The relative efficiency of honeycomb selection and other procedures for mass selection in winterrye (*Secale cereale L.*)

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THE RELATIVE EFFICIENCY OF HONEYCOMB SELECTION AND OTHER PROCEDURES FOR MASS SELECTION IN WINTERRYE *(Secale cereale L.)*

Proefschrift
ter verkrijging van de graad van
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dr. C.C. Oosterlee,
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ABSTRACT

Bos, I. (1981) The relative efficiency of honeycomb selection and other procedures for mass selection in winterrye *(Secale cereale L.)* (X) + 172p., 20 figures, 80 tables, 69 references.
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The efficiency of a one-generation application of honeycomb selection was studied in comparison with a one-generation application of other procedures for mass selection. These alternatives included random selection, truncation selection, grid selection and selection with independent culling levels. The result of honeycomb selection, which was continued during 3 successive generations was also established. The aim of the selection was a decreased culmlength while maintaining or improving grain yield.

The obtained results showed that it was possible to promote such a recombinant plant type by honeycomb selection, but the efficiency of this new method was somewhat disappointing. The cause for this is environmental diversity occurring within groups of 7 plants.

For better results of mass selection it was suggested to base the selection on different plant characteristics (harvest index or grain yield per ear) or to modify grid selection in such a way that per grid a variable number of plants is selected.

Free descriptors: *Secale cereale*, autotetraploids, mass selection, honeycomb selection, truncation selection, grid selection, heritability, genetic correlation, additive genetic variation, competition.

STELLINGEN

1. De waarneming bij een sporofytisch incompatibiliteitssysteem, dat volledige dominantie van het ene allel ten opzichte van een ander allel veel vaker optreedt in het stuifmeel dan in de stempel is ontoereikend als rechtvaardiging voor een methode van S-allel identificatie, waarbij de heterozygoot uitsluitend als moeder wordt gebruikt.

D.J. Ockendon, 1975. Euphytica 24: 165-172.

2. Het oordeel van Mayo, dat recente successen van de plantenveredeling, bijvoorbeeld op het gebied van de granen, meer te danken zijn aan wetenschappelijke inbreng vanuit het terrein van de statistiek dan vanuit de genetica wordt door te weinigen gedeeld.

O. Mayo, 1980. The theory of plant breeding (p. 5).

3. Omdat honingraatselectie alleen correctie mogelijk maakt voor milieuvariatie welke zich voordoet over oppervlakten die groter zijn dan die welke wordt ingenomen door een zesring, maar niet voor variatie over oppervlakten kleiner dan een zesring, betekent deze selectiemethode nauwelijks een verbetering ten opzichte van eerder gepropageerde methoden voor massaselectie.

Dit proefschrift.

4. De bewering dat de maximale waarde van de coëfficiënt van dubbele reductie slechts 1/7 of 1/8 zou zijn is onjuist.

R.W. Allard, 1960. Principles of plantbreeding (p. 393).

5. Het door Mayo aan R.A. Fisher toegeschreven citaat dat, in geval van genetische analyse van een kwantitatieve eigenschap, het aantal loci "één van de minst modificeerbare kenmerken van een polygeen systeem is" mag niet gebruikt worden als rechtvaardiging van gebrek aan interesse in dat aantal loci.

O. Mayo, 1980. The theory of plant breeding (p. 61).

6. Zij die er van uitgaan, dat de inteeltcoëfficiënt van een in Hardy-Weinberg evenwicht verkerende F_2-populatie van een zelfbevruchtend gewas gelijk is aan nul hanteren niet een gangbare definitie van de inteeltcoëfficiënt, nl. de kans dat een diploïd individu op één locus 2 allelen bevat die identiek zijn door afstamming.

D.S. Falconer, 1964. Introduction to quantitative genetics (p. 61).

7. De mogelijkheid dat in een graangewas, bestaande uit een kruisingspopulatie dan wel uit een zuivere lijn, verschillen in halmlengte eerder een gevolg dan een oorzaak van verschillen in concurrentie-vermogen zijn, wordt in de plantenveredeling onvoldoende onderkend.

Dit proefschrift.

8. De veronderstellingen die ten grondslag liggen aan Spitters' conclusie dat de rangorde voor de opbrengst van een aantal genotypen, die in een mengsel geteeld worden, niet afhangt van de plantdichtheid van het mengsel zijn niet alleen onduidelijk gespecificeerd, maar ze lijken ook aanvechtbaar gezien de verkregen conclusie.

C.J.T. Spitters, 1979. Competition and its consequences for selection in barley breeding (p. 86).

9. De mogelijkheden om op voor de teelt van snijmais bestemde percelen winterrogge te telen als groenbemestingsgewas zijn in Nederland nog onvoldoende onderzocht.

10. De veronderstelling dat bij een onregelmatige stand van een graangewas de potentiële opbrengstderving door het optreden van open plantplaatsen tot op zekere hoogte gecompenseerd wordt door extra uitstoeling van naburige planten is niet altijd te rechtvaardigen.

C.J.T. Spitters, 1979. Competition and its consequences for selection in barley breeding (p. 230, 231).

11. De ontwikkeling van concepties op het gebied van de resistentieveredeling wordt geremd door de gebrekkige wijze waarop velen het genetisch jargon hanteren.

12. Zij die voorstander zijn van een effectieve regeling van het kindertal, maar tegelijkertijd bezwaren aanvoeren tegen volledige deelname van een in gezinsverband levende vrouw aan het maatschappelijk leven, geven blijk van een dualistische visie op een in essentie causale samenhang.

13. Door verbetering van bouwkundige voorzieningen moet het de bezoeker aan het receptie-loket van het Wageningse belastingkantoor mogelijk gemaakt worden met opgeheven hoofd te communiceren met de ontvanger; momenteel is zulks alleen mogelijk als men bij voorbaat door de knieën gaat.

Proefschrift van I. Bos
The relative efficiency of honeycomb selection and other procedures for mass selection in winterrye (Secale cereale L.)
Wageningen, 27 november 1981

Aan Marianne Boers,
aan Margreet en Dirk

WOORD VOORAF

De voltooiing van dit proefschrift schenkt me veel voldoening. Door de afronding, van een deel van mijn onderzoek, in deze vorm voldoe ik niet alleen aan een morele verplichting, maar komt tevens tot uitdrukking, dat de grote of kleine inspanningen die vele anderen zich terwille van mij getroost hebben niet tevergeefs zijn geweest.

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Om de arbeidspieken af te vlakken mocht ik profiteren van de voortreffelijke assistentie van de vakantiehulpen Richel Hildebrand en Rudi Keij.

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CONTENTS

1 INTRODUCTION

1.1 METHODS OF MASS SELECTION

Mass selection is a breeding procedure which has been applied since the beginning of the domestication of plant species. With this procedure individual plants are selected (visually or on the strength of a more or less formal criterion) because of their individual phenotypic performance. The next generation is grown from the bulked seeds of the selected plants. The results of this method have been impressive. One should realize, for instance, the difference in number of grains on ears of present-day maize and that on the oldest, subfossilic ears found in Southern-Mexico, which date from about 5200 before Christ (Frakken,1965). Not only the earsize, but also the region in which the crop can be grown increased enormously. Further, the sugar content of sugar beets was increased from about 6%, at the end of the 18th century, to about 10% in 1868. (From then on family selection, introduced by De Vilmorin, was applied to increase sugar content.) Thus good results were obtained by application of primitive forms of mass selection for very many generations.

Lonnquist (1964) summarized the most important features of mass selection, indicating the following advantages:

(i) The simplicity of the selection technique is at its utmost.

(ii) Because selection can be applied in each of the succeeding generations a small progress per generation can, eventually, result in a larger gain than that attained by using methods requiring more than one generation per cycle (e.g. reciprocal recurrent selection).

(iii) Large-size populations can be handled. In such populations a high intensity of selection can be applied without considerable risk of important random genetic drift for alleles on loci that are not under selection pressure.

He also mentioned some disadvantages. The criterion used for selection is the phenotypic value of individual plants. This phenotypic value is determined not only by the genotype of the plant, but also by the growing conditions of the site (read: macro-environment), by the weather conditions of the growing season and by interactions among these 3 factors. Further there is the summed effect of influences on the phenotype which cannot be specified individually. These influences comprise micro-environmental conditions (including competition by neighbouring plants) as well as internal physiological developments. Together all these influences, each of which might be of minor importance on its own, are responsable for a large part of the considerable variation which can in general be observed for characters of agricultural interest. For many characters the phenotypic differences rely, therefore, only partly on genetic differences.

Another disadvantage of mass selection is the genetic heterogeneity of the population resulting from a programme of mass selection. This very phenomenon illustrates that mass selection cannot approach very quickly the final goal of selection: exhaustion of the genetic variation for characters of interest. This disadvantage manifests itself especially if mass selection is in the form of truncation selection, i.e. selection of the best phenotypes when considering the whole population.

Application of truncation selection means simply selection of all plants from the selection field that surpass a certain level. If selection is for yield all plants yielding more than a defined lower level are selected. More levels are defined (for each character one) if selection is for more than one character. This type of truncation selection is called selection with independent culling levels.

With truncation selection there is no correction for differences among environmental conditions prevalent within the selection field. This disadvantage can be removed partly by decreasing the variation in environmental conditions to which the plants to be compared are submitted. Gardner (1961) therefore divided the plants in a selection field, planted with the maize variety Hays Golden, into small areas (which he called strata), each containing 40 plants. In each stratum (also being called grid) the 4 highest yielding plants were selected. With 4 generations of selection the yield had increased from 79.3 bu/acre to 97.4 bu/acre. The linear regression of relative yield (i.e. the yield expressed as an percentage of that of the unselected variety) on the number of selection interventions amounted to 3.93%. Another yardstick for the average progress per generation is the geometric mean of the total progress over 4 generations (22.8%). This amounted to 5.3% per generation. Considerable fluctuations around these means did show up.

This remarkable success stimulated a revival of interest in mass selection, especially in the United States where, because of the success of hybrid maize research on mass selection had been neglected since about 1925. An interesting summary on procedures and results of mass selection in the 10 years following Gardners publication was given by Le Cochec (1972).

Verhalen et al. (1975) applied grid selection in a cotton variety known to be genetically variable for fiber length. Truncation selection was applied for comparison. The selection field was arbitrarily subdivided into three 20×60 m grids. Within each grid 100 plants were visually selected and from these plants the upper and lower 10% were chosen, on the basis of fiber length, both in each grid and over the whole selection field. Plants bordering skips in the same row or in an adjacent row were excluded from consideration. Because of overlapping not (2×3×10)+(2×30)=120 different plants were selected, but only 85. Despite this overlapping about half of the plants selected by the one method were not selected by the other.

Therefore it was supposed that one selection method should be superior to the other. The fiber length of the offspring of the 85 plants was measured to determine the selection response. In 6 out of 8 comparisons the result of grid selection was significantly better than that of truncation selection.

As was mentioned by Verhalen et al. (1975) an increasing similarity of the environmental conditions for the plants to be compared can be expected at decreasing grid sizes. This means an improvement of the opportunities for selection response.

Presumably the minimal size for grid selection is effectuated by so-called honeycomb selection (Fasoulas, 1973, 1976, 1977, 1979; Fasoulas & Tsaftaris, 1975). In the 1973 publication honeycomb selection was presented as a method of selection for self-fertilizing crops, to enable breeders to distinguish high yielding genotypes, even if these were represented by single plants. The procedure was announced to be applicable under heterogeneous soil conditions. Selection could start already in the F_2 of self-fertilizing crops.

The central idea was that growing conditions for contiguous plants are more similar than those for non contiguous plants. Comparison of the performance of a single plant with the performance of its neighbours would give the best impression of the genotypic value of the central plant. A fair comparison is possible when the plants are grown in a regular hexagonal pattern (the honeycomb pattern), because then each plant has 6 neighbours, each at the same distance. A plant should be selected if it is yielding better than each of its 6 neighbours.

Although soil heterogeneity seemed to be considered as the most restrictive factor for the success of selection, competition was mentioned as another influence that masks the genotypic value. By growing the plants in the selection field in absence of competition, the plants can show their genetic potential under their private soil conditions. Fasoulas (1973) admitted that it was unclear "whether plants selected on the basis of very low competition or without competition would perform well in solid stand". Because preliminary results had shown him that the yielding ability of a (wheat?) genotype, selected without competition, was not affected at high plant density he dared to grow an F_2 population of wheat in a honeycomb selection field at interplant distances of 50 cm. Nevertheless it was stated that interplant distance deserved further investigation. Because the method was only illustrated no decisive evidence on its worth for practical application could be derived.

In a next paper (Fasoulas & Tsaftaris, 1975) more attention was given to competition as a cause for the lack of success of single plant selection. It was advocated that selection should be done under conditions without competition, i.e. at very low density.

In an experiment with 7 hybrid maize varieties (the structure of the varieties was not given) it was observed that the ranking of the varieties was the same, regardless of whether the varieties were grown as single plants (without competition) or in a normal density (monocultures with intragenotypic competition). The same was found in an experiment with 7 cotton varieties.

In a selection experiment with cotton superior plants were selected in an F_2 population grown under noncompetitive conditions in a honeycomb pattern (interplant distance 90 cm). The progenies of the selected plants were grown at three densities. High yielding progenies were said to maintain their superiority across the three planting densities, but in Fig. 2 (l.c.) a change in ranking of the 2 parental varieties is manifest.

For an obligate cross-fertilizing crop like rye monogenotypic varieties are not grown and then the plants are exposed to intergenotypic competition. Fasoulas & Tsaftaris (1975) exclude this category of crops from their concept of constant ranking of monogenotypic varieties across densities.

Spitters (1979) mentions experiments with self-fertilizing crops showing spacing dependent ranking (p.77, l.c.). Briggs and Faris (1979) found at 2 sites contrasting agreements between the performance of cultivars in space plantings and in solid seedings. More evidence should therefore be acquired before it can be stated that, in general, genotypes having the highest yield under noncompetitive conditions also have the highest yield in monocultures, grown at normal density.

In rye it is practically impossible to make use of genetically homogeneous material as a check (see section 2.1). Therefore, it was decided to measure progress by selection by comparing the performance of offspring of plants selected on purpose with that of the offspring of plants selected at random. The result of random selection was thus the point of reference to measure the results of other selection methods.

1.2 AIMS OF THE EXPERIMENTS

Honeycomb selection was proposed as a method enabling the breeder to start selection already in the F_2 generation of a self-fertilizing crop. In an F_2 population in general all plants will have an unique genotype for a complex character such as kernel yield. Because honeycomb selection was announced to be the best method for identification of superior genotypes, each represented by only one plant, its application to cross-fertilizing crops was not excluded. The procedure appeared therefore also suitable for heterogeneous populations of outbreeding crops.

The method was applied to rye to collect evidence on the usefulness of the method under conditions of practical breeders. Its relative efficiency compared with other methods of mass selection was studied. These other methods comprised random selection, truncation selection, grid selection and selection with independent culling levels.

Because in rye it is as important to develop material with shorter culms as it was in wheat, simultaneous selection for improved yield and decreased culmlength was applied. This was done by honeycomb selection and by selection with independent culling levels.

As a substrate for selection on the one side the diploid winterrye variety Dominant was used and on the other an autotetraploid population of winterrye, developed at our institute. As was anticipated using the variety Dominant meant a difficult starting point for realizing selection responses. On the contrary the autotetraploid population, having a broad genetic base, was never submitted to artificial selection before. This population was assumed to afford an easier starting point for realizing selection responses.

The experiments with autotetraploid rye are described in chapter 6, the experiments based on Dominant material are described in the other chapters.

1.3 RYE AS AN AGRICULTURAL CROP

Data, derived from the USDA issue Agricultural Statistics (1978), on the area and yield of rye are reproduced here in Table 1. Compared to 1975 the total area increased with 7.8% to about 16.2 million ha. Fifteen years earlier, in 1961, the world's total acreage amounted to 28.5 million ha (Bushuk, 1976). A drop in acreage of 43% has thus occurred since 1961. The total production decreased from 35 million tons in 1961 to 29.4 million tons in 1976, a decrease of 16%. (To compare: the total acreage of wheat amounted to 232.4 million ha in 1976.) The 1980 issue of Agricultural Statistics provides data for 1979. The world total rye area amounted to 13.28 million ha, the mean yield was 1.61 tons/ha and the total production 21.4 million tons. Thus the long term trend of rye to decline as an agricultural crop was continued.

In the Netherlands the decline in the area was even more pronounced. Figure 1, based on data of several issues of the Dutch list for varieties, presents the area of rye in the Netherlands since 1945.

The dramatic decrease of the Dutch rye area can be explained largely by the lag in development of the rye yield per ha as compared to that of wheat (see Table 2; source: Landbouwcijfers, 1975, 1977). The additional yield of wheat tends to increase. The ratio in yield however being fairly constant. The yield potential of rye appeared to be reasonable during our experiments: in one of the largest experiments (crop 10) the grain yield was 6300 kg/ha. Kupers (1975) observed in a trial field a yield of 4.7 ton per ha. Clearly, agronomists and breeders have devoted much more efforts in the past to wheat than to rye. Besides, it is a common practice to grow rye on worse soils. The little interest of farmers to grow rye will certainly not rest on the costs of growing, nor on the farmers price per 100 kg (see Table 3; source: Landbouwcijfers, 1977).

Table 1 Area, yield per ha and production of rye. Data of 1976.

continent	country	area (1000 ha)	yield (tons/ha)	production (1000 tons)
America	Canada	251	1.75	440
	U.S.A.	283	1.35	381
	Argentina	340	0.97	330
	others	25	1.16	29
Europe:EEC:	Belg.&Lux.	17	2.94	50
	Denmark	72	2.97	214
	France	114	2.49	284
	Germany	663	3.17	2100
	Italy	16	2.19	35
	Netherlands	21	3.10	65
	U.K.	8	2.38	19
rest:	Austria	120	3.42	410
	Portugal	211	0.70	148
	Spain	225	0.95	214
	Sweden	122	3.50	427
	Czechoslovakia	186	3.02	561
	GDR	600	2.43	1455
	Poland	2934	2.36	6922
	USSR	9035	1.55	13991
	others	313	1.80	563
Africa:	South Africa	89	0.04 (?)	4 (?)
Asia:	Turkey	530	1.40	740
Oceania:	Australia	28	0.54	15
World total		16203	1.81	29397

Table 2 Mean yield (in kg/ha) of winterwheat and winterrye in the Netherlands

	'51/'55	'56/'60	'61/'65	'66/'70	'71/'75	1976	1977	1978	1979
wheat	3900	4500	4600	4700	5200	5700	5400	6800	6100
rye	2800	2900	2900	3100	3300	3100	3500	4000	4000
difference	1100	1600	1700	1600	1900	1800	1900	2800	2100
ratio	1.39	1.55	1.59	1.52	1.58	1.84	1.54	1.70	1.53

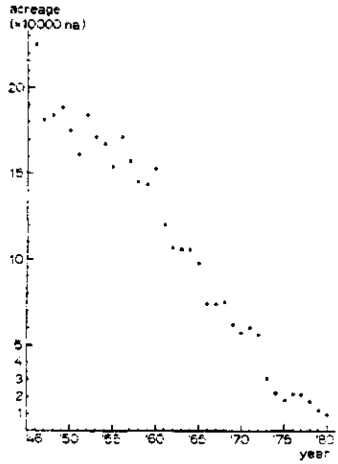

Figure 1 Area of rye in the Netherlands since 1945.

Rye is mainly used in mixed fodders. When rye is the only ingredient in the fodder the results are mostly bad, especially with pigs and chicken. Wieringa (1967) established that the growth inhibition caused by feeding rye rests on resorcinols in the pericarp of the kernel. Hoffman and Wenzel (1977) developed a nondestructive colorimetric method to determine the alkylresorcinol content of individual rye kernels. Selection to decrease the content to the level found in wheat appears to be possible because Becker et al. (1977) observed considerable variation in rye for 5-alkylresorcinol content.

One of the reasons for the lower yield of rye then in wheat is its greater culmlength. Because of that the risk of lodging after giving a certain amount of fertilizer is greater for rye than for wheat. Another possible disadvantage of the long culms is the lower harvest index that could be associated with that. Products of the photo-synthesis should preferably be allocated to production of kernels and not to straw production. Still another reason for the lower yield of rye is its shorter growing season: rye is harvested earlier than wheat. It has been observed that shortness of the

Table 3 Farmers prices (Dfl/100 kg) for wheat and rye

	'55	'60	'65	'70	'75
wheat	25.15	30.25	35.45	37.55	43.20
rye	21.25	20.75	29.20	32.10	41.45

culms is sometimes associated with an improved ability to survive cold winters. This forms, especially in Eastern Germany, an additional reason to breed rye with short culms (Sturm & Engel, 1980).

Shortening of the culms can be forced by application of chemicals. Kuizenga (1975) observed, after treatment of Dominant with ethrel (also called etephon), significant shortening of the culms, decreased lodging(especially when 90 or 120 kg N/ha was given) and a higher number of ears. The yield increase did not suffice to counterbalance the costs of the treatment. Kühn et al. (1977) found after simultaneous application of CCC and ethrel an effective reduction in strawlength, coinciding with a much improved lodging resistance.

It is clear that, in the long run, it is more economic to develop new varieties with shorter culms. In the present experiments attention was given to this goal.

1.4 HINTS FOR READING

It was thought better to prevent the use of abbreviations as much as possible. Nevertheless a few are used throughout the text. They are:

G for grid

H for honeycomb

ICL for independent culling levels

R for random

T for truncation

These abbreviations are used in connection with the words selection, plant and family. For example: "ICL-selection" is selection of plants in accordance with the criteria for selection with independent culling levels; an "ICL-plant" is a plant selected through "ICL-selection"; an "ICL-family" is the offspring of an "ICL-plant".

If a character is measured on parental plants as well as on their offspring the parental observation is represented by x and the observation on the offspring by y. Underlining of a variable means that it is a stochastic variable.

In Figure 2 the pathway of the experiments is outlined. Throughout the text crop numbers are mentioned, referring to certain experiments. To see the position of these experiments in the whole programme one should use Figure 2 as a guide.

The meaning of "yield" is weight of the ears of an individual plant, "kernel yield" is the weight of the kernels produced by an individual plant. By plant density is meant: the number of plants per m^2; by ear density: the number of ears per m^2.

Throughout the text levels of significance are indicated by:

* : $P < 0.05$

** : $P < 0.01$

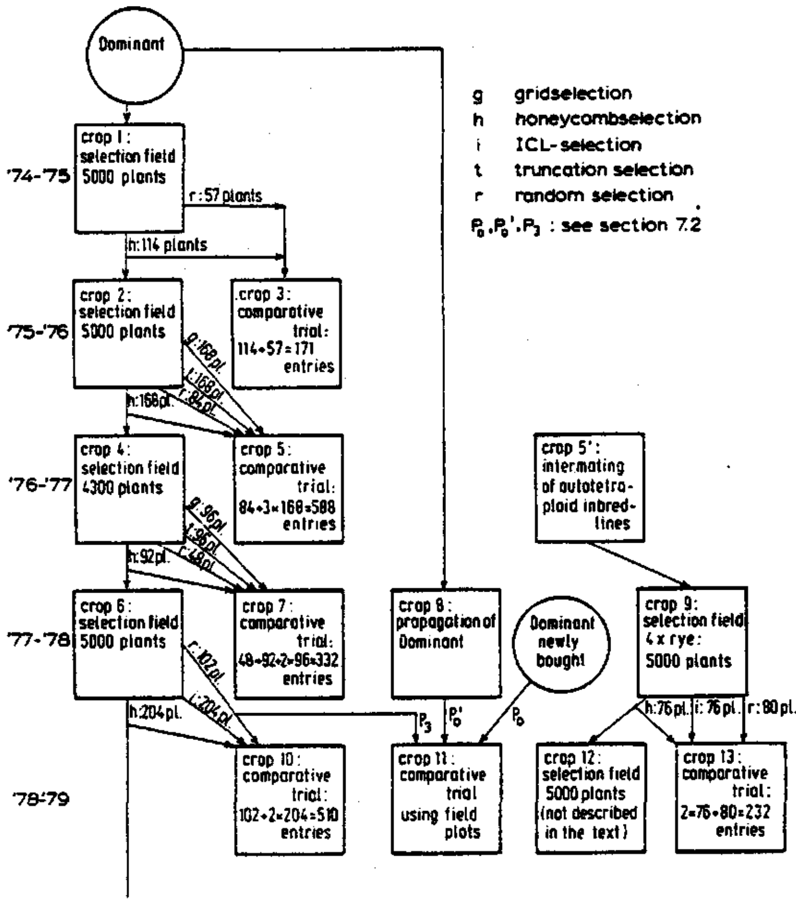

Figure 2 Pathway of the experiments.

***: P < 0.001

The meaning of the symbol ~ is 'approaches the value of'; the symbol ≃ indicates identity in probability distribution.

2.1 MATERIAL AND METHOD

The material

As indicated in section 1.2 the variety Dominant was chosen as substrate for the selection experiments with diploid winterrye. During the years of the experiments Dominant was the most widely grown rye variety in the Netherlands. It is a synthetic variety based on about 12 inbred components, which are maintained by socalled sibmating (Mastenbroek, 1975). The variety was therefore assumed to contain enough genetic variation for further improvement by continued application of an effective mass selection method. Honeycomb selection was given the opportunity to prove itself to be such an effective method. Data on the amount of genetic variation actually present within the variety was gained in the course of the experiments.

The lay-out of the selection field

Fasoulas & Tsaftaris (1975) mentioned two honeycomb designs:

(i) The ranking honeycomb design.
This design can be used for ranking genotypes when, per genotype, several plants (e.g. 14 to 56) are grown.

(ii) The screening honeycomb design.
This design was proposed for selection of superior genotypes when each genotype is represented by only one plant. By insertion of plants of a check genotype at prescribed sites the yield of each plant can be compared with the average yield of its 6 neighbours as well as with the average yield of the 3 nearest check plants.

The use of clones or pure lines as genetically homogeneous checks is conceivable for rye but was not applied. Pure lines are rather difficult to produce and to maintain. (Owing to its gametophytic incompatibility system (Lundqvist, 1956) rye is an obligate allogamous crop). Furthermore they have a performance far below that of non inbred rye material. Therefore pure lines were not used.

Cloning of rye plants is feasible, but cloning will result in rather heterogeneous clones, because the splitting of the plants to be cloned results in plant parts differing in size and recuperation ability. Such heterogeneous clones are not suited as check material.

The honeycomb pattern of planting was, therefore, applied without inclusion of check plants. The pattern is depicted in Figure 3. When the distance between 2 plants equals d cm the area per plant equals the area of a regular hexagonal with side $\frac{1}{3}\sqrt{3}$ d cm. This area amounts to $\frac{1}{2}\sqrt{3}\,d^2\,cm^2$.

To plant a selection field in this pattern, the soil is marked in 2 orthogonal directions. The crossing points of the markation lines indicate the location of some of the plants. Each crossing point of the diagonals through the rectangulars marks the position of one of the remaining plants. The distance between 2 parallel markation lines is either $\sqrt{3}$ d cm or d cm.

The soil conditions for a central plant and those for its 6 neighbours will be the more similar the smaller d. It is then more likely that a central plant which performs better than its neighbours, does so because of its superior genotype. The smaller d the better the elimination of the disturbing influence of soil heterogeneity. However, the disturbing effect of intergenotypic competition increases when d decreases. Fasoulas (1973) applied d=50 cm in wheat and Fasoulas & Tsaftaris (1975) applied d=90 cm for maize and d=100 cm for cotton. Apparently, they chose to exclude competition effects rather than to minimize effects of soil heterogeneity. As indicated in section 1.1 it is uncertain, especially for cross-fertilizing crops, whether genotypes having the highest yield under non-competitive conditions are also superior when grown at normal density. The principle of selecting under competitive conditions resembling those under normal growing conditions was therefore followed. (The spatial distribution of the plants in a honeycomb selection field is more in agreement with a distribution after broadcasting than the distribution after sowing in rows.)

In the present case selection fields the interplant distance was chosen to be d=15 cm. This was considered to be the smallest distance, yet offering a possibility of walking across the crop without damaging the plants. The area per plant amounts then to 195 cm^2, which corresponds with 51.3 plants per m^2. Because 250 small-grain plants per m^2 is considered to be the optimal number, the present plant density was still rather low.

Whether the applied interplant distance represents a satisfactory compromise between the mentioned advantages and disadvantages of a certain plant density was unknown at the start of the experiments. Some experiences on the effect of plant density on the result of honeycomb selection are given in section 8.5.

Hamblin (1975) stated that selection for yield should be attempted only at normal crop densities. However, Hamblin et al. (1978) observed for wheat a much better elimination of the disturbing effect of soil heterogeneity (using a moving average) under low density (6.25 plants per m^2) than under high density (625 plants per m^2). It should be remembered that these 2 densities represent 2 extremes.

As a last illustration of opposing opinions on the optimal plant density for selection we cite Valentine (1979): "Chebib et al. (1973) concluded that the efficiency of single plant selection for 11 characters (including grain yield) in wheat could be doubled by sowing uniform sized seed in close-

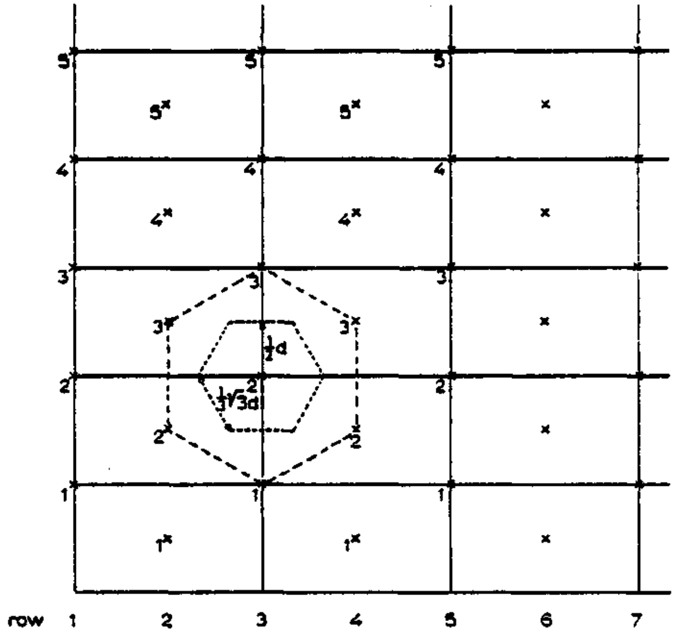

Figure 3 The honeycomb pattern. The plants are indicated by a cross. The heavy lines correspond to the lines marked in the soil of the selection field. The wide-dotted hexagon indicates a central plant with its 6 neighbours, the narrow-dotted hexagon indicates the area per plant. The intrarow distance between two plants equals d; the interrow distance amounts 0.5 $d\sqrt{3}$ (In the actual experiments d=15 cm).

planted relative to wider spaced stands sown with unsorted seeds. For this reason the honeycomb design suggested by Fasoulas (1973) may not result in single plant selection of the maximal efficiency".

The selection field

The number of plants for the selection field was based on the available manpower and set at about 5000 plants. These plants were to grow at an intrarow (=interplant) distance of d=15 cm and an interrow distance of $\frac{1}{2}\sqrt{3}$ d=13 cm (see Figure 3). For 5000 plants, each with an area of $\frac{1}{2}\sqrt{3}\ d^2$ =195 cm^2, about 100 m^2 was needed, i.e. a square field measuring 10×10 m^2. This field was provided with a border having a width of 1 m. The total field measured therefore about 12×12 m^2. The field contained 93 rows (total width of the field 92×13=1196 cm), each consisting of 79 or 80 plants (80×15=

1200 cm). Before sowing or planting, 80 parallel markation lines were drawn in one direction and 47 lines were then drawn at right angles with the former. This resulted in 80×47=3760 plant positions on crossing points (of which 80×46=3680 were used) and 79×46=3634 positions on crossing points of imaginary diagonals; in total 7314 plant positions.

The plants considered for selection were the 66 plants in the middle of the 76 central rows (i.e. 66×76=5016 plants). For application of honeycomb selection one should know the performance of the neighbour plants in the border. The plants observed were therefore the 68 plants in the middle of the 78 central rows (i.e. 5304 plants). These plants occupied an area of 1020×1014=1034280 cm^2, i.e. 103,428 m^2, the border excluded. The position of every plant was described by 2 coordinates: the row number and the number of the plant within the row. The position was thus given by the so-called row-plant number.

2.2 THE PLANTS OF CROP 1

2.2.1 The growing of the crop

On 6 and 7 October, 1974 8526 not disinfected kernels of Dominant were sown in a mixture of peat and soil (Trio), most of them in Jiffy pots (1 kernel per pot) and the rest, destined to form the border, in boxes. Because of heavy rainfall and damage by mice, only 85% of the kernels emerged. Additional sowing was therefore done on 31 October and 5 November. The condition of the young plants was bad. The reason for this was the unprecedented heavy rainfall, which from October up to and including March, 1975 amounted to 641 mm. The occurrence of frost was not worth mentioning. Transplantation of the plants from the nursery to the selection field could not be done until 10 April, 1975. Some of the plants showed already a short culm.

After this adverse beginning the conditions improved considerably. The plants survived the transplantation well and a nice crop developed. April was wet and cold, May and June were cool and dry, July was normal. In the first decade of August there was a heatwave, which accelerated full maturation. The harvest took place from 5-9 August. From each plant the length (in cm) of the longest culm (excluding its ear) and the number of ears were recorded. This was done in the field, immediately after lifting the plants. The ears were cut off and stored in a bag, labelled with the row-plant number. After 2 weeks of drying the ears were threshed and kernel yield per plant was assessed. The 3 observations were noted down on a map. Figure 4 shows a part of it.

In deviation from the described procedure the selection fields of later years were not established after transplantation of seedlings. Further, they were harvested without simultaneous recording of culmlength and earnumber.

Table 4 Summary of the observations on plants belonging to crop 1. n: number of observed plants, $\bar{x}$: mean, s: standard deviation, cv_p: coefficient of phenotypic variation.

character		all plants (n=5260)	selected plants	
			H-selection (n=114)	R-selection (n=57)
culmlength	$\bar{x}$	145.7	142.2	150.2
(cm)	s	13.4	6.9	12.8
	cv_p	0.092	0.049	0.085
earnumber	$\bar{x}$	4.89	7.80	4.96
	s	2.38	2.98	2.55
	cv_p	0.487	0.382	0.515
kernel yield	$\bar{x}$	95.2	160.9	103.8
(dg)	s	64.7	61.4	69.8
	cv_p	0.680	0.381	0.672

2.2.2 Some statistical properties

The 78×68=5304 plant positions can be divided in (2×68)+(76×2)=288 plant positions in the border (marked with * in Figure 4) and 76×66=5016 plant positions enclosed by this border. Kernel yield was recorded on 5260 plants, viz. 280 in the border and 4980 inside the border. No kernel yield record was obtained from 5304-5260=44 positions. Data on the plants belonging to crop 1 are summarized in Table 4. The mean earnumber amounted to 4.89. Thus, on the basis of the intended plant density (i.e. 51.3), the eardensity was 250.9. This amounts to only 63% of the optimum of 400 ears per m^2 (Kupers, 1975), whilst the plant density was only 21% of the plant density considered to be optimal (i.e. 250). The extreme regular distribution of the plants in the selection field must have partly been responsible for this compensation for the low plant density. The compensation as regards kernel yield can even be considered to be about complete, because the mean kernel yield per m^2 amounted to 51.3×95.2=4884 dg (=4884 kg/ha). In view of the low plant density, the poor condition of the seedlings and the late time of transplantation this was indeed a surprisingly high kernel yield.

The mean kernel yield per ear was 95.2/4.89=19.5 dg.

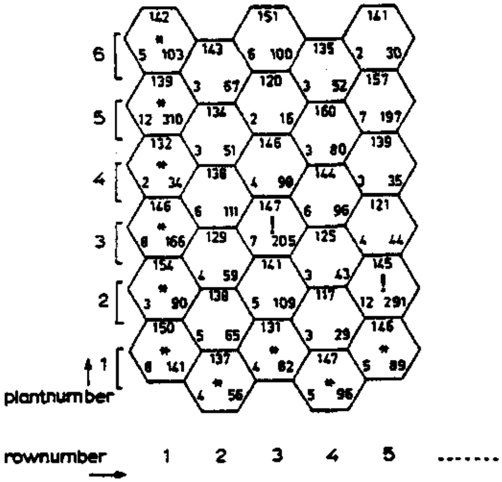

Figure 4 A part of the map of crop 1.
Each hexagon contains the observations on a single plant; the upper number is the length (in cm) of the longest culm, the lower left number is the number of ears, the lower right number is the kernel yield (in dg). The hexagons marked with * belong to the border, those marked with ! had a kernel yield surpassing that of each neighbour.

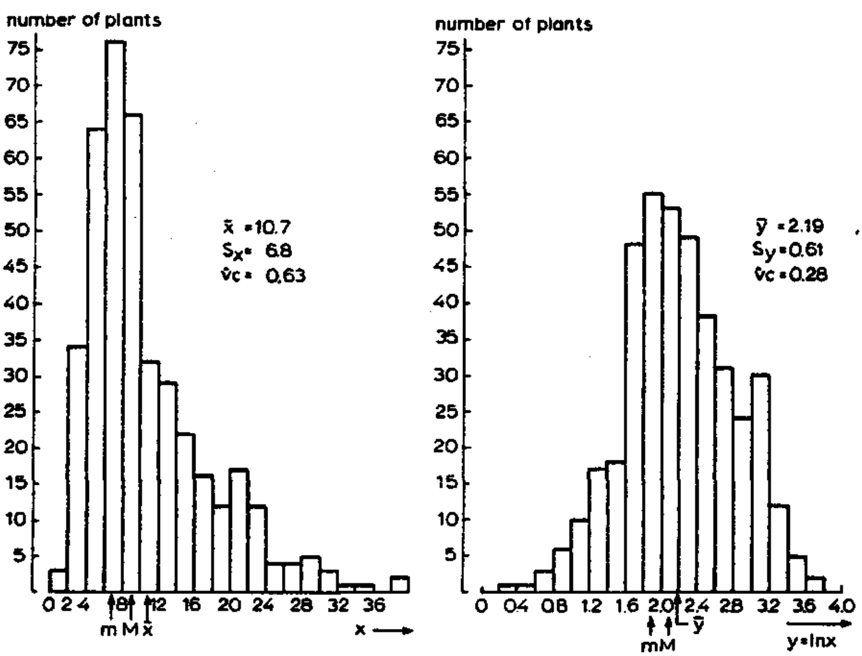

Figure 5 The distribution of $\underline{x}$, the kernelyield (in g) of 403 plants (row 1, 2, ..., 6 of crop 1). The right histogram depicts the distribution for ln$\underline{x}$.
M:median; m:mode.

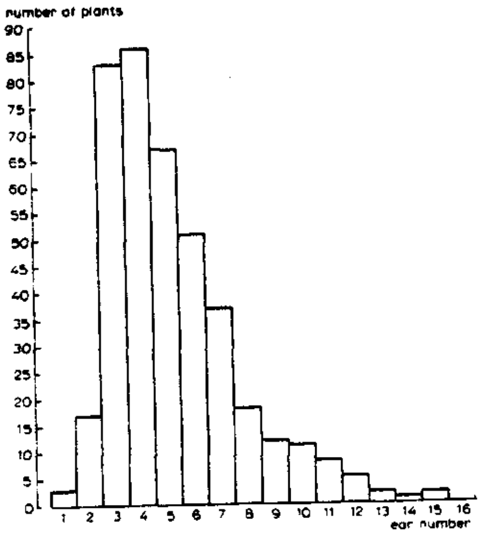

Figure 6 The distribution of the earnumber of 403 plants (row 1, 2, ..., 6 of crop 1).

The probability distribution of kernel yield

In Figure 5 the histogram for kernel yield of 403 plants (row 1,2,...,6 of crop 1) is given. The skewness (see Snedecor & Cochran, 1967) for the untransformed kernel yields (x) amounted $\hat{\gamma}_1$=1.392***, that for the transformed data (i.e. for ln(x) amounted to $\hat{\gamma}_1$=-0.019. The significant positive skewness of the untransformed data was taken away by the simple transformation and the coefficient of variation was halved.

According to Spitters (1979) positive skewness for yield can be explained by competition. From the literature he derived the general rule that in situations without interplant competition the distribution is normal (l.c., p.91). From this one could conclude that in crop 1 Fasoulas' ideal of absence of competition was not prevalent.

The skewness for kernel yield will rest on the similar skewness for earnumber, see Figure 6. (The correlation of kernel yield and earnumber was 0.90; see Table 5.) More data on the distribution for culmlength, yield and earnumber of the plants in the selection fields are given elsewhere. The conclusion is that the often assumed normal distribution for a quantitative character could not be justified here for yield.

Table 5 Phenotypic relation of characters of plants from crop 1. The characters are: WE: weight of the ears, (in dg); WK: weight of the kernels (in dg); NE: earnumber; CL: culmlength (in cm).
The relation between WE and WK was studied:
(i) : per ear (n=201)
(ii) : per plant (n=111)
The relations between WK and CL and between NE and CL was studied:
(i) : for 203 plants
(ii) : for 17 plants with NE>7
(iii): for 180 plants with NE<8

	WE	WK	NE
WK	(i): WK=0.881WE-0.0179 $\overline{WK}$=2.068 $\overline{WE}$=2.368 r_1=0.998 (ii): WK=0.886WE-0.167 r_2=0.997		
NE		r=0.90 (n=203)	
CL		(i) : r=0.52*** (ii) : WK=0.44CL-47.73 r=0.65*** (iii): WK=0.15CL-13.73 r=0.59***	(i) : r=0.36*** (ii) : CL=3.88NE+128.93 r=0.36 (iii): CL=2.53NE+127.47 r=0.54***

Some phenotypic correlations

The individual threshing of every plant of crop 1 was timeconsuming. In the case of a high correlation between the weight of the ears of a plant and the weight of the kernels produced by the same plant (here indicated by yield, resp. kernel yield) threshing can be omitted. The kernel yield is then characterized sufficiently by the weight of the ears: selection can then be based on weight of the ears and the threshing confined to the ears of the selected plants.

The phenotypic correlation was estimated for the following situations:

(i) per ear: r_1 was calculated from all 201 ears of 43 random plants from row 26 and 27,

(ii) per plant: r_2 was calculated from 111 random plants from row 23 and 24.

From Table 5 it can be seen that both correlations approached unity.

Therefore in all later experiments "yield" was observed in stead of kernel yield. It was derived that 2.068/2.368 or 87.3% of the yield could be attributed to the kernels. The regression coefficient indicated 88.1%.

The phenotypic correlation of earnumber and kernel yield was estimated from 203 plants (from row 23, 24 and 28). This correlation (r=0.90) was high (as could be expected). Indirect selection for yield via selection for earnumber was, however, rejected (see the end of section 2.3.4).

A scatter diagram suggested that for strong tillering plants there was another relation between kernel yield and culmlength than for moderately tillering plants. The correlation between kernel yield and culmlength was estimated therefore for:

(i) all 203 plants mentioned before

(ii) for the 17 plants with at least 8 ears

(iii) for the 186 plants with less than 8 ears

The correlations were moderately high, but significant. High kernel yield was associated with great culmlength, but this association was weaker for moderately tillering plants than for strong tillering plants. These correlations are estimates for a heterogeneous population. They do not imply that a homogeneous short-straw population should consist of poor producing plants. From the observed association one may not conclude that, by selection of recombinants, it is impossible to gain a short-straw, high producing type of plant.

A positive relation (in a segregating population) of culmlength and yield appears also in other small grains (e.g. McKenzie and Lambert (1961) for barley).

In a dense stand, which is more in accordance with a normal crop density, there will be many more plants with a small number of ears (say at most 7). For those plants a weaker positive phenotypic correlation between culmlength and kernel yield was observed. Selection in a wider stand for short culms does not have to be very disadvantageous for kernel yield when the plants are grown in dense stand. Nevertheless, truncation selection for short culms was not performed, because the shortest plants produced no kernels at all (or only a few). These plants were considered to suffer from some deficiency.

The phenotypic correlation of earnumber and culmlength was estimated for the same group of plants. The estimates were low, which suggest that it must be possible to gain a short, good tillering (thus good producing) plant type.

2.2.3 The actual selection

Honeycomb selection

Application of the simple criterion for honeycomb selection, i.e. a plant should yield more than each of its neighbours, resulted in selection of

692 plants. The portion of selected plants was 692/4980=0.139, not very different from the expected portion (0.15 according to Fasoulas (1973)).

The mean kernel yield of these 692 plants amounted to 195.4 dg, the coefficient of variation was 0.413.

This number of selected plants was considered to be too large to comprise the offspring of each selected plant in the comparative trial (crop 3). The honeycomb criterion was therefore adjusted as follows:

(i) the yield should be higher than that of each of the 6 neighbours

(ii) the culmlength should be less than the mean culmlength of the 6 neighbours.

This modification has been applied in all selection fields described in the present text. Honeycomb selection in this text refers therefore to application of this double criterion. The second criterion was inspired by the desire to breed rye with shortened culms. By this a stiffer crop can be gained, preventing lodging at higher amounts of fertilizer. It supplies an alternative way to get a higher yield per ha in addition to direct selection for kernel yield. The urgent need for that was shown in section 1.3. The two criteria for selection together aimed at breaking the positive correlation of culmlength and kernel yield (see former section). By applying these criteria plants were selected that had a short culm but yielded all the same satisfactory. This way of honeycomb selection resembles selection for a high harvest-index (=kernel yield/biomass).

Harvest index is a plant character that is not very sensitive for the positive relation between kernel yield and earnumber (this positive relation manifests itself very clear when varying plant density). Selection for harvest-index should thus be effective at an irregular stand of the crop (see Donald & Hamblin, 1976), because the influence of interplant distance is of minor importance. In section 6.3.4 more considerations on this subject and experimental results are given.

One hundred and fourteen of the 692 plants that were selected initially met the requirement for the second criterion. When selecting, the fact was neglected that some plants had less than 6 neighbours.
Because less than 1% of the plants was missing this will have concerned only a few selected plants. Moreover it appeared that the number of neighbours did not play an important role (see concluding remarks).

Because of the positive correlation of kernel yield and culmlength, primarily those plants from the group of 692 were selected that yielded less than the average of this group (see Table 4).

Random selection

As announced at the end of section 1.1 progress by selection was measured by comparing the performance of offspring of intentionally selected plants with that of the offspring of random plants. Because 114 plants were selected by H-selection, 57 plants were selected at random. (The reason for

Table 6 The mean kernel yield of the n_k plants with k neighbours. Row 1, 2, ..., 15 of crop 1

k	n_k	mean kernel yield (dg)
3	1	72.0
4	3	123.7
5	27	100.2
6	916	102.6

this will be explained in section 2.3.1.) The R-selection was carried out using a random permutation table. The observations on the 57 R-plants are summarized in Table 4.

Two restrictions were imposed:

(i) only plants not selected by H-selection were considered. Later this restriction was judged to be wrong. It was, therefore, only applied in crop 1;

(ii) only plants yielding at least 80 kernels were considered. This restriction was imposed because the lay-out of crop 3 required 80 kernels per entered offspring. This restriction must have been the main reason for the fact that the mean yield of the R-plants exceeded that of all plants in crop 1 by 8.6 dg.

Concluding remarks

It has been considered to use the following as a second criterion for H-selection: the culmlength should be less than that of each neighbour. Application of this on a random sample revealed that considerably less than 100 plants should then be selected. To avoid the risk of random drift a less restrictive second criterion was chosen: the culmlength should be less than the mean culmlength of the 6 neighbours.

The mean kernel yield of plants with 3,4,5 or 6 neighbours was established from 15 rows, in order to observe the effect of the number of neighbours on the kernel yield of the central plant. The result is shown in Table 6. There was no clear tendency that the yield of the central plant is the higher the lower the number of neighbours. Such a tendency could be expected as an effect of increased area per plant. However, the occurrence of missing plants might indicate poor local growing conditions. Indeed, the one plant of Table 6 having only 3 neighbours was a poor yielder. Obviously, the local conditions on the spot were adverse.

2.3 THE RESULT OF THE SELECTION

2.3.1 Material and method for crop 3

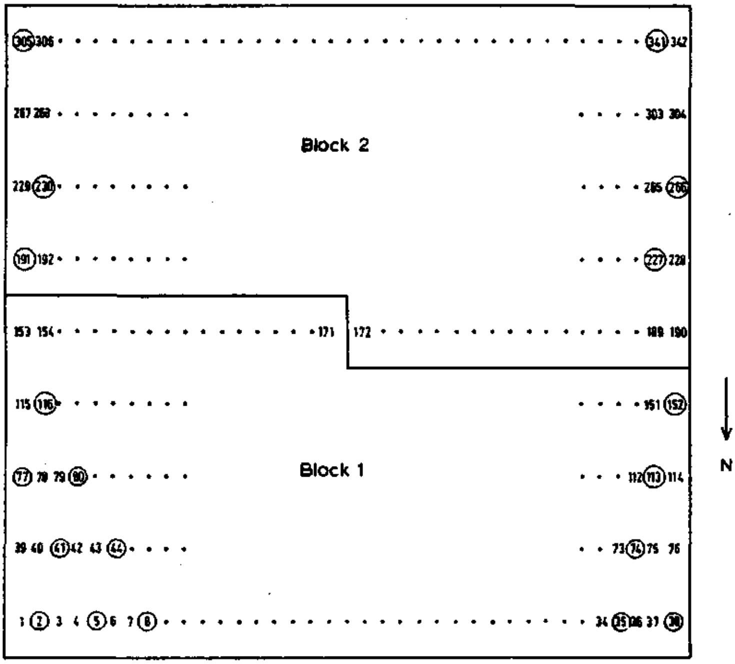

Figure 7 Position of the plots in crop 3. The encircled plotnumbers indicate plots with an R-family.

The material included in crop 3 comprised 114 H-families and 57 R-families (see section 2.2.3). Crop 3 was laid out to compare the performance of the H-families with that of the R-families (see section 2.3.6). By this method some interesting quantitative genetic parameters could be estimated from observations on the R-plants (crop 1) and on their offspring in crop 3 (see section 2.3.4 and 2.3.5). Such estimations could not be made if the selection response was measured by comparing the performance of the H-families (or a mixture of them) with the performance of plants grown from a mixture of the seeds of the not-selected plants.

The comparative trial was laid out in a form similar to that advocated for wheat by Shebeski (1970), who planted a control plot adjacent to every F_3 plot. This meant in the present case that - in general - an R-family plot was bordered on both sides by an H-family plot. Each plot comprised a single row of 20 plants plus a label. To be able to discriminate individual plants at the time of harvesting, the chosen interplant distance (within a row) was 5 cm. The length of a plot measured 21×5=105 cm, the width (i.e. the interrow distance) 25 cm.

The trial was in twofold. Each complete block comprised 114+57=171 plots.

The lay-out of crop 3 is depicted in Figure 7. The dimensions of the trial field, excluding the 1 m border all around, were: width 38×25= 950 cm, depth 9×105=945 cm. The total area (89.775 m^2) was considered to be small enough to plant complete blocks. However, because small environmental differences might occur among plots located at a distance of one or a few meters from each other (e.g. a temporary puddle), Shebeski's method to eliminate the influence of local differences in soil conditions was adopted. This procedure is especially applicable if the check is genetically uniform (a clone, a pure line, or an F_1 hybrid). This was not the case here, but the method was applied as well, because:

(i) in this way one can be sure that both R- and H-families will be evenly distributed across the trialfield

(ii) this design offers an alternative for measuring selection responses (see section 2.3.6).

Applying a randomization procedure the families were assigned a plotnumber. The plants grew in a rectangular stand. The area per plant was 5×25=125 cm^2, i.e. 80 plants per m^2. Here again the plant density was much lower than the optimal density. (The precise density was 20 plants per 21×5×25=2625 cm^2, i.e. 131.25 cm^2 per plant or 76.2 plants per m^2.)

Because 2 kernels were sown per plant position for 2 blocks 2×2×20=80 kernels per family were needed. These kernels were disinfected with Aa-tirit (containing Lindane and Thiram) and stored in one bag per family. First 40 kernels were taken out to sow block 1 and then the remaining 40 kernels were sown in block 2. The border was sown with a random sample of kernels from crop 1. After sowing appropriate measures were taken against damage by birds and large rodents. The trial was sown on 28 and 29 October, 1975 in the same field as crop 1.

From 15 to 19 March, 1976 the rye plants were singled. The crop had a good development. Most of the plant positions contained 2 plants. Because the plants were firmly rooted, the lifting of one of the 2 plants must have had some influence on the other plant. Empty positions were filled up by supernumerary plants from the same plot. These positions were not marked. (Later experiences learned that this transplantation had a drastic adverse effect on growth and production of the concerned plants.) The filling up of empty positions could not always be done completely, because it had to be done within a single plot and in some cases not enough plants were available. Ten plots at the most will have contained less than 20 plants on 19 March, 1976. From 25 May onward the crop flowered. After mid June an attack by brown rust (Puccinia graminis f.sp.secalis) became apparent. Because of the drought (see section 3.2.1) the crop was harvested already from 20 to 22 July, 1976. Per plot all plants were lifted and collected in a sheaf.

2.3.2 The observations

Each plot in crop 3 was harvested as a small sheaf. After drying, the following observations were done:

(i) per plant: culmlength: the distance (in cm) between roots and ear, along the longest culm
earnumber: the number of ears with at least 1 kernel
yield: total weight (in dg) of the ears

(ii) per plot: the number of broken ears
the weight (in dg) of the broken ears.

The time required per sheaf for these observations was about 10 minutes (when done by 2 persons). The observations sub (ii) are part of the respective totals per plot. The totals and the means per plant are thus the same as those obtained when there were no broken ears. When the ear on the longest culm was missing, the culmlength of the longest complete ear was recorded. A too short culmlength was then registered. This fault affected total culmlength and mean culmlength.

Some considerations on the number of plants per plot

The anticipated number of plants per plot for crop 3 was 20. Because of several causes the actual number of plants was, for some plots, less at the time of harvest. In fact even the actual number stayed unknown because the registered number of plants could deviate from the actual number. Transplantation during thinning, to fill up empty plant positions could not guarantee the number of plants aimed at: there may have been too few plants and mistakes in counting may have occurred. During and after the harvest several causes for a further deviation from the pursued number of plants occurred:

(i) notwithstanding the interplant distance of 5 cm the tillers of 2 neighbours were entangled in such a way, that they were taken for one plant
(ii) one plant produced tillers in such a way that it was considered as 2 entangled plants. Accordingly, this plant was wrongly torn in 2 parts
(iii) at the time of lifting some plants broke at the levels of the roots and the tillers of these plants were divided in 2 or more groups. When recording the observations then 2 or more plants were registered.

This last cause for a false number of plants has probably happened rather often. The registered number of plants is then too high. A false number has a direct (mainly negative) impact on the mean yield (calculated by dividing the weight of all ears belonging to a sheaf by the number of plants). The effect on mean culmlength will be less. In sections 5.3 and 6.3 the variation of the number of plants per plot is studied more precisely.
Two trains of thoughts were followed as regards the further analysis:

(i) a parent plant with a good genotype will, after open pollination, produce an offspring containing relatively many good plants. The progenies can, therefore, be judged on the basis of mean performance per plant. Such a mean may be biased downwards, especially for yield, because of fault (iii) stated above. Grain plants are assumed to take in general a profit from having, during their ontogeny, an empty neighbouring position. Because the justification for this assumption was questioned at the end of section 2.2.3 it is supposed here that the bias downwards will turn the scale.

(ii) a parent plant with a good genotype will, after open pollination, produce a good progeny. The progenies can, therefore, be evaluated on the basis of total yield per plot. Then the errors, mentioned before, in the registered number of plants do not play a role.

In conclusion a light preference for the second train of thoughts existed. Both approaches however were performed.

2.3.3 Comparison of the 2 blocks

Besides there possibly being a block effect from soil differences, also the way of sowing could give rise to such a block effect. Each progeny was grown both on a plot in block 1 and on a plot in block 2. To compare the 2 blocks pairs of plots were compared. Every pair was represented by a plot in each of the 2 blocks.

The observations for progeny j on the plots in block 1 and block 2 are indicated respectively by $\underline{y}_{1j}$ and $\underline{y}_{2j}$. There is a block effect δ if

$$E(\underline{y}_{1j} - \underline{y}_{2j}) = E\underline{d}_j = \delta \neq 0$$

The null hypothesis (to be tested) and the alternative hypothesis are:
H_0: the 2 blocks afford the same results (i.e. $\delta=0$)
H_a: the 2 blocks afford different results (i.e. $\delta\neq0$).
It is assumed that $\underline{d}$ is normally distributed. The test statistic $\underline{t}$ is

$$\underline{t} = \frac{\bar{\underline{d}}\,\sqrt{p}}{\sqrt{\underline{s}_{\underline{d}}^2}} \qquad (2.1)$$

When Student's t-distribution with p-1 degrees of freedom is indicated by $\underline{t}_{p-1}$, p being the number of pairs (in crop 3 holds p = 171), then under H_0:

$$\underline{t} \simeq \underline{t}_{p-1} \qquad (2.2)$$

In the first 7 columns of Table 7 the results of the tests are presented. These are not very consistent: for culmlength the 2 blocks showed a highly significant difference for growing conditions, for earnumber the growing conditions may be considered to be the same, for yield the growing conditions are just significantly different.

Table 7 Comparison of the blocks in crop 3. The characters are: (1) mean culmlength (cm), (2) total number of ears per plot, (3) mean earnumber, (4) total yield (dg) per plot, (5) mean yield (dg). The meaning of the symbols is: $\bar{x}_i$: mean across the plots of block i; $\bar{d}=\bar{x}_1-\bar{x}_2$; r: correlation coefficient.

character	$\bar{x}_1$	$\bar{x}_2$	$\bar{d}$	s_d	t	$P(\lvert \underline{t}_{170}\rvert > \lvert t\rvert)$	$r_{x_{1j},x_{2j}}$	t_r	$P(\underline{t}_{169}>t_r)$
(1)	121.165	119.987	1.177	4.428	3.47	0.0006	0.698	12.66	~ 0
(2)	70.386	70.280	0.106	14.58	0.094	0.925	0.197	2.62	0.005
(3)	3.596	3.625	-0.029	0.7087	-0.5387	0.5908	0.208	2.77	0.003
(4)	1363.54	1307.62	55.92	302.71	2.416	0.0167	0.253	3.39	~ 0
(5)	69.375	67.124	2.247	14.93	1.9683	0.0507	0.242	3.24	~ 0

The greater culmlength and yield in block 1 as compared with block 2 may result from the way of sowing. When sowing block 1 the larger kernels were unvoluntary taken out of the bags by preference. Thus for block 2 inferior kernels remained. Another cause might be the careless way of irrigation of a neighbouring trial. Because of this block 1 was partly irrigated as well. Because the summer of 1976 was unprecedently warm and dry this single irrigation may have had a lasting effect on culmlength and yield. (At the time of the irrigation the earnumber was already determined.)

The correlation of the observations $\underline{y}_{1j}$ and $\underline{y}_{2j}$ was also estimated. The estimates and the result of testing H_0: "the correlation is zero" are presented in the last 3 columns of Table 7.

The pairing was done because of the common ancestor. The significant positive correlation indicates that this really increased the precision when testing the null hypothesis. Nevertheless the correlation coefficients were rather low, except for mean culmlength. For earnumber and yield there was hardly a difference between the estimate for the totals and that for the means.

The low correlation coefficient indicated a relatively large environmental variation among the plots within a block. This could be caused by:

(i) the fact that the neighbours of a family in block 1 are different from the neighbours of the same family in block 2

(ii) the number of plants per plot (aimed to be 20) being too small, i.e. this number was not large enough to indicate the genetic value of the family to a reasonable degree. (This has been studied. See section 5.3.2 and 6.3.2.)

The total weight of all ears of all plants amounted to 456769 dg, i.e. 45.7 kg. According to a calculation for crop 1 (grown one year before), 87.3% of the weight of the ears could be attributed to the kernels (such a portion is called here: the conversion factor; see section 2.2.2). The derived kernel yield was therefore 39.91 kg on an area of 89.775 m². This corresponds with 4445 kg/ha. The conversion factor for crop 2 (grown in the same year as crop 3, but on a different piece of land where the effect of the extreme drought of 1976 was much more adverse) amounted to only 70.5% (see section 3.2.3). The mean earnumber in crop 3 was 3.61, so that per m² 3.61×80=288.8 ears were produced. The mean kernel yield per ear was thus 4445/288.8=15.4 dg.

2.3.4 The relation between R-plants (crop 1) and their offspring (crop 3)

Introduction

The study of the relation between a random set of parents and their offspring after random mating was undertaken to estimate a few typifying quantities. To facilitate further reading first 2 random variables are defined:

$\underline{x}_j$:= the observation (for some character) on the random parental plant j

$\underline{y}_j$:= the weighted average of the observations (for the same character) of the members of the family of half sibs, having plant j as their common parent

For the suffix j it holds that j=1,...,n; n being the number of randomly selected parents. The typifying quantities to be estimated are:

(i) the heritability in narrow sense (h_n^2) of the character
From the linear regression of $\underline{y}$ on $\underline{x}$, i.e. from $\hat{y}$=a+bx, h_n^2 can be estimated by

$$\hat{h}_n^2 = 2b \tag{2.3}$$

(see Falconer (1960), p. 169).

(ii) the additive genetic variance (σ_a^2) of the character.
From the covariance of $\underline{x}$ and $\underline{y}$, i.e. from cov ($\underline{x}$,$\underline{y}$), σ_a^2 can be estimated by

$$\hat{\sigma}_a^2 = 2\ \hat{\text{cov}}\ (\underline{x},\underline{y}) \tag{2.4}$$

(see Falconer (1960), p. 153)

(iii) the genetic correlation (ρ_g) between characters. This is treated in the introduction of section 2.3.5.

The former estimations for a certain character can only be justified when a few assumptions hold for that character. These assumptions are:

(i) epistatic interaction does not play a role in the genetic part of the determination of the phenotypic value

(ii) the parental population is in linkage equilibrium

(iii) the parents form a random sample

(iv) the parents give rise to an offspring after random mating.

These assumptions deserve some comments. The justification of the first assumption offers difficulties. If there is epistasis, then the following relations hold for any pair of loci:

- for the genetic covariance of parent and offspring

$$\text{cov}(\underline{g}_P,\ \underline{g}_{HS}) = \tfrac{1}{2}\ \sigma_a^2 + \tfrac{1}{4}\ \sigma_{aa}^2 \tag{2.5}$$

- for the genetic variance among families of halb sibs

$$\text{var}(\underline{g}_{HS}) = \tfrac{1}{4}\ \sigma_a^2 + \frac{1}{16}\ \sigma_{aa}^2 \tag{2.6}$$

These expressions are given by Falconer (1960), p.157. Mather (1974) writes $\frac{1}{2} D_r$ for σ^2_a and $\frac{1}{4} I_r$ for σ^2_{aa}. He gives the full expressions for D_r and for I_r in terms of main effects of genes and of their interaction effects.

From formula (2.5) and (2.6) estimates for σ^2_a and σ^2_{aa} can be derived as follows

$$\hat{\sigma}^2_a = 8\ [\hat{var}(\underline{g}_{HS}) - \tfrac{1}{4}\ \hat{cov}(\underline{g}_P,\underline{g}_{HS})] \qquad (2.7)$$

$$\hat{\sigma}^2_{aa} = 8\ [\hat{cov}(\underline{g}_P,\underline{g}_{HS}) - 2\ \hat{var}(\underline{g}_{HS})] \qquad (2.8)$$

An application is illustrated in section 5.3.3. A drawback is that no statistical test for testing H_o: "$\sigma^2_{aa}=0$" was known to the author. Therefore the study of epistasis was not done systematically. Throughout the present text it is taken for granted that epistasis could be neglected.

Even in the case of absence of epistasis the assumption that the population is in Hardy-Weinberg equilibrium for the relevant loci is not enough. The more stringent assumption of linkage equilibrium, implied in the derivation of formula (2.3) and (2.4), is required. The original variety Dominant is a synthetic variety (see section 2.1). The material used in crop 1 will have been Syn-2 or Syn-3 material. Therefore, crop 1 was only approximately in linkage equilibrium. Crop 2, 4 and 6 were established after selection (after flowering) and thus neither a linkage equilibrium nor a Hardy-Weinberg equilibrium could be expected to occur in these crops. The second assumption will hold therefore only approximately.

It has already been stated (section 2.2.3) that a restriction was laid on the sampling of the random plants (these plants should produce enough kernels to grow an offspring. Supposition (iii) is thus a little bit affected. According to Falconer (1960, p.170) selection does not affect the regression of offspring mean on the parental value, because "the covariance is reduced to the same extend as the variance of the plants.... But the covariance is not a valid measure of the additive genetic variance". A citation from Kempthorne (1957, p.329) says: "This will only be true if the regression of y on x is linear throughout the range of x. In the present case this will be true if there are no dominance deviations". Spitters (1979, p.217) takes it that "for non-normal frequency distributions, the regression generally deviates from linearity".

In our experiments it was assumed to be impossible to prove a significant deviation of linearity (because of the wide scattering of the (x,y)-points). For convenience sake it was therefore supposed that regression yields an unbiased estimate for h^2_n, even if there is some selection among the parents. The additive genetic variance however could be underestimated.

As far as the fourth assumption is concerned one should realize that, because of the gametophytic self-incompatibility, some outbreeding may occur, i.e. that more heterozygotes arise than expected according to random mating.

Table 8 Duration of flowering of 9 plants in crop 7 which started shedding pollen grains on 1 June, 1978.

6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	date in June
1	4	1		1										2	number of plants finishing flowering
3	3.25	6		2										6.5	mean earnumber of those plants

Because of the large size of the population (about 5000 plants) the magnitude of this surplus can be neglected. Further one may assume that some assortative mating occurs for the time of flowering. This could have an impact on the tillering, e.g. early types produce less culms. However, the possibility of a measurable deviation of random mating was rejected because assortative mating for time of flowering appeared to be neglectable: the duration of flowering is so long, that no effective assortative mating will take place. This is based on the following observation.

On 1 June, 1978 labels were attached to 9 plants in crop 7 which started shedding pollen grains the same day. From then on these plants were observed every day, to see whether at least 1 ear was flowering or had to start flowering. The date on which this was not longer the case was recorded. The results are summarized in Table 8. From 11 until 17 June it was cool (15-20°C) and some rainfall occurred. The 2 plants that ended flowering on 20 June did not flower continuously. They produced small, late developing ears (possibly a result of the low plant density). With the other 7 plants the duration of flowering was not clearly related to the earnumber. It was thus observed that, notwithstanding the nice weather, flowering lasted about 1 week. This appears long enough to state that it can not be justified to say that in Dominant there is assortative mating for the time of flowering in a measurable degree.

All the foregoing considerations together mean that only a restricted value can be attached to the estimates. In addition to this the lack of normality in the distribution of the characters studied (see e.g. section 2.2.2) makes statistical tests based on the normal distribution inappropriate. The results of these tests present therefore only an indication. This applies throughout the present text.

Frey and Horner (1957) advised to calculate the regression of offspring mean on the parental value for the standardized observations in stead of the original observations in case of an effect of the year on level and on variation of the observations. The result equals the coefficient of correlation of the original observations. The quantitative genetic interpretation of this correlation is, however, not as simple as that of the regression.

Table 9 Estimates, for 3 characters, of the numerical values of the quantities mentioned in section 2.3.4. The estimates are based on observations on 57 R-plants in crop 1 and their progeny in crop 3.

estimated quantity	culmlength (cm)	earnumber	yield (dg)	adjusted yield (dg)
α	94.58	3.53	66.51	68.57
β	0.194	0.0145	0.0221	0.0301
ρ	0.481	0.0794	0.151	0.210
t_r	4.07	0.59	1.13	1.60
$P(\underline{t}_{55}>t_r)$	~0	0.557	0.262	0.116
$\bar{x}$	150.2	4.96	103.8	7.58
$\bar{y}$	123.65	3.60	68.8	
σ^2_x	163.6	6.53	4869.1	5100.7
σ^2_y	26.50	0.22	104.3	
h^2_n	0.387	0.029	0.044	0.060
$cov(\underline{x},\underline{y})$	31.67	0.09	107.7	
σ^2_a	63.34	0.19	215.5	
$vc_a(=\sigma_a/\bar{x})$	0.053	0.088	0.141	

The numerical value of the heritability, estimated by correlation of offspring and parents, accounts, besides for disturbing effects of other sources (e.g. competition), also for the disturbing effect of genotype x year interaction. Genotype × year interaction will decrease the correlation between parents and offspring but not necessarily the regression of offspring on parent. Because the parental plant and its offspring share their cytoplasm the heritability estimates include variation for genetic factors transmitted by the cytoplasm.

The additive genetic variance can also be estimated after application of mating design 1 (Comstock and Robinson, 1948, 1952). Then the estimate is biased upwards because of inclusion of effects of genotype x year interaction. In that case also the variation for genetic factors transmitted by the cytoplasm is included.

Based on observations on R-plants and on their offspring after open pollination the following quantities were estimated:

- the parameters α and β of the linear function $y=\alpha+\beta x$
- the correlation ρ of $\underline{x}$ and $\underline{y}$
- the t_r-value for testing H_0:"$\rho=0$" against the alternative hypothesis H_a: "$\rho>0$". (This results in the same t-value as obtained after testing H_0: "$\beta=0$" against H_a:"$\beta>0$").
- the right tailed critical level $P(\underline{t}_{n-2}>t_r)$
- the mean of $\underline{x}$ and of $\underline{y}$

- the variance of $\underline{x}$ and of $\underline{y}$
- the heritability in narrow sense (h^2_n)
- the covariance of $\underline{x}$ and $\underline{y}$
- the additive genetic variance (σ^2_a)
- the coefficient of additive genetic variation, i.e. $cv_a=\sigma_a/\bar{x}$

The actual relation

Because neither a block effect nor a possible family x block interaction was considered to be of primary interest, the observations on the 2 plots per family were pooled. The totals were summed and weighted averages per plant were calculated. These averages form the basis for the results presented in the rest of this chapter. Table 9 presents for culmlength, earnumber and yield estimates of the quantities mentioned before. Figures 8 and 9 present for culmlength and yield the scatter diagrams for the relation between open pollinated parent and offspring mean.

Just for comparison with Table 9 for the 114 H-plants and their offspring a number of the parameters mentioned before were estimated as well. The results are presented in Table 10.

The means of $\underline{x}$ and $\underline{y}$ were very different in Table 9. Several causes may be mentioned for this:

(i) the plants of crop 1 were grown in a hexagonal pattern, the area per plant being 195 cm^2 (plant density 51.3). The plants in crop 3 were grown in a rectangular pattern; the area per plant amounting to 125 cm^2 (or - more precise - 131.25 cm^2 (plant density 76.2); see section 2.3.1). This was an advantage for yield of the parents.

(ii) the yield of the parents was kernel yield. For the plants of crop 3 it was total weight of the ears per plant. This means an advantage for the offspring.

(iii) the seedlings of the parental plants grew under extremely wet conditions. Their descendants grew under unprecedented dry conditions. (Rainfall of February through Juli 1976 amounted only 167 mm.) This drought will have been the main cause for the lower performance of the plants in crop 3.

Only for culmlength a significant correlation was established, indicating that r, and thus h^2_n, was significantly greater than zero. For earnumber and for yield r (and thus h^2_n) was not significant. When the assumptions for the test could be justified this would mean that the population did not contain additive genetic variation for these 2 characters.

Absence of additive genetic variation would mean that Dominant represents a population with the maximal mean genotypic value (in as far as it is in linkage equilibrium). Then the population is homogeneous for loci with incomplete dominance, but polymorphic for loci with overdominance. It was of course uncertain to what degree this conclusion was true under the prevail-

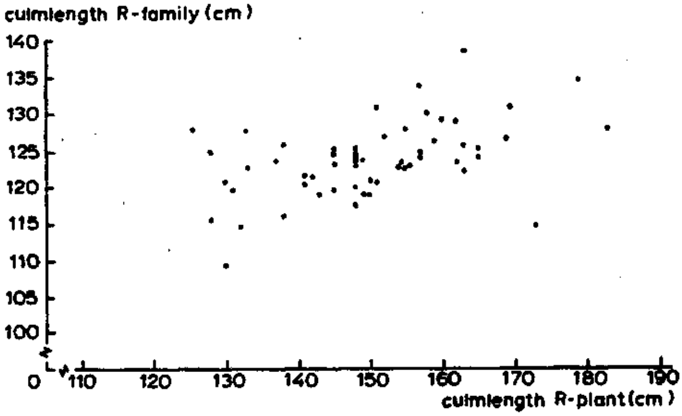

Figure 8 Scatter diagram for the culmlength (in cm) of random parents (x) and their offspring (y).
The material concerned 57 random plants in crop 1 and their progeny in crop 3. The regression line is given by Y=94.6 + 0.194x.

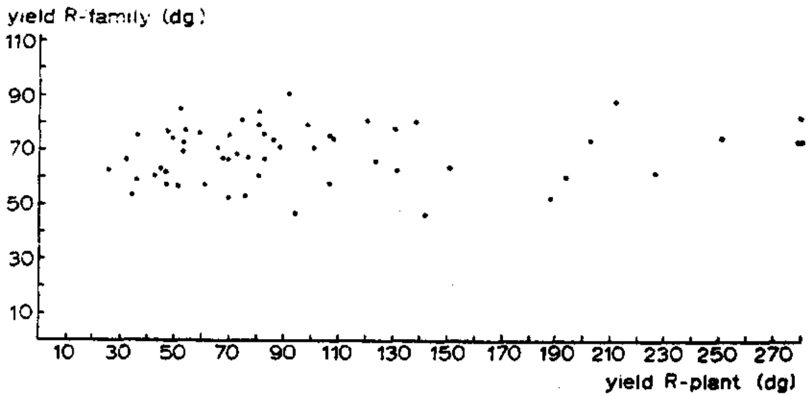

Figure 9 Scatter diagram for the yield (in dg) of random parents (x) and their offspring (y). The points mark kernel yield of 57 random plants of crop 1 and weight of the ears (mean per plant) of their progeny in crop 3. The regression line is given by y=66.5 + 0.022x.

ing situation. In any case these results mean that the possibilities to realize a selection response for earnumber and for yield are restricted. When one should succeed in decreasing the mean culmlength by selection, the result could be an increased harvest index (notwithstanding the positive phenotypic correlation of culmlength and kernel yield (viz. $r=0.52$; see Table 6)) or - given a constant biomass - even a higher kernel yield. To study how this all would work out it was decided to continue the programme.

A high heritability for culmlength ($h^2_n=0.67$) and a low one for earnumber ($h^2_n=0.042$) were also estimated for the winterrye variety Petkus (Bos, 1970). The low estimate for the heritability for yield will partly be caused by genotype x year interaction. (This creates differences between the ranking of the parents and that of their offspring.) It will also be caused partly by the low additive genetic variation (see vc_a in Table 9) and by the effects of the incidental micro-environmental conditions, pertaining to the parental plants.

This last suggestion was studied further. This was done by calculating the regression of offspring mean on parent in a different way: not x (the phenotypic value, i.e. the yield, of the parent) was used, but x': the yield of the plant diminished by the mean yield of its neighbours. The result (see Table 9, right column) is hardly better than that for the original procedure: the correlation of x' and y was not significant. This kind of adjustment was criticized by Baker & McKenzie (1967) because of the danger of overadjustment. They proposed an alternative which is illustrated in section 8.2.

By means of the coefficient of variation one can compare the variation for different characters of plants of the same population. In Table 9 estimates for the coefficient of additive genetic variation (cv_a) are given. The value for yield is the highest but it still has a low value. When comparing cv_a with cv_p in crop 1 (see Table 4) then it appears that for culmlength, i.e. the character with the highest heritability, the difference between cv_a and cv_p was the lowest.

The low heritability of earnumber implied that this character could not be used for indirect selection for yield. This was suggested by the high phenotypic correlation of earnumber and kernel yield ($r=0.90$; see Table 6).

Heritability estimates are mainly of interest only to those who obtained the estimates, because the level of the estimates reflects their material tested under their conditions. Therefore comparisons with estimates reported in the literature were hardly made.

Table 10 Estimates, for 3 characters, of the numerical values of some of the quantities mentioned in section 2.3.4. The estimates are based on observations on 114 H-plants and their progeny in crop 3.

estimated quantity	culmlength (cm)	earnumber	yield (dg)
α	81.53	3.71	72.43
β	0.264	-0.014	-0.026
r	0.401	-0.103	-0.169
$P(\underline{t}_{112}>t_r)$	~0		
$\bar{x}$	142.23	7.80	160.9
$\bar{y}$	119.04	3.60	68.21
σ_x^2	48.3	8.89	3763.7
σ_y^2	20.9	0.173	90.3

Table 11 Analysis of variance for the n R-families in crop 3, 5, 7, 10 or 13

source of variation	df	MS	$\varepsilon(\underline{MS})$
R-families	n-1	MS_F	$\sigma^2+2\sigma_f^2$
blocks	1	MS_B	$\sigma^2+n\sigma_b^2$
error	n-1	MS_E	σ^2
total-CT	2n-1		

After H-selection lower (and even negative) estimates for the correlation between parents and offspring were obtained (Table 10) than when R-selection was applied (Table 9). The cause for this could be a diminished genetic variation among progenies, which could indicate that the selection had some effect.

The additive genetic variance σ_a^2 could also be estimated from the n R-families in the comparative trials. The variable of interest is

$\underline{x}_{ij}$:= the mean of the observations on the members in block i of the j^{th} family of half sibs (i=1,2; j=1,...,n).

The analysis of variance is given by Table 11. The component σ_f^2, written in formula (2.6) as $var(\underline{g}_{HS})$, represents the genetic variance among the R-families. According to the relation

Table 12 Analysis of variance for 3 characters of the 57 R-families in crop 3

source of variation	df	culmlength			earnumber			yield		
		SS	MS	f	SS	MS	f	SS	MS	f
R-families	56	2938.24	52.47	6.07***	25.48	0.455	2.36***	11748.5	209.8	2.76***
blocks	1	15.11	15.11	1.75	0.11	0.107	0.55	24.7	24.7	0.33
error	56	484.40	8.65		10.83	0.193		4245.1	75.8	
total-CT	113	3437.75			36.42			14018.4		

$$var(\underline{g}_{HS}) = \frac{1}{4} \sigma^2_a \quad (2.9)$$

the additive genetic variation can also be estimated from an analysis of variance. Relation (2.9) is given by Falconer (1960), p.154. It is based on the assumption that maternal effects, as defined by Mather and Jinks (1971) are lacking. If this assumption does not hold, maternal effects contribute to σ^2_f. The estimate of σ^2_a will then be biased upwards. Such a bias is also present when σ^2_a is estimated from relation (2.4). The present estimate is

$$\hat{\sigma}^2_a = 2(MS_F - MS_E) \quad (2.10)$$

Table 12 presents the actual analysis of variance. For each of the 3 characters a highly significant variation among the R-families was detected. Thus, for each character significant additive genetic variation was observed. This may seem to deviate from the results reported before. However, there the significance of $\hat{h}^2_n$ was tested. The estimates for σ^2_a, derived from Table 12 are:

- culmlength 87.64 cm^2
- earnumber 0.524
- yield 268.0 dg^2

These estimates are higher than those in Table 8. This can be caused by the influence of genotype x year interaction, which is not excluded here.

For blocks no significant differences were obtained. This seems to impair the conclusion in section 2.3.3. However, that test for paired samples included all 171 pairs and here only the R-families were dealt with.

2.3.5 *Genetic correlations*

Introduction

There are several ways to estimate the genetic correlation between characters. The use of these methods is illustrated in several sections, especially in section 3.3.4, 4.3.4 and 6.3.4. Here only 2 estimators are introduced.

Table 13 Genotypic correlations, estimated by application of formula (2.11) or (2.12) on data from the 57 R-plants in crop 1 and their offspring in crop 3, and phenotypic correlations (also presented in Table 6).

	r_g		r_p
characters	form.(2.11)	form.(2.12)	(Table 6)
culmlength-earnumber	0.54	0.29	0.36
culmlength-yield	0.68	0.45	0.52
earnumber-yield	0.89	0.61	0.90

To understand the structure of the estimators the following quantities are defined:

$\underline{x}_{kj}$:= the observation for character k on the j^{th} R-plant

$\underline{y}_{kj}$:= the weighted average of the observations for character k on the members of the progeny of the j^{th} R-plant

The estimators are given by Becker (1975), p.130. They are:

$$r_g(k,k') = \frac{\hat{cov}(\underline{x}_k,\underline{y}_{k'})+\hat{cov}(\underline{x}_{k'},\underline{y}_k)}{2\sqrt{\hat{cov}(\underline{x}_k,\underline{y}_k)\cdot\hat{cov}(\underline{x}_{k'},\underline{y}_{k'})}} \qquad (2.11)$$

and

$$r_g(k,k') = \sqrt{\frac{\hat{cov}(\underline{x}_k,\underline{y}_{k'})\cdot\hat{cov}(\underline{x}_{k'},\underline{y}_k)}{\hat{cov}(\underline{x}_k,\underline{y}_k)\cdot\hat{cov}(\underline{x}_{k'},\underline{y}_{k'})}} \qquad (2.12)$$

They are called the arithmetic method resp. the geometric method. In accordance with Becker (loc.cit.) "the sign of the correlation calculated by the geometric method is determined from the sign of the correlation obtained by the arithmatic method". In cases where the arithmatic method could not be applied the sign of the phenotypic correlation was taken.

The actual correlations

The estimates for ρ_g are given in Table 13. For comparison the estimates for ρ_p in Table 6 are given as well.

The arithmatic method for estimating ρ_g gave higher values than the geometric method. The rank orders were not only the same for the 2 methods, but also equal to that for the phenotypic correlation. The mean genetic correlation of culmlength and yield approached the phenotypic correlation.

The prospects for selection of a plant type with a high production and a decreased culmlength were thus not completely lacking, but rather unfavourable. Later in the programme (see chapters 5 and 6) direct selection for the recombinant plant type was applied by means of ICL-selection.

2.3.6 The actual result of selection

Introduction

The comparative trial was laid out to determine if purposeful selection gave some response. To that end the mean performance (for means per plant or for totals per plot) of the n=114 purposeful selected families was compared with the mean of the m=57 R-families. The null hypothesis H_0: "the means are the same" (i.e. selection gave no response) was tested against the alternative hypothesis H_a: "the means are different" (i.e. selection gave response). This null hypothesis was tested in this chapter with Wilcoxon's nonparametric test for comparison of 2 means and in the other chapters with its equivalent: the test of Mann and Whitney. This was done because:

(i) it was thought that the variance among the purposeful selected families could be smaller than that among the R-families (Compare Table 9 with Table 10 for σ^2_{y}.)

(ii) the distribution of the family means could deviate from the normal distribution.

In section 5.3.5 these reasons for application of a non-parametric test are evaluated.

The application of Wilcoxon's test (see Snedecor and Cochran (1967), p.130) to crop 3 passed as follows: the weighted family means were ordered from the lowest (rank number 1) to the highest (rank number 171). The sum of the rank numbers for the m R-families amounted to w. Under H_0 for the approximation of the distribution of $\underline{w}$ by

$$\underline{w} \simeq \varepsilon\underline{w} + \sigma_w \underline{\chi} \quad (2.13)$$

it holds that

$$\varepsilon\underline{w} = \tfrac{1}{2}\, m(n+m+1) \quad (2.14)$$

and $$\mathrm{var}(\underline{w}) = \frac{1}{12}\, mn(n+m+1) \quad (2.15)$$

In the present case this gave

$$\underline{w} \simeq 4902 + 305.2\ \underline{\chi}$$

Table 14 Weighted means per plant for 3 characters of the plants of crop 3

	selection procedure	
character	H-selection (n=114)	R-selection (n=57)
culmlength (cm)	119.0	123.6
in %	96.3	100
earnumber	3.60	3.60
in %	100	100
yield (dg)	68.21	68.80
in %	99.1	100

Result for mean culmlength

The sum of the rank numbers of the 57 R-families amounted to w=6646.5 (that for the 114 H-families was thus 8059.5). Because a decreased culmlength was aimed at by selection, relatively high rank numbers might occur among the R-families. Therefore, a right-tailed test was applied:

$$P(\underline{x} > (6646.5-4902)/305.2) = P(\underline{x} > 21.6) \sim 0$$

Thus the null hypothesis was rejected: the selection had resulted in families with a reduced culmlength. As can be seen from Table 14 the mean culmlength of the plants of the H-families was 4.6 cm less; a decrease of 3.7%.

Result for yield per plant and for total yield from 2 plots

For yield per plant the sum of the rank numbers of the 57 R-families amounted to w=5036. Now a left-tailed test had to be applied:

$$P(\underline{x}<(5036-4902)/305.2) = P(\underline{x}<0.44) = 0.66$$

Thus selection did not result in a significantly increased yield per plant (see Table 14).

For total yield from 2 plots the sum of the rank numbers of the R-families was w=5098. The corresponding left-tailed critical level (i.e. 0.74) indicated that also for total yield per plot no selection response was realized.

Discussion

The result of honeycomb selection in crop 1 was not spectacular. There was no response for yield. Culmlength decreased 3.7%. The disappointing result for yield indicated that by H-selection - in contrast to the intention - no genetically superior plants were selected. The selected plants were only phenotypically superior over their neighbours. This could be the result of favourable circumstances during and after the transplantation (which took place as late as 10 and 11 April, 1975). Such a transplantation was not applied in the later selection fields. The decrease in culmlength was hardly associated with a decrease in yield. It appeared thus to be possible to break the positive correlation of culmlength and yield.

As was announced in section 2.3.1 the evaluation was also done otherwise: for each H-family the mean score per plant was expressed as a percentage of the mean score of the adjacent R-family. This was done both for culmlength and for yield. The average percentages were:

	culmlength	yield
block 1	96.7	103.6
block 2	96.1	101.3
total	96.4	102.4

According to this yardstick the selection resulted in plants having a 3.6% decreased culmlength, but yielding 2.4% more. This confirms the earlier conclusion for culmlength, but not that for yield. In section 6.3.5 this measure for selection response is criticized.

From Table 4 one might derive that the R-plants possessed a greater culmlength and that they yielded more than the average plant in crop 1. This could rest on the requirement that the R-plants should produce enough kernels to permit inclusion in crop 3. The result of the selection (positive for culmlength, negative for yield) could possibly be explained partly by this.

3.1 MATERIAL

Crop 2 consisted of a mixture of kernels produced by the H-plants in crop 1. The number of kernels used per H-plant depended on the yield of the H-plant concerned. The reason was that large differences in yield were observed among the H-plants. Such differences could partly rest on genetic variation, which was the assumption when preparing the sowing of crop 2. At the time it was not yet known that, except for culmlength, there was no important genetic variation among the H-plants (see Table 9).

It was thus believed better to include in the mixture more kernels of the higher yielding than of the lower yielding H-plants. This will occur automatically when mass selection is done by bulking seeds of the selected plants. The number of kernels from a certain H-plant to be included in the mixture, was determined as follows.

When the yield of the i^{th} H-plant amounts to x_i dg, then the total yield of all N H-plants amounts to $X = \sum_{i=1}^{N} x_i$ dg. The relative contribution of plant i to the total yield X is x_i/X.

The total area of the selection field and the 1 m border contained 92 rows, each with 79 or 80 plant positions; i.e. 7314 positions in all. The number of kernels of plant i to be included in the mixture is therefore 7314 (x_i/X) when sowing one kernel per position and $7314(2x_i/X)$ when sowing two kernels per position. (Variation for individual kernel weight was neglected in this approach: from plants differing for kernel size but having the same yield equal numbers of kernels were included in the mixture. So, selection for kernels size was avoided.)

The total yield of the 114 H-plants in crop 1 amounted to 18350 dg (see Table 4). Because 2 kernels were sown per position, the number of kernels used from the i^{th} plant, yielding x_i dg, was $7314\ (2x_i/18350)=0.8x_i$.

The mixture was disinfected with Aatirit and sown on 27 October, 1975. The lay-out of crop 2 was exactly the same as that of crop 1. Crop 2, however, was grown direct from sown kernels; crop 1 was grown after transplantation of the included plants in the seedling stage. Again attack by large rodents and birds was prevented.

The previous crop, potatoes, had been harvested only one month before, which might have had a lasting effect on crop 2 (see section 8.1).

3.2 THE PLANTS OF CROP 2

3.2.1 The growing of the crop

The plants of crop 2 emerged well and showed a good stand in the early spring of 1976 after a mild winter. Most of the plant positions were occupied by 2 plants. Thinning out to one plant took place between 15 and 19 March. The removal of one of the two plants disturbed sometimes the remaining individual. Empty positions were filled up by transplantation of supernumerary plants. Thus, 19 March all positions were occupied. To destroy loose silky-bent (Apera spica-venti (L.) P.B.) a spray with Simazine and DNOC was applied.

The drought of the spring and summer was unprecedented. The monthly rainfall from March through July amounted to respectively 29,9,28,38 and 33 mm. Because of the drought the leaves curled and died by mid-June. Brown rust was hard to detect. The crop was harvested as early as 14 to 19 July, 1976.

3.2.2 Some statistical properties

At the harvest 78 rows, each comprising in principle 68 plants, were lifted. Of each plant culmlength, earnumber and yield were recorded in the manner described in section 2.3.2, sub (i). Because of the strong phenotypic correlation of kernel yield and weight of the ears (see section 2.2.2) weight of the ears was recorded as yield.

In the third column of Table 15 summarized data on the plants of crop 2 are presented. As indicated in section 2.2.2, the number of plants envisaged was 5304, i.e. 288 forming a border that enclosed 5016 other plants. From the numbers of plants presented in the table one can derive the number of lacking observations, e.g. for yield 5304-5263=41. The cause for this was that 9 plants were absent and 32 plants did not produce any kernel. The plant positions were thus occupied in a high degree.

Comparison of Tables 4 and 15 shows that in crop 2 the means for all plants were much lower than those in crop 1. It appears reasonable to ascribe this to the severe drought of the summer of 1976. The coefficient of phenotypic variation for yield was somewhat lower in crop 2 than in crop 1. The cause of this may have been that the plants of crop 1 were first sown in Jiffy pots and transplanted later. The drought may also have partly been responsible for it.

The total yield of all plants amounted to 263154 dg. According to the conversion factor for crop 2 (see section 3.2.3) the kernel yield was 70.5% of the crude yield. The estimated kernel yield per m^2 was thus $(0.705\times263154)/103.428=1793.7$ dg. This low value indicates how unfavourable, even for rye, the growing conditions were. Calculated from the mean yield, the kernel yield per m^2 was $51.3\times50.0\times0.705=1803.2$ dg. This is somewhat too high a fig-

Table 15 Summary of the observations on plants belonging to crop 2.
n: number of observed plants; $\bar{x}$: mean; s: standard deviation; cv_p: coefficient of phenotypic variation; min: minimum; max: maximum

character	quantity	all plants	selected plants			
			H-selection (n=168)	G-selection (n=168)	T-selection (n=168)	R-selection (n=84)
culmlength (cm)	$\bar{x}$	113.5 (n=5266)	110.6	122.2	122.6	113.0
	s	14.5	7.40	9.58	9.75	10.2
	cv_p	0.127	0.067	0.078	0.080	0.090
	min		86	91	91	77
	max		135	149	149	138
earnumber	$\bar{x}$	3.34 (n=5268)	4.90	6.08	6.23	3.73
	s	1.44	1.43	1.43	1.36	1.31
	cv_p	0.432	0.292	0.235	0.218	0.351
	min		2	3	4	2
	max		11	11	11	7
yield (dg)	$\bar{x}$	50.0 (n=5263)	85.0	116.5	117.5	56.95
	s	28.9	20.3	18.0	17.4	22.7
	cv_p	0.578	0.239	0.155	0.148	0.399
	min		40	95	102	16
	max		165	235	235	123

ure because the actual plant density was less than 51.3 (the density aimed at). The mean kernel yield per ear was (0.705×50)/3.34=10.6 dg.

3.2.3 *The methods of selection*

Section 1.1 introduced the procedures for mass selection that are to be compared. These procedures were, on the one side, honeycomb selection (the new procedure) and, on the other, grid selection and truncation selection (conventional procedures). Random selection was applied as well. These 4 methods were applied to crop 2. So, 4 groups of plants were selected, whose progenies were compared in crop 5 (see section 3.3). The ways in which the methods were applied, are described here.

Honeycomb selection

The double criterion for H-selection, described in section 2.2.3, was applied. In contrast to the selection in crop 1, only plants with 6 neighbours were considered for H-selection. (When 2 neighbours incidentally had the same yield, which was for either better than the yield of the remaining 5 neighbours, then the second part of the criterion was applied for the shortest of the 2 plants.)

The first part of the criterion was met by 684 plants (i.e. 684/5263 ×100=13%) and the full criterion by 168 plants (3.2%). In Table 15 (4^{th} column) data on these 168 H-plants are given. Their mean culmlength was 2.9 cm less than that for all plants. Application of the approximate t-test:

$$t' = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2}}} \qquad (3.1)$$

(see Snedecor & Cochran (1967), p.115) showed that this difference was significant. In crop 1 (see Table 4) the difference was 3.5 cm.

The mean kernel yield was 68.6 dg. Therefore 100(68.6/85.0)=80.9% of the yield was due to kernel yield. The conversion factor calculated for the R-plants was only 70.5%. The difference may rest on better seedset of the H-plants.

Grid selection

The basic idea behind grid selection is the assumption that by gridding the selection field the plants are grouped in such a way, that the environmental conditions for plants belonging to the same group are more similar than for plants belonging to different groups. When selecting the best phenotypes within a grid plants are compared which grew under relatively similar conditions. Thus the probability that the selected plants have superior genotypes is increased.

The disturbing effect on the phenotype of local environmental conditions is partly removed in grid selection, but - as might be assumed - not as efficiently as in honeycomb selection. The relative efficiency of G-selection and H-selection could be studied empirically by comparing the results of the 2 methods.

For a fair comparison equal numbers of plants should be selected for each method. Thus 168 G-plants were selected, i.e. the 14 best yielding plants in each of 12 grids. The size and the orientation of the grids was chosen in an arbitrary manner. The 12 grids comprised the central 76×66=5016 plant positions of the selection field. Thus each grid contained 76/4=19 rows with 66/3=22 plant positions. The dimensions of a grid were: width: 19×13=247 cm; length: 22×15=330 cm. Figure 20 gives the same partition for crop 9.

Only plants with 6 neighbours were considered for G-selection. If more than 1 plant showed the lowest yield required for selection then the plant to be selected was chosen at random. In this way the number of plants selected within a grid was always 14.

In Table 15 (5^{th} column) data on the 168 G-plants are presented. The G-plants were about 10% longer than the H-plants; they produced 24% more ears and yielded 37% better. These differences can partly be explained by the fact, that H-selection aimed at reduced culmlength combined with improved yield (negatively correlated aims), while G-selection aimed only to increase yield.

Truncation selection

The simplest form of mass selection is the so-called truncation selection. Plants that come closest to the level desired by the breeder are selected without any correction for the effect of variation in environmental conditions. Just as with H-selection 168 plants were selected. These were plants yielding at least 102 dg.

As 175 plants produced at least this minimum requirement for yield, 7 of the 10 plants producing 102 dg were discarded at random. Only plants from the central 76×66=5016 positions and only plants with 6 neighbours were taken into consideration.

In Table 15, 6^{th} column, data on the T-plants are presented. Their mean culmlength and yield were comparable to those of the G-plants.

The lower bound for T-selection was determined as follows. It was assumed (notwithstanding the skewness reported in section 2.2.2) that the distribution for yield was normal and could be given by

$$\underline{x} \simeq 50.0 + 28.9\,\underline{\chi} \qquad \text{(see Table 15)}$$

Then for selection of 168 plants (the portion 168/5266=0.032) the threshold x' for selection follows from

$$P(\underline{\chi} > 1.855) = 0.032$$

Thus $x'=50+(1.855\times 28.9)=103.6$ dg.

For the sake of security, first the plants yielding at least 98 dg were selected. This comprised 226 plants.

The selection differential S (see Falconer (1960), p.192) amounted to 117.5-50.0=67,5 dg and thus the calculated intensity of selection was

$$i = \frac{S}{s_p} = \frac{67.5}{28.9} = 2.34$$

For a normal distribution this would be equal to 2.243 (see Becker (1975), Table 3).

Random selection

For random selection, just as in crop 1 (see section 2.2.3), we selected only half as many plants as for H-selection. Thus 84 R-plants belonging to the 5016 central positions were sampled by drawing 84 pairs of lottery tickets (indicating together the row-plant number).

Two restrictions were imposed:

(i) only plants with 6 neighbours were considered for selection. This ensures that the random plants form a sample out of the population of plants which came into consideration for the other selection methods. Further, by requiring a fixed number of neighbours a cause for diversity among the R-plants is removed.

(ii) only plants yielding at least 60 kernels could be admitted. This restriction was imposed because of the lay-out of crop 5.

In the last column Table 15 presents data on the R-plants. Their mean yield was 6.95 dg higher than that of all plants. This may have been caused by applying restriction (ii).

For each R-plant the number of kernels (k) was established. Also their joint weight (w) was determined. From these observations it was derived that:

$\bar{k}$	= 132.5	$\bar{w}$	= 40.2 dg
s_k	= 68.0	s_w	= 21.4 dg
vc(k)	= 0.51	vc(w)	= 0.53

The phenotypic correlation of k and w amounted to r_p=0.94. The mean single kernel weight was only 40.2/132.5=0.303 dg. Because the mean yield of the R-plants in crop 2 amounted to 56.95 dg (see Table 15) the weight of the kernels was estimated to be (40.2/56.95)×100=70.5% of the weight of the ears. This was a low portion when compared with the conversion factor for crop 1 (i.e. 87.3%; see section 2.2.2). The serious effect of the drought was thus clearly reflected by the mean single kernel weight and by the conversion factor.

Comparison of groups of selected plants

For the 4 mentioned procedures 168 H-, 168 G-, 168 T- and 84 R-plants were selected. Because some plants were used with 2 or 3 procedures the total number of selected plants was only 401 instead of 3(168)+84=588. Table 16 presents a classification of the selected plants on the basis of the procedure(s) for which the plants were selected. The ranking of the classification depended on the number of plants belonging to the groups.

It is clear that by H-selection a distinct group of plants was selected: only 37 of the 168 H-plants were also selected with another procedure. The probable reason for it was that the selection aimed at both a reduced culmlength and a better yield. In contrast G- and T-selection were largely equivalent, because with those methods selection was only for yield. The 22 plants in group HGT had the highest mean yield; their mean culmlength was 10.6 cm less than that of the GT-plants. It was not unexpected that only 12 of the 84 R-plants were also selected by other procedures.

Table 16 Classification of the 401 plants, selected in crop 2, in accordance with the procedure(s) for which the plants were selected.
n: number of plants; $\bar{x}$: mean; s: standard deviation; min: minimum; max: maximum.

group	n	culmlength (cm)				earnumber				yield (dg)			
		$\bar{x}$	s	min	max	$\bar{x}$	s	min	max	$\bar{x}$	s	min	max
H	131	110.0	7.6	86	135	4.56	1.19	2	9	77.3	13.5	40	101
GT	119	124.7	9.2	106	149	6.17	1.39	4	11	119.4	17.8	102	235
R	72	112.9	10.7	77	138	3.56	1.25	2	7	51.5	18.3	16	98
HGT	22	114.1	7.3	91	126	6.59	1.50	5	11	121.5	18.6	102	165
T	19	123.0	9.5	103	138	6.21	1.08	4	8	105.5	8.3	102	139
G	18	119.4	7.2	107	131	5.28	1.36	4	9	98.5	2.0	95	101
HR	7	109.9	3.6	106	115	4.43	0.98	3	6	77.3	11.8	59	91
GH	4	109.3	2.4	106	111	5.50	1.29	4	7	97.8	2.6	95	100
HT	4	110.5	4.7	106	117	6.75	1.50	6	9	102.8	0.5	102	103
GRT	4	118.5	9.4	107	128	5.75	0.96	5	7	110.5	8.5	104	123
GR	1	121				3				96			
	401												

3.3 THE RESULT OF THE SELECTION

3.3.1 *Material and method for crop 5*

The lay-out of the comparative trial (crop 5) was analogous to crop 3 (see section 2.3.1). The plots consisted again of 21 positions alongside a single row: 1 position for the label and 20 for a plant. The interrow distance was 25 cm, the intrarow distance 5 cm. For the comparative trial 2 complete blocks were sown, with - in general - 2 kernels per plant position. The complete blocks had to include offspring of 168 H-plants, 168 G-plants, 168 T-plants and 84 R-plants (in total 588 half sib families). Quite a number of plants were selected according to 2 or 3 procedures. Thus 80, 160 or 240 kernels from a selected plant were required for crop 5. When there were not so many kernels, but more than 60, 120 or 180 respectively, at some plant positions only 1 kernel was sown in stead of 2. When there were still less kernels available bulk seed was sown all over the pertaining plot, for as many selection procedures as necessary. Then the available kernels were used, with decreasing priority, as H-, G- or T-material. The actual number of objects was thus lower than the intended number:

type of families	number of objects		
	intended	actual	replaced by bulk
H	168	159	9
G	168	165	3
T	168	151	17
R	84	84	0
	588	559	29

The R-families were bordered on both sides by H-, G- and T-families. Thus crop 3 consisted of units of 7 plots sown with respectively T,G,H,R,H,G,T material. Although the plotnumbers for the diverse types of material were preset, it was determined by a randomization procedure which specific family had to be grown on a certain plot.

The width of the trial field was 10 units of 7 plots, i.e. 70×25=1750 cm. The complete trial, 2x588=1176 plots, consisted of 16 strips with 70 plots plus 1 strip with 56 plots and 14 bulk plots. The length of the field was thus 17×105=1785 cm. All around the trial field a 1 m border was sown. The area of the trial measured 2 (blocks)×559 (plots)×1.05×0.25=293.475 m^2.

The trial was sown 18-22 October, 1976. The emergence was good; most plant positions were occupied by 2 plants. Because of unfavourable weather conditions the thinning was done as late as 14-28 March, 1977. The plants were already too large by that time and the thinning must therefore have caused some damage to the plant that remained on the plant position. On 4 April Simazine was sprayed (primarily to exterminate loose silky-bent). The flowering (i.e. shedding of pollen) started 31 May. According to a visual impression the crop was rather heterogeneous.

When the harvest took place (5-15 August, 1977), many plants were divided, which led later to the registration of too many plants per plot. In section 2.3.2 some considerations on the effect of a variable number of plants per plot were given. The observations (see section 2.3.2) were done after storage in a non-mouse-proof room. Because of mice many ears lost almost all their kernels. Thus where the character yield is concerned, the results were less accurate for mean yield per plant as well as for total yield.

3.3.2 Comparison of the 2 blocks

Crop 5 was sown in the same way as crop 3. Again all kernels from a certain parent plant were kept in one paper bag. This implied that earlier sown plots (in block 1) may have been sown with seeds of another seed quality than later sown plots (in block 2). Differences between the blocks could therefore be the result of differences in soil conditions as well as of differences in seed quality.

Table 17 Comparison of the blocks in crop 5. The characters are: (1) mean culmlength (cm), (2) total number of ears per plot, (3) mean earnumber, (4) total yield per plot (dg), (5) mean yield (dg). The meaning of the symbols is: $\bar{x}_i$: mean across the 559 plots in block i; $\bar{d}=\bar{x}_1-\bar{x}_2$; r: correlation coefficient.

character	$\bar{x}_1$	$\bar{x}_2$	$\bar{d}$	s_d	t	$P(\lvert \underline{t}_{588}\rvert > \lvert t\rvert)$	$r_{x_{1j},x_{2j}}$	t_r	$P(\underline{t}_{587} > t_r)$
(1)	143.8	143.1	0.7	10.03	1.65	0.10	0.291	7.18	~ 0
(2)	61.2	56.7	4.5	22.07	4.82	~ 0	0.105	2.48	0.007
(3)	3.34	3.12	0.22	0.969	5.37	~ 0	0.116	2.75	0.003
(4)	1070.0	1067.1	3.8	499.1	0.18	0.85	0.114	2.70	0.004
(5)	57.9	58.1	-0.2	16.89	-0.28	0.78	0.114	2.71	0.003

The null hypothesis H_0: "the 2 blocks afford the same results" was tested in the same way as in section 2.3.3. Formula (2.1) and formula (2.2) were applied with p=559 (the number of pairs of plots in crop 5).

The results of the tests are presented in Table 17. Only for the characters total number of ears per plot and mean earnumber the null hypothesis had to be rejected in favour of the alternative hypothesis that the 2 blocks afforded different results. It was remarkable that H_0 was only rejected in crop 5 for exactly these characters, in contrast to the results of crop 3. Because of these contradictory results the supposition that in block 1 larger kernels were sown than in block 2 was not supported in crop 5. Nevertheless, the comparative trials grown later were sown in a different way.

The correlation between the observations for an object in the 2 blocks is also given in Table 17. These correlations were very low, especially when compared with those for crop 3 (see Table 7), but always significantly greater than zero. Again the repeatability was at its highest for culmlength. In section 2.3.3 a few comments on the meaning and the causes for the low numerical values were given.

The total number of ears in crop 5 was 65941. Because the area of the crop measured 293.475 m² the ear-density was 224.7. In the same way it was established that the mean yield per m² was 4072.67 dg. According to the conversion factor for crop 4 (see section 4.2.2) this corresponded to a kernel yield of only 0.67×4072.7=2728.7 dg per m². The mean kernel yield per ear was therefore only 2729/224.7=12.1 dg. These low values were not in accordance with the visual impression of crop 5. Post-harvest losses might be responsable for that.

3.3.3 The relation between R-plants (crop 2) and their offspring (crop 5)

Skewness was studied from the observations on the n=84 R-plants and from the observations on their offspring. It was studied for the mean per plant as well as for the total of 2 plots. The skewness was estimated according to Pearson & Hartley (1970). To test H_0: "there is no skewness" against H_a: "there is skewness" the standard deviation was derived from the approxima-

Table 18 Skewness ($\sqrt{b_1}$) for some characters observed on 84 R-plants (in crop 2) and their offspring (in crop 5).

		offspring	
character	R-plants	mean per plant	total from 2 plots
culmlength	-0.64*	-0.87**	
earnumber	0.82**	-0.27	-0.54*
yield	0.68*	-0.16	-0.40

tion $\sqrt{6/n}$=0.267. The results are summarized in Table 18. Like in section 2.2.2 it was established that the assumption of normality could not always be justified.

In section 2.3.4 the assumptions and limitations of estimates of quantitative genetic parameters were discussed. These parameters are estimated here from the 84 R-plants in crop 2 and their offspring. Table 19 presents for culmlength, earnumber and yield estimates for all quantities mentioned in the introduction to section 2.3.4. The relation between parents and offspring is expressed graphically in Figs. 10,11 and 12 respectively for the 3 characters.

Table 19 Estimates, for 3 characters, of the parameters mentioned in section 2.3.4. The estimates are based on observations on 84 R-plants in crop 2 and their offspring in crop 5.

estimated parameter	culmlength (cm)	earnumber	yield (dg)
α	119.9	3.15	54.62
β	0.20	-0.01	0.024
ρ	0.32	-0.03	0.04
t_r	3.01	-0.27	0.38
$P(\underline{t}_{82}>t_r)$	0.002	0.605	0.354
$\bar{x}$	113.0	3.73	56.95
$\bar{y}$	142.5	3.11	56.00
σ_x^2	104.4	1.72	515.3
σ_y^2	41.9	0.25	176.8
h_n^2	0.40	0	0.048
$cov(\underline{x},\underline{y})$	20.87	-0.02	12.47
σ_a^2	41.74	0	24.94
vc_a	0.057	0	0.088

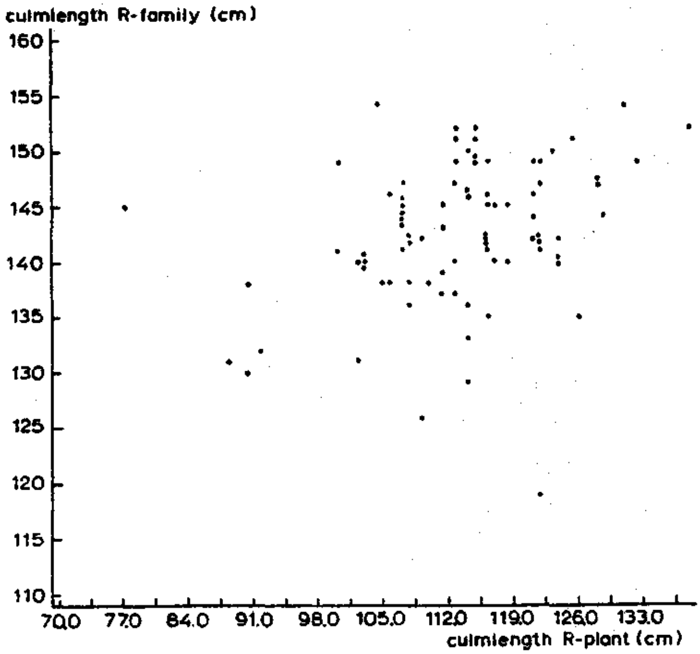

Figure 10 Relation between the mean culmlength of the members of an R-family (y) and the culmlength of their common parent (x); y and x in cm. The relation is depicted for 84 R-plants (crop 2) and their offspring (crop 5).

For comparison with Table 19 also estimates for some of the parameters of interest were derived for the H-, the G- and the T-plants. These are presented in Table 20.

Discussion

The skewness in crop 4 was studied from a sample, formed by the 84 R-plants, from crop 4. One of the restrictions imposed on the sampling meant truncation in such a sense, that the lowest yielding plants were not admitted. This will have biased upwards the estimates for skewness.

Table 19 allows a comparison of the mean values for the R-plants ($\bar{x}$) and for their offspring ($\bar{y}$). This requires some commenting:

(i) the parents produced culms about 30 cm shorter. This illustrates the drastic effect of the drought prevailing in crop 2 on culmlength;

(ii) the parents produced more ears than their offspring, but the yield was about the same. The parents suffered from the drought (especially

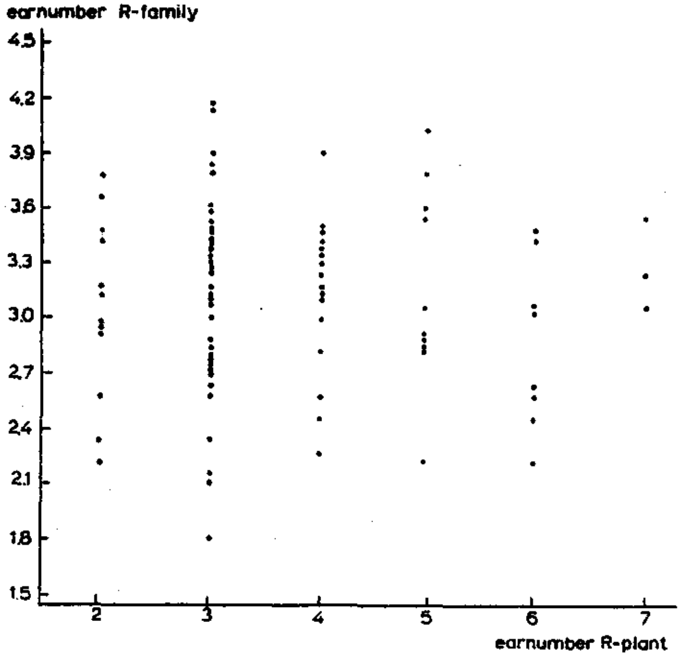

Figure 11 Relation between the mean earnumber of the members of an R-family (y) and the earnumber of their common parent (x).
The relation is depicted for 84 R-plants (crop 2) and their offspring (crop 5).

for yield), but grew at a lower plant density than their offspring. Considering their growing conditions, the latter gave a disappointing yield (see section 3.3.2).

Because of the significant skewness the results of the statistical tests (see Table 19) for significance of the heritability should be taken as an approximation. Only for culmlength significance of h^2_n was established.

The estimates for the heritability had about the same numerical values as those of crop 1 (see Table 9), whereas the coefficients of correlation between parental value and offspring mean were somewhat lower than for crop 1. A large difference between the estimates for the additive genetic variance was, however, observed for yield. A decline in genetic variation was not yet evident. Indeed, because of the poor results of the selection in crop 1 (see section 2.3.6) such a decline could hardly be expected.

The estimates for the coefficient of additive genetic variation were, except for culmlength, still lower than in crop 1 (see Table 9). Again the difference with the estimates for the coefficient of phenotypic variation was smallest for culmlength.

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Table 20 Estimates, for 3 characters, of some of the parameters mentioned in section 2.3.4. The estimates are based on observations on n plants selected in crop 2 and their offspring in crop 5.

		selection procedure		
character	estimated parameter	H-selection (n=159)	G-selection (n=165)	T-selection (n=151)
culmlength(cm)	β	0.287	0.236	0.201
	ρ	0.372	0.398	0.336
	t	5.02	5.39	4.48
	$P(\underline{t}_{n-2}>t)$	~0	~0	~0
	$\bar{x}$	110.56	122.41	123.56
	$\bar{y}$	141.44	144.37	145.51
earnumber	β	-0.001	0.009	-0.065
	ρ	-0.002	0.026	-0.156
	t	-0.029	0.332	-1.979
	$P(\underline{t}_{n-2}>t)$	0.511	0.370	0.972
	$\bar{x}$	4.96	6.09	6.23
	$\bar{y}$	3.30	3.23	3.26
yield (dg)	β	0.022	-0.057	-0.117
	ρ	0.033	-0.080	-0.159
	t	0.412	-1.025	-2.02
	$P(\underline{t}_{n-2}>t)$	0.340	0.847	0.974
	$\bar{x}$	85.96	116.81	117.47
	$\bar{y}$	58.57	58.25	59.77

In conclusion: the indication obtained in chapter 2 that Dominant, the substrate for the experiments, contained only a small amount of additive genetic variation for yield was confirmed. The restrictions to be attached to the operational value of the estimates should, of course, be kept in mind. In this stage of the experiments better prospects were assumed for the experiments with autotetraploid material (see chapter 6), which was derived from diverse origins.

The additive genetic variance was also estimated from an analysis of variance for the n=84 R-families. This was explained in section 2.3.4. The analysis of variance is presented in Table 21.

Only for earnumber significant differences between the 2 blocks (plus confounded factors) were detected. This confirms the conclusion drawn in section 3.3.2.

The R-families appeared to differ only significantly for culmlength (critical level about 0.01), indicating significant additive genetic variation for this character (conform the results obtained before).

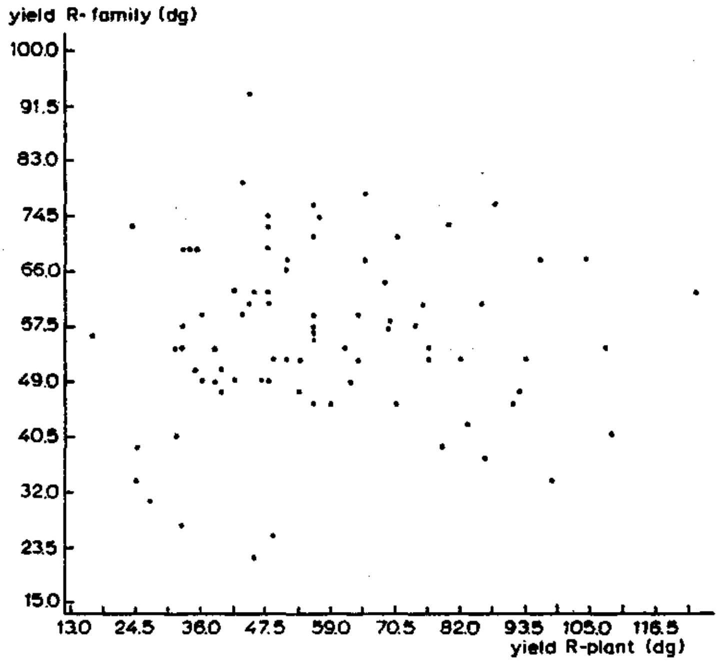

Figure 12 Relation between the mean yield of the members of an R-family (y) and the yield of their common parent (x); y and x in dg. The relation is depicted for 84 R-plants (crop 2) and their offspring (crop 5).

The estimates for σ_a^2, to be derived from Table 21, are:

culmlength: 71.6 cm^2
earnumber : 0.112
yield : 193.2 dg^2

These estimates are higher than those in Table 19. Again the reason for this might be the influence of genotype x year interaction. Such influence is excluded when the estimates are based on covariance of parents and offspring. The estimates are somewhat lower than those for crop 3.

Table 21 Analysis of variance for 3 characters of the 84 R-families in crop 5

source of variation		culmlength (cm)			earnumber			yield (dg)		
	df	SS	MS	f	SS	MS	f	SS	MS	f
R-families	83	7426.1	89.5	1.67*	43.98	0.530	1.12	30966.4	371.1	1.35
blocks	1	72.1	72.1	1.34	8.07	8.07	17.0***	887.4	887.4	3.21
error	83	4453.5	53.7		39.34	0.474		22947.7	276.5	
total-CT	167	11951.7			91.39			54801.5		

Table 22 Genotypic correlations, estimated by application of formula (2.11) or (2.12) on data from the 84 R-plants of crop 2 and their offspring in crop 5, and phenotypic correlations, estimated from observations on those R-plants.

characters	r_g		r_p
	form (2.11)	form (2.12)	
culmlength-earnumber		0.77	0.15
culmlength-yield	0.83	0.79	0.32**
earnumber-yield		2.18	0.79***

3.3.4 Phenotypic and genetic correlations

Coefficients of phenotypic correlation were estimated from the observations on the 84 R-plants. The estimates are presented in the last column of Table 22. Significant positive correlation was established for culmlength and yield and for earnumber and yield. All 3 estimates were lower than the corresponding values in Table 13. The rank of the correlations was the same for crop 1 and 2.

In section 2.3.5, 2 formulas were given to estimate genetic correlation from the relation between parents and offspring. Application of formula (2.11) presented difficulties because of the negative estimate of the covariance of parents and offspring for earnumber. Only the genetic correlation for culmlength and yield could be estimated: r_g=0.83 (see Table 22). This estimate was much higher than that for the phenotypic correlation; thus confirming again difficulties in selection of the desired recombinant plant-type.

When using formula (2.12) negative signs of covariances cancel out and unreliable estimates result (see Table 22, 3rd column). According to this formula negative as well as positive genetic correlations are possible. Clearly, these 2 formulas have their drawbacks. Therefore 2 other, possibly more reliable ways to estimate the genetic correlation are illustrated here. These methods imply application of the expression given by Falconer (1960, p.318) for the relation between the expected response for character y, when there is selection for character x, and the response for character x itself. The expression can be written as

$$CR(y)=\rho_g(x,y)\sqrt{\frac{\sigma_a^2(y)}{\sigma_a^2(x)}}\cdot R(x) \qquad (3.2)$$

and also as

$$CR(y)=\rho_g i(y)\ \sqrt{h_n^2(y)\cdot h_n^2(x)}\ \sigma_p(y) \qquad (3.3)$$

in which i represents the selection intensity. The estimates for ρ_g obtained in this way could be called realized genetic correlation.

In the following, estimates for the genetic correlation of culmlength and yield are derived from these 2 expressions:

(i) The direct response to T-selection for yield (x) was R=59.77-56.0=3.77 dg (Table 23); the correlated response for culmlength (y) was CR=145.5-142.5=3.0 cm (Table 23). The estimates for the additive genetic variance of the 2 characters are 24.94 and 41.74, respectively (Table 19). Substitution in formula (3.2) gives r_g=0.62 as the estimate for the genetic correlation of culmlength and yield.

(ii) The intensity of T-selection in crop 2 was 2.3 (see section 3.2.3). The estimates for the heritability were 0.40 for culmlength and 0.05 for yield (Table 19). The phenotypic standard deviation for culmlength was given in Table 15 and was s=14.5 cm. Thus formula (3.3) yields, for CR=3 cm, as estimate for ρ_g the value r_g=0.63.

3.3.5 The actual result of selection

Introduction

Crop 5 was to give indications on the relative efficiency of the methods for mass selection applied to crop 2. For fair comparison of G-, H- and T-selection always 168 plants, each with 6 neighbours, were selected (3.2%). However, not enough seed was available to grow 168 progenies for each selection procedure. Especially no fair comparison was possible because H-selection was both for yield and culmlength, whereas G- and T-selection were only for yield. In a later stage (see chapters 5 and 6) H-selection was compared with ICL-selection (also aiming at a recombinant planttype).

Kruskal and Wallis' median test (Siegel, 1956), was used to test the hypothesis H_0: "the 4 methods resulted in equivalent progenies" against the alternative hypothesis H_a: "the 4 methods resulted in non-equivalent progenies". The distribution of the test statistic $\underline{H}$ was, for H_0 being true, approximated by

$$\underline{H} \simeq \chi^2_{k-1} \qquad (3.4)$$

(k=number of treatments; here k=4), see Pearson & Hartley (1972), p.49. This test statistic was used to test H_0 against H_a. The corresponding critical level is given by

$$P(\chi^2_{k-1} > H).$$

Table 23 Weighted means per plant for culmlength, earnumber and yield; and means for total yield from 2 plots. Results from crop 5.

character	selection procedure			
	H-selection (n=159)	G-selection (n=165)	T-selection (n=151)	R-selection (n=84)
culmlength (cm)	141.4	144.4	145.5	142.5
in %	99.2	101.3	102.1	100
earnumber	3.30	3.23	3.26	3.11
in %	106.1	103.9	104.8	100
yield (dg)	58.6	58.3	59.8	56.0
in %	104.6	104.0	106.7	100
total yield (dg)	2164	2113	2183	2058
in %	105.2	102.7	106.1	100

In case of rejection of H_0 for a certain character Mann-Whitney's test was applied for pairwise comparison of the 4 methods (Pearson & Hartley (1972), p.46).

Actual results

Table 23 presents the results of crop 5. Application of the Kruskal and Wallis test revealed that only for culmlength H_0 had to be rejected:

character	H	critical level
culmlength	35.4	0
earnumber	6.3	0.096
yield	3.0	0.396
total yield	2.6	0.460

Mann-Whitney's test further revealed that

(i) both G- and T-selection resulted in plants with significant longer culms than the plants from R-selection

(ii) H-selection resulted in plants with significantly shorter culms than the plants from G- or T-selection.

H_0 was not rejected for other contrasts.

Discussion

Only a few contrasts appeared to be statistically significant. Thus most of the discussion to follow concerns rather tendencies than proven shifts.

As could be expected from the positive correlation of yield and culmlength the methods selecting only for yield (G and T) resulted in plants with not only an increased yield, but also - as a correlated response - with an increased culmlength. In contrast, H-selection resulted in plants with an

Table 24 Predicted responses ($\hat{R}$) and realized responses (R) after H-, G- and T-selection for culmlength, earnumber and yield; b: *regression of offspring mean on parental value, S: selection differential.*

character	b	H-selection			G-selection			T-selection		
		S	$\hat{R}$	R	S	$\hat{R}$	R	S	$\hat{R}$	R
culmlength (cm)	0.2	-2.9	-0.58	-1.1	8.7	1.74	1.9	9.1	1.82	3
earnumber	-0.01	1.56	-0.0156	0.19	2.74	-0.0274	0.12	2.89	-0.0289	0.15
yield (dg)	0.024	35.0	0.84	2.6	66.5	1.596	2.3	67.5	1.62	3.8

increased yield and a decreased culmlength. Thus, as a consequence of the double criterion applied with this method, H-selection succeeded in pushing forward the desired recombinant planttype. The direction of the responses agreed with the intended and expected trends but their actual sizes were rather small and insignificant.

The results of H-selection in crop 2 do not only confirm those of H-selection in crop 1, but they even surpass those: indeed with this method it was possible to select recombinants with offspring that yielded about 5% more and had culms about 1% shorter than observed on the offspring from random plants.

Grid selection was applied because it was considered to be superior to T-selection (see section 3.2.3). This was not confirmed by the results of selection in crop 2: G-selection gave a yield improvement of about 4%, but the response to T-selection was larger (about 6.5%). The cause of this might be the fact that, with G-selection in the applied form, from each grid a fixed number of plants is selected. Thus, necessarily, in some grids not all genotypically superior plants are selected and in other grids plants not having a superior genotype are selected. Indeed, the average yield of the plants only selected by G-selection (see Table 16) was clearly less than that of the plants in group GT. Especially when the differences in growing conditions among grids are neglectable, it is not improbable that T-selection is superior to G-selection. This will be discussed further in section 8.6.

The small discordance between the results for yield per plant and those for total yield from 2 plots might rest on a variable number of plants per plot. This is studied in detail in chapters 5 and 6.

The response to selection (R) can be predicted by the expression.

$$R=b.S \tag{3.5}$$

(see Falconer (1960, p.188)). In this formula b represents the regression of offspring mean on parental value and S represents the selection differential. Estimates for b are given in Table 19; S can be derived from Table 15. Predicted and realized responses (derived from Table 23) can be compared in Table 24.

For culmlength and yield the predictions were always more conservative than the realizations. The correlation between prediction and realization, estimated from these 6 pairs of figures, was as high as 0.86.

From Table 15 it appears that the R-plants yielded 11.4% better than the average plant in crop 2. Because of this the realized response observed in crop 5 might be biased downwards for yield.

The result of selection in crop 2 was also measured differently. For culmlength as well as for yield for each plot the mean observation per plant was expressed as percentage of the mean observation per plant in the contiguous plot with an R-family. Thus in each series of 7 plots, plot 1,2,3,5,6 and 7 were related to plot 4. The average percentage for each selection method was:

selection method	culmlength	yield
H	99.42	113.44
G	101.74	116.95
T	102.42	120.67

The results derived for culmlength were about the same as in Table 23, but for yield the mean percentage was much higher. In section 6.3.5 this deviation will be discussed.

4 *SELECTION IN CROP 4*

4.1 MATERIAL

The selection experiment was continued with a new selection field: crop 4. This crop was grown from a mixture of kernels produced by 168 H-plants in crop 2. The number of kernels from each H-plant to be included in the mixture was determined in the same way as for crop 2 (see section 3.1).

The total kernel yield of the 168 H-plants in crop 2 was X=11517 dg. Thus, because per plant position 2 kernels were sown in crop 4, the number of kernels used from the i^{th} H-plant, with kernel yield x_i dg, was $7314\ (2x_i/11517) \sim 1.3x_i$.

The lay-out was exactly the same as that for crop 2. After disinfection with Quinolate the trial was sown on 12 and 13 October, 1976 on a humusrich, sandy patch of soil. The field was fenced with wire netting; mice were kept off by scattering poisoned wheat kernels on the borders.

4.2 THE PLANTS OF CROP 4

4.2.1 The growing of the crop

Soon after sowing it appeared that the emergence was bad, notwithstanding the favourable conditions for germination.

The mild winter was followed by a relatively warm first half of March, 1977. Thinning out of supernumerary plants and filling up of empty positions was done on 9 and 10 March. At that time it appeared that the soil was burrowed by moles. This burrowing could be the cause of the bad stand. After transplantation for the sake of securing a field without open plant positions, only 64 rows with 80 plants each remained (a total of 5120 plants in stead of 7314). After this was done the weather conditions stayed favourable and on inspection on 17 March a positive impression was gained. On 4 April weeds were killed by spraying Simazine. On 3 May it was observed that transplanted plants stayed behind when compared with not transplanted plants. Partly because of that the whole field gave a heterogeneous impression. From 7 May ears emerged and by the end of May pollen began to shed. At the harvest on 2-5 August 58 rows, each with 74 plant positions, were lifted (4292 plant positions). In this way only a narrow border (about 40 cm) was provided, which was done to keep the proper selection field as large as possible.

4.2.2 Some statistical properties

After harvesting of crop 4 the usual plant observations (culmlength, earnumber and yield) were made as described in section 2.3.2, sub (i).

The third column of Table 25 gives a summary of the observations on all plants in crop 4. The intended number of plants, i.e. the number of plant positions, was 4292. These can be partitioned in plant positions in a border (2×74+56×2=260 positions) and those enclosed by the border (4032 positions). From the number of plants, given in Table 25, one can derive that from 4292-4075=217 plant positions (about 5%) no observation was recorded. This concerned mainly plant positions on which the transplanted individual did not survive. The occupied plant positions gave rise to a heterogeneous crop. Comparison of Tables 4, 15 and 25 learns that the coefficients of phenotypic variation for earnumber and for yield in crop 4 were about twice as high as in crop 1 or 2. For culmlength it was hardly higher. This agrees with the higher heritability of culmlength as compared with that for earnumber and yield (see Tables 8 and 19).

The total yield of all 4075 plants amounted to 298956 dg. On the basis of observations on random plants out of crop 4 it was calculated that the kernel yield amounted to 67% of the yield (see next section). The estimated kernel yield per m^2 was thus (0.67×298956)/(4292×0.0195)=2393 dg. This is only half as much as for crop 1. The reason for this must be the adverse effect of the transplantation of so many plants.

The low yield was associated with a low ear density (only 12331/(4292×0.0195)=147). The mean kernel yield per ear was estimated at (0.67×83.4)/3.03=16.2 dg.

Coefficients of phenotypic correlations among the characters were estimated from observations on 48 random plants. These are treated in section 4.3.4.

4.2.3 The methods of selection

The methods for mass selection applied to crop 4 were the same as those applied to crop 2, viz. honeycomb selection, grid selection, truncation selection and random selection. The progenies of the 4 groups of selected plants were compared in crop 7 (see section 4.3).

Honeycomb selection

The heterogeneity of crop 4 led to a somewhat different application of honeycomb selection. Application of the 2 criteria of section 2.2.3 resulted in selection of only 26 plants. When plants with only 5 neighbours were also considered for selection, still only 33 plants met the requirements. To avoid a dangerous genetic narrowing it was decided to continue the programme

Table 25 Summary of the observations on plants belonging to crop 4; n: number of observed plants; $\bar{x}$: mean; *s: standard deviation;* cv_p*: coefficient of phenotypic variation; min: minimum; max: maximum*

character	quantity	all plants (n=4075)	selected plants H-selection (n=92)	G-selection (n=96)	T-selection (n=96)	R-selection (n=48)
culmlength (cm)	$\bar{x}$	122.1	121.7	146.6	149.0	135.3
	s	21.8	8.96	10.2	9.89	15.3
	cv_p	0.179	0.074	0.069	0.066	0.113
	min		92	113	113	97
	max		139	172	172	170
earnumber	$\bar{x}$	3.03	5.07	10.7	11.5	3.9
	s	2.69	2.71	2.8	2.45	3.2
	cv_p	0.888	0.535	0.261	0.214	0.821
	min		1	5	7	1
	max		13	20	20	17
yield (dg)	$\bar{x}$	73.4	137.6	369.7	393.8	109.7
	s	90.5	94.3	103.6	84.4	117.3
	cv_p	1.23	0.685	0.280	0.214	1.07
	min		24	229	298	21
	max		499	660	660	604

on the basis of more than these 33 plants. Therefore, in addition, 59 plants were selected which yielded more than each of their 6 neighbours and which had a culmlength less than 130 cm. Tho total number of selected plants amounted thus to 92, or 2.3%.

Table 25 shows in the 4th column data on these 92 H-plants. According to formula (3.1) their mean culmlength was not different from the mean culmlength of all plants but, at the same time, their yield was twice as high. Therefore, notwithstanding absence of decreased culmlength, it can be stated that recombinant planttypes were selected.

Grid selection

Throughout the experiments the principle was followed to select, for each of the selection methods to be compared, the same number of plants as for H-selection. This principle served to get a fair comparison of the efficiency of the methods. It is admitted, of course, that the methods required different efforts to apply them. Thus these efforts should be related to the results before drawing conclusions on the efficiency of the methods in economic sense.

To select as many plants with G-selection as with H-selection in each of 12 grids the 8 highest yielding plants were selected (under the restriction that they had 6 neighbours). Thus 96 (=2.4%) plants in all were selected (4 more than for H-selection).

The 12 grids contained the central 56×72=4032 plant positions. Each grid contained 19 (or 18 rows) with 72/4=18 plant positions. Thus 8 grids had

19×18=342 plant positions (grid size 247×270 cm) and 4 grids 18×18=324 plant positions (grid size 234×270 cm).

Table 25 gives summarized data on the 96 G-plants (5^{th} column). It appears that the heterogeneity of crop 4 was associated with positive skewness for the 3 characters of interest. Selection of the 2.4% best yielding plants means then selection of outliers, i.e. plants yielding more than 5 times the average yield. Dropping the restriction of having 6 neighbours would result in selection of still more extreme phenotypes.

It is worth noticing that, in contrast to the results of G-selection in crop 2, the G-plants in crop 4 exhibited for yield a larger standard deviation than all plants together (see Table 25). So, after G-selection, the phenotypic variation was increased (significance level less than 0.05).

The reason for this is a point of speculation. First: the remark does not hold in relation to the R-plants. Next: it is possible that the drawback of G-selection, which was mentioned in section 3.3.5, was responsable for this. This drawback is the fact that in each grid a fixed number of plants has to be selected. Thus, necessarily, in some grids poor plants have to be selected.

Truncation selection

The number of highest yielding plants to be selected was fixed at 96, the same as for G-selection. To achieve this, a lower bound for yield had to be chosen. This was done in the following way.

It was assumed that the distribution for yield was normal and thus was given by

$$\underline{x} \approx 73.4 + 90.5\,\underline{\chi} \text{ (see Table 25)}$$

For T-selection of 2.4% the lower bound x' for selection is given by

$$P(\underline{\chi} > 1.99) = 0.024,$$

from which follows that x'=73.4+(90.5×1.99)=253.5 dg. As it was known that there was positive skewness, as a first threshold a minimum yield of 300 dg was chosen. This requirement was met by 107 plants, 13 of which were rejected because of having less than 6 neighbours. Therefore, in addition to the 94 acceptable plants, 2 other plants were selected, which yielded 299 dg and 298 dg respectively.

Data on the 96 T-plants are presented in Table 25, 6^{th} column. Compared with the G-plants the T-plants were on the mean even still more extreme yielders.

Random selection

Again half as many plants as for the other selection methods were chosen at random, by drawing pairs of lottery tickets. Only plants belonging to the central 56×72=4032 plant positions were considered for selection. Two further restrictions were implied (see also section 3.2.3):

(i) only plants with 6 neighbours were acceptable;

(ii) only plants yielding at least 20 dg were admitted. Such plants were predicted to yield at least the 50 kernels, which were required for crop 7.

These restrictions were rather prohibitive because 98 plants had to be sampled to get the 48 acceptable R-plants. The 50 non-admitted plants were rejected for the following reasons: 3 plants were absent, 13 had less than 6 neighbours, 23 yielded less than 20 dg and 11 plants yielded insufficiently and had less than 6 neighbours. Thus the second restriction was by far the most prohibitive.

Data on the R-plants have been summarized and are presented in the last column of Table 25. It appears that the mean yield of the R-plants exceeded the mean yield of all plants with 36.3 dg (or 49.5%); the mean culmlength was larger by 13.2 cm (10.8%). Thus the admitted R-plants may not be considered as a representative sample of all the plants in crop 4. The truncation for yield will have promoted the positive skewness for yield and for earnumber (see section 4.3.3).

For 20 of the 48 R-plants the number of kernels (k) was established and their joint weight (w) was recorded. From these observations it was calculated that:

$\bar{k}$	= 242.4	$\bar{w}$	= 103.0 dg
s_k	= 277.1	s_w	= 122.0 dg
vc(k)	= 1.14	vc(w)	= 1.19 dg

The phenotypic correlation of k and w was r_p=0.996. Thus the mean single kernel weight must have been rather constant across the plants. The regression of k on w is given by

$$\hat{k} = 9.47 + 2.26\ w$$

From this relation the mean single kernel weight can be fixed as 1/2.26= 0.44 dg. (The mean single kernel weight was also calculated as $\Sigma w_i/\Sigma k_i$. This resulted in 0.425 dg.) The relation predicts for w=20 that k=54.7. (Restriction (ii) was based on this result.)

The mean yield of the 20 plants amounted to 153.7 dg. Therefore the weight of the kernels was estimated at 100(103/153.7)=67.0% of the weight of the ears. The linear regression of kernel yield (y_k) on (crude) yield (y_e) was established as

Table 26 Classification of the 252 plants, selected in crop 4, according to the procedure(s) for which the plants were selected.
n: number of plants; $\bar{x}$: mean; s: standard deviation; min: minimum; max: maximum.

group	n	culmlength (cm)				earnumber				yield (dg)			
		$\bar{x}$	s	min	max	$\bar{x}$	s	min	max	$\bar{x}$	s	min	max
H	81	121.1	8.9	92	139	4.57	2.14	1	11	118.2	71.1	24	499
GT	58	149.9	8.4	135	172	11.7	2.73	7	20	419.9	90.4	298	660
R	40	134.6	14.5	97	170	2.93	1.46	1	8	74.5	56.0	21	293
T	29	150.3	7.9	135	164	10.9	1.83	7	15	338.9	30.2	299	402
G	29	144.0	8.5	130	166	8.55	1.70	5	12	264.4	20.5	229	296
HGT	5	125.4	8.6	113	137	11.4	1.52	9	13	384.0	33.8	360	441
HR	4	121.3	5.4	116	128	4.75	2.50	2	8	146.3	82.6	67	247
GH	2	136.0	4.2	133	139	10.0	1.41	9	11	288.5	0.7	288	289
RT	2	161.0	1.4	160	162	11.5	0.71	11	12	362.5	82.7	304	421
GRT	2	151.5	9.2	145	158	14.0	4.24	11	17	489.0	162.6	374	604
	252												

$$\hat{y}_k = -16.19+0.775\ y_e$$

According to this relation the conversion factor amounts to 77.5%. The high correlation of y_k and y_e was confirmed once more: r_p=0.997.

The mean kernel yield per ear was 20.2 dg, about the same as found in crop 1 (i.e. 20.7 dg).

Comparison of groups of selected plants

Altogether 92 H-plants, 96 G-plants, 96 T-plants and 48 R-plants were selected in crop 4. Some plants were selected according to more than 1 selection method and therefore the total number of selected plants amounted to 252 in stead of 92+2(96)+48=332. A classification, on the basis of the procedure(s) for which the plants were selected, is given in Table 26.

Again it is remarkable that by H-selection distinct plants were selected: only 11 out of the 92 H-plants were also selected otherwise. The similarity of G- and T-selection appeared again: 58 of the 96 plants were selected by both methods. The 5 plants in group HGT yielded 35.9 dg less than the GT-plants (=8.5%), but their culmlength was 24.5 cm less (=16.3%). Only 8 out of 48 R-plants were also selected by other procedures.

4.3 THE RESULT OF THE SELECTION

4.3.1 Material and method for crop 7

The comparative trial (crop 7) included offspring of 92 H-plants, 96 G-plants, 96 T-plants and 48 R-plants, a total of 332 families. Because quite a number of plants were selected for 2 or 3 selection methods it was decided

Table 27 Comparison of the 2 blocks in crop 7. The characters are: (1) mean culmlength (cm), (2) total number of ears per plot, (3) mean earnumber, (4) total yield per plot (dg), (5) mean yield (dg). The meaning of the symbols is: $\bar{x}_i$: the mean across the 332 plots in block i; $\bar{d}=\bar{x}_1-\bar{x}_2$; r: correlation coefficient.

character	$\bar{x}_1$	$\bar{x}_2$	$\bar{d}$	s_d	t	$P(\underline{t}_{331}<t)$	$r_{x_{1j},x_{2j}}$	t_r	$P(\underline{t}_{330}>t_r)$
(1)	144.7	146.4	- 1.7	0.347	-4.90	~0	0.52	10.9	~0
(2)	46.3	50.8	- 4.5	0.767	-5.74	~0	0.10	1.91	0.028
(3)	2.47	2.80	- 0.33	0.041	-8.09	~0	0.094	1.72	0.044
(4)	1132.3	1296.0	-163.7	24.1	-6.78	~0	0.108	1.97	0.025
(5)	60.4	71.4	- 11.1	1.27	-8.67	~0	0.104	1.89	0.030

to sow only 1 kernel per plant position. By doing so problems of shortage of kernels (see section 3.3.1) were avoided and also the disadvantage from thinning out (i.e. damaging the remaining plant) was taken away. In fact, it was the intention to replace the thinning out in the spring by filling, some time after sowing, empty plant positions with additional kernels.
Thus, after threshing, for each of the 252 selected plants 2, 4 or 6 bags were filled with 20 kernels each (depending on whether a plant was selected for 1, 2 or 3 selection methods). Therefore, in contrast to the former comparative trials, not 252 bags with 80, 160 or 240 kernels were prepared, but 332×2=664 bags with 20 kernels each. This was done to prevent the possibility, mentioned in section 3.2.2, that a block effect rested partly on differences in seed quality.

The lay-out of crop 7 was similar to that of crop 5. Again the crop consisted of units of 7 plots sown with respectively T,G,H,R,H,G and T material. Altogether there were 48 such units per block, i.e. 48×7=336 plots per block. To realize this, in addition to the 92 plots with an H-family 4 plots were sown from bulk material. By a randomization procedure the plotnumber for a certain type of family was established.

Again 70 plots formed a strip with a width of 70×25=1750 cm and a depth (equal to the plot length) of 105 cm. The experimental material occupied 9 complete strips plus a strip with 42 plots. The total depth was 10×105= 1050 cm. To the west 5 border rows were sown, to the east 7 border rows. To the south and to the north a 1 m border was sown. Inter- and intrarow distances were again 25 and 5 cm respectively. The crude area amounted to 20.5×12.5=256.25 cm².

Just before sowing the kernels were disinfected with Quinolate. The experiment was sown on 31 October and 1 and 7 November, 1977. During and after sowing the weather conditions were bad. The precipitation in November amounted to 185 mm. Because of this it was impossible to provide, some time after sowing, each open plant position with an additional kernel. Notwithstanding the observation that soon after sowing some temporary puddles occurred in the field, the visual impression on the emergence was favourable.

The crop suffered from moles (up to end January, 1978), couch grass and loose silky bent. These weeds occurred primarily in block 1. In April they

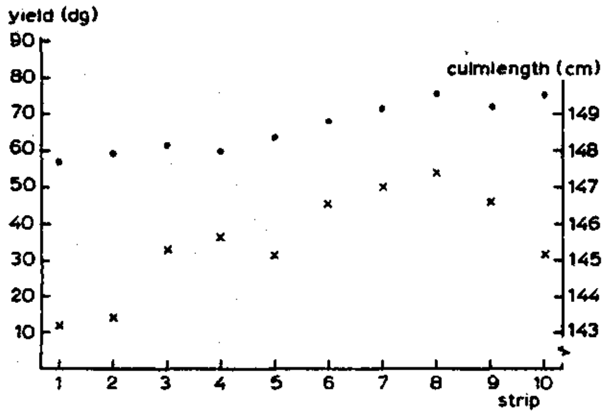

Figure 13 Mean culmlength (x) and mean yield (•) of the plants in each of the 10 strips in crop 7.

were suppressed twice by hoeing. Early May the crop was rather thin and heterogeneous. After 16 May lots of ears emerged. Pollen shedding began on 30 May. From half June some brown rust could be detected. The weeds occurred again. The crop did not lodge. It was harvested 4, 7 and 8 August and stored, after drying, in a mouse-proof cabin. On each plant of each of the 664 sheafs the observations mentioned in section 2.3.2 were done.

4.3.2 Comparison of the 2 blocks

Because of the nuisance of localized weed it was expected that block 2 afforded better growing conditions than block 1. Therefore the hypothesis H_o: "block 1 and 2 afforded the same results" was tested against H_a: "block 1 afforded worse results than block 1". To execute the test, formulae (2.1) and (2.2) were applied with p=332.

The results are summarized in Table 27. They show that H_o had to be rejected in favour of its alternative. The plants in block 2 had longer culms, produced more ears and had a higher yield.

The mean culmlength and the mean yield in each of the 10 strips forming crop 7 was determined. Each strip comprised 70 plots (containing together 1400 plant positions), excepting strip 10 which comprised 42 plots. In Figure 13 the means are plotted against the stripnumber. From the figure a clear trend in growing conditions becomes evident: the plants in strip 1 were the shortest (143.2 cm) and produced lowest (56.4 dg), those in strip 8 were the longest (147.4 cm) and produced highest (75.1 dg). For unknown reasons this trend was not continued in strip 9 and 10 for culmlength. Anyway, uniformity within the blocks, which was assumed for the sake of convenience (since then complete blocks can be grown; see section 2.3.1) did not occur.

Table 28 The correlation in crop 7 between the observations in block 1 and block 2. The characters are: (1) mean culmlength, (2) mean number, (3) mean yield.

character	H-families (n=92)	G-families (n=96)	T-families (n=96)	R-families (n=48)
(1)	0.59**	0.35**	0.37*	0.66**
(2)	0.09	0.10	-0.03	0.22
(3)	0.12	0.05	0.01	0.27*

Table 29 Skewness for some characters observed on 48 R-plants in crop 4 and their offspring in crop 7.

		offspring	
character	R-plants	mean per plant	total from 2 plots
culmlength	0.09	0.17	
earnumber	2.33***	0.06	0.07
yield	2.46***	0.45	0.29

This was already observed in crop 3 (section 2.3.3).

The correlations between the observations in block 1 and 2 were very low and hardly significant, with the exception of those for mean culmlength. Like before, culmlength showed the best repeatability.

These correlations were also estimated for each selection method separately. The estimates are presented in Table 28. It is surprising to note how different these estimates were. The R-families showed the highest correlations. This could have been caused by the higher diversity among the R-families (compare s_y^2 in Table 30 with s_y^2 in Table 31).

The number of ears amounted in block 1 to 15361 on 6234 plants and in block 2 to 16860 on 6034 plants. Thus, the total number of ears was 32221 on an area as large as 2×332×1.05×0.25=174.3 m². The ear density was only 184.9. This is rather low; not only when compared with the ear density in crop 3 (288.8) and in crop 5 (224.7), but also when compared to farmers crops. (In 1978 the ear density was established also in 2 farmers crops. In one it amounted to 258 (row distance 0.2 m), in the other to 400 (row distance 0.25 m).) In block 1 the mean earnumber was 2.46, in block 2 it was 2.79.

The number of plant positions per block amounted to 332×20=6640. Thus, the registered number of plants was clearly less than the number of plant positions, especially in block 2. Keeping in mind that the registered number of plants tends to be biased upwards (see section 2.3.2), it was concluded that many plant positions were not occupied. This could rest on the bad germination conditions, especially for block 2, a part of which was sown one week later than block 1. In sections 5.3 and 6.3 the number of plants per plot and its effect on plot totals and means per plant are discussed.

The lower mean earnumber in block 1 is explained by the competition exercised by the grassy weeds in that block.

The mean yield per m^2 was (806197/174.3)=4625 dg. The conversion factor for crop 6, see section 5.2.2, implies for crop 7 a kernel yield per m^2 of 0.863×4625=3991 dg. The mean yield per ear was 806197/32221=25.0 dg, the mean kernel yield per ear 21.6 dg. Thus the mediocre yield of crop 7 was put forward by heavy ears.

4.3.3 The relation between R-plants (crop 4) and their offspring (crop 7)

The observations on the n=48 R-plants in crop 4 and on their offspring in crop 7 were studied for skewness. The estimates for skewness are presented in Table 29. According to Table 34.B in Pearson and Hartley (1970) their was only significant positive skewness among the parents for earnumber and for yield. Because of the high phenotypic correlation of these 2 characters ($r=0.96$; see Table 33), it is not surprising that positive skewness for both of the characters was established. The occurrence of the skewness must partly rest on the truncation which was applied when sampling the R-plants (see section 4.2.3).

If one applies tests based on normality when there is no normality conclusions will be made that can not be fully justified. The interpretation of results should then be done with reserve. This applies especially when the null hypothesis H_0: "there is no correlation of parents and offspring (i.e. $\rho=0$)" is tested against the alternative H_a: $\rho>0$.

The parameters mentioned in section 2.3.4 were estimated from the observations on the R-plants and on their offspring. These estimates are presented in Table 30. The relation between R-plants and their offspring was not essentially different from that described in section 3.3.3 and therefore no graphical illustration is given here.

Estimates for some parameters of interest were also derived from the H-. the G- and the T-plants and their offspring. These are given in Table 31.

Discussion

The means for the R-plants and for their offspring are given in Table 30. It appears that for earnumber and for yield, the mean of the parents was about 50% higher than that of their offspring. Several causes can be held responsable for this:

Table 30 Estimates, for 3 characters, of the parameters mentioned in section 2.3.4. The estimates are based on observations on 48 R-plants in crop 4 and on their offspring in crop 7.

estimated parameter	culmlength (cm)	earnumber	yield (dg)
α	117.6	2.69	63.76
β	0.21	-0.01	0.017
ρ	0.50	-0.078	0.15
t_r	3.97	-0.528	1.02
$P(\underline{t}_{46}>t_r)$	~0	0.80	0.16
$\bar{x}$	135.3	3.90	109.7
$\bar{y}$	146.4	2.65	65.7
σ^2_x	233.6	10.22	13759
σ^2_y	41.7	0.187	185.6
h^2_n	0.43	0	0.034
$cov(\underline{x},\underline{y})$	49.8	-0.107	238.3
σ^2_a	99.6	0	476.6
vc_a	0.073	0	0.199

(i) From Table 25 one can derive that the 48 R-plants in crop 4 differed from the mean of all plants: they had a greater culmlength, they produced more ears and yielded much higher. The main reason for this will be the requirement that the R-plants should yield at least 20 dg. In section 4.2.3 it was indicated that this was the most important reason to reject random plants as R-plants: 34 out of 50 rejected plants yielded less than 20 dg. In addition to this bias there might have been a random error because only 48 plants were sampled from a very heterogeneous population.

(ii) The plants in crop 4 grew at a lower density than their offspring in crop 7. This could decrease culmlength and increase earnumber (and thus yield).

(iii) The early spring weather conditions were better for crop 4 than for crop 7 (which suffered from competition by weeds).

(iv) The clear positive skewness among the R-plants makes that the mean was less suited as a measure for central tendency than the median. For positive skewness the mean is larger than the median. (Indeed: the average earnumber of the R-plants was 3.9, whereas the median amounted to 3 ears.)

The estimates for h^2_n (see Table 30) agreed rather well with those obtained before (see Tables 9 and 19). The same is true for the correlation coefficients; sometimes called heritability in standard units, see Frey and Horner (1957).

Table 31 Estimates, for 3 characters, of some of the parameters mentioned in section 2.3.4. The estimates are based on observations on n plants, selected in crop 4, and on their offspring in crop 7.

		selection procedure		
character	estimated parameter	H-selection (n=92)	G-selection (n=96)	T-selection (n=96)
culmlength(cm)	β	0.10	0.29	0.31
	ρ	0.16	0.60	0.58
	t	1.51	7.11	6.99
	$P(\underline{t}_{n-2}>t)$	0.07	~0	~0
	$\bar{x}$	121.7	146.6	149.0
	$\bar{y}$	142.8	146.3	147.1
	σ^2_y	29.4	24.6	24.4
earnumber	β	0.02	0.004	-0.01
	ρ	0.14	0.03	-0.07
	t	1.32	0.29	-0.66
	$P(\underline{t}_{n-2}>t)$	0.09	0.39	0.75
	$\bar{x}$	5.1	10.7	11.4
	$\bar{y}$	2.55	2.57	2.75
	σ^2_y	0.146	0.159	0.169
yield (dg)	β	0.03	0.01	-0.001
	ρ	0.21	0.04	-0.005
	t	2.06	0.52	-0.05
	$P(\underline{t}_{n-2}>t)$	0.02	0.30	0.52
	$\bar{x}$	137.6	369.7	393.8
	$\bar{y}$	62.4	65.3	69.4
	σ^2_y	141.9	153.5	175.2

The estimates for σ^2_a are rather changeable (compare Tables 9, 19 and 30), but those for cv_a are quite consistent. The gaps between vc_a and vc_p are enorm (see Tables 4, 15 and 25); even for culmlength the difference is a factor 2. Because for culmlength σ_a was estimated at about 10 cm one might speculate that a decrease of 20 cm in culmlength should be possible. The negative effect of such a decrease on the yield should be restricted by selection for yield (e.g. by tandem selection).

In Table 31 for some parameters estimates derived from selected plants and their offspring are given. For culmlength the correlation between parents and offspring was not significant after H-selection (which implied selection for decreased culmlength). For the other selection procedures, which did not consider culmlength, a significant correlation was established. For yield

Table 32 Analysis of variance for 3 characters of the 48 R-families in crop 7

source of variation	df	culmlength (cm)			earnumber			yield (dg)		
		SS	MS	f	SS	MS	f	SS	MS	f
R-families	47	3928.3	83.6	4.74***	3.18	0.0677	0.28	2768	58.9	0.28
blocks	1	69.2	69.2	3.92	17.58	17.58	73.4***	17348	17348	81.0***
error	47	829.2	17.6		11.25	0.239		10060	214.1	
total-CT	95	4826.7			32.01			30176		

the situation was the reverse: a significant correlation after H-selection (which implies weak selection for increased yield); no correlation after the other procedures (which imply direct selection for increased yield). It was a surprise to observe for culmlength that after G- and T-selection higher estimates for β were obtained than after R-selection. A possible explanation for this is proposed in section 5.3.3.

Like before, the additive genetic variance was also estimated by means of an analysis of variance (see also section 2.3.4). This analysis is given in Table 32. For culmlength no significant block effect was found. This appears to be contrary to the judgment in section 4.3.2. However, in that section all families were taken into account and here only R-families were considered.

Significant differences among families were only observed for culmlength and thus only for this character significant additive genetic variation was found (confirming Table 30). The estimate was 131.9 cm^2; again higher than the estimate resulting from offspring-parent regression (s_a^2=99.6; Table 30).

4.3.4 *Phenotypic and genetic correlations*

The coefficients of phenotypic correlation between the characters were estimated from data on the 48 R-plants. The estimates are presented in the last column of Table 33. The null hypothesis H_0: "the phenotypic correlation is zero" had to be rejected in all cases in favour of positive correlation. The estimates were close to those for crop 1 (see Table 13).

Like in section 3.3.4, application of formulas (2.11) and (2.12) presented difficulties to estimate the genetic correlation between characters. The reason for this was the negative estimate for earnumber for the covariance of parents and offspring. Therefore only estimates for the genetic correlation of culmlength and yield are presented in Table 33. Again the estimates exceeded the estimates for the phenotypic correlation.

Because G- and T-selection were applied here on the univariate character yield, again the approaches given by formulas (3.2) and (3.3) were applied to estimate ρ_g for culmlength and yield. This passes for the 2 formulas as follows:

Table 33 Genotypic correlations, estimated by application of formula (2.11) or (2.12) on data from the 48 R-plants in crop 4 and their offspring in crop 7, and phenotypic correlations, estimated from observations the same R-plants in crop 4.

characters	r_g		r_p
	form (2.11)	form (2.12)	
culmlength-earnumber		0.77	0.51***
culmlength-yield	0.90	0.80	0.56***
earnumber-yield			0.96***

(i) The direct response to T-selection for yield was R=69.45-65.66=3.79 dg (Table 34). The correlated response for culmlength was CR=147.1-146.42= 0.68 cm. The additive genetic variances of the 2 characters were estimated to be 476.6 dg² resp. 99.6 cm² (Table 30). Substitution in formula (3.2) yields r_g=0.39. For G-selection this resulted in r_g=0.56 (with R=-0.35 dg and CR=-0.09 cm!).

(ii) The intensity of the T-selection for yield amounted to i=S/s_p=(393.8-73.4)/90.5=3.54 (see Table 25). Culmlength and yield possess as estimated heritabilities 0.43, resp. 0.034 (Table 30). The phenotypic standard deviation for culmlength was estimated at 21.8 cm. The resulting estimate for ρ_g is then r_g=0.073. The estimate derived from the result of G-selection equals r_g=0.01.

The above calculated "realized genetic correlations" were lower than those resulting from application of formulas (2.11) and (2.12). This was also the case in section 3.3.4, but now it was more evident, especially when applying the second alternative (based on formula (3.3)). This could be caused by the small correlated response for culmlength (only 0.68 cm after T-selection and even -0.09 cm after G-selection), which - in turn - could be the result of the fact that the mean culmlength of the R-plants exceeded the mean culmlength of all plants by 13.2 cm (10.8%).

Singh (1977) presented as correlations (in 1968) between number of effective tillers and dry earweight r_p=0.70* and r_g=0.15. At the time of ear emergence the correlations between plant height and dry earweight were r_p=0.29 and r_g=0.56 in 1967 and r_p=0.24 and r_g=0.19 in 1968. Plant height at the time of ear emergence was expected to be the most effective character for indirect selection before flowering for total dry weight. The heritability for the number of effective tillers was reported to be 0.15.

4.3.5 The actual result of selection

Table 34 Weighted means per plant for culmlength, earnumber and yield; and means for total number of ears from 2 plots and for total yield from 2 plots. Results from crop 7.

character	selection procedure			
	H-selection (n=92)	G-selection (n=96)	T-selection (n=96)	R-selection (n=48)
culmlength (cm)	142.76	146.33	147.10	146.42
in %	97.5	99.9	100.5	100
earnumber	2.55	2.57	2.75	2.65
in %	96.2	97.0	103.8	100
yield (dg)	62.40	65.31	69.45	65.66
in %	95.0	99.5	105.8	100
total number of ears	94.34	94.39	102.02	97.65
in %	96.6	96.7	104.5	100
total yield (dg)	2311	2399	2574	2421
in %	95.5	99.1	106.3	100

Introduction

Crop 7 should reveal the relative efficiency of the 4 methods for mass selection which were applied to crop 4. A really fair comparison was excluded, not only because slightly different numbers of plants were selected for the methods, but primarily because H-selection was for both yield and shortness, whereas G- and T-selection were only for yield.

First Kruskal and Wallis' test was applied to see if the methods yielded differences at all. Next Mann and Whitney's test was used in cases for which such overall differences were established, for pairwise comparison of the 4 methods.

Actual results

Table 34 contains means for families descending from the plants selected in crop 4. The results of Kruskal and Wallis' test were:

character	H	critical level
culmlength	33.6	0
earnumber	13.9	0.003
yield	13.4	0.003
total number of ears from 2 plots	13.6	0.003
total yield from 2 plots	12.1	0.007

Thus for each character the methods gave rise to different groups of families. Application of the Mann-Whitney test was done for the most interesting contrasts. These are studied according to the hypotheses given below. Depending on the alternative hypothesis the critical level was one or two tailed:

character	hypotheses H_o	H_a	P
culmlength	H=R	H<R	0.001
	H=T	H<T	~o
	H=G	H<G	~o
	T=R	T>R	0.250
	G=R	G>R	0.486
earnumber	H=R	H>R	0.894
	T=R	T>R	0.105
	G=R	G>R	0.851
yield	H=R	H>R	0.887
	H=T	H≠T	~o
	H=G	H≠G	0.229
	T=R	T>R	0.041
	G=R	G>R	0.607
	T=G	T≠G	0.015
total yield from 2 plots	H=R	H>R	0.848
	H=T	H≠T	0.001
	H=G	H≠G	0.424
	T=R	T>R	0.056
	G=R	G>R	0.670
	T=G	T≠G	0.009

Discussion

The result of the H-selection was disappointing: the culmlength of the H-families was indeed less than that of the R-families, but they yielded 5% less. The culmlength was significantly decreased by H-selection when compared with any of the other methods (which did not aim al reducing culmlength). The relative high value of the heritability for culmlength promised such a selection response. The yield of the H-families did not differ significantly from that of the R-families. The aim of H-selection, i.e. selection of a recombinant plant type, was not convincingly approached by the selection in crop 4.

Comparison of H-selection with G- and T-selection is not fair for yield because H-selection also aimed at (and succeeded in) reducing culmlength.

The results of the tests for yield and those for total yield from 2 plots were of the same tenor. The preference for total yield as a measure for selection response (see section 2.3.2) did not influence the conclusions.

The result of G-selection were about nill. In contrast, T-selection was significantly better than any of the other methods, as far as yield was concerned. Superiority of T-selection over G-selection was not expected because

Table 35 Predicted responses ($\hat{R}$) and realized responses (R) after H-, G- and T-selection for culmlength, earnumber and yield; b: regression of offspring mean on parental value, S: selection differential.

character	b	H-selection			G-selection			T-selection		
		S	$\hat{R}$	R	S	$\hat{R}$	R	S	$\hat{R}$	R
culmlength (cm)	0.21	-0.4	-0.08	-3.66	24.5	5.15	-0.09	13.2	2.77	0.68
earnumber	-0.01	2.04	-0.02	-0.10	7.67	-0.08	-0.08	8.47	-0.08	0.15
yield (dg)	0.017	64.2	1.09	-3.26	296.3	5.04	-0.35	320.4	5.45	3.79

of the similarity of the 2 methods: 58 of the 96 T-plants were also selected as G-plants. Indeed the other 38 G-plants were clearly inferior (Table 26).

In section 8.6 causes for the poor relative efficiency of G-selection will be elaborated in comparison with T-selection.

A general remark concerning the results is the fact that the R-plants were not representative for all plants in crop 4. They yielded on the average 49.6% more than all plants. This hampers manifestation of the desired selection response for yield. Further they were 10.8% longer, which promoted the observation of reduced culmlength after H-selection.

Response to selection was again predicted by means of equation (3.5). Estimates for β are given in Table 30; the selection differentials can be derived from Table 25. Table 35 presents both the predicted responses and the realized responses. The resemblance is poor: the correlation between the two amounted to 0.54, and only to 0.30 when the response for yield after T-selection, was omitted. The cause for the bad correspondence could be the fact that the R-plants were not representative.

The result of the selection in crop 4 was again measured by means of percentages, calculated with the R-family in each unit of 7 plots as a base. The mean percentage for each selection method was:

selection method	mean performance (in % of standard)	
	culmlength	yield
H	100.1	104.2
G	97.7	99.6
T	100.7	114.4

The results deviate from those in Table 34, especially for yield. In section 6.3.5 the reason for this, skewness for the distribution of the percentages, is studied in more detail.

5 *SELECTION IN CROP 6*

5.1 MATERIAL

In crop 4 H-selection was applied for the third time. The 92 selected plants gave together a mixture of kernels from which crop 6 was grown. This mixture was formed by including $7314(x_i/X)$ kernels from the i^{th} H-plant ($i=1,...,92$). Thus the mixture provided only one kernel for each plant position. The total yield of the H-plants amounted to $X=12657$ dg; so from a plant yielding x_i dg $0.6x_i$ kernels were included in the mixture.

The lay-out was the same as before (see section 3.1), except that now only 1 kernel per plant position was sown (the reasons for this were given in section 4.3.1). The central 78 rows comprised the 78×68=5304 plant positions that were of relevance for the experiment. The plants on rows 76, 77 and 78 were given more attention. They formed part of a study concerning the effect of the weight of a sown kernel on the performance of the plant emerging from such kernel (see section 8.4).

After disinfection with Quinolate the kernels were sown from 17 to 19 October, 1977. At the same time wire netting was put up around the trial.

5.2 THE PLANTS OF CROP 6

5.2.1 The growing of the crop

Soon after sowing the conditions became rather adverse. Because of the heavy precipitation (185 mm in November) it was not possible to provide open plant positions with an additional kernel. However, this omission did not appear to be serious because the emergence was judged to be good. The crop did well and on 19 April, 1978 it was still good: the low number of empty plant positions was associated with a good covering of the soil. The first ears emerged on 7 May. Pollen shedding was abundant on 28 May. Attacks by brown rust and by mildew were restricted. Lodging did not occur. The plants were lifted from 31 July to 3 August. Culmlength and earnumber were recorded near the field to minimize post-harvest losses: only the ears were transported (per plant packed together).

5.2.2 Some statistical properties

Observations on all harvested plants are summarized in the 3^{rd} column of Table 36. From this table one can derive that no observation was obtained for 5304-5110=194 plant positions (3.6%). Comparison of the selection fields

Table 36 Summary of the observations on plants belonging to crop 6; n: number of observed plants; $\bar{x}$: mean; s: standard deviation; cv_p: coefficient of phenotypic variation; min: minimum; max: maximum

character	quantity	all plants	plants in row 76-78	selected plants		
				H-selection	ICL-selection	R-selection
culmlength (cm)	n	5111	200	204	204	102
	$\bar{x}$	158.8	157.7	152.0	147.9	159.1
	s	12.5	11.0	7.3	4.6	11.6
	cv_p	0.079	0.070	0.048	0.031	0.073
	min		118	127	127	134
	max		184	170	153	200
earnumber	n	5110	200	204	204	102
	$\bar{x}$	4.07	4.11	5.51	5.93	4.10
	s	1.42	1.67	1.51	1.30	1.40
	cv_p	0.348	0.406	0.275	0.219	0.343
	min		1	2	3	2
	max		12	9	11	11
yield (dg)	n	5107	200	204	204	102
	$\bar{x}$	102.2	103.7	142.5	144.6	101.9
	s	36.0	41.0	30.0	16.8	31.7
	cv_p	0.352	0.395	0.211	0.116	0.312
	min		20	83	126	55
	max		316	260	215	223

by means of Tables 4, 15, 25 and 36 shows that the mean culmlength in crop 6 was at its highest (combined with the lowest coefficient of phenotypic variation). Also for earnumber and for yield cv_p was lower than ever before. The means for these 2 characters were higher than in crop 2 or 4. The favourable visual impression of crop 6 was thus confirmed by these statistics.

The total yield of all plants amounted to 521894 dg. The kernel yield to yield ratio in crop 6 was estimated at 0.862 (see next section). Thus the mean kernel yield per m² was approximately (0.862×521894)/103.428=4355 dg. The mean kernel yield per ear was (0.862×102.2)/4.07=21.7 dg. The ear density was 20821/103.428=201.3.

The plants in rows 76, 77 and 78

The 204 plant positions in rows 76, 77 and 78 yielded 200 plants. These plants formed part of a different study (see section 8.4). In addition to the usual characters the following types of observations were done on each harvested plant:

- kernel number : the number of produced kernels
- kernel yield : the weight (in dg) of the produced kernels
- spikelet number : the number of spikelets
- straw yield : the weight (in dg) of the straw; roots and ears excluded

The relavant statistics for culmlength, earnumber and yield are given in Table 36, those for the additional characters in Table 37. For the usual characters there was a high degree of similarity between the statistics for

Table 37 Summary of observations on additional characters of the 200 plants in row 76, 77 and 78 of crop 6. $\bar{x}$: mean; s: standard deviation; cv_p: coefficient of phenotypic variation; min: minimum; max: maximum.

quantity	kernel number	kernel yield (dg)	spikelet number	straw yield (dg)
$\bar{x}$	224.9	89.4	134.3	136.4
s	88.0	35.7	53.1	57.2
cv_p	0.39	0.40	0.40	0.42
min	35	15	24	19
max	613	278	351	390

all plants and those for the 3 rows. Remarkably, the coefficient of phenotypic variation for 6 of the 7 characters amounted to about 0.40, whereas for culmlength it was only 0.07. The mean kernel yield covered 86.2% of the (crude) yield. The coefficient of linear regression of kernel yield to yield gave the conversion factor 87%.

The mean weight of a single kernel was determined from the mean yield and the mean kernel number. It amounted to 0.398 dg. This mean pertains to all kernels produced by a plant: to the kernels in the main ears, containing the larger kernels, as well as to those in the later emerging accessory ears, which produce smaller kernels. The variation in kernel weight and size within and among plants was not assessed in this study; the effect of the individual kernel weight on the performance of the plant emerging from that kernel is quantified in section 8.4.

The mean number of kernels per spikelet can be used as a yardstick for fertility. Assuming that with complete seedset each spikelet contains 2 kernels this value, i.e. 1.675, means a seedset of 83.7%. The mean number of spikelets per ear amounted to 134.3/4.11=32.7; the mean yield per ear to 25.2 dg and the mean kernel yield per ear to 21.7 dg.

In the present experiments harvest index was defined as the ratio of the weight of the ears of a plant to the weight of the aerial plant parts. It was always established for mature harvested, dried plants. The gross harvest index for the 200 plants in rows 76-78 was calculated as 103.7/(103.7+136.4)= 0.432. More details on harvest index are given in section 6.2.2.

Seedset, conversion factor and mean weight of a single kernel were also determined for each individual plant. Thus a number of interesting coefficients of phenotypic correlation between characters could be estimated. These are presented in Table 38.

The correlation of yield and culmlength amounted only to 0.30%. This value was low when compared with earlier estimates (see Table 13 and Ta-

Table 38 Phenotypic correlations (r_p) estimated from observations on the 200 plants in row 76-78 of crop 6.

characters	r_p
culmlength-earnumber	0.15*
culmlength-yield	0.30***
earnumber-yield	0.86***
yield-kernel yield	0.998***
yield-kernel number	0.94***
yield-seedset	0.18**
yield-conversion factor	0.12
kernel yield-conversion factor	0.17**
kernel yield-seedset	0.21**
conversion factor-seedset	0.46***
conversion factor-kernel weight	0.26***

ble 33), but it was confirmed by the estimate for the 102 R-plants in crop 6 (r_p=0.31; see Table 40). It seems unlikely that this was achieved by continued H-selection, aiming at a recombinant plant type (see section 8.3). The positive correlation of kernel yield and conversion factor was lower than expected. It explains only partly the low conversion factor for crop 2 (section 3.2.3) and means that the conversion factor is more or less independent of yield; at least within this experiment.

5.2.3 The methods of selection

Honeycomb selection was applied in the usual way, i.e. good yielding plants with a relatively short culm were selected. As an alternative also selection with independent culling levels for yield and culmlength was applied.

The reason for this was that H-selection, aiming to reduce culmlength and to improve yield, should be compared with an alternative method aiming the same and not with methods (like G- or T-selection) which aim to improve only yield. This objection against comparison of H-selection with G- or T-selection was expressed already several times (e.g. in the introduction to section 4.3.5).

Random selection served as yardstick and provided data to estimate genetic parameters. The progenies of the 3 groups of selected plants were grown in a comparative trial (crop 10; see section 5.3).

Honeycomb selection

The number of plants with 6 neighbours and satisfying the usual requirements for H-selection amounted to 205, i.e. to 100(205/5110)=4%. This high number reflects the fact that only 3.6% of the plant positions did not contain a plant. It was reduced to 204 because only even numbers of H-plants could be admitted to crop 10. Data on these 204 H-plants are summarized in the 5th column of Table 36. Their mean culmlength was about 7 cm less than that of all plants in crop 6.

ICL-selection

When truncation selection is applied to two or more characters simultaneously, using independent levels of truncation, socalled selection with independent culling levels is applied (Simmonds, 1979; p.177). Independence means here that only plants satisfying each level are selected. When determining the levels, the level for the one factor will be determined in correspondence with the level(s) for the other factor(s). To approach the present aim, i.e. good yielding plants with a reduced culmlength, the determination of the levels for yield and culmlength was done arbitrarily. The levels were determined after inspection of a scatter diagram, showing yield and culmlength of the 200 plants in rows 76-78 of crop 6. The ultimate goal, i.e. selection of 204 ICL-plants in crop 6, was of course included in the consideration. Based on the diagram it was decided to select plants yielding at least 126 dg and having a culmlength of 154 cm at most. The number of plants satisfying these levels was 244. This number was reduced to 204 plants by further refinements. The 204 ICL-plants finally selected yielded at least 126 dg and had at most a culmlength of 153 cm.

Statistics on the 204 ICL-plants are presented in Table 36, 6th column. From this table the standardized levels can be calculated. For yield it was (126-102.2)/36=0.66 and for culmlength (153-158.8)/23.5=-0.46. Assuming normality, it means that the selected plants belonged to the 25% best yielding plants and to the 32% plants with the shortest culms. Thus for yield a somewhat higher selection intensity was applied than for culmlength. However, this rests on an assumption which appeared to be false.

The choice of the culling levels should be made with great care. To exploit phenotypic variation with similar strength for each character one could decide to choose levels with the same standardized value. Absence of normality presents then a deviation from the supposed similarity of selection intensities. A choice which takes into account the relative economic importance of the different characters appears attractive. Practical execution would suffer however from the same problem as with index selection: how to determine relative economic values of several characters? Even when they have been determined, such relative values should be adjusted from time to time depending on the prices. Young & Weiler (1961) indicated how the levels had to be chosen when the expected economic result per individual had to be maximized. In the present study a different goal was pursued, viz. the development of good yielding material with relatively short culms. (Of course such a plant type is expected to have a positive N-response, due to lodging resistence, and therefore to yield an improved financial result.)

The levels could also be chosen in such a way that the ratio of the heritabilitues would be the same as the ratio of the absolute values of the standardized levels, or the same as the ratio of the selection intensities. Here again absence of normality would cause biases. Furthermore it should be realized that weighing of the levels with the heritabilities could mean that the strength of selection for a character becomes variable. Then ICL-selection would include an element of tandem selection.

Random selection

The number of plants selected at random was 102. They were sampled by drawing pairs of lottery tickets indicating row-plant numbers. This was continued until 102 acceptable plants had been chosen. In contrast to the procedure in crop 4, see section 3.2.3, the requirement that the selected plants have 6 neighbours was omitted (by mistake). Because of the low percentage of empty plant positions (3.6%) only few R-plants will have had less than 6 neighbours. The R-plants were required to yield at least 55 dg, to ensure at least 2×40=80 kernels for crop 10 (see section 5.3.1). Afterwards this requirement appeared to be too high. From the 200 plants in rows 76-78 the next linear relation between number of kernels (k) and yield in dg (y) was established: k=15.5+2y. Thus 80 kernels could be expected from a plant yielding 33 dg. The truncation level of 55 dg appeared therefore to be higher than necessary, even when kernels were used for additional sowing (to fill empty plant positions in crop 10).

To sample 102 R-plants 119 pairs of row-plant numbers had to be drawn. So, 17 of the sampled plant positions did not contain a plant or contained a plant yielding less than 55 dg. The truncation for yield was therefore only of minor influence owing to be good yielding level of crop 6. This appears also when comparing the last column of Table 36 with columns 3 and 4.

Comparison of groups of selected plants

Because of overlapping, the H-, the ICL- and the R-plants numbered together 441 in stead of 510. The manner in which the selection methods overlapped is shown in Table 39. In contrast to the expectation, by far the most plants selected by H-selection were not selected by ICL-selection as well. ICL-selection succeeded better in selecting short culmed, good yielding plants than did H-selection (compare both H with R and I with R). This is also illustrated by Table 36. The interesting group HI is the most promising. The performance of the offspring of these 60 plants is treated in section 5.3.5.

Table 39 Classification of the 441 plants, selected in crop 6, according with the procedure(s) for which the plants were selected. n: number of plants; $\bar{x}$: mean; s: standard deviation; min: minimum; max: maximum; I=ICL

group	n	culmlength (cm)				earnumber				yield (dg)			
		$\bar{x}$	s	min	max	$\bar{x}$	s	min	max	$\bar{x}$	s	min	max
H	140	153.7	7.4	131	170	5.31	1.61	2	9	139.0	33.6	83	260
I	139	148.0	4.5	131	153	5.86	1.28	3	9	142.4	15.9	126	215
R	93	159.7	11.9	134	200	3.90	1.16	2	9	97.8	30.0	55	223
HI	60	147.6	5.1	127	153	5.97	1.19	4	9	150.1	18.2	126	208
IR	5	148.6	2.6	146	152	6.60	2.70	4	11	138.6	6.8	132	147
HR	4	157.3	3.6	154	162	5.50	1.00	5	7	150.8	17.9	137	176
	441												

5.3 THE RESULT OF THE SELECTION

5.3.1 Material and method for crop 10

To compare the result of the 3 selection methods a comparative trial (crop 10) was sown in which offspring of the 441 plants selected in crop 6 was included. The material comprised 204 H-families, 204 ICL-families and 102 R-families, that is 510 entries in all. The trial comprised two complete blocks, each containing 510 plots. The plotsize was 21 positions (20 plants + 1 label) alongside a single row for the H- and for the ICL-families and 42 positions (40 plants + 2 labels) alongside 2 contiguous rows for the R-families. Plots with an R-family were thus twice as large as the other plots. This was done to check the supposition that a plotsize of 20 plants was insufficient (see section 2.3.3).

Thus for each H- and for each ICL-family 2 bags with 20 kernels each were prepared and for each R-family 2 bags with 40 kernels each. The kernels in the 1020 bags were disinfected with Quinolate immediately before sowing.

The lay-out of crop 10 was analogous to those for earlier comparative trials. Now the crop consisted of units of 5 plots sown respectively with an ICL-, H-, R-, H- and an ICL-family. One such unit comprised 6 rows. Its length alongside the rows measured 1.05 m, its width 1.5 m. Each complete block contained 102 of such units. Given the plotnumber (and thus the type of family) it was determined by a randomization procedure which family of the prescribed type should be grown on it.

A strip contained 12 units of 5 plots (=6 rows) each. Its width measured 72×0.25=18 m, its length 1.05 m. Each block comprised 8.5 strips. The complete trial contained 17 strips, covering an area of 18×17×1.05=321.3 m^2. Three border rows were sown on both sides. The other sides received a 1 m border.

The trial was sown 18, 19 and 20 October, 1978. The field was fenced with wire netting, which could not prevent mice and birds from eating the emerging kernels. Therefore a net was installed above the trial field on 31 October.

Table 41 The number of plant positions and the number of registered plants for each type of families in crop 10.

type of families	number of rows per block	number of plant positions per block	block 1: number of registered plants	block 1: occupation of plant positions (in %)	block 2: number of registered plants	block 2: occupation of plant positions (in %)
H	204	4080	3921	96.1	3893	95.4
ICL	204	4080	3923	96.2	3910	95.8
R	204	4080	3856	94.5	3802	93.2
	612	12240	11700	95.6	11605	94.8

Table 40 Comparison of the 2 blocks in crop 10. The characters are: (1) mean culmlength (cm), (2) total number of ears per plot, (3) mean earnumber, (4) total yield per plot (dg), (5) mean yield (dg), (6) number of plants per plot. The meaning of the symbols is: p: the number of pairwise compared plots, $\bar{x}_i$: the mean across the plots in block i; $\bar{d} = \bar{x}_1 - \bar{x}_2$; r: correlation coefficient.

character	families included in the test	p	$\bar{x}_1$	$\bar{x}_2$	$\bar{d}$	$s_{\bar{d}}$	t	$P(\lvert t_{p-1} \rvert > \lvert t \rvert)$	r_{x_1,x_2}	t_r	$P(t_{p-2} > t_r)$
(1)	all	510	136.4	137.4	- 1.05	6.7	-3.51	~0	0.43	10.8	~0
	H	204	136.4	127.7	- 1.30	7.0	-2.65	0.009	0.35	5.3	~0
	ICL	204	134.4	135.3	- 0.84	7.0	-1.70	0.09	0.31	4.6	~0
	R	102	140.3	141.3	- 0.97	5.6	-1.76	0.08	0.48	5.4	~0
(2)	H	204	82.1	84.9	- 2.9	17.7	-2.32	0.02	0.20	2.9	0.002
	ICL	204	82.4	83.6	- 1.3	16.0	-1.12	0.26	0.30	4.4	~0
	R	102	161.8	167.5	- 5.6	28.6	-2.00	0.05	0.12	1.2	0.125
(3)	all	510	4.29	4.44	- 0.16	0.87	-4.02	~0	0.15	3.4	~0
	H	204	4.28	4.47	- 0.19	0.94	-2.85	0.005	0.11	1.6	0.060
	ICL	204	4.29	4.38	- 0.09	0.83	-1.57	0.12	0.23	3.3	0.001
	R	102	4.29	4.51	- 0.22	0.80	-2.73	0.007	0.07	0.7	0.252
(4)	H	204	1870.0	1977.0	-107.0	34.4	-3.11	0.002	0.27	3.9	~0
	ICL	204	1851.1	1013.4	- 62.3	31.9	-1.95	0.05	0.30	4.4	~0
	R	102	3794.5	3975.2	-180.7	77.8	-2.32	0.02	0.07	0.7	0.236
(5)	all	510	97.8	103.2	- 5.41	24.7	-4.95	~0	0.20	4.6	~0
	H	204	97.5	104.2	- 6.65	26.6	-3.57	~0	0.18	2.6	0.005
	ICL	204	96.5	100.2	- 3.68	24.0	-2.19	0.03	0.26	3.8	~0
	R	102	100.7	107.1	- 6.38	21.9	-2.94	0.004	0.05	0.5	0.295
(6)	H	204	19.2	19.1	0.14	2.73	0.72	0.47	0.08	1.2	0.119
	ICL	204	19.2	19.2	0.06	2.50	0.36	0.72	0.12	1.7	0.045
	R	102	37.8	37.3	0.53	3.77	1.42	0.16	0.19	1.9	0.027

Open plant positions were given an additional kernel on 7, 8 and 9 November. These emerged from 15 November onwards. These seedlings probably were not able to make up the leeway. January and February 1979 were extremely cold. The trial field was covered with snow during the whole period. Early March the crop had a reasonable appearance. The number of open plant positions seemed to be restricted. On 5 April Dicuran (containing chloretoluron) was sprayed, mainly to kill loose silky bent. On 9 April 15-11-22 NPK fertilizer was provided (60 kg N/ha). March and April were gloomy and wet. In May the crop developed quite quickly. Ears emerged from about 18 May, poller shedding started on 31 May. Notwithstanding heavy showers on 31 May and on 4 June (27 mm in 90 minutes) the crop did not lodge. The crop was harvested from 6 through 13 August.

For each plant of each of the 1020 sheaves the culmlength was recorded. Earnumber and yield were observed per plot. This procedure proved to be more efficient than that described in section 2.3.2. In addition to the reasons mentioned there for deviation of the actual number of plants from the intended number, it should be stressed here that crop 7, 10 and 13 were grown from 1 kernel per plant position. Thus imperfect filling up of empty plant positions or loss of plants after that intervention are additional causes for a deficit. The other causes for false registration of the actual number of plants remained in force as before. Because the number of plants per plot is of importance when determining plot totals and means per plant, this factor was studied for crop 10 and for crop 13.

5.3.2 Comparison of the 2 blocks

By means of the test given by formulae (2.1) and (2.2) the 2 blocks in crop 10 were compared. The test results are summarized in Table 40. They show that the growth conditions in block 2 were more favourable than those in block 1. In block 2 the mean culmlength, the mean earnumber and the mean yield surpassed the corresponding values for block 1. In general, this was true both for all families together as well as for the types of families separated. For total number of ears per plot and for total yield per plot the same was found. The ICL-families showed the general trends but mostly not statistically significant.

The significantly higher mean earnumber and mean yield were associated with higher totals per plot but the critical levels of the means were always smaller than those of the corresponding totals. The explanation for this is the higher number of plants in block 1. Table 41 affords a comparison of the number of plant positions per block and the registered number of plants. Calculated for the 2 blocks together the percentage of plant positions occupied by a plant amounted to 95.2%. This value is biased upwards because with registration more plants were counted than there actually were in the field (see section 2.3.2). This is shown by the observation that rather often an excess of plants per plot was registered. The portion of plots for which the number of registered plants exceeded the number of plant positions amounted to:

type of families	block 1	block 2
H	0.235	0.240
ICL	0.275	0.240
R	0.167	0.064

The portion of plots for which a false number of plants was registered was at least as large as the given portion. Therefore a continuation of the analyses only for means per plant was considered to be less reliable. In stead of this, for earnumber and for yield means per plant position were analysed as well. These were derived from their respective plot totals (which could be observed with relatively good precision). For culmlength there was a direct relation between the number of registered plants and the sum of their culmlengths. No reliable value for mean culmlength per plant position could therefore be obtained. (A prohibitive factor for the analyses of plot totals was the fact that plots with an R-family contained 40 plant positions in stead of 20.)

The number of registered plants per plot exceeded rather often the number of plant positions. The mean number of registered plants per plot, however, failed to exceed the intended number of plants (see Table 40). Therefore, the means per plant always exceeded the means per plant position. This is illustrated by Table 46 and Table 48. It is also exemplified by the fllowing: for the R-families 3856+3802=7658 plants were registered; thus 93.85% of the plant positions were occupied (see Table 41). The mean performance per plant will then amount to about 1/0.9385=1.0655 times the mean performance per plant position. For yield the actual ratio was 103.7/97.1=1.068, for earnumber 4.39/4.12=1.0655 (see Table 46).

The mean number of plants per row amounted for H-families (3921+3893)/408=19.15, for ICL-families 19.19 and for R-families 18.77. For the R-families it amounted thus to 98.0% and 97.8% of that for the H- resp. ICL-families. The occupation within rows of R-families was thus about 2% less than that for the other types of families. This was probably due to poorer seed quality. The lower portion of plots with an excess of registered plants follows, of course, from the lower occupation.

The lower number of plants per row for the R-families might influence totals per plot and means per plant in a different way. The totals per plot might tend to be lower because they are sums of fewer plants. The means per plant might tend to be higher because of decreased interplant competition. These suppositions were confirmed by correlations between the number of plants per plot on the one side and totals per plot and means per plant (for earnumber and yield) on the other side (see Table 42).

Table 43 presents, for each type of families, the total number of ears and the total yield in each of the 2 blocks. The ear density over the whole crop amounted to (50053+51470)/321.3=316. This is a fair ear density; not only because of the low plant density (76.2, see section 2.3.1), but also compared with former results (from 184.9 in crop 7 to 288.8 in crop 3). The mean yield per m^2 amounted to 2345219/321.3=7299.2 dg. On the strength of the conversion factor for crop 6, grown one season before, i.e. 0.862 (see section 5.2.2), this corresponded with a kernel yield per m^2 of 6292 dg. Thus crop 10 yielded well, owing to both a fair ear density and a reasonable mean yield per ear (2345219/101523=23.1 dg).

The correlation between x_1 (an observation on a family in block 1) and x_2 (the same observation on the family in block 2) was established for all

Table 42 Correlation between the number of plants per plot on the one side and totals per plot and means per plant on the other side.

type of families	block	earnumber		yield	
		total per plot	mean per plant	total per plot	mean per plant
H(n=204)	1	0.44***	-0.21***	0.38***	-0.12*
	2	0.32***	-0.28***	0.22***	-0.25***
ICL(n=204)	1	0.43***	-0.14*	0.28***	-0.16**
	2	0.34***	-0.28***	0.30***	-0.19**
R(n=102)	1	0.31***	-0.26**	0.24**	-0.25**
	2	0.29**	-0.36***	0.22*	-0.35***

families together, as well as for each type of families (see Table 40). In general the estimates were less than 0.35, but significant owing to the large number of observations. Mean culmlength was an exception. For this character the correlation among the R-families, which were grown on plots with a doubled number of plant positions, was clearly higher than that obtained for the other types of families. The reverse was true for the other characters.

The correlations for means per plant were always less than for totals per plot. The cause of this appears to be the bias with which the number of plants per plot was determined.

Discussion

The problems connected with the determination of the number of plants per plot impose the question whether it is sensible to design comparative trials that allow the harvesting of individual plants. The present comparative trials consisted of a 25×5 cm plant position pattern (interrow distance 25 cm, intrarow 5 cm), which implied a plant density (80) far below that for

Table 43 The total number of ears and the total yield (dg) for each type of families in crop 10

type of families	block 1		block 2	
	number of ears	yield	number of ears	yield
H	16739	381475	17324	403300
ICL	16809	377615	17065	390328
R	16505	387034	17081	405467
	50053	1146124	51470	1199095

Table 44 Coefficient of phenotypic variation among the families for total yield and for mean yield per plant

character	total yield			mean yield per plant		
type of families	H	ICL	R	H	ICL	R
block 1	0.21	0.20	0.16	0.20	0.20	0.17
block 2	0.21	0.20	0.13	0.21	0.20	0.14
blocks pooled	0.17	0.16	0.11	0.16	0.16	0.11

commercial crops (250). For an interrow distance of 25 cm the commercial density implies 62.5 plants per m alongside a row, which under practical conditions consists of a narrow band rather than of a straight line. Thus the commercial density implies rather strong interplant competition, reducing the yield per plant. Indeed, the smaller density in crop 10 did not prevent the crop from yielding as much as about 6300 kg/ha. Thus objections against a plant density that is less than the commercial density will hold only for still smaller densities than applied in our comparative trials.

A disadvantage of comparative trials at the commercial density is the fact that systematic differences among the entries for percentage of emergence and percentage drop outs then remain hidden. Now such a difference was discovered: the R-families produced less plants per row than the other types of families.

Thus comparative trials that enable individual harvesting are still preferred but it was decided to take 2 measures:

(i) to approach the commercial density somewhat better in later experiments (not described in the present text) only 15 cm was applied as interrow distance. This implies a plant density of $\frac{25}{15}\times 80=133.33$. This interrow distance was advocated by Bogulawski & Debruck (1972) and by Dörre (1979), p.35.

(ii) the lifting of the plants at harvest should be done with more care. Individual plants should be lifted individually or the soil around the plants should be loosened before lifting.

The supposition in section 2.3.3 that a plotsize of 20 plants might be insufficient to reflect the genetic value of a family was not supported by higher correlation coefficients between corresponding plots containing 40 in stead of 20 plants.

Obviously, the environmental variation between plots belonging to different blocks but containing the same family were the main reason for the correlation to be as small as observed. Nevertheless it was unexpected that, except for mean culmlength, for the R-families even smaller correlation coefficients were obtained than for the other types of families. This was associated with smaller variances among the families (compare Table 46 with

Table 45 Skewness for some characters observed on 102 R-plants in crop 6 and their offspring in crop 10.

character	R-plants	offspring	
		mean per plant	total from 2 plots
culmlength	0.38	-0.18	
earnumber	1.95**	0.22	-0.11
yield	1.31**	0.04	-0.18

Table 48). In crop 7 the reverse was observed for the correlations as well as for the variance (see section 4.3.2).

For yield the variation among the plots, as measured by the coefficient of phenotypic variation (see Table 44), was minimal for the R-families; thus showing in this respect a beneficial effect of the increased plotsize. The table shows that it was unimportant how the yield was measured. For mean culmlength the coefficients, calculated after pooling the plots amounted to 0.037 for the H-families, to 0.035 for the ICL-families and to 0.036 for the R-families.

In conclusion, the lower correlation coefficients for the R-families remain enigmatic.

5.3.3 The relation between R-plants (crop 6) and their offspring (crop 10)

Skewness was determined for the n=102 R-plants in crop 6 and for their offspring in crop 10. The results (see Table 45) show that there was positive skewness among the parents for earnumber and for yield (the correlation between these characters amounted to r_p=0.76). In contrast to the situation in section 4.2.3 the skewness in this case can hardly be ascribed to the requirement of a minimal yield produced by the R-plants. Such requirement was not a serious restriction in crop 6 when sampling R-plants (see section 5.2.3). The skewness for these characters was in crop 6 less pronounced than in crop 4.

The skewnesses presented in Table 45 for the totals from 2 plots are, of course, the same as those that would be obtained for the corresponding means per plant position.

The caution advocated before, e.g. in section 4.3.3, for analysis and interpretation in case of skewness applies here again.

The parameters mentioned in section 2.3.4 were now estimated from the observations on the R-plants on the one side and from the mean per plant as well as from the mean per plant position on the other side, i.e. from data on the offspring. The estimates are presented in Table 46. The values obtained confirm the trends observed before. The estimates based on offspring

Table 46 Estimates, for 3 characters, of the parameters mentioned in section 2.3.4. The estimates are based on observations on 102 R-plants in crop 6 and on their offspring in crop 10.

estimated parameter	offspring performance in mean per plant			offspring performance in mean per plant position	
	culmlength(cm)	earnumber	yield(dg)	earnumber	yield(dg)
α	103.3	4.37	98.9	4.14	92.0
β	0.24	0.005	0.048	-0.005	0.05
ρ	0.59	0.02	0.13	-0.02	0.15
t_r	7.24	0.17	1.33	-0.19	1.52
$P(\underline{t}_{100}>t_r)$	~0	0.43	0.09	0.58	0.07
$\bar{x}$	159.1	4.10	101.9	4.10	101.9
$\bar{y}$	140.8	4.39	103.7	4.12	97.1
$\sigma^2_{\underline{x}}$	135.6	1.97	1007.6	1.97	1007.6
$\sigma^2_{\underline{y}}$	22.0	0.18	131.7	0.16	111.2
h^2_n	0.47	0.01	0.095	0	0.10
$cov(\underline{x},\underline{y})$	32.0	0.01	47.9	-0.01	50.37
σ^2_a	64.0	0.02	95.7	0	100.74
vc_a	0.050	0.034	0.096	0	0.098

mean per plant position are similar to those based on offspring mean per plant. Notwithstanding the occurrence of skewness it appears justified to conclude that for earnumber and for yield there was no significant heritability.

The estimates for the heritability of culmlength increase steadily from generation to generation (viz. 0.39; 0.40; 0.43 and 0.47 respectively). The confidence intervals show, however, that no significance has to be attached to this.

The confidence interval, with confidence level 1-γ, for the coefficient β for linear regression is given by

$$\underline{b} - z\underline{s}_{\underline{b}} < \beta < \underline{b} + z\underline{s}_{\underline{b}} \qquad (5.1)$$

in which $P(\underline{t}_{n-2}>z)=\frac{1}{2}\gamma$ and $\underline{s}^2_{\underline{b}}=\underline{s}^2/\{(n-1)s^2_{\underline{x}}\}$ (see Corsten (1973), p.98). Because

$$\bar{h}^2_n=2b \qquad (2.3)$$

it follows that $\hat{var}(\underline{\bar{h}}^2_n)=4\hat{var}(\underline{b})$. (5.2)

For n=102 and γ=0.05 we find z ~ 1.98. Confidence intervals for β and for h^2_n are given in Table 47. The intervals show that the former estimates belong all to the confidence intervals determined from the present data.

For some parameters estimates were obtained, which were derived from observations on the H-and the ICL-plants and on their offspring. These are presented in Table 48.

Discussion

Table 47 Confidence intervals, with confidence level 0.95, for β and for h_n^2 (see section 2.3.4), calculated from s^2- and s_b-values for the R-plants and their offspring.

	s^2	s_b	confidence interval	
culmlength (cm)	14.55	0.0326	$0.18<\beta<0.30$	$0.34<h_n^2<0.60$
earnumber	0.18	0.0301	$-0.05<\beta<0.06$	$-0.11<h_n^2<0.13$
yield (dg)	130.7	0.0358	$-0.02<\beta<0.12$	$-0.13<h_n^2<0.24$

On the question how to choose a reasonable number of families (N) and a reasonable number of plants per family (n) there is no straight answer. In section 6.2.3 there is the guess that a sample of N=38 R-plants would be too small. Originally the number of plants per family was established at 40, but in crop 10 as well as in crop 13 it was fixed on n=80. A complicating factor is formed by the differences in heritability among the characters. Thus the numbers for N and n that will satisfy depend on the character of interest.

To tackle this problem when estimating h^2 the argument developed by Falconer (1960), p.179 was followed. The variance of the estimator $\underline{b}$ for the regression of offspring mean on parental value can approximated by

$$\hat{var}\ (\underline{b}) \sim \frac{1}{N} \cdot \frac{s_y^2}{s_x^2}$$

The smaller var($\underline{b}$) the better the precision of the estimate for h^2.

Falconer showed that $s_y^2 = \frac{1+(n-1)t}{n} \cdot s_x^2$; in which t represents the phenotypic intraclass correlation (see Falconer (1960), p.232), i.e. $t=\sigma_b^2/\sigma_t^2$, where

σ_b^2:=the component of variance between families

σ_t^2:=the (total) phenotypic variance.

Thus

$$\hat{var}(\underline{b}) \sim \frac{1+(n-1)t}{Nn} .$$

According to Falconer this approximation is minimal for $n_m = \sqrt{(1-t)/t}$ when the total number of observed plants, i.e. T=N+Nn, is fixed. Because $\sigma_b^2/\sigma_t^2=\frac{1}{4}h^2$ var($\underline{b}$) is minimal for $n_m= \sqrt{(4-h^2)/h^2}$.

In the present situation when applying to above expression, we obtained for culmlength n_m=2.74 because h^2=0.47 (see Table 46). Thus a family size of 3 plants would be obtimal as far as culmlength is concerned. For yield we found n_m=6.41 and for earnumber n_m=20. From these results it must be concluded that, in the current experiments, the applied family sizes were too large and that the number of families was too small. Of course, this conclusion is only valid when we intend to maximize the precision of the estimation of h^2 via regression of offspring mean on parental value.

Table 48 Estimates, for 3 characters, of some of the parameters mentioned in section 2.3.4. The estimates are based on observations on 204 plants selected in crop 6 and their offspring in crop 10.

character	estimated parameter	offspring performance in mean per plant		offspring performance in mean per plant position	
		H-selection	ICL-selection	H-selection	ICL-selection
culmlength (cm)	β	0.35	0.32		
	ρ	0.50	0.31		
	t	8.31	4.64		
	$P(\underline{t}_{202}>t)$	~0	~0		
	$\bar{x}$	152.0	147.9		
	$\bar{y}$	137.0	134.9		
	σ^2_y	25.2	22.9		
	$cov(\underline{x},\underline{y})$	18.5	6.9		
earnumber	β	-0.02	-0.02	-0.04	-0.03
	ρ	-0.06	-0.05	-0.11	-0.06
	t	-0.85	-0.77	-1.57	-0.85
	$P(\underline{t}_{202}>t)$	0.80	0.78	0.94	0.80
	$\bar{x}$	5.50	5.93	5.50	5.93
	$\bar{y}$	4.37	4.33	4.17	4.15
	σ^2_y	0.276	0.274	0.294	0.295
	$cov(\underline{x},\underline{y})$	-0.05	-0.04		
yield (dg)	β	0.02	-0.005	0.02	-0.02
	ρ	0.04	-0.005	0.03	-0.02
	t	0.55	-0.07	0.44	-0.31
	$P(\underline{t}_{202}>t)$	0.29	0.53	0.33	0.62
	$\bar{x}$	142.5	144.6	142.5	144.6
	$\bar{y}$	100.6	98.2	96.2	94.1
	σ^2_y	252.9	243.7	259.7	238.5
	$cov(\underline{x},\underline{y})$	18.5	-1.3		

The R-plants grown in crop 6 and their offspring in crop 10 offered an opportunity to study the modifying influence of the growing conditions in 2 successive seasons. For earnumber and for yield the mean of the parents was about equal to the mean of the offspring, especially when the latter was expressed as mean per plant position. For culmlength the parents exceeded their offspring quite clear.

The next 2 considerations on this comparison are pointed out:

(i) among the offspring the culm elongation started very late, owing to the cold spring. This could be the cause for the culms of the offspring to be 159.1-140.8=18.3 cm shorter than those of the parents (Table 46);

(ii) the parental plants had a plant density of 51.3, those of the offspring 76.2. Notwithstanding the cold winter and the difference in plant density the earnumber in crop 10 was as good as in crop 6. The reason for this could be better soil conditions for crop 10.

The correlation coefficients, i.e. the heritability in standard units, fit in with the earlier estimates, except for culmlength, for which a clearly higher value was found.

For some parameters also estimates were derived from observations on selected plants and on their offspring (Table 48). For H-selection and for

ICL-selection about the same results were obtained. For culmlength the estimates for β were very surprising. They were very significant and did not belong to the confidence interval established for the R-plants. The same phenomenon was observed after G- and T-selection in crop 4 (see section 4.3.3).

For earnumber and for yield no significant correlation was obtained. Means per plant and means per plant position yielded very similar results.

Comparison of Table 46 with Table 48 shows that the variances among the R-families were lower than those among to H- or ICL-families. This was quite unexpected. Apparantly, selection raised the genetic variation. This appeared also from the increased correlation coefficients for culmlength.

The selection aims at promoting a recombinant plant type. This causes the population to leave an equilibrium at which the mean fitness of the population is at its maximum and the additive genetic variance of the fitness is minimal. Deviations from this equilibrium are associated with increased additive genetic variance for fitness, which appears to be associated on its turn with increased additive genetic variance for culmlength and for yield. The covariances between parent and offspring were lower for the H- and the ICL-plants than for the R-plants and thus it seems that the foregoing speculation deserves rejection. However, it was indicated in section 2.3.4 that in case of selection such covariances are not valid measures of the additive genetic variances.

The absence of decrease in course of time of the estimate for the coefficient of additive genetic variation (vc_a) as well as the increase of the heritability estimate for culmlength might be explained by the same speculation.

The estimates for vc_a (see Table 46) agreed well with those in Table 19, and also fairly well with those in Table 9 and Table 30. Compared with Table 30 the present estimates are somewhat lower but this might rest on an incident. On the basis of the stability throughout the generations of the estimates for vc_a it is concluded that the success of the selection was so restricted that it dit not result in a clear decrease of genetic variation. This phenomenon is frequently observed for long-term experiments with mass selection. The nicest example is the mass selection programme in maize continued over 70 generations (Dudley, 1974).

It did not matter whether vc_a was estimated from means per plant or from means per plant position.

An analysis of variance for the R-families yielded alternative estimates for σ_a^2 (see section 2.3.4). Such analyses are presented in Table 49. The results for testing block effects are about the same as those given for the R-families in Table 40. Exactly the same results should have been achieved if pairing of the plots was not applied. In that case the relation $f(1,101) = t_{101}^2$ would hold exactly (see Snedecor & Cochran (1967), p.267). Because of the low values of the correlation coefficients, except for culmlength (see Table 40), the advantage of pairing was neglectable.

Table 49 Analysis of variance for 5 characters of the 102 R-families in crop 10

character		source of variation R-families (df=101)	blocks (df=1)	error (df=101)
mean culmlength	SS	4447.9	48.3	1584.5
	MS	44.0	48.3	15.7
	f	2.81***	3.08	
mean earnumber per plant	SS	37.03	2.39	32.4
	MS	0.367	2.39	0.321
	f	1.14	7.45**	
mean yield per per plant (dg)	SS	26946.4	2077.3	24213.2
	MS	266.8	2077.3	239.7
	f	1.11	8.67**	
mean earnumber per plant position	SS	32.45	1.02	25.76
	MS	0.321	1.02	0.255
	f	1.26	3.99*	
mean yield per plant position(dg)	SS	22457.4	1041.0	19463.2
	MS	222.4	1041.0	192.7
	f	1.15	5.40*	

Only for culmlength significant differences among the R-families were detected. Thus only for this character significant additive genetic variation was determined. The estimate for σ_a^2 for this character was 2(44.0-15.7)=56.6 cm^2, for yield it was 54.2 resp. 59.4 dg^2. In contrast to our expectation, that higher estimates would be got from the analysis of variance than from the offspring-parent regression, in crop 10 the reverse was obtained. This might have been an incidental deviation.

For each R-plant and its offspring (pooled over the 2 blocks) the mean yield per ear was determined.
The mean and the coefficient of phenotypic variation for this character were estimated to be:

	R-plants	R-families
$\bar{x}$(dg)	25.5	23.6
vc_p	0.20	0.08

The estimates for vc_p were lower than those presented in Table 36 (except for culmlength) and Table 37 for the R-plants and those presented in Table 44 for yield of the R-families. This was associated with a much higher heritability, i.e. $\hat{h}^2_n$=0.29 (which was significantly positive, $\hat{\rho}$=0.40), than obtained for yield (h^2_n=0.095, see Table 46). The coefficient of additive genetic variation amounted only 0.107. Nevertheless selection for yield per ear offers better perspectives for progress than selection for yield per plant. Patyna & Grochowsky (1978) reported for rye that 'grain weight per ear seems to be the most effective parameter of selection'.

As a correlated response to such a selection one should anticipate a decreasing earnumber because, for the R-plants, the correlation of yield per ear and earnumber amounted to -0.38. This means that the ears produced by a plant have a smaller weight the larger the earnumber of that plant. However, this association appeared to be rather weak. More details of relevance for this association are given in section 6.2.2.

In section 2.3.4 formulae, i.e. (2.7) and (2.8), were presented to estimate genetic variance due to additive genetic effects (σ^2_a) and the genetic variance due to additive × additive interaction (σ^2_{aa}). Substitution of the required estimates, given by Table 46 and 49, yields the following estimates for these 2 vaiances:

for culmlength:

$$\hat{\sigma}^2_a = 8\ [(44.0-15.7)/2-(32.0/4)]=49.2\ cm^2$$

$$\hat{\sigma}^2_{aa} = 8\ [32.0-2(44.0-15.7)/2]=29.6\ cm^2$$

for yield:

$$\hat{\sigma}^2_a = 8\ [(266.8-239.7)/2-(47.9/4)]=12.6\ dg^2$$

$$\hat{\sigma}^2_{aa} = 8\ [47.9-(266.8-239.7)]=166.4\ dg^2$$

For culmlength the estimate for σ^2_a is only a little bit smaller than the estimate presented in Table 46. The estimate for $\hat{\sigma}^2_{aa}$ shows that epistasis is of minor importance. For yield the estimate for σ^2_a is much smaller than that obtained before. Further epistasis is here an important source of variation. In section 5.3.5 these estimates are used to predict the response to selection. When applying the formulae (2.5) and (2.6) one should always remember that these formulae pertain only to pairs of loci. Further the estimates are based on assumptions ((ii) through (iv), see section 2.3.4) which do not always hold.

5.3.4 Phenotypic and genetic correlations

Coefficients of phenotypic correlation between the characters were estimated from observations on the 200 plants in rows 76, 77 and 78 of crop 6 as well as on the 102 R-plants in crop 6. The former are presented in Table 38, the latter in Table 50. The 2 groups of estimates are quite similar.

The genetic correlations were estimated by application of formulae (2.11) and (2.12), as well as by means of an analysis of covariance. (In fact an

Table 50 Phenotypic correlations (r_p) estimated from observations on the 102 R-plants in crop 6; genotypic correlations (r_g) estimated from the same observations and from observations on the offspring of the R-plants. The 3 methods to estimate ρ_g are explained in section 5.3.4; +: correlation could not be determined.

characters	r_p	r_g offspring performance in mean per plant (1)	(2)	(3)	id. in mean per plant position (1)	(2)
culmlength-earnumber	0.10	-1.38	-1.31	-0.96	+	+
culmlength-yield	0.31***	0.07	0.07	-0.29	0.20	0.16
earnumber-yield	0.76***	0.03	+	-0.42	-0.28	+

analysis of variance was made for the sum of the observations for the 2 characters. From this analysis of variance and from those for each of the characters themselves (see section 5.3.3 and Table 49) estimates of genetic variances and genetic covariances were obtained.) The results are presented in Table 50, in which (1), (2), resp. (3) refer to the 3 methods mentioned here.

Application of formulae (2.11) and (2.12) was in some cases impossible because of negative estimates for some of the covariances included in these formulae. Further the 2 formulae yielded unrealistic estimates for the genetic correlation of culmlength and earnumber.

The estimates derived from analyses of covariance are all negative. They do not confirm earlier estimates for the genetic correlation; neither those obtained from formulae (2.11) and (2.12), nor those obtained from correlated responses after single trait selection. In general, of course, negative correlations are expected to occur quite often because of physiological restrictions. Thus greater culmlength is expected to be associated with decreased earnumber and decreased yield. However, such a negative relationship is not expected for earnumber versus yield.

Altogether it is concluded that the methods to estimate genetic correlations which were applied in chapters 2, 3, 4 and 5, yield conflicting and sometimes unrealistic estimates. The realized genetic correlations (see section 4.3.4) appear to be the most satisfying.

5.3.5 *The actual result of selection*

The results

Crop 10 was grown to establish the results of the different selection

Table 51 Weighted means per plant for culmlength, earnumber and yield; means per plant position for earnumber and yield; mean number of plants per family. Results from crop 10.

character	selection procedure				
	H-selection (n=204)	ICL-selection (n=204)	R-selection (n=102	HI-selection (n=60)	index selection (n=19)
culmlength (cm)	137.04	134.87	140.84	135.25	137.40
in %	97.3	95.3	100	96.0	97.6
earnumber	4.37	4.33	4.39	4.42	
in %	99.5	98.6	100	100.7	
yield (dg)	100.57	98.13	103.70	100.90	102.80
in %	97.0	94.7	100	97.3	99.13
earnumber per plant position	4.17	4.15	4.12	4.20	
in %	101.2	100.7	100	101.9	
yield (dg) per plant position	96.17	94.11	97.12	95.98	95.52
in %	99.0	96.9	100	98.8	98.35
number of plants per family	38.30	38.40	75.08		
occupation of plant positions (%)	95.75	96.00	93.85		

methods applied in crop 6. The means of the families obtained after H-, ICL- and R-selection are presented in Table 51.

Using Kruskal and Wallis' median test to test H_o: "the 3 selection procedures afford equivalent progenies" against its complementary two-tailed alternative H_a (see formulae (3.4) with k=3 selection methods), the following test results were arrived at:

character	H	critical level
culmlength	86.7	~0
earnumber	0.851	0.654
yield	9.2	0.01
earnumber per plant position	1.16	0.559
yield per plant position	2.87	0.24

Most attention should be given to the yardstick mean per plant position, because this is equivalent to performance per unit area, which is the interest of the farmers.

For culmlength H_o was rejected, for earnumber it was not rejected, for yield only when expressed as mean per plant.

Next, for the characters for which H_o was rejected, Mann-Whitney's test was applied to study interesting contrasts of selection procedures. The null hypothesis tested was H_o: "the 2 selection procedures afford equivalent progenies", the alternative hypothesis was two-tailed or one-tailed, depending on the character and on the selection procedures under comparison. The critical level was one- or two-tailed accordingly. The results were:

character	hypothesis		critical level
	H_o	H_a	
culmlength	H=R	H<R	~0
	ICL=R	ICL<R	~0
	ICL=H	ICL≠H	~0
yield	ICL=H	ICL≠H	0.15

By H-selection as well as by ICL-selection the culmlength was decreased. After ICL-selection the decrease was larger than after H-selection. The yield of the H- and the ICL-families was, completely in contradiction to the objective, lower than that of the R-families.

Discussion

As indicated in section 5.3.2 and shown by Table 51, the R-families occupied their plant positions about 2% worse than the H- and ICL-families. Thus for earnumber and yield, expressed as mean per plant, the results of H- and ICL-selection were about 2% worse than the results expressed as mean per plant position (or, which is equivalent, as totals per family).

The earnumber per plant position was minimal for the R-families. This could partly rest on incomplete compensation of the worse occupation of plant positions by better tillering and partly by a correlated response of H- and ICL-selection on tillering (which is improbable because H- and ICL-families yielded less).

The results of the H- and the ICL-selection were not completely in accordance with the objectives. The offspring of the H- and the ICL-plants showed, it is true indeed, a decreased culmlength, but their yield was not increased. The yield even tended to be less than that of the R-families. Thus the recombination aimed at was not approached in a convincing degree: the decrease in culmlength (3% for the H-families, 4% for the ICL-families) was accompanied by a decrease in yield (1% for the H-families, 3% for the ICL-families). It was not a surprise to observe that the decrease of the culmlength after ICL-selection was larger than that after H-selection. This was expected because the ICL-plants had a smaller culmlength than the H-plants (Table 36).

It had to be anticipated of course that the results should be restricted because H-selection as well as ICL-selection aimed at realizing synchronously conflicting objectives. Further, the lack of a significant heritability for yield promised this kind of results. Because both crop 6 and crop 10 can be considered to be experiments with an excellent quality the meaning of the present results may not be belittled.

In such a situation one has to look for different approaches. Two such alternatives, both belonging to the group of methods for mass selection, are elaborated here:

(i) It is a well-known fact, also observed in the present experiments, that methods for mass selection are poor in detecting superior genotypes. Therefore it was interesting to study the offspring of plants that were selected by H-selection as well as by ICL-selection. In general different plants were selected by these 2 methods. Nevertheless, 60 of the 348 selected by H-selection or by ICL-selection (the union of the plants selected for these 2 methods) belonged to the intersection of the 2 sets of selected plants (see Table 39). As remarked in section 5.2.3 this group of selected plants was the most promising: the mean culmlength of these HI-plants amounted to 147.6 cm (11.5 cm less than for the R-plants), their mean yield to 150.1 dg (48.2 dg more than for the R-plants). The mean performance of the offspring of the HI-plants, which were grown on 120 plots in each block, are presented in Table 51.

From the results it appears that HI-selection suffered from the same drawbacks as H- and ICL-selection. Thus the intersection of the plants selected by H- or by ICL-selection did not yield a clearly better progeny than did H-selection or ICL-selection alone.

(ii) Simultaneous selection, aiming at improvement for more than one character, is said to be most efficient when the selection is for a socalled index (Falconer (1960), p.324). In the present situation the ultimate goal would already have been attained when a population was obtained with decreased culmlength, which is not combined with a decrease for yield. The improvement aimed at concerns then character x (culmlength). The other character y (yield) is only considered to promote the efficiency of the selection. The relative economic weight of y amounts then to zero. According to Falconer (1960), p.328 index selection can then be applied by using as an index

$$I = p_x + w\, p_y \qquad (5.3)$$

in which p_i: = phenotypic value for character i

$w = \sigma_x\{\rho_g h_y - \rho_p h_x\}/\{\sigma_y(h_x - \rho_g \rho_p h_y)\}$

For crop 6 the next estimates were obtained: $\hat{\sigma}_x$=12.5 cm, $\hat{\sigma}_y$=36.0 dg (Table 36); $\hat{\rho}_p$=0.31, $\hat{\rho}_g$=-0.29 (Table 50); $h_x=\sqrt{0.47}=0.68$, $h_y=\sqrt{0.095}=0.31$ (Table 46).

Thus one gets w=-0.15.

A negative value for w means, according to Falconer, that "the phenotypic correlation between x and y is chiefly environmental in origin. The secondary character then acts as an indicator of the environmental deviation".

The resulting formula to calculate the index values, i.e. $I=p_x-0.15p_y$, was used to determine the index value for each R-plant in crop 10.

To select the recombinant plant type plants with low index values should be selected. The mean index value of the 102 R-plants amounted to 143.82, its standard deviation to 11.15. Thus among the R-plants those plants with an index value of less than 133 were selected. These yielded 19 plants with for mean culmlength 145.2 cm, mean earnumber 4.95 and mean yield 113.32 dg. Compared with all R-plants (see Table 36) these plants had a clearly smaller culmlength.

The mean index value of the 19 selected R-plants amounted to 128.2; the range of their index values being 123.8 through 132.2. The means for culmlength and yield of the offspring of the 19 selected R-plants are presented in Table 51. They show that the results of index selection, obtained from this small study, are as disappointing as those for the other methods of selection. Absence of significant correlation among the 102 R-plants between index value and yield confirms this result.

In section 2.3.6 2 reasons were mentioned for applying non-parametric tests to study the result of selection. The first reason, variances among purposeful selected families being smaller than those among R-families, was illustrated by referring to Table 9 and Table 10. Comparison of Table 30 with Table 31 yields another illustration. In the present chapter the reverse was observed for the relative sizes of the variances (compare Table 46 with Table 48). The second reason, deviation for the family means from the normal distribution, was verified several times (Table 18, 29 and 45). Only in Table 18 significant negative skewness for culmlength was indicated. Thus, indeed, both reasons could be justified by experiences obtained in the course of the experiments.

Responses to selection were predicted by applying equation (3.5). The estimates for β and the selection differentials used in the predictions were derived from Table 46, resp. Table 36; the realized responses were derived from Table 51. Thus Table 52 presents predicted and realized responses, expressed as means per plant position. As already expected the agreement was very poor: for culmlength the realized responses exceeded their predicted values, for yield the reverse was true.

According to Griffing (1960), p.327 the response after one cycle of mass selection equals

$$(i/\sigma^2)(\sigma^2_a + \tfrac{1}{2}\sigma^2_{aa}) \qquad (5.4)$$

in which $i=S/\sigma$, the selection intensity.

Because here selection was applied after flowering only half this quantity was calculated here. The selection intensity for H-selection amounted for culmlength to $i=-6.8/\sqrt{135.6}=-0.584$; further $\hat{\sigma}^2_a=49.2$ cm² and $\hat{\sigma}^2_{aa}=29.6$ cm² (see end of section 5.3.3). The resulting prediction equals

$$\tfrac{1}{2}(-0.584/135.6)(49.2+\tfrac{1}{2}(29.6))=-0.14 \text{ cm.}$$

This prediction is hardly better than the prediction given by equation (3.5). Thus the unreliability of estimates of genetic parameters is illustrated here once more. This proves that the assumptions underlying the applied models were inadequate to describe the population genetic and quantitative genetic

Table 52 Predicted responses ($\hat{R}$) and realized responses (R) after H- and ICL-selection for culmlength, earnumber and yield. b: regression of offspring mean on parental value, S: selection differential

	H-selection				ICL-selection		
character	b	S	$\hat{R}$	R	S	$\hat{R}$	R
culmlength (cm)	0.24	-6.8	-1.63	-3.8	-10.9	-2.62	-5.97
earnumber	-0.005	1.44	-0.007	0.05	1.86	-0.009	0.03
yield (dg)	0.05	40.3	2.02	-0.95	42.4	2.12	-3.01

contributions to the observed phenotypic diversity. Interactions of genotype and environment, extrachromosomal inheritance, coupling of genes and absence of linkage equilibrium were implicity assumed to be unimportant. Clearly such simplifications belittle the underlying complexity of the come about of the phenotypes.

6.1 MATERIAL

Introduction

In section 1.2 it was already stated that choosing Dominant as a substrate for the experiments implied a difficult starting point for the realization of selection responses. During the years of the experiments it was the most widely grown rye variety in the Netherlands; possibly the best variety at the time. Indeed, potential differences in efficiency among the selection methods, if present at all, could not be demonstrated at a very convincing level.

To enable the methods to show such potential differences when applying them in a population combining a greater genetic diversity with a lower agronomic value, the methods applied in crop 6 were also applied under the same environmental conditions in crop 9. Crop 9 was a newly developed autotetraploid population.

Autotetraploid rye

Owing to the application of colchicine autotetraploid rye has been available since 1938. The performance of the first tetraploid varieties remained in general below that of the diploid varieties; notwithstanding the higher single kernel weight. This rested mainly on inferior tillering and on incomplete seed set (Bremer-Reinders, 1958). This incomplete seed set is caused not only by appearance of aneuploids (which have a reduced fertility), but might also be the result of imperfect isolation from diploid rye. Natural cross-pollination between diploid and tetraploid material yields sterile triploids which mostly abort in the embryonic stage. Thus large-scale growing of tetraploid rye should be associated with appropriate isolation from diploid rye.

The baking quality of flour of autotetraploid grains would differ favourably from that of flour of diploid grains. Kuckuck & Peters (1977) reported that, in the past 10 years, increasingly more positive data on the yield of tetraploid rye are obtained, especially from Eastern Germany, the USSR, Poland and Czechoslovakia. The variety Belta would perform rather well: the mean kernel yield (after a 4 year trial) amounted to 4250 kg/ha; the thousand kernel weight to 49 g. These should be compared with the diploid variety Benjakonsja which yielded 3280 kg/ha and had a thousand kernel weight of 30 g.

Improvements in comparison with the earlier autotetraploids are: shorter culms, better lodging resistance, improved winter hardiness, improved tillering, higher protein content, better N-response and improved seedset (from 60% increased to 75-78%, see Bremer-Reinders, 1958).

The autotetraploid material in crop 9

Around 1950, material belonging to the next 16 rye varieties were treated with colchicine:

1	Amelander	9	Carsten
2	Oude Terschellinger	10	Hellkorn
3	Akkerrogge	11	Hohenauer
4	Heertvelder	12	Kings rye
5	Kruiprogge	13	Steel rye
6	Ottersumse	14	Pekka
7	Leuvenumse	15	Vanoise
8	Brandts Marien	16	Wloszanowo

Varieties 1 to 7 inclusive were old Dutch land varieties, most of which have been lost over the years. Varieties 8 to 11 inclusive are of German origin, 12 and 13 are Swedish, 14 is Finnish, 15 originates from the French Alps and 16 is Polish. Bremer & Bremer-Reinders (1954) reported their experiences with autotetraploidy of some of these varieties.

All of the 16 varieties were maintained in autotetraploid condition until 1974-1975, when the 15th generation after continued selfing was grown. The varieties were thus maintained as mixtures from kernels obtained after selfing in stead of as mixtures from kernels obtained after open pollination. In this context the next conclusion of Lundqvist (1958) is of interest: "fertilization after selfing really occurs more easily in the tetraploids and, probably, the observed weakening of self-incompatibility is an intrinsic property of polyploidy in rye".

On the long run the applied procedure results in maintenance of each separate variety as a heterogeneous population of tetraploid plants with a high degree of homozygosity.

If, for a certain locus A-a, the original portion of heterozygotes (AAAa, AAaa and Aaaa) amounts to H_0, then this portion decreases after 1 generation of selfing to $H_1 \sim (\frac{5}{6})\ H_0$ (see Li(1976)). After 15 generations of selfing the portion of heterozygotes is decreased to about $(\frac{5}{6})^{15}\ H_0 = 0.065\ H_0$, i.e. to about $(1/16)^{th}$ of the original portion. This corresponds with the decrease of the frequency of heterozygotes which follows from 4 generations of selfing in a diploid species.

During the maintenance both random loss of genes and selection will have changed the genetic make-up of each variety. The random loss of genes follows from the fact that in every generation only 1 ear of about 40 plants was selfed to obtain the kernels for the next generation. Selection must have occurred for reduced self-incompatibility, as well as for improved course of the meiotic process.

To study the agronomic potential of the autotetraploid material from 1975 the 16 varieties were pooled to get a broadly based autotetraploid population. Thus in 1975 from each variety a number of openpollinated ears were harvested. The kernels in those ears originated from crossfertilization (by pollen from the same variety or by pollen from a different variety) or from selffertilization.

Of all openpollinated ears with more than 20 kernels single rows of 20 kernels were sown in a field on 28 and 29 October 1976 for the purpose of intermating. The total number of rows was 600, interrow and intrarow plant distances being 25 and 5 cm respectively. The field was isolated from diploid rye.

Further, at least 3 kernels of each of the 600 ears were used for cytogenetic screening, to check that the cells in the root tips of the seedlings contained $2n=4x=28$ chromosomes. This proved to be right (see Geersing (1977)). Also in another survey, comprising about 30 plants from each of 5 varieties, all plants appeared to be autotetraploid.

At lifting on 15, 16 and 17 August 1977 almost each of the 600 entries yielded a small sheaf. From each sheaf 25 kernels of 1 representative plant were used to form a mixture from which crop 9 should be grown.

The lay-out of crop 9 was similar to that for crop 6 (see section 5.1), in which also 1 kernel per plant position was sown. For a good comparison crop 6 and its offspring were grown under like conditions as those for crop 9 and its offspring. Of course, mutual pollination between diploid and tetraploid material was prevented by spatial isolation.

After disinfection with Quinolate crop 9 was sown on 20 and 21 October, 1977. Wire netting was put up around the trial.

6.2 THE PLANTS OF CROP 9

6.2.1 The growing of the crop

Just as described in section 5.2.1 for crop 6 also for crop 9 adverse weather conditions did not allow the provision of empty plant positions with an additional kernel. The emergence appeared to be good, but after the winter, i.e. after a period with a snow cover lasting 3 weeks, a considerable number of plant positions did not contain a plant. During the spring and the summer the plants had to compete with loose silky bent. Because of a thunderstorm on 6 May, 1978 a small part of the field (about 4 m^2) lodged. This part recovered only partly and suffered later in the season severely from mildew. In the course of May the plants became rather tall. On 29 May the length of the crop was estimated to be 190 cm. Both quantitative and qualitative variation among the plants was observable. Most of the plants showed waxy cuticula, some plants were waxyless; some plants produced neck hairs, some plants did not. From 30 May pollen was shed. The attack by mildew became more severe than ever observed for the other trials described in this text. The plants were lifted 14 to 17 August 1978. Culmlength and earnumber were recorded near the field; ears and straw were artificially dried before yield and straw yield were determined.

6.2.2 Some statistical properties

In addition to the usual observations also the weight of the straw of individual plants was registered for each mature plant. It was determined after removal of their roots and their ears.

The performance of the tetraploid rye was compared with that of the diploid rye. The results of the comparisons are given throughout the next of this chapter. The differences are summarized and discussed in section 6.3.5.

A summary of all observations on all plants is given in Table 53, 3^{rd} column.

The number of plants was about 4470. They were obtained from 5304 plant positions. No observation was thus available from 834 plant positions (15.7%). Among the diploids (crop 6) the percentage of drop outs was only 3.6%. Thus the germination and/or the winterhardiness of the tetraploid material was inferior when compared with the material forming crop 6.

Comparison of columns 3 of Table 36 and Table 53 shows that the culmlength of the tetraploid plants exceeded the culmlength of the diploid plants by 20.9 cm (13%). The tetraploids produced 9% less ears (notwithstanding the higher percentage of drop outs) and yielded 12% less. The mean straw yield was 0.5% higher than that mentioned in Table 37. The weight of the aerial plant parts averaged (89.9+137.1)=227.0 dg. In the present text this weight is defined as biomass. For the 200 diploid plants measured in crop 6 it amounted on the average to (103.7+136.4)=240.1 dg.

The coefficient of phenotypic variation was higher for all characters, especially for yield.

The total yield of all plants was 401879 dg. According to the conversion factor, determined for crop 9 (see section 6.2.3), this corresponded with a kernel yield equal to 0.854(401879)=343205 dg. The mean kernel yield per m^2 was 343205/103.428=3318.3 dg. Under the given conditions (comprising both material and environment) the tetraploids yielded 76% of the yield of the diploids.

The mean kernel yield per ear was (0.854×89.9)/3.69=20.8 dg. This was less than for the diploids and in contradiction to what we expected.

The eardensity was only 16501/103.4=159.6, which is quite low.

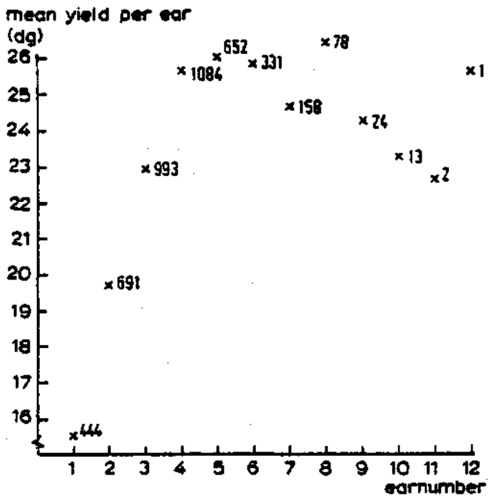

Figure 14 Mean yield per ear (in dg) plotted against the earnumber. The number of plants concerned is indicated near the crosses. Data from crop 9.

Discussion

The straw yield was observed because it was thought (see section 2.2.3) that selection for a recombinant plant type could be achieved by selection for an increased harvest index. According to Spitters (1979), p.189, the problem of competition, which is a disturbing factor when selecting for yield, is circumvented by selection for harvest index. This is a second recommendation in favour of selection for harvest index. Perspectives and aspects of such a selection criterium are discussed throughout this chapter.

The correlation between mean yield per ear and earnumber was 0.29 (n=4471). This positive relation is shown in Figure 14. This figure was obtained after classifying all plant according to their earnumber. For each earnumber class the mean yield per ear is depicted. Figure 14 shows that the mean yield per ear is less when the number of ears decreases. This trend is contradicted by a reverse relation for plants producing 8 ears or more. In fact in crop 9 the mean yield per ear reached a maximum (about 26 dg) for plants with 5 ears, the optimum number of ears in this respect. In such situation the correlation should not be interpreted in terms of general trends. The correlation was also estimated for the 80 R-plants in crop 9. This yielded $r= -0.17^{ns}$.

6.2.3 The methods of selection

Table 53 Summary of the observations on plants belonging to crop 9. n: number of observed plants, $\bar{x}$: mean; s: standard deviation; cv_p: coefficient of phenotypic variation; min: minimum; max: maximum.

			selected plants		
character	quantity	all plants	H-selection	ICL-selection	R-selection
culmlength	n	4473	76	76	80
(cm)	$\bar{x}$	179.7	179.9	169.8	185.7
	s	19.3	7.9	5.4	15.0
	vc_p	0.107	0.044	0.032	0.081
	min	68	158	151	144
	max	232	198	177	216
earnumber	n	4473	76	76	80
	$\bar{x}$	3.69	5.51	6.93	4.25
	s	1.72	1.46	1.43	1.45
	vc_p	0.466	0.264	0.206	0.342
	min	1	3	4	2
	max	12	10	11	10
yield (dg)	n	4471	76	76	80
	$\bar{x}$	89.9	161.5	184.6	121.1
	s	57.0	38.1	40.0	48.6
	vc_p	0.635	0.236	0.216	0.401
	min	1	108	141	55
	max	346	292	328	346
straw yield	n	4473	76	76	80
(dg)	$\bar{x}$	137.1	199.9	238.1	174.1
	s	71.3	40.7	46.3	53.5
	vc_p	0.520	0.204	0.195	0.307
	min	5	136	160	87
	max	405	319	352	374

Honeycomb selection

Because many plant positions were not occupied the restriction of considering only plants with 6 neighbours was dropped. Also plants with 5 neighbours were accepted. Thus 30 plants with 6 neighbours and 46 plants with 5 neighbours were selected, because they yielded at least as high as each of their neighbours, and their culmlength was less than the mean culmlength of their neighbours.

The 4th column of Table 53 presents summarized data on these 76 H-plants. The selection for reduced culmlength is counter-balanced by the selection for improved yield (which implies selection for increased culmlength). Thus the resulting selection differential for culmlength was negligible: the mean culmlength of the H-plants was equal to that for all plants. Their yield was 71.6 dg (79.6%) higher. Such result of H-selection was also achieved in crop 4 (section 4.2.3).

ICL-selection

Just as in crop 6 also in crop 9 ICL-selection was applied. The determination of the selection (=culling) levels was based on a scatter diagram illustrating yield and culmlength of the 76 R-plants (see next paragraph). Thus plants yielding at least 141 dg and with a culmlength of at most 179 cm were selected. The number of plants selected for these criteria was 122, clearly more than the desirable number of 76. The successive steps to reduce the number of ICL-plants were:

culmlength(cm)	yield(dg)	number of ICL-plants
≤179	≥141	122
≤178	≥141	113
≤177	>141	102
≤176	≥141	88
≤175	≥141	78
≤175	≥142	75

By adding to this last group a plant included in the last but one group with culmlength 164 cm and yield 141 dg the group of 76 ICL-plants, to be selected in crop 9 was stated. The number of neighbours was not taken into consideration. In Table 53, 5th column, data on these plants are presented. (From that it appears that the maximum culmlength encountered was 177 cm. Indeed, on abuse a plant with culmlength 177 cm and yield 193 dg was included as well.)

The standardized levels amounted to (175-179.7)/19.3=-0.24 for culmlength and to (142-89.9)/57.0=0.91 for yield. In case of normality this would mean that the ICL-plants belonged to the 41% plants with the shortest culms and to the 18% best yielding plants. It would mean further that for yield the selection intensity was much higher than for culmlength.

On the average the ICL-plants had a culmlength which was 9.9 cm (5.5%) less than that of all plants. Their yield was 94.7 dg (105%) higher. Compared with the H-plants the ICL-plants approached better the desired recombinant plant type. How this would work out in the offspring was, of course, a matter of speculation because the levels used were purely arbitrary. Formal criteria to define the culling levels could not be given (see section 5.2.3).

Random selection

It was decided that the number of plants selected at random should be 80 in stead of only the 38 which would be sampled for the comparative trial (crop 13) if that trial was to have the same design as the former comparative trials. This was done as the guess was that sampling only 38 R-plants would be not enough.

In accordance to H-selection and ICL-selection also for R-selection the number of neighbours of the sampled plants was not considered. The restriction that the R-plants should have a minimal yield, 55 dg in this case, had to be applied of course to ensure the availability of enough kernels for crop 13. Afterwards this minimum appeared to be too high. The linear relation between number of kernels (k) and yield in dg (y) among the 80 R-plants was k=27.3+1.4y. Thus 80 kernels could be expected from R-plants yielding 37.6 dg. The surplus of kernels for the applied minimum yield, i.e. [27.3+(1.4×55)]-80=24.3 were (partly) used for additional sowing on empty plant positions in crop 13 (see section 6.3.1).

The restriction meant that 123 row-plant numbers had to be sampled before 80 admissable R-plants were obtained. The R-plants could thus not considered as a representative sample from crop 9. This appears also from the last column of Table 53: on the average the R-plants had longer culms, produced more ears and yielded better than all plants in crop 9. (By chance the best yielding plant in crop 9 happened to be included in the group of R-plants.) This promotes a positive selection response for culmlength but it hampers positive response for yield.

Additional observations on the R-plants

The next observations were recorded on the R-plants as well:
kernel number: the number of produced kernels
kernel yield : the weight (in dg) of the kernels
spikelet number: the number of spikelets

A summary of these observations is presented in Table 54. The coefficients of phenotypic variation were of the same order as those presented for the other characters (except culmlength) observed on the R-plants.

The mean kernel yield covered 100(103.4/121.1)=85.4% of the yield. This conversion factor could also be determined as the coefficient of linear regression of kernel yield to yield, i.e. 0.865.

The mean single kernel weight amounted to (103.4/196.7)=0.526 dg, which was 32% higher than that for the diploid material.

As in section 5.2.2 the mean number of kernels per spikelet was used to measure fertility. When complete seedset implies 2 kernels per spikelet here a seedset of 100(196.7/140.2)/2=70.1% was derived. This seedset is somewhat (5%) lower than the figure cited from Bremer-Reinders (1958), see section 6.1.

Table 54 Summary of observations on additional characters of the 80 R-plants in crop 9. $\bar{x}$: mean; s: standard deviation; cv_p: coefficient of phenotypic variation; min: minimum; max: maximum. Harvest index and yield index are defined in section 6.2.3.

quantity	kernel number	kernel yield (dg)	spikelet number	harvest index	yield index
$\bar{x}$	196.7	103.4	140.2	0.404	0.367
s	71.6	42.4	47.8	0.052	0.054
vc_p	0.36	0.41	0.34	0.13	0.15
min	92	44	72	0.22	0.19
max	464	307	349	0.49	0.48

The obtained seedset amounts to 84% of the seedset which was established for crop 6. The mean number of spikelets per ear was 140.2/4.25=33, which was equal to that for the diploid material. Thus, the larger earsize of the tetraploid plants was not associated with a larger number of spikelets. The mean yield per ear was 121.1/4.25=28.5 dg and the mean kernel yield per ear 24.5 dg (both figures are 13% higher than for the diploid plants). The ears of the tetraploid plants contained less kernels than the ears of the diploids, but their weight was higher because of the higher single kernel weight.

The formal definition of harvest index is: ratio of kernel yield to total biomass (Donald & Hamblin, 1976). However, it is not feasable to determine this quantity for a large number of plants. Therefore it was defined in the present text as: ratio of the weight of the ears of a plant to the weight of the aerial plant parts. For the R-plants also the ratio of kernel yield to the weight of the aerial plant parts was determined. For shortness this ratio was designated here as yield index.

The harvest index for crop 9 as a whole can be determined from data in Table 53. This yields: 89.9/(89.9+137.1)=0.396. Data on harvest index and yield index of the individual R-plants are included in Table 54. The coefficient of phenotypic variation of harvest index appeared to be relatively small.

Table 55 comprises a number of interesting coefficients of phenotypic correlations between characters observed on the R-plants. (Correlations estimated for all plants are presented in Table 67 and discussed in section 6.3.4).

The correlation between yield and culmlength was still lower than that presented in Table 38 for the diploid material. Harvest index and yield index were closely related (r=0.97). Thus harvest index gives a good impression of yield index. The correlation of harvest index and yield amounted to only 0.55. Thus by selection for harvest index not only high yielding plants will be favoured. The relation between harvest index of a parental plant and

Table 55 Phenotypic correlations (r_p) estimated from observations on the 80 R-plants in crop 9

characters	r_p
culmlength-earnumber	-0.03
culmlength-yield	0.22*
earnumber-yield	0.82***
yield-kernel yield	0.99***
yield-straw yield	0.83***
yield-kernel number	0.95***
kernel yield-kernel number	0.94***
harvest index-yield index	0.97***
harvest index-yield	0.60***
harvest index-culmlength	0.16
harvest index-earnumber	0.38***
straw yield-earnumber	0.74***

the yield performance of its offspring is discussed in section 6.3.3.

The correlation of harvest index and culmlength, i.e. r_p=0.16, did not deviate significantly from zero. Thus the suggested negative relation (see section 1.3) was not observed. This relation is discussed more fully in section 6.3.4).

In section 2.2.3 it was supposed that H-selection, in the form in which it was performed, would imply selection for increased harvest index. The mean harvest index of the H-plants amounted to 0.446, which indeed exceeds the mean harvest index of the R-plants. Also the mean harvest index of the ICL-plants, i.e. 0.437, was higher than that of the R-plants.

Comparison of groups of selected plants

The total number of plants selected in crop 9 was 216, i.e. 76 H-plants, 76 ICL-plants and 80 R-plants. The manner in which the selection methods overlapped is shown in Table 56. Like in section 5.2.3 by far the most plants selected by H-selection were not selected by ICL-selection as well. The interesting group HI comprised only 11 plants. The differences between the H- and the I-group were larger in the tetraploid material (Table 56) than in the diploid material (Table 39).

Table 56 Classification of the 216 plants, selected in crop 9, according to the procedure(s) for which the plants were selected.
n: number of plants; $\bar{x}$: mean; s: standard deviation; min: minimum; max: maximum; I=ICL.

		culmlength (cm)				earnumber				yield (dg)			
group	n	$\bar{x}$	s	min	max	$\bar{x}$	s	min	max	$\bar{x}$	s	min	max
R	76	186.6	14.8	144	216	4.14	1.39	2	10	118.0	47.1	55	346
H	64	182.0	6.24	164	198	5.20	1.30	3	10	155.9	33.9	108	245
I	61	169.9	5.30	151	177	6.95	1.49	4	11	183.7	39.0	143	328
HI	11	169.6	5.39	161	175	7.09	1.14	5	9	190.7	49.0	141	292
IR	3	172.3	0.58	172	173	5.67	0.58	5	6	176.0	45.7	142	228
HIR	1	158				8				196			
	216												

6.3 THE RESULT OF THE SELECTION

6.3.1 Material and method for crop 13

To compare the results of the 3 selection methods a comparative trial (crop 13) was sown which comprised offspring of all 216 plants selected in crop 9. Thus 76 H-families, 76 ICL-families and 80 R-families were included in the trial; 232 entries in all. The trial comprised 232 plots in each of 2 blocks. The plotsizes were the same as in crop 10 (see section 5.3.1). Altogether 464 bags were prepared, each containing 20 or 40 kernels disinfected with Quinolate.

In crop 13 the plots sown with an R-family did not form the centre of units of 5 plots, as in crop 10. In that case only 38 R-families would be included in the trial and such was considered to be too few (see section 6.2.3). The lay-out used instead is shown in Figure 15. From the figure it appears that H-families were as often neighbour to an R-family as to an ICL-family.

The families were allotted at random to a plot of their type. A strip contained 19 H-families (each on a single-row plot), 19 ICL-families (idem) and 20 R-families (each on a two-row plot). Its width was $(19+19+(2\times20))\times 0.25=19.5$ m, its depth 1.05 m. The complete trial contained 8 strips, covering $8\times19.5\times1.05=163.8$ m². The border covered 0.75 m on the south- and the north-side and 1 m on the other sides. The border was sown from remnant seed of crop 9.

The trial was sown on a sandy soil, rich in humus, on 11 and 12 October, 1978. Immediately after sowing the field was fenced with wire netting. The emergence in strip 1 was 93.3%. On 7 November plant positions which were not occupied were provided with an additional kernel. Such kernels emerged from 20 November onwards.

In the late autumn it appeared that the plants in strip 8 suffered from wet soil conditions because there was a depression on the spot.

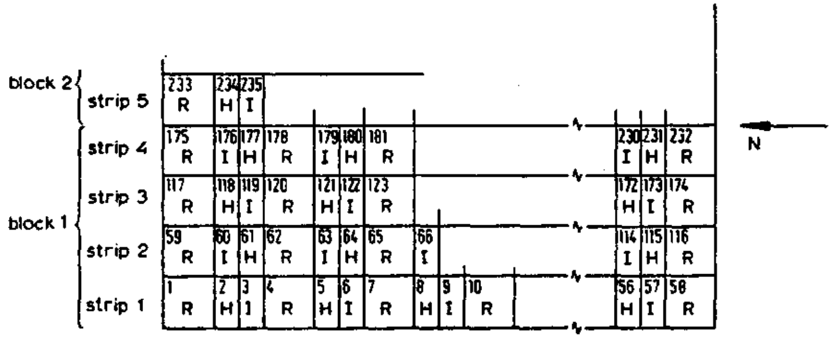

Figure 15 Plan of the trialfield on which crop 13 occurred.
Crop 13 comprised 2 blocks, each consisting of 4 strips with 58 plots.
The plotnumbers as well as the type of family grown on the plots are indicated. H: H-family; I: ICL-family; R: R-family.

The growing conditions were the same as those for crop 10 (see section 5.3.1). On 31 May 1979 the first ears shed pollen. Powdery mildew occurred after 15 June. The plants of crop 13, which did not lodge, were lifted 14 and 15 August.

For each plant of each of the 464 sheaves (=plots) the culmlength was recorded. Earnumber and yield were observed per plot. For each of the sheaves of the 160 plots containing an R-family the weight of the straw was recorded as well.

The sowing of only 1 kernel per plant position instead of 2 meant an additional cause for registration of a number of plants per plot which differed from the intended number (see end of section 5.3.1).

Through several causes no observation was obtained for some plots. The number of plots for which observations were available for the analyses to follow are given by Table 57. The quality of the observations per plot will be variable. The recorded number of plants per plot will deviate quite often from the actual number. On the other hand the reliability of the records for yield (and straw yield) will have been reasonable.

6.3.2 Comparison of the 2 blocks

The 2 blocks were compared by applying the test given by formulae (2.1) and (2.2). The test results are summarized in Table 58.

For all families together the growing conditions in the 2 blocks were not very different: the plants in block 1 produced significantly longer culms, but they yielded somewhat less. The plants of the R-families yielded in block 1 less straw than in block 2.

Table 57 **Number of plots for which observations became available. Crop 13; (i): block 1; (ii): block 2. The underlined numbers indicate completeness of the desired data.**

	H-families		ICL-families		R-families		total	
	(i)	(ii)	(i)	(ii)	(i)	(ii)	(i)	(ii)
culmlength	75	75	76	74	79	80	230	227
earnumber	76	75	76	74	80	79	232	228
yield	76	75	76	74	80	79	232	228
straw yield	0	0	0	0	80	79	80	79
number of plants	70	75	76	74	80	79	232	228

The smaller mean yield in block 1 for the H- and the ICL-families was associated with a higher total yield per block. That lower mean yield rested thus on the larger number of plants per plot in block 1 (in which the plants became taller).

The lower mean straw yield in block 1, associated with a larger total straw yield per plot, followed also from the larger number of plants in the plots of block 1.

The numbers of plant positions and the registered numbers of plants are given in Table 59. This table reveals again that in block 1 more plant positions were occupied than in block 2. Furthermore it discloses that in both blocks the R-families yielded fewer plants than the other types of families. The occupation pooled over the 2 blocks amounted to 90.7%, which is clearly less than the corresponding figure (i.e. 95.2%) for the diploids. Thus the winterhardiness of the tetraploids is somewhat less than that of the diploids.

At several occasions it has been stated that the registered number of plants is biased upwards. This is illustrated by the portion of the plots for which more plants were registered than there were plant positions available:

type of family	block 1	block 2
H	0.053	0.053
ICL	0.053	0.027
R	0.050	0.013

Of course, because of the lower level of occupation of plant positions, such excesses occurred here not as often as in crop 10.

In section 5.3 the analyses were continued for means per plant as well as for means per plant position. This was not done here because the results of those 2 lines of analyses were rather similar.

Table 58 Comparison of the 2 blocks in crop 13. The characters are: (1) mean culmlength (cm), (2) total number of ears per plot, (3) mean earnumber, (4) total yield per plot (dg), (5) mean yield (dg), (6) mean straw yield (dg), (7) total straw yield per plot (dg), (8) number of plants per plot. The meaning of some symbols is: p: the number of pairwise compared plots; $\bar{x}_i$: the mean across the plots in block i; $\bar{d} = \bar{x}_1 - \bar{x}_2$; r: correlation coefficient.

character	families included in the test	p	$\bar{x}_1$	$\bar{x}_2$	$\bar{d}$	s_d	t	$P(\lvert \underline{t}_{p-1} \rvert > \lvert t \rvert)$	r_{x_1,x_2}	t_r	$P(\underline{t}_{p-2} > t_r)$
(1)	all	225	151.3	149.2	2.07	6.7	4.64	~0	0.44	7.32	~0
	H	74	150.1	147.7	2.40	7.1	2.92	~0	0.26	2.28	0.013
	ICL	74	150.7	149.0	1.64	7.2	1.96	0.05	0.28	2.47	0.008
	R	77	152.9	150.7	2.18	5.9	3.25	~0	0.64	7.21	~0
(2)	H	75	55.0	53.0	2.0	10.6	1.64	0.11	0.30	2.69	0.005
	ICL	74	55.0	52.3	2.7	10.1	2.27	0.03	0.19	1.64	0.053
	R	79	109.2	102.2	7.0	17.8	3.51	~0	0.23	2.07	0.021
(3)	all	228	2.93	2.98	-0.05	0.57	-1.37	0.17	0.11	1.66	0.049
	H	75	2.90	2.98	-0.08	0.59	-1.25	0.22	0.19	1.65	0.051
	ICL	74	2.93	3.00	-0.07	0.62	-1.01	0.32	0.05	0.42	0.336
	R	79	2.95	2.95	~0	0.51	~0	~1	0.08	0.70	0.242
(4)	H	75	1207.6	1189.2	18.3	292.3	0.54	0.59	0.28	2.49	0.008
	ICL	74	1199.3	1152.3	47.0	287.6	1.41	0.16	0.30	2.67	0.005
	R	79	2354.9	2226.8	128.0	454.3	2.50	0.01	0.43	4.17	~0
(5)	all	228	63.7	65.9	-2.21	16.7	-2.00	0.05	0.19	2.91	0.002
	H	75	63.6	67.2	-3.53	18.0	-1.70	0.09	0.20	1.74	0.043
	ICL	74	63.9	66.3	-2.43	18.1	-1.16	0.25	0.12	1.03	0.154
	R	79	63.5	64.2	-0.74	13.9	-0.47	0.64	0.28	2.56	0.006
(6)	R	79	71.0	74.7	-3.72	14.7	-2.26	0.03	0.04	0.35	0.363
(7)	R	79	2634.8	2585.4	49.4	471.6	0.93	0.36	0.23	2.07	0.021
(8)	H	75	19.0	17.9	1.1	2.1	4.50	~0	0.23		
	ICL	74	18.8	17.5	1.3	2.5	4.57	~0	-0.03		
	R	79	37.1	34.8	2.4	4.4	4.73	~0	0.02		

Table 59 The number of plant positions and the number of registered plants for each type of families in crop 13.

type of families	block 1				block 2			
	number of rows	number of plant positions	number of registered plant	occupation of plant positions(%)	number of rows	number of plant positions	number of registered plants	occupation of plant positions(%)
H	76	1520	1437	94.5	75	1500	1342	89.5
ICL	76	1520	1431	94.1	74	1480	1295	87.5
R	160	3200	2973	92.9	158	3160	2748	87.0
	312	6240	5841	93.6	307	6140	5385	87.7

Table 60 Correlation between the number of plants per plot on the one side and totals per plot and means per plant on the other side.

type of families	block	earnumber		yield		straw yield	
		total per plot	mean per plant	total per plot	mean per plant	total per plot	mean per plant
H(n=76)	1	0.40***	-0.07	0.35***	-0.05		
	2	0.42***	-0.40***	0.14	-0.40***		
ICL(n=76)	1	0.18	-0.30**	0.27**	-0.10		
	2	0.48***	-0.33**	0.29**	-0.27*		
R(n=80)	1	0.28**	-0.24*	0.26**	-0.11	0.38***	-0.13
	2	0.54***	-0.26**	0.40***	-0.17	0.34***	-0.33***

Pooled over the 2 blocks the H- and the ICL-families occupied 91.4% of their plant positions: the R-families 90.0%, i.e. 1.4% less. This could follow from a poorer seed quality.

The correlations between the number of plants per plot on the one hand and totals per plot and means per plant on the other are presented in Table 60 for earnumber, yield and straw yield. The same trends as for the diploids can be observed from this table. In general the correlations in block 2 deviated more from zero than those in block 1.

Table 61 presents, for each type of families, the total number of ears and the total yield. For the R-families the total straw yield is given as well.

The total number of ears on the 619 rows amounted to 33033. The area occupied was 619×1.05×0.25=162.4875 m^2. Thus, the ear density was 203.3. This is rather low, especially when compared with the corresponding figure for the diploids, i.e. 316. Causes for this are the worse winterhardiness and the worse tillering of the tetraploids. Pooled over the whole trials the mean earnumber amounted to 33033/11226=2.94 in crop 13 and to 101523/23305=4.36 in crop 10. The mean yield per m^2 was 721953/162.4875=4443 dg. The conversion factor for crop 12 amounted to 0.80, thus the mean kernel yield per m^2 was estimated to be 3554 dg. Given the weather conditions and the plant density this was assumed to be a reasonable performance for this young autotetraploid population.

The mean yield per ear was calculated to be 721953/33.33=21.9 dg, which was less than that for the diploids (i.e. 23.1 dg).

The correlation between the performance of a family in block 1 and the performance of the family in block 2 was estimated for all types of families pooled as well as for the separate types of families (see Table 58). In general they were not significant and less than 0.35. Mean culmlength was an exception. For this character, which showed in the former experiments with diploid rye a relatively good repeatability, the correlation among the R-families was twice as high as among the other types of families. It should be remembered in this context that the R-families were grown on plots with a doubled plotsize. This resulted only for culmlength in an increased correlation.

Discussion

Most probably the cause for lower numbers of plants per plot in block 2 was the greater wetness of the soil in block 2, especially in strip 8. For each strip of crop 13 the mean number of plants per plot, the mean culmlength and the mean yield was determined. These means are plotted in Figure 16 against the stripnumber. It appears that the mean number of plants per plot in strip 7 and strip 8 was lower than that in the other strips. At the same time the mean yield was high in these strips. In strip 5 the mean

Table 61 The total number of ears, the total yield (in dg) and the total straw yield (dg) for the types of families in crop 13.

type of families	block 1				block 2			
	number of rows	number of ears	total yield	total straw yield	number of rows	number of ears	total yield	total straw yield
H	76	4172	91466		75	3976	89194	
ICL	76	4200	91758		74	3872	85268	
R	160	8739	188348	210827	158	8074	175919	204249
	312	17111	371572		307	15922	350381	

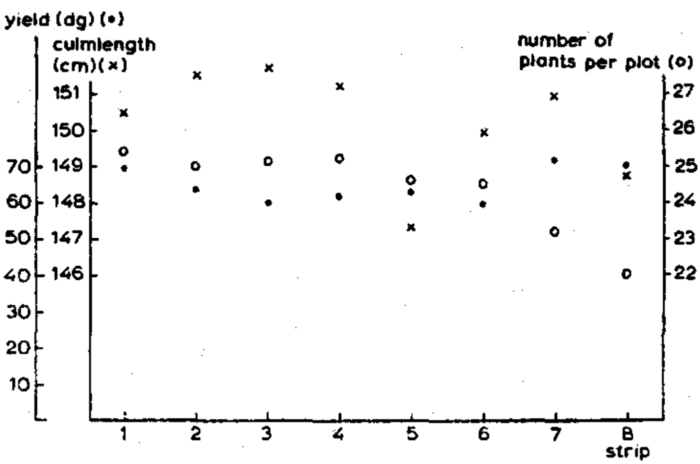

Figure 16 Mean yield (•), mean culmlength (x) and mean number of plants per plot (o) in each strip of crop 13.

culmlength was remarkably low. Figure 16 proves that the supposition of uniform growing conditions within a block could not be justified.

The establishment in section 5.3.2 that a larger plotsize did not inflate the correlation coefficient, except for culmlength, was arrived at also for the tetraploid material in crop 13.

Correlations for means per plant were always less than the corresponding ones for totals per plot. This reflects the better quality of the observations which concerned plot totals.

6.3.3 The relation between R-plants (crop 9) and their offspring (crop 13)

Introduction

The development of models for inheritance of quantitative characters is much more advanced for diploids than for tetraploids. Levings & Dudley (1963) discussed some possibilities to estimate for allogamous autotetraploid populations interesting quantitative genetic parameters. In case of absence of inbreeding, of double reduction and of epistasis the genetic variance in a tetraploid population can be written as

$$\sigma^2_g = \sigma^2_a + \sigma^2_d + \sigma^2_t + \sigma^2_f \qquad (6.1)$$

In this expression σ^2_a and σ^2_d *represent* the variance *components* that *are* well-known for diploid populations. The components σ^2_t and σ^2_f represent genetic variance due to the intra-locus interaction of the 3, resp. 4 alleles present within an individual.

For the former assumptions it was derived that

- the genetic covariance of parent and offspring is given by

$$\mathrm{cov}(g_P, g_{HS}) = \frac{1}{2}\sigma^2_a + \frac{1}{6}\sigma^2_d \qquad (6.2)$$

- the genetic variance between families of half sibs equals

$$\mathrm{var}(g_{HS}) = \frac{1}{4}\sigma^2_a + \frac{1}{36}\sigma^2_a \qquad (6.3)$$

These 2 expressions, which pertain to the same quantities as expressions (2.5) and (2.6), contain the component σ^2_d because in autotetraploids the gametes comprise 2 alleles per locus.

Notwithstanding the appearance of this component σ^2_d in the expressions (6.2) and (6.3) Levings & Dudley (1963) stated: "For prediction of short term response to selection twice the parent-offspring regression should be an adequate estimate of h^2_n". This is the usual approach for allogamous diploids for a character that is observed after flowering. The assumptions which should hold to justify such estimation were discussed in section 2.3.4. A few additional remarks on the effect of autotetraploidy are given here.

Because of confounding of the effects of inter-locus interaction and the effects of intra-locus interaction estimation of σ^2_{aa} by solution of formulae (2.5) and (2.6) would be biased by σ^2_d. The reverse is true when σ^2_d is estimated by solution of the expressions (6.2) and (6.3). Thus for autotetraploids the relative importance of the role of epistasis in the genetic variance is still more difficult to ascertain than for diploids.

The assumption of random mating equilibrium, both per locus and across loci, might sometimes be justifiable. However, in autotetraploids the attainment of such equilibria requires more generations of random mating than in

Table 62 Skewness for some characters observed on 80 R-plants in crop 9 and their offspring in crop 13.

character	R-plants	offspring (mean per plant)
culmlength	-0.57*	-0.44
earnumber	1.10***	0.17
yield	1.42***	0.63*
straw yield	1.01***	0.26
harvest index	-0.90***	-0.08

diploids. Thus for the R-plants from the young population grown as crop 9 and for their offspring the assumption of random mating equilibrium can not be justified. The weakening of self-incompatibility in this autotetraploid material allows even a certain degree of inbreeding. In section 6.2.3 it was already indicated that the R-plants did not form a representative sample of crop 9.

The warning in section 2.3.4 not to set too much value to the estimates of quantitative genetic parameters applies even more in the case of autotetraploidy. The translation of estimates of statistical quantities in terms of estimates of quantitative genetic parameters deserves utmost reserve. The observation by Speckman (personal communication) that during the meiosis of this tetraploid material relatively many bivalents and few quadrivalents were formed - this indicates a diploid behaviour of the chromosomes - may not weaken the above restriction.

Results

In Table 62 the estimates of skewness for several characters of the 80 R-plants and their offspring are presented. According to Pearson & Hartley (1970), Table 34.B, there was significant skewness for each character mentioned for the R-plants. The positive skewness for earnumber, yield and straw yield will partly rest on the strong positive phenotypic correlations between these characters (see Table 55). The degree of skewness for yield, and also for its associated characters, will have been enhanced by the requirement that the R-plants should yield at least 55 dg.

The established skewnesses imply that tests based on normality can not fully be justified. Then the results have only an indicative value. This pertains especially when testing the null hypothesis H_0: "the regression of offspring on parent is zero", i.e. H_0: $\beta=0$, against H_a: $\beta>0$. This test is done by testing the null hypothesis H_0: "there is no correlation between offspring and parent", i.e. H_0: $\rho=0$, against H_a: $\rho>0$.

Table 63 Estimates, for 5 characters, of the parameters mentioned in section 2.3.4. The estimates are based on observations on 80 R-plants in crop 9 and on their offspring in crop 13.

	character				
estimated parameter	culmlength(cm) (n=77)	earnumber (n=79)	yield(dg) (n=79)	straw yield(dg) (n=79)	harvest index (n=79)
α	109.0	2.91	57.4	70.5	0.37
β	0.23	0.007	0.05	0.012	0.23
ρ	0.56	0.037	0.28	0.089	0.52
t_r	5.85	0.32	2.53	0.79	5.34
$P(\underline{t}_{n-2}>t_r)$	~ 0	0.37	0.006	0.22	~0
$\bar{x}$	185.7	4.25	121.1	174.1	0.404
$\bar{y}$	151.9	2.94	63.7	72.6	0.466
σ^2_x	225.2	2.11	2357.2	2862.0	0.003
σ^2_y	37.8	0.075	84.1	55.6	0.001
h^2_n	0.46	0.014	0.10	0.02	0.46
$cov(\underline{x},\underline{y})$	51.9	0.0148	123.9	35.8	0.0006
σ^2_a	103.8	0.0296	247.8	71.7	0.0012
vc_a	0.055	0.040	0.130	0.049	0.086

The results of this test as well as estimates for the parameters mentioned in section 2.3.4 are presented in Table 63. The relation between R-plants and their offspring is illustrated in Figure 17 for the character harvest index.

For some parameters estimates were obtained from the H- and the ICL-plants and their offspring as well. These are presented in Table 64.

Discussion

The autotetraploid material was included in the experiments because it was hoped that this material would offer better opportunities to realize selection responses (see section 1.2). Nevertheless for culmlength, earnumber and yield the obtained estimates for the additive genetic variance and for the heritability in narrow sense were similar to the corresponding estimates obtained for the diploid material (compare Table 63 with e.g. Table 46). The perspectives on the strength of these estimates are therefore disappointing. It should be realized however that the operational value of the estimates is controversial.

The estimate for the heritability of yield was higher than ever obtained for the diploid material, it was even significant, but its value was still

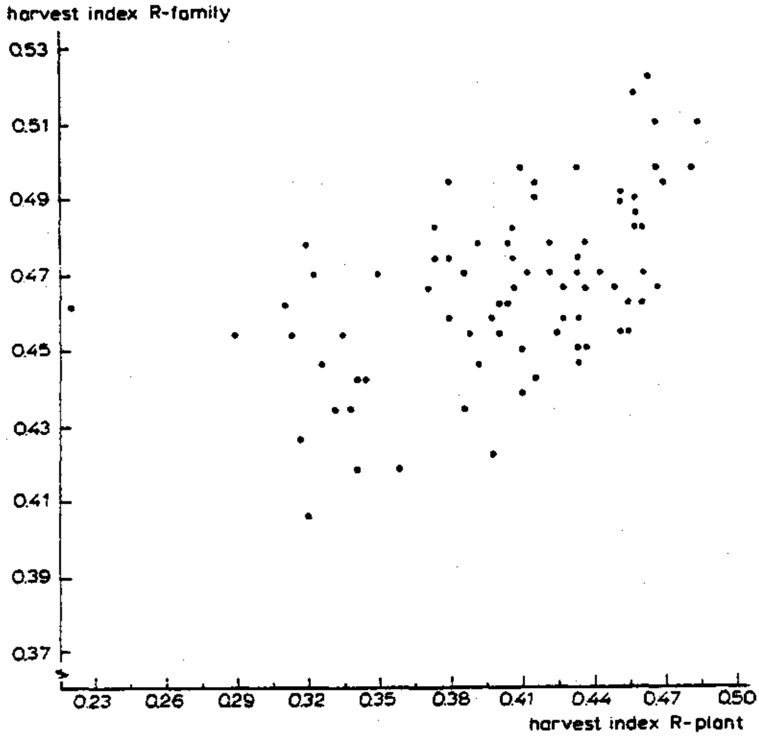

Figure 17 Relation between the mean harvest index of the members of an R-family (y) and the harvest index of their common parent (x). The relation is depicted for 80 R-plants (crop 9) and their offspring (crop 13).

low. The estimates for straw yield and for earnumber were both very unfavourable. The estimates for culmlength and harvest index were rather promising. The value for culmlength confirmed earlier estimates for diploid material. The estimate for harvest index was very surprising: h_n^2=0.46. The correlation between parents and offspring amounted to r_p=0.52. These estimates were obtained notwithstanding an exceptional low harvest index, i.e. 0.22, for one of the R-plants (see Figure 17). This plant had a culmlength of 170 cm, it yielded 66 dg, the 124 spikelets on the 4 ears contained only 137 kernels (seedset 55%). Its straw yield was 234 dg. Possibly one or more ears were lost from this exceptional plant. After withdrawing of this R-plant from the calculations the next estimates were obtained for harvest index: h_n^2=0.53, r_p=0.55.

The suggestion in section 6.2.2 to apply truncation selection for harvest index appears to be applicable indeed. The more so because the correlation between harvest index of the parent and yield of its offspring amounted to 0.42 (and also to 0.42 after withdrawing the exceptional R-plant).

Table 64 Estimates, for 3 characters, of some of the parameters mentioned in section 2.3.4. The estimates are based on observations on plants selected in crop 9 and on their offspring in crop 13. The values for $\bar{x}$ are derived from Table 53.

character	estimated parameter	selection procedure	
		H-selection	ICL-selection
culmlength(cm)	n	74	74
	β	0.16	0.10
	ρ	0.28	0.11
	t	2.47	0.94
	$P(\underline{t}_{n-2}>t)$	0.008	0.18
	$\bar{x}$	179.9	169.8
	$\bar{y}$	149.0	149.9
	σ^2_y	20.5	22.7
earnumber	n	75	74
	β	-0.006	-0.02
	ρ	-0.025	-0.10
	t	-0.21	-0.85
	$P(\underline{t}_{n-2}>t)$	0.58	0.80
	$\bar{x}$	5.51	6.93
	$\bar{y}$	2.93	2.96
	σ^2_y	0.13	0.10
yield (dg)	n	75	74
	β	0.056	0.06
	ρ	0.20	0.25
	t	1.74	2.19
	$P(\underline{t}_{n-2}>t)$	0.04	0.02
	$\bar{x}$	161.5	184.6
	$\bar{y}$	65.1	64.8
	σ^2_y	114.2	95.8

In contrast to the present finding, Donald & Hamblin (1976) obtained for harvest index such a low estimate for its heritability that they concluded that harvest index is not suited for indirect selection for yield in case of intergenotypic competition.

Spitters (1979), p.189 and 190, observed absence of association within pure lines of barley, between harvest index and biomass of individual plants. He therefore concluded that harvest index would not be influenced 'by competition that originates from non-genetic causes'. Also intergenotypic competition appeared hardly to influence harvest index. The masking effect of intergenotypic competition on the genotypic value for yield or for biomass would thus be circumvented by selection for harvest index.

Thus far it is not known of this applies to diploid and tetraploid rye. Because of the favourable perspectives experiments to assess this were started in 1981.

The coefficients of correlation presented in Table 63 for the tetraploid material were generally higher than those for the diploid material (Table 46).

The additive genetic standard deviation amounted for culmlength 10.2 cm. When the breeding value for culmlength of the individual plants would have a normal distribution, then 2.28% of the plants would have a breeding value for culmlength of at least 2×10.2=20.4 cm below the population mean. Likewise 2.28% of the plants would have a breeding value for yield of at least 2×15.7=31.4 dg above the population mean. Because of the positive correlation between culmlength and yield the combination of the 2 conflicting 'limits of selection' in a recombinant plant type will be a hard job.

Comparison of the parental means ($\bar{x}$) with the means of the offspring ($\bar{y}$) affords an oppertunity to study the modifying effect of the prevailing growing conditions on the performance of succeeding generations. Except for harvest index the parents performed better for each character (see Table 63). The following considerations are relevant in this context:

(i) the winter and spring conditions for crop 13 compare unfavourable with those for crop 9. This will be the main cause for the large differences between the 2 generations for culmlength and earnumber. The smaller culmlength of the offspring might have caused their higher harvest index;

(ii) the parents had a plant density of 50, their offspring a density of 80. The tillering of the plants did not reflect this difference. This is most probably due to the dominating effect of the adverse growing conditions for crop 13;

(iii) the R-plants did not form a representative sample of crop 9. On the average they were taller and yielded better than the respective means for all plants.

The estimates presented in Table 64 are based on observations on selected plants and on their offspring. After H-selection there was still a significant correlation between parents and offspring for both culmlength and yield. After ICL-selection this was only obtained for yield.

In contrast to what was obtained for the diploids (see section 5.3.3) now for culmlength smaller values for β were obtained after H- and after ICL-selection than after R-selection. Also the variance among the families was smaller.

However, for yield somewhat larger values for β were obtained after H- or ICL-selection. This could be an incident, although the variance among the families was also larger than among the R-families. Thus here again the possibility of increased genetic variation after selection was open. A possible explanation for this is given in section 7.4.

The estimates for vc_a corresponded rather well with those for the diploid material (compare e.g. Table 63 with Table 46). Their values were much lower

Table 65 Analysis of variance for 4 characters of the 80 R-families in crop 13.

character		source of variation		
		R-families (df=79)	blocks (df=1)	error df=76)
mean culmlength (cm	SS	5868.9	182.7	1315.5
	MS	74.3	182.7	17.3
	f	4.29***	10.6**	
mean earnumber	SS	11.86	0.014	9.7
	MS	0.15	0.014	0.128
	f	1.18	0.11	
mean yield (dg)	SS	13625	57.2	7172
	MS	172.5	57.2	94.4
	f	1.83**	0.606	
mean straw yield (dg)	SS	9083	642.8	8175
	MS	115	642.8	107.6
	f	1.07	5.98*	

than those for vc_p (see Table 53 and 54). Even for culmlength and for harvest index vc_p was about twice as large as vc_a.

An analysis of variance for the R-families is presented in Table 65. Based on expression (6.3) it was supposed that the genetic variance between families is primarily due to σ_a^2. Estimates of σ_a^2 were thus obtained in the usual way (by equating expression (6.3) to expression (2.9)). By that the contribution by σ_d^2 was ascribed to σ_a^2. Thus an additional cause for overestimation of σ_a^2 was built in. The obtained results did not sustain this consideration.

Table 58 was confirmed by the establishment of a significant block effect for mean culmlength and for mean straw yield. Table 63 was confirmed by the establishment of a significant family effect (which implies significant genetic variation) for mean culmlength and for mean yield. The estimates for σ_a^2, which were obtained from Table 65, amounted to 114 cm^2 for culmlength and to 156.2 dg^2 for yield. Table 63 presented 103.8 cm^2 resp. 247.8 dg^2 as estimates derived from the regression analysis. Thus for yield, the character which reacts very sensitive on environmental variation, a much lower value was obtained. This deviates from our expectation that the analysis of variance will tend to result in higher estimates for σ_a^2 (due to inclusion

Table 66 Analysis of variance for 3 characters of the 76 H-families and of the 76 ICL-families in crop 13

character		*H-families* source of variation			*ICL-families* source of variation		
		H-families (df=75)	blocks (df=1)	error df=73)	ICL-families (df=75)	blocks (df=1)	error df=73)
mean culmlength (cm)	MS	42.4	213.5	25.0	44.9	99.2	25.9
	f	1.7*	8.5**		1.7*	3.8	
mean earnumber	MS	0.255	0.250	0.175	0.212	0.198	0.194
	f	1.5	1.4		1.1	1.02	
mean yield (dg)	MS	238.1	456.7	163.7	206.1	219.6	163.6
	f	1.46	2.79		1.26	1.34	

in the estimate of genotype × environment interaction as well as to the neglect of σ_d^2). In section 7.4 the results, obtained in course of the experiments, of the 2 methods for estimating σ_a^2 are discussed.

This kind of analysis of variance was also made for the H-families and for the ICL-families (see Table 66). The results confirm those presented in Table 58. Estimates for the (additive) genetic variance amounted for the H-families to 34.8 cm² for culmlength and to 148.8 dg² for yield. For the ICL-families we obtained 38 cm² resp. 85 dg². These estimates were always less than the estimates obtained from the analysis of variance for the R-families. So this type of analysis did not support the suggestion of increased genetic variance for yield after H-selection or after ICL-selection.

Just as in section 5.3.3 for the diploid material here also yield per ear was studied as a character for indirect selection. Mean and coefficient of phenotypic variation amounted to:

	R-plants	R-families
$\bar{x}$(dg)	28.9	21.7
vc_p	0.24	0.12

The parents produced heavier ears than their offspring. Possible causes for this might be the worse winter and spring conditions for crop 13 as well as the larger plant density for the R-families.

The regression of offspring mean on parental value amounted for yield per ear to 0.182 (while r=0.51***). Thus its heritability in the narrow sense was estimated to be 0.36, which is much higher than the value for yield (i.e. 0.10). Therefore also for this tetraploid material it appears attractive to start indirect selection to improve kernel yield by selecting for high yield per ear. Experiments to verify this were started in 1981.

6.3.4 Phenotypic and genetic correlations

Coefficients of phenotypic correlations were estimated for all plants in

Table 67 Phenotypic correlation (r_p) estimated from observations on all plants in crop 9 and on the 80 R-plants in crop 9; genotypic correlations (r_g) were estimated from observations on these R-plants and on their offspring. The 3 methods to estimate ρ_g are explained in section 6.3.4.
+: correlation could not be determined

characters	r_p		r_g		
	all plants (n=4471)	R-plants (n=80)	(1)	(2)	(3)
culmlength-earnumber	0.31***	-0.03	0.47	0.27	0.03
culmlength-yield	0.53***	0.22*	0.58	0.30	0.34
earnumber-yield	0.84***	0.82***	0.45	0.42	0.16
culmlength-straw yield	0.53***	0.19*	1.47	1.19	
culmlength-harvest index	0.41***	0.16	-0.03	+	
earnumber-straw yield	0.83***	0.74***	-1.79	-1.77	
earnumber-harvest index	0.41***	0.38***	1.81	1.35	
yield-straw yield	0.91***	0.83***	0.60	0.60	
yield-harvest index	0.61***	0.60***	1.02	0.98	
straw yield-harvest index	0.33***	0.09	0.30	0.29	

crop 9 as well as for the 80 R-plants sampled in crop 9 (see Table 67). The latter were already presented in Table 55. The observation that the R-plants could not be considered as a representative sample of crop 9 (see section 6.2.3) is confirmed by the large difference between corresponding phenotypic correlations in the 2 sets. Comparison of the r_p values in Table 67 with those in Table 50 shows however that the rank of the correlations determined for each set is the same for all sets.

Because of skewness of the distribution for the characters the result of the test of H_0: $\rho_p=0$ against H_a: $\rho_p\neq0$ deserves cautious treatment.

The positive correlation between culmlength and harvest index was at its highest (and only then significant) for all plants ($r_p=0.41$). Among the R-plants it was $r_p=0.16$, among the ICL-plants $r_p=0.04$ and among the H-plants $r_p=-0.07$. Thus the positive correlation among all plants is due to positive correlation among plants which did not came into consideration for selection.

Selection for increased harvest index, which was advocated in section 6.3.3, does not necessarily mean that, as a correlated response, the culmlength will increase. It is interesting to compare the above correlations with the mean harvest index for all plants (0.37), for the R-plants (0.41), the ICL-plants (0.44) and the H-plants (0.45). It seems that the correlation between culmlength and harvest index is the lower, the higher the mean harvest index.

The genetic correlations were estimated by means of expressions (2.11)

Table 68 Weighted means per plant for culmlength, earnumber and yield; mean number per plants per family. Results from crop 13

character	selection procedure			
	H-selection	JCL-selection (n=74)	R-selection	HI-selection (n=12)
culmlength (cm)	149.0 (n=74)	149.9	151.9 (n=77)	148.8
in %	98.1	98.7	100	97.9
earnumber	2.93(n=75)	2.96	2.94(n=79)	3.06
in %	99.7	100.7	100	104.1
yield (dg)	65.14(n=75)	64.76	63.67(n=79)	68.26
in %	102.3	101.7	100	107.2
number of plants per family	36.88(n=75)	36.31	71.9(n=79)	34.4 (n=11)
occupation of plant positions (%)	92.2	90.8	89.9	85.6 (n=11)

and (2.12) as well as by means of an analysis of covariance. The respective results are presented in Table 67.

Because of the large differences among estimates for the same pair of characters not too great an importance should be attached to the presented values for r_g. This is clearly exemplified by the figures for the correlation between culmlength and earnumber.

The genetic correlation between culmlength and yield was moderately high; that between yield and harvest index was high and that between harvest index and culmlength was negligible. These 3 values deserve a positive appreciation, but their reliability is quite small.

6.3.5 The actual result of selection

The results

Crop 13 was grown to observe the result of the different selection methods. The means of the families are presented in Table 68.

Kruskal and Wallis' median test was applied to test H_0: "the 3 selection methods yielded equivalent offspring" against its alternative H_a: "the 3 methods did not yield equivalent offspring". Thus formula (3.4) with k=3, yielded next results:

character	H	critical level
culmlength	12.2	0.002
earnumber	0.23	0.893
yield	1.17	0.556

H_0 had to be rejected only for culmlength, thus only for this character the test of Mann-Whitney was applied. This was done in the manner described in section 5.3.5. The results were:

null hypothesis	alternative hypothesis	critical level
H=R	H<R	~0
ICL=R	ICL<R	0.007
H=ICL	H≠ICL	0.315

So the culmlength was significantly decreased by H-selection as well as by ICL-selection. Both these methods were equivalent in this respect.

The plots with H-families and those containing ICL-families comprised equal numbers of plant positions. Therefore the H-families were compared with the ICL-families for total number of ears per family as well as for total yield per family. The results of the test of Mann-Whitney were:

character	H_0	H_a	critical level
total number of ears	H=ICL	H≠ICL	0.824
total yield	H=ICL	H≠ICL	0.369

No significant differences were obtained, notwithstanding differences between the 2 methods for the plants which were selected (see selection 6.2.3).

Discussion

In all selection fields (except crop 6) R-selection implied selection of plants with longer culms and higher yield than the respective means of all plants. This promotes the observation in the comparative trials of a selection response for culmlength but it hampers such observation for yield. From this point of view a better procedure would have been to destine from each plant in the selection field a few kernels (e.g. 3) to form a mixture to be grown as the standard in the comparative trial. However, such procedure is rather laborious. Furthermore it does not allow estimation of statistical quantities on a family basis. (Some of such quantities might be interpreted in quantitative genetic terms.) As a partial way-out, from 1981 the offspring of modal plants will be used as standard.

In section 7.1 it is explained that progress by one cycle of mass selection might be negligible or even be negative. Thus not to much attention should be given to the development of procedures measuring response to one cycle of mass selection.

From Table 68 it appears that the R-families occupied a lower percentage of their plant positions than did the other types of families (see also section 6.3.2). The reason for this was suggested to be an inferior seed quality. (The bearing of seed quality, as measured by single kernel weight, is treated in section 8.4.) This lower occupation of the available plant positions was not associated, as might be expected, by an increased earnumber.

The result of the selection corresponded with the aims: the offspring of the H-plants and that of the ICL-plants produced shorter culms than the R-families whilst their yield was better than that of the R-families. H-selection performed slightly better than ICL-selection with view on promoting a recombinant plant type. This could not be expected immediately after the selection. Table 56 shows that the ICL-plants reflected better our desire to promote a recombinant plant type than did the the H-plants. Nevertheless the H-families came closer to that goal than the ICL-families.

This could rest on the fact that, unlike H-selection, for ICL-selection no restriction of the environmental influence on the phenotypic value was pursued. On the whole the result of H-selection and that of ICL-selection differ so little that no meaning should be attached on the difference.

From a practical point of view one might prefer to apply ICL-selection in stead of H-selection, because in that case one can reject inferior plants immediately, while for H-selection one has to observe all plants. However for application of HI-selection (see later), which turned out to give quite good results one also has to observe every plant in the selection field.

The response to selection was only significant for culmlength. This could be expected because of the much higher heritability of this character. As mentioned at the beginning of this discussion it could also be expected because the R-plants deviated from crop 9 as a whole by a larger culmlength (which enhanced positive selection response for culmlength). Absence of significant selection response for yield can be explained by a similar reasoning.

The H-families did not differ from the ICL-families for total number of ears per family (neither for total yield per family). This could be the combined effect of the H-families having a smaller earnumber but a better occupation of plant positions.

From Table 56 it can be seen that the 11+1=12 plants which were selected by H-selection as well as by ICL-selection, came closer to the selection goal than either the H-plants or the ICL-plants.

Although there were only 12 such HI-plants the performance of their offspring deserved interest. Table 68 shows that the offspring of the HI-plants did very well: the mean culmlength of the 840 offspring plants was 2.1% lower than that of the R-families, their yield was 7.2% better.

Compared with HI-selection in crop 6 this kind of selection seemed to perform much better in crop 9. Experiments to clarify the efficiency of HI-selection better were initiated in 1981.

Notwithstanding the observation that the selection responses were in the desired directions these responses were rather small. Three causes are supplied for this:

(i) It appeared that the genetic variation, as measured by vc_a, in crop 9 was hardly larger than that in crop 6 (compare Table 63 with Table 46). This could rest on both natural selection and random drift during the years before the present experiments (see section 6.1).

(ii) Selection against a recessive genotype responds in a tetraploid population with a much smaller decrease in the frequency of the recessive allele than in a diploid population (Bos(1974), p.87). Thus in autotetraploids responses tend to be small compared with those in diploids.

(iii) The visible result of selection is the net result of artificial selection which aims at changes for characters of agronomic interest (with a correlated response for fitness) and of natural selection which aims at an increase of the mean fitness (Falconer (1960), p.330-332). This net result of selection will be small when there is a strong tendency to genetic homeostasis. It is possible that such tendency is stronger in autotetraploid populations than in diploid populations. This would hamper efforts to realize selection results.

The tetraploid plants in crop 9 were grown under the same conditions as the diploid plants in crop 7. Next list contains the mean performances of the 2 types of rye material:

character	diploids	tetraploids	id.,as % of the diploids
drop outs (%)	3.6	15.7	
culmlength (cm)	158.8	179.7	113
earnumber	4.07	3.69	90.7
yield (dg)	103.7 †	89.9	86.6
straw yield (dg)	136.4 †	137.1	100.5
biomass (dg)	240.1 †	227.0	94.5
kernel yield (dg)	89.4 †	76.7	85.8
yield index	0.372†	0.338	90.3
kernel yield (dg/m²)	4355	3318	76.2
kernel yield per ear (dg)	21.7 †	20.8	95.9
single kernel weight (dg)	0.398†	0.526††	132
spikelets per ear	32.7 †	33 ††	101
kernels per spikelet	1.675†	1.403††	84
seed set (%)	83.75 †	70.1 ††	84
ear density	201.4	159.6	79.2

† data from the 200 plants in row 76, 77 and 78

†† data from the R-plants

Table 69 Performance of the H- and the ICL-families, expressed as a percentage of the performance of the R-families.

character	type of families	n	min	max	arithmatic mean	geometric mean
culmlength	H	147	82.2	110.6	98.0	97.8
	ICL	148	85.7	111.1	98.7	98.5
earnumber	H	150	54.1	171.0	101.2	100.0
	ICL	149	65.1	157.8	102.5	101.2
yield	H	150	56.5	188.4	105.1	102.3
	ICL	149	50.1	204.3	104.7	101.9

When studying the above list one should realize that the differences are not only due to the difference in ploidy but also to differences in gene-frequencies. The diploid population was derived from Dominant (a successfull commercial variety), the tetraploid population was based on a mixture of land varieties originating from different parts of Europe. Further self-incompatibility might be weakened or even be absent in the autotetraploid plants. Thus some inbreeding depression might be present in crop 9.

The result of the selection in crop 9 was also determined by means of expressing the performance on plots with the H- and the ICL-families as a percentage of the performance on neighbouring plots with an R-family (each H- and each ICL-family was adjacent to an R-family; see Figure 15). The performances were expressed as means per plant. These means were used to calculate the percentages. Table 69 presents characteristics of the distribution of these percentages.

For culmlength the arithmatic means presented in Table 69 confirm those in Table 68 quite good, but for earnumber and for yield higher values were obtained. A possible cause for this is the tendency of positive skewness which seems to be present for these characters (compare the location of minima and maxima with the means). Such skewness occurs rather often for ratios or percentages. The geometric mean is then a better yardstick for the centre of the distribution than the arithmatic mean. This geometric mean can easily be derived from the arithmatic mean of the logarithmic values of the individual figures.

Indeed the geometric means, presented in Table 69 are closer to those in Table 68 than the arithmatic means. Herewith a solution has been given for the problem indicated at the end of section 4.3.5.

It was concluded that an experimental design with fixed positions for the plots with the diverse types of families does not imply an improvement with regard to a design for a comparative trial in which the families are randomly allocated to the plots without any restriction. This detracts nothing of

Table 70 Predicted response ($\hat{R}$) and realized response (R) after H- and ICL-selection for culmlength, earnumber and yield; b: regression of offspring mean on parental value, S: selection differential

		H-selection			ICL-selection		
character	b	S	$\hat{R}$	R	S	$\hat{R}$	R
culmlength (cm)	0.23	0.2	0.05	-2.9	-9.9	-2.28	-2.0
earnumber	0.007	1.82	0.01	-0.01	3.24	0.02	0.02
yield (dg)	0.05	71.6	3.58	1.47	94.7	4.73	1.09

the value of growing check plots on fixed positions under conditions of practical breeding (e.g. when rating in the field under heterogeneous soil conditions).

Response to selection can be predicted by means of equation (3.5). This equation should hold irrespective of the ploidy level. Predicted responses, calculated from estimates for β (see Table 63) and from S (derivable from Table 53), and realized responses are compared in Table 70. The correspondence between predictions and realizations was rather good when measured by the coefficient of correlation (r=0.76). Nevertheless, there were large differences between prediction and realization.

In the present case the main reason for the differences between prediction and realization must have been the use of a biased sample of R-plants. Another explanation which could be applicable was indicated by Spitters (1979), p.218. This rests on the possibility that the linear relationship between offspring and parent among the sampled plant material differs from that among the selected material. Table 70 is based on the regression of offspring on R-plants. The regressions obtained after H- resp. ICL-selection were given in Table 64. They amounted resp. to 0.16 and 0.10 for culmlength, to -0.006 and -0.002 for earnumber and to 0.056 and 0.06 for yield. Thus for culmlength too high a value for b might have been applied in Table 70.

7 *THE CUMULATIVE EFFECT OF CONTINUED HONEYCOMB SELECTION*

7.1 INTRODUCTION

It is a well-known fact that the result of a single application of mass selection for a quantitative character is strongly influenced by incidental circumstances. This has been reported for maize by Gardner (1978) when selecting for yield and by Dudley (1974) for selection for oil and protein content. The progress which has been realized by selection in a certain year is cancelled another year. Evidently, the phenotypes selected in a certain year represent other genotypes than those selected in the next generation. This follows from the fact that the growing conditions for the population to be selected vary. Not only the location (and thus the soil) but especially the weather can vary considerably. Because genotype × environment interaction is an important factor with yield, the phenotypes preferred one year may largely represent genotypes that, because of their phenotypes, were rejected a generation before. In this sense one might say that continued mass selection for a character that is greatly modified by genotype × environment interaction, resembles tandem selection, where different goals of selection are pursued in different generations. The progress by selection effected in a single application of mass selection could then be positive, nil or even negative. It is therefore better to evaluate the cumulative effect of continued mass selection. In the present study it was investigated what was the effect of 3 successive interventions through honeycomb selection on the original populaton.

7.2 MATERIAL AND METHOD

In the season 1978-79 a comparative trial (crop 11) was grown. It comprised 3 entries which were labelled P_o, P'_o and P_3. The meaning of these labels is:

- P_o: the original variety Dominant as it was obtained from the breeder in the summer of 1978
- P'_o: this material was obtained by a single multiplication (crop 8) of remnant seed left after starting the experiments with crop 1
- P_3: this denominates the population obtained after application of honeycomb selection during 3 successive generations followed - in crop 6 - by a single generation with intermating in the absence of selection.

Seed quality is a rather important factor when comparing the performance of different entries (see section 8.4). Therefore, in addition to P_o a multiplication of P_o was made under the same climatic conditions that prevailed

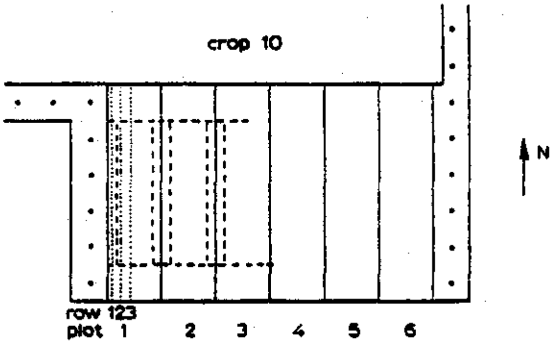

Figure 18 Scheme of lay-out for crop 11. The dotted area indicates the border.

in crop 6 (from which P_3 was obtained). This should warrant similar seed quality of P'_o and P_3. (The large influence of the season on mean single kernel weight can be illustrated by comparing the value for crop 2, i.e. 0.303 dg, with that for crop 4, i.e. 0.425 dg.)

Because P_o consists of a synthetic variety in the Syn-2 or the Syn-3 generation (see section 2.3.4) the effect on the genetic composition of an additional generation of intermating in crop 8 will have been small. Thus the genetic compositions of P_o and P'_o were assumed to be almost identical.

P_3 was obtained by sampling 102 R-plants in crop 6. These R-plants formed a representative sample (see section 5.2.3).

Crop 8 was sown on 7 November, 1977. It covered 3.75×9=33.75 m², i.e. 15 rows each 9 m long (interrow distance 25 cm). The crop was quite heterogeneous. It suffered from powdery mildew since the beginning of May, 1978. On 14 August the plot was harvested with a mini-combine. The yield amounted to 96500 dg, which corresponds with only 2859 dg/m².

The 3 entries of crop 11 (P_o, P'_o and P_3) were compared at normal crop density. A plot comprised 6 rows each 6 m long. The interrow distance was again 25 cm. A single plot covered thus 9 m². Because the trial was in twofold 6 plots in all were grown (see Figure 18).

It is generally accepted that a plant density of 250 in a commercial grain crop is optimal. (The Dutch list of varieties 1978 advises a sowing rate of 90 kg/ha, i.e. 90 dg per m². A mean single kernel weight of 0.40 dg (see section 5.2.2) implies then 225 kernel per m².) A number of 250 plants per m² means for each entry a total of 2×9×250=4500 plants. To realize this per entry 12 bags (for each row 1 bag) each containing 170 dg were prepared. Thus per row about 170/0.4=425 kernels were sown. This corresponds with 2×6×425=5100 kernels per entry. To obtain these 50 kernels from each of the 102 R-plants in crop 6 were used to form P_3.

After disinfection with Quinolate the kernels were sown on 18 October,

Table 71 Mean culmlength (cm) of n random plants from the centre (n=80), the middle (n=120), or the whole area of the plots in crop 11.

entry	replication 1			replication 2		
	centre	middle	whole	centre	middle	whole
P_0	145.7	145.9	146.4	142.3	143.2	142.9
P_0'	149.8	148.9	150.3	151.5	150.5	150.6
P_3	140.7	140.3	139.8	142.2	142.2	142.8

1978. The external growing conditions were the same as those for crop 10 (see section 5.3.1) because crop 10 and 11 were grown as each other's neighbour. Of course, the plant density in crop 11 was much higher. Probably because of this on 21 May, 1979 the plants in crop 11 were about 20 cm taller than those in crop 10. Since about half June the border between crop 10 and crop 11 had lodged.

Crop 11 was harvested on 13 and 14 August 1979. Each plot was harvested as 12 sheaves, because every row within a plot was harvested as follows: the first and the last meter of a row were harvested together as a small sheaf, the intermediate 4 metre of the same row were harvested as a larger sheaf (this is illustrated in Figure 18 for 3 rows of plot 1). The larger sheaves from rows 2,3,4 and 5 comprise the centre of a plot, the larger sheaves from row 1 to 6 inclusive the middle of the plot. In this way it was possible to obtain results on the basis of:

(i) the centre of the plots
(ii) the middle of the plots
(iii) the whole area of the plots.

The following observations were obtained:

culmlength: the culmlength was determined in the usual way (in cm). It was observed on 10 random plants of each smaller sheaf and on 20 random plants of each larger sheaf;

kernel yield: per plot all ears were cut off and threshed. The weight of the kernels was recorded (in dg) as kernel yield per plot.

In the next section the simultaneous comparison of P_0, P_0' and P_3 is elaborated. However, P_0' was assumed to be a better standard than P_0 because of the reasons mentioned in the beginning of this section (concerning seed quality and additional intermating). Therefore the comparison concerning only P_0' and P_3 was also elaborated.

7.3 RESULTS

The mean culmlengths, determined for each entry of the comparative trial,

Table 72 Kernel yield (in dg/m^2) of the centre (4 m^2), the middle (6 m^2), or the whole area of the plots (9 m^2) in crop 11.

entry	replication 1			replication 2		
	centre	middle	whole	centre	middle	whole
P_0	3683	3949	4694	5969	6140	6459
P_0'	5066	4975	5277	6091	5902	6092
P_3	5706	6072	6193	5080	5177	5661

are presented in Table 71. It appears from this table that the 3 bases for comparison yielded about the same means. However, the 2 replications differed somewhat: the plants of P_0 were in replication 1 a little bit longer than in replication 2 (3.5 cm when expressed for the whole plot), whereas those for the other entries were somewhat shorter. The critical levels of the f-values from analyses of variances amounted, according to the F-table (df=2,2), respectively to 0.085 (f=10.78; centre), 0.084 (f=10.96; middle) and 0.110 (f=8.06; total area). Thus the 3 entries did not differ significantly for mean culmlength.

The data for kernel yield were transformed to kernel yield per unit area, i.e. to dg/m^2. The performances of the entries are presented in Table 72. Now it appears that, within a replication, the basis for comparison really matters when comparing the entries; especially for replication 2. Within replication 1 P_3 was always superior. Within replication 2 P_0 was superior on the basis of the middle of the plots as well as on the basis of the whole plot, but P_0' was superior on the basis of the centre.

Comparison of the 3 entries shows that the best entry in replication 1, i.e. P_3, appeared to be worst in replication 2. The reverse was true for entry P_0.

It was preferred to compare the kernel yields on the basis of the whole plots. However, the f-value obtained from the pertaining analysis of variance, amounted to only 0.097. Thus the 3 entries differed neither significantly for kernel yield.

For culmlength as well as for kernel yield there was not a significant replication effect. Thus by neglecting replication as a potential source of variation a new experimental design was awarded to the trial. The means of the entries, calculated on the basis of the whole plot, are presented in Table 73. The performances are also expressed as percentages of the performance of P_0' (which was preferred as a check to measure selection responses).

The analysis of variance neglecting replications as a source of variation indicated significant differences among the 3 entries for culmlength; for each basis of comparison. Using a pooled estimate for the residual variance

Table 73 Mean performance of the entries in crop 11. The presented figures pertain to data on the basis of the whole area of the plots.

entry	culmlength		kernel yield	
	in cm	in %	in dg/m²	in %
P_0	144.7	96.1	5577	98.1
P_0'	150.5	100	5685	100
P_3	141.3	93.9	5927	104.3

the contrast P_3-P_0' appeared to be significant, whereas for the contrast P_3-P_0 no significance was observed.

For kernel yield no significant differences were detected after neglection of the classification into replications.

7.4 DISCUSSION

Comparison of the 3 bases for measuring the performance of the entries learned again that culmlength is a character with a relatively high degree of repeatability, whereas kernel yield is highly modified by inscrutable, incidental influences. Nevertheless the critical levels obtained for culmlength were too high to declare the 3 entries to differ significantly for culmlength, unless replications was dropped as a source of variation. This rested presumably on the low number for degrees of freedom.

At the end of section 7.2 it was stated that P_0' might be a more appropriate standard than P_0. Therefore P_3 was also compared with only P_0'. In applying the t-test to compare the means equality of residual variance was assumed, because significant differences between the residual variances were not obtained. For culmlength the t-test revealed that the P_3-plants produced significant shorter culms than the P_0'-plants. This was found for each basis of comparison. The critical level was about 0.01. Thus our variant for H-selection succeeded in reducing culmlength. The reduction amounted to 6.1% (see Table 73).

For kernel yield the t-test did not show a significant superiority of the P_3-material. The t-values amounted to 0.498, 0.289, resp. -0.309 for comparison on the basis of the whole, the middle, resp. the centre of the plots (df=2).

Notwithstanding our inability to present for kernel yield statistically significant results the figures afforded by Table 73 indicate favourable outcomes. After 3 generations of continued honeycomb selection, aiming at both a reduced culmlength and an increased kernel yield indeed a reduced culmlength (6.1%) combined with an improved kernel yield (4.3%) was obtained. This was brought about by selection in selection fields with a plant density of only 51.3. The overall mean yield of crop 11 amounted to 5763 dg/m², a really satisfying yield level. (However, for the neighbouring crop 10, with a plant density of only 80, a kernel yield of 6292 dg/m2 was derived. This was discussed in section 5.3.2.) Compared with P_0 as a check the decrease in culmlength is only 2.3%, but then improvement for kernel yield amounts to 6.3%.

The overall mean culmlength in crop 11 amounted to 145.5 cm. In the neighbouring crop 10 it was 140.84 cm among the R-families (see Table 51). Thus the higher plant density in crop 11 was associated with a somewhat lower kernel yield per m² and an increased culmlength.

Altogether it appeared that honeycomb selection succeeded in pushing forward the desired recombinant plant type. The shifts, effectuated by 3 generations continued H-selection (6.1% for culmlength, 4.3% for kernel yield) may seem to be small. Three considerations with respect to this are elaborated here:

(i) Our aim was to realize at the same time a decrease in culmlength and an increase in yield. This goal was in conflict with the positive phenotypic (and presumably also genotypic) association of culmlength and yield. Thus our expectations should be accordingly.

(ii) In the introducton to this chapter the difficulty to realize selection responses caused by genotype × environment interaction was stressed. In the present set of trials this may have played an important role, because in 3 seasons the weather conditions were unique as far as we can recall. (Thus confirming the statement by McKenzie & Lambert (1961) 'that normal weather is something that does not occur very frequently').

First the wetness of the autumn of 1974 was unpreceded. This affected crop 1. Next, the spring and summer of 1976 were extremely hot and dry. Especially crop 2 suffered from this. Thirdly, the winter and early spring of 1979 were colder than ever recorded. This had an impact on crops 10, 11 and 13.

In addition to this it should be remembered that in the selection fields the plant density amounted to 51.3 and in crop 11 to about 250. Genotype × plant density interaction also belongs to the complex of genotype × environment interaction.

It must be possible to apply honeycomb selection at higher plant densities. The circumstances in the selection field are then closer to those in commercial crops. Another advantage of higher plant density in the selection field will be replacement of interspecific competition by weeds through intraspecific competition. The absence of intraspecific competition, advocated by Fasoulas & Tsaftaris (1975), by growing the plants in the selection fields at wide interplant distances implies a threat by interspecific competition from weeds. This was experienced in barley by Spitters (1979), p.176.

(iii) Honeycomb selection can only eliminate masking environmental effects as far as they are operative over areas larger than those covered by a group of 7 plants, i.e. a central plant and its 6 neighbours. However, within such group there remains diversity for a number of factors influencing the phenotype. These factors concern kernel size, positioning of the kernel after sowing (depth as well as orientation), hindrance by clods, pebbles or leaves, gluttony of mice or rabbits, competition (inter- and intraspecific), micro-climate. A few of these factors can be controlled (e.g. kernel size; see section 8.4), but as far as such control is not effectuated still superior phenotypes in stead of superior genotypes are favoured by honeycomb selection. The result of the selection will then disappoint. In section 8.1 the effectivity of honeycomb selection to correct for environmental heterogeneity covering areas larger than that covered by a group of 7 plants is considered.

As a philosophy on realizing a lasting selection response one might deliberate that the selection should be continued long enough if one wants to realize a lasting improvement. Owing to canalisation at the improved level of expression such improvement should last, at least partly, even if the selection is not longer applied. As an illustration for this one can consider the result of selection for increased number of abdominal chaetae in Drosophila (see Mather & Jinks (1971), Fig. 4). After 20 generations the selection was relaxed and the number of chaetae fell. However, a higher level of expression was maintained than occurring in the original population. Falconer (1960), Fig. 12.1 and 12.2, refers to similar observations.

There is a buffering against an improved level as long as canalisation aims at preserving the expression of the current level. Thus the genetic homeostasis at the current level should be broken and canalizing selection should promote a situation in which the new phenotype, i.e. the improved level, is produced by quite a number of genotypes. Thus the ultimate product of the selection should be a population with not only an improved level of expression for one or more characters, but also with a restricted variation around that level.

This speculation can be extended to explain the maintenance or even increase of the variance among families after selection. Such an increase was observed for culmlength as well as for yield (see section 5.3.3 and 6.3.3).

It is possible that, owing to natural selection a population has reached a genotypic composition that is in the equilibrium which is wellknown as balanced polymorphism due to heterozygote advantage. Such a stable equilibrium is conceivable when natural selection favours heterozygotes at loci which are directly or indirectly responsable for components of fitness. For loci with overdominance the equilibrium is characterized by gene frequencies implying maximal mean genotypic value as well as minimal additive genetic

Table 74 Summary of estimates of the phenotypic mean ($\bar{x}$), the phenotypic standard deviation (σ_p), the coefficient of the additive genetic variation and the heritability. Crop 9 concerns autotetraploid material.

	phenotypic parameters		genetic parameters			
			(O,P)-regression			anova
	$\bar{x}$	$\hat{\sigma}_p$	$\hat{\sigma}^2_a$	$v\hat{c}_a$	$\hat{h}^2_n$	$\hat{\sigma}^2_a$
culmlength (cm)						
crop 1	145.7	13.4	63.3	0.053	0.39	87.6
2	113.5	14.5	41.7	0.057	0.40	71.6
4	122.1	21.8	99.6	0.073	0.43	131.9
6	158.8	12.5	64.0	0.050	0.47	56.6
9	179.7	19.3	103.8	0.055	0.46	114.0
yield (dg)						
crop 1	95.2	64.7	215.5	0.141	0.04	268.0
2	50.0	28.9	24.9	0.088	0.05	193.2
4	73.4	90.5	476.6	0.199	0.03	-
6	102.2	36.0	95.7	0.096	0.09	54.2
9	137.1	71.3	247.8	0.130	0.10	156.2

variance (Falconer (1960), p.137). Artificial selection implies direct or indirect selection for components of fitness. Thus for the loci with overdominance, which control (in)directly fitness, the gene frequencies are forced to deviate from their equilibrium values. As a consequence the additive genetic variance is increased after artificial selection.

Table 74 presents for yield and for culmlength a summary across the selection fields of estimates of the phenotypic mean, the phenotypic standard deviation, the additive genetic variance and the heritability. The summary shows the above mentioned possibility that the genetic variation is maintained even when selection is continued. This is illustrated by all genetic parameters presented in the table. The dimensionless parameters vc_a and h^2_n deserve our greatest attention in this respect. The gradual increase in the diploid material for the heritability of culmlength was already indicated in section 5.3.3. No significance was attached to that. The estimates for σ^2_a are rather changeable, especially for yield. This might rest on climatic diversity among the seasons in which the crops were grown.

In general the estimates for σ^2_a from the offspring-parent regression were smaller than those obtained from an analysis of variance. This is in accor-

Table 75 The phenotypic (ρ_p) and the genetic correlation (ρ_g) between culmlength and yield

crop	ploidy-level	$\hat{\rho}_p$	$\hat{\rho}_g$ [1]
1	2x	0.52 (n=203) [2]	0.68 (n= 57)
2	2x	0.32 (n= 84)	0.83 (n= 84)
4	2x	0.56 (n= 48)	0.90 (n= 48)
6	2x	0.30 (n=200)	
6	2x	0.31 (n=102)	0.07 (n=102)
9	4x	0.22 (n= 80)	0.58 (n= 80)
9	4x	0.24 (n= 80) [2]	
9	4x	0.21 (n= 80) [3]	

[1] based on expression (2.11)

[2] correlation of culmlength and kernel yield

[3] correlation of culmlength and biomass

dance with the fact that effects of genotype × environment interaction are included when the latter method of estimation is applied (see section 2.3.4).

The phenotypic means proved to be very changeable, especially for yield. There was no clearcut relation between the means and their corresponding standard deviation. Such a relation occurs in case of socalled scale effects (Falconer (1960), p.293).

Especially in section 5.3.4 it was concluded that diverse methods to estimate ρ_g, the genetic correlation between 2 characters, gives very different results. Nevertheless there was great interest in the genetic association between culmlength and yield. The trend in course of the generations is given in Table 75. Especially the last but one estimate for ρ_g is rather deviating. A specific development of ρ_g was not observed and neither expected (see section 8.3).

Direct selection for reduced culmlength was not applied in the set of experiments described in the present text. This was omitted because it are the shortest plants which yield in general no kernels at all. They were considered to be genetically deficient (see section 2.2.2). Nevertheless in crop 12 T-selection was applied for reduced culmlength. Plants with a culmlength less than 100 cm were selected. This comprised 44 plants who produced few kernels, having a bad seed quality. Table 76 presents characteristics of these 44 plants as well as of all plants in crop 12.

The mean emergence after sowing the kernels produced by the 44 plants amounted to 59.5%, the plant density of these offspring plants was thus only 0.595×80=47.6. The mean yield of the offspring plants amounted to

Table 76 Summary of the observations on plants belonging to crop 12: n: number of observed plants; $\bar{x}$: mean; s: standard deviation; min: minimum; max: maximum.

character	quantity	all plants (n=5101)	plants with culmlength less than 100 cm (n=44)
culmlength (cm)	$\bar{x}$	148.8	87.5
	s	16.5	12.4
	min	30	30
	max	190	98
earnumber	$\bar{x}$	3.97	1.73
	s	1.68	1.02
	min	1	1
	max	11	5
yield (dg)	$\bar{x}$	69.7	7.68
	s	41.5	6.56
	min	1	1
	max	272	26

38.6 dg, their mean culmlength to 140.8 cm. When compared with the means obtained for the R-families, i.e. 39.0 dg per plant position, resp. 148.8 cm, one might conclude that T-selection for reduced culmlength appears attractive. Therefore experiments to obtain more evidence were started in 1981.

8 *ADDITIONAL NOTES CONCERNING THE REDUCTION OF MASKING EFFECTS BY ENVIRONMENTAL VARIATION AND COMPETITION*

8.1 THE EFFICIENCY OF HONEYCOMB SELECTION TO REDUCE EFFECTS OF SOIL HETEROGENEITY

It has been stressed in section 7.4 that honeycomb selection does not succeed in unravelling environmental deviation and genotypic value in so far as such environmental deviations occur within groups of 7 plants. Among the factors causing differential growing conditions within a hexagon, which were mentioned in section 7.4, depth of sowing is suspected to be relatively important. This was suggested by observation during thinning of crop 2. The two plants growing in the same hole were rather similar in appearance: quite often both plants were excellent or normal or inferior. The micro-environment within a hole is the same for the 2 plants in that hole and because of the high degree of modification by the environment the two phenotypes in the hole are very similar. Honeycomb selection of course fails to account for variation in the environmental contributions to the phenotypes which occur within a hexagon, but it should account for environmental variation occurring on larger areas than that of a hexagon.

In April, 1976 differences of growing conditions in crop 2 could visually be observed: within the crop alternating parallel strips could be distinguished which differed for leafiness of the plants. The strips were parallel with the rows of the crop grown before on this lot, i.e. potatoes, and with the direction of ploughing. Thus the preceding crop or the ploughing could be responsable for the strips that disclosed systematic differences in soil fertility. The estimated width of a strip was about 1½ m.

Later in the season it was impossible to discern this phenomenon by eye, but it could be proved that there was a lasting effect. This was established as follows.

The rows of crop 2 were perpendicular to the direction of the strips. Thus the mean yield of the first plant in the even rows was determined; subsequently the mean yield of the first plant in the odd rows, then the mean of the second plant in the even rows, etc. (see Figure 3). This resulted in 2×68=136 means, each based on 39 plant positions. The moving average of 7 of such means is depicted in Figure 19. This figure shows that clear maxima occurred for rownumbers (now counted in a transverse direction) 7, 26, 45 and for 78, 97 and 115. Thus at an interval of 18 or 19 rows, i.e. 18.5×7.5=138.75 cm. The maximum between row 45 and row 78, expected at row 62, was less convincing.

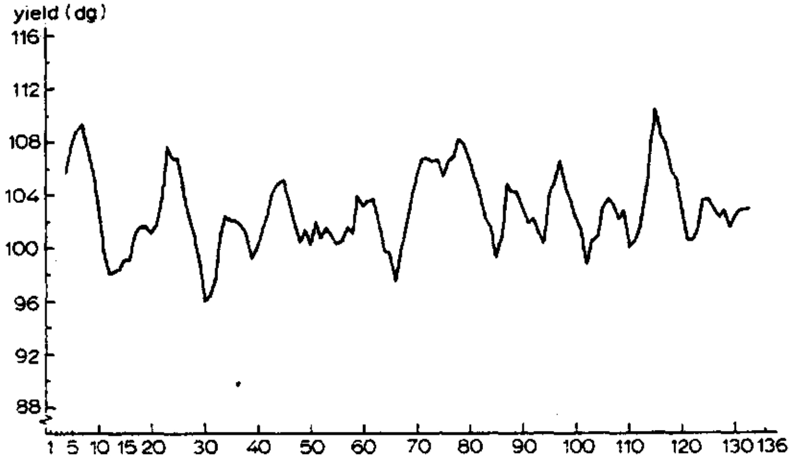

Figure 19 Moving average, determined for 7 mean yields of plants on 39 plantpositions. Results from crop 2.

To support the suggestion of a cyclic alternation of rows differing in soil fertility the null hypothesis H_o: "there is a random alternation" was tested against H_a: "there is a cyclic alternation" by means of the one-sample runs test. Thus the n-1=135 signs of differences of n=136 successive means were determined. The number of runs, i.e. series of equal signs, amounted to s=77. The normal approximation for $\underline{s}$ is given by

$$\underline{s} \approx \frac{2n-1}{3} + \sqrt{\frac{16n-29}{90}}\,\underline{\chi} \qquad (8.1)$$

(see Lindgren (1976), p.501).

The left tailed critical level amounted to $P(\underline{s}<77)=P(\underline{\chi}<-2.73)\approx 0.003$ and thus H_0 deserved rejection.

For mass selection it holds that the better the elimination of variation for the environmental deviation included in the phenotype, the more efficient the selection procedure. The procedures for mass selection that were applied to crop 2 were T-selection, G-selection and H-selection. The correlation between the mean yield of the plants in a transverse row and the number of plants selected in that row afforded an indication on the quality of the applied selection methods: the lower the correlation, the better the selection method. This correlation amounted to 0.68 for T-selection, to 0.71 for G-selection and to 0.44 for H-selection. All 3 correlations were significant and thus neither method succeeded to neglect the cyclic alternation in soil fertility completely. This was true even for H-selection, probably because that method does not eliminate differences across a distance less than 15 cm. However, H-selection performed much better than T- or G-selection. G-selection was even inferior when compared with T-selection, not only in the present aspect but also according to the response to selection (see section 3.3.5).

A different kind of trend in soil fertility was visually observed and later statistically confirmed in crop 12 (which is not described further in this text). For each row the mean was determined for culmlength, earnumber and yield. For culmlength and yield there appeared to be a positive correlation between mean and rownumber. These correlations amounted respectively to 0.39*** and 0.56***. According to the linear regression equations the mean values were predicted for row 1 and for row 78. The predictions amounted for culmlength to 146.9 cm, resp. 150.6 cm and for yield to 62.0 dg, resp. 77.3 dg.

In case of such soil heterogeneity, prevailing over a distance of several meters, honeycomb selection will perform better than truncation selection and also better than grid selection. (The size and orientation of the grids are factors which are partly decisive for the success of grid selection).

8.2 THE MEAN PERFORMANCE OF THE NEIGHBOURS AS A CONCOMITANT VARIABLE WHEN EVALUATING THE CENTRAL PLANT

Introduction

Soil heterogeneity masks the inherent genotypic value of the observable phenotypes. Therefore, in a selection field plants should be compared which have grown under similar conditions. For Fasoulas (1973) a group of 7 plants in a hexagon formed such a group of plants growing at similar conditions. He suggested to select the central plant when it produces better than any of its neighbours.

Many more methods have been proposed to unravel the disturbing effect of soil heterogeneity (see Spitters (1979) for a short summary of those methods). One of them is the suggestion by Baker & McKenzie (1967). They advocated to use the performance of nearby check plots as a covariable, which should be related to the performance of the plot under study. The value of the covariable indicates the local soil fertility. In the present study this was applied by regression of the performance of the central plant on the mean performance of its neighbours. This was done for the 102 R-plants belonging to crop 6. The regression equation should yield for each R-plant a predicted value, expressing the performance that might be expected from an arbitrary genotype. Subsequently the adjusted performance of the central plant was calculated by diminishing its actual value by the predicted value. This adjusted performance is expected to be positive in case of a central plant with a superior genotypic value and negative in case of a central plant with an inferior genotypic value. The influence of individual differences in growing conditions within a hexagon (see section 7.4) is neglected in this approach.

In the case of a better correspondence between the adjusted performance and the genotypic value than between the unadjusted performance and the genotypic value the correlation between offspring mean and parental value should be higher for the adjusted performance than for the unadjusted performance.

Results and discussion

The correlations obtained amounted to:

	performance of parent	
	unadjusted	adjusted
culmlength	0.59	0.59
yield	0.13	0.12

The estimates of the correlation mentioned for the unadjusted performances were already presented in Table 46. They are not lower than the estimates obtained after adjusting the performance in the described manner. Also the heritability estimates were not affected by the adjustment. Thus Baker & McKenzie's (1967) preference to apply a correction based on an analysis of covariance in stead of correction by means of a subtraction was not supported. The correction by means of subtraction was already illustrated in section 2.3.4. That adjustment implies diminishing of the phenotypic value of the central plant by the mean performance of its neighbours. (Such adjustment was rejected by Baker & McKenzie because it often results in overadjustment. In any case it did not yield attractive results in section 2.3.4).

The explanation for the failure of the present method for adjustment is a matter of speculation. In section 7.4 it was indicated that the performance of individual plants depends strongly on individual conditions afforded by the micro-environment. Thus the mean of the 6 neighbours might be an inexact measure for the environmental conditions of the central plant, because it rests on only 6 phenotypes, each of which heavily depends on individual in stead of common environmental conditions. Furthermore, the phenotype of the central plant is only weakly determined by the common environment and highly modified by its own micro-environment.

Honeycomb selection aims to select plants with a superior genotypic value. The method is expected to be efficient in case of mass selection in a population, which is grown under a pattern of environmental conditions which is too fine-grained for efficient grid selection. Such fine-grained pattern of environmental conditions tends to induce a positive correlation between $\underline{p}$ (the phenotypic value of a plant) and $\underline{p}_n$ (the mean phenotypic value of its neighbours). On the contrary intraspecific competition tends to induce a negative correlation. The net result of the 2 conflicting trends affords an indication of the perspectives of H-selection. The correlation obtained for the 102 R-plants in crop 6 amounted to 0.29*** for culmlength and to 0.28*** for yield. This correlation was higher the larger the number of rows in crop 6, across which it was determined. This rests on the fact that the mean yield per plant, calculated per row, depended on the rownumber. Thus, just as described in section 8.1 for crop 12, there occurred also in crop 6 a trend in the selection field: the correlation between rownumber and mean yield per plant, calculated per row, amounted here to 0.45***.

The condition for decreasing the environmental variance by adjustment was determined for the simple method of adjusting given by

$$\underline{p}' = \underline{p} - \underline{p}_n$$

i.e. the adjustment applied in section 2.3.4. For the usual basic model for quantitative genetics (see Falconer (1960), p.112) this implies for individual plants

$$\underline{p} = \underline{g} + \underline{e}$$

as well as

$$\underline{p}' = \underline{g} + \underline{e}'$$

Thus

$$\underline{e}' = \underline{p}' - \underline{g} = (\underline{p} - \underline{p}_n) - (\underline{p} - \underline{e}) = \underline{e} - \underline{p}_n$$

and

$$\text{var}(\underline{e}') = \text{var}(\underline{e} - \underline{p}_n) = \text{var}(\underline{e}) - 2\,\text{cov}(\underline{e},\underline{p}_n) + \text{var}(\underline{p}_n)$$

Because

$$\text{cov}(\underline{e},\underline{p}_n) = \text{cov}(\underline{p},\underline{p}_n),$$

while

$$\text{cov}(\underline{g},\underline{p}_n) = 0,$$

we obtained

$$\text{var}(\underline{e}') < \text{var}(\underline{e})$$

if

$$2\text{cov}(\underline{p},\underline{p}_n) > \text{var}(\underline{p}_n)$$

or if

$$2\rho(\underline{p},\underline{p}_n)\sigma_p > \sigma_{p_n} \qquad (8.2)$$

In the case that this inequality holds the environmental variance decreases by applying the adjustment. We obtained for plants in crop 1 (see section 2.3.4):

	$2r\hat{\sigma}_p$	$\hat{\sigma}_{p_n}$
culmlength (cm)	6.81	6.96
yield (dg)	18.11	22.60

This reveals that truncation selection based on the unadjusted performances offers better perspectives than T-selection based on the adjusted performances. Especially for yield the adjustment led to an increase in environmental variance.

Spitters (1979), p.206 also tried to determine the conditions under which the adjustment

$$\underline{p}' = \underline{p} - \underline{p}_n$$

leads to decreased environmental variance. He assumed

(i) absence of interplant competition. This is in accordance with Fasoulas & Tsaftaris (1975) who claim that (honeycomb) selection should occur in absence if interplant competition;

(ii) that the phenotypic covariance between plants in the hexagon is of equal size for each pair of plants, viz. equal to the covariance of the central plant and a neighbour.

Spitters (loc.cit.) derived that

$$\text{var}(\underline{e}') < \text{var}(\underline{e})$$

when the correlation between neighbours exceeds 1/7. This yardstick seems useless in the present situation because competition will have occurred at the applied interplant distance. Further the second assumption appears undefendable.

8.3 INFLUENCE OF COMPETITION ON THE RELATION BETWEEN CULMLENGTH AND YIELD

According to Spitters (1979), p.180 juvenile growth is the main factor determining competitive ability. Thus plant height would be of minor importance. Spitters (1979), p.169 observed absence of association between the plant height of a barley variety in monoculture and its competitive ability. Therefore it is assumed in the following that differences in culmlength should be considered as effects of competition rather than as causes for competition. The same reasoning might hold for yield. Thus the positive correlation between culmlength and yield, which is frequently observed in heterogeneous populations of small grains might be the result of interplant competition. On the strength of this assumption it is understandable that, notwithstanding the absence of this association between populations, it might be present within populations. Indeed there exist dwarf varieties, especially for wheat, which give a good yield. Within such varieties as well as within crosses between such varieties the positive association will be present again. The same will have occurred within crops 10 and 11. However, the plants of crop 11 had longer culms but yielded less than the plants of crop 10. Thus between these 2 crops the association was absent.

The genotypic value of a certain genotype depends on the growing conditions afforded. Thus at higher plant density a certain genotype might have a genotypic value for culmlength which is different from the genotypic value at lower plant density. It is conceivable that at increased plant density the genotypic values have a larger (genotypic) variance for culmlength. On the contrary it is quite well possible that in absence of competition (owing to low plant density) there is hardly genotypic variation for culmlength. At such low density possible differences in juvenile growth have no meaning as competitive advantage or disadvantage.

If the former speculation is right selection for decreased culmlength should occur preferably at higher plant density because genetic variation for culmlength will be magnified by the higher plant density.

In section 2.2.3 it was said that the honeycomb selection aimed at breaking the positive phenotypic and genetic correlation of culmlength and yield. Table 75 presents estimates for ρ_p and for ρ_g in course of the generations. The estimates for ρ_g were discussed in section 7.4. They were considered to be inconclusive because no reliable way to estimate ρ_g appeared to be available.

In fact our goal was to decrease mean culmlength, while maintaining or even increasing the yield, and not to break the correlation coefficient. That would even be impossible if indeed that correlation is not an inherent property of the material but rather a result from interplant competition.

8.4 THE EFFECT OF THE WEIGHT OF THE SOWN KERNEL ON THE PERFORMANCE OF THE PLANT EMERGING FROM THAT KERNEL

The restricted response to honeycomb selection was partly ascribed to the inability of H-selection to account for environmental deviations owing to variation in growing conditions within a hexagon. One of the factors mentioned in this respect (see section 7.4) was kernel size. Thus the disturbing effect of variation for the size of the kernels from which the plants are grown, on the yield of the plants might partly be responsable for the low estimates of the heritability of yield. If there is indeed a relation between kernel size and plant performance, variation in kernel size, which might be partly independent from the variation in the genotypic value of the germ in the kernel, can be partly responsable for the low value of the heritability.

The association between the size of a single kernel and the performance of the plant grown from that kernel was studied in wheat by Austenson & Walton (1970). For weight of the kernel they established a significant correlation with plant yield (r=0.20) and also with earnumber (r=0.22).

Christian & Gray (1941) concluded "that unequal competition between adjacent plants in heterogeneous wheat populations, sown at approximately field spacings, may occur as a result of variation both in initial seed weight and in genotype. The effect is of considerable magnitude and is alone sufficient to make the selection of individual plants for yielding ability in segregating generations unreliable". They also wrote: "Much of the variation due to interplant competition could be eliminated by grading the seed according to size or weight and sowing only seed of approximately the same weight in one plot. This would not, of course, overcome the unequal competition between plants resulting from unlike genotypes".

McMillan (1935) reported that for individual wheat plants of the variety Baroota Wonder, sown at rectangulars of 15.2×5.08 cm, there was a significant correlation between initial kernel weight and yield ($r=0.38$) and earnumber ($r=0.35$).

It might be possible that the positive effect of a larger kernel size rests on a better competitive ability. In that case the effect would be larger at high plant density than at low plant density. Because the plant density in the honeycomb selection fields amounted only to 51.3 it was studied whether the kernel weight exerted still an effect on plant performance at this low plant density. This was studied for winterrye, for the winterwheat variety Arminda and for the springbarley variety Vada (see De Jong (1978)). Only the results concerning rye are reported here.

The weight of the kernels destined for the plant positions in rows 76, 77 and 78 in crop 6 was individually determined (in 10^{-4} g) prior to sowing. Statistics on the resulting plants were discussed in section 5.2.2. Correlations between the kernel weight on the one side and characteristics of the mature plant on the other side are presented in Table 77. It appears that even at this low plant density the initial kernel weight exerted an important influence on the yield components of the mature plant.

It was verified whether the plants selected by H-selection for yield only originated from larger kernels than the plants that were not selected. Only the 133 plants in rows 76 and 77 came into consideration for H-selection because the plants in row 78 (the last row) could serve only as neighbours and not as central plants. The number of selected plants amounted to 20, i.e. 15% (in accordance with Fasoulas (1973)). Indeed the initial kernel weight pertaining to these 20 plants was significantly higher than that of the other 113 plants ($t_{131}=3.69^{***}$). Thus indeed H-selection failed to account for this source of intra-hexagon variation. As a consequence since 1979 the kernels to be used for a selection field have been graded by sieving.

8.5 THE EFFECT OF PLANT DENSITY ON THE RESULT OF HONEYCOMB SELECTION

Spitters (1979), p.22, described an experiment with a mixture of 12 bar-

Table 77 Correlations between the weight of the sown kernel on the one side and characteristics of the mature plant on the other side (n=200).

mature plant characteristic	r
culmlength	0.10
earnumber	0.33***
yield	0.42***
straw yield	0.45***
kernel yield	0.45***
number of spikelets	0.38***
number of kernels	0.41***
harvest index	-0.02

ley varieties, which could be visually distinguished after harvesting. Equal numbers of plants from each variety were included in the mixture. This mixture was grown at a triangular pattern of plant positions at a plant density of 80 as well as at a plant density of 3.2 (the latter density was in accordance with the density recommended by Fasoulas & Tsaftaris (1975) for wheat, i.e. using an interplant distance of 60 cm). Further the 12 varieties were grown in monoculture (at a plant density of 80 as well as at a commercial density), under similar growing conditions.

Based on the criterium for selection of individual plants, which was proposed by Fasoulas (1973), plants were selected for yield; in the mixture of 480 plants at the higher density as well as in the mixture of 624 plants at the lower density. By application, in the second instance, of truncation selection eventually at both densities about 10.3% of the plants was selected (corresponding with 50, resp. 64 plants). Table 78 presents the origin, i.e. the variety of the selected plants as well as the rank of the varieties (see Spitters (1979), Table 37).

To study the accordance of the 3 methods for determining the monoculture yield, rank correlation coefficients were calculated, or rather d^2 values (see Snedecor & Cochran (1967), p.194), whose critical values for n=12 are given by Corsten (1973). Absence of correspondence (d^2=217.5) between method (1) and (2) was mainly due to the behaviour of L98 (see Table 78). Bigo and L98 were responsable for a non-significant correspondence between methods (1) and (3), for which d^2 amounted to 174.5. Methods (2) and (3), both based on commercial density, confirmed each other (d^2=95*), notwithstanding Bigo. Method (2) was based on a one year experience (the same year in which the honeycomb selection was applied); method (3) on several years. L98 and

Table 78 Distribution (in %) of the plants, selected after honeycomb selection applied in a mixture of barley varietes, according to their variety. The rank for the yield - from lowest (1) to highest (12) - in monoculture is also given: (1) yield per plant of spaced plants (5×25 cm), see Spitters (1979), Table 27; (2) monoculture yield per row after sowing at a rate of about 110 kg/ha, see Spitters (1979), Table 38; (3) monoculture yield as obtained in national tests, see Spitters (1979), Table 6.

variety	density in the mixture				rank for yield in monoculture		
	80		3.2				
	%	rank	%	rank	(1)	(2)	(3)
Varunda	2	4	2	3.5	6.5	5	9
Tamara	20	11	16	10	10	11.5	12
Belfor	12	9.5	25	12	6.5	10	8
Aramir	4	5.5	11	9	12	7	11
Camilla	12	9.5	9	8	5	11.5	10
Golden Promise	0	2	5	5	1	4	5
Balder	4	5.5	6	6.5	4	8.5	6
WZ 704068-14	0	2	19	11	8	6	7
Goudgerst	32	12	0	1.5	3	3	4
L98	6	7	2	3.5	11	1	3
Titan	0	2	0	1.5	2	2	1
Bigo	8	8	6	6.5	9	8.5	2

Bigo were mainly responsable for inconsistencies in the correspondence between methods of measuring monoculture yield. These 2 varieties do not have any agricultural importance. At the time of the experiment only the varieties Aramir and Belfor (see the list in Table 78) were commercially grown (27% of the total springbarley area in 1977).

It appears best to measure the ability of honeycomb selection for detection of superior varieties by comparing the result of H-selection with the monoculture yield as measured by method (3). This comparison is also based on d^2 values. For H-selection at a density of 80 we obtained $d^2=210$, and for H-selection at a density of 3.2 $d^2=101.5^*$. Thus for H-selection at a density of 80 no significant association was obtained between the frequency with which a homozygous barley genotype was selected and the monoculture yield performance in a commercial density. On the contrary, for H-selection at a density of 3.2 a significant positive association was obtained. Thus Fasoulas' (1973) hypothesis that selection should occur in absence of interplant competition was supported. The upper 6 varieties, according to method

(3), were represented by 54% of the plants selected at a density of 3.2.

Spitters (1979) reported in section 8.3.2 (loc.cit.), that the correlated response (for yield in monoculture), brought about by H-selection in the mixture, was positive for selection at the lower density. This was based on method (2), for which we obtained d^2=154 (selection at the higher density), resp. d^2=67.5*** (selecton at the lower density).

The heritability at the higher density was somewhat higher than that at the lower density, but the correlation between the yield in mixture and the kernel yield in monoculture was negative at the higher density and positive at the lower density (see Table 24, loc.cit.).

This experimental support of Fasoulas' (1973) and Fasoulas & Tsaftaris' (1975) preference to select in absence of interplant competition is based on incidental, derived evidence. No general conclusion may be drawn from it. On the strength of general considerations Spitters (1979), section 8.3.3, prefers selection at high density. He arrived also at this conclusion in section 5.6.

Briggs & Faris (1978) observed in one location a clear relation between the performance of barley genotypes at wide spacing (61×61 cm) and the performance of these genotypes in commercial density, but not in another location.

8.6 SOME REMARKS ON GRID SELECTION

The results of grid selection that were obtained in crop 2 (see section 3.3.5) and in crop 4 (see section 4.3.5) were rather disappointing. In stead of a better response than that for T-selection, which was expected (see section 3.2.3), a worse response was obtained. It was suggested in section 3.3.5 that a reason for the disappointing response of G-selection could be the custom of selecting in each grid the same, predetermined number of plants. It is evident that, as a matter of chance, in each grid the number of plants with a superior breeding value will be a random variable. Thus it is unwise to select a fixed number of plants per grid, in stead of a variable number. In fact, H-selection can be considered as G-selection in moving grids (comprising at most 7 plants) in such a way that in some grids one plant is selected and in others none.

Other reasons for the disappointing response are the arbitrary ways in which size, shape and orientation of the grids were determined.

The first point mentioned here, i.e. selection of a fixed number of plants per grid, was considered somewhat better. This was done by superimposing on crop 9 a division of the selection field in 12 parts. The division was equal to that described for G-selection in crop 2 (see section 3.2.3;see Fig.20). Table 79 presents for each grid mean and phenotypic standard deviation.

The number of plant positions per grid was 19×22=418. In the lodged part of crop 9 (see section 6.2.1), i.e. in grid 11, the number of plants was

Table 79 **Means ($\bar{x}$) and standard deviations (s) for culmlength, earnumber, yield and straw yield in each of the 12 grids superimposed on crop 9. The numbers of plants pertain to the number of plants for which the yield could be assessed.**

grid	number of plants	culmlength(cm)		earnumber		yield(dg)		straw yield(dg)	
		$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
1	365	176.0	18.9	3.74	1.77	85.0	57	131	73
2	344	174.2	20.7	3.79	1.73	80.0	56	131	73
3	358	183.0	18.7	3.07	1.22	82.7	46	123	58
4	351	178.4	19.3	3.91	1.74	99.7	60	144	70
5	363	182.4	19.4	3.42	1.51	82.4	50	124	63
6	362	185.6	21.0	3.53	1.58	88.9	56	135	71
7	346	186.1	18.6	3.50	1.61	90.0	53	138	68
8	354	182.0	17.0	3.67	1.57	94.6	59	137	70
9	365	183.0	16.8	3.74	1.63	92.6	55	136	66
10	356	181.1	17.5	3.42	1.64	87.7	58	136	72
11	326	173.7	18.3	3.90	1.96	90.6	61	157	82
12	346	175.9	18.4	4.40	1.98	103.3	63	156	79

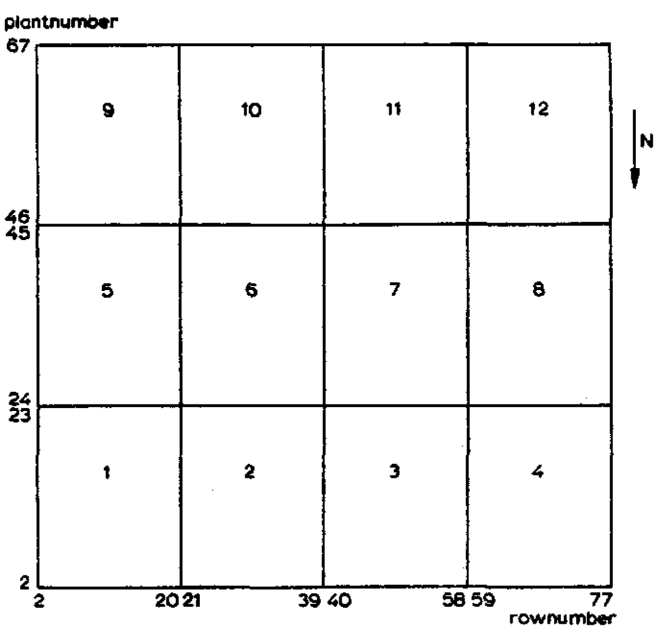

Figure 20 Partition of crop 9 in 12 grids.

lowest: owing to lodging some plants were lost.

By analyses of variance H_o: "the grids contain equivalent groups of plants" was tested against the alternative H_a: "the grids do not contain equivalent groups of plants". To do this the test statistic F(=MS between grids/MS within grids) was calculated. The obtained F-value was for culmlength 18.5***, for earnumber 13.6***, for yield 5.5*** and for straw yield 7.6***.

Thus the between-grids component of the phenotypic variance appeared to be significant. This component is entirely of environmental nature. The within-grids component contains environmental as well as genetical contributions. For yield the estimate for the between-grids component of variance amounted to 40.1 dg^2 and that for the within-grids component to 3178 dg^2.

When applying grid selection the between-grids component of variance is eliminated from the phenotypic variance (see also Spitters (1979), p.195). Gridding thus reduces the environmental component of the phenotypic variance and promises better prospects for G-selection than for T-selection.

It has been suggested (Van der Veen, personal communication) that a better procedure for G-selection would be selection of plants with the best adjusted performance. The adjustment implies diminishing of the actual performance of each plant by the mean performance of all plants in the same grid. After such adjustment T-selection across all grids is applied, so as to find plants with the best adjusted performance. Then, indeed, in different grids different numbers of plants will be selected and the disadvantage of selection of a fixed number of plants per grid is eliminated.

An objection against this arises when the grids differ for variation within the grid. In a relatively homogeneous grid the number of plants with a high adjusted value will be low and in a relatively heterogeneous grid that number will be high. Indeed, the null hypothesis H_o: "the within-grid variances are homogeneous" had to be rejected for all characters. (The significance of the test statistic of Bartlett-Box might also be due to absence of normality.)

Because of the heterogeneity of the variance within a grid a further step in the adjustment was applied: the actual performance of the plants was diminished by the grid mean and the difference was divided by the standard deviation of the plants in the grid. This adjustment implies standardization per grid. The adjustment should be followed by T-selection (based on the adjusted performances).

This modification was applied for yield. All plants with a standardized value greater than 2 were selected. This yielded 128 plants, i.e. 100(128/4236)=3.0%. (In case of normality, 2.28% of the plants would be selected.) The mean yield of the 128 plants amounted to 231.8 dg and their mean culmlength to 191.0 cm. Comparison of this mean yield with the means in Table 53 reveals that the 128 plants yielded much more than the H-plants or the ICL-plants in crop 9. This rests on the fact that culmlength was not

Table 80 Summary of the observations on plants belonging to crop 9 and their offspring. The plants were selected for yield after standardization per grid. For comparison data on the R-families in crop 13 are included as well.

character	quantity	plants in crop 9	offspring in crop 13	R-families in crop 13
culmlength (cm)	n	27	26	77
	$\bar{x}$	176.2	150.5	151.9
	min	161	137.7	133.3
	max	203	156.4	164.9
earnumber	n	27	26	79
	$\bar{x}$	7.7	3.02	2.94
	min	5	2.54	2.37
	max	10	3.69	3.69
yield (dg)	n	27	26	79
	$\bar{x}$	236.9	68.8	63.67
	min	197	52.1	45.4
	max	346	89.2	92.8
straw yield (dg)	n	27	3	79
	$\bar{x}$	276.9	72.2	72.6
	min	226	64.7	58.6
	max	374	82.3	88.9

taken into consideration in the present study. (Indeed the mean culmlength of the 128 plants exceeded the means presented in Table 53 considerably.) The number of plants selected in a grid ranged from 9 (in 4 grids) to 16 inclusive (in 1 grid).

From 23 of the 128 plants offspring plants were included in crop 13. Because 4 of the 23 plants were included twice, a total of 27 plots with offspring plants was grown in each block of crop 13 (24 plots with 120 plant positions and 3 plots with 40 plant positions). Table 80 presents data on these plants and on their offspring. For comparison also the performance of the R-families in crop 13 is given in this table. The results of T-selection for yield after standardization per grid were rather surprising. The culmlength of the offspring of the selected plants was reduced by 1.4 cm (~1%) whereas their yield was 5.1 dg (=8%) better. Of course this is the result of only a small, preliminary study of the potential of T-selection after standardization per grid, but these results justify further study to the efficiency of this modified use of gridding. Such study was started in 1981.

SUMMARY

Chapter 1 Individual plants are selected under mass selection. The next generation is grown from bulked seed of the selected plants. Whereas the selection aims to pick out plants with a superior genotypic value, the actual selection is based on the phenotypic value. This phenotypic value of an individual plant is partly determined by the environmental conditions for that plant. For separate plants these environmental conditions are different because they comprise a number of influences (including differences in competitive ability among the plants). With truncation selection for one or more characters (the latter is called selection with independent culling levels) there is no correction at all for the environmental contribution to the phenotypic value. By application of grid selection the similarity of the environmental conditions for the plants to be compared is improved, thus reducing the variation for the environmental contribution to the phenotypic value.

With honeycomb selection the grid size is minimal, which implies minimization of the masking effect of the environment. Because this last method appeared very attractive its efficiency under practical conditions was compared with that of other methods for mass selection. The substrate for the study was winterrye; diploid material (the variety Dominant) as well as autotetraploid material (developed at the Institute of Plant Breeding, Wageningen). The experiences with the tetraploid material are described in chapter 6.

The goal of selection was a recombinant plant type, combining a good yield with a reduced culmlength. The pathway of the experiments is outlined in figure 2.

Chapter 2 When planting a honeycomb selection field one has to consider the plant density. The higher the plant density the smaller the area covered by a group of 7 plants (a central plant plus its 6 neighbours) and thus the more uniform some of the growing conditions within such group. On the other hand the disturbing effects of interplant competition increase at higher plant density. In the present experiments a plant density of 51.3 plants per m^2 was applied in the selection fields. Crop 1 as well as the other selection fields (except crop 4) comprised 5304 plant positions containing a plant to be observed.

After harvest for each plant kernel yield, earnumber and culmlength were registered. For kernel yield and earnumber the frequency distributions showed positive skewness. Because of the high phenotypic correlation between kernel yield and weight of the ears in later experiments only the weight of

the ears was registered (under the heading of yield). The phenotypic correlation between earnumber and kernel yield amounted to 0.90. The phenotypic correlation between culmlength and kernel yield was about 0.6. This promised difficulties to realize the goal of the selection (i.e. obtaining a recombinant plant type).

With honeycomb selection plants yielding more than each of their 6 neighbours and with a culmlength less than the mean culmlength of the 6 neighbours were selected. To establish the selection response random plants were selected at the same time (socalled random selection). Selection response was measured by comparing offspring of the intentionally selected plants with offspring of the random plants.

The quality of the observations on the plants in the comparative trial is discussed. It is concluded that the actual number of plants per plot might be lower than the registered number. Therefore total yield per plot appeared to be a safer criterion for evaluation than mean performance per plant.

A second reason to select random plants and to grow their offspring was the desire to obtain estimates for the heritability, the additive genetic variance and the genetic correlation between characters. Because the assumptions underlying the estimators could be justified only partly, the estimates should be used as rough indicators for the mode of polygenic inheritance.

For culmlength the estimate for the heritability in narrow sense amounted to 0.39, for yield to 0.04. The genetic correlation between these 2 characters was estimated to be 0.45 by the one estimator and 0.68 by the other.

From the comparative trial (crop 3) it appeared that the selection did not result in an increased yield, but for culmlength a significant reduction was established.

Chapter 3 The second selection field, i.e. crop 2, was grown from kernels from plants selected by honeycomb selection in crop 1. The lay-out was the same as for crop 1. The crop suffered severely from the unprecedented drought. After harvest the expressions for the characters yield, earnumber and culmlength were registered. In addition to honeycomb selection and random selection now also truncation selection and grid selection were applied. The first method aimed to reduce culmlength whilst maintaining or increasing yield, whereas the latter 2 methods aimed to increase yield.

The lay-out of the comparative trial (to compare the performances of the offspring of the 4 types of families) was analogous to that for crop 3: the plots consisted again of 21 plant positions alongside a single row. The correlations between the performances of the corresponding plots in the 2 blocks were very low; ranging from 0.11 for earnumber to 0.29 for culmlength. The heritability estimates had about the same numerical values as one generation before. Genetic correlations between culmlength and yield were now also estimated from correlated selection responses. The obtained value (about 0.62) deviated rather from the value (i.e. 0.83) obtained from the conventional estimator.

The comparative trial indicated only for culmlength significant differences among the 4 types of offspring: after grid selection or truncation selection the culms were significantly longer than after random selection or honeycomb selection. In contrast to our expectation after grid selection the yield was not as good as after truncation selection.

Chapter 4 The third selection field (crop 4) was grown from a mixture of kernels of the plants selected by honeycomb selection in the second selection field (crop 2). The emergence of crop 4 was extremely bad. Very many plants had to be transplanted to obtain a field without open plant positions. This resulted in a heterogeneous crop.

The selection methods applied in crop 2 were also applied in crop 4. The offspring of the 4 groups of selected plants were compared in a comparative trial, consisting of 2 complete blocks. The correlations between the observations in the 2 blocks were very low and hardly significant, with the exception of those for mean culmlength (r=0.52***). The heritability estimates amounted to 0 (earnumber), 0.03 (yield) and 0.43 (culmlength). The genetic correlation between culmlength and yield was estimated by several procedures. The resulting estimates were greatly in conflict. Clearly all 4 methods have their drawbacks and no reliable procedure appeared to be available.

The result of honeycomb selection in crop 4 was disappointing: the culmlength was significantly reduced (2.5%), but also the yield was reduced (5%). The results of grid selection were about nil. Truncation selection resulted in a significantly increased yield (compared with any of the other 3 methods of selection).

Chapter 5 The fourth selection field (crop 6) was grown from a mixture of kernels from the 92 plants selected by honeycomb selection in the previous selection field (crop 4). The field was established by sowing one kernel per plant position. Only 3.6% of the plant positions did not yield a plant. The selection methods which were applied comprised honeycomb selection, selection with independent culling levels and random selection. The culling levels were chosen arbitrarily. Their choice promoted good yielding plants with a reduced culmlength. The offspring of the selected plants were compared in crop 10. The plots containing families from plants selected at random consisted of twice the usual number of plants. Except for culmlength this did not result in a higher correlation between the observations on corresponding plots in the 2 blocks. A promising heritability estimate, i.e. 0.29, was established for mean yield per ear.

Again no reliable estimates for genetic correlations were obtained. Estimates derived from correlated selection responses were considered the most trustworthy.

From the comparative trial it appeared that honeycomb selection as well as selection with independent culling levels succeeded in decreasing the culmlength. However, yield decreased as well (but not significantly). Neither index selection nor selection of plants selected by honeycomb selection as well as by selection with independent culling levels yielded better results.

Chapter 6 The methods of selection described in the preceding chapter were also applied on autotetraploid plants. The selection field (crop 9) was grown in the usual lay-out. It was located near crop 6 and the diploid and tetraploid material was compared for many characters. Straw yield was observed in addition to the usually observed characters. The plants selected by random selection should produce more than a minimal yield regarding the comparative trial. Because of this these plants formed a biased sample from crop 9: they yielded more and produced longer culms. This hampered the observation of realization of the pursued goal of selection for yield, but for culmlength such observation was promoted. Again the offspring of plants selected at random were grown on plots with twice the usual size. This resulted only for culmlength in an increased correlation between corresponding plots.

For the autotetraploid material the justifications for estimating quantitative genetic parameters were even more disputable than for the diploid material. For culmlength, earnumber and yield the obtained estimates for the additive genetic variance and for the heritability in narrow sense were similar to the corresponding estimates for the diploid material. For harvest index the heritability estimate amounted to as much as 0.46. Yield per ear appeared an attractive character for indirect selection.

The offspring of the selected plants showed significant reduction in culmlength after honeycomb selection and after selection with independent culling levels. The plants selected by both these 2 methods gave very promising offspring (yielding 7.2% better, whereas the culmlength was reduced by 2.1%).

Chapter 7 The results presented in the preceding chapters confirm the experiences obtained elsewhere that the result of a single application of mass selection is strongly influenced by accidental circumstances. Therefore the cumulative effect of 3 successive generations with honeycomb selection was studied at normal plant density. No statistically significant positive results were obtained for yield because the number of replications for the concluding trial amounted only 2. Nevertheless favourable results were obtained: 3 generations of continued honeycomb selection resulted in plants with a reduced culmlength (6.1%) combined with an improved kernel yield (4.3%). Thus indeed the applied variant of honeycomb selection succeeded in pushing forward the desired recombinant plant type.

Genotype x environment interaction and environmental diversity occurring within groups of 7 plants were discussed as factors hampering the response to honeycomb selection. Some considerations were given to explain the maintenance, notwithstanding selection, of additive genetic variation. This intricate phenomenon has been reported already several times.

Across the years the estimates for the additive genetic variances obtained from the offspring-parent regression were in general smaller than those obtained from an analysis of variance. Such can be expected by realizing that effects of genotype x environment interaction are included when the latter method of estimation is applied.

A preliminary study concerning the efficiency of direct selection for reduced culmlength gave attractive results. This line of study will be continued.

Chapter 8 Some ways in which environmental variation and competition mask the genotypic value of an individual plant are considered. In the first section it is shown that, at least in crop 2, honeycomb selection succeeded better in eliminating the environmental deviation included in the phenotype than either truncation selection or grid selection. Grid selection was slightly worse than truncation selection in this respect. Of course, honeycomb selection fails to account for phenotypic variation which is caused by differences in environmental conditions occurring within a hexagon. Such differences exist for e.g. depth and positioning of the sown kernels.

The suggestion to use the mean performance of a nearby group of plants as a covariable, which should be related to the performance of the plant(s) under consideration was experimentally evaluated. This suggestion was put forward as a method to eliminate the environmental deviation contained in the observable phenotypic value of the plants considered for selection. In the present study the suggestion was tested by regression of the performance of the central plant on the mean performance of its neighbours. This was done for the 102 R-plants belonging to crop 6. The adjusted performance of the central plant was calculated by subtracting the predicted value from the actual value. This adjusted value should reflect the genotypic value better than the actual value. Thus the correlation between the parental value and its offspring mean should be higher for the adjusted performance than for the unadjusted performance. However, this was not observed and evidences in favour of the suggestion could not be demonstrated. The reason for this could be an overwhelming influence of individual micro-environmental growing conditions on the phenotypic value. The condition for decreasing the environmental variance by adjustment was given for a simple method of adjusting. It was shown that in crop 1 the condition was not met.

In section 8.3 the idea is put forward that differences in plant height are effects of competition rather than causes for differences in competitive ability. The same reasoning might hold for yield. Thus the positive correlation between culmlength and yield might partly be the result of interplant competition. If true, such a relation will exist within any population with interplant competition. Thus the goal of the selection programme should not be the breaking of the correlation but the decrease of the culmlength, whereas the yield is maintained or even improved.

As known from the literature the size of a kernel has an effect on the performance of the plant emerging from that kernel (see section 8.4). According to Spitters (1979) this would rest on a better competitive ability during the juvenile stage of plants obtained from larger kernels. Thus variation for kernel size is one of the factors causing variation for the environmental deviation component of the phenotypic value. The dependency of mature plant characteristics on the initial kernel size was established in case of the present plant density at the present triangular pattern of plant positions. It appeared indeed, that, for the growing conditions prevailing in the selection fields, the initial kernel weight exerted an important influence on the yield components of the mature plant. Plants selected for yield by honeycomb selection originated from heavier kernels than plants that were not selected. As a consequence since 1979 the kernels to be used for a selection field have been graded by sieving.

The effect of plant density on the result of honeycomb selection was studied by deriving data from an experiment with a mixture of 12 spring barley varieties (see section 8.5). The mixture was grown at a triangular pattern of plant positions at a plant density of 80 as well as 3.2. For both densities 10.3% of the plants were selected by honeycomb selection. The percentage with which a barley variety occurred in the group of selected plants was related to the rank of the variety when tested as a monoculture in national tests. At a density of 80 no significant association was obtained, but at a density of 3.2 it was. Thus Fasoulas' hypothesis that selection should occur in absence of interplant competition, was supported.

The experiments described in chapters 3 and 4 showed that, in contrast to our expectation, the result of grid selection was not as good as the result of truncation selection. The custom of selecting in each grid the same predetermined number of plants was assumed to be a major reason for the disappointing response of grid selection. Therefore a modification was experimentally evaluated for crop 12. This modification implies standardization per grid for the character of interest, followed by truncation selection for the standardized value. In crop 12 the 128 plants with a standardized yield greater than 2 were selected. This meant that the number of plants selected in a grid ranged from 9 to 16 inclusive. From 23 of these plants the offspring was compared with the offspring of plants selected at random in crop 12. It appeared that the former group of offspring yielded 8% better. Further study on the efficiency of this modification was started in 1981.

SAMENVATTING

Bij massaselectie worden individuele planten geselecteerd. De volgende generatie wordt verkregen uit een mengsel van zaden van de geselecteerde planten. Het doel van de selectie is het afzonderen van planten met een superieure genotypische waarde. De feitelijke selectie is echter gebaseerd op de fenotypische waarde. Deze fenotypische waarde van een individuele plant wordt mede bepaald door de groeiomstandigheden voor die plant. Die groeiomstandigheden zijn van plant tot plant verschillend omdat ze uit een complex van condities bestaan (inclusief de concurrentieverhoudingen tussen planten). Bij afknottingsselectie voor één of meer eigenschappen (in het laatste geval spreekt men van selectie met onafhankelijke selectiedrempels) wordt er in het geheel geen rekening gehouden met de bijdrage van de groeiomstandigheden aan de fenotypische waarde. Bij toepassing van vakselectie is er een grotere uniformiteit in groeiomstandigheden van de te vergelijken planten. Hierdoor wordt de variatie van de bijdrage van de groeiomstandigheden aan de fenotypische waarde verminderd.

Bij honingraatselectie is de vakgrootte minimaal. Het maskerende effect van de groeiomstandigheden op de genotypische waarde wordt dan geminimaliseerd. Omdat deze laatste methode erg aantrekkelijk leek werd haar doeltreffendheid vergeleken met die van andere methoden voor massaselectie. Het onderzoek werd uitgevoerd met winterrogge; zowel met diploid materiaal (het ras Dominant) als met autotetraploid materiaal, dat op het IvP ontwikkeld was. Het doel van de selectie was een planttype, waarbij een goede opbrengst samengaat met geringere halmlengte. Het verloop van de proefnemingen wordt door figuur 2 in beeld gebracht.

Bij het aanleggen van een honingraatselectieveld moet men de plantdichtheid in overweging nemen. Hoe groter de plantdichtheid, hoe kleiner de oppervlakte die door een groep van 7 planten (een centrale plant en haar 6 buren) in beslag genomen wordt en hoe uniformer sommige groeicondities binnen zo'n groep. Aan de andere kant nemen de storende effecten van concurrentie tussen de planten toe bij hogere plantdichtheid. In het onderhavige onderzoek werd in de selectievelden een plantdichtheid van 51,3 planten per m^2 toegepast. Teelt 1 en de overige selectievelden (behalve teelt 4) omvatten 5304 plantplaatsen voor planten doe geobserveerd dienden te worden.

Na de oogst van teelt 1 werd voor elke plant de korrelopbrengst, het halmgetal (d.w.z. het aantal aren per plant) en de halmlengte geregistreerd. Voor korrelopbrengst en voor halmgetal werden frequentieverdelingen met een positieve scheefheid verkregen. Op grond van de zeer hoge fenotypische correlatie van korrelopbrengst en het gewicht van de aren werd in latere proefnemingen volstaan met registratie van het gewicht van de aren (kortheids-

halve onder de kop: opbrengst). De fenotypische correlatie van halmgetal en korrelopbrengst bedroeg 0,90. De fenotypische correlatie van halmlengte en korrelopbrengst was ongeveer 0,6. Dat beloofde problemen bij de realisatie van het doel van de selectie: verkrijging van een zgn. recombinant planttype.

Bij de honingraatselectie werden de planten met een hogere opbrengst dan elk van hun 6 buren en met een halmlengte die kleiner was dan de gemiddelde halmlengte van de 6 buren geselecteerd. Om het resultaat van de selectie vast te stellen werden tegelijkertijd willekeurige planten geselecteerd (z.g. lotingsselectie). Het selectieresultaat werd gemeten door vergelijking van de nakomelingen van de opzettelijk geselecteerde planten met de nakomelingen van de willekeurig geselecteerde planten.

De kwaliteit van de waarnemingen aan de planten van de vergelijkende proef werd in beschouwing genomen. Hierbij werd vastgesteld dat het feitelijke aantal planten per veldje vaak kleiner was dan het geregistreerde aantal. De totale opbrengst per veldje leek daarom een veiliger maatstaf bij de beoordeling dan de gemiddelde opbrengst per plant.

Een tweede reden voor selectie en nateelt van willekeurige planten was de wens schattingen te verkrijgen voor de erfelijkheidsgraad, de additieve genetische variantie en de genetische correlatie van de eigenschappen. Omdat de veronderstellingen die ten grondslag liggen aan de schatters slechts ten dele gerechtvaardigd konden worden kunnen de schattingen slechts als ruwe indicatie voor de wijze van de polygene overerving dienen.

Voor halmlengte bedroeg de schatting voor de erfelijkheidsgraad in engere zin 0,39; voor opbrengst 0,04. De genetische correlatie van deze 2 eigenschappen werd door de ene schatter op 0,45 geschat maar door de andere schatter op 0,68.

Uit de vergelijkende proef (teelt 3) bleek dat de selectie niet resulteerde in een hogere opbrengst, maar voor halmlengte werd een significante afname vastgesteld.

Het tweede selectieveld (teelt 2) bestond uit nakomelingen van de planten die in teelt 1 door honingraatselectie waren geselecteerd. De proefopzet was gelijk aan die voor teelt 1. De planten leden ernstig onder de ongekende droogte van 1976. Na de oogst werden opbrengst, halmgetal en halmlengte geregistreerd. Behalve honingraatselectie en lotingsselectie werden nu ook afknottingsselectie en vakselectie toegepast. De eerste methode beoogde reductie van de halmlengte bij gelijkblijvende of toenemende opbrengst, terwijl de laatste 2 methoden een hogere opbrengst beoogden.

De opzet van de vergelijkende proef, waarin de prestaties van de nakomelingen van de 4 typen geselecteerde planten werden vergeleken, was analoog aan die voor teelt 3: de veldjes bestonden opnieuw uit 21 plantplaatsen langs één rij. De correlaties van de prestaties van overeenkomstige veldjes in de 2 blokken waren erg laag. Ze lagen tussen 0,11 voor halmgetal en 0,29 voor halmlengte. De schattingen van de erfelijkheidsgraad waren ongeveer gelijk aan die, welke een generatie eerder verkregen waren. De genetische correlatie van halmlengte en opbrengst werd nu tevens geschat uit het gecorreleerde selectieresultaat. De verkregen waarde (circa 0,62) week nogal af van de waarde (n.l. 0,83) verkregen met de conventionele schatter.

De vergelijkende proef onthulde alleen voor halmlengte significante verschillen tussen de 4 typen nakomelingschappen: na vakselectie of afknottingsselectie waren de halmen significant langer dan na lotingsselectie of honingraatselectie. In tegenstelling tot wat verwacht werd bleef de opbrengst na vakselectie achter bij die na afknottingsselectie.

Het derde selectieveld (teelt 4) werd verkregen uit een mengsel van korrels van planten, die in het tweede selectieveld door honingraatselectie waren geselecteerd. De opkomst van teelt 4 was uiterst slecht. Om een selectieveld zonder open plantplaatsen te verkrijgen moesten erg veel planten verspeend worden. Dit resulteerde in een heterogeen gewas.

De selectiemethoden die in teelt 2 waren toegepast werden ook in teelt 4 toegepast. De nakomelingen van de 4 groepen geselecteerde planten werden vergeleken in een proef die uit 2 volledige blokken bestond. De correlaties van de waarnemingen in de 2 blokken waren erg laag en nauwelijks significant; behalve voor halmlengte (r=0,52***). De schatting van de erfelijkheidsgraad bedroeg voor halmgetal 0, voor opbrengst 0,03 en voor halmlengte 0,43. De genetische correlatie van halmlengte en opbrengst werd op diverse manieren geschat. De verkregen schattingen waren erg tegenstrijdig. Het werd duidelijk dat elke schattingsprocedure bezwaren kent. Een goede methode lijkt niet beschikbaar te zijn.

Het resultaat van honingraatselectie in teelt 4 was teleurstellend: de halmlengte nam weliswaar significant af (2,5%), maar ook de opbrengst nam af (5%). De resultaten van vakselectie waren ongeveer nihil. Afknottingsselectie resulteerde in een significant toegenomen opbrengst (t.o.v. elk van de 3 andere selectiemethoden).

Het vierde selectieveld (teelt 6) werd verkregen uit een mengsel van korrels van de 92 planten, die door honingraatselectie waren geselecteerd in het voorafgaande selectieveld (teelt 4). Er werd één korrel per plantplaats gezaaid. Slechts 3,6% van de plantplaatsen bevatte uiteindelijk geen plant. De selectiemethoden die werden toegepast waren: honingraatselectie, selectie met onafhankelijke selectiedrempels en lotingsselectie. De selectiedrempels werden niet volgens een formeel criterium gekozen. De keuze was zodanig dat planten met een goede opbrengst en een relatief geringe halmlengte geselecteerd werden. Nakomelingen van de geselecteerde planten werden in teelt 10 vergeleken. De veldjes met families, die afkomstig waren van gelote planten, omvatten tweemaal het gebruikelijke aantal planten. Behalve voor halmlengte resulteerde dat niet in een hogere correlatie van de waarnemingen aan overkomstige veldjes in de 2 blokken. Voor opbrengst per aar werd een interessante schatting van de erfelijkheidsgraad verkregen, n.l. 0,29.

Opnieuw werden er geen bevredigende schattingen voor de genetische correlatie verkregen. Aan de schattingen op basis van gecorreleerde selectieresultaten werd de voorkeur gegeven.

Uit de vergelijkende proef bleek dat zowel honingraatselectie als selectie met onafhankelijke selectiedrempels er in slaagden de halmlengte te verminderen. De opbrengst nam evenwel ook af (hoewel niet significant). Noch door indexselectie, noch door selectie van de planten, die zowel aan de criteria voor honingraatselectie voldeden als aan de criteria voor selectie met onafhankelijke selectiedrempels, werden betere resultaten verkregen.

De zojuist beschreven selectiemethoden werden ook toegepast op een populatie van autotetraploide planten (teelt 9). Het selectieveld was op de gebruikelijke wijze aangelegd. Het lag in de nabijheid van teelt 6. Voor een groot aantal eigenschappen werden het diploide en het tetraploide materiaal vergeleken. In aanvulling op de steeds waargenomen eigenschappen werd ook de stro-opbrengst geregistreerd. De door lotingsselectie afgezonderde planten dienden met het oog op de vergelijkende proef meer dan een minimale opbrengst te hebben. Deze planten waren daardoor niet representatief voor teelt 9: ze brachten meer op en ze waren langer. Dit belemmerde de waarneming van realisatie van het beoogde selectiedoel voor opbrengst, maar voor halmlengte werd zo'n waarneming bevorderd. Nakomelingen van de gelote planten werden opnieuw op veldjes met tweemaal het gebruikelijke aantal planten geteeld. Alleen voor halmlengte resulteerde dat in een toegenomen correlatie van overeenkomstige veldjes.

Voor het autotetraploide materiaal waren de voorwaarden voor het schatten van kwantitatief-genetische parameters nog moeilijker te rechtvaardigen dan voor het diploide materiaal. Voor halmlengte, halmgetal en opbrengst kwamen de schattingen voor de additieve genetische variantie en voor de erfelijkheidsgraad overeen met de vergelijkbare schattingen voor het diploide materiaal. Voor oogstindex bedroeg de schatting van de erfelijkheidsgraad maar liefst 0,46. Opbrengst per aar bleek een aantrekkelijke eigenschap voor (in)directe selectie.

De nakomelingen van de geselecteerde planten vertoonden een significante afname van de halmlengte: zowel na honingraatselectie als na selectie met onafhankelijke selectiedrempels. De planten die door elk van deze twee methoden werden geselecteerd gaven opmerkelijk gunstige nakomelingen (met een opbrengst die 7,2% beter was, terwijl de halmlengte 2,1% was afgenomen).

De verkregen resultaten bevestigen de elders opgedane ervaring, dat het resultaat van een eenmalige toepassing van massaselectie in hoge mate beïnvloed wordt door incidentele omstandigheden. Daarom werd het cumulatieve effect van 3 opeenvolgende generaties met honingraatselectie bestudeerd bij een normale plantdichtheid (teelt 11). Door een te klein aantal herhalingen resulteerde deze afsluitende beproeving niet in statistisch significante, positieve resultaten voor korrelopbrengst. Er werden desondanks gunstige uitkomsten geboekt: toepassing van honingraatselectie gedurende 3 opeenvolgende generaties resulteerde in planten met een geringere halmlengte (6,1%), gecombineerd met een verbeterde korrelopbrengst (4,3%). De toegepaste variant voor honingraatselectie bewerkstelligde dus inderdaad recombinatie in de beoogde richting.

Genotype x milieu interactie en heterogene groeicondities binnen de zesringen met 7 planten werden besproken als factoren die het resultaat van honingraatselectie beperken. Er werd een poging gedaan een verklaring te geven voor het wel vaker geconstateerde verschijnsel dat, ondanks de selectie, de additieve genetische variantie niet afnam.

In het algemeen waren de schattingen voor de additieve genetische variantie, verkregen uit de covariantie van nakomelingschap en ouderplant, kleiner dan die verkregen uit een variantie-analyse. Dit stemt overeen met hetgeen verwacht wordt op grond van de overweging, dat effecten van genotype x milieu interactie bijdragen aan de schatting ingeval de laatste schattingsmethode wordt toegepast.

Een oriënterend onderzoekje naar de doeltreffendheid van directe selectie op geringe halmlengte gaf aantrekkelijke uitkomsten. Dit onderzoek zal worden voortgezet.

In het laatste hoofdstuk wordt een aantal mogelijkheden voor verdoezeling van de genotypische waarde van een individuele plant in beschouwing genomen. Het betreft zowel milieuvariatie als concurrentie. In de eerste paragraaf wordt aangetoond dat, althans in teelt 2, honingraatselectie er beter in slaagde de milieu-bijdrage aan de fenotypische waarde te elimineren dan afknottingsselectie of vakselectie. Vakselectie was in dit opzicht enigszins inferieur vergeleken met afknottingsselectie. Honingraatselectie slaagt er natuurlijk niet in fenotypische variatie, welke berust op verschillen in groeicondities binnen een zesring met ten hoogste 7 planten te elimineren. Zulke verschillen bestaan bijvoorbeeld voor zaaidiepte en voor oriëntatie van de gezaaide korrel.

De suggestie het gemiddelde van een nabij gelegen groep planten te gebruiken als een covariabele die gerelateerd zou moeten worden aan de prestatie van de in beschouwing zijnde plant(en), werd proefondervindelijk op haar waarde onderzocht. Deze suggestie werd gepropageerd als een methode om de milieu-bijdrage aan de fenotypische waarde van de ter beoordeling staande planten te verdisconteren. In het onderhavige onderzoek werd de suggestie beproefd door regressie van de prestatie van een centrale plant op de gemiddelde prestatie van de bijbehorende buurplanten. Dit werd gedaan voor de 102 gelote planten uit teelt 6. De gecorrigeerde prestatie van de centrale plant werd berekend door de feitelijke prestatie te verminderen met de voorspelde prestatie. De gecorrigeerde waarde dient de genotypische waarde beter te weerspiegelen dan de feitelijke waarde. De correlatie van de ouderlijke waarde en het nakomelingschapsgemiddelde zou dus hoger moeten zijn voor de gecorrigeerde prestatie dan voor de niet-gecorrigeerde prestatie. Dit werd echter niet gevonden zodat er geen aanwijzingen ten gunst van de suggestie werden verkregen. De reden hiervoor kan een overstelpend grote invloed van individuele, tot het micromilieu beperkte invloeden op de fenotypische waarde van de centrale plant zijn. De voorwaarde voor afname van de milieuvariantie ten gevolge van correctie werd voor een eenvoudige correctiemethode gegeven. Er werd aangetoond dat in teelt 1 niet voldaan werd aan die voorwaarde.

Verder werd de gedachte uitgewerkt, dat verschillen in plantlengte eerder een gevolg zijn van concurrentie dan een oorzaak voor verschillen in concurrentievermogen. Voor opbrengst zou hetzelfde kunnen gelden. De positieve correlatie van halmlengte en opbrengst zou dus voor een deel kunnen berusten op tussenplantconcurrentie. Indien dit idee juist is zal zo'n relatie binnen elke populatie met tussenplantconcurrentie bestaan. Het doel van een selectieprogramma dient dan niet te zijn het breken van de correlatie, maar afname van de halmlengte met behoud van de opbrengst of zelfs met toename daarvan.

Zoals uit de literatuur bekend is is de grootte van een korrel van invloed op de prestatie van de plant die uit die korrel groeit. Volgens Spitters (1979) zou dat berusten op een sterker concurrentievermogen tijdens de juveniele fase van de uit grotere korrels verkregen planten. Variatie in korrelgrootte is daardoor één van de groeifactoren welke bijdragen aan de milieuvariantie. De afhankelijkheid van eigenschappen van de volwassen plant van het gewicht van de uitgangskorrel werd vastgesteld bij de onderhavige plantdichtheid en bij het onderhavige plantverband. Inderdaad bleek dat ook onder de groeiomstandigheden van een selectieveld (teelt 6 in dit geval) het gewicht van de uitgangskorrel in belangrijke mate bepalend was voor de opbrengstcomponenten van de volwassen plant. De planten die door honingraatselectie op opbrengst werden geselecteerd waren uit zwaardere korrels afkomstig dan de niet-geselecteerd planten. Op grond hiervan worden de korrels die gebruikt worden voor een selectieveld sinds 1979 gesorteerd op grootte.

Het effect van plantdichtheid op het resultaat van honingraatselectie werd bestudeerd op grond van gegevens ontleend aan een onderzoek van Spitters (1979) met een mengsel van 12 zomergerstrassen. Het mengsel werd in een driehoeks-plantverband geteeld; bij de dichtheden 80 en 3,2 planten per m². Bij beide plantdichtheden werd 10,3% van de planten geselecteerd door honingraatselectie. Het percentage waarmee elk gerstras vertegenwoordigd was in de groep geselecteerde planten werd gerelateerd aan het rangnummer van het ras volgens de opbrengst in nationale beproevingen. Bij een dichtheid van 80 was er geen significante correlatie, maar wel bij een dichtheid van 3,2. De hypothese van Fasoulas dat selectie in afwezigheid van tussenplantconcurrentie zou moeten plaatshebben werd dus gesteund.

Het onderzoek toonde aan dat, in tegenstelling tot onze verwachting, het resultaat van vakselectie niet zo goed was als dat van afknottingsselectie. De gewoonte om in elk vak hetzelfde, vooraf bepaalde aantal planten te selecteren zou hiervan de oorzaak kunnen zijn. Daarom werd in teelt 12 een modificatie toegepast. Deze impliceerde voor elk vak standaardisatie voor de van belang zijnde eigenschap, gevolgd door afknottingsselectie gebaseerd op die gestandaardiseerde waarden. De 128 planten met een gestandaardiseerde opbrengst groter dan 2 werden geselecteerd. Het hierdoor geselecteerde aantal planten per vak varieerde van 9 tot en met 16. Van 23 van deze planten werd de nakomelingschap geteeld en vergeleken met de nakomelingen van de gelote planten uit teelt 12. De eerste groep nakomelingen produceerde 8% meer. Verder onderzoek naar de doeltreffendheid van deze modificatie is in 1981 aangevangen.

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