shanghwa.
Turkey: Aegean Regional Agricultural Research Institute (ARARI), Izmir.

The cooperation between east and west European countries through the Eucarpia gene bank committee is developing very well. The UNDP/FAO proposals for a European Cooperative Program should improve the situation even more.

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with the collaboration of
W.L. Brown on maize
J.G. Boonman on grasses
J. Sneep on man-made species
H. Lamberts on institutions

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4 Current breeding methods

The first and more general part of this chapter is concerned with techniques. It begins with a survey of the modes of reproduction of crop plants and the methods of breeding appropriate to each type. The usefulness of mutations is discussed and they are seen to be of value in breeding certain vegetatively propagated food and ornamental crops and certain specialized seed crops. Special attention is given to the complexities of breeding for important quantitative properties such as yield, earliness etc. Next follows a consideration of the intensity of selection appropriate to each stage in a balanced selection programme, and an example is given of an advanced, computerized trial lay-out and data-processing system which is already in operation. In view of the successes that the breeding of hybrid varieties has had in food crops and the probability that their use will continue to increase, a large section deals with the basic techniques applied in the production of hybrids, viz. those involving the use of male sterility, fertility restoration and self incompatibility. An outline is given of the difficulties and opportunities associated with apomixis. The second part of the chapter provides examples of breeding procedures appropriate to various types of crops, arranged as follows: a vegetatively propagated crop (potato); self-pollinated cereals (mainly wheat, with discussions on the prospects of hybrid wheat and hybrid rice); cross-pollinated crops (grasses, maize, sugar beet and sunflower). Of the crops in the last group, the grasses are still being bred by classical methods; maize is predominantly bred for hybrid production, even in developing countries; sugar beet varieties are likewise mostly hybrids, those of western Europe being triploid; and sunflower is a crop in which a shift from conventional varieties to hybrid varieties is in progress.

General

CLASSIFICATION OF CROPS

Crops can be classified according to their system of propagation and the relevant methods of breeding into:

1 Vegetatively propagated crops: potato, cassava, sugar cane etc.
2 Autogamous crops: wheat, rice, barley, soya bean, tobacco etc.
3 Allogamous crops: maize, rye, sugar beet, sunflower, oil palm, many grasses etc.

Between groups 2 and 3 there is an intermediate class of crops which are partly self pollinated and partly cross pollinated, such as *Vicia faba*, *Brassica napus* and sorghum. The breeding methods appropriate to this class are basically no different from those used for groups 2 and 3 and will therefore not be treated separately. Group 3 can be subdivided into two classes of importance for breeding: crops in which selection can take place before flowering, e.g. sugar beet and cabbage; crops in which selection cannot take place until after flowering, e.g. maize and rye.

Any attempt to modify the principal methods used in breeding or to develop alternative methods must take into account the following properties of plants:

– Dioecy. Inbreeding by self fertilization is not feasible. The sexes may differ in their value as a crop. Sex manipulation to give pure male or female strains may be possible. Examples are asparagus, spinach and papaya.

– Monoecy. Inbreeding by self fertilization is possible. Hybrid varieties can be produced. Sex manipulation to give pure female strains may be possible. Examples are maize (emasculation easy), castor oil plant (emasculation difficult) and cucumber.

– Hermaphrodite flowers. Emasculation is not readily effected. Male sterility or self incompatibility is necessary for hybrid production, especially in self-pollinated crops. Examples include *Brassica*, tomato, rye, wheat and rice.

– Persistent capacity of the plant for sexual reproduction. This property facilitates breeding, especially in the case of selection after flowering. Examples are oil palm, coffee, coconut and many grasses.

– Capacity for vegetative propagation and maintenance. This property increases the precision of selection, facilitates diallel crossing and allows increased seed production per genotype. The advantages are the same as for the preceding property. It also facilitates breeding by procedures such as the polycross. Examples are sugar beet, Brussels sprouts and many grasses.

Vegetatively propagated crops

In these crops, improvement is achieved mainly through careful choice of parents, followed by the production of a large F_1 population and selection for favourable characteristics. Selection in early years is mainly for characteristics with high h_b^2 (broad-sense heritability), the clones from every F_1 seedling maintained being subjected to increasing selection intensity in successive years. Once the clones contain a sufficient number of plants, selection for wide adaptability and for characters with low h_b^2 is also carried out.

Infection of the plants by viruses constitutes a major hazard during maintenance and propagation. Measures must also be taken against other pathogens transmitted by vegetatively propagated material.

In order to introduce desirable characters, especially various kinds of resistance, much use is made of crosses with related species. This normally necessitates recurrent back crossing. Fertility is not particulary important as a varietal character. Thus many potato varieties are male sterile or only moderately fertile.

Autogamous crops

Improvement in self-pollinated or, more strictly, autogamous crops began with the selection of wild progenitors and proceeded to selection from land races. Although land races in Europe were subjected to intensive selection in the last quarter of the 19th and the first quarter of the 20th century, they are now used primarily as a source of special characters. In developing countries land races still comprise a wealth of adapted genotypes. Considerable progress is possible by means of simple breeding methods such as line selection (corresponding to half-sib family selection in allogamous crops); this procedure ensures that the strains obtained are well adapted.

Methods using crosses and back crosses as a source of genotypic variability were being applied by the end of the 19th century and have since then grown in importance. Back crosses are necessary when parental material from the areas of diversity is used. Also of growing importance is the use of multiple crosses to combine characteristics distributed among more than two parents. Mass selection is now little used in autogamous crops. Another method which is now little favoured involves growing in bulk up to about the F_7 in order to test almost pure lines. The procedure is time-consuming, favourable genotypes are easily lost and even many years of multiplication provide no information on genotype × year interaction; the advantages of a possible natural selection pressure, even in cereals, do not outweigh all this.

Almost all current selection methods are based on line selection and its modifications. In a programme of line selection, selection for yield is often not introduced until the F_5. Considering the many factors involved in yield, this entails a distinct possibility that favourable alleles may be lost in early generations (Sneep, 1977), and it is therefore usually desirable to advance selection for yield to an earlier stage. Selection for performance in dense populations rather than selection of single plants in spaced plantings is receiving increasing attention.

As a means of obtaining homozygous lines in a short time from many populations in a restricted area, without the risk of unwanted spontaneous selection pressure, use may be made of the 'single seed descent method' (Brim, 1966). This method involves harvesting one seed per plant from the F_2 to the F_6 and sowing them in the greenhouse in order to raise two or three generations per year depending on the crop. However, the method has its disadvantages: if favourable gene combinations are not to be lost in the course of early generations, large numbers of plants are required; also, the procedure provides no possibility of obtaining information on genotype × year interactions. Another method of obtaining homozygous lines is by means of chromosome doubling in haploids. Doubled haploids allow a rapid evaluation of a particular cross combination, but the method has so far found little application in practice. Its further use will depend largely on how far the production of haploids can be simplified (cf. Chapter 8, pp. 330-341). Adequate data on the utility of these methods are not yet available.

Use is also made of F_1 hybrids in autogamous species. In certain cases the hybrid varieties are produced by manual pollination, as for example in tomato. In a number of crops cytoplasmic male sterility is being sought with a view to the economic production of hybrid varieties (see 'Male sterility for hybrid production', pp. 120-134, 'Hybrid wheat', pp. 167-172 and 'Hybrid rice', pp. 173-174). Purely genic male sterility is difficult to handle on a large scale.

Diallel analyses in self-pollinated species are little used in applied breeding. They are an important adjunct to breeding, allowing the analysis of general and specific combining ability, but their predictive value is uncertain as the procedure has so many prerequisites that it can hardly be applied to breeding material. Moreover in many species a full diallel analysis is very laborious.

Multilines The possibility of using multilines, i.e. mixtures of nearly isogenic lines, in autogamous crops has attracted the attention of many plant breeders in recent years. To prevent an epidemic spread of air-borne diseases such as rust in wheat, the cultivation of multiline mixtures in which the lines differ only in their resistance to different races of the pathogen is sometimes advocated. An important drawback in breeding multilines is that many repeated back crosses of an existing outstanding variety to several resistance sources are required. This is a time-consuming process and has the result that by the time the multiline is introduced it is already outyielded by newly bred conventional varieties. An example may be cited from the Netherlands. In 1966 the wheat variety Tadorna was admitted to the Recommended List of Varieties. It was resistant to yellow rust and outyielded the leading variety Manella by 10% (Table 4.1). Some years later it became susceptible to a new strain of yellow rust, and by 1971 it had lost its superiority over Manella in all areas where rust was important. In the meantime a multiline variety of Tadorna, called Tumult, was developed which, in trials in 1975, outyielded Tadorna by 9% in the areas where rust was prevalent. During the same period, however, other new varieties bred along conventional lines surpassed the average yield level whereas by 1975 the yield of Manella was 6% below the average and that of Tumult was also below the average.

Mixtures of varieties, similar in agronomic properties such as earliness, height,

Table 4.1. Comparison of the yields of Tadorna, its multiline version Tumult and Manella in the Netherlands. (Calculated from trial results, RIVRO).

	Yields in % of the mean of all accepted wheat varieties In areas where yellow rust is:	
	important	unimportant
1966 Manella	103	100
Tadorna	111	112
1971 Manella	96	98
Tadorna	98	106
1975 Manella	95	92
Tadorna	91	101
Tumult	97	98

grain size etc. but differing in race-specific resistance, can serve the same purpose as the multiline, but here the difficulty of achieving agricultural uniformity is more serious. In this respect, mixtures of sister lines from multiple crosses (involving more than two parents) may be expected to have certain advantages, since they are, or may be, related in several traits and since they have a broader spectrum of resistance than two-parent lines.

There is little support for the suggestion that in the absence of diseases mixtures are better yielding than each of the components (cf. Chapter 2, pp. 67-70): mixtures are only justified where they can prevent epidemics.

Multiple crosses Where it is desired to combine more than two distinct characters which are only available in more than two parents, wheat breeders in particular are turning to the use of multiple crosses. Some breeders, however, are not aware that the frequency of favourable alleles in an $F_1 \times F_1$ cross is considerably lower than in a conventional F_2 generation. The same is true of the succeeding generations. For this reason multiple crosses cannot be used for combinations of more than approximately ten favourable alleles without risking the loss of a large proportion of them (Sneep, 1977).

Allogamous crops

As in autogamous crops, selection in allogamous crops started with mass selection, followed by such improvements as half-sib family selection and full-sib family selection.

Mass selection In its simplest form, mass selection is now practised only in crops of minor economic importance or in crops that have undergone little breeding. Its use is justifiable only for characteristics with high heritability and even then it is not very efficient, especially if the alleles to be eliminated are present in low frequencies. Mass selection after flowering is even less efficient than mass selection before flowering.

Modifications worthy of consideration are:

– The stratified or grid system; here the best plants from each square of the selection field are retained (Gardner, 1961).

– The honeycomb system (Fasoulas,1973); here the plants are sown in hexagons and the best plant of every set is selected.

Both systems aim at reducing the effect of location on selection, by comparing each selected plant with its neighbours.

Half-sib family selection This method involves an evaluation of the progeny from each mother plant. As each mother plant has been fertilized by more than one father plant, it may be said that the mother plants have been open pollinated. Since the half-sibs often flower simultaneously, separating them from each other can be a costly procedure and is rarely worthwile. For this reason the method is more frequently applied to crops that can be selected before flowering (i.e. crops grown for their vegetative parts) than to seed crops. The system used for the latter crops is the remnant-seed procedure (known as ear-to-row selection in maize).

Generally speaking, it may be said that half-sib selection is based on general combining ability, the entire population being used as a tester.

A variant of the half-sib selection procedure is the polycross method, described by Frandsen (1940) and Tysdal et al. (1942). The polycross is particularly suitable for cross-pollinated crops which can be propagated and maintained vegetatively for purposes of breeding (e.g. many grasses and some legumes). This procedure and its many variants have been used to develop a great number of synthetics (cf. 'Grasses', pp. 181-183).

Full-sib family selection Here selection is carried out in the progeny of a mother plant which has been pollinated by only one father plant. Continued full-sib family selection leads to a rapid narrowing of the population. In effect, full-sib family selection is a test for specific combining ability. It is an effective means of selecting against unfavourable characters, particularly against recessive alleles that can be detected before flowering. To achieve maximum efficiency in selecting for traits not apparent until after flowering, all full sibs must flower separately. The procedure is therefore very expensive. Here the remnant seed method would be an alternative.

Simple recurrent selection This method is of value where selection cannot be applied until after flowering and where either enforced selfing or vegetative maintenance is possible. Where the plants are self fertilized, only the desirable phenotypes are retained on harvesting. To offset the effects of self fertilization, the good I_1s are intercrossed in the next season. After this a new cycle can be started. Where the plants are vegetatively maintained, desirable plants are allowed to flower together in the second season to produce the starting population for a new cycle. This method, in fact, is comparable to mass selection before flowering.

Other recurrent selection methods are merely used as one part of a total breeding scheme. Most are used as part of a complex hybrid breeding procedure.

Hybrid varieties or F_1 hybrids are becoming important in an increasing number of cross-pollinated crops. Maize is the best-known example ('Maize', pp. 190-203), but west European sugar beet hybrids may be cited as example involving advanced production techniques ('Sugar beet', pp. 203-215). In the production of hybrid varieties, increasing use is being made not only of cytoplasmic male sterility but also of self incompatibility, especially in *Brassica* ('Incompatibility as a tool in plant breeding', pp. 134-139). Chemical methods of emasculation are not yet suitable for large-scale application, and the same is true of purely genic male sterility ('Male sterility for hybrid production', pp. 120-134).

Varietal maintenance in cross-pollinated crops involves selection for uniformity and is therefore a continuation of the breeding procedure. In minor crops mass selection is still an important method. In the case of synthetics, the practice of keeping the seed of the parental components in cold storage is increasing, a procedure which assures the stability of the variety over a number of years.

Cytoplasm In choosing female parents, the breeder needs to consider the effect of cytoplasm on the pattern of genetic variation and therefore on heritability. It is regrettable that our knowledge in this field is so meagre, with respect to both allogamous and autogamous species.

MUTATION BREEDING

Micke (1976) puts the total number of varieties developed from induced mutations up to December 1975 at 197 (Table 4.2). If this figure is considered in the light of all the effort expended on mutation breeding, it gives little cause for satisfaction. In a comparison of the results of mutation breeding with those of classical breeding methods our vote will definitely be in favour of the latter, especially where the crop concerned has a wide genotypic variation that can readily be exploited in crosses.

Whether induced or spontaneous, mutants may nevertheless be useful in cases where little genotypic variation exists. As a means of enhancing genotypic variation in crops that because of sterility or for other reasons cannot be crossed – as is the case in certain species of *Iris* and *Alstroemeria* – mutations may in fact be extremely advantageous. It is therefore hardly surprising that vegetatively propagated ornamental crops occupy such a prominent position in Table 4.2. The probability that in

Table 4.2. Number of commercial varieties from induced mutations up to December 1975 (after Micke, 1976).

	Direct mutations	Varieties from crosses with mutants
1. Field crops		
a. propagated by seed	87	36
b. propagated vegetatively	9	1
subtotal	96	37
2. Ornamental crops		
a. propagated by seed	—	4
b. propagated vegetatively	60	—
total	156	41
	Grand total: 197	

certain ornamentals virtually any novelty will be of interest is probably relevant here. Induced mutations are also increasing in importance in ornamental crops that are readily crossed. Here changes in flower colour and/or shape may be induced which leave the rest of an often highly heterozygous but genetically well-balanced complex practically unaffected (Broertjes & van Harten, 1978).

Among properties that can be induced by mutation are short straw, high protein quality and resistance. It is well known that genic male sterility can be induced by means of mutagenic treatment. Mutagenic treatments may also be of service in chromosome engineering.

Notwithstanding, the conclusion that mutation breeding is not a panacea for all plant breeding problems is inescapable. The method offers possibilities but is also subject to severe limitations. Except in cases involving a change from a dominant to a recessive character in certain vegetatively propagated ornamental crops, it cannot be expected to compete seriously with classical breeding. Induced mutations constitute only one tool among the many available to plant breeding. As such they are useful.

METHODS FOR QUANTITATIVE TRAITS

In general, selection for quantitative (polygenic) traits such as yield is preferably carried out in early generations. The reason for this is that by the time advanced generations have been reached, especially under intensive selection for other characters, most of the desired combinations of favourable alleles will have been lost. The same is true, to a lesser extent, in the absence of selection pressure. The following difficulties are associated with selection in early generations:
– the number of entries is very high;
– only small quantities of seed are available, so that trials cannot always be replicated;
– variance between entries is lower than in later generations, especially in autogamous crops;
– genetic variation within progenies cannot be distinguished from random variation, making it difficult to select between entries;
– space and labour requirements are high.

In early generations with many entries, nonreplicated trials with many (replicated) controls must suffice. In contrast, advanced generations have the following advantages:
– they produce enough seed to allow testing in lattice designs with genotype × location interactions and even genotype × location × season interactions;
– genetic variance between entries is greater, so that selection is easier.

On the other hand there is a limit to the numbers of locations, replications and years the breeder can employ ('Balance in multistage selection', pp. 112-115). In view of these varied requirements, the breeder must strike a balance between range of material, generation of selection and magnitude of selection pressure.

The efficiency of selection depends on two components. The first is the ratio of genotypic to phenotypic variation, or heritability in the broad sense h^2_b. Minimizing the error variation increases h^2_b, decreases the chance of a wrong choice of material and promotes the efficiency of selection in early generations. The second is the ratio of fixable genetic variation to total genetic variation, or heritability in the narrow sense (h^2_n). The selection response R (sometimes denoted by G_s) is directly proportional to h^2_n. Yield is a complex variable, and some of its components can be selected more efficiently than yield itself. The same is true of other polygenic quantitative characters. A suitable selection index, i.e. an index in which various values for different selection criteria are combined, is useful where there is an adverse association between the desired component characters.

Where full selection is only possible after flowering, breeding methods in allogamous crops are complicated and the response is slow. In such cases efficiency can be enhanced by modified breeding schemes, or by means of indirect selection involving a character (or characters) which can be observed before flowering and which is highly correlated with final performance after flowering. If more than one such character is used, the term 'indirect index selection' is appropriate. The efficiency of index selection depends largely on the magnitude of the associations and their heritability.

BALANCE IN MULTISTAGE SELECTION

Heritability and genetic gain must be seen in the context of a multistage selection procedure that is designed to attain the greatest possible response by the end of the last stage, though not at the end of each single step. To guarantee a rapid selection advance the number of years must be low, but for biological reasons it is not always possible to reduce the number of years to correspond exactly to the number of stages of selection, as for example where the amount of seed is inadequate or where additional generations are required to achieve homozygosity.

Multistage selection can be illustrated by reference to the varietal testing phase. In year s or stage s, a perfomance test is carried out at P_s locations, with R_s replications at each. Out of N_s selections tested, N_{s+1} selections are chosen, corresponding to a selected fraction $\alpha_s = N_{s+1}/N_s$. These N_{s+1} selections are tested further during the next stage, provided that another trial year has been planned. Table 4.3 shows the different quantities for a three-stage selection procedure. Selection can be based on the mean performance x_s of a genotype as averaged over $P_s \cdot R_s$ plot values. But it is also possible to include data from earlier years if these are reliable.

For quantitative characters with a normal distribution, it is possible to predict the selection response. The total number of test plots, the test capacity C, is often limited. This can make it difficult to allocate or distribute the plots among number of locations P_s, number of replications R_s and number of genotypes N_s in such a way as to obtain maximum selection response: the condition $C = P_1R_1N_1 + P_2R_2N_2 + P_3R_3N_3$ must be met. As breeding work is of a continuous nature and the breeder may begin

Table 4.3. Tabulation of a three-stage selection process.

Stage	Number of locations	Number of replications	Number of candidates	Fraction selected	Mean of candidate	Optimum selection based on
1	P_1	R_1	N_1	$\alpha_1 = N_2/N_1$	x_1	x_1
2	P_2	R_2	N_2	$\alpha_2 = N_3/N_2$	x_2	$b_{21}x_1 + b_{22}x_2$
3	P_3	R_3	N_3	$\alpha_3 = N_4/N_3$	x_3	$b_{31}x_1 + b_{32}x_2 + b_{33}x_3$

with a fresh procedure each year, the limitation mentioned applies to tests within one year for all selection procedures, and also to tests within one selection procedure for all the years concerned.

In Table 4.3, selection optima are given for a few situations. It is assumed that, in testing the selections, masked variances interact with the genotypic variance as follows:

genotypes × locations: $\sigma^2{}_{tp}/\ \sigma^2{}_t = 0.5$
genotypes × years: $\sigma^2{}_{tq}/\ \sigma^2{}_t = 0.5$
genotypes × locations × years: $\sigma^2{}_{tpq}/\ \sigma^2{}_t = 1.5$
total deviation: $\sigma^2{}_e/\ \sigma^2{}_t = 4.0$
$\sigma^2{}_t$ - the genotypic variance between genotypes
$\sigma^2{}_{tp}$ - the genotypes × locations interaction variance
$\sigma^2{}_{tq}$ - the genotypes × years interaction variance
$\sigma^2{}_{tpq}$ - the genotypes × locations × years interaction variance

These coefficients of variation are mean values taken from estimated values found in the literature for yield in self-pollinated cereal species. It is further assumed that only one genotype is finally selected, so that $N_1 = 1$. Where $N_4 > 1$, the corresponding values (e.g. N_1) must be multiplied by N_4.

Table 4.4 gives the results of the optimal allocations for three different test capacities (C) and for two situations for number of replications. For each test capacity, the first line applies to cases in which the number of locations is unlimited, the second to cases in which tests can be performed at a maximum of three locations. The optimum number of locations at the first stage is always 1, while at the last stage it varies from 7 to 17. As would be expected, the greater the value of C, the smaller the fraction selected. The accuracy of the test increases with an increase in P_3 or C (see last column). Here H is the square of the coefficient of correlation of the genotypic values for the genotypes with the best estimated values. The percentage indicates the heritability obtained over all three stages.

The larger the test capacity, the greater the maximum obtainable selection response G_s. However, the rates of increase decline. The selection response decreases

Table 4.4. Optima of a three-stage selection for number of locations (P_S), number of candidates in the first stage (N_1), fraction selected (α_S in %), selection response (G_S) and heritability (H) obtained in the finally chosen candidates as computed for several test capacities (C), the greatest possible number of locations (P_{max}) and two replications.

C	P_{max}	P_1	P_2	P_3	N_1	α_1	α_2	α_3	G_S	H
Optima for $R_1 = 1, R_2 = 2, R_3 = 3$										
300	–	1	3	7	140	11	21	31	1.97	0.62
	3	1	3	3	160	11	22	26	1.93	0.54
900	–	1	5	13	432	7	14	24	2.35	0.68
	3	1	3	3	564	8	16	14	2.23	0.54
1500	–	1	5	17	717	7	11	18	2.52	0.69
	3	1	3	3	995	7	14	10	2.35	0.54
Optima for $R_1 = 2, R_2 = 2, R_3 = 3$										
300	–	1	4	7	80	13	26	37	1.91	0.64
	3	1	3	3	97	13	28	28	1.86	0.55
900	–	1	6	13	245	9	17	27	2.30	0.69
	3	1	3	3	323	10	21	15	2.17	0.55
1500	–	1	6	17	425	8	14	21	2.46	0.71
	3	1	3	3	559	9	18	11	2.29	0.55

by 2 to 3% when the number of replications in the first stage is increased from 1 to 2. The optimal number of locations may appear to be high, especially for high test capacities, and could be regarded as the upper limit. The reason for this lies in our simplified assumptions. A relatively strong limitation to only 3 test locations reduces the selection response by 2 tot 7%, with the largest decrease for the greater test capacities.

From a great number of similar calculations of the optimum it appears that the advantage of multistage selection lies in the fact that a great many individuals can be entered during the first stage and that right up to the last step an adequate degree of accuracy can be attained. Also, the optima lie on a very slightly curved line, so that the selection tests can be located over a relatively wide range. This goes far towards meeting the requirements of the practical breeder.

To ensure the greatest possible genetic gain, the following points must be observed in applying multistage selection:

- At the first stage the number of individuals must be as high as possible. This involves keeping the costs per individual to a minimum.
- The earlier the stage of selection, the smaller the optimal selected fraction, i.e. selection must be most intense during the first stage. According to Finney's selection rule, $\alpha_1 = \alpha_2 = \ldots = \alpha_k = \sqrt[k]{N_{k+1}/N_1}$, i.e. at each step the same fraction is selected. An optimum result would be attained if these values were kept somewhat lower in the first stages and somewhat higher at the last stage.

These principles are applicable not only to the variety testing phase but also to advanced generations of crosses.

At each step it becomes more expensive to record observations; hence the rules of multistage selection are also applied to the scoring of characters. At the first stage, selection is for the best genotype as opposed to selection for certain characters. In this way, selection among hundreds or even thousands of genotypes is feasible, and this is what is done for example in selecting among potato seedlings, S_0 plants of maize or F_2 ears of cereal species. Genotypes lacking a desired character will often be eliminated early in the next generation. The fact that a group of characters is recorded as a whole instead of many single measurements being made, makes scoring economically more attractive.

The later the selection stage, the less satisfactory a simplified scoring system will be and the greater will be the need to quantify the superiority of the better genotypes for single characters: yield and yield components, quality and quality components, early maturity, straw strength, resistance etc. must be indicated by figures. Data must be collected from several locations, years and replications. Only in this way is it possible to form a reliable decision concerning the introduction of a new variety, with or without recommendations for cultivation.

From the viewpoint of selection response, cases in which genotypes can be selected on the strength of their expected performance are particularly advantageous. For instance, in autogamous crop species, crosses can be made between parents that have already shown good performance for the characters desired. Similarly, in breeding double hybrids, estimates of performance can be made on the basis of the results obtained from single hybrids of the parental combinations. For such predictions, epistatic gene action is mostly left out of consideration, for to take this into account would often require additional estimations at considerable cost.

The breeder faces many questions with regard to (1) the choice of initial material, (2) the optimal size for an S_0 or F_2 generation, depending on the expected mean value and genetic variance of the parental material, (3) the heritability of the desired characters, (4) existing genetic correlations etc. All these can have a bearing on the kind and size of the initial populations to be used.

A COMPREHENSIVE INFORMATION HANDLING SYSTEM

The collection and evaluation of data on newly developed strains involve testing in replicated trials laid out over a number of years and locations. The number of experimental strains produced by the breeder can run into thousands, but the time available for the evaluation of trial data, between harvest and the next sowing, is often short and imposes a severe limitation on the amount of data that can be handled. The use of the computer enables the breeder to handle extensive data more accurately and more rapidly than would otherwise be possible. Indeed, without a suitable electronic processing unit, it would be impossible to carry out the large breeding programmes now in hand in a number of crops. The system used by Van der Have will be briefly described below.

Trial lay-out

A number of experimental designs with varying randomization, number of entries, replications and lay-outs are prepared and stored in the computer, each with a catalogue number. The designs stored are randomized block, incomplete block (balanced or partially balanced), latin square, single replication trial with two standards in blocks of 12 entries, and special treatments such as a main plot with nitrogen application as subplot.

When the breeder knows the kind of materials to be tested, the number of entries and the place, a field lay-out is prepared manually (Fig. 4.1). Each trial is given a number, for administrative purpose, the first cipher being the crop number and the last the year index.

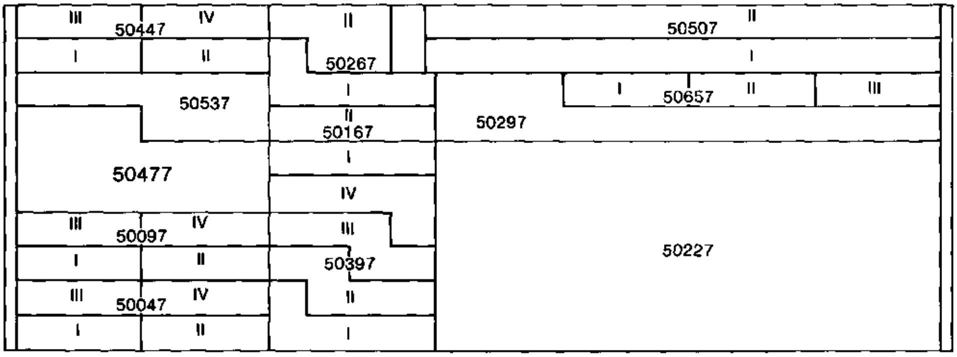


Fig. 4.1. Trial field lay-out. General view. Arabic numerals are trial numbers. Roman numerals are replicates.

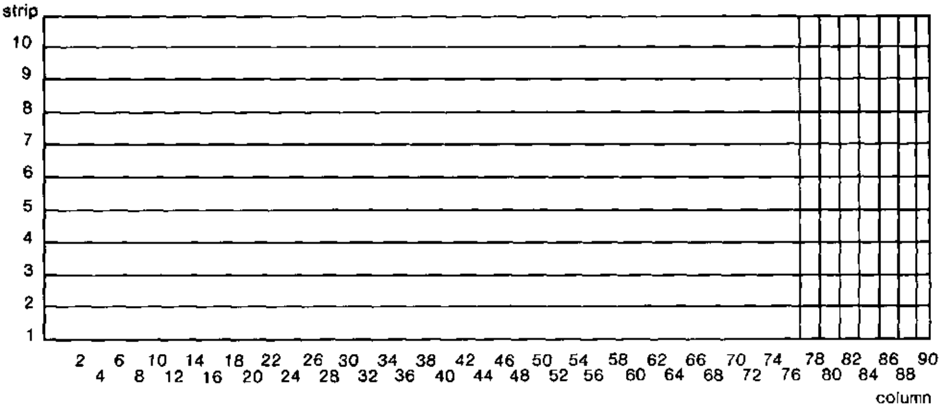


Fig. 4.2. Trial field lay-out. Detailed partitioning of the field. Each plot is identified by its strip number and column number.

Production of documents

The field lay-out gives the trial number, appropriate catalogue number, number of plots per trial, number of replications, number of labels per plot, and first and last column per strip (Fig. 4.2). With this information, the appropriate catalogue number is retrieved from the computer, and using this the seed list, self-sticking labels, the trial survey, the field book and the 'punch' document are produced (Fig. 4.3).

– Seed list. This is a working list used for the manual preparation of the seed samples

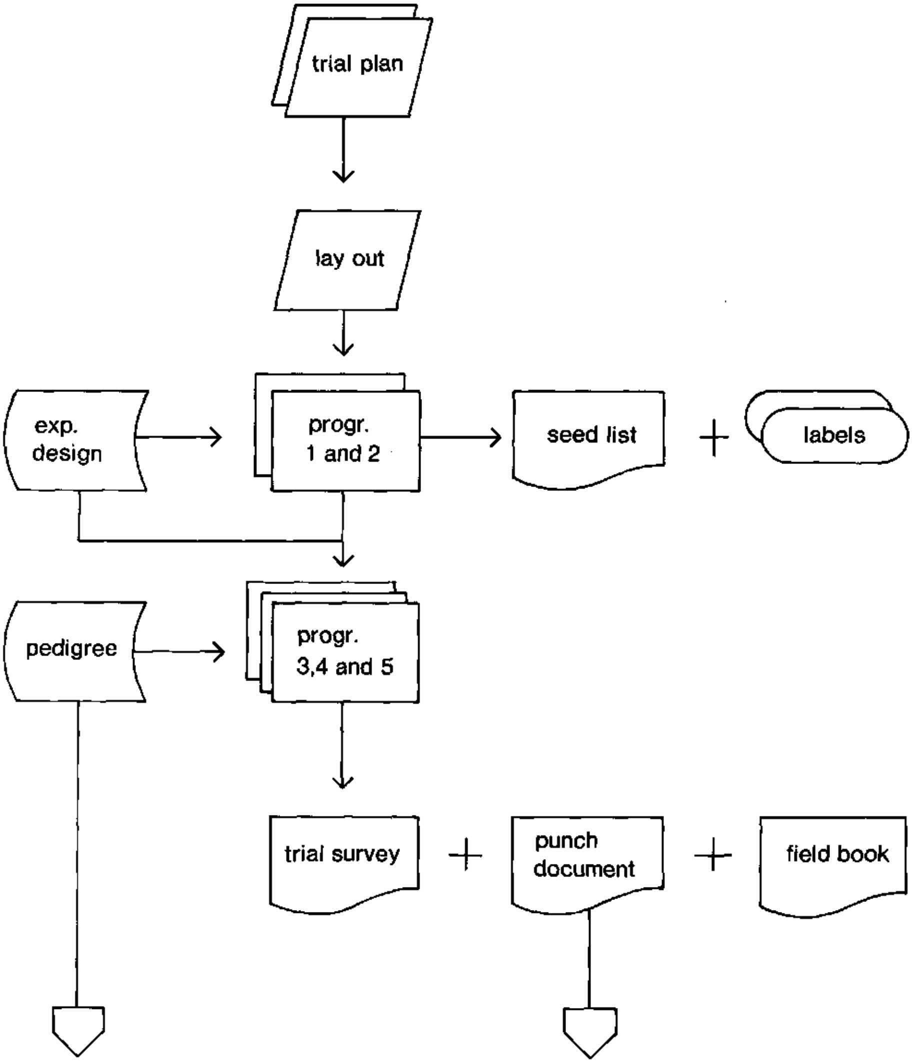


Fig. 4.3. Flow chart of the production of documents.

per plot to be drilled in the trial. The first column in the list is the entry number, followed by the strip-column numbers indicating where the entry is sown: there will be as many strip-column numbers as there are numbers of replications. During the preparation of the seed, the seed identification of each entry will be added to the list by hand.

– Self-sticking labels. Each label contains the entry number, strip-column numbers and the trial number. There are as many labels as there are bags needed per plot and this depends upon the sowing machine, whether 2-row, 4-row etc. The labels are fixed by machine on to the seed bags, appropriate bag sizes being used for each particular crop. The labels are in order of entry and plot, and the bags when filled are sorted according to strip-column number. This minimizes errors in filling and in sowing.

After sowing, each plot is given a number which will serve as identification until harvest. The pedigrees and seed-lot numbers are manually prepared and punched on cards or recorded on diskettes. The following documents are then printed:

– Trial survey. This gives a convenient and compact inventory of the complete material under test. It tabulates, per entry, the plot numbers which correspond to the number of replications and the seed-lot number and pedigree or variety name.

– Field book. In the field book, plot number and pedigrees are listed according to position in the field. It contains appropriate headings for the characters to be observed and blanks for written comments. The characteristics are entered in quantified form.

– 'Punch' document. All trial observations which are not automatically recorded are written on this document, from which they will be transferred to cards or diskettes. It contains the entry number, plot number and block number and the appropriate headings for the observations made per crop.

Data collection

Almost all observations are quantified to give scores on a scale of 1-9 or 1-5, or actual measurements. For purposes of uniformity, descriptions of the methods of scoring or measurement used for each character are available for consultation. Most of the observations for maize and cereals are made in the field and handwritten in the field book and then transferred to the punch document, while for sugar beet trials, many of the data are determined in the laboratory and the process is fully automated. The samples from sugar beet trials are identified in the laboratory by plot number on an optical reader card, and the root weights (gross and net) and the chemical analysis data (sugar content, potassium, sodium and nitrogen) are automatically registered on paper tape. Photographs of various steps in production of documents and data collection are given in Fig. 4.4.

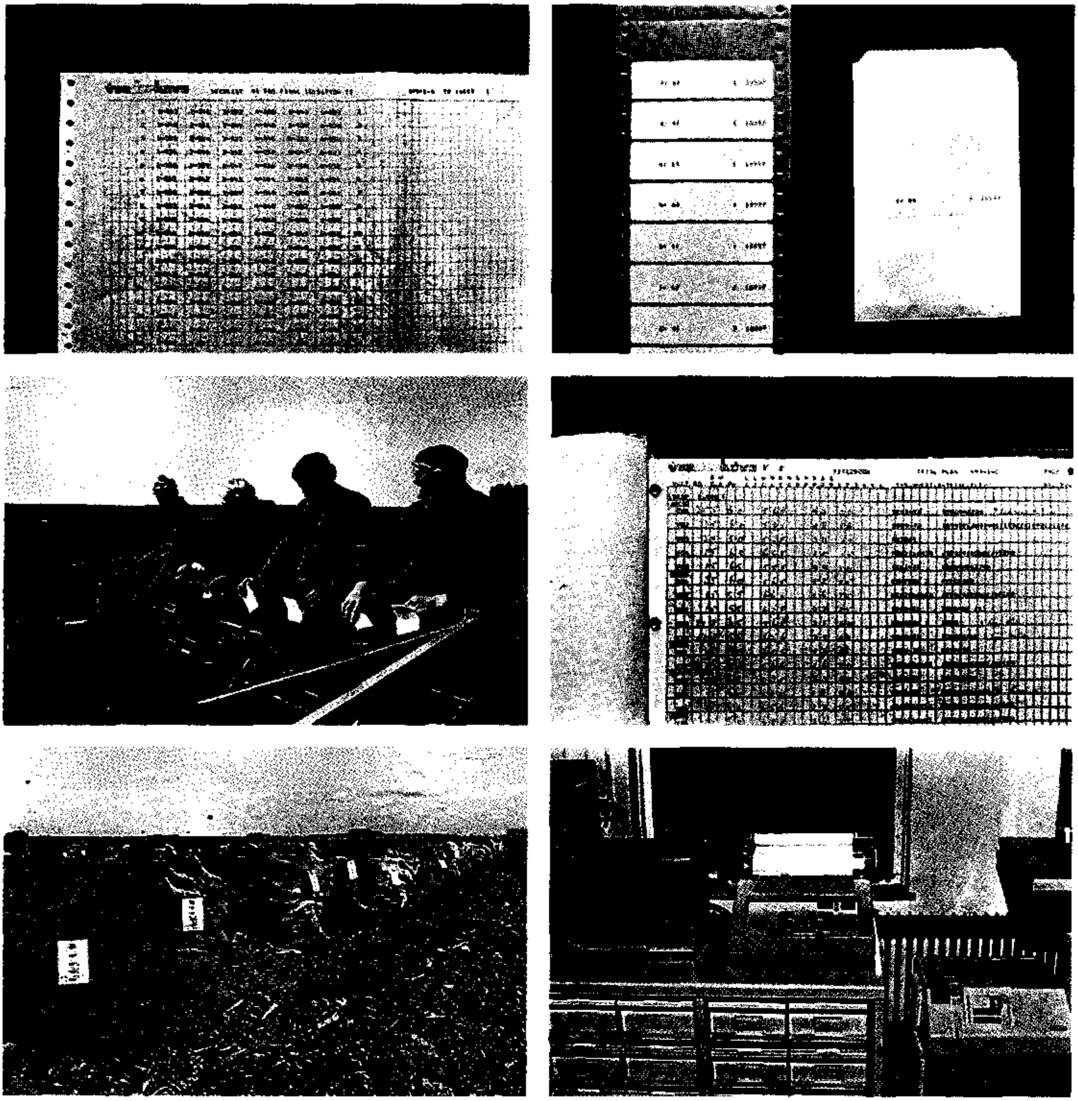


Fig. 4.4.

a. Top left – Seed list showing object numbers and corresponding plot numbers.

b. Top right – Self-sticking labels with object number and plot number (strip and column).

c. Centre left – Bags of seed in sowing equipment (Øyjord).

d. Centre right – Field book containing field observations.

e. Bottom left – Harvested sugar beets in bags showing field number suitable for optical reader.

f. Bottom right – Recording of chemical analysis on printer and on tape.

(Photographs: M. de Goffau).

Data processing

The field observations on the punch document are transferred to cards or diskettes. Punching and mechanical errors are checked through a CHECK program and corrected before any statistical analysis is performed. The steps in the data processing are shown in Fig. 4.5. A precalculation program (pre-cal) for every crop is available for transforming the raw data (e.g. yield per plot to dt/ha, root yield and sugar content to sugar yield etc.) and for testing the plausibility of the data. Analysis of variance per trial is processed by means of an appropriate computer program. The results are presented in a manner convenient for the breeder, the individual trial results being given together with an analysis of variance table and a table of means of the characters observed. A maximum of 20 characters are included in the table, the means being expressed relative either to the trial mean or to the mean of standards or in absolute values. Each line in the table contains entry number, pedigree and variety name and the 20 characters. This facilitates study of the performance of each variety or line and comparison between them. A computer program summarizes results from similar trials in different locations to give the mean performanc of a variety or line over a number of places. Results over years are summarized in the same way. The calculation of the mean performance of each variety over locations and/or years is based on the principle described by Cochran & Cox (1957). The means per variety are weighted means based on the standard deviation of the trials, with the most reliable trials having the greatest effect on the means.

The procedures described above are the normal routine. In addition to these, depending upon the need for further information, there are special programs for the analysis of regression correlation, multiple regression and genotype-environment interaction, based on Finlay & Wilkinson (1963) and Eberhart & Russell (1966). The general and specific combining ability programs are used to analyse the results of diallel and partial diallel crossing systems in hybrid crops. With a comprehensive information handling system of this kind, large populations can be screened for many characters, and efficiency in selection will be increased without increasing manual labour.

MALE STERILITY FOR HYBRID PRODUCTION

Introduction

When in 1880 Beal published his startling results of crosses between maize populations from distant locations, he could hardly have realized that he was initiating a development so far unmatched in the history of plant breeding. It had already been observed by Koelreuter (publications 1761/1766), Darwin and other early scientists that in outbreeding crops crossing gave better results than selfing. But after Beal's publication the knowledge of this finding was put to more direct use. Large-scale investigations in maize revealed the deleterious effects of inbreeding, the most strik-

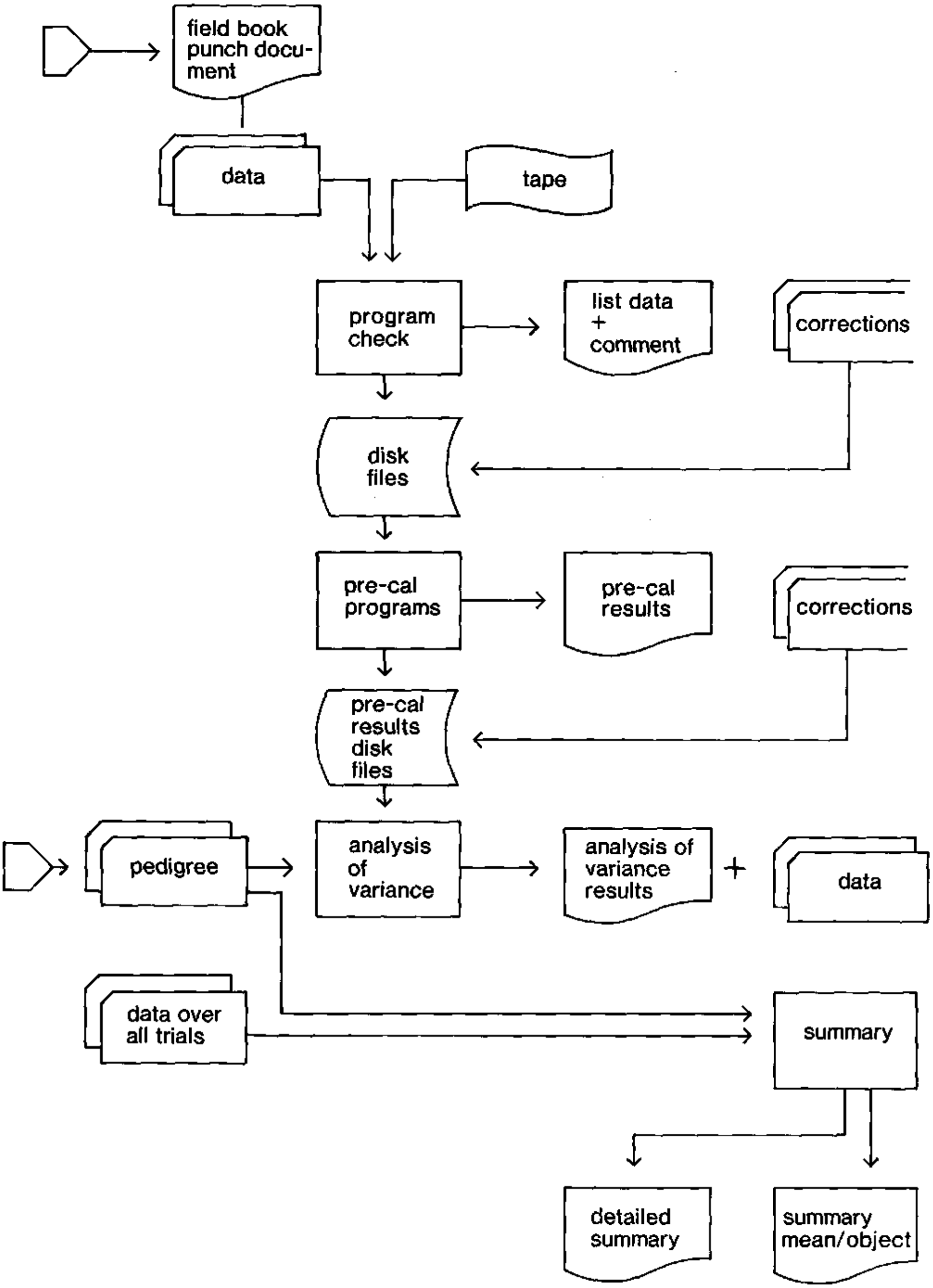


Fig. 4.5. Flow chart of data processing.

ing of these being reduced productivity and decline in vigour. On the other hand, it was noticed that crossing particular inbred lines resulted in progeny far superior to the parents in vigour and many other characters. This superiority of the F_1 or hybrid offspring was called hybrid vigour or heterosis. For a long time the use of heterosis was confined to maize, but after the discovery of mechanisms that enable the breeder to perform crosses between inbred lines in other crops, hybrid breeding underwent rapid evolution. Today hybrid varieties of many crops are grown commercially, including allogamous and autogamous crops, field crops and vegetables, and ornamentals as well as fruit crops.

The production of hybrid varieties in maize was largely facilitated by the occurrence of male and female flowers in separate inflorescences. To achieve hybridization, alternating rows of seed lines and pollinator lines were planted. The seed lines were detasselled before they shed their pollen and were then left to be pollinated by the paternal lines. In a crop like sorghum, however, with its countless, tiny, bisexual flowers grouped in one big inflorescence, emasculation caused enormous problems. Emasculation by hand with tweezers is an extremely laborious and time-consuming job; moreover, seed set is often low as a result of mechanical damage to the ovaries. Alternative methods of emasculation, like removal of the anthers by vacuum suction or killing the pollen grains with hot-water treatments, have been of some use, but in most cases they do not appear to be sufficiently reliable.

Attention was accordingly directed to processes in the plant which reduce or prevent the formation of male sex organs or microspores. In the sections that follow, the origin of male sterility and its utilization in hybrid breeding will be treated in detail.

The spectacular spread of hybrid crops since the early fifties is mainly due to the following advantages of hybrid varieties:

- Yields are high as a result of hybrid vigour.
- Desirable dominant characters are readily combined.
- Crop development and the harvested product are both uniform, owing to genetic homogeneity.
- The breeder is protected against fraudulent use of his breeding products (of importance especially in countries without breeders' rights).

Hybrids also have a number of disadvantages:

- Extensive use of a single cytoplasmic source in cross-pollinated species may result in increased vulnerability to epidemic diseases and pests.
- Hybrid seed is comparatively expensive.
- Farmers are forced to buy new sowing material each season.

Before considering the possibilities and implications of hybrid production on the basis of male sterility, we may state the requirements which hybrids in general must meet:

- They should show heterosis for yield and/or other desirable characteristics. To cover the extra expenses connected with the production of hybrid seed, the yield must be substantially higher than that of standard varieties.

– For a maximum yield of seed or fruit the ability to produce pollen must be optimal. Crops grown for their vegetative parts (beets, vegetables, ornamentals) do not have to meet this requirement.

– Seed production must be economic. The need to compensate the higher cost of hybrid seed by a gain in yield for the farmer sets a ceiling on the seed production costs. In some species this has led to the development of three-way or double-cross hybrids instead of single crosses, in order to eliminate the inbreeding depression of the parents in the certified seed production blocks. The elimination of inbreeding depression apparently compensates for the drawbacks of double crosses (loss of uniformity, reduced hybrid vigour, need for complex line combinations). In a number of crops, such as barley, poor pollen dispersal by the male parent and poor pollen interception by the stigmas of the female parent are a source of difficulty.

Definition and classification

Male sterility can be defined as the incapacity of plants to produce or to release functional pollen. Male sterility may result from total absence of male sex organs, which is the normal condition of female plants in dioecious species and of female flowers in monoecious species, but which , as an anomaly, can also be observed in hermaphrodite species. In other cases plants are seen in which the anthers develop normally, but in which irregularities in the development of the microspores cause abortion of the pollen grains. This form of nonfunctioning of the male sex is called pollen sterility. It is met with, in different frequencies, in many plant species. Pollen sterility sometimes occurs spontaneously under extreme environmental conditions. It can also be induced by certain chemicals (cf. 'Chemical induction of male sterility', p. 131). However, it is commonly controlled by hereditary factors, in which case there are three possible modes of control:

– Pollen sterility is governed by one or occasionally more genes: genetic or genic male sterility.

– Pollen sterility is brought about by extrachromosomal hereditary particles: cytoplasmic male sterility.

– Pollen sterility results from the concerted action of both extrachromosomal factors and genes: cytoplasmic/gen(et)ic male sterility.

The cases of male sterility just mentioned are designated true male sterility. A last and comparatively rare type of male sterility is seen, for instance, in tomato. Here normal viable pollen is formed but the pollen is not released because of a defect in the dehiscence mechanism of the anther. This phenomenon is called functional male sterility.

Monoecy

Monoecious plants are characterized by the presence of two types of flower, namely male (stamens present, no pistil) and female (pistil present, no stamens). In some crops these two types develop successively, as in cucurbits. In other crops both flower types appear simultaneously and are arranged in separate inflorescences. Maize, with its tassels and ears, is a classic example of this category.

Monoecious crops of the last type are suitable for hybrid breeding. Inbreeding is easily achieved by repeated pollination of stigmas by the male flowers of the same plant. The same method is applied in the maintenance and multiplication of the inbred lines to be used as parents. In the crossing blocks maternal and paternal lines are sown in separate rows. The male flowers or inflorescences of the seed lines are then removed and pollination and fertilization by the pollinator rows takes place.

Despite its simplicity, the procedure described is far from perfect. Screening the seed rows for male flowers is a tedious job and there is always a chance that some flowers will be overlooked. Most of the difficulties would be overcome if plants of a monoecious crop could be transformed into completely female plants. If the female character were then introduced into the breeding stock, the female lines produced could serve as female parents in a hybrid programme. This is in fact what has been done in parthenocarpic salad cucumber in several west European countries.

Several investigators have made extensive studies of the inheritance of sex in cucumber (Shiffriss et al., 1964; Kubicki, 1972; Galun, 1973). Treatment with gibberellins or silver nitrate (de Ponti & Kho, 1977) is able to bring about a temporary reversal from female to male sex. By treating genetically female cucumber plants at the right stage of development, a number of viable pollen-producing flowers are induced, with the result that the plants can be propagated simply by selfing or sibbing. All offspring will be completely gynoecious again.

The final step is the production of commercial hybrid seed. The use of a monoecious line as male parent would result in an incompletely female hybrid which would be liable to form a certain amount of seed and hence to produce irregularly shaped fruits. A better method is to start from two gynoecious lines, one of which is forced to produce pollen by means of high doses of gibberellins or silver nitrate. An alternative approach may be to utilize a monoecious pollinator and to furnish both parental lines with modifying genes that promote femaleness. The hybrid will then be heterozygous for sex but will have a strong tendency to femaleness as a result of the action of the modifiers.

The application of sex reversal in hybrid production is also practised in castor-oil beans (Zimmerman & Smith, 1966). It is worth mentioning that in maize, too, female and male plants may occur in addition to the normal monoecious types: these are the tassel-seed and silkless types.

Dioecy

In dioecious species male and female flowers or inflorescences occur on different plants. The sex ratio is genetically determined. Sex generally is under the control of one major gene pair: MM = female, Mm = male. Where specific sex chromosomes have been identified, female plants are denoted by XX and male plants by XY.

Dioecy is the normal condition of a limited number of crop plants, e.g. asparagus, spinach, hops, hemp, date palm and papaya.

The classic hybridization procedure in a dioecious crop includes the following steps.

– Development of inbreds. Since selfing is impossible owing to the unisexual nature of individual plants, inbreeding is effected by sibbing within a progeny.

– Maintenance and multiplication of inbreds. This is effected by sib crossing male and female plants within an inbred.

– Hybrid seed production. Inbreds are planted in alternating rows in an experimentally determined ratio. The seed-parent rows have to be rogued of male plants as soon as differentiation between male and female plants is possible. After flowering the pollinator rows are discarded and the seed parents are harvested at ripening (Webb & Thomas, 1976). This method is very laborious.

Many investigators have sought suitable alternative procedures. Attention has so far been devoted mainly to the development of pure male or female lines from intersexual plants. This can also be of importance as a breeding aim in itself, e.g. pure female varieties in papaya, pure male varieties in asparagus (male plants having a better yield).

Intersexuality includes all transitional forms between pure female and pure male individuals. Intersexuals have been shown to occur in most dioecious crops, particularly in asparagus, spinach and hemp. The character is believed to be controlled by modifier genes, which occur along with the major sex genes *(M/m)* or the sex chromosomes(X/Y).

Several hypotheses have been developed with respect to the number and action of genes governing intersexuality in asparagus (Franken, 1969; Wricke, 1973) and spinach (Bemis & Wilson, 1953; Janick & Stevenson, 1955). In spinach, for example there is a gradual transition from pure androecy to complete gynoecy accompanied by strong genotype-environment interactions. This circumstance largely prevents genetic analysis and prohibits the decisive classification of plants into sex categories. If a slight amount of contamination is accepted, hybrids can also be made using predominantly female seed lines, which can be maintained rather easily.

In asparagus, haploids (X) are occasionally found in twin seeds and will give rise on diploidization to completely homozygous females. It may prove possible to derive male inbreds by repeated back crossing to such homozygous female plants. Haploid males (Y) and females (X) can be raised by anther culture and these will be YY and XX respectively after diploidization. Hybridization between XX and YY lines with good combining ability would furnish a completely male (XY) heterotic offspring.

We have not yet considered chemical treatment. It is a remarkable fact that chemical compounds which strongly influence sex expression in both monoecious and male-sterile bisexual crops apparently fail to do so when applied to dioecious crops. The few recorded attempts to induce sex conversion with gibberellins and other chemicals have all had negative results, except in hemp (Mohan Ram & Jaiswal, 1972a, 1972b).

Genetic male sterility

In genetic or genic male sterility, pollen abortion is controlled by chromosomal factors. It is found in several crops, e.g. tomato, barley, sorghum and *Phaseolus* (Jain, 1959). Except in a few instances, genetic male sterility is governed by one recessive gene (*ms*). Some crops (barley, tomato) possess many *ms* loci.

The recessive nature of the *ms* gene is a serious drawback to its practical exploitation. The propagation of parental lines and production of hybrid seed using this kind of sterility is visualized in Fig. 4.6. Removal of the fertile plants in the crossing block necessitates a large labour force. Besides this, twice as many plants have to be raised as are strictly needed for seed production. The most troublesome factor, however, is that selection against fertile plants in the mother line can only be carried out at a very late stage of development, during or just before flowering. Consequently, if any fertile plants flower early or escape notice, there is a considerable risk that some of the male-steriles will be fertilized by them. This will result in reduced heterosis and loss of uniformity of the commercial seed.

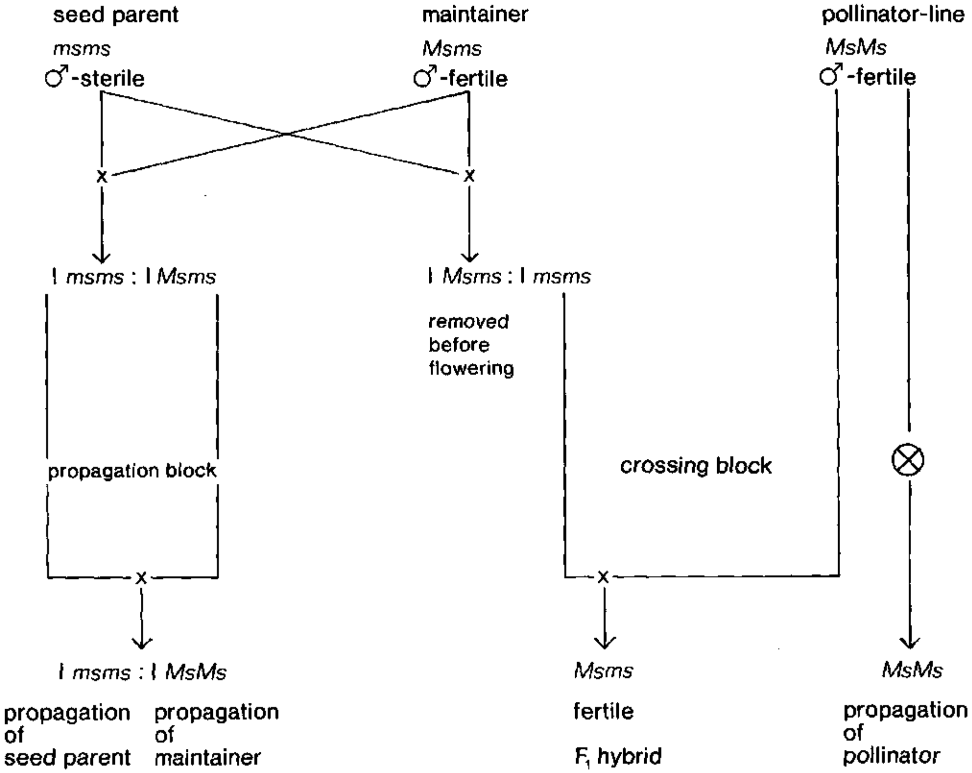


Fig. 4.6. Propagation of parental lines and production of hybrid seed with the aid of monofactorially inherited genic male sterility. Crossing: ×. Selfing: ⊗

In several crops procedures have been developed which enable early screening of the mother lines for fertile individuals. Most of these methods are based on pleiotropic action of the *ms* alleles or on marker genes closely linked to the *Ms/ms* locus. A case of linkage between *ms* and marker genes is mentioned in the contribution on sunflower (p. 220).

The most elaborate procedure for using genetic male sterility is that developed by Ramage (1965, 1975) in barley. The essential feature of this so-called 'balanced tertiary trisomic' system or BTT system is the presence of an extra chromosome composed of parts of two nonhomologous chromosomes. The extra chromosome contains the *Ms* allele, whereas the normal homologous chromosomes contain *ms* genes. The supernumerary chromosome is not transmitted by the pollen grains. Consequently diploid progeny of a trisomic are always sterile *(msms)*, whereas trisomic descendants are fertile *(Msmsms)*. Since some selection against trisomics also takes place in the egg cell, the selfed progeny of a trisomic plant consist of about 70% *msms* individuals and 30% *Msmsms* types. The two homologues of the second chromosome included in the extra chromosome carry the recessive allele of a marker gene (e.g. *r* = green stem), whereas the extra chromosome possesses the matching allele *R* (red stem). Consequently, sterile and fertile segregates can be distinguished easily.

The BTT system, ingenious though it is, has obvious shortcomings. Apart from the complexity of the procedure, BTT plants are often weak, and have reduced female fertility and low pollen production. This last fact aggravates the problem of poor pollen dispersal which in any case characterizes this self-pollinated crop.

In conclusion, it can be stated that, as long as procedures are lacking which enable early and reliable screening of male-steriles without affecting the vitality of the plants concerned, genic male sterility will be of only limited value as a tool for hybrid seed production. Crops which produce large quantities of seeds per fruit and which command a high seed price (e.g. tomato) are a possible exception.

Cytoplasmic and cytoplasmic/genic male sterility

As early as 1908 the German biologist Correns (1908), one of the rediscoverers of the Mendelian laws, found that in crosses between female and hermaphrodite plants of summer savory *(Satureja hortensis)* all progeny showed the sex expression of the (female) maternal parent. To explain this result, von Wettstein (1924) advanced the hypothesis that the development of anthers in the female is suppressed by a specific condition of the cytoplasm. Later, more cases were found in which dysfunction of the anthers or abortion of the developing microspores was the result of the action of so-called sterilizing cytoplasm. Such cases of male sterility are denoted by the term cytoplasmic male sterility (CMS). Sterilizing cytoplasm is generally indicated as (*S*) in distinction to the normal fertilizing (*F*) or (*N*) cytoplasm. Crossing between a CMS plant and a male-fertile partner results in a completely male-sterile progeny, since the plasmagenes responsible for sterility are transferred from the mother to all the offspring via the egg cells: the paternal parent only provides a naked nucleus and does not affect the cytoplasmic constitution.

Cytoplasmic male sterility may occur spontaneously. This is seen for example in beet, onion, maize, carrot and red pepper *(Capsicum)*. The frequency of occurrence of CMS mutants varies between crops and even between varieties within the same crop. Thus Owen (1945) noticed 2% CMS plants in the sugar beet variety US1; in a selection derived from this variety there were 6%. CMS mutants have also been observed in west European and Polish sugar and fodder beets, although in much lower frequencies (0.01-0.03%). It should be realized that these forms of cytoplasmic male sterility are not necessarily identical. It is a matter of dispute whether the (*S*)-cytoplasms in European and American onions are identical or not. In maize, the crop investigated in most detail, over 30 different sources of CMS have been detected since the publication of Rhoades' (1933) classical article on cytoplasmic male sterility. Most of these, however, have been shown to be identical with one of the three major types C, S or T.

Most CMS sources result from crosses between distantly related plants. These crosses may be intraspecific (sorghum, flax), interspecific *(Capsicum, Brassica, Nicotiana, Oryza, Phaseolus, Triticum)* or even intergeneric *(Aegilops* spp. × *Triticum aestivum)*. In all these cases the genomes of the 'wild' CMS parent are replaced by those of the cultivated crop by repeated back crossing. The final product has the genotype of a breeding line or commercial variety embedded in the sterilizing cytoplasm. Recent compilations of sources of CMS have been published by Krupnov (1971) and Laser & Lersten (1972).

Earlier it was shown that the offspring of a cytoplasmically male-sterile plant are identical to the maternal parent with respect to this character. In many cases of CMS, however, it is found that particular crosses result in fertile progeny. The explanation of this deviating behaviour is that some plants carry genes which counteract the sterilizing action of the cytoplasm. Such genes are called 'restorer genes' or *Rf* genes. This implies that sterility actually results from the concerted action of sterilizing cytoplasm and nonrestorer genes *(rf)*. Strictly speaking, the term cytoplasmic/genic male sterility is applicable to such situations. In practice, however, the term cytoplasmic male sterility, and its abbreviation CMS, is commonly used. Examples are given in the contributions on sugar beet (pp. 203-215) and sunflower (pp. 216-223). As the great majority of hybrids are based on CMS (the abbreviation CMS being a applied to all cases involving sterilizing cytoplasm) we will discuss the implications of this system at greater length.

The basic method of hybrid production based on CMS includes the following steps:

- introduction of the CMS character into the breeding stock used as mother lines,
- maintenance of the CMS line and its fertile isogenic counterpart,
- introduction of *Rf* genes into the pollinator lines,
- production of hybrid seed by alternating male-sterile seed rows and male-fertile pollinator rows.

The CMS character is introduced by repeated back crossing with the breeding material as the recurrent parent, combined with selection for paternal phenotypes. The resulting line (A-line) will be isogenic to the male parent except for male sterility. It can easily be maintained by crossing it to its fertile counterpart (B-line), which is propagated by selfing. In sugar beet breeding the term O-type is in use instead of B-line.

Rf genes are introduced into the paternal line by crossing the paternal line to a restorer source, followed by repeated back crossing to the inbred line. To identify the restored plants back-cross progenies must be test crossed to a male-sterile line. The restorer genes are introduced in order to ensure the pollen fertility of the hybrid plants. Fertile hybrids are essential in crops like maize and wheat from which the reproductive parts are harvested. But in crops which are grown for their vegetative parts (onion, beet, grasses), male fertility of the hybrid crop is of no value, so that there is no need for restorer genes. The procedure of hybrid seed production of a seed crop on the basis of CMS is presented in Fig. 4.7.

In actual practice the production of hybrid seed on a CMS basis is often rather complicated for the following reasons:

- Male sterility must be stable. Instability would lead to partial self fertilization or intercrossing of the mother line, giving rise to heterogeneity and lower yield of the commercial seed.
- Fertility restoration is generally under the control of more than one gene. Consequently more than one *Rf* gene must be introduced into the breeding material.
- The expression of *Rf* genes is affected by the genetic background. This means that

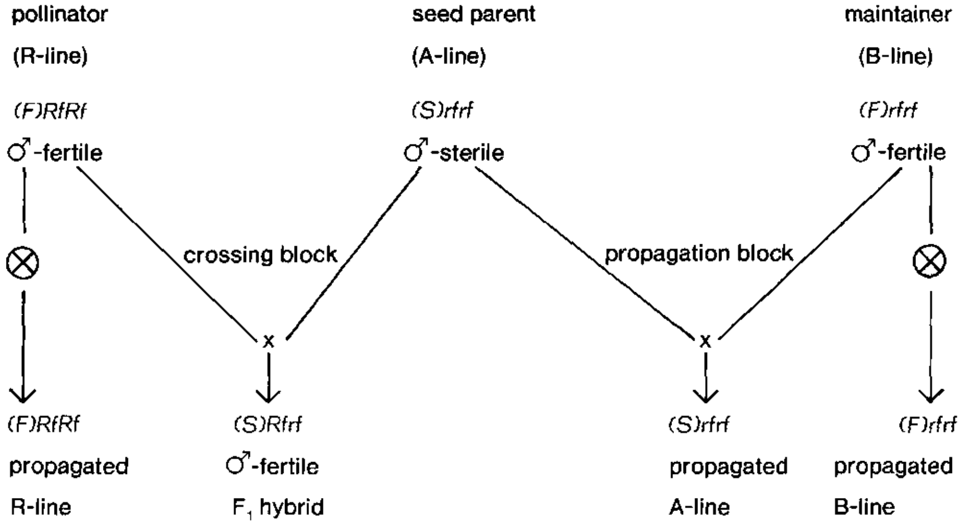


Fig. 4.7. Hybrid seed production based on cytoplasmic/genic male sterility in a food or seed-producing crop. Crossing: ×. Selfing: ⊗

after the introduction of a restorer gene into a particular inbred, the *Rf* gene may fail to be expressed or it may show incomplete activity.

– The most embarrassing factor is the susceptibility of restorer genes to environmental influences. The fertility expression of restored wheat plants has been shown to vary with day length, temperature, relative humidity, light intensity and plant density. In the garden petunia it has been observed that both low and high temperatures adversely affect pollen development (van Marrewijk, 1969). Indications of fertility shifts occurring under the influence of evironmental conditions are found in many other plants. It appears to be the heterozygous restored plants in particular that are sensitive to changes. This constitutes a threat to CMS hybrid production, as hybrids are heterozygous for the restorer character.

– In some crops, abnormalities in growth, development or plant morphology are observed in connection with the introduction of (*S*) cytoplasm or *Rf* genes. Some CMS petunia varieties for example exhibit flower-bud abortion ('blindness') and erect instead of bushy plant habit. A dramatic example of a CMS-associated character is found in the susceptibility of maize with Texas cytoplasm to southern corn leaf blight in the US Corn Belt in 1970. Total yield losses were estimated to run as high as 15% in that year (p. 202).

Male sex suppression and sex reversal in hermaphrodite plants

In several species that are normaly bisexual, mutants are found with reduced stamens or even without stamens. Stamenless mutants have been recorded for various crops, including tomato, maize, sorghum and tobacco. In other crops mutants are observed in which the androecium is converted into petals (all double-flowering ornamental crops), carpels (e.g. carrot, cabbage) or pistils (e.g. maize, papaya, carrot, primrose). The last phenomenon, known as pistillody, is a case of sex reversal. Interspecific hybridization may also sometimes result in suppression of the male sex, ranging from atrophy of the anthers *(Solanum rybinii* × *S. chacoense)* to a reduction of the androecium to staminodes or rudimentary organs (peony hybrids, *Streptocarpus wendlandii* × *S.-rexii)*.

Several forms of reduced maleness are utilized in the production of F_1 hybrids in ornamentals. Partial restoration of maleness in petaloid carnation, achieved by growing the plants under poor nutritional conditions, enabled Reimann-Philipp (1976) to create acceptable hybrids. The 'Cinderella' mutant of *Begonia semperflorens* (Reimann-Philipp & Seidel, 1963), with its sterile, misshapen anthers, and the stamenless 'Femina' type of *Tagetes* (Bolz, 1961) also appear well suited to the production of hybrid varieties. Both mutants are recessive. This means that they have to be propagated by back crossing to the corresponding heterozygous dominant form and that the male segregates of the seed line have to be eliminated prior to crossing with the pollinator line. The offspring will display the normal fertile type of inflorescence. In major crops, plant types exhibiting sex transformations of this kind have not yet been applied in hybrid breeding.

Functional male sterility

Functional male sterility differs from all other forms of sterility in that plants produce normal amounts of viable pollen. Owing to a defective dehiscence mechanism the anthers do not open and pollen is not shed.

The presence of viable pollen makes functional male sterility very attractive for hybrid breeding. Inbreeding and line propagation can be performed by selfing of plants after opening the pollen sacs with the aid of tweezers. When using the functionally sterile parent as the seed line in the crossing block no further provision is needed to ensure an all-hybrid offspring. Unfortunately this attractive sterility mechanism only occurs in a limited number of crops. The crop which has been most investigated so far is tomato (Larson & Paur, 1948; Roever, 1948), but the character is also found in egg plant, cabbage and *Streptocarpus*.

The use of functional male sterility in tomato is limited by two factors:

- Nondehiscence is sensitive to environment. Depending on weather conditions, up to 50% self fertilization may thus occur in the seed lines.
- The stigmas of the tomato are hidden within a cone of connate stamens. Hence cross pollination is severely impeded. This problem can be by-passed, however, by the use of mutants with exserted stigmas.

Several tomato hybrids based on functional male sterility have been released in Bulgaria (Daskalov & Georgiev, 1976).

Chemical induction of male sterility

In the section on monoecy it was mentioned that gibberellins are able to induce sex reversal in gynoecious plants. Similarly, some restoration of fertility is observed after treating male-sterile barley plants with gibberellic acid (Kasembe, 1967). Surprisingly enough, in some other crops a reverse activity of gibberellic acid is observed, i.e. suppression of pollen development. Other chemical compounds also appear to have this pollen-killing effect. They are known collectively as gametocides.

Gametocides with an absolute effect are the golden dream of every breeder. They would make it possible to produce male-sterile versions of any breeding stock on demand without the need for a laborious and expensive back-cross programme. What is even more important, they would enable a hybrid to be commercialized in minimal time. With the present procedure of introducing male sterility into A-lines by back crossing, the breeder 'loses' about four years. Thus his hybrid combination of today has to compete with normal varieties which are perfected about four years later. Consequently he runs the risk of being late in the market. According to Chopra et al. (1960), a gametocide that can be used for the production of hybrid seed should fulfil the following criteria:

- The treatment should cause only pollen abortion and not affect ovule fertility.
- It should have no mutagenic effect.
- The method of application should be easy and economical.

Table 4.5. List of common gametocides and crops with positive response.

Chemical	Crops
Gibberellins (GA_3; GA_{4+7})	lettuce, onion, rice, maize, sunflower
Maleic hydrazide (MH)	wheat, tomato, onion
FW 450; Mendok (sodium 2,3-dichloroisobutyrate)	cotton, tomato, groundnut, sugar beet
Ethrel; Ethephon (2-chloroethanephosphonic acid)	wheat, rice, sugar beet

– The precise dosage when applied at a certain stage of growth in the life cycle of the plant should give consistent results, i.e. the effects should be reproducible.
– There should be no undue hazards either to man or plant.

Since these criteria were formulated, much experience with an increasing number of gametocide compounds has been gained. In Table 4.5 a compilation is given of widely used chemicals and the crops on which they are effective. Although progress has certainly been made in producing a reliable gametocide, so far no compound has been developed which meets all the requirements mentioned above. The shortcomings of present-day gametocides are the following:
– Pollen abortion is incomplete and erratic.
– Treatments are only effective for short periods and at particular stages in the development of the plant.
– Because of the short duration of the effect, treatments have to be repeated.
– Female fertility is adversely affected, resulting in comparatively low seed set.
– Harmful side effects are evoked, such as leaf deformation, stunting of the plant, or wilting.
– The high dosage, the many repetitions needed and the high cost make the treatments uneconomic.

Although gametocides are not yet suitable for large-scale application in hybrid seed production fields, they may be of value for the determination of specific combining ability between plants or lines in crops in which emasculation by hand is not feasible or is cumbersome. Fertility-restoring chemicals in the case of genically male-sterile plants (comparable to the gibberellins and $AgNO_3$ situation in cucumber) would also be attractive for hybrid breeding in other crops.

Prospects

Male sterility can be an aid in the production of hybrid seed. However, the many imperfections at present associated with it hamper its efficient use. These imperfections have been described in the foregoing sections. The more important impediments to an effective application of genic and cytoplasmic male sterility are the following:
– Sterility and restoration of fertility are sensitive to environmental conditions, which may cause a breakdown of either sterility or restored fertility at inconvenient

moments.

– The breeder is dependent on accidental sources of sterility, which can often only be incorporated in his breeding material by means of crosses.

Efficient use of male sterility is highly dependent on our ability to check the interaction between male sex expression and environmental conditions. To achieve this, direct research into the behaviour of male-sterile plants and plants with restored fertility under varying environments is necessary. The resulting knowledge would be of aid in choosing the right environments for line propagation and hybrid seed production.

In order to obtain futher sources of sterility, the breeder may try to induce male sterility by means of chemicals which suppress the development of the male sex organs or kill the microspores. But a great deal of research has still to be done on such sterility-inducing aids before it will be possible to predict and reproduce plant reactions while avoiding undesirable side effects. The question is, how far present chemicals meet the breeder's requirements, and this brings us to the core of the matter in so far as the practical value of male sterility is concerned. For male sterility is really only of practical value if it is available whenever the breeder requires it and if fertility can likewise be restored whenever required. Investigations should therefore be directed towards finding 'foolproof' male sterility inducing substances without undesirable side effects.

When such substances are available, there will be no need for (1) incorporating the male sterility character via crosses into A-lines, (2) concurrently maintaining a male-sterile A-line and its fertile isogenic maintainer line (B-line) or (3) introducing *Rf* genes into the pollinator line (C-line). To elucidate this, Fig. 4.8 shows the produc-

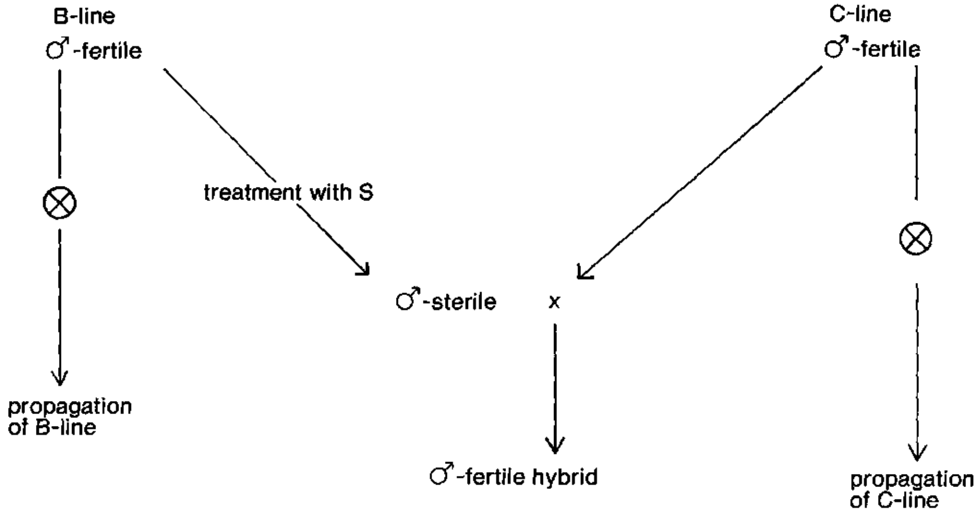


Fig. 4.8. Maintenance and production of hybrid seed with the male sterility inducing substance S. Crossing: × Selfing: ⊗

tion of hybrid commercial seed using a (hypothetical) male sterility inducing substance. Apart from the advantages already mentioned, the system illustrated has the invaluable benefit that the fertility of the hybrid remains stable, thus guaranteeing a good seed set.

Taking into account the great advantages, it is suprising that so little fundamental research is being done on the sterility-regulating substances. Rather than carrying out indiscrimate experiments with hormones and other chemicals to induce male sterility, research workers should try to unravel the chemical and physical background of the phenomenon of sterility.

The successive steps of such a study would be to determine:

1 the morphological, cytological and anatomical deviations occurring in and around the androecium,
2 the biochemical changes accompanying it,
3 the causes of these changes.

The first two points would give only preliminary information, but would provide a basis for the further study of the physiological processes that govern male sterility. Many authors have observed deviations in the development and chemical composition of the stamens in male-sterile plants. These deviations relate to the development of the tapetum (the cell layer investing the growing pollen cells and playing a role in the nutrition of these cells), the composition of free aminoacids and proteins, and the differences in enzyme activity in the anthers of male-sterile and fertile plants. Since certain of the deviations are apparently similar for diverse crops and for different types of sterility, there is a legitimate hope that one basic principle, perhaps with a number of variants, underlies all these phenomena. If such a basic principle is found, it may be possible to interfere in its action and thus work towards realizing the dream of every breeder: to have sterility 'on demand'.

INCOMPATIBILITY AS A TOOL IN PLANT BREEDING

Introduction

Incompatibility constitutes a widespread natural barrier against inbreeding in plants. Since it is based on the interaction of products from specific alleles at one or more incompatibility loci in the style and those from identical alleles in the pollen or sporophyte, it is expressed most commonly as self incompatibility, and rather less frequently as cross incompatibility within a species or between closely related species. Incompatibility is thus one of the outbreeding mechanisms of the plant kingdom.

The discovery of different incompatibility systems, and their genetical elucidation over the years (one-locus gametophytic in the 1920s, one-locus sporophytic in the late 1940s and two-locus gametophytic in the 1950s), excited much interest among breeders, owing to their potential as a new tool in breeding F_1 hybrids and synthetics (Pearson, 1932; Odland & Noll, 1950; Burton & Hart, 1967). The current application of the one-locus sporophytic system in cruciferous vegetables is the result of decades of breeding research. Studies on the application of this and other systems in other crops are now also in progress. In the present contribution various problems, results and approaches will be discussed.

One general problem arises from two basic requirements which strictly speaking are mutually exclusive. On the one hand, in order to breed F_1 hybrids, homozygous lines are required, and this means that repeated selfing of lines must be possible. On the other hand, if hybrid seed is to be produced from these lines in the field, the possibility of self and sib fertilization must be completely excluded. As with other problems in plant breeding, a compromise solution must be sought.

Production of inbred lines

Many devices have been reported for circumventing or overcoming self incompatibility in the development of inbred lines: bud pollination, high or low temperatures, high relative humidity, irradiation of styles, hormone treatment of pollen or pistils, increased CO_2 content, double pollination, use of pollen mixtures, treatment of stigmas with ether-soluble pollen-coat material, mechanical methods such as steel-brush pollination, electrically aided and thermally aided pollination, clipping of the styles and ovule pollination. However, none of these methods is generally applicable; their effect depends on the nature of the *S* alleles, the genetic background, the age and vigour of plant and flower, the type of crop and the incompatibility system. And in all cases of genetically controlled, environmentally induced or mechanically enforced pseudocompatibility there is the danger of unintentionally imposing selection for weak *S* alleles or for a genetic background favouring self-seed set. The production of agronomically promising lines which prove to be useless owing to weak *S* alleles or an unfavourable genetic background is to be avoided.

In recent literature various suggestions have been made for producing inbred lines more quickly, efficiently and safely. These suggestions will be critically discussed below.

Hermsen (1974) drew attention to the potentialities of monohaploids obtained through parthenogenesis or anther culture. The production and doubling of such monohaploids would enable completely homozygous lines to be produced in only two generations, with little risk of lowering the level of self incompatibility. However, the frequency of viable monohaploids is generally extremely low owing to inbreeding depression, lethal genes and other factors.

Litzow & Ascher (1977) pointed out the potential of interaction type V of the one-locus sporophytic system. This is a self-compatible interaction type, involving a reverse dominance relationship of *S* alleles in pollen and style. Their proposed scheme for the development of inbred lines is given in Fig. 4.9. Obvious advantages of the scheme are: no bud pollination is required; no selection for pseudocompatibility is involved; it provides an automatic test of the strength of the *S* alleles in each generation, because all plants have to be selfed in order to identify S_aS_b; tests for

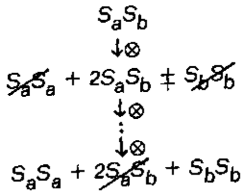


Fig. 4.9. Development of inbred lines using interaction type V. (from: Litzow & Ascher, 1977).

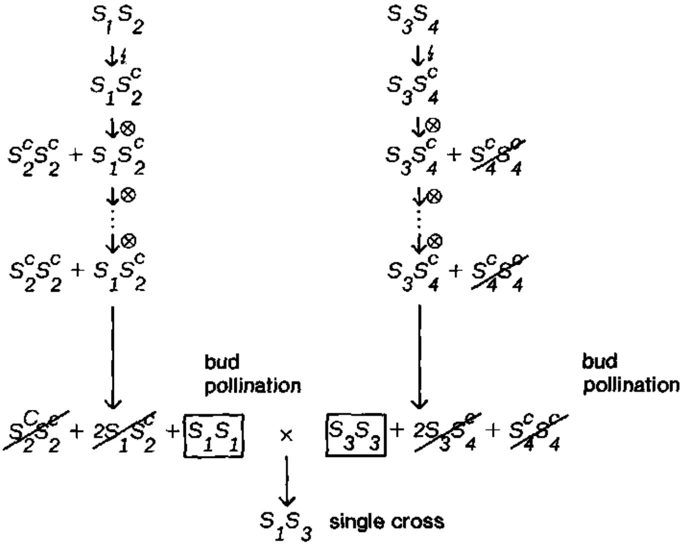


Fig. 4.10. Procedure for the production of self-incompatible inbred lines using permanent self-incompatibility mutations. Radiation: ⚡ . Self fertilization: ⊗. (from: van Gastel & de Nettancourt, 1975).

combining ability are possible in each generation; and inbreeding can be stopped at any time. Only the homozygous lines are self incompatible and suitable for use as parents of single crosses or as seed parents in three-way crosses. A disadvantage is that no double crosses can be made, because the singles are self compatible. However, the greatest drawback is that type V occurs so rarely, owing to the fact that natural selection (inbreeding depression after selfing) acts against it.

Van Gastel & de Nettancourt (1975) proposed a method for using permanent self-compatibility mutations for the production of self-incompatible inbred lines with a gametophytic system. Their proposal, which relies on induced mutations, is summarized in Fig. 4.10. Once the desired mutations have been obtained, time-saving is the obvious advantage, since only one bud pollination is needed. However, it is doubtful whether the method can be applied in breeding, for it may well prove both difficult and laborious to find the appropriate mutations. Furthermore, the method provides no opportunity for testing *S* alleles in the intermediate stages. In some crops self-compatibility alleles (S_f) or extremely weak *S* alleles have been found. These could be used in a breeding programme in the same way as self-compatibility alleles induced by irradiation.

Singles, doubles and compromises

Single-cross hybrids are usually more productive and uniform than doubles. Figures have been given by Nieuwhof (1968) for Brussels sprouts. But single-cross seed, being produced from generally weak inbred lines, is very expensive. Three-way hybrids provide one solution, but there are a number of other useful compromises. One approach is to stop inbreeding while the lines are still reasonably vigorous and when uniformity and hybrid vigour in the singles are at an acceptable level. A large stock of self seed from inbreds of this kind which show promise could be made in one generation and stored for use in future years (Haruta, personal communication, 1968; Fabig, 1973), in order to prevent further inbreeding depression.

Another practical approach to the production of near-isogenic lines is given in Fig. 4.11. The same procedure is applied to S_cS_d. The number of bud pollinations is optimal when the near-isogenic pairs of *S*-homozygous lines produce reasonably vigorous singles, while the doubles from these singles have an acceptable uniformity and hybrid vigour. It is apparent that this method would be even more efficient if interaction type V, self-compatibility mutations or S_f alleles could be included as described above.

The one-locus gametophytic system in red clover

Kendall & Taylor (1969), Duncan et al. (1973) and Anderson et al. (1974) studied the potential of the one-locus gametophytic system in *Trifolium pratense*. The observation that clones grown at about 40 °C produce 8-10% self seed can be made use of in inbreeding.

Because the individual plants are of little value in forage crops as compared with horticultural crops, the sophisticated and expensive methods used in breeding hybrid

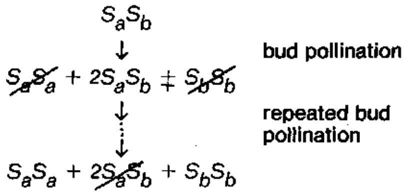


Fig. 4.11. Production of near-isogenic lines. (from: Nieuwhof, 1968).

varieties of cole crops (cabbage, cauliflower, Brussels sprouts etc.), for example, are not worthwhile in forage crops. For red clover the following method has been proposed:

- Superior I_1 plants with different *S* alleles and 8-10% pseudocompatibility at high temperatures are propagated vegetatively.
- The I_1 clones are grown in the field in a region with high temperatures for production of large quantities of I_2 seed.
- The I_2 plants are grown at normal temperatures in order to produce single-cross seed.
- Single-cross seed samples from various sources are mixed and the mixture is sown. In this way double-cross seed is obtained.

Self incompatibility in self-pollinated crops

Various methods of introducing self incompatibility into self-compatible crops are in use. Denna (1971) discusses the problem involved in attempts to introduce self incompatibility into tomato, lettuce and *Phaseolus* beans from related wild species. Martin (1968) has produced a self-incompatible counterpart of the tomato variety Tiny Tim. The three crops mentioned are insect pollinated, but do not produce nectar, so that natural pollination depends on pollen-collecting insects. Because such insects do not visit male-sterile flowers, a cytoplasmic male sterility (CMS) system with restorers is not feasible and it is necessary to use self incompatibility to replace expensive hand pollination. Certain problems may then arise: many self pollinators are not attractive to insects (e.g. lettuce); F_1 hybrids intended for fruit production (e.g. tomato) would have to be self compatible or able to produce parthenocarpic fruits; F_1 hybrids of ornamentals should preferably be self incompatible, as the flowers would then last longer (Reimann-Philipp, 1965); unilateral incompatibility may intervene and barriers to crossing with normal varieties may be introduced, as happened in the case of Tiny Tim (Martin, 1968).

Mackay (1976) was successful in introducing fully functional *S* alleles into the self-pollinating allotetraploid species *Brassica napus*. He used two sources, viz. *B. campestris*, one of the ancestral species of *B. napus*, and a newly synthesized *B. napus* from *B. campestris* × *B. oleracea*. Whereas the former can provide only one *S* locus, the latter can provide two, one from each parental species. Methods of producing F_1 hybrid swedes are being developed (Gowers, 1975).

A completely different approach underlies the attempts of Larsen et al. (1973) to select self-incompatible plants in a highly heterogeneous barley population. Because complementary genes apparently determine the incompatibility system not only in grasses, but also in *Beta vulgaris* and *Ranunculus acer*, Larsen and his colleagues assume that such genes may be dispersed throughout self-compatible crops, such as barley, and that it may be possible to assemble and combine them to give self-incompatible plants. Results have not yet been published.

Prospects

Continued research may be expected to result in the wider utilization of incompatibility as a tool in plant breeding. In *Brassica* and *Raphanus* crops, it is likely that normal commercial varieties will increasingly be replaced by F_1 hybrids, and that double-cross hybrids will tend to replace the singles. Nieuwhof (1974) suggested introducing the stronger *S* alleles from winter cultivars of cauliflower into summer cultivars, which in general are fairly self compatible. It is also possible that introducing the best *S* alleles from other *Brassica oleracea* varieties into cauliflower would facilitate breeding hybrid cauliflower cultivars. Incompatibility studies have also been, and are being, carried out on a large number of ornamentals belonging to many plant families, particularly the Compositae, Solanaceae and Scrophulariaceae. Where a CMS-restorer system is lacking, incompatibility is the alternative in those self-incompatible species in which F_1 hybrids are commercially attractive. Application of the gametophytic system seems feasible in clovers. It may be anticipated that research in this field will continue and that the procedures may improve to the point where they can be applied commercially.

The feasibility of utilizing *S* alleles from wild species in crops like tomato and lettuce remains speculative and will depend on the extent and results of future investigations. It should not be forgotten that, even in cole crops, it is only as a result of large-scale investment in research that it has finally become possible to utilize incompatibility commercially. The investigations of Larsen et al. (1973) in barley are of interest from the scientific point of view. Barley is an economically important crop in which a CMS-restorer system is not yet available and for which other systems like the balanced tertiary trisomics are not completely satisfactory. However, even if self incompatibility is eventually found in barley, its genetics is likely to be rather complicated and for that reason any practical application would seem unlikely.

APOMIXIS

In the widest sense, apomixis in plants includes all modes of asexual propagation, whether by seed or by vegetative reproduction from the somatic tissues of the mother plant. In the latter case, neither embryo nor seed is produced, examples being certain kinds of vivipary and bulbil formation in the inflorescence.

In this contribution only apomixis in the narrow sense of asexual propagation via the seed will be considered. The phenomenon is encountered in many families and is well-known in the Gramineae, the Rosaceae and the Compositae (Doll, 1971; Bashaw, 1974).

In many apomicts that reproduce by seed, embryo sac formation is generally the result of either apospory or diplospory. In apospory an unreduced ($2n$) embryo sac (with a $2n$ egg cell) arises from a somatic ($2n$) cell. Diplospory is a form of apomixis in which the embryo sac develops from an archesporial cell without a preceding meiosis. The result in this case is also a $2n$ embryo sac with a $2n$ egg cell. In both apospory and diplospory $2n$ embryos are formed, either from the unfertilized egg cell or from another cell in the embryo sac (Gustafsson, 1946/1947).

A more or less distinct form of apomixis is adventitious embryony, in which a neighbouring somatic cell penetrates the embryo sac and develops into a $2n$ embryo (*Citrus* (Fig. 4.12), mango etc.). In addition to the adventitious embryo, a normal embryo is often generated sexually from the egg cell.

The process whereby a cell in an embryo sac develops into an embryo at the n level, without undergoing fertilization, is also included by some authors under apomixis. The cell may originate within the embryo sac (apogamy) or it may be a male gamete that has penetrated the embryo sac (androgenesis *sensu stricto*).

In many apomicts endosperm formation requires fertilization of the polar nuclei. This phenomenon is called pseudogamy. Apomicts of this type often have good pollen formed via normal reduction division.

The frequency of apomixis may vary not only from species to species, but also from variety to variety and even from plant to plant. When propagation is entirely asexual, we speak of obligate apomicts. When propagation is occasionally via a sexual process, the term facultative apomict is used. For plant breeding this classification is important.

Apomixis has some advantages for breeding:

- Any genotype of an apomict, even one with an aberrant chromosome number, can be maintained unchanged by seed (certain *Poa* species).
- In most cases there is no transmission of viruses via apomictic seed (e.g. *Citrus*).
- Both aposporous and diplosporous plants can occasionally give rise to plants with altered ploidy, as for example where triploids may be formed as a result of pollination (*Poa* species).
- The occasional apomictic development of unfertilized cells of the reduced embryo sac can lead to haploidy (*Asparagus*).

Apomixis also has certain disadvantages:

- It is practically impossible to reproduce obligate apomicts sexually. Since pollination does not result in fertilization, new genotypes are not readily produced.
- An apomictic species is liable to form a number of fixed genotypes and may then be more prone to epidemics.

Various attempts have been made to recombine obligate apomicts such as *Poa pratensis* in spite of their being virtually incapable of sexual reproduction. The following procedures have been used:

- Appropriate manipulation of the environment may assist sporadic sexual (amphimictic) reproduction (see p. 187).
- A facultative apomict of the same species may be crossed as female parent with the obligate apomict. The best apomictic plants may then be identified among the progeny.
- A related nonapomictic species may be crossed as female parent with the apomict to give a hybrid which is then crossed with another genotype of the apomictic species or with an analogous hybrid. This procedure allows the apomictic species to be

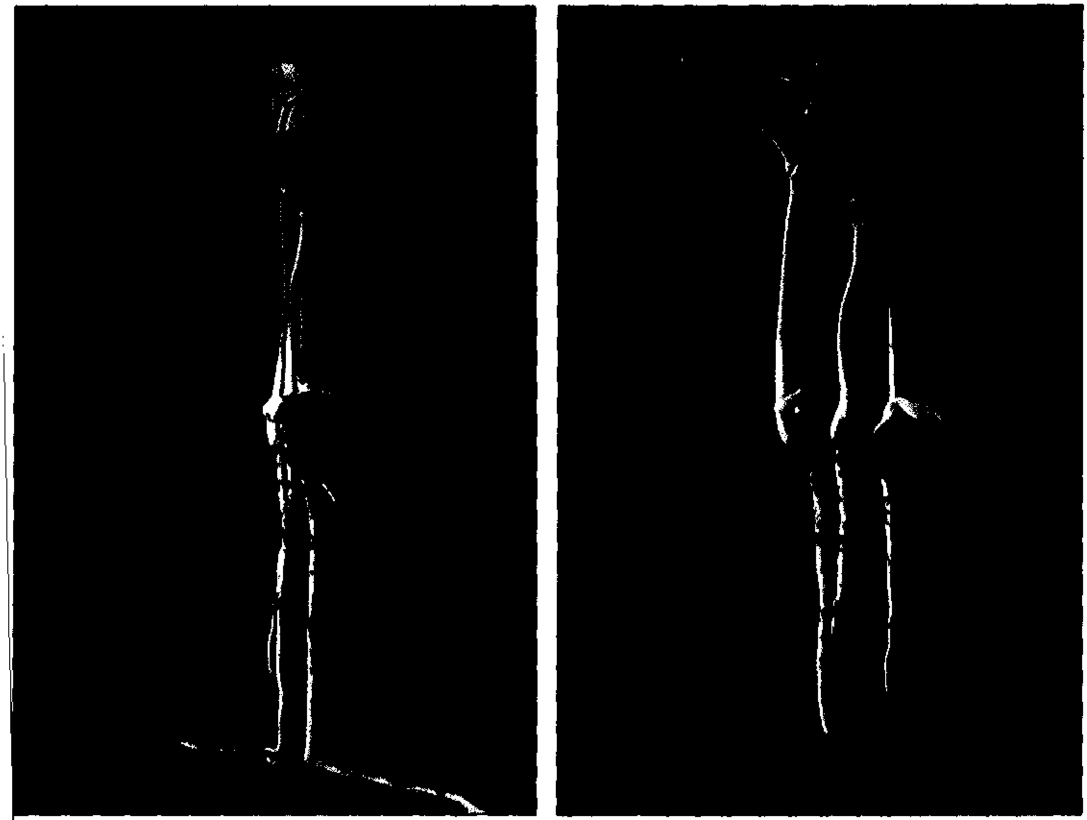


Fig. 4.12. Nucellar embryony in citrus. Left: three plantlets from one seed. Right: plantlets separated. (Photographs: IVP).

reestablished in the form of new genotypes.
– Mutagenic interference with apomixis may be of use, but no clear-cut results have been obtained.

Where applicable, the first method seems to be the most attractive.

In addition to attempts to overcome the disadvantages of apomictic species for purposes of breeding, endeavours have been made to incorporate apomixis in naturally amphimictic crop species, with a view especially to fixing a varietal genotype and possibly hybrid vigour. In crops that are propagated vegetatively (via tubers, bulbs, shoots etc.), apomictic reproduction via seed (usually with consequent exclusion of virus transmission) would be a very attractive proposition.

For autogamous crops the possibility of permanently fixing heterosis by the introduction of apomixis would be highly desirable, but this is still a distant prospect. The same is true to some extent of some allogamous crops. However, any innovation of this kind would require further study of the genetic background of apomixis. In the cases investigated so far, the genetics of apomixis is rather complicated (Nogler, 1978).

Potatoes

The main problems encountered in potato breeding are the following:
– It is difficult to produce wide genotypic variation, with favourable genes for yield, a diversity of quality characters and resistance to pests and diseases.
– Inadvertent selection of genotypes susceptible to environmental influences can cause trouble and it is advisable to test clones at the earliest possible stage in the regions for which they have been bred.
– The propagation rate is low.
– Breeding material and selections are liable to become infected with viruses. The best places for breeding and maintenance of varieties are regions with a cool climate where aphids (virus vectors) are less prevalent than elsewhere.
Outside South America the potatoes grown have been limited to rather a narrow genetic base. In order to meet all the requirements of growers and consumers, new introductions of both Solanum tuberosum and related species from the centres of diversity should be used in breeding. Work on broadening the genetic base is in progress. New approaches include breeding at the diploid level and returning to the tetraploid level by means of techniques involving the use of unreduced gametes. The possibility of producing hybrid populations from true seed is receiving attention. This may be of particular importance for regions subject to heavy virus infection, as true seed does not normally carry viruses or soil-borne diseases.

CONVENTIONAL METHODS

Introduction

As the potato (*Solanum tuberosum*) is a vegetatively propagated crop, diseases are easily transmitted to the next generation. This is especially true of virus diseases and can lead to marked decreases in yield. In general, virus diseases are not transmitted by seed and as early as the 18th century it was observed that potato plants grown from seed were often much more vigorous than those propagated from tubers. These observations encouraged the use of occasional sexual reproduction to improve vigour. It was soon observed, however, that the generations obtained from seed segregated into many different types, and this in turn was an incentive to breeding work.

The production of virus-free seed potatoes is very important and a scheme is given in Chapter 9 (p. 137). The conditions required (cool weather and few aphids) are favourable in north temperate regions. This has enabled the Netherlands to develop an export market for seed potatoes and to combine this with breeding programmes aimed at producing varieties specially adapted to the conditions and requirements of the many countries where seed potatoes are imported.

Commercial potato breeding in the Netherlands is carried out by a few large companies, some tens of medium-sized companies and more than a hundred private individuals. Besides this, there are two state institutions for basic breeding research whose work is of importance for the breeding work carried out by the private companies. One is the Institute for Plant Breeding (IVP) of the Agricultural University, which conducts research on breeding methods, including new techniques in potato breeding. The primary function of the second, the Foundation for Plant Breeding (SVP), is to produce breeding material, including potato material, for Dutch breeders. For the small breeder, the SVP produces seeds and clones which can be used for practical selection in the field without much equipment. The larger companies, which carry out their own crossing programmes, can obtain parents from the SVP in which certain desired characteristics, very often resistances of various kinds, have been incorporated by means of interspecific crosses.

Breeding objectives

In view of the importance of seed potatoes for export, a broad scale of selection criteria to suit both national and international requirements is applied by Dutch breeders. The most important criteria are described below.

Potatoes for different purposes Potatoes are used for human consumption, for feed and also for the starch industry. The different uses have different requirements. Among varieties for human consumption, the requirements vary according to consumer preferences in different countries and according to whether they are to be boiled or used for the preparation of chips (French fries), crisps, mashed potato etc. For the potato starch industry, dry matter content and the quality of the starch are important, and where protein is to be extracted from the waste water, a high protein content is desirable as this allows a more economic extraction. For varieties for feed, the requirements parallel those for starch varieties.

Yield Scheijgrond (1978) reports on yield increases obtained in the Netherlands in varieties bred for the starch industry and Fig. 4.13 shows some results obtained in the trials of the Government Institute for Research on Varieties of Cultivated Plants (RIVRO) and also in commercial cultivation over the period 1948-1977. In the trials, the increase in yield attributable to the introduction of higher-yielding varieties was 0.35% per year for tonnage and 0.28% per year for under-water weight. In commercial cultivation, the increases have been so spectacular that yields can now be obtained which were undreamed of 30 years ago. This is partly due to the introduction of improved varieties but also to better techniques of *Phytophthora* control.

Stability of yield In many cases one or more factors limit production and prevent the full yield potential from being realized. The priority given to any one factor in a breeding programme will depend on its effect and on the circumstances in which it exerts this effect. It can be a matter of some importance whether priority is given to breeding for high potential yields or to breeding in order to overcome the constraints

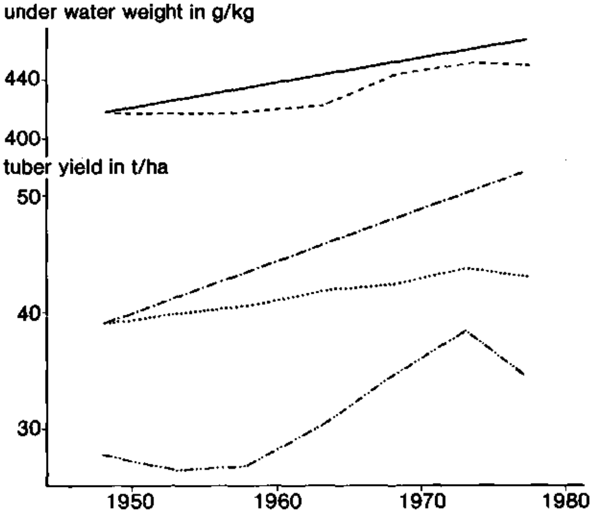


Fig. 4.13. Potato yield and under-water weight increases in RIVRO trials, Netherlands, 1948-1977. Actual under-water weight —— (annual increase 0.5%); change due to variety improvement --- (annual increase 0.28%). Actual tuber yield –·– (annual increase 1.2%); change due to variety improvement ····· (annual increase 0.35%). For comparison: commercial tuber yields –··– (annual increase 1.0%). (from: Scheijgrond, 1978).

(such as diseases) that prevent the attainment of potential yields. The most important diseases are considered below.

– Virus diseases. For many developing countries, where potato growing is on the increase, the possibility of multiplying imported seed potatoes for one or two generations within those countries is of importance; this would entail the use of varieties with improved resistance to virus diseases. Resistance to the mosaic viruses A, X, S and M and also to the dangerous virus Y^N is already in use in breeding, and commercial varieties with good field resistance to virus A or X are available. Material with reasonable field resistance to Y^N is likely to be released soon. Breeding for resistance to leaf roll virus is hampered by the polygenic nature of the resistance.

– Potato blight (*Phytophthora infestans*). This important fungal disease can attack both leaves and tubers and can lead to severe reductions in yield. In the past, *R* genes conferring complete resistance have been introduced from wild species such as *S. demissum* into commercial varieties, but this resistance breaks down rapidly on the appearance of new pathotypes of the pathogen, resulting in severe attack and heavy losses. The only solution would seem to be to breed for horizontal resistance (Chapter 6, p. 265). Leaves and tubers are not necessarily similar in susceptibility.

– Potato cyst nematodes (*Globodera rostochiensis* and *Globodera pallida*). Where potatoes are included too frequently in the crop rotation, as is liable to occur where potato growing is profitable, attack by these nematodes is frequent and can cause very heavy losses. Breeding for resistance, based on available sources in a number of *Solanum* species, is of great importance (Chapter 6, pp. 285-287).

– Wart (*Synchytrium endobioticum*). This fungus, which can cause complete loss of a crop, can remain in the soil for years. At the beginning of the century most varieties were susceptible. Many countries ruled that all new varieties were to be resistant, and prohibited the cultivation of susceptible varieties in infected areas. Resistance is simply inherited and many resistant varieties have been released, but the possibility of new pathotypes appearing requires continued attention.

– Scab (*Streptomyces scabies*). The occurrence of scabby tubers can reduce the salability of the crop. The disease is associated with certain soil types and is favoured by dry periods at the beginning of tuber formation. Varieties differ greatly in susceptibility, but inheritance is complex. For light soils, tolerant varieties are required.

– Spraing, characterized by rings, streaks and spots in the tubers, is caused by the tobacco rattle virus, which is transmitted by soil-borne stem eelworms. It can be important on sandy soils. Varieties differ in resistance, and testing in infected soils allows adequate selection.

– Diseases and pests of importance for the tropical zone. A typical disease of the humid tropics is bacterial wilt, *Pseudomonas solanacearum*. Resistance is now available in the AVRDC acc. 1282-19. In hot and dry conditions the fungal diseases *Alternaria solani*, *Verticillium dahliae*, *V. albo-atrum* and *Fusarium oxysporum* can be injurious. Existing differences in resistance are being exploited. In warm climates many insects can occur on potato, including *Phthorimaea operculella*, *Epilachna*, *Leptinotarsa decemlineata* (Colorado beetle), *Epicauta* spp., cutworms and many others. A great number of aphids are generally also found. As these are vectors of many virus diseases, it is necessary to produce seed potatoes in cool aphid-free regions. Potato breeding is hardly feasible in aphid-infested regions and is therefore mainly concentrated in northern countries.

– Storage diseases (*Phoma exigua* var. *foveata* and *Fusarium* sp.). *Phoma* can cause heavy losses in potatoes harvested and stored under cold conditions. It is not clear whether the differences between varieties are due to differences in growth rate of the fungus or to differences in harvest damage. Another storage disease, caused by *Fusarium* sp., occurs especially after a hot season and can lead to severe losses of seed potatoes. Varietal differences are sufficiently great to permit breeding for resistance.

– Extreme weather conditions. In breeding varieties for hot, dry areas, it is important to include parents with tolerance of such conditions in the crossing programme. When long dry spells are followed by rain, growth may be renewed, leading to the formation of misshapen and undesirable tubers. Varietal differences are considerable and the years in which the phenomenon occurs should be used to advantage in breeding.

Time of maturity The yield of a variety is much influenced by its earliness. Late varieties are inherently capable of yielding more, but as a late harvest is always a risk in rainy areas on heavy soil, early varieties are preferred, especially since the introduction of mechanical harvesting. In the starch industry, too, early-maturing varieties are required to extend the season. For areas where potatoes are grown for the beginning of the new marketing season, the preference likewise is for very early varieties.

Time of tuber formation Among varieties with similar maturity there may nevertheless be considerable differences in the time at which tuber formation begins. For later-ripening varieties in particular, it is necessary to select for earliness of tuber initiation in order to make seed potato production economically practicable. Varieties for the early market should also be characterized by early tuber initiation. Time of maturity and time of tuber initiation are both influenced by day length and will therefore vary in the same variety grown at different latitudes.

Dormancy An adequate dormancy period is a prerequisite for good storage ability.

Suitability for cutting of seed potatoes In a number of countries, especially around the Mediterranean, farmers prefer large seed potatoes, on account of their lower price. These seed potatoes are cut into pieces each containing at least one eye. This procedure has a special advantage in the production of potatoes for the early market, because many of the plants form only one stem and will produce a few large tubers, which are suitable for an early harvest. Varieties show clear differences in their suitability for cutting. This characteristic should therefore be taken as a selection criterion in breeding for areas where the practice is prevalent.

Breeding procedure

In comparison with the breeding schemes used for most other crops, the breeding procedure for potatoes is relatively simple. In essence, it consists in making crosses and producing F_1 clones, which are then subjected to continuous selection and vegetative multiplication. The method in use at the Ropta breeding station of De Friese Maatschappij van Landbouw in the Netherlands is described in detail below. More complicated methods which may be turned to account in the future are surveyed in another contribution (pp. 153-158).

Choice of parents Many characters are of importance in the development of new varieties, and this complicates the choice of parents for the production of F_1 seed in which desired characters are combined with each other. Less favourable characters can never be completely avoided. The heterozygosity and the autotetraploid condition of potato will result in a very variable F_1. Experimental knowledge of the inheritance of the characters of parents in use in breeding projects is now quite extensive, but the theoretical background is still far from complete. Practical experience is therefore an important guide in devising a crossing programme. A large number of combinations are made and from each cross only a fairly small number of clones are examined. The parents used may be donors of resistance genes, either already developed in the breeding programme or obtained from other stations, or they may be older selections from the programme and commercial varieties. Althought it is generally true that virus disease are not transmitted by seed, healthy parental material is essential since otherwise it will be a constant source of infection in the breeding station.

Hybridization and seed production Although self fertilization is possible in some varieties, the breeder will generally prefer to start by crossing two parents with a view to combining their desirable characters. Crosses made in the field are liable to suffer losses from wind, rain, heat and drought and most breeders therefore prefer to work in the greenhouse. The following technique is used. Tubers of the chosen parents are placed on a brick and covered with sand and peat. The roots grow over the brick and when they have penetrated the soil on which the brick is lying, the covering sand is washed away (Fig. 4.14a). Removal of the tips of the stolons, which would otherwise produce new tubers, is then possible. This promotes vigorous stem growth and enhances flowering. Flowering can also be induced by grafting a potato shoot on to a tomato rootstock, but this gives weaker growth.

In planning a crossing programme it has to be borne in mind that many varieties are male sterile and that male parents are therefore in short supply. Certain varieties which set seed without artificial pollination, mostly through self fertilization, can be assumed to have fertile pollen and can therefore be used as a male parent. When such a variety is used as female parent, emasculation should be effected in unopened flowers one or two days before crossing. A variety which because of its self incom-

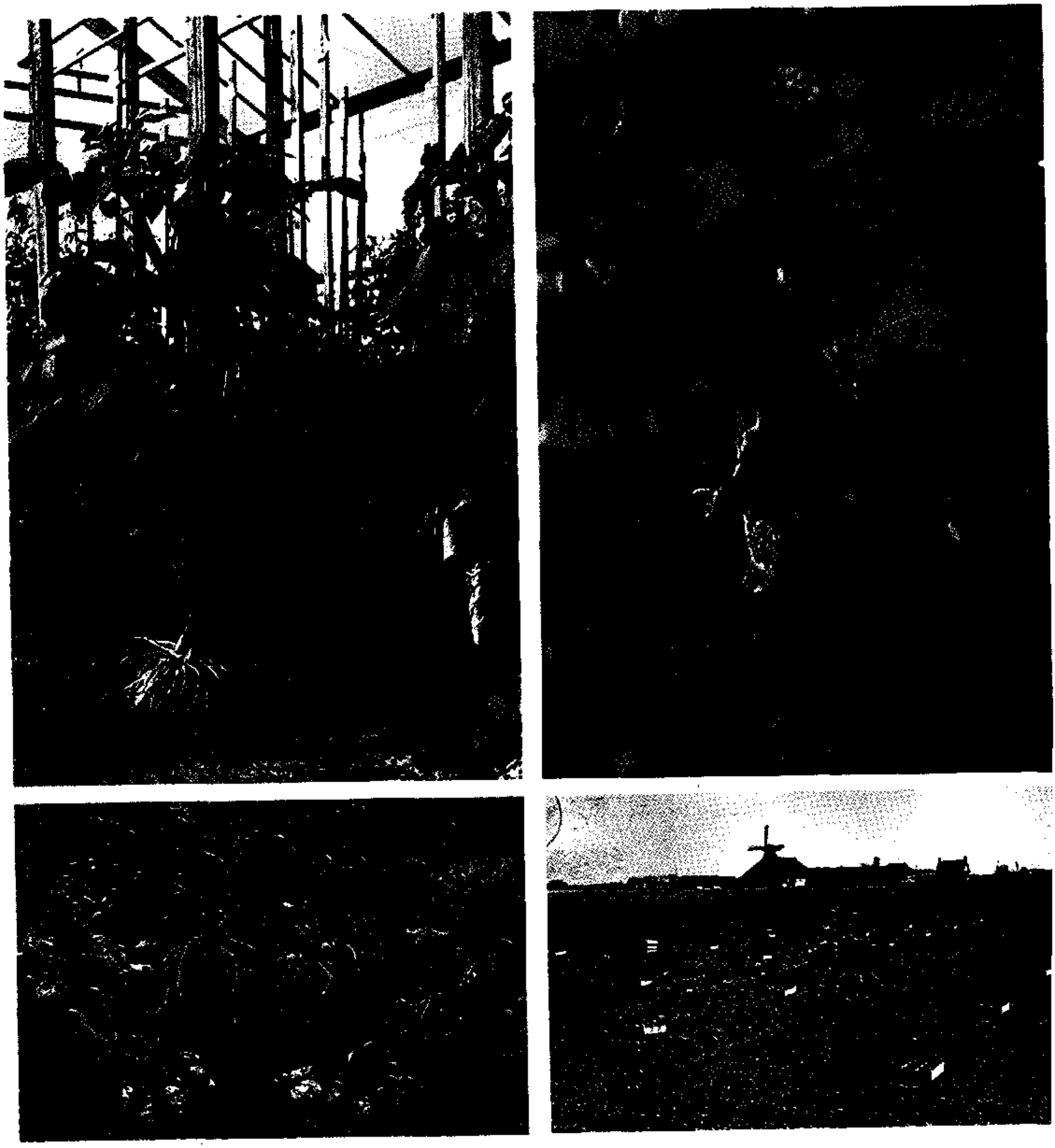


Fig. 4.14.

a. Top left – Potato on brick with stolons washed free.

b. Top right – Seedlings artificially infected with virus Y, showing differences in resistance.

c. Bottom left – Four different plants from one cross in a first-year field test.

d. Bottom right – Planting of second-year field test.

(Photographs: Ropta).

patibility requires artificial pollination in order to set seed may nevertheless be male fertile, in which case it can be used as either male or female parent; in the latter case emasculation is unnecessary.

Another problem is poor nicking (unsynchronized flowering) of the parents. This can be prevented by planting the male parents in the greenhouse as well as the female parents. The luxuriant growth of plants in the greenhouse ensures a long period of pollen production. The pollen can be stored under appropriate conditions, and pollen can also be collected from the field as long as the outdoor male parents are flowering.

To make a cross, pollen from ripe anthers is applied to the stigmas of all the flowers of one of the inflorescences of the female parent, which is then labelled. To facilitate pollen collection, inflorescences may be cut from the male parent one or two days in advance and placed in a jar of water. Excised inflorescences can also be used as female parents, but the harvest of seeds will be smaller than from intact inflorescences. The berries appear within a few weeks and to prevent losses they are bagged with nylon netting of large mesh. When ripe, they are harvested separately from each cross, and their contents (10-300 seeds) are removed and smeared on an unglazed flower pot. After a couple of days the seeds are collected and can, if necessary, be stored for years under suitable conditions.

Growing the seedlings The following spring the seeds are sown on moist filter paper under black plastic film for germination at room temperature. Rate of germination depends on the cross and the age of the seed. When sufficient seeds have germinated, the filter paper is placed on a layer of soil in the greenhouse and covered with a layer of garden mould. The seedlings emerge after a couple of days and on reaching the four-leaf stage they are transplanted into flower pots. Although all the seeds from one cross differ genetically, the number of seeds used to produce seedlings is normally limited to about 500 per cross.

In programmmes of selection for resistance, artificial infection may be used at this stage for purposes of selection, as is the case for *Phytophthora infestans* and potato virus Y^N (Fig. 4.14b).

Differences between the seedlings are small initially but become more marked later. Around the end of June the greenhouse plants are mature and the biggest tuber from each pot is harvested for planting next year. Tubers from one cross are put together in one bag. Little selection is possible in the first season and normally only 5-10% of the plants are discarded. The harvested tubers are stored for about 10 months, a storage temperature of 2-4 °C being used up to February to prevent sprouting and consequent loss of vigour.

After the first harvest at the end of June the greenhouse can be used for a second culture of seedlings. The yearly production at Ropta comprises 90,000 genetically distinct tubers.

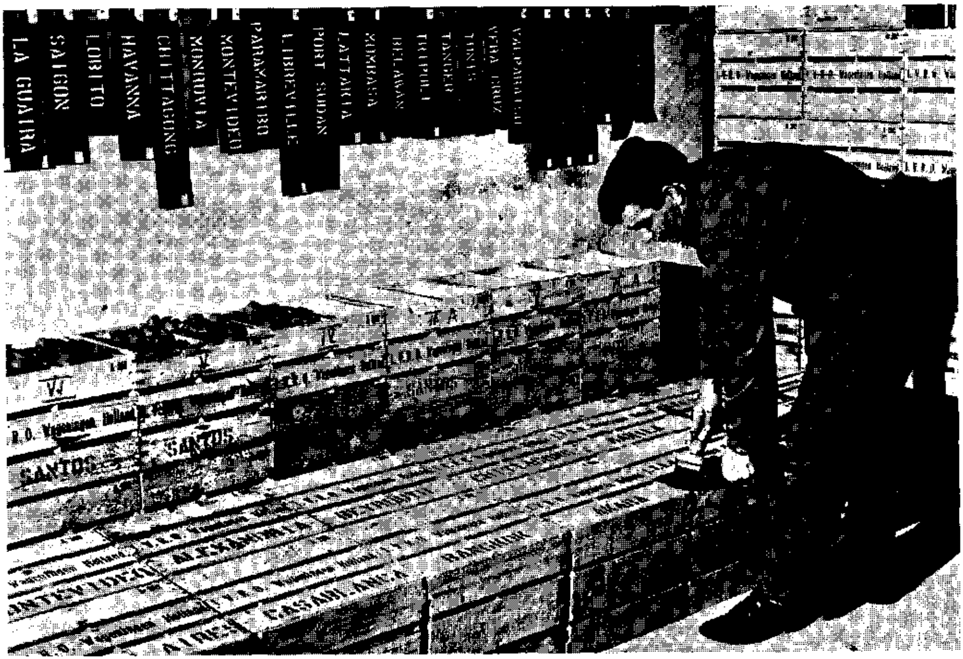


Fig. 4.15. Seed potato lots of experimental varieties for international NIVAP tests ready for shipment (Photograph: RIVRO).

First-year field test After chitting, the potatoes are planted out in the field in blocks, each comprising one cross. Wide variation is seen within and between crosses (Fig. 4.14c). Rapid growth and early tuber formation are important characters allowing early harvest or early haulm destruction, thus preventing virus infection transmitted by aphids. Selection against undesired plant types and diseases can be applied several times during the course of the growing season. Early in August all plants are harvested and judged individually for yield, uniformity and number of tubers, tuber shape, depth of eyes and length of stolons. The number of plants retained varies from 1 to 25% depending on the cross. Of the original 90,000 tubers, an average of about 10% may be retained, giving about 9000 selected single plants each with 4 to 12 tubers which are kept and stored separately. By discarding or cutting the tubers before planting in the following year, the final number of tubers per plant is brought to six of medium size. Immediately after harvesting, one tuber of each plant is sent to the Plant Protection Service, for screening against cyst nematodes of pathotype A. Many susceptible clones are eliminated at this stage. In subsequent years the remaining clones will be screened against other pathotypes.

Second-year field test The six tubers of each clone are planted out in single-row plots, with gaps of 1 m between clones to facilitate mechanical harvesting (Fig. 4.14d). In addition to the 9000 plots planted with the new clones, the trial includes 500 plots planted with about ten standard commercial varieties. The seed potatoes are now of normal size and this facilitates comparison between clones. Selection in the field starts early. All entries with undesirable plant type, poor soil coverage, virus infection, too high susceptibility to *Ph. infestans, Alternaria* etc. are eliminated. When aphids begin to appear, with consequent danger of virus infection, the haulms are destroyed by spraying with appropriate chemicals and harvesting starts a week later. A small one-row harvester is used. Good clones are selected visually for the characters mentioned above. Of the 9000 clones, about 1000 are retained, with about 60 tubers per clone. These are again screened by the Plant Protection Service for nematode resistance and susceptible clones may be discarded before planting. Methods of storage and preparation for planting are the same as in the previous year.

Third-year field test The clones are planted out in plots of 3 rows of 9 plants. Selection is carried out during the growing season as in the previous year. To ensure that healthy plant material will be available, the haulms of two rows per plot are removed before the appearance of aphids and the seed potatoes are left in the soil until the whole trial is harvested. The third row of each plot is used for observations on disease resistance, time of maturity and yield. The trial is harvested when the majority of the entries are mature. The yields of the seed potato rows and the third row are evaluated and on the basis of this and of field notes the number of clones retained for further testing is reduced to about 175. The tubers from the third row are used for determining cooking type and quality, suitability for the preparation of chips, under-water weight (dry matter content), resistance to *Synchytrium endobioticum* and, again, nematode resistance.

Up to and including the third year only one plot per clone is planted, for the following reasons:

- material of each clone is limited,
- large numbers of clones have to be tested,
- selection criteria other than yield are important,
- the number of standards used is adequate for comparison, provided the trial soil is sufficiently uniform.

For later tests the number of trial locations is increased, rather than the number of plots per clone per trial.

One difficulty in the selection procedure up to this stage is the detection of virus infections. Since differences in leaf characters are very marked, small differences due to virus infection are not readily observed. Mechanically transmitted viruses such as X and S can be particularly dangerous. For this reason selection for virus-free material is practised during the winter season. Sprouting is induced in 150 tubers of each clone, by means of a heat shock applied in December. From each tuber a piece containing one eye is planted in the greenhouse while the tubers are returned to cold storage. After six weeks, the greenhouse plants are tested for viruses X, S, M, Y^N and A. The tubers corresponding to all greenhouse plants suspected of virus infection are discarded so that only healthy seed potatoes are used for the fourth year.

Subsequent field tests From the fourth year onwards, selection work involves (1) separate multiplication of healthy seed potatoes to maintain the clones still under test and (2) comparison of mature plants of the clones for agronomic characters. The agronomic trials are laid out in different locations, including one where scab is prevalent and one on a sandy soil where rattle virus occurs. From the fifth year the breeder starts his own trials in several countries, in order to obtain information on reaction to climate, day length, different soils and growing systems. Also in the fifth year, preliminary tests with replications by locations only and with only one plot per clone per location are initiated in the Netherlands by RIVRO. Varieties which continue to give satisfaction in these tests are finally tested in trials at several locations with more than one replication per location. On the basis of these test trials a variety is admitted to the Recommended List or rejected. Besides this, world-wide international tests of young varieties are conducted by NIVAP (Nederlands Instituut voor Afzetbevordering van Pootaardappelen) (Fig. 4.15). Table 4.6 gives a survey of selection pressure and the multiplication for one selection series.

Table 4.6. Course of a selection series started in 1965 and ending in the commercial release of one new variety in 1979.

Year	Number of selections	Seed production per clone	Number of trials		
			Netherlands		abroad
			trials	replications	trials
1965	several hundred crosses	–	–	–	–
1966	95,000 seedlings	–	–	–	–
1967	90,000 plants	1 plant	1	none	–
1968	9,000 clones	6 plants	1	none	–
1969	1,000 clones	18 plants	1	none	–
1970	175 clones	150 plants	6	none	–
1971	40 clones	250 plants	6	none	6
1972	15 clones	350 plants	9	yes	10
1973	5 clones	1000 plants	9	yes	15
1974	4 clones	0.05 ha	11	yes	15
1975	3 clones	0.2 ha	16	yes	22
1976	2 clones	0.5 ha	± 36	yes	32
1977	1 clone	1.0 ha	± 44	yes	35
1978	1 clone	2.5 ha	± 44	yes	⟩100
1979	1 clone	5.0 ha	± 44	yes	⟩100
1980 and following		distribution to seed potato producers			

Concluding remarks

In countries like the Netherlands, where the potato is already an important crop, varietal improvement in resistance to nematodes, viruses and *Phytophtora infestans* is desirable. Where seed potatoes are exported on a large scale, as in the Netherlands, breeding objectives should take into account the requirements of the importing countries. For developing countries aiming to increase potato cultivation on account of its potentialities as regards both quantity and quality (cf. Chapter 1, p. 41), adapted varieties with adequate resistance to viruses are needed. Expeditions to centres of origin of the potato have already provided valuable sources of disease resistance. The conservation of genetic resources is of extreme importance for the breeder (Chapter 3). New breeding procedures are discussed below, but for practical breeders the traditional method described above can be expected to remain important for some decades and to provide significant improvements in varieties.

NEW APPROACHES IN POTATO BREEDING

Possible reasons for slow progress in breeding

The traditional and most widely applied breeding procedure is to intercross superior autotetraploid parents and select the best F_1 individuals. Such selection is laborious and the chances of finding a superior new genotype are extremely remote, for on meiosis the optimally balanced, highly heterozygous genotype of each parent divides into numerous and diverse male and female gametes, and these, on crossing, are fertilized by a completely random process which cannot be controlled in any conventional way. The breeder's usual procedure is to try to make a rational choice of parents based on his knowledge of their breeding value. However, such knowledge is also laborious to acquire and is available for only a small number of parental lines. Some breeders (Broertjes & van Harten, 1978) have tried to induce desirable changes in useful varieties by mutagenic treatment, leaving the overall genotype largely intact. Hitherto, however, little has been achieved along these lines, owing to the autotetraploidy of potato and the randomness of induced mutations.

Another reason for the relatively slow progress made in conventional potato breeding during the last 50 years is mentioned by Simmonds (1960). He draws attention to the narrowness of the genetic base of potato, the result in part of the small number of introductions from South America originally imported into Europe and in part of further reductions in variation through extensive losses due to disease.

In the present contribution, certain promising new approaches will be discussed. Some of these are on the verge of being applied in practice, others may reach that stage in due course.

Model for an optimal selective mating in tetraploid potato

The basic procedure for the complete control of the selection and fusion of gametes can be summarized in four steps.

1 Raising plants from gametes (= haploids), thus allowing the production of so-called 'gametic samples' from different sources (cf. Chapter 8, pp. 330-341).

2 Vegetative propagation of the haploids to enable a reliable evaluation of their genotypes for various kinds of resistance, yielding ability and quality characters.

3 Assessment of the combining ability of the haploids by test crossing.

4 Fusion of somatic cells from haploids selected for good agricultural characters and combining ability.

Steps 1 and 2 can be carried out with relative ease by any breeder. For step 3 the lack of fertility of most haploids is an obstacle. Step 4 is not feasible because somatic cell hybridization is not yet a routine method. In the following sections the best compromise solution attainable at present will be indicated.

Breeding tetraploid potato at the diploid level

Steps 2 and 3 mentioned above basically constitute a selection programme at the diploid level. Such a programme has been developed by several breeders to give a breeding scheme complete in itself. Van Suchtelen (personal communication), for example, obtained diploid *Solanum tuberosum* clones showing remarkable performance and fertility, and workers at Wisconsin, USA, (Hougas, Peloquin, Ross, Rowe and their students) achieved good results by introducing the diploid cultivated species *S. phureja* into their haploid programme as a source of fertility and genetic diversity. In spite of these successes, however, questions as to whether it will be possible to replace tetraploid varieties by diploid ones in the future generally have to be answered in the negative.

On theoretical grounds (Mendoza & Haynes, 1974), the potential of tetraploids may by expected to surpass that of diploids, since, as has been shown in a number of crops, e.g. lucerne (Busbice & Wilsie, 1966; Dunbier & Bingham, 1975) and rye (Lundqvist, 1966), multiallelism (more than two alleles per locus) plays an important role in the performance of tetraploid varieties. For this reason, breeding at the diploid level will probably remain only an intermediate stage in potato breeding; but as such, it has a number of advantages. In the first place, diploids can by hybridized directly with most diploid wild species, and these are an important source of genes for various kinds of resistance, for adaptability etc. In addition, fewer back crosses are needed in order to eliminate undesirable wild characters. It is possible to carry out inheritance studies and to combine useful characters more efficiently and hence with smaller populations at the diploid level than at the tetraploid level. Finally, the examination of gametic samples of tetraploid parental lines can give information on the various good and bad characteristics and hence on the breeding value of such lines, thus providing the possibility of removing unfavourable genes from the breeding material.

Return to the tetraploid level

Once a diploid clone of value has been obtained, the breeder encounters the problem of raising the ploidy level without disturbing the balanced genotype. Colchicine treatment should be avoided, as may be concluded from both experimental evidence (Skiebe, 1966; Mendoza & Haynes, 1974) and theoretical considerations (colchicine-induced tetraploids at most have two different alleles per locus). Fusion of somatic cells of the selected diploids is a possible alternative, and would result in an autotetraploid carrying both the cytoplasm and the intact genotypes of both parents. In this connection a good 'combining ability' of idiotypes is important. The fact that somatic cell fusion may be carried out between very young parental plants allows a saving of time; moreover, flowers are not needed and hence there is no problem of sterility. However, imperfections in technique are still an obstacle to the application of this potentially powerful method in plant breeding (cf. Chapter 8, pp. 353-355).

The best feasible compromise is to make use of numerically unreduced gametes (also referred to as $2n$ gametes) from diploid clones. Many diploid *Solanum* species produce not only normal n gametes but also a certain proportion of $2n$ gametes. When crossed with diploids, autotetraploids give rise to predominantly tetraploid offspring, since the triploid hybrid embryos as a rule do not survive owing to defective endosperm. It is particularly relevant in the present context to know what proportion of the genotype of a selected diploid is transferred intact to the progeny, because this proportion determines not only the degree of heterozygosity (or vigour) and uniformity of the tetraploid progeny, but also the extent to which useful gene combinations from the selected diploid will be transmitted to the offspring (Hanneman & Peloquin, 1968; Mendiburu, 1971; Mendiburu & Peloquin, 1971; Quinn et al., 1974; Mok & Peloquin, 1975; Mok et al., 1976; den Nijs, 1977). Peloquin and his students, who have made important contributions to our knowledge of the origin of $2n$ gametes and their value in potato breeding, distinguish between two basically different modes of origin, viz. first-division restitution (FDR) and second-division restitution (SDR). In both cases the parental chromosome number, $2n$, is reduced to n during the first meiotic division. The $2n$ number is then restituted either as a consequence of the failure of formation of the first-division wall, leading to FDR, or as a result of incomplete second meiotic division, leading to SDR. According to these authors, with FDR an average of 80% of the original diploid genotype is transferred intact to the progeny, whereas with SDR the proportion is only 40%. FDR and SDR are independent phenomena, based on single recessive genes (Mok & Peloquin, 1975), and therefore easy to manipulate. It is evident that FDR is the more promising mechanism for practical potato breeding.

In a few cases tetraploid plants have been obtained from diploid × diploid matings (Mendiburu & Peloquin, 1971). Triploid hybrids may also originate from such matings and these, if FDR is involved, are more promising than the triploids which occasionally arise from the fusion of n gametes in tetraploid × diploid matings.

In conclusion, it may be said that an extension of breeding at the diploid level can be recommended and should aim at developing highly heterozygous diploid clones in which many useful characters are accumulated, including recessivity at the FDR locus. In view of the relatively slow progress at the tetraploid level, interest in breeding at the diploid level and in making use of 2*n* gametes in potato breeding may be expected to increase in the future.

Broadening the genetic basis of potato breeding

Solanum species related to the potato are of great importance in its improvement. On the one hand, wild and cultivated species from the gene centre, South and Central America, have been and are being widely utilized for introducing genes controlling specific characters, mostly various types of resistance, into existing varieties by crossing and back crossing under continuous selection. On the other hand, a completely different use of *Solanum* species, especially cultivated ones, is becoming increasingly important in connection with breeding for yield potential under stress conditions. This aims at broadening the genetic basis of breeding and at selecting genotypes adapted to certain environmental conditions, such as long-day conditions in temperate zones and relatively high minimum temperatures in the lowland tropics. As early as 1960, Simmonds suggested that pure *S. tuberosum* has a limited potential in breeding. He initiated an adaptation programme in England, starting with tetraploid *S. tuberosum* ssp. *andigena* (Simmonds, 1961, 1966) and soon afterwards including diploid *S. phureja* and *S. stenotomum.* All these species are grown in South America and are adapted to short-day conditions. Simmonds' intention was to repeat within a few decades what had previously taken centuries: namely, the selection of potatoes adapted to European long-day conditions from South American material. His work is being continued in Scotland by Glendinning (1976), working on tetraploids. Using a different approach, other workers have taken up the idea and have obtained evidence which supports Simmonds' views and results (Budin & Soboleva, 1971; Haynes, 1972; Plaisted, 1972; Maris, unpublished). The International Potato Center (CIP) at Lima, Peru, was early to recognize the significance of this approach to breeding potatoes for developing countries and not only established close cooperation with various workers but also initiated a high-priority programme along these lines to find potato clones adapted to the severe stress conditions of the lowland tropics (Mendoza & Estrada, 1977). The potential contribution of wild species to such programmes has as yet hardly been studied systematically. Incidental observations, however, suggest that wild species have positive effects on several quantitative characters, including yield, quality and leaf roll resistance. Among species which warrant systematic investigation in this respect are *S. chacoense, S. vernei, S. sucrense, S. demissum, S. microdontum* and *S. sparsipilum.*

Wide crosses in Solanum

Distantly related species are mostly either largely or entirely cross incompatible with cultivated potato, and so-called wide crosses should be attempted only where the wild species involved carry valuable genes not known to occur in more closely related species. Good examples of such species are *S. bulbocastanum* (unique genes for resistance to *Phytophthora infestans*) and *S. brevidens* (unique genes for resistance to leaf roll). Introgression of genes in wide crosses is limited, owing not only to the low number of hybrid plants that can be obtained but also to the dilution of desirable genes that results from the use of bridging species (Hermsen & Ramanna, 1973) or other devices and from the relatively large number of back crosses needed. Genes may also be lost through elimination of chromosomes from hybrids (Ramanna & Hermsen, 1971).

Before wide crosses are attempted, it is advisable

- to evaluate fully the wild species for the desired characters;
- to accumulate genes, especially polygenes, aimed at upgrading those characters;
- to combine genes for different desirable characters, normally scattered over different accessions;
- to study the genetics of the wild species, with a view to avoiding erratic genetic ratios due to interspecific barriers.

Such a prebreeding programme may prevent disappointment at advanced stages, after much labour has been expended.

Somatic hybridization, even if successful, does not appear to be a promising method for wide crosses. It allows two different parent plants to produce only one new hybrid, and this has twice the chromosome number of the parents. Even without the occurrence of chromosome elimination during vegetative growth, the hybrid may fail to flower, and if it does flower there is a good chance of sterility due to genetic, plasmon-genic or genomic unbalance. Back crosses in such cases are often more difficult to make than the original cross, but somatic hybridization cannot be applied twice in succession owing to the increase in chromosome number. There is thus a real risk of reaching a dead end.

A few remarks on crossability are relevant to wide crosses. Crossability is generally determined by the genotypes of both parental species (Hermsen et al., 1977) and is also affected by environmental factors. For this reason, unless the crosses under study are made using a broad range of genetic variation in the parental species and are carried out on a large scale under a variety of environmental conditions, it is necessary to be cautious in concluding that two species cannot be intercrossed. Several reports on noncrossability have later had to be retracted.

Hybrid populations from true seed: implications for breeding

Hybrid varieties grown from true seed are a challenge to the potato breeder. If they were competitive with normal varieties in yield, quality, uniformity and resistance, they would be a breakthrough in potato breeding. The use of seedlings has some obvious advantages in cultivation. True seeds do not carry soil-borne diseases or viruses and, apart from new infections *in situ*, they will as a rule produce healthy seedlings. Transportation is safe, easy and cheap and the same is true for storage. Finally, there is no loss of a potential food as planting material, as is the case with seed tubers. The parents of a hybrid population for a developing country should have good combining ability for yield, and especially for reliability of yield; that is to say, wide adaptability and a wide range of disease resistance are essential for a hybrid population. It also is desirable that the parents should be complementary with regard to resistance to biotic and abiotic factors, so that the hybrid population or the greater part of it combines the parental resistances and preferably shows transgression for any polygenic resistance.

Uniformity is not as urgent a requirement in developing countries as in developed countries. Complete homozygosity and hence a genetically uniform hybrid population may be feasible at the diploid level with the aid of monohaploids (van Breukelen et al., 1977). Completely homozygous tetraploids are, however, more difficult to produce and to handle in a breeding programme than diploids. Furthermore, at the tetraploid level it is desirable to produce a double cross in order to reach a satisfactory level of heterozygosity, and this implies loss of uniformity.

The following is proposed as an acceptable and realistic produce for breeding suitable hybrid populations. Both tetraploid and diploid lines are bred. The tetraploids should be lines or varieties known to produce acceptably uniform progeny, whereas the diploids should preferably be homozygous and have the FDR mechanism for producing $2n$ gametes. With this starting material either a double or a three-way cross may be produced according to the following breeding scheme:

$$\begin{tikzcd}
\text{tetraploid} \times \text{tetraploid} \arrow[d] & & \text{diploid} \times \text{diploid} \arrow[d] \\
\text{tetraploid single cross} & \times \arrow[d] & \text{diploid single cross with FDR} \\
& \text{tetraploid double cross} &
\end{tikzcd}$$

The use of one superior tetraploid parent in place of the tetraploid single cross would give a tetraploid three-way cross.

It would be possible to streamline hybrid seed production, for example, by introducing cytoplasmic male sterility into one diploid parent. The species *S. verrucosum* is a good source of cytoplasmic male sterility (Abdalla & Hermsen, 1972). Hybrid seed can then be harvested from the male-sterile diploid single cross in a seed production field with the tetraploid parent as pollen parent. It is clear that acceptable hybrid varieties cannot be bred within a few years and that only extensive research by skilled scientists over several years can lead to success, especially for developing countries. The International Potato Center in Peru has shown a lively interest in the problem and may contribute a great deal to the realization of this approach in developing countries.

Autogamous small grains

In this group of crops, choice of parents, the creation of genotype variation and the application of appropriate selection procedures within and between progenies are the main stages in breeding. Varietal purity and maintenance also require attention. Although, in principle, continued line selection from the F_3 to about the F_7 with parallel yield trials, is a possible method, in practice it proves unwieldy. The main complication in a wheat breeding programme is the requirement for wide genetic variation on the one hand and for intensive selection, especially subsequent to the F_2, on the other: a compromise procedure is described. Back crossing is a well-known procedure often used in transferring a limited number of genes from a donor variety into a locally adapted variety: an example of a back-crossing system, as applied at the National Plant Breeding Station at Njoro, Kenya, is given. A cytoplasmic male sterility and restorer system is available in wheat. In producing F_1 hybrids, breeders have encountered difficulties in maintaining pure male sterility, in restoring full fertility, in synchronizing the times of stigma receptivity and pollen shedding in the parents and in ensuring adequate cross pollination, especially under unfavourable weather conditions. Nevertheless, progress is being made in exploiting heterosis in this important cereal. Scattered attempts to breed hybrid rice have been made over the years. In recent years, following the identification of a useful source of cytoplasmic male sterility, massive efforts at developing hybrid rice have been made in China, where several hybrids are now grown on a commercial basis. These hybrids appear to outyield conventional hybrids by nearly 20%, but the high cost of F_1 seed production restricts their wide adoption.

CONVENTIONAL METHODS

Basically, all conventional breeding methods for self-pollinated cereal varieties follow more or less the same pattern, in which three stages can be distinguished:
- creation of genetic variation,
- selection,
- purification and maintenance.

The breeding method actually chosen will be determined by the relative emphasis to be placed on each of these three stages.

Genetic variation, which is the basis of any breeding programme, can be achieved in several ways. Normally some form of crossing programme (single crosses, multiple crosses, back crosses etc.), using manual crossing techniques, is applied, but population techniques, using genic or cytoplasmic male sterility, can also be used. In addition, mutagenic techniques may come into consideration, if it appears that recombination of the available natural sources of genetic variation affords little prospect of reaching a specified breeding objective. In any case, the degree of genetic variability, which is the starting point of the breeding programme, should be carefully adjusted according to the facilities available for the subsequent selection procedure. For a given availability of labour and facilities, the breeder can choose between two possibilities in deciding on an appropriate selection procedure for his breeding programme:

- an intensive selection procedure, based on a limited pool of genetic variability (e.g. a relatively small number of crosses);
- a less intensive selection procedure, with emphasis on producing a large pool of genetic variation.

If he works with a limited number of crosses, or with parents of limited diversity, the breeder risks losing an important part of his experimental material. On the other hand, if he uses less intensive selection methods, he must face the fact that he will never be able to screen the full genetic potential of each cross. Also, he will have to find a means of reducing unwanted selection pressures (e.g. competition effects) to a minimum. A complete pedigree selection system is, in general, the safest but also the most elaborate method of screening breeding material for genetic potential. Bulk selection systems, or combinations of bulk and pedigree selection, may be useful when the breeder has to economize on labour while preserving a broad genetic variation in his programme.

The system that the breeder chooses for the purification and maintenance of his selected strains will mainly depend on two factors:

- the selection system he has used,
- purity regulations in the country for which his variety is intended.

If he uses a pedigree selection system, work on the purification of his most promising strains can begin in relatively early generations, owing to the fact that all the breeding material is available as plant progenies or ear progenies in all generations. If he uses a bulk selection system, purification of the strains cannot begin until the strains have been isolated.

As it is hardly possible to discuss all the advantages and disadvantages of the various selection systems used in cereal breeding, two wheat (*Triticum aestivum*) breeding systems only are described in the following pages. One is adapted to requirements in western Europe and another, with a minimum of technical requirements, has given good results in a developing country.

A simplified method of bulk and pedigree selection

Autogamous cereal varieties can be bred by pure pedigree selection starting in the F_2, or by a method in which multiplication up to the F_6 or F_7 is done in bulk, after which pedigree selection starts. The pedigree method is very labour intensive and with the bulk method losses of good combinations easily occur.

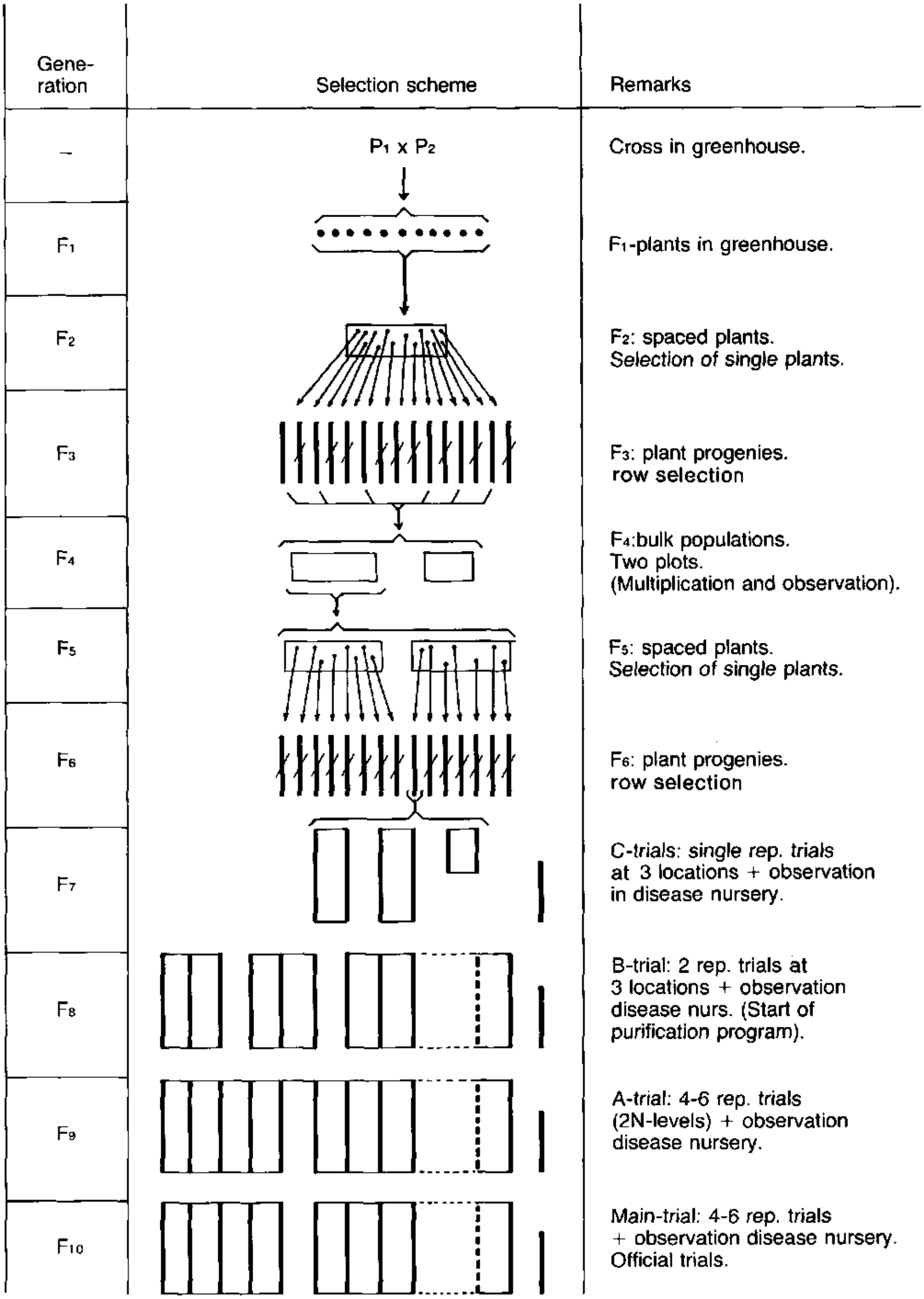
In the simplified method here described an attempt is made to combine the advantages of both methods.

A diagram of the selection procedure is given in Fig. 4.16. The procedure shown in the diagram begins with a single cross ($P_1 \times P_2$), but in an actual breeding programme, both single, multiple and back crosses are used. The progenies of the single crosses can only be included in the selection procedure if the parents are both well adapted and complement each other with respect to important characters like disease reaction and straw characters. Where the single crosses involve primitive or unadapted parents, the F_1s are first back crossed once or twice with adapted varieties. Possible parents require careful study and care should also be taken in deciding which F_1s are to be back crossed and which are sufficiently promising to be entered in the selection procedure without further back crossing.

Parental material and the F_1 generations are grown in the greenhouse (Fig. 4.17a). The number of F_1 plants grown from each cross is limited (8 F_1 plants for single crosses and 24 F_1 plants from multiple crosses). In order to determine whether putative F_1 plants are true hybrids, they are compared with the female parent. A weak negative selection is carried out in F_1s from multiple crosses, mostly for straw length and disease reaction. The resulting F_1 plants are harvested in bulk per cross.

In the F_2 generation, the material is sown in plots at a very low seeding rate in order to obtain spaced plants in which single-plant selection is possible. Each F_2 population resulting from a single cross is sown in one standard plot of about 10 m^2, containing about 500 plants. A population resulting from a multiple cross is expected to show greater genetic and morphological variability and is therefore sown in two plots at the same seeding rate, in which plants infected with the most prevalent races of yellow rust are planted out. Plots with control varieties, sown at the same seed rate, are included at regular intervals. Negative selection is effected several times during the growing season by cutting back single plants which show undesirable characters. After ripening, positive selection is carried out by harvesting a number of single plants from each population. The number of plants harvested from a population depends on the information available about the parents and on the observations made on the F_2 material during the growing season. The selected plants are threshed in the field (Fig. 4.17b), and can thus be selected also for seed quality. At this stage of selection, hardly any populations are discarded completely.

Each F_3 line is grown in a single 3 m row, commonly sown by Øyjord equipment (see Fig. 4.4c). Infection rows and control varieties are sown at regular intervals. During the growing season, information on important characters like disease, straw characters, earliness etc. is collected. No roguing is carried out. At the end of the growing season, the best plant progenies are selected from every cross population, as much of the variability within the population being preserved as possible. In the selected plant progenies, single ears are harvested by hand from the best plants, again preserving as much as possible of the variability within the progeny. The total number of ears harvested from one cross population is fixed (being determined by the quantity of seed needed for sowing the F_4 generation), but the number of plant



Generation	Selection scheme	Remarks
–		Cross in greenhouse.
F_1		F_1-plants in greenhouse.
F_2		F_2: spaced plants. Selection of single plants.
F_3		F_3: plant progenies. row selection
F_4		F_4:bulk populations. Two plots. (Multiplication and observation).
F_5		F_5: spaced plants. Selection of single plants.
F_6		F_6: plant progenies. row selection
F_7		C-trials: single rep. trials at 3 locations + observation in disease nursery.
F_8		B-trial: 2 rep. trials at 3 locations + observation disease nurs. (Start of purification program).
F_9		A-trial: 4-6 rep. trials (2N-levels) + observation disease nursery.
F_{10}		Main-trial: 4-6 rep. trials + observation disease nursery. Official trials.

Fig. 4.16. Breeding scheme for wheat varieties (simplified method of bulk and pedigree selection).

progenies from which these ears are harvested may be very different from one cross population to another.

In this way, after fairly rigorous selection for agronomic characters in the F_3 narrowed F_4 populations are produced. These F_4 populations are each sown on two plots on different soil types, together with control varieties: one plot is a 10 m^2 plot on clay soil with artificial yellow rust infection, sown at 50% of the normal seed rate, and the other is a 5 m^2 observation plot on sandy soil, sown at the normal seed rate. During the growing season, no selection is carried out in either of these plots. As much information as possible on the performance on the two soil types is recorded. The plots on clay soil are harvested by combine (Fig. 4.17c) and their yield is recorded. The plots on sandy soil are not harvested separately; they are left standing as long as possible so as to obtain a good impression of straw characters and susceptibility to ear diseases.

After harvesting, when yield has been determined, selection for grain size is effected by means of rigorous grading. A sample of the seed is reserved for quality tests: protein content, flour yield, kernel hardness and dough properties.

In the F_5 generation, the populations are sown on two plots, in the same way as the F_2 populations from multiple crosses, i.e. as spaced plants, with yellow rust infection. As in the F_2 generation, roguing is carried out during the growing season and positive selection after ripening. The number of plants to be harvested in a population is now determined on the basis of the following information:

- yield and field observations in the F_4,
- field observations in the F_5,
- quality tests carried out in the previous year,
- variability within the population (number of F_3 lines which have contributed to the population and observations in the F_4 and F_5).

The selected plants are harvested separately, as in the F_2.

In the F_6 generation, plant progenies are sown in the same way as in the F_3. Besides being selected for agronomic characters, the plant progenies are now also selected for homogeneity. Promising nonsegregating plant progenies are harvested in separate progeny bulks. In promising plant progenies which are still segregating, two or more single plants are harvested, which are then reentered with the F_6 plant progenies in the next year. To avoid later problems during the purification of lines, it is essential that no segregating lines be included in the yield trials.

About 0.5 kg seed is harvested from each plant progeny in the F_6, this being sufficient for two locations in nonreplicated yield trials and a third location on sandy soil for observation. Yield trials (Fig. 4.17d) are carried out on different soil types and in different climatic conditions. All the lines in yield trials are also sown in disease nurseries with yellow rust infection. There are four levels of yield trials:

- C-trial (F_7 or later): nonreplicated trials, limited to three locations.
- B-trial (F_8 or later): two-rep trials at three locations in the country concerned and first-year trials at several locations in neighbouring countries. Besides the yield trials, seed production plots are sown, at a low seeding rate. Off-types are rogued from

Fig. 4.17.
a. Top left – Growing F_1 plants in the greenhouse.
b. Top right – Threshing F_2 single plants in the field.
c. Bottom left – 'Hege' combine harvester.
d. Bottom right – Yield trial.
(Photographs: M. de Goffau).

these plots, in order to produce relatively pure seed for the next year's yield trials. In addition, 30 single plants are harvested separately from each seed production plot. These plants form the basis for the purification programme and all further seed productions of the variety.

– A-trial (F_9 or later): 4 – 6-rep yield trials at three locations within the country and extended yield trials in neighbouring countries. One yield trial with two different nitrogen levels.

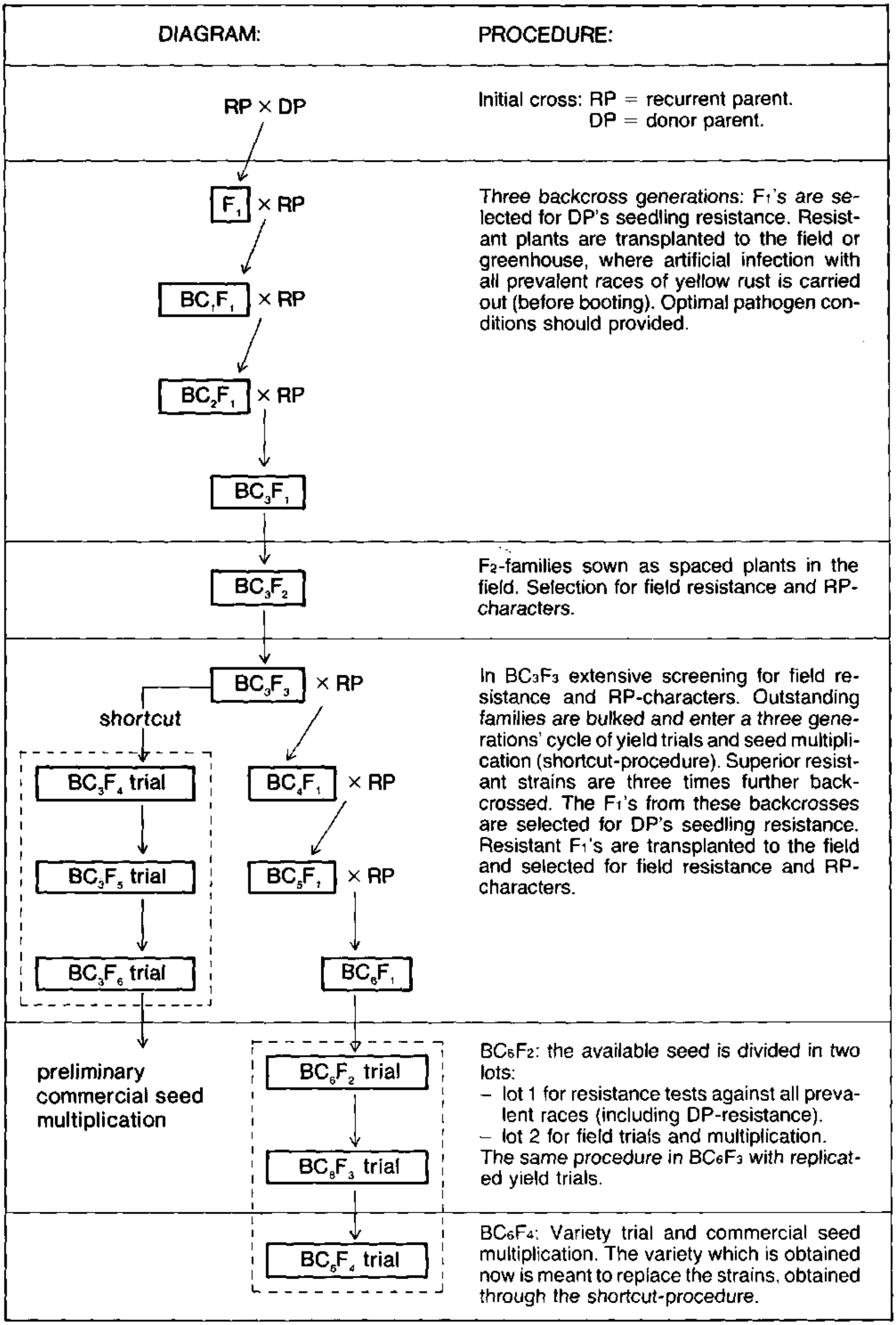
– Main trial (F_{10} or later): trials containing all lines or varieties which are in state trials of countries for which the varieties are intended. The trials are carried out in the same way as the A-trial. A limited number of lines which have reached the last stage of official trials are tested in a special trial for reaction to different treatments, e.g. nitrogen levels, CCC treatment and fungicide treatments. After two to four years of state trials, a variety may be included in recommended lists, i.e. when it has reached about the F_{12} generation.

In deciding upon the generation in which line purification should be started, the breeder has to make a compromise. If the purification programme begins at a late selection stage, the material will have reached a very high level of homozygosity, so that little genetic segregation can be expected. However, considerable amounts of pure seed will then have to be produced in a very short time. Starting at an earlier stage has the advantage that the purification work can be spread over several generations, but it also has two disadvantages: (1) there is a greater likelihood that segregation will occur in the material; (2) purification programmes have to be undertaken for a large number of lines which are still in trial, and most of this work will prove useless, becuse the majority of the lines will be discarded in the course of selection. A diagram of the purification procedure is given in Chapter 9 (Fig. 9.4).

Introducing new characters by back crossing

Back-cross methods in cereal breeding programmes are successful only for very narrow breeding objectives. The breeder may well succeed in improving an existing variety for a single or a few characters by back-cross methods, provided that the character is simply inherited. If the breeding objective involves polygenic characters, or several independently inherited characters, other methods are more appropriate. Furthermore, the expression of the character which is to be introduced by back crossing should be sufficiently pronounced and independent of environment to allow the breeder to select for it at all stages of back crossing and subsequent selection, and it should be possible to detect the character before flowering. Recessive characters are more difficult to introduce and in this case the feasibility of using a possible linkage with a dominant character should be investigated.

An advantage of the use of back-cross methods is that lines with a high level of homozygosity can be obtained in a very short time. This means that sufficiently homogeneous material can be released quickly. Back-cross breeding methods can be considerably speeded up, moreover, if more than one generation can be grown each



PROCEDURE:

Initial cross: RP = recurrent parent.
DP = donor parent.

Three backcross generations: F_1's are selected for DP's seedling resistance. Resistant plants are transplanted to the field or greenhouse, where artificial infection with all prevalent races of yellow rust is carried out (before booting). Optimal pathogen conditions should provided.

F_2-families sown as spaced plants in the field. Selection for field resistance and RP-characters.

In BC_3F_3 extensive screening for field resistance and RP-characters. Outstanding families are bulked and enter a three generations' cycle of yield trials and seed multiplication (shortcut-procedure). Superior resistant strains are three times further backcrossed. The F_1's from these backcrosses are selected for DP's seedling resistance. Resistant F_1's are transplanted to the field and selected for field resistance and RP-characters.

BC_6F_2: the available seed is divided in two lots:
- lot 1 for resistance tests against all prevalent races (including DP-resistance).
- lot 2 for field trials and multiplication.

The same procedure in BC_6F_3 with replicated yield trials.

BC_6F_4: Variety trial and commercial seed multiplication. The variety which is obtained now is meant to replace the strains, obtained through the shortcut-procedure.

Fig. 4.18. Breeding scheme for wheat varieties (back-cross method).

year. The selection procedure can be very simple; only the characters of the recurrent parent and the new character being introduced from the donor parent have to be taken into consideration.

Fig. 4.18 illustrates a back-cross method used at the National Plant Breeding Station, Njoro, Kenya, for the improvement of local wheat varieties for yellow rust resistance *(Puccinia striiformis)*. The first step in this procedure is a cross between the recurrent parent (RP) and a donor parent (DP). The recurrent parent may be a well-adapted local variety, lacking resistance to a new race of yellow rust. The donor parent may be a nonadapted resistant variety. The choice of the recurrent parent as well as the donor parent should be carefully considered. The recurrent parent should be of proven agricultural value, for no essentially new characters will be introduced in the course of the selection procedure, apart from the target disease resistance. The genetic background of the donor parent's resistance should be known and, if possible, the breeder should be aware of any close linkage between the donor parent's resistance and any undesired characters.

This breeding procedure has proved very successful in Kenya, because it allows varieties which are a clear improvement over existing varieties to be released within a very short time. There is hardly any improvement that appeals more to the farmer than marked differences in disease reaction. As a short-cut procedure for the preliminary release of commercial seed, the method appeals to the breeder but it can only be applied if requirements regarding varietal purity are not too strict, or if purity requirements do not need to be met until material can be released from the final back-crossing cycle.

HYBRID WHEAT

There are four prerequisites for the economic production of hybrid wheat *(Triticum aestivum)*:

1 Stable cytoplasmic male sterility and/or reliable gametocides should be available.
2 Stable genetic and/or chemical fertility restoration should be practicable .
3 It should be possible to ensure a high level of cross pollination.
4 The F_1 varieties should produce much more than the best other varieties available.

We will discuss the four requirements in turn.

Production of male-sterile plants

Genetic male sterility is unsuitable for crops like wheat and barley. It cannot be used to breed male-sterile lines (A-lines) because a number of the plants will be fertile. A BTT (balanced tertiary trisomic) system (cf. p. 127) is attractive in principle, but there are three major objections to it: first, the production of BTTs is laborious and time-consuming; second, BTT plants are generally weak, with reduced pollen and seed production; and third, the extra chromosome is liable to be transmitted (the frequency of transmission being up to 17% for barley), with the result that fertile plants appear in the male-sterile population. Such fertile plants will pollinate a higher proportion of the neighbouring male-sterile (isogenic) sister plants than will the intended pollen parent.

Cytoplasmic male sterility (CMS) is found in wheat. The most frequently used is that conferred by cytoplasm of *Triticum timopheevi*, but 'sterilizing' cytoplasms of other species are also available. The *timopheevi* cytoplasm appears to be stable under all weather conditions, but there are indications that it has certain drawbacks (Sage, 1976). For instance, in Yugoslavia it has been observed that plants with *timopheevi* cytoplasm produce seed with a reduced germinating capacity and are more cold sensitive; however, they have a larger flag leaf area and a higher content of chlorophyll a + b in the flag leaf (Jošt et al., 1975.) Yield figures are not yet available. In England it has been found that *timopheevi* versions of Minister (a Belgian winter wheat with fertility-restoring capacity) and of other varieties are liable to sprout in the ear, a characteristic not observed in the varieties themselves (Sage et al., 1973). In addition, lower yields have been recorded in spite of optimal pollination conditions, a possible reason for this being the degeneration of the vascular bundles in the rachis of the spikelets.

It would be useful to investigate other sources of CMS, not only in *Triticum* (including other sources of *T. timopheevi*) but also in rye and *Aegilops* species. The use of a greater diversity of sterilizing cytoplasms may prevent disease epidemics similar to that affecting maize with Texas-CMS (cf. pp. 202-203).

Gametocides Most published gametocide research has been carried out with Ethrel (2-chloroethanephosphonic acid) (Hughes et al., 1974; Dotlačil & Apltauerová, 1978; but see also Jan et al., 1976). The action of Ethrel is specific, i.e. it only sterilizes florets at a certain stage of development, immediately before meiosis of the pollen mother cells. Since there are differences in stage of floret development within one ear, one plant and one field, several applications of Ethrel are needed and even then not all florets necessarily become male sterile. Any fertile floret remaining will pollinate itself and neighbouring florets, giving rise to selfed seeds. Too early an application of Ethrel prevents the emergence of the ear. For granular Ethrel, it has been shown that the slow but continuous release of relatively low quantities of Ethrel, absorbed through the roots, causes almost 100% male sterility (Fairey & Stoskopf, 1975). Further research is needed to confirm these data.

The action of Ethrel is affected by the environment, and genetic effects also play a part. Selection should be directed towards genotypes which are readily sterilized. If the ideal gametocide, consistent and systemic in action, could be found, a single treatment of the grains would suffice. In view of the possibility that the use of gametocides may in the end prove to be the only practicable way of producing hybrid wheat, it may be said that research on gametocides by chemical companies and plant breeding stations is still on too small a scale.

Fertility restoration

Genetic fertility restoration Fertility-restoring genes, or *Rf* genes, (cf. p. 129) have been found in bread wheats (*T. aestivum*) and related species (Zeven, 1968; Hughes & Bodden, 1977). The action of Rf_{ae} genes (found in *T. aestivum*) seems to be strong, whereas that of the Rf_{tim} genes is weak. The weaker the *Rf* genes, the more of them are needed, their effects being additive.

But breeding a restorer line (R-line) with more than two *Rf* alleles is more difficult than breeding an R-line with only one pair of *Rf* alleles. Hence the search for *Rf* genes with really effective action. There are indications that such a gene is available in west European varieties such as Minister and Primépi. This gene is probably identical to the one found in central European spelt varieties (*T. spelta*).

The breeder sometimes experiences trouble from unwanted fertility restoration in A-lines and from inadequate fertility restoration in R-lines and F_1 hybrids. The genetics of male sterility and fertility restoration in some material is rather complex, and not well understood. It appears that genetic background and environment may cause unexpected changes in the expression of male sterility or fertility restoration. For this reason, the breeder should be careful to check his A-lines and their specific maintainer lines for sterility genes and for *Rf*-inhibitor genes, and also for minor *Rf* genes which may restore fertility under certain environmental conditions. He should also check his R-lines for the presence of *Rf* alleles which may restore fertility in the heterozygous condition, irrespective of the genetic background of the F_1 hybrid and of the environment. More research is needed on these matters.

In addition, investigation is needed into the effects of sudden changes in weather immediately before or during flowering. In the bread wheat variety Penjamo 62 in Tunisia it was observed that a sudden drop in temperature of 8-10 °C resulted in male-sterile plants. Such drops in temperature may be caused by sudden rain showers. The breeder should therefore aim at stability in his A-lines, maintainer lines, R-lines and F_1 hybrid varieties. The possibility of an unexpected and perhaps considerable interaction between idiotype and environment cannot be excluded, which would mean that F_1 hybrid varieties can be bred only for regions with a limited environmental range.

The introgression of inactive *Rf* alleles or *Rf* alleles with only a slight action can be prevented by breeding R-lines with the sterilizing (*S*) cytoplasms specific for those alleles. Even so, it would still be possible for the desired *Rf* genes in the R-lines to be lost inadvertently owing to the homozygous condition of another *Rf* gene or genes. Similarly, the unnoticed introgression of a sterility gene or an *Rf*-inhibitor gene into an A-line will be harmful.

Chemical fertility restoration Research into stable fertility-restoring (gametoficant) chemicals is required. If gametoficants were available, there would be no need to develop R-lines and dependence on unstable genetic restorer capacity would be eliminated. A systemic chemical of this kind would be ideal.

Level of cross pollination

Selection should be aimed at female flowering (open flowering, prolonged stigma receptivity) and male flowering (open flowering, abundant light-weight pollen grains, prolonged pollen-grain viability). In some regions, environmental factors may have an effect on cross pollination; for example, high temperatures (above 19 °C) and/or low relative humidity (below 60%) shorten the life of both stigma and pollen. Selection for resistance to these factors should be undertaken. Weather conditions before flowering may affect the degree of overlap between the flowering periods of A-lines and R-lines. Simultaneous development of these lines should be an aim of selection. In the Netherlands the seed set on male-sterile plants varies in general from 10 to 80% (de Vries, 1974). Rain hinders cross pollination .

The difficulties encountered in ensuring sufficient cross pollination have the advantage that little isolation is needed in hybrid wheat seed production. In work on experimental crosses in the Netherlands for instance, hybrid production using unlimited numbers of different pollinators in the same field has proved feasible. This is done by separating the hybridization blocks, each of which consists of seven plots, by means of cotton screens, as shown in Fig. 4.19. (To make the lay-out clearer, the photograph shows the field with one set of screens removed). In each block of seven, plots 1, 3, 5 and 7 are sown to one pollinator and plots 2, 4 and 6 to three different male-sterile lines. The field illustrated produces 90 different hybrids. The percentage of crossing between blocks is so low that the level of seed purity is acceptable for experimental purposes.

Yield superiority of F_1 hybrids

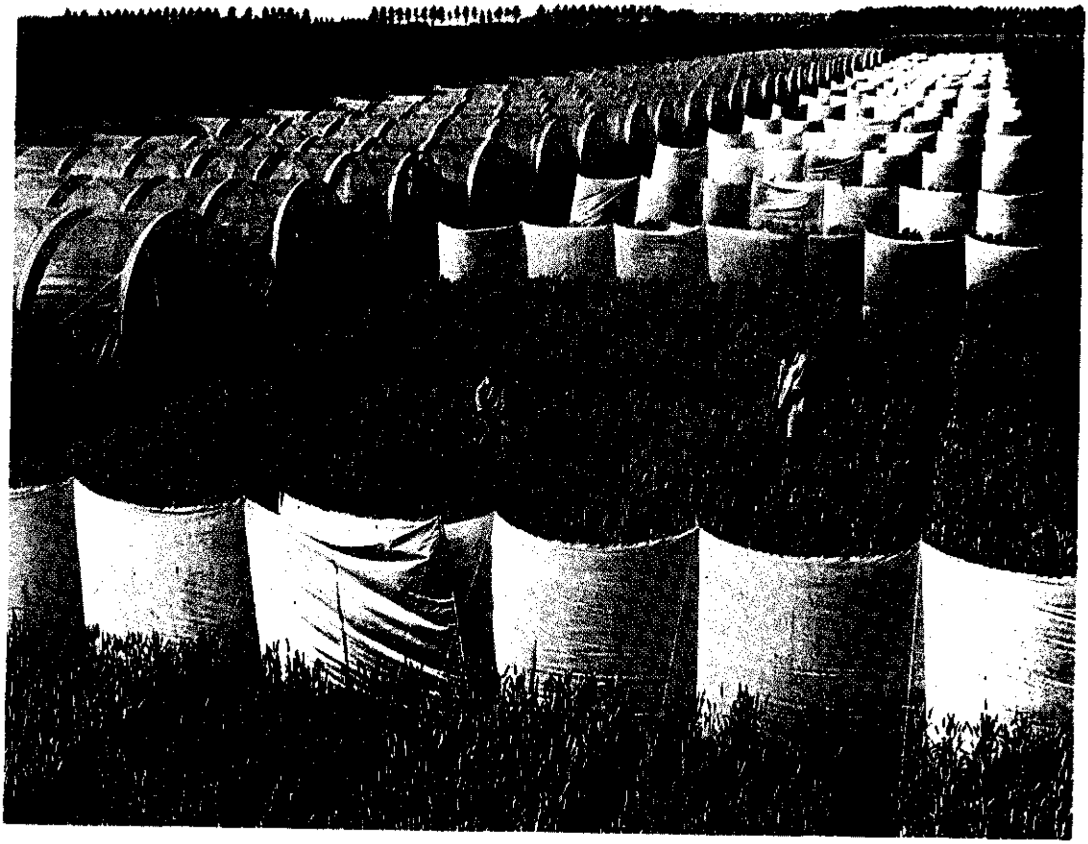
F_1 varieties should produce so much more than the best varieties available that the use of the more expensive hybrid seed nevertheless gives the farmer an extra profit. A high degree of heterosis for yield has been observed in certain combinations. However, this in itself is not enough: the difference in yield between an F_1 and the best varieties available must be sufficient to cover the cost of breeding and use of hybrid varieties.

At Wageningen, Netherlands, it was found (in a single trial of six hybrid combinations at one site in one year) that there was no relationship between the heterosis effect and plant density (Zeven, 1972). If this conclusion is generally valid, it will be possible to test F_1s at low density.

More research on the cultivation of hybrid varieties is needed. There are frequent

Fig. 4.19. Production field of 90 experimental wheat hybrids involving 30 different pollen parents each crossed on three different male-steriles. (Photograph: M. de Goffau).

Fig. 4.20. Plot combine for harvesting and weighing grass plots. (Haldrup 1500). Capacity: ± 100 plots per man hour. (Photograph: M. de Goffau).



references in the literature to the general combining ability (GCA) and specific combining ability (SCA) of varieties. A variety with good GCA can be used in many combinations. However, SCA should not be disregarded, as a combination with high SCA may give a higher yield than a combination between good general combiners.

The results so far obtained for percentage heterosis in relation to the best available variety are not encouraging. The yield increase may well be so small that the extra costs of breeding a hybrid variety are not recovered. The buffering effect of the hexaploid may reduce heterotic effects (Zeven, 1972). From practical experience, Geling (personal communication) suggests that a hybrid variety should yield at least 15% more than the best available variety in order to cover its breeding costs. It may be worth noting that in western Europe a yield increase of 20% would mean an additional 1000 kg/ha, whereas in the USA it would mean only an additional extra 500 kg/ha. The latter may be easier to attain than the former. This suggests that it may be feasible to grow hybrid wheat in the USA but not in western Europe.

In countries with little or no legislation for plant variety protection, hybrid varieties may be of economic importance.

Conclusion

It appears that, of the four requirements for the economic production of hybrid wheat, the first (stable CMS) and the second (stable fertility restoration) can more or less be met. The third (good cross pollination) needs further investigation. In regions characterized by variable weather it will remain an uncertain factor. It would be possible to by-pass this difficulty by propagating hybrid seed in an area with stable weather conditions, but this could increase the costs of organization and transport, and the parent lines would moreover have to be resistant to diseases present in that area.

It is too soon to reach any final conclusions regarding the future of hybrid wheat. There are still many problems to be solved. Results obtained so far, however, are not very encouraging. When a suitable gametocide becomes available the prospects of hybrid wheat can be expected to improve. The great advantage of this – apart from the reduction in breeding work, since neither A-lines nor R-lines would be needed – would be the rapidity with which a hybrid combination would become available. The good combination of today will be available as F_1 hybrid variety tomorrow. At present, the breeding of A-lines and R-lines takes so much time that the good combination of today has to compete with conventional varities that become available 5-10 years later.

The full development of hybrid maize took about 50-60 years of research. Hybrid wheat is now at a stage comparable to that of hybrid maize in the mid-1930s. While the final outcome cannot yet be predicted, it would be unfortunate if wheat breeders concluded on the basis of the limited data now available that hybrid wheat has no future and in doing so lost the opportunity to take advantage of heterosis in one of the world's most important cereals.

HYBRID RICE

Heterosis has frequently been found in hybrids of rice (*Oryza sativa*), though sometimes the so-called hybrid vigour is not true F_1 superiority or heterobeltiosis but superiority over the midparent value (Chang et al., 1973). The use of F_1 hybrids in commercial rice production hinges on the extent of heterobeltiosis and the ease and cost of producing F_1 seed.

During the last few decades, several rice workers have been engaged in the identification and improvement of sources of cytoplasmic male sterility, or cytosterility. Considerable progress has been made in obtaining male-sterile lines from *spontanea* forms of *O. sativa*, Indica varieties from India, Taiwan and the IRRI, Indica × Sinica (Japonica) hybrids, and a number of Chinese varieties. Similarly, good maintainer lines and fertility-restoring sources have been found (Chang, 1964; Watanabe, 1971; Athwal & Virmani, 1972; Carnahan et al. 1972; Li, 1977). However, much remains to be done in finding male parents producing abundant pollen and specific cross combinations that would perform well both in grain yield and seed set.

In 1974 there was a major breakthrough in the commercial production of hybrid rice in mainland China. The cytosterile source was collected from Hainan Island in late 1970 and was probably a hybrid between a red-awned wild rice plant (*spontanea*) and a local Indica variety. Pollen sterility apparently resulted from an interaction between incompatible cytoplasm and nucleus. The sterile plant was used by researchers in Kiangsi, Hunan and Kwangsi provinces to produce the male-sterile lines. The maintainers were largely developed from local Indica varieties during 1973. Most of the useful restorers were of the Indica type, including IR24 and IR26. Experimental planting of F_1 hybrids began in 1974, and by 1976 about 130,000 mou (8670 ha) of F_1 hybrids were being grown. Hybrid seed production ranged between 1.50 and 5.25 t/ha. The highest yields obtained from the F_1 hybrids were around 12 t/ha. The yield increases compared with existing varieties ranged between 10 and 30%, averaging about 20% or slightly more.

The superior performance of hybrid rices was ascribed to their vigorous root system, vegetative growth vigour, high tillering ability, larger and dense panicles, heavy grains, and wide adaptation in the middle Yangtze River basin and in south China across many topographical and soil types (Hunan Provincial Rice Research Institute, 1977; Li, 1977; Yuan, 1977). A comparative study of the hybrid Nan U-2 and the improved pure-line variety Kuang Yu 73 revealed the following characteristics of the hybrid: larger leaf area, lower photosynthetic efficiency per unit leaf area, lower nitrogen and phosphorus contents of the shoot, higher root activity, larger root system, lower respiration intensity and lower photorespiration rate. When compared to its three parental lines, the hybrid showed a faster decline in photosynthetic activity during the ripening stage, a sustained high root activity and a higher requirement for potassium. Both maternal and paternal influences on the above physiological activities were noted (Hunan Agricultural College, Department of Chemistry, 1977). The extent of heterosis was proportional to the genetic diversity between the parents (Kwangsi Rice Heterosis Utilization Cooperative Team, 1977).

Studies made in Hunan Province indicated that the highest frequency of cross pollination and seed set (74%) occurred during early September when the daily mean temperature was 22 °C or above. The male and female parents were planted on different dates to ensure simultaneous flowering. The flowering time of the pollen parents appeared to be more readily affected by the date of transplanting. The flowering date of the pollen parent could also be modified by drainage or irrigation, nitrogen top-dressing, clipping of the flag leaf, and foliar application of a suitable chemical ('920' or gibberellin) or chemicals. It was also possible to increase pollen production by the male parents and to increase the spikelet number of the female parents by modifying cultural practices. Panicle exsertion and seed set could be enhanced by clipping of the flag leaf, stripping the sheath of the flag leaf and spraying with '920'. The range of seed set obtained from the same hybrid planted at six production brigades (a brigade is a unit under a commune) with varying ratios of male and female plants (2:5 or 2:6) was from 33 to 45% (Hunan Agricultural Bureau & Revolutionary Committee of Yan-pai-du Commune, 1977).

The sterile anthers generally contained less proline than those of the maintainer and restorer lines. Retardation of sugar metabolism and a decrease of aminoacids were associated with male sterility (Kwangsi Teachers' College, 1977). The critical phase appears to be the binucleate stage of the pollen mother cells, when the activities of cytochrome oxidase, polyphenol oxidase and ATPase become lower, respiration rate increases, and hydrogen peroxide is formed, resulting in little accumulation of starch and protein (Kiangsi Communist University, Department of Agronomy, 1977).

The costs of producing F_1 seeds by labour-intensive practices and supplementary measures such as hand-assisted cross pollinations were not discussed or considered by the Chinese workers.

The planted area of hybrid rice in China reached about 500,000 ha in 1978. The extensive use of F_1 hybrids was made possible partly by the distinctly lower rate of seeding (about 1/4) that is needed for transplanting each unit area of land, owing to the greater growth vigour and higher tillering ability of the hybrids over the conventional varieties. During the drought of 1977 and 1978, the hybrids proved to be more resistant to water stress, as they have more vigorous root systems than their parents.

Grasses

This group of crops is characterized by a great natural wealth of genotypes. Hence new varieties can often be produced with little or no breeding. Many cultivated grasses are propagated by seed, but often they can be maintained and reproduced vegetatively. This allows special breeding methods to be applied, such as the polycross and its variants. The occurrence of apomixis, as in Poa pratensis, may give rise to difficulties in breeding but *can sometimes be circumvented by physiological manipulation. Intergeneric crosses are receiving attention, but the seed set of their progeny tends to be low. Cytoplasmic male sterility has been available for some years in some species and can be used in breeding* F_1 *hybrids. The production of commercial hybrids with good performance remains a challenge to the breeder.*

INTRODUCTION

The grasses in cultivation today are those found growing in the wild yesterday. Within a species, no clear-cut distinction can as yet be drawn between cultivated and wild, for both may exist together in the same or adjacent associations. On one side of the fence we may find a sown pasture developed from plants collected from the old grassland on the other side. Similarly, the mown grass verges lining a street may well be based on material picked by breeders from the pavement.

Domestication, a term loosely applied at best, therefore has little relevance in discussing grasses, except perhaps when narrowed down to certain aspects of seed production. It is here that grasses have been exposed in very recent times to the same forces of selection as led to the birth of some of our cereals a few thousand years ago.

The grass breeder is in fact charged with the task of subjecting wild material to agricultural uses whose horizons are obscure. What do yield and quality mean in forage grasses as compared with cereals or other crops in which storage organs are the harvestable part? Even when grass yield is expressed in terms of metabolizable energy, its actual value can only be realized in terms of the grazing animal. To comprehend the chain of events that links the assessment of the individual spaced plants of the breeder's choice with the ultimate grazing value of the ensuing variety is the challenge faced by the grass breeder.

The immediate benefit of forage grasses is mainly sought in their conversion to meat, milk and fibre, but often as not high value is also attached to the soil-ameliorating effects of grass swards, both in primitive shifting cultivation and in the sophisticated cropping schedules of mechanized agriculture. A grass break can work wonders where biocides and fertilizers fail. Numerous instances can be cited of grasses grown in rotation with crops to achieve control of pests, diseases and weeds, to charge the soil with organic matter, to improve the infiltration of scarce rainfall, and to combat erosion. In cases where the farmer is better at crop husbandry than at animal husbandry it may well be that the contribution of such grass breaks to the economy is made through the soil rather than through the rumen. Grasses protect the crop production capacity of the soil and in many instances the soil itself. Had *Pennisetum clandestinum* (Kikuyu grass) not found its way in recent decades into the Andes and other mountain areas and crept up the slopes to rescue land abused by deforestation, overcropping and overgrazing, irreversible damage would have been done to land resources and water catchment systems.

In order to raise the productivity of land and to be able to exploit new and better husbandry techniques, modern agriculture requires new varieties. But in order to protect his variety and, indeed, his own interests, the breeder also has to meet certain requirements of legislation. These various requirements should not be regarded as mutually exclusive. In fact, many of the farmer's and breeder's interests overlap.

Only three home-bred grass varieties were mentioned in the 1930 Dutch Recommended List, while the other grasses described originated from foreign stocks. By 1978 this number had increased to 135, and many of these varieties have also found their way into the agriculture of other countries in Europe and elsewhere.

In this article we outline some of the aims and procedures of grass breeding, bearing in mind that the excellence of the varieties of tomorrow will depend on the use we make of nature's gifts today.

BREEDING OBJECTIVES

In view of the rather involved grass-animal-farm relationships, the many genera and species involved, and the nature of the plant itself, breeding objectives in forage crops are often regarded as complicated. The aim is the improvement not merely of one harvestable part of the plant, but rather of the plant as a whole.

One basic requirement common to all crops is that the variety should be composed of sufficiently uniform genotypes to ensure varietal stability over successive generations of seed multiplication and to ensure that it can be recognized with the means usually employed to distinguish individual varieties. In addition, the breeding of herbage crops is concerned, directly or indirectly, with the following:

- herbage yield and its seasonal distribution,
- nutritive value,
- seed production,
- resistance to adverse weather conditions,
- persistency.

A situation in which all characters need to be improved simultaneously from an initially low level will rarely be encountered. More often than not, work will be concentrated on species and varieties which are already popular and improvement will be sought in a few characters which are considered to be limiting. Characters rarely vary independently and care must be taken that improvement in one character is not nullified by a correlated negative response in another of agricultural importance.

Herbage yield and its seasonal distribution

Herbage yield is one of the commonest characters measured in plant breeding programmes, and this applies not only where a direct yield increase is the objective of the breeder. Tolerance to biotic and abiotic factors, longevity of the sward and even rapidity of seedling growth are also usually assessed by measuring the yield, though certain refinements are possible, such as the inclusion of parameters of sward structure and leaf : stem ratios.

The number of livestock that can be maintained by the farmer is restricted by the occurrence of periods of poor herbage growth rather than by the total annual yield. Equally, an increase in total annual herbage yield may not be essential if most of the extra feed produced comes at a time when a surplus is already giving rise to management problems. However, strategic application of nitrogen, suitable conservation practice and judicious grazing management all help to distribute the supply of feed throughout the year.

Herbage is usually assessed either visually or by cutting and weighing (Fig. 4.20). Both methods are simple and both are of great value, provided it is realized that the grazing animal is the final arbiter. Evaluation using the grazing animal is important at many critical stages in the development of a breeding programme and can be simple and meaningful if judiciously applied. Direct grazing trials, however, are too unwieldly and rigid to permit proper interpretation of the results. In any case, there seems little point in letting a grazing trial show the best of three selections, if 97 have already been rejected on the basis of very simple evaluation methods.

Nutritive value

When simple techniques for screening large numbers of plants for digestibility, which is the main component of nutritive value, first became available in the 1960s, hopes were high that breeding would achieve a breakthrough in selection for nutritive value. High digestibility, where the material tested is comparable, usually results in better voluntary intake and better animal production. In temperate grasses, digestibility of the organic matter is usually of the order of 70-75%, but it is lower in tropical grasses, where it hardly exceeds 60%, so that a large proportion of the herbage cannot be utilized effectively.

The application of the *in vitro* digestibility technique in Kenya brought to light a promising degree of plant-to-plant variability in existing ecotypes of Rhodes grass (*Chloris gayana*) and setaria (*Setaria sphacelata*). Ranges were found of more than 15-20% digestibility units and relatively high estimates of heritability were established. However, it was subsequently found that much of this variability was secondary and could be accounted for by variation in heading date and herbage yield. Early-heading plants are higher in digestibility than late-heading plants, when compared at the same morphological stage, but when compared on the same date the late-heading plants are higher in digestibility.

It appears that there is larger scope for improving nutritive value in tropical grasses than in temperate grasses because of the lower level in the former. In Bermuda grass (*Cynodon dactylon*), the variety Coastcross was developed by crossing the variety Coastal with a highly digestible introduction from Kenya and selecting the hybrid having the best digestibility at different periods of regrowth (Burton et al., 1967). The new variety exceeded the Coastal parent by 12.3% in digestibility over a 4-year period. Steers grazing Coastcross in a triplicate grazing test for four years made 39% better average daily gains than those grazing Coastal Bermuda grass (Utley et al., 1974). It must be realized, however, that inherent plant characteristics (the greater amount of structural carbohydrates in tropical grasses) and climatic conditions (the higher temperatures of tropical areas) do not allow large increases in quality. However, proper grazing management could in itself make a considerable contribution to the improvement of nutritive value.

Seed production

The ability of a grass to produce seed in commercial quantities has often dictated its success in agriculture, regardless of its virtues as herbage. Also, where all varieties are regarded by the farmer as being much the same, those with the cheapest seed will be the most popular.

Vegetative propagation is the only practicable means of establishing tropical grasses such as Pangola digit grass (*Digitaria decumbens*), Bermuda or star grass (*Cynodon* spp.) and elephant grass (*Pennisetum purpureum*). Even when mechanized, vegetative propagation invariably involves more work and higher costs than multiplication by seed and can be an active deterrent to the setting up of grass establishment programmes in developing countries.

More critical, however, is the fact that vegetatively propagated grasses, by their very nature, comprise only one or a few genotypes and are therefore more prone to serious disease problems. Pangola digit grass has been severely attacked by Pangola stunt virus in Central America and by rust in Australia. Star grass in Kenya is commonly attacked by a wide range of pests and diseases even in its natural habitat. Elephant grass has also become more and more liable to fungus attack in recent years.

Seed yields of tropical grasses are very low in comparison with those of temperate grasses. This is largely due to the extended heading, flowering and seed maturation patterns displayed by these grasses. However, a better understanding and application of the correct cultural techniques have gone a long way towards solving some of the practical problems. In addition, breeding is an obvious way of increasing the seed yield of varieties with a large variation in heading date and in seed yielding potential.

Traditionally, seed yield has been regarded as incompatible with herbage quality and with longevity of the sward under grazing. However, a thorough investigation of the material will often give the breeder the clues he needs in order to be able to combine desirable traits within one variety. In Kenya new varieties of Rhodes grass and setaria, the two most commonly sown grasses, have been developed that combine high herbage and seed yields, while in the Netherlands the early perennial ryegrass variety Cropper (*Lolium perenne*) also combines these two characters.

Restistance to adverse weather conditions

Seasonality of production is pronounced in many climates, even during the active growing season, in response to often small variations in temperature and rainfall and also to physiological changes in the plant itself. The breeder's aim is to extend production in periods which affect growing conditions adversely, such as drought and cold.

Some grasses have a better ability to maintain a certain amount of green leaf in dry periods than others. Rhodes grass and setaria, for instance, produce equal amounts of dry matter annually, but the former produces a greater proportion in the transitional period between the rainy and the dry season.

In north-western Europe attempts have been made to introduce the ability to grow at low temperatures from Mediterranean into local varieties of ryegrass. Difficulties have been encountered, however, in reconciling the desirability of low-temperature growth with the need for winter hardiness.

Persistency

The persistency of a grass is expressed by the maintenance of a certain yield level over a number of years and is closely related to the grass's ability to survive adverse weather conditions, its resistance to diseases, its competitive ability in mixtures and the type of management imposed.

Lack of persistency will soon give irregular open swards, as shown in Table 4.7 (Schejgrond & Vos, 1961). An open sward is not only invaded by weeds and hence less productive, but it is also more susceptible to cold and frost. It is clear from the table that breeders have broken the correlation between lateness of heading and high persistence in *L. perenne* and have produced early varieties with high persistence.

Table 4.7. Ground cover of different varieties of *Lolium perenne* (from Scheijgrond & Vos, 1961).

Varietal type	% Cover	
	After 3 years' frequent mowing of pure swards	After 3 years' grazing of grass/clover mixtures
Late, persistent	90	85
Late, moderately persistent	40	40
Medium late, persistent	90	75
Medium late, nonpersistent	5	5
Early, persistent	85	80
Early, nonpersistent	2	12

BREEDING METHODS

Ecotype breeding

Grasses display considerable differentiation into populations adapted to various natural or man-made environments; these plant populations are often referred to as ecotypes. In breeding, seed or vegetative material is collected from as many ecotypes as possible and screened in comparative trials. Promising introductions are multiplied directly for commercial use. It is necessary to realize, however, that though the general appearance of the ecotype may seem uniform, nevertheless considerable variation exists within the ecotype. This could lead to a genetic shift during seed multiplication, and if application is then made for breeders' rights, objections could be raised on grounds of lack of intravarietal uniformity.

Phenotypic selection

In order to improve uniformity the next step is to examine the extent of variability within the ecotypes and to select plants of similar appearance.

Cross-pollinating grasses are highly heterogeneous and the individual plants are highly heterozygous. As grasses have only recently been subjected to intensive cultivation and artificial selection, the greater part of the variation present in ecotypes is additive, so that considerable progress can be expected from phenotypic selection. The success of phenotypic selection depends on how accurately plants with a superior breeding value, based on the additive effects of polygenes, can be recognized from their phenotypic expression. The presence of nonadditive gene effects, due to dominance, epistasis and environmental effects, is a hindrance to their identification. A powerful tool in minimizing these environmental effects is the use of repetitive measurements on the same plants and clonal replicates.

Initial selection is usually made from plants grown at wide spacing. However, the performance of spaced plants may be different from performance under sward conditions, for in the absence of competitive stress, poor plants can excel, while under sward conditions these plants would vanish.

Compared with plants in drilled field conditions, spaced plants may give too optimistic an impression of seed-yielding ability, but they are convenient for scoring for time of head emergence, growth habit, disease resistance and winter hardiness. One solution of the problem is to evaluate the single plants in a dense sward of another genus. A further refinement can be used in rhizomatous and stoloniferous grasses. In such grasses, monogenotypic swards can be established. To prevent the individual swards from invading each other, barriers of a different type of grass can be planted or sown between them, thus subjecting all swards to equal competition.

Phenotypic selection can be applied in two different ways. Negative selection can be applied by removing off-types from the space-planted field before flowering, the remaining plants being allowed to intercross for seed production. With positive selection, promising plants are picked out either for further evaluation in replicated clonal rows or for intercrossing with other similar plants to produce seed.

Phenotypic and genotypic selection

To obtain information on the genotypic value of the plants, progenies from selected plants grown in a suitable mating design are tested to allow superior parent plants to be identified. Breese & Hayward (1972) have raised a number of objections, on genetic grounds, against progeny tests, as they may squander genes that are additive in action, thereby making dominance and epistasis more important than they originally were. But one of the main practical reasons for establishing progeny tests is the difficulty of obtaining meaningful measurements on individual plants, whereas seed progenies can be sown out in little swards.

The mating designs used in grass breeding are:

- the polycross,
- the top cross,
- inbreeding,
- the diallel cross.

The polycross Plants that have been selected phenotypically (about 50) are multiplied vegetatively in a greenhouse (Fig. 4.21) and planted in a polycross in such a way that in each replicate (normally 8 replicates) one clone is surrounded by four other clones, with a view to making panmixis as complete as possible. The clones included in the polycross are also planted in a clone collection for future reference and maintenance.

Seed is harvested per clone, enabling the breeder to select for seed production characters simultaneously, and the individual progenies are included in a progeny test. The plants that produce outstanding progenies are selected, and isolated crossing plots are established from the clones maintained in the clone collection.

It has to be borne in mind, however, that the original polycross as described by Frandsen & Frandsen (1948) is only applicable to those grasses that can be maintained vegetatively for a number of years. Difficulties are encountered in clonal collections of perennial ryegrass for example, which can be heavily affected by virus diseases, while Westerwolds ryegrass (*L. multiflorum* ssp. *gaudini*) cannot be maintained vegetatively at all. Clones of setaria and Rhodes grass can be maintained for four or five years without serious problems.

In the polycross progeny test, selection is carried out for general combining ability, which depends on the additive variance of the phenotypically selected clones. But if only four or five plants are selected, specific combining ability, which depends on dominance and epistasis, may assume importance, and here no information is available. Therefore, in order to safeguard the final selection, the polycross must be followed by a diallel cross between the four or five selected plants, which is rather time consuming. To limit the risk of a large specific combining ability effect, the first

multiplication of the new variety can be established from the remnant seed of the progenies of the best clones. This has the further advantage that it is easier to store seed samples for a number of years than to maintain clones for a long period.

One of the major objections to the polycross method is that total panmixis is rarely encountered, especially where the number of plants is large. Also, if overdominance is the cause of good combining ability between the clones, the polycross method will lead to an equilibrium of gene frequencies, instead of an accumulation of favourable dominant genes.

The top cross In the top cross the phenotypically selected plants are intercrossed with a common pollen parent, which may be a variety. On the basis of the performance of the top-cross progenies, final selections are made. The comments made on the polycross, regarding the maintenance of the vegetative material, also apply to the top-cross method. In comparison with the polycross method the top cross is much easier to execute. Both methods yield a large quantity of seed. The choice of the common pollen parent is of paramount importance. Thus an advantage of the polycross compared to the top cross is that no external pollen source is used.

Inbreeding Selected plants are self fertilized (Fig. 4.22) and the S_1 progenies are raised for evaluation. The degree of inbreeding depression reflects the amount of additive variance present. On the basis of the performance of their progenies, parent plants are selected.

The major disadvantage of inbreeding is the occurrence of random drift and the rapid fixation of genes. Moreover not all plants are self compatible, and to discard these plants is thought to be risky as they may possess favourable characteristics. Only small amounts of seed are harvested and hence progeny tests can only be conducted as spaced plants or in drilled rows.

The diallel cross Selected plants are crossed in all combinations and on the basis of the performance of their progenies selection is made for general and specific combining ability. This method is very laborious and only little seed is harvested.

Ploidy breeding

In the Netherlands breeding for autotetraploidy in perennial ryegrass (*Lolium perenne*) and Italian ryegrass (*L. multiflorum*) started in 1949. In 1963 the first tetraploid varieties appeared on the Recommended List of Varieties. The breeding of polyploids in perennial ryegrass was initiated with the aim of improving winter hardiness, while in Italian and Westerwolds ryegrass the aim was to increase varibility

Fig. 4.21. Vegetative multiplication of grasses in a greenhouse. (Photograph: M. de Goffau).

Fig. 4.22. Production of seeds by self pollination of *Lolium multiflorum*. (Photograph: M. de Goffau).

within the species (Wit, personal communication). The material obtained – the original plants were genetically as diverse as possible – was allowed to intercross and ample variation was present in the segregating progeny for further selection.

The chromosome number is usually doubled by treatment of germinating seeds with the alkaloid colchicine. Apart from the colchicine concentration and the duration of the exposure, plant vigour, genotype and growing conditions play an important role in the success of the treatment. Several important characters are affected by chromosome doubling. The difference in appearance between tetraploid and diploid *L. perenne* is shown in Fig. 4.23. Van Bogaert (1975) compared diploid and tetraploid varieties of *Lolium* species for the following characters:

– 1000-grain weight. That of tetraploid varieties was 72 to 84% higher than that of diploid varieties.

– Seed yield. An increase of up to 59% compared to diploid varieties was observed in tetraploid varieties, but this was mainly due to the higher 1000-grain weight. Thus the total number of seeds harvested from the tetraploids was smaller.

– Forage yield. The yield of green matter of tetraploid varieties of Westerwolds, Italian and perennial ryegrass was on average 18%, 13% and 8% higher, respectively, than that of the corresponding diploid varieties. But the dry matter yield of tetraploid and diploid varieties was approximately the same owing to the lower dry matter content of the former.

– Disease resistance. Chromosome doubling had a favourable effect.

– Winter hardiness. Contradictory results have been obtained in various studies but from the Dutch list of varieties it appears that there is little difference between tetraploid and diploid varieties.

– Tillering and persistency. Tetraploid varieties had a less dense sward than diploid varieties and did not withstand grazing to the same degee.

– Nutritive value. Livestock undoubtedly preferred tetraploid varieties. In considering voluntary intake the lower dry matter content of the tetraploid varieties has to be taken into account.

Hybrids based on male sterility

When conventional methods of breeding to increase herbage yield have been exhausted, it should be possible to develop varieties with hybrid vigour. Because of the self-incompatibility system in many grass species it is, in theory, feasible to produce hybrids of this kind. But so far no workable means of exploiting them commercially have been developed.

A prerequisite for the production of hybrid families or populations is the presence of male sterility in the mother plant. In the Netherlands male sterility was introduced

Fig. 4.23. Comparison of a diploid (left) and a tetraploid (right) shoot of *Lolium multiflorum*. (Drawings: A. Koornneef).

into *Lolium* species (Wit, 1974) by crossing with autotetraploid meadow fescue (*Festuca pratensis*) and back crossing the hybrid with *Lolium*. The inheritance of the male sterility is probably of the nuclear cytoplasmic type.

Once male-sterile plants (A-types) have been developed, maintainers of male sterility (B-types) and pollinators (C-types) having a good combining ability with the A-type must be sought. The flowering times of the three types should be similar.

So far there is little to show which *Lolium* species as pollinator will have the highest combining ability with *L. perenne* as A-type, but preliminary indications are that as far as yielding ability is concerned the best results are obtained with *L. multiflorum* ssp. *gaudini*. Promising results have also been obtained with *L. multiflorum* as pollinator. However, when these short-duration types are used as pollinators the hybrids often show a tendency to lack persistency. *L. perenne* can also be used as a pollinator. In this case, inbreeding, followed by an extensive crossing programme to test the combining ability of the pollinator, must precede the final crossing.

Complementation in production patterns is also an important criterion in seeking a suitable combination of A-types and C-types. This complementation is more marked in the components of interspecific hybrids than in those of intraspecific hybrids. In intraspecific combinations, complementation is mostly associated with differences in flowering time, so that commercial seed production will be very difficult, if not impossible.

Interspecific and intergeneric crosses

Deficiencies in the material to be improved can be made good by crossing with genera or species in which the deficient character is highly developed. Intergeneric hybridization between ryegrass and fescue species seems promising in this respect. Hybrids between *L. perenne* and *F. pratensis* occur naturally in old Dutch pastures as diploids and triploids, but are sterile owing to an unbalanced chromosome composition. Artificial hybrids display the same character, but by chromosome doubling the balance can partly be restored. In this way hybrids (allopolyploids) between ryegrass and *F. arundinacea*, *F. pratensis* and *F. rubra* have been developed. A few varieties have been bred, but the cytological instability and difficulties of seed production still cause problems in many cases.

Varieties have been developed from crosses between perennial and Italian ryegrass. In tropical countries crosses have been made between elephant grass (*Pennisetum purpureum*) and bulrush millet (*P. typhoides*) to combine the forage production of the former with the drought tolerance and seed production characteristics of the latter.

Methods for apomictic species

Apomixis (asexual seed development) is a method of reproduction reported to occur in over 100 species of perennial grasses, the most important of which are *Poa pratensis* (smooth-stalked meadow grass on Kentucky bluegrass) among the temperate grasses and *Cenchrus ciliaris* (buffel grass) among the tropical grasses. Apomixis is particularly prevalent in the latter. It is usual to draw a distinction between obligate apomicts, which reproduce only by apomixis, and facultative apomicts, in which the same ovule is capable of either apomictic or sexual reproduction. Most known apomictic grasses are pseudogamous, i.e. they require pollination for seed development and their pollen is usually effective in fertilizing sexual plants.

Obligate apomicts such as *P. pratensis* and *C. ciliaris* lack natural variability within ecotypes and it has traditionally been impossible to combine desirable characteristics through hybridization. Fortunately, both grasses have useful natural ecotypes which have been developed into varieties. Some of the *P. pratensis* varieties are listed in Tables 4.8 and 4.9. Of buffel grass at least five clearly distinct ecotypes are in widespread use in tropical and subtropical Australia. However, sustained progress now seems to depend on finding or even inducing cross-compatible sexual plants. In common with other vegetatively propagated plants, apomicts are highly heterozygous and wide variability can be released if the apomictic barrier is broken. Conversely, the apomictic mechanism circumvents problems of sterility and has been an effective evolutionary tool in genome preservation, polyploidy build-up and permanent fixation of heterosis.

It is the possibility of being able to reproduce hybrids indefinitely by seed that has aroused the interest of breeders in obligate apomicts. The first prerequisite is the production of cross-compatible sexual plants and second the control of the reproductive processes in such a way that apomixis is maintained in the hybrids.

Among grasses, most obligate apomicts of importance have by now been found to contain some sexual types, which have been used in many breeding programmes. However, such plants are few and are not always cross compatible with the apomicts.

A method of inducing sexuality in *P. pratensis* was developed in the 1960s by Funk at Rutgers University, New Jersey, USA, (Funk & Han, 1967), and was later successfully applied by the Mommersteeg and Van der Have breeding stations in the Netherlands. According to this method, male and female parent plants of good potential are raised in the greenhouse in January, February and March at staggered intervals so as to ensure overlapping flowering periods. A 20-hour day length and a diurnal 16/8-hour temperature regime of 16 °C/10 °C are maintained until the start of flowering, when the temperature is raised to 18 °C/15 °C. Just prior to anthesis 2-5 panicles of the female parent are bagged together with 15-20 panicles of the pollen parent, the latter being arranged above the former. The pollination bag is connected with a device that shakes the plants every 20 minutes, day and night, freeing pollen for pollination. The pollination bags are removed after a fortnight and three weeks later seed is harvested from the female parent.

Seedlings are raised and transplanted to the field. Only those which deviate phenotypically from the female parent are selected for clonal evaluation and subsequently for turf performance. Remnant seed is used for assessment of the degree of apo-

Table 4.8. Results of *Poa pratensis* hybridization (male parent specified).

Female parent	Male parent	Aberrant progeny as % of total progeny	Hybrids as percentage of aberrant progeny				
			hybrids selected for clonal production	hybrids selected for turf evaluation	hybrids with promising turf performance (A)	hybrids with (A) and high degree of apomixis (B)	hybrids with (A) and (B) and promising seed production
Parade	Baron	26	38	26	3,7	1,6	0,8
	Geronimo	20	60	58	4,5	4,5	4,5
Baron	Bristol	19	23	14	9,3	4,7	2,3
	Parade	20	44	11			
	Kimono	23	57	21			
	Geronimo	20	25				
	Glade	18	25				
Geronimo	Parade	10	23	19	1,6	1,6	1,6
Bristol	Baron	18	31	17	7,1	5,3	2,7
	Parade	21	10				
	Entopper	24	21				
Kimono	Baron	8	28	3			
Enmundi	Baron	4	18				
	Bristol	4	19				
	Geronimo	3	13				
Entopper	Baron	13	15				
	Bristol	14	32				
	Geronimo	11	43				
Glade	Baron	14	20				
	Entopper	12	23				
Nugget	Baron	26	39				
	Saskia	24	30				
Fylking	Parade	14	69				
	Saskia	14	53				

mictic reproduction. A high degree of apomixis and good seed yielding ability determine the ultimate selection of hybrid plants.

The results thus far obtained can be summarized as follows:

– The percentage of aberrant progeny depends almost entirely on the female parent. Large varietal differences occur. The choice of the male parent has little influence (Table 4.8).

– The percentage of hybrids selected for further evaluation depends on the female as

Table 4.9. Results of *Poa pratensis* hybridization (male parent not specified).

Female parent	Male parent	Aberrant progeny as % of total progeny	Hybrids as percentage of aberrant progeny				
			hybrids selected for clonal evaluation	hybrids selected for turf evaluation	hybrids with promising turf performance (A)	hybrids with (A) and high degree of apomixis (B)	hybrids with (A) and (B) and promising seed production
Merion	several	9	39	21	1,6	1,6	0
Geronimo	several	10	26	17	0,9	0,9	0,9
Parade	several	20	50	36	4,3	2,7	1,6
Baron	several	20	39	18	9,6	6,0	3,6
Bristol	several	20	24	13	5,7	4,6	2,3
Entensa	several	39	40	15	2,5	1,5	0
Monopoly	several	58	26	17	0,4	0,4	0,4
Kimono	several	7	29	7			
A34	several	11	57	23			
Enmundi	several	4	17				
Glade	several	12	22				
Entopper	several	13	30				
Fylking	several	15	59				
Nugget	several	27	37				

well as on the male parent. Again large varietal differences occur (Table 4.8 and 4.9).

Androgenesis has been observed in a few cases, though this was largely confined to the varieties Entensa and Monopoly.

Vegetative propagation

Many stoloniferous perennial tropical grasses are propagated vegetatively, thus eliminating problems of seed production and allowing sterile hybrids with desirable traits to be exploited. Both Coastcross 1 Bermuda grass (*Cynodon dactylon*) with high digestibility and Transalva digit grass (*Digitaria decumbens*) with Pangola stunt virus resistance are sterile but since both grasses are normally vegetatively propagated they are widely utilized. Some outstanding clones of elephant grass have been obtained in the Kenya breeding programme and are ready for release. It has been estimated that 5-6 million hectares of Coastal Bermuda grass has been established by vegetative propagation in the south-eastern USA.

Maize

The unique morphology of this monoecious species, in which all the male flowers are borne in a terminal panicle, makes it relatively easy to effect a total emasculation. Partly for this reason, maize was the first important crop to lend itself to large-scale hybridization. Today, hybrids dominate the maize-growing area of all developed countries and their use is increasing in some developing countries. Notwithstanding the many investigations into other breeding methods for maize, it would seem that the latter will not become serious competitors to the present system of hybrid production.

EARLY HISTORY

Selection in maize (*Zea mays*) probably dates back to the beginning of domestication of the species. Certainly some selection was necessary to transform the wild ancestor of maize into a plant whose domestication is so complete as to require the aid of man for its survival. The first Europeans to reach the Americas found the American Indians growing all the major classes of maize known today.

The white man apparently contributed little to the improvement of maize prior to the 18th century. Presumably he was content to use the types acquired from the American Indian. However, as the early white settlers began migrating westward early in the 19th century they carried with them those types of maize they had been growing on the eastern seaboard. As they moved westward through Pennsylvania, Ohio and on to what is now the central Corn Belt, the varieties of maize brought along from the northern and southern seaboards were hybridized both accidentally and intentionally to produce better-adapted and higher-yielding types. For example, the yellow dent maize which now dominates the USA and much of Europe arose as result of combining the late-maturing soft dents from the south-eastern USA with the early-maturing 8-10-rowed flints from the north-east. This maize was the product of the white man's art and was unknown to the American Indian.

From the early 1800s to the early 1900s, selection within yellow dent maize by American farmers resulted in the evolution of numerous varieties representing a range of maturity adaptation extending from the deep south to as far north as Minnesota, Wisconsin and Michigan. The better known of these farmer breeders were James and Robert Reid, Isaac Hershey and George Krug (Wallace & Brown, 1956).

All the early improvement of maize came about through the application of some form of mass selection. That the total result was positive is unquestionable, yet the effectiveness of the methods employed was limited by the lack of control of the male parent and the absence of any progeny testing. Beginning in the late 1800s, additional progress was made through the use of controlled varietal hybridization (Beal, 1877). Despite the yield improvement attributed to varietal hybridization, the method was not felt to be sufficiently practical to be used commercially. Instead, the attention of maize breeders was directed to the use of a new technique, ear-to-row selection, which was first used in 1896 at the Illinois Experiment Station by Hopkins (1899). The method proved to be effective when applied to traits such as protein and oil percentage, ear height, plant height etc., but it was not particularly effective in improving yield (Smith & Brunson, 1925).

THE INBRED-HYBRID METHOD

Hybrid maize, based on the use of inbred lines, owes its development to East (1908), Shull (1909) and Jones (1918, 1922). Shull's discovery of the vigour and productivity of crosses of inbred parents of maize was the by-product of a study of the inheritance of kernel row number. East, who obtained results similar to those of Shull and at about the same time, recognized the need for a practical method of producing hybrid seed. He suggested that varietal crosses were perhaps a solution to the problem, but it remained for Donald Jones, a student of East, to devise a technique which made hybrid maize production practicable. His invention of the double cross, which combines four inbred parents, is a cross of two unrelated single crosses. With this advance, hybrid maize was on its way and by 1938 was being planted on about 55% of the maize acreage in the USA. By 1945 virtually all the maize acreage in the USA was planted with hybrid seed. Shortly after World War II hybrids were quickly accepted in western Europe and have since almost completely dominated the commercial maize acreage of those countries.

The early hybrids consisted almost solely of double crosses and three-way crosses, although it has long been known that the best single crosses significantly outyield the best doubles of comparable maturity. It also has been shown recently that select single crosses are as dependable in yield as the best doubles (Eberhart & Russell, 1969). So, for these reasons, plus the improvement in vigour of new inbred lines, there has been a growing trend towards the use of single crosses and a corresponding decrease in the use of doubles. It is estimated that 80-90% of the hybrid maize used in the USA in 1977 consists of single crosses or some modified form of single crosses.

GENE ACTION AND POPULATION IMPROVEMENT

In 1914, G.H. Shull, the inventor of hybrid corn, proposed the word 'heterosis' to describe the unusual vigour of the F_1 resulting from hybridization of two inbred lines of maize. Maize inbreds typically are less than 30% as productive as their hybrid progeny. Shull defined heterosis as 'the stimulating effect of the union of unlike germ cells' (Shull, 1946).

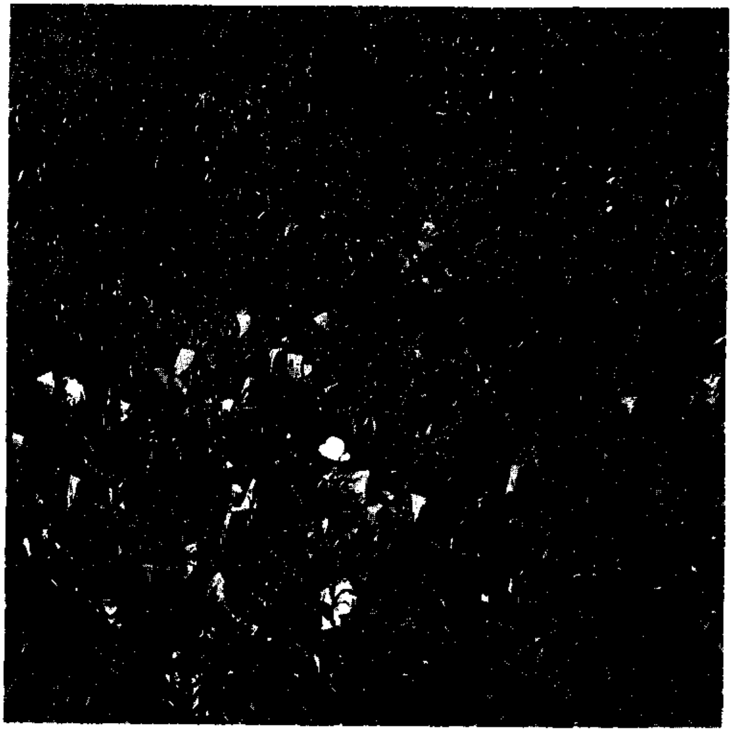
Since then, geneticists have conducted hundreds – perhaps thousands – of experiments designed to explain the genetics of hybrid vigour in more detail. They have proposed numerous theories of gene action and how it might cause hybrid vigour, each couched in the genetical terms of its time. Starting in about the mid-1940s, quantitative geneticists began to develop a methodology for investigating the problem. A pioneering paper by Robinson et al. (1949), which itself was built on a theory advanced in 1935 by Sewall Wright, proposed a method for studying the genetic variability in maize by using advanced hybrid generations. The genetic variance was partitioned into various components, to show the relative importance of additive, dominance and epistatic (interaction of nonallelic genes) genetic variance. It was assumed that results of experiments using these techniques would help breeders to plan more efficient breeding schemes.

However, even before the quantitative genetics theory and information on gene action were available, maize breeders attempting to develop improved hybrids had proposed several schemes of population improvement and had tried out some of them. In all cases, these breeding schemes were aimed at producing improved inbred lines which could be used to make superior hybrids.

The 'pedigree method' is perhaps the simplest technique and is still widely used. It consists in self pollinating F_1 hybrids of well-tested, desirable inbred lines (Fig. 4.24). The resulting new inbred lines are then tested in hybrid combination, to find those inbreds which combine some of the best traits of both parents. A variation of this technique is to self the first or second back-cross progenies on the assumption that lines resembling the recurrent parent but having desired traits from the nonrecurrent parent could be selected. In either case the original population consists of the whole body of first-cycle inbred lines (one or both of them adapted to a given locality), and the improved population is the total number of derived second-cycle lines. It is clearly hard to quantify the limits of the populations, the selection intensity or the total effort expended in this type of population improvement. Virtually all maize breeders used the pedigree method in the early days of hybrid maize improvement. It still works and it still is widely used, although not as universally as in former times.

A second type of population improvement, 'recurrent selection', was developed along more formal lines as a direct consequence of some of the early quantitative genetic studies of maize. Breeders have developed major subdivisions of the technique, usually called (a) simple recurrent selection, (b) recurrent selection for general combining ability, (c) recurrent selection for specific combining ability and (d) reciprocal recurrent (or recurrent reciprocal) selection (Sprague, 1955). Variations of these subdivisions include 'reciprocal full-sib selection' (Hallauer, 1973), 'reciprocal selection with inbred line tester from reciprocal populations' (Eberhart et al., 1973) and 'recurrent selection for general combining ability based on S_1 testing' (Genter, 1971).

Fig. 4.24. Inbreeding nursery for maize. Top: general view showing bags for pollen collection on tassels. Bottom: selfings; background, pollen collection; foreground, pollination. (Photographs: Pioneer Hi-Bred International Inc.)



Tables 4.10 to 4.15 summarize results of recurrent selection over the past 30 years in the USA. Table 4.10, listing synthetic populations developed for the USA, shows that we have many synthetic populations, of broad genetic diversity. Table 4.11, showing average yield gains of 60 kg/ha per generation for synthetics *per se*, and 50 kg/ha/generation for crosses of synthetics, indicates slow progress in their improvement. These slow rates of gain seem especially discouraging when they are compared with data showing that the pedigree method, over the past 40 years, has resulted in genetic yield gains for hybrids of about 70 to 80 kg/ha per generation (Duvick, 1977). (Before about 1955, recurrent selection and the pedigree method both required about one year per generation. Since 1955, both methods utilizing winter generations can average nearly two generations per year). Since the synthetics were usually selected only for yield, whereas breeders using the pedigree method necessarily selected for yield plus all other useful traits (presumably a more difficult task), one might have expected that yield gains for recurrent selection would have been larger than those achieved with the pedigree method. The relative effort put into the two techniques is probably not equal; propably more effort has been expended on the pedigree method, but nevertheless for the past 25 years a large part of the research effort of maize breeders at the top USA Corn Belt universities (Nebraska, Iowa State, Illinois, Purdue, Minnesota), plus much work at North Carolina, has gone into recurrent selection theory and practice. If the formal recurrent selection methods were clearly superior to the pedigree method they should have shown better results by now. For example, the original inbred-hybrid method was an easy success, based on much less effort and thought than has gone into recurrent selection.

Table 4.12 shows that synthetic populations, improved by recurrent selection, virtually never yield as much as control hybrids. If stalk and root strength plus other important traits are considered, as in Table 4.13, the synthetics without exception are greatly inferior. This means that synthetics cannot compete on the farm with hybrids.

Synthetics in hybrid combination approach the yields of hybrids (Table 4.14), but overall agronomic performance (example in Table 4.15) again indicates that they cannot compete on the farm with today's hybrids.

USE OF IMPROVED POPULATIONS

Two questions frequently asked are: (1) would synthetics *per se* be as good as hybrids today (in the USA) if comparable amounts of breeding effort had been used for both types, and (2) will synthetics improved by recurrent selection be good sources of inbred lines?

The answer to question 1 appears to be 'No'. It is unlikely that more work would have made synthetics fully as good as the best hybrids. Few people outside the maize-breeding fraternity are aware of the poor performance of even the best synthetics with regard to traits other than yield, nor do they understand the very great

Table 4.10. Synthetic populations[1] (adapted to the USA) listed in published literature since 1967. Most synthetics have been carried through several cycles, so that the total number of synthetics is several times the total shown here.

Cornelius & Dudley (1974)
Synthetic O.P.

Genter & Eberhart (1974)
Virginia Corn Belt Southern Synthetic (VCBS)
Krug Hi Synthetic 1 (BSK)
Stiff Stalk Synthetic (BSSS)
Nebraska Hays Golden (NHG)
Pioneer Hi-Bred Corn Belt Synthetic (PHCB)
Pioneer Hi-Bred West Indian Synthetic (PHWI)

Eberhart et al. (1973)
BSCB1
BSSS (HT)

Hallauer (1973)
Pioneer Two-ear Composite (PHPRC)

Russell et al. (1973)
Alph
WF9 × B7

Stuber et al. (1973)
Jarvis Golden Prolific O.P.
Indian Chief O.P.

Hallauer (1972)
Iowa Stiff Stalk Synthetic 2 (BSSS2)
Iowa Long Ear Synthetic (BSLE)
Iowa Two-ear Synthetic (BSTE)
Pennsylvania Intermediate Synthetic (PaSI)
Iowa Corn Borer Synthetic 9 (BSCB9)
Erto (Eto × 6 early US inbred lines) (BS2)
Tuxlan (BSTL)
BSSS × BSCB1 (BS6)

Hallauer & Sears (1972)
Eto (C4)

Troyer & Brown (1972)
Zapalote
Mexican
West Indian

Brown & Allard (1971)
6 California flint inbreds (Pool A)
6 Corn Belt dent inbreds (Pool B)

Carangal et al. (1971)
Synthetic A High Yield (Syn. A-HY)
Synthetic A High Combining (Syn. A-HC)

Eberhart (1971)
10 high yield single crosses (FR)
BSAA × BSBB (AB)
58 elite inbred lines (BSAA)
44 elite inbred lines (BSBB)
Gaspe Flint × Eto and Gaspe Flint × (Peru 330 × Narino 330) (GFE)
50% US × 50% Exotic (CBK)
US, European and Tropical (SK)
US Hybrids (SCS)
Jarvis × Indian Chief (JIC)
Jamaican Synthetic-Yellow × Caribbean Composite (JYC)

Penny & Eberhart (1971)
Iowa Corn Borer Synthetic 1 (BSCB1)

Sentz (1971)
8 elite inbred lines (Minnesota Synthetic 3)

Lonnquist & Lindsey (1970)
Krug Yellow Dent ($K_{II(A)}$)

Efron & Everett (1969)
12 synthetics, US × tropical (MRM)
12 synthetics, US × teosinte (MTM maize-like)
12 synthetics, US × teosinte (MTM teosinte-like)

Duclos & Crane (1968)
Purdue Exotic Synthetic (Ex syn.)

Hallauer & Sears (1968)
Corn Borer Synthetic 3 (CB Syn. 3)
Michigan 250 × Mexican Jala (Purdue MJ)

da Silva & Lonnquist (1968)
Krug test-cross progeny selection ($K(S_1)$ syn-2)
Krug full-sib families (K(FS)syn-2)

Lonnquist & Williams (1967)
Iowa State Stiff Stalk (SSS_{III})
25 inbred lines (B_{IV})

Webel & Lonnquist (1967)
Hays Golden O.P.

Table 4.11. Yield gain per cycle and per generation in several recurrent selection programmes.

Authors	Method[1]	Material	Cycles	Gen./Cycle	Population per se			Top cross		
					gain/cycle		gain/gen.	gain/cycle		gain/gen.
					in kg/ha	in %	in kg/ha	in kg/ha	in %	in kg/ha
Lonnquist (1949)	b	Krug High Syn-3	2	3	640	27.4	210			
Webel & Lonnquist (1967)	b	Hays Golden	4	1[2]		9.4				
Penny (1968)	b	Stiff Stalk Syn.	3	3	350	7.4	120	90	1.4	30
	d	Stiff Stalk Syn.	4	3	100	2.0	30	60	1.0	20
	c	Stiff Stalk Syn.	6	3	130	2.6	40	150	2.4	50
	Pedigree	Stiff Stalk Syn.	1	10	240	5.0	20	80	1.3	10
Hallauer & Sears (1969)	b	Krug	6	1[3]	80	1.6	80			
	b	Iowa Ideal	5	1[3]	70	1.4	70			
Horner et al. (1969)	a	Broad Base Comp.	2	4[4]	−190	−5.2	−50	100	2.7	30
	b	Broad Base Comp.	2	3	0	0	0	150	4.1	50
	c	Broad Base Comp.	2	3	−200	−5.6	−70	60	1.5	20
Burton et al. (1971)	b	BSK(HT)	4	3	100	1.6	30	100	1.4	30
	b	BSK(S)	4	3[5]	250	4.1	80	190	2.6	60
Penny & Eberhart (1971)	d	BSSS	3	3	140	2.5	50			
	d	BSCB1	3	3	−60	−1.1	−20			
	d	BSSS × BSCB1	4	3				120	1.8	40
Hallauer (1973)	d	BSTE	1	6	940	16.9	160			
	d	PHPRC	1	6	1120	20.4	190			
	d	BSTE × PHPRC	1	6				−70	−1.0	−10
Russell et al. (1973)	c	Alph	5	3	210	4.8	70	310	4.5	100
	c	WF9 × B7	5	3	160	4.0	50	130	1.8	40
Eberhart et al. (1973)	d	BSCB1	5	3	50	0.9	20	120	1.8	40
	d	BSSS	5	3	20	0.5	10	150	2.3	50

	b	BSK	4	3[5]	120	2.5	40	–40	–0.6	–10
	b	BSSS	7	3	–30	–0.5	–10	10	0.1	0
	b	NHG	12	1[3]	50	1.0	50	10	0.2	10
	b	PHCB	9	1[3]	40	0.9	40	20	0.3	20
	b	PHWI	9	1[3]	20	0.3	20	30	0.5	30
Average					170	4.0	60	110	1.8	50

1. Methods as follows:
a. simple recurrent selection
b. recurrent selection for general combining ability
c. recurrent selection for specific combining ability
d. recurrent reciprocal selection.
2. Progeny row half-sib selection.
3. Mass selection.
4. S_2 selection.
5. S_1 selection.

Table 4.12. Yields of synthetic varieties *per se* compared with control hybrids.

Authors	Variety, hybrid	Yield in t/ha syn.	Yield in t/ha hybrid	Yield of syn. in % of hybrid
Lonnquist (1949)	Syn-3 High	5.9		93.6
	US 13 (double cross)		6.3	
Webel & Lonnquist (1967)	Hays Golden-C4			99.0
	Nebr. 501D (double cross)			
Eberhart (1971)	Mean of nine synthetics	5.3		62.3
	Mean of four hybrids		8.5	
Eberhart (1971)	Mean of six synthetics	4.2		65.6
	Mean of four hybrids		6.4	
Hallauer (1972)	Mean of nine synthetics	6.2		75.6
	Mean of four hybrids		8.2	
Hallauer (1973)	Mean of two synthetics	6.6		97.0
	Mean of six hybrids		6.8	
Russell et al. (1973)	Mean of two synthetics	4.9		65.3
	Mean of three hybrids		7.5	
Eberhart et al. (1973)	Mean of four synthetics	5.8		79.5
	Mean of four hybrids		7.3	
	Mean of synthetics	5.6		79.7
	Mean of control hybrids		7.3	

importance of specific combining ability for yield with regard to the important final 5% of yield advantage. It is likely that synthetics improved by recurrent selection would be better today if they had been selected for all useful traits rather than for yield alone, but theoretical as well as practical results agree in showing that in the end the best given selection is always a hybrid, not a synthetic.

The answer to question 2 is that synthetics can be a good source of inbred lines, although to date they have produced only a few truly superior lines. The low rate of improvement for yield of synthetics in crosses is discouraging, for this trait is predictive of the rate of improvement of inbreds derived from synthetics. A careful search for the reasons for the generally slow progress in improvement of synthetics needs to be made. A critical comparison with progress achieved by means of the pedigree method should be made, with the aim of drawing attention to any strong points in the pedigree method which might be applied to the methodology of recurrent selection. For example, does the increased precision gained by longer, more extensive testing for identification of inbred lines (pedigree method) counterbalance the increased time per cycle required by the pedigree method? Did the emphasis on yield

Table 4.13. Performance of 13 synthetics and 5 hybrid controls in central Iowa, 1974 (Pioneer Hi-Bred International Inc. Exp. 35081).

Synthetic, hybrid	Yield	Moisture and lodging in % of mean value of the trial		
	in t/ha	moisture	not RL[1]	not St.L.[2]
BS4	6.7+	87–	63	104
BS3	6.6+	97	108	94
BS10(FR)C2	6.4+	88–	98	98
BSSS(R)C6	5.9	106	112	102
BS11(FR)C2	5.9	100	104	102
BSCB1(R)C6	5.8	90	92	95
Eto(M)C6	6.0	99	64	90–
BS7	5.0	91	98	95
BS2	5.5	79–	35–	96
BS15	5.7	99	86	85–
BS8	4.5–	100	107	85–
BSL(S)C4	4.4–	103	80	94
BS5	3.6–	69–	89	88–
Av. of synthetics	5.5	93	87	94
Mo17 × B73	10.2+	81–	127	110+
3301	9.8+	87–	142+	110+
3780	8.4+	75–	136	108
3325	8.1+	104	141	110+
3549	7.5+	82–	132	110+
Av. of hybrids	8.8	86	136	110
Total means	5.5	25	69	91

+ = 2 standard deviations or more above mean.
– = 2 standard deviations or more below mean.
1. RL = root lodged.
2. St.L. = stalk lodged.

alone in early recurrent selection schemes actually detract from dependable yielding ability because accessory traits (root strength, disease and insect resistance and drought tlerance) are important yield components in a broad sense under widespread cultivation? (For example, ability to overcome disease and insect attack is a necessary preliminary to the expression of 'true' yield potential.)

These remarks are not intended to discourage attempts to develop improved populations and inbreds from them by means of recurrent selection. We need the genetic diversity such breeding techniques can offer. But we also need to improve their rates of gain.

Table 4.14. Yields of advanced-generation synthetics in hybrid combination.

Authors	Synthetic crosses, or hybrid controls	Yield in t/ha	
Hallauer & Sears (1968)	36 syn. × syn. crosses	6.2	
	Best cross: SS Syn. × Pa Int. Syn.	7.1	
	5 hybrid controls		6.7
Carangal et al. (1971)	Syn. A-HY C2 × testers	5.4	
	Syn. A-HC C × testers	5.5	
	3 hybrid controls		5.6
Eberhart (1971)	36 Corn Belt syn. × syn. crosses	6.0	
	Best cross: BSSS2 × FR	7.7	
	4 SX hybrid checks		8.5
	Best hybrid: N28 × Mo17		9.3
	15 southern US syn. × syn. crosses	5.1	
	Best cross: PHWI(MT) × JIC	6.1	
	4 hybrid controls		6.4
	Best hybrid: Dixie 55		7.0
Hallauer (1972)	36 syn. × syn. crosses	7.0	
	Best cross: BSSS2 × PaSI	7.7	
	4 SX hybrid controls		8.2
	Best hybrid: Mo17 × N28		9.0
Russell et al. (1973)	2 B14 × syn. crosses	8.3	
	Best cross: B14 × Alph C5	8.5	
	2 SX hybrids		8.1
	Best hybrid: B37 × B45		8.6
	Alph C5 × (WF9 × B7)C5	7.4	
Eberhart et al. (1973)	2 syn. × syn. crosses	7.6	
	Best cross: BSCB1(R)C5 × BSSS(HT)C7	7.7	
	4 hybrid controls		7.3
	Best hybrid: B37 × B45		8.2
Genter & Eberhart (1974)	21 syn. × syn. crosses	6.4	
	Best cross: VCBS(S)C4 × PHWI(M)C9	7.1	
	Hybrid controls		7.6
	Best hybrid: 'Local hybrid 1'		7.8
	2 syn. × syn. crosses	7.3	
	Best cross: BSSS(HT)C7 × BSCB1(R)C5	7.8	
	Hybrid controls		7.6
	Best hybrid: 'Local hybrid 1'		7.8
	B14 × BS12(HI)C5	7.8	
	Hybrid controls		7.6
	Best hybrid control 'Local hybrid 1'		7.8
	Av. Syn. crosses	6.7	
	Av. Hybrid controls		7.4
	Av. Best syn. crosses	7.5	
	Av. Best hybrid controls		8.0

Table 4.15. Performance of B14A × Alph C5 *vs.* 110 SX hybrids in 4 locations in Iowa and Missouri, 1974 (Pioneer Hi-Bred International Inc. Exp. 32061).

	In t/ha	As % Ear Moisture	As % Not RL[1]	As % Not St.L.[2]
B14A × Alph C5	4.9–	22	40–	91–
110 experimental SX hybrids	6.0	22	68	93

– = 2 standard deviations or more below mean.

1. RL = root lodged.
2. St.L. = stalk lodged.

BREEDING FOR IMPROVED NUTRITIONAL QUALITY

Since about 1965 (Mertz et al., 1964), maize breeders around the world have worked intensively on development of opaque-2 maize, high in lysine and tryptophan. But today, very little acreage is planted to this type of maize anywhere in the world. Opaque-2 grain in developed countries should be especially useful for feeding to pigs, because the farmer can then reduce supplementation with soya bean meal. In developing countries where maize is consumed directly by humans, opaque-2 grain could relieve malnutrition and would reduce the need for dietary supplementation with expensive, less productive pulses.

Opaque-2 maize has not been widely accepted in the developed countries because its yields are about 10% less than those of normal-endosperm counterparts, and prices of soya beans in relation to maize are usually sufficiently low that the savings in soya bean meal supplementation do not counterbalance the yield loss. Another problem has been that opaque-2 hybrids usually have reduced resistance to ear and kernel rots. Varieties with satisfactory resistance can be selected, but some of the first releases were so disastrously poor in resistance that many farmers have been prejudiced against later releases.

In the developing countries (these are usually in the tropics), the taste and texture preferences of the people who eat the maize plus the need for resistance to ear rots and grain insects have been important problems. Breeders in developing countries have concentrated on developing disease and insect-resistant opaque-2 maize with flinty kernel texture (opaque-2 grain characteristically is soft and floury). This involves handling multiple factors in addition to the opaque-2 gene. There appear to have been no successful releases for the tropics up to the time of writing.

Opaque-2 maize must be regarded as a new crop species, to be handled as such, and must find its own niche.

USE OF THE HAPLOID METHOD

About 25 years ago new techniques made it relatively easy to identify and select haploid maize plants (Chase, 1974). The haploid system appeared likely to be of great practical benefit to maize breeders, since it would reduce the number of generations required for developing inbred lines from an average of five or six down to two. Today, however, the haploid technique is not used by maize breeders.

The following three reasons may explain why the technique was not adopted. Despite the use of gene markers for preliminary identification of haploid plants and of the squash technique for positive identification, the percentage of haploids identified and saved was low, and because diploidization was difficult the percentage of haploid plants producing diploid progeny was even lower. The effort expended in producing a single inbred line was therefore greater than that expended in conventional methods. The saving in time might have made the greater effort worthwhile but, at about the time the haploid technique was introduced, advances in the protection of maize by fungicides and insecticides made it possible to grow one or even two winter generations in the southern USA, Hawaii or Latin American countries. This meant that the development time for producing inbreds by conventional means was halved and the haploid technique thus was no longer much faster than conventional inbreeding methods.

A third reason why breeders favour the conventional methods is that useful types of selection for highly heritable traits can be made during the several generations of inbreeding. Such types of selection can be made much more easily and cheaply than selection for yield, which requires the use of relatively expensive yield trials with numerous replications. Thus it may really be more efficient to take a little more time to develop an inbred line and, by so doing, to reduce the number of lines that must be tested in hybrid form in expensive yield trials. However, if techniques now developing (for example, large-scale production of haploids from anther culture) can be applied to maize, the haploid technique may yet become popular and useful.

USE OF MALE STERILITY TO ELIMINATE DETASSELLING

Cytoplasmic male sterility was extremely successful as a technique to eliminate detasselling until 1970, when a race of *Helminthosporium maydis* (*Cochliobolus heterostrophus*) specific to T cytoplasm spread over most of the eastern United States in epidemic form causing yield reductions averaging about 15% (Tatum, 1971). The use of T cytoplasm was discontinued immediately and it is now used by only a few producers in the western parts of the maize-growing regions where *C. heterostrophus* does not occur owing to the dry summer climate. Other sterile cytoplasms, for example S and C, have not been attacked by the specific race (race T) of *C. heterostrophus* but they are not as easy to use as T cytoplasm and up to the present have not been used nearly as widely as was T cytoplasm before 1970.

Techniques utilizing chromosomal-genic combinations causing male sterility have been proposed but are not yet in use (see review in Duvick, 1972). In theory, the techniques seem to be workable but in practice the time required for conversion to the proper chromosomal-genic type is extremely long and in some cases sterility in maintainer lines is high enough to cause serious difficulties in producing foundation lots of male-sterile parents.

Major chemical companies have experimented with chemicals which could produce male sterility or a delay in pollen shedding sufficient to make it possible to detassel more cheaply. Up to now, however, none of the chemicals have produced satisfactory results.

Sugar beet

The evolution of sugar beet from a fodder crop (ca. 1800) to an important, highly improved source of sugar has been unusually rapid. The breeding procedure commonly practised up to the middle of the 19th century was mass selection, after which family selection, accompanied by analysis of the sugar content, became the principal method. Apart from a significant increase in sugar yield per hectare, the most notable developments in sugar beet breeding have been: the production of hybrid varieties by means of cytoplasmic male sterility; the introduction of triploid hybrids; the discovery of the monogerm character, which, combined with modern cultivation techniques, has eliminated singling and thinning; and improvement of root shape, thus facilitating machine harvesting. As a result sugar beet cultivation is well on the way to total mechanization. Since World War II, breeding has largely suppressed bolting, thus allowing earlier sowing. This, in turn, has extended the growing season and increased yield. The improvement of juice purity has made the extraction of sugar more economic.

HISTORICAL INTRODUCTION

The use of *Beta vulgaris* as a vegetable for human consumption goes back to prehistoric times. The use of the roots for feed started much later, probably in Spain, and was introduced into Germany around 1700 by the Mennonites when they came to the Palatinate from the Netherlands. In 1747 Marggraf discovered that these fodder beets contained a sugar identical with that from sugar cane. Some time later, in Silesia, Achard found that it was possible to extract sugar from the white Silesian beet. It is thought that these beets contained around 5-7% sugar, from which Achard was able to recover half of the available quantity; he started mass selection in 1786 and from 1802 to 1810 he used his selected material for the production of beets for his sugar factory. Work on selection and seed production was continued by the von Koppys, father and son, whose sugar factory was in operation in Silesia from 1805 to 1830. Later they continued selection for the export of sugar beet to France. By about

1830 the sugar content of their 'variety' had reached 9%, from which the factories were able to extract two thirds.

Up to 1856 the only method of selection in use was mass selection, and the sugar content was assessed by determining the specific gravity, a method still used in potatoes. In 1856 Vilmorin started family selection and introduced the polarimeter for determining sugar content. At the beginning of the twentieth century, selection on the basis of juice purity was introduced and the sugar content was further raised to about 17%.

The next basic developments in breeding occurred between 1930 and 1940. In 1934, in Russia, Bordonos and Savitsky discovered the property of monogermy. The monogermy of most varieties in the Western world, however, derives from a second source discovered by Savitsky in 1948 in the USA, where he found five monogerm plants among 300,000 plants of the open-pollinated variety Michigan Hybrid.

The promising results of hybrid maize breeding in the USA led breeders of other crops in that country to seek ways of introducing the same breeding technique into other crops by the use of male sterility, and in 1942 Owen reported that he had found male-sterile sugar beets in which the sterility was caused by a combination of cytoplasmic and genetic factors. He proposed a scheme which would enable the breeder to use this sterility in the production of hbrid varieties.

In 1938 Schwanitz announced that he had obtained tetraploid sugar beets through the use of colchicine. Early attempts to develop better varieties at the tetraploid level were unsuccessful but in 1940 Peto and Boyes reported the superiority of triploids. European breeders made use of this superiority by producing the so-called 'polyploid' varieties; these varieties are obtained by using a mixture of diploid and tetraploid families for seed production and hence they consist of mixtures of diploid, triploid and tetraploid plants.

Comparison of existing breeding methods

Sugar beet varieties now in use or under development can be divided, according to whether male sterility is used or not, into two groups, namely hybrid varieties and open-pollinated varieties. A second division into four groups is possible according to ploidy level: diploid, 'polyploid', triploid and tetraploid. A combination of these two groupings gives us seven different ways of producing varieties. Thus open-pollinated varieties can be divided into diploid, polyploid and tetraploid varieties, while hybrids based on the use of male sterility can be divided into diploids, triploids from diploid male-steriles, triploids from tetraploid male-steriles and tetraploid hybrids.

In Table 4.16 a subjective estimation is given of the opportunities for improvement provided by these different types of varieties. A score of 1 means that improvement of the given character in a variety from the stated type is easy, whereas a score of 9 means that this is difficult. Assuming that the characters listed are all of equal value, a comparison of the total scores for the various methods indicates that triploid and diploid hybrid breeding is more promising than other systems. Clearly, however,

Table 4.16. Evaluation of existing types of varieties (with a view to breeding genetically monogerm varieties) (1 = high, good; 9 = low, bad).

	Open-pollinated varieties (without use of male sterility)			Hybrid varieties (based on the use of male sterility)			
	diploid	'polyploid'	tetraploid	diploid	triploid on $2n$ ms	triploid on $4n$ ms	tetraploid
Approximate year of introduction of first commercial variety (multigerm or monogerm)	1802	1951	1966	1955	1959	1974	–
Seed characters							
seed size	9	5	3	7	6	1	1
germination	1	5	7	1	5	3	7
seedling vigour	3	5	7	1	3	1	7
other seed characters	5	9	7	3	1	7	9
Seed production							
varietal maintenance	7	9	7	1	1	3	5
insensitivity to contamination	1	3	5	5	9	7	9
Variety improvement							
introducing new characters	5	7	9	3	1	3	5
increasing the range of varieties available	5	7	9	2	1	4	3
breeding for disease resistance	7	9	9	3	1	9	7
breeding for bolting resistance	9	7	1	5	3	5	1
results obtained hitherto	5	3	7	1	1	7	9
Total score	57	69	71	32	32	50	63

the various characters differ in value, so that the choice of system cannot be based on the total score but will depend partly on the value alloted to special characters, and even after this decision has been taken more than one choice will remain.

In this respect there are also clear differences between countries. In the USA and Europe all new varieties introduced are genetically monogerm, but whereas for historical reasons diploid hybrids are mostly in use in the USA, the majority of current varieties in Europe are triploid. In areas where multigerm seed is still used this is mostly 'polyploid'. Diploid open-pollinated varieties have practically disappeared from the Western world. Tetraploid varieties and hybrids are hardly in use. Triploid hybrids produced from tetraploid male-sterile monogerm parents are now being introduced; they offer certain advantages, but the handling of tetraploid male-steriles is difficult (Bosemark, 1977).

In view of the importance of hybrid varieties the following section will describe the breeding of triploid hybrids based on diploid male-steriles. Schemes for breeding diploid hybrids are in some respects similar to those for breeding maize hybrids and in others to those for breeding triploid sugar beet hybrids.

BREEDING OF TRIPLOID HYBRIDS BASED ON DIPLOID MALE-STERILES

The development of a hybrid involves three distinct components, for each of which an independent breeding scheme may be applied:

- male-sterile cytoplasm,
- families carrying the genes for maintenance of male sterility (O-types),
- tetraploid pollinators.

Male-sterile cytoplasm

Male-sterile plants are to be found in all diploid open-pollinated varieties and also in *B. maritima*. In some cases this male sterility is of purely genetic origin, while in others it is based on a combination of cytoplasmic and genetic factors. This latter type of sterility is particularly suitable for the production of hybrid varieties. For practical purposes it is assumed, in accordance with Owen's hypothesis, that this sterility is based on a cytoplasmic factor (plants carrying this factor are designated (S) whereas with normal cytoplasm are designated (N) and on at least two recessive genes designated x and z. A male-sterile plant thus has the formula $(S)xxzz$. When such a plant is crossed with a male-fertile plant carrying the recessive genes for sterility (formula $(N)xxzz$) and designated an O-type, the offspring of the male-sterile plant will also be male sterile.

If, on being crossed with a selected O-type, a male-sterile plant found in a diploid *B. vulgaris* population gives a male-sterile progeny, this plant may prove to be a new source of cytoplasmic male sterility. To dermine whether this is so is not easy, since at least six back crosses are necessary before families can be obtained in which the only difference, if any, is located in the cytoplasm. Savitsky observed differences in sterility between lines containing different cytoplasms, and in the Van der Have breeding programme small differences in yielding capacity have also been detected, together with slight indications of differences in disease resistance. Such differences, especially the last-mentioned, make further investigation of different sources of cytoplasm desirable.

Fig. 4.25. Isolation cages for sugar beet hybridization and self pollination.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Development of new O-types ((N)xxzz)

Although Owen (1950, in Knapp, 1958) states that O-types are very common in most diploid open-pollinated varieties, experience shows that is not easy to find O-types capable of maintaining 100% male sterility. To identify O-types, it is necessary to make experimental crosses between a male-sterile plant and single plants selected from a population. If the progeny of the male-sterile plant crossed with the selected pollen parent is male sterile, it may be concluded that the selected pollen parent is *(N)xxzz*.

A good technique for the development of new O-types is as follows. A single *(S)xxzz* plant and a plant with normal cytoplasm are grown together in an isolation cage (Fig. 4.25) and cross-pollinated seed is harvested from the male-sterile plant and self-pollinated seed from the fertile plant. If the progeny from the sterile plant has an acceptable level of male sterility, new pair crosses are effected between the *(S)xxzz* progeny and the progeny from self pollination. In the following generation, if the progeny from the male-sterile plant is still 100% male sterile, it may be assumed that the S_2 family used as pollinator for two generations is of the type *(N)xxzz*. This family may then be tested for other desired characters. The new O-types may be used to pollinate an existing cytoplasmically male-sterile family and selection for seed and root characters may then be applied on the basis of the performance of the F_1 progenies.

Development of tetraploid pollen parents

Doubling the chromosome number in beet material presents no problems. Treatment of germinating seeds with a 0.2% colchicine solution at 30 °C for 15 hours generally gives a satisfactory percentage of plants showing a response. Such plants are transplanted, vernalized and checked for chromosome number before flowering. Chromosome numbers must also be checked in the succeeding generations. Although tetraploid populations are readily produced by this method, their further improvement is not an easy matter, especially where the tetraploid is to be used as the male parent of a triploid hybrid. It is therefore essential that the diploid material used for chromosome doubling should undergo selection for all desired characters before doubling of chromosomes is effected.

In general, it is possible to maintain the combining ability of a tetraploid population by mass selection for the most important characters, namely, root weight, sugar yield, juice purity, bolting resistance and root shape, and also, where required, for resistance to certain diseases. Such populations can sometimes be improved by selecting tetraploid single-plant progenies on the basis of the performance of their triploid hybrids and recombining large numbers of the selected single-plant progenies in a polycross. Among the advantages of the hybrid technique are, firstly, the fact that only small quantities of the pollen parent are needed for hybrid production. Using 1 kg of seed of a pollen parent it is possible to produce commercial seed for 300 to 600 ha of sugar beets from the male-sterile diploid monogerm plants. Secondly, vegetative multiplication of selected pollen parents is generally not difficult.

It may be mentioned that the best triploid hybrid combinations are obtained by using the F_2 of the cross between tetraploid plants or families. One method of crossing two tetraploid families is as follows. Two tetraploid populations which have given good hybrids are chosen, plants with a green hypocotyl being selected from one and plants with a red hypocotyl from the other. The two groups of plants are multiplied separately in isolation plots to give sufficient seed for mass selection. The following year, 500 plants are selected from each of the two mass-selection fields for use in pair crosses in the next generation. These pair crosses are effected in isolation cages between plants with red and green hypocotyls from the respective populations, seed being collected only from the plants with green hypocotyls. The hybrid plants, identified after sowing by their red hypocotyls, are used to produce the F_2 and at the same time they can be test-crossed with a diploid male-sterile monogerm single cross.

On the basis of the triploid test crosses, the majority of the hybrids will be eliminated, and the resulting small quantity of selected F_2 seed is used to make a new series of test crosses. The tetraploid F_2 progenies that have given good results in the triploid combinations are then produced on a large scale by multiplying the remnant F_1 seed. If necessary a larger stock can be produced trough vegetative propagation of the F_1 plants.

Production and testing of experimental hybrids

It has already been mentioned that the introduction of different sources of cytoplasmic male sterility is very time consuming, since at least six back crosses with the O-type are required to produce male-sterile families differing only in their cytoplasm. In view of the possible hazards associated with the use of only one source of cytoplasm it may be desirable to use a mixture of various sources and it will certainly be desirable to continue testing for resistance to certain diseases in the localities where the diseases occur.

After preliminary screening for general combining ability of the male-sterile families and the tetraploid pollinators, partial and complete diallel crossing programmes are carried out with a view to further selection for both general and specific combining ability. If for instance 16 new male-sterile families with their corresponding O-types have been retained from the first selection mentioned in the section 'Development of new O-types', each of these male-sterile families can be crossed with four different O-types. To allow the general combining ability of the male-sterile families and the O-types to be calculated, it is necessary that if, for instance, male-sterile family A is crossed with the O-types E, F, G and H and the male-sterile family B is also crossed with the O-type E, the combinations B × F, B × G and B × H should not occur. The 64 new male-sterile single crosses obtained are now combined with 64 developed tetraploid pollinators. The partial diallel is shown in Fig. 4.26. This cross-

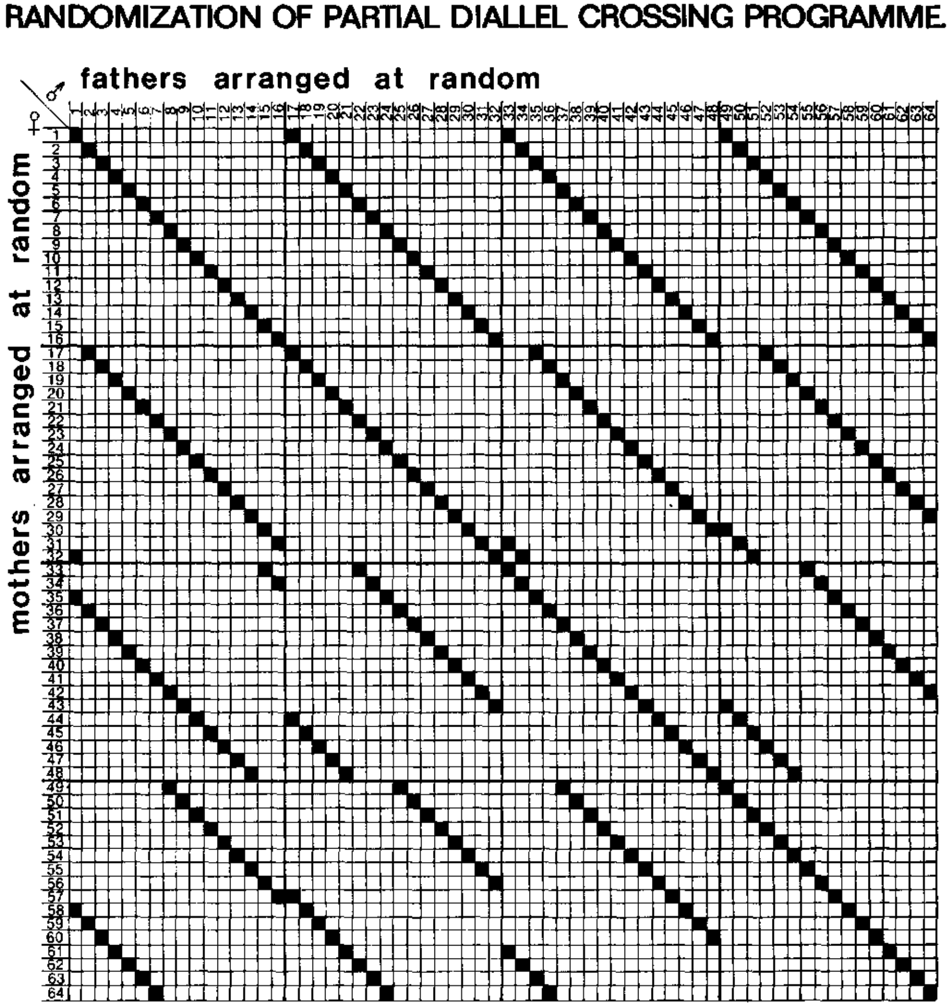


Fig. 4.26. Partial diallel.

ing programme gives 256 experimental crosses in which each male-sterile occurs 16 times, each O-type 16 times and each tetraploid pollen parent four times. From the results of trials of these 256 test crosses the general combining ability of each male-sterile, each O-type and each tetraploid parent can be calculated. In addition, the data obtained provide a possibility of checking for the occurrence of specific combining ability in the 256 test crosses. The selected four male-steriles with their fertile counterparts out of the initial 16 will give six different single crosses (excluding reciprocal crosses). With the 16 tetraploid pollen parents selected out of the 64 used in the partial diallel, 96 experimental crosses can be made for further testing under different climatic conditions and in different years. After a final selection, large quantities of genetically identical material can be built up for commercial distribution.

The breeding scheme employing the selection method described above is given in Fig. 4.27 for the development of the tetraploid pollen parents and in Fig. 4.28 for the development of the male sterile-families and the triploid crosses made with the tetraploids from Fig. 4.27.

SELECTION CRITERIA

In developing the components of a triploid variety, preselection is practised in order to obtain suitable material.

Preselection at the diploid male-sterile level

– Male sterility. Continuous control of sterility is exercised in all generations, including single crosses.
– Monogermy. Selection is made first for 'monogermy' of the flowers. Only plants which on this basis are practically monogerm are maintained. In addition, it is necessary to test the selected lines for polyembryony.
– Seed quality. This is an important character because field emergence has to be high to allow monogerm seed to be drilled to a stand. Seed quality is determined in seed from the single crosses, since the values obtained in the pure lines are not comparable owing to differences in inbreeding depression. Important characters in this respect are germination, especially after five days, germination at low temperatures and 1000-germ weight; this last is correlated with 1000-'seed' weight, but owing to differences in pericarp it is necessary to make the final selection on the basis of seedling weight determinations. Germination vigour, tested under adverse conditions, can also be an important selection criterion.
– Seed yield. In this respect it is of economic importance to select single crosses with a good seed yield and it is especially important to obtain material which produces a high yield of seed of desirable shape and size.

Preselection at the tetraploid level

Preselection for various characters is also necessary at the tetraploid level.
– Tetraploidy. Tetraploid pollinators should be tested for chromosome level in the first generations of multiplication. A certain percentage of aneuploid plants occurs regularly in tetraploids and selection for a low percentage is not very effective as aneuploids reappear during further multiplication and their frequency soon returns to the original level.
– Pollen fertility and pollen production. It is possible to select good pollinators by allowing pollen from tetraploid parents to compete with pollen from diploid plants carrying a colour marker in the production of experimental hybrids.
– Disease resistance. In general, moderately resistant hybrids can be obtained by selection in the tetraploid pollinator alone. Crosses between a susceptible male-sterile

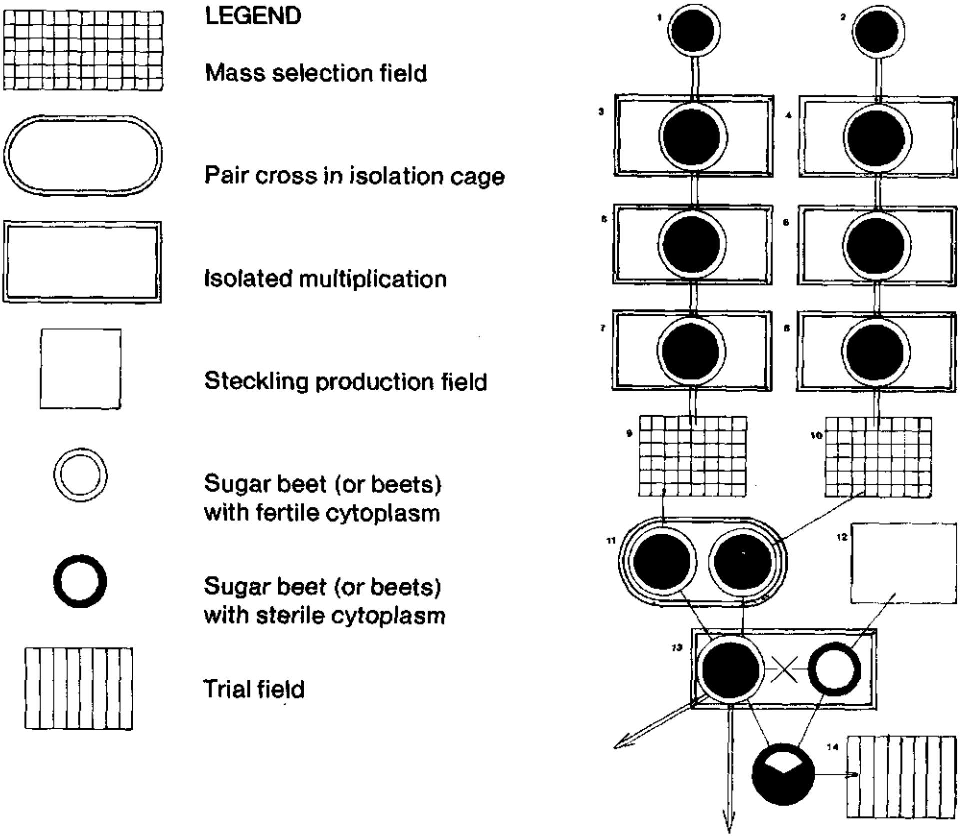


Fig. 4.27. Procedure for the production of tetraploid pollinators for triploid sugar beet hybrids.

Fig. 4.27. *Year 1:* Colchicine treatment of diploid populations with green hypocotyls (1) and with red hypocotyls (2) in order to double chromosome number. *Year 2:* Production of C_1 seed of 'green' population with selection for green (3) and 'red' population with selection for red (4). *Year 3:* Production of C_2 seed of 'green' population (5) and 'red' population (6). *Year 4:* Production of c_3 seed of 'green' population (7) and 'red' population (8). *Year 5:* Mass selection of tetraploid beets (c_4 generation) of populations. *Year 6:* Pair crosses between beets from tetraploid populations for production of F_1 tetraploid seed (11), and production of stecklings of male-sterile single cross for triploid hybrid production in year 7 (12). *Year 7:* Selection of F_1 hybrids from pair crosses with the aid of hypocotyl colour, and crosses of F_1 with male-sterile stecklings for production of triploid test hybrids. *Year 8:* Multiplication of tetraploid F_1 to give tetraploid F_2, and trial of the triploid hybrids (14).

Fig. 4.28. *Year 1:* Mass selection of two diploid monogerm populations (1 and 2), and production of male-sterile stecklings (3). *Year 2:* Caging of single plants from population 1 with male-sterile stecklings (4) and of single plants from population 2 with male-sterile stecklings(5). *Year 3:* Second generation pair crosses of progenies from of year 1 after elimination of families with poor sterility (6 and 7), and production of stecklings of unrelated male-sterile monogerm line for test crosses (8). *Year 4:* Isolation for production of second back cross. Self pollination and crosses with male-steriles, and, in same isolation field, production of F_1 hybrids between I_2 lines and the unrelated male-sterile monogerm line. *Year 5:* Test of seed plants of hybrids from year 4 (11) and test of general combining ability for sugar yield of same crosses for selection of suitable new O-types (12). *Year 6:* Multiplication of selected monogerm O-types and production of third back cross of O-types to the malesterile. *Year 7:* Further

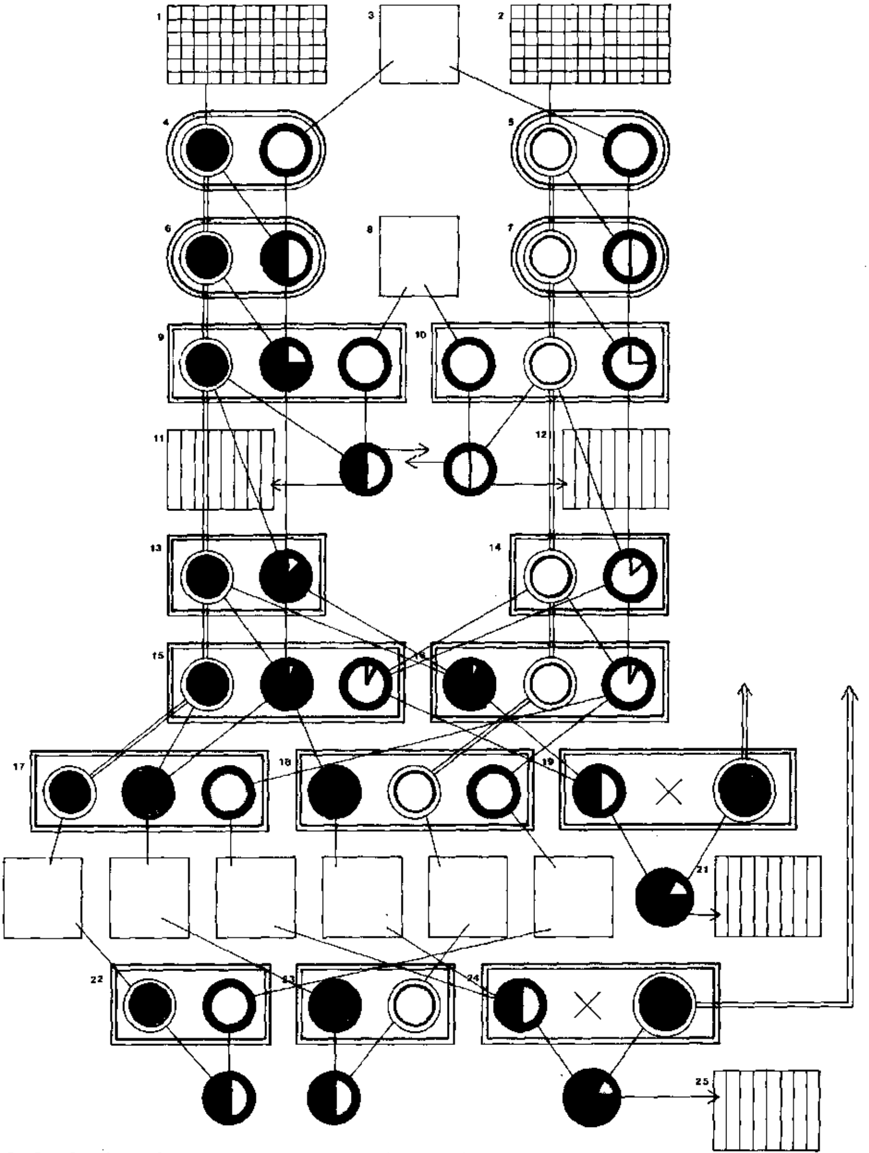


Fig. 4.28. Production of male-sterile parents and triploid sugar beet hybrids.

multiplication of selected monogerm O-types and their male-sterile counterparts, with partial diallel to obtain male-sterile single crosses. *Year 8:* Further multiplication and back crossing of monogerm O-types and male sterile counterparts and production of test crosses of single crosses with tetraploid pollinators from Fig. 4.27. *Year 9:* Production of stecklings of new O-types, male-sterile counterparts and single crosses for seed production in year 10, and trial of experimental triploid hybrids (21). *Year 10:* Seed production with parents selected in trial 21, and complete diallel of all selected monogerm O-types and male-sterile counterparts. Further crosses based on trial results of year 9 between tetraploid pollinators from Fig. 4.27 and monogerm single crosses selected in trial 21. *Year 11:* Production of monogerm male-sterile elite seed and further tests of experimental triploid hybrids produced in year 10 for final selection of commercial varieties.

single cross and a pollinator having good resistance will generally have an acceptable degree of resistance. In addition, if there is risk of disease in the seed-production field, resistance at the diploid male-sterile level may also be required, but in most cases it is more convenient to transfer seed production to an area where the given disease is not present, so that resistance breeding can be restricted to the tetraploid level.

– Sugar content. The influence of the tetraploid parent on the sugar content of the triploid hybrids is twice as great as that of the diploid male-sterile, and any one male-sterile will give very different triploid hybrids depending on the tetraploid pollinators used.

–Juice purity. The same applies to juice purity as to sugar content.

– Bolting resistance. The bolting resistance of a triploid hybrid is likewise influenced more by the tetraploid than by the diploid parent. Furthermore, the bolting resistance of a tetraploid population is better than that of the diploid population from which it derives. Thus a high bolting resistance can be achieved by rigorous selection in the diploid population before chromosome doubling. The correlation between the bolting resistance of a tetraploid and that of the triploids produced from it is generally very close, and indeed, susceptibility to bolting from the diploid male-sterile side can be partially masked on hybridization with a good bolting-resistant tetraploid.

When all preselection at the diploid and tetraploid levels has been completed, the main selection work is carried out at the triploid level in experimental hybrids produced from the preselected diploid and tetraploid parents.

Final selection at the triploid level

Final selection involves all the above characters, and in addition sugar yield, root shape, fanginess and the height, shape and uniformity of the crown.

RESOURCES FOR THE SUGAR BEET BREEDER

For many years, breeders have habitually used available commercial varieties as their main source of breeding material. The development of new O-types, single crosses or polycrosses from previously created O-types may also provide useful material. (In the case of single crosses, it is advantageous to use hypocotyl colour as a marker, as self compatibility may have arisen as a result of inbreeding in the development of O-types.) Whether commercial varieties or crosses of previously created O-types are used, the genetic base remains relatively small and therefore additional basic material has been sought elsewhere. Fodder beet varieties have for instance been introduced into sugar beet breeding programmes. Attempts have also been made to use other varieties from the *B. vulgaris* group; Savitsky, for instance, states that it is possible to obtain additional genes for sugar content from Swiss chard (*B. vulgaris* var. *cicla*). Other representatives of the genus have also been studied. Resistance to *Cercospora*, for example, was introduced into sugar beet from *B. maritima* by Munerati in 1932, and such species as *B. lomatogona*, *B. webbiana* and *B. procumbens* have all been tested as sources of new characters. Their crosses are highly sterile, however, and it is only recently that some success has been achieved, an example being the introduction of nematode resistance from other *Beta* species into *B. vulgaris* (Savitsky, 1975, 1978).

RESULTS OBTAINED IN PRACTICE

Early in the 17th century the yield was about 20 t/ha, and the sugar content about 6%, giving a sugar yield of 1.2 t/ha from which only 0.6 t/ha could be extracted. Under good conditions, extractable sugar yields in north-western Europe can now reach 7-9 t/ha. Scheijgrond (1978) calculated the yield increase in the Netherlands and his results are given in Fig. 4.29. The sugar yield obtained in trials was 10 t/ha. The total increase due to variety improvement over the same period was 10%, or 0.35% per year. In the same period the mean yield on farmers' fields rose from 6.5 t/ha to 7.2 t/ha. From a publication of the Netherlands Mechanization Centre (Stichting Mechanisatie-Centrum, 1971), conclusions regarding a further improvement can be drawn. Owing to the introduction of genetically monogerm seed and herbicides, together with full mechanization, the 290 man hours formerly needed for the cultivation of 1 ha of sugar beet (excluding the hours needed for general farm maintenance work) has been reduced to 13.0 hours. From these data it can be shown that whereas in Achard's time the production was about 4 kg sugar/man hour, after World War II this figure was raised to 23 kg sugar/man hour in the Netherlands. By 1980, when the total sugar-beet area under full mechanization in the Netherlands is expected to reach 25%, the figures for fully mechanized farms are likely to be 550 kg/man hour.

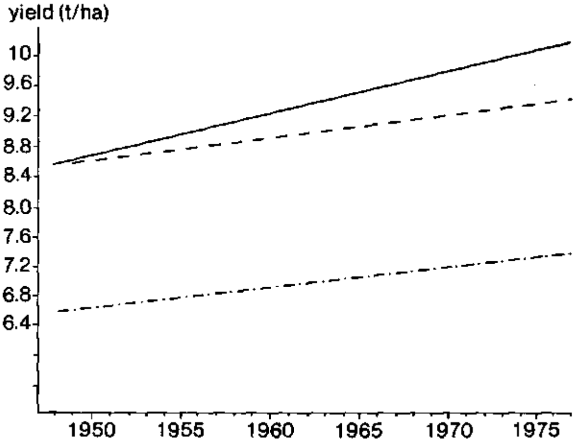


Fig. 4.29. Sugar yield increases in RIVRO trials, Netherlands, 1948-1977. Actual yields —— (annual increase 0.64%); change due to variety improvement – – – (annual increase 0.35%). For comparison: commercial yields –·– (annual increase 0.40%) (from: Scheijgrond, 1978).

Sunflower

Breeding of sunflower began in about 1900 as simple mass selection in land races in the USSR and resulted in better-adapted types and in local varieties resistant to broomrape and sunflower moth. The first step towards scientific breeding was half-sib family selection and the second the head-to-row method or remnant seed procedure. One result of the latter method was the improvement of the oil content from about 33% in the 1920s to more than 50% after World War II. The development of hybrids with high specific combining ability began as early as 1919 in the USSR, but owing to the absence of male sterility their production on an economic scale was not successful. Landmarks in hybrid production were the discovery of genetic male sterility (1965), of cytoplasmic male sterility (1969) and finally of fertility-restoring genes (1970). With the application of these last two tools, hybrid breeding developed successfully. Large acreages are now under hybrids in Rumania, the USA and elsewhere. The sunflower is the first major oil crop to join the ever-growing list of cultivated species in which heterosis is being exploited through the use of F_1 *hybrids.*

FROM LOCAL POPULATIONS TO HIGH-OIL VARIETIES

The introduction and widespread cultivation of sunflower (*Helianthus annuus*) as an oil crop in Russia, late in the nineteenth century, was accompanied by the development of the first local peasant-bred varieties. These varieties appear to have been bred with the aim of producing unbranched types with a single head and large seeds. Another aim of popular selection was a sunflower adapted to cultivation as a field crop, a fact which explains its remarkable drought tolerance and the existence of types differing in maturity period, ranging from the late strains first introduced into cultivation to early and midlate types. Local selection for resistance to broomrape (*Orobanche cumana*) and sunflower moth (*Homoeosoma nebulella*) also played an important role in the early days of sunflower breeding, when the heavy losses inflicted by these two noxious organisms placed the whole sunflower crop in jeopardy.

Scientific sunflower breeding, initially based on the local strains bred by popular selection, began in Russia at Kharkov, Krasnodar and Saratov in 1910-1912. The attention of breeders was directed primarily to the control of broomrape and sunflower moth. In the case of the latter, selection proved effective from the very outset, owing to the presence of an impenetrable layer in the pericarp. This character, controlled by one dominant gene, has been repeatedly used in breeding and is present in all modern sunflower cultivars. The control of broomrape attack was more difficult, and is still a matter of concern, in view of the appearance of new races of this parasite. Attention was also paid to improving the main morphological and physiological characteristics, and the resulting open-pollinated varieties consequently showed increased yielding capacity and uniformity.

In the early stages of breeding, the method of mass selection was widely employed to improve yielding capacity and adaptability. Subsequently, individual selection by family groups played an important role. This method consists in sowing seed from selected single plants separately, by families, in the same spatially isolated nursery, followed by selection of the best heads among these families. As selection is performed only on the maternal line, there is no possibility of controlling the genetical contribution of the male parent.

The development of varieties with a high oil content by V.S. Pustovoĭt constituted a crucial stage in sunflower improvement. While the first cultivars released between 1912 and 1926 contained only 30-33% oil in the dry seeds, after World War II, Pustovoĭt and other Russian breeders obtained open-pollinated varieties with 48-52% oil, and thus contributed to the rapid development of sunflower as a crop not only in the USSR but throughout the world.

Pustovoĭt's method of individual selection with progeny testing and controlled

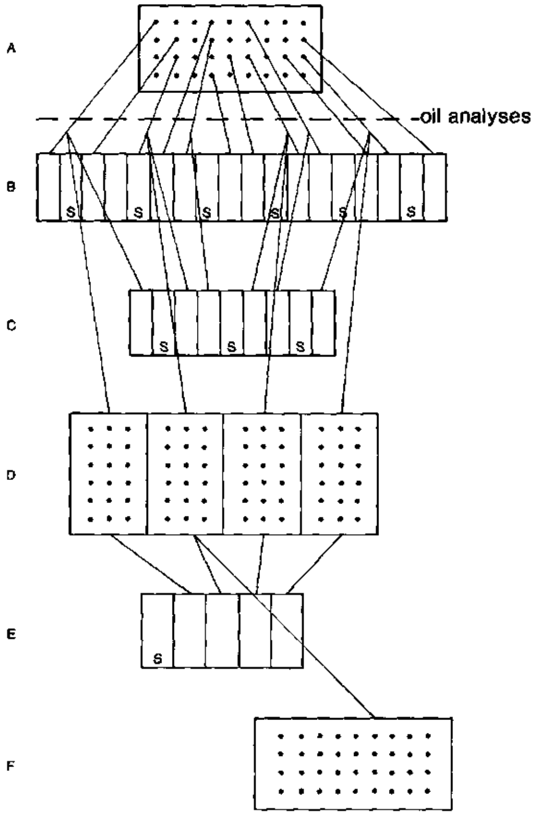


Fig. 4.30. Breeding scheme for sunflowers (combined head-to-row and remnant-seed method). A. Original material. Isolated selection fields (new open-pollinated varieties, intervarietal hybrids, superior families from mutual pollination field). B. Progeny testing nursery, first year. Replicated trials with standard variety (S) for comparison. C. Same, second year. D. Isolation field for mutual pollination of best families. E. Competitive trials. F. Start of new selection cycle.

pollination of the best families (combined head-to-row and remnant-seed method), makes it possible to avoid the contamination of valuable families by pollen from uncontrolled families (Pustovoït, 1963). Fig. 4.30 outlines the method in schematic form. Essentially, it works as follows: a small part of the seed from each elite plant is sown in the progeny-testing nursery, one row per elite plant, in two replications, every third row being a control. When each progeny has been completely evaluated, the remnant seed of the female parents giving the best families, usually 10-20, is sown in a spatially isolated multiplication field the next season, for mutual pollination. For this purpose, the families should have a different genetic background, but should be alike in height, flowering date and maturity. Each entry in the controlled pollination field is harvested separately, the plants being threshed individually and the seeds kept in numbered bags. After laboratory analyses, seed from the selected plants is utilized in two ways: that from the best plants is retained for the next breeding cycle and the remainder is combined to give the seed stock of each family, which is then tested in preliminary trials.

THE INBRED-HYBRID METHOD

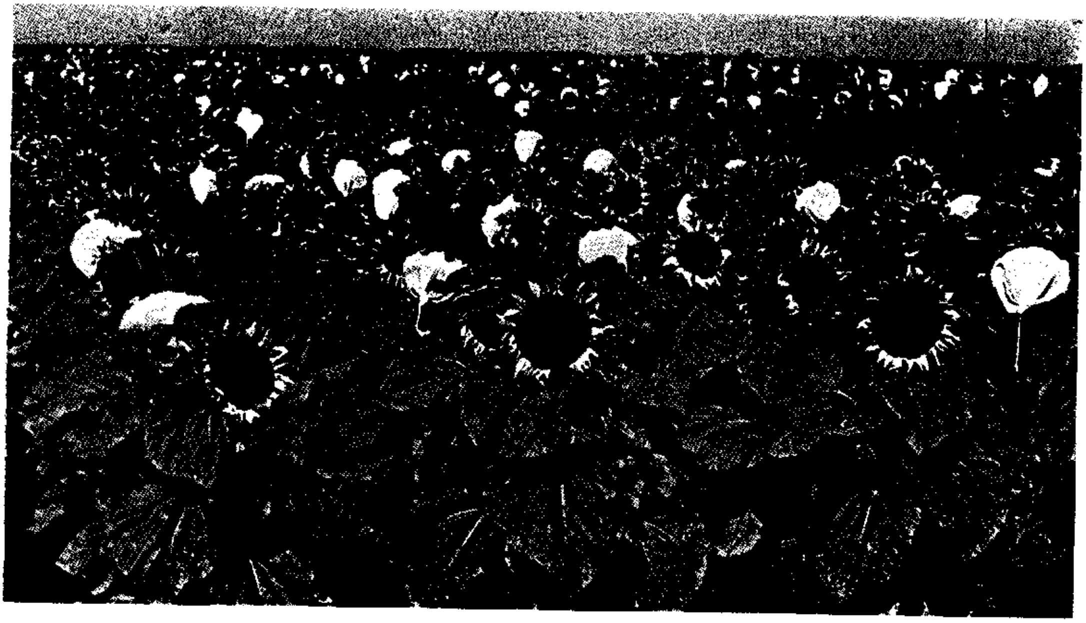
Modern sunflower breeding is particularly associated with the utilization of heterosis in the production of superior hybrids. Nevertheless, this is not a new approach. Improvement by inbreeding was initiated in 1919 at Saratov, in the USSR, where it continued for almost two decades, and was afterwards developed at Voronezh and Krasnodar (Plachek, 1930, 1936; Shcherbak, 1937; Yagodkin, 1937). Although the experimental F_1 hybrids obtained at this early stage showed evident heterosis, there were problems in using these hybrids in practice: the principal difficulty was that of producing a satisfactory proportion of hybrid seed in the absence of a suitable type of male sterility.

The next stage in using the F_1 hybrid method was reached after World War II. It began in Canada, where the first top-cross hybrids were obtained, along with a range of inbred lines carrying genes for rust resistance but having thick husks and a low seed oil content (Putt, 1964).

Extensive work on selecting inbred lines from open-pollinated high-oil varieties was initiated in Romania two decades ago (Vrânceanu, 1967b), and soon afterwards in the USSR, at Krasnodar (Gundaev, 1971). Subsequently, such work has also been developed in the USA, France, Bulgaria, Yugoslavia and other countries where sunflower has recently been introduced as a crop.

In the course of selecting inbreds, various strains with monogenic male sterility were identified, and this stimulated interest in developing commercial hybrids (Gun-

Fig. 4.31. Inbreeding nursery for sunflower. (Photograph: A.V. Vrândeanu).



daev, 1965; Leclercq, 1966; Putt & Heiser, 1966; Vrânceanu, 1967a). Using the linkage detected by Leclercq (1966) between the allele for male fertility, *Ms*, and the dominant gene *T*, which determines the red anthocyanin coloration of the entire plant, the first commercial hybrids were produced in Romania and France (Vrânceanu, 1974).

The breeding of hybrid sunflowers has been greatly assisted by the discovery of cytoplasmic male sterility among progenies of the interspecific cross *H. petiolaris* × *H. annuus* (Leclercq, 1969). The main difficulty encountered in the practical exploitation of this type of male sterility lies in the extremely low frequency of genes for pollen fertility restoration (*Rf* genes) in the cultivated sunflower. Such genes have been identified in wild sunflower species and in certain material derived from them (Kinman, 1970; Enns, 1972), and also in certain obsolete sunflower cultivars (Vrânceanu & Stoenescu, 1971). The main emphasis in current breeding work on sunflower inbreds is on the introduction of *Rf* genes into the genotypes of the best inbred lines (Vrânceanu & Stoenescu, 1978), with a view to the large-scale production of

Table 4.17. Performance of sunflower single hybrids in FAO network trials, 1976 (seed yield at 0% moisture).

Cultivars[1]	Source	Romania (Fundulea)		Bulgaria (Toshevo)		Hungary (Iregszemcse)		Yugoslavia (Novi Sad)		Italy (Pisa)		France (Aude)	
		q/ha	rank	q/ha	rank	q/ha	rank	q/ha	rank	q/ha	rank	q/ha	rank
Romsun 52	Romania	31.1	2	32.9	1	24.6	3	39.8	2	32.4	4	32.2	1
Sorem HT-64[2]	Romania	29.5	5	25.0	9	22.1	6	29.3	3	33.3	1	31.1	2
H-223	Spain	28.2	7	30.3	3	25.6	2	39.0	4	30.7	6	29.5	4
H-489	Spain	27.9	8	30.3	3	26.1	1	35.8	9	29.1	8	28.2	7
Relax	France	27.9	8	28.5	6	18.2	11	40.5	1	29.3	7	28.2	7
Sorem 82	Romania	30.6	3	24.4	10	24.4	4	32.6	13	29.1	8	30.1	3
Romsun 59	Romania	32.2	1	30.0	5	20.9	7	33.1	12	31.7	5	27.7	8
Airelle	France	27.6	10	30.4	2	19.8	10	38.5	5	22.5	13	29.1	5
H-465	Spain	28.4	6	30.2	4	20.8	8	36.3	8	26.2	11	26.6	11
Romsun 53	Romania	29.6	4	26.9	8	20.3	9	35.5	10	33.1	2	25.8	13
Yu NS-65	Yugoslavia	27.7	9	22.5	12	16.9	13	39.8	2	32.5	3	26.8	10
Sorem 80	Romania	29.5	5	21.9	13	17.7	12	37.8	6	27.4	10	27.0	9
Peredovik[3]	USSR	27.1	11	27.7	7	24.6	3	34.5	11			28.8	6
Helios 322	Bulgaria	27.6	10	25.0	9	24.3	5	28.4	14	28.9	9	25.4	14
Remil	France	24.4	12	24.1	11	20.3	9	36.6	7	25.2	12	26.0	12
LSD 0.05		1.6		1.1		2.8		5.6		6.3		3.8	
CV %		4.0		7.3		8.1		9.2		8.1		7.9	

1. In order of average performance.
2. Three-way hybrid.
3. Control open-pollinated variety; original seeds from Krasnodar, USSR.

Table 4.18. Performance of two Romanian sunflower hybrids in Romania in 1977.

Cultivars	Genetic structure	Cultivated area (ha)	Average yield (kg/ha)	(%)
Romsun 53	single hybrid	116,338	1858	140
Romsun 52	single hybrid	24,078	1714	129
Record	open-pollinated variety	332,159	1449	109
VNIIMK 8931	open-pollinated variety	31,014	1325	100

commercial hybrids on the basis of cytoplasmic male sterility. Fig. 4.31 shows parts of an inbreeding nursery.

The superiority of the first sunflower hybrids compared with the best open-pollinated varieties has been confirmed in rigorous experiments conducted in various countries. This is illustrated in Table 4.17, which presents data obtained in the FAO Co-operative Network on Sunflower in 1976. Better hybrids are continually being released in various countries. Owing to the uniformity and improved lodging resistance of the hybrids, seed losses due to shattering before and during mechanical harvesting have been substantially reduced, with the result that the gains in yield provided by the best sunflower hybrids grown in large commercial fields are in fact higher than those obtained in test plots. Thus the single hybrid Romsun 53, grown on a large area in Romania in 1977, outyielded the open-pollinated varieties VNIIMK 8931 and Record by 40 and 28% respectively (Table 4.18).

OPEN-POLLINATED VERSUS HYBRID VARIETIES

The remnant-seed procedure (head-to-row method), as elaborated and successfully exploited by Pustovoĭt for the production of high-oil open-pollinated varieties, is a form of recurrent selection with a cycle of two or three years, by means of which gene frequencies within the population are gradually altered while at the same time the genetic diversity necessary for selection is maintained. Such a method is especially effective when, as a result of recombination, the genes which determine the required characters become concentrated in a reduced number of individuals. In this connection, an instructive example is provided by the remarkable efficacy of selection for reduced husk percentage and increased oil content in sunflower seeds.

Another advantage of this method is the fact that it permits improvement of the combining ability of the breeding material. By means of progeny tests, the best hybrid combinations obtained when various types are crossed with the general tester (the initial population from which the elite plants were extracted) can be identified. Although such combinations cannot be reproduced anew, types with good combining ability are selected and their frequency increased, so that by multiplying this material, new combinations with some degree of heterosis appear. In many cases, the increases in yield observed in the progeny-testing nursery are reduced when the families are multiplied by controlled pollination, but the new population finally obtained has an increased yielding capacity and oil percentage.

The breeding methods employed in the improvement of open-pollinated varieties, however, have some serious disadvantages, such as inadequate control of the male parent and continued segregation due to the heterozygosity of the individuals which form the population. For this reason, conventional methods are not very effective in selecting for disease resistance, one of the main objectives in sunflower breeding. Thus the Argentine varieties Impira, Guayacán, Cordobés and Manfredi, developed by mass selection from cross populations obtained by crossing indigenous varieties with certain wild species, are either only partially rust restistant, with approximately 30-40% susceptible plants, or completely without specific resistance, after having been initially very resistant (Luciano & Davreux, 1967). G.V. Pustovoït (1968) notes that, as a consequence of repeated back crossing to cultivated sunflower, the initial immunity of interspecific hybrids to downy mildew (*Plasmopara helianthi*) has not been maintained in later generations, and that the extensive heterozygosity of the hybrids makes it difficult to develop stable immune cultivars.

In spite of the obvious success of selection for high oil content, present-day open-pollinated varieties are not superior to old ones in respect of seed yield. Morozov (1971) points out that no increase in seed yield has been observed in new varieties over the past 30 years, the substantial increases obtained in oil yield being attributable to the higher oil percentage in the kernel and the higher proportion of kernel in the harvested seed.

The main current problem, therefore, is the further improvement of productivity by increasing seed yield and, as far as possible, the oil content of the seed. This goal can be attained only by exploiting the hybrid vigour of the F_1 produced by hybridization of two inbred lines. Although, on account of the very limited number of male-sterile and restorer inbreds initially available, the number of high-yielding commercial hybrids is still quite small, as may be seen from Tables 4.17 and 4.18, nevertheless, the experimental hybrids obtained after only a decade of hybrid sunflower breeding have been characterized by higher and higher seed yields. The yields have often reached more than 4 t/ha, and have been accompanied by oil contents of 53-55%, a level very close to the biological upper limit of this trait. The inbreeding method has facilitated the rapid selection of inbred lines with thin husks and a high kernel oil percentage, which can then be combined to give superior hybrids with reproducible heterosis.

The F_1 hybrid method has proved very efficient in breeding for disease resistance. It permits the level of homozygosity to be increased and the genes for resistance to be controlled and transferred to other inbred and hybrid genotypes without difficulty. When new pathogen races appear, the specific resistance of a hybrid can be reestablished rapidly by the incorporation of more effective resistance genes in the parental lines. Thus, following the identification of the first gene conferring resistance to *P. helianthi* (Vrânceanu, 1970), breeding has advanced so rapidly that today no hybrid would be accepted without being resistant, whereas among open-pollinated varieties bred by interspecific hybridization and conventional breeding methods, none with resistance to this serious disease has been released or widely grown over the past 25 years. It is worth mentioning that it is not only vertical or monogenic resistance that can be easily incorporated into the parents of a hybrid, but also horizontal or polygenic resistance, such as that conferring an acceptable degree of tolerance to the sunflower rots incited by *Sclerotinia sclerotiorum* and *Botrytis cinerea.*

Unlike conventional breeding methods the F_1 hybrid method facilitates the construction of a morphological and physiological ideotype of sunflower, i.e. a model plant which may be expected to yield a greater quantity or quality of grain and oil in a defined environment. It should be possible progressively to improve and introduce into the general type the characters of the model – strong stem with short internodes, large and compact head, slight inclination of the head, erect leaves etc. – and thus develop a new type of cultivar.

Because of their genetic uniformity, single hybrids have hitherto been more vulnerable than open-pollinated varieties to climatic variations and to the heat or water stress encountered in various ecological zones (Vrânceanu & Stoenescu, 1972). For this reason, it is not easy to produce a single hybrid of the 'universal' or widely adapted type, of which the open-pollinated Russian cultivar Peredovik is an example. However, single hybrids could be substantially improved with respect to their adaptability to the natural climatic and soil conditions of specified areas. This would involve testing a large range of hybrids, in order to identify those best adapted to a given locality. At present, attention is also being paid to three-way hybrids, which are superior in adaptability and yield stability.

Sunflower may be cited as an example of a crop in which the breeding of both varieties and hybrids is still actively in progress. In fact, there is no question of competition between the two methods: there is merely a choice imposed by current breeding objectives and requirements. Open-pollinated varieties are still of interest in arid zones or in marginal areas not very favourable to this crop, such as those in the developing countries of Asia, Africa and South America or even in some countries with advanced agriculture. Hybrids, on the other hand, are intended for an intensive agriculture, capable of exploiting their high yielding ability.

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with the collaboration of
M.T. Morales and K.B. Geling on information handling
G.A.M. van Marrewijk on male sterility for hybrid production
J.G.T. Hermsen on incompatibility as a tool in plant breeding
G.E. van Dijk on apomixis
J. Trip on potato breeding
J.G.T. Hermsen on new approaches in potato breeding
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A.C. Zeven on hybrid wheat
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D.N. Duvick and W.L. Brown on maize breeding
A.J.T. Hendriksen on sugar beet breeding
A.V. Vrânceanu on sunflower breeding

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5 Crop adaptation

For the breeder aiming at surpassing the adaptive level of existing varieties, an understanding of the environments in which a future variety is to be grown is of particular importance. The high-yielding varieties (HYVs) of wheat and rice have been successful mainly because of the wide ecogeographic adaptation and high response to irrigation and nitrogen application associated with their improved plant type. In general, future crop varieties should be suitable for the mechanized cultivation, dense planting and fertilizer applications used in advanced agricultural systems. A further means of increasing crop production per hectare per year is the use of varieties adapted to multiple cropping. For the less favoured farmer, stability of crop production is more important than high yields based on high investments. Thus, for example, drought resistance may be essential, especially for the subsistence farmer. Suitability for minimum cultivation also deserves attention from breeders. Discussions of genotype × environment interactions presented in this chapter throw light on the magnitude of environmental effects on varietal adaptation and performance and should help to further the efficiency of breeding for well-adapted varieties.

Adaptation in plant breeding

INTRODUCTION

Before the advent of the HYVs (high-yielding varieties) in cereals, farmers' varieties were characterized by numerous genotypes which had specific adaptation to local ecological conditions and agronomic practices or had locally preferred quality features, or both. The HYVs of wheat and rice have amply demonstrated that, with wide adaptation, the plant breeder's product can cover a wide ecogeographic area, that seed of the improved genotypes and the associated technology can spread rapidly and that the impact on crop production can be considerable.

It is important for plant breeders to recognize the components that confer wide or specific adaptation, so that selection procedures can be tailored to meet the breeding objectives. It is equally important to understand the interaction between plant traits related to adaptability and the prevailing range of environmental conditions. Where such interactions are in favourable directions, stability in production can also be realized.

Wide adaptation refers to the relatively low levels of response of the genotype to an array of environmental conditions, whereas specific adaptation focuses on the maximum genotypic response to a highly specific factor or factors of the environment. Specific adaptation also means a much lower level of productivity in other ranges of environment. The plant breeder's job is to exploit such genotype-environment interactions in the interest of maximum production, lowest possible inputs and the farmers' needs. This chapter discusses the various component traits associated with wide or specific adaptation, the identification of genotypes with varying levels of adaptation, the genetic basis of homoeostatic properties responsible for genotype-environment interactions, appropriate testing procedures for the choice of parental material and evaluation of hybrid progenies for acceptable levels of interactions, and the role of heterosis or heterozygosity in the stability of production.

IMPLICATIONS IN PLANT BREEDING

Genotypic and populational adaptation

Adaptability is that property or ability of a genotype or population of genotypes which permits subsequent alteration of the norms of adaptation in response to changed selection pressures (Simmonds, 1962), whereas adaptation is a state of fitness to a given environment. Simmonds (1962) describes four categories of adaptation:

- Specific genotype adaptation is the close adaptation of a corresponding genotype to a limited environment. For the production of rice in a deep-water area, a variety's capacity for rapid internode elongation during flooding is an essential feature of its specific adaptation.
- General genotypic adaptation is the capacity of a genotype to produce a range of phenotypes compatible with a range of environments. This can be illustrated by the semidwarf wheats and rices which can be grown over a wide array of environmental conditions or a wide geographic area.
- Specific population adaptation is the aspect of specific adaptation of a heterogeneous population that is attributable to interaction between components rather than to the adaptation of components themselves. A composite or a varietal mixture giving stable production corresponds to this category.
- General population adaptation is the capacity of heterogeneous populations to adapt to a variety of environments. Synthetic varieties of forage crops are an example. This property of adaptation is specific to an individual genotype or a group of genotypes and is termed homoeostasis. Populations that are heterogeneous have a greater capacity to stabilize productivity over a range of changing environments because such heterogeneity provides a higher degree of population buffering. Similarly, heterozygous individuals have better buffering ability than homozygotes and such a property constitutes physiological homoeostasis.

Environmental factors affecting adaptation

Variation in the environment comprises predictable and unpredictable changes. The first category includes topography and soil type, and climatic conditions such as day length. Agronomic practices such as sowing date, method of seeding and fertilizer rates can be superimposed on these environmental variations.

In northern areas, low temperatures during the crop growing period sometimes affect plant growth and crop yield. This constitutes one of the factors of stress in those areas. In Hokkaido, Japan, cool-weather tolerance has been of primary importance in rice. Although recent rice yields have attained the level of 5 t/ha, which is well above the average recorded in Japan, once every four years or so there is a cool year, in which a critical low temperature occurs during meiotic division of the pollen mother cells, and yields in such years are usually significantly lower than those of the average year. Today, however, yields in a cool season are higher than those in normal seasons 20 years ago. Thus, the level of the critical temperature has dropped, and breeding has led to improved resistance to low temperature. Low temperature is still a stress factor, but the degree of damage it causes is changing.

CATEGORIZATION OF ENVIRONMENTS

In order to identify superior genotypes that can give reproducible performance, the breeder evaluates his breeding materials over a number of locations or seasons. At the same time, he can use the experimental data for categorizing the environments of the test sites. This information will improve the efficiency of regional testing and enhance our knowledge of varietal adaptation.

Using appropriate statistical analyses, Horner & Frey (1957) were able to adopt an optimum pattern of subdivision for the oat breeding programme in Iowa, USA, by reducing the test sites from nine to four. Similarly, in Japan, Konishi & Sugishima (1964), using heading date as the main criterion, were able to choose three sites to represent the barley-producing areas of Kyushu. The use of the rank correlation method allowed Gotoh & Fujimori (1960) to subdivide the soya bean producing area in the Tokachi district of Hokkaido Island into three groups. Cluster analysis, used by Abou-El-Fittouh et al. (1969), led to the adoption of five major areas and subareas for the cotton-producing states of the USA.

ASSESSMENT OF YIELD STABILITY

Components of variance

Sprague & Federer (1951) used the components of variance to compare the genotype × environment interactions of single-cross and double-cross maize hybrids. They obtained smaller interactions from the double-cross hybrids than from the single crosses. However, more recent data obtained by several workers in the USA and Canada have shown that some single crosses are more widely adapted than the standard double-cross hybrids.

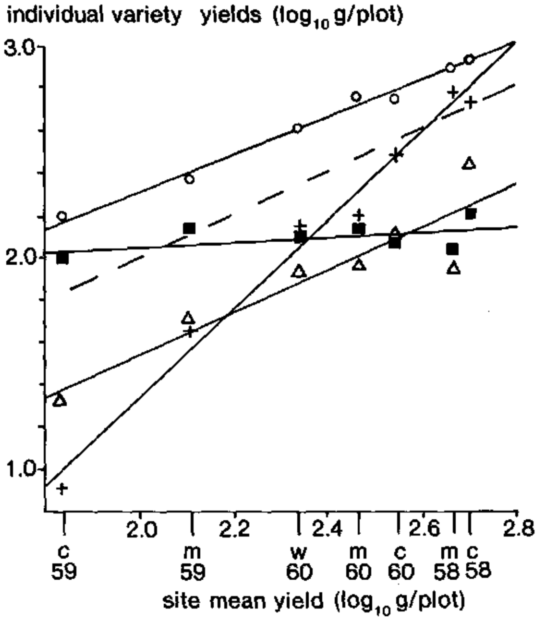

Fig. 5.1. Regression lines, showing the relationship of individual yields of four varieties and population mean of 277 varieties of barley grown at different sites and seasons. Atlas ○, Provost +, Bánkúti Korai ■, BR 1239 Δ . Population mean ––– c, Clinton; m, Minlaton; w, Waite Institute. 58, 59, 60 represent 1958, 1959, 1960 (from: Finlay & Wilkinson, 1963).

Regression analysis

Since the mid-1960s regression analysis has been increasingly used to measure yield stability over a wide range of environments. Finlay & Wilkinson (1963) first analysed the yield stability of 277 barley varieties grown at three locations for three years. They identified four situations with regard to yield stability (Fig. 5.1). Atlas was a high-yielding and stable variety with a regression coefficient of $b = 0.90$; BR1239 was low yielding and stable, with $b = 1.05$; Bánkúti Korai was a relatively high-yielding variety in poor environments, with $b = 0.14$; Provost was an unstable variety giving extremely low yields in poor environments but high yields in favourable environments, with $b = 2.13$.

This technique is useful in quantifying the adaptation of a number of cultivars on the basis of multilocation testing. However, linear regression analysis, to be useful, should account for most of the variation of the dependent variable (yield) with little or insignificant deviations from linearity. Sometimes this is not the case, owing to the following limitations:

1 The testing environments are restricted in number and diversity and the entries included are already highly selected and therefore not sufficiently representative to

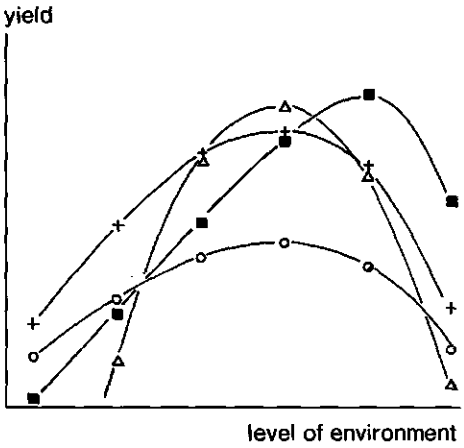

Fig. 5.2. Typical yield response curves of four different genotypes (+, ■, O and Δ) to levels of an environmental factor such as temperature or nutrient supply (from: Knight, 1970).

fit the random model for linear regression. The environmental index suffers from the same limitation where there is a restricted number of related genotypes with a similar past history of selection or origin.

Knight (1970) discusses problems of the biological interpretation of results from regression studies and makes some important points, which are brought out in Fig. 5.2. This shows typical yield response curves of different genotypes to levels of a single environmental factor such as temperature or nutrient supply. Genotypes 1 and 2 have optima at different levels of environments, genotypes 1 and 3 have similar ranges in response but different overall yields, and genotype 4 shows a restricted adaptation and range in response. The response curve of genotype 1 corresponds to the average response of a large number of genotypes and it will have the average linear regression. The other genotypes are atypical.

A substantial portion of the variation in the barley material used by Finlay & Wilkinson happened to fit the linear regression model. This is not so in a number of crops, including hybrids of sorghum and millet and advanced cultivars of rice and wheat, when grown under a diversity of conditions in the humid and semiarid tropics. The deviation from linearity may become more pronounced under moisture stress. However, the experimental evidence on sorghum and millet hybrids indicates that by using appropriate male parents on the same male-sterile female parent, it is possible to choose hybrids with limited deviations from linearity. The degree of deviation from a linear model would thus appear to be under genetic control, even in F_1 hybrids with maximum heterozygosity, which is considered by some to confer greater buffering capacity over environments.

2 A comparison of the regression coefficients of single-cross, three-way cross and double-cross hybrids of maize has again shown that the claim that double crosses are more widely adapted than single crosses is not justified (Lynch et al., 1973).

3 In addition to the regression coefficient (*b*), Eberhart & Russell (1966) used a second parameter, the mean square deviation from regression (s_d^2, to describe yield stability. Their definition of a stable variety is one with $b = 1.0$ and $s_d^2 = 0$. This second stability parameter (s_d^2) appeared to be very important. As large values of s_d^2 were obtained for some lines and crosses, the data were fit to a quadratic model. The reduction in the deviation mean square was negligible, however, so that large deviations were not caused by a quadratic response. On the other hand, Schnell & Schmidt (1975) have shown that quadratic regression is more appropriate to the study of the yield and adaptation of medium-maturity hybrids of maize than linear regression.

Most of the regression analyses of adaptation have made use of yield and environmental data, the varieties being classified as stable, medium and highly responsive to environmental improvement. However, stability is equally important for other characters like flowering time and duration of flowering and maturity, some flexibility being required to allow recovery from stress when more favourable conditions reassert themselves during the same crop season. Stability is also necessary for characters like grain size, number of secondary branches of the panicle and grain filling, all of which are important contributors to yield. Some components of yield are mutually compensatory and may be so for their stability also. With regard to grain quality, protein content and quality, which are highly influenced by environment, further study is needed, since there appears to be genetic variability for relative stability for these attributes in the major cereals. Similar studies would be worth undertaking in oil seeds, legumes and tuber crops.

Principal component analysis

Okuno et al. (1971) applied principal component analysis (PCA) to the data obtained by the International Rice Adaptation Experiment in 1968. They concluded that PCA may be useful for the categorization of environmental conditions and for the classification of varieties for yield stability. This kind of approach was employed by Suzuki & Kikuchi (1975) to relate the adaptability of rice varieties to meteorological factors recorded at seven sites, also using the data of the International Rice Adaptation Experiment. They applied PCA to the meteorological records, calculated simple and multiple correlations between yields and such records, and carried out cluster analysis of experimental sites in respect of yields. Although the results were not conclusive, partly owing to insufficient data on climatic and cultural conditions, it seems that this kind of approach may be applicable to analyses of environmental index and varietal response to the environmental complex in the future.

SELECTION FOR YIELD STABILITY

Yield stability is genetically controlled and, as has been shown for maize (Scott, 1967), selection for yield stability can be effective.

It is possible to select for yield stability using two contrasting environments (locations or seasons). Oka (1967) called this method 'disruptive seasonal selection'. An example is provided by rice breeding in Taiwan, traditionally based on successive selections in the first (spring) and second (autumn) seasons, which greatly differ in the changing pattern of temperature and day length. Products of such a selection process, the Ponlai varieties, are adapted to both crop seasons in Taiwan (Chang, 1961). They were found to be highly productive in different African countries and in India when grown under intensive management (Shastry, 1966; Chang, 1967a).

Oka (1967) grew segregating materials in two successive seasons in order to select dual-season types of soya beans in Taiwan. Desirable lines were selected in one season and grown in the next. By means of this method, high-yielding lines with low photoperiod sensitivity, determinate growth and short stature were bred. When these were grown at seven locations and their stability tested using the method of Finlay & Wilkinson, it was found that they showed wide adaptation, and that the so-called disruptive seasonal selection had been effective in selecting for stability (Tsai et al., 1970).

As is well known, Mexican wheat varieties perform well not only in the Asian countries but also in Canada. The stability of the Mexican wheat varieties is attributable to an aggregate of characters including insensitivity to photoperiod, stiff straw, high response to nitrogen, resistance to many rusts etc. According to Borlaug (1965), at CIMMYT, Mexico, two generations of segregating materials were grown and selected each year to accelerate the breeding programme. The plants were grown in a winter nursery at sea level in north-west Mexico at latitude 27°N and in a summer nursery at 2800 m altitude near Mexico City at latitude 18°N. Some selections were even grown at 3100 m in Colombia at latitude 4°N. Selection of the best material at each of the test sites in turn resulted in a gene pool of high-yielding and widely adapted lines for final selection. This approach is also an example of disruptive seasonal selection.

The relatively low photoperiod sensitivity of IR8, TN1 and Tainan 3 rices is a major contributory factor to their yield stability (Oka, 1966; Chang, 1967a). Other attributes are a moderately long basic vegetative phase (BVP), moderately high tillering ability, low response to variations in temperature and high panicle fertility. A rather long BVP ensures a minimum period of leaf and tiller production. High tillering ability compensates for variations in planting density. IR8 tolerates high temperatures of both water and air but is rather sensitive to low night temperatures (Chang & Vergara, 1971). High panicle fertility at a high rate of nitrogen fertilization is one of the desirable features of the semidwarf rices (Yoshida, 1972). The rather short plant stature and stiff culm of the Ponlai varieties of Taiwan provide good lodging resistance, but the semidwarfs are superior in lodging resistance and hence in nitrogen responsiveness (Chang, 1967b). The short-statured varieties are best adapted to shallow and continuously irrigated conditions.

Analysis of the data from the 3-year International Rice Adaptation Experiments of IBP/UM has also demonstrated that yield stability is a genotypically controlled character. Photoperiod-sensitive varieties are more variable in yield than insensitive ones when tested at different sites. When only insensitive and weakly sensitive varieties were tested, however, yield stability differed significantly according to varietal genotype (Japanese International Biological Program, unpublished). When measured on a logarithmic scale, yield stability appeared in many cases to be weakly positively correlated with mean yield (Oka, 1975). Analysis of the IBP Adaptation Experiments yield data and pertinent climatic data by Suzuki & Kikuchi (1975) also showed the importance of varietal responses to temperature and photoperiod.

The stability of panicle length was strongly and positively correlated with yield stability ($r = 0.90$). On the other hand, the stability of panicle number (per m^2) showed a weaker, negative relationship with that of panicle length and of grain yield. This suggests that a certain degree of plasticity at the tillering stage and stability during panicle development result in yield stability (Morishima & Oka, 1975).

RELATION BETWEEN GENERAL AND SPECIFIC ADAPTIVENESS

The performance of a widely adapted variety may sometimes be affected by a specific factor or factors. Sanbuichi & Gotoh (1969) calculated *b* values (regression coefficients) for five soya bean varieties in Hokkaido, Japan, from data taken at seven locations during six years. The *b* values for locations were lower in the cultivars Kogane-jiro and Tokachi-shiro than in other varieties. However, their *b* values for years were higher than those for cultivars. These two varieties are well adapted over wide areas but are sensitive to cool weather conditions. On the other hand, Karikachi and Kitami-shiro, both tolerant of cool conditions, showed high *b* values for locations and low values for years.

Similarly Joppa et al. (1971) analysed the adaptiveness of five high-yielding and six low-yielding varieties of spring wheat. The data were obtained at 15 to 20 locations during 10 years. On the basis of *b* values, they estimated the adaptation of varieties to fertile or poor environments. For example, Polk showed a low *b* value. It performed relatively well in poor environments, so they concluded that this variety could be recommended for poor or unfavourable environments. Joppa et al. (1971) found s_d^2 (mean square for deviations from regression) to be a useful indicator for specific genotype × environment interaction, and they believed that it depends on the reaction to certain diseases. Varieties Crim and Justin showed low values of s_d^2, and were considered to be stable varieties; as the s_d^2 value of the rust-susceptible variety Marquis was large, this variety seems to belong to the unstable group.

Thus, it appears necessary to examine concurrently the general and specific adaptiveness of each variety in order to assess the biological parameters related to adaptation.

LIMITATIONS OF THE WIDELY ADAPTED HYVs

Wheat

The semidwarf wheats do not set seed well when high humidity prevails during flowering period. Moreover, they are susceptible to aluminium toxicity of the soil. Such ecoedaphic limitations have restricted the spread of the CIMMYT-Mexican wheats in many areas of Latin America.

Rice

The short stature of the semidwarf rices makes them unsuitable for planting in areas where the depth of water exceeds 30 cm during the vegetative growth stage or 50 cm at the flowering stage. The semidwarfs also lack the high level of drought resistance necessary for dryland culture in the drier regions and are without tolerance to the lower temperatures which prevail at high altitudes in the tropics or subtropics. In the Ponlai varieties of Taiwan, the grain dormancy which is essential for growing in the monsoon season is absent.

Adaptation to production systems

MECHANIZATION

Mechanization has contributed to increased yields and reduced production costs by making it possible to plant and harvest on time and by facilitating multiple cropping. Furthermore, deeper ploughing is now possible and fertilizers can be applied and seeds planted in one operation. It is therefore desirable that modern cultivars should be bred to suit mechanized cultivation: uniform seed size or feasibility for pelleting, uniform germination and emergence, stiff straw, suitable plant or ear height for combine-harvesting are among the characters required.

Outstanding examples of successful breeding include grapes, tomatoes, sorghums and sugar beet (see Chapter 4, pp. 203-215).

Cereals

Lodging resistance Lodging is sometimes a constraint in mechanized harvesting. In cereals, lodging at angles of recline of 45° and 90° at the ripening stage can lead to average yield losses of about 25% and 40%, respectively. Such losses are attributable mainly to reduced photosynthesis during the ripening period, impeded translocation of photosynthates from vegetative organs to the grains, and grain losses at harvest. Consequently, lodging resistance remains an important project for cereal breeders. Pinthus (1973) has documented the lodging resistance of cereals, covering plant characters associated with lodging, relations between growing conditions and lodging, and breeding for lodging resistance.

Semidwarfs of wheat and rice Lodging is initially induced by the weight of the leaves and culms themselves and the heavy load of grains on ripening. Serious lodging results when strong winds and a heavy load of raindrops cause further loading on the leaves and culms. To reduce the stress on culms, the centre of gravity of the plant should be lowered. It is well known that the semidwarfing genes originating from Norin 10 are widely used for this purpose in wheat breeding, providing stiff straw and tolerance to heavy fertilization.

The important contributions of IR8 and other high-yielding rice varieties and of the CIMMYT-Mexican wheats to the Green Revolution are due to their stiff straw and semidwarf stature. Other characters associated with lodging resistance in rice are short basal internodes, thick and symmetrical culm tissues, erect leaves, and tight-wrapping leaf sheaths (Chang, 1967b). Lodging resistance is an essential requisite of nitrogen responsiveness and high yielding ability. A quantitative analysis of lodging resistance in rice by path analysis has been described by Chang & Vergara (1972). Lodging-resistant genotypes are generally less affected by cultural practices such as heavy nitrogen, deep water and dense planting than susceptible ones (Chang, 1967b).

A similar situation is known in some other crops. For example, the semidwarfing gene (*uz*) has been found in barley originating from Japan and Korea. In sorghum, the production of F_1 hybrids with short stature makes combine harvesting possible and is the principal reason for the growing importance of sorghum as a world crop in recent years.

Semidwarfness in wheat has been reported to be due to either recessive or nondominant alleles at one to three independently inherited loci. The semidwarfing genes sd_1 (rht_1) and sd_2 (rht_2) have been widely used in wheat breeding programmes.

McNeal et al. (1972) bred three height classes of composites in spring wheat by back crossing Centana (with normal plant height) to Norin 10 × Brevor. They were grown under various fertility levels at 22 locations in Montana in the USA. The short composite, presumed to have two dwarfing genes, showed the poorest yield throughout the experiments. On the other hand, the medium composite with one dwarfing gene performed very well under fertile conditions, and its yield surpassed that of the donor parent. Pepe & Heiner (1975) crossed Era, which has the sd_2 gene from Norin 10 × Brevor and gives high yields, with Chris Mutant, which has short plant stature and a higher protein content than Era. The dwarfing genes of Era and Chris Mutant were independently inherited. In F_5 lines random recombination was observed between genes for height, grain yield and protein percentage. Thus it may be expected that further use can be made of semidwarfing genes of different origin to increase yield under fertile conditions where severe lodging is the most important problem in production.

The nature of lodging resistance in rice appears to be more complex than in other small grains, owing to the enormous genetic diversity of rice varieties. In addition to mechanical properties, viscoelasticity plays an important role. Moreover, rice varieties differ markedly in the time of onset of senescence before grain ripening. Late senescence is generally associated with lodging resistance.

Mechanism of lodging The degree of reduction in yield due to lodging is determined by the type of lodging. Culm breakage causes the severest losses, followed by the bending type of lodging and root lodging. Culm breakage occurs in the internodes; bending is due to the reclining of the culms at the nodes; and factors affecting root systems cause the so-called root lodging. Lodging itself is attributable to many factors, such as culm length, height of the centre of gravity, ear height, culm weight and total weight of plant; and, of course, quality of culms plays an important role in this phenomenon.

Oda et al. (1966) studied the mechanisms of lodging in wheat and barley in relation to the following characters: thickness of culm wall; culm diameter; cross-sectional area of culm wall; section modulus, Z; bending moment, M, of culm at breaking, measured using stem samples derived from the basal 10 cm at the time of milk ripeness; secondary moment of inertia, I; Young's modulus, E, measured by a modified Olsen-type stiffness tester; bending rigidity, EI, or resistance to bending; bending stress, σ (where $M = \sigma Z$), or resistance to breaking. Their conclusions may be summarized as follows:

- M and EI can both be used to express culm stiffness. They are closely correlated with each other and with dry weight per unit culm length.
- Cultivars with the same degree of stiffness (σ) fall into two groups, in one of which stiffness is related to culm diameter and in the other to thickness of culm wall.
- The same degree of bending rigidity is expressed by different factors in different cereals. In barley it is affected mainly by I and in wheat by E.
- The lodging index L ($L = l^2 W/w M$, where l is culm length, W is total fresh weight per tiller and w is culm dry weight per tiller) is closely and inversely correlated with lodging resistance in the field.
- The bending resistance R ($R = 3\,EI\,s/l^3$, where s is bending distance), measured by a spring-balance, is closely correlated with lodging resistance in the field.
- In highly resistant cultivars, M is above 800 g cm and EI is above 8 g, except in cultivars with extremely short culms.

Lodging resistance index Various indices expressing lodging resistance have been devised for cereals. Murphy et al. (1958) used a snap score for the evaluation of lodging resistance in oats. In the snap test a handful of culms is pulled to a reclining position and allowed to snap back into place. The force required to pull the grain culms from an erect position and the rapidity and resilience with which the grain culms become erect are recorded on a scale from one to ten. The correlation between snap score recorded and actual lodging percentage in the World Oat Collection was very high, namely 0.80. They also used cL_r, which is the lodging resistance factor devised by Grafius & Brown (1954). It is computed from F/b, where F is the force required to induce lodging, measured by hanging a weight on the stem, and h is the plant height. Murphy et al. (1958) combined the following factors, which seemed to be closely related to resistance: I = percentage lodging + 0.80 percentage curvature + 0.64(10 snap score) + 0.36(100 − 1.47 cL_r). They applied this index to the World Oat Collection and were able to identify highly resistant strains originating from Scotland. These methods of evaluating lodging resistance seem to be reliable for use in selection.

NB

When a large number of rice accessions are to be evaluated, the simple approach of gently pushing the culms of flowering plants back and forth at a distance of about 30 cm from the ground may be used. This simple test indicates culm stiffness and resilience (Chang & Bardenas, 1965).

Peas

Peas are traditionally a crop of lighter land in temperate climates. They may be harvested when the fruits (pods) are green for fresh consumption or for freezing or the fruits may be allowed to ripen when the crop is harvested as 'dried peas' for human consumption or for stock feed.

When grown on a 'market garden' scale, the crop may be staked and the climbing habit exploited to provide the maximum light penetration into the crop and to place the pods in a drier atmosphere where disease will be less damaging to yield and the seeds will develop with the minimum of blemishes.

On the field scale, however, the crop is semiprostrate or prostrate depending upon the weather conditions or crop maturity. The prostrate habit frequently causes difficulties in harvesting by machine. The process is slow, harvesting losses may be heavy and there may be a high production of blemished seed which will reduce the marketability of the crop.

In the last decade genetical investigations have demonstrated the means by which some of the problems of the pea crop can be ameliorated by breeding. New varieties will incorporate one or more major genes causing the plant to develop either without leaves but with stipules or with neither leaves nor stipules. It might be thought that a drastic reduction in the photosynthetic area of the plant would have an adverse effect on yield but this proves not to be so. New plant types in which photosynthesis is carried out only by the stem, tendrils and pods prove to be capable of providing a full yield.

The new leafless varieties, the first of which are now in registration trials, have the additional benefit that they are not prostrate. The plants of a crop are held together by their tendrils and because the weight of the leaves is not present this is sufficient to keep the crop erect. Consequently it ripens more early, seed blemishing is diminished and the crop may be harvested easily by combine harvesters, just like a small-grained cereal. The pea crop therefore provides an excellent example of the way in which a change in the plant model profoundly affects mechanization.

DENSE POPULATIONS

Heavy applications of fertilizers and dense planting are two important ways of obtaining higher crop yields, and increased lodging resistance has made it possible to take advantage of both practices in cereal growing (Chapter 2, p. 52). Both involve increasing the leaf area index (ratio of leaf area to area of soil) in earlier stages of growth. However, too large a leaf area causes mutual shading within the canopy, and reduces the photosynthetic activity of the leaves. To increase the penetration of light, the leaf arrangement in the canopy must be improved, and ideal types for higher yields in such conditions have in fact been proposed. In this section we will deal with relations between plant type and spacing and planting density.

Rice

It is well known that in subtropical and tropical areas semidwarf cultivars, such as IR8 and related varieties, are extensively grown, owing to their high yields under favourable conditions.

As Tanaka et al. (1968) have pointed out, the plant type of leading cultivars in Hokkaido, Japan, has changed remarkably. For example, the old cultivar Akage, released in 1905, has a few large panicles with large droopy leaves, whereas Yukara, a representative modern cultivar released in 1962, has many effective tillers with upright leaves. In general, new cultivars tend to have shorter stature, high and plastic tillering capacity, a larger leaf area but smaller light extinction coefficients owing to their upright leaves, and a high harvest index. IR8 has the remarkable characteristic that it does not lodge and is still highly productive when its leaf area index is as high as 9 (Yoshida et al., 1972). Chandler (1969) feels that the upright leaf character is even more important at high levels of nitrogen fertilization, when enhanced tillering would otherwise cause excessive shading. The high tillering ability of the semidwarfs enables them to adapt to a range of spacings. A relatively short growth duration is generally associated with high yield among genotypes having the improved plant type.

Dryland cereals

Donald (1968) has made the provocative suggestion that a high-yielding ideotype for wheat should have a short, strong stem; few, small erect leaves; an erect spike with awns; and a single culm per plant. While no experimental evidence is available to support the uniculm concept, it appears that a sufficient number of grain-bearing tillers per unit area is essential to high yield. Rather than a high number of vegetative tillers, high tillering economy in terms of a high proportion of spikes to the total number of tillers is important.

Limited evidence suggests that erect leaves in densely planted maize may be a desirable trait (Winter & Ohlrogge, 1973). Because barrenness becomes more serious in densely planted populations, prolificacy (more than one ear per plant) in maize hybrids may insure more stable yields with different densities (Collins et al., 1965). Hybrids developed from three isogenic prolific selections were more productive than those from their original inbred (Duvick, 1974).

For any dryland cereal, the choice of an appropriate population density must take into consideration the supply of soil moisture, level of soil fertility, evapotranspiration losses from the crop, and the growth duration in relation to climatic conditions.

IRRIGATED CULTURE

The application of irrigation water to rainfed dryland crops such as wheat and sorghum not only permits heavier fertilization and higher crop yields but also requires a modification of plant type. The best-known example of technological improvements involving seed, fertilizer and water is the so-called Green Revolution and the two main cereals involved in it, semidwarf wheats and semidwarf rices. The sorghums grown in irrigated areas are largely the short-statured hybrids.

The decrease in plant stature due to the incorporation of the semidwarfing gene (in rice) or genes (1 to 3 in wheat and sorghum) is a major factor in conferring lodging resistance and nitrogen responsiveness under well-watered and well-fertilized conditions. The erect leaves associated with semidwarfs reduce the load of water drops on the leaf canopy during rain showers. Although the semidwarfs of rice are similar in plant height, they differ markedly in lodging resistance, owing to variations in outside culm diameter, thickness of culm tissues, elongation of the basal internodes, and wrapping of the lower internodes by the leaf sheaths (Chang & Vergara, 1972). Nitrogen responsiveness in rice is associated with a high harvest index or grain-to-straw ratio (Yoshida, 1972; Yoshida et al., 1972).

In semidwarf wheats, high yields are associated with large number of grains per spike but not consistently with high harvest index or erect leaves (CIMMYT, 1976). Where semidwarf wheats carry different height genes, selection for tall individuals among the semidwarf genotypes may lead to increased yields (Gale & Law, 1977).

The physiological contributions made by various component traits of the improved plant type to high yields in rice have been reviewed and discussed by Yoshida et al. (1972). Genetic control of such traits has been elucidated by Chang and his coworkers (Chang & Li, 1979). A summary of the physiological and genetical interpretations of the improved plant type is presented in Table 5.1 (Chang, 1979).

Because of the lush vegetative growth generally associated with irrigated culture and heavy fertilization, the microclimate around the semidwarf plants may become so modified as to lead to heavier insect infestation or pathogen infection or both. Therefore, genetic resistance to pests is of much greater importance for an irrigated crop than for an unirrigated crop. The heavy epidemics and rapid changes in the composition of a pest population that are associated with continuous monoculture of the same crop in the tropics, such as the semidwarf rices grown in irrigated areas, are

Table 5.1. Plant characters associated with high yielding potential of irrigated rice in the monsoon season (adapted from Table 1 in Yoshida et al., (1972) and the publications and unpublished data of Chang and coworkers (see Chang & Li, 1979)).

Plant part	Desirable characteristics	Physiological and ecological contribution	Genetical control and correlations
Leaf	Erect	Increases sun-lit leaf area, permitting even distribution of incident light; decreases load of raindrops on leaf surface.	Erectness recessive to droopiness; largely associated with semidwarfism; correlated with high yields.
	Short and small	Associated with erectness and even distribution of leaves in a canopy.	Polygenic control of leaf length and leaf area; broad leaf dominant to narrow.
	Thick	Associated with erectness and higher photosynthetic rate.	
Culm and leaf sheath	Short thick culms, tight leaf sheaths	Provide lodging resistance and nitrogen responsiveness.	One recessive gene and modifiers control shortness; culm length correlated with panicle length.
Tiller	Upright and compact	Permits light penetration into canopy.	Multigenic control in most crosses; upright tillers associated with semidwarfism.
	High tillering capacity	Adaptive to various spacings; can compensate for missing hills; permits faster leaf area expansion in transplanted crop.	Dominant trait; largely additive effect, some dominance effect; associated with semidwarfism.
Panicle	High fertility at high nitrogen	Allows high doses of nitrogen responsiveness.	Associated with semidwarfness and relatively short panicles.
	High harvest index	Associated with high grain yield.	Multigenic control; negatively correlated with growth duration; associated with early and sustained growth vigour.

a great challenge to the plant breeder (Chang, 1979).

Irrigated fields tend to dry out more slowly than rainfed fields near the harvest season. Strong root anchorage is another requisite for irrigated crops; otherwise, lodging due to uprooting is likely to occur. Since irrigation water adds to the cost of crop production, an early-maturing genotype with similar yielding ability to a late-maturing one will not only produce more grain per unit area of land per day but also a higher monetary return per unit area per day.

HIGH AND LOW FERTILITY CONDITIONS

In order to obtain profitable returns from heavy fertilization, an ample supply of soil moisture is essential. When soil moisture is limiting, the fertility level as well as the crop population density needs to be adjusted accordingly. The close relationship between water supply and fertilizer efficiency may be expressed by the following equation (World Meteorological Organization, 1975): $E = \Sigma\ P/(150 + 0.45\ \Sigma\ d) - 50$, where E is efficiency of applying fertilizer in percent relative to optimum conditions, $\Sigma\ P$ is the annual precipitation in mm; and $\Sigma\ d$ is the sum of the mean diurnal values of moisture deficit of air in mb.

According to this equation, the efficiency in unirrigated areas under winter grain in the Crimea, USSR, is 25% relative to the efficiency in the northern regions of the forest-steppe zone. Comparison of the potential evaporation and precipitation gives only an approximation of the dependence of efficiency on the degree of aridity of an area.

To obtain a consistent effect from fertilizer application, the plant breeder must take into account agrometeorological conditions as well as soil fertility. In 35% of years in the Crimea, aridity reaches the limit at which fertilizers produce no positive effect; the effect from nitrogenous fertilizers under these conditions can even be negative. Considerable success has been achieved in predicting the efficiency of fertilizer dressings from long-range climatic data.

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Like the application of irrigation water, heavy fertilization would generally lead to (1) a denser and closed leaf canopy, entailing changes in the microclimate around the lush-growing plants, (2) lodging susceptibility, (3) predisposition of the plants to disease infections or insect attacks, (4) more intense weed growth and (5) changes in crop quality. The plant breeder should therefore pay attention to early growth vigour or high tillering ability, resistance to lodging, resistance to diseases and pests affected by nitrogen, the harvest index, and changes in crop quality due to increased nitrogen content. Generally speaking, nitrogen responsiveness is correlated with thick leaves and early maturity.

While breeding for high fertility conditions has received much attention and has been widely practised in recent years, breeding for efficient crop production under low fertility conditions has remained theoretical rather than practical. Again, low soil fertility is frequently associated with limited soil moisture. Cultivars adapted to low soil fertility generally have good ability for stand establishment, thin, pale-green leaves, a long growth duration, good drought resistance or an extensive root system, a low harvest index and a short grain-filling period. While a deep and well-distributed root system enables the plant effectively to extract water and nutrients from the soil, an efficient use of water and nitrogen is equally important. Otherwise, a deep-rooted cultivar may quickly exhaust the inherent fertility of the soil and render the soil unproductive after the initial benefit of requiring little or no fertilization. Wheat and pearl millet genotypes differ in the pattern of protein accumulation in the grain from flowering to maturity – those with rapid accumulation soon after flowering may have an advantage over those with maximum accumulation at a later stage when water stress is likely to occur (Anon., 1977). In areas with a limited crop season, early maturity and rapid grain ripening are again important. Low fertility areas are frequently affected by other stress factors, so that a complex situation arises which makes it difficult for a plant breeder to compare strains for relative efficiency of nutrient utilization.

ADAPTATION TO DROUGHT-PRONE CONDITIONS

Drought annually decreases the yield of dryland crops over vast areas of agricultural land. The incidence of drought is generally higher in the semiarid regions than in the humid tropics. But partially irrigated fields and high rainfall areas are not totally immune from the adverse effects of drought. In tropical areas, drought frequently precedes or follows a flood.

Understanding drought

Breeding crop plants for drought-prone conditions requires an appreciation and knowledge of the environmental factors which interact with rainfall deficits to create the array of complexes collectively referred to as 'drought'. The variability (across and within seasons) and range of these salient environmental factors are extremely location-specific.

A brief discussion of agricultural drought and the associated environmental factors and cultural systems with special emphasis on rice has been provided by O'Toole & Chang (1978, 1979). Although many edaphic, biotic and agronomic factors characterize the location specificity of drought and its consequences on crop yield, the primary considerations are the rainfall pattern or distribution and the soil's capacity to supply the crop's water requirement between rainfall events. Thus the first step in planning a varietal improvement effort must be a comprehensive 'diagnosis' of the direct (water deficit) and indirect (attendant physical, chemical and biological changes) contributing factors. The compilation and analysis of rainfall data with reference to the traditional cropping schedule of rainfed farming will aid in determination of the crop growth stages prone to water deficit conditions. Equally important is a survey of the regional soil characteristics, especially texture, depth and drainage characteristics. These climatic and edaphic analyses, in combination with identification of problematic yield-determining growth stages, determine the appropriateness of employing specific adaptive mechanisms. The importance of this 'diagnostic' step cannot be overemphasized and should be a continual process which attempts to clarify objectives (O'Toole & Chang, 1978).

Selection of adaptive mechanisms

Empirical selection among traditional cultivars or hybrid progenies under drought-prone conditions or conditions of drought simulation has been the most common and surprisingly efficient approach in selecting and breeding genotypes adapted to this stress (Chang et al., 1975; Hurd, 1971). Although successful, this method of selecting for 'field resistance' or 'phenotypic acceptability', without investigating the causal factors, may prove limited in scope.

Adaptive mechanisms or the component traits making up 'field resistance' have been classified as escape, avoidance, tolerance and recovery mechanisms.

Escape mechanisms allow the crop to undergo their yield-determining growth stages during periods of adequate moisture. This adaptation has been broadly selected for in rainfed agricultural systems. Early maturity (see Asana, 1976; Derera et al., 1969, for wheat; Krishnamurthy et al., 1971, for rice; Blum, 1970, for sorghum) and photoperiod sensitivity (Oka, 1958; Vergara & Chang, 1976) are two alternative traits which ensure the completion of the drought-sensitive reproductive stages during periods of adequate moisture.

Early seedling vigour and rapid stand establishment will enable a cultivar quickly to attain a good crop stand within the limited crop season.

Avoidance If a rainless period does occur, the crop's initial means of continuing growth and development is to avoid internal stress. Initially, this is by uptake of stored soil water to meet evaporative demand. Later, if soil water becomes limiting, control of water loss from shoot to atmosphere may be invoked.

Adaptive mechanisms enabling a crop to maintain water uptake would be combinations of a denser root habit (greater root-soil interface/cm^3 of soil) with deeper rooting. The traditional upland rices of Southeast Asia and West Africa have such deep and thick roots (Chang et al., 1972) that they compare favourably with those of a wheat cultivar (IRRI, 1975). Similar findings have been reported from several dryland cereals (Hurd, 1971, 1974, 1976). Through the analysis of nitrogen reductase activity and the determination of root depth and distribution by ^{32}P tagging, the improved pearl millet hybrids of India have been found to utilize applied nitrogen and, hence, available soil moisture more efficiently than their parents (Anon., 1977). Semidwarfs of wheat have equally extensive or even better root systems than tall cultivars (Lupton et al., 1974), but semidwarf rices generally have shallower and finer roots than the traditional upland rices (Chang et al., 1972, 1974). Mass screening of rice cultivars and breeding lines in a simulated upland culture (Chang et al., 1974) provides an indirect scoring of the root system (IRRI, 1976; Parao et al., 1976). On the other hand, like most biological characteristics, root development in rice has shown genotype-environment interactions (Chang et al., 1972). Moreover, a balance exists between the relative amounts of shoot and root growth (IRRI, 1976).

Selection for root characteristics is, however, a problem. Hitherto, techniques for direct field observation of roots have proved too laborious for use in breeding and selection. Observations of root system development such as those described by Hurd (1968), or used in India (Anon., 1977) or at IRRI, Philippines (IRRI, 1975), will allow a cursory evaluation of the germplasm but cannot be used for a large-scale breeding programme except to verify the results of *in situ* growth and yield tests (Hurd et al., 1972; Hurd, 1976). However, the very close relationship between root studies and field drought screening suggests field screening by visual scoring as an indirect means of screening for root system development (IRRI, 1976). The values for leaf-water potential determined at dawn can also serve as an indicator of the tester variety's root system (O'Toole & Chang, 1978).

Stomatal resistance has been investigated as a tool in determining drought resistance in sorghum (Blum, 1974; Henzell et al., 1976), rice (IRRI, 1973, 1975) and wheat (Kaul, 1974). Evaluation of stomatal resistance, however, presents problems. In view of the dynamics of stomatal behaviour and the variability of environmental factors contributing to drought, meaningful and repeatable screening procedures would be difficult to develop. The possibility of using stomatal resistance as a general selection criterion for drought resistance appears remote for most crop plants.

Cuticular ?

High cultivar resistance to water loss has been noted as a potential attribute of drought-resistant crop species (Martin & Juniper, 1970; Ebercon et al., 1977). Yoshida & de los Reyes (1976) compared the cuticular resistance of sorghum, maize and several rice cultivars from different origins. They reported cuticular resistance values of 116 and 112 s/cm for sorghum and maize respectively, while the rice cultivars tested ranged from 68 to 30 s/cm. It was subsequently found that the epicuticular wax deposition varied between rice cultivars with differing cuticular resistance values (IRRI, 1976). The amount of epicuticular wax on the leaf appears to be indicative of the cuticular resistance and lends itself to rapid screening. Ebercon et al. (1977) developed a colorimetric test to quantify wax removed by dipping sorghum leaves in chloroform.

Leaf rolling, perhaps the most universally obvious symptom of drought, has been identified as a resistant and alternatively as a susceptible trait. Rolling of leaves indicates a decrease in turgor pressure potential, indicating that the plant is no longer completely avoiding internal water stress. Parker (1968) stated that some grasses of the Mediterranean region reduce transpiration by as much as 46 to 63% by leaf rolling.

The onset of leaf rolling, the extent of rolling and the elasticity in unrolling among rice cultivars during a diurnal cycle of water stress have been extensively used in IRRI's breeding programme as an indirect score of drought resistance (Chang et al., 1974; Loresto et al., 1976; O'Toole & Chang, 1979). A parallel trend in leaf rolling score and leaf-water potential (O'Toole & Moya, 1978) suggests that the leaf rolling score could be a convenient selection tool for rice breeders.

The basic purpose of incorporating avoidance mechanisms is to maintain a favourable internal plant water balance for a longer time under drought-prone conditions. The advent of portable field equipment for the measurement of plant water potential has greatly aided selection for the combined effect of avoidance mechanisms (Blum, 1974; O'Toole & Moya, 1978). Blum et al. (1978) has shown aerial infrared photography to be another practical means of screening for relatively high leaf water potential in large sorghum breeding nurseries.

Tolerance Drought tolerance is another adaptive mechanism frequently mentioned in the literature but rather difficult for plant breeders to make use of. In discussing tolerance we must first make the assumption that escape and avoidance are precluded. It is then possible to assume that the plant is actually suffering internal water stress and is exhibiting the capacity to withstand it.

Unfortunately, in studying differences in tolerance between crop species and between varieties, workers too often utilize only severe or sustained water stress. The information thus obtained has only limited applications in plant breeding. For situations where drought occurs during crop establishment or early vegetative stages, for example in the establishment of forage species or transplanted rice, sources of tolerance have been identified by utilizing artificial selection techniques (Wright & Jordan, 1970; De Datta & O'Toole, 1977). Varietal differences have been demonstrated by means of heat tolerance tests (Sullivan, 1972), proline accumulation (Singh et al., 1972) and desiccation survival (Levitt, 1972). These tests may be of use provided the basic characters they are based on can be empirically related to field conditions (Wright & Jordan, 1970; Sullivan & Ross, 1979). Recent progress in understanding crop response to water deficits has been reviewed by Begg & Turner (1976). As this area of research expands we may expect better insights into plant tolerance of internal water deficits and the evolution of more satisfactory screening methods.

Recovery Droughts vary in duration but when rainfall does commence the trait of rapid recovery and return to active growth and development is important. Recovery is not well understood at present but its merits are obvious and selection for it should be a part of the process of improving crop varieties. Good recovery ability in rice appears to be phenotypically correlated with vegetative growth vigour, high tillering ability, a shallow root system, and rather long growth duration (IRRI, 1975; Loresto et al., 1976). By repeated hybridization, testing and selection, progress has been made in combining moderate levels of drought resistance (via avoidance) with recovery ability (IRRI, 1976).

Heritable nature of adaptive mechanisms

Work at IRRI has shown that all of the adaptive mechanisms studied in rice are heritable (IRRI, 1975; O'Toole & Chang, 1978), though each trait is likely to be controlled by a complex of quantitative genes. Aberrant segregation has been observed in crosses between tall, traditional upland varieties and semidwarf lowland varieties, indicating restrictions in genetic recombination (Hung & Chang, 1976).

The proper selection of parents for specific traits is therefore crucial (Chang et al., 1975; Hurd, 1976). Moreover, three-way or double crosses appeared more effective than single crosses for recombining different traits from diverse parents (IRRI, 1975, 1976).

By crossing diverse parents in large numbers, followed by testing and selection of large segregating populations in appropriate environments, a full spectrum of genetic materials adapted to various moisture-edaphic conditions can be developed (Chang et al., 1975; IRRI, 1978b).

Choice of selection criteria

In general, drought escape is the breeder's first line of defence. Second, if drought occurs, the ability to avoid internal stress will help to reduce yield losses. Third, if the crop exhausts the available soil water resources, it should be able to tolerate internal water stress. And finally, droughts vary in duration but the recovery of the crop when rain does come may be crucial if the plants are to catch up and fully use the remaining growing season so as to regain the lost yield potential.

In addition to drought resistance, early growth vigour, moderate tillering capacity, light green leaves, and good grain filling are essential agronomic characteristics that are generally associated with stable yields under drought-prone conditions (Roy & Murty, 1970; Chang et al., 1972; Eslick & Hockett, 1974).

Drought resistance and yield performance

Varietal differences in yield performance obtained from field trials in rainfed culture are often difficult to interpret simply on the basis of absolute yields in a single season or at a few sites. The proportional reduction in yield due to water stress, as compared with the yield obtained under well-watered conditions, is a more meaningful criterion than absolute yield (Blum, 1973; Chang et al., 1974; Asana, 1976). By comparing yield levels, growth stages at which water stress occurred, rainfall distribution or soil moisture, and the delay in maturity due to stress in a multicriterion comparison at multiple sites over a number of crop seasons, it was possible to elucidate varietal differences in rice yield levels and apply them to farm conditions (Chang et al., 1975; IRRI, 1975, 1976).

Breeding strategy

Breeding methodology for drought resistance has been discussed by Hurd (1969, 1971, 1976), Rao et al. (1971) and Chang et al. (1975). Blum (1978) reviews two major breeding strategies currently being employed. The first, which assumes that a variety giving superior yields under optimal growing conditions will also yield relatively well in suboptimal conditions, handles yield and stability as one complex. In so doing, it requires an improvement in yield under optimum conditions which may often be irrelevant in breeding for suboptimal environments.

According to the second approach, superior cultivars for drought-prone environments should be selected *in situ*, with the particular environment applying the appropriate selection pressures. Although appealing, this approach has the disadvantage that the great variability associated with drought-prone environments makes progress slow and often calls for the testing of large populations which decreases the efficiency of the total programme.

A third alternative proposed by Blum (1978) involves the selective incorporation of relevant drought-resistance factors into cultivars with superior yielding ability under optimum conditions, thus making them better adapted to the suboptimal conditions. It is analogous to the strategy employed by plant pathologists in their efforts to incorporate disease resistance into superior lines. This strategy requires the combined efforts of plant breeders, crop physiologists, biochemists, meteorologists and soil physicists to assure the available germplasm is fully exploited.

MULTIPLE CROPPING

Multiple cropping includes an array of cropping sequences that all produce more than one crop within a year. In the broad sense, multiple cropping could refer to (1) a continuous monoculture of the same crop, such as rice following rice, (2) a continuous culture of two or more different crops such as wheat-rice or rice-rice-soya bean, (3) ratoon crops from one planting, such as ratooned rice or sorghum, (4) mixed planting of two or more crops in the same field sown at about the same time, such as upland rice and maize, maize and beans, or a grain and vegetable mixture, or (5) interplanting of different crops in the same field in a relay pattern, such as vegetables or tobacco transplanted between rows of lowland rice shortly before the rice is fully mature (Dalrymple, 1971; Cheng, 1972; Baker & Norman, 1975; Andrews & Kassam, 1976; Harwood & Price, 1976; Okigbo & Greenland, 1976).

Cultivars designed for multiple cropping schemes should generally have the following characteristics: early maturity, uniform ripening, photoperiod insensitivity, high yield per unit area per day, relatively small crop residues, and, in the case of the relayed type of intercropping, suitability for mechanized harvesting and processing. In some cases, a photoperiod-sensitive genotype may suit specific growth periods better than insensitive genotypes.

The best-known example of improved cultivars that have greatly increased the cropping intensity indexes in the tropics are the semidwarf rices. With one directly seeded crop followed by a transplanted crop under rainfed culture, two harvests are feasible within the usual span of a traditionally single-crop rainy season (IRRI, 1975). Some of the most intensive cropping schemes may be found in Taiwan (Cheng, 1972; Chao, 1975), mainland China (Anon., 1975) and Indonesia (Syarifuddin et al., 1975). The contributions of the Ponlai rice varieties to multiple cropping in Taiwan have been discussed by Iso (1954) and Huang et al. (1972).

In addition to the plant characteristics mentioned above, the following are important:

- Adaptation to heavy fertilization and supplementary irrigation (for short-season crops).
- Adaptation to dense planting.
- Disease and insect resistance under heavily fertilized, well watered and densely planted conditions.
- Quality features suited to special market demands (e.g. early-season types) or processing needs.
- Specific characteristics that would benefit the companion or succeeding crop, e.g. provision of shade at seedling stage, tolerance to shade at a later stage (thus reducing evapotranspiration of the shorter-statured crop), elastic straw adapted to trampling, or tolerance to drought or water-logging.
- Plant characteristics that would benefit both crops, e.g. resistance to a common disease or insect, different rooting depths, or varying nutrient requirements.
- Adaptation to minimum tillage.
- Other improvements leading to reduced labour costs.

In developing cultivars adapted for multiple cropping, the plant breeder and the agronomist have to tackle concurrently problems related to land preparation techniques, modification of existing farm machinery, improvement of harvest techniques, variety-system interactions, and related economic considerations. Bradfield (1972) and Francis et al. (1976) describe interesting experiences in developing improved systems for multiple cropping in tropical areas. Other aspects related to multiple cropping systems have been discussed in two workshops held at IRRI (IRRI, 1976, 1978a) and a symposium sponsored by the American Society of Agronomy in 1975 (Papendick et al., 1976).

MINIMUM CULTIVATION

While agronomic practices and agricultural machinery are being rapidly developed for minimum cultivation, only in recent years have plant breeding efforts been directed towards cultivars suited to the new technology. Nevertheless it may not be unreasonable to postulate a number of breeding objectives that the crop scientists need to consider: rapid seed germination, quick and vigorous stand establishment, rapid early plant growth, strong root growth, good competitive ability against weeds, such as is conferred by a rapidly expanding and luxuriant leaf canopy, resistance to soil-borne pathogens, and low sensitivity to the phytotoxicity of herbicides. While good vegetative vigour is essential in grain crops, the plant breeder should seek a balance between vegetative growth and grain production. A rapidly growing and relatively early-maturing genotype may come nearest to the above requirements.

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with the collaboration of
J.C. O'Toole on drought conditions
R. Riley on peas
B.R. Murty on fertility conditions

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6 Resistance to pests and diseases

Resistance, when it can be achieved, is the best method of control of pests and diseases, being free from the adverse side effects sometimes resulting from the use of pesticides. As a cheap, simple and effective means of improving stability of yield, it may be of particular importance in developing countries. But while it is often a relatively easy matter to obtain resistance, the maintenance of resistance can present problems. Historically, plant breeders have introduced a considerable number of resistance genes into crops, but the pathogen unfortunately often has a remarkable ability to adapt to the gene-for-gene type of resistance. Nevertheless, this simple type of resistance has in some cases lasted for many decades. A prerequisite to the breeding of long-lasting resistance is a full understanding of the host-parasite relationship. Once this knowledge has been acquired the breeder can turn his attention to devising methods of controlling epidemics by means of non-race-specific resistance. Like the pathogens causing diseases, insect pests are able to respond to resistance by developing virulent new biotypes. They can respond in the same way to insecticides. Screening methods and host-parasite relationships are more complicated for insect pests than for fungal or bacterial pathogens; insects are mobile and few methods are available for mass screening. More and better screening procedures are required. Work on breeding for nematode resistance is in progress, examples being resistance to cyst nematodes in potato (a vegetatively reproduced crop) and soya bean (a seed crop). In some cases screening for virus resistance presents few difficulties, while in others it is complicated by the fact that the virus is transmitted by an insect or other vector. A little-explored field deserving more attention is postharvest resistance. Promising results have, however, been obtained, for example in groundnut (Chapter 10, p. 412). Although long-lasting resistance can probably never be attained in all crops, nevertheless a system of integrated pest control whose central core is non-race-specific resistance will probably provide the most successful approach to stabilizing yield near its full genetic potential.

Disease resistance

INTRODUCTION

The remarkable ability of many parasites to adapt to introduced resistances (and indeed also to pesticides) is not only well known, but also of grave concern to all who have to cope with the rapidly increasing world demand for agricultural produce. This is the case especially where food crops are concerned. Adaptation to host resistance (physiological races) has been reported from viruses, bacteria, fungi, higher plants (*Orobanche*), nematodes and insects. Resistance to pesticides has been found among bacteria, fungi, mites and insects.

To gain an insight into the ability of a parasite to adapt to its changing environment, a detailed study of the host-parasite relationship is necessary. A basic feature of host-parasite coexistence is the fact that the parasite must circumvent or resist the defence mechanisms of the host, while the host must likewise avoid or resist the parasite to a certain extent.

TYPES OF RESISTANCE

The classification of resistance discussed in this paper distinguishes two groups, namely 'avoidance' and 'true resistance' and is based on the differences in the mechanisms involved. The mechanisms characteristic of the first group reduce the chances of contact between the prospective host tissue and the parasite, whereas those characteristic of the second operate from the moment of contact between the host tissue and the parasite.

Avoidance, involving a heterogeneous group of mechanisms, often depends on the structure of the entire plant, of certain plant parts or of certain plant tissues. A few examples are:

- The resistance of barley cultivars (*Hordeum vulgare*) with closed flowering to loose smut, *Ustilago nuda* (Pederson, 1960).
- The resistance of tall wheat cultivars (*Triticum aestivum*) to glume blotch, *Septoria nodorum*, where the height of the plant impedes the spread of the inoculum to the upper plant parts (Brönnimann et al., 1973).
- The resistance of sugar cane (*Saccharum officinale*) to smut, *Ustilago scitaminea*, depending on the morphology of the emerging ratoon buds (Waller, 1970).
- The resistance of rubber clone LCB870 (*Hevea brasiliensis*) to *Hevea* mildew, *Oidium heveae*, where the period of susceptibility, i.e. the period during which the young leaf has a thin cuticle, is reduced; normal cuticle thickness is attained in 10 to 11 days, about 7 days earlier than in most other clones (Ferwerda, 1969).

True resistance reduces the rate of colonization or growth of the parasite from the first moment of contact between the host tissue and the parasite. It implies an intimate contact between host and parasite and it involves the expression of their mutual interaction. Typical examples are:

- Resistance of the hypersensitive type. This type is used very frequently in resistance breeding and is generally controlled by a number of major genes. Where investigated in detail, the resistance genes appear to operate in a gene-for-gene relationship with the virulence genes in the parasite (Flor, 1971; Day, 1974).
- Partial resistance. This type is expressed as a reduction in the rate of epidemic build-up, occurring in spite of a susceptible reaction to infection. The reduction may be the result of a lower infection frequency, a longer latent period and/or reduced spore production.

GENETICS OF HOST-PARASITE RELATIONSHIPS

Resistance and pathogenicity have been shown to follow normal patterns of inheritance (Day, 1974), and may be governed oligogenically or polygenically. Within genes there is frequently dominance, and between genes intergenic interactions are often encountered. Cytoplasmic inheritance of resistance and probably also of pathogenicity has been observed.

Although this knowledge is useful to the breeder, the most important aspect of the genetics of host-parasite relationships is the observation that resistance genes in the host can operate on a gene-for-gene basis with virulence genes in the parasite. Flor (1956) was the first to formulate the gene-for-gene concept based on his classic work on the system involved in flax (*Linum usitatissimum*) and flax rust (*Melampsora lini*). The importance of the gene-for-gene relationship lies in the fact that it results in the race-specific, differential or vertical types of resistance (VR). All gene-for-gene relationships will give a race-specific pattern when different host cultivars are tested against various parasite genotypes (isolates, races or strains). The converse, that all race-specific host-parasite relationships indicate the operation of gene-for-gene systems, is probably also true, but has not been proved as yet.

There are in fact two types of gene action to be discerned in host-parasite relationships: firstly the gene-for-gene relationship, and secondly independent gene action. If there is no gene-for-gene (or gene-for-genes, genes-for-gene or genes-for-genes) interaction, the host genes and the parasite genes must act independently of each other. In this case it can be shown that there is no interaction between host cultivars and parasite genotypes when these are tested against each other. There is no race specificity. The variation in resistance and the variation in pathogenicity are independent of each other. This is non-race-specific resistance, as recognized by van der Plank (1963, 1968, 1975), who designated it horizontal resistance (HR). Robinson (1976) developed this concept further.

The presence of race-specific or cultivar-isolate interaction effects, therefore, can be said to indicate the presence of resistance genes that operate on a gene-for-gene basis. The absence of such effects, however, does not necessarily mean the absence of gene-for-gene action, as will be shown later.

Returning to the two resistance groups distinguished above, we may ask what types of gene action they represent, whether HR or VR. In the case of avoidance it is difficult to envisage any specificity between the host and parasite. Those plant structures which reduce the probability of contact are generally of a kind to which the parasite has no corresponding adaptations. To adapt itself to such structures, the parasite might well have to undergo drastic biological changes likely to be beyond its evolutionary capacity, at least over short periods such as decades.

The genes governing these forms of resistance generally have no specific counterparts among the genes of the parasite. Gene-for-gene relationships are not likely to be involved and the host-parasite relationship can be expected to be characterized by non-race-specific effects. With regard to animal parasites, which are capable of sense perception and movement, many plants have evolved warding-off mechanisms. Such avoidance mechanisms, which can be of a chemical (repellents, distractants) or morphological nature, are in general fairly unspecific, affecting groups of parasites rather than single species. Although somewhat different in nature from the kinds of avoidance described above, they too are unlikely to be governed by gene-for-gene systems.

With respect to true resistance the situation appears to be quite different. Here the resistance operates when the host cells and those of the parasite are in intimate contact. Genes governing resistance may have – in terms of the parasite – a specific action, which can be counteracted, or annulled, by genes in the parasite, which also have a specific action. Each stepwise increase in resistance may result in a corresponding stepwise change in the parasite. A gene-for-gene coevolution of host and parasite is not difficult to envisage. It is even plausible that all true resistance genes, i.e. genes operating when host tissues and parasite are in intimate contact with each other and involving complicated biochemical pathways on both sides, act on a gene-for-gene basis with virulence genes in the parasite.

In short, resistance and pathogenicity genes can operate either independently of each other (as suggested for avoidance mechanisms) or in accordance with a gene-for-gene relationship (as indicated for true resistance). Independently of this, resistance and pathogenicity may each be governed by one or a few genes or polygenically.

It is through a combination of these two, *type of gene action* and *numbers of genes* involved, that either race-specific (vertical) or non-race-specific (horizontal) host-parasite relationships arise.

HORIZONTAL AND VERTICAL RESISTANCE

Van der Plank (1963, 1968, 1975) distinguishes horizontal (HR) non-race-specific or uniform resistance and vertical (VR), race-specific or differential resistance. The former, he assumes, is stable, the latter not. This has been further elaborated by Robinson (1976). To test the type of resistance, a number of host genotypes are tested against a number of parasite genotypes (van der Plank, 1968, 1975). Where all nonenvironmental variation in the resulting disease severity can be explained by differences between host cultivars and by differences between isolates or strains of the parasite (main effects), we are dealing with HR and with horizontal pathogenicity, the effects being additive. There are no interactions. In the case of VR and vertical pathogenicity the nonenvironmental variation in disease severity shows interactions between cultivars and isolates, as already mentioned in connection with the gene-for-gene concept.

The consequence of this interaction is that the ranking of the cultivars according to their level of resistance depends on the isolate of the parasite used. Table 6.1 shows this. Under the combined effects of HR and VR, cultivar II is the most resistant when isolate 2 is used, but the most susceptible when tested with isolate 4; with HR the

Table 6.1. Disease severities (in percentages of affected plants or tissue) of four cultivars inoculated with four isolates. A. Main effects only (horizontal resistance only). B. Main effects and cultivar × isolate interaction effects together (horizontal plus vertical resistance).

Cultivar	A main effects only					B main and interaction effects				
	isolates				mean	isolates				mean
	1	2	3	4		1	2	3	4	
I	10	20	30	40	25	10	30	40	20	25
II	20	30	40	50	35	50	10	20	80	40
III	30	40	50	60	45	20	30	60	50	40
IV	40	50	60	70	55	40	70	60	50	55
mean	25	35	45	55	40	30	35	45	50	40

ranking of the cultivars is independent of the isolates. Both van der Plank (1975) and Robinson (1976) state unequivocally that HR is based on independent gene action between host and parasite, i.e. genes for HR cannot operate on a gene-for-gene basis. It is here that some confusion arises. HR as measured by van der Plank is the property of a population of host genotypes tested against a population of parasite genotypes; it is not a property of genes.

Let us therefore consider first of all how HR (no cultivar-isolate interaction) arises. It can arise from host genes acting independently of parasite genes, as van der Plank (1968, 1975) and Robinson (1976) conclude correctly, but it can also derive from the action of genes operating on a gene-for-gene basis, provided the resistance of the host and the pathogenicity of the parasite are both polygenically controlled. Parlevliet & Zadoks (1977) compared two models (the additive model and the interaction model) in which resistance and pathogenicity were governed by five minor genes each. In the 'additive model' the genes in the host and the genes in the pathogen showed additive action (independent gene action, no interaction) and consequently no gene-for-gene relationships. In the 'interaction model' the five resistance genes acted on a gene-for-gene basis with the five pathogenicity genes. In the additive model the variance in disease severity was entirely due to main effects, the interaction variance being nil. In the interaction model most of the variance was due to main effects too, but a small proportion had to be attributed to interaction effects. This proportion appeared to be so small that it would be difficult to distinguish it from the error variance in most experiments. This implies that with normal experimental procedures the two modes of gene action cannot be distinguished from each other in polygenic systems, or, in other words, polygenic systems operating on a gene-for-gene basis will be classified as HR according to van der Plank's test.

Parlevliet (1976, 1977) showed that the polygenically controlled partial resistance of barley to *Puccinia hordei* behaved precisely as described in the interaction model, with a large variance component for main effects and a very small one for interaction effects. From this and other data reported Parlevliet & Zadoks (1977) concluded that polygenically controlled true resistance most probably operates on a gene-for-gene basis with minor genes in the parasites.

It is now possible to draw a few general conclusions regarding avoidance and true resistance. The avoidance mechanism, with host and parasite genes generally acting independently of each other, can be expected to exhibit the characteristics of HR. The resistance may be governed by any number (one or more) of genes. This is in agreement with the ideas of van der Plank and Robinson. The resistance may also be expected to be stable, as already mentioned, since it is unlikely that the parasite will readily undergo the changes required in its own biology to overcome this resistance.

With true resistance, assumed to operate generally on a gene-for-gene basis, the situation is different. When the resistance and pathogenicity are under simple genetic control (very often monogenic), vertical resistance will be observed. The resistance is very often unstable, but not necessarily so (van der Plank, 1975; Robinson, 1976; Parlevliet & Zadoks, 1977). In the case of polygenic control, the resistance is for all practical purposes horizontal, being non-race-specific and, as far as known data go, stable. Parlevliet & Zadoks (1977) concluded that polygenic true resistance is stable owing to genetic homoeostasis in the parasite population. In order to overcome such polygenic resistance, the parasite would have to change its genetic constitution at several or many loci, a change which it could scarcely achieve without a serious loss in overall fitness.

A similar situation appears to exist in the parasite-pesticide relationship. Dekker (1976) reviews the situation with regard to fungicides. Many of the conventional fungicides are rather unspecific, being able to interfere with the fungal metabolism at several or many sites (multisite inhibitors). Resistance to such fungicides is rare, probably because the fungus would have to change at a number of loci in order to become resistant. On the other hand, where the fungicides are site-specific, as are many systemic fungicides, resistance frequently appears to develop, though not invariably. Here a monogenic change generally suffices to confer resistance.

To summarize, it is clear that two different types of HR can be envisaged: avoidance and polygenic true resistance. Both are non-race-specific and stable, but the causes of their stability are different.

SELECTION FOR RESISTANCE: PAST AND PRESENT

In the past 70 to 80 years, breeding in general and breeding for disease resistance in particular have increased rapidly in importance. Resistance to parasites, especially in field crops grown for food, has become a major aim in crop improvement. In order to increase the efficiency of selection, breeders have sought cheaper screening methods allowing better discrimination between resistant and susceptible plants. This required good control of the disease level; artificial epidemics were induced, trial fields or greenhouse benches were infested artificially with soil pathogens, the pathogens were applied directly to the plants or plant parts to be tested, or the plants were subjected to toxins extracted from pathogens. Where possible, seedlings or germinating seeds were used to save space and time.

All these improvements in the screening methods did indeed increase the efficiency of selection greatly. Unfortunately, the resistances favoured in this way were the monogenic, complete or nearly complete true resistances, i.e. those classified as vertical and very often unstable.

Many of the screening methods at present in use are unsuitable for distinguishing the various levels of a polygenic true resistance. The amounts of pathogen applied are often too high and the plant stage tested may be wrong. Similarly, screening for avoidance mechanisms by the use of heavy applications of pathogen under conditions deviating from the normal field situation is unlikely to be efficient. In many cases, avoidance mechanisms only reach their optimum effectiveness under field conditions.

SELECTION FOR RESISTANCE: THE FUTURE

It would be an exaggeration to regard the approach to resistance breeding summarized in the preceding section as a complete failure (Robinson, 1976). In fact many types of resistance with a relatively simple mode of inheritance have been and are still being used with success. It is, however, the failures that attract attention; and there are many failures, especially among certain serious diseases in important crops. It is for host-parasite relationships of this kind, and not for the success stories, that revised breeding approaches are needed.

Where resistance genes have 'broken down' within a relatively short time after introduction, the following approaches may be especially appropriate. Parlevliet & Zadoks (1977) suggested that the stability of true resistance depends on genetic homoeostasis operating in the parasite population. The more strongly this homoeostasis operates, the less the parasite population is able to alter in response to the introduced resistance. The more diversified the environment of the parasite, they suggested, the more pronounced genetic homoeostasis becomes. And it should therefore be our goal to increase the diversity of the parasite's environment. This can be done genetically, by the breeder, or nongenetically, by means of crop protection measures (see below).

Genetic diversification is an approach whereby the parasite is obliged to cope not with single resistance genes (with which it appears to cope very ably), but with a variety of resistance genes. Diversity among resistance genes can be pursued in several ways. The multiline approach and the gene deployment method have been discussed by Frey et al. (1973). In these methods the genes used are the so-called major, vertical genes.

Another approach is that of using HR, either avoidance or polygenic true resistance. In both cases screening should preferably be conducted in the field, as nearly as possible under natural conditions, so that the disease pressure is little higher than is normally experienced in the field. In order to accumulate polygenes and/or genes governing different mechanisms of both the avoidance and the true resistance types, it is essential that the selection intensity per selection cycle be low, and that recombination be permitted to occur as frequently as possible. This implies repeated crossing and selection. Only under such conditions is it possible to accumulate a maximum number of resistance genes. A high selection pressure leads more quickly to a certain level of HR, but the level achieved will be lower than that attained under continuous low selection pressure. Inadequate recombination has the same effect.

Moderate, continuous selection with frequent recombination allows simultaneous selection for other characters, including resistance to other diseases. Moderate selection for HR may be effected by removing only the most susceptible plants, lines or families in each selection cycle. Initially this may seem very time consuming, but it should be realized that, once a reasonable level of HR in most of the material has been reached, the maintenance of that level is not difficult, as shown for example in the polygenic resistance of maize (*Zea mays*) to *Puccinia sorghi* and of barley (*Hordeum vulgare*) to *Puccinia hordei.*

INTEGRATED CONTROL OF PESTS AND DISEASES

There are three important points to be taken into account in crop protection:

- It is unrealistic to hope ever to achieve adequate long-term resistance to all pests and diseases in all our crops.
- In some host-parasite systems an adequate level of long-term resistance may well be unobtainable.
- The diversification of crop protection by methods other than resistance can help to increase the stability of the resistance genes. By diversifying the environment, as already pointed out, the genetic homoeostasis of the parasite population, i.e. its tendency to resist genetic change, can be increased.

A consideration of these three points makes it clear that it is necessary to make use of all the control methods available. They should be applied against each host-parasite system as an integrated control system. The more the various methods are used in conjunction with each other, the more they will tend to reinforce each other and the more they will diversify the environment of the parasite. And hence, too, the duration of resistance and of pesticide effectiveness will be extended. For the long-term protection of as many crops as possible, it appears that the use especially of horizontal resistance, in conjunction with a variety of other control measures, is the optimal system.

Insect resistance

INTRODUCTION

The increasing complexities of insect pest control in recent years, and the growing awareness of such problems as pest resistance to insecticides, rising costs of insecticide application, destruction of useful insects and other fauna, accumulation of undesirable residues, environmental pollution etc., all associated with the large-scale use of broad-spectrum insecticides, have emphasized the critical need for effective control measures which are relatively free of adverse side effects. The use of insect-resistant crop varieties offers one promising possibility.

Crop varieties that are resistant have the unique advantage of providing an inherent control which involves no expense or environmental pollution problems and is generally compatible with other methods of insect control. The cultivation of resistant plants is not subject to vagaries of weather, as are chemical and biological control measures, and in certain situations the use of resistant varieties constitutes almost the only effective means of control. Host plant resistance is especially valuable where crops are low in value per hectare, in particular in developing countries where crops are planted on small holdings and the economic constraints and lack of technical knowledge limit the proper use of costly insecticides. Also, resistant varieties control even a low pest density whereas use of insecticides is justifiable only when the density reaches the economic injury level. Painter's book *Insect resistance in crop plants* (1951) was a milestone in making agricultural scientists cognizant of the importance of breeding for insect resistance in crop plants.

GENERAL ASPECTS

Painter (1951) defined varietal resistance to insect pests as 'the relative amount of heritable qualities possessed by the plant which influence the ultimate degree of damage done by the insect. In practical agriculture, it represents the ability of a certain variety to produce a larger crop of good quality than do ordinary varieties at the same levels of insect populations.'

He classified resistance into three categories:

- Nonpreference: a plant is unattractive to the insect pest for feeding, oviposition or shelter. Recently, Kogan & Ortman (1978) have suggested the term 'antixenosis' to replace nonpreference.
- Antibiosis: the host plant has adverse effects on the growth and survival of the insect and its progeny.
- Tolerance: the plant can withstand a heavy insect attack and still produce a good crop.

A plant's resistance may involve one or more of these factors. Antibiosis is considered the most important, but under certain circumstances nonpreference can be of equal value, particularly when brief infestations cause severe plant damage. Some examples of the latter are feeding by stem borers, which causes white head in rice, and insect transmission of virus diseases. In field plantings, nonpreferred crop varieties frequently escape infestation and even when insects are caged on nonpreferred hosts, they lay fewer eggs and produce smaller populations than on susceptible hosts. Thus, both nonpreference and antibiosis influence or even disrupt one or more of the following stages of an insect's establishment on a plant: (1) orientation, (2) feeding, (3) metabolic utilization of food, (4) growth, (5) survival and egg production, (6) oviposition (Saxena, 1969) and (7) hatching (Pathak & Saxena, 1976).

Tolerance is attributable to plant vigour and is more or less independent of effects on the insect. Tolerant varieties do not inhibit insect populations and under certain conditions may even be responsible for the build-up of a larger population than is found on susceptible varieties, which are killed when a certain level of infestation is reached. However, the ability of tolerant plants to survive infestations for a longer period permits a longer exposure of the insects to their natural enemies. Tolerance is frequently valuable in integrated pest control.

Varietal resistance should not be misconstrued as 'immunity', which is a rarity among crop plants. Varietal resistance, as defined above, is generally a *relative* quality: under severe infestations even resistant varieties succumb and are subject to significant crop losses.

REQUIREMENTS IN BREEDING FOR RESISTANCE

Success in breeding for resistance depends on effectively identifying resistance and incorporating it in varieties with other desirable agronomic characters. Genetically diverse germplasm collections and an intensive search for resistance are necessary if suitable sources of resistance are to be selected. Resistance to a particular pest is frequently, but not always, found in varieties or selections from areas where the pest is indigenous. Diverse germplasm offers greater chances of selecting resistant material than does material with a relatively narrow genetic base. Diverse sources of resistance also provide an insurance against new pest biotypes which may thrive on some resistant varieties with a narrow genetic base if these are planted extensively (see Chapter 3, p. 91).

Efficient methods of mass screening are essential to the identification of resistant genotypes. Techniques of mass-rearing of the insect pest and screening of varieties for resistance should be based on a knowledge of the bionomics of the pest and the physiology of the crop plant. A close collaboration between entomologists and plant breeders is essential in a varietal resistance programme and, in addition, collaboration with plant pathologists, agronomists and other problem-area scientists is necessary for combining insect resistance with desirable plant characters. Such programmes require adequate support of research systems which encourage interdisciplinary problem-orientated research, as exemplified by the Genetic Evaluation and Utilization Program of the International Rice Research Institute (IRRI) (see Chapter 3, p. 89).

In most cases, so far, breeding for resistance has been accomplished without a knowledge of the causes of resistance or its genetics. However, such knowledge is important. In a few crops, the physical and chemical characters of the plant that impart resistance have been identified and these are mentioned in the sections which follow. It is expected that as the role of these factors and their inheritance in plants is better understood, genetic manipulation of resistance will become much more effective.

PROGRESS IN MAJOR CROPS

Significant progress has been made in recent years in several major agricultural crops. Important sources of resistance have been identifed and bred into suitable crop varieties, which are now being planted over large acreages. Some of these varieties are resistant to several insect species, diseases and even some physiological disorders and adverse soil conditions. Selected examples are reviewed below.

Grapes

The earliest and most spectacular case of resistance as a major source of insect control is the use of American rootstocks resistant to phylloxera, *Phylloxera vitifoliae*, discovered in about 1870. This discovery saved the grape and wine industry in many parts of Europe and is still a major means of control of this pest of European grape varieties (*Vitis vinifera*).

Lucerne

The use of resistant varieties in lucerne (*Medicago sativa*) is now well established, effecting an annual saving of ca. 300,000 t of insecticides in the USA alone (Schalk & Ratcliffe, 1977).

The spotted alfalfa aphid, *Therioaphis trifolii* (= *Th. maculata*), after its first appearance as a lucerne pest in 1954 in New Mexico, USA, spread rapidly to 30 states and in Kansas alone caused damage estimated at 8 million dollars (Painter, 1968). Since 1960, when the resistant varieties Lahontan, Moapa and Condy were released, several further varieties resistant to biotypes which had overcome the resistance of earlier varieties have been released.

Some of the resistant varieties proved susceptible to the pea aphid, *Acyrthosiphon pisum*, and its biotypes, and attempts were made to combine resistance to the two pests (Howe et al., 1965). The variety Dawson, developed by 1967, combined resistance not only to these two pests but also to the potato leafhopper, *Empoasca fabae*, and to bacterial wilt (Kehr et al., 1968). The resistance of lucerne to its pests is attributed to antibiosis caused by higher saponin content, particularly medicagenic acid, which is predominant in some resistant varieties (Horber et al., 1974).

Cotton

The cotton boll weevil, *Anthonomus grandis*, and the cotton bollworm, *Heliothis zea*, have long been pests and the pink bollworm, *Pectinophora gossypiella*, and the tobacco budworm, *Heliothis virescens*, are becoming a major problem in several important cotton-growing areas. Pilot programmes for developing resistant cottons (*Gossypium* spp.) have involved screening of a wide variety of germplasm.

The mechanisms of resistance have been identified in a few cases. For example, red colour of the foliage, combined with hairiness and absence of stem glands, is involved in resistance to the cotton boll weevil (Stephens, 1957). Hairiness of the foliage is reported to increase resistance to cotton leafhoppers, *Empoasca* spp., cotton aphid, *Aphis gossypii*, cotton leafworm, *Spodoptera littoralis*, and spider mites, *Tetranychus* spp. Hairiness of the flower buds was found to impede the feeding of boll weevils on the bracteoles enclosing the flower buds and exerted antibiosis effects on the larvae (Stephens & Lee, 1961). Pubescence was also found to obstruct the movements of pink bollworm larvae (Smith et al., 1975).

In many cases, however, the existence of an association between hairiness and resistance has not been confirmed. For example, in India, the leafhopper *E. devastans* heavily infests the hairy U4 variety which is resistant to *E. fascialis* in Africa (Husain & Lal, 1940). Also hairiness has been reported to increase infestation by the cotton aphid, spider mites (Pollard & Saunders, 1956) and the cotton fleahopper, *Pseudatomoscelis seriatus* (Lukefahr et al., 1970). Conversely, smooth-leaved cottons have shown promise for bollworm resistance by reducing sites for oviposition (Lukefahr et al., 1971).

The so-called Frego bract character reduces oviposition by the boll weevil (Jenkins & Parrott, 1971) but increases susceptibility to other pests such as *Lygus* bugs and fleahoppers (Maxwell, 1977). The polyphenol gossypol occurs in much higher concentration in the seed and green parts of glanded than of glandless varieties (Lukefahr & Houghtaling, 1969). Glandless varieties, bred to reduce gossypol concentration in the seed to a level nontoxic to nonruminants, proved susceptible to about 10 different insect pests while the glanded varieties were resistant. Toxic effects of gossypol were demonstrated by spraying it on a number of pests of cotton and by mixing it in a diet used for rearing *H. zea* (Bottger et al., 1964). Cottons with a high gossypol content in the flower buds (2-3 times the amount found in cultivated varieties) inhibited larval growth and suppressed populations of *H. virescens* (Lukefahr & Houghtaling, 1969).

Efforts have been made to transfer the high-gossypol character into good agronomic cottons for the Cotton Belt (Sappenfield et al., 1974) and good agronomic types that carry the character are now available (Maxwell, 1977). The single source used so far is Socorro Island *G. hirsutum*.

The antibiosis against *Heliothis* larvae shown by the flower buds of a few wild races of *G. hirsutum* and by extracts made from them could not be explained by gossypol concentration but is attributable to certain 'x-factors', among which at least three chemicals, called heliocides, have been identified (Lukefahr et al., 1974; Maxwell, 1977). Recently, condensed tannin from flower buds of certain *G. hirsutum* lines has been reported to have a strong antibiotic activity against *H. virescens* (Chan et al., 1978).

Potato

Impressive levels of resistance to a number of insect pests are readily available in several tuber-bearing *Solanum* species, but these have not been fully utilized in breeding.

Varietal differences in insect susceptibility of potato (*S. tuberosum*) were recorded as early as 1938. Resistance to potato leafhopper in the variety Sequoia was nearly as effective as insecticides (Sleesman, 1938). This resistance in certain wild potatoes is attributed to the feeding-deterrent effect of the solanaceous alkaloidal glycosides tomatine, solanine and leptine I, and the aglycones solanidine and demissidine (Dahlman & Hibbs, 1967). It should be noted that these compounds are also toxic to man. Their concentrations are, however, rather higher in the foliage than in the tubers. Resistance to pests such as the potato aphid, *Macrosiphum pisum*, the green peach aphid, *Myzus persicae*, the potato leafhopper, the Colorado beetle, *Leptinotarsa decemlineata*, and spider mites, *Tetranychus* spp., has been confirmed in several wild potato species and is attributed to glandular insect-trapping hairs on the foliage and stem (Gibson & Turner, 1977). These hairs may be of two types. Those of type A have 4-lobed heads which rupture when an insect alights and release a quick-setting liquid which traps the insect. Although adults of Colorado beetle are not deterred from feeding, young larvae either get entangled or so coated in the sticky secretions that they are unable to feed, and die in a few days. A few wild potato species have additional elongate B-type hairs which secrete a sticky droplet at their tips. Spider mites, although light enough to walk over the lobed hairs without rupturing them, fail to escape the sticky ooze from B-type hairs. White flies, however, are not only light but produce a powdery wax, which covers the sticky secretions and allows the flies to escape.

A few fertile, tetraploid hybrids of the wild species *S. berthaultii* with cultivated potato are available (Gibson, 1974), so it may be possible to breed agriculturally useful cultivars having one or both types of hairs.

Maize

Progress in breeding for resistance has been most impressive in cereal crops, such as maize, wheat, oats, barley, rye, sorghum and rice. Varieties of maize (*Zea mays*) resistant to several insect pests, e.g. European corn borer, *Ostrinia* (= *Pyrausta*) *nubilalis*, corn earworm, *Heliothis zea*, corn leaf aphid, *Rhopalosiphum maidis*, and chinch bug, *Blissus leucopterus*, have been developed and are being planted over millions of hectares in the USA, which produces almost half of the world's total maize crop.

Cultivation of borer-resistant varieties has led to significant economic savings by reducing the annual application of insecticides by about 22,000 t, and has also increased yields considerably (Schalk & Ratcliffe, 1977). Damage on resistant varieties is reduced, as the pest fails to build up in large numbers. Physiological inhibitors responsible for borer resistance have been identified in maize (Beck & Smissman, 1961). Klun et al., (1967) demonstrated that DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) in the leaves of inbreds conferred resistance to first-brood larvae and noted a significant correlation between the concentration of DIMBOA in the leaf whorl tissues of several inbreds and their degree of resistance to first-brood larvae (Klun et al., 1970; Reed et al., 1972). Analysis of breeding material for DIMBOA content has even been used as a method of screening for resistance to first-brood larvae (Russell et al., 1975). Recently, DIMBOA was also found to be the primary chemical factor in the nonpreference mechanism of resistant dent maizes (Robinson et al., 1978). However, many accessions from the tropics have a low DIMBOA content but are resistant (Sullivan et al., 1974; Scriber et al., 1975), and inbred B52 has a low DIMBOA concentration but is resistant to the second-brood larvae (Guthrie et al., 1971). The chemical basis of second-brood resistance thus remains to be resolved. Since the feeding habits of the second-brood larvae are different from those of the first brood, DIMBOA is unrelated to second-brood resistance. Nevertheless, resistance to stalk rot, stem rust, and herbicides has also been attributed to DIMBOA.

Resistance to corn earworm has been attributed in certain varieties to tight kernel husks which help confine the larvae longer in the husks, increasing the probability of cannibalism among the larvae (Painter, 1951), or forcing them to feed on silk channels which, in certain genotypes, contain a lethal biochemical factor (Walter, in Guthrie & Walter, 1961). The silks of Zapalote Chico maize contain a feeding deterrent or growth inhibitor affecting the larvae (Straub & Fairchild, 1970). Three species of *Tripsacum,* including Florida gamagrass, have been found to be highly resistant to the corn leaf aphid and if this resistance in Florida gamagrass is not inherited in a complex manner, probably it can be transferred to maize (Branson, 1972).

Wheat

Among the major insect pests of wheat (*Triticum aestivum*) are the Hessian fly, *Mayetiola destructor*, the wheat stem sawfly, *Cephus cinctus*, the cereal leaf beetle, *Oulema melanopus* and the greenbug, *Schizaphis graminum.* The cultivation of resistant varieties has reduced the Hessian fly and wheat stem sawfly from a very serious problem, with annual crop losses of 10 million dollars in the USA alone (Gallun et al., 1975), to the status of minor pests. By 1974, nearly 16 million acres in the USA were planted to cultivars resistant to Hessian fly, and by 1977 more than 28 resistant varieties had been released (Gallun, 1977).

Resistance to Hessian fly is mainly due to antibiosis, as larvae feeding on resistant plants generally die while those that survive remain small in size (Gallun, 1978). The chemical basis of this resistance has not been fully elucidated, although hemicellulose and silica contents appear to be implicated.

Since selection pressure of resistant cultivars on Hessian fly is severe, it has led to the appearance of new biotypes of the pest. However, a few biotypes were known even before resistant varieties were released for cultivation. Eight biotypes (the Great Plains or GP biotype and biotypes A, B, C, D, E, F and G) have now been isolated in the USA (Gallun, 1977). They are morphologically alike but can be identified by the differential varietal reactions of wheat seedlings having different sources of resistance. Recently, a ninth, biotype L, has been isolated from a greenhouse population of biotype D (Sosa, 1978). Biotype L is able to survive and infest cultivars with the Ribeiro source of resistance (H_5 gene) to the other known biotypes.

A gene-for-gene relationship has been suggested between genes for resistance in wheat and genes for virulence in Hessian fly (Hatchett & Gallun, 1970; Gallun, 1977). Since there are now four resistance genes (Seneca-H_7H_8, Monon-H_3, Knox 62-H_6, and Abe-H_5) capable of differentiating among biotypes, theoretically a total number of 16 biotypes would be possible (2^n, where $n = 4$). The first eight biotypes (GP, A, B, C, D, E, F and G) have been identified in the field or laboratory. The laboratory isolation of the ninth or L biotype strongly supports the gene-for-gene concept and points to the possibility that similar selection could also occur in the field. In fact, a major shift of this kind in biotype frequency was recorded in Indiana where biotype B replaced biotype A as the predominant biotype (Hatchett & Gallun, 1968).

Further studies by Gallun (1978) on the genetic interrelationship between varieties of wheat, biotypes B and C and progenies of the hybrids of the two biotypes have indicated that the gene for virulence to Monon wheat in biotype B and the gene for virulence to Knox 62 wheat in biotype C are on separate chromosomes. The allele *M* in biotype C that causes it to be avirulent to Monon is located near the centromere; the allele *K* in biotype B that causes it to be avirulent to Knox 62 is at a considerable distance from the centromere. During spermatogenesis in the Hessian fly, paternally derived centromeres and the attached chromatin are eliminated. Crossing over occurs prior to the elimination of the chromatin.

Inundative releases of the dominant avirulent biotype of Hessian fly have been considered as a novel possibility for suppressing field populations of virulent biotypes of the pests and have shown promise in small-scale field tests (Foster, 1977).

Sawfly-resistant cultivars are now being cultivated on large areas in Canada and the USA where wheat could not be grown economically earlier because of the sawfly problem and lack of appropriate control methods. The solid stems of Rescue and other resistant varieties result in the sawfly eggs being mechanically damaged and desiccated and restrict the movement of the newly emerged larvae (McNeal et al., 1971; Wallace et al., 1973). Stem solidness is controlled by one or more dominant, recessive, or complementary genes, depending on the parents used, the crosses and the ploidy involved (Wallace & McNeal, 1966).

The cereal leaf beetle is a recent threat in the USA. Natural infestations in Michigan state have caused losses in yield of up to 55% in spring wheat (Webster et al., 1972) and 23% in winter wheat (Gallun et al., 1967). Pubescence of the leaves has been found to provide protection by deterring oviposition by the beetle and feeding by the emerged larvae (Gallun et al., 1973; Wellso, 1973; Hoxie et al., 1975). While the length of hairs or trichomes on seedling leaves of some resistant cultivars was found to be about 250-300 μm and the density of pubescence ranged from 30-70 leaf hairs per mm^2, the susceptible wheats had fewer than 10 hairs/mm^2 (Webster, 1977). Leaf pubescence in wheat is probably quantitatively inherited (Ringlund & Everson, 1968), and as many as three additive genes may determine length of hairs (Leisle, 1974).

R*ice*

Resistance to the striped stem borer, *Chilo suppressalis*, and the yellow stem borer, *Tryporyza incertulas*, the two most destructive borer species in Asia, was studied earlier than resistance to other pests of rice (*Oryza* spp.). Over 14,000 rice varieties have been screened for resistance to the striped borer at the International Rice Research Institute (IRRI), Philippines, in field and greenhouse experiments. Lines which were initially resistant were retested under controlled levels of infestation (Pathak et al., 1971; IRRI, 1974-1977). The resistant varieties not only inhibit oviposition but also exert adverse effects on the growth and development of larvae emerging from eggs laid on them. Consequently, infestations are much lower on resistant than on susceptible varieties. Many varieties, particularly those of the Ponlai and Japonica types, are moderately resistant during the vegetative stage of plant growth but become susceptible after panicle emergence. In the field, these varieties generally have few dead hearts but frequently suffer heavily from white head damage. The change in susceptibility is probably due to differences in susceptibility of different plant parts. A few Indica varieties have uniformly low infestation at all stages of plant growth.

A general correlation between susceptibility or resistance to stem borers and several physical characters such as plant height, length and width of the flag leaf, culm height and diameter, percentage of the stem cross-sectional area occupied by vascular bundle sheaths, and number of tillers was recorded by Pathak et al. (1971) (Table 6.2). Although each of these characteristics appeared to influence stem borer response, none by itself appeared to be the main cause of susceptibility or resistance.

Evidence is increasing that biochemical factors may determine susceptibility or resistance of rice plants to stem borers. A chemical substance from rice, called 'oryzanone' (*p*-methylacetophenone), was found to attract ovipositing moths, which laid more eggs on a treated than on an untreated surface (Munakata & Okamoto, 1967).

Table 6.2. Correlations between rice plant characters and percentages of tillers infested with striped borer (from: Patanakamjorn & Pathak, 1967).

Plant character	Correlation coefficient
Elongated internodes, number	0.632**
Third elongated internode, length	0.715**
Flag leaf, length	0.798**
Flag leaf, width	0.836**
Culm height	0.796**
Culm, external diameter,	
at half its length	0.672**
at one-fourth its length from the base	0.785**
Culm, internal diameter	
at half its length	0.671**
at one-fourth its length from the base	0.790**
Tillers per plant, number	-0.756**
Stem area occupied by vascular bundle sheaths (percentage)	-0.756**

** Significant at the 1% level.

The odour of oryzanone also attracted the borer larvae. Incorporation of fresh plant extracts of resistant and susceptible varieties into artificial diets showed that the borer larvae had a definite preference for susceptible (Rexoro) over resistant (TKM6) varieties and had significantly poorer growth on the resistant variety Taitung 16 (Das, 1976).

Recent studies at IRRI showed that the striped borer moths oviposited heavily on surfaces treated with the odorous extract of the susceptible Rexoro variety, very little on untreated surfaces, and none on surfaces treated with the odorous extract of the resistant TKM6. The effect of odour was so strong that moths oviposited heavily on the resistant TKM6 after it was sprayed with the susceptible Rexoro extract, but oviposition was inhibited when Rexoro was sprayed with the odorous extract of TKM6 (Fig. 6.1).

Efforts are being made to augment the level of resistance to striped borer in rice varieties by diallel crossing among moderately resistant lines. TKM6 has proved a valuable parent and has been used extensively in several countries in breeding for resistance. IR20, the first resistant variety of improved plant type, was developed by crossing TKM6 with Peta^3 × Taichung Native 1 (TN1). Several progenies from diallel crosses showed higher resistance than any of their parents. In a screenhouse experiment, the progenies of the moderately resistant parents, TKM6 and CR94, both had lower dead-heart incidence than those of other crosses (IRRI, 1977).

Studies on varietal resistance to yellow stem borer have been limited because of the problems in rearing this insect. However, some succes was achieved by rearing it on

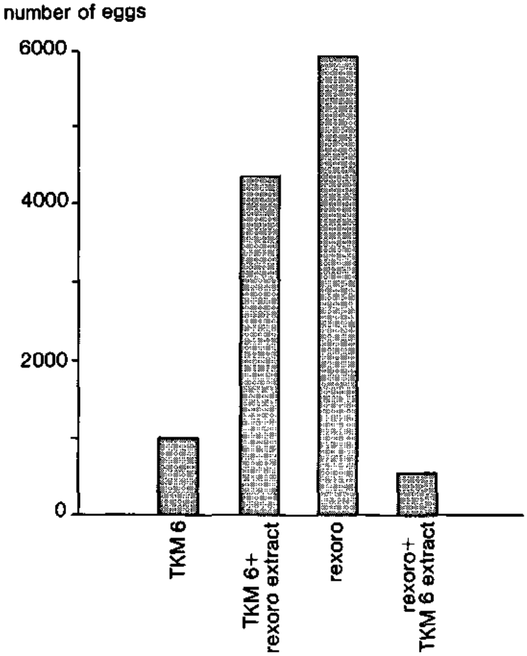

Fig. 6.1. Ovipositional response (number of eggs per 20 females) of striped borer moths on plants treated with ether extract of steam distillates of resistant (TKM6) and susceptible (Rexoro) rice plants (from: IRRI, 1977).

plants grown inside a screenhouse and allowing the moths to oviposit on the test varieties growing in adjacent nursery beds. Thus, several hundred varieties from field selections were critically evaluated and ten of them identified as moderately resistant (Manwan, 1975). A breeding line, IR1820-52-2, exhibited maximum resistance. Progeny of this line showed a significantly lower incidence of dead heart than other test lines (IRRI, 1977). Resistance to borer in these lines was due to larval antibiosis, since borer moths did not show much preference during oviposition on test varieties.

Breeding for resistance to rice leafhoppers and planthoppers had become a major objective at IRRI and within the last decade excellent sources of resistance to the green leafhopper, *Nephotettix virescens*, the brown planthopper, *Nilaparvata lugens*, and the white-backed planthopper, *Sogatella furcifera*, have been identified and bred into high-yielding varieties. This had a marked economic impact because some of the earlier high-yielding varieties, which had become popular in many countries, proved to be highly susceptible to these pests.

Screening procedures for resistance to these insects are simple and rapid and many thousands of rice accessions collected from all over the world have been evaluated. Insects caged on resistant varieties had slower growth and higher mortality than

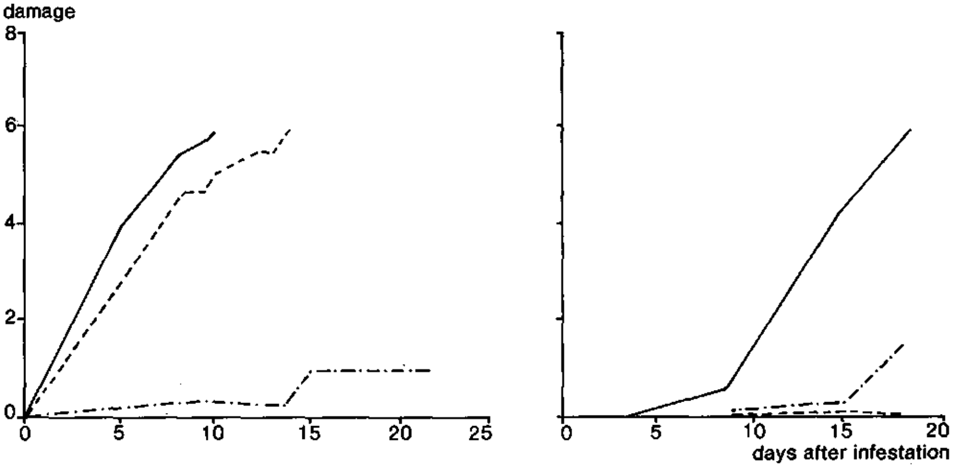

Fig. 6.2. Damage caused on caging 100 first-instar nymphs on resistant and susceptible rice varieties. Left: brown planthopper, right: green leafhopper, TN1 ——, Pankhari 203 – – –, Mudgo – · – (from: Pathak et al., 1969).

those on susceptible varieties. Even a large population of these insects caged on resistant plants barely caused noticeable damage, while the susceptible variety was killed (Fig. 6.2).

The hoppers exhibited distinct nonpreference for certain varieties. This response was gustatory rather than visual, mechanical or olfactory, as insects did not show differences in alighting upon different varieties, but their feeding was not sustained on resistant varieties. The white-backed planthopper females started feeding promptly on the susceptible TN1 plants and fed continuously but on resistant plants they often did not start feeding for the first 20 to 39 minutes and their feeding durations were short (Fig. 6.3) (IRRI, 1977). Similarly, brown planthopper females did little feeding on resistant varieties but ingested large quantities of sap from susceptible varieties (Fig. 6.4) (Saxena & Pathak, 1977). The weight gain was small on resistant varieties as against susceptible varieties and was related to the amount of sap sucked by the insects from the plants. The green leafhopper also excreted more honeydew on the susceptible variety TN1 than on the resistant varieties Pankhari 203 and IR8, but differences were not as marked as for the brown planthopper (Cheng & Pathak, 1972).

The reduced feeding by hoppers on resistant varieties is probably due to either absence of feeding stimulants or presence of feeding deterrents or repellents for these insects. The resistance of variety Mudgo to biotype 1 of brown planthopper has been attributed to its low asparagine content as compared with the susceptible TN1 variety (Sōgawa & Pathak, 1970).

Although both susceptible and resistant varieties may be quite suitable for egg-laying, the hatching of eggs laid on resistant varieties may be impaired. Despite nearly equal oviposition by brown planthopper biotype 1 on the resistant Mudgo,

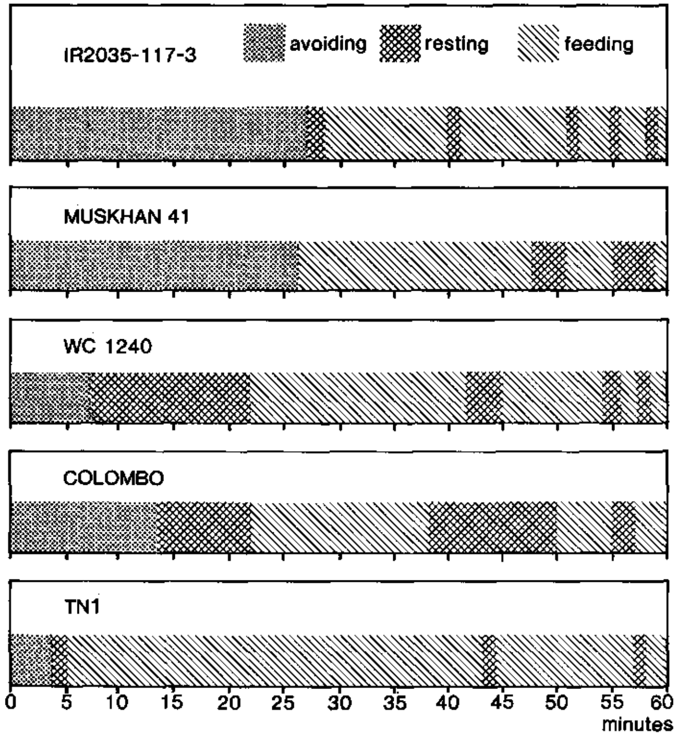

Fig. 6.3. Duration of feeding of white-backed planthopper caged on resistant and susceptible (TN1) rice varieties (from: IRRI, 1976).

IR26 and ASD7 and the susceptible IR20, IR8 and TN1, hatching was significantly less on the resistant varieties (Table 6.3) (Saxena & Pathak, 1977). On the nonhost barnyard grass, *Echinochloa crus-galli*, both oviposition by the brown planthopper and hatching were reduced. That the plant's internal chemistry influences the hatching of the hopper eggs became evident in an experiment in which eggs laid in the susceptible TN1 variety hatched normally upon artificial transplantation into the leaf sheaths of another TN1 plant, while those transplanted identically into barnyard grass had very low hatching.

Breeding for resistance to hoppers was started at IRRI in 1967. A cross between Mudgo (resistant) and IR8 (improved plant type) produced progeny resistant to brown planthopper but poor in grain quality. Since then, several high-yielding resistant varieties (IR26, IR28, IR30, IR32, IR34, IR36, IR38, IR40, IR42) have been developed and released. These varieties are also resistant to a number of other insect pests and diseases. In 1975, two new genes for resistance to brown planthopper were identified, bringing the total to four (Lakshminarayana & Khush, 1977). Similarly, two genes were identified for resistance to green leafhopper (Siwi & Khush, 1977). These genes are being incorporated into material of improved plant type. Many countries are now using local as well as IRRI improved lines or varieties in breeding

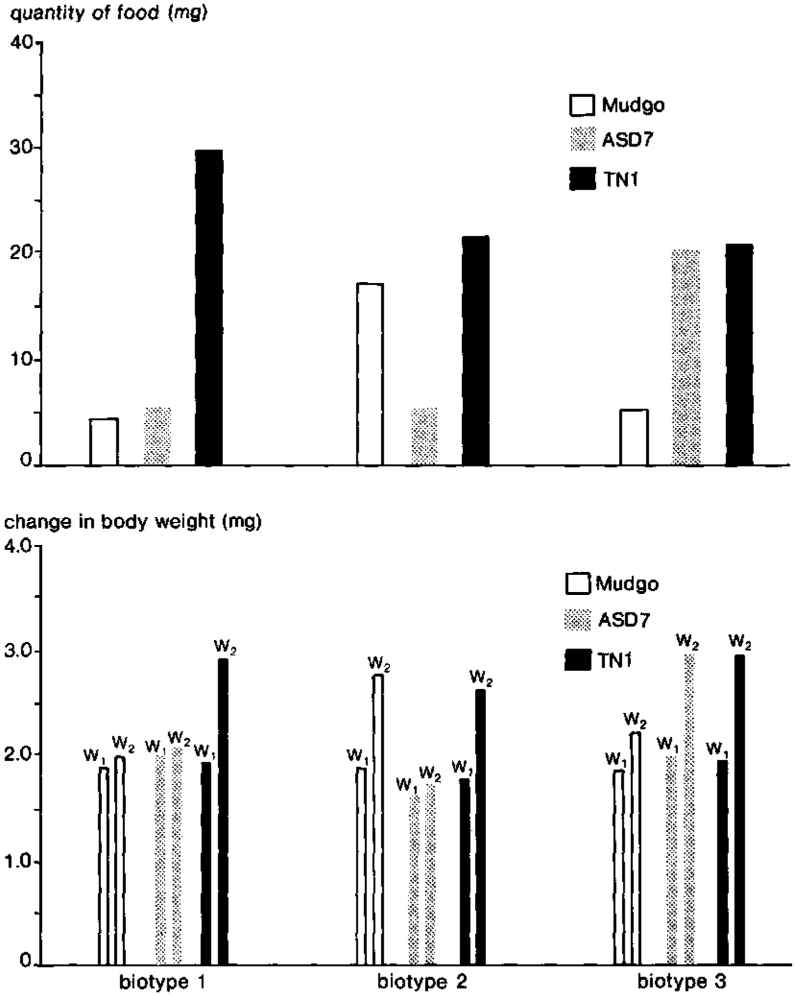

Fig. 6.4. Quantity of food ingested per female in 24 h and change in body weight of female in 24 h of three biotypes of brown planthopper allowed to feed on Mudgo, ASD7 and TN1 rice varieties. W_1 initial weight, W_2 weight after 24 h (from: Saxena & Pathak, 1977).

for resistance to these insects.

Breeding for resistance to the white-backed planthopper started in 1975. About 450 resistant lines were found among more than 4000 entries tested. N22, ARC6003, and Dharia were used as donor parents and IR28, IR32, and IR38 as recurrent parents in a back-crossing programme. Breeding lines with resistance to white-backed planthopper and multiple resistance to diseases and other insects are now available.

At least three biotypes of the brown planthopper have been recorded. Besides these, the populations in southern India (Kalode, personal communication) and in

Table 6.3. Oviposition and hatching of brown planthopper (biotype 1) eggs on resistant and susceptible rice varieties and on barnyard grass, IRRI, 1975-76 (Saxena & Pathak, 1977).

Test plants	Eggs laid/10 females/24 h[1, 2] (No.)	Eggs hatched[1, 3]
Mudgo	328 ab	68 b
ASD7	348 ab	78 b
IR26	292 ab	74 b
IR20	325 ab	95 a
IR8	309 ab	90 a
TN1	400 ab	91 a
Barnyard grass	205 a	18 c

1. In a column, any 2 means followed by a common letter are not significantly different at 5% level.
2. Based on values transformed to Log x, base 10.
3. Based on values transformed to Arcsin sqs (x).

Taiwan (Cheng, personal communication) appear to belong to different biotype(s). Differential resistance to these biotypes was recorded in rice varieties possessing *Bph1* and *bph2* genes (Athwal et al., 1971; Athwal & Pathak, 1972). Two new resistance genes, *Bph3* and *bph4,* which impart resistance to all known biotypes, have recently been identified in some tall traditional varieties at IRRI (Lakshminarayana & Khush, 1977) and have been transferred by back crossing into semidwarf experimental lines. In 1976, IRRI screened 6262 rices from the germplasm bank and identified 48 that were resistant to all three biotypes.

To monitor brown planthopper biotypes and to identify resistant material, an International Rice Brown Planthopper Nursery has been established in many countries. The nursery consists of a uniform set of varieties. If particular rices are resistant in one area but susceptible in another, the insects at the two locations are suspected of being different biotypes.

The monogenic resistance of rice to brown planthopper makes it more vulnerable when several biotypes coexist than would polygenic resistance. Therefore present breeding endeavours envisage utilizing both major and minor genes for resistance.

Green leafhoppers in Bangladesh (Rezaul Karim, personal communication) and in Indonesia (Harahap, personal communication) may have biotypes different from that in the Philippines. The rice variety Pankhari 203, which was highly resistant to green leafhoppers at IRRI, was susceptible in Bangladesh and Indonesia.

Recent progress in studies on insect resistance and on breeding for resistance have been summarized by Pathak (1972, 1977) and Khush (1977a, 1977b).

Insect pest problems are encountered even after harvesting. About 20 species of insects damage paddy or rough rice, parboiled rice, brown rice and milled rice during storage. Although sources of resistance and the grain characteristics imparting resistance have been identified in some cases, little progress has been made in breeding for resistance to storage pests.

UTILIZATION OF RESISTANCE IN PEST MANAGEMENT

Natural resistance to insect pests has been discovered in many crop plants in the world. This resistance is mostly moderate but sometimes high. In most cases, resistance has been found in the unimproved germplasm. Cultivation of such varieties may have been a factor in pest suppression in the past, but the growers were not aware of their inherent resistance.

Utilization of host plant resistance is now recognized as the most valuable component in pest management programmes. Earlier concern that resistance is frequently associated with poor quality and low yield has largely been overcome by incorporating the resistance into high-yielding varieties of good quality. Depending on its level, resistance can be used either as the principal method of control or can be integrated with other methods to develop appropriate pest management systems. For example, rice varieties resistant to brown planthopper generally do not need insecticidal protection against this insect, but they do need protection from other pests to which they are susceptible. On the other hand, rice varieties resistant to striped borer will need insecticidal protection even from striped borer if infestation become severe. Thus a combination of varietal resistance and insecticidal treatments provides a more complete pest control programme than the use of either method alone.

Obviously, resistant varieties do not adversely affect the natural enemies of insect pests. On the other hand, the restless behaviour of pests on resistant varieties exposes them to predators which may devour more small-sized insects on resistant plants than larger insects on susceptible hosts. Thus, cotton bollworm larvae hatching from eggs placed on plant apices remained longer on Frego-type resistant cotton and were more exposed to predators than larvae on the susceptible DPL Smooth Leaf variety (Lincoln et al., 1971). Consequently, predators killed twice as many larvae on the resistant variety as on the susceptible variety.

Varietal resistance and cultural practices can be used synergistically for pest control. Planting of a resistant variety around a susceptible one may prevent a migrating pest from reaching the susceptible hosts. Conversely, a susceptible variety planted around a nonpreferred variety may serve as a trap crop for the pest. Researchers in Louisiana, USA, showed that when 10 to 20% of a field was planted with green cotton around a red cotton, which is nonpreferred by boll weevils, the insects concentrated in the green rows (Maxwell, 1977). Only the green portion of the field was sprayed, thus protecting predators and parasites in the major red portion of the field. Commercial lines of red cotton are now available for cultivation.

Use of insect-resistant varieties may limit the spread of insect-transmitted diseases. Rice variety IR8 is resistant to the rice delphacid, *Sogatodes orizicola*, in Colombia but is susceptible to hoja blanca virus transmitted by this insect. Fields of

IR8 remained virtually virus free, apparently because of its resistance to the vector, while other susceptible rice varieties growing in adjacent plots were heavily infested (Jennings & Pineda T., 1970). Similarly, many rice varieties resistant to leafhoppers and planthoppers exhibit field resistance to virus diseases because of their resistance to the vectors, although they are susceptible to the viruses.

Potatoes resistant to cyst nematodes

When the modern work on breeding potatoes (*Solanum tuberosum*) resistant to cyst nematodes was started in 1952, only a single species of potato cyst nematode was recognized, *Heterodera rostochiensis*. It is now known that there are two species, both of which have a number of pathotypes. There has also been a change in genus nomenclature, the two species now being known as *Globodera rostochiensis* and *G. pallida*. In South America *G. rostochiensis* occurs from the Peru-Bolivian border southwards while in Peru and northwards the dominant species is *G. pallida*. In western Europe *G. rostochiensis* is the commoner species in both Germany and the Netherlands, but in the UK the two species are about equally common, *G. rostochiensis* being predominant in some districts and *G. pallida* in others.

Modern work on breeding for resistance to cyst nematodes was made possible by Ellenby (1952) who screened the Commonwealth Potato Collection (CPC) for resistance using a nematode population which would now be identified as *G. rostochiensis* pathotype Ro1. He found resistance in the wild diploid species, *S. vernei*, and also in five accessions of Andigena tetraploid cultivated potatoes (*S. tuberosum* ssp. *andigena*). One of the latter, CPC1673, has been widely and successfully used in breeding many nematode-resistant varieties, particularly in west European countries (Toxopeus & Huijsman, 1952).

The resistance of CPC1673 is due to a single dominant gene H_1; this, together with an easy and efficient test for resistance, made the breeding of varieties resistant to *G. rostochiensis* Ro1 relatively easy. Ellenby's test for resistance was simple: tubers or small pieces of tuber were planted in a nematode-infested soil and the root-balls examined about ten weeks later. Susceptible plants had hundreds of cysts (developing females) while resistant plants had no, or few, cysts. This is the criterion of resistance which has been used by all subsequent workers.

Later work showed that resistant plants with gene H_1 produced a root diffusate with a larval-hatching power as high as that of susceptible plants and that the roots of resistant plants were invaded by a similar number of larvae to those of susceptibles. But mature females, i.e. new cysts, were not able to develop in the roots of resistant plants. This type of resistance to nematodes appears to be the usual type in other crop species for other nematode species (Howard & Cotten, 1978). Because of the high larval invasion, resistant potatoes may suffer considerable damage but, because hatched larvae do not produce mature females, the growing of resistant varieties reduces the density of nematode infestation so that subsequent potato crops yield more than after crops of susceptible varieties.

Although in many parts of western Europe most potato cyst nematode infestations are predominantly by *G. rostochiensis* pathotype Ro1, there are also infestation by other pathotypes of *G. rostochiensis* and by pathotypes of *G. pallida.* Gene H_1 gives no resistance to such infestations and it has also been found that the continued growing of potatoes with gene H_1 can change nematode populations from predominantly Ro1 to mostly Pa3 or some other pathotype to which gene H_1 gives no resistance. In South America there are probably more pathotypes of both species than have been found in Europe.

The problem now to be solved in western Europe is the production of varieties resistant to pathotypes Ro2 and Ro3 of *G. rostochiensis* and to pathotypes Pa1, Pa2 and Pa3 of *G. pallida.* This has been tackled by breeding from several accessions of the wild diploid species *S. vernei* and there has been some success in the Netherlands, where a few varieties with resistance to Ro1, Ro2 and Ro3 are now available. Resistance to *G. pallida* is of particular importance in the UK where about half the potato cyst nematode infestations are by *G. rostochiensis* Ro1 and about half by pathotypes of *G. pallida.* Resistance to *G. pallida* is shown by *S. vernei* and also by a few clones of Andigena (Howard et al., 1970).

It has been claimed that the resistance of *S. vernei* is due to polygenes and that it is a non-race-specific type effective against all pathotypes. This now seems unlikely as different clones bred from *S. vernei* can be used as differential hosts to recognize different pathotypes of both nematode species (Canto Sáénz & Mayer de Scurrah, 1977; Kort et al., 1977). The resistance may be due to a few major genes plus several modifiers . It differs from that controlled by gene H_1 for resistance to Ro1 (and by gene H_2 from the wild species *S. multidissectum* for resistance to Pa1) in that in progenies from resistant × susceptible there is no clear-cut distinction between resistant and susceptible offspring, there being a more or less continuous range in the number of cysts found on root-balls. It is therefore necessary to decide where to draw the line between resistant and susceptible. Although it was at first suggested that the resistance of some Andigena clones to pathotypes of *G. pallida* was due to a single dominant gene, H_3, segregations in later generations from crosses of resistant × susceptible were similar to those obtained in the breeding work using *S. vernei* as a source of resistance.

The somewhat lower resistance of resistant clones bred from *S. vernei* has led to the suggestion that such material would best be used in an integrated control system using both nematicide treatment and resistant varieties. Field experiments have shown that by using such a system reductions in nematode populations can be obtained with varieties which in pot experiments have about 10% of the number of cysts found on the susceptible controls. The use of a nematicide in integrated control usually leads to satisfactory yields in the year of treatment.

So far consideration has been given to only a single type of resistance to cyst nematodes, the type which leads to a marked reduction in numbers of cysts produced. Potato varieties do, however, differ considerably in their tolerance to nematode attack, some varieties suffering a smaller reduction in yield at high nematode densities (Huijsman et al., 1969). Little or no work has been done on breeding for tolerance.

Potato cyst nematode infestations are common in many of the world's main potato growing regions, producing marked reductions in yield even when there are no obvious haulm symptoms. Although nematicide treatment can produce satisfactory yields, it is costly and also usually results in no decrease in the nematode population. There would therefore appear to be an important place for resistant varieties in nematode control and resistant varieties should continue to be very valuable.

It is also possible that the new varieties bred for nematode resistance may have other valuable characters; for example CPC1673 has contributed resistance to virus X to the gene pool as well as gene H_1, and Maris Piper, so far the most successful variety in the UK with gene H_1, has very good cooking quality. Resistance to *G. pallida* and to the rarer pathotypes of *G. rostochiensis* is proving harder to obtain than resistance to Ro1 of *G. rostochiensis* but it should be achieved soon.

Soya beans resistant to cyst nematodes

Damage to soya beans (*Glycine max*) caused by the cyst nematode, *Heterodera glycines*, was first observed in Japan (Good, 1973). Soya beans grown in heavily infested soil are stunted and may undergo a yellowing that progresses upwards from the lower leaves. Death of the plant may occur in heavily infested soil. Losses in yield due to nematode have been estimated to be as high as 90% of the possible production. In the cyst nematode the eggs are retained in the body of the female and at maturity the cuticle of the adult female thickens to form a lemon-shaped leather-like encasement or cyst containing the eggs. The cyst remains attached to the plant root until the roots decay, after which the cyst can remain in the soil for several years. Hatching of the eggs is accelerated when susceptible plants such as soya beans are grown. A diffusate from the soya bean roots apparently stimulates hatching of the eggs.

A high degree of resistance to the soya bean cyst nematode is found in the Peking cultivar. Caldwell et al. (1960) reported that this resistance is conditioned by three independent recessive genes, rhg_1, rhg_2 and rhg_3. A fourth, dominant, gene, Rhg_4, was later found by Matson & Williams (1965) to be involved in the inheritance of resistance.

Four races of the nematode are recognized. The first resistant variety grown in the USA was Pickett, released in 1966. The Bedford variety (Hartwig & Epps, 1978) was released to soya bean growers having problems with race 4 of the nematode.

Authors: J.E. Parlevliet on disease resistance
M.D. Pathak and R.C. Saxena on insect resistance
H.W. Howard on potato cyst nematodes
D.E. McCloud on soya bean cyst nematodes

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7 Opportunities and problems in the developing world

Until recently the economic efficiency of crop production has usually been measured in terms of monetary input and output. The balance between energy input and output is however of growing importance, and this is affected by such factors as water-use efficiency, nitrate assimilation and harvest index. Its improvement by cultural practices and plant breeding is desirable. A further important means of saving energy and preventing losses would be provided by improvements in systems of distributing agricultural produce. In order to reach the biological ceiling of production, much time and research are still required. In the meantime, if the gap between the potential yields attainable through the application of present knowledge and the actual yields achieved by farmers could be bridged, especially in developing countries, a great step forward would have been taken. This requires an active and well organized extension service, preferably with demonstration plots in farmers' fields. An example of the rapid acceptance of recent developments in plant breeding is provided by the introduction of adapted semidwarf varieties of wheat and rice in countries such as India. Demonstrations in farmers' fields have served both to introduce the varieties and to alter cultural practice, the result in India being to raise total wheat production from about 12 million t in 1964/65 to over 31 million t in 1977/78. Although the introduction of high-yielding varieties has been criticized by sociologists as being more profitable to the relatively large farmer than to the small farmer, the available data from India reveal no significant relationship between size of land holding and yield of cereal crops. The new agricultural technology as such has no built-in sources of social discrimination. Sociologists should however be aware that there is no biological solution to the problem of the inadequate capacity of marginal farms for mobilizing inputs and taking risks. Without appropriate inputs, high yields are impossible. The increase in yields due to the new varieties and methods cannot be held to blame for social problems which can only be solved in the socioeconomic field. However, the new technology should be encouraged to develop in harmony with the socioeconomic needs of an area. Next to high food production, stability of the food supply is of prime importance. Stability may be sought within a crop, but an alternative is to grow a diversity of crops. In many parts of the developing world the potato affords an attractive additional food crop. Plant breeding can often play an important role in the partial fulfilment of the need for high and stable yields. It requires well-equipped breeding stations, good facilities for variety testing and seed multiplication and, last but not least, demonstrations of new varieties in farmers' fields and efficient seed distribution.

Breeding for efficient utilization of energy sources

Energy input in agriculture can be divided into solar energy and cultural energy. All forms of energy introduced into agriculture as a consequence of the domestication of plants and animals are referred to as 'cultural energy'. The purpose of cultural energy is to maximize the economic output of green plants through the utilization of solar energy. The efficiency of both solar and cultural energy conversion and the relative cost-benefit relationships of the different forms of cultural energy used in a specific farming system will determine the efficiency and cost-competitiveness of that system. Hence, the whole area of bioenergetics in relation to farming systems requires attention. Each component of the solar and cultural energy cycle and the 'double tandem' use of energy through the plant-animal-man food chain needs study. With the assistance of plant physiologists, breeders will have to develop appropriate screening procedures for identifying genotypes with superior efficiency in converting each of the cultural energy inputs indicated in Fig. 7.1 into the desired output.

Until recently, the economics of crop production was assessed mainly in terms of monetary input and output. This will no doubt continue to be the major consideration with farmers in times to come. However, the recent awakening to the energy needs of technology has led to a critical analysis of the energy input-output relationship in agricultural production and food utilization.

Pimental et al. (1973) showed that maize production in the USA gave an energy

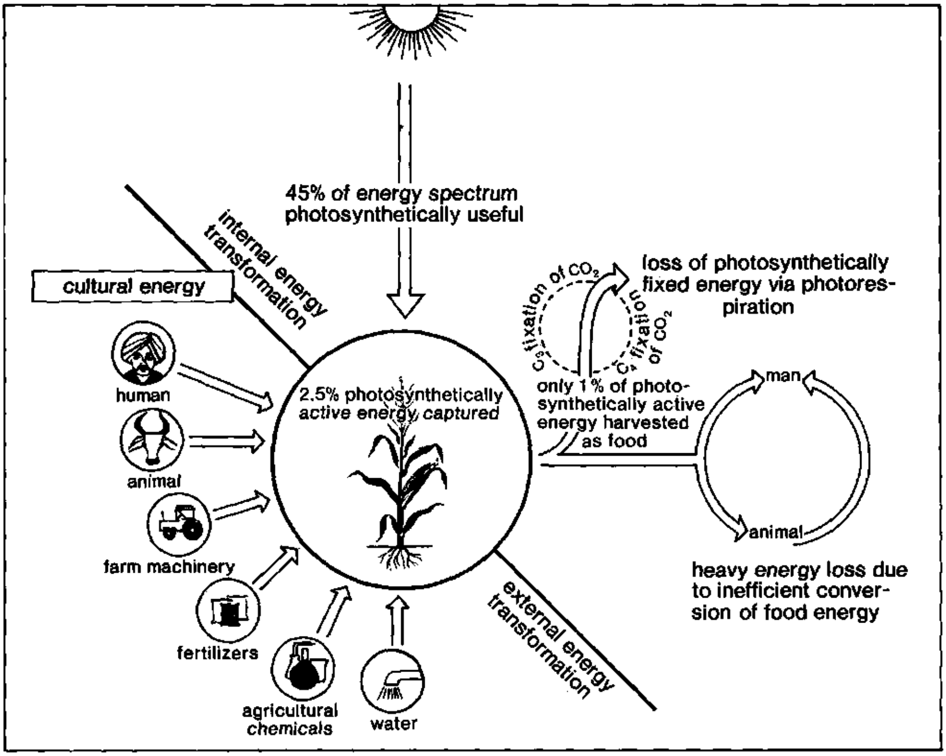

Fig. 7.1. Energy input and losses in agriculture.

input: output ratio of 1: 2.82; straw was not taken into consideration, otherwise this figure might be higher. The major items of energy input in the USA, according to this study, were heavy machinery, petrol and fertilizers. The last item was the most significant input. However, a further analysis showed that by the time a farm product reaches the consumer, more energy has been invested than harvested: the energy balance sheet shows a negative value.

In developing countries like India the items of energy investment are relatively low and the energy used for food processing and marketing is nearly negligible as compared with the USA. Current farming practice involves a low input of mechanical energy but a relatively high investment of human and animal energy. Plant breeders should be conscious of the need for developing an agricultural technology in which productivity improvement is not simultaneously accompanied by a heavy loss in the efficiency of energy conversion.

Because of their ability to fix nitrogen, many pulse crops may leave considerable quantities of nitrogen in the field; hence biological nitrogen fixation can provide a feasible method of saving nonrenewable forms of energy. In addition to the urgent need to grow more pulses for food, this is yet another cogent reason for growing legumes in multiple and intercropping systems.

An important characteristic of the new plant types of dwarf varieties of wheat and rice is their ability to apportion as much as 50% of the total dry matter produced during the life of the crop to grain formation. It is this harvest index in favour of the grain, as against straw and leaf, that confers on the new varieties the ability to give higher yields at low, medium and high levels of fertilizer application. Hence, contrary to the view sometimes expressed, the relevance of appropriate high-yielding varieties increases as fertilizers rise in price and become less readily available (cf. Fig. 7.2). Work on developing varieties for optimum response to high, low and zero input conditions is in progress.

The average farmer in various parts of the tropics has a small and often fragmented holding, his capacity for taking risks is low, his resources are poor and he is often illiterate. In spite of these handicaps, he is receptive to new ideas and can decide what is useful and what is not. Poverty makes it essential for him to base his decisions not on yield per hectare but on stable income per hectare. Hence, a profit-maximizing technology characterized by stability of income and low risk appeals to him more than a mere production-maximizing technology.

Analysis of gaps and constraints

There are two major gaps with which agricultural scientists are concerned. The first is the difference between the biological ceiling of production and the highest experimental yield obtained so far. Details relating to this difference, which may be designated a 'research gap', are discussed in Chapter 2. In order to develop screening and selection procedures for breeding varieties which can help to bridge this gap, the possible constraints and approaches must be identified. A breakdown of the different

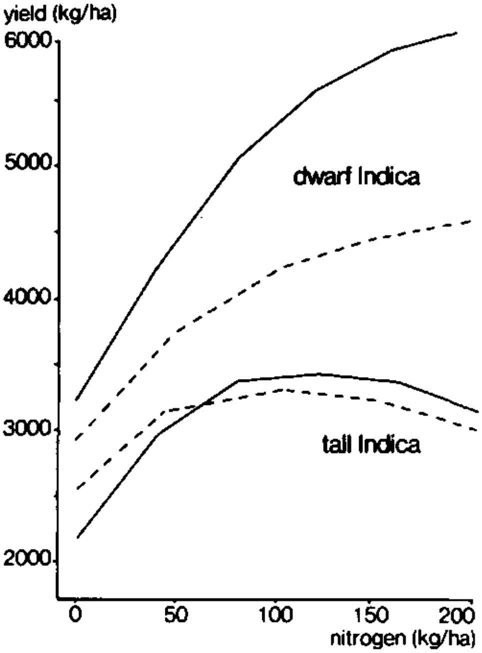

Fig. 7.2. Response of dwarf and tall Indica varieties to different levels of nitrogen application; — winter season; --- rainy season.

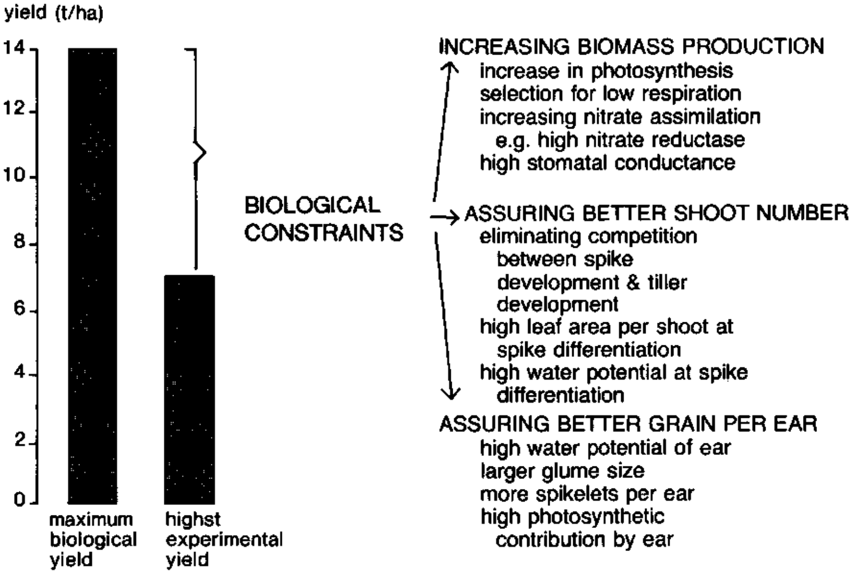

Fig. 7.3. Analysis of the gap between the biological ceiling and experimental station yields in wheat.

possibilities in bread wheat is given in Fig. 7.3.

The second gap is the difference between experimental yields and actual farm yields, and it represents the untapped yield reservoir existing at current levels of technology. The highest priority should be given to bridging this gap. This requires a detailed constraints analysis by an interdisciplinary team consisting of plant breeders, agronomists, statisticians and social scientists, in order to estimate the relative importance of the different constraints in a given area and to promote appropriate remedial action. A hypothetical breakdown of constraints is given in Fig. 7.4. In most farming systems in developing countries, the present average yields represent barely 20 to 25% of the experimental yields.

Some of the approaches which may be useful in studying the two gaps are described below.

MAJOR COMPONENTS OF THE RESEARCH GAP

Introduction

Since the rediscovery of Mendel's laws of inheritance at the beginning of this century, considerable progress has taken place in improving the yield potential of major economic plants. Both conventional breeding procedures and special techniques like mutation and polyploidy breeding have been employed. Although yield improvements have generally been gradual, there have also been occasional sudden leaps. One such leap resulted from the commercial exploitation of hybrid vigour, first in maize and subsequently in other crops, and another from the repatterning of plant architecture to suit the need for water and fertilizer application, for example by

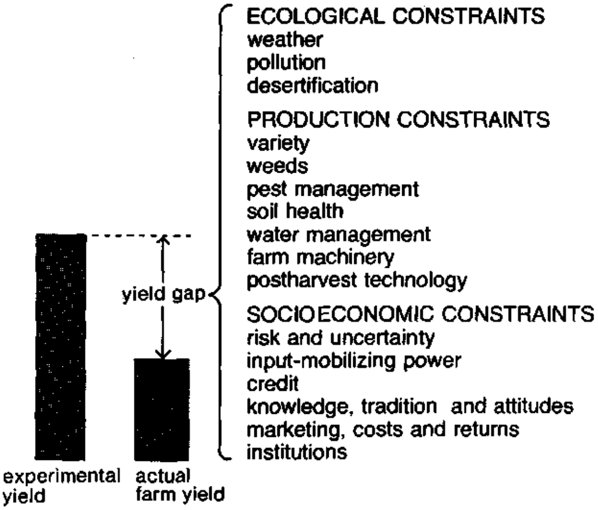

Fig. 7.4. Analysis of the gap between experimental station yields and farm yields.

introducing the Norin dwarfing genes into wheat and the 'dee-geo-woo-gen' dwarfing gene into rice. While another leap in yield may not be easy to make in wheat or rice (in these crops greater breeding priority should therefore be given to stability of yield), in general, steady improvements leading ultimately to the achievement of the theoretical potential postulated by plant physiologists should be possible. For this purpose, greater interdisciplinary cooperation among plant breeders and plant physiologists is necessary.

So far, much of the increase in yield potential has taken place through increased apportionment of the total photosynthates to the plant organs of economic value, such as grain in cereals. The next major breakthrough in yield improvement may be possible only when genotypes with a capacity for a greater production of total biomass are identified.

The challenge is particularly great in pulses and oilseeds. On an average, 1 g of glucose can produce 0.83 g of carbohydrates, 0.40 g of protein with nitrate as nitrogen source and 0.32 g of lipids. Hence, there may be a calorie penalty if there is an increase in protein or lipid content and a protein or lipid penalty if there is an increase in calorie yield. An optimum balance between the two will have to be developed in different crops under different growing conditions. For this purpose detailed analysis of 'yield potential constraints' on the lines already indicated for wheat in Fig. 7.3 and as shown for chickpea in Fig. 7.5 will be necessary.

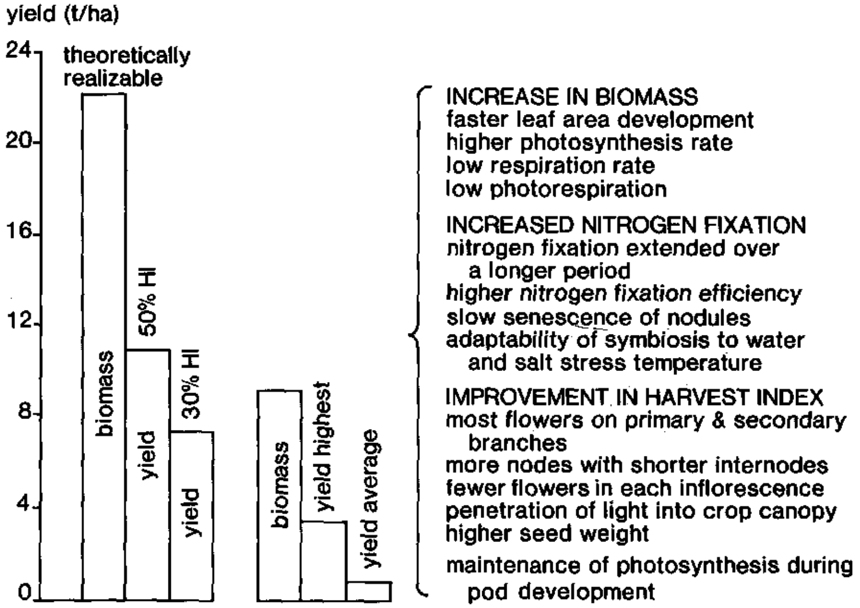

Fig. 7.5. Analysis of the gaps between biological ceiling, experimental station yields and farm yields in chickpea. HI, harvest index.

Dry matter production

If there is no limitation of water and nutrients, dry matter production should equal net photosynthetic production. Here a distinction must be made between photosynthate production and photosynthesis rate. The total net photosynthate is equal to photosynthetic surface × photosynthesis rate per unit area minus respiration. Where the photosynthetic surface consists essentially of leaves, it is defined by number of leaves × leaf size, and leaf size in turn is defined by number of cells × size of cells.

Sinha & Khanna (1975) and Sinha (1976) have shown that the number and size of leaves from different parents can combine to produce a larger total leaf area in F_1 hybrids. In a further study it was observed that complementation in cell number and cell size could be responsible for the greater leaf size of F_1 hybrids, thus providing a mechanism for producing a larger leaf area during the entire growth cycle of the plant.

Nitrate assimilation and dry matter production

Nitrogen is one of the major inputs in agricultural crop production. Hageman et al. (1967) concluded that the enzyme nitrate reductase (NR) can be a limiting factor in the utilization of nitrate and consequently in dry matter production and yield.

Genetic variability in NR activity is known and it has been shown that this enzyme in maize is controlled by two genes (Warner et al., 1969). In a study of inbreds and hybrids it was observed that only the low × low-NR types gave heterosis whereas high × low or high × medium resembled the better parent (Hageman et al., 1967). In a recent study using seven male parents and three female parents in sorghum, Mishra et al. (1978) observed that the high-NR parents showed no heterosis with either low or medium parents. This study shows that the high-NR character has relatively high heritability and if it could be combined with high leaf area, a high NR potential could be achieved. An example of this is provided in a study of maize by Balusubramanian et al. (1977), in which the hybrid was intermediate between the parents but had a higher leaf area which ultimately gave higher total NR at any given time during crop growth.

Water-use efficiency

Water is one of the limiting factors in crop production. Consequently, improvement in water-use efficiency can be advantageous. In temperate countries, the period of maximum solar interception is generally characterized by adequate precipitation. Unfortunately, in the tropics and subtropics the period of maximum insolation often tends to be also the period of minimum precipitation. Hence, research on the effective application and use of water as well as larger investments in irrigation are both essential in the tropics. Downes (1969) compiled data on water-use efficiency in various dicotyledonous and monocotyledonous plants and concluded that the C_4

Table 7.1. Water use efficiency in C_3 and C_4 species. Data obtained in field experiments (from: Downes, 1969).

Class	Water use efficiency in mg dry weight/g water	
	C_4 species	C_3 species
Dicotyledons	3.44	1.59
Monocotyledons	3.14	1.49

plants in both groups had more than double the efficiency of C_3 plants (Table. 7.1). Water-use efficiency is further influenced by environmental conditions; the higher the evaporation demand, the lower the efficiency. In view of the problem of limited water availability, it would be useful to obtain information on genetic variability in water-use efficiency (Singh & Sinha, 1978). In addition, the effect of moisture stress at different stages of growth and development on yield should be critically assessed. In wheat, for example, lack of moisture at the stage of crown root initiation has an adverse effect on tillering and hence on yield.

Flowering habit

Flowering time is important for the establishment of the 'sink' (cf. Chapter 2, pp. 59-61) in most grain crops. Recent studies in various crops indicate that flowering time is under genetic control, so that this character can be manipulated along with vegetative characters to provide a mechanism for complementation between vegetative and reproductive structures.

Improvement in harvest index

The harvest index in cereals is defined as the ratio of economic yield to the total biological yield above ground. In grain crops this depends upon the apportionment of dry matter between the grains and the remaining plant parts. The final grain harvest does not allow precise determination of the partitioning of the dry matter produced before anthesis and that produced after anthesis. Therefore, growth analysis studies to determine the role of the vegetative phase in relation to the reproductive phase are important. It is also necessary to understand when the grain potential or 'sink' potential is determined. It is common knowledge that shortening of the vegetative phase by manipulating temperature or day length, or both, also reduces the size of the spike. Thus there is a minimum requirement for vegetative growth, or in other words, the harvest index cannot exceed a certain maximum. This maximum has not yet been reached.

GAP BETWEEN EXPERIMENTAL AND ACTUAL FARM YIELDS

Introduction

In 1965, the Government of India introduced a National Demonstration Programme to provide opportunities for scientists to demonstrate in farmers' fields the economic viability of the new technology. These demonstrations are generally laid out in the fields of the poorer farmers, since the yields obtained in demonstrations in the fields of rich farmers would be liable to be attributed to the effects of affluence rather than of technology. If the average yield obtained in farmers' fields in the national demonstrations is compared with the average yield for in the area concerned, we get a measure of the degree to which yield can be improved at a particular time and at a particular level of technology. Studies, preferably multidisciplinary, can then be conducted to identify the factors responsible for the gap between the yield of the demonstrations and of the area as a whole.

The size of the gap and the factors determining it may vary widely according to the agroecological and socioeconomic conditions of each area. Some of the major constraints responsible for the low average yields in various parts of the tropics are indicated in Fig. 7.4. The constraints can be overcome through appropriate blends of technology, services, social or community action (particulary relevant for small holdings) and public policies.

A study by the International Rice Research Institute (IRRI, 1977) on some of the major yield-reducing factors operating in the fields of Asian rice farmers has given the following results.

Bangladesh

It was found that the productivity of rice can be improved by about 1 t per hectare by growing modern varieties with adequate inputs during the boro season. However, in transplanted aman rice, the spread of modern varieties was limited by deep water and by the need for photoperiod sensitivity in the case of late plantings.

Indonesia

The yield gap in the area studied was very small in the wet season but was about 1.3 t per hectare during the dry season. During the wet season poor pest control was a major factor. Increasing fertilizer application above the levels now used in the wet-season crop in coastal areas is therefore unlikely to be profitable unless pests are controlled.

Philippines

In the wet season the yield gap ranged from 0.4 to 2 t per hectare, fertilizers and insect control being equally important factors at most locations. The gap ranged from 0.9 to 2 t per hectare in the dry season, fertilizers accounting for about two-thirds of the gap. Insect damage was the second most important component, accounting for 30-50% of the gap.

Sri Lanka

During the wet season, a yield gap of over 1 t per hectare was observed in four complex experiments. Fertilizer, insect control and weed control contributed to the gap, insect control making the greatest contribution.

Taiwan

Yields in farmers' fields ranged from 5 to 7.2 t per hectare according to farmers' inputs. The yield gap was 0.8 t per hectare, with fertilizer contributing about 60% of the gap in both seasons. Thus, rice production in Taiwan has reached an optimum level from both the physical and the socioeconomic points of view. Under such conditions farmers respond to price incentives, and economic factors act as the major determinants of the farmer's yield target.

Thailand

Inadequate fertilizer use was the dominant constraint in all the three seasons during which the study was conducted, causing a gap of about 0.5 t per hectare during the wet season and 1.5 t per hectare during the dry season. Insects and weeds reduced yields by 0.1-0.3 t per hectare.

Measures for bridging the gap

During 1977, the Indian Council for Agricultural Research (ICAR) and IRRI organized a joint survey of the rice-growing areas in eastern India (Bihar, Orissa and West Bengal) to identify the major factors influencing rice yield in this region during the south-west monsoon period. In this region no yield improvement has been observed in spite of the introduction of HYVs of rice (Fig. 7.6). This team has made the following recommendations:

– Since the performance and profit of existing high-yielding varieties with costly inputs are uncertain, scientists should develop a technology which combines good yield with reliability and security of profit to farmers. This is necessary especially if small and marginal farmers are to be helped to adopt the technology. Out of a total rice area of 37 million hectares in the country, the area under deep (50 cm and

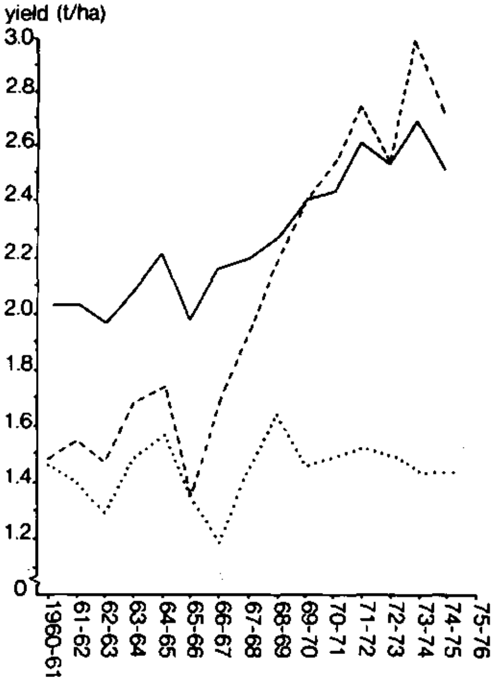

Fig. 7.6. Improvement in rice yields in different parts of India, 1960/61-1975/76; — South India; --- North India; · · · East India.

above), semideep (30 to 50 cm) and intermediate (15 to 30 cm) water depths is about 10 million hectares. Hence, rapid testing and release of promising strains for these areas are necessary.

- Diversification of varieties and periodic replacement of varieties are important for a high-stability technology. States should develop the capacity and organization for multiplying and distributing seed of new varieties rapidly and to change a variety once every 3 to 4 years.
- Early planting and short-duration varieties may reduce damage from floods and waterlogging in some areas. Community nurseries could help small and marginal farmers to adopt these practices.
- Fertilizer application poses problems in such areas. 'Supergranules' of urea could be placed under the soil. This would require a simple implement for placing the granules at the appropriate depth.
- Minor elements, particularly zinc, appear to be deficient in several soils. A suitable testing programme to assess response to zinc is necessary. The role of sulphur in increasing yield also needs study.
- Better pest surveillance is required. Pest-resistant varieties should be popularized.

– Water distribution systems, on-farm management of water and drainage need to be improved.

– Attention should be given to postharvest technology, including the use of community grain driers driven by solar energy and organic fuels like paddy husk, coal, weeds, etc., and to the popularization of cheap storage structures.

Variety improvement in wheat

Before the introduction of the new technology based on semidwarf varieties of wheat (*Triticum aestivum*) in 1966-67, the highest wheat production recorded in India was in 1964-65, when about 12 million t were produced. The production during 1977-78 was about 31 million t. It may be appropriate to describe briefly the scientific developments which led to this progress.

MEXICAN DWARF WHEATS IN INDIA

In 1962 the yield potential of genotypes carrying the Norin dwarfing genes was recognized in Mexican material received from N.E. Borlaug and raised at the Indian Agricultural Research Institute (IARI), New Delhi, and a new possibility for increasing wheat production in India became apparent. Earlier wheat-breeding work in India had been confined solely to the tall wheats, which had the inherent limitation of lodging whenever intensive agricultural practices were followed. The dwarf wheats, besides having stiffer and shorter straw, were relatively photoinsensitive and were capable of giving high yields with high doses of fertilizers, water and other inputs. Their harvest index was also more favourable.

Immediate steps were taken to exploit the potentialities of the dwarf wheats: by direct introduction, by selection, by mutation breeding and by hybridization with Indian wheats.

Direct introduction

Of the different dwarf wheats obtained from Mexico, two varieties, Sonora 64 and Lerma Rojo 64-A, were superior. These were extensively tested in 1964 at 155 locations in the country, and in 1965 about 250 t of seed of Lerma Rojo 64A and Sonora 64 were imported from Mexico for testing in farmers' fields. On the basis of the favourable reactions of farmers, the government of India imported 18,000 t of seed of these two varieties from Mexico in 1966. This enabled the planting of about 20,000 hectares with these wheats during 1966-67. One more variety, PV18 from Mexico, also proved outstanding in the Punjab. However, all these wheats had red grains, which were not liked by farmers and consumers, and subsequently they had to be replaced by varieties with greater consumer appeal.

Selection

Some of the advanced-generation wheat material received in 1963 from Mexico segregated for characters like rust resistance, shattering, maturity and grain type, and it was possible to select strains which were promising under different conditions. This line of work yielded varieties like Kalyan Sona, Sonalika, Chhoti Lerma and Safed Lerma, which became very popular with farmers because of their high yields, rust resistance, amber or white grains and adaptability to different soil and climatic conditions. Kalyan Sona and Sonalika are still extensively cultivated all over India, while the cultivation of Chhoti Lerma and Safed Lerma is restricted to small areas in peninsular India.

Mutation breeding

Since Sonora 64 and Lerma Rojo 64A were satisfactory apart from their red grains, mutation breeding was initiated at the IARI to alter the colour of the grain. This line of work yielded Sharbati Sonora from Sonora 64 and Pusa Lerma from Lerma Rojo 64A, both possessing amber grains.

Hybridization with Indian varieties

Extensive breeding work was initiated in 1963 to transfer the desirable short and stiff straw of the semidwarf wheats into well-adapted Indian wheats. Among the excellent results of this programme are Hira, Moti, Janak, Arjun, Pratap, Girija, Shailaja, WG357, WG377, WL711, WL410, Raj 911, NI747-19, NI5439 and Shera. These wheats were released either by the Central Subcommittee for the Release of Varieties of the Government of India or by the Varietal Release Committees of the States. Seeds of several other promising prerelease strains are being multiplied by such seed agencies as the National Seeds Corporation, State Farms Corporation of India Ltd., and the Tarai Development Corporation.

Every year some 600 to 700 new strains developed under the All-India Coordinated Wheat Improvement Project of the ICAR are tested all over the country, to locate superior and disease-resistant varieties for release to farmers.

CONTROL OF PATHOGENS, PESTS AND WEEDS

Wheat, fortunately, does not suffer from any serious insect attack in India, although dwarf varieties whose leaves show slow aging may be attacked by cutworms and army worms in March. Two weeds, wild oats and *Phalaris minor*, have become very important in the Punjab. Fortunately, standard methods of eliminating them have been developed at the Punjab Agricultural University and elsewhere. What is now needed is sustained community action on the part of all farmers in each village so that these weeds are not allowed to shed their seeds on to the soil.

The most important reason for instability in wheat production in the past has been disease epidemics. Among diseases, the rusts cause the greatest damage. Black, brown and yellow rusts (*Puccinia graminis, P. recondita* and *P. striiformis*) are all important in India. These are also known as stem, leaf and stripe rusts, respectively. *P. striiformis* is confined more to the foothills of the Himalayas and north-west India. *P. graminis*, though prevalent all over the country, normally appears in epidemic form only in southern, central and eastern parts of India. *P. recondita* occurs throughout the country.

Considerable attention is being paid to the control of rust epidemics. A National Disease Survey and Surveillance system in wheat is being operated cooperatively by wheat pathologists at the IARI and Agricultural Universities. A national rust control strategy has also been developed which involves study of the dissemination of wheat rust spores in different parts of the country in order to identify the '*Puccinia* path'. It should be possible to obstruct the path and hence delay the spread of the disease by growing genetically different resistant material in the different zones (Fig. 7.7). This varietal deployment principle is valid for many of the air-borne plant pathogens, and also has the effect of minimizing selection pressure on the pathogen. An example of its application is provided by north India, where a large proportion of the *P. recondita* inoculum comes from the oversummering foci along the Nepal part of the Himalayas to parts of north Bihar and east and central Uttar Pradesh. All along the narrow foothills of Haryana, the Punjab, Himachal Pradesh and Jammu and Kashmir, infections develop from the Indian Himalayan sources. Foci are established in the foothills and north-eastern India by mid-January and in favourable weather the disease then spreads to other zones. During the epidemic year 1972-73, Kalyan Sona was the predominant variety of north-west India, while north-eastern India was under local and native improved wheats. As these local wheats were infected by almost all the

Fig. 7.7. Wheat growing zones in India of importance in the prevention of rust epidemics by the gene deployment method. I, source of infection; II, area of early inoculation build-up; III, major wheat belt.

leaf rust races, the appropriate races from the east were able to infect Kalyan Sona and cause an epidemic. On the other hand, during 1975-76, the weather was favourable for the rust but no epidemic developed. Investigations showed that within this period Kalyan Sona was replaced to some extent by WG357, WG377, Arjun and Sonalika in north-west India; the north-eastern region had Sonalika and the Nepal hills Sonora 64, Lerma Rojo and Sonalika as the predominant varieties. These varieties had different resistance genes. As a result, the race from one zone could not infect the crop of another zone. Hence, disease development was delayed and an epidemic averted.

Jensen (1952) suggested an interesting method of avoiding the pressure on the pathogens that leads to the development of epidemics. This method consists in breeding and growing a variety which is homogeneous in growth and morphological characters, but differs in genetic resistance to different races of the pathogen. This is the 'multiline' method of breeding and is now reaching the stage of being field tested (see Chapter 4, p. 107, Table 4.1).

Bhatia (1976) and his coworkers at the IARI have established the importance of developing grain varieties resistant to storage pests. Varietal differences in resistance to *Sitophilus oryzae* and *Rhyzopertha dominica* have been observed in wheat, Kalyan Sona being resistant to both of these pests and also to *Trogoderma granarium*. The resistance of Kalyan Sona to *S. oryzae* is polygenically determined and has high heritability. Differences in resistance to storage pests have also been detected among barley varieties.

AGRONOMIC MEASURES FOR SEMIDWARF WHEATS

The agronomy of the new dwarf wheats is entirely different from that of the tall wheats. To exploit their potentialities to the full, agronomists have developed an appropriate technology. This covers the time of sowing, seed rate, depth of seeding, row spacing, time and frequency of irrigation, fertilizer doses, not only of major elements like nitrogen, phosphorus and potassium but also of minor elements like zinc and sulphur, herbicide application etc., and also the separate agronomic practices needed for irrigated and rainfed wheat cultivation.

As new wheats are developed, suitable agronomic techniques for growing them are worked out at the all India level. The new wheats are also tested simultaneously in simple fertilizer trials as well as in cultivators' fields under various management practices. It was through the National Demonstrations of the new wheats and cultural practices on farmers' fields that farmers became convinced of their yield potential. Having seen what could be done on their own fields, the farmers themselves brought about the 'wheat revolution'.

SOCIAL IMPLICATIONS OF NEW TECHNOLOGY

Are the advances in agricultural science, including plant breeding, in step with the desired movements in society? Since the immediate social goals of developing countries include the removal of gross inequalities in the economic situation of different sections of the population, as well as the provision of jobs to all who need them and the improvement of nutritional standards, it is appropriate to ask:

- How far is the new technology relevant to farmers with small holdings?
- Is the new technology labour-displacing?
- Has the differential rate of yield improvement in a cereal like wheat and a grain legume like chickpea had an adverse nutritional effect?
- Can technology help to stabilize yield in addition to increasing it?

Some data from India which may help us to answer these questions are discussed below.

For farms of different sizes

The Agricultural Census of 1970-71 showed that a large number of operational holdings (32.9%) in India are below 0.5 hectare in size (Table 7.2). Hence, it is of interest to know whether farmers with small holdings can benefit from the new agricultural technology. The available data from National Demonstrations and sample surveys reveal no significant relationship between the size of land holdings and the yields of cereal crops (Tables 7.3 and 7.4), indicating that the technology itself has no built-in seeds of social discrimination. It should, however, be emphasized that there is no biological solution to the problem of the inadequate input-mobilizing and risk-taking potential of small and marginal farmers. There is a posi-

Table 7.2. Number of operational holdings - All India (from: Anonymous, 1975).

Size class in ha	Number $\times 10^6$	Percentage
< 0.5	23.2	32.9
0.5- 1.0	12.5	17.7
1.0- 2.0	13.4	19.0
2.0- 3.0	6.7	9.5
3.0- 4.0	4.0	5.7
4.0- 5.0	2.7	3.8
5.0-10.0	5.3	7.5
10.0-20.0	2.1	3.0
20.0-30.0	0.4	0.6
30.0-40.0	0.1	0.1
40.0-50.0	0.05	0.1
> 50.0	0.05	0.1
Total	70.5	100.0

Table 7.3. Relationship between the size of land holding and yield in National Demonstrations.

Size of land holding in ha	Number of farms with a cereal yield below or above the target of 1 t/a							
	1972-73		1973-74		1974-75		1975-76	
	below	above	below	above	below	above	below	above
0-2	142	138	68	70	141	128	203	203
2-4	160	154	135	145	165	193	296	317
4-6	140	145	101	150	120	153	139	196
>6	189	200	218	291	198	217	254	274
Total	631	637	522	656	624	691	892	990

Table 7.4. Percentage of cases exceeding target of 1 t/ha in different sizes of land holding in National Demonstrations.

Size of land holding in ha	Percentage			
	1972-73	1973-74	1974-75	1975-76
0-2	49.3	50.7	47.6	50.0
2-4	49.0	51.8	53.9	50.5
4-6	50.9	59.8	56.0	58.5
>6	51.4	57.2	52.3	51.9

tive relationship between input and output and it is not possible to obtain high yields with no inputs. Nonmonetary inputs can help improve yield to some extent, but these often require cooperative endeavour on the part of a community. Hence, small and marginal farmers can best be aided through appropriate public policy measures in land reform, credit insurance, pricing and marketing and through the organization of necessary services like input supply and effective extension advice.

For employment

Citing field data from Bangladesh, India, Indonesia, Malaysia, Pakistan, the Philippines, Sri Lanka and Thailand, a recent study by the International Labour Organization (ILO, 1977) indicates that employment per hectare and yields and added value per hectare rise as the average size of farm declines. The report states that small farmers typically use production technologies, cropping patterns and rotation systems which are more productive than those used by large farmers. Specifically, small farmers tend to cultivate any given crop with more labour-intensive techniques, to choose combinations of crop and livestock which are more labour intensive and, finally, to use their land more intensively, even at the risk of exhausting soil fertility.

Table 7.5. Labour days per hectare for HYVs of wheat and rice (from: Lakdawala, 1977).

State	District	Crop and variety	Year	Labour days per ha
Punjab	Ferozepur	wheat HYV	1967-70	68.20
		wheat local	1967-70	52.23
Uttar Pradesh	Muzzaffarnagar	wheat HYV	1966-69	63.12
		wheat local	1966-69	59.00
	Deoria	wheat irrigated	1966-69	100.12
		wheat unirrigated	1966-69	57.63
Punjab	Ferozepur	paddy HYV	1967-70	91.88
		paddy local	1967-70	78.92

It is obvious that if a capital-intensive and highly mechanized high-yield technology is introduced, there could be an adverse impact on the employment of agricultural labour. The introduction of an appropriate technology could, however, lead to greater opportunities for gainful employment for the following reasons:

- The crop itself will need intensive care involving weeding, manuring, irrigation and pest control.
- Multiple cropping involving the cultivation of 2-3 crops in a year may be possible.
- Mixed farming involving crop and animal husbandry can be introduced.
- Increased production will necessitate greater attention to postharvest technology, such as packaging, storage and transport operations.

Data on the number of labour days per hectare needed for high-yielding varieties (HYVs) of wheat and rice in the Punjab and Utter Pradesh, India, are given in Table 7.5.

It will be seen that HYV programmes can help to generate more employment. However, their impact on employment should be continuously monitored, so that the technology released is in harmony with the socioeconomic conditions of the area. Scientists, including plant breeders, should keep employment generation as a specific objective of technology development. A good example of this approach is provided by hybrid cotton, seed of which is produced in India by hand emasculation and pollination.

For energy and protein production

In 1966, when several parts of India faced serious drought, the HYV programmes designed to popularize varieties or hybrids of rice, wheat, maize, sorghum and pearl millet possessing the capacity to respond well to good management (involving the application of fertilizer and water) were initiated in areas with assured water supplies. As is well known, the wheat programme was very successful (Table 7.6). Several

Table 7.6. Sample surveys for assessment of HYV programme (from: IASRI, 1978).

State	Average yield in t/ha for farms of sizes:				
	< 1 ha	1-2 ha	2-4 ha	4-8 ha	> 8 ha
Bihar	1.65	1.67	1.76	1.66	1.75
Gujarat	2.31	2.56	2.70	2.31	2.45
Haryana	1.54	1.70	1.80	2.02	1.84
Madhya Pradesh	3.41	2.42	2.54	2.66	3.06
Maharashtra	1.35	1.30	1.29	1.32	1.34
Karnataka	2.18	2.59	1.65	2.45	2.62
Punjab	1.94	2.35	2.23	2.28	2.43
Rajasthan	1.47	1.89	1.93	2.08	2.00
Uttar Pradesh	1.76	1.78	1.92	2.13	2.51
West Bengal	2.37	2.04	2.30	2.59	2.60

studies have indicated that the expansion of wheat acreage in the major wheat-growing states such as the Punjab, Haryana, Uttar Pradesh, Bihar, Madhya Pradesh and Rajasthan has primarily been at the expense of chickpea, pigeon pea, other pulses and barley. As a result, there has been a decline in per caput availability of pulses in India. This has led to the question whether the wheat revolution has in fact had an adverse nutritional impact.

Ryan & Asokan (1977) of the International Crops Research Institute for the Semiarid Tropics (ICRISAT) have recently analysed the available data on this question. They concluded that if the HYVs of wheat had not been introduced, the annual trend production of energy in the six Indian states mentioned earlier would have been 13.5% less than it actually was during the year 1974-75. In fact, compared with the situation in 1965-66, the actual production of nutrients in the six major wheat-growing states was higher by the following percentages during 1975-76: total production 22, protein 20, energy 22, lysine 7, methionine and cystine 21, tryptophan 33, leucine 16 and isoleucine 12. Hence, according to this study, the substitution of wheat for chickpea and other crops after 1966-67 led to an increase in the production not only of energy per hectare but also of protein. Ryan & Asokan calculate that, per additional hectare of wheat, a further 35 kg of protein and 10.6×10^3 kJ of energy were produced, over and above what could have been obtained had chickpea been grown in that area (Table 7.7).

Thus, in the case of wheat, a primarily yield-orientated plant breeding strategy has had a favourable effect on the nutritional well-being of the people. A similar strategy may be desirable for other cereals and also grain legumes. If, moreover, high yield and good nutritional quality can be combined, the consumer receives a nutritional bonus at no extra cost. For this reason adding a nutritional dimension to plant breeding programmes is important. In the case of tuber crops like cassava, a suitable intercropping system with a grain legume would help to achieve a simultaneous improvement in energy and protein yield.

Table 7.7. Trend levels of production of protein and energy per hectare from wheat and chickpea in the six major wheat-growing states of India in 1964-65 and 1974-75 (from: Ryan & Asokan, 1977).

Crop	Yield in kg/ha		Protein in kg/ha		Energy in kJ/ha × 10^6	
	1964-65	1974-75	1964-65	1974-75	1964-65	1974-75
Wheat	900	1414	106	167	13.0	20.5
Chickpea	615	657	105	112	9.3	9.9

From what has been stated above, it should not be concluded that we ought to replace grain legumes with high-yielding cereals. A combined legume-cereal diet compensates the deficiency of lysine in the cereal and promotes a balanced nutrition. Also, there is a limit to the quantity of cereal that growing children can consume. Hence it would be wrong to assume that nutritional needs can be met entirely by cereals, although this may be theoretically feasible. What is clear, however, is that unless the yield potential of grain legumes can be improved, the farmer will replace a low-yielding pulse crop with a high-yielding cereal, particularly if he has access to irrigation. The only way of avoiding shifts of this kind will be to develop a standard high-yield technology for pulses without any sacrifice of quality. The alternative of providing high price incentives in favour of the pulse crops may defeat the very purpose for which a higher production of pulses is needed. Recent advances in research on pulses are encouraging from the point of view of improving yield.

For yield stability

Since crop or credit insurance is not yet available in most developing countries, imparting stability to yield is essential if the small farmer is to be insulated from undue risks. The two major factors causing yield instability are pest epidemics and weather aberrations. Through a series of crop-rescue techniques and alternative cropping strategies to suit different weather models it is now possible to reduce the adverse effects of aberrant weather. A suitable disease control strategy can help to reduce the risk of extensive epidemics. As mentioned above, the gene deployment strategy adopted in India for rust resistance in wheat has been effective in minimizing infection during a season very favourable to the pathogen.

Potato cultivation

INTRODUCTION

'The potato is the richest of nature's gifts and all the problems concerning the potato depend on man's wisdom' R.N. Salaman, 1949.

Chapter 1 provides a comparison of the nutritive value and energy production (calories) of potatoes (*Solanum tuberosum*) and other crops. Data summarized in Table 7.8 (van der Zaag, 1976) clearly demonstrate that an extension of potato culture in developing areas could bring about considerable improvements in food production. Total world production is given in Table 7.9.

The potato is grown in some 120 countries covering a total area of about 20 million hectares. Its total production is about 292 million t, averaging 13.3 t per hectare. The area and the production per continent are roughly as shown in Table 7.9. The potato's wide adaptability to soil and climate is illustrated by the fact that it is grown from the Arctic Circle (northern Sweden and Finland) to the Cape of Good Hope in South Africa and from South America, Mexico and North America in the west to China, Japan, the Philippines, Indonesia, Australia and New Zealand in the east. In most tropical and subtropical countries, however, the main sources of energy in the food are rice, maize, sweet potato, cassava and sago, and the potato is still regarded as a luxury product. By increasing the potato acreage, and more especially the yield per hectare, total potato production could be increased considerably, and

Table 7.8. Comparison of yield and of energy and protein production per hectare per day in potato and tropical food crops, latitudes 30°N to 30°S (from: van der Zaag, 1976).

	Yield 1970/72 in t/ha			Energy in kJ/ha per dag ×10³			Protein in kg/ha per day		
	Latin America	Africa	Asia	Latin America	Africa	Asia	Latin America	Africa	Asia
Potato	7.3	6.8	9.1	153	144	193	1.0	0.9	1.2
Cassava	13.8	7.7	9.2	225	125	150	0.2	0.1	0.2
Sweet potato	9.8	4.1	6.3	290	120	187	0.9	0.4	0.6
Yam	11.0	9.3	4.3	144	121	57	0.7	0.6	0.3
Beans (dry)	0.62	0.41	0.31	56	37	28	0.9	0.6	0.5
Chickpeas	0.81	0.55	0.66	82	56	67	1.1	0.7	0.9
Rice	1.70	1.35	1.80	116	92	122	0.6	0.4	0.6
Maize	1.28	1.20	1.07	142	133	119	0.9	0.8	0.8

Table 7.9. Total world production of potatoes (from: van der Zaag, 1976).

	Area in ha ×10³	Production in t ×10³
Europe (incl. USSR)	15,000	200,000
North and Central America	700	18,000
South America	1,000	8,000
Asia	5,000	56,000
Africa	400	4,000
Oceania	500	1,000

this, together with lower prices, would allow the potato to reach a much greater section of the population than is at present the case. Storage facilities in particular, to allow an even supply of potatoes, would also need drastic improvement.

Potatoes can be grown on nearly all types of soil, though very heavy clay soils are not favourable to its cultivation. In tropical and subtropical countries, cleared forest soils and volcanic soils are particularly suitable on account of their loose structure, but cultivation on brownish red loam soils is also possible. Generally speaking, the potato grows best in the cool and rainy climate characteristic of west European countries, where it will give yields of 50-60 t per ha. Both excessively low temperatures (e.g. frost in mountainous regions) and excessively high temperatures (e.g. in tropical, humid lowlands) have an adverse effect. Optimum tuber initiation takes place at temperatures between 16 °C and 19 °C, few or nor tubers being formed at 25-30 °C. In the subtropics therefore the planting time is shifted to the cooler periods of autumn (August/September/October) or to the winter (December/January/February), while in tropical areas potatoes are grown in the cooler mountainous regions or on high plains.

At high temperatures photosynthesis decreases while respiration increases, with the result that at 30 °C net photosynthetic rate is about half that at 20 °C. Where temperatures are high, especially at night, tuber production is low, but where differences between day and night temperatures are marked, as for example in Egypt and tropical highland areas, tuber production is favourably affected. A high light intensity also has a favourable effect on tuber growth.

PRODUCTION IN THE TROPICS AND SUBTROPICS

Figs. 7.8 and 7.9 (van der Zaag, 1976) show the percentage increases in area and total production over the period 1962-1973 for the whole world, the temperature zone and the tropical zone (Fig. 7.8) and for Latin America, Africa and Asia (Fig. 7.9). From these figures it appears that total production in tropical countries has increased by more than 60% (from 9.2 to nearly 15 million t). The increase has been particularly marked in Asia and Africa (from 3.4 to 6.4 million t in Asia and from 1.1 to 1.8 million t in Africa).

In farm trials under optimum growing conditions in the tropical yields up to 30-40 t/ha have been achieved, figures for variety trials in Bangladesh being up to 32 t/ha, in Senegal up to 31 t/ha and in Brazil 38 t/ha (van der Zaag, 1974). This reveals the remarkable difference that exists between present yields and potential yields in the tropics. Low yields are not primarily the result of environmental factors such as temperature and short day, but rather of faulty agronomic methods such as the use of poor (degenerated) seed of unadapted varieties, inadequate fertilizer application, poor weed control, insufficient water supply (irrigation), lack of control of diseases and insects and deficient storage facilities (losses of stored tubers by rotting may amount to 30% or more). The growth period of the potato is short (3-3½ months) compared with some traditional tropical crops, for example 5-6 months in sweet potato, 9 months in yam and 11-16 months in cassava.

In the shadow of growing food crises, attention has focused on the potato (Sawyer, 1975). The International Potato Center (CIP) founded in Lima, Peru, in 1972 is working to improve potato cultivation and to disseminate knowledge for the greater utilization of the potato as a basic food in developing countries. Breeding

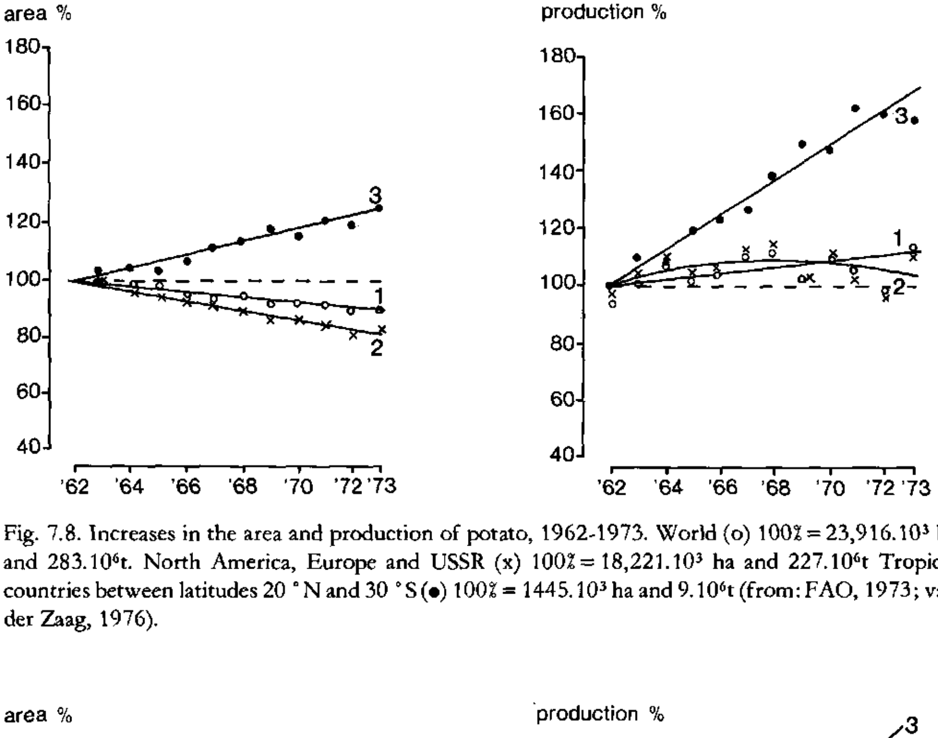

Fig. 7.8. Increases in the area and production of potato, 1962-1973. World (o) 100% = 23,916.10³ ha and 283.10⁶t. North America, Europe and USSR (x) 100% = 18,221.10³ ha and 227.10⁶t Tropical countries between latitudes 20 °N and 30 °S (●) 100% = 1445.10³ ha and 9.10⁶t (from: FAO, 1973; van der Zaag, 1976).

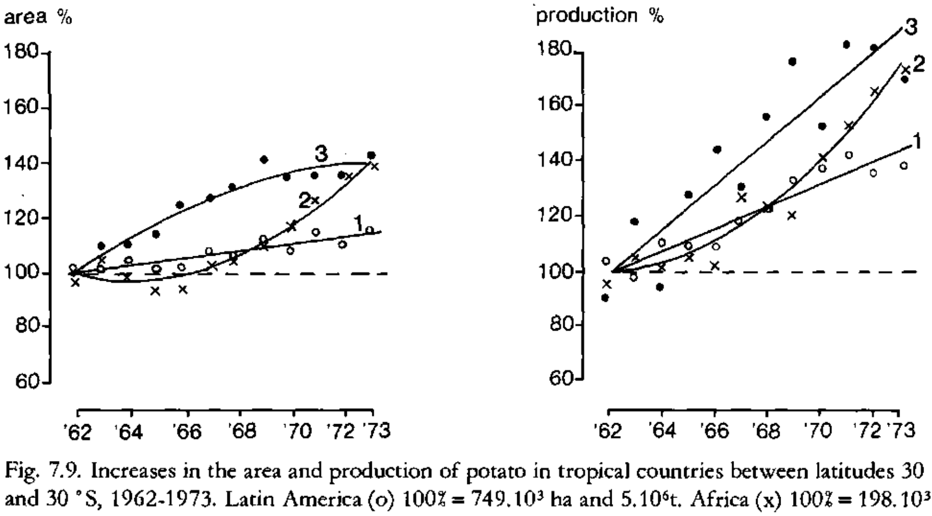

Fig. 7.9. Increases in the area and production of potato in tropical countries between latitudes 30 °N and 30 °S, 1962-1973. Latin America (o) 100% = 749.10³ ha and 5.10⁶t. Africa (x) 100% = 198.10³ ha and 1.10⁶t. Asia (●) 100% = 489.10³ ha and 4.10⁶t (from: van der Zaag, 1976)

work has aimed at resistance to various kinds of diseases, the clones produced being tested in tropical countries. Attempts to select clones suitable for the tropical lowlands and also for the cold conditions (light frosts) of the tropical highlands are in progress. It is arguable, however, that the time and effort expended in breeding potatoes for the hot and humid tropical lowlands might be better used in the selection of new varieties and improvement of the cultivation of root crops such as cassava, sweet potatoes and yams, which are better suited to growing under these extreme climatic conditions.

SEED SUPPLY

By using only reasonably healthy seed tubers in the developing countries, yield can be increased considerably. If sufficient material is to be available for propagation, it will be necessary to import a certain quantity of certified or basic seed from western Europe. The production of certified seed potatoes is a long, complicated and expensive procedure (cf. Chapter 9, p. 375). In order to save foreign currency it will be desirable to multiply this material once or perhaps twice, in isolated areas which as far as possible are free from aphids.

In this respect, van der Zaag (1977) has made the following calculations. The total area under potatoes in all developing countries is about 2,500,000 ha. The total quantity of seed imported annually by these countries can be estimated at about 250,000 t. Following a single multiplication of this seed (with a multiplication factor of 1-7), about 1,750,000 t seed would be available. By using an average of 1.5 t per hectare, it would be possible to plant roughly 1,200,000 ha, i.e. about the half of the area. This alone could double the yields. Some developing countries have started their own seed potato programmes with the assistance of foreign agriculturists or of experts trained abroad. Needless to say, the production of local seed is desirable in a country with two harvests per calender year, where the most important planting time is during the period when no seed potatoes are available in countries with a temperate climate.

VARIETAL RESEARCH

The choice of the right variety for the area in which it is to be grown is of decisive importance. Hence it is of some consequence that on the one hand breeders working in temperate countries should send their clones to their potential customers at early stages of selection and that on the other hand the recipient countries should have a reliable trial system. A reliable system for detecting valuable clones and varieties can also be the starting point for a simple breeding programme where the climate is suitable.

STORAGE

The increasing acreage and production in the tropics and subtropics necessitate good storage facilities. The following aspects are important:

- Storage of ware potatoes between harvests, in order to spread the supply regularly over the whole year and to avoid price fluctuations. At present much of the harvest is likely to come on to the market all at once, leading to considerable losses through wastage.
- Storage of a part of the crop for new planting when for financial or climatic reasons total seed potato requirements cannot be met by imports.
- Temporary storage of local seed and/or imported seed, allowing proper timing of distribution to the growing areas.

The Institute for Research on Storage and Processing of Agricultural Produce (IBVL) at Wageningen provides advice in a number of countries on the correct storage of potatoes (e.g. the construction of potato stores); similar advice is provided under the Dutch aid projects for the development of cooperation in agriculture.

Mechanization and diversification of labour use

If real income is to be improved, labour must gradually be withdrawn from the routine operations of farming and diverted to the wide variety of occupations basic to scientific agriculture. The process of modernization of agriculture opens up a whole series of new job opportunities, for example in the production and marketing of seeds, fertilizers, pesticides, machinery, pumps and other equipment related to water use, processing and storage equipment and other inputs. Various agro-based industries can also be promoted. Transport and sale of agricultural produce and banking and business activity provide considerable opportunities for additional employment. Thus, modernization of agriculture does not merely mean the replacement of human labour by machines but implies removal of human drudgery, improvement of the human energy input-output ratio and above all, diversification of labour use.

In the USA over 50% of the population is engaged in industrial, commercial and other activities related to agriculture, although only about 5% of the population is engaged in the physical operations of farming. In Japan, a country with small holdings, it formerly took about 1600 to 2000 man hours to produce 4 t of rice on one hectare of land. It now takes only 750 man hours to produce 4.7 t on the same area. This is due to the mechanization of farm operations, starting with transplanting and ending in harvesting. On a per ton basis, where it previously took 400 to 500 man hours it now takes only 160 man hours to produce a given quantity of grain. The per man productivity has thus increased by 300%. At the same time, new avenues of employment in the production of power tillers, transplanting equipment, fertilizer drills, sprayers and reapers have been opened up.

The same process of mechanization occurred in South Korea, with the result that the average yield of rice has risen in that country to about 5 t per hectare. In addition, because of the time saved, rice farmers have been able to take up supplementary activities like poultry keeping, dairying or silk worm rearing. If methods of supplementing income are not provided, the old saying 'paddy and poverty go together' will continue to remain valid.

In India, the highest degree of mechanization is found in the Punjab, where multiple cropping and mixed farming are widely prevalent. In other areas, where problems of unemployment and underemployment are serious, mechanization has to proceed in such a manner that employment-generation programmes suffer no setback. In other words, what is needed is a relevant mechanization programme which will:

- reduce human drudgery and facilitate the correct timing of farm operations,
- increase crop and human productivity,
- facilitate maximum returns from the available sunlight, water and land resources,
- promote diversification of labour and organization of subsidiary and agro-based industries.

Organization of plant breeding research

BREEDING

Poor experimental station facilities and inadequate access to genetic variability have been the breeder's major handicaps in many developing countries. Progress in yield improvement has, therefore, been rather slow. Also, selection work in the past was often aimed at suitability for low soil fertility conditions, so that varieties tended to be selected for performance under adverse conditions rather than for the ability to give good yields under good conditions of management. The Indica-Japonica hybridization programme in rice, started in 1952 at the instance of FAO, was the first serious attempt to develop varieties for response to fertilizer application. Today both additional genetic variability and improved conditions for screening and selection are available to breeders in many developing countries. Emphasis in selection has shifted from the performance of individual plants in segregating generations to the performance of populations. Also, cooperation between plant pathologists, agronomists and plant breeders is increasing.

TESTING VARIETIES

Once a suitable selection has been made, it will be necessary to have its performance assessed by means of a statistically designed multilocation testing procedure. In India this is achieved through the All-India Coordinated Research Projects, which serve as national networks of cooperative experiments involving scientists working in different research institutions. The All-India Coordinated Research Project for every major crop is structured in the following manner:

- The country is divided into appropriate agroclimatic zones with particular reference to the maturity characteristics necessary.
- In each agroclimatic zone, a major centre is established, along with supporting testing centres.
- Coordinated trials are laid out both in the main and testing centres. Such trials may include special testing programmes for specific resistance characters, such as brown planthopper and gall midge resistance in rice, leaf rust resistance in wheat etc.
- Data from all these trials are collected and analysed statistically and presented at an annual workshop which is attended by all the workers concerned.
- The workshop considers all the available data and recommends varieties (i.e. prerelease varieties) for field testing in farmers' fields.
- The varieties recommended for on-farm testing are grown in suitable 'minikit' trials.
- On the basis of the data from the coordinated trials and 'minikit' trials, the most promising strains are recommended either by a State Release Committee or a Central Release Committee, depending upon whether the variety shows specific or wide adaptation.

The precise procedures adopted vary from country to country. In general, all countries have a varietal release procedure which necessitates collating data from multilocation trials. In West Africa, several countries have joined together to form the West African Rice Development Association (WARDA). WARDA arranges coordinated trials more or less on the lines of the All-India Coordinated Crop Research Projects. In China, much of the research is done in farmers' fields. This has been referred to as an 'open door research policy'. The procedure seems to have considerable merit in that the farmer and the breeder work closely together and the farmer also helps in the selection process.

MULTIPLICATION AND DISTRIBUTION

The chain of seed production involving breeder's, foundation and certified seed has not evolved very far in many developing countries. In India there is a National Seeds Corporation organized by the government which funtions as the top coordinating agency for the production and distribution of quality seed. The National Seeds Corporation is concerned primarily with foundation seed production. Various states of India have their own state seed corporations. In addition, there are some private seed companies. The certification agency is usually the state government. Certified seed is sold to farmers through cooperatives and other organizations engaged in input supply. The Central Seed Committee has to approve all varieties. Unless a variety is approved, it cannot be certified. The breeders themselves are assigned the task of supplying the required quantities of breeder's seed. Since India is a large country with varied disease problems in different parts of the country, some system of home quarantine will also be desirable to ensure that seed-borne diseases are not carried from one state to another.

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with the collaboration of
J.A. Hogen Esch on potatoes

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8 Methods for the future

Plant breeding is a technology which has the practical purpose of producing material objects – the variety or cultivar – which offer advantages over preexisting varieties in terms of absolute yield, stability of yield, agronomic convenience or quality of the market produce. The application of the technology exploits knowledge drawn from many scientific disciplines, but since the changes incorporated in a new variety must be determined genetically, genetics is the central science. Genetics must in this sense be interpreted widely to include cytogenetics and genetical aspects of biometry and cell and molecular biology. Much research in genetics relative to plant breeding has the purpose of improving the precision of the methods by which new genotypes can be constructed to fit identified objectives, and it is with the outcome of such research that this chapter is principally concerned.

The concepts discussed have been applied in only the recent past, or they await application or need further research before their feasibility and potential value can be fully assessed. The topics considered illustrate the greater and greater precision of genetic manipulation that is becoming available to the plant breeder. An example of this progression is the advance from changes in the numbers of sets of chromosomes present (in plants with altered ploidy), via changes in the number of individual chromosomes (in aneuploids), to the movement of particular chromosome segments (in induced translocations), until finally we have the prospect of altering individual molecules of DNA by restriction endonuclease technology.

The increasing importance to plant breeding of cell biology is illustrated by the advances made in the technology of cell and tissue culture. These procedures are making it possible to produce haploid sporophytes by anther culture, rapidly to multiply valuable new genotypes by micropropagation and, potentially, to produce hybrid genotypes, beyond the bounds possible by sexual hybridization, by means of protoplast fusion and regeneration.

Of particular interest is the way in which new developments in more than one technology will be necessary in the future before practical results can be expected. Thus the methodology for the isolation of protoplasts and their regeneration into complete plants must be mastered in the more recalcitrant crop groups, such as the legumes and cereals, before transformation by DNA insertion can be exploited in such crops.

The contribution on symbiotic nitrogen fixation in this chapter concentrates on the systems that already exist in nature in the legume- Rhizobium *relationship. The possibility cannot be ignored of incorporating, in the cells of nonleguminous crops, alien DNA carrying the information for nitrogen fixation. However, the problems of making such a modification of nonlegume crops are formidable. Not only is the genetic information specifying nitrogenase production complex but it must also be associated with a means of excluding oxygen from the zone of nitrogenase activity, since nitrogen fixation only occurs in the absence of atmospheric oxygen. In addition, it must be remembered that there is an energy cost to nitrogen fixation. Consequently some of the products of* *photosynthesis that might previously have contributed to the economic yield of the crop might be diverted to driving the nitrogenase activity.*

It may be predicted that, in the future, plant breeders will find it necessary to consider genetic activities of the cell other than those determined by nuclear genes. So far, apart from the use of cytoplasmically inherited male sterility, plant breeding has concentrated almost exclusively on the effects of the nuclear genes. But the mitochondria and the chloroplasts also have genomes, consisting of DNA which encodes information that is vital for the functioning of the organism. One of the first examples of a concern with nonnuclear inheritance was the theory of mitochondrial complementation, which suggested that mixtures of mitochondria from different genotypes might operate with greater efficiency than isolates from either alone. It was thought that this would be indicative of the heterotic benefit provided by hybrids between the two plant genotypes from which the mitochondria were isolated. In practice mitochondrial complementation has proved to be an uncertain phenomenon and not a test that is helpful to those seeking highly heterotic hybrids. Nevertheless, breeding for modifications of the mitochondrial and chloroplast genomes may soon come to occupy more of the attention of plant breeders, since such important characters as disease resistance are now known to be controlled in part by mitochondrial genes.

Finally in this introduction attention must be drawn to the exciting way ahead for plant breeding made possible by recent advances in genetic engineering. Present knowledge of the molecular biology of DNA and particularly of the ways by which alien sequences may be inserted using restriction endonuclease technology open up the prospect of precisely tailoring the plant genome to meet the breeder's objectives. There can be little doubt that the next one or two decades will see the application to plant breeding of highly sophisticated molecular biological procedures that will transform the precision of genetic manipulation.

Chromosome manipulation and plant breeding

INTRODUCTION

In most plant breeding programmes, the synthesis of new and improved genotypes relies upon the processes of recombination and segregation that occur in the progenies of heterozygous individuals within a crop. Alternatively, where attempts are made to modify a single genetic locus, or a single plant character, the breeder may resort to induced mutation. In both of these situations the entities being manipulated by the breeder are single genes that are potentially, within the limitations of linkage, capable of independent segregation from other genes.

Occasionally there is advantage in manipulating not single genes but large arrays of associated genes. Such arrays may consist of all of the genes in a set of chromosomes, or on a single chromosome, or on a substantial segment of chromosome. Where these procedures are followed, plant breeders are applying the techniques of cytogenetics, which is the name of the discipline in which the procedures of genetics are used to study the nucleus and chromosomes and the techniques of cytology (or cell science) are used to study inheritance.

MANIPULATING SETS OF CHROMOSOMES

The experimental manipulation of entire sets of chromosomes may be of three kinds:

– The reduction from the normal chromosome number ($2n$) to the haploid number (n), as described elsewhere in this chapter ('Haploids, origin and potentials').

– The increase, within a species, from the normal diploid number ($2n$) to a higher multiple, such as triploid ($3n$) or tetraploid ($4n$) or analogous changes when the initial number is polyploid. Reference has been made to the use of autotriploid varieties of sugar beet (Chapter 4, p. 203) and to the use of autotetraploid Italian ryegrass and red clover (Chapter 4, p. 183).

– The combination in a synthetic allopolyploid, or amphiploid, of the full complements of chromosomes of two distinct species.

The production in breeding programmes of synthetic amphiploids reiterates in principle the course of evolution of some crops. For example, the 42 chromosomes of bread wheat (*Triticum aestivum*) were assembled, by natural hybridization of wild grasses with 14 chromosomes and the doubling of the chromosome number of the hybrids. The capacity to exploit synthetic amphiploids in breeding depends upon the ability artificially to hybridize the species concerned, to cultivate the resulting hybrids and to induce aberrations of cell divisions that cause the chromosome number to be doubled. The characteristic feature of interspecific hybrids is that, because of distinctions between the chromosomes of the parental species, there is no regular chromosome pairing at meiosis, so that the hybrid fails to produce genetically balanced gametes and is therefore sterile. By contrast, following doubling of the chromosome number, each chromosome is represented twice and so has a partner with which it pairs at meiosis. Consequently genetically balanced gametes are produced and the amphiploid is fertile.

Triticale is probably the best-known synthetic amphiploid crop. It has been subject to intensive breeding research and varieties have been released in Canada, Hungary and Mexico. The forms of triticale most likely to be used in agriculture have 42 chromosomes comprising the set of 28 from *Triticum turgidum* – the rivet and durum wheats – and the set of 14 from rye, *Secale cereale*. The advantage of triticale over its parental species resides principally in the high spikelet number per spike, derived from rye, and the larger number of fertile florets per spikelet and the greater grain size, derived from wheat. Other hoped-for benefits are the combination of resistances to disease, derived from each parent, and the higher grain lysine content from rye. However, at present difficulties are created by some chromosomal instability, inadequately developed grain endosperm, premature sprouting of the grain, low frequency of tillering and yield levels which rarely equal those of bread wheat.

Detailed descriptions of our scientific knowledge of triticale will be found in MacIntyre & Campbell (1974).

Two other examples of the use of synthetic amphiploids in agriculture or in variety production are the so-called 'hybrid ryegrass' and synthetic *Brassica napus* (oilseed rape). Hybrid ryegrass is a tetraploid combining the chromosome sets of perennial ryegrass (*Lolium perenne*) and Italian ryegrass (*L. italicum*). Hybrid ryegrass has the rapid early growth and high nutritive value of Italian ryegrass and the persistency of perennial ryegrass and greater genetic stability than is found in the interspecific hybrid at the diploid level (Breese et al., 1975). *B. napus* ($2n = 38$) is the natural allotetraploid derived from *B. campestris* ($2n = 20$) and *B. oleracea* ($2n = 18$). By resynthesizing *B. napus* from its parents and hybridizing the natural and synthetic tetraploid it has been possible to introduce useful genetic variation from the diploid species into the tetraploid (Olsson, 1963).

ANEUPLOIDS

The manipulation of intact single chromosomes in plant breeding and in relevant research makes use of plants that have chromosome numbers different from those that are normal in the species. Such plants are called *aneuploid* because they do not have the good, or *euploid*, number. The following are the designations given to the range of aneuploids most commonly used in plant breeding where the euploid is designated $2n$:

Nullisomic – $2n-2$ lacks both chromosomes of one homologous pair
Monosomic – $2n-1$ lacks one chromosome
Trisomic – $2n+1$ has one chromosome present three times
Tetrasomic – $2n+2$ has one chromosome present four times

Thus in bread wheat, in which the euploid is $2n = 42$, nullisomics are $2n - 2 = 40$, monosomics are $2n - 1 = 41$, trisomics are $2n + 1 = 43$, and tetrasomics are $2n + 2 = 44$.

Fully effective work depends upon the availability of a complete set of a particular type of aneuploid. That is where stocks or lines have been constructed and identified, with each chromosome, in turn, present in a particular aneuploid condition.

Complete sets of monosomics are available in the following crop species:

	(*Triticum aestivum*)	$2n = 42$, with 21 monosomic lines
Oats	(*Avena sativa*)	$2n = 42$, with 21 monosomic lines
Tobacco	(*Nicotiana tabacum*)	$2n = 48$, with 24 monosomic lines

Complete sets of trisomics are available in the following crop species:

	(*Triticum aestivum*)	$2n = 42$, with 21 trisomic lines
Oats	(*Avena sativa*)	$2n = 42$, with 21 trisomic lines
Tomato	(*Lycopersicon esculentum*)	$2n = 24$, with 12 trisomic lines
Spinach	(*Spinacia oleracea*)	$2n = 12$, with 6 trisomic lines
Chilli	(*Capsicum annuum*)	$2n = 24$, with 12 trisomic lines
Rye	(*Secale cereale*)	$2n = 14$, with 7 trisomic lines
Rice	(*Oryza sativa*)	$2n = 24$, with 12 trisomic lines
Sorghum	(*Sorghum vulgare*)	$2n = 20$, with 10 trisomic lines

Access to an extensive list of references to plant aneuploids is provided in Khush (1973).

USE OF ANEUPLOIDS IN GENETIC STUDIES

Both trisomics and monosomics have been used to provide information on the chromosomal location of genes of significance in varietal synthesis. Such information is of importance in enabling breeders to dermine the likelihood of synthesizing genotypes with desired combinations of beneficial alleles.

The determination of which chromosome in the complement carries a particular genetic locus depends upon the distorted segregation that occurs for allelic differences when the chromosome with the relevant locus is in either the monosomic or the trisomic condition.

When a chromosome is in the monosomic condition it is not transmitted from meiosis to 50% of the gametes and therefore the genes that it carries do not segregate according to the ratios expected of chromosomes in the disomic condition. In practice, therefore, if the chromosomal location is sought of a dominant allele in a euploid genotype, this genotype is hybridized with the set of lines monosomic, in turn, for every chromosome of the complement and carrying a recessive allele at the same locus. The F_2 generation will segregate with the expected 3 dominant : 1 recessive phenotype from monosomic hybrids derived from all of the monosomic parental lines except for that which was monosomic for the chromosome carrying the dominant allele. In such hybrids the dominant allele will be in the hemizygous condition in the F_1 generation, so the recessive phenotype will not be displayed in the F_2 generation except perhaps in the rare nullisomic progeny.

Alternatively, if the chromosome location of a recessive allele is sought in an unknown genotype, a set of monosomic F_1 hybrids is again created by hybridization with the parental lines carrying the dominant allele and monosomic, in turn, for every chromosome of the complement. The recessive phenotype will be displayed by the F_1 monosomic for the chromosome carrying the recessive allele while the remainder of the monosomic F_1s will display the dominant phenotype.

More complex analyses are required where two or more loci are involved in the determination of a character. Nevertheless the procedures are relatively straightforward and valuable guidance to breeders has arisen from genetic analyses based on monosomics. Detailed descriptions of the procedures of aneuploid analysis are given by Sears (1953) and Khush (1973).

Trisomics have been widely used to ascertain the chromosomal location of genes in the provision of information for breeders on the genetic structure of crop species. The methodology is analogous to that involved when monosomic hybrids are used, except that trisomic hybrids are produced. Where the locus under study is on the trisomic chromosome there is distortion from the usual disomic segregation in the back-cross or F_2 generation (for references see Khush, 1973).

Further refinement of gene location has been developed by making use of telocentric chromosomes, which are misdivision products from which one arm has been deleted. They arise, often in monosomics, by aberrant division at meiosis of unpaired chromosomes. The extent of the disassociation in segregation of a particular allele from the telocentric or the complete homologous chromosome permits the estimation of linkage between the relevant locus and the centromere (Sears, 1962).

INTERVARIETAL CHROMOSOME SUBSTITUTION

A technique which makes use of aneuploids has been elaborated very effectively in bread wheat, initially for breeding research and now for application to variety production. Known as intervarietal chromosome substitution, the technique results in the transfer of a single unchanged pair of chromosomes of a donor variety into a recipient variety where it replaces the homologous pair. This is achieved by using monosomic lines of the recipient variety as the recurrent seed parent so that the chromosome to be replaced is absent from most egg cells. When this recurrent monosomic parent is pollinated by the donor parental variety, or by one of the monosomic back-cross progeny, a euhaploid pollen grain will usually achieve fertilization. Therefore, the resulting monosomic offspring will have the donor monosomic chromosome but will lack the recipient homologue while the background chromosomes will, according to the stage of the back-crossing programme, increasingly revert to the gene content of the recipient variety. Following the completion of back crossing, the final monosomic derivative is allowed to self pollinate and this leads to the segregation of a small proportion of euploid progeny in which the substituted donor chromosome is in the disomic condition while the background chromosomes will have reverted largely to their genetic status in the recipient variety. This procedure is being used by C.N. Law and his colleagues at the Plant Breeding Institute, Cambridge, UK, to introduce, into developing varieties, chromosome 5B^s/7B^s from the variety Bersée (Johnson, 1976). This chromosome carries several genes that apparently determine durable resistance in mature plants to stripe (yellow) rust – *Puccinia striiformis.* The use of intervarietal chromosome substitution ensures that the several genes determining rust resistance will be held together in new varieties.

An additional procedure that can be employed in the refinement of established intervarietal substitution lines permits recombination to occur in the substituted chromosome. The disomic substitution line is hybridized with the recipient variety. The resulting hybrids are heterozygous only in the substituted chromosome whereas all the other, background, chromosomes are homozygous. Among the derivatives of such hybrids selection can be practised for recombination in the substituted chromosome and thus, in breeding work, its precise gene content can be adjusted (Law & Worland, 1973).

ALIEN GENETIC VARIATIONS

In some breeding programmes desirable genetic variation for particular characters is not available within the crop species concerned. It is then necessary to seek it by induced mutation or by genes from other species. Sometimes alien genes can be incorporated from species so closely related to the crop species that in hybrids between them chromosomes derived from each parent will pair together at meiosis and recombine. Where such hybrids are fertile the incorporation of alien genes in the crop presents no more difficulty than the transfer of genes intraspecifically from one variety to another. There are many examples of the successful use of genetic variation from other species by this means but only two will be mentioned, namely the introduction of late blight resistance into the potato (*Solanum tuberosum* ($2n = 48$)) from *S. demissum* ($2n = 72$) (Howard, 1970) and the introduction of stem rust resistance into wheat (*Triticum aestivum* ($2n = 42$)) from *T. timopheevi* ($2n = 28$) (Allard, 1949).

Breeding procedures of greater complexity are needed when, in interspecific hybrids, there is little or no meiotic pairing and recombination between chromosomes derived from the two parents. Such hybrids may give rise to genetically stable and sexually fertile synthetic amphiploids following the doubling of the chromosome number and reference has been made to the opportunities for using these earlier. However, there are often disadvantages in attempting to combine the total genetic structures of two species and greater advantage in attempting to incorporate in the recipient crop species some limited, perhaps single, genetic attribute of a donor species.

There has been a progressive evolution of the cytogenetic methodology aimed at achieving this objective and more work in this field has concentrated on wheat, and its relatives, than on any other crop group. In this discussion, therefore, the principles will be discussed using wheat as a model.

The first step in the limitation of the amount of genetic material transferred to wheat from a related alien source involves the construction of so-called 'alien chromosome addition lines'. In these a single pair of chromosomes from another species is added to the full complement of wheat chromosomes. Plant material of this kind has been most extensively studied in the wheat-rye combination (Riley & Chapman, 1958). Initially the wheat-rye amphiploid (triticale) is constructed and then back crossed to the wheat species parent. The back-crossing programme is continued, using wheat as the recurrent parent, and during the process the rye chromosome content of the derivatives is diluted until only one rye chromosome remains, while the full complement of wheat chromosomes is retained. Such monosomic addition plants are then allowed to self pollinate and among the resulting progeny those plants are selected which have the alien chromosome in the disomic condition. In these, since the alien chromosome is paired, meiosis is regular and the addition condition true breeding and stable.

Of course, from any combination of species, as many distinct addition lines can be created as there are chromosomes in the haploid complement of the donor species. In the case of lines with the addition of *Secale*, *Aegilops* or *Agropyron* chromosomes to wheat, the addition lines differ phenotypically from the recipient wheat varieties. However, while some beneficial changes of phenotype occur there are also usually disadvantageous modifications, particularly reduced yield. As a result, as yet, no alien chromosome addition line has been used as a commercial variety.

The next step, after the introduction of alien genetic variation by the addition of single chromosome pairs, involves the replacement of a pair of chromosomes of the recipient species by an alien pair. This can be achieved in wheat because its polyploid status permits marked deviations into aneuploidy. Derivatives of the procedure are called 'disomic chromosome substitution lines'. They are achieved by hybridizing wheat monosomics with disomic addition lines to produce plants in which a wheat chromosome and the alien chromosome are simultaneously monosomic. The complete replacement of the wheat monosomic may be attained in the next generation either by selfing the doubly monosomic plants or two generations later following the hybridization of the doubly monosomic individuals with the disomic addition line.

Disomic substitution lines frequently display attributes of the phenotype conditioned by genes on the alien chromosome. They are moreover frequently more fertile and more stable from generation to generation than disomic addition lines. It is consequently not suprising that wheat varietes have been employed commercially which carry an alien chromosome pair substituting for a wheat pair. The rye-chromosome substitution varieties of wheat that have been used most widely all have the 1R pair of rye replacing the 1B pair of wheat. Varieties with this constitution, which it should be said arose fortuitously from hybridization programmes using rye or triticale as a parent, include Orlando, Zorba, Weique, Neuzucht, Riebesel 47/51 (Zeller, 1973) and Clement.

It is important to emphasize that alien chromosomes can only be substituted for recipient chromosomes to which they are related genetically. Thus the substituted and substituting chromosomes will probably have evolved from the same chromosome of the common ancestor of the donor and recipient species. Much of their gene content may therefore be similar in activity, linkage order and dispersion among noninformational nucleotide sequences.

Despite the success of disomic substitution lines, in general, the amount of alien genetic material introduced into such genotypes is too extensive for the retention of the genotypic balance of the organism. This probably arises because, despite their similarity, there has been no adjustment, by selection, of the gene contents to permit efficient interactions between the alien chromosome and the chromosomes of the recipient species. This leads to the conclusion that the introduced alien chromosomal material should be limited, as far as possible, to only that restricted segment necessary to incorporate in the recipient the single desired phenotypic modification from the donor. E.R. Sears of the University of Missouri, USA, had the earliest and clearest insight into this problem and sought to solve it by the use of induced translocation (Sears, 1956). The procedure was to expose to X rays wheat plants carrying the monosomic addition of an alien chromosome causing a qualitative beneficial modification of the phenotype. Subsequently selection was practised for euploid plants displaying the beneficial phenotypic modification. These proved to carry chromosome translocations (interchanges) in which a segment of the alien chromosome, carrying the useful gene, had been incorporated in a wheat chromosome. Selection was then practised, in the progeny, to obtain the translocation chromosome in the homozygous condition. The resulting plants had minimal disturbance of the phenotype while displaying the beneficial alien attribute, which was a form of disease resistance. The translocation homozygotes could then be used as parents to permit the transfer of this resistance into commercial varieties.

Several other workers have subsequently applied the principles established by Sears and valuable forms of alien desease resistance have been introduced into commercial wheat as a result (see Sears, 1972). As with whole chromosome substitution the success of the Sears method depends upon the alien chromosome segment replacing a genetically similar segment. However, the likelihood of this occuring is low since induced translocation, while probably not entirely at random, is not precise as to the homology of the break points in the participating chromosome, even when the chromosomes exchanging segments are homoeologous.

ALIEN INTRODUCTION AND INDUCED RECOMBINATION

The theme followed in these descriptions of the methodology of introducing alien variation into crops has been the need to minimize the size of the introduced alien chromosome segment. The range of manoeuvres used has been imposed by the lack of meiotic chromosome pairing and recombination between the chromosomes of the crop species and those of the other species from which a potentially useful gene was sought. That is to say there is a meiotic barrier.

In the wheat group, genetic means have been developed by the use of which it is possible to surmount the meiotic barrier. The procedure depends upon the finding that a single gene, at the *Ph* locus on chromosome 5B, acts to prevent genetically related chromosomes, that are not fully homologous, from pairing together at meiosis. The effect of this activity, in polyploid wheat, is to restrict pairing to fully homologous partners, to the exclusion of genetically related homoeologues derived from different parental ancestor species (for references see Riley, 1974).

Removal of the *Ph* allele, or genetic suppression of its activity, causes wheat chromosomes to pair in hybrids with homoeologous chromosomes derived from other species. Recombination also takes place so that segments of wheat chromosomes can be replaced by genetically corresponding segments of alien chromosomes. This system is only just coming into use in the mid–1970s but the initial indications are favourable in that there is minimal disturbance of the genetic balance of wheat (Riley et al., 1968; Sears, 1972). This may compensate to some degree for failure to diminish, as fully as might be desirable in some examples, the size of the alien chromosome segment incorporated.

CONCLUSIONS

Manipulation of the chromosome composition of certain crop plants can be achieved in ways that permit a more precise specification of the genotype than is possible by conventional breeding methods. Consequently it may be anticipated that such methods will increasingly be employed, especially with polyploid crop species. They have already been of practical value in the transfer of alien disease resistance into crops. However, the introduction of alien variation is most likely to be successful when there is the least possible disturbance of the genotype of the recipient species. The final outcome of the advancing methodology of alien gene transfer may lie in the development of the means of transforming plant cells by the introduction of specific DNA molecules by techniques often referred to as 'genetic engineering'.

Haploids, origin and potentials

INTRODUCTION

The smallest number of chromosomes differing in structure and gene content in an organism forms one functional entity and is called a genome. This basic chromosome number, which is symbolized by x, is characteristic of each species and in economically important crops is generally in the range of 5-20. Autoploids contain one or more copies of one basic genome (Fig. 8.1, above). Alloploids derive from two or more diploid species and therefore contain two or more different basic genomes (Fig. 8.1, below). The number of chromosomes in somatic or diplophase cells is indicated by $2n$, because they originate from the fusion of n chromosomes from the male parent with n from the female, n being the number of chromosomes in gametes or haplophase cells.

Haploids are autonomous sporophytic plants which, owing to their origin from a gametic cell in the embryo sac or in the pollen grain, have the gametophytic chromosome number. The haploid embryo arises either from the egg cell (gynogenesis) or from a gametophyte cell other than the egg cell (apogamy), or else from a male gamete (androgenesis). When it originates from the pollen grain, it usually does so from the vegetative cell, and only in anther or pollen culture *in vitro.*

Parallel to the distinction between autoploid and alloploid crops (Fig. 8.1), haploids can be subdivided into autohaploids and allohaploids, as indicated in Table 8.1.

On the basis of breeding behaviour the following categories may be distinguished.

1 Functional monoploids. These include all haploids from diploid and alloploid crops. They are characterized by having only unpaired chromosomes (no homologous pairing) and hence by exhibiting complete sterility. On spontaneous or induced doubling of the chromosome number, this sterility is generally converted into complete fertility and the plants become completely homozygous.

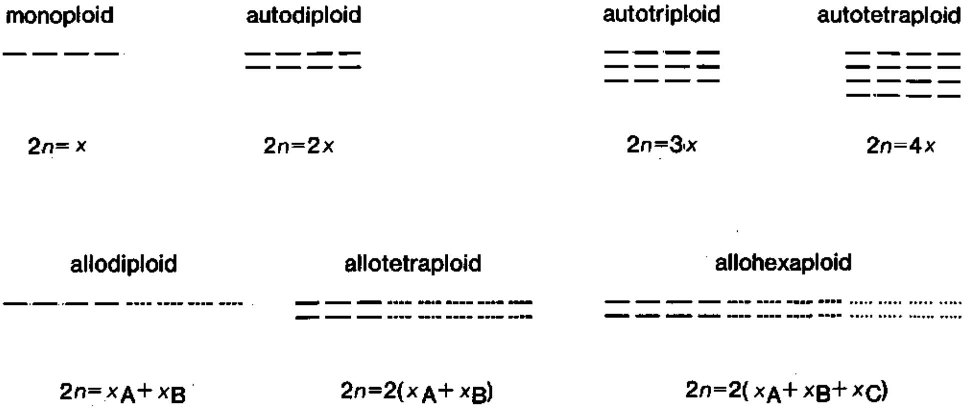

Fig. 8.1. Schematic representation of the genomic structure of some autoploids and alloploids, with their genome formulas. The letters A, B and C indicate the genomes of the different diploid species which constitute the alloploids.

Table 8.1. Types of drops and derived haploids in relation to genome composition

Crops	Genome formula	Derived haploids	Genome formula
monoploids[1]	$2n=x$	none	
autodiploids[2]	$2n=2x$	monohaploids	$2n=x$
autotriploids[3]	$2n=3x$	different, mostly aneuploid	
autotetraploids[4]	$2n=4x$	autodihaploids	$2n=2x$
autohexaploids[5]	$2n=6x$	autotrihaploids	$2n=3x$
allodiploids[6]	$2n=x_A+x_B$	monohaploids	$2n=$ either x_A or x_B
allotetraploids[7]	$2n=2(x_A+x_B)$	allodihaploids	$2n=x_A+x_B$
allohexaploids[8]	$2n=2(x_A+x_B+x_C)$	allotrihaploids	$2n=x_A+x_B+x_C$

1. Natural monoploid cultivars include cv. Kleiner Liebling of *Pelargonium zonale* and a clone of *Thuja plicata* f. *gracilis*, both propagated vegetatively for many years before the discovery of their monoploidy.
2. Many crops.
3. *Musa acuminata* (seedless banana), *Citrullus vulgaris* (seedless water melon), *Beta vulgaris* (triploid varieties), maintained either vegetatively or by tetraploid-diploid matings.
4. *Solanum tuberosum* (potato), *Medicago sativa* (lucerne), *Dactylis glomerata* (cocksfoot).
5. *Phleum pratense* (timothy).
6. *Solanum ajanhuiri* (a diploid potato).
7. *Gossypium hirsutum* and *G. barbadense* (cotton), *Nicotiana tabacum* (tobacco), *Arachis hypogaea* (groundnut), *Triticum durum* (macaroni wheat), *Brassica napus* (rapeseed).
8. *Triticum aestivum* (bread wheat), *Avena sativa* (oats).

2 Functional diploids. These include autodiploids, autodihaploids, all pure alloploids (except allodiploids) and all colchicine-doubled monoploids mentioned under 1. This category as a rule shows normal meiosis and fertility and simple disomic inheritance. Autodihaploids are largely male-sterile and in addition retain a relatively high degree of heterozygosity owing to their origin from heterozygous autotetraploid crops.

3 Functional polyploids. These include autopolyploid crops ($2n = px$, where p 2) and induced autopolyploids. This category of plants shows complicated polysomic inheritance of characters, and triploids, pentaploids etc. (where p is odd) are largely sterile.

HAPLOIDS IN NATURE

Haploids of higher plants arise through abnormal processes and are therefore rare in nature. Nevertheless spontaneous haploids occur in many plant families. They arise via gynogenesis, androgenesis or apogamy and are often associated with polyembryony. Their frequency is extremely low: approximately 1 ‰ parthenogenetic and 0.1 ‰ androgenetic haploids.

Polyembryonic seeds may contain 0-2 haploid embryos. The natural frequency of polyembryonic seeds has been studied in about 50 plant species (for review see Lacadena, 1974) and amounts to 0.01-0.20 %. In view of these low frequencies, the collection of haploids from such material in sufficiently large numbers for practical application would be extremely laborious and it would be difficult to avoid genetic drift in outbreeders.

INDUCTION OF HAPLOIDS

Methods have been developed to enable the breeder to increase the frequency of haploids, to induce haploid formation in species which have hitherto not produced them and to facilitate the detection of haploids in plant populations. A useful survey of methods of producing haploids is presented in the *Proceedings of the first international symposium on haploids in higher plants* (Kasha, 1974).

In vitro induction

In vitro induction using anthers and microspores, but not ovules, has been and is being applied on a large scale. Success requires use of the correct growth media and knowledge of the optimal microspore stage at the outset of the experiment. Temperature and light are also important, and a cold shock may be effective (Nitsch & Norreel, 1973).

The chances of obtaining haploids are greater where differentiation is induced without intermediate callus formation than where a callus phase intervenes (Fig.

Fig. 8.2. Haploid plantlets obtained *in vitro* from anthers of *Solanum bulbocastanum* (left, with callus) and *S. verrucosum* (right, with roots). (Photographs: E. W. M. van Breukelen).

8.2). In the latter case higher ploidy levels are commonly found. Sunderland (1974) has summarized the results obtained in the decade since 1963 when the first pollen haploids were obtained in *Datura innoxia.* Progress has been rapid and haploids have been produced by means of anther culture in nearly 60 species. However, 90% of these species belong to two plant families only, the Solanaceae and the Gramineae, and it is as yet only in tobacco and *Datura* that the method has become a routine procedure.

In vivo induction

In vivo induction of haploids takes place in the embryo sac, as is true of natural or spontaneous haploids. Research on this type of induction started after World War II. The modes of origin of haploids from an embryo sac vary but in all cases either cross or self pollination is a prerequisite and the haploids then arise following abnormal fertilization processes. The frequency of the haploids is genetically controlled. All mother plants with a high haploid-producing ability will produce a high proportion of egg cells with a genotype favouring parthenogenetic development. Different male parents (or, more correctly, pollinators) may differ considerably in haploid-inducing ability. Other factors which may influence the frequency of haploids (Lacadena, 1974) are chemicals (Illies, 1974), delayed pollination (Chase, 1969) and alien cytoplasms (Tsunewaki et al., 1968).

Before we discuss mechanisms of haploid production *in vivo*, it should be pointed out that several genera are known to produce a certain proportion of so-called $2n$ gametes, which, owing to abnormal meiosis, have the unreduced number of chromosomes (e.g. *Solanum*, *Medicago*, *Primula*, *Raphanus*, *Brassica*, *Trifolium* and *Matricaria*). Such gametes may give rise to 2*n* plants through parthenogenesis or androgenesis. In the following such plants will not be considered further.

Gynogenesis is the production of an embryo (plant) from an unfertilized egg cell. This phenomenon has been studied in detail in *Zea mays* and *Solanum tuberosum* (Fig. 8.3).

In the case of intraspecific or interspecific diploid × diploid crosses, the seeds formed may have either diploid hybrid embryos or monohaploid embryos but all will

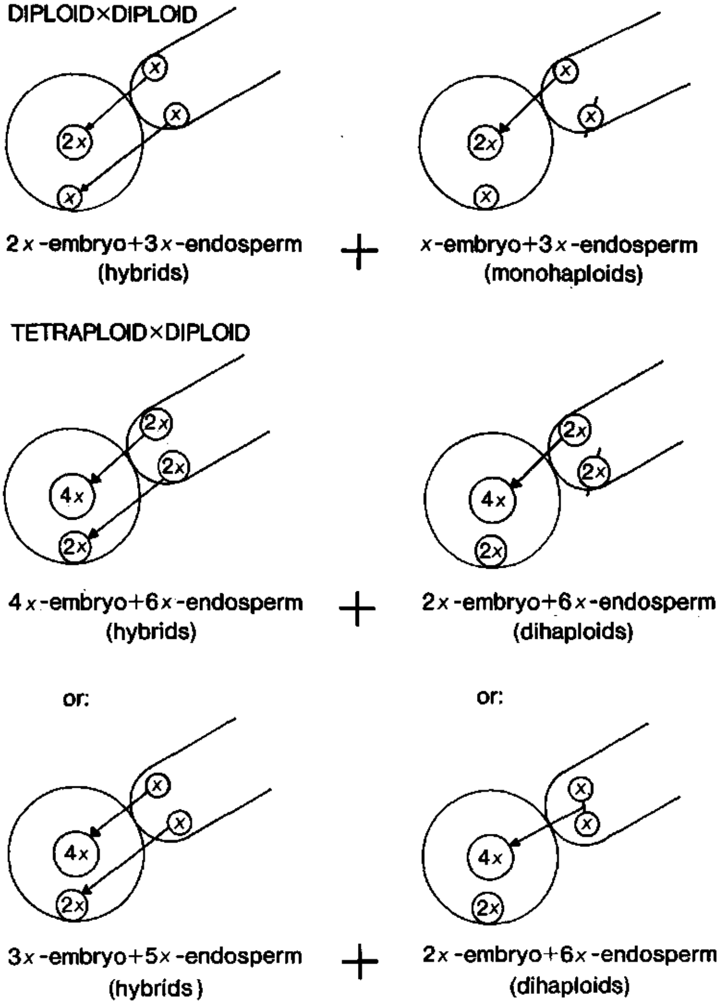

Fig. 8.3. Possible modes of origin of parthenogenetic haploids from diploid × diploid and tetraploid × diploid matings respectively. Arrows indicate fertilization. An oblique line through a nucleus means the loss of that nucleus (above and centre right). A line connecting nuclei (below right) indicates fusion of those nuclei.

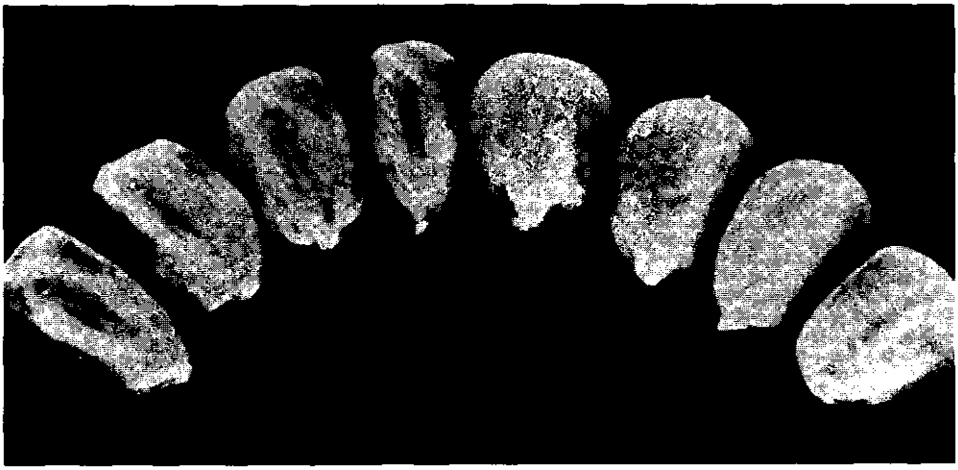

Fig. 8.4. 'Purple embryo marker' in maize. Seeds with stripes contain hybrid embryos, those without contain monohaploid embryos (from: Sarkar, 1974).

have triploid endosperm (Fig. 8.3, above). The average frequency of monohaploids in maize is 0.1%, but this has been increased by selection to 3%. The detection of seeds with monohaploid embryos in seed samples is facilitated by the use of dominant embryo colour markers according to the principle *aa* × *AA* ⟶ hybrids + *a* monohaploids, which can be separated by the presence/absence of embryo colour (Fig. 8.4).

Apart from maize, ***Populus tremula***, ***Beta vulgaris***, ***Brassica oleracea***, diploid ***Solanum*** species and dihaploid ***Solanum tuberosum*** have all yielded monohaploids from diploid × diploid crosses.

In the case of interspecific tetraploid × diploid crosses, the seeds have either hybrid embryos or dihaploid embryos (Fig. 8.3). The hybrids are predominantly tetraploid and originate from $2n$ gametes of the male parent. Triploid hybrid embryos mostly fail to survive owing to the degeneration of the pentaploid endosperm. Seeds with tetraploid hybrid or dihaploid embryos contain viable hexaploid endosperm. The dihaploids may originate in two ways, viz. via $2n$ gametes from the pollen parent (Fig. 8.3, centre) and via normally reduced male gametes (Fig. 8.3, below). In the first case, as in maize, one male nucleus is lost, while the other fertilizes the secondary nucleus of the embryo sac; in the second case, the two male nuclei fuse and together fertilize the secondary nucleus. In both cases the $2x$ egg cells remain unfertilized and, if they carry genes for parthenogenesis, develop parthenogenetically. In ***S. tuberosum*** the frequency of dihaploids may be up to 90% of the plants. Here, too, the frequency is highly dependent on male and female genotypes. As in maize, dihaploids are detected by means of a dominant marker, in this case embryo-spot (Fig. 8.5), which is highly effective and based on two complementary genes (Hermsen & Verdenius, 1973): ***aaaabbbb*** ♀ × *AABB*♂ → *AAaa* ***BBbb*** hybrids + ***aabb*** haploids.

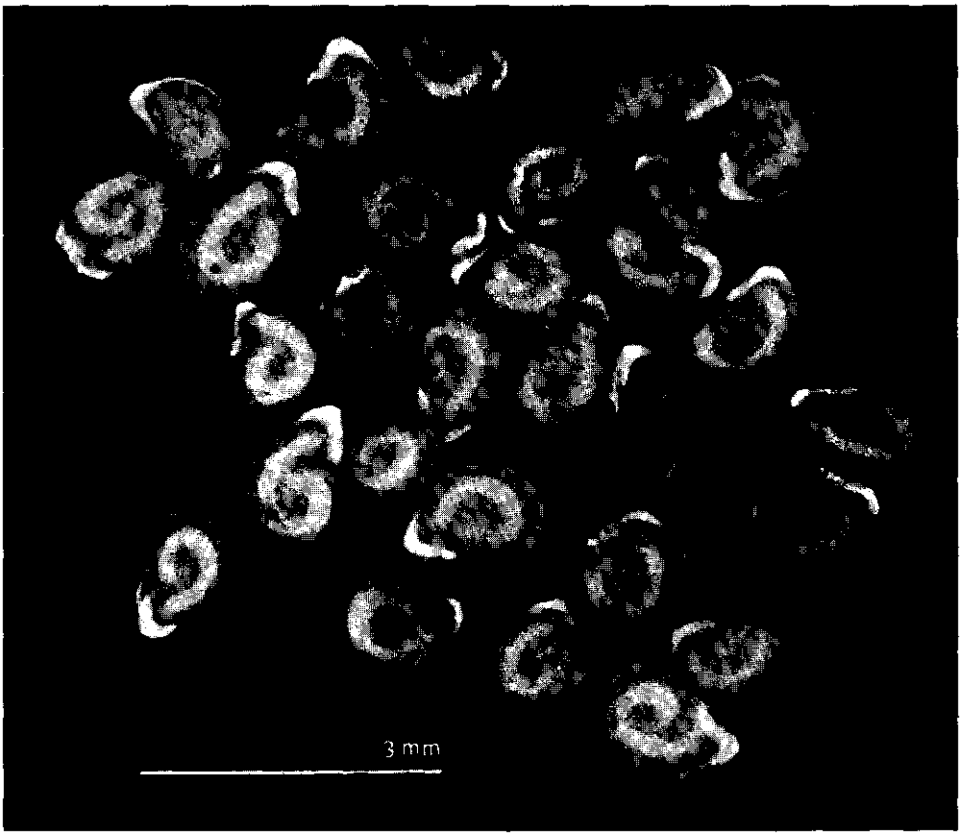

Fig. 8.5. 'Embryo-spot', a dominant marker in *Solanum phureja*. Seeds are from a cross tetraploid cultivar × *S. phureja*. Spotted seeds produce hybrid plants, unspotted seeds dihaploids. (Photograph: IVP.)

In *Medicago sativa* (autotetraploid) the diploid species *M. falcata* is used as pollinator for dihaploid induction (Bingham, 1969). In *Solanum tuberosum*, the pollinator used is the diploid species *S. phureja* (Hougas et al., 1964). In strawberry (octaploid), Janick & Hughes (1974) succeeded in obtaining tetrahaploids by using *Potentilla anserina* as pollinator.

Androgenesis Whereas in recent literature the term androgenesis has been used to denote plants derived from pollen grains, it is used here to designate the situation where, after a male nucleus has entered the egg cell, the egg nucleus is eliminated and the male nucleus develops into a haploid plant containing the chromosome set of the male gamete only together with the cytoplasm of the female parent. Pandey (1973) proposes that the latter type of androgenesis be called 'ovule androgenesis' to distinguish it from 'anther androgenesis', in which there is no participation of the female cytoplasm. The average frequency of (ovule) androgenesis in maize is 0.00125%. The discovery by Kermicle (1969) of a recessive mutant *ig* (indeterminate gametophyte) increased this frequency 2000 times, viz. to 2.3%.

In order to select androgenetic haploids, a marker gene which is dominant in the female and recessive in the male parent is required: *AA* ♀ × *aa* ♂ → *Aa* hybrids + *a* haploids.

Semigamy is an abnormal type of fertilization whereby male and female gametes participate in embryo formation but caryogamy does not occur. In cotton, chimerical haploid plants with sectors of maternal and paternal origin develop from semigamic crosses (Fig. 8.6). Semigamy, which may be described as a combination of gynogenesis and androgenesis, has been found in *Cooperia*, *Zephyranthes*, *Rudbeckia* and *Gossy-*

Fig. 8.6. Part of a semigametic haploid cotton plant from the cross *Gossypium hirsutum* × *G. barbadense*. The dark spots on the left are oil glands, which are superficial only in *G. barbadense* (from: Turcotte & Feaster, 1967).

pium. The phenomenon has been studied extensively in cotton (Turcotte & Feaster, 1967, 1974). Semigamy has a genetic basis and occurs when the egg cell has the appropriate genotype. The frequency may reach 5%.

Selective chromosome elimination Crosses of *Hordeum vulgare* or *Triticum aestivum* with certain wild *Hordeum* species, particularly *Hordeum bulbosum*, result in normal fertilization. Since the endosperm fails to develop beyond initial stages, the provision of nutrition through the use of embryo culture is necessary to prevent starvation and death of the embryos. In the surviving embryos, a gradual elimination of all *H. bulbosum* chromosomes takes place in early developmental stages (Table 8.2). The resulting plants are then haploids of barley and wheat respectively. The elimination of *H. bulbosum* chromosomes is independent of the direction of the cross and occurs at both the diploid and tetraploid levels. There is one exception: diploid *H. vulgare* × tetraploid *H. bulbosum* results in triploid hybrids. In all other cases elimination takes place (Kasha & Kao, 1970; Barclay, 1975). It has been demonstrated that in interspecific *Hordeum* crosses, elimination is genetically controlled by genes on chromosomes 2 and 3 of *H. vulgare*. However, crossability between the species is based on one dominant gene in *H. vulgare* (Pickering & Hayes, 1976). It is estimated that, given good crossability, an average of 10 haploids can be produced by one worker per day.

Table 8.2. Elimination of chromosomes in young embryos of diploid *Hordeum vulgare* × diploid *Hordeum bulbosum* (Subrahmanyam & Kasha, 1973).

Age of embryo (days)	Number of cells per embryo		Number of cells with 7 chromosomes	
	total	with countable chromosomes	absolute	in %
3	37	7	3	42.9
4	75	11	0	0
5	199	27	10	37.0
6	370	50	26	52.0
7	772	99	68	68.7
8	1178	176	160	90.9
9	2306	229	170	77.3
10	4710	241	218	90.5
11	7430	460	431	93.7

POTENTIAL APPLICATIONS OF HAPLOIDS

Monohaploids

As already pointed out, monohaploids are haploids derived from functional diploids. The important point here is that a monohaploid has unpaired chromosomes only, resulting in aneuploid and therefore sterile gametes. For monohaploids to be of direct use, the chromosome number in the somatic cells must be stable and vegetative propagation would have to be possible. Monohaploids are of great value for the study of phylogenetic relationships in alloploid species, for genetic studies (since they give rise to simplified segregation ratios) and for mutation research (since the mutations are directly visible). Their direct use in plant breeding, however, will rarely be possible, though it may be feasible in some ornamentals.

The potential value of monohaploids for breeding is mainly based on the possibility of obtaining completely homozygous, fertile plants by doubling the chromosome number. In some species spontaneous doubling is observed, but in most cases colchicine treatment or tissue culture is necessary. By this means, homozygous diploid lines can be obtained in two seasons, whereas with repeated selfings 5-6 generations are needed. Homozygous lines are not only important in breeding hybrid varieties. The use of doubled monohaploids can also increase the selection efficiency of other breeding procedures, since it allows the quick and accurate testing of lines at any stage of a breeding programme. In principle, testing is possible in a population of homozygous lines derived from gametes of F_1 plants. Ideally, such a population should contain all possible genotypes, and its size would then be dependent on the heterozygosity and genetic diversity of the parents. However, as the production of homozygous lines is generally laborious and hence a limiting factor, it is preferable to postpone the use of the monohaploid method to a later generation, e.g. the F_3, when the heterogeneity and heterozygosity of the population have decreased. In countries where pure-line varieties of self-fertilizing crops are required in order to meet registration and inspection requirements, the monohaploid method would be an excellent tool, once it is possible to produce haploids on a practical scale at a reasonable cost. The use of monohaploids in breeding uniform potato populations to be raised from true seed is discussed elsewhere (Chapter 4, pp. 000).

Androgenetic monohaploids having the genotype of the male parent and the cytoplasm of the female may be used to introduce cytoplasmic male sterility (CMS) quickly into homozygous lines as follows:

CMS line × homozygous diploid
↓
CMS androgenetic monohaploid
↓ colchicine
CMS homozygous diploid line

This method would be particularly useful where a commonly used sterilizing cytoplasm for some reason has to be replaced by another, an example being the Texas cytoplasm in maize which appears to be associated with susceptibility to *Cochliobolus heterostrophus.*

A few groups of crops deserve special attention in connection with the use of monoploids. Strictly dioecious crops like asparagus allow sib fertilization only, an inbreeding procedure three times as slow as selfing. The process of inbreeding is even slower in crops with a long juvenile period, like forest trees, many tropical crops, horticultural trees and shrubs, tulip and lily. The production of homozygous lines in these groups is feasible only by the monohaploid method. Finally, mention should be made of self-incompatible crops, which have a natural barrier against selfing. Enforced selfing is time-consuming and may impose a selection pressure for reduced self incompatibility, which would make the lines less useful, or even useless, as parents of hybrid cultivars. Here the production of monohaploids would not only save time but would also remove the risk of reducing self incompatibility.

Dihaploids

The advantages of dihaploids are a consequence of the genetics and breeding of autotetraploid crops. Tetrasomic inheritance is complicated. The selection and recombination of favourable characters at the tetraploid level is much more laborious and requires larger populations than at the diploid level. Furthermore, the crossability of diploid wild species with dihaploids is far greater than with autotetraploids, and fewer back crosses are needed to improve the agricultural performance of interspecific hybrids. These considerations are particularly relevant to potato breeding, for in this crop dihaploids can be produced at will. In addition, wild diploid *Solanum* species are an invaluable source of genes for resistance to various diseases and pests. As pointed out elsewhere (Chapter 4, p. 155), selected diploid genotypes may be transferred nearly intact to tetraploid progeny via $2n$ gametes in tetraploid × diploid crosses.

Since haploids can be used to expedite and refine the breeding process and to adapt existing breeding methods to crops for which such methods are not otherwise suitable, they unquestionably provide a powerful tool in plant breeding. Their utility has already been demonstrated in a number of crops, while in others the results are promising. Bearing in mind all the available information, it would appear that the promotion of research on haploids is justified.

SOMATIC HYBRIDIZATION AND HAPLOIDS

Somatic hybridization would gain a new dimension, were this technique to be applied to haploids, especially monohaploids. If it were possible for the breeder to fuse the protoplasts of his monohaploids, there would be no need to double the chromosome number or to cross homozygous lines in order to determine combining ability, for the fusion of protoplasts from two monohaploids produces a diploid single-cross hybrid in one step. Furthermore, the breeder would not be dependent on the flowering and fertility of the monohaploids.

Cell cultures from monohaploids are also potentially powerful tools. A single mutant cell among some millions would escape detection in a differentiated organism, but in a cell culture on a selective medium it would become manifest. Perhaps in due course the plant breeder will find that some of the elegant techniques used in microbiology will also prove applicable to cell or protoplast cultures of monohaploids of higher plants.

Breeding for symbiotic nitrogen fixation

INTRODUCTION

There is reason to believe that the more efficient exploitation of symbiotic nitrogen fixation may help to alleviate the world food problem, which in many areas involves a shortage of adequate protein. Although there are other systems capable of fixing nitrogen, legumes are, from the agronomic point of view, the most important proteinaceous crop both for human consumption and animal feed. The ability to fix nitrogen resides in the root nodules, which are formed as the result of a specific symbiotic relationship with a *Rhizobium* species, a small rod-shaped bacterium often present in the soil. These bacteria are presumably initially attracted by the roots, and then undergo rapid multiplication in the rhizosphere. The site of infection is generally the root hair, which is invaded by way of an infection thread. The plant responds by increased cell division in the infected region, giving rise to the characteristic nodular structure. The bacteria are released from the infection thread into plant cells having a double chromosome number. Inside the nodule, the bacteria are transformed into bacteroids, these being large, often branched cells, containing the nitrogen-fixing enzyme nitrogenase. At the same time, a red pigment is synthesized, leghaemoglobin, which is important in the transfer of oxygen within the nodule and which gives it the red colour characteristic of an active, functional nodule.

Although symbiotic nitrogen fixation has been studied for almost a century, it is only in recent years that there has been a rapid increase in our understanding of the process, mainly as a result of the application of novel methods and the concerted efforts of many scientists from different fields. However, little progress has been made in exploiting the knowledge acquired to improve the yield of leguminous crops. In fact, any success obtained so far has been based on selecting effective

Rhizobium strains for a particular crop by trial and error.

Little attention has been given to nitrogen fixation in legume breeding programmes. This is undoubtedly due to our meagre knowledge of the genetic background of the process. Genetic studies in recent years have concentrated on the rhizobia, owing to the demonstration of nitrogen-fixing *(Nif)* genes in bacteria. But the genetic contribution of the host plant is equally important, and further progress will depend on our knowledge of the host factors controlling symbiosis.

GENETIC VARIATION OF THE RHIZOBIUM/LEGUME SYMBIOSIS

Symbiotic nitrogen fixation depends on the interaction between host plant, microbial symbiont and environment. Both partners of the symbiotic association are subject to genetic variation; hence great variation exists in type of nodulation, amount of nitrogen fixed and, ultimately, yield of the plant.

Variation within bacterial strains is well known and is utilized in selecting valuable *Rhizobium* strains for inoculating leguminous crops. *Rhizobium* strains differing in ability to infect and to nodulate a specific host have been isolated. The number and size of the nodules induced may also vary, depending on the *Rhizobium* strain used. In addition, variation in the functioning of the nodules due to the bacteria has been observed, ranging from ineffective (non-nitrogen-fixing) to highly effective, as evidenced by the growth of the plants. Besides these symbiotic characteristics, much attention has been given to variation in the competitive ability of *Rhizobium* strains, which enables the bacteria to establish themselves on the roots and in the soil in competition with indigenous *Rhizobium* strains and other microorganisms in the soil.

The importance of the host plant in the symbiosis was first recorded in trials using different plant cultivars inoculated with a single *Rhizobium* strain. Progress in this field is rather slow, but from experiments with clovers, peas, soya bean and some other legumes, it is evident that the variation observed by changing the *Rhizobium* strain can also be obtained by changing the host plant. At present, plant genotypes are available which fail to form nodules (nonnodulating), produce few nodules (sparsely nodulating) or produce numerous nodules (profusely nodulating) with the same *Rhizobium* strain. The nodules produced can be ineffective, intermediate or very effective. The time of appearance of the nodules and the onset and termination of nitrogen fixation are also largely controlled by the host plant.

Equally important is the effect of the environment on symbiosis, and failure to form nodules or to fix nitrogen can be ascribed to factors like extreme temperatures, low pH and lack or excess of soil moisture. Recently, another type of variation, not expressed under optimum conditions but only under some environmental stress, has been demonstrated (Lie, 1971; Pate, 1976). This type of variation is important in view of the possibility it offers of selecting plant and bacterial strains capable of effecting symbiosis under adverse conditions, for example at low or high temperatures and in problem soils.

Host genes controlling symbiosis

Heritable host factors controlling either nodule formation or nitrogen fixation have been detected in clovers (Nutman, 1954, 1961, 1969), lucerne (Gibson, 1962), pea (Gelin & Blixt, 1964; Lie, 1971; Lie et al., 1976), soya bean (Williams & Lynch, 1954) and *Centrosema* sp. (Bowen & Kennedy, 1961). Through the use of plant genotypes defective in symbiotic ability, it is possible to identify genes responsible for a particular part of the process. It must be emphasized that the expression of symbiosis depends on the particular *Rhizobium* strain used. For this reason, if a clear-cut genetic analysis is to be possible, the assay must be carried out under bacteriologically controlled conditions using a single *Rhizobium* strain and, as shown below, also under environmentally controlled conditions.

Failure to form root nodules: host resistance

In a resistant plant selected from a population of normally nodulating red clover plants *(Trifolium pratense)*, the failure to form nodules was due to a recessive gene acting together with a cytoplasmic factor. Unfortunately, further research was complicated by the fact that the resistance factor was linked to a factor which reduced plant vigour and caused some chlorosis (Nutman, 1969).

A line in which nonnodulation was due to a recessive gene was also obtained in soya bean *(Glycine max)*. The resistance is not complete and, under some environmental conditions and with certain *Rhizobium* strains, a few nodules may be obtained (Clark, 1957). This gene was introduced into other soya bean varieties, and a number of isogenic lines differing only in the possession of this factor are now available for use in assessing nitrogen fixation under field conditions.

Many primitive genotypes of peas *(Pisum sativum)*, originating in the Middle East and Central Asia, fail to form nodules with *Rhizobium* strains isolated from European cultivated peas. In one genotype, cultivar Afghanistan, the failure is due to a major gene (Holl & LaRue, 1976; Lie et al., 1976). Infection of the root hairs takes place but instead of nodules small swellings, consisting of hypertrophied cells, are induced on the roots. In another genotype, cultivar Iran, no nodules are formed at 18-20 °C, the normal growth temperature of peas. But nodulation occurs when the plants are grown at 26 °C or exposed for only a few days to this temperature. This temperature-sensitive nodulation is due to another gene (Lie, 1971; Lie et al., 1976). There are many other genotypes, particularly from the Afghanistan region (Lie, 1978), resistant to one or more *Rhizobium* strains, but further genetic analysis is needed to differentiate the genes.

Factors controlling nodule number and time of nodulation

Host control of nodule number has been observed in many plant species, resulting in plants having either a low number of nodules (sparse nodulation) or a high number (profuse nodulation) (Bowen & Kennedy, 1961; Gelin & Blixt, 1964; Nutman, 1969). In subterranean clover and pea, two genes controlling nodule numbers have been detected (Gelin & Blixt, 1964; Nutman, 1969). In the case of peas (Gelin & Blixt, 1964), yield is correlated with nodule number, but in general sparsely and profusely nodulating plants give the same yield. In the latter case low number is compensated by the larger size of the individual nodules, resulting in an equal volume of nodule tissue in both cases.

The time of appearance of the first nodule is vital for the development of the plant. Early-nodulating plants have the advantage that the period of nitrogen deficiency, before the nodules are formed, is reduced. There is great variability in time of nodulation in clovers, and this property seems to be multifactorially controlled (Nutman, 1969).

Factors controlling nitrogen fixation: the problem of ineffectiveness

Ineffectiveness, which is often a sign of incompatibility between the two partners, may be caused by different factors. The most common type is the early degeneration of bacteroid-containing tissue, reducing the period of nitrogen fixation to almost zero. Ineffective nodules are usually small, white and present in large numbers, scattered all over the root system. In contrast, effective nodules are large, red and present in limited numbers on the upper part of the root system.

Failure to fix nitrogen often occurs when plants are inoculated with *Rhizobium* strains derived from other, related, hosts; for instance, ineffective nodules are formed on subterranean clover with *Rhizobium* strains from red or white clovers. Similar observations have been made in peas: plant genotypes belonging to the *abyssinicum* and *fulvum* types formed ineffective nodules when inoculated with *Rhizobium* strains effective on the cultivated pea (Lie, 1978).

In red clover, genes causing ineffectiveness were described by Nutman (1969). One gene prevented the transformation of bacteria to bacteroids in the nodule. Another gene induced tumorization, resulting in a few plant cells containing *Rhizobium,* completely surrounded by dividing plant cells.

Genes causing ineffectiveness were also found to be present in soya bean and peas. In general, small white nodules were obtained, but from a cross between a primitive and a cultivated pea genotype, some F_2 segregates were obtained which produced normal, red, but non-nitrogen-fixing nodules. A functional nitrogenase was claimed to be present in these nodules, but a defect in the carbohydrate metabolism of the nodule was presumed to be the cause of this type of ineffectiveness (Holl & LaRue, 1976).

SELECTION AND BREEDING FOR IMPROVED NITROGEN FIXATION

Shortage of nitrogen is often a limiting factor in plant growth, and under these conditions, plants having the property of nitrogen fixation have a competitive advantage over other plants. It may be assumed that in primitive agriculture, where no fertilizer nitrogen is available, plants bearing highly effective nodules have unintentionally been selected and used for further breeding. It is therefore not surprising that many of our cultivated legumes are well nodulated.

This is the case in peas, for example, where effective symbiosis has been observed in advanced cultivars originating from all over the world (Lie et al., 1976). This is probably due to a common trait introduced long ago into the genetic constitution of the ancestors of the cultivated pea and perpetuated in further selections. As reported by Gelin & Blixt (1964), the pea variety Monopol, which is a genotype with good nodulation, has been repeatedly used in the breeding programme in Sweden.

Another example is found in lucerne, *Medicago sativa* (Gibson, 1962). It appears that the most successful genotypes, Du Puits, Hunter River and Hairy Peruvian, are also genetically the best adapted for nitrogen fixation. Problems in nodulation may arise when the genotype Rambler, derived from *Medicago falcata*, is used as a source of the useful characteristic of creeping-rootedness. *M. falcata* and Rambler are poor nitrogen fixers when growing in symbiosis with local *Rhizobium* strains and the same is true of progeny from crosses of *M. sativa* and *M. falcata*. These results show how dangerous it can be to neglect the property of nitrogen fixation in the breeding programme.

Few attempts have been made to select leguminous plants directly for improved nitrogen fixation. By selection and crossing of plants with different amounts of nodule tissue, white clover plants with an increased volume of nodule tissue were obtained (Mytton & Gareth Jones, 1971). However, this property was maintained only for the first two generations after which it diminished. Moreover, an increase in nodule tissue is not always accompanied by increased nitrogen fixation, indicating that other factors than amount of nodule tissue limit the efficiency of nitrogen fixation. Red clover plants with an improved nitrogen-fixing capacity were obtained by crossing plants selected for high nitrogen fixation. The acquired property was found to be very specific and pertained to one *Rhizobium trifolii* strain only and not to two others tested (Nutman et al., 1971). Problems may arise if such plants are grown in soils with a mixed population of *Rh. trifolii* strains unless the specific bacterial strain concerned can be used as a successful inoculant.

An important feature is the duration of the period of nitrogen fixation, i.e. time between onset and termination of the process. In temperate regions, onset is delayed by low temperatures in spring. The selection of symbiotic systems with a lower temperature optimum would have a marked effect on ultimate yield. Termination of nitrogen fixation is often associated with the reproductive phase of the plants, presumably owing to a redirection of translocation in favour of the developing pods. Prolonging the vegetative phase by removing the pods or by other means may increase the amount of nitrogen fixed (Hardy & Havelka, 1976). However, many cultivated plants have a determinate growth habit and prolonging the vegetative phase may not always be feasible.

To estimate the growth potential of a leguminous plant, it is essential to differentiate between the growth potential which is independent of nitrogen fixation and that which is dependent on it. Therefore it is necessary to compare plants supplied with sufficient combined nitrogen with plants which are dependent upon nitrogen fixation. When the full potential of plant growth under local conditions is known, the symbiotic potential can be assessed.

In formulating a breeding programme, it is also essential to know whether nitrogen fixation *per se* is limiting to plant growth. The early observation that carbohydrate supply limits nitrogen fixation has been substantiated by recent experiments using an increased CO_2 supply to the shoots (Hardy & Havelka, 1976). Increased CO_2 supply to the roots and nodules may sometimes raise the efficiency of nitrogen fixation by increasing the production of organic acids serving as precursors of aminoacids (Mulder & van Veen, 1960). These experiments demonstrate that nitrogenase is not limiting and that a substantial increase in nitrogen fixation can be obtained by increasing the carbohydrate supply to the nodules. Selection for higher net photosynthesis may be a key to the more efficient exploitation of biological nitrogen fixation.

CONSERVATION OF A GENE POOL FOR SYMBIOTIC NITROGEN FIXATION

Owing to their agronomic importance, research priority is given to cultivated plants and very little attention is paid to wild or primitive legumes. The origin of the cultivated legumes, as of many other crops, is not easily traced, but in view of the many characteristics that the various cultivars of a crop have in common, it must be assumed that they originate from a limited number of ancestors. There is growing concern that the spread of modern agriculture is tending to replace low-yielding, highly variable forms by a high-yielding, but genetically uniform crop. One of today's most important tasks is to collect and conserve wild and primitive plant material in order to maintain a gene pool for our cultivated crops.

It is often assumed that the *Rhizobium* gene pool is adequately maintained in the culture collections of various research institutes, which usually contain *Rhizobium* strains effective for agronomically important crops. Without denying the value of these collections, it is questionable whether much of the potential of rhizobial genetic material is actually represented in them. *Rhizobium* strains are isolated from root nodules, and by using a certain plant genotype as a trap plant, a specific group of rhizobial strains is unconsciously selected and other strains remain undetected. Selection depends in part on the characteristics of the host and in part on bacteria, such as competitiveness and ability to colonize the roots.

A further reason for conserving *Rhizobium* strains from wild and primitive legumes is that in the course of time breeding work may result in plant material requiring specific *Rhizobium* strains not previously used for cultivated plants. Therefore, it is important that the original variability of the *Rhizobium* gene pool should be conserved.

Results with peas provide an illustration. When advanced pea genotypes from different parts of the world were tested for symbiotic nitrogen fixation, little variation was observed. However, when primitive or wild material was examined, a high degree of genetic variability was detected, especially in plants from the centre of origin of these legumes (Norris & 't Mannetje, 1964; Lie et al., 1976; Lie,1978). Further, by using a primitive plant genotype from Afghanistan as a trap plant, specific *Rhizobium* strains were isolated from soils in the Middle East and Central Asia. These strains seem to be limited to these areas. The results clearly demonstrate that the centres of origin contain not only valuable plant material, but also *Rhizobium* strains having specific properties not present in strains isolated from advanced cultivars (Lie, 1978).

Although *Rhizobium* strains can grow as saprophytes in the soil, their occurrence and distribution are related to the presence of host plants. The number of *Rhizobium* cells in a soil declines gradually after the disappearance of the host plant. In modern agriculture the inoculation of legumes with an effective *Rhizobium* strain is often recommended. Besides being a good nitrogen fixer, such a strain should be aggressive with regard to competition with other rhizobia of the same type and able to persist and establish itself in the soil. With repeated use, these inoculant strains may in the long run replace the less agressive native *Rhizobium* flora. The situation is aggravated by the disappearance of indigenous legumes and by agricultural management techniques which tend to equalize the soil environment.

NITROGEN FIXATION IN THE RHIZOSPHERE

In recent years it has been suggested that cereals may benefit from nitrogen fixation by free-living bacteria in the rhizosphere. This is corroborated by observations that many *Azotobacter* cells are present in the rhizosphere of sugar cane and grasses like *Paspalum*. More recently, a nitrogen-fixing *Spirillum* species has been detected in the rhizosphere of many tropical plants, including maize (Döbereiner & Day, 1976). In these cases, loose associations (associative systems) are established between the roots and the bacteria, so that the situation is different from that obtaining in the root nodule.

It is not surprising to find nitrogen-fixing bacteria in the soil and in the rhizosphere, but their contribution to the nitrogen economy appears to be of the order of only a few kg N per hectare per year. Some workers have indeed claimed that some hundreds of kg of nitrogen can be fixed by associative systems, which would thus be comparable with symbiotic systems, but careful experiments have not substantiated this. Their technique involves incubating the roots overnight in order to equilibrate the system. But during this period a great increase in number of bacterial cells occurs (enrichment culture), as a result of the release of nutrients by wounded plant root cells, resulting in an unrealistically high rate of nitrogen fixation. In fact, if the roots are assayed directly after sampling, a low nitrogen-fixing activity, corresponding to a few kg N per hectare per year, is found (Burris, 1977).

Nevertheless, the presence of N_2-fixing bacteria in the rhizosphere and the possibility of a close association with the roots are of considerable academic interest. A certain specificity in the associative systems has been claimed, some plant cultivars being more successful than others in establishing an association with the bacteria. However, unless new facts come to light, the contribution to the nitrogen economy is at best a minor one.

TRANSFER OF NITROGEN-FIXING (NIF) GENES TO OTHER ORGANISMS

An intriguing feature of symbiotic nitrogen fixation is that only a limited number of plants, including legumes and nonlegumes like alder, *Casuarina* spp. and others, are capable of forming nitrogen-fixing root nodules. Unfortunately, this property cannot be transferred to other plants by intergeneric crosses. Although recent work has shown that it is possible to produce hybrid cells by somatic fusion of plant cells having no cell walls (protoplasts), attempts to obtain hybrid cells between a legume and a cereal have not been very successful. The main problem is to regenerate intact plants from the hybrid cells.

So far, only procaryotic cells, bacteria and blue-green algae, have been found to carry *Nif* genes and some years ago the transfer of these genes between two related bacterial species, *Klebsiella pneumoniae* and *Escherichia coli*, was achieved (Dixon & Postgate, 1972). The idea of introducing *Nif* genes into the plant genome to obtain novel nitrogen-fixing systems is obviously attractive, but the problems of transferring genes from a procaryotic bacterium to a eucaryotic plant are taxing in the present state of genetic technology, one difficulty being the regeneration of intact plants from recombinant cells. There can be no guarantee of success in the near future.

Furthermore, it should be borne in mind that our cultivated crops, as a result of selection and breeding, are often specialized with respect to the synthesis of specific products, e.g. starch in cereals and proteins in legumes. Whether it is at all possible to construct a superplant with the dual function of synthesizing starch and protein while excelling in both is questionable. Perhaps the best short-term alternative is to use the presently available leguminous plants and to apply conventional breeding practices to improve their nitrogen fixation. However, before any progress can be made, more research is needed to characterize the genetic background of the host plant and the microbial symbiont in this process.

Mitochondrial complementation and combining ability

Assessment of combining ability is an essential part of many breeding programmes, particularly in the breeding of hybrid varieties. It is a time-consuming procedure, however, since it necessitates testing the progenies of numerous crosses for yield potential, and more rapid methods of testing could therefore be of great importance. A method which seemed to be promising was discovered by McDaniel & Sarkissian (1966). The basis of this method is a relationship between heterosis and the oxidative and phosphorylative activity of isolated mitochondria. Oxidative phosphorylation, the energy-generating process of mitochondria, is characterized by:

- ADP/O, the ratio between molecules of ADP converted and atoms of oxygen consumed. The ADP/O ratio is a measure of the efficiency of oxidative phosphorylation, i.e. the transfer of energy from substrate to ATP.
- RC (respiratory control), the ratio of oxygen uptake in the presence of ADP to oxygen uptake in the absence of ADP. The RC is a measure of coupling between oxidation and phosphorylation.
- Rate of oxygen uptake per unit of mitochondrial protein.

McDaniel & Sarkissian (1966, 1968) and Sarkissian & Srivastava (1967) found that mitochondria isolated from scutella of a heterotic hybrid of maize exhibited higher ADP/O, RC and oxygen uptake than mitochondria from the inbred parental lines. This phenomenon was termed 'mitochondrial heterosis'. They also observed that the activity of a 1 : 1 mixture of mitochondria of those parental lines was higher than the activity of the parental mitochondria; this phenomenon was called 'mitochondrial complementation'. Mitochondrial heterosis and complementation were not observed with a nonheterotic hybrid. Similar results were obtained with wheat (Sarkissian & Srivastava, 1969) and barley (McDaniel, 1971). It was suggested that the combining ability of breeding lines be predicted by assessing mitochondrial complementation (McDaniel, 1971; Sarkissian, 1972; Srivastava, 1972). The attractiveness of the technique stimulated research in other laboratories, which reported mitochondrial complementation for wheat (Sage & Hobson, 1973; Barratt & Flavell, 1977) and sugar beet (Doney et al., 1972). But negative results were also published (Zobl et al., 1972; Ellis et al., 1973; Doney et al., 1975; van Gelder & Miedema, 1975; Hanson et al., 1975). The above results raise at least two questions:

- What is the significance of genetic variation in mitochondrial activity in relation to plant growth and yield?
- What is the cause of the contradictory results on mitochondrial complementation?

Before discussing these questions in detail we must consider the influence of techniques and plant material on mitochondrial activity. Mitochondria are isolated at low temperatures (0 - 4 °C). ADP/O and RC are determined at 23 - 27 °C. During isolation from plant tissues, oxidation and phosphorylation can be uncoupled by mechanical disruption or by chemical components from the cells. This results in low RC values. Mitochondria with RC values below about 3 are not very suitable for studying oxidative phosphorylation, although in one of the earliest reports RC values as low as 1.3 to 1.4 were reported (McDaniel & Sarkissian, 1968). In the investigations cited above (except Doney et al., 1972, 1975), mitochondria were isolated from scutella or shoots of young dark-grown seedlings, as young tissues are the most suitable source of mitochondria showing tight coupling. Both RC and ADP/O decline with the age of the seedling tissue (Sarkissian, 1972; McDaniel, 1973). Flavell & Barratt (1977) observed that within one wheat variety RC and ADP/O were affected by nitrogen content and size of the seeds. Mitochondrial complementation has only been demonstrated with α-ketoglutarate as a substrate; with substrates like NADH and succinate, a higher oxygen uptake was observed, but no complementation or heterosis (McDaniel & Sarkissian, 1968; see also Hanson et al., 1975). Oxidation of the latter substrates was less sensitive to uncoupling. It appears, therefore, that various nongenetic factors influence the *in vitro* activity of mitochondria. Variation of ADP/O *in vitro* is no proof that a similar variation occurs *in vivo*, but may be the result of uncoupling due to the technique of isolation and/or of differences in the suitability of the tissue as a source of mitochondria showing tight coupling. This assumption is sustained by the high correlations detected between RC and ADP/O (van Gelder & Miedema, 1975; Flavell & Barratt, 1977). Furthermore there is no evidence that the activity of mitochondria from young seedlings is indicative for later stages of plant development (see also Sinha & Khanna, 1975).

If genetic variation in mitochondrial activity is a real phenomenon, what is its significance for plant growth and yield? Flavell & Barratt (1977) found a positive correlation between grain yield and ADP/O and RC in nine wheat varieties. A variation in ADP/O from 1.99 to 2.13 was associated with a variation in grain yield from 98 to 120 (arbitrary units). Calculations by Penning de Vries et al. (1974) revealed that an increase of ADP/O of this order improves the efficiency of utilization of glucose by 0.8, 1.5 and 4.5% at relative growth rates of 1, 0.1 and 0.01 $g.g^{-1}$ day^{-1}, respectively. In rapidly growing plants the efficiency of oxidative phosphorylation has little effect because most of the carbohydrates are directly used for the synthesis of cell constituents. Sinha & Khanna (1975) reported that in germinating maize no heterosis was observed in the utilization of [^{14}C] sucrose or [^{14}C] glucose. Although statistically significant relationships have been demonstrated between mitochondrial activity and seedling vigour or grain yield, there is no evidence for a causal relationship (cf. Flavell & Barratt, 1977). A considerable literature shows that many genes and many processes are involved in heterosis and hybrid vigour (Manwell & Baker, 1970; Sinha & Khanna, 1975).

Mitochondrial complementation is more relevant for plant breeding than mitochondrial heterosis, as it may enable combining ability to be predicted without the necessity of making the crosses. Contradictory results reported in the literature, however, may indicate that mitochondrial complementation is difficult to reproduce or is restricted to combinations of special genotypes. Ellis et al. (1973) were unable to reproduce the results of McDaniel (1971) and Sarkissian & Srivastava (1969), using the same genotypes of barley and wheat and employing the same technique. Sage & Hobson (1973) tested mitochondrial activity (ADP/O) in six parental lines of wheat and nine parental mixtures, and the same material was tested by Barratt & Flavell (1977) by a slightly different technique, but whereas the former were unable to show significant differences between mitochondrial mixtures and parental mitochondria, in the latter's study, one mitochondrial mixture out of the nine showed an ADP/O significantly higher than the midparental value. To determine the reproducibility of the measurements we have calculated correlation coefficients relating the ADP/O ratios of the two investigations. For parental lines (average of three sets of experiments), we found $r = -0.435$ and for mitochondrial mixtures $r = -0.220$. Thus the ADP/O of genotypes and mitochondrial mixtures was not reproducible at all. Moreover the ADP/O levels were different; the average ADP/O for mitochondrial mixtures was 2.91 in Sage & Hobson's study and 2.36 in that of Barratt & Flavell. Mitochondrial complementation (calculated on the basis of the midparental value) showed a correlation coefficient of +0.764 ($0.01 < P < 0.05$), which is rather low for a screening technique ; omission of the highest value led to a nonsignificant correlation coefficient of +0.556. Here again it appears that mitochondrial activity cannot readily be reproduced by different workers. Barratt & Flavell (1977) reported one other case of significant mitochondrial complementation out of three combinations of wheat. Unfortunately, data on the mitochondrial activity of the hybrid, which are essential for the whole concept, were not reported.

In some reports claiming mitochondrial complementation, the parental mixtures and the hybrids exhibited ADP/O values far above the theoretical maximum of 3 (Sarkissian & Srivastava, 1969; Srivastava et al., 1969). Here mitochondrial complementation may be attributed to artefacts. In other reports (Sarkissian & Srivastava, 1967; McDaniel & Sarkissian, 1968; Doney et al., 1972), mitochondrial complementation was associated with very low ADP/O values of parental lines. In a study on maize, six inbred lines exhibited ADP/O values ranging from 2.60 to 2.73 (van Gelder & Miedema, 1975). In our opinion, low ADP/O values are the result of imperfect isolation techniques or plant properties affecting mitochondrial characteristics during isolation.

The above discussion clearly shows that mitochondrial complementation is not a generally occurring phenomenon. The poor reproducibility indicates that we are probably dealing with artefacts or experimental errors. To our knowledge no breeding company or institute is using the technique of mitochondrial mixing in screening for combining ability. Combining ability is a very complicated phenomenon and no technique neglecting this complexity can be expected to replace conventional breeding methods.

Applications of tissue culture to plant breeding

INTRODUCTION

Plant tissue culture technology has been available to the plant breeder for more than two decades, yet its impact on plant breeding has been minimal. Recent methods of plant tissue culture involving the isolation and genetic manipulation of plant protoplasts have greatly stimulated interest in this area, and we will later discuss the extent to which we think these new methods will aid the plant breeder. To gain some perspective, however, we will first consider the use and limitations of the presently available methods, such as embryo culture, cell and callus culture and clonal propagation.

CURRENT APPLICATIONS

Tissue culture has been more extensively applied in certain crops such as sugar cane than in the cereals and legumes, where present difficulties in technique have largely restricted its use to the *in vitro* culture of embryos for purposes of interspecific hybridization.

In sugar cane (*Saccharum officinale*), the use of cell suspensions has allowed variability to be introduced by treatment with colchicine, and such treatment has also enabled plants to be produced with doubled chromosome numbers. When resistance to a fungal disease is located at the cell level, cell selection can be applied to cell suspension cultures to obtain clones resistant to the fungal toxins, as in the case of *Helminthosporium sacchari*, the causal agent of eye spot in sugar cane. One of the difficulties, however, is that few cell suspensions are single-cell systems and that the selection procedures are usually not adequate, except in a few instances. Furthermore, unless regeneration from cells to whole plants is possible, methods involving cell suspensions and selection are useless. As has been stressed by Heinz et al. (1977), no particular advantage is derived from propagation by tissue culture in sugar cane unless selection towards one particular characteristic can be achieved, as has been done for eye-spot resistance.

For horticultural crops, propagation principally by meristem culture is now standard practice for certain high-cost species, particularly those requiring a high degree of uniformity. When such species, e.g. orchid species and strawberry, are propagated vegetatively they often contain systemic bacteria, fungi or viruses which affect yield and appearance, but by means of tissue-culture techniques clean material with a low virus index can frequently be produced. Subsequent propagation by *in vitro* culture is often much more rapid than for example by bulb formation.

In the case of tree species, vegetative propagation is generally preferred to sexual propagation because genetic characteristics are better maintained. Tissue culture methods show promise for the clonal propagation of elite coconut palms (Eeuwens & Blake, 1977). In tree breeding, use has been made of one of the oldest applications of tissue culture in plant breeding, namely embryo culture. Where there is incompatibility between the embryo and maternal tissues, or where endosperm development ceases prematurely, embryos in seeds resulting from interspecific hybridization do not normally germinate; a main objective of isolated embryo culture is therefore to germinate such embryos. Embryo culture has been used as a tool to obtain hybrid plants in difficult crosses in barley, sweet clover, fruit trees, forest trees and various vegetable crop plants. It has a further use, for example in the cross *Hordeum bulbosum* × *H. vulgare*, where directional elimination of chromosomes results in the production of immature embryos which yield haploid *H. vulgare* plants if embryo culture is employed (see 'Haploids, origin and potentials').

It is, however, clear that such tissue-culture methods, although well established as methods for the plant breeder, are in fact only rarely used in plant breeding; there is a reluctance amongst breeders to use these *in vitro* aseptic methods unless they are absolutely essential. As a result there is little accumulation of expertise or of current results from these methods and this in itself tends to detract from their usefulness in plant breeding.

Another technique, that of *in vitro* pollination or fertilization, may be particularly useful where there is a real need for crosses which cannot be obtained by normal pollination procedures, for example where self incompatibility is present (Rangaswamy, 1977). This would probably also prove useful where more distant hybridizations are attempted, but these techniques have not yet been integrated into the armoury of the plant breeder.

As has been stressed by D'Amato (1977), a meristematic cell line from a true shoot apex is probably the only kind of cell line endowed with genetic stability; culture of such meristematic apices ensures genetic stability of the *in vitro* propagated progeny. In tissue cultures of other material, it is always possible for various chromosomal abberrations to occur. Such changes can be kept to a minimum by maintaining plant material for the shortest possible time in culture.

APPLICATIONS FOR THE FUTURE

Plant genetic manipulation

Totipotency of plant cells provides the basis of several approaches in which the aim is to induce genetic modifications of the plant cell which will survive through culture and be expressed phenotypically in the whole plant. Such modifications may be expected to be sexually transmissible and therefore of real value to the breeder.

In general, the approaches to plant genetic manipulation are well defined and in certain cases their feasibility has been demonstrated. The basic problem in their application is the unavoidable fact that, although tissue culture of most species of horticultural or agricultural interest is possible, relatively few such species, to date, have exhibited reproducible and efficient plant regeneration, even what is agriculturally perhaps the most important group, the Gramineae. It is therefore against this background of restricted plant regeneration that the methods of genetic manipulation should be assessed.

Somatic cell hybridization

Cell fusion provides the opportunity for the combination of two genomes between any pair of species and of any ploidy level. In order to achieve cell fusion the plant cell wall is enzymatically degraded to release the protoplast. Fusion of protoplasts can be induced readily, thus producing heterocaryons which, when maintained under conditions permitting cell-wall regeneration and division, can lead to the production of somatic hybrid tissue; a prerequisite is that nuclear fusion (occurring during mitotic division) takes place and that chromosomal stability ensues. Plants regenerated from such tissues would, in their simplest form, possess the unreduced chromosome complements of both parents (nuclear hybrid) (Power et al., 1976) and in some cases both cytoplasms ('cybrid') (Belliard et al., 1977). Superficially regarded, the potential of such a process is enormous in terms of novel hybrid generation; however, owing to basic biological incompatibility, many species combinations will undoubtedly fail.

The main problem is probably not one of feasibility but rather of the identification of the specific cases where there is an actual need to produce a new (somatic) hybrid for use in breeding. Somatic hybridization is a process designed to generate genetic variability; but it must be pointed out that, for many of the major crop species, and in particular the cereals, lack of genetic variability is not the limiting factor for their further improvement. The chief constraint is the difficulty of identifying and isolating desired recombinants.

Perhaps the most practical application of cell-fusion methods, particularly for the near future, is the manipulation of extrachromosomally inherited features such as male sterility. Since protoplast fusion leads to cytoplasmic hybridization as a result of cytoplasmic mixing, it would be possible to isolate potentially useful plant types even where the nuclei fail to fuse, or where unidirectional chromosome elimination takes place. Somatic hybridization would clearly also have a role to play in crop improvement in certain vegetatively propagated species or where avoidance of a sexual cycle is desirable, and also, perhaps most important of all, where sexual hybridization proves impossible. The somatic hybrid may be more fertile than the conventionally produced F_1, assuming that the latter can be produced at all, and the back cross may also be more readily achieved via somatic hybridization, though here the repeated addition of chromosomes is likely to be a serious drawback. Somatic hybridization also offers the possibility of transferring potentially lethal genes in the heterozygous state.

In applying somatic hybridization to specific breeding problems, the main concern will be with aspects of gene-pool expansion, disease and pest control, quality and yield, matters which, in somatic hybridization as in conventional breeding, are likely to be resolved at the intrageneric level. In many cases, conventional hybrids between species can be produced only by unilateral pollination. The somatic hybrids of such species combinations could possess a mixed cytoplasm contributed by both parents, unlike the sexually derived hybrid which has the cytoplasm of the maternal parent only. The situation could also be brought about in which the cytoplasm of the hybrid was donated solely by the obligatory paternal species, thus creating a unique nuclear/cytoplasmic combination. To date, somatic hybrids have been produced between sexually compatible species at both the interspecific (e.g. *Daucus, Nicotiana, Petunia*) and intraspecific (e.g. *Nicotiana, Datura*) levels.

It should also be pointed out that in many cases the somatic hybrid of a novel species combination would be of little direct value; its exploitation would rely entirely on conventional breeding procedures.

Cell mutants and plant modification

Since the production of protoplasts provides the researcher with a large population of single cells, it is possible to apply microbial techniques of mutagenesis and selection to higher plant systems. Selected cell lines, possessing chemically induced or radiation-induced chromosome or point mutations, could be regenerated into plants, and these plants might retain and express the selected characteristic. Such newly acquired characteristics might prove to be sexually transmissible. It is in fact possible to select cell lines resistant to specific herbicides, fungal toxins, pollutants, extremes of temperature and high salt concentrations. The main problem, often encountered, is that of plant regeneration, since regeneration capacity is lost very rapidly during disorganized growth in culture. Among other biochemical mutants, those resistant to the presence of aminoacid analogues in the medium could be expected to overproduce specific aminoacids, such as lysine; in cereals, this might result in grain with an increased percentage of lysine if whole plants could be regenerated from such mutant cell lines. However, it does not follow that increased percentages of lysine in the cereal grain will necessarily result from cell cultures containing increased pools of free aminoacids such as lysine. A weakness of this approach is that certain genes may not be active at the single-cell level. Similarly, specific tissue functions may take place only when the cell is an integral part of the intact plant.

Besides the above-mentioned kinds of mutants, morphological mutants may be expected following mutagenic treatment of embryonic cells. In many cases, however, mutagenic treatment is unnecessary and undesirable, since the availability of efficient cloning systems permits the handling of very large numbers of cells and protoplasts and therefore affords the opportunity to detect naturally occurring mutations.

Finally, it should be stressed that the maintenance of plant tissues in culture results in an accumulation of polyploid and aneuploid cells or spontaneous mutations, all of which will have an influence on plants regenerated from such cells.

Uptake of foreign particles, plasmids and genetic materials

Plant protoplasts can readily be induced to take up small particles (up to three microns). Larger bodies, such as cell organelles, can also enter protoplasts as a result of fusion and active uptake processes. The evidence for uptake of genetic material in the form of nuclei, bacteria, blue-green algae and extracted DNA is convincing. The effect on the protoplast/cell of such input information is, however, at best fleeting and in most cases nonexistent. The most promising approach to cell modification is likely to be that of gene transfer, whereby specific genes, inserted into plasmids (extrachromosomal bacterial DNA) acting as vectors, are incorporated into the host genome. When such plasmids, for example the Ti plasmid of *Agrobacterium tumefaciens* (responsible for crown-gall tumour formation in many plants), enter protoplasts, their influence on the host cell should be readily detected, since the growth requirements of the transformed cell will alter, particularly in relation to hormonal requirements. This altered growth would provide the basis for the selection of modified cell lines. By supplying plant cells with the modified plasmid and selecting against nontumerous growth, or wild-type (normal) cells, it may be possible to isolate altered cell lines.

There are two problems connected with this approach: firstly, plant regeneration from tumorous tissues is difficult, but this could be overcome by using noninducible strains; and secondly, many plant characteristics are polygenic functions. It is therefore difficult, at this stage, to imagine that major phenotypic modifications will be achieved by this approach alone.

The direct insertion of DNA into the host genome, although more difficult, also offers the possibility of plant genetic manipulation.

The availability of these two approaches to cell modification provides the tissue culturist and plant breeder with perhaps more hope than ever before that *in vitro* propagation of plant tissues will lead to the production of new plant types of benefit to man.

Ti plasmids as potential vectors for genetic engineering in plants

INTRODUCTION

One way of obtaining a plant species with a new character would be through the direct incorporation of the appropriate gene or genes in the plant genome. In bacteria, DNA transformation is the classical way of accomplishing this. In higher plants, although data indicating that DNA is taken up by cells have been obtained, no firm evidence has yet been presented for true transformation. Studies on the plant crown gall tumour caused by *Agrobacterium tumefaciens* have demonstrated that in this material we have a natural case of 'genetic engineering' of plant cells by a bacterium. By transferring a particular type of DNA, the bacterium induces tumour cells, and these then produce compounds that can be used efficiently by the bacterium as a sole source of nitrogen. In the past few years much knowledge has been gained regarding the molecular basis of crown gall formation. This knowledge is now finding applications which can be of benefit to man. For detailed information on research on the physiology, molecular biology and genetics of crown gall the reader is refered to recent review papers (Beiderbeck, 1977; Braun, 1978; Schell, 1978; Gordon et al., 1979; Hooykaas et al., 1979).

THE CROWN GALL DISEASE

The crown gall tumour is characterized by non-self-limiting cell proliferation. It arises when *A. tumefaciens* infects wound sites. Virulent agrobacteria attack a great number of species and families, mostly dicotelydons; monocotyledons do not appear to be susceptible to the tumour-inducing stimulus of the bacterium. Like *Rhizobium, Agrobacterium* is a member of the Rhizobiaceae, which are gram-negative bacteria often present in the soil. In nature crown galls are frequently induced at or just below soil level in the root crown, where wounds readily occur. Wounding is an essential precondition for tumour formation. *A. tumefaciens* cells penetrate into the intercellular spaces and into damaged cells filled with wound exudate, and at these sites the bacteria multiply and interact with adjacent healthy cells; they do not, however, penetrate into the latter, but act by attaching themselves to the cell walls, from which a tumour-inducing principle is transferred into the cell. Only conditioned cells appear to be susceptible to transformation. These are cells in the wound region which are stimulated to divide as a response to wounding. Tumour induction has to be accomplished, however, before cell division takes place; after that the cells are no longer susceptible. Experiments on stems of *Kalanchoe daigremontiana* have shown that at 25 °C tumour induction is completed within about 20 hours. Thereafter unlimited cell proliferation occurs even when the bacteria are killed. With the exception of the meristematic tissues of the stem and the root tips all organs of the plant are susceptible to crown gall formation.

NEWLY ACQUIRED PROPERTIES OF CROWN GALL CELLS

A typical feature of the crown gall is its capacity to produce phenotypically identical tumours when bacteria-free explants of it are grafted on healthy plants. This character is related to a new heritable property of the crown gall cells which allows them to grow and to divide on a basic culture medium without the added auxin and cytokinin normally needed for sustained cell division in tissue culture. In principle, the ability of crown gall cells to grow independently of phytohormones can be used to select such cells from a population containing a large number of normal cells. Many normal cells are often present in the tumour and are stimulated to divide by growth factors produced by the tumour cells. It is because of this phenomenon of cross-feeding that normal cells cannot easily be eliminated in tissue culture, even if the crown gall tissue is cultured on a phytohormone-free medium. Selection of crown gall cells can only be achieved by the isolation of single cells or protoplasts from the callus tissue.

Another newly acquired property which is frequently observed is the capacity to synthesize one of two types of unusual aminoacid derivatives, an example of the one type being octopine, N^2-(D-1-carboxyethyl)-L-arginine, and of the other type nopaline, N^2-(1,3-dicarboxypropyl)-L-arginine. The synthesis of one or the other type of aminoacid derivative is specified by the tumour-inducing bacteria and not by the host plant. It is conceivable that during the period spent in the tumour the bacteria actually profit from the tumour-specific compounds, since they not only induce the compound in the tumour but are able to utilize it specifically as a sole source of nitrogen. *A. tumefaciens* strains that induce octopine-producing tumours catabolize octopine but not nopaline and are therefore called octopine strains. Strains that induce nopaline-producing tumours catabolize nopaline and not octopine and are

Fig. 8.7. Nopaline-producing crown gall with teratomas on a stem of *Kalanchoe daigremontiana*.

called nopaline strains. These aminoacid derivatives are not in themselves responsible for the neoplastic condition of crown gall cells: a number of wild-type as well as mutant *A. tumefaciens* strains have been isolated which induce tumours without these compounds. Octopine and nopaline-producing plant tumours differ in their regenerative capacity. When nopaline-producing tumours develop on the upper half of stems or on leaves of plants with a high regenerative capacity they often form leaf-like teratomas (Fig. 8.7). Teratomas are not formed on octopine-producing plant tumours. The difference between the two tumour types suggests that octopine and nopaline bacteria modify plant cells differently.

TI PLASMIDS

Each *A. tumefaciens* cell harbours one or more large plasmids. One of these extra-chromosomal DNA elements carries genes which are essential for its oncogenic capacity. This particular plasmid is called the tumour-inducing plasmid or Ti plasmid. Ti plasmids range in size between 95 and 160 megadaltons, which means that they can code for about 150 proteins. The role of the Ti plasmid in inducing tumours has been demonstrated by plasmid-curing and plasmid-transfer experiments. When *A. tumefaciens* cells are cultured at a temperature of 35 °C instead of 28 °C, which is the normal growth temperature, the Ti plasmid is sometimes lost. 'Cured' bacteria from which the plasmid has been lost are avirulent and have also lost the capacity to catabolize the unusual aminoacid derivatives. When the Ti plasmid is reintroduced into such bacteria by DNA transformation or through conjugation with virulent bacteria they again become virulent and are able to utilize octopine or nopaline. If the

Ti plasmid is received from an octopine strain the recipient becomes an octopine strain, regardless of whether it originally was an octopine or a nopaline strain; similarly when the recipient acquires the Ti plasmid of a nopaline strain it becomes a nopaline strain. Apparently octopine and nopaline strains harbour different types of Ti plasmid. Hence one type is called an octopine Ti plasmid and the other a nopaline Ti plasmid. These plasmids obviously not only carry genes which determine oncogenicity but also genes which determine whether octopine or nopaline will be synthesized in the tumour cell as well as genes for utilizing these compounds. Oncogenicity and the synthesis of one or the other unusual aminoacid derivative in crown gall cells are an expression of the presence of a fragment of the Ti plasmid in these cells. This fragment, which is not necessarily of the same size in different crown gall callus tissues, is called T-DNA. It is not yet known whether the complete Ti plasmid is transferred and processed in the plant cells or whether only a fragment produced in the bacterium is transferred to the plant cells.

T-DNA

The size of the T-DNA in different octopine-producing crown gall callus tissues appears to vary between a few percent to about 10% of the Ti plasmid. In all cases studied so far the T-DNA is derived from the same region of the plasmid. Nopaline-producing crown gall cells also contain T-DNA. Although most of the T-DNA from octopine and nopaline Ti plasmids does not exhibit DNA homology, part of it shows

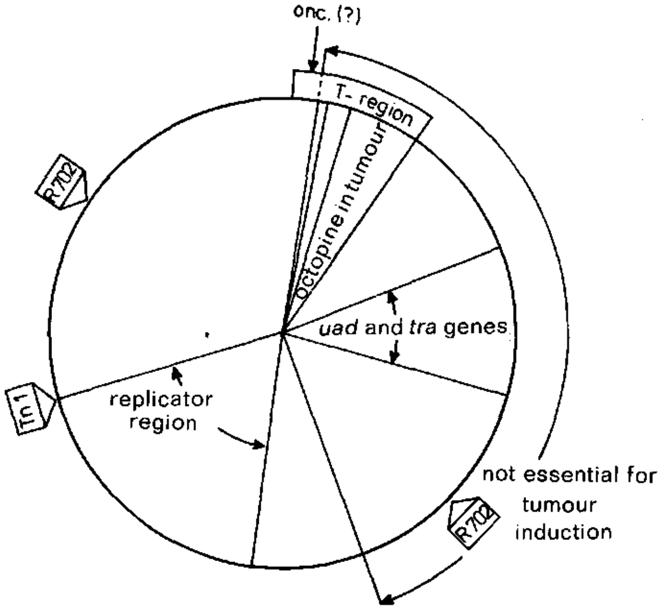

Fig. 8.8. Genetic map of an octopine Ti plasmid, showing T-region, position of presumed gene(s) for oncogenicity (arrowed), two insertion sites of the R702 plasmid position of Tn 1 insertion.

about 100% DNA homology. It is thought that genes on this conserved region are essential for oncogenicity. A T-DNA and the presumed position of a gene or genes for oncogenicity in an octopine Ti plasmid is shown in Fig. 8.8. The number of copies of the righthand region of the incorporated T-DNA in tumour cells appears to be greater than the number of copies of the lefthand region. The DNA in between has intermediate values (Merlo et al., 1978). This interesting observation is important in relation to a gene dose effect. In principle, the more copies of a gene there are, the more protein is likely to be synthesized. At least part of the T-DNA has been shown to be transcribed in RNA in tumour cells. A portion of these RNA molecules is bound to polyadenylic acid, which is characteristic of eucaryotic messenger RNA (mRNA). This means that T-DNA transcripts are subject to a eucaryotic control system. Whether the RNA is also translated into protein is not yet known. If it is translated, possible candidates for the protein are the enzymes lysopine dehydrogenase and nopaline dehydrogenase, which catalyse the synthesis of octopine and nopaline. In planning to use the Ti plasmid as a vector for genetic engineering in plants it is first necessary to know which part of the T-DNA is essential for oncogenicity, in order to make it possible to replace the remaining part by the genes which it is desired to introduce into the plant cells. It is probable that the oncogenicity region is needed for the integration of foreign DNA into the plant genome. New genes should be linked to this region, since integration in the genome is a prerequisite for stability of maintenance in progeny cells. It is also necessary to know whether there are genes outside the T-region which are required for virulence. These questions can be answered by the isolation of plasmid mutants; transposon insertion mutants and deletion mutants are particularly suitable.

GENETIC MAP OF AN OCTOPINE TI PLASMID

Transposons are discrete DNA structures which usually carry genes for antibiotic resistance. They are often present in the drug resistance plasmids or R plasmids which occur in many bacterial species. R plasmids are self transmissible and because of this can be exchanged between different bacterial species. In many cases they have been found to be responsible for the spread of antibiotic resistance that follows upon the extensive use of antibiotics. R plasmids can also be transferred to agrobacteria. When both an R plasmid and a Ti plasmid are present in a bacterium two things can happen. Either the complete R plasmid becomes integrated with the Ti plasmid or, if it carries a transposon, the transposon promptly passes or 'jumps' into the Ti plasmid. A typical property of a transposon is its ability to insert itself in any type of DNA present in the bacterium, independently of the recombination system which normally controls DNA recombination. Because of this property transposons are often called 'jumping genes'.

The position of the insertions in a plasmid can be determined by the use of certain enzymes known as restriction endonucleases. These enzymes break DNA at specific sites giving a digest of a plasmid consisting of fragments of different sizes. These fragments can be separated by electrophoresis on agarose gels. Since each enzyme cleaves DNA at sites specific for the enzyme, the fragmentation pattern in the gel is dependent on the enzyme used. The sequence of the fragments in the plasmid for a certain restriction endonuclease can be determined by DNA-DNA hybridization and the use of different enzymes. In this way a physical map of a plasmid can be made on which the specific cleavage sites of the enzymes are fixed positions. Since both R plasmids and transposons have a fixed size their insertion position in the Ti plasmid can easily be mapped by restriction enzyme analysis. This is shown in Fig. 8.8 for R plasmid 702 and for a position of the transposon Tn 1, which carries genes for carbenicillin resistance. By the use of transposon insertions a fine mapping of Ti plasmid functions can be made. Each insertion takes place at a different site and prevents the expression of the gene in which the insertion occurs.

Ti plasmids with inserted transposons are also useful for the isolation of deletion mutants. In deletion mutants part of the DNA is eliminated. Deletions often start at the ends of transposons, which allows plasmid mutants to be isolated which have deletions that start from the different transposon insertion sites.

Studies with these different types of plasmid mutants (Koekman et al., 1979) have shown that the right side of the octopine Ti plasmid, as shown in Fig 8.8, is not essential in tumour formation. Even when the deletions extend far into the T-DNA, the bacteria are still able to induce tumours on *Kalanchoe* stems, although the tumours grow slowly. These tumours, however, do not synthesize the enzyme lysopine dehydrogenase. The position of the gene determining this enzyme is indicated on the genetic map in Fig. 8.8. Also indicated are the regions carrying genes of the plasmid replicator, genes for the utilization of octopine (*uad* genes) and genes for conjugation (*tra* genes). Generally many *tra* genes are involved in the conjugation mechanism and presumably at least a number of them are located at the indicated region.

The data available so far demonstrate that, except for the left side of the T-DNA, with its presumed region of oncogenicity, the rest of the T-DNA can in principle be replaced by genes useful for the genetic engineering of plants. In relation to the expression of these genes it is important to note again the observation of Merlo et al. (1978) that the right side of the T-DNA has the largest copy number. Schell (1978) and coworkers at Ghent, Belgium, studied the question of whether foreign genes in T-DNA would be transferred and maintained in plant cells. For this purpose they used a nopaline Ti plasmid mutant with a transposon insertion in the nonessential part of the T-DNA. A transposon for streptomycin resistance was used. They made the important observation that T-DNA with the transposon is present in callus tissue derived from crown galls induced by this mutant and is maintained during subculturing. Expression of this transposon in the plant cells has not yet been reported. But in any case, it has been demonstrated clearly that foreign genes unrelated to the Ti plasmid can be incorporated in the plant genome. Because the frequency of tumour induction by *A. tumefaciens* is high and the DNA is well protected in this bacterium, it may be considered desirable to use this organism, carrying a modified Ti plasmid, as a tool for genetic engineering in plant cells; but in order to do so, it is necessary to know the number and position of all virulence genes. It appears that several sites on the left side of the octopine Ti plasmid, which are located far from the T-region, are important for virulence, for we have found that insertions at these sites cause avirulence. It is not yet known whether the corresponding genes have a transient function in the plant cell in those cases where the complete Ti plasmid appears to be transferred, or whether they are needed for the bacterium to accomplish tumour induction.

TRANSFORMATION OF PROTOPLASTS

Transformation of single cells is a prerequisite if cells with newly acquired properties are to be selected. The development of an *in vitro* system for the transformation of single cells by either *A. tumefaciens* or Ti plasmid DNA would be important. It has recently been found that cell-wall regenerating protoplasts isolated from leaves of a tobacco mutant (*Nicotiana tabacum*), which is resistant to streptomycin, can be transformed by *A. tumefaciens.* A large number of calluses were obtained which had acquired the capacity for phytohormone-independent growth and which synthesized lysopine dehydrogenase. Interestingly, several of the calluses developed shoots (Marton et al., 1979), and these tumour shoots retained the capacity to synthezise lysopine dehydrogenase, as did callus tissues obtained from protoplasts isolated from the small leaves of the shoots. Shoot development from octopine-producing callus tissues is remarkable because this is not generally observed to occur in octopine calluses derived from crown galls induced on plants.

Preliminary data from our laboratory at Leiden, Netherlands, and the laboratory of Cocking in England suggest that *Petunia* and tobacco protoplasts can also be transformed with Ti plasmid DNA. If it appears that this system allows transformation to be effected reproducibly and with a sufficiently high frequency, then it will be possible to determine whether T-DNA alone is sufficient for plant cell transformation. The possibility of transformation using T-DNA alone would reduce the problems of 'engineering' the Ti plasmid by means of recombinant DNA technology. Problems may however arise where there is too large a number of virulence genes. Another reason why transformation of protoplasts by means of DNA would be an important breakthrough in studies on the genetic engineering of plant cells is that it might facilitate the transformation of cells from monocotyledons which are not susceptible to *A. tumefaciens.*

PLANTS FROM TUMOUR CELLS

As mentioned earlier, teratomas can develop from nopaline-producing crown galls on plants. The first evidence that these teratomas develop from tumour cells came from experiments with cloned lines of nopaline-producing tobacco crown gall tissues performed by Braun (1978). Under suitable conditions more or less well-developed shoots were obtained. When the best-developed shoots were grafted on to the apices of healthy plants of another tobacco variety some of them formed morphologically and functionally normal apical shoots that flowered and set seed. It was shown that the tumour shoots still synthesized nopaline dehydrogenase, were not susceptible to *A. tumefaciens* and contained T-DNA. Haploid tissues derived from anthers and plants of the F_1 generation obtained from teratoma-derived seeds after self pollination lack nopaline dehydrogenase and T-DNA (Merlo et al., 1978). The loss of T-DNA may be due to some repair mechanism acting during meiosis. If it appears that T-DNA is always lost during meiosis, this would be a serious obstacle to genetic engineering. However, this would not constitute a problem in vegetatively propagated species such as potato and cassava.

FUSION OF NORMAL CELLS WITH CROWN GALL CELLS

By means of cell fusion different genotypes can be combined *in vitro*. Somatic cell hybridization has been shown to be possible by means of the fusion of protoplasts. This procedure might be useful for transmitting new genes which are integrated in the genome of a crown gall cell into the chromosomal background of another plant species. It might also be of use when problems are encountered in the regeneration of plants from 'engineered' cells. It is conceivable that when these cells are fused with cells of a plant species with a high regenerative capacity in tissue culture, fusion products will be obtained from which shoots will develop. We have tested this possibility for a cloned octopine-producing tobacco crown gall callus which could not be induced to form shoots under any conditions. The crown gall tissue was derived from a leaf tumour on the tobacco cultivar White Burley. Protoplasts isolated from the cloned callus tissue were fused with protoplasts isolated from leaves of a mutant of the tobacco Petit Havana, which was resistant to streptomycin. The selection of fusion products was based on the properties of the tumour protoplasts, such as white colour of the callus, hormone-independent growth and the synthesis of lysopine dehydrogenase, and on the properties of the other parent, such as hormone-dependent growth, streptomycin resistance and formation of green callus tissues. After fusion a small number of calluses were obtained which were green, phytohormone independent and streptomycin resistant. They also synthesized lysopine dehydrogenase and regenerated shoots spontaneously. In this way shoot cultures were obtained giving plantlets which, compared to normal tobacco plants, had acquired three new properties. These are: streptomycin resistance, acquired by selection of mutant cells in tissue culture, the capacity to synthesize lysopine dehydrogenase, and resistance to *A. tumefaciens*, acquired via Ti plasmid genes.

PERSPECTIVES

From a technical point of view it may be concluded that the first steps on the long road leading to successful genetic engineering in higher plants through the integration of new genes have been taken. It can be expected that in the near future 'artificial' plants will be obtained with selected new genes. What types of genes should be incorporated and how do we isolate these genes? It is clear that many plant characters are polygenic, with poorly characterized genes. This makes them unsuitable. In the case of a protein for which the aminoacid sequence is known or for which the mRNA can be obtained in a pure form, the corresponding DNA sequence can be synthesized *in vitro*. Methods of synthesizing DNA enzymatically from an RNA template or by chemical means are developing rapidly. By means of recombinant DNA technology the synthesized gene can be integrated first in a Ti plasmid derived vehicle and thence in the plant genome.

It should also in principle be possible to integrate the *nif* genes of *Rhizobium*, which carry the information for a nitrogenase complex active in N_2 fixation. This would confer on plant cells the capacity for nitrogen fixation. The nitrogenase enzyme complex, however, is very sensitive to oxidation by oxygen. In root nodules induced by *Rhizobium* on leguminous plants the nitrogenase of bacteroids is protected from inactivation by leghaemoglobin, a plant gene product formed in the nodules. The haemoglobin maintains the concentration of dissolved oxygen at a level that is sufficient to support ATP formation through oxidative phosphorylation but insufficient to inactivate the nitrogenase of the bacteroids. If the gene for leghaemoglobin is linked to the *nif* genes and both together are integrated in the plant genome the result might be nitrogen-fixing plant cells. It has proved possible to isolate the mRNA for leghaemoglobin and this can be used to synthesize enzymatically a DNA copy that can be linked to the *nif* genes. Recent studies indicate that the *nif* genes of *Rhizobium* are clustered on a large plasmid (Nuti et al., 1978). This would make them available for genetic engineering experiments. However, even if the procedures prove effective, it remains to be seen whether the energy-consuming process of nitrogen fixation interferes seriously with plant development. If it does, then the induction of nitrogen-fixing tumours on plants at a suitable moment in their development might be an interesting alternative in a number of cases.

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with the collaboration of
J.G.T. Hermsen on haploids
T.A. Lie and E.G. Mulder on symbiotic nitrogen fixation
P. Miedema and W.M.J. van Gelder on mitochondrial complementation and combining ability
E.C. Cocking and J.B. Power on applications of tissue culture
R.A. Schilperoort on Ti plasmids as potential vectors for genetic engineering

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9 Seed production and distribution

Improved varieties are of great importance for agriculture, but equal importance should be attached to the production of high-quality seed that can reach the farmer through efficient and reliable distribution channels. Efforts to improve seed distribution in the developing world are being sponsored by the SIDP and promoted under bilateral agreements between developed and developing countries. Before a new variety is accepted, it has to be tested for distinctness, homogeneity, stability and, where breeders' rights are involved, also for newness. Finally, if the variety is found to have good agronomic value, it is entered in a varietal list. In many countries this is a recommended list only; elsewhere it is a compulsory list. The maintenance of the variety and the production of breeder's seed are the responsibility of the breeder. The subsequent production of basic seed is often the combined responsibility of the breeder and the seed inspection service, and certified seed is then produced by farmers under the supervision of an inspection service. The complete seed production cycle thus takes at least six years. Special maintenance and production procedures are applicable to vegetatively propagated crops (e.g. potato), open-pollinated crops (e.g. perennial ryegrass) and hybrid varieties (e.g. maize and sugar beet). The ultimate aim of an inspection service is to guarantee that the seed the farmer buys is true to type and of good quality. Regulations on variety quality, seed quality, plant variety protection and plant quarantine play a role in breeding and the import and export of seed. In countries without plant variety protection, breeding work in all crops, including autogamous and vegetatively propagated crops, may be carried out at state institutes, while the private breeding stations mostly concentrate on hybrid varieties. In countries where plant variety protection exists, private breeders are generally numerous and work on many different crops, the result being a wide choice of varieties for the farmer. Various systems for the supply of good seed are to be found in both the developed and developing world. Selected examples are the systems in use in the Netherlands, Kenya, Tunisia, Taiwan and Romania.

Introduction

The word 'seed' in the present chapter should be understood to include both seed and other propagating material, unless otherwise indicated. The aim of any seed production and distribution system should be to supply farmers with reliable seed of varieties which have demonstrated their good performance in extensive tests. A supply of good-quality seed can be an effective means of improving food production; even in the absence of new and better varieties, adequate supplies of reliable seed of existing varieties would have a favourable effect. In addition, the effect of plant breeding on food production will depend on the efficiency of seed distribution: only if the improved varieties reach the farmer through a reliable seed distribution channel will he be able to use them effectively to produce more food.

The efficiency of a seed distribution system depends on:
- the variety evaluation system,
- the system of varietal maintenance,
- the availability of new and better varieties,
- the control of seed production.

Many countries have regulations or laws aimed at promoting the efficient distribution of seed. Countries differ in their approach, however, and some of the differences are crucial, being the result of different views on plant breeders' rights. Problems relating to these regulations are discussed in this chapter.

Variety evaluation

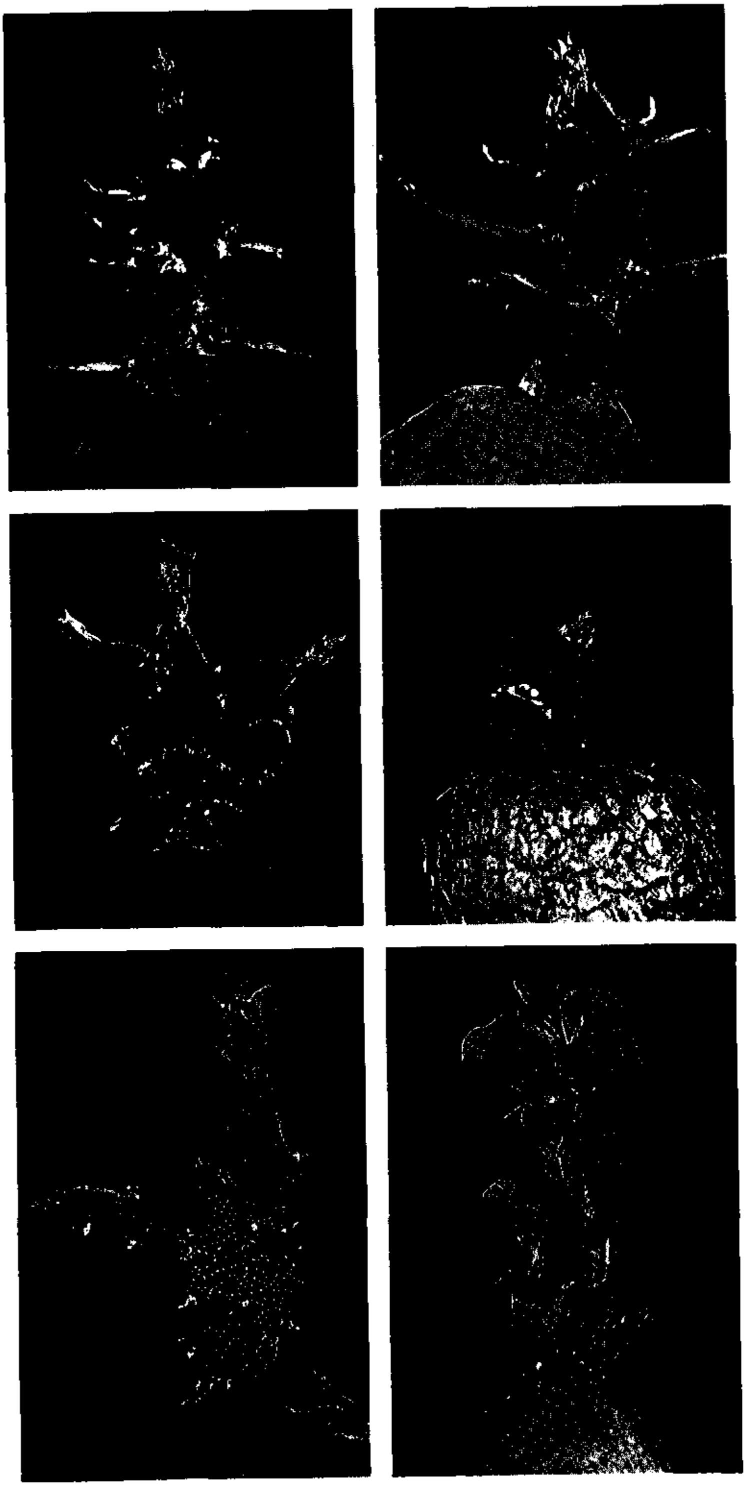
The evaluation of a variety comprises two stages:
- establishment of distinctness, homogeneity and stability,
- establishment of agronomic value.

Evaluation is normally carried out by an independent authority, i.e. one which is completely independent of the parties concerned. The latter may be plant breeders, agricultural processing industries, seed producers, seed companies etc. Independence is necessary to ensure proper evaluation. Mudra (1975) considers that the best form of organization is undoubtedly a governmental agency or at least an independent committee charged with the supervision and control of all activities related to variety evaluation.

DISTINCTNESS, HOMOGENEITY AND STABILITY

When a new variety is submitted for evaluation, the first point that has to be established is its distinctness. For this purpose a description of the morphological characters of the variety has to be made, special attention being given to those features which distinguish the variety from existing varieties. Various morphological characters, and in some cases physiological characters too, may be suitable for this purpose. An example of a character used in distinguishing potato varieties is given in Fig. 9.1. This shows a series of photographs of sprouting potatoes differing in pigmentation. Such photographs are prepared and used as a standard of reference in distinguishing potato varieties by the Dutch Government Institute for Research on Varieties of Cultivated Plants (RIVRO). Establishment of distinctness is necessary for the identification of the variety in the seed production fields by the inspection service. It also has to be shown that a new variety is sufficiently different from existing varieties to make the much more expensive determination of agronomic value worthwhile.

Homogeneity of a variety is required by growers, processors, consumers and agricultural engineers (cf. Chapter 3, p. 90 and Table 3.1). Homogeneity is also required for the identification of a variety in the seed production field, to ensure that a variety is stable and, where applicable, for purposes of varietal protection. Howev-



er, it is important that homogeneity requirements should not be too rigorous; they should preferably not be more stringent than is necessary for the preservation of distinctness. Homogeneity should never be a goal in itself. Spitz (1975) points out that legislation and the structure of the seed industry must be realistic and that it is therefore necessary to take into account the present state of agriculture within the economy and the alternative paths offered for its development.

Stability is a characteristic desired by the farmer, because only a stable variety will perform in accordance with expectations based on the results of tests of the variety for agronomic value.

AGRONOMIC VALUE

For the establishment of agronomic value an efficient system of testing is necessary. Guidelines are given in Chapter 4, pp. 112-120, and further information can be found in Mudra (1975) and in many other textbooks. The scope of testing should be such that significant yield differences amounting to only a few percent can be determined. Special observation trails may also sometimes be necessary, for instance to determine differences in disease resistance under artificial infection.

For new varieties showing marked differences in development, growth habit etc., it may be of importance to ensure that the agronomic practices used in the trials are in accordance with the specifications supplied by the breeder for the particular variety.

If the results of the examination for distinctness, homogeneity, stability and agronomic value are favourable the new variety can be released for use by farmers. In many countries this means that the variety will be entered in a variety list. Some countries have a compulsory list, which means that only seed of varieties placed on the list may be sold. Other countries have a recommended list only, in which case rejected varieties cannot be excluded from use. In 1975 the European Economic Community (EEC) published its first list of accepted cultivars valid for the whole community. A variety accepted in any EEC member state will normally be entered in the EEC list after two years, but member states can exclude any variety from use in their country provided that cogent reasons can be produced. The fifth edition of this list is currently available (EEC, 1979).

Certain regulations relating to the international seed trade are laid down in the Organisation for Economic Co-operation and Development Council Decisions of 11 February 1970 (OECD, 1970), and a list of cultivars eligible for certification is published each year. In the 1978 list (OECD, 1978), the following crops are eligible for OECD seed certification: herbage and oil crops, cereals, beet, subterranean clo-

Fig. 9.1. Sprouting potatoes differing in pigmentation. (Photographs: RIVRO.)

ver and similar species and maize. There are now 34 participating countries, in which a total of 560 companies and institutions are responsible for the maintenance of the accepted varieties; two thirds of these companies are located in the nine countries of the EEC.

Variety maintenance

To ensure the stability of accepted varieties a suitable varietal maintenance system is essential. The appropriate method will depend on the mode of reproduction of the crop, whether vegetative or sexual, and in the latter case on whether seed is set by self fertilization or cross fertilization. The choice of system will also depend on the multiplication rate of the cultivar. In vegetatively propagated crops, the major problem is the prevention of virus infection, as described below for potato. Our other examples of varietal maintenance procedures relate to autogamous crops (small grains), crops in which both vegetative and sexual propagation is possible (perennial ryegrass), and allogamous crops (maize and sugar beet). Although each method has many possible variants, the essential feature in each case is that no genetic changes occur during maintenance, or in other words that the stability of the variety is assured.

POTATOES

Fig. 9.2. presents the scheme used for the maintenance of a potato variety (*Solanum tuberosum*) in the Netherlands. Six different generations of seed potatoes are recognized for purposes of certification. These are indicated by the letters S, SE, E, A, B and C. In international trade the generations S, SE and E are known as basic seed potatoes and the generations A, B and C as certified seed potatoes. The first four years of selection (at least) are handled by basic seed potato producers approved by the Netherlands General Inspection Service for Field Crops (NAK). For a new variety the basic seed producer is usually the breeder. As starting material for each new cycle of maintenance single-plant selections are made within a field of third-generation clones. These single-plant selections will produce first-year clones in the next generation. The clones are verified as being true to type and free from virus infection. Each clone is harvested individually and planted out the following year for the production of the second-year clones. Similar selection is carried out in the second and third years. The third-year clones are continued as separate lines for the fourth and fifth years (the symbol S in the third to the fifth generations applies to the separate single-plant clones).

At the same time a mixture of seed potatoes from the third-year and older clones will be certified as class SE and used for distribution to other seed potato producers. These other producers multiply the class SE potatoes to give class E seed potatoes, which then in the next generation become class A seed potatoes and in the following generation are classed as B or C according to the degree of virus infection. The seed

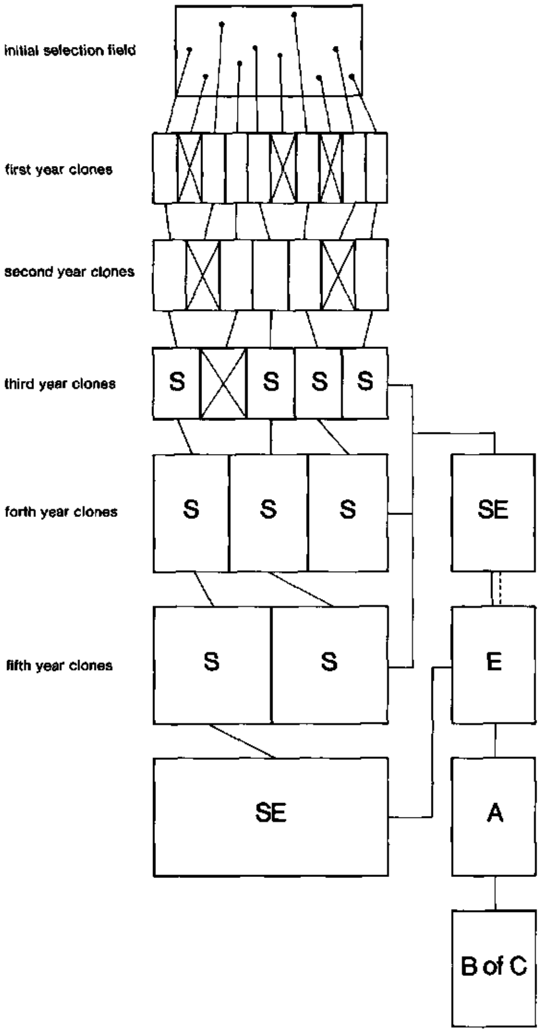


Fig. 9.2. Variety maintenance in potatoes.

potatoes of class S are never more than five generations removed from the initial plant selections. All seed potato production fields are harvested or at least defoliated before the first major aphid flights occur, in order to prevent virus infection. Classes B and C are used as seed for commercial potato production.

The Netherlands exports large quantities of seed potatoes, with the result that many countries prefer to have their seed potatoes classified according to the Dutch system rather than the system which distinguishes only basic and certified seed.

PERENNIAL RYEGRASS

As shown in Chapter 4, p. 180, a variety of perennial ryegrass (*Lolium perenne*) may be selected in different ways: it may originate from selected clones or it may be based on a single seed stock. Whatever the source, the initial seed multiplication requires about one hectare, and whether the variety is of clonal origin or is derived from a single seed stock, such as a selected variety cross, the initial material must be propagated vegetatively until enough material is available for planting the seed production field.

The cultivation, drying, cleaning etc. of the first seed multiplication requires the utmost care so that the final product has a high germination rate, is free from other seeds, especially weeds, and has a moisture content varying between 6 and 8%. The first seed multiplication may yield about 500 kg of breeder's seed. Stored at a temperature of 3 °C and a relative humidity of 30% this seed will maintain its germination capacity for a minimum of ten years.

The breeder's seed is used for the production of prebasic seed. A production area of about one hectare of prebasic seed will usually suffice for several years. In the scheme shown in Fig. 9.3 the first seed production from the prebasic seed in turn gives sufficient basic seed for the production of certified seed in years 4, 5, 6 and 7. For further production of certified seed a new production of prebasic seed has to be set up in year 4. In the example given, one ton of breeder's seed will cover the needs of at least 15 years of certified seed production.

In the course of multiplication, problems may arise from the presence of impurities, such as seeds of other grass species or, more seriously, of noxious weeds. It is not always possible to remove these impurities, in which case the material must be discarded. In estimating the quantities of prebasic and basic seed needed, it is therefore desirable to allow a wide safety margin, so that it will be possible to repeat any stage of multiplication if necessary.

AUTOGAMOUS SMALL GRAINS

Fig. 9.4 gives a scheme for the maintenance of a variety of wheat (*Triticum aestivum*), barley (*Hordeum vulgare*) or oats (*Avena sativa*). As a first step in maintaining a variety, ear selections are taken either from a field sown with breeder's seed or, in the case of a variety which has been in existence for some time, from three-year-old lines, the third year in the maintenance cycle being the last year in which all lines are multiplied separately.

In the following year, the selected ears result in first-year lines which are sown out in 80 cm rows. All lines containing plants which are not true to type or which are infected with seed-borne diseases are eliminated and the lines retained are threshed separately and sown out in plots of about 12 m^2 for the production of second-year lines. The same procedure is followed for these lines and produces selected lines with a yield of around 4 kg per line.

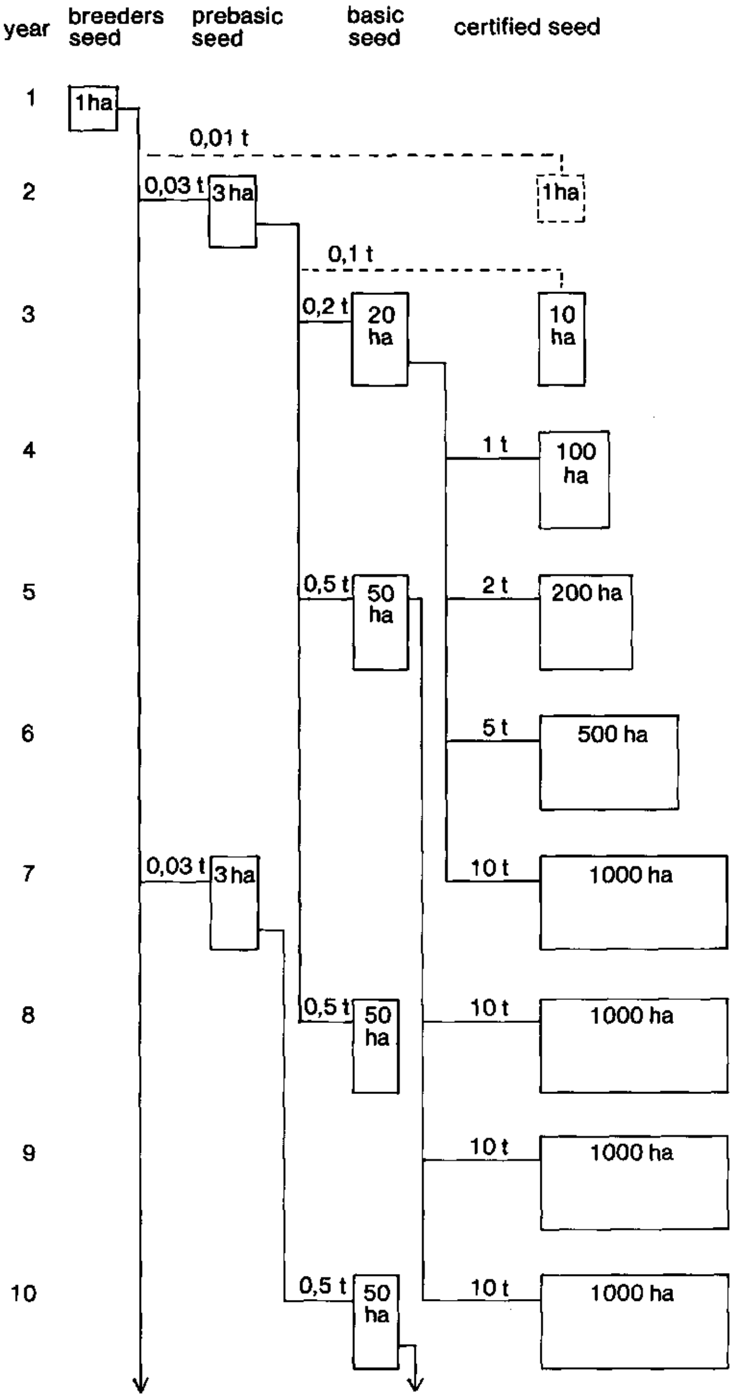


Fig. 9.3. Variety maintenance in perennial ryegrass.

This seed is used to produce third year-lines which are sown out in fields of 200 m^2, and at this stage the retained lines yield about 60 kg of seed. The seed harvested from these lines is mixed together to give the prebasic seed for the production of basic seed, which in turn will be used to produce the certified seed. The multiplication of the prebasic seed is controlled by the breeder and generally also by the inspection service, whereas the production of certified seed is mostly carried out by growers under contract with seed firms, under the supervision of the inspection service. The scope of the maintenance procedure depends on the amount of seed necessary. In general it can be stated that, to produce 1000 kg of prebasic seed, 100 ear selections are required in the first year.

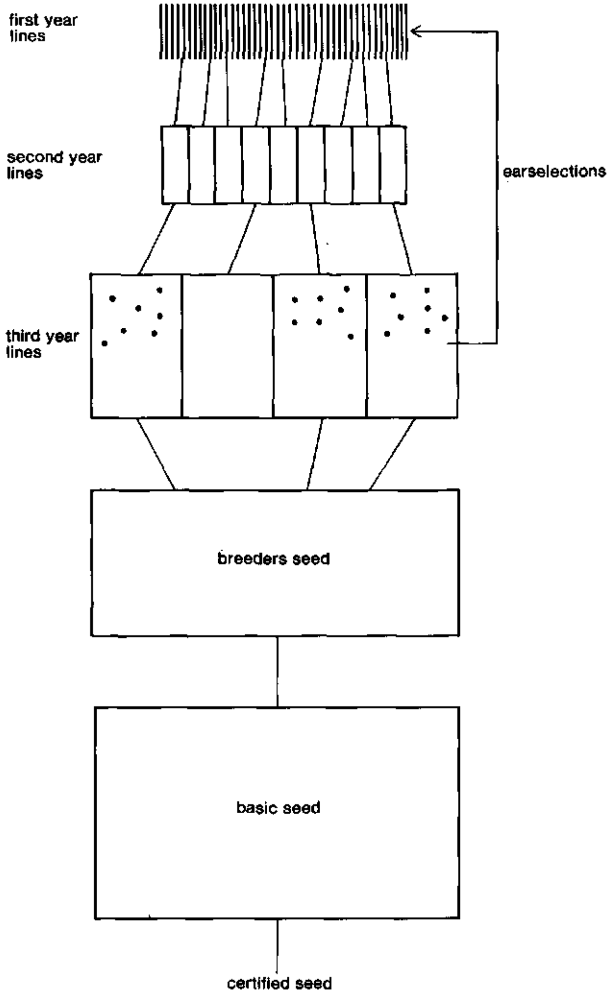


Fig. 9.4. Variety maintenance in an autogamous cereal.

MAIZE

The maintenance of a hybrid variety of maize (*Zea mays*) is based on the maintenance of its parental components, which are usually homozygous inbred lines. The maintenance of an inbred line starts with the production of breeder's seed. This seed is produced from a number of self-pollinated plants, which have all been verified as being true to type. The verification procedure involves ear-to-row sowing of control seeds of the self-pollinated ears, using a special trial corn planter (Fig. 9.5). The remnant seed of the rows which are true to type is then bulked as breeder's seed. A sufficient quantity of breeder's seed, usually several kilograms, is placed in cold storage to provide the nucleus for future seed multiplication. With proper management this seed stock may last ten years or more before renewal becomes necessary.

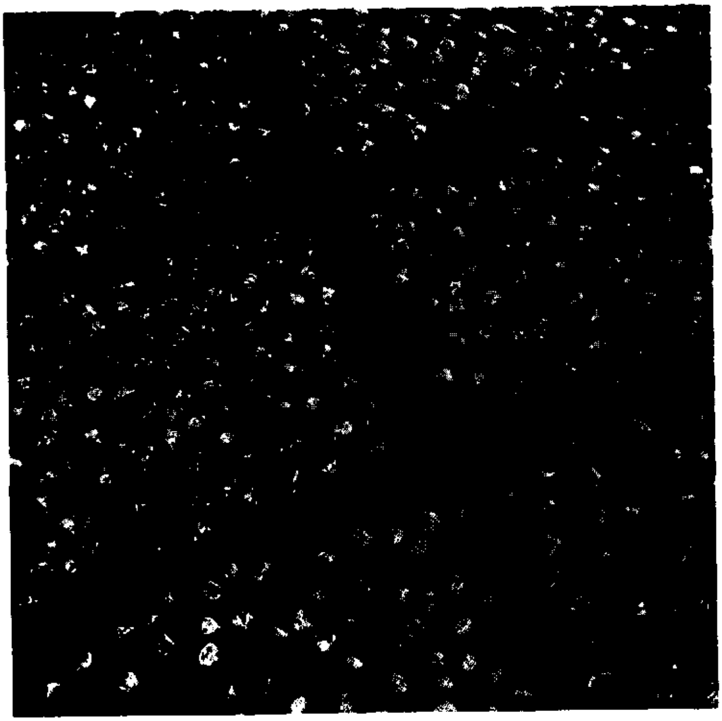
The next step is to grow a small quantity of breeder's seed in an inbred increase nursery. The plants are hand pollinated, either by selfing or by sibbing. Selfing serves to maintain the inbred line in its pure condition, while sibbing tends to prevent an excessive loss of vigour.

Seed from the inbred increase nursery is used to grow the inbred maintenance seed stock, which is produced in a well-isolated block by natural random sib mating. The purity of the seed harvested is verified in a grow-out. In most cases, any outcrosses that occur in an inbred line are readily detected.

The inbred maintenance seed or prebasic seed is used in turn for the production of basic seed. Basic seed may be either an inbred line, a single cross, or a cross between sister lines, depending on the type of hybrid. If the basic seed is an inbred line, it is produced in an isolated increase block. If it is a single cross, the seed is grown in an isolated crossing block in which the female parent is detasselled. Before the parent seed is used, its genetic purity should again be verified in grow-out tests. To save time this is often done during the winter, at a location with a suitable climate. Basic seed of proven genetic purity may then be used in the following year to produce the certified hybrid seed. To facilitate hybrid seed production, different colours of seed dressing may be used to distinguish male and female parents. An example of this is shown in Fig. 9.6.

The multiplication factor for maize may be roughly set at 1 : 100. Thus every hundred hectares of maize requires about one hectare of seed production. The actual figure depends on the type of hybrid; seed production of double and three-way crosses normally requires less space than that of single crosses.

The production of adequate amounts of hybrid seed requires several years of advance planning. It is common practice to keep fairly large buffer stocks of the different seed generations in cold storage available, as a safeguard both against crop failure and against unexpected demands.



SUGAR BEET

The special problems associated with the maintenance of a triploid sugar beet hybrid (*Beta vulgaris*) as compared with a maize hybrid are related to the greater difficulty of controlling the purity of the basic material and to its greater genetic complexity. Favourable features of the crop are the possibility of vegetative multiplication, the high multiplication rate (1 : 1000 for the production of breeder's seed and 1 : 300 for the production of certified seed) and the possibility of annual seed production for experimental purposes parallel to the biennial commercial production. This last feature allows the breeder to produce experimental quantities of a hybrid two years before he produces the genetically identical certified seed, thus giving him an extra two years of yield tests before the certified seed is issued to farmers.

As shown in Chapter 4 (sugar beet, p. 213), the prebasic material of a triploid hybrid consists of a diploid male-sterile line, a diploid pollinator (O-type) and a tetraploid F_1 cross or mixture of F_1 crosses.

Basic seed is produced in two isolated fields. In the first a single cross of the two diploid lines is produced by planting out alternating rows of male-sterile plants and pollinators in a ratio of two rows of the pollinator to four or six rows of the male-sterile line. Only the single-cross seed is harvested and the pollinator rows are destroyed before the seed is ripe. The utmost care should be taken to ensure that no seed from the pollinator is mixed with the seed harvested from the sterile plants. The second field is used for the production of the F_2 of the tetraploid. Both fields should be large enough to provide sufficient basic seed for at least four years of certified seed production. The basic seed is stored under optimum conditions and before being used for certified seed production it is tested for varietal purity, sterility and ploidy. Not less than two years before the stock runs out, a new production of basic seed is set up, which is tested in the same way prior to certified seed production. The production fields for basic seed are controlled by the breeder. The fields of the male-sterile single cross are checked plant by plant for sterility in the female rows, and in the case of monogerm seed production female and male parents are both checked for the monogerm character. As both characters are genetically recessive, their frequency will decrease in the next generation. Hence isolation is also extremely important.

The basic seed is delivered to the grower of certified seed under the seal of the inspection service. For this reason, although the responsibility for the production of

Fig. 9.5. Special planter for maize trials. Operators drop contents of seed packets into a separate unit for each row. (Photograph: Pioneer Hi-Bred International Inc.)

Fig. 9.6. Germination tray for cold test of maize seed. Different entries are distinguished by coloured seed dressings. Similar dressings are used for distinguishing male and female parents. (Photograph: Pioneer Hi-Bred International Inc.)

basic seed rests entirely with the breeder, the fields are also inspected by the inspection authority.

For the production of certified triploid seed two male rows alternating with six female rows are planted out (or sown, in case of direct seed production). For the production of diploid hybrids, a lower ratio of male rows can be used. The male rows are eliminated before the hybrid seed is harvested from the female rows.

In the case of the production of triploid monogerm hybrids it is possible to use a mixture of the female and male parents as basic seed. The pollinator in this case is tetraploid multigerm stock which produces seeds which are so much bigger than the monogerm hybrid seed that they are readily removed.

Fig. 9.7. Checking sugar beet seed lots for outcrosses. General view of the glasshouse. (Photograph: M. de Goffau.)

The production of the certified seed is controlled by the inspection service and control by the breeder is not required by law, but the risk of outcrossing and low germination in this crop is so great that practically all breeders also carry out their own field inspections at this stage. Despite all these controls, crosses produced by stray pollen from garden beets, fodder beets and, most dangerous of all, annual beets, may still be present and in the autumn most breeders therefore check each seed lot by sowing samples in the glasshouse at a temperature of 20 °C and under continuous light of high intensity (Fig. 9.7 and 9.8). Under these conditions unwanted outcrosses can be recognized six weeks after sowing.

Fig. 9.8. Checking sugar beet seed lots for outcrosses. The seedlings are being checked for colour and stem elongation. Foreground right: outcrosses. (Photograph: M. de Goffau.)

Availability of new varieties

The extent to which new varieties are available in a country depends on the one hand on the amount of breeding activity within that country and the possibility of importing varieties and on the other hand on government regulations controlling the release of new varieties. Breeders may be private persons, companies or government institutions. In many countries both private and government breeders are active but in other countries practical breeding work is exclusively or predominantly carried out by one or other of these groups. Much depends on whether or not a country grants plant breeders' rights. At a meeting of the California Seed Association, White (1971) remarked that the first consequence of the signing of the Plant Variety Protection Act on December 24, 1970, in the USA would be that the seed industry research programme would be vastly expanded. Previously American seed companies had largely restricted their breeding efforts to hybrid programmes because of the protection for the breeder afforded by hybrids, but as a result of the act conventional breeding of such crops as soya beans and cereals increased considerably. The attitude of private breeders to the breeding of autogamous crops is in fact frequently found to depend on whether or not their country has plant breeders' rights; the attitude of foreign breeders to the export of their varieties into other countries shows a similar dependence.

As far as hybrid varieties are concerned the breeder is automatically protected and hence he will be interested in establishing a market even in countries without plant variety protection. There will however be some differences relating to certified seed production. In a foreign country with breeders' protection the breeder will normally be willing to produce the certified seed in that country for local use and even for export to other countries, but in a country that provides no protection he will prefer to import the certified seed, and this makes the seed more expensive for the recipient country.

In the case of potato varieties, nature provides another kind of protection, due to the rapid degeneration undergone by potato varieties unless they are reproduced under stringent conditions of virus control. In general, potato breeders rely on this protection and readily export their varieties even to countries that have no variety protection.

It is clear that private breeders will generally not be interested in breeding or importing their varieties of autogamous crops into countries without plant variety protection. In such countries the farmer is dependent on local state breeding stations for new and better varieties. Landenmark (1975) points out that in a country where breeding work is entirely in the hands of a single government institute, regulations controlling variety release are important for the protection of the farmer. For autogamous crops the existence of plant variety protection will make a larger range of varieties available.

Government regulations controlling the release of new varieties can also have an adverse effect, for example when they result in excessive bureaucracy and cause delays in the introduction of the new varieties. Unreasonable requirements for homogeneity, varietal purity, purity of inbred lines etc. may not only delay the introduction of a good variety but can even result in its rejection. Here again governments should take a pragmatic view and adapt their demands to the requirements of the farmers in their country.

Seed production control

The purpose of the control systems used in the seed industry is to guarantee that the seed a farmer buys belongs to the variety he has ordered and is of good quality. This involves control of the identity and purity of the variety and control of the more important properties of the seed itself. Seed treatment and packaging also require attention. Finally, certification provides the farmer with the assurance that the seed he is buying has passed all necessary controls.

Field inspection

Field inspection involves identification of the variety, determination of varietal purity, and recognition of seed-borne diseases, noxious weeds and plants of other crops. Isolation is also controlled: in autogamous crops the distance between seed production fields of different varieties of the same species must be sufficiently great to prevent mechanical mixing, and in allogamous crops it must be sufficiently great to prevent cross pollination. The actual distance depends on the species, on whether hybrid or open-pollinated seed is being produced, on ploidy, on the nature of the differences between the varieties in the adjacent fields and on the size of each field.

Seed testing

Laboratory seed tests include verification of identity and varietal purity, in so far as this is possible. The next step is the determination of moisture content and analytical purity, the sample being separated into pure seed, seed from other crops, weed seeds and inert impurities. The pure seed is used for the determination of germination and health. International rules for seed testing have been published by the International Seed Testing Association (ISTA, 1976).

Precontrol and postcontrol

For the precontrol tests, a sample of the seed lot intended for multiplication is sown by the inspection service on control plots for comparison with plots of an authentic sample of the cultivar. The control field is kept under observation throughout the growing season, thus enabling the inspector to check the seed lot for identity, varietal purity and health.

For the postcontrol tests a sample of each seed lot harvested is again sown by the inspection service to check the effectiveness of the control work in the production field of the previous season.

SEED TREATMENT AND PACKAGING

Seeds are often treated with chemicals as a protection against seed-borne and soil-borne diseases, and against insects and birds. Systemic fungicides are also in use to protect the plants from later infection with such fungi as mildew or rusts. Formerly organomercury fungicides were used extensively, but more and more countries are now prohibiting these fungicides in order to protect the environment. The use of HCH-based insecticides is being discouraged for the same reason. In producing seed for any particular country or region it is therefore necessary to determine first what sort of seed protection is advisable and second which chemicals are permitted. In treating the seed, special care is needed to ensure a uniform dressing of all the seeds.

In warm and humid climates special care should be taken in packaging the seed for retail distribution. Where the conditions of storage between time of delivery and time of sowing are unfavourable, and especially where the atmosphere is very humid, moisture-proof packaging may be desirable but in this case the seed should be subjected to extra drying to reduce the moisture content (in the case of cereals to below 9%).

CERTIFICATION

When a seed lot has passed through the control measures mentioned above and been found adequate, it can receive certification. Certain certificates issued by official seed testing stations are based on laboratory analyses only, and do not require field inspection. Many countries, however, have seed certification schemes in which the entire seed production process is subject to supervision. Schemes of this kind can promote the availability of high-quality seed of tested varieties. They also expedite the introduction of superior new varieties and improve the stability of existing varieties. Certified seed will automatically promote its own further use when the farmer discovers that certified seed generally yields more than seed retained from his own harvest.

Regulations

ON VARIETAL QUALITY

Regulations governing the quality of new varieties are commonly applied in industrial crops. Often they are not required by law but are specified by the industry. Sugar beet factories, for example, lay down quality requirements for sugar beet varieties, such as minimum values for sugar content and juice purity. The regulations differ between countries, and the breeder should be aware of the different requirements.

Another example is provided by barley, where a distinction is often made between malting varieties and feed varieties. In the case of wheat, regulations on baking quality may be laid down by law, or they may merely be formulated by the milling and baking industry.

A regulation of a more general nature is the so-called GRAS ('generally recognized as safe') regulation in the USA, which was originally applicable to food and food additives but which is now also applicable to new varieties. The object of the GRAS regulation is to prevent a significant decline in the nutrient content of food crops (Senti & Rizek, 1975). A decline of this kind might result from the introduction of varieties with a reduced content of an important nutrient, e.g. a vitamin. In the USA oranges and tomatoes are regarded as important sources of vitamin C and new varieties of these crops should not have a significantly lower level of vitamin C than existing varieties. It is also desirable to prevent any increase from occurring in the content of toxic substances as a result of breeding (Gabelman, 1975). Solanine is a toxic compound present in potatoes, large genetic differences in content being found between varieties. A high level of solanine is found in the variety Lenape, which had to be withdrawn from the market for that reason.

ON SEED QUALITY

Seed certification is often covered by a law governing all aspects of breeding, seed production, seed certification and seed merchandizing. The first step to legal control in the seed trade involves the establishment of quality requirements for seeds.

The International Seed Testing Association (ISTA) was founded in 1924 with a view to standardizing the rules for the required laboratory tests. Member laboratories have all adopted the international rules and they use the International Seed Analyses certificate for recording the results of analyses. However, these certificates give little to no information on the identity or varietal purity of the seed lot. For these important properties a complete control procedure as described in the previous paragraphs is necessary, and this may well lead to a legalized seed certification programme.

Once a country has established a system of seed certification on a national level, it can adopt the OECD schemes and thus enter more readily into the international seed trade, and this then may have an important bearing on the country's import and export of certified seed.

ON PLANT VARIETY PROTECTION

Attempts to provide monetary incentives for plant breeding seem to have begun in the first quarter of the present century, when certain agricultural associations in the Netherlands began to offer modest premiums for outstanding varieties. Interest in promoting statutory schemes for the remuneration of breeding work grew during the 1920s, and in 1930 the Plant Patent Act was promulgated in the USA. This was based on a patent system not altogether suitable for the protection of breeders, as it covered only certain asexually propagated crops, excluding those propagated by tubers. The act was of no practical value as far as food crops were concerned, but it was an instance of the increasing recognition being accorded to breeding work.

In Germany the 1934 'Verordnung über Saatgut' (Seed Ordinance 1934) gave the breeder the sole right of sale of his varieties, on the condition that this did not work against the common good; government approval of the breeder's variety was a preliminary requirement. By this time, breeders' rights had begun to attract the attention of the legal profession, as appears from a doctoral thesis published in the Netherlands (van Harreveld, 1934).

A scheme to ensure adequate remuneration for breeders was introduced in the Netherlands in 1937 by the NAK for field crops. Under this scheme, which was approved by the government, an extra charge was made for the inspection of certified seed of a new variety, and from the fees collected in this way the breeder could be paid in proportion to the acreage of his varieties inspected.

It soon became apparent that a developing agriculture required not only better varieties but also a greater diversity of varieties suitable for mechanized farming methods. In attempting to meet these needs, breeding techniques became more complex and as greenhouses, laboratories and other equipment became necessary, the expenses of breeding also increased. Under these conditions, if private breeders were to continue to produce new varieties, they would have to receive compensation for their labour and expenses; otherwise, they would hardly be able to function and their undoubtedly valuable work would be seriously hampered. The only alternative would be to place all breeding work in the hands of public institutions – an alternative which generally found little favour in western Europe.

In the USA, however, where prior to 1972 there was no real protection for breeders, public or semipublic institutions were at that time responsible for a large part of varietal improvement work. This is perhaps one reason why private breeders in the USA have always been interested in hybrid varieties, which, in effect, have a built-in system of protection. In the Federal Republic of Germany and the Netherlands, where breeders' rights have been recognized for many years, much useful work has been done by private breeding firms and there are breeders actively working on a wide range of crops, including autogamous crops.

The Netherlands 'Plant Breeders' Decree 1941' gave the Dutch breeder the sole right over his variety on the condition that the variety was sufficiently distinct, homogeneous and stable and had not been put on the market before. It also authorized the regular publication of the *Descriptive List of Varieties of Field Crops* and gave legal status to the inspection service, thus helping to secure the production of high-quality seed. In the case of potatoes and cereals, the decree entitled anyone who so wished to propagate listed varieties, but part of the fees for the inspection of the propagation fields, supplemented by money from public funds, were credited to the breeder. There were also safeguards against misuse.

However, the Plant Breeders' Decree of 1941 was not without its opponents. Certain seed firms, for instance, which had been engaged in the growing and marketing of practically the entire range of available varieties of vegetable crops, saw it as a threat to their competence to maintain their overall range. These objections gradually faded as the seed firms themselves began to undertake more breeding work, and eventually, when their efforts had actually resulted in new varieties, they gave their full support to the decree. This may be regarded as evidence for the stimulating effect that exclusive ownership of a variety can have on breeding.

The year 1961 was of paramount importance for the protection of breeders' rights in western Europe, for that was the year that saw the conclusion of the 'Convention International pour la Protection des Obtentions Végétales' (International Convention for the Protection of New Varieties of Plants), commonly known as the Paris Convention. The purpose of the Convention was to ensure that the breeder should have the sole right of marketing propagating material of his variety and/or of licensing its propagation and commercialization. In order to qualify for protection the variety had to be distinct, homogeneous, stable and new. To prevent misuse, protection was to be of limited duration but was to last at least 15 years. Article 9 allowed for the restriction of the free exercise of a breeder's sole right where such restriction would be in the public interest, and Article 5 permitted free use of the protected variety by any breeder as a source of variation in breeding new varieties. The Convention underwent revisions in 1972 and 1978. The most recent revision is not yet in force but it includes amendments which facilitate the joining of new members.

The present member states party to the Convention are Belgium, Denmark, France, Germany (Federal Republic of), Italy, the Netherlands, South Africa, Sweden, Switzerland, the United Kingdom and the USA.

The Paris Convention does not provide for the protection of the varietal name as a trade-mark, the reason for this being that a breeder's right is of limited duration only, whereas trade-mark protection is unlimited. Within each member state, national legislation safeguards the public interest against incidental misuse. For example, section 42 of the Netherlands Seeds and Planting Materials Act of 1967 reads: 'The holder of a plant breeder's right shall grant such licences as are necessary to stock the market with propagating material on reasonable terms and conditions.' The holder of the breeder's right is also obliged to furnish the licensee with sufficient propagating material, at a reasonable price, to allow him to make full use of the licence. Should the breeder fail to fulfil these obligations, the Board for Breeders' Rights may grant an obligatory licence on conditions laid down by the Board. In fact, as far as food crops are concerned, such a situation has not once arisen in the last eleven years.

Analogous provisions exist under the national laws of the other member states, but, as in the Netherlands, they have rarely or never had to be enforced. Indeed, the very fact that a wide distribution of his varieties is a principal concern of any breeder, and that it is to this end that he engages in open competition, would normally preclude any attempt to limit distribution.

The practical inspection of varieties for registration involves the comparison of the new varieties with existing varieties of the same group in the trial field and the preparation of varietal descriptions. This is carried out by a neutral institution. The description of a new variety must be sufficiently detailed and distinct to allow ownership to be legally proved when required.

In some countries, written descriptions are submitted by the breeder himself without prior field inspection. In practice, these have proved inadequate, and countries with long experience in handling breeders' rights, such as the Federal Republic of Germany and the Netherlands, normally require that the descriptions submitted be based on field inspections.

The preceding discussion of breeders' rights and governmental regulations on the introduction of new varieties applie to Europe rather than to the USA. In the USA for example the breeder is free to release and market new varieties without prior approval of any government agency.

Certification is used but is not a universal requirement and with some crops the farmer has come to rely upon the reputation of the breeder as a substitute for certification. The Plant Variety Protection Act of 1970 has stimulated research programmes by the private seed industry, but many unprotected varieties are still being released by private breeders.

On the whole, the developing countries have not as yet reached the stage of introducing detailed legislation of the kind described above. In due course, however, they will require more extensive information, better guarantees of quality, and incentives to encourage breeding work. Objective, descriptive varietal registers will be important, as will the availability of reliable seed and propagating material at reasonable prices; here a system of propagation under the supervision of an inspection service may be appropriate. The value of such a system has recently been shown in Kenya. The next step might well be to introduce a scheme for the protection of the breeder's property, this being the procedure which in fact has been followed in countries which now have legislation on plant breeders' rights.

For those developing countries which do not wish to depend completely on state institutions for their new varieties, the system of breeders' protection provides a means of stimulating private breeding effort. It also results in greater diversification among breeders, and as such may be regarded as beneficial for both agriculture and horticulture.

ON PLANT QUARANTINE

The breeder may sometimes have to take plant quarantine regulations into account. If he wishes to import genetic material from elsewhere he must be familiar with the regulations of his own country, and if he is interested in testing material abroad he must be aware of the import requirements of the relevant countries. The same applies to seed-exporting companies and importers of basic or certified seed. Hitherto countries have differed widely in their requirements in this respect, but FAO has for some years been attempting to standardize the regulations. The International Plant Protection Convention of 1951 was established with this purpose in view. A uniform phytosanitary certificate is now in use.

The EEC is also in the process of formulating uniform phytosanitary regulations for all member states. When these become effective, the import regulations for material imported from outside the EEC will apply equally to all member countries, and the regulations between EEC countries will be identical.

The regulations will also affect the import of dangerous diseases or diseased plants for experimental work. A breeder who wishes to breed for resistance to a disease which does not occur in his country will have to submit his plans to the responsible authority and his research will then be subject to restrictions determined by the authority.

There is ample evidence that pests and diseases can be introduced through the importation of infected material; even pollen can be a carrier of disease. Hence it is clear that plant quarantine measures can play an important role in minimizing the risks of spreading diseases to disease-free areas. It is desirable, however, that any regulations imposed should not be more stringent than is required to prevent the spread of disease. Regulations that are too strict could seriously limit the effectiveness of plant breeding and the use of imported seed in the improvement of agricultural production.

Seed industry development

INTRODUCTION

The importance of good-quality seed for raising food production has long been recognized. An interest in collaborative programmes for the development of the seed industry in the developing world exists in most developed countries. As an example of action taken to promote the use of better seed we may cite the ISTA training course held in 1964 in Kenya. Following this, A.F. Schoorel (then president of ISTA) and H.B. Goettsch (director of the Regional Inspection Service in the Netherlands) became consultants on seed legislation, inspection and certification to the government of Kenya, with the result that in 1971 the governments of Kenya and the Netherlands agreed to collaborate in the establishment of a seed unit (Anon., 1971). A second example is provided by the Federal Republic of Germany, where in December 1976 a meeting was organized by the Ministry of Economic Cooperation, the German Foundation for International Development and the Society for Technical Cooperation (GTZ) to survey projects organized by the GTZ and to discuss future projects. The GTZ was at that time involved in seed production activities in 17 countries. The report of this meeting by Rohrmoser & Seidel (1977) contains much information of use for the promotion of seed production in the developing world.

The 15th and 16th sessions of FAO, the second World Food Congress and the first session of the Committee on Agriculture drew the attention of the world to the importance of the distribution of good seed. On the basis of the recommendations subsequently made, FAO initiated the international Seed Industry Development Programme (SIDP) in September 1973.

Some examples of existing seed industries are given below. Spitz (1975) considers that the seed industry has reached its highest development in the Netherlands and the essential features relating to that country are therefore given first. The next example is the situation that has developed in Kenya in the course of collaboration between Kenya and the Netherlands. An account of a seed project from Tunisia and Taiwan follows and finally some interesting aspects of the Romanian law are noted.

THE NETHERLANDS

Basic research in breeding is carried out at several institutions. The Foundation for Agricultural Plant Breeding (SVP) and the Institute for Horticultural Plant Breeding (IVT) work in close association with practical breeders, and have representatives of the private and cooperative breeding companies on their boards. Another important institute is the Institute of Plant Breeding (IVP) of the Agricultural University in Wageningen, which works in close contact with the Department of Genetics of the same university. Basic material produced by the IVP is passed to the SVP for further work and thence eventually to the practical breeder. The Institute for Phytopathological Research (IPO) carries out important work on screening for disease resistance. The Institute for the Application of Atomic Energy in Agriculture (ITAL) conducts mutation research which, as would be expected, has been most successful in ornamental plants. As a result of the close cooperation between institutes and breeders, the material developed by these institutes has an impact on the development of new varieties which is considered by breeders to be much greater than could be achieved by the institutes alone.

Nearly all practical breeding of agricultural crops is conducted by private and cooperative breeding companies. New varieties are submitted to RIVRO for registration tests (distinctness, homogeneity, stability and newness) and determination of agronomic value. New varieties from other countries receive exactly the same treatment as new Dutch varieties. A variety which passes the registration tests becomes a registered variety, and one which also passes the test for agronomic value is entered in the *Descriptive List of Varieties of Field Crops*, published annually.

Seed production and certification are under the control of the breeders and/or the NAK as follows:

- Breeder's seed: control by the breeder.
- Basic seed: control by the breeder and NAK.
- Certified seed: control by NAK.

Seed certification is obligatory. Imported seed has to arrive certified according to EEC or OECD rules. The cost of the certification organization is covered by the fees charged by the organization for inspection and certification.

KENYA

The 1971 agreement between the Kenyan and Dutch governments initiated a rapid development of the seed industry. The purpose of the agreement was to increase agricultural production in Kenya by improving the seed used by farmers. Within less than five years Kenyan farmers were using certified seed, i.e. good-quality seed of improved varieties, on more than 40% of the agricultural area. This figure is a mean value for all crops; for maize the figure is about twice as high.

It is worth noting that the scheme was especially effective as far as the small farmer was concerned, as may be concluded from the fact that in the 1974/75 season nearly 800,000 bags of 10 kg each of hybrid maize were retailed. Although the project was initiated by an agreement between governments, its success depended very much on the availability of good locally bred varieties, especially of maize, on the Kenyan and Dutch technicians in the Kenya Inspection Service (KIS) and on the active role played by the seed trade, in particular the Kenya Seed Company, which in 1976/77 produced 13,000 t maize, 8000 t wheat, 3000 t sunflower and 11 t grasses.

Another reason for these rapid results can be found in the pragmatic approach of the government and the inspection service to such problems as varietal purity. As pointed out earlier, it is important that countries introducing schemes for seed industry development should not impose regulations that are more stringent than necessary. The regulations in force in Kenya are in fact not sufficiently in line with the rules set up by the 1961 Paris Convention to allow Kenya to become a member of the International Union for the Protection of New Varieties of Plants (UPOV). However, Kenya has already joined the OECD and can therefore export its varieties under the OECD scheme; this is in fact already being done for hybrid maize seed and grass seed. By means of agreements between foreign breeders and local seed companies, it is also possible for foreign varieties to be multiplied legally in Kenya under the certification scheme controlled by the KIS.

At present, breeding work is restricted almost entirely to state institutions, but following recent developments private breeding companies may be expected to show an interest in establishing breeding projects of their own. Because of the wide variation in its climate, together with the existence of a plant variety protection law, the opportunities offered by Kenya are very attractive. The prospects of breeding and seed production of tropical grasses are good (the area lies in a gene centre for tropical grasses), with possibilities of exporting under the OECD scheme. There should also be good opportunities for potato breeding and potato seed production at high altitude, especially now that the Asian Vegetable Research and Development Center (AVRDC) has made breeding material with resistance to bacterial wilt (*Pseudomonas solanacearum*) available.

TUNISIA

A different scheme for the introduction of higher-yielding varieties, at present limited to cereals, has been developed by the Tunisian government. Here the aim is to promote the use of the new varieties without cost to the farmer, especially the small farmer. Breeding is conducted by state breeding stations, and the new varieties are multiplied by cooperatives under government contract. The seed is then put at the disposal of farmers, who can exchange their own seed for an equal quantity of seed of the new varieties without payment. The price paid by the government to the cooperatives for the seed produced is about the double consumption price. If the government of Tunisia wished to enlarge the choice of varieties available to the farmer, one way of doing so would be to offer the same conditions to foreign breeders.

TAIWAN

Taiwan has a simple and extensive network for rice seed multiplication and distribution. The district agricultural improvement stations grow foundation seed which is then turned over to the farmers' association (cooperative) for multiplication of registered seed. Two or more 'demonstration farmers' (model farmers) in each village are delegated to produce extension seed from the registered seed. The extension seed is inspected, tested and certified by the station staff before it is accepted by the farmers' association. Other farmers who so wish may exchange their own ordinary grain for the same amount of pure seed from the cooperative. In turn the government pays the model farmer a 15% premium through the cooperative for his services as seed grower.

Under this barter system the ordinary rice farmer has no need to travel beyond the township to obtain pure seed of a popular or a new variety, and in the latter case he has a chance to examine the variety while it is standing in the seed field. The convenience and efficiency of the systeem make most rice farmers willing to renew their seed stocks once every three years. Through frequent contact with the farmers, extension workers can become familiar with their preferences for certain varieties and this information is channeled to the station staff, extension offices and farmers' associations who jointly plan the annual seed multiplication and distribution operation.

ROMANIA

The Romanian law on seed production, use and quality control has features of special interest (Anon., 1974). It resembles the UPOV regulations at many points but there are also some marked differences. One similarity is the division made between breeding activities on the one hand and the testing and introduction of new varieties on the other, the Academy of Agricultural and Forestry Science being responsible for the former and the State Committee for the Testing and Homologation of Varieties for the latter. The Committee maintains an up-to-date state register of accepted varieties and hybrids.

Seed production is carried out on 'specialized units', and the seed production fields are subject to field inspection. The regulations state that: 'Should any specialized units fail to apply the measures provided in the seed and planting material production technologies, thus being unable to attain the quantitative and qualitative plan figures, they shall be liable to penalties and the licence granted to them by the Ministry of Agriculture, Food Industry and Water Management will be withdrawn.' A feature found in few other countries is that every individual farmer is legally obliged to change his seed at intervals: annually in the case of maize, sorghum, two-rowed barley and rice, every 1-3 years in the case of potatoes and every 2-3 years in the case of cereals, pulses, fodder crops and other crops. Another unfamiliar requirement is that a new variety must have a yield superiority of at least 10% if it is to be accepted on the basis of improved yield. However, new varieties can also be accepted on account of their superiority in other physiological or qualitative characteristics compared with the best varieties or hybrids grown in the relevant area.

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with the collaboration of
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W.L. Brown on plant variety protection in USA
T.T. Chang on seed industry development in Taiwan

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10 Perspectives

A major challenge in world food production is the increase in world population, with the resulting increase in demand not only for food, but also for greater employment and income generation, especially in rural areas. In addition, the conservation of renewable and nonrenewable resources is of far-reaching importance. If these challenges are to be met, not only must agricultural research be undertaken, but its findings must be made available to farmers. National food security systems should be set up which will provide for the establishment of (1) ecological security, to maintain fertility and prevent desertification, (2) technological security, to ensure that an appropriate diversity of varieties and agricultural techniques is available, (3) social security, allowing adequate purchasing power to the consumer and a reasonable return to the producer, (4) education in nutrition and (5) adequate food reserves in areas of potential need. The contribution that breeders can make, and have already made, to higher and more stable food production will be enhanced by international collaboration, especially in the conservation and distribution of genetic resources and the establishment of screening nurseries. Here the International Research Institutes have an important role to play. Local plant breeding stations, on the other hand, are of importance mainly in breeding varieties for specific areas. In addition, private breeding stations, especially in Europe, North America and Japan, have bred large numbers of varieties. Although the trend towards internationalization of breeding companies will probably continue, small specialized stations will probably also continue to exist, especially in countries with breeders' rights. The acquisition of some plant breeding companies by large chemical enterprises is a recent development whose relative advantages and disadvantages for plant breeding cannot yet be assessed. Breeding aims common to both developing and developed countries include high and stable yields and high quality, including quality for processing and storage. An additional task for breeders in developing countries is to assist in increasing the potential of agriculture for generating employment. They must breed varieties suitable for different conditions within a wide range of management levels and growing methods, such as high-density monoculture, intercropping, mixed cropping, three-dimensional crop canopies, crop-livestock integrated production systems and kitchen gardening. In developed countries, specialized breeding aims include high production per man hour, and suitability for processing or for value-added products. In the progress of plant breeding towards all these goals during the rest of this century, there is no doubt that current breeding methods will remain important. Work on breeding hybrid varieties will certainly increase, and in breeding for pathogen resistance the change in emphasis from vertical to horizontal resistance will probably persist. The use of haploids, polyploids and interspecific and intergeneric crosses, assisted by chromosome engineering and the new techniques of protoplast fusion, will continue to attract attention. The implications of DNA manipulation in vitro and of DNA transfer in higher plants with respect to practical breeding remain to be seen, but conceivably such techniques may prove to be the first steps in a future evolution guided by man.

Food production and security levels

INTRODUCTION

Food is the first in the hierarchy of man's needs. It is more than 10,000 years since man, in his attempt to ensure more reliable food supplies, changed from being a food gatherer to producing food by domesticating plants and animals. This process started two significant developments. First, various forms of what we may term cultural energy (energy inputs into agriculture other than solar energy) were introduced to enable green plants to give stable and higher yields. The relative contributions of the different forms of cultural energy (cf. Fig. 7.1) to agricultural production have varied with time and over geographic regions. Second, from among the millions of species recorded in the world flora and fauna, only a few plants and animals were chosen for domestication. Thus, there are now only about 30 plant species whose individual world production exceeds 10 million t per year and six animal species whose production in the form of meat exceeds 1 million t per year. Such dependence of the food needs of the growing world population upon a few species has increased the vulnerability of food production systems to the hazards of weather aberrations and pest epidemics, and the problems arising from this dependence are compounded by the fact that at present less than 10 countries in the world have surplus food grains for the export market. A beneficial consequence of this dangerous situation has been the initiation in recent years of steps for developing global and national food security systems.

While the need to accelerate agricultural advance is becoming increasingly urgent, man's course of spoiling his agricultural assets is proceeding unabated. This includes the entire process of desertification, which has been defined as a diminution or destruction of the biological potential of the land ultimately resulting in desertlike conditions. The subject was reviewed at a UN conference held at Nairobi in 1977. Immediate action to combat desertification is essential, since apart from the extreme deserts an area of about 45 million km^2 of productive land distributed among 100 countries and comprising about 30% of the world's land surface is threatened. Lowdermilk (1953), in a study of the conquest of the land through 7000 years, has stressed that, while maintaining soil fertility is the duty of the farmer, conserving the physical integrity and production potential of the soil as a resource is the duty of each nation. In a series of thought-provoking publications Lester Brown, Eric Eckholm and their associates of the World Watch Institute have drawn attention to the fact that apart from the rapid depletion of earth's nonrenewable resources, even the potential for renewable wealth is being destroyed (Brown et al., 1976). The impact of man's activities on the climate, such as the effects of increasing carbon dioxide and of the release of nitrous oxides, freons and other trace chemicals on the ozonosphere is also a matter of serious concern. Above all, the path of agricultural advance followed so far relies heavily on nonrenewable forms of energy, and if the same path is followed in the future, the improvement of food production could find itself in a blind alley.

Progress in applying science and technology to the utilization of available soil, water, air, sunlight and biological resources has raised hopes for our agricultural future. Methods of drawing up agricultural balance sheets, which show the production assets and liabilities of each area, have been elaborated and advances have been made in adapting the architecture and growth rhythms of plants to suit specific agrometeorological and management conditions. Similarly, integrated animal production systems involving genetic upgrading, better nutrition and health care and improved processing and marketing have been developed. New vistas of production have also been opened up in both fresh-water aquaculture and mariculture, in addition to capture fisheries. With regard to forestry, land management systems involving integrated approaches to sylviculture and agriculture (termed 'agroforestry') are emerging. Above all, developments in postharvest technology are helping to minimize storage losses and to allow the elaboration of value-added products from all parts of plants and farm animals.

WORLD FOOD PRODUCTION

Challenges

The relentless growth in population, particularly in poor nations, following rapid advances in preventive and curative medicine in recent years presents the greatest challenge to mankind, not only for producing food in the quantities and of the quality needed for the existing and expanding population, but also for generating the economic growth rate essential for full employment. Hence agricultural growth should be viewed not merely in terms of the production of certain quantities of food but also in terms of employment and income generation in rural areas.

A second major challenge is that of preserving the renewable nature of our renewable resources (Brown et al., 1976). This can be done only if the entire community in each country cooperates in ensuring that there is no depreciation in basic agricultural assets. Unfortunately, awareness of this necessity is yet to become widespread.

A third major challenge is in the area of energy supply and management in agriculture and aquaculture. Technologies will have to be developed and promoted which involve the principles of organic recycling and integrated approaches to pest management and nutrient supply. When solar power becomes economically attractive, new prospects may be opened up by combining various uses of solar energy during the production and postharvest phases with techniques such as no tillage or minimum tillage and other methods of minimizing the energy input requirements.

A fourth area of considerable significance is the development of crop-livestock integrated production systems. Livestock production has assumed importance in rich countries in order to meet the dietary preferences of their populations. But also in many of the so-called MSA countries (i.e. those most severely affected by malnutrition), the integration of animal husbandry with agriculture has become essential, since this is the only immediately feasible method of enhancing the income of small farmers and reducing underemployment among landless labourers. How can this situation be reconciled with the much higher energy needs of the plant-animal-man food chain compared with the plant-man food chain (cf. Fig. 7.1)? Obviously, technologies of livestock management based on a complementary relationship between animal and man need to be developed. Mixed farming has always been a way of life of farmers in many developing countries. The ruminant is ideal for such a symbiotic production system, since all cellulose material and some aminoacids which cannot be digested by man can be converted by the animal into a nutritious food for man. Crop-livestock-fish integrated production systems offer even greater opportunities for achieving high energy output-input ratios.

A fifth area of immediate relevance to the food problem is the initiation by governments of appropriate programmes for exploiting the unused yield potential existing at current levels of technology. This will call for massive efforts in extension work, in organizing relevant services based on constraints analysis and, above all, in introducing public policy measures which would stimulate both production and consumption.

Finally, governments will have to grapple with the problem of distribution. As is evident from the data presented earlier (cf. Fig. 1.5), world food production is sufficient to feed the millions who are malnourished today provided there is equitable distribution; this would involve less use of grain for feed. The deadline of 1984 set by the World Food Congress for ensuring that no human being goes to bed hungry could be advanced to an earlier date, if we can humanize our science and technology. Unless this happens, global action to meet man's need for food, energy and other basics may not be forthcoming. Until all global planning for the future and all development of technology are subjected to the one test prescribed by Mahatma Gandhi – 'Will this benefit the poorest man ?' – it is unlikely that an international food security system will come into existence. The prevailing conditions under which, with every rise in gross national product, there is an increase in the sufferings of the poorest nations and the poorest groups within nations owing to the increased demand for food by wealthier nations and wealthier groups within nations, can be altered only by public policies designed to bring about equitable distribution. By what means can a nation build a national food security system which can insulate its people from hunger arising from weather-induced crop failures and/or inadequate purchasing power?

Opportunities

While available projections of population, per caput income and demand for food, on the one hand, and production and marketable surpluses of food, on the other, reveal a possible world food gap of about 45 million t by 1985, an encouraging sign is the growing awareness among developing countries that the needs and claims of agriculture should have overriding priority. National, regional and global efforts in agricultural research and development are growing. Analysis of gaps and constraints in major crop production systems in several MSA countries has shown that while the gap between potential and actual farm yields is high, the constraints are such as can be remedied fairly speedily.

Global weather-monitoring programmes sponsored by WMO (World Meteorological Organisation) are also making rapid progress and agrometeorology is emerging as a major science. Yield forecasting techniques are being perfected. Weather satellites and remote sensing techniques have added a new dimension to research in this area. Hence, given adequate international cooperation, reliable early warning systems of likely food shortages can be developed. The time is therefore appropriate for governments to launch a programme of building strong national food security systems. Once food security systems are developed on a national scale, it will be relatively easy to build an international system.

COMPONENTS OF A NATIONAL FOOD SECURITY SYSTEM

Ecological security

If the ecological infrastructure necessary for sustained agricultural advance is not preserved and strengthened, desertification processes will damage both agriculture and aquaculture. Nothing should be done which will cause unfavourable changes in either macroenvironment and microenvironment. To ensure this, every country should form a national movement for the promotion of economic ecology. Economic ecology, unlike an ecology strictly concerned with conservation, is intended to maximize the economic benefits from a given ecological milieu and to minimize the risks and hazards associated with that environment. Guidelines for achieving ecological security along with agricultural progress should be drawn up by an interdisciplinary team of scientists for each area.

Technological security

Technological development should be tailored to specific ecological, economic and social conditions, and precautions should be taken to ensure that it is not in itself a source of social discrimination. The major aim of agricultural technology in countries with very little scope for bringing additional land under cultivation should be to increase continuously the economic yield per hectare of land or water surface without detriment to the long-term production potential of soil and water. Moreover, improvements in productivity must be brought about without seriously increasing the consumption of nonrenewable forms of energy. Nor should improvements in yield be made at the cost of stability of production. Where the probability of weather-induced instability in yield is high, owing to such causes as floods and drought, alternative cropping strategies, such as growing more drought-resistant crops like sorghum in drought-prone areas, and crop-rescue techniques should be developed to suit different weather models. Postharvest technology should receive as much attention as production technology, so that both farmer and consumer can derive full benefit from the products marketed.

Plant and animal breeders should adopt a 'cafeteria approach' (cf. p. 412) in the selection of genotypes of crops and farm animals for different farming systems. This approach may also be recommended to production agronomists for the development of technologies suited to farmers with varying input-mobilizing capacity. Meteorologists should measure the impact of different weather parameters on the entire system and not merely on components of it, if their data are to be of use in designing more efficient systems. 'Farming system meteorology' will involve much greater attention to microenvironment in crop canopies and to adapting the sequential use of land to weather conditions in such a way as to permit optimum perfomance of the crops and animals farmed.

Social security

As an essential component of national food security programmes, appropriate measures in social security should be taken to provide, on the one hand, all the inhabitants of the country with their minimum needs of food and, on the other, the producers of food with adequate remuneration for their labour. Several developing countries like India now have large grain reserves. However, many people still go hungry to bed, largely because of their inadequate purchasing power. Inability to purchase food is frequently due to lack of opportunities for employment. Therefore the nutrition problem will have to be dealt with both through increasing production and through increasing opportunities for gainful employment. The government of India, for example, has launched a Food for Work programme involving the distribution of substantial quantities of wheat and rice for payment to workers employed in such work as soil and water conservation, provision of drinking water supply etc. Another project introduced in some parts of India like Maharashtra is the Employment Guarantee Scheme which is intended to help provide everyone in need of a job with the opportunity to work.

Social security for farmers is as important as social security for consumers. Farming is a risky activity and until the harvested produce has been safely sold the farmer cannot know what the final return for his labour and investment will be. Integrated input-output pricing policies are required which will be both remunerative to the farmer and reasonable to the consumer. Japan, for example, has been able to stimulate rice production very rapidly through a favourable input-output price ratio between fertilizer and grain (Table 10.1). Every country will have to give serious attention to this problem of maintaining an appropriate balance between input and output prices, keeping in view the twin objective of stimulating production and promoting consumption.

Table 10.1. Input-output price relationship of rice. Note: in case of India, figures at (i) relate to open market prices, and figures at (ii) relate to procurement prices (based on data from: IRRI).

Country	Cost of 1 kg of nitrogen in Rs	Cost of 1 kg of paddy in Rs	Cost of 1 kg of nitrogen in terms of kg of paddy
Japan	5.94	7.82	0.76
Korea	4.63	3.49	1.32
Philippines	4.06	1.30	3.12
India	3.50	0.89 (i)	3.93 (i)
		0.85 (ii)	4.12 (ii)
Nepal	3.49	1.14	3.06
Indonesia	3.09	1.54	2.00
Sri Lanka	2.52	1.54	1.63
Bangladesh	1.95	1.22	1.60
Thailand	2.52	0.81	3.11
Pakistan	2.52	0.81	3.11
Taiwan	2.93	1.46	2.07

Education in nutrition

Attempts to change food habits have everywhere met with great resistance and can often take many years. However, if successful, they can have a tremendous impact on the quantity and especially on the quality of the available food. If for instance a food crop, not used as such in a given area, proves to be capable of outyielding an established crop, its introduction could mean an improvement in the energy production per hectare for the country concerned, provided the population can be persuaded to accept the new crop in their diet. Thus, in a drought-prone area where the population habitually consumes maize, the amount of food available could be much increased if maize were to be partly substituted by sorghum.

What may be of even greater importance is the influence that acceptance of a greater variety of food could have on the nutritional balance of the diet. In this respect, the cultivation and consumption of more vegetables are important, especially as a source of minerals and vitamins in the diet. Improved methods of preparing meals also have an effect and should receive attention in programmes of education in nutrition. One result of success in this field would be to render unnecessary many demands to change the nutritional value of crops by breeding.

Building up food reserves

Every MSA country should try to build up a grain reserve which can help it not only to meet the anticipated shortfall in a bad year but also to run an effective public distribution system. Countries which are not normally self sufficient in their food requirements would obviously have to maintain adequate stocks by imports so that in years when production is adversely affected by weather in the traditional food-exporting countries, prices are not allowed to rise abnormally. Every country will have to devise an appropriate grain reserve policy based on ecological, economic, logistic and other considerations. The reserve may be not only of cereals but also of grain legumes, oilseeds and other crops, depending on needs and availability. Such a buffer stock can also help to ensure that prices of farm produce do not fall below an economic level. In addition to maintaining a basic reserve and sufficient operational stocks, it will be prudent to have contingency plans for increasing the production from irrigated areas in years when there is widespread drought. Thus, an integrated grain reserve policy and a programme for the efficient use of production potential during emergencies, on the basis of early warning from crop-weather watch groups, should help to launch every country on the path of self reliance in food.

International collaboration in plant breeding

Exchange of plant material, both conscious and unconscious, occurred even before the birth of agriculture. The origin of the tetraploid cottons (*Gossypium hirsutum* and *G. barbadense*) from Old and New World diploids is an exemple. Following Vavilov's elaboration of the concept of centres of diversity and origin of crop plants, efforts in systematic plant exploration, collection and exchange have gained in momentum and scope. In 1973 this ultimately resulted in the establishment, by the Consultative Group on International Agricultural Research (CGIAR), of an International Board for Plant Genetic Resources (IBPGR). The major task of the IBPGR is to organize an international network of plant genetic resources centres, and to ensure that diverse germplasm of important food crops and other plants is adequately collected, satisfactorily conserved, evaluated and documented, and is made available for use by plant breeders and other scientists all over the world. If this task is not carried out properly, the fruits of thousands of years of natural and human selection will be denied to posterity.

Plant collections will have to be maintained as follows:

- as working collections maintained by plant breeders,
- in medium-term storage in national institutes,
- in long-term storage at suitable international/national centres,
- in centres of diversity for the *in situ* maintenance of variability.

The International Research Institutes funded by CGIAR (Table 10.2) have an important role to play in the collection, classification, evaluation, storage and distribution of genetic material relating to the crops in which they work (see Chapter 3). In addition to serving as repositories of germplasm collections, the International Research Institutes assist plant breeders all over the world by:

- establishing 'hot spot screening' nurseries for important diseases (e.g. in Toluca valley in Mexico for screening for resistance to *Phytophthora infestans* in potato);
- conducting international trials of promising genetic material from different

Table 10.2. The International Agricultural Research Institute Network (from: Wortman & Cummings, 1978).

Centre	Programme	Year founded	Headquarters	Agroclimatic area served
International Rice Research Institute	Rice, multiple cropping	1960	Philippines	Rainfed and irrigated areas - subtropical/tropical
International Maize and Wheat Improvement Center	Wheat, maize, barley, triticale	1966	Mexico	Rainfed and irrigated areas - temperate/tropical
International Institute of Tropical Agriculture	Maize, rice, cowpeas, soya beans, lima beans, cassava, yams, sweet potatoes, and farming systems	1968	Nigeria	Rainfed and irrigated areas - lowland tropics
International Center of Tropical Agriculture	Beans, cassava, beef and forages, maize, rice and swine	1969	Colombia	Rainfed and irrigated tropics - 1000 meters to sea level
International Potato Center	Potatoes	1972	Peru	Rainfed and irrigated areas - temperate-to-tropical
International Crops Research Institute for the Semi-Arid Tropics	Sorghum, millets, groundnuts, chickpeas, pigeon peas	1972	India	Semiarid tropics
International Laboratory for Research on Animal Diseases	Blood diseases of cattle	1974	Kenya	Mainly semiarid tropics
International Livestock Centre for Africa	Cattle production	1974	Ethiopia	Humid-to-dry tropics
International Center for Agricultural Research in Dry Areas	Wheat, barley, lentils, broad beans, oilseeds, cotton, and sheep farming	1976	Lebanon, Syria, Iran	Mediterranean

national programmes under diverse environmental conditions, to help identify genotypes with wide as well as specific adaptation;

- organizing bibliographic services, seminars and symposia and monitoring tours;
- assisting in manpower development.

Since there are now International Research Institutes covering all the major food crops and ecological zones of developing countries and since many national institutions in developed countries also have international collaboration projects through bilateral or multilateral funding, plant breeders can look forward to reaping the benefit in their future work.

Plant breeding as a commercial enterprise

INTRODUCTION

It may be assumed that it was at that time in prehistory when man first changed from being a hunter and food gatherer to being a food grower that plant breeding began. As a food grower he would soon have realized that it was worthwhile to take the seeds of the best plants for the next crop. We cannot date the beginning of this first and primitive stage of mass selection, because it was before the dawn of written history.

Probably mass selection remained the main type of breeding until about the middle of the ninteenth century. From then on, more sophisticated methods such as line and family selection were introduced. At about the same time intraspecific crosses were increasingly used by breeders. This development was considerably accelerated by the rediscovery of Mendel's laws and is in marked contrast to the efforts of scientists of the eighteenth century and the first half of the nineteenth, who were more interested in interspecific and even intergeneric crosses. Following the rapid development of agriculture in the western hemisphere, by the second half of the nineteenth century plant breeding was well on the way to becoming a profession.

THE FARMER – PLANT BREEDER

Who were the first professional plant breeders and in what circles did they originate? Most of them were farmers, vegetable growers or seed growers who, against a general background of agriculture, gradually began to specialize. Today plant breeding is a highly specialized profession requiring skilled breeders and ever-increasing levels of investment, labour and facilities. And in fact, it was often the need for large investments that led what had originally been family concerns to become limited companies: this was particularly true of enterprises concerned not only with the growing of various crops but also with the production, cleaning and sale of seed.

INTERNATIONAL BREEDING COMPANIES AND MULTINATIONALS

To make such investments profitable an expansion of sales beyond the national uptake capacity was necessary, with the result that the companies became international. Internationalization was a matter not only of extending sales but also of collaborating with breeding companies in other countries.

A further development that has occurred only in the last decade is the acquisition of some plant breeding companies by multinationals and other large enterprises, mainly producers of chemicals. The underlying motives are not all clear, but they probably include diversification, and the more efficient exploitation of those sections of the organization concerned with testing and sales. Such combinations may have certain advantages:

- They facilitate investment in the further facilities required for the development of plant breeding methods.
- They provide a world-wide organization for receiving information on varieties, developments in agriculture etc.
- They provide a world-wide testing and sales organization.
- They facilitate international cooperation.

However, they may also entail certain disadvantages:

- There is the risk that breeding will be regarded as a short-term commercial enterprise which must be capable of showing a profit at any time. This can endanger continuity.
- Breeding work may be depersonalized. This could have a deleterious effect, since the profession of plant breeding needs personal involvement, being not only a science but also an art.
- There is a risk of creating monopolies and trusts. Monopolies, even state monopolies, can be harmful because they may maintain unnecessarily high seed prices while failing to maintain adaquate seed quality. In countries with plant breeders' rights, regulations exist which give the government power to compel the breeder to issue licence contracts for muliplication at a reasonable breeder's fee.

These risks must be eliminated, if possible, in advance.

On the other hand many small breeders are still in existence. They mostly concentrate on only one or a few crops and contract out their seed growing and sales to specialized organizations. In the Netherlands, for instance, there is still a remarkable number of small breeders of potatoes, who have made and are making valuable contributions to the breeding of potato varieties. There are several reasons for this:

- Their interests are protected by laws on plant breeders' rights.
- They can benefit from government extension on plant breeding procedures and make use of the basic material made available by state plant breeding stations.
- The breeder limiting himself to a specific crop almost inevitably develops special skills.
- Last but not least, the small breeder is usually characterized by devotion to breeding and love of plants.

PLANT BREEDING AS A PROFESSION

Plant breeding is already an extremely captivating profession and is likely to become more so in the future. It will certainly grow in complexity, for increasingly it will need to synthesize results from related and supporting branches of science. Probably the best answer to this challenge will be to form strong teams of well-equipped specialists working in close cooperation with breeders in the field.

Breeding techniques applicable in the future

GENERAL

Current breeding methods

The methods described in Chapter 4 will remain the most important methods in the near future and will probably continue to undergo further gradual improvement. One component of progess will certainly be the extensive application of quantitative genetics and biometrics. Another will be the improvement of field trial systems and the computerized handling of relevant information.

With regard to selection procedures, the need for screening large numbers of plants will have to be met. As our knowledge of crop physiology increases, the possibility of index selection is likely to increase: indirect selection and selection using independent culling levels can be especially useful in allogamous crops in which final selection cannot be completed before flowering.

F_1 hybrids

In view of the success of hybrid varieties both in food crops and ornamentals, there are good grounds for expecting that their use will continue to increase. Today a wide range of techniques and properties is used in the production of hybrids: hand crossing (tomato, cotton in India), cytoplasmic male sterility (sugar beet), cytoplasmic male sterility in conjunction with fertility-restoring genes (sorghum, maize), functional male sterility (tomato in Bulgaria), self incompatibility (Brussels sprouts and other *Brassica* crops), and shift in sex expression (parthenocarpic cucumber). Genic male sterility is unlikely to be of more than limited interest for the breeder unless drastic improvements in its application can be made.

Future research will probably concentrate on exploiting cytoplasmic male sterility (where necessary in conjunction with fertility-restoring genes), on developing reliable methods of inducing male sterility, probably by means of chemicals, and, in the case of genic male sterility, on seeking fertility-restoring environments or chemicals. The application of incompatibility in hybrid breeding will probably remain limited to crops in which cytoplasmic male sterility is not found and in which male sterility cannot be induced. In autogamous crops the introduction of outcrossing mechanisms is of importance.

The breeding of inbred lines is time consuming, and it will be worthwhile to simplify and perfect methods of making inbreds by doubling haploids.

Apomixis

Whereas it is desirable for purposes of recombination to eliminate apomictic behaviour in apomictic crops, it may sometimes be useful to introduce the character into certain amphimictic crops, for example in order to allow a highly heterozygous genotype of a vegetatively propagated crop to be reproduced from seed which would probably be virus-free. Another possible benefit of introducing apomixis into amphimictic plants would be the possibility of fixing heterosis. Further research into the genetics of the phenomenon and appropriate methods of manipulation are required.

Mixtures

Mixtures within a species do not normally yield more than the best component (cf. Chapter 2, pp. 67-70). The same is true of mixtures of crops which have the same sowing and harvest time. Mixtures of the following types can, however, be useful:
- leguminous and nonleguminous crops,
- crops differing in their main growing period,
- crops with different canopy levels and a lesser light requirement for the lower one,
- lines of autogamous crops differing in genes for resistance to a major disease (cf. Chapter 4, pp. 107-108).

The traditional method of breeding the near-isogenic lines of the last-mentioned type is to back cross several resistance donors to a common recurrent parent. This takes rather a long time, especially in the case of winter cereals. A reasonable alternative to this type of mixture might be a mixture of near-isogenic sister lines derived from a multiple cross with four parents having different genes for resistance. A less homogeneous mixture could be made up of varieties resembling one another but having different resistance genes.

Breeding for stability of yield

The total dry matter production of a species per hectare has a biological maximum, depending on the latitude (available solar energy) and the availability of minerals and water. The yields achieved by west European farmers in good growing seasons, with control of diseases and pests, are close to this biological ceiling. Where this is the case, the designation of future breeding priorities will require some hard thinking.

The most likely candidates are improved stability of yield, improved sinks and extension of the growing season of the crop. Yield stability is an obvious and important objective where the capacity for producing maximum dry matter yield exists but cannot be expressed in every season because of pests and diseases, drought etc. Once the total dry matter ceiling has been reached, attention may be given to the improvement of the sink capacity of those parts of the plant which are used economically, e.g. the grain in the case of cereals. The next stage could then be to breed for an extended growing season, allowing a longer period of use of incoming energy. Here sugar beet provides a good example: because of the bolting resistance that has been bred into modern varieties, the farmer can sow early in spring, and consequently the total number of days of assimilation is considerably increased and likewise the yield.

In developing countries there is a clear need not only for higher yields but also for greater stability of yield. In many cases, optimal growing conditions do not exist and the control of pests and diseases is very limited. Here a stable high yield is a main objective of breeding.

Resistance breeding

Breeding for resistance to fungi, viruses and bacteria has certainly achieved some remarkable successes, but there have been not a few disappointments owing to the formation of new strains of the pathogens, especially in host-pathogen combinations involving a relatively simple gene-for-gene relationship. Today the general aim in breeding for resistance is stable or long-lasting resistance; in many cases this is in fact horizontal resistance, which is genetically more complicated and hence more difficult for the breeder to manipulate than resistance based on a gene-for-gene relationship (cf. Chapter 6, pp. 264-267).

A good start has been made in breeding for resistance to insects. In general, screening for insect resistance is more complicated than screening for resistance to fungi. In view of the need for more and improved methods of screening large numbers of plants, this is a field in which collaboration with entomologists could be fruitful.

Haploids, polyploids and wide crosses

Haploids as a tool in plant breeding are growing in importance and further developments in the technique of making haploids can be expected. Polyploidization is a neccessary complement to their use and here somatic cell fusion can be increasingly used adjunct to traditional techniques.

A field likely to continue to receive special attention in connection with the application of techniques of haploidization, polyploidization, somatic cell hybridization and chromosome manipulation is that of interspecific and intergeneric hybridization. Although most of the products of interspecific and especially intergeneric crosses are unlikely to find direct use as crops, except perhaps in some ornamentals, their value as sources of genetic diversity is undoubted and this will probably be their main contribution to future breeding in existing crops.

DNA transfer

The breeder viewing with interest the results of recent work on the transfer of plasmids from bacteria to higher plants is prompted to wonder how soon the techniques will have developed far enough to be applied in crop breeding. Any projection of future progress in this field must however remain highly speculative.

Converting C_3 plants into C_4 plants

C_4 plants have a higher potential rate of biomass production than C_3 plants (see Chapter 2, pp. 70-77). Most C_4 crop plants are grown in tropical and subtropical zones (sorghum, sugar cane, maize, some grasses). Of these, maize *(Zea mays)* is also grown in temperate zones, but except where daily temperatures are above 15 °C, it cannot reach its optimum production in these regions and hence is grown mainly for silage rather than grain; moreover, low spring temperatures shorten the growing season so that only early varieties can be used. Should the conversion of C_3 plants into C_4 plants ever be achieved, the products would be of only limited use in the temperate zones, though in tropical and subtropical regions the new possibilities of improved biomass production might prove very useful. However, the likelihood of such a conversion is still very remote, and other methods of increasing yields through plant breeding must be sought.

Adapting crops to new environments

Breeders are sometimes urged to develop varieties of crops for regions or conditions to which the crops are not adapted.

Their efforts have in some cases been attended by success, as for example in the potato *(Solanum tuberosum)*. This crop, as a result of breeding, is able to produce high yields far outside its centre of diversity. One of the characters eliminated from potato by breeding is sensitivity to day length, and the same is true of soya bean *(Glycine max)*, a short-day plant. Another example is the sunflower *(Helianthus annuus)*, which has actually attained its greatest importance and distribution in regions remote from its centre of diversity (America), namely in south-eastern Europe and the Middle East. In this case, important diseases characteristic of the centre of diversity were not carried to the new growing areas, and the varieties that were bred became so well adapted that they outyielded the varieties in the areas of origin (see Chapter 4, pp. 216-223).

It may be asked, however, whether it is really useful to expend a great deal of effort in breeding, say, a potato variety adapted to tropical lowlands, when rice and many other crops are easily grown there already? What proportion of plant breeding work can justifiably be devoted to projects of this kind without prejudice to other important tasks? Any attempt to answer these questions must take into consideration a number of interrelated factors, including the following:

- The urgency of other breeding aims such as resistance and increased yields in crops which are already adapted.
- The effort required *versus* the expected gain.
- The feasibility of growing the crop in question in the regions to which it is to be adapted.
- The costs of transport from the production belt to the sites of consumption.
- The possibility of growing alternative crops.

In connection with the last-mentioned point there is a further question for consideration, namely the desirability of growing crops under energy-consuming conditions (e.g. in hothouse culture) for off-season production. Clearly it would be absurd to waste breeding potential on producing, say, coffee varieties for growing in Europe: it is better for all concerned to import coffee from tropical countries. But the answer is by no means always so clear cut. Every case will have to be considered individually on its own merits.

Breeding nutritionally balanced varieties

Another proposal sometimes put to breeders is that they should produce varieties which combine in one plant all the main nutrients in the correct proportions for a well-balanced diet. To reshape a species which yields mainly carbohydrates into one which also supplies adequate protein and fat is a task of such magnitude that it is unlikely ever to be satisfactorily achieved. The grower who dreams of raising a crop which is a complete 'food package' in itself would be well advised to turn his attention to growing a diversity of crops. The breeder's full attention can then be given to the more appropriate tasks of increasing yield and yield stability.

DEVELOPING WORLD

Introduction

Most of the developing countries lie in the tropical or subtropical regions of the world. These regions have a rich flora and fauna and have been the centres of origin of most economic plants. Many of the countries are densely populated and experience the twin problems of low productivity and highly unstable production. The size of an average farm holding is only of the order of 1 to 2 hectares in several countries, including India, Bangladesh, Sri Lanka etc. Between 50 and 70% of the population depends upon agriculture for a living. Even in a plantation crop like rubber, over 60% of the rubber production in Malaysia comes from small holders. Hence, some of the urgent tasks facing plant breeders in developing countries are:

- Development of crop varieties which, by their suitability for multiple and relay cropping, mixed cropping and mixed farming systems, can help to raise the yields and nutritional value of crops on small holdings and also the income from them.
- Stabilizing production by introducing greater resistance to fluctuations in weather

and to pest epidemics.

- Improving the ratio of conversion of different forms of cultural energy into food energy, so that improvements in productivity are not simultaneously accompanied by an exponential consumption of nonrenewable forms of energy (cf. Chapter 7, pp. 293-295).
- Breeding varieties that combine high yields with high stability and high nutritional quality.
- Breeding varieties with resistance to the production of mycotoxins and better quality for storage, processing, transportation and utilization. This is desirable, for example, in maize and groundnut, where contamination with toxigenic strains of *Aspergillus flavus* under inadequate drying and storage conditions can give rise to aflatoxins causing liver disease. Improved postharvest technology would also be an aid in the preparation of value-added products in rural areas, thereby enhancing the potential for income and employment generation in villages.
- Breeding varieties of industrial crops able to respond to chemical treatments conferring greater capacity to resist commercial competition from synthetic products, e.g. natural rubber *versus* synthetic rubber, natural cotton and jute *versus* synthetic fibres etc. For example, it is known that some genotypes of cotton (both *Gossypium arboreum* and *G. hirsutum*) respond well to chemical finishing treatments which can impart to their fibres some of the 'easy-care' properties (such as the drip-dry and wrinkle-free characters) for which the synthetic fibres are preferred by the consumer. Some varieties are also more suitable than others for synthetic/natural fibre mixtures. Cooperation between breeders and technologists is important in all industrial crops.

The 'cafeteria' approach to crop breeding

Plant breeders in developing countries with predominantly small holdings will have to assist in making agriculture an instrument not only of improving food production but also of generating more jobs and income in the rural sector. Farmers differ greatly in their capacity to mobilize inputs and take risks. Hence, scope for a choice of varieties based on the level of management (with particular reference to input application) which different small holders can adopt, will have to be provided. This we may term the 'cafeteria' approach. Varieties which are respectively suitable for high-density monoculture, intercropping, three-dimensional crop canopies, crop-livestock integrated production systems, agroforestry and integrated agriculture and aquaculture farming systems, should be designed and developed.

Breeding for improved farming systems

Since the decisions of farmers are influenced by the entire system of farming around which their daily life revolves, a brief review is given below of some of the existing and emerging farming systems in Asia.

Multiple cropping systems in irrigated areas Various two, three and even four-crop sequences are now being followed. In promoting multiple cropping systems, attention should be paid to ensuring both that grain and fodder legumes find a place in the rotation and also that crops having the same pests and diseases are not grown in succession. Unscientific multiple cropping could compound pest and soil fertility problems disastrously. On the other hand, the presence of both grain and fodder legumes in the rotation will contribute towards improved human as well as soil nutrition. A rotation involving mung bean (*Vigna radiata*), rice and wheat is a good method of combining cereals and legumes in North West India. The short-duration varieties of pigeon pea (*Cajanus cajan*) have made a pigeon pea – wheat rotation possible. A rotation of jute (*Corchorus*), rice and wheat is becoming popular in parts of Assam and West Bengal in India and also in Bangladesh.

The introduction of relative insensitivity to photoperiod and temperature through breeding has been responsible for the development of 'period fixed' rather than 'season bound' varieties. In breeding varieties for multiple cropping, yield per day should be used as a selection criterion in segregating generations. Other factors like seed dormancy will also need attention, since if a crop attains maturity before the complete withdrawl of the monsoon rains, so that there is rainfall at harvest time, the grains will sprout. A few examples of the different kinds of multiple cropping sequences involving food crops which are becoming popular in different parts of India are given in Tables 10.3 to 10.5.

Rainfed farming In high-rainfall areas the production potential is similar to that of irrigated areas. However, in the unirrigated semiarid areas, commonly referred to as dry-farming areas, considerable production risks exist. The main crops grown in such areas are grain legumes, sorghum, millets and oilseed crops. It is also possible to grow a wide variety of fruit trees and thus help to meet the nutritional needs of the area concerned. Research in semiarid areas should be directed towards water and soil conservation and land-use planning based on knowledge of precipitation, evapotranspiration and the moisture-holding capacity of the soil. Contingency plans should be developed and introduced so as to minimize the risk of total loss of crops during aberrant weather. In addition, more profitable crops should be sought for the semi-arid areas: there are many underexploited plants of potential economic value.

Plant breeders should develop varieties which can be grown in flood-free seasons in flood-prone areas, and also drought-escaping varieties which can be grown in drought-prone areas. This requires cooperation between breeders and agrometeorologists.

Mixed and intercropping Various combinations are sown particularly in unirrigated areas. Not all the combinations currently grown are scientifically sound. Intercropping systems should therefore be developed which are based on the extent to which the companion crops are able to interact beneficially or 'cooperate'. Among the major components of such cooperation are:

Table 10.3. Production potential, crop duration and labour requirement of important annual crop sequences[1] in North Western Region of India (1974/75 to 1976/77).

Centre	Crop in sequence (duration)			Total crop duration in days	Labour requirement in man days	Yield in kg/ha			Total yield in kg	
	kharif[2]	rabi[3]	summer			kharif[2]	rabi[3]	summer	grain	others
Palampur	Ma 119	Wh 185	Fallow	304	181	5,254	4,328	-	9,582	-
	Ma 120	Po 103	Po 122	344	396	7,124	6,715	9,985	7,124	16,700
	Ri 108	Po 100	Po 125	333	450	6,150	10,377	20,157	6,150	30,534
Talab Tillo	Ri 97	Wh 178	Fallow	275	235	1,790	2,856	-	4,646	-
	Ma 98	Po 94	Wh 110	302	341	3,357	14,135	2,580	5,937	14,135
	Ma 98	Ra 85	Po 90	273	298	3,071	16,485	10,575	3,071	27,060
Ludhiana	Ma 95	Wh 168	Fallow	263	181	4,089	5,013	-	9,102	-
	Ma 95	Wh 168	Mu 68	331	273	4,862	5,204	1,044	11,110	-
	Ma 95	Wh 168	MF 62	325	251	4,151	5,261	36,280	9,412	36,280
	Ma 95	Po 93 + Po 93	Mu 68	349	488	4,684	19,772 + 18,627	1,201	5,885	38,399

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1. Ma = Maize, Ri = Rice, Wh = Wheat, Po = Potato, Ra = Radish, Mu = Mung bean, MF = Maize as fodder.
2. Kharif season: June to October.
3. Rabi season: October to April.

Table 10.4. Production potential, crop duration and labour requirement of important annual crop sequences[1] in Northern Region of India (1974/75 to 1976/77).

Centre	Crop in sequence (duration)						Total crop duration in days	Labour requirement in man days	Yield in kg/ha			Total yield in kg	
	kharif[2]		rabi[3]		summer				kharif[2]	rabi[3]	summer	grain	others
Pantnagar	Ma	105	Wh	144	–		249	181	3,910	4,537	–	8,447	–
	Ma	106	Wh	130	Mu	65	310	273	3,718	4,788	638	9,144	–
	Ma	105	Po	86	Wh	109	300	341	3,722	14,590	4,353	8,075	14,590
	Ma	100	La + Wh	93 101	Mu	59	353	325	3,233	863 + 3,742	246	7,221	863
Pura	Ma	79	Wh	139	Mi	61	279	233	3,704	4,007	982	8,693	–
	Pi	152	Wh	121	Mi	61	334	225	1,988	4,550	1,027	7,565	–
	Ma	79	Po + Wh	72 108	CF	61	320	411	3,791	17,866 + 4,491	28,763	8,282	17,866 + 28,763
	Ri	95	Po + Wh	72 109	CF	60	336	465	3,924	17,066 + 4,436	27,559	8,360	17,066 + 27,559
Varanasi	Ri	102	Wh	127	Ri	103	332	365	4,259	4,861	4,029	13,149	–
	Ri	105	Wh	127	Mu	61	293	327	5,110	5,136	1,773	12,019	–
	Ri	105	Wh	127	Mi	64	296	287	4,830	4,909	2,284	12,023	–

1. Ma = Maize, Pi = Pigeon pea, Ri = Rice, Wh = Wheat, Po = Potato, La = Lahi, Mu = Mung bean, Mi = Millet, CF = Cowpea as fodder.
2. Kharif season: June to October.
3. Rabi season: October to April.

Table 10.5. Production potential, crop duration and labour requirement of important annual crop sequences[1] in Eastern Region of India (1974/75 to 1976/77).

Centre	Crop in sequence (duration)						Total crop duration in days	Labour requirement in man days	Yield in kg/ha			Total yield in kg	
	kharif[2]		rabi[3]		summer				kharif[2]	rabi[3]	summer	grain	others
Bhubaneshwar	Ri	71	Ri	95	Ri	106	272	390	3,133	3,749	4,807	11,689	–
	Ri	102	Ma	105	Co	57	264	298	4,583	4,048	3,677	12,308	–
	Ri	102	Po	76	Se	73	251	342	4,785	19,876	1,103	5,888	19,876
Chiplima	Ri	100	Po	86	Ri	101	287	420	2,949	13,480	3,778	6,727	13,480
	Ri	100	To	87	Ok	111	298	254	3,337	9,701	4,796	3,337	14,497
Kalyani	Ri	94	Wh	121	Ri	96	311	365	4,700	3,021	4,710[4]	12,431	–
	Ri	94	Po	83	Ri	96	273	420	4,482	14,803	5,356	9,838	14,803

1. Ri = Rice, Ma = Maize, Po = Potato, To = Tomato, Wh = Wheat, Co = Cowpea, Se = Sesame, Ok = Okra.
2. Kharif season: June to October.
3. Rabi season: October to April.
4. Based on data for two years only.

- efficient interception of sunlight,
- ability to tap nutrients and moisture from different depths of the soil,
- nonoverlapping pest sensitivity,
- use of legumes for promoting biological nitrogen fixation and increasing protein availability.

Multilevel or three-dimensional cropping In garden lands, where a wide variety of plantation crops, fruit trees, palms and other tree crops are grown, it is possible to design a crop canopy allowing more efficient utilization of vertical space. The effective use of both horizontal and vertical space should be taken into account in breeding varieties for cultivation in three-dimensional crop canopies. Efficiency in such a cropping system will again depend on the extent of cooperation among the crops in the system. In studies at the Central Plantation Crops Research Institute in India, coconut, cocoa and pineapple proved a good combination (Fig. 10.1): they can intercept sunlight efficiently in a combined canopy and also remove nutrients and moisture from different depths of the soil. The introduction of grain and fodder legumes into such three-dimensional crop canopies will provide opportunities for animal husbandry. A careful study of all the major garden-land cropping systems based on the extent of symbiosis and synergy that the different components of the system exhibit will be useful in developing specifications for ideotypes with efficient performance in three-dimensional crop canopies.

Kitchen gardening and home fish gardening Kitchen gardening can be one of the most efficient systems of farming from the point of view of solar and cultural energy conversion. Vegetables rich in β-carotene and iron need to be developed and popularized (cf. Chapter 1, pp. 40-42). If planned intelligently and scientifically, the use of backyard gardens, roof gardens and other sites for growing vegetables and fruits wherever possible around mud huts as well as brick houses can make a substantial contribution to improved nutrition. Where small ponds are available in large numbers, home fish gardening can be an excellent method of supplementing nutrition and income.

Forestry and agroforestry The importance of improving the productivity of forests cannot be overemphasized. Agroforestry has been defined as a sustainable management system for land which increases overall production, combining agricultural crops, tree crops, forest plants and/or animals simultaneously or sequentially. Sylvipastoral, sylvihorticultural, sylviagricultural and other combined land-use systems are extremely important for meeting the food, feed, fuel and fertilizer needs of people in many hilly regions. Plant breeders have yet to turn their attention to the breeding of varieties suitable for such systems of sylviculture.

Shrubs and trees suitable for raising plantations for fuel energy in villages and initiating what is sometimes called a 'gasoline' agriculture need to be identified and improved.

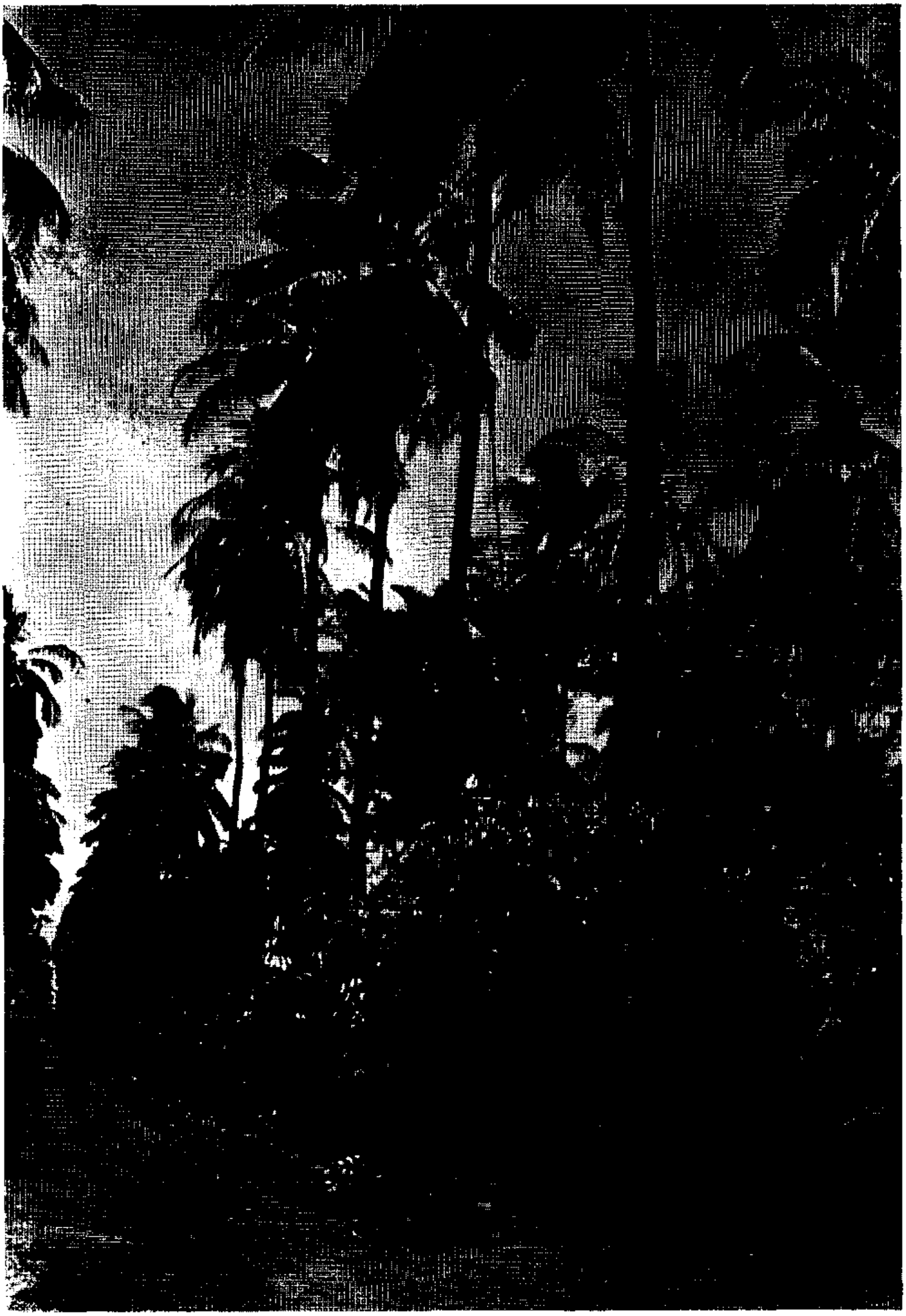

Fig. 10.1. Mixed cropping of coconut, cocoa, peppers and pineapple in India. (Photograph: Royal Tropical Institute, Netherlands.)

Mixed farming systems may involve crop-livestock, crop-fish and crop-livestock-fish production programmes. In Southeast Asia fishing in rice fields is common. Minimal use of chemical pesticides will be important in such systems so as to avoid fish mortality and the transfer of toxic residues through the plant-animal-man food chain. This will involve the incorporation of genetic resistance in the crops and the development of integrated pest management systems.

Sea farming There are considerable opportunities for spreading scientific sea farming practices involving an appropriate blend of capture and culture fisheries. The rate of growth of oysters, mussels, prawns, lobsters, eels and a wide variety of marine plants and animals is high in tropical oceans. If along with such integrated sea farming practices, the cultivation of suitable economic trees like casuarina, cashew nut and coconut can be popularized along the coasts, thriving coastal agriculture-cum-mariculture systems can be developed. Plant breeders will have to select suitable genotypes of the above species and other plants which can grow well on coastal sandy soils. In addition to improving income and nutrition, such farming systems can help to arrest sea erosion.

Relevant changes in agronomic practice To realize the yield potential of a given plant type, it is necessary that appropriate changes be introduced into agronomic practice. The following are some of the important developments now taking place:

- Use of minimum or appropriate tillage suitable for multiple and intercropping systems.
- Use of high plant density leading to dense crop canopies.
- Development of a weed-free environment.
- Integrated nutrient supply, involving controlled release of fertilizer, use of nitrification inhibitors, foliar feeding and low-cost anhydrous ammonia, and of *Azolla,* bacterial, algal and other microbial fertilizers.
- Better on-farm management of water, including drip irrigation in arid land.
- Integrated pest and disease management involving agronomic, genetic, biological and chemical methods of control.
- Use of growth regulators in fruit trees and ripeners in sugar cane.
- Organic recycling leading to crop-livestock, crop-fish and crop-livestock-fish integration.

DEVELOPED WORLD

Breeding for production per man hour

In the developed world it may be expected that breeding for high production per man hour of agricultural labour will increasingly prove to be at least as important as breeding for higher yields. As an example of this kind of development we may cite the stiff straw required in grain cereals and silage maize if these are to be suitable for mechanized harvesting. This is now such an important character that new varieties which are inferior in this respect to existing varieties will not be accepted by the farmer even if they are significantly higher yielding. Another example is the monogerm character in sugar beet varieties: new multigerm varieties, regardless of what other favourable characters they may possess, are of no importance for future use in developed countries. A further example is provided by the silage maize hybrids bred for cool climates, which because their higher production per man hour have replaced mangels in several countries.

Industrial crops

Another character likely to gain in importance is suitability for processing. In breeding sugar beet, for example, it may be expected that in the future more emphasis will be laid on juice purity. At present the price obtained by the farmer for sugar beets is generally based on sugar yield, but it is probable that 'in future' sugar content and extractable sugar yield, as well as or instead of sugar yield, will be taken into account in fixing prices.

In addition, the introduction of new crops as raw material for the chemical and pharmaceutical industries will probably become more important, especially in countries where agricultural overproduction in certain crops is so high that they could with advantage be replaced by crops of local value or suitable for export.

Protein and oil crops

Within the European Economic Community proposals have been made to encourage the cultivation of protein crops, such as *Vicia faba*, and breeders have been requested to produce varieties giving higher and especially more stable yields of these crops. If the success of such projects is to depend on protective measures, such as import levies, consideration should also be given to their possible effects on exports of such products from the developing world.

In many countries there was opposition to the protection of sugar beets because it acted against the efforts of developing countries to export cane sugar. In this case there were many arguments in favour of the continued protection of sugar production in the developed world: these included the fact that the crop is of economic importance to farmers and is important in crop rotations, that numerous factories are in existence and that some 40% of world sugar production comes from beet. If protection of protein production is also to be introduced in the developed world, it is essential to scrutinize closely the question whether such protection can in any way be justified.

With respect to oil crops it must be borne in mind that generally speaking the yield of oil per hectare in tropical countries is much higher than the yield that can be obtained in the temperate zones. Here the same problems have to be faced.

Since the period normally needed to complete a breeding cycle is 15 years, it must be stressed that the plant breeder should consider very carefully before embarking on a breeding project that results in products whose value is based on protective measures which may be abandoned at any time as a consequence of changing political views.

Value-added products

Agricultural products which for one reason or another are considered to have an extra value over and above that normally attached to the crop are sometimes also of importance in developed countries and this may have consequences for the breeder. Potato breeding in the Netherlands provides an example. In that country the export of seed potatoes has assumed such proportions that the suitability of potato varieties for other countries can be as important as suitability for the home market. Because of the higher value of seed potatoes as against ware potatoes, long-distance export can still be economically worthwhile.

Impact of breeding

ON PERFORMANCE

Fig. 1.12 illustrates the effect of improvements in agricultural techniques and of the introduction of higher-yielding varieties on crop yields in the USA. We see that no improvement whatsoever has been obtained for beans and only a moderate improvement for soya beans but that the results for maize and groundnuts are very good. Fig. 4.17 and Fig. 4.37 show the results for potatoes and sugar beets in the Netherlands. Here the increase over the high yield levels already attained in 1930 is partly due to improvement in cultivation techniques and partly to the introduction of higher-yielding varieties. By considering the two factors separately it is possible to show that the yield increase due to the introduction of better varieties since 1930 was 0.8% per year for potatoes and 0.4% per year for sugar yield. Similarly, for spring wheat the yield increase due to breeding has been shown to be 1% per year over the same period.

Similar calculations were made in England at the National Institute of Agricultural Botany (Silvey, 1978) and the results are given in Fig. 10.2 for wheat and in Fig. 10.3 for barley. The increase in yield due to breeding was 1.8% per year over a period of 30 years in wheat, accounting for 67% of the total yield increase. For barley the corresponding figures are 1% per year and 50% of the total increase.

Similar data for maize (Russell, 1974; Duvick, 1977) were obtained from uniform trials of hybrids representing each decade from the 1930s up to and including the 1970s. Although considerable interaction was observed between genotypes and seeding rates, the two sets of experiments gave similar results and indicated that, of the total gain in yield per hectare per year, the proportion due to breeding was 57 to 63%. It seems clear, therefore, that somewhat more than half of the yield gain

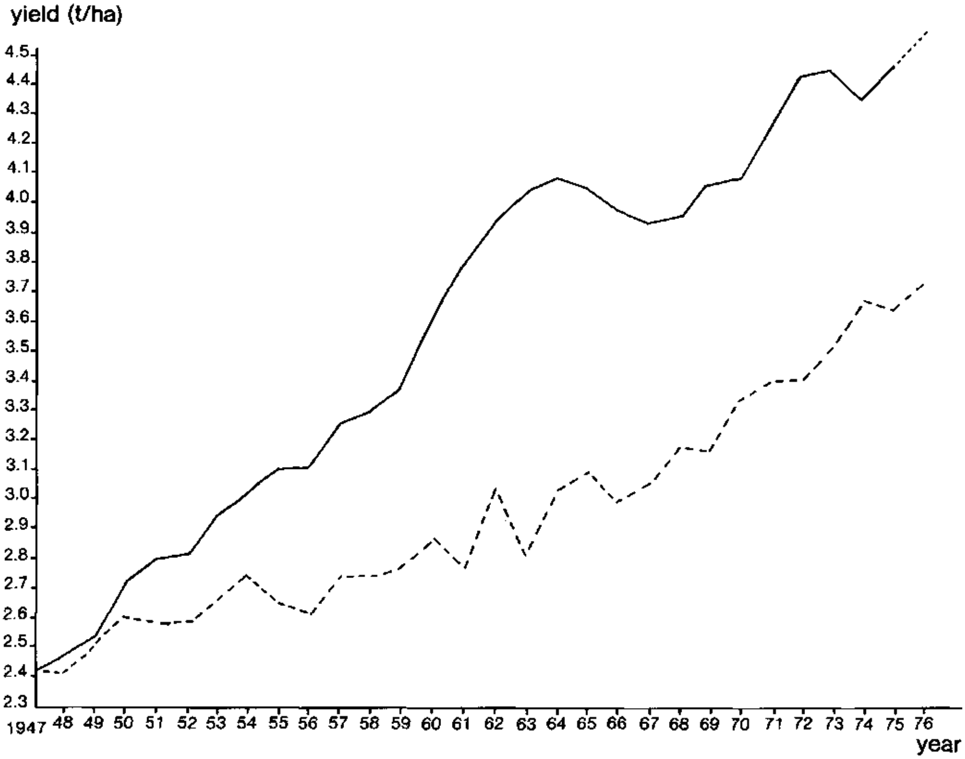

Fig. 10.2. Yield increases in spring and winter wheat in the UK, 1947-1976; — total yield increase, 15-year moving average, --- yield increase due to variety (from: Silvey, 1978).

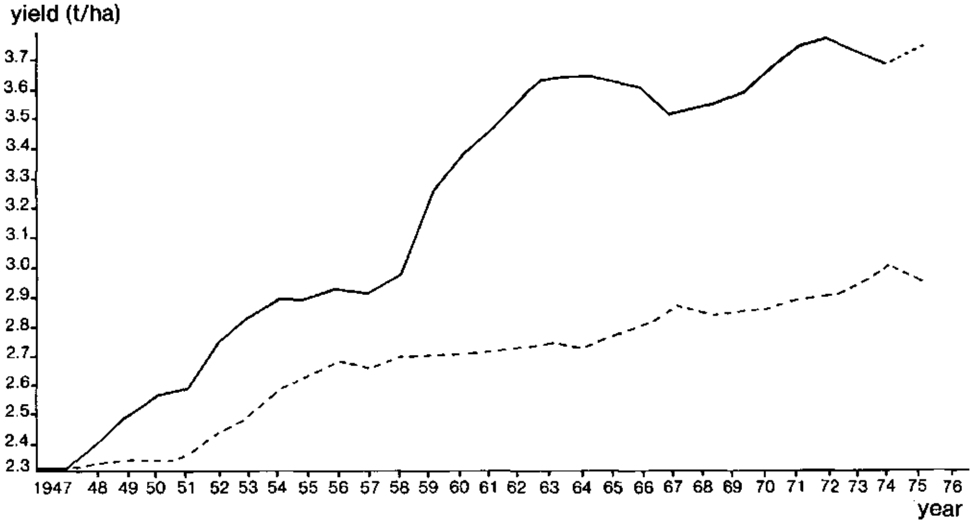

Fig. 10.3. Yield increases in spring and winter barley in the UK, 1947-1976; — total yield increase, 15-year moving average; --- yield increase due to variety (from: Silvey, 1978).

achieved in maize hybrids over a 40-year period is attributable to genetics. This figure of about 50% for the proportion of the total yield improvement attributable to new varieties seems to be generally valid.

The figures in Table 10.6 have been calculated from data on cereals given by FAO on the yield increase in various countries over the period 1950-1978. Here again we see exceptionally high figures for maize, though in this case the increase in the USA is below the other countries. The reason may be that by 1950 hybrid maize was being grown in 78% of the USA maize area whereas in other countries it was not until after

Table 10.6. Changes in cereal yields in different countries from 1948 to the present. Note: Figures are mean yields per crop season. For rice, in which the growth period has been reduced and two crops or more per year can now be grown, the total effect on annual yield will be greater than shown here. (Based on Sehgal, 1977).

Crop	Country	Yields			
		in t/ha	in % of yield 1948/52		
		1948/52	1961/65	1972	1976
Rice	India	1.11	133	145	158
	Indonesia	1.61	109	140	162
	Japan	4.25	118	139	130
	Philippines	1.18	107	120	157
	Thailand	1.31	134	136	144
	USA	2.56	170	206	202
	Mean	2.00	129	148	158
Wheat	Bulgaria	1.24	146	299	285
	France	1.83	160	250	202
	Hungary	1.38	135	225	263
	India	0.66	127	209	217
	Mexico	0.88	230	302	340
	Pakistan	0.87	95	137	157
	Romania	1.02	143	234	235
	USA	1.12	152	196	181
	USSR	0.84	114	175	182
	Mean	1.09	145	225	229
Maize	Bulgaria	0.98	258	441	422
	France	1.36	222	321	249
	Hungary	1.77	147	225	222
	Italy	1.84	178	292	298
	Romania	0.81	218	379	317
	Spain	1.55	151	232	255
	USA	2.49	167	245	208
	Yugoslavia	1.34	169	249	283
	Mean	1.52	189	265	282

1950 that hybrid maize was introduced and was able to make its contribution to yield increases.

For rice the smallest increase is seen in Japan, possibly because yields were already very high in the period around 1950 (about three times the average yield of the other areas mentioned), with the result that the introduction of HYVs (high-yielding varieties) in this area has had much less impact than elsewhere.

The impact of HYVs of wheat may be the reason for the leap in wheat yield data for Mexico in 1961/65; for India, where HYVs were not yet of importance in 1961/65, a similar leap is seen in the figure for 1972. Assuming that here, too, 50% of the yield increases are the effect of plant breeding, we may conclude that the effect of plant breeding on yield level in agriculture is very substantial. The table demonstrates that in the developed world breeding by traditional methods continues to make an important contribution to the constant rise in yield, but there is also a clear influence of the HYVs on the one hand and of the introduction of the hybrid technique in maize on the other hand.

Not only does plant breeding affect yield but it is also essential for the development of varieties better suited to mechanization, processing, suitability for transport etc., as pointed out in Chapter 5. An example of the influence on production per man hour or agricultural labour is given in Chapter 4 ('Sugar beet', p. 215).

Another very important factor, but one which is rather difficult to demonstrate, is any concrete fashion, is the catalytic influence of the introduction of better varieties on developments such as the use of fertilizers, agricultural machinery etc.

ON GENETIC DIVERSITY

The introduction of HYVs and hybrids has created some uneasiness in view of the possibility that the consequent narrowing of the genetic base of our agricultural crops may increase the danger of epidemics. This is in fact a matter of great concern to many plant breeders, and they have given their support to the action now under way for the creation of gene banks. The necessity for collecting and maintaining genetic material is stressed in Chapter 3. The dangers associated with a narrow genetic base became apparent in the now classic example of the southern corn leaf blight epidemic on all maize in the USA carrying T-cytoplasm (cf. Chapter 4, p. 202). Although the importance of gene conservation must not be underrated, mention must also be made of the fact that although the epidemic caused a mean yield loss in the USA of 15% in the year of the epidemic, nevertheless, as a result of efficient organization and the alertness of American breeders, the negative effect was eliminated within a year: in the year following that of the disaster, yields were back to normal and further yield increases were obtained in subsequent years.

Notwithstanding, the loss of land races and primitive forms of our crops should be avoided. Serious losses have already occurred but there is still a very wide range of material available which should be saved. As far as the broad genetic base is concerned, it is probable that most material of any value is still available in the gene centres. Even in such a densely populated area as north-western Europe, where agriculture is highly mechanized, all the different forms of perennial ryegrass (*Lolium perenne*) for which this area is a gene centre are still to be found. Whereas land races are in grave danger of disappearance, the effect of the introduction of better-yielding varieties on the occurrence of the wild relatives of cultivated species in other gene centres will probably be less serious.

With regard to trees and shrubs the danger of losing valuable material is also considerable and in Brazil, for instance, projects for the reclamation of vast areas of tropical forest should be examined carefully for the possibility of undesirable side effects of this kind.

We cannot, however, agree with those who propagate the view that, in order to safeguard land races which are of value as genetic sources, new high-yielding varieties should not be introduced into developing countries. We regard it as unacceptable to ensure genetic conservation by denying to the poorest part of the world the opportunity of benefiting from the results of plant breeding.

On the other hand, these local varieties or land races are important and they ought to be saved. Here there is an important task for the developed countries, viz. to set up a joint programme with developing countries for the preservation, study and description of this genetic pool. The developed world could supply the means and techniques for collection and maintenance in the gene centres themselves, and could also provide facilities for duplicate storage and study in the developed world, thus ensuring that the material is preserved and used in the best possible way.

Among the positive results of plant breeding activity in this field, mention may be made of the following: the development of varieties combining characters originating from different areas, for instance those combining the high yielding capacity of varieties from developed agricultural areas with the disease resistance of primitive forms from other areas; the introduction of day-length neutrality into day-length sensitive crops; and the introduction of improved cold tolerance and winter hardiness into cold-susceptible crops. A further activity in which plant breeders are engaged is the distribution of genetic material in regions outside its normal area of use, in order to extend the range of genetic diversity in the new varieties that they are creating. Finally it may be noted that the major goal of all the methods described in Chapter 8 is a broadening of the genetic base beyond the natural limits of the plant.

Retrospect and prospect

We can look back with legitimate pride and satisfaction on the accomplishments of plant breeders during this century. There has been great progress in improving the yield potential of crops as well as ensuring their security from ravages due to the unholy triple alliance of pests, pathogens and weeds. There has also been improvement in the nutritive quality, consumer acceptance and suitability for processing and storage in various economic plants. Nevertheless it must be admitted that we have not been able to introduce any new crop plant into cultivation. The only man-made cereal, triticale, has yet to achieve real commercial importance. The scope for domesticating and improving some of the underutilized plants will have to be seriously examined in coming years, since many are known to have a great capacity for biomass production as well as being sources of useful natural products. Examples are *Chenopodium* species for use as food material and *Parthenium argentatum* for rubber production.

Recent advances in genetic engineering provide some hope of enlarging the gene pool available to plant breeders for designing new and more hardy plant types. In the immediate future, however, we will have to depend largely on the techniques often referred to as 'conventional', which still provide sure and speedy methods of achieving many of our objectives.

It is tempting to try to estimate the relative importance that the various techniques for the development of new varieties are likely to have in the near future. The techniques described in Chapter 4 under 'Current breeding methods' are clearly still able to produce valuable results, and it is they that should principally engage the efforts of the practical breeder, especially in areas where breeding is less advanced. The techniques discussed in Chapter 8 under 'Methods for the future' are as yet hardly far enough developed to be of use in practical breeding programmes. Fig. 10.4 illustrates the possible relative impacts of various techniques in the next 20 years. A large proportion of the crop varieties in use by the year 2000 may be expected to have originated by means of current breeding methods. Second in importance may be the

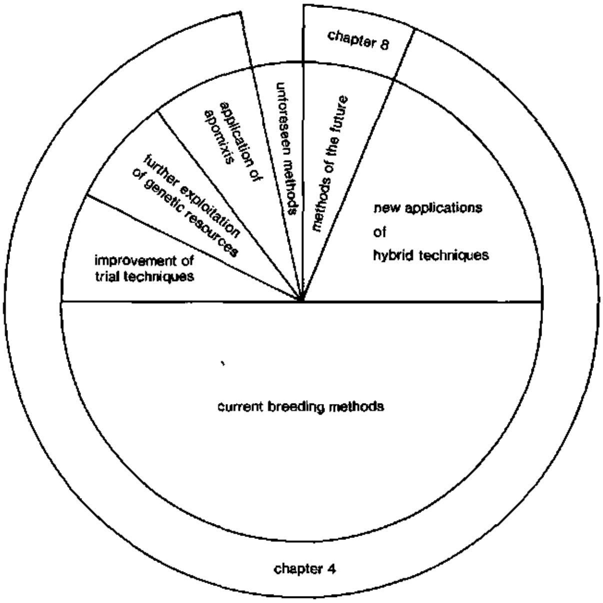

Fig. 10.4. Relative future importance of various breeding techniques (conjectural).

extension of hybrid techniques to new crops. Further applications of apomixis and more sophisticated techniques in breeding and testing for yield and stability could have some impact. Some useful material may also come from results of new investigations of genetic resources and rather less from cell, genome, chromosome, gene and DNA manipulations and finally from unforeseen developments.

Therefore, while working and waiting for new breakthroughs, we should intensify our efforts to improve the productivity of both terrestrial and aquatic farming systems. Calculations by Buringh and coworkers (cf. Chapter 2, pp. 48-51) indicate an absolute maximum world production potential of nearly 50,000 million t per year in grain equivalents of a standard cereal crop. Since average world production in recent years has only been of the order of 1300 million t, the postulated production potential is nearly 40 times the present level of production. This vast untapped production reservoir is the most hopeful feature of the world food scene. Since the tropics and subtropics where most of the developing countries lie are blessed with abundant sunlight, it is these countries that have the greatest opportunity for achieving a substantial increase in current production levels. From being importers of food, as most of them are today, they are capable of becoming the world's granary. Given an appropriate blend of political will and professional skill, it should be possible to convert the potential into reality. Plant breeders will have to play a catalytic role in this process of transformation of stagnant agricultural systems.

It has been stated that hybrid maize in the USA not only helped to increase maize production in that country but also initiated a chain reaction in the improvement of farming as a whole. This is because farmers who saw the benefit of fertilizer application and improved management practices in hybrid maize, proceeded to apply improved methods to other crops as well. Another recent example of progress in one crop having a far-reaching effect on an entire farming system is seen in the Punjab of India. Here the modern phase of agricultural transformation started with the release of the dwarf and fertilizer-responsive varieties of wheat. The farmers who obtained high yields in wheat then adopted the new technology in rice, potato and other crops, and thus the areas of the wheat revolution also became the centres of the rice revolution. Where vision is limited, action is equally circumscribed. Hence it can be regarded as a duty of plant breeders to enlarge the vision of political leaders, extension workers and above all the farming community. This can be done provided plant breeders also take interest in organizing demonstrations in the fields of small farmers. To the farmer 'seeing is believing' and hence good demonstrations can trigger mass agricultural movements.

In the poor nations, agriculture should not merely help to provide more and better-quality food but should also become an important instrument of economic growth, particularly of income and employment generation. It is for this reason that we have laid considerable stress on strategies which can help to withdraw some of the labour population from the routine operations of farming through a properly planned programme of diversification of land, water and labour use. The potential of tropical agriculture for diversified land use and for the harvesting of solar energy, is illustrated by a Chinese saying that the same plot of land can appear brown, black and green on the same day. Brown represents a crop which is about to be harvested, black the empty soil after the removal of the crop and green the transplanted seedlings which are planted on the same day.

It is sometimes stated that we are now in an age of technology and computers. Modern technological advances are indeed remarkable and we can be proud of them. Reaching the moon is no longer a science fiction. It remains a fact, however, that millions of people on this earth are still unable to meet their minimum needs, including food. Our aim, therefore, should be to channel the techniques and tools offered by modern science and technology into growing two blades of grass where only one grew before. The population expansion means that, like Alice through the Looking Glass, we have to run twice as fast to remain where we are. It is hence necessary to emphasize that unless an age of humanism, in which the highest priority in all developmental programmes is given to providing the minimum needs of every human being, is superimposed upon the age of science and technology, there can be no happy world. In working towards this goal, the plant breeder has an important part to play. A successful plant breeder is one who understands the characteristics of his material in relation to the environment in which the plant is to be cultivated. Modern experimental techniques can help the plant breeder to improve the precision and speed of his work. It cannot, however, help him to provide successful varieties unless he has intimate contact with both the plant and the environment in which it is to be cultivated. Hence plant breeding will always remain as much an art as a science. We would, therefore, like to conclude this book by expressing the hope that plant breeders around the world, both young and old, will remain close to the earth and, by working together with the farmers who finally have to convert the products of plant breeding into more and better food, will help to make the problem of hunger a problem of the past.

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Abbreviations of organizations and institutes mentioned in the text

ACC	Administrative Committee on Co-ordination (of the United Nations)
ARARI	Aegean Regional Agricultural Research Institute, Turkey
AVRDC	Asian Vegetable Research and Development Center, Taiwan
CABO	Centrum voor Agrobiologisch Onderzoek (Centre for Agrobiological Research), Netherlands
CATIE	Centro Agronómico Tropical de Investigación y Enseñanza (Tropical Agricultural Research and Training Center), Costa Rica
CENARGEN	Centro Nacional de Recursos Geneticos (National Genetic Resources Center), Brazil
CGIAR	Consultative Group on International Agricultural Research
CIAT	Centro Internacional de Agricultura Tropical (International Center for Tropical Agriculture), Colombia
CIMMYT	Centro Internacional de Mejoramiento de Maíz y Trigo (International Maize and Wheat Improvement Center), Mexico
CIP	Centro Internacional de la Papa (International Potato Center), Peru
CSIRO	Commonwealth Scientific and Industrial Research Organization, Australia
EEC	European Economic Community
ECP	European Cooperative Program
FAO	Food and Agriculture Organization of the United Nations
GTZ	Gesellschaft für Technische Zusammenarbeit (Society for Technical Cooperation), Federal Republic of Germany
IAEA	International Atomic Energy Agency
IBP	International Biological Programme
IBPGR	International Board for Plant Genetic Resources
IBVL	Instituut voor het onderzoek van Bewaring en Verwerking van Landbouwprodukten (Institute for Research on Storage and Processing of Agricultural Produce), Netherlands
ICA	Instituto Colombiano Agropecuario (Colombian Agricultural Institute), Colombia
ICARDA	International Center for Agricultural Research in Dry Areas, Syria
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics, India

IICA	Instituto Interamericano de Ciencias Agrícolas (Inter-American Institute of Agricultural Sciences), Costa Rica
IITA	International Institute of Tropical Agriculture, Nigeria
INCAP	Institute of Nutrition of Central America and Panama
INIA	Instituto Nacional de Investigaciones Agrícolas (National Institute of Agricultural Research), Mexico
INRA	Institut National de Recherche Agronomique (National Institute of Agricultural Research), France
IPC	*see* CIP
IPO	Instituut voor Plantenziektenkundig Onderzoek (Institute for Phytopathological Research), Netherlands
IRAT	Institut de Recherches Agronomiques Tropicales et des Cultures Vivrières (Institute for Tropical Agricultural Research and Food Crops), France
IRRI	International Rice Research Institute, Philippines
IRTP	International Rice Testing Program
ISTA	International Seed Testing Association
ITAL	Instituut voor Toepassing van Atoomenergie in de Landbouw (Institute for the Application of Atomic Energy in Agriculture), Netherlands
IUNS	International Union of Nutritional Sciences
IVP	Instituut voor Plantenveredeling (Institute of Plant Breeding), Netherlands
IVT	Instituut voor de Veredeling van Tuinbouwgewassen (Institute for Horticultural Plant Breeding), Netherlands
KIS	Kenya Inspection Service, Kenya
LISA	Laboratory for Information Science in Agriculture Fort Collins, Colorado, USA
NAK	Nederlandse Algemene Keuringsdienst voor Zaaizaad en Pootgoed van Landbouwgewassen (Netherlands General Inspection Service for Field Crops), Netherlands
NAS/NRC	National Academy of Sciences/National Research Council, USA
NIAB	National Institute of Agricultural Botany, UK
NIVAP	Nederlands Instituut voor Afzetbevordering van Pootaardappelen (Netherlands Potato Consultative Institute), Netherlands
OECD	Organisation for Economic Co-operation and Development
OPEC	Organization of the Petroleum Exporting Countries
ORSTOM	Office de la Recherche Scientifique et Technique de l'Outre-Mer (Overseas Office for Scientific and Technical Research), France
PAG	Protein-Calorie Advisory Group of the United Nations System
RIVRO	Rijksinstituut voor Rassenonderzoek van Landbouwgewassen (Government Institute for Research on Varieties of Cultivated Plants), Netherlands

SABRAO	Society for the Advancement of Breeding Researches in Asia and Oceania
SIDP	Seed Industry Development Programme (FAO)
SVP	Stichting voor Plantenveredeling (Foundation for Agricultural Plant Breeding), Netherlands
UNDP	United Nations Development Programme
UPOV	Union internationale pour la Protection des Obtentions Végétales (International Union for the Protection of New Varieties of Plants)
USDA	United States Department of Agriculture, USA
VIR	Vsesoyuznyĭ Nauchno-Issledovatel'skiĭ Institut Rastenievodstva imeni N.I. Vavilova (Vavilov Institute of Plant Industry), USSR
WARDA	West African Rice Development Association
WHO	World Health Organization
WMO	World Meteorological Organization

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For abbreviations see List of abbreviations of organizations and institutes mentioned in the text (pp. 430-432).

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Boonman, J.G., Glas, D.J. & Wijk, A.J.P. van p.: 175-189.
Cocking, E.C. & Power, J.B.: p. 351-356.
Duvick, D.N. & Brown, W.L.: p. 190-203.
Gelder, W.M.J. van: see Miedema, P..
Geling, K.B.: see Morales, M.T..
Glas, D.J., Roothaan, M.E. & Wolff, F. de: p. 376-378.
Glas, D.J.: see Boonman, J.G..
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Hintzen, J.J.: p. 186-189.
Hogen Esch, J.A.: p. 41 and p. 312-317.
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Lie, T.A. & Mulder, E.G.: p. 341-348.
Marrewijk, G.A.M. van: p. 120, 122-134.
Miedema, P. & Gelder, W.M.J. van: p. 348-351.
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Mulder, E.G.: see Lie, T.A..
O'Toole, J.C.: p. 250-255.
Parlevliet, J.E.: p. 262-269.
Pathak, M.D. & Saxena, R.C.: p. 270-285.
Power, J.B.: see Cocking, E.C..
Roothaan, M.E.: see Vettel, F. and Glas, D.J..
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Schilperoort, R.A.: p. 356-364.
Trip, J.: p. 143-153.
Vettel, D., Strube, H.G. & Roothaan, M.E.: p. 159-167.
Vrânceanu, A.V.: p. 216-223.
Wijk, A.J.P. van: see Booman, J.G..
Wolff, F. de: see Glas, D.J..
Zeven, J.A.: p. 167-172.

All contributors to text and to corresponding lists of references are named at the ends of the chapters.

Errata

page

59 5th paragraph, the beginning of the 3rd sentence "However, this is not the case . . ." should read "This is indeed the case . . ."

59 5th paragraph, the beginning of the 4th sentence "Here the shortening of the growing period has influenced all the developmental phases of the plant in approximately the same way, as is illustrated. . ." should read "The shortening of the growing period influenced here only the length of the vegetative phase, as is illustrated . . ."

87 1st paragraph, 12th line "Frankel and Hawkes, 1976" should read "Frankel and Hawkes, 1975"

91 (Table 3.1) Add "(Adapted from Day 1973)" after the title of the table

96 1st paragraph, 5th line, insert "-LISA" after "IBPGR"

100 1st paragraph, 6th line, "Nordic" should read "Nodic"

101 10th line, "Chang, T.T. 1978." should read "Chang, T.T. 1979."

101 after 34th line, insert "Day, P.R. 1973. Genetic variability of crops. Ann. Rev. Phytopathol. 11:293-312."

103 21st line, "Hernandez X., E." should read "Hernandez, X.E."

103 after 23rd line, insert "Williams, J.T. 1976. A bibliography of plant genetic resources. Supplement. CGIAR/IBPGR, Rome. 36 pp."

133 bottom line of figure caption should read "Crossing: ×. Selfing: ⊗"

174 5th paragraph, 1st line "500,000 ha" should read "5 million ha"

240 2nd paragraph, 1st line "Oka (1963) grew segregating materials" should read "Oka (1963) proposed to grow segregating materials"

257 6th reference, "Baker, E.F.I. & Nopman, D.W.," should read "Baker, E.F.I. & Norman, D.W.,"

257 9th reference (Blum, A., 1973), the title should read "Components analysis of differential yield responses to drought of some sorghum hybrids."

260 21st reference, "Rao, M.J.B., Murth, K.S.," should read "Rao, M.J.B., Murthy, K.S.,"

261 5th reference, "Biological Reviews 37:422-465" should read "Biological Reviews 37:442-465"

431 INRA, "de Recherche Agronomique" should read "de la Recherche Agronomique"

431 LISA, "in Agriculture Fort Collins" should read "in Agriculture, Fort Collins"

432 WARDA, "West African" should read "West Africa"