PHYSIOLOGICAL POTENTIAL OF CROP PRODUCTION

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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

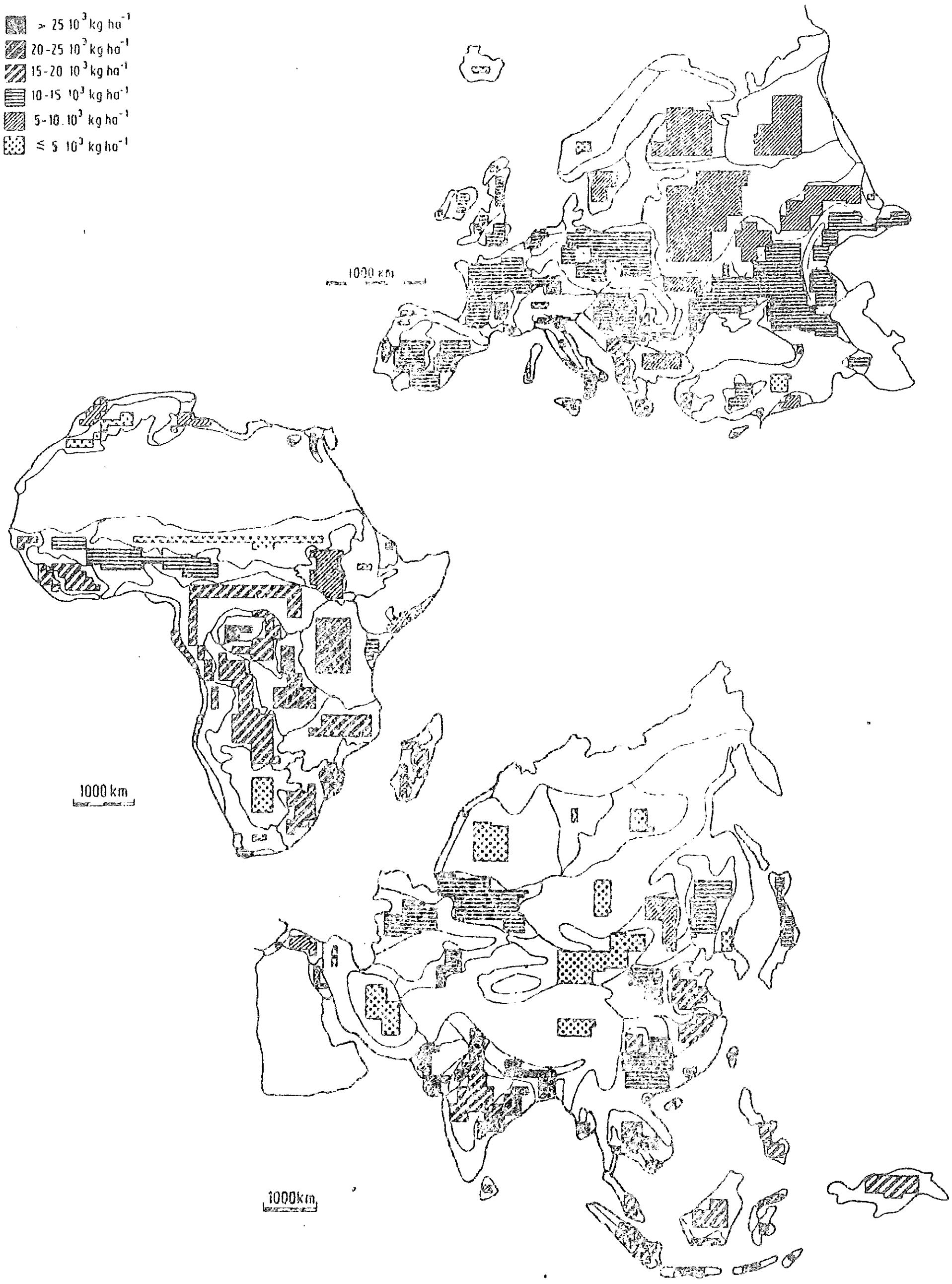
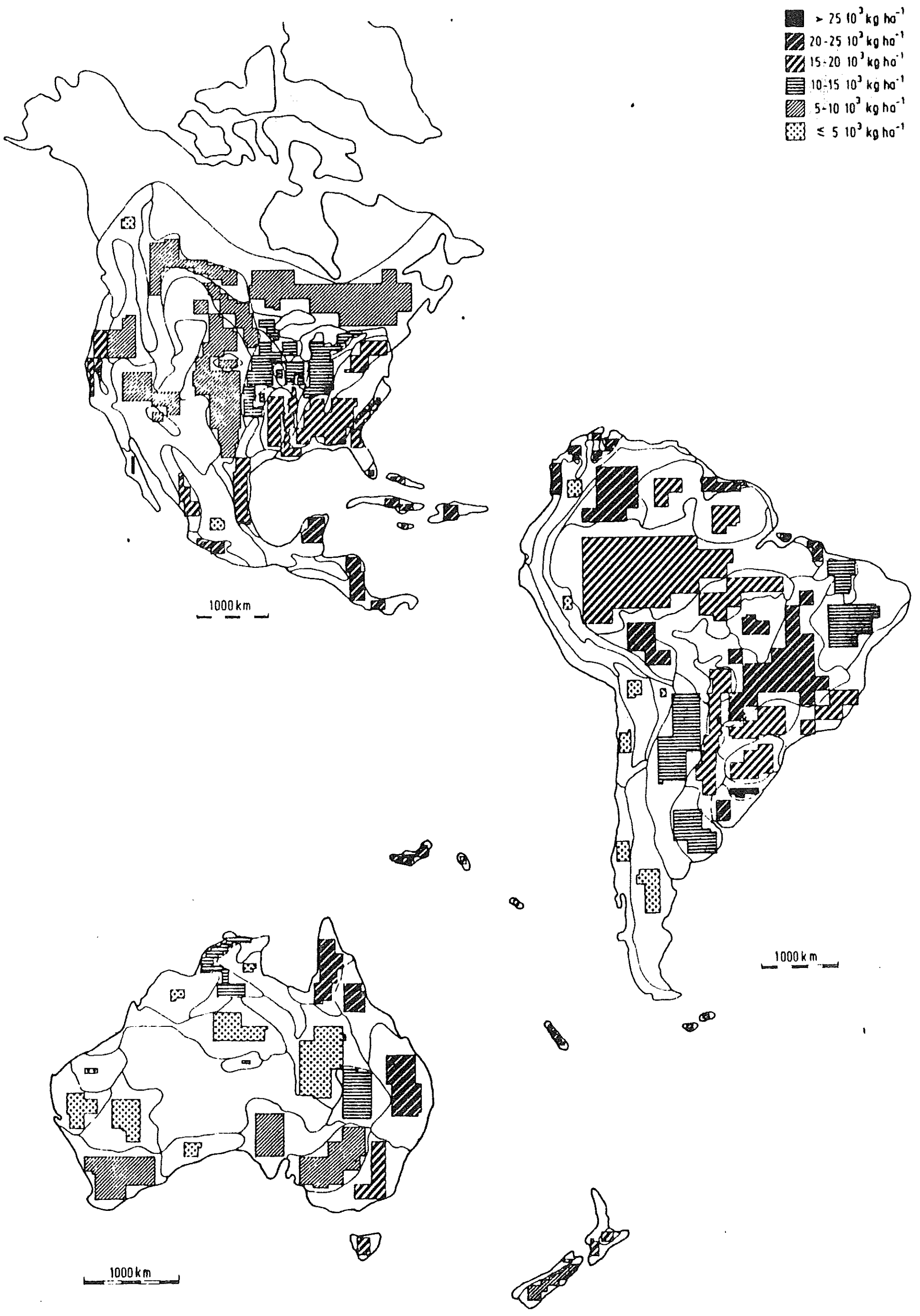


Fig. 2.1. Broad soil regions with their area of potentially arable land marked by the shaded area per region and its average potential yield, in kg grain eq. ha^{-1} $year^{-1}$ indicated by the type of shading. Water and soil constraints are taken into account (from: Buringh et al., 1975).


> 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}
≤ 5 10^3 kg ha^{-1}
1000 km
1000 km
1000 km

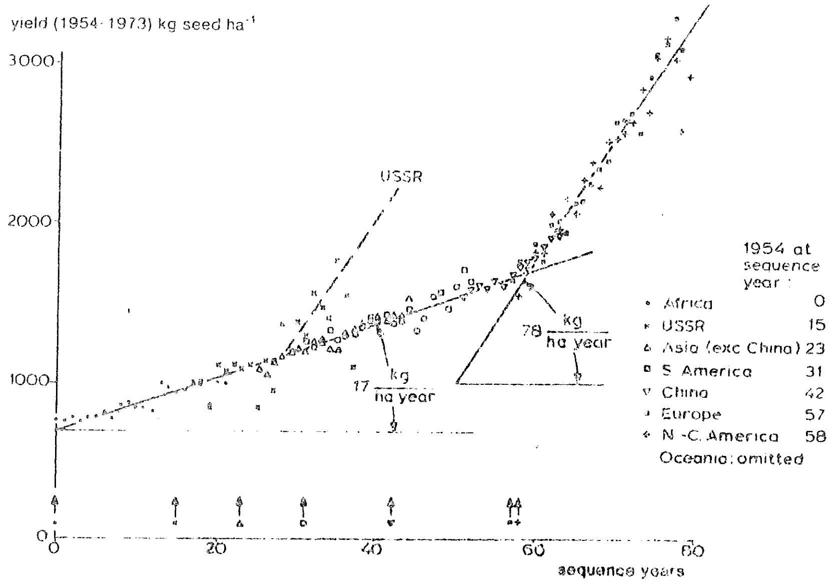


Fig. 2.2. Yields from 1954 to 1973 in the main regions distinguished by FAO, ordered along a continuous yearly time scale. The position of the year 1954 is marked by an arrow for each region. Oceania, with an average yield of 1200 kg ha⁻¹, is omitted because of the erratic fluctuations in the reported 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

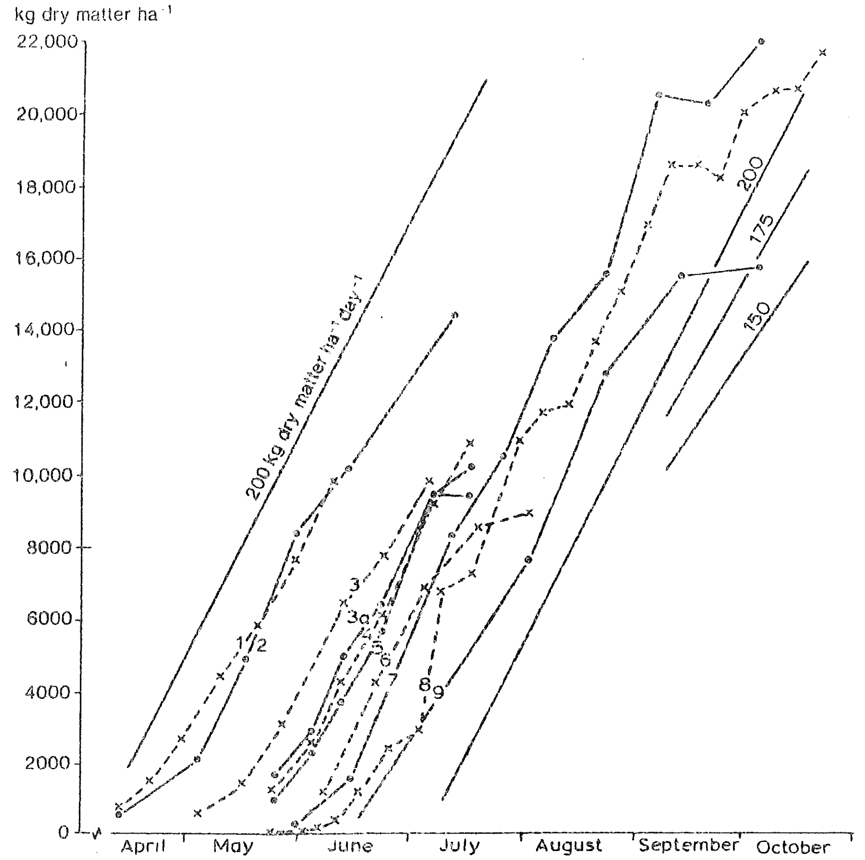


Fig. 2.3. The growth rates of the main agricultural crops in the Netherlands under (near-)optimal growth conditions; compared to the curves corresponding to 200, 175 and 150 kg ha^{-1} day^{-1}. 1. Grass (Alberda, 1960). 2. Wheat (de Vos, 1965). 3. Oats + barley (de Wit, 1960). 3.a. Oats + peas (de Wit, 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

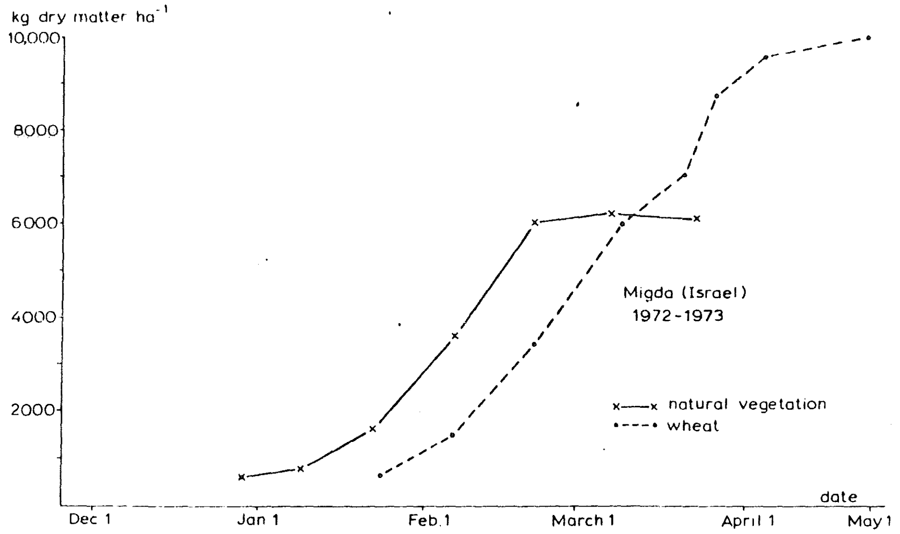


Fig. 2.4. The growth of wheat and natural grassland in Migda (Israel) under (near-)optimal water and nutrient supply (from: van Keulen, 1975).

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

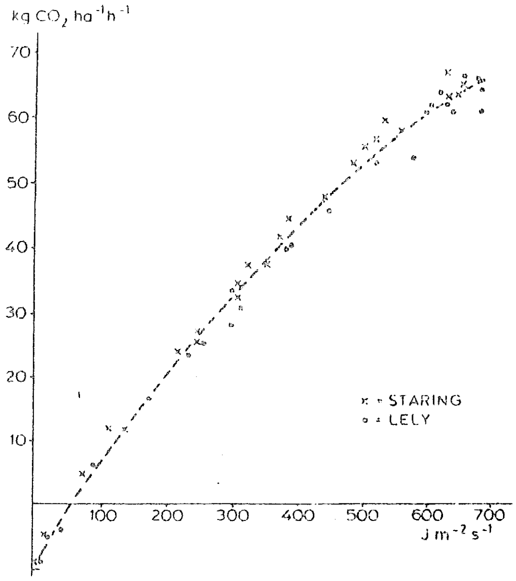


Fig. 2.5. Net CO$_2$ assimilation as a function of light intensity, as measured under field conditions for Staring and Lely, two wheat varieties from 1940 and 1970, respectively.

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%

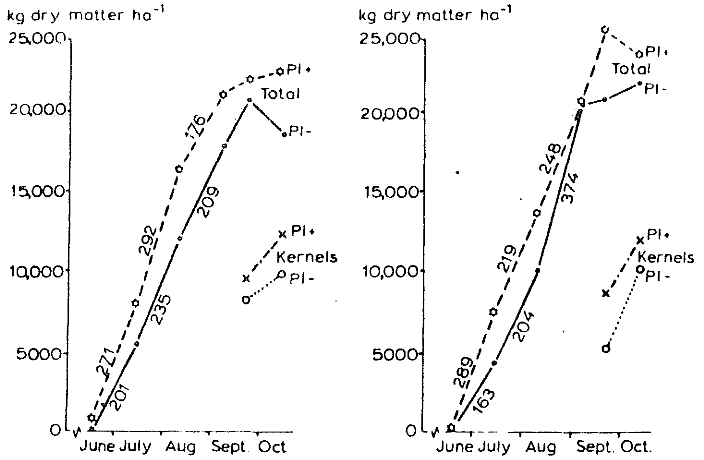


Fig. 2.6. Dry matter yields of two maize varieties, Capella (left) and Pioneer hybrid 3853 (right), grown from 25 April (sowing) to 20 May under plastic (Pl+) and control (Pl—). Numerals upon the growth curves indicate crop growth rate in kg dry matter ha^{-1} day^{-1} for the period concerned (from: 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 $210 \times 40 = 8400$ 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

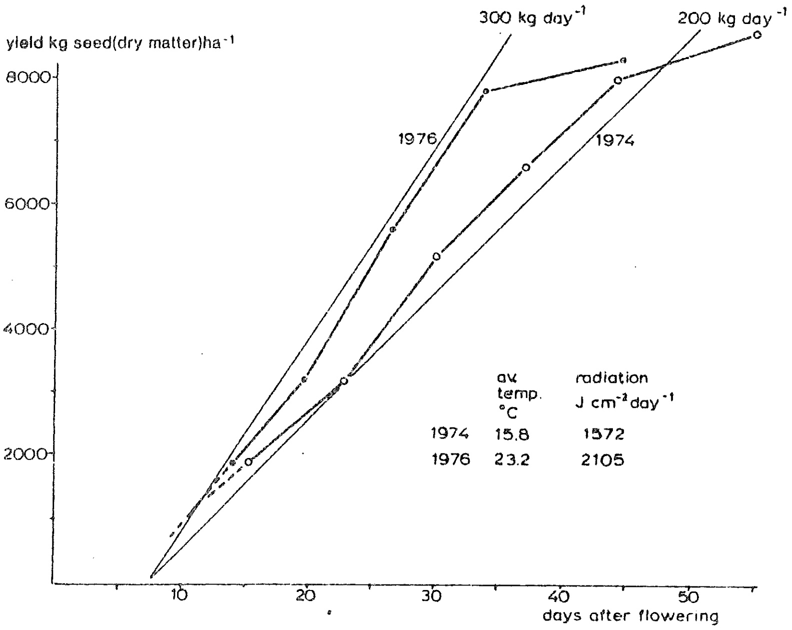


Fig. 2.7. Course of grain growth during two seasons with an extreme difference in weather conditions (wheat).

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

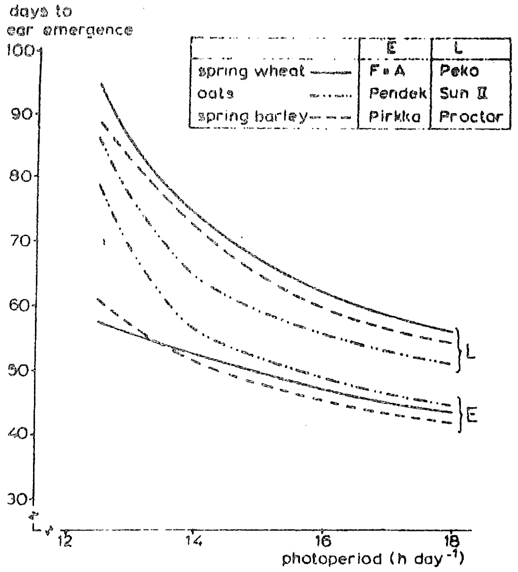


Fig. 2.8. Photoperiod response curves for some early (E) and late (L) varieties of cereals (from: de Vos, 1971).

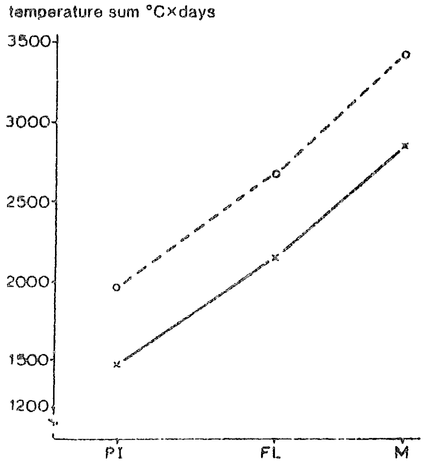


Fig. 2.9. Temperature sum required for panicle initiation (PI), flowering (FL) and maturity (M) for two rice varieties, IR8 (o --- o) and B9C-Md-3-3 (x —— x) grown in Indonesia (Paransih Isbagijo, personal communication).

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

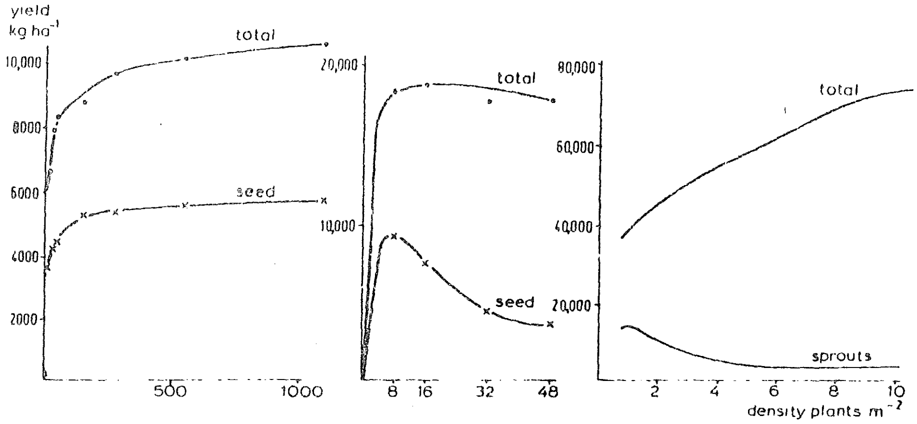


Fig. 2.10. Relation between plant density and yield (total and economic) for barley (left), maize (centre) and Brussels sprouts (right).

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

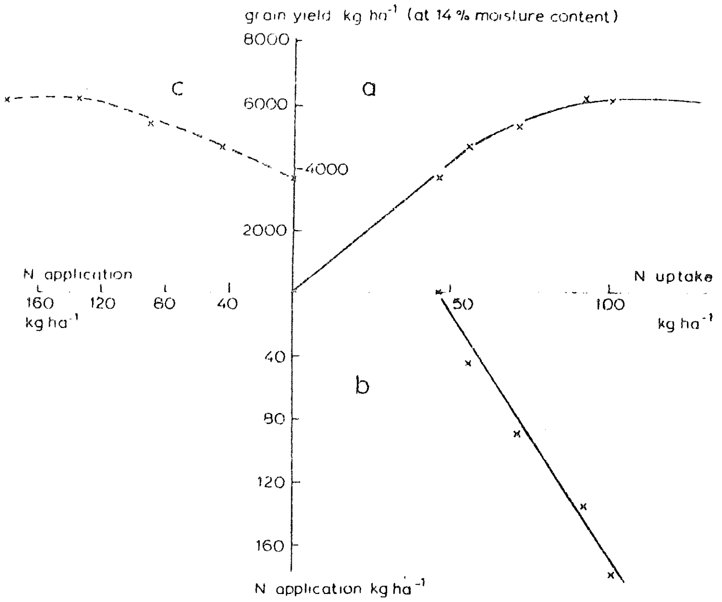


Fig. 2.11. Relation between N uptake and grain yields (a), between N application and N uptake (b), and between N application and grain yield (c) for IR5 rice grown in Muara, Indonesia, dry season 1971 (from: van Keulen, 1977).

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-

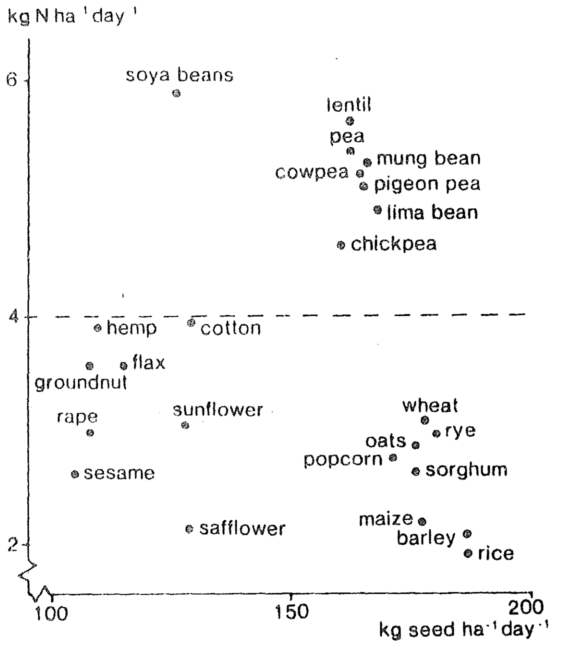


Fig. 2.12. Seed production rate and nitrogen requirement of the seed, both in kg ha^{-1} day^{-1}, for 24 crop species with an assumed available photosynthate of 250 kg ha^{-1} day^{-1} (from: Sinclair & de Wit, 1975).

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

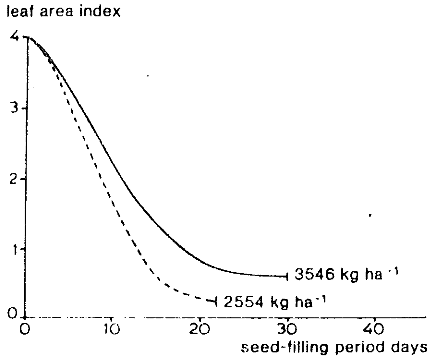


Fig. 2.13. Simulated changes in leaf area indices with time for soya bean crops with an initial leaf area index of 4, and two rates of root nitrogen supply (4 kg N ha^{-1} day^{-1} —— and 2 kg N ha^{-1} day^{-1} ---). Final seed yields in kg ha^{1} are presented in lower, righthand portion of figure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

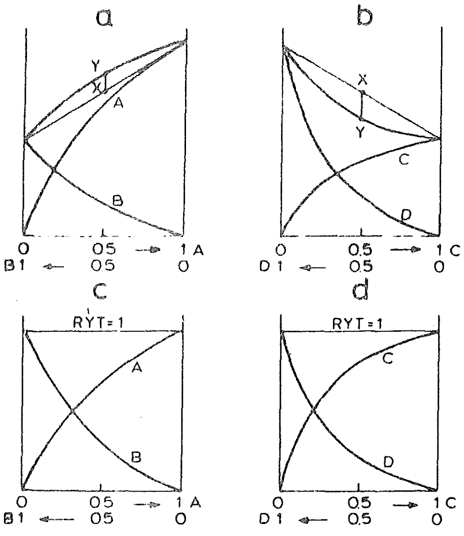


Fig. 2.14. Two typical replacement diagrams with a relative yield total (RYT) equal to one, in absolute (above) and relative (below) terms. The difference Y—X is the competitive ability.

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

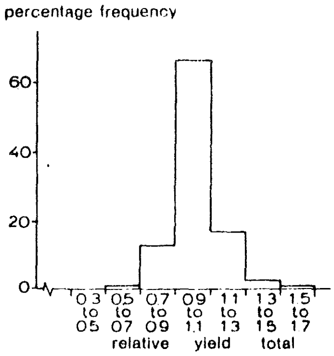


Fig. 2.15. Distribution of values of relative yield total (RYT), excluding legume/nonlegume combinations (from: Trenbath, 1976).

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. RYT's 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

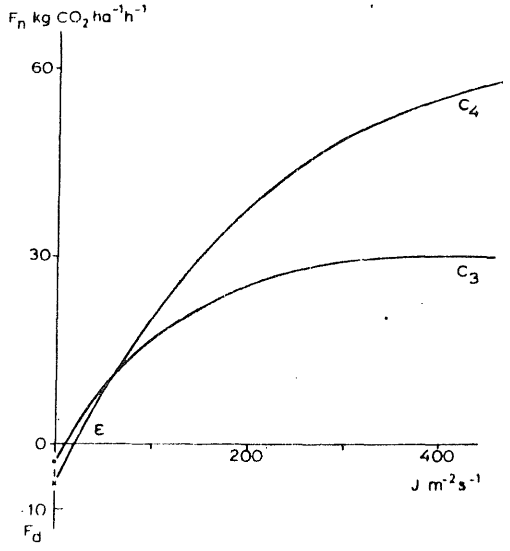


Fig. 2.16. Characteristic net CO_2 assimilation functions (F_n) of individual leaves for C_3 and C_4 plants.

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

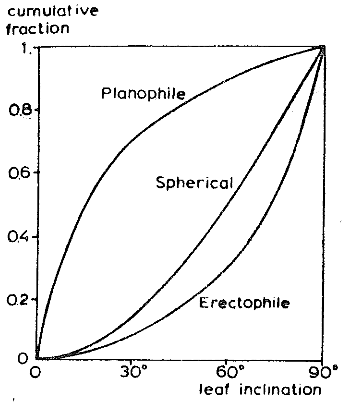


Fig. 2.17. The cumulative distribution of the inclination of leaves for three types of leaf angle distribution (from: de Wit, 1965).

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

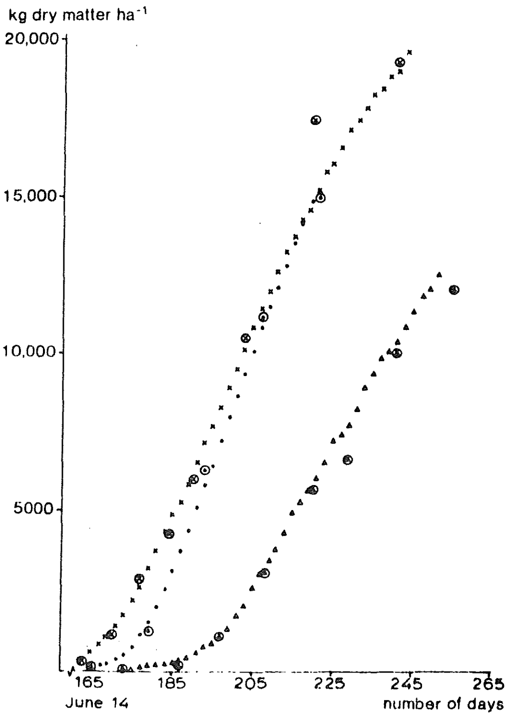


Fig. 2.18. Simulated and measured (circled) dry matter production of maize in Ames (Iowa, USA, 1963), Davis (California, USA, 1968) and Flevoland (Netherlands, 1972) at a plant density of 10 plants m^{-2}. Ames ×, Davis • and Flevoland Δ.

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

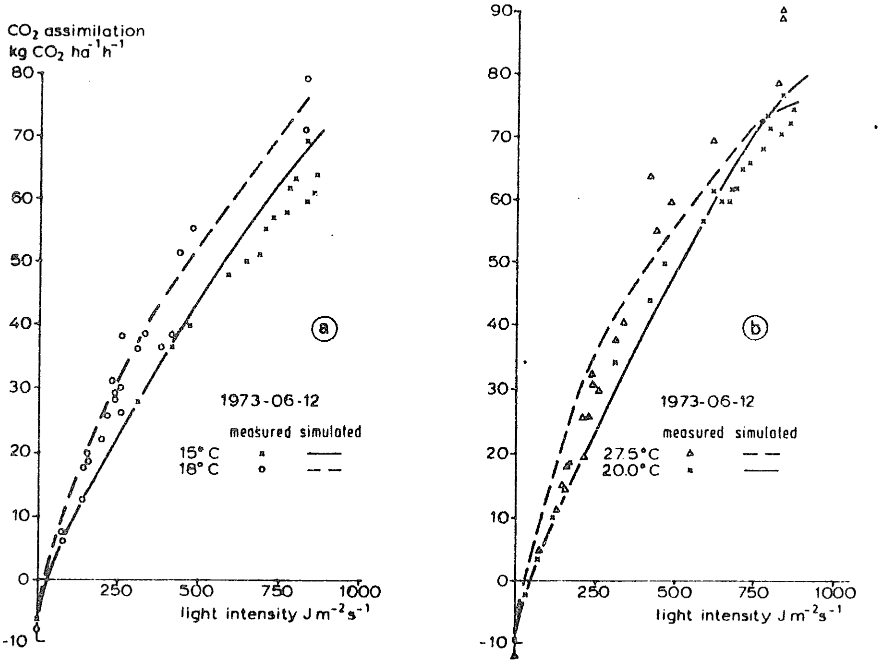


Fig. 2.19. CO_2 assimilation at four temperatures as a function of light. Species: *Zea mays* cv. Caldera 535; density: 3 × 3 cm (a), 4 × 4 cm (b); sowing date: 1973-06-01; measuring date: 1973-06-12; location Droevendaal, Wageningen; LAI: 17.5 m^2m^{-2} (a), 14.7 m^2m^{-2} (b); dry weight shoot: 3708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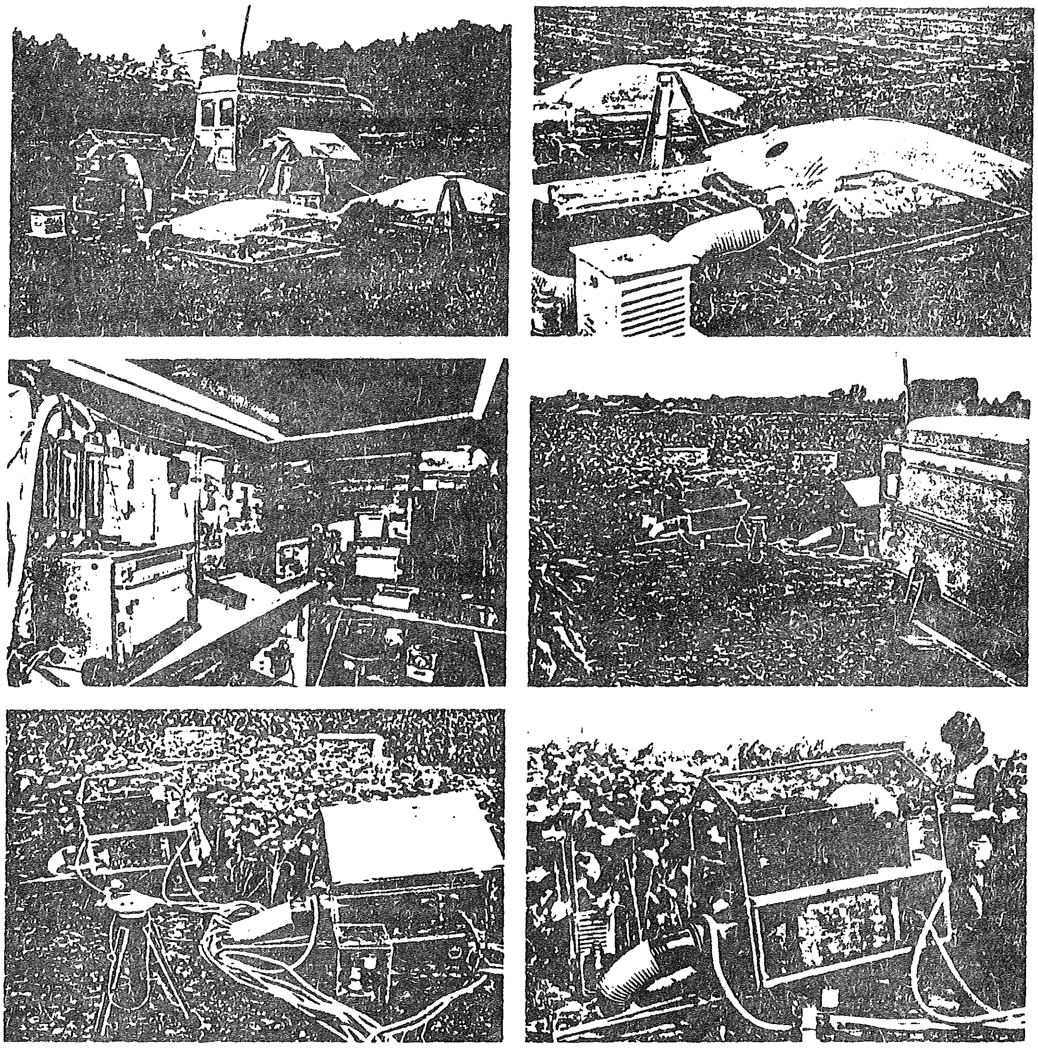

Fig. 2.20.
Top left – The mobile equipment ('photomobile') for measuring photosynthesis, respiration and transpiration in the field. Plant chambers as used for a grass crop.
Top right – Plant chambers of photomobile as used for grass. In the foreground a Stephenson hut (for recording temperature) and 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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