# Competition and its consequences for selection in barley breeding

C.J.T. Spitters

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dr. H.C. van der Plas,
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# Abstract

Spitters, C.J.T. (1979) Competition and its consequences for selection in barley breeding. Agric. Res. Rep. (Versl. landbouwk. Onderz.) 893, ISBN 90 220 0712 X, (x) + 268 p., 48 figs, 58 tables, 310 refs.
Also: Doctoral thesis, Wageningen.

The influence of competition is discussed and quantified for unselected bulk propagation, single-plant selection and yield testing of progenies in row plots. A mathematical model is introduced that defines the influence of intergenotypic competition and density of stand on the response to selection. The model is verified with the results of mixtures and monocultures of barley varieties. Intergenotypic competition usually increases the genetic variance considerably, but hardly affects the environmental variance. Selection for yield in a segregating population, i.e. in a mixture, results in a correlated response for monoculture yield.

Delaying selection for yield until the late generations of a segregating population is not handicapped by competition and natural selection. Methods to account for competition in single-plant selection and in yield testing of progenies in row plots are discussed. The selection response is independent of the spacing provided that certain prerequisites are satisfied. Alternating the plants or rows with those of a standard variety is of no use in reducing the competitional bias. Given the present nursery equipment, 3-row plots with all three rows considered in selection for yield, seem the most suitable type of microplot.

Free descriptors: competition model, selection response, yield testing, field plot technique, microplots, density of stand, mixtures, soil heterogeneity, bulk propagation, natural selection, small grains, wheat.

This thesis will also be published as Agricultural Research Report 893.

# Stellingen

1. De conventionele kwantitatief-genetische analyse is van weinig waarde indien de beschouwde eigenschap, zoals de meeste kwantitatief-overervende eigenschappen, door concurrentie wordt beïnvloed.

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2. Additieve biometrische modellen, zoals het additief-dominantie-model in de kwantitatieve genetica, missen een biologische basis en dienen vervangen te worden door modellen die die basis wel bezitten. Deze laatste modellen zullen in het algemeen multiplicatief zijn.

3. Het vergelijken van selectiemethoden naar hun responsies, die verkregen zijn door in een splitsende populatie volgens die methoden te selecteren, verschaft nauwelijks enig inzicht in de verschillen tussen de onderzochte selectiemethoden.

4. In het gebruik van de 'realized heritability' toont de 'black box'-benadering in de plantenveredeling zich op zijn zwartst.

5. Het concurrentiemodel van De Wit (1960) houdt geen rekening met het feit dat de afstand tot waar een plant zijn invloed kan uitstrekken aan een biologische limiet is gebonden. Dit kan leiden tot belangrijke afwijkingen van hetgeen op grond van het model verwacht wordt.

C.T. de Wit, 1960: Versl. landbouwk. Onderz. 66(8).
Dit proefschrift

6. De discrepantie tussen de opvattingen van onderzoekers en die van praktische kwekers ten aanzien van de te volgen selectieprocedure zou aanmerkelijk verkleind worden indien de onderzoekers in belangrijke mate zouden deelnemen aan de veldwerkzaamheden op de onderzoeksinstellingen.

7. Het belang van de statistiek voor de praktische veredeling ligt veel meer in de proefveldtechniek en de gegevensverwerking dan in de kwantitatieve genetica.

8. Het achtergrondsvak voor de teeltrichtingen vam de Landbouwhogeschool dient een integratie van de relevante vakgebieden te omvatten. Dit is het beste te realiseren via een systeem-analytische benadering.

9. Het feit, dat de Minister van Landbouw blijkens de memorie van toelichting op de begroting van 1980 de inkomensverdeling binnen de Nederlandse landbouw niet als zijn taakveld onderkent, moet als typerend voor het gevoerde overheidsbeleid in deze sector worden beschouwd.

10. De kijk van niet-wetenschappers op de wetenschap zou aanmerkelijk realistischer zijn indien zij de resultaten van wetenschappelijke theorieën en modellen even gemakkelijk zouden kunnen verifiëren als de resultaten van de meteorologische modellen waarop de weersvoorspellingen berusten.

Proefschrift van C.J.T. Spitters
Competition and its consequences for selection in barley breeding
Wageningen, 12 december 1979

# Woord vooraf

Een omvangrijk proefschrift waaraan uitgebreide experimenten ten grondslag liggen is alleen mogelijk met de hulp van velen. Vanaf deze plaats wil ik iedereen bedanken die op enigerlei wijze aan de realisatie van het onderzoek heeft bijgedragen.

Promotor prof.dr.ir. C.T. de Wit was een uitstekende leermeester. Zijn altijd weer alternatieve benaderingen, zijn vermogen uiteenlopende vakgebieden te integreren, zijn provocerende opmerkingen en zijn vermogen om achter vele zaken een gefundeerd vraagteken te zetten hebben mij steeds geïnspireerd. Co-promotor prof.dr.ir. J. Sneep heeft het onderzoek naar de implicaties van concurrentie voor de plantenveredeling aangekaart als onderwerp voor een promotie-assistentschap. Ik ben hem met name erkentelijk voor het door hem in mij gestelde vertrouwen door mij als promovendus aan te nemen.

Ir. I. Bos heeft kritisch en consciëntieus het manuscript doorgewerkt, hetgeen een bron vormde van constructieve discussies. Dit geldt ook voor prof.dr. R.S. Loomis (Univ. California, Davis) die veel correctiewerk verrichtte en mij enige Engelse grondregels bijbracht. Verschillenden hebben onderdelen van het manuscript beoordeeld; met name dr.ir. A.C. Zeven en prof.dr.ir. J.H. van der Veen.

De experimenten zijn grotendeels verricht op het Instituut voor Plantenveredeling (I.v.P.). Velen hebben bij het veldwerk meegeholpen. In het bijzonder wil ik de heer H. Masselink bedanken voor zijn inzet en zijn technische raadgevingen. Van het proefveldpersoneel dat onder zijn leiding stond noem ik met name de heren J. van den Brink en H.B. Blekkink. De heer H.E. de Ruiter (Theoretische Teeltkunde) heeft geassisteerd bij vele veldwerkzaamheden en het verzamelen van gegevens in 1977. De heren C.M. Levering en W. Muyres hebben een belangrijk deel van de plantselectieproef van 1977 voor hun rekening genomen als onderdeel van hun doctoraalstudie.

De heer C.A. Hoveyn (CABO) heeft mij ingewijd in de proefveldtechniek en mijn kijk op de statistiek verhelderd. Gebruik van zijn statistische standaardpakketten voor computerverwerking bespaarde mij veel tijd. Hierbij heb ik assistentie ondervonden van de dames C. van Grootheest en J. Jochemsen. Ook bij de heer M. Keuls (Wiskunde) kon ik altijd aankloppen met statistische problemen.

Het vele typewerk werd op uitstekende wijze verzorgd door Mw. C.G. Uithol-van Gulijk (Theoretische Teeltkunde) en Mw. T.T. Nijenhuis-Rijmers (Tekstverwerking). De heer G.C. Beekhof (BGD) verzorgde het tekenwerk. Mw. E. Brouns-Murray corrigeerde het Engels en besteedde ruime tijd aan de bespreking van de correcties.

De Landbouwhogeschool ben ik erkentelijk voor de mogelijkheid dit onderzoek te verrichten, het PUDOC voor de verzorging van de uitgifte van het proefschrift en het CABO voor zijn gastvrijheid en onderzoeksfaciliteiten.

Wil, jij gaf mij de nodige morele en ook daadwerkelijke steun.

# Curriculum vitae

Kees Spitters werd geboren op 13 april 1951 te 's-Hertogenbosch. Op het Sint-Janslyceum aldaar volgde hij de HBS-b opleiding met 6-jarige cursusduur. In 1969 begon hij zijn studie aan de Landbouwhogeschool te Wageningen (studierichting Plantenveredeling), waar hem in 1974 het ingenieursdiploma met lof werd uitgereikt. Van november 1974 tot maart 1978 was hij promotie-assistent bij de vakgroepen Theoretische Teeltkunde en Plantenveredeling van de Landbouwhogeschool. Sinds maart 1978 is hij als wetenschappelijk ambtenaar werkzaam bij de vakgroep Theoretische Teeltkunde.

# Contents

# 1 Introduction

## 1.1 INTERGENOTYPIC COMPETITION AND CEREAL BREEDING

Plant breeders aim at finding superior genotypes in genetically heterogeneous populations. Such selection is an involved task since phenotypic expression is determined not only by genotype but also by environment. Diversity of the environment within the selection field, together with random variation, bias selection.

The environment of a plant consists of physical growth factors and the neighbouring plants which interfere with that plant. Interference is usually a competition for the same growth requisites, like water, light, and nutrients. These are present in a limited supply. The competition between the plants for the limited resources results in an uneven sharing of these resources.

As a result of competition between the genotypes, the performance of a genotype in a heterogeneous, mixed population differs from its performance in a homogeneous monoculture. In this way intergenotypic competition complicates selection since selection must be carried out in a genetically heterogeneous stand, whereas the selected genotypes have ultimately to perform in a homogeneous monoculture. When the genotypes are evaluated in a mixed population, some genotypes, the weak competitors, are underestimated with respect to their yielding ability in monoculture. On the contrary, the yielding ability of other genotypes, the strong competitors, is overestimated in the mixture. Hence, due to intergenotypic competition the performance in the selection nursery may be poorly related to yielding ability under agricultural conditions. Therefore, intergenotypic competition biases the outcome of selection.

Intergenotypic competition may make itself felt at several stages of a breeding programme. Let us consider the different steps of such a programme and the ways by which competition exercises its influence (Fig. 1). The discussion is focussed on selection for yield in self-fertilizing small grain crops.

Generally, the programme starts with the establishment of a segregating population, from which individual plants are selected. To avoid the enormous error variation inherent to single plants, the progenies of the plants are tested in subsequent generations. Breeders apply many variants of this so-called 'line selection' method. Present practice in cereal breeding is illustrated well by the results of a questionnaire sent in 1966 to a cross-section of the world's wheat breeders to determine the basic breeding methods they use. The results were reported by Shebeski (1967) and Briggs (1969). Most breeders practise pedigree breeding systems where in the second generation, the $F_2$, spaced plants are rigorously selected for characters such as resistance to disease, stiffness of straw and height. The progenies of the selected plants are generally

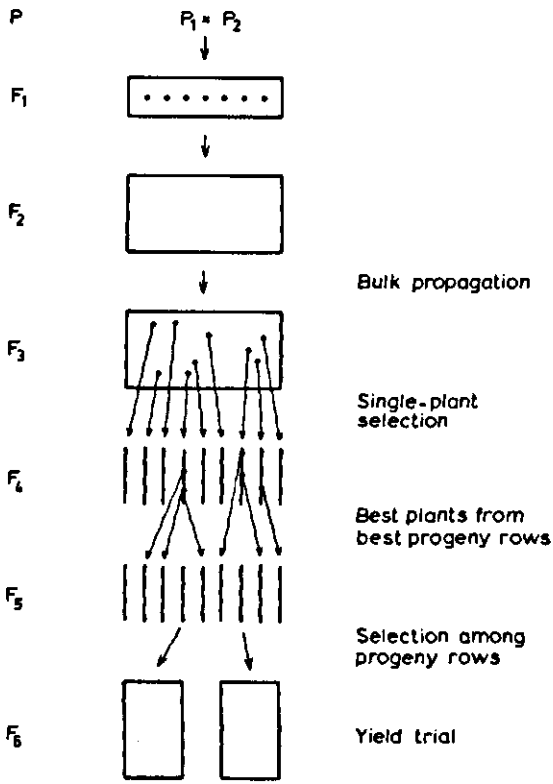


**Fig. 1. A selection scheme for self-fertilizing cereals. Dots indicate single plants, lines indicate progeny rows, and rectangles denote field plots.**

grown in rows. In each row a single progeny is sown. The rows are used for a visual assessment of desirable agronomic traits on a line basis, commonly followed by visual selection of single plants within the selected lines. This procedure is continued for some generations, until in later ones yield testing is started. Very few breeders are engaged in methods of selecting for yield on a quantitative basis in the generations prior to $F_4$. In contrast to the pedigree method, Mac Key (cited by Briggs, 1969) indicated that in his own programme, and in those of many European wheat and barley breeders, mass selection is conducted until $F_4$ in order to start pedigree selection at a level of greater homozygosity.

When the programme is based on a cross between two homozygous parents, the segregating $F_2$ is the first generation where intergenotypic competition plays a role. Unselected bulk propagation of the heterogeneous $F_2$ carries natural selection with it, which favours the types that produce the largest number of descendants. In this way competition may involve a strong dilution or even loss of desirable alleles.

For example, in a mixture of five rice varieties grown by Jennings & de Jesus (1968) during four cycles of bulk propagation, the two vigorous, tall, leafy varieties tended to crowd out the vegetatively small, short-statured varieties by overshading them. However, pure stands of the latter consistently and substantially outyielded the highly competitive varieties. Hence, the yield per plant of the desired short types was depressed

by the taller ones. Hence, selection of single plants for yield, and also for vigour or general appearance, may be biased by competition.

The progenies of the selected plants are evaluated in separate rows, each progeny in a single row. Since the yield of the border rows of a field plot may be significantly affected by the adjacent plots, yield evaluation of the progenies sown in rows may be confounded by competition between the genetically different rows. Since the lines are segregating, the plants within the rows suffer also from intergenotypic competition. Therefore, reselection of individual plants from the selected lines is also complicated by competition.

## 1.2 EARLY GENERATION YIELD TESTING

Selection for yield on a quantitative basis rarely starts in generations prior to $F_4$. Most breeders prefer a step-by-step policy: in early generations many lines are discarded on the basis of simply inherited traits and general agronomic appearance in order to test a moderate number of promising progenies in advanced generations in field plots for yield performance. Intergenotypic competition will influence only the border rows of field plots and is therefore of minor importance in yield tests of traditional breeding programmes.

On the other hand, several authors, especially Shebeski (1967), stated that yield testing has to start in the early generations. This involves yield testing in microplots, especially single-row plots, because of the large number of entries to be tested and the scanty seed supply of each entry. In contrast to the field plots used in conventional yield testing, the microplots may be seriously affected by interplot competition.

Shebeski (1967) pointed to the disadvantages of delaying selection till late generations. When the two homozygous parents of a cross differ for yield at n independent loci, $(3/4)^n$ of the $F_2$ plants can be expected to possess the best alleles for each of the n loci in either homozygous or heterozygous condition. With further generations this portion decreases considerably to $(5/8)^n$ in $F_3$, $(33/64)^n$ in $F_6$ and $(1/2)^n$ in $F_\infty$ (Table 1). The expected portions only hold for an equal fitness of each genotype and for independence of the loci. Independence of the loci involves absence of linkage and absence of inter-locus interaction. Yield, as a typically quantitative character, is determined by a large number of genes, i.e. n is large. Hence, the breeder who delays selection until later generations or who makes too few reselections from the selected lines, will have to settle for genotypes with fewer desirable alleles than possible.

From a theoretical point of view, yield testing should start in $F_2$, but owing to the poor reliability of yield of single plants, yield testing is recommended to begin in $F_3$. The efficiency of early generation selection has been studied mostly by the correlation between the yields of $F_3$ lines in microplots, usually single rows, and the yields of related family means or bulks in later generations. Such a correlation has to be interpreted with caution as the correlation coefficient tends to be higher when the genetic variation in the population is larger.

In barley, McKenzie & Lambert (1961) found correlations between yields in $F_3$ and

Table 1. The additive and dominance fraction of the genetic variance, D and H respectively, and the frequency of the plants having all of the independent desired alleles, in successive generations derived from a cross between two homozygous parents of a self-fertilizing species. As an example, it is assumed that there are 21 independent loci for yield.

| Generation | Genetic variance | Frequency of plants with desired alleles |
|---|---|---|
| $F_1$ | 0 | 1 |
| $F_2$ | 0.50 D + 0.25 H | $24000 \times 10^{-7}$ |
| $F_3$ | 0.75 D + 0.19 H | $520 \times 10^{-7}$ |
| $F_4$ | 0.88 D + 0.11 H | $57 \times 10^{-7}$ |
| $F_5$ | 0.94 D + 0.06 H | $17 \times 10^{-7}$ |
| $F_6$ | 0.97 D + 0.03 H | $9 \times 10^{-7}$ |
| $F_\infty$ | D | $5 \times 10^{-7}$ |

$F_6$ of 0.31 and 0.54 for the two populations studied. The $F_3$ lines were tested in unreplicated 1-row plots. The authors concluded that testing lines in $F_3$ for yield would not be a reliable method of obtaining the best material out of a cross. However, they considered the findings not too discouraging. In winter wheat, Utz et al. (1973) found variable and low correlations between the yields of 1-row plots in $F_3$ and the yield of field plots in $F_5$ and $F_6$. Over two populations the correlation coefficients averaged 0.23. In spring wheat, Knott & Kumar (1975) observed correlations between $F_3$ yields and $F_5$ yields of 0.29 and 0.14 for the two populations studied. The $F_3$ yields were measured in three times replicated 1-row plots. When in the $F_3$ the 36 highest yielding $F_3$ lines (20%) were selected, only 17 of the 36 highest yielding $F_5$ lines would have been recovered.

Shebeski (1967) and DePauw & Shebeski (1973) reported in spring wheat high correlations between $F_3$ lines and their related $F_5$ families. The simple correlation coefficient was 0.56 and the rank correlation amounted 0.85. They tested the $F_3$ lines in 3-row plots of which the yield was expressed as percentage of adjacent control plots.

Briggs (1969) and Briggs & Shebeski (1971) observed rank correlations between the yield of $F_3$ lines in unreplicated 3-row plots and the mean yield of related $F_5$ families of 0.83, -0.09, and 0.31 for three spring wheat populations, respectively. However, early generation yield testing was successful in that in each of the three populations the highest yielding $F_5$ families were derived only from $F_3$ lines which were relatively high yielding. Based on their own results and a review of the literature on this subject, Briggs & Shebeski (1971) stated that, although the supporting evidence is not strong, yield testing of unreplicated $F_3$ lines might be a worthwhile procedure.

The moderate success of early generation yield testing is ascribed to (a) interaction between genotype and year because a comparison of the generations is not made in the same year, (b) heterozygosity in early generations that may give rise to high-yielding heterotic genotypes which do not breed true in the following generations, and (c) experimental error introduced by the use of microplots.

Early generation yield testing may be compared with yield testing in later genera-

tions by selecting the same population according to both methods. This was done in spring wheat by Knott & Kumar (1975), Seitzer & Evans (1978), and Knott (1979), and in soybeans by Raeber & Weber (1953), Voigt & Weber (1960), Luedders et al. (1973), and Boerma & Cooper (1975). The advantage of early generation yield testing over yield testing in late generations was absent or small. The general opinion was that it is questionable whether the gain, if present, of early generation yield testing justifies the extra work involved. One might object that too few reselections were made in the subsequent generations to exploit the theoretical advantages of early-generation yield testing fully. Furthermore, the difference between selection methods was confused by other factors, so that the comparison was complicated.

Despite the theoretical advantages, commercial breeders do not start selection for yield on a quantitative basis in early generations. In the early generations, most breeders select the lines only visually for qualitatively inherited characters and for a general good appearance. What are the arguments to delay yield testing to the late generations?

*Cost* Yield testing is expensive.

- Early generation yield testing requires that a large number of plant progenies are screened for yield. However, many plants and many lines can already be discarded on visual grounds. Visual selection is very cheap compared with laborious yield tests. Therefore, the lines are selected visually in order to test, later on, only a moderate number of promising lines for yield.
- One reason for the low cost of visual selection is that it can be done in single headrows and it makes little demands on the uniformity of the plots. On the other hand, yield testing requires a high uniformity of the microplots which, moreover, must be larger than single headrows.
- To exploit the theoretical advantage of early generation yield testing fully, many reselections must be made in subsequent generations and all reselections must be tested for yield.
- Eventhough some high-yielding genotypes are lost in conventional breeding, a breeder aims to maximize the response per unit cost instead of to maximize the response whatever the costs.

*Heterozygosity* In self-fertilizing species, once a cross between two homogygous parents has been made, the homozygosity increases in each of the subsequent generations. $F_6$ and $F_7$ plants already show a high degree of homozygosity.

- When single plants are selected from the late generations, the resulting lines tend to breed true.
- Together with the homozygosity, the additive portion of the genetic variation increases considerably with advanced generations at the cost of the dominance fraction (Table 1). This facilitates selection.
- Dependent on the ratio between the dominance and the additive portion of the genetic variance, the total genetic variance may increase with advanced generations (Table 1).

Hence, due to the high degree of heterozygosity in the early generations, the plants

in these generations are not true to seed, the additive part of the genetic variance is relatively small, and also the genetic variance may be smaller.

*Identification* The theoretical advantage of early generation yield testing cancels out the disadvantage of a high degree of heterozygosity in the early generations and that of the large expenses of yield testing only when the genotypes with the favourable alleles are identified to a large extent. However, the identification will be poor.

- For example, in my trials with 12 pure-line varieties that differed greatly in their year of release, the yields of the eight highest-yielding varieties were not significantly different at $P \leq 0.10$ (Table 16). The varieties were laid out in a randomized design with 24 replications in such a way that the average yield of each variety was based on 48 bordered rows of 2 m length. The variation coefficient was only 2.8%. Hence, the detection of the genotypes, with alleles favourable for yield, is very poor when yield testing is done in unreplicated 3-row plots or in unbordered 1-row plots.
- History shows that most progress through breeding has involved adaptation to improved husbandry rather than increase of the ability to yield under optimal, disease-free conditions. Potential crop growth rate has not been augmented by breeding (de Wit et al., 1979), while the enhancement of grain/biomass ratio contributed only moderately to the increase of yield in course of time by breeding. On the other hand, genotypes are mainly differentiated in yield by secondary characters. In the previous example, there was a reduction in the influence of lodging and disease (Section 2.2), which probably contributed to the small differences in yield between the varieties. Selection for the secondary characters can conveniently be done visually so that high-yielding types are partly identified visually.
- The genotype with the highest yield at a certain location and in a certain year does not necessarily yield best at another location or in another year. Yield shows a large genotype x location and genotype x year interaction.
- Under absence of dominance effects, that is when the loci are isomeric, a genotype with all the desired alleles for yield in heterozygous condition is expected to have the same yield as a genotype with only half of the desired alleles but with each of these alleles in homozygous condition. Then, the yield of genotype AaBb equals that of AAbb and aaBB. However, the prospects of the former genotype are much better than those of the latter. This isomerism restricts the efficiency of early generation selection.

*Other considerations*

- A high yield is not the only prerequisite for a successful variety. Resistance against diseases, winter hardiness and straw-stiffness contribute to the reliability of the crop and with it to the success of a variety. Also quality aspects, date of ripening and suitability for mechanical harvesting may be of importance.
- In visual selection, allowance can be made for yield determining factors that exhibit themselves differently from year to year and from location to location. For example, in some years or at some locations a disease may be not epidemic, whereas usually this disease reduces the yield of susceptible varieties seriously. One may say that a breeder, in visual selection, partly accounts for genotype x year and genotype x location interaction.

In conclusion, early generation yield testing is unrealistic and, therefore, inadvisable. It is likely that the response per unit cost is greater in the conventional breeding procedure than in early generation yield testing. In early generation yield testing, a large number of lines of each cross must be tested. However, yield testing of the same number of lines but derived from several populations after rigorous visual selection, probably results in a higher response. The approach about the genetically optimal stage to start selection, shows that visual selection has to start as early as possible in order to keep the favourable characters together. Independent of ones opinion about yield testing in early generations, microplots may be useful to screen a large number of lines for yield. Therefore, in later sections, the effect of competition on yield testing in microplots is studied.

## 1.3 CONSEQUENCES OF COMPETITION FOR BREEDING, REVIEW OF LITERATURE

In this section the literature on the demonstration of intergenotypic competition and the consequences of competition for selection is summarized. Special attention is paid to ways to avoid or to reduce competition or to make allowance for it. A division is made into three stages of a breeding programme, namely unselected bulk propagation, plant selection and progeny testing (Fig. 1). For an outstanding overall survey on plant competition, the reader is referred to Donald (1963).

### *1.3.1 Unselected bulk propagation and natural selection*

Since Darwin developed his theories about evolution and about natural selection as one of its driving forces, some scientists have studied the possibility of leaving selection partly to nature for choosing agronomically desired types. They considered that natural selection would favour genotypes that are best adapted to a particular environment and give the highest yield in this environment, and that natural selection would eliminate, at least, the less adapted types.

Another reason to harvest all plants 'en masse' and to resow the bulked seed during several generations is based on the increase of the homozygosity with subsequent generations in a self-fertilizing species. As an additional advantage, large numbers of genotypes may be screened with very little expense on land and labour.

Bulk breeding has some disadvantages compared with early generation selection. Because of the homozygosity, the frequency of the plants possessing all favourable alleles decreases with successive generations (Section 1.2). Due to natural selection, some desired types may be diluted or even crowded out. During the period of bulk propagation, no information is obtained about genotype x year and genotype x location interaction. Moreover, the number of years from making the cross and the release of a variety is increased. However, most breeders, using bulk propagation, start selection of plants already in $F_4$.

Sometimes a bulk population is grown for more generations without artificial selection to prolong the effect of natural selection and to subject newly arisen segregants

to this selection pressure too. The population has mostly a very diverse genetic base, which may have been created in different ways. $F_1$'s or $F_2$'s of many crosses may be bulked into one composite population or multiple crossing may be practised till finally a single composite cross is made. The composite-cross method as part of a cereal breeding programme was advocated mainly by Suneson (1956, 1964, 1969) and was based on work of Harlan & Martini (1929) and Suneson & Stevens (1953) with barley composites.

In addition to the disadvantages mentioned for a few generations of bulk propagation, it must be noted that in the composite-cross method: (a) the progress in the late generations may be too slow to be of value for a breeder, (b) the final yield level is mostly lower than that of commercial varieties, and (c) a high yield level of the population does not guarantee that a large number of high-yielding lines can be derived.

This work is focused on competition and its consequences for selection on yield in self-fertilizing cereals. Thus, the critical issue for bulk propagation is whether natural selection favours genotypes with a high grain yield in pure culture. A closely related problem is the association between yield in mixed and pure culture. The last problem is crucial for plant selection and progeny testing, where selection is based on performance in segregating populations. The relation between competitive ability and pure-culture yield is of basic importance for both previous associations.

Natural selection favours those genotypes producing the largest number of descendents, i.e. producing the largest number of viable kernels. The reproductive rate of a genotype relative to that of the other components in the mixture does not only depend on the number of grains which the given genotype would produce in pure culture. It is also a function of its competitive ability and the grain production of the associated genotypes. Moreover, and usually of minor importance, the genotypes differ in seed size and consequently a larger number of kernels does not necessarily imply a higher yield in grain weight.

The relation between yield in mixed and pure stand, which affects the efficiency of plant selection and progeny testing, is less complicated. It is determined by the competitive ability of the given genotype relative to that of its neighbours (see Section 4.1 for mathematical expression).

Intergenotypic competition in cereals is mostly studied by growing mixtures of cultivars and comparing the results with the performance of these cultivars under agronomical practice. The competitive ability of a cultivar is estimated from its survival in mixtures grown for several generations or from its relative yield in annual mixtures. The agronomic performance of a cultivar is measured as its popularity with local farmers or as its yield in regional variety trials or, most directly, as its yield in adjacent monoculture plots.

*Relation between survival in mixture and yield in monoculture* Harlan & Martini (1938), in their classic experiment, mixed seed of 11 barley varieties in such a way that a mixture was obtained that contained equal numbers of plants of each variety. A random sample was drawn from the harvested seed to establish another plot in the next generation. This procedure was applied at 10 U.S. experiment stations for a period of from 4 to 12 years.

At each location a census was made annually to determine the variety of the plants and from that the progressive changes in the composition of the mixture. At all locations there was a rapid elimination of some cultivars, while it was also quickly evident which variety would eventually dominate the population. The constitution of the group of surviving varieties was different at each locality, as was the group of the eliminated ones. The dominating cultivars were, in general, the varieties most successful in commercial growing in the region in question. However, there were some distinct exceptions. On the other hand, the rapidly eliminated types were usually those less adapted to the local conditions and consequently the agronomically inferior ones.

Blijenburg & Sneep (1975) showed that the only variety well adapted to local conditions rapidly dominated a mixture of eight barley varieties grown during 6 successive years.

On the contrary, sometimes a negative association is observed. Jennings & de Jesus (1968) found that in a mixture of five rice varieties the two vigorous, tall varieties crowded out the erect, short-statued cultivars, whereas in pure culture the latter had the highest yield. Jennings & Herrera (1968) sampled the tall and dwarf segregates in the $F_2$ to $F_6$ from a cross between a tall rice variety and an erect dwarf type. The tall and dwarf segregates represented two highly contrasting plant types differentiated essentially by a major gene that affected also tillering, number, length and angle of leaf. This locus for height had also a pronounced effect on yielding ability because yield trials of random $F_6$ lines showed that under commercial growing conditions the dwarf lines by far outyielded the tall ones. The percentage dwarf plants observed in the $F_2$ to $F_6$ was much less than would be expected in absence of competition.

Suneson & Wiebe (1942) and Suneson (1949) grew a mixture of four barley varieties for 16 years, which resulted in the practical extinction of two varieties. One of these two varieties had a significant higher yield and leaf-disease record than any of the others when grown in monoculture in adjacent plots as well as in state-wide variety trials. However, the winning variety in mixture, 'Atlas', had the greatest popularity among farmers (Suneson, 1949; Allard, 1960, p. 139). However, a pertinent conclusion about the relation between survival in mixture and yield in monoculture cannot be drawn from this experiment, because the differences in monoculture yield were small. Moreover, when more extensive variety trials are considered (Suneson & Ramage, 1962), the rank in monoculture yield was changed and in favour of 'Atlas', the winning variety in the mixture. Allard & Adams (1969) did a separate competition experiment with these varieties and also found 'Atlas' to be the winner, but also the variety with the highest yield in monoculture.

*Relation between yield in mixture and yield in monoculture* Jensen & Federer (1965) showed prominent interrow competition among four wheat cultivars. Despite the significant competition effects, there was a general correspondence between the yield of a cultivar when bordered by itself and the yield of that cultivar when bordered by the others. A positive relationship between yield in mixed culture and that in pure stand was also reported by Kannenberg & Hunter (1972) in two competitional diallels of maize hybrids. A competition diallel is a design where the genotypes are grown in monoculture and in all possible 1 : 1 mixtures.

On the other hand, already in 1912 Montgomery concluded from his binary varietal mixtures of winter wheat and oats that '...when left in competition the variety which is the best yielder when placed alone may not always dominate, but, on the other hand, a less productive type may be best able to survive competition'. Gustafsson (1951) called this phenomenon the 'Montgomery effect'. An inverse relationship between the yields in mixed and pure stand was also observed by Christian & Gray (1941) and Khalifa & Qualset (1974) both in wheat and Wiebe et al. (1963) in barley.

*Relation between competitive ability and monoculture yield* Competitive ability is defined and estimated in different ways. These differences in calculation are ignored in this section.

Of the previous mentioned literature Jensen & Federer (1965), Kannenberg & Hunter (1972), and Blijenburg & Sneep (1975) demonstrated a good agreement between pure-culture yield of the varieties and their competitive ability in mixture. Stadler (1921) evaluated border effects of plots in barley, wheat and oats. In all experiments, involving a total of 316 entries, he recorded positive correlations between his coefficient of competition and yield of the centre rows. The correlations were significant in five out of seven experiments. Although in general the higher yielding varieties were favoured in competition, the reverse frequently occurred. Allard (1960, p. 142), summarizing some literature on competition in varietal mixtures and in bulk populations, claimed that agronomically poor types are also poor competitors.

As reported earlier, a negative association between either yield or survival in mixture and pure-culture yield is frequently found. This points to the occurrence of a negative correlation between competitive ability and pure-culture yield in the experiments concerned. Hamblin & Rowell (1975) showed such a correlation to be significantly in a population of 200 $F_5$ barley lines. In a trial with five oat varieties, Smith et al. (1970) found the variety with the lowest monoculture yield to be the strongest competitor.

As some authors reported a positive correlation and others demonstrated a negative one, it is not surprising that there were also reports of an inconsistent relationship. Then, both the group of the strongest competitors and the group of the weak competitors included varieties showing a high yield in pure stand as well as low-yielding ones. Sakai (1955) concluded from an experiment with mixtures and pure stands of 12 barley varieties, that no sign of association of competitive ability with yield, or with any of the other characters measured, was detected. In an experiment with six barley varieties, Piano & Ceccarelli (1976) found no correlation between yield in monoculture and competitive ability in mixture. Oka (1960) tested the competitiveness of $F_{10}$ lines derived randomly in $F_6$ of crosses between Indica and Japonica types of rice. Competitive ability, measured by increase or decrease in panicle number, did not show a significant correlation with number of panicles in monoculture.

*Conclusion* There may be a positive or a negative association or none at all between the ability of a genotype to compete well in mixture and its yield in pure stand. Hence, negative relations between either survival or yield in mixture at one hand and pure-culture yield on the other hand are frequently found. Consequently, when bulk propagation

is practised there is a considerable chance that natural selection causes a dilution or even loss of desirable genes as a result of crowding, especially in breeding programmes where wide crosses of distinct plant types are handled. Care has to be taken in extending conclusions derived from variety mixtures to segregating populations because variety mixtures consist of a few, selected, homozygous genotypes.

*Methods to account for natural selection* The most obvious way to avoid outcrowding due to natural selection is to replace natural by artificial selection. This is realised most expediently by the pedigree method. Applied in its purest form, this method involves selection of individual $F_2$ plants followed by choice of single plants from the selected lines in $F_3$ to $F_5$. Hence, it removes most of the effect of natural selection among plants within the segregating progenies. When the pedigree method is adopted, where line selection is taken up from the highly heterozygous $F_2$, the advantage of the bulk method that only nearly pure lines are handled is lost.

The 'single-seed descent method', advocated among others by Brim (1966), combines both the minimization of competitional bias due to natural selection (Empig & Fehr, 1971; Tee, 1971; Tee & Qualset, 1975) and the high degree of homozygosity attained at the stage when the first selections are made. In this method only one seed is taken from each $F_2$ plant to produce a $F_3$ plant, which process is repeated to $F_6$ or $F_7$. Selection and yield testing in late generations was discussed in Section 1.2.

To slow down the effects of natural selection, Khalifa & Qualset (1975) suggested growing the bulk at wider spacings than the normal ones. Jennings & Herrera (1968) proposed to subdivide the population into separate groups based on the character assumed to be important in competition. The adverse effects of natural selection may partly be counterbalanced by removing undesired types from the population (negative mass selection) or selecting desired types and bulking the selected plants (positive mass selection).

### *1.3.2 Single-plant selection and competition*

It has long been recognized by breeders that single-plant selection for yield, particularly in $F_2$, is not effective. Accordingly, when a breeder has to select individual plants, he does not make quantitative measurements but, in general, he chooses disease-free plants of moderate height and general good appearance. The same holds for selection of single plants from lines in the pedigree method. When the population is sown at a normal density, the breeder only selects single ears because he cannot distinguish individual plants.

In the literature, the poor response of plant selection for yield was demonstrated by a low and non-significant, or even negative correlation between the yield of $F_2$ or $F_3$ plants and that of the progenies in field plots in later generations (e.g. McGinnis & Shebeski, 1968; Alber, 1969; Hamblin & Donald, 1974). The unsuccessfulness of single-plant selection for yield is also illustrated by the experiments where random and selected $F_2$ plants gave similar results in $F_3$ plots (e.g. Grafius et al., 1952; Shebeski, 1967; McGinnis & Shebeski, 1968). Consequently, a very low heritability is usually found for yield of single plants. Nevertheless, some positive results of plant selection for yield

have been reported (Boyce et al., 1947; McGinnis & Shebeski, 1968; Alessandroni & Scalfati, 1973; Skorda, 1973).

It is obvious, however, that any method which makes single-plant selection reliable would considerably improve the efficiency of breeding. It would facilitate the screening for yield of very large samples.

The lack of success of $F_2$-plant selection is explained by (1) the very large experimental error proper to single-plant measurements, (2) the high degree of heterozygosity in $F_2$, so that selected plants do not breed true and their hybrid vigour extinguishes in successive generations, (3) genotype x year interaction when the selected plants are compared with their progenies in different years, and (4) intergenotypic competition.

The large experimental error partly originates from a poor plot technique, which may be improved by accurate spacing and methods to account for soil heterogenity. In selection nurseries, where identification of single plants is desired, plant spacings are wider than in the farmer's field. Because single-plant performance under wide-spaced conditions is not necessarily related to population performance under close spacings, this may be a source of error.

Intergenotypic competition is brought about by the segregating nature of the population in which selection is practised. As was seen, there is no consistent relation between yield in mixed stand, i.e. the environment where is selected in, and that in pure culture, i.e. the environment where is selected for. Hence, competition may complicate individual-plant selection. For example, in the extreme case where the rank of the genotypes is reversed by mixing them, the low-yielding plants should be chosen. Wiebe et al. (1963), dealing with such a situation in their barley experiments, concluded that in their material 'one should save the poorest plants rather than the good ones'.

What is the importance of competition in biasing the result of plant selection? Christian & Gray (1941), who studied mixed populations of wheat, stated that 'the effect (of interplant competition) is of considerable magnitude and is alone sufficient to make the selection of individual plants for yielding ability in segregating generations unreliable'. Hamblin & Donald (1974) considered competition to be responsible for their poor results of plant selection in barley where $F_3$ single-plant yield was not related to yield of $F_5$ in field plots. $F_5$ yield did however show a significant inverse correlation with plant height and leaf length in $F_3$ as well as in $F_5$. Consequently taller plants with longer leaves presumably gained competitive advantage over their neighbours in a mixed population, but they were inferior to shorter plants with respect to pure-culture yield. Hamblin & Rowell (1975) confirmed in these $F_5$ lines the negative relation between competing ability and yielding capacity.

Chebib et al. (1973) found that the contribution to the total variation among wheat plants in their experiment came from wide plant spacing, followed by differences in seed size, competition between seed size classes and intergenotypic competition in decreasing order. Briggs et al. (1978) observed a low heritability for grain yield per plant in a mixture of 12 accurately spaced barley varieties. They alternated within a row of plants, plants of a check variety with plants of the 12 other varieties. As control, in the adjacent rows only the check variety was sown. They expected that an increased variation between plants of the check variety in the mixed rows, compared with that in the adjacent

control rows, might be an explanation of the poor heritability. However, for grain yield the variation of the check did not increase in the mixed rows. Therefore, the authors concluded that the effect of competition could not be used alone as simple explanation for the poor heritability of single-plant yield. Neither Chebib et al. (1973) nor Briggs et al. (1978) paid attention to the consequence of intergenotypic competition, most important in selection, that the yield of a genotype in mixture is expected to deviate from its yield in monoculture.

The previous literature is not unanimous about the degree to which competition accounts for the poor results of single-plant selection. Probably the main reason for the difference of opinion is that the effects of intergenotypic competition on the outcome of selection is poorly quantified.

Some authors suggested methods to avoid or to correct for competition. Most of them (Christian & Gray, 1941; Fasoulas, 1973, 1976, 1977; Fasoulas & Tsaftaris, 1975; Shebeski, 1967) advocated the use of very wide spacings.

Hinson & Hanson (1962) illustrated in soybeans that at wide spacing there is a decrease in the error from intergenotypic competition on plant selection accompanied, however, by an increase in the error from a differential response of the genotypes to spacing. De Wit (1960) pointed out that spacing experiments are an extreme form of competition experiments and that response to spacing can be expressed in terms of crowding coefficients. Hence, it is obscure whether any competitional bias is removed by wide spacing.

When a trait is relatively insensitive to competition and has a high correlation, either positive or negative, with pure culture yield, an indirect selection for yield may be practised by such a trait. Hamblin & Donald (1974) stated that vegetative characters, in their study plant height and leaf length, may provide a valuable selection criterion for yielding capacity. Jennings & Aquino (1968) proposed removal, during bulk breeding, of obviously competitive and undesirable plants which were in their rice programme the tall and leafy types. Christian & Gray (1941) suggested mathematical correction for competing ability where this may be associated with some traits. However, they did not specify a method of correction.

Plants originating from large seeds show a competitive advantage over those from small seeds (Montgomery, 1912; Kiesselbach, 1918; Christian & Gray, 1941; Helgason & Chebib, 1963; Sandfaer, 1970; Chebib et al., 1973; and others). In the wheat populations of Chebib et al. (1973) difference in seed size and competition between plants grown from different seed size fractions contributed more to the total error variance than did intergenotypic competition. Both Christian & Gray (1941) and Chebib et al. (1973) advocated grading of seed from segregating populations according to size or weight and sowing only seeds of approximately the same size together in one selection plot.

### *1.3.3 Progeny testing and competition*

Progenies of selected plants are, in general, evaluated in rows. Each row contains a single progeny. Commonly, these first-year lines are only visually selected for simply-inherited characters and general appearance, while yield testing is delayed until the se-

cond or third year of line evaluation. Then sufficient seeds are available for testing a moderate number of promising lines in field plots. In contrast, yield testing in single-row or in few-row microplots has often been suggested. It allows screening for yield of a large number of entries. Microplots are also required for early generation yield testing because of the short seed supply in $F_3$ and the large number of progenies to be tested.

LeClerg et al. (1962), reviewing the literature on field plot technique, claimed a general correspondence for yield between single-row plots and field plots. However, a more moderate reliability of single-row testing has frequently been reported. Together with the large random variation in single-row yields, this forms the main reason for the rare use of single-row yield testing in commercial breeding programmes.

To improve effectiveness of yield testing in microplots, the experimental error has to be reduced. Competition between adjacent, genetically different rows is often mentioned as an important component of the experimental error. For example, Montgomery (1913, p. 47) observed that a certain strain of wheat tested in single-row plots gave a very poor appearance, whereas the same strain tested in square 'centgener' plots provided a much better comparative appearance. He concluded (p. 61) that there is some competition between adjacent rows, especially when varieties very different in growth habit are planted side by side.

Interrow competititon has mainly been studied by comparing outer and inner rows of field plots. The border rows give an estimate of yield in a competitive situation while the centre rows represent a pure culture. Discussion on border effects was started in the first decades of this century. In extensive varietal trials of small grains Hayes & Arny (1917), Kiesselbach (1918, 1919) and Stadler (1921) showed strong border effects and they concluded that there is obvious competition between adjacent rows when these rows consist of different varieties. On the other hand, Love (1919) and Stringfield (1927) found only occasional indications of yield disturbance from interrow competition. From these early findings, the Committee on Standardization of Field Experiments of the American Society of Agronomy concluded that, 'When varieties are planted adjacent to each other, without the intervention of alleys, certain ones may effect others adversely. When plats are flanked or surrounded by alleys it is known that the yields are increased and that all varieties are not influenced alike.' They recommended '.... that two drill rows from either side of each plat in the case of small grain .... be either removed before harvest or left unharvested' (Wiancko et al., 1924).

Brown & Weibel (1957) grew varieties of winter wheat and oats in 4-row plots with 30 cm between rows within a plot and 60 cm between plots. The accumulated effect of wide plot spacing and interplot competition resulted in highly significant border effects and, in two out of four experiments, also in significant border x variety interactions. However, they concluded that this interaction may be too small to cause concern in a breeding programme dealing with such plots.

Although the above-mentioned studies were directed to border effects in varietal testing, the findings are also appropriate to the evaluation of progenies in single rows. In the latter situation the effect of competition will even be more pronounced because a particular row differs in its genetic constitution from both its neighbours. More recently interrow competition was demonstrated by, among others, Jensen & Federer

(1964, 1965), Rich (1973), Smoček (1973), Haniš et al. (1976), all in wheat, and by Smith et al. (1970) in oats.

From the many studies where competition between rows was clearly demonstrated, it is generally stated that competition may or will seriously complicate selection for yield in single rows. However, few authors have quantified the degree of competitional bias. Stringfield (1927) measured the standard deviation for yield in border and centre rows of 3-row plots in wheat. He concluded that there was little evidence that competition brought about greater variation. Hanson et al (1961) showed that in soybeans the effects of inter-row competition were major sources of variation and did overshade the genetic differences. On the other hand, Thorne & Fehr (1970), also studying soybeans, observed in their analysis of variance also a significant interaction between strains and competition situations, but the variance of this interaction was much smaller than the genetic variance. From a study with four grain sorghum hybrids, Ross (1973) claimed that, if an additional error of five percent can be tolerated above the normal experimental error, single-row plots may be satisfactory.

Many suggestions have been made to overcome or to reduce the bias in yield testing that arises from intergenotypic competition between rows. The following discussion is restricted to a maximum sample size of three rows per line. The seed required for three rows, with 100 seeds per row, corresponds with the amount of seed normally produced by a single spaced plant.

(1) Use of 2-row or 3-row plots rather than single rows. Evidently, the effect of interplot competition will be less severe with an increased number of rows per plot. For example, Shebeski (1967) used 3-row plots for early-generation yield testing. However, it might be a point of discussion whether unreplicated 3-row plots outweigh a three-fold replication of single-row plots.

(2) Use of bordered plots. Within this context this implies that only the middle row of 3-row plots is harvested for yield, whereas both the outside rows are discarded. A satisfactory correpondence of this type of plots with field plots was demonstrated by, among others, Klages (1933), Torrie et al. (1943), and Rasmusson & Lambert (1961). The method has often been proposed for preliminary varietal testing. More recently it was put forward by Jensen & Federer (1964), Schultz & Brim (1967), and Sneep (1977) for selection purposes. However, Stringfield (1927) found, in his experiments with wheat and oats, that yield of 3-row plots was much more reliable when based on all three rows than based on only the centre row. So, in his study, the removal of competition did not counterbalance the advantage of a greater sample size. Additional disadvantages of bordered plots are increased expenditure and environmental variation due to a larger block size.

(3) Wide distances between rows or plots. For instance, in order to minimize interplot competition in his breeding programme, Shebeski (1967) used 3-row plots with plots 60 cm apart and a row distance of 15 cm. Fasoulas (1973, 1976, 1977; Fasoulas & Tsaftaris, 1975) applied this method in an extreme way in his 'Ranking Honeycomb Design', where progenies were evaluated as widely spaced single plants replicated several times throughout the nursery. On the other hand, there is severe criticism on the use of wide spacings

to reduce competition (see Section 1.3.2).

(4) Bordering all plots with rows of one common variety. Hanson et al. (1961) and Thorne & Fehr (1970) advocated the use of an intermediate competitor as common border for all plots in the nursery.

(5) Grouping strains of similar habit. Montgomery (1913) and Love (1919) suggested grouping of similar strains, especially with respect to earliness and height. They realised that competition will be less severe when the competing phenotypes are more alike.

## 1.4 DEFINITION OF PROBLEM AND GENERAL METHODOLOGY

In a selection nursery neighbouring genotypes interfere with each other. Due to this interference the performance of each will be changed. For some the performance will be enhanced, for others it will be diminished. With respect to yield in self-fertilizing small grain crops it was concluded that there was a positive or a negative relationship or none at all between the ability of a genotype to compete well in a mixed population and its yield in pure culture. Therefore, the rank of genotypes in a segregating population may be markedly different from their rank in monoculture.

The numerous findings of significant competition effects show that competition between genetically different plants and rows may confound selection and decrease its reliability. However, the opinions about the significance of intergenotypic competition in disturbing the outcome of selection are different. The main reason is that the extent to which intergenotypic competition biases the efficiency of selection is not well quantified. Therefore, the quantification of the degree of competitional bias, in terms of change of response to selection, is the main objective of the present research. An accurate definition of the competitional bias provides also a better understanding of the ways in which competition complicates selection.

The quantification of competitional bias requires a mathematical approach. Many competition models have been described in the literature (Section 3.3), so the approach is based on one of them. It was necessary to extend beforehand the chosen competition model to a model describing plant-to-plant and row-to-row competition because most of the existing models are restricted to changes in the average performance of a variety in a variety mixture (Section 4.2). The deterministic competition model had to be converted into a stochastic form (Section 4.3) since selection is a game of chances so that the theory on selection is based on calculus of probabilities.

The model is tested and illustrated with data from field experiments (Chapters 8 and 9). At the same time, methods of plant selection and progeny testing are evaluated experimentally, together with alternatives that are claimed to reduce or remove the bias due to intergenotypic competition.

The experiments were carried out with varieties of spring barley (*Hordeum vulgare* L). The varieties were sown in monoculture and in different types of mixtures. The use of varieties, instead of segregating populations, has several advantages, especially in self-fertilizing species where all plants belonging to a variety can be considered to be nearly identical to genotype. The efficiency of a method can directly be calculated after selection has been practised since the monoculture yield of a genotype selected

from the mixed population is given by its yield in adjacently grown monoculture plots. Therefore, the evaluation of a method is not disturbed by heterozygosity, genotype x year and genotype x location interaction. As the plants of a variety all have about the same genotype, the genotypes may be replicated throughout the nursery. This facilitates the estimation of the components of the variance among plants and rows. The discussion is not concerned with the fact that genotypes, selected from a segregating population, do not breed true since that problem is independent of the question of competitional bias in selection (Section 4.4.1). Therefore, pure-line varieties are used in the study of the competitional bias in selection in segregating populations. The use of varieties in competition studies is discussed further in Section 2.4.

## 1.5 NOTE TO THE READER

It is suggested that the reader starts with Chapter 4 where a model for the effect of competition on selection is introduced. After the description of the experiments (Chapter 2),he may turn directly to Chapter 7, 8 or 9 where the consequences of competition for bulk propagation (Chapter 7), selection of single plants (Chapter 8), and testing of progenies in row plots (Chapter 9) are discussed in combination with the competition model. These chapters may be read independently, even without knowledge of the theory presented in Chapter 4. In Chapter 5, a model is introduced to quantify the effect of density of stand on the outcome of selection. In Chapter 3, the reasoning is given why the competition model is based on the basic competition model of de Wit (1960). Chapter 6 deals with the estimation of the competition effects from the different types of experimental design.

# 2 Field layout and material

## 2.1 FIELD PLOT DESIGN

In the experiments, mixtures of barley varieties are used to study the effects of intergenotypic competition on selection of unknown genotypes in segregating populations. The advantages and disadvantages of this technique are discussed in Section 1.4 and 2.4. Some details of the trials are summarized in Tables 2 and 3. The first part of the trial number refers to the year of experimentation.

### *2.1.1 76-1 Monocultures and binary mixtures*

To estimate the pure-culture performance and competitive ability of 12 varieties (nos 3, 4, 5, 7, 9, 10, 11, 12, 13, 16, 17 and 18, Table 6), monocultures and binary mixtures were grown with 'Varunda' as the common associate. The mixture plots consisted of alternating rows of the two components. Each row was sown with a single cultivar. Hence, 'Varunda' was grown in every second row. Each mixture plot was situated between both their corresponding monoculture plots, giving a unit of three plots. A randomized block design with three replicates of the 12 three-plot units was laid out.

Table 2. Details of the experiments dealing with either rows or plots as basic units.

| Characteristic | Experiment | | |
|---|---|---|---|
| | 76-1 | 76-3 | 77-2 |
| Experimental unit | plot | row | row |
| Soil | loamy sand | sandy (clay) loam | sandy clay loam |
| Row direction | NS | EW | NS |
| Row distance (cm) | 11.5 | 20 | 20 |
| Plot size: sown ($m^2$) | 1.4x6.5 | 0.20x2.10 | 0.20x2.00 |
| harvested ($m^2$) | 0.9x5.5 | 0.20x1.80 | 0.20x1.70 |
| Rows per plot | 12 | 1 | 1 |
| Seed rate (kernels $m^{-2}$) | 275 | 250 | 250 |
| Plants per $m^2$ | 260 | . | 180 |
| % Dry matter of recorded weights | 100 | 86 | 89 |

Table 3. Details of the experiments dealing with single plants as basic units.

| Characteristic | Experiment | | |
|---|---|---|---|
| | 76-2 | 77-1 | |
| Soil | loamy sand | sandy clay loam | |
| Row direction | NS | NS | |
| Plant spacing ($cm^2$ $plant^{-1}$) | 6x25 | 5x25 | 52x60 |
| | | 10.4x12 | |
| % Dry matter of recorded weights | 93 | 92 | 90 |

*2.1.2 76-2 Plant selection*

To study single-plant selection, the 12 varieties were planted out in the field in peat pots at 6 x 25 $cm^2$ $plant^{-1}$. The planting took place according to three arrangements, which were randomized within a main plot. The field layout is comparable with that of Exp. 77-1 and is given in Fig. 3. There were two main plots, grown adjacent to Exp. 76-1. The main plots had very different drought stress so that they were handled as two different treatments. The arrangements were:

(a) Multicomponent mixture. The 12 varieties were arranged in a randomized block design with 32 replicates per main plot. Thus, 12 plants per replicate were grown (see Fig. 3b).

(b) Multicomponent mixture, where plants of the studied varieties were alternated with plants of the standard 'Varunda'. Consequently, every second plant is a standard. A randomized block design with 18 replicates per main plot was used (see Fig. 3c).

(c) Multicomponent mixture, where plants of the studied varieties were alternated with three standard plants. So, three out of four plants belong to the standard. Again, the randomized block design was replicated 18 times.

(d) Monocultures. Each monoculture plot had five rows of 20 plants per row. The 12 central plants of each of the three middle rows were harvested. This makes a sample size of 36 plants per plot. The varieties were grown in a randomized block design with two replicates. The replicates coincided with the main plots.

With arrangements b and c, I aimed at studying methods of correction for competition by means of inserted standard plants. Furthermore, the standards facilitate correction for soil heterogeneity.

*2.1.3 76-3 Line selection*

To investigate procedures of line selection, six varieties (nos 3, 5, 7, 9, 13 and 18, Table 6) were grown in rows, each row containing one variety. The field layout is comparable with that of Exp. 77-2 which is shown in Fig. 4. The following arrangements were used:

(a) Single-row plots;

(b) Three-row plots;

(c) Single-row plots with every second row a standard row of 'Varunda';
(d) Single-row plots at 60 cm interrow spacing instead of the 20 cm which was used in arrangement a to c. Every third row was sown with the standard;
(e) Uniformity trial with only 'Varunda' rows, where 180 rows were sown per strip.
(f) Monocultures in eight-row plots. The six central rows were harvested for yield.

The monocultures were laid out in a six times replicated randomized block design. Each arrangement is laid out as a strip of a number of rows grown side by side (Fig. 4).

The four former arrangements were randomized in a block design with three replicates, and so these arrangements yielded 12 strips. Arrangement f was situated at the end of the strips of arrangement b and c. Six uniformity strips were incorporated, in such a way that each third strip of the 18-strips nursery only consisted of 'Varunda' rows. Within any arrangement the varietal plots were randomized within blocks. Per strip, there were 19, 7, 8 and 6 blocks for arrangements a, b, c, and d, respectively. Monoculture performance was estimated from the six central row of the eight-row plots and from the central rows of the three-row plots.

*2.1.4 77-1 Plant selection*

The layout of the experiment was similar to that of Exp. 76-2. However, the seeds of the varieties were accurately spaced by hand, two kernels being sown at each place and the plants being singled after emergence. The few places where no seedling emerged, were filled with plants in peat pots. Twelve varieties (nos 1, 2, 3, 6, 7, 8, 12, 13, 14, 15, 16 and 17, Table 6) were used in several arrangements (Figs 2, 3, Table 4).

(a) Monocultures at a spacing of 5 x 25 $cm^2$ per plant. Each monoculture plot had four rows of 60 plant places per row. The 25 central plants of each of both central rows were harvested. Thus the sample size was 50 plants per plot. The varieties were grown in a four-times replicated randomized block design.

(b) Multicomponent mixture at a spacing of 5 x 25 $cm^2$ per plant. Within a plot the varieties were randomized as single plants in a block design with eight replicates. The plots of the arrangements b, c and d were randomized together in a block design with five replicates (Fig. 2).

Table 4. Details of plant-selection experiment 77-1.

| Type | Spacing $cm^2 plant^{-1}$ | Subplots per plot | Replicates of plots | Plants per variety |
|---|---|---|---|---|
| a. Monocultures | 5x25 | | 4 | 200 |
| b. Multicomponent mixture | 5x25 | 8 | 5 | 40 |
| c. Mixture with alternated standard | 5x25 | 4 | 5 | 20 |
| d. Screening honeycomb design | 10.4x12 | 8 | 5 | 40 |
| e. Screening honeycomb design | 52x60 | 13 | 4 | 52 |
| f. Ranking honeycomb design | 52x60 | 13 | 4 | 52 |

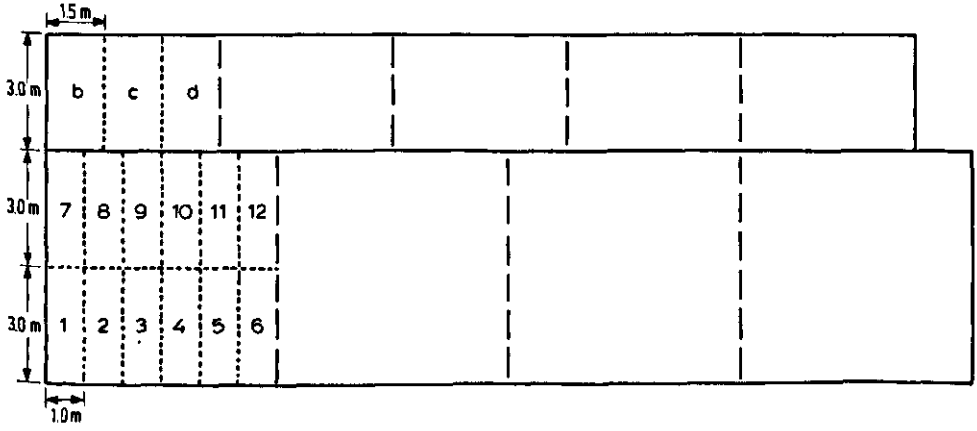


Fig. 2. Topography of the plots in plant-selection experiment 77-1. At the bottom are the monocultures (Exp. 77-1a). The monoculture plots, denoted by a number representing the cultivar, were arranged in a randomized block design with four replicates. At the top, plots of the other arrangements are given: multicomponent mixture (b), multicomponent mixture with inserted standard plants (c), screening honeycomb design (d). The plots b, c, d were randomized together in a block design with five replicates.

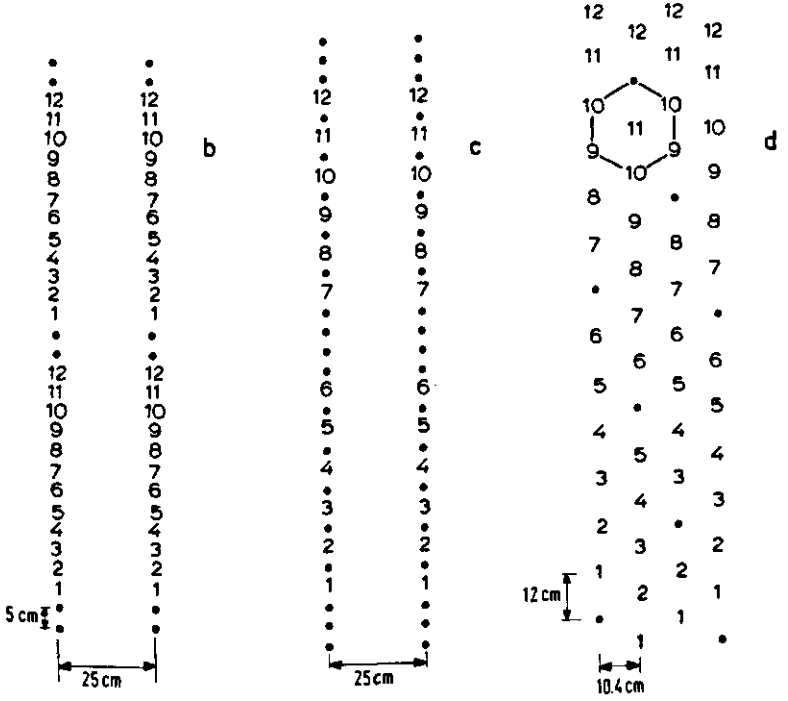


Fig. 3. Arrangement of the plants in Exp. 77-1 in a multicomponent mixture (b), a multicomponent mixture with standard plants alternately inserted (c), and a screening honeycomb design (d). The standard plants, represented by dots, have a fixed position. The plants of the other cultivars, represented by the cultivar number, were randomized in a replicated block design. Twelve plants, each of a different cultivar, together with the appropriate standard plants, made up a replicate. In Arrangements b and d there were eight and in c there are four replicates per plot. Hence, for each arrangement half of a plot is presented in the figure. Border rows were present but they are not drawn in the figure.

(c) Multicomponent mixture where the plants of the studied varieties were alternated with plants of the standard 'Varunda'.

(d) 'Screening honeycomb design' at a triangular planting pattern of 10.4 x 12 $cm^2$ $plant^{-1}$, The nomenclature 'honeycomb design' was introduced by Fasoulas (1973) for the field layout of a multicomponent mixture at a triangular spacing (Fig. 3d). 'Screening' denotes that the genotypes are non-replicated within the trial. This situation is simulated by growing replicated varieties instead of the unique genotypes. With triangular spacing any plant is the centre of a hexagon and its neighbours are at the angular points of the hexagon. Plants of a standard variety are inserted in such a way that any hexagon contains one plant of the standard variety. For details of the design see Fasoulas & Tsaftaris (1975).

(e) 'Screening honeycomb design' at a spacing of 52 x 60 $cm^2$ $plant^{-1}$. Each plot enclosed a randomized block design with 13 replicates per plot. The plots of this arrangement and that of f were randomized together and replicated four times (Fig. 4). The sparse stand is used to demonstrate the problems that complicate the removal of interplant competition by means of very wide spacings.

(f) 'Ranking honeycomb design' at a spacing of 52 x 60 $cm^2$ $plant^{-1}$. Fasoulas & Tsaftaris (1975) aimed at ranking progenies or varieties according to their yielding ability by a replicated design of single plants. Within each trial seven genotypes are used, one standard variety and six unknown entries. Due to the triangular pattern, it is possible to surround a given genotype by each of the other six. Six varieties together with 'Varunda' as standard were replicated 13 times within a subplot. As 12 varieties were studied, there where two subplots. Both subplots constitute a plot. As mentioned, the ranking and the screening plots at wide spacing were randomized with each other.

For technical reasons the arrangements were separated in three groups: (1) monocultures (Arrangement a); (2) mixtures at narrow spacing (Arr. b to d), (3) mixtures at wide stand (Arr. e and f). The trials of group 1 and 2 were grown adjacent to each other as the central strip in the line selection field of Exp. 77-2 (Figs 2, 4). Group 3 was randomized with the row arrangements of Exp. 77-2 (Fig. 4).

*2.1.5 77-2 Line selection*

The field layout (Fig. 4) was similar to that of Exp. 76-3 and the varieties were the same as in Exp. 77-1. The arrangements were randomized with the wide honeycomb designs of Exp. 77-1, and replicated four times in a block design.

(a) Monocultures and binary mixtures in six-row plots. A plot with a binary mixture composed of alternating rows of the studied variety and 'Varunda' as common associate. The mixture plot was situated between two plots with the corresponding pure cultures. This gave a three-plot unit. In the mixtures all six rows were considered since each of them is bordered by the associate genotype (Fig. 4). In the monocultures only the four central rows were studied in order to exclude border effects. Twelve three-plot units and next to them 12 additional monocultures were in two adjacent strips, which were replicated four times. So the monocultures were repeated eight times in total.

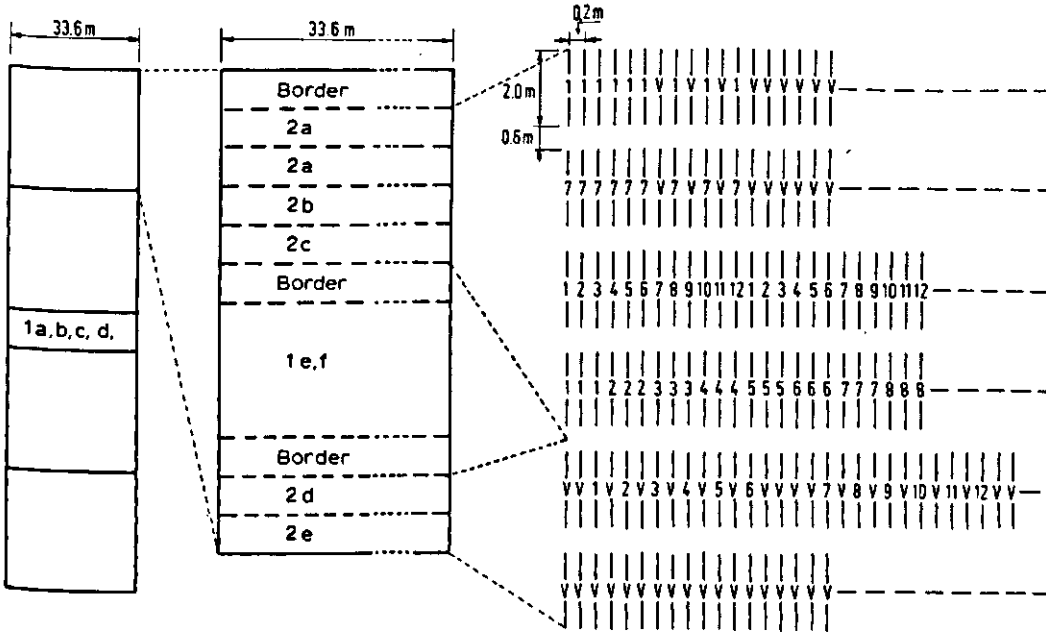


Fig. 4. Field layout of Exp. 77-1 (single plants) and Exp. 77-2 (rows).
On the left: Topography of the four replicates of the row arrangements (Exp. 77-2) and the plant arrangements at wide stand (Exps 77-1e and f). The plant arrangements at narrow spacing (Exps 77-1a to d) formed the central strip in the nursery.
In the centre: A single replication consisting of strips with monocultures and binary mixtures (2a), single-row plots (2b), three-row plots (2c), single-row plots alternated with standard rows (2d), uniformity trial (2e), single-plant arrangements at wide stand (1e,f), and border strips. The arrangements were randomized within a replicate.
On the right: Arrangement of the rows within the strips. A number denotes the cultivar sown in the row, while V stands for rows with the standard cultivar 'Varunda'. The position of the standard is fixed. In the figure, the other varieties are presented in a fixed rank, but in the field, they were randomized in block designs. Drawn are for Arr. 2a two three-plot units with the six-row binary mixtures situated between their component six-row monoculture plots, for Arr. 2b two replicates of single-row plots, for Arr. 2c 2/3 replicate of three-row plots, for Arr. 2d one replicate.

(b) Single-row plots with the varieties in a randomized block design with 12 replicates per strip.

(c) Three-row plots with four replicates per strip.

(d) Single-row plots, every second row being the standard 'Varunda'. Here, the varieties were replicated five times per strip.

(e) Uniformity trial of 150 'Varunda' rows per strip.

Hence, there was a hierarchy: rows per plot, plots per replicate, replicates per strip, strips per block (Fig. 4). Several extra strips were inserted to border the wide honeycomb designs so that herbicides and fungicides could be sprayed and a top-dressing of fertilizer could be given without the experimental strips being damaged by tractor wheels (Fig. 4).

## 2.2 HUSBANDRY AND GROWING CONDITIONS

Single plants were planted out in the field (Exp. 76-2) or directly sown in the right place (Exp. 77-1). The single plants were marked by coloured sticks so that the individual plants and their genotype could easily be determined. At harvest the plants were labelled and stored in a shed. Thereafter, they were dried in an oven and measurements were made.

The line-selection field was sown with a 'Seedmatic' drill (Hoeser et al., 1974), which enabled the sowing of small separate rows, each row with 100 kernels belonging to a single variety. The 100 kernels per row is a commercial rate of about 110 kg $ha^{-1}$. The rows were individually reaped with a hook and bundled. The bundles were labelled and hung in a ventilated shed to dry. When the percentage dry matter remained constant, aboveground biomass was determined and, after threshing, the grain weight per row.

My main objective was to study competition and its consequences for selection on yielding ability. Therefore, factors such as weeds, disease and lodging, which interfere with yield capacity were controlled. Weeds were removed by herbicides, and the wide spacing of Exp. 77-1 was supplementarily hoed by hand. The seeds were dressed with fungicide. Mildew (*Erysiphe graminis* f. sp. *hordei*), the main disease, was controlled by spraying with fungicides. Partly due to the dry weather, no lodging occurred in 1976. In 1977, the plant mixtures and the tall varieties in the line-selection field were supported by a frame of strings. Late in the season the complete nursery lodged, but on a moderate scale. Hence, lodging did not bias the results.

The two growing seasons were very different. For The Netherlands, 1976 was extremely dry and hot, while 1977 was cool and wet (Table 5). As a result of the differences in weather, the crop was harvested in the middle of July in 1976 and mid August in 1977. Obviously the drought stress was much more extreme on sand (Exp. 76-1,2) than on loam (Exp. 76-3).

The yield level of the habitat may be characterized by the mean yield of the 50% highest yielding varieties. At 85% dry matter, this was 4.8 tonne $ha^{-1}$ on loamy sand and 5.1 tonne $ha^{-1}$ on sandy (clay)loam in 1976, and 4.9 tonne $ha^{-1}$ on sandy clay loam in 1977. Tables 2 and 3 show which trials were sown on which soil.

Table 5. Weather data of the growing seasons.

| Characteristic | 1976 | | | | 1977 | | | |
|---|---|---|---|---|---|---|---|---|
| | April | May | June | July | April | May | June | July |
| Mean temperature at 150 cm (°C) | 7.1 | 13.3 | 17.8 | 19.2 | 6.2 | 11.9 | 14.6 | 16.7 |
| Total precipitation (mm) | 7 | 34 | 35 | 29 | 50 | 55 | 64 | 68 |
| Global irradiance (100 J $cm^{-2}$) | 464 | 547 | 618 | 575 | 364 | 543 | 425 | 484 |

## 2.3 MATERIAL

Barley varieties were used to simulate the effect of selection of unknown genotypes in segregating populations. This approach is discussed in Sections 1.4 and 2.4.

The varieties were chosen to express a wide variety of agronomic characters, especially yield and those morphological traits which presumably contribute to competitive ability. Evidently, the more varieties involved in an experiment the better a segregating population will be approached. Technical reasons limit the number of varieties to a moderate number.

The cultivars are reviewed in Table 6 with respect to their land of breeding, year of release and relative yield in Dutch national variety trials. It is claimed that this relative yield represents the commercial value of the varieties under local conditions. The yield data are corrected for effects of year and site. However, the data may be

Table 6. Varieties used in the experiments with their land of breeding, year of release and 'relative' yield on clay/loam and sand. Years between brackets denote the first year of Dutch national test for varieties which did not come into the market. The 'relative' yield is the relative yield of the varieties in the Dutch national yield trials, derived from 'Rassenbericht' (IVRO, Wageningen), except that of Camilla ('Resultaten Rassenproefvelden 929', IVRO, Wageningen), Varunda (IVRO, Wageningen, pers. commun.), Titan (Blijenburg & Sneep, 1975), L 98 (J. Sinke, Wageningen, pers. commun.), Golden Promise (Rowe & Doodson, 1976), Belfor and Proctor uniculm (my own experiments with field plots of 22 $m^2$), W.Z. 704068-14 (personal estimate).

| Variety | | Origin | Year of release | Relative yield | |
|---|---|---|---|---|---|
| | | | | clay/loam | sand |
| 1. | Tamara | Neth. | 1978 | 100.0 | |
| 2. | Aramir | Neth. | 1973 | 96.7 | 88.6 |
| 3. | Camilla | Neth. | (1972) | 96.4 | |
| 4. | Piccolo | Neth. | (1974) | 95.2 | 85.2 |
| 5. | Julia | Neth. | 1968 | 91.2 | 82.0 |
| 6. | Varunda | Neth. | 1974 | 88.2 | 80.7 |
| 7. | Belfor | Neth. | 1971 | 87.7 | 86.1 |
| 8. | WZ 704068-14 | Neth. | | 86.0 | |
| 9. | Minerva | Neth. | 1955 | 85.5 | 77.8 |
| 10. | v.d. Have 198-71 | Neth. | (1974) | | |
| 11. | Proctor | GB | 1953 | 83.2 | |
| 12. | Balder | Sweden | 1942 | 77.9 | 69.8 |
| 13. | Golden Promise | GB | 1966 | 76.4 | |
| 14. | Goudgerst | Sweden | 1913 | 74.8 | 67.2 |
| 15. | L98 | Ethiopia | | 73.7 | |
| 16. | Bigo | Neth. | 1924 | 67.5 | 52.9 |
| 17. | Titan | Canada | 1943 | 52.0 | |
| 18. | Proctor uniculm | GB | | 31.4 | |

biased by variety x year and variety x site interactions.

Bigo, Titan and WZ 704068-14 are four-rowed, L98 is six-rowed and the other varieties are two-rowed. Titan is the only variety with naked seeds. Goudgerst, Bigo and L98 are pure-line selections from land varieties. Uniculm is a mutant from Proctor, showing only one or two culms per plant.

## 2.4 APPROPRIATENESS OF VARIETY MIXTURES IN THE SIMULATION OF SEGREGATING POPULATIONS

In the experiments, mixtures of varieties are used to study the influence of intergenotypic competition on selection in segregating populations. Transposition of the findings obtained from variety mixtures to segregating populations may be biased by the differences that exist between both. The bias will be discussed.

The varieties in the variety mixtures are, compared with the genotypes in segregating populations, homozygous, small in number and selected genotypes. The varieties were selected by breeders from segregating populations because they distinguished themselves in an agronomically favourable way from the other phenotypes in the populations. I chose from the assortment of varieties those types that were assumed to represent a wide variation in yield and in those morphological traits which presumably contribute to competitive ability.

The goal of the present study is to design a model to define and to quantify the consequences of competition on yield testing. Variety mixtures were used to test the model and, especially, to illustrate the model. Because the model is restricted to yield testing, it does not matter whether the selected genotypes maintain their expected performance in the next generation (Section 4.4.1). Hence, effects of heterozygosity and mode of reproduction are not under discussion. Therefore, the homozygosity of the varieties is no limitation. Variety mixtures are even preferable above segregating populations because the plants of a variety all have about the same genotype. Thus it is possible (a) to grow a genotype in monoculture and mixture at the same time, and (b) to replicate the genotypes within a population. The former provides estimates of the competitive ability and the agronomical value, measured by the monoculture yield, of the genotypes. The latter supplies estimates of the appropriate variances within the population.

A disadvantage of the randomized block designs used is the negative genetic correlation between the experimental units within a block (Section 8.5). However, the consequences are relatively unimportant. In future experiments, a completely randomized block design would be preferable.

The secondary goal of the study is to acquire a general view on the magnitude of the parameters that are characteristic for the model. These parameters are ratios of variances and covariances (Section 4.4). For a discussion of the usefulness of correlation coefficients estimated from variety mixtures, see Sections 6.4 and 7.3.3. The other parameters were discussed in Section 6.3.2. It was concluded that care has to be taken in the interpretation of the parameters estimated from variety mixtures.

# 3 Comparison of competition models

A great variety of methods are applied in the analysis of competition experiments. The complexity of the model depends on the complexity of the ecosystem studied. For example, the analysis of a natural community of several species with overlapping generations, a large spatial and temporal heterogeneity, changing population size, irregular and changing patterns of plant density and cross fertilization among the many genotypes within each species will demand a by far more complex model than the analysis of a mechanically constructed mixture of only a few known genotypes of a single self-fertilizing annual species grown at a given density in a rather homogeneous environment and with given frequencies. The first situation is typical for ecological field studies, while the latter is characteristic for varietal mixtures and to a lesser extent for breeding nurseries. An intermediate position is taken by competition of crops against weeds and mixtures of pasture and forage crops, especially when they consist of several perennial species with overlapping generations.

Because this study is directed to competition and its consequences for selection in cereal breeding, simple models like those used in agronomy will be satisfactory. Hence a discussion of these is necessary.

## 3.1 DESIGN OF EXPERIMENTS

In agronomy, different experimental designs are used to study competition among genotypes. The plan depends on the objectives of the experimenter. Of basic interest are studies about morphological and physiological components of competitive ability, studies of the evolution of cultivated crops, fitness theories, and analysis of unusual types of interaction.

More practical studies can be related to the production of commercial mixtures, which are superior to the best of their components grown in pure culture. Superior is interpreted as higher yielding, better yield stability over environments, less susceptible to disease, or improved quality of the crop product (review by Trenbath, 1974). On the other hand, when a farmer wishes to grow two crops, the question is whether some mixture of both is more favourable than a mean of their pure cultures. Due to practical problems peculiar to growing mixtures the farmer will usually choose to grow the pures.

Involved in the study of commercial production of mixtures is the determination of the optimal proportions of the components and the likely shifts in the composition of such mixtures when they are grown for one or more generations. Often the research deals with grazed and fodder crops, although numerous reports are published about cereal mixtures too. Other fields of practical research are the study of the depressing effect of weeds on crop yield and the consequences of competition for breeding.

To achieve some of the foregoing aims the following designs are used:

(1) Growing different genotypes in mixtures and their pure cultures. Most experiments are annual and involve two-component mixtures. The set of populations can be arranged as

- mixtures with one or more testers;
- a replacement series which is the result of generating a range of mixtures of equal density by starting with a monoculture of component i and progressively replacing plants of i with those of component j until a monoculture of j is produced;
- a competition diallel where the components are compared in all pairwise combinations of 1:1 binary mixtures together with the pure cultures;
- multi-row plots in which the central rows give an estimate of the performance in pure culture and the border rows supply an estimate of mixture yields.

(2) Construction of a mixture of several genotypes followed by comparison of the relative propagation rates of the genotypes after one or more generations of bulk propagation. In these fitness experiments, natural selection is the driving force.

## 3.2 METHODS OF ANALYSIS

The early approach to competition was qualitative: the data were presented in tables without further analysis or a graphical display is used (see e.g. Sakai, 1955).

More recently in agronomy, competition experiments are mostly analysed with either an 'additive' or a 'proportional' model. Trenbath (1978) stated that the additive model is based on the expectation that in a mixture of two components i and j, the gain in yield per plant by i over its monoculture equals the loss in yield per plant by j compared with its own monoculture. He expressed this by

$$Y_{ij} - Y_{ii} = -(Y_{ji} - Y_{jj}) \qquad (3.1)$$

where $Y_{ij}$ the yield per plant of i in mixture with j, and $Y_{ii}$ the yield per plant of i in monoculture.

The proportional model is based on the expectation of equality of the proportional increase of i and the proportional decrease of j. Trenbath (1978) represented this by

$$\frac{Y_{ij} - Y_{ii}}{Y_{ii}} = -\frac{Y_{ji} - Y_{jj}}{Y_{jj}} \qquad (3.2)$$

However, the foregoing is a simplification. Only the simple additive models satisfy Eqn 3.1. Most additive models consist of a linear combination of parameters describing the effects of competition, monoculture performance and interaction effects. Moreover, it will be shown in Section 3.3 that in the proportional model of de Wit (1960) Eqn 3.2 only holds for 1:1 mixtures, and even then only in those situations where both components compete for the same space. The proportional or 'multiplicative' models are better characterized by multiplicativity of the effects of monoculture performance and competition.

*3.2.1 Additive models*

Diverse additive models are used. They may be grouped according to the experimental design to be analysed.

(1) Fitness experiments. Because the fitness models, devised to study natural selection, are not appropriate to describe the effect of competition on single-plant and line selection, they are not discussed here. The term 'fitness' is defined as the ability to produce fertile descendents.

(2) Replacement series. Replacement series are substitution series of two components represented by the two monocultures and a number of intermediate mixtures, all at equal density. Following an additive approach, the response to various numbers of the associate is considered to be additive. The performance per plant is regressed against the number of plants of the other component in the mixture (Sakai, 1955, 1957; Schutz & Brim, 1967). A positive slope indicates that the performance of the component studied is enhanced at an increased number of associates and, consequently, the former is found to be the stronger competitor. A negative slope points to a weak competitive ability. Departure from additivity is noticed by deviation of the regression from linearity.

(3) Competition diallels. There is an extensive quantative-genetic theory on diallel crosses, where a number of genotypes is crossed in all pairwise combinations including crossing each genotype with itself. The genetic analysis of the progenies is based on additive genetic effects and departure from additivity measured as dominance effects. A number of authors adapted the genetic models to the treatment of competition diallels by developing a reasoning and nomenclature adjusted to competition rather than a genetic context. Frequently, the analysis is slightly modified.

Competition diallels are the most appropriate designs to estimate and to test the additive effects as well as the effects indicating deviation from simple additivity.

For illustration the model of Eberhart et al. (1964) is given. In this the yield of i in mixture with j is expressed as

$$\underline{Y}_{ij} = \mu + \underline{s}_i + k + \underline{sk}_i + \underline{c}_{ij} + \underline{e}_{ij}$$

where $\mu$ is the overall mean of pure stands; $\underline{s}_i$ the effect of i on pure-stand yield; k is the overall competition effect; $\underline{sk}_i$ the effect of i in competition; $\underline{c}_{ij}$ the competition effect due to the specific combination of i and j; and $\underline{e}_{ij}$ the residual error. The $\underline{c}_{ij}$-component denotes the deviation from pure additivity. (Stochastic variables are underlined).

Usually, the additive model is applied in combination with an analysis of variance to test the significance of the competition effects and the departure from additivity. The The latter is similar to the genetic dominance effects. The analyses proposed by Sakai (1961), Williams (1962), Helgason & Chebib (1963), Eberhart et al. (1964) and Chalbi (1967) resemble the analysis introduced by Hayman (1954a) for a diallel set of crosses. The William's analysis was used by McGilchrist (1965) in an essentially similar way but with a different parameterization, and elaborated by Gallais (1970). McGilchrist &

Trenbath (1971) incorporated the proportional concept of 'relative yield total' of de Wit & van den Bergh (1965) into the additive Williams/McGilchrist model. Thus a kind of mixed model arose. Hay (1974) proposed an analysis for situations where the individual components of the mixture cannot be distinguished from each other. Wright (1975) extended the Hayman approach to allow for linear, quadratic, cubic and quartic effects.

Another analysis in terms of genetic parameters, imitated in the study of competition, is the $W_r$-$V_r$ analysis introduced by Jinks (1954) and Hayman (1954b). Harper (1965) was the first who treated a diallel set of mixtures in this way. His approach was followed by England (1965), Hill & Shimamoto (1973), Wright (1975) and others. The analysis is based on a regression of $W_r$ on $V_r$. $W_r$ denotes the covariance of the rth diallel array entries with the non-recurrent monoculture value, i.e. cov ($Y_{ii}$, $Y_{ri}$). $V_r$ designates the variance among the entries of the rth array, i.e. var ($Y_{ri}$). However, the quantities are difficult to interpret in competition terms, also due to the partial confounding of additive and interaction effects. Furthermore, already in quantitative genetics this method is criticized.

As a sequel to the $W_r$-$V_r$ analysis, Durrant (1965) proposed the $W_r$-$W_c$ analysis of reciprocal differences in genetic diallels and also modified the formula for use in a mixture diallel. Here $W_r$ is regressed on $W_c$, which points to the covariance of the associated cth entries with the non-recurrent monoculture values. This technique was applied and discussed by Norrington-Davies (1967, 1968, 1972).

In plant breeding, genotype-environment interaction is often analysed by linear regression of the yield of each genotype in turn on an environmental index. Mostly the Finlay & Wilkinson (1963) model is applied. The use of this method to analyse competition diallels was discussed by Jacquard (1970), Jacquard & Caputa (1970), Wright (1971), Breese & Hill (1973), and Hill (1973). The model for the yield of i in mixture with j runs as

$$\underline{Y}_{ij} = \mu + g_i + (1+\underline{\beta}_i)\,\underline{c}_j + \underline{s}_{ij} + \underline{e}_{ij}$$

where $\mu$ the overall mean, $g_i$ the effect of i, $\underline{c}_j$ the effect of j on its mixture associate, $\underline{\beta}_i$ the coefficient of regression of performance of i on an environmental index, $\underline{s}_{ij}$ any discrepancy due to interaction between i and j. In the competition diallel the associate means give the environmental index, that is the index to gauge the response of competitors to the range of environmental conditions supplied by the associates.

As far as competition diallels are considered no detailed comparison of the models is given because (1) it falls beyond the scope of a global inventory of methodology in the analysis of competition experiments, (2) all techniques are well-known with respect to genetic studies in plant breeding, (3) the reader may consult the reviews of Jacquard & Caputa (1970), Hill & Shimamoto (1973) and an extensive one of Trenbath (1978), who paid special attention to measurements of agressiveness and productivity.

Stadler (1921, p. 32) was probably the first to use a proportional measure of competitive ability. He did not suggest wider use of his coefficient of competition than the quantification of border effects in field plots. Moreover, his approach was solely empirical.

De Wit (1960) developed a comprehensive proportional model, of which the principles had already been published by de Wit & Ennik (1958). The theory is initialized by the analogy between distillation and competition phenomena. The relation between the composition of the mixture sown and that of the harvest product runs parallel to the relation between the composition of the liquid and vapour phase for mixtures of solvents. Activity coefficients showing the departure from Raoult's law are transformed to 'crowding coefficients' in competitive situations.

The model is appropriate to a diversity of competition experiments, for instance binary mixtures as well as multicomponent blends, mixtures differing in relative frequencies of the components (e.g. replacement series), shifts and survival in populations grown over several generations, mixtures grown at different densities as well as density response of pure cultures. The theory was subsequently extended with the concept of 'relative yield total' (de Wit & van den Bergh, 1965) and simulation techniques (Baeumer & de Wit, 1968; de Wit, 1970; de Wit & Goudriaan, 1974). An outline of the model is given in Section 4.1. The proportional model results in curvilinear relations in a replacement diagram (Fig. 5). This is in contrast to the additive models which give rise to straight lines in such a diagram.

Sandfaer (1970) gave a physiological justification of the proportional model. A

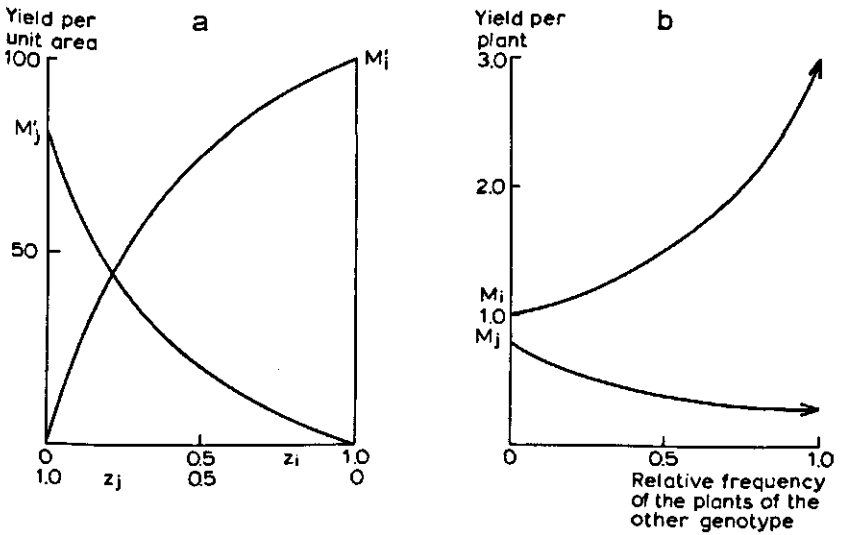


Fig. 5. (a) Relation between the relative seed frequency and the yield of two genotypes i and j, generated by substitution of the arbitrary values $k_{ij}=3$, $M_i'=100$ and $M_j'=80$ into Eqn 4.6. (b) The same relation as in a, except that the yields are expressed per plant.

higher monoculture yield of genotype i compared with genotype j is interpreted as a higher efficiency of resource utilization of i. It is to be expected that the genotypes utilize growth factors with the same efficiency in mixture as in pure. Hence, a certain yield increase in the high-yielding genotype requires a less amount of resources than the same yield increase in the low-yielding genotype, and vice versa. This difficulty is overcome by weighting the yield differences with the efficiency factors measured by the monoculture yields.

### 3.3 COMPARISON OF THE DE WIT MODEL WITH ADDITIVE MODELS

When we compare the de Wit model with the additive models, we see that:

(1) The de Wit model better fits the data of competition experiments. Hence, the effect of competition appears to be proportional rather than additive. This will be demonstrated below.

(2) A solely additive model does not hold because of the significant deviation from additivity, which is generally found in the experiments. On the contrary, there is mostly no deviation from the de Wit assumptions. Both features are discussed below.

(3) The de Wit model is the most universal one. The formulae are appropriate to a great variety of designs, whereas most of the additive models are restricted each to a specific experimental design.

(4) The de Wit model has a high predictive value and with it a wide applicability. Within the same physical environment and dealing with the same genotypes, estimates from a particular experiment can be easily transferred to quite different designs with other combinations of the genotypes. Thus the results can be generalized to a high degree. Due to the design-specific nature of most additive models, these are mainly descriptive. This is reinforced by the usually significant interaction effects, which are connected with specific combinations of mixture components. In my opinion the ideal model for biological interaction should not contain statistical terms of interaction, but only 'main effect' parameters peculiar to the single components.

(5) In the de Wit model the genotypes are characterized by only a few basic parameters: monoculture performance, crowding ability, and relative frequency in the mixture. Several additive models swell because a large number of parameters including interactions effects are incorporated to fit the data.

(6) The de Wit model mainly deals with relative values. Dimensionless quantities facilitate, among others, comparison of experiments, treatments or species with highly different performance level and comparison of traits measured with different dimensions.

(7) In contrast to the purely empirical additive models it has a more rational foundation due to the physiological justification. A mathematical model based on the underlying biological processes itself is always preferable to an empirical model for data fitting.

(8) Due to the complicated error structure of his multiplicative model and also for other reasons, de Wit paid little attention to statistical aspects. Thomas (1970), Torssel et al. (1976), and Machin & Sanderson (1977) proposed a procedure of estimation and statistical testing of the de Wit parameters in a replacement series. For a number

of other designs, a statistical analysis, in accordance with the de Wit model, will be introduced in Section 6.2. On the other hand, the additive approaches are already accompanied by an extensive statistical analysis.

It must be noticed that the additive and the proportional model, as defined in Eqns 3.1 and 3.2, are essentially the same for a 1:1 binary mixture when the monocultures do not differ in yield. This can be shown by substituting $Y_{ii} = Y_{jj}$ in these equations, which leads to equivalence of both. An experimental illustration can be derived from the data of Hill (1974, his Table 2), who grew five genotypes of perennial ryegrass in two seasons in monocultures and in all 1:1 binary mixtures. In the first season all monoculture yields differed significantly from each other ($P < 0.10$) and the author found in five out of ten binary mixtures a significant deviation from his additive model. In the second season there were no significant differences between monocultures ($P > 0.10$) and also no significant deviation from the additive model was detected.

*Deviation from simple additivity* The diallel arrangement facilitates testing of deviation from additivity and consequently it enables testing of the adequacy of an additive model. Only competition diallels dealing with genotypes of only one species are discussed, because interspecific competition is of no importance in cereal breeding. The mixtures involved in the diallels are 1:1 mixtures. Due to the scarcity of published diallels in cereals, mainly fodder crops are considered. If not mentioned otherwise, biomass productivity is the trait under consideration.

Applying modified approaches of the Hayman analysis, significance of interaction effects to particular combinations of the components in mixture, was reported by Sakai (1961) for number of ears in wheat, and by Eberhart et al. (1964) for grain yield of single crosses in maize. For biomass production, significant interaction effects were reported by England (1965) in perennial ryegrass and cocksfoot, Chalbi (1967) in lucerne, Gallais (1970) in cocksfoot, and Hill (1974) in perennial ryegrass. Wright (1975) found in Italian ryegrass significant quadratic effects in an alternative analysis.

In the $W_r$-$V_r$ analysis of competition experiments, regression coefficients which are either non-significant or far from slope unity reflect a deviation from the model. This was found by Harper (1965) in flax and linseed, England (1965) in perennial ryegrass and cocksfoot, and Wright (1975) in Italian ryegrass. When this aberrance is not obtained, it does not exclude the presence of combination-specific competition effects. Therefore the non-significant departure from unity slope reported by Harper (1965) in one of the two diallels, by England (1965) in some of his experiments, and by Hill & Shimamoto (1973) in perennial ryegrass does not confirm additivity of competition effects.

When the yield of each genotype in mixture is regressed on the associate means, heterogeneity among linear regression denotes deviation from the additive model. Significance of this term was observed by Breese & Hill (1973) in a diallel of several grass species, by Hill (1973) in perennial ryegrass even when a deviant genotype was omitted, and by England (1974) in ryegrass and cocksfoot.

On the other hand, no deviation from simple additivity was detected in one of the perennial ryegrass diallels of Hill (1974). As was already mentioned this was accounted for by the absence of differences among pure cultures.

Weakness of the additive models is also suggested by the observation that the total yield of a mixture predominantly exceeds its midcomponent monoculture yield: for a 1:1 mixture:

$$Y_{ij} + Y_{ji} > Y_{ii} + Y_{jj}$$

which shows inequality of Eqn 3.1. Evidence for this tendency is found in the reviews of Donald (1963) and Trenbath (1974) with respect to biomass.

It is emphasized again that a universal and predictive model should not contain interaction effects describing competition between specific combinations of genotypes.

*Deviation from proportionality* The adequacy of the de Wit model can be tested by means of the relative yield total (RYT) introduced by de Wit & van den Bergh (1965). When the mixture components compete for the same growth requisites, RYT should equal unity. The RYT is defined to be $\sum_{i=1}^{n} (O_i'/M_i')$ where n the number of genotypes in the mixture, and $O_i'$ and $M_i'$ the yield of a genotype i in the mixture and in its monoculture, respectively. The yields are expressed per unit area. When we express O and M per plant, the RYT becomes $\sum_{i=1}^{n} (z_i O_i/M_i)$ where $z_i$ the relative seed frequency of i in the mixture. The present discussion deals with 1:1 mixtures, so we have to substitute $z_i = z_j = \frac{1}{2}$. The relative yield total for a 1:1 mixture is then

$$RYT = \frac{Y_{ij}}{2Y_{ii}} + \frac{Y_{ji}}{2Y_{jj}} = 1$$

which is equivalent to Eqn 3.2. Hence, Eqn 3.2 describes the de Wit model only for 1:1 mixtures.

One of the basic assumptions of de Wit is that RYT = 1. This is assumed for 1:1 mixtures as well as for any mixture of two or more genotypes, whatever the relative seed frequencies of the genotypes in the mixture. RYT = 1 is then an operational definition of competition for the same resources. Competition for the same resources will be the case in mixtures of genotypes belonging to the same species or related plant species, while in mixtures of, for example, grasses with leguminous species competition is often for not entirely the same resources (de Wit, 1960; de Wit et al., 1966; van den Bergh, 1968). De Wit (1960) developed models for such situations too, but these are not discussed here.

Trenbath (1974, 1978) found the mean RYT for biomass of 572 mixtures to be 1.027 $\pm$ 0.006 and concluded that under the conditions used, competition for the same resources appeared to be the norm. In his review, mixtures of different species, mainly fodder crops, were involved too. Hence the fit to RYT = 1 will even be slightly underestimated, although mixtures of leguminous with non-leguminous species were omitted.

Returning to grain yield in cereals, Sandfaer (1970, p. 32) calculated RYT values in barley mixtures from data published by Allard and co-workers, and found them close to unity. The same held for his own barley experiments, except when a particular variety was involved. That variety caused a fall of RYT below unity due to carriage of a virus. The virus caused a high percentage of sterile flowers in that variety as well as in

the other variaties when they were grown in mixture with the carrier variety (Sandfaer 1970, 1977). Blijenburg & Sneep (1975) concluded from the RYT values for a mixture of eight barley varieties that there was no indication that these varieties influenced each other in any other way than by competition for the same growth requisites.

In the experiments described in Chapter 2, RYT values were computed. None of them showed deviations of RYT from unity, neither for grain yield nor for biomass (Table 11), although competition effects were highly significant. It is concluded that a strictly proportional model is adequate in the analysis of competition between genotypes belonging to the same or related species, and particularly for the competition effects among the varieties used in this study.

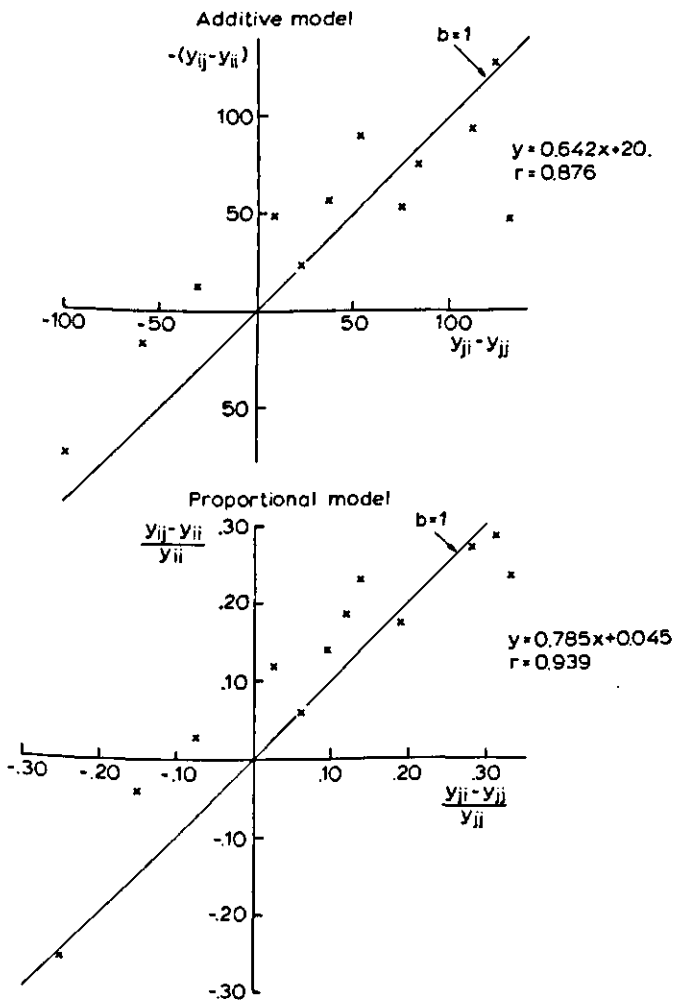


Fig. 6. Data fitting of the additive model with absolute increases and decreases with respect to monocultures and the proportional model with proportional increases and decreases with respect to monocultures. $Y_{ij}$ denotes the grain yield (g $m^{-2}$) of genotype i in mixture with j. Exp. 76-1.

*Data fitting of the models* Trenbath (1972, 1978) compared the data fitting of both types of model. He plotted the biomass data of 133 published binary mixtures derived from 8 references, according to the two sides of Eqn 3.1 as well as according to both sides of Eqn 3.2 (see Fig. 6). He observed that the functional regression line of the 'proportional' graph had a slope considerably closer to $45^{o}$ than that of the 'additive' graph. Therefore, he concluded that the proportional model provided a superior fit.

For illustration, the same technique is applied with the grain yield data of Exp. 76-1. Fig. 6 confirms the superior fit of the proportional model, although in this trial the differences among monocultures were not large.

In the experiments, discussed above, only varieties were involved. In general, the monoculture differences between varieties are large relative to those between the entries tested in a breeding nursery. We have seen that when pure stands perform evenly, for 1:1 mixtures several additive models are equivalent to the proportional model. Consequently, in the analysis of competitive phenomena in breeding nurseries, the advantage of superior fit by the proportional model is reduced. However, the other advantages stand and the universality of the proportional model becomes even more important.

It is concluded that simple additivity of competition effects does not hold, whereas the assumption of proportionality seems adequate. Competition experiments should be analysed with the de Wit model rather than with an additive one, because of the many advantages of the former. Hence, the de Wit model is adopted in the present study.

# 4 Analysis of bias due to competition

In the present chapter the competiton model of de Wit is explained in full. Because the model is designed for mean yields of the components of a mixture, it is extended here to describe the interference between single adjacent plants and rows since these are the basic units of artificial selection. The ultimate interest of breeders is the response to selection, therefore the bias due to competition is modelled in terms of decrease in the response to selection.

## 4.1 DE WIT MODEL

*Available space* The model introduced by de Wit (1960) is based on the assumption that, in a mixture of two genotypes, the 'space' occupied by one genotype and that confiscated by the other relate to each other according to

$$A_i : A_j = b_i z_i : b_j z_j \tag{4.1}$$

The 'crowding coefficient' b denotes the competitive ability of the subscripted genotype and the 'relative seed frequency' z its portion in the total number of kernels planted. Thus $z_i = Z_i/(Z_i+Z_j)$, where Z is the number of grains of the subscripted genotype in the mixture sown. All mixtures are sown at the same density, so $Z_i+Z_j$ = constant.

The term 'space' summarizes all growth requisites like light, water and nutrients for which the genotypes compete. The space is supposed to be uniformly distributed over and in the field.

It is supposed that the total available space is a constant, say unity. This is expressed by

$$A_i + A_j = 1 \tag{4.2}$$

This expression implies that the genotypes exclude each other and crowd for the same space. One may say that they occupy the same ecological 'niche'.

The output yield in mixture (O') of a genotype is assumed to be proportional to the space acquired by that genotype in mixture, hence

$$O'_i = A_i M'_i \qquad \text{and} \qquad A_i = \frac{O'_i}{M'_i} \tag{4.3}$$

where M' is the monoculture yield of the subscripted genotype. The yields O' and M' are provided with an accent to denote that they are expressed per unit area. The O and M without an accent are used when the yield is expressed per experimental unit, that is

per plant or per row. The physiological justification of proportionality was given in Section 3.2.2 and experimental evidence in Section 3.3. The rational background holds for biomass productivity, but the equations are applicable to grain yield and number of kernels too. For parts of plants, especially morphological traits, they become less certain.

*Relative yield total* The 'relative yield' (RY) introduced by de Wit & van den Bergh (1965) denotes the same as the term 'available space'. Thus

$$RY_i = A_i = \frac{O'_i}{M'_i}$$

For example, in a 1:1 mixture there is no competition or both genotypes are equally competitive when the RY of each equals one half. A higher, or lower, value indicates that the particular genotype occupied more, or less, space than its share allotted according to the relative seed frequency.

In analogy to the available space, the sum of relative yields is unity, when competition is for the same resources. The 'relative yield total' becomes

$$RYT = RY_i + RY_j = 1$$

*Relative crowding coefficient* When the space is unevenly shared between the genotypes, the unequal share is described by the ratio of the crowding coefficients. This ratio is termed the 'relative crowding coefficient':

$$k_{ij} = \frac{b_i}{b_j} \tag{4.4}$$

From Eqn 4.1 we see that, regardless the value of RYT, the relative crowding coefficient can be estimated as

$$k_{ij} = \frac{A_i}{A_j}\,\frac{z_j}{z_i} = \frac{RY_i}{RY_j}\,\frac{z_j}{z_i} = \frac{O'_i/M'_i}{O'_j/M'_j}\,\frac{z_j}{z_i} \tag{4.5}$$

It follows that $k_{ji} = 1/k_{ij}$. The relative crowding coefficient of i with respect to j expresses to what extent i is able to occupy space allotted to j. If $k_{ij} = 1$, both genotypes are equally competitive or there is no competition at all. When $k_{ij} > 1$, genotype i is more agressive than j, while the reverse is true when $k_{ij} < 1$.

An expression for the yield in mixture can be derived. We substitute Eqn 4.2 into Eqn 4.1 and the resulting expression for $A_i$ into Eqn 4.3. Replacing the ratio of the two crowding coefficients by the relative crowding coefficient (Eqn 4.4) we obtain for the yield in mixture

$$O'_i = \frac{k_{ij}z_i}{k_{ij}z_i + z_j}\,M'_i \tag{4.6a}$$

and

$$O'_j = \frac{k_{ji}z_j}{k_{ji}z_j + z_i} M'_j = \frac{z_j}{z_j + k_{ij}z_i} M'_j \qquad (4.6b)$$

*Relative reproductive rate* The 'reproductive rate' of a genotype is defined as the ratio of its number of seeds harvested and its number of seeds sown. When the output yield in mixture is expressed in number of kernels per unit area, then the reproductive rates become

$$a_i = \frac{O'_i}{Z_i} \text{ and } a_j = \frac{O'_j}{Z_j} \qquad (4.7)$$

The 'relative reproductive rate' of i with respect to j becomes

$$\alpha_{ij} = \frac{a_i}{a_j} = \frac{O'_i}{O'_j} \times \frac{Z_j}{Z_i} = k_{ij} \frac{M'_i}{M'_j} \qquad (4.8)$$

This quantity denotes the 'relative fitness' or 'survival value' of the genotype in mixture.

*Multicomponent mixture* The equations describing the effect of competition within mixtures of two components may be extended to mixtures of more than two components. For n genotypes the basic equation 4.1 is rewritten as

$$A_1 : A_2 \ldots\ldots : A_n = b_1z_1 : b_2z_2 : \ldots\ldots : b_nz_n \qquad (4.9)$$

in which the sum of the relative spaces remains a constant, say one. Equation 4.6 describing the yield of genotype i in mixture is recast in the form

$$O'_i = \frac{b_iz_i}{b_1z_1 + b_2z_2 + \ldots + b_nz_n} M'_i \qquad (4.10)$$

because $O'_i = A_iM'_i$.

*Implications for breeding* The aim of breeding is to select genotypes which perform better than the existing varieties. In present agriculture the varieties are grown in monoculture, therefore the monoculture yield M' is the character selected for. Selection has to take place in a segregating population, so selection is based on yield in mixture O and the relation between $O'_i$ and $M'_i$ becomes crucial in single-plant selection and progeny testing. In unselected bulk propagation the association between survival of a genotype, measured as $\alpha_{ij}$, and its monoculture yield $M'_i$ is essential. Of fundamental interest is the relation between competitive ability, measured by $b_i$, and the respective yield of the pure stand $M'_i$.

## 4.2 COMPETITION BETWEEN NEAREST NEIGHBOURS

The de Wit model gives an expression for the yield of a genotype in a mixture, averaged over all individuals of that genotype in the mixture. However, selection is for individual units. In plant selection, a single plant is the unit of selection. In line selection, mostly a row of plants, all belonging to the same line, is the unit of selection.

Competition between units of selection falls within two limits. In one limit, all units of the population compete with each other to the same degree ('diffuse competition'). This implies that the yield of a unit depends on the genotypic composition of the entire population. In the other limit, only the nearest neighbours compete with each other ('nearest-neighbour competition'). Then, the yield of a unit depends on the genotype of its nearest neighbours and is, therefore, independent of the genotypic composition of the entire population.

The model of de Wit describes only diffuse competition. It is therefore necessary to develop a model to define competition between nearest neighbours. Models for nearest-neighbour competition were already given by Hanson et al. (1961), Geidel & Haufe (1968, 1970) and Rawlings (1974). However, these models are purely additive and do not suit the aim of the present study. Therefore in this section, another model is developed from the de Wit model to describe competition between nearest neighbours.

### *4.2.1 A model for competition between nearest neighbours*

For the moment, we shall restrict ourselves to a line-selection field, where individual rows are the unit of selection. A row competes only against its nearest neighbours (Section 4.2.2). When we represent each row by a letter denoting the genotype of the plants sown in that row, the arrangement (Arr.) of a mixture of the genotypes h and i is given by

h i h i h i h i (Arr. 4.1)

According to Eqn 4.10 the yield of i in mixture is

$$O_i' = \frac{z_i b_i}{z_i b_i + z_h b_h} M_i'$$

When we express the yield per row instead of per unit surface, we obtain

$$O_i = \frac{b_i}{z_i b_i + z_h b_h} M_i \qquad (4.11)$$

$O_i = O_i'/Z_i$ and $M_i = M_i'/Z_{tot}$ and, therefore, $O_i/M_i = O_i'/z_i M_i'$.
Note that when the yields are per row or per plant, O and M are without an accent. As $z_i = z_h = \frac{1}{2}$, the yield of i in the 1:1 mixture is

$$O_i = \frac{b_i}{\frac{1}{2}b_i + \frac{1}{2}b_h} M_i \qquad (4.12)$$

When we substitute every second h row by a j row, we have the arrangement

h i j i h i j i (Arr. 4.2)

We assume an experimental evidence (Section 4.2.2) that a row is only affected by its direct neighbour rows. That is, the effect of second and higher-order neighbours is neglected. Under this assumption, the yield of h in Arr. 4.2 equals the yield of h in a mixture where h and i are planted alternately (Arr. 4.1). Thus, the yield of h in Arr. 4.2 is given in accordance with Eqn 4.12 as

$$O_h = \frac{b_h}{\frac{1}{2}b_h + \frac{1}{2}b_i} M_h$$

and, in the same way, the yield of j as

$$O_j = \frac{b_j}{\frac{1}{2}b_j + \frac{1}{2}b_i} M_j$$

The expression of $O_i$ is less easy to derive. It is not allowed to substitute $z_i = \frac{1}{2}$ and $z_h = z_j = \frac{1}{4}$ into Eqn 4.10. For in Arr. 4.2 h and j do not compete with each other, as it is assumed that only adjacent neighbours compete with each other. When we represent the yield of i as $O_i = xM_i$, where x an auxiliary variable, then it holds for Arr. 4.2 that the sum of the relative yields O'/M' equals

$$RYT = \frac{1}{2}x + \frac{1}{4}\frac{b_h}{\frac{1}{2}b_i + \frac{1}{2}b_h} + \frac{1}{4}\frac{b_j}{\frac{1}{2}b_i + \frac{1}{2}b_j}$$

When the genotypes compete for the same space (RYT = 1, Section 4.1), x can be solved from both equations and substituted into $O_i = xM_i$. We find for the yield of i situated between h and j

$$O_{i,hj} = \left(\left(1 - \frac{b_h}{b_i + b_h}\right) + \left(1 - \frac{b_j}{b_i + b_j}\right)\right) M_i = \frac{b_i(2b_i + b_h + b_j)}{(b_i + b_h)(b_i + b_j)} M_i =$$

$$\frac{2b_i^2 + b_i b_h + b_i b_j}{b_i^2 + b_i b_h + b_i b_j + b_h b_j} M_i \qquad (4.13)$$

When we substitute in Arr. 4.2 all rows, except one row of i and both its neighbours, by rows with different genotypes, we have

d e f g h i j k (Arr. 4.3)

Under the assumption that the effect of second and higher-order neighbours is negligible, the yield of i in the arrangements 4.2 and 4.3 is expected to be the same and thus

equals Eqn 4.13.

When a rough approximation is satisfactory, one may suppose that h and j are equally competitive. Than $b_h = b_j = b$ and Eqn 4.13 can be simplified to

$$O_{i,hj} = \frac{2b_i}{b_i+b} M_i$$

*In a line-selection field, the genetic constitution of a line is genetically unique.* When each line is sown as a single row, Arr. 4.3 represents a part of the field. The yield of a line i is given by Eqn 4.13.

*4.2.2 Effect of second and higher-order neighbours*

4.2.2.1 Literature

The literature on the degree to which a plant or a row extends its competitive influence on successive neighbours is scarce. Jensen & Federer (1964) showed marked effects of interrow competition in wheat where the rows were 30 cm apart. The effect of a row sown with a standard variety on successive rows of the adjacent 3-row plots was restricted to the first row adjacent to the standard. The standard variety appeared to be a strong competitor. Gomez (1972) grew rice varieties in 10-row plots at a plant spacing of 20 x 20 cm. Not only the first border row was affected by adjacent plot competition, but frequently the second row too. However, the last situation occurred when the variety in the adjacent plot lodged. In winter wheat, Rich (1973) found indications that a variety of normal height affected the second row of an adjacent plot sown with a semi-dwarf variety. The interrow spacing ranged from 15 to 30 cm.

Some information can be derived from the distance effect of alleys. These experiments can be translated to adjacent row competition by considering an empty row, i.e. the alley, as the weakest competitor possible. Arny & Hayes (1918) and Arny (1921) studied wheat, barley and oats in 17-row plots with a row spacing of 15 cm. Due to the 45 cm cleaned alley, the yield of the outside border rows materially increased and, in the majority of cases, the yield of second and third rows also, but to a less extent. In the 1918 experiments the enhancement averaged 98, 15 and 10% for the first, second and third rows, respectively. Hulbert & Remsberg (1927) found in a similar experiment, that a 60 cm alley usually affected the second border row. Robertson & Koonce (1934), in wheat, used irrigated plots separated by small dykes. From their Table 4, it can be derived that the border effect extended to the first and second rows, but not to the third one. In the experiments from both latter references, the yield increase of the second rows was small relative to that of the first rows.

On the other hand, McClelland (1929, 1934), in oats and wheat at a row spacing of 20 cm, found no effect on the second border row due to alleys of one and two empty rows. In wheat, Miller & Mountier (1955) observed that only the yield of the first border rows of 7-row plots changed when the spacing between the plots increased from 18 to 71 cm. The rows within the plots were spaced 18 cm apart. Gomez & Gomez (1976, p. 230) studied the effect of alleys ranging in width from 20 cm (control) to 140 cm, on successive rows

of 10-row rice plots planted at a rate of 20 x 20 cm. They found that only the outermost row gave significant higher yields than the center rows.

As a general feature, the yield of the first border is considerably increased due to the alley effect. Some authors found also an enhancement of the second row, but to a much lesser extent. The width of the alley mostly exceeded the width of a single empty row. So, the experiments overestimate considerably the distance effect of an empty row. and even more the influence of a weak competitor. The different row spacings used by the authors complicate the interpretation. Nevertheless it seems that the influence of a single row is probably limited to its first neighbours, but more experimental evidence is needed. In small cereals, I did not find any publication on the effect of an individual plant on its consecutive neighbour plants.

4.2.2.2 Experiments

The influence of a row on its consecutive neighbour rows is investigated in barley by raising rows all having the same genotype, called the producer genotype P, except that every 11th row in the 1976 experiment and every 9th row in the 1977 experiment is replaced by a row consisting of the aggressor genotype A. In this way, sets of P rows are obtained where the influence of the aggressor A on the producer P decreases with successive rows of P. We can represent the arrangement of 1977 by

$$P_4\ P_3\ P_2\ P_1\ A\ P_1\ P_2\ P_3\ P_4$$

where each letter represents a single row and its subscript denotes the order with respect to A. Fourteen and sixteen of such P sets were grown in 1976 and 1977, respectively. The layout of the experiments is similar to that described in Section 2.1 for line selection.

In each year two situations were considered. Firstly, A is an empty row, the weakest aggressor imaginable, and P consists of the variety 'Belfor'. Secondly,'Belfor' is the aggressor, thought to be strongly competitive, while the producer P is a presumably weak competitor, 'Camilla' and 'Golden Promise' in 1976 and 1977, respectively.

The effect of an empty row on successive 'Belfor' rows is presented in Fig. 7. The first row, bordering the empty row, has a considerably higher yield than the other rows. But no yield difference among the latter can be detected. It is concluded that in both experiments the effect of the empty row is restricted to its first neighbour.

The other experiments with rows failed to show significant competition effects, that is the first row did not yield differently from the other rows. Probably, this result was brought about by the small differences in competitive ability between the varieties involved. It is not possible to predict beforehand which varieties are weak and which are strong competitors.

From my experiments, I conclude that at least a row of a weak competitor, bordered with rows of a stronger competitor, restricts its competitive influence only to its first neighbour rows.

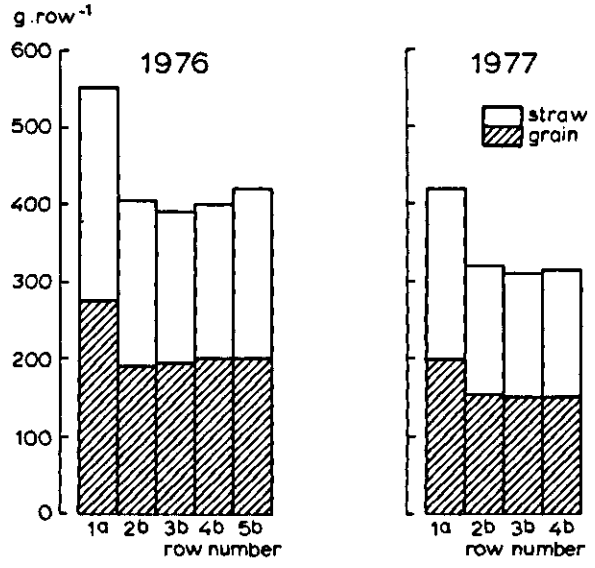


Fig. 7. Influence of an empty row on grain yield and biomass of successive rows of 'Belfor' in two years. Rows followed by the same letter are not significantly different at $P < 0.05$ according to the Student-Newman-Keuls test.

Similar experiments were done with single plants at a spacing of 5 cm between plants within a row and 25 cm between rows. The grains were accurately spaced by hand, sowing two kernels at each place and singling the plants after emergence.

In 1977, the influence of an empty place on consecutive 'Belfor' plants, located in the same row, was studied. Averaged over 40 replicates, aboveground biomass was

| $P_1$ | $P_2$ | $P_3$ | $P_4$ | $P_5$ | $P_6$ | |
|---|---|---|---|---|---|---|
| 10.3 | 10.8 | 9.2 | 11.0 | 9.9 | 10.0 | g plant$^{-1}$ |

The yields are not significantly different (S.E. of mean = 0.70 g plant$^{-1}$).

A similar trial was carried out in 1978 with the cultivar 'Varunda'. A strong aggressor was established by sowing six grains on a plant place without singling the plants on this place after emergence. A weak aggressor was obtained by an empty plant place. The results are given in Fig. 8. When the influence of an aggressor is restricted to its direct neighbour, it is expected that the first neighbour of the strong aggressor has a lower yield and the first neighbour of the weak aggressor has a higher yield compared with the neighbours of higher order. However, it appears that in this experiment this was not the case (Fig. 8). The outcome cannot be ascribed to competition effects, which are too small to be demonstrated. For, when the yields of 12 varieties in monoculture were compared with their yields in a mixture of all varieties, the competition effects were highly significant (Table 14). This experiment was as equally discriminative as the abovementioned experiments because the standard deviation belonging to the treatment means was similar in the multicomponent mixture (SE = 0.79 g), the experiments in 1978

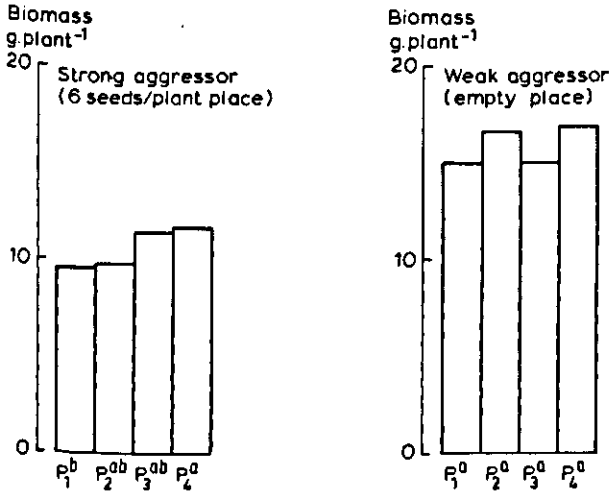


Fig. 8. Influence of a strong aggressor and of a weak aggressor on biomass of consecutive 'Varunda' plants situated in the same row as the aggressor. Plants are spaced 5 cm within the rows 25 cm apart. The strong aggressor was established by sowing six grains on a plant place. The biomass of the strong aggressor averaged 46.0 g per plant place. The weak aggressor is formed by an empty plant place. The subscript of the producer P denotes the order with respect to the aggressor. Producers followed by the same letter are not significantly different at $P < 0.05$ according to the Student-Newman-Keuls test.

with a strong aggressor (SE = 0.60 g) and that with a weak aggressor (SE = 0.74 g), and the experiment in 1977 with a weak aggressor (SE = 0.70 g). Moreover, the differences in competitive ability in the latter experiments are expected to be larger than those between the varieties in the multicomponent mixture. Hence, if competition were restricted to adjacent plants, this would have been demonstrated in the experiments. However, the consecutive neighbours did not yield differently.

In contrast to the small differences in yield between the treatments within a trial, the experiment with the strong aggressor provided a distinctly lower yield than the experiment with the weak aggressor (Fig. 8). Each experiment consisted of three rows and the experiments were situated side by side. Inspection of the mean yield per row revealed that a systematic fertility gradient cannot be the cause of the difference in yield level. This result strongly suggests that the difference in yield level must be due to a difference between the aggressors.

The previous findings suggest that a plant does not only influence its direct neighbours, but also affects its neighbours of higher order, even to a considerable degree. Increase of plant density will enhance this effect. When the conclusion holds for these trials with contrasting competitors, the conclusion will also be true for a less extreme situation, for example a plant-selection nursery with competing genotypes.

Thus the yield of a genotype in mixture is affected by the relative seed frequencies of the genotypes rather than by the genetic make-up of its surrounding neighbours. Then the sowing pattern does not influence the yield of the components in the mixture. This can be tested in Exp. 77-1 where a mixture of 12 varieties was grown according to a rectangular plant arrangement at 5 x 25 $cm^2$ $plant^{-1}$ (Exp. 77-1b) as well as according to a

triangular planting pattern at 10.4 x 12 $cm^2$ $plant^{-1}$ (Exp. 77-1d). In the joint analysis of variance for biomass and in that for grain yield, the variety x stand interaction was not statistically significant ($P > 0.10$). This agrees with the findings of Naylor & Bebawi (1977). They found no differences, neither in the yields of barley nor in the yields of oats, when barley and oats were planted according to different arrangements of the species in a 1:1 ratio at a spacing of 3.5 x 3.5 $cm^2$ $plant^{-1}$.

From the trials with rows, complemented with the findings reported in the literature, it is concluded that in the small grains a row influences only its adjacent neighbour rows (nearest-neighbour competition). In the experiments with individual plants, however, each plant strongly affected neighbours of higher order too (diffuse competition). More experimental evidence is required to confirm for the small cereals the diffuse nature of the competition between single plants.

There may be situations where these conclusions do not hold. (a) When a row is placed between two empty rows, the row affects its second neighbours. This can be seen from the relation between row distance and yield, which relation is linear only at very wide row spacings (Section 5.1.2). (b) At extremely small row distances, the influence of a row may reach farther than only its adjacent neighbours. (c) In mixtures, other than those of small cereals, the yield of the genotypes or species is sometimes influenced by the planting pattern (Harper, 1961; Donald, 1963; Mack & Harper, 1977). This implies that then the competition between plants is not purely diffuse but tends to be restricted between nearest neighbours.

*Summary* In small grains, a row influences only its adjacent neighbour rows (nearest-neighbour competition). A single plant, however, strongly affects neighbours of higher order too (diffuse competition). Therefore, when single rows are the experimental unit the nearest neighbour concept must be applied, but when individual plants are involved, the original model of de Wit seems more appropriate.

### *4.2.3 Comparision between nearest-neighbour competition and diffuse competition*

The differences between the original de Wit model, that describes diffuse competition, and the model developed in Section 4.2.1 to describe competition between nearest neighbours are pointed out. Moreover, it is illustrated which erroneous results are reached when the de Wit model is applied to a situation where competition is only between nearest neighbours.

Competition between single plants can be approached as diffuse competition. Under diffuse competition, all plants in the population compete with each other to the same degree. Thus the yield of a single plant depends on the genotypic composition of the entire population. Then, the yield of the genotypes in the population is independent of the planting pattern and is independent of the mutual arrangement of the genotypes. In absence of environmental variation, all plants belonging to the same genotype show the same yield. Diffuse competition is described by the original model of de Wit.

A row competes only against its adjacent neighbour rows so that the yield of a row depends on the genotype of its adjacent neighbours, but is independent of the genotypic

composition of the population. The yield of a genotype in the population, where each genotype is sown in a separate row, depends on the planting pattern and on the mutual arrangement of the genotypes. In absence of environmental variation, all rows sown with the same genotype differ in yield when each row has genetically different neighbours. Competition between adjacent neighbours is described by the nearest-neighbour concept.

Experiment 77-2 (Section 2.1.5), where competition between rows is studied, enables a comparison of both models. The crowding coefficient b is estimated from the monocultures and 1:1 alternated mixtures (Exp. 77-2a) according to the procedure described in Section 6.2.2. The de Wit model and the nearest-neighbour concept are equivalent for 1:1 alternated mixtures and so they supply identical estimates. However, the models disagree with each other for 1:1 mixtures where the genotypes are not alternately grown, for binary mixtures with relative seed frequencies unequal to a half, and for mixtures consisting of more than two components.

In the mixture where the 12 cultivars occur at the same frequency (Exp. 77-2b), the yield expectation of genotype i is according to de Wit given by Eqn 4.10 as

$$O_i' = \frac{b_i}{b_1+\ldots.+b_{12}} M_i'$$

The crowding coefficient b is on a relative scale so that an arbitrary level may be chosen for it (Section 6.2.1). For convenience, we set the average of the b s to unity. When we substitute this value and we express O and M per row, we have

$$O_i = b_i M_i \qquad (4.14)$$

In the nearest-neighbour concept, Eqn 4.13 gives the expected yield of i in the mixture as

$$\underline{O}_i = \varepsilon \left(\frac{b_i}{b_i+\underline{b}_h} + \frac{b_i}{b_i+\underline{b}_j}\right) M_i$$

Note that i is fixed and h and j are stochastic. Stochastic variables are underlined. An approximation is found by the 'method of statistical differentials' (Section 4.3.1.2). The second and higher-order terms in the Taylor series expansion appeared to be relatively very small. Hence, we can approximate the expected yield of i in a multicomponent mixture as

$$\underline{O}_i = \frac{2b_i}{b_i+\overline{b}} M_i \qquad (4.15)$$

The yields as they are expected according to Eqns 4.14 and 4.15 are presented in Table 7 and are compared with the yields observed in the multicomponent mixture (Exp. 77-2b). The predictions are based on the variables M and b, which were derived from Exp. 77-2a. Hence, prediction and observation are independent from each other because they are based on different experiments.

$$\text{var } \underline{p} = \text{var } \underline{g} + \text{var } \underline{e} \qquad (4.17)$$

when cov($\underline{g}$,$\underline{e}$) is neglected.

However, the model does not hold when the character studied is subjected to competition. We have seen in Section 1.3 that the yield of entries in a selection nursery can be considerably affected by competition. Consequently, the model must be extended for competition effects.

*Additive competition models* When competition effects are supposed to be additive, the right-hand side of Eqn 4.16 has to be enhanced with a stochastic variable measuring the deviation due to competition. So the phenotypic performance appears in the form

$$\underline{p} = \mu + \underline{g} + \underline{c} + \underline{e}$$

where $\underline{c}$, the competition component, has expectation zero. Neglecting the covariances with $\underline{c}$, the partitioning of the phenotypic variance takes the form

$$\text{var } \underline{p} = \text{var } \underline{g} + \text{var } \underline{c} + \text{var } \underline{e} \qquad (4.18)$$

Sakai (1951) was probably the first to recognize competition as a source of variation among plants. He introduced the partitioning of variance as it is given in Eqn 4.18 and emphasized the competitional variance in genetic as well as breeding work (Sakai, 1953). Additive approaches of competition effects and their components of variance are numerous. Section 3.2.1 reviews a number of models which are accompanied by an analysis of variance to test the significance of the competition effects. The competitional variance is frequently split into a number of additive components, but the model remains essentially based on Eqn 4.18. Theoretical genetic models dealing with competition and operating at the level of effects and frequencies of single genes, were given by, among others, Singh (1967), Hühn (1969, 1970), Griffing (1967a, b), Gallais (1976), and Hamblin & Rosielle (1978). Sakai & Mukaide (1967) and Hühn (1972, 1975) tried to estimate competitional variances in standing forests. Also Skinner (1961) and Hogarth (1977) used an additive model to account for competition in their genetic studies in sugarcane.

In Section 3.3 it was shown that the additive models are inferior to the de Wit model, so a further discussion of the former would be pointless.

### *4.3.1 Components of variance in a proportional competition model*

#### 4.3.1.1 Basic model

For the moment, we shall restrict ourselves to a line-selection field with single rows as experimental unit. Let a row, sown with a random genotype i, be situated between a row with a random genotype h and a row with a random genotype j. According to Eqn 4.13, the yield of a row sown with i is expected to be

$$\underline{O}_{i,hj} = \frac{\underline{b}_i(2\underline{b}_i+\underline{b}_h+\underline{b}_j)}{(\underline{b}_i+\underline{b}_h)(\underline{b}_i+\underline{b}_j)}\ \underline{M}_i \qquad (4.13)$$

The pure-stand yield of i, expressed in genetic terms, equals $\underline{M}_i = \mu+\underline{g}_i$. The expectation for a row with i in the mixture can now be rewritten as

$$\underline{O}_{i,hj} = \underline{c}_{i,hj}(\mu+\underline{g}_i) \qquad (4.19)$$

where $\underline{c}$, the competition coefficient, equals

$$\underline{c}_{i,hj} = \frac{\underline{b}_i(2\underline{b}_i+\underline{b}_h+\underline{b}_j)}{(\underline{b}_i+\underline{b}_h)(\underline{b}_i+\underline{b}_j)} \qquad (4.20)$$

with $\varepsilon\ \underline{c} = 1$ (Eqn 4.13).

Elaborating the model to allow for random and environmental errors, the phenotypic performance of i located between h and j is recast in the form

$$\underline{P}_{i,hj} = \underline{c}_{i,hj}(\mu+\underline{g}_i)+\underline{e}_i \qquad (4.21)$$

The variable $\underline{c}$ denotes the genetic component of competition, that is it only involves the competition effects due to genotype. Within a pure stand, where all genotypes are identical to each other, competitional differences between adjacent rows arise from environmental and random causes. This type of competition is explained by the residual error $\underline{e}$. This component contains also the error due to random variation in interrow distances.

When not mentioned otherwise, $\mu$ refers to the population mean in monoculture, that is the average monoculture yield of the genotypes. The population mean in mixture is obtained from Eqns 4.13 and 4.19 by the method of statistical differentials (Section 4.3.1.2). Taking into account the quadratic terms, this gives

$$\mu_{mix} = \mu_{mono} + \mathrm{cov}(\underline{c},\underline{g}_{mono}) \qquad (4.21a)$$

Interaction and correlation of the genetically determined effects, $\underline{g}$ and $\underline{c}$, with the environmental error $\underline{e}$ is assumed to be absent. This approach is useful for a single selection nursery.

#### 4.3.1.2 Method of statistical differentials

Before dealing with components of variance, the method of statistical differentials is outlined. This method will be frequently used. When functions are non-linear, approximate variances and covariances can be found by the method of statistical differentials described by, among others, Kempthorne & Folks (1971, p. 130).

Let $\underline{x}$ and $\underline{y}$ be random variables and $\underline{U} = f(\underline{x},\underline{y})$ a differentiable function of $\underline{x}$ and $\underline{y}$. Suppose the means are given by $\varepsilon\underline{x}$ and $\varepsilon\underline{y}$, the variances by var $\underline{x}$ and var $\underline{y}$, and the

covariance by cov $(\underline{x}, \underline{y})$.

Expanding $\underline{U}$ in a Taylor series about $\epsilon\underline{x}$ and $\epsilon\underline{y}$ gives

$$\underline{U} = f(\underline{x},\underline{y}) = f(\epsilon\underline{x},\epsilon\underline{y}) + (\underline{x}-\epsilon\underline{x})\frac{\delta f}{\delta x} + (\underline{y}-\epsilon\underline{y})\frac{\delta f}{\delta y} + \text{higher order terms}$$

where the derivatives are to be evaluated at $\epsilon\underline{x}$ and $\epsilon\underline{y}$. If higher order terms are neglected, we have

$$\epsilon(\underline{U}) = f(\epsilon\underline{x},\epsilon\underline{y}) + \epsilon(\underline{x}-\epsilon\underline{x})\frac{\delta f}{\delta x} + \epsilon(\underline{y}-\epsilon\underline{y})\frac{\delta f}{\delta y}$$

Because $\epsilon(\underline{x}-\epsilon\underline{x}) = \epsilon\underline{x}-\epsilon\underline{x} = 0$ and $\epsilon(\underline{y}-\epsilon\underline{y}) = \epsilon\underline{y}-\epsilon\underline{y} = 0$
this can be simplified to

$$\epsilon(\underline{U}) = f(\epsilon\underline{x},\epsilon\underline{y})$$

The variance of $\underline{U}$ is found from its definition to be

$$\text{var } \underline{U} = \epsilon(\underline{U}-\epsilon(\underline{U}))^2 = \epsilon\left((\underline{x}-\epsilon\underline{x})\frac{\delta f}{\delta x} + (\underline{y}-\epsilon\underline{y})\frac{\delta f}{\delta y}\right)^2$$

$$= \left(\frac{\delta f}{\delta x}\right)^2 \text{var } \underline{x} + 2\left(\frac{\delta f}{\delta x}\right)\left(\frac{\delta f}{\delta y}\right) \text{cov } (\underline{x},\underline{y}) + \left(\frac{\delta f}{\delta y}\right)^2 \text{var } y$$

where the derivatives are to be evaluated at $\epsilon\underline{x}$ and $\epsilon\underline{y}$.

The method of statistical differentials can also be applied to two or more differentiable functions. If $\underline{U} = f(\underline{x},\underline{y})$ and $\underline{V} = g(\underline{x},\underline{y})$, then the approximate covariance of $\underline{U}$ and $\underline{V}$ is given by

$$\text{cov } (\underline{U},\underline{V}) = \epsilon(\underline{U}-\epsilon\underline{U})(\underline{V}-\epsilon\underline{V}) = \epsilon\left((\underline{x}-\epsilon\underline{x})\frac{\delta f}{\delta x} + (\underline{y}-\epsilon\underline{y})\frac{\delta f}{\delta y}\right)\left((\underline{x}-\epsilon\underline{x})\frac{\delta g}{\delta x} + (\underline{y}-\epsilon\underline{y})\frac{\delta g}{\delta y}\right)$$

$$= \left(\frac{\delta f}{\delta x}\cdot\frac{\delta g}{\delta x}\right) \text{var } \underline{x} + \left(\frac{\delta f}{\delta x}\cdot\frac{\delta g}{\delta y} + \frac{\delta f}{\delta y}\cdot\frac{\delta g}{\delta x}\right) \text{cov}(\underline{x},\underline{y}) + \left(\frac{\delta f}{\delta y}\cdot\frac{\delta g}{\delta y}\right) \text{var } \underline{y}$$

where the derivatives are to be evaluated at $\epsilon\underline{x}$ and $\epsilon\underline{y}$.
If $\underline{U} = f(\underline{x},\underline{y},\underline{z})$ and $\underline{V} = g(\underline{x},\underline{y},\underline{z})$ the expressions become

$$\text{var } \underline{U} = \left(\frac{\delta f}{\delta x}\right)^2 \text{var } \underline{x} + \left(\frac{\delta f}{\delta y}\right)^2 \text{var } \underline{y} + \left(\frac{\delta f}{\delta z}\right)^2 \text{var } \underline{z} +$$

$$+ 2\left(\frac{\delta f}{\delta x}\right)\left(\frac{\delta f}{\delta y}\right) \text{cov}(\underline{x},\underline{y}) + 2\left(\frac{\delta f}{\delta x}\right)\left(\frac{\delta f}{\delta z}\right) \text{cov}(\underline{x},\underline{z}) + 2\left(\frac{\delta f}{\delta y}\right)\left(\frac{\delta f}{\delta z}\right) \text{cov}(\underline{y},\underline{z})$$

$$\text{cov}(\underline{U},\underline{V}) = \left(\frac{\delta f}{\delta x}\cdot\frac{\delta g}{\delta x}\right) \text{var } \underline{x} + \left(\frac{\delta f}{\delta y}\cdot\frac{\delta g}{\delta y}\right) \text{var } \underline{y} + \left(\frac{\delta f}{\delta z}\cdot\frac{\delta g}{\delta z}\right) \text{var } \underline{z} +$$

$$+ \left(\frac{\delta f}{\delta x}\cdot\frac{\delta g}{\delta y} + \frac{\delta f}{\delta y}\cdot\frac{\delta g}{\delta x}\right) \text{cov}(\underline{x},\underline{y}) + \left(\frac{\delta f}{\delta x}\cdot\frac{\delta g}{\delta z} + \frac{\delta f}{\delta z}\cdot\frac{\delta g}{\delta x}\right) \text{cov}(\underline{x},\underline{z}) +$$

$$+ \left(\frac{\delta f}{\delta y}\cdot\frac{\delta g}{\delta z} + \frac{\delta f}{\delta z}\cdot\frac{\delta g}{\delta y}\right) \text{cov}(\underline{y},\underline{z})$$

These expressions can be expanded for situations where more than three random variables are involved.

4.3.1.3 Phenotypic variance

The phenotypic variance among rows can be derived from Eqn 4.21. Omitting the subscripts for the moment, we have

$$\text{var } \underline{p} = \text{var } (\underline{c}\mu + \underline{c}\,\underline{g} + \underline{e}) = \text{var } (\underline{c}\mu + \underline{c}\,\underline{g}) + 2 \text{ cov } ((\underline{c}\mu + \underline{c}\,\underline{g}), \underline{e}) + \text{var } \underline{e}$$

Since the genotypes are randomly distributed across the field, there is no expected correlation between genotype and environment, that is

$$\text{cov}((\underline{c}\mu + \underline{c}\,\underline{g}), \underline{e}) = 0$$

and therefore

$$\text{var } \underline{p} = \text{var}(\underline{c}\mu + \underline{c}\,\underline{g}) + \text{var } \underline{e} \qquad (4.22)$$

The genetic component can be worked out as

$$\text{var}(\underline{c}\mu + \underline{c}\,\underline{g}) = \text{var}(\underline{c}\mu) + \text{var}(\underline{c}\,\underline{g}) + 2 \text{ cov}(\underline{c}\mu, \underline{c}\,\underline{g})$$

$$= \mu^2 \text{ var } \underline{c} + \text{var}(\underline{c}\,\underline{g}) + 2\mu \text{ cov}(\underline{c}, \underline{c}\,\underline{g}) \qquad (4.23)$$

Application of the method of statistical differentials (Section 4.3.1.2) gives the approximations

$$\text{var}(\underline{c}\,\underline{g}) = (\varepsilon\underline{c})^2 \text{ var } \underline{g} + 2(\varepsilon\underline{c})(\varepsilon\underline{g}) \text{ cov}(\underline{c},\underline{g}) + (\varepsilon\underline{g})^2 \text{ var } \underline{c} = \text{var } \underline{g}$$

$$\text{cov}(\underline{c},\underline{c}\,\underline{g}) = (\varepsilon\underline{g}) \text{ var } \underline{c} + (\varepsilon\underline{c}) \text{ cov}(\underline{c},\underline{g}) = \text{cov}(\underline{c},\underline{g})$$

since $\varepsilon\underline{g} = 0$ and $\varepsilon\underline{c} = 1$.
Substitution into Eqn 4.23 gives

$$\text{var}(\underline{c}\mu + \underline{c}\,\underline{g}) = \mu^2 \text{ var } \underline{c} + \text{var } \underline{g} + 2\mu \text{ cov}(\underline{c},\underline{g})$$

Combining this expression with Eqn 4.22, we find

$$\text{var } \underline{p} = \text{var } \underline{g} + 2\mu \text{ cov}(\underline{c},\underline{g}) + \mu^2 \text{ var } \underline{c} + \text{var } \underline{e} \qquad (4.24)$$

The competitive ability of a genotype is characterized by its crowding coefficient (Section 4.1). Hence, it is useful to express the competition coefficient $\underline{c}$ and its variance as a function of the crowding coefficient $\underline{b}$ and its variance, respectively.

When we transpose the expression for the competition coefficient $\underline{c}$ (Eqn 4.20) to the variance, we obtain

$$\text{var } \underline{c}_{i,hj} = \text{var } \frac{\underline{b}_i(2\underline{b}_i+\underline{b}_h+\underline{b}_j)}{(\underline{b}_i+\underline{b}_h)(\underline{b}_i+\underline{b}_j)} \tag{4.25}$$

After $\underline{c}$ is differentiated to $\underline{b}_i$, $\underline{b}_h$ as well as $\underline{b}_j$, the method of statistical differentials provides

$$\text{var } \underline{c}_{i,hj} \approx \frac{3}{8} \text{ var } \underline{b} \tag{4.26}$$

It was assumed that the genotypes are allotted to each other at random; that is that the bs are uncorrelated and their mutual covariances equal zero. In the calculation, the bs were set to the arbitrary level $\epsilon\underline{b} = 1$. This is allowed as the crowding coefficients $\underline{b}$ are scale independent. Only their ratios, the relative crowding coefficients k, have significance (Section 6.2.1).

From Eqn 4.20 we see

$$\text{cov}(\underline{c}_{i,hj},\underline{g}_i) = \text{cov}\left(\frac{\underline{b}_i(2\underline{b}_i+\underline{b}_h+\underline{b}_j)}{(\underline{b}_i+\underline{b}_h)(\underline{b}_i+\underline{b}_j)}, \underline{g}_i\right)$$

Differentiation of $\underline{c}$ and $\underline{g}$ to $\underline{b}_i$ and $\underline{g}$ supplies, after use of the differential method,

$$\text{cov}(\underline{c}_{i,hj},\underline{g}_i) \approx \tfrac{1}{2} \text{ cov}(\underline{b}_i,\underline{g}_i) \tag{4.27}$$

where again $\epsilon\underline{b}$ was set to unity and, when $i \neq j$, $\text{cov}(\underline{b}_i,\underline{b}_j)$ and $\text{cov}(\underline{b}_j,\underline{g}_i)$ equal zero as the genotypes are allotted to each other at random.

Substitution of Eqns 4.26 and 4.27 into Eqn 4.24 gives for the phenotypic variance in mixed culture

$$\text{var } \underline{p} = \text{var } \underline{g} + \mu\text{cov}(\underline{b},\underline{g}) + \frac{3}{8}\mu^2 \text{ var } \underline{b} + \text{var } \underline{e} \tag{4.28}$$

At first sight, it may be curious that the population mean $\mu$ appears in the expression of var $\underline{p}$. The reason is that $\underline{g}$ is on an absolute scale and $\underline{b}$ on a relative scale. To bring $\text{cov}(\underline{b},\underline{g})$ and var $\underline{b}$ on the level of the absolute scale, the multiplication factors $\mu$ and $\mu^2$ are used, respectively.

Substitution of Eqn 4.27 into Eqn. 4.21a gives for the average yield of the genotypes in mixture

$$\mu_{mix} \approx \mu_{mono} + \tfrac{1}{2} \text{ cov}(\underline{b},\underline{g}_{mono})$$

4.3.1.4 Genetic and environmental variance

In the present study, selection nurseries are simulated by growing varieties rather than unknown genotypes. Only a moderate number of varieties are used and these are replicated several times throughout the nursery. Therefore, the phenotypic variance can be

partioned into two components, one describing the variance between different genotypes and the other the variance between rows of the same genotype. This approach facilitates the separation of the effects of intergenotypic competition into (i) the change in the genetic variation among the entries and (ii) the increase of the environmental variation.

*Variance between genotypes* The expected yield of a fixed genotype i in mixture is given by

$$\underline{O}_i = (\varepsilon \underline{c}_{i,hj})(\mu + \underline{g}_i)$$

Eqn 4.20 defines the expected competition effects on i as

$$\varepsilon \underline{c}_{i,hj} = \varepsilon\left(\frac{b_i(2b_i+\underline{b}_h+\underline{b}_j)}{(b_i+\underline{b}_h)(b_i+\underline{b}_j)}\right)$$

Note that the effects of i are not stochastic but fixed, because genotype i is fixed. The genotypes are allotted to each other at random, therefore $\varepsilon \underline{b}_h = \varepsilon \underline{b}_j = 1$ and we observe, according to Eqn 4.15

$$\varepsilon \underline{c}_{i,hj} \simeq \frac{2b_i}{b_i+\overline{1}}$$

The variance among genotype means is

$$\text{var } \underline{O} = \text{var}\left(\left(\frac{2\underline{b}}{\underline{b}+\overline{1}}\right)(\mu + \underline{g})\right)$$

which can be worked out to

$$\text{var } \underline{O} = 4\,\mu^2 \text{ var}\left(\frac{\underline{b}}{\underline{b}+\overline{1}}\right) + 4 \text{ var}\left(\frac{\underline{b}\,\underline{g}}{\underline{b}+\overline{1}}\right) + 8\,\mu \text{ cov}\left(\frac{\underline{b}}{\underline{b}+\overline{1}}, \frac{\underline{b}\,\underline{g}}{\underline{b}+\overline{1}}\right)$$

After employment of the differential method and subsequent substitution of $\varepsilon \underline{b} = 1$ and $\varepsilon \underline{g} = 0$, we arrive at

$$\text{var } \underline{O} \simeq \text{var } \underline{g} + \mu \text{ cov}(\underline{b},\underline{g}) + \tfrac{1}{4}\,\mu^2 \text{ var } \underline{b}$$

To distinguish the genetic variance in presence of intergenotypic competition from that in absence of intergenotypic competition, we call them var $g_{mix}$ and var $g_{mono}$, respectively. Hence, var $g_{mono}$ is the variance between the genotypes when they are grown in monocultures. The variance among genotype means in mixture becomes

$$\text{var } g_{mix} \simeq \text{var } g_{mono} + \mu \text{ cov}(\underline{b},g_{mono}) + \tfrac{1}{4}\,\mu^2 \text{ var } \underline{b} \qquad (4.29)$$

Evidently, in a line-selection field where each line is sown in a separate row, the above-mentioned genetic variance is the genetic variance between lines.

*Variance within genotypes* Returning to Eqn 4.21, we write for the kth replicate of genotype i

$$\underline{p}_{i,hj_k} = \underline{c}_{i,hj}\ (\mu + \underline{g}_i) + \underline{e}_{i_k}$$

When the variance among plants all belonging to genotype i is considered, the effect of i is fixed. In monoculture of i

$$\underline{p}_{i,ii_k} = c_{i,ii}\ (\mu + g_i) + \underline{e}_{i_k}$$

hence

$$\text{var } \underline{p} = \text{var } \underline{e}$$

In mixture

$$\underline{p}_{i,hj_k} = \underline{c}_{i,hj}\ (\mu + g_i) + \underline{e}_{i_k}$$

Since i is fixed, we find

$$\text{var } \underline{p}_{i,hj_k} = \text{var}(\underline{c}_{i,hj}\ (\mu + g_i) + \underline{e}_{i_k})$$

$$= (\mu + g_i)^2 \text{ var } \underline{c}_{i,hj} + \text{var } \underline{e}_{i_k}$$

For the competitional variance, Eqn 4.25 gives

$$\text{var } \underline{c}_{i,hj} = \text{var } \frac{b_i(2b_i+\underline{b}_h+\underline{b}_j)}{(b_i+\underline{b}_h)(b_i+\underline{b}_j)}$$

Note that since genotype i is fixed, its crowding coefficient $b_i$ is a non-stochastic parameter. The differential method produces

$$\text{var } \underline{c}_{i,hj} = \frac{2b_i^2}{(b_i+1)^4} \text{ var } \underline{b}$$

Hence, it follows that

$$\text{var } \underline{p}_{i,hj_k} = \frac{2(\mu+g_i)^2 b_i^2}{(b_i+1)^4} \text{ var } \underline{b} + \text{var } \underline{e}$$

which is the environmental variance within genotype i in mixed stand. So we can write

$$\text{var } \underline{e}_{i_{mix}} = \frac{2(\mu+g_i)^2 b_i^2}{(b_i+1)^4} \text{ var } \underline{b} + \text{var } \underline{e}_{mono}$$

Since

$$\text{var } \underline{e}_{mix} = \epsilon \text{ var } \underline{e}_{i_{mix}}$$

and $\epsilon g_i = 0$ and $\epsilon \underline{b}_i = 1$, we obtain

$$\text{var } \underline{e}_{mix} = \text{var } \underline{e}_{mono} + \frac{1}{8} \mu^2 \text{ var } \underline{b} \qquad (4.30)$$

As a matter of course, Eqn 4.30 can also be obtained directly as the difference of Eqns 4.28 and 4.29.

*Summarized expressions* We express the phenotypic performance in mixture as

$$P_{mix} = \underline{g}_{mix} + \underline{e}_{mix}$$

and the phenotypic variance in mixture as

$$\text{var } P_{mix} = \text{var } \underline{g}_{mix} + \text{var } \underline{e}_{mix}$$

Writing the Eqns 4.29 and 4.30

$$\text{var } \underline{g}_{mix} = \text{var } \underline{g}_{mono} + \mu \text{ cov}(\underline{b}, \underline{g}_{mono}) + \tfrac{1}{4} \mu^2 \text{ var } \underline{b} \qquad (4.29)$$

$$\text{var } \underline{e}_{mix} = \text{var } \underline{e}_{mono} + \frac{1}{8} \mu^2 \text{ var } \underline{b} \qquad (4.30)$$

Hence, we have

$$\text{var } P_{mix} = \text{var } \underline{g}_{mono} + \mu \text{ cov}(\underline{b}, \underline{g}_{mono}) + \frac{3}{8} \mu^2 \text{ var } \underline{b} + \text{var } \underline{e}_{mono} \qquad (4.31)$$

It is evident that this latter Eqn is essentially the same as Eqn 4.28.

## 4.4 RESPONSE TO SELECTION

### *4.4.1 Central question*

The ultimate interest of breeders is the response to selection. Consequently, the ideal model describing the implications of competition for selection should express the bias due to competition in terms of change in the response to selection.

In genetics, the term 'response' is used for the progress in generation t+1 made by selection in generation t. Hence, the central question is: to what extent are the genotypes with the highest yield in generation t+1 chosen when selection is for the phenotypes with the highest yield in generation t.

Selection is done, necessarily, in a heterogeneous population. Hence, selection for yield of individual plants or individual rows of plants occurs in a mixture. However,

as the farmer grows his varieties in monoculture, the breeder aims at selecting the genotypes with the highest yield in monoculture. Therefore, we must reformulate the central question: to what extent are the genotypes with the highest yield in monoculture in generation t+1 chosen when selection is for the phenotypes with the highest yield in a mixture in generation t.

As will be shown in Section 4.4.3 by Fig. 12, we may divide the central question into three:

(1) To what extent are the highest-yielding phenotypes in the mixture in generation t also the highest-yielding genotypes in that mixture in that generation?

(2) To what extent do the genotypes selected in the mixture in generation t produce a superior yield if they were grown in monoculture in that generation?

(3) To what extent do the genotypes selected in generation t maintain their expected monoculture yield in generation t+1?

The first question refers to the degree that the genotypes that are able to yield high in the particular mixture are identified. The expected yield of the selected genotypes differ from the expected yield of the unselected genotypes. This difference, I call the direct response to selection, written as $R_{mix}$ or $R_{mix,t}$.

The second question defines the influence of intergenotypic competition on the outcome of selection. The genotypic yield in mixture and the genotypic yield in monoculture are correlated. Therefore, selection in mixture brings about a correlated response for monoculture yield, written as $CR_{mono}$ or $CR_{mono,t}$.

The first and second questions deal with yield testing. In combination, they form the question: to what extent are the genotypes with the highest yield in monoculture identified by selection for the phenotypes that yield the most in mixture? It does not matter whether the selected genotypes maintain their expected yield in the next generation. Hence, it does not matter whether the genotypes are heterozygous or homozygous and whether they are self-fertilizers or cross-fertilizers.

It is the third question that concerns the effect of heterozygosity and mode of reproduction. The genotypic yield in monoculture in generation t and the genotypic yield in monoculture in generation t+1 are correlated. Therefore, selection in generation t results in a correlated response for monoculture yield in generation t+1, written as $CR_{mono,t+1}$.

As was stated in the foregoing, in genetics the term 'reponse' is used for the progress in the next generation. However, I call this progress the correlated response in generation t+1, written as $CR_{mono,t+1}$. The attention of the reader is drawn to this unusual use of the term response in this paper.

*Summary* The progress that is made by selection is divided into three parts. Each part is considered separately. The advantage of this approach is that the influence of competition on the outcome of selection is defined independent of the effects of heterozygosity and mode of reproduction. The present paper is restricted to yield testing, that is to the first and second part of the total progress.

Let us consider the distribution given in Fig. 9 for the yields of individual phenotypes in the mixed population. The population mean is represented by $\bar{p}$. We select the phenotypes in the shaded area. Their yields average $\bar{p}_s$. The difference between the mean yield of the selected phenotypes and the population mean is called the selection differential

$$S_{mix} = \bar{p}_s - \bar{p}$$

The selected phenotypes constitute together a new population. The distribution of the phenotypic values of the selected phenotypes is given by the truncated (shaded) curve of Fig. 9. The distribution of their genotypic values, in the mixture where they are grown, is given in the lower part of Fig. 9. The average genotypic value of the selected plants in the mixture is denoted by $\bar{o}_s$.

The change in the average genotypic performance, brought about by selection, is termed the response to selection

$$R_{mix} = \bar{o}_s - \bar{o}$$

It is emphasized that, throughout this paper, I apply the term 'response' for the change in average genotypic performance within the generation of selection. The study is restricted to changes in the composition of the genotypes within the generation of selection. Hence, it does not matter that the genotypes are not true to seed, i.e. that they are not constant over generations because of heterozygosity and cross-fertilization (Section 4.4.1).

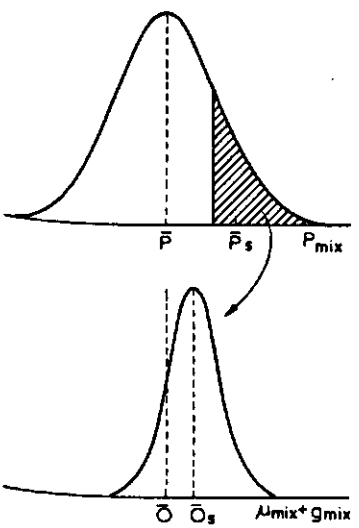


Fig. 9. Distribution for phenotype of a mixed population before selection (top) and for genotype after selection in the mixture (bottom). Symbols are explained in Section 4.4.2.

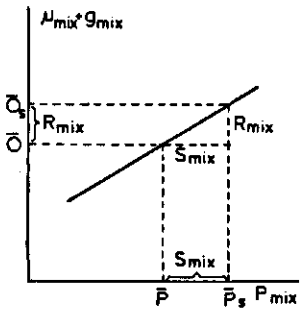


Fig. 10. Regression of genotype on phenotype in mixture, showing the selection differential $S_{mix}$ and the response to selection $R_{mix}$.

Suppose that the regression of the genotypic value on the phenotypic value is a linear function (Fig. 10, Section 9.1.3). The slope of the regression line is

$$b_{R.S} = \frac{R_{mix}}{S_{mix}}$$

Consequently, the response to selection

$$R_{mix} = b_{R.S}\, S_{mix}$$

Note that in this equation, b denotes the regression coefficient instead of the crowding coefficient.

Substitution of the statistical definition for the regression coefficient provides

$$R_{mix} = \frac{\mathrm{cov}(g_{mix}, p_{mix})}{\mathrm{var}\, p_{mix}} S_{mix}$$

After substitution of Eqn 4.16 for the phenotypic performance, the expression can be simplified to

$$R_{mix} = \frac{\mathrm{var}\, g_{mix}}{\mathrm{var}\, p_{mix}} S_{mix}$$

The portion of the phenotypic variation that is attributed to genetic differences is termed the 'heritability'. In formula

$$h^2 = \frac{\mathrm{var}\, \underline{g}}{\mathrm{var}\, \underline{p}} = \frac{\mathrm{var}\, \underline{g}}{\mathrm{var}\, \underline{g} + \mathrm{var}\, \underline{e}}$$

Hence,

$$R_{mix} = h^2_{mix}\, S_{mix}$$

Division of the selection differential S by the phenotypic standard deviation, transforms S to a dimensionless parameter termed the 'intensity of selection' i. Falconer (1960, p. 194) showed that under a normal distribution of the measurements, i

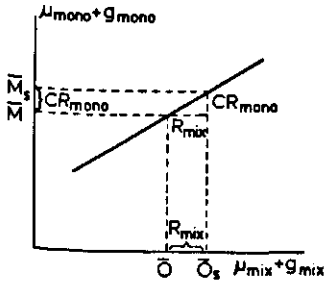


Fig. 11. Regression of genotype in monoculture on genotype in mixture showing the relation between the response to selection for mixture yield ($R_{mix}$) and the correlated response for monoculture yield ($CR_{mono}$).

is a simple function of the percentage selected. Now we have for the response to selection

$$R = h^2 S = \frac{\text{var } \underline{g}}{\text{var } \underline{p}} \; S = i \, \frac{\text{var } \underline{g}}{\sqrt{\text{var } \underline{p}}} \tag{4.32}$$

or

$$R = i \, h^2 \sqrt{\text{var } \underline{p}} = i \, h \sqrt{\text{var } \underline{g}} \tag{4.33}$$

Our aim is to select for monoculture yield by means of selection for yield in a mixture. Mixture yield is the auxiliary trait in the indirect selection for the target trait monoculture yield. When we select for mixture yield, a response $R_{mix}$ is the result. When mixture yield and monoculture yield are correlated, a correlated response for monoculture yield, $CR_{mono}$, will be the result of selection for yield in mixture. Assuming a linear relation between mixture yield and monoculture yield (Fig. 11), we have

$$CR_{mono} = b_{mono.mix} \, R_{mix} \tag{4.34}$$

The statistical definition of the coefficient of linear regression supplies

$$CR_{mono} = \frac{\text{cov}(g_{mix}, g_{mono})}{\text{var } g_{mix}} \, R_{mix} \tag{4.35}$$

Substitution of $R_{mix}/\text{var } g_{mix}$ by $i_{mix}/\sqrt{\text{var } p_{mix}}$ (Eqn 4.32) gives

$$CR_{mono} = i_{mix} \, \frac{\text{cov}(g_{mix}, g_{mono})}{\sqrt{\text{var } p_{mix}}} = i_{mix} \, r_g \, h_{mix} \sqrt{\text{var } g_{mono}} \tag{4.36}$$

where $r_g$ the coefficient of the genetic correlation between yield in mixture $\underline{O}$ and yield in monoculture $\underline{M}$, that is

$$r_g = \frac{\text{cov}(g_{mix}, g_{mono})}{\sqrt{\text{var } g_{mix} \; \text{var } g_{mono}}} \tag{4.37}$$

Without intergenotypic competition, that is if each genotype were grown in monoculture, the response to selection is given by Eqn 4.33 as

$$R_{mono} = i_{mono}\, h_{mono} \sqrt{\text{var } g_{mono}} \tag{4.38}$$

Now the bias due to intergenotypic competition is defined as the ratio of the correlated response of pure-culture yield, when selected on mixed-culture yield, to the response in a hypothetic mixture without intergenotypic competition. Consequently,

$$\text{degree of competitional bias} = \frac{CR_{mono}}{R_{mono}} \tag{4.39}$$

Division of Eqn 4.36 by Eqn 4.38 gives

$$\frac{CR_{mono}}{R_{mono}} = \frac{i_{mix}}{i_{mono}}\, r_g\, \frac{h_{mix}}{h_{mono}} \tag{4.40}$$

with the square root of the ratio of the heritabilities

$$\frac{h_{mix}}{h_{mono}} = \sqrt{\frac{\text{var } g_{mix}}{\text{var } p_{mix}} \cdot \frac{\text{var } p_{mono}}{\text{var } g_{mono}}} \tag{4.41}$$

$CR_{mono}/R_{mono}$ measures to what extent the outcome of selection is affected by intergenotypic competition. On the other hand, $CR_{mono}/R_{mix}$ measures to what extent the conventional genetic estimation of the response to selection is biased by intergenotypic competition (Section 8.2.2).

*Summary* The effect of intergenotypic competition on the outcome of selection is quantified. For that, yield in monoculture is considered to be the character which has to be improved, while selection is done for yield in mixture. Selection for yield in mixture brings about a correlated response for yield in monoculture. An expression for the correlated response is derived. The degree of competitional bias is defined as the ratio of this correlated response to the direct response in a mixture without intergenotypic competition.

### *4.4.3 Position of the competition model within the genetic theory*

All equations given in Section 4.4.2 hold irrespective of whether the genotypes are heterozygous or homozygous and irrespective of whether a self-fertilizing or a cross-fertilizing species is involved. This is of fundamental importance for the position of the competition model within the genetic theory. Hence, it will be explained in detail.

We may combine Fig. 10 for the direct response to selection and Fig. 11 for the correlated response to selection into one figure (Fig. 12). At the same time, allowance may be made for the drop in response from the generation of selection, generation t, to the next generation, generation t+1. This is done by plotting in the third quadrant, the relation between monoculture yield in generation t and monoculture yield in genera-

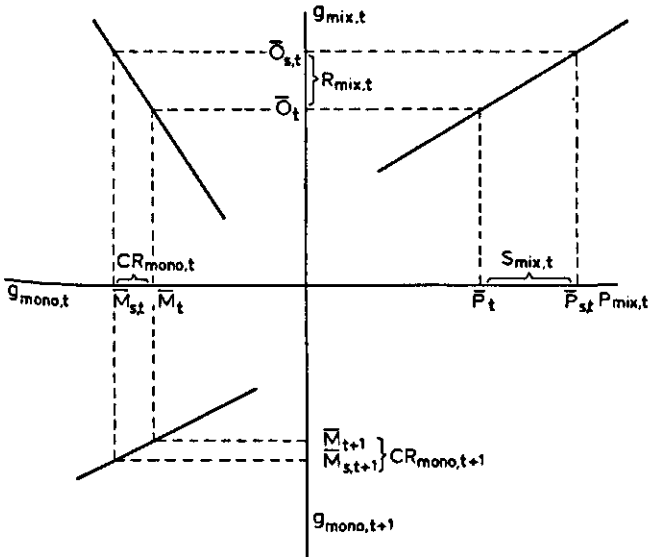


Fig. 12. Regression of genotype in generation t+1 on genotype in generation t, in relation to Figs 10 and 11.

tion t+1. Suppose that this relation is linear, as will be discussed later on. The response for yield in monoculture in generation t+1, brought about by selection for yield in mixture in generation t, is then

$$CR_{mono,t+1} = b_{mono,t+1} \,.\, _{mono,t}\, CR_{mono,t}$$

The selection response for monoculture yield declines from generation t to generation t+1 because the selected genotypes are, in general, heterozygous and, therefore, not true to seed. The drop depends on the degree of heterozygosity, the generation of selection, the method of selection, and the mode of reproduction of the species. In quantitative genetics, there is an extensive theory on the expression for the regression coefficient of $g_{mono,t+1}$ on $g_{mono,t}$ as a function of the above-mentioned factors. When single plants are selected from the $F_\infty$ of a self-fertilizing crop, the regression coefficient equals one because all plants are homozygous and thus true to seed.

In the conventional genetic models, some effects of intergenotypic competition are assumed to be absent and others are even neglected. In more detail:

(1) In the conventional genetic models, it is assumed that the genotypes do not differ in their reproductive rate with respect to the studied character. Otherwise, the gene fequencies would change in successive generations. For yield, the assumption is not valid. The genotypes differ in competitive ability and they differ in monoculture yield. This leads to differences in reproductive rate between the genotypes (Eqn 4.8).

(2) Conventional genetic models neglect that the yield of a genotype in a population is expected to differ from the yield of the same genotype in another population because

of intergenotypic competition. For, the expected yield $O_i$ of a genotype i depends on the genotypic composition of the population (Eqns 4.13 and 4.14).

Intergenotypic competition will, therefore, seriously bias the conventional genetic analyses of yield. In the genetic analyses, the components of the phenotypic variance are estimated from the variation observed in different types of populations. For example, from the variation between $F_2$ plants, from that between plants within $F_3$ lines and from that between the means of $F_3$ lines. However, the genotypic composition of the $F_2$ and $F_3$ will be different due to natural and artificial selection and, in self-fertilizing species, due to the growth to homozygosity. Moreover, the genotypes within a line are more alike than the genotypes of the entire population and so the effects of intergenotypic competition are smaller within a line. Furthermore, competition between lines, sown in microplots, is less severe than competition between individual plants. Hence, the competitive relations are different in each of the populations. Therefore, the yield $O_i$ of a fixed genotype i is different when grown as plant in an $F_2$-population, when grown as plant within an $F_3$ line, and when grown as an $F_3$ line. Furthermore, these yields of genotype i differ from its yield in monoculture and, in self-fertilizing species, the monoculture is the ultimate aim of selection.

In conclusion, the conventional interpretation of the genetic components of yield in different types of populations is wrong because no account is made of intergenotypic competition. Therefore, the estimates of the components of the variance for yield are wrong. Based on the present competition model, genetic analyses may be developed that account for intergenotypic competition.

Now, the assumptions underlying Fig. 12 will be discussed. The assumptions are:

(1) The relations in the first, second and third quadrant are linear. This generally implies that the quantities, which are plotted on the axes, each show a normal frequency distribution (Section 9.1).

(2) The relations are mutually independent. Only then is it allowed to expand the correlated response for monoculture yield in generation t by

$$CR_{mono,t} = b_{g_{mono,t} \cdot P_{mix,t}} S_{mix,t} = b_{g_{mix,t} \cdot P_{mix,t}} b_{g_{mono,t} \cdot g_{mix,t}} S_{mix,t}$$

and the correlated response for monoculture yield in generation t+1 by

$$CR_{mono,t+1} = b_{g_{mono,t+1} \cdot P_{mix,t}} S_{mix,t} = b_{g_{mix,t} \cdot P_{mix,t}} b_{g_{mono,t} \cdot g_{mix,t}}$$

$$b_{g_{mono,t+1} \cdot g_{mono,t}} S_{mix,t}$$

It can be worked out that the assumption of mutual independency implies that the partial correlation coefficients of the quantities, that are plotted on the axes, equal zero. This will be specified under 2a and 2b.

(2a) For the relations in the first and second quadrant, the partial correlation coefficient is

$$r_{g_{mono,t}\, p_{mix,t} \cdot g_{mix,t}} = 0$$

That is, for a fixed value of $g_{mix,t}$, $g_{mono,t}$ and $p_{mix,t}$ are uncorrelated. When we change from the genetic to the competitional notation we may write, for a fixed value of the genotypic mixture yield $O_t$

$$\mathrm{cov}(\underline{M}_t, (O_t + \underline{e})) = 0$$

or

$$\mathrm{cov}(\underline{M}_t, \underline{e}) = 0$$

When the genotypes are distributed at random across the field, the assumption is valid.

(2b) For the relations in the first to the third quadrant, the partial correlation coefficient is

$$r_{g_{mono,t+1}\, p_{mix,t} \cdot g_{mono,t}} = 0$$

That is, for a fixed value of the monoculture yield in generation t, the monoculture yield in generation t+1 and the mixture yield in generation t are uncorrelated. It follows that for a fixed value of the genotypic monoculture yield $M_t$

$$\mathrm{cov}(\underline{M}_{t+1}, (\underline{c}_t M_t + \underline{e}_t)) = 0$$

or

$$\mathrm{cov}(\underline{M}_{t+1}, (\underline{c}_t M_t)) = 0$$

where $\underline{c}$ the competition coefficient (Eqn 4.20). For the change in monoculture yield from generation t to generation t+1, we may introduce the empirical relation

$$\underline{M}_{t+1} = \underline{d}\, \underline{M}_t$$

Now we may write, for a fixed $M_t$,

$$\mathrm{cov}(\underline{d}\, M_t), (\underline{c}_t\, M_t)) = 0$$

or

$$\mathrm{cov}(\underline{d}, \underline{c}_t) = 0$$

Hence, for a fixed value of $M_t$, $\underline{c}$ and $\underline{d}$ are uncorrelated. The monoculture yield of the genotypes in generation t differ from that of their progenies in generation t+1 because the genotypes are not true to seed. In self-fertilizing species, this is due to hetero-

zygosity. Then, the change in yield, and with that $\underline{d}$, is proportional to the degree of heterozygosity. So, the above-mentioned partial correlation coefficient is zero when $\underline{c}$ and $\underline{d}$ are uncorrelated within a group of genotypes having the same monoculture yield. That is, within such a group, there is no correlation between the competitive ability and the degree of heterozygosity of a genotype. Note that this is fundamentally different from: there is no correlation at all between competitive ability and monoculture yield. Uncorrelatedness of $\underline{c}$ and $\underline{d}$ at a fixed value of $M_t$ will be a reasonable assumption. The uncorrelatedness is required to connect, without restrictions, the genetic theory on the regression of $g_{mono,t+1}$ and $g_{mono,t}$ to the competition model.

*4.4.4 Progeny testing in single rows (nearest-neighbour competition)*

In a line-selection programme in small grains, the progenies of the selected plants are usually sown in rows, each progeny in a single row. Let selection of the progenies be for yield. As the rows compete with each other, the yield of the progenies in the line-selection field measures their yield in a mixed stand. Selection for yield in the mixed stand gives a correlated response for monoculture yield. The basic equations for the correlated response and the competitional bias have already been in Section 4.4.2. In the present section, the equations are elaborated for progeny testing in single rows, that is yield testing in a situation where competition is restricted to adjacent neighbour rows.

The phenotypic yield of a row with a random genotype i, situated between a row with the random genotype h and a row with the random genotype j, can be derived from Eqns 4.20 and 4.21 as

$$P_{i,hj} = \frac{\underline{b}_i(2\underline{b}_i+\underline{b}_h+\underline{b}_j)}{(\underline{b}_i+\underline{b}_h)(\underline{b}_i+\underline{b}_j)}(\mu + g_i) + \underline{e}_i \qquad (4.42)$$

The phenotypic, genetic and environmental variance in mixture were already expressed in Eqns 4.31, 4.29 and 4.30, respectively. Now we need the expression for the covariance between the genotypic yield of a random genotype i in mixture, $\underline{O}_i$, and the genotypic yield of that genotype in monoculture, $\underline{M}_i$. For the random genotype i, we have for its genotypic yield (i.e. the expected yield) in monoculture

$$\underline{M}_i = \mu + g_i$$

and for its genotypic yield in mixture (Eqn 4.15)

$$\underline{O}_i = \frac{2\underline{b}_i}{\underline{b}_i+1}(\mu + g_i)$$

The genetic covariance can be written as

$$\mathrm{cov}(\underline{O}_i,\underline{M}_i) = \mathrm{cov}(g_{mix},g_{mono}) = \mathrm{cov}\left(\frac{2\underline{b}_i}{\underline{b}_i+1}(\mu + g_i),(\mu + g_i)\right)$$

With omission of the subscripts and repeated use of the differential method

$$\mathrm{cov}(g_{mix}, g_{mono}) = \mathrm{var}\, g_{mono} + \tfrac{1}{2}\mu\, \mathrm{cov}(\underline{b}, g_{mono}) \qquad (4.43)$$

Substitution of Eqn 4.31 for the phenotypic variance in mixture and Eqn 4.43 for the genetic covariance into Eqn 4.36, gives for the correlated response for monoculture yield, after selection on mixture yield,

$$CR_{mono} = i_{mix} \frac{\mathrm{var}\, g_{mono} + \tfrac{1}{2}\mu\, \mathrm{cov}(\underline{b}, g_{mono})}{\sqrt{\mathrm{var}\, g_{mono} + \mu\, \mathrm{cov}(\underline{b}, g_{mono}) + \tfrac{3}{8}\mu^2\, \mathrm{var}\, \underline{b} + \mathrm{var}\, e_{mono}}} \qquad (4.44)$$

The degree of competitional bias was defined by the ratio of the correlated response of monoculture yield, when selected on yield in mixture, to the response in a hypothetic mixture where competition is absent (Eqn 4.39). The expression for the competitional bias is found by division of Eqn 4.44 by Eqn 4.38. From the resulting expression the bias originating from selection in presence of competition can be estimated for a nursery of which the variables $\mu$, var $g_{mono}$, var $e_{mono}$, var $\underline{b}$ and cov($\underline{b}$, $g_{mono}$) have already been estimated.

The expression for CR/R is not easy to interpret. To gain a better view and to give general opinions, an expression in terms, of dimensionless variables is preferable. Moreover, dimensionless quantities enable an easier comparison of experiments with divergent fertility levels and traits with different dimensions. In breeding, the heritability $h^2$ is a widely used dimensionless quantity. Here we use the heritability in monoculture $h^2_{mono}$, abbreviated by $h^2$. For competition studies, it is useful to introduce the coefficient $r_{bg}$ for the correlation between $\underline{b}$ and $\underline{g}$, which is by definition

$$r_{bg} = \mathrm{cov}(\underline{b}, \underline{g}) \,/\, \sqrt{\mathrm{var}\, \underline{b}\ \mathrm{var}\, \underline{g}} \qquad (4.45)$$

and the 'competitive stress', which is defined as

$$\gamma = \mu^2\, \mathrm{var}\, \underline{b} \,/\, \mathrm{var}\, \underline{g} \qquad (4.46)$$

Hence, the competitive stress $\gamma$ measures the competition effects relative to the genetic variance in monoculture. Since $\underline{b}$ is a relative quantity, the multiplication factor $\mu^2$ brings the numerator on the scale of the denominator. The parameter $\gamma$ is also useful to compare different traits with respect to their sensitivity to competition.

The competitional bias CR/R, that is the ratio of Eqns 4.44 and 4.38, can be worked out to

$$\frac{CR}{R} = \frac{i_{mix}}{i_{mono}} \frac{1 + \tfrac{1}{2} r_{bg} \sqrt{\gamma}}{\sqrt{1 + r_{bg} h^2 \sqrt{\gamma} + \tfrac{3}{8} h^2 \gamma}} \qquad (4.47)$$

For its constituents (Eqn 4.40), the coefficient of the genetic correlation between $\underline{O}$ and $\underline{M}$ (Eqn 4.37) and the square root of the ratio of the heritability in mixture

and that in monoculture (Eqn 4.41), we find respectively,

$$r_g \simeq \frac{1 + \frac{1}{2} r_{bg} \sqrt{\gamma}}{\sqrt{1 + r_{bg} \sqrt{\gamma} + \frac{1}{4}\gamma}} \tag{4.48}$$

and

$$\frac{h_{mix}}{h_{mono}} \simeq \sqrt{\frac{1 + r_{bg} \sqrt{\gamma} + \frac{1}{4}\gamma}{1 + r_{bg} h^2 \sqrt{\gamma} + \frac{3}{8} h^2 \gamma}} \tag{4.49}$$

*4.4.5 Single-plant selection (diffuse competition)*

From a segregating population, single plants are selected. Suppose that selection is for yield. A segregating population is a mixture of many genotypes. Therefore, the yield of a plant in the population is the yield of the plant in a mixture. However, the breeder aims at selecting plants that yield high in monoculture. Selection for yield in the mixture brings about a correlated response for monoculture yield. The correlated response is different from the response if selection were applied in a hypothetic population without intergenotypic competition. The bias due to competition was defined in Eqn 4.39 as the ratio of both responses.

In Section 4.4.4 expressions were derived for the correlated response and the competitional bias when single rows are the unit of selection. However, the equations do not hold when single plants are selected, because the yield of a single plant in mixture is described by an equation that differs from that for the yield of a row in a mixture of rows (Eqn 4.14 and 4.13, respectively). In small grains, these equations are different because the influence of a row is restricted to its first neighbour rows (nearest-neighbour competition), whereas an individual plant strongly affects its neighbour plants of higher order too (diffuse competition) (Section 4.2.2). Now, the expression for the components of variance, the selection response and the competitional bias are given for single plants as unit of selection. The equations can easily be derived in analogy to those for rows (Sections 4.3 and 4.4.4) and are, therefore, only summarized.

The expected yield of genotype i in a multicomponent mixture is given by Eqn 4.14 as

$$O_i = b_i M_i \tag{4.14}$$

Rewritten in terms of the stochastic genetic model, the phenotypic yield of a plant of a random genotype i is

$$\underline{p}_i = \underline{b}_i (\mu + \underline{g}_i) + \underline{e}_i \tag{4.50}$$

where $\mu$, $\underline{g}$ and $\underline{e}$ refer to monocultures. The population mean in mixture is found from Eqn 4.21a as

$$\mu_{mix} = \mu_{mono} + \text{cov}(\underline{b}, \underline{g}_{mono})$$

For the phenotypic variance in mixture we can derive, similar to the derivation of Eqn 4.28,

$$\text{var } \underline{P}_{mix} = \text{var } \underline{g}_{mono} + 2\mu \text{ cov}(\underline{b}, \underline{g}_{mono}) + \mu^2 \text{ var } \underline{b} + \text{var } \underline{e}_{mono} \quad (4.51)$$

In analogy with Section 4.3.1.3, the phenotypic variance in mixture is split into the genetic variance in mixture

$$\text{var } \underline{g}_{mix} = \text{var } \underline{g}_{mono} + 2\mu \text{ cov}(\underline{b}, \underline{g}_{mono}) + \mu^2 \text{ var } \underline{b} \quad (4.52)$$

and the environmental variance in mixture

$$\text{var } \underline{e}_{mix} = \text{var } \underline{e}_{mono} \quad (4.53)$$

The covariance between the genotypic yield in mixture and the genotypic yield in monoculture is obtained in a way similar to Eqn 4.43 as

$$\text{cov}(\underline{g}_{mix}, \underline{g}_{mono}) = \text{var } \underline{g}_{mono} + \mu \text{ cov}(\underline{b}, \underline{g}_{mono}) \quad (4.54)$$

Substitution of Eqns 4.51 and 4.54 into Eqn 4.36 gives for the correlated response for monoculture yield, after selection on mixture yield,

$$CR_{mono} = i_{mix} \frac{\text{var } \underline{g}_{mono} + \mu \text{ cov}(\underline{b}\ \underline{g}_{mono})}{\sqrt{\text{var } \underline{g}_{mono} + 2\mu \text{ cov}(\underline{b}, \underline{g}_{mono}) + \mu^2 \text{ var } \underline{b} + \text{var } \underline{e}_{mono}}} \quad (4.55)$$

The bias from intergenotypic competition was defined by the ratio of the correlated response of monoculture yield, when selection is for yield in mixture, to the response in a hypothetic mixture where intergenotypic competition is absent (Eqn 4.39). Hence, the degree of competitional bias is found by division of Eqn 4.55 for the correlated response by Eqn 4.38 for the direct response to selection.

In Section 4.4.4, it was pointed out that an expression of the competitional bias as a function of dimensionless parameters may be preferred. As dimensionless parameters were introduced: the heritability in monoculture $h^2$, the coefficient $r_{bg}$ of the correlation between $\underline{b}$ and $\underline{g}$ and the competitive stress $\gamma = \mu^2 \text{ var } \underline{b}/\text{var } \underline{g}$. It can be seen that

$$\frac{\text{var}(\underline{M}_i - \underline{O}_i)}{\text{var } \underline{M}_i} = \frac{\text{var}((\mu + \underline{g}_i) - \underline{b}_i\ (\mu + \underline{g}_i))}{\text{var } (\mu + \underline{g}_i)} \approx \frac{\mu^2 \text{ var } \underline{b}}{\text{var } \underline{g}} = \gamma$$

This only holds for diffuse competition because only then does $\underline{O}_i = \underline{b}_i\ (\mu + \underline{g}_i)$, which can be seen from Eqn 4.14.

It can be derived, that the degree of competitional bias

$$\frac{CR}{R} = \frac{i_{mix}}{i_{mono}} \frac{1 + r_{bg}\sqrt{\gamma}}{\sqrt{1 + 2r_{bg}h^2\sqrt{\gamma} + h^2\gamma}} \quad (4.56)$$

For its constituents (Eqn 4.40), the coefficient of the genetic correlation between $\underline{O}$ and $\underline{M}$ (Eqn 4.37) and the square root of the ratio of the heritability in mixture and that in monoculture (Eqn 4.41), we find respectively,

$$r_g \approx \frac{1 + r_{bg}\sqrt{\gamma}}{\sqrt{1 + 2r_{bg}\sqrt{\gamma} + \gamma}} \tag{4.57}$$

and

$$\frac{h_{mix}}{h_{mono}} \approx \sqrt{\frac{1 + 2r_{bg}\sqrt{\gamma} + \gamma}{1 + 2r_{bg}h^2\sqrt{\gamma} + h^2\gamma}} \tag{4.58}$$

## 4.5 INTERPRETATION OF THE MODEL

How can we interpret the measure CR/R for the bias that arises from competition? When we suppose that without competition a positive response to selection $R_{mono}$ is obtained, a positive ratio $CR_{mono}/R_{mono}$ indicates that selection in a mixed population results in progress for yield. When the ratio is smaller than unity, that is $CR_{mono} < R_{mono}$, the gain from selection is less than it would be if competition had not masked the genetic performances. When the ratio exceeds unity, that is $CR_{mono} > R_{mono}$, competition is even advantageous to selection because it magnifies the differences between the entries to such an extent that it more than counterbalances a decline due to the correlated response. On the other hand, when the ratio is negative, that is $CR_{mono} < 0$, the effect of competition is of such a size that the end result of selection is negative. Then, preferentially genotypes are selected with a strong competitive ability but with a lower than average monoculture yield.

The ratio CR/R only measures the degree of competitional bias. The actual progress due to selection is predicted by the correlated response CR itself.

To gain a better view on the competitional bias CR/R, this has to be broken down in simpler components. A first step is the partitioning into the coefficient $r_g$ of the correlation between the expected yield in mixture and that in monoculture and the square root of the ratio of the heritability in mixture and that in monoculture $h_{mix}/h_{mono}$ (Eqn 4.40, Fig. 13). For convenience, here and in what follows, the intensity of selec-

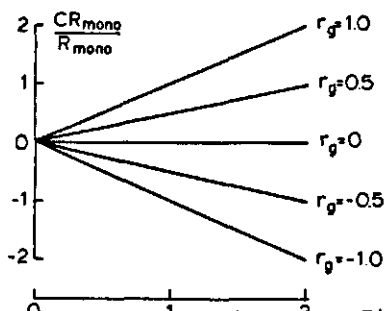


Fig. 13. Graphical presentation of $CR_{mono}/R_{mono} = r_g\, h_{mix}/h_{mono}$.

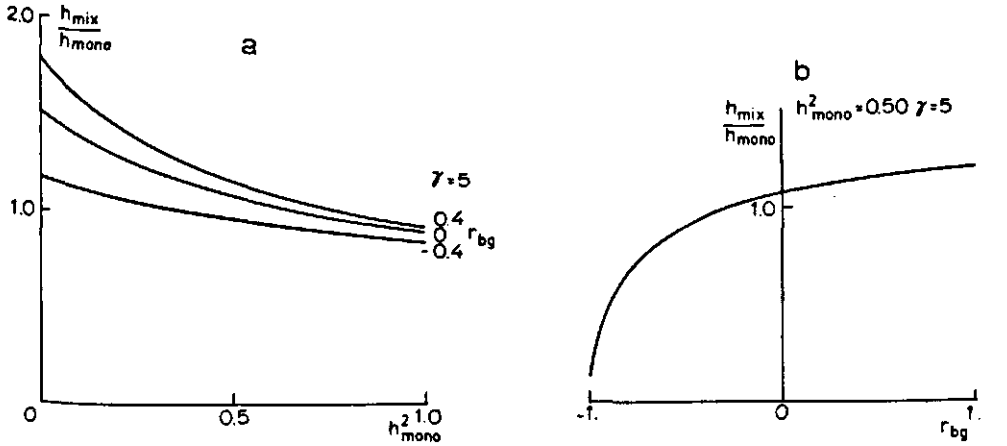


Fig. 14. The square root of the ratio between the heritability in mixture and that in monoculture $h_{mix}/h_{mono}$ as a function of the heritability in monoculture $h^2_{mono}$, the competitive stress $\gamma$, and the genetic correlation $r_{bg}$ of competitive ability and monoculture yield. Competition is assumed to be between rows.

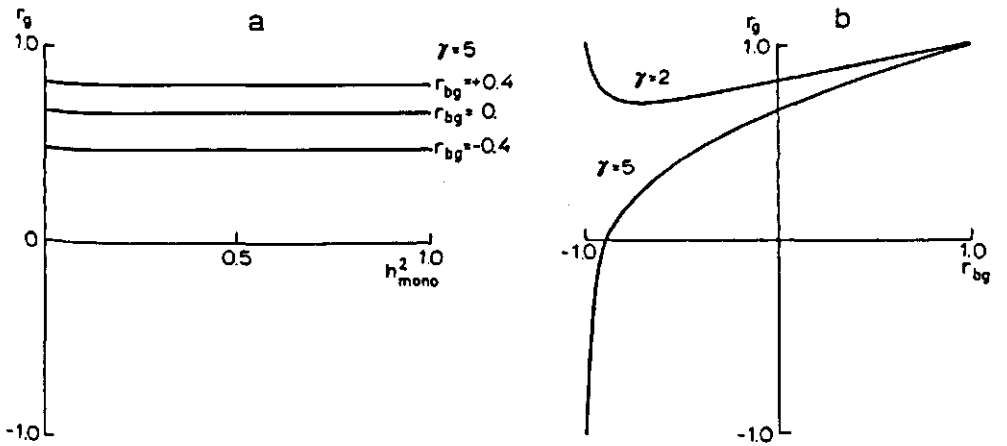


Fig. 15. The genetic correlation $r_g$ of yield in mixture and monoculture as a function of the heritability in monoculture $h^2_{mono}$, the competitive stress $\gamma$, and genetic correlation $r_{bg}$ of competitive ability and monoculture yield. Competition is assumed to be between rows.

tion in mixed and pure culture is supposed to be the same.

As a second step, both variables, $r_g$ and $h_{mix}/h_{mono}$, can be split into some components. This is done in Section 4.4.4 for progeny testing in single rows and in Section 4.4.5 for selection of individual plants. For these two situations, two different models were necessary since the competition effect of a row is restricted to its first neighbour rows (nearest-neighbour competition) whereas a single plant strongly affects neighbours of higher order also (diffuse competition) (Section 4.2.2). For both situations, some general rules can be derived. Most of them are easy to understand, while others can be derived by differentiating the appropriate equations. The trends for progeny testing are

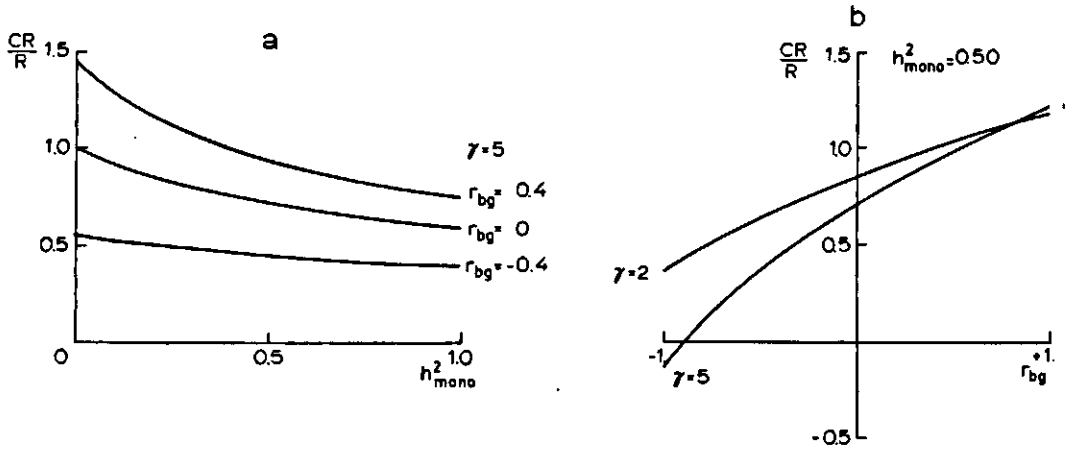


Fig. 16. The ratio of the correlated response in monoculture when selected in mixture and the direct response to selection in monoculture CR/R as a function of the genetic correlation $r_g$ of competitive ability and monoculture yield. The selection intensity in mixture is supposed to be equal to that in monoculture. Competition is assumed to be between rows.

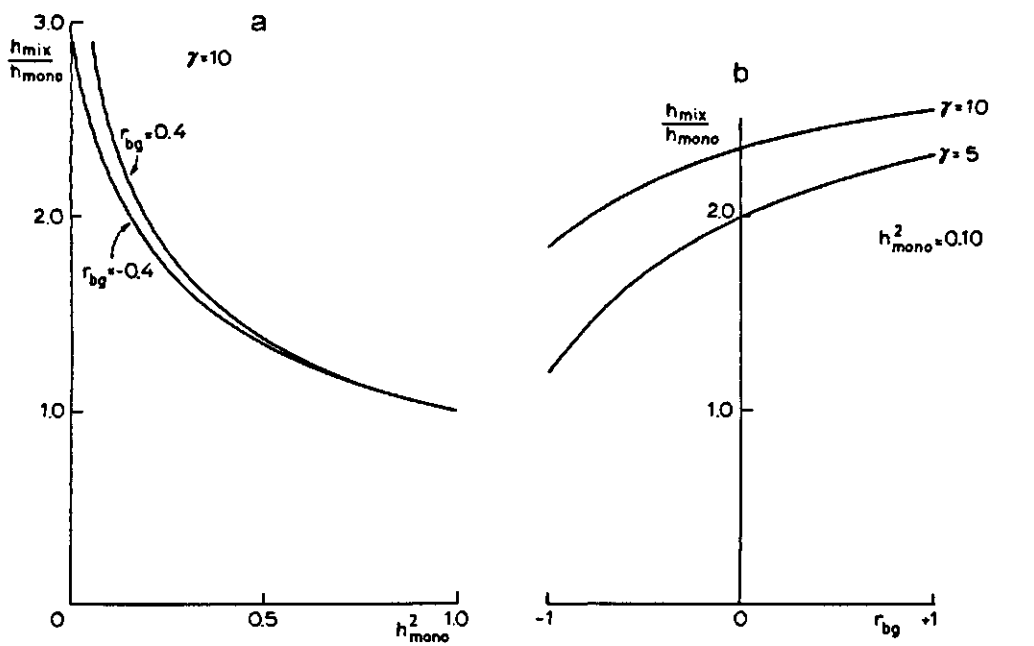


Fig. 17. Similar to Fig. 14, but competition is assumed to be between single plants.

illustrated in Figs 14 to 16, and that for plant selection in Figs 17 to 19.

The ratio of the heritability in mixed and pure stands increases as $h^2_{mono}$ decreases, as $r_{bg}$ increases and, in general, as $\gamma$ increases (Eqns 4.49 and 4.58; Figs 14 and 17). The coefficient $r_g$ of the genetic correlation between the yield in mixture and that in monoculture, does not depend on $h^2_{mono}$, but, in general, increases the higher $r_{bg}$ is and the lower $\gamma$ (Eqns 4.48 and 4.57; Figs 15 and 18). The ratio CR/R of the correlated re-

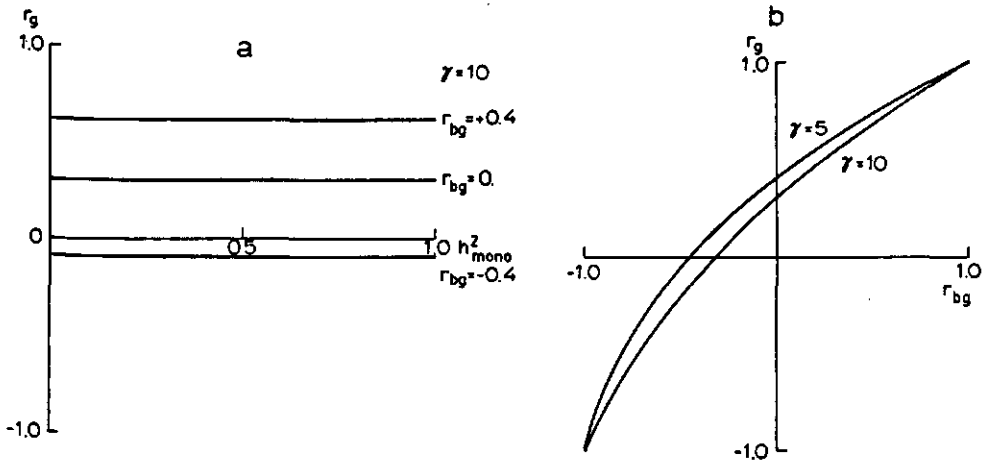


Fig. 18. Similar to Fig. 15, but competition is assumed to be between single plants.

sponse CR in monoculture yield, brought about by selection in mixed stand, and the response R to hypothetic selection in absence of intergenotypic competition is the product of $r_g$ and $h_{mix}/h_{mono}$ (Eqn 4.40). Hence, the effect of $h^2_{mono}$, $r_{bg}$ and $\gamma$ on CR/R can be summarized from the former relations as

| | $h^2_{mono}$ | $r_{bg}$ | $\gamma$ |
|---|---|---|---|
| $h_{mix}/h_{mono}$ | - | + | + |
| $r_g$ | . | + | - |
| CR/R | - | + | $\pm$ |

In conclusion, CR/R increases the higher the coefficient $r_{bg}$ of the genetic correlation between competitive ability and monoculture yield, and its absolute value increases the lower the heritability in absence of intergenotypic competition $h^2_{mono}$ (Eqns 4.47 and 4.56; Figs 16 and 18). The competitive stress $\gamma$ has a variable influence due to its opposite effects on the heritability ratio and the genetic correlation (Figs 16b and 19b).

Changing the input variables $r_{bg}$ and $h^2_{mono}$ brings about a larger modification of the output variables when competition is among single plants than when competition is among rows. Hence, the competition effects are more marked in the model for diffuse competition than in the model for nearest-neighbour competition (Section 4.2.3).

The influence of intergenotypic competition on (1) the genetic variance and (2) the environmental variance will be discussed.

(1) The genetic variance in mixed stand is unequal to that in pure, var $g_{mix} \neq$ var $g_{mono}$ (Eqns 4.29 and 4.52). The genetic variance in mixture can be less than the genetic variance in monoculture, as when competition smoothes the differences among the genotypes. For example, Hozumi et al. (1955), in maize, observed a tendency towards equalization of plant height. The reduced amount of light received by the shorter plants caused an etiolated growth, that is an accelerated shoot elongation of those plants. The lower

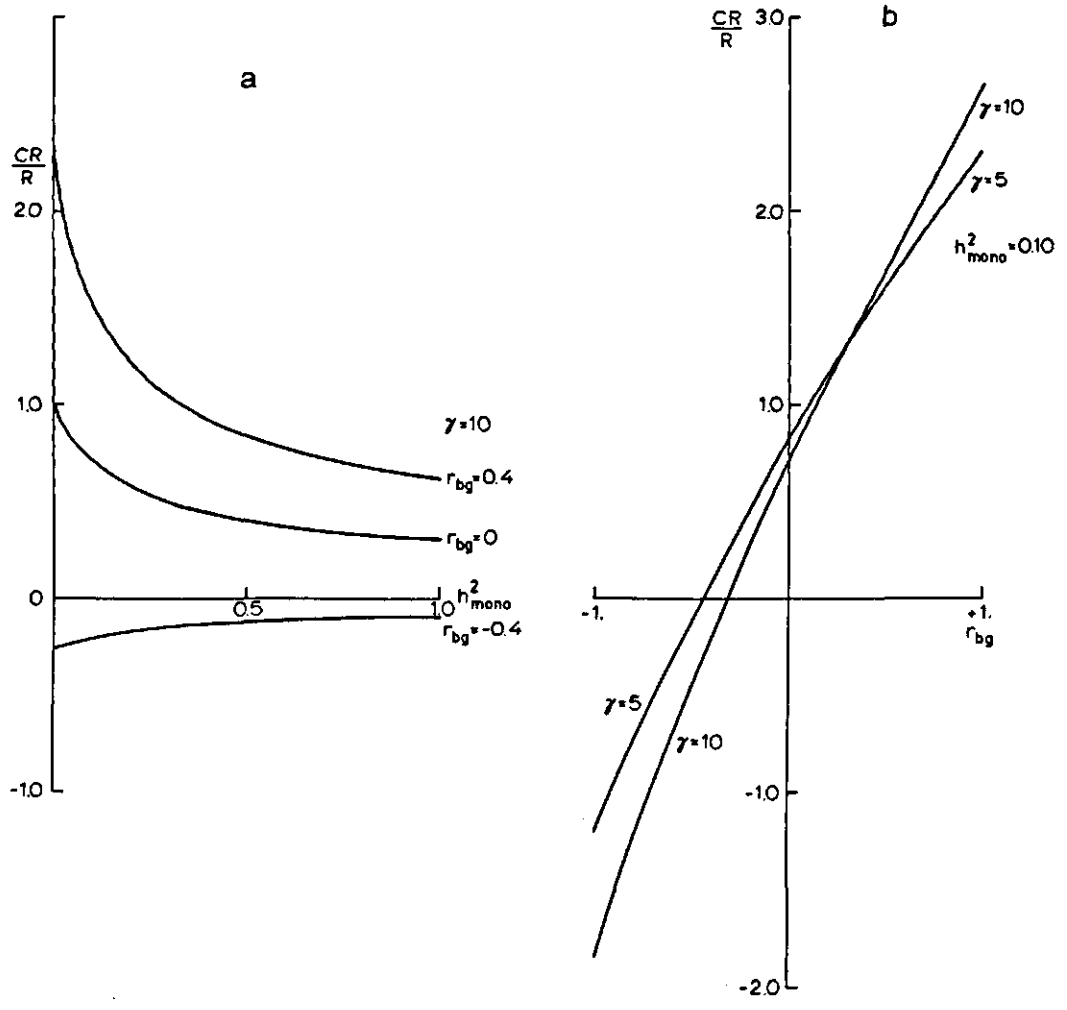


Fig. 19. Similar to Fig. 16, but competition is assumed to be between single plants.

genetic variance in mixture decreases the genetic portion of the total variance, i.e. the heritability.

However, for yield an enhancement of the genetic variance due to mixing is more likely. Equations 4.29 and 4.52 show that when cov($\underline{b}$,$g_{mono}$) is not too strongly negative, then var $g_{mix}$ exceeds var $g_{mono}$. This can be formulated more exactly by using the parameters $r_{bg}$ and $\gamma$. We find for rows (Eqn 4.29) that var $g_{mix}$ > var $g_{mono}$ when $r_{bg} > -\frac{1}{2}\sqrt{\gamma}$. For single plants (Eqn 4.52) we find $r_{bg} > -\frac{1}{4}\sqrt{\gamma}$. In Section 6.4, it is concluded that, in barley, the correlation coefficient $r_{bg}$ of competitive ability and pure-culture yield will, on the whole, be close to zero and probably slightly positive. Consequently, an increased genetic variance due to competition will be the rule, especially when the competitive stress $\gamma$ is large. Experimental evidence is to be found in the literature. Hinson & Hanson (1962) grew four soybean varieties in monoculture and a mixture of all

four. The variance among varietal means was larger in mixture than in monoculture for all five spacings studied. Magnified differences among genotypes in mixture compared with monoculture were demonstrated for forage yield in lucerne (Rotili & Zannone, 1971; Rotili et al., 1976), red clover (Rotili et al., 1977a), *Dactylis glomerata* L. (Rotili & Zannone, 1977b), and *Festuca arundinacea* Schreb. (Rotili et al., 1977c).

(2) The environmental variance in mixture. When competition is between rows (nearest-neighbour competition), the environmental variance is enlarged by a genetic component, var $\underline{e}_{mix}$ > var $\underline{e}_{mono}$ (Eqn 4.30). However, when competition is between single plants (diffuse competition), the environmental variance in mixture equals that in pure stand, var $\underline{e}_{mix}$ = var $\underline{e}_{mono}$ (Eqn 4.53). This paradox will be explained.

(a) Competition between rows. A monoculture is a genetically homogeneous stand and a mixture is a genetically heterogeneous one. Hence, in monoculture, all rows have an identical genetic environment, whereas, in mixture, the genetic make-up of the neighbourhood differs from row to row. Since adjacent rows interfere with each other, the variation in genetic environment enlarges the environmental variation in mixture (Eqn 4.30).

(b) Competition between single plants. It seemed appropriate to describe the yield of an individual plant in mixture by the equation given by de Wit (1960) (Section 4.2.2). De Wit assumed that the yield of a plant in mixture is affected by the relative seed frequencies of the genotypes in the mixture, but that the yield of the plant is not influenced by the genotype of its nearest neighbours (Section 4.2.3). Then any plant in the mixture competes with a group of plants of which the genetic composition agrees with the relative seed frequencies in the entire mixture. Hence, the genetic composition of the competing group is identical for any plant in the mixture. Therefore, there is, in fact, no variation in genetic environment between the plants. Consequently, when this assumption holds, var $\underline{e}_{mix}$ = var $\underline{e}_{mono}$.

As was already argued in Section 4.2.3 the two models may be considered as the limits of a real situation. In the model for progeny testing, it is assumed that a row is protected, by its adjacent neighbours, against all competitive influences of rows other than the adjacent rows so that competition is restricted to nearest neighbours. On the other hand, in the model for single-plant selection, it is supposed that there is no protection by the adjacent neighbours at all so that competition is diffuse. In Section 4.2.2 it was shown that for barley, and probably for all small grains, the assumptions are justified. However, the models are not by definition a model for progeny testing in row plots and a model for single-plant selection, respectively. For example, when for a crop has been found that a plant mainly competes with its adjacent neighbours, the row-competition model may be adopted or some intermediate of the two models.

In Chapter 5 the model will be extended to allow for selection at spacings different from the commercial one. In later sections, the model is tested with actual data of selection experiments in barley, dealing with single plants (Section 8.2) as well as with rows (Section 9.1). Moreover, the experiments give an additional illustration of the use and interpretation of the competition model. Some general opinions about the consequences of intergenotypic competition for plant selection and progeny testing will be given.

# 5 Bias in selection due to spacing and competition

## 5.1 INTRODUCTION

Selection of plants at wider spacings than the commercial one is often supposed to be useful and is therefore frequently applied (Sections 1.3.2 and 1.3.3). The arguments are: (1) easier screening of individual plants, especially in visual selection, (2) decrease or removal of intergenotypic competition, and (3) increase of seed production per plant to obtain a sufficient amount of seed for progeny tests of reasonable size. The second argument holds also for the selection of progenies in widely-spaced single-row plots.

However selection at a wide stand involves selection in an environment which deviates from normal growing conditions. This introduces a source of error. When a number of genotypes are grown at various densities, the yield differences and sometimes even the rank of the genotypes varies from density to density. In other words, there is interaction between genotype and density. A review of some literature on the differential response to spacing and on how to quantify the differential response is appropriate. It is also necessary to consider the density response of a single genotype. There is an enormous amount of literature on this subject, but it will suffice to give a general picture on the density-response curve and to summarize the models that describe that curve.

A sparse stand weakens interplant competition, but, except at very wide spacings, this competition cannot be removed completely. Hence, it seems useful to quantify the effects of wide spacing combined with that of decreased interplant competition on the efficiency of selection. A model for the bias in selection at different spacings requires formulae for response to spacing and density dependence of the competition effects.

As was already stated in Section 4.4, the ultimate interest is the response to selection. Consequently, the ideal model describing the implications of wide spacing and intergenotypic competition for selection should express the bias, caused by these factors, in terms of change in response to selection. A procedure may be applied analogously to that used in Sections 4.3 and 4.4 where the bias due to competition was quantified: the effect of spacing and intergenotypic competition on yield is described in terms of a stochastic equation. From this, expressions for the phenotypic, genetic and environmental variance are derived and, finally, a formula is constituted for the correlated response for monoculture yield at normal spacings brought about by selection for yield in a mixture at wide spacings. For a better understanding of the bias that results from selection in mixture at wide stands, it is convenient to separate the bias into (1) the bias due to selection among monocultures at wide stands i.e. without intergenotypic competition and (2) the bias from the presence of intergenotypic competition.

*5.1.1 Review of literature*

*Differential response to spacing* Already in 1925, Engledow (1925) showed an example where the rank of two wheat varieties changed over spacings. The differential response to spacing is mostly evaluated by the component for genotype x density interaction in an analysis of variance. When cultivars of small grains were grown at different seed rates, significant interactions of that type were found. Examples have been reported in barley by Immer (1941) and Kirby (1967), in winter wheat by Pendleton & Dungan (1960), in rice by Kariya & Yamamoto (1963), and in oats by Jones & Hayes (1967). Sometimes the interaction is found to be non-significant, but this can often be traced back to a narrow range of densities studied. Then there are no or only small yield differences between the spacings.

The interaction with genotype can be significant not only for plant spacing but also for row spacing. That was observed in wheat, barley and oats by Harrington (1941) and in barley by Finlay et al. (1971). In winter wheat Lashin & Schrimpf (1962) recorded a different reaction of varieties to row spacings.

The differential response to density has also been characterized in other ways. Sakai & Iyama (1966) expressed density response in terms of linear regression of plant performance on spacing. Twelve barley cultivars showed significant differences in their regression coefficients. Škorpík (1972), in wheat, found the correlation with grain yield at a commercial rate to decrease with increasing plant spacing.

In $F_2$ populations of spring wheat, Nass (1978) selected for total ear weight per plant at a normal rate of 260 seeds $m^{-2}$ and at a low rate of 26 seeds $m^{-2}$. Selection at the higher density resulted in $F_4$ lines with a greater mean yield and in more $F_4$ lines located in the top 15% when the lines are ranked to their yield.

Evidently, genotype-specific responses to spacing are also found in other crops. Mentioned are the fodder crops, where at the initial stages of the traditional breeding programmes the genotypes are selected as spaced plants aimed to perform in swards (Lazenby & Rogers, 1962). The ranking of strains for production at a wide spacing is often found to be quite different from that in dense swards. See for a review Lazenby & Rogers (1962) and for additional evidence Rumbaugh (1963), Davies & Reusch (1964), Lazenby & Rogers (1964), Rotili (1969), and Rotili & Zannone (1971).

The poor agreement between the performance of a genotype under wide-spaced conditions and its performance in commercial stand lowers the efficiency of selection. Therefore it is rather surprising that little attention has been paid to predict the influence of wide spacing on the response to selection.

*The density-response curve* The general picture of the density-response curve in small grains was described by, among others, Holliday (1960) and Donald (1963) in their reviews. The yield of biomass per unit area shows an asymptotic curve: the yield increases with density, but at higher densities with a lower rate. Also the curve for grain yield rises to a maximum but then declines with increasing density. The total curve is approximately parabolic in shape and there is a wide range of densities giving near-maximal grain yield.

The density beyond which grain yield declines is strongly affected by the growing

conditions (Kirby, 1970). In barley, grain yield in Canadian field trials diminished already when the seed rate increased from 50 to 100 kg $ha^{-1}$ (Stoskopf & Reinbergs, 1966). Under British conditions Kirby (1967, 1969, 1970) and Willey & Holliday (1971) observed a yield depression from densities of about 400 plants $m^{-2}$ (160 kg $ha^{-1}$) onwards. On the other hand, in field plots in Sweden the grain yield gradually increased over the entire range of densities up to 300 kg $ha^{-1}$ (Bengtsson & Ohlsson, 1966). In the Netherlands, de Wit (1968) also reported a continuous enhancement even up to a dressing of 1100 kg $ha^{-1}$. Therefore, when secondary factors such as water and nutrient shortage, lodging and diseases are not overruling, grain yield may also show an asymptotic curve (Fig. 20).

Various mathematical expressions are proposed for the yield-density relation. For a review the reader is referred to Willey & Heath (1969). Among others, de Wit (1960) introduced a model, which appears to fit well the asymptotic curve of spacing experiments. Since breeding work deals predominantly with suboptimal densities, that is spacings wider than the commercial one, the model is appropriate in the present study for grain yield too. Moreover, de Wit worked it out as a special case of his competition model, so that it is likely that the model presented in Chapter 4 can be extended to allow for density effects.

De Wit (1960) considered response to spacing in terms of change in interplant competition. The differential response of the genotypes to spacing can be attributed to differences in competitive ability. As the degree of interplant competition declines from dense stands to spaced plants, genotypes which can more fully occupy the increased space available are favoured. Those are the more competitive ones. For example, in wheat, Fischer & Kertesz (1976) observed that the yield of erect-leaved genotypes in field plots was 6% above that of the non-erect genotypes, but as spaced plants their mean yield was 12% below that of the others. The non-erect types were supposed to be the stronger competitors. In an experiment with 12 varieties of rice, grown in mixtures and in monocultures at different spacings, Kawano et al. (1974) found a strong correlation between spacing response in monoculture and competitive ability in mixture. Wilcox & Schapaugh (1978) grew two soybean genotypes in mixture and monoculture at nine spacings. They found that the stronger competitor in mixture also used the extra space, supplied by the wide spacings, much more effectively. Therefore, competitional bias is not removed by increasing

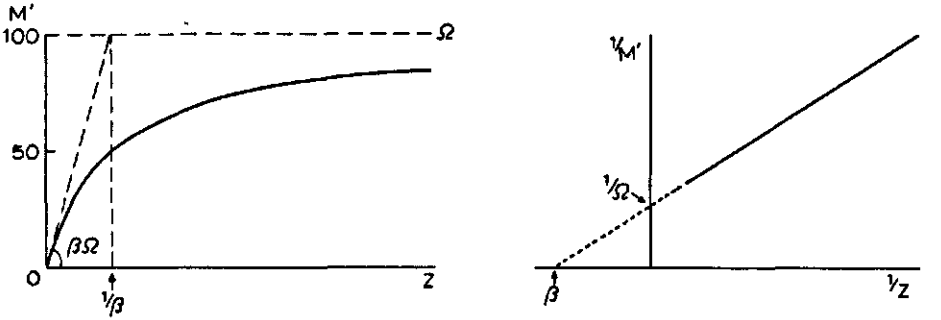


Fig. 20. Relation between yield per unit area and density in plants or kernels per unit area. For explanation of symbols see text. Modified after de Wit & Goudriaan (1974, Fig. 37) and de Wit (1960, Fig. 20).

spacing. Indeed, interplant competition disappears but a new component of competition, namely competition against empty space appears.

## 5.2 DE WIT MODEL OF DENSITY RESPONSE

De Wit stated that spacing experiments are an extreme form of competition experiments, namely a series of mixtures where one of the genotypes does not grow at all. The approach was introduced by de Wit & Ennik (1958) and elaborated by de Wit (1960). For a summarized version see de Wit (1961). Early applications were given by de Wit (1959) for sugar beets and by Reestman & de Wit (1959) for potatoes.

Assume that in a mixture of i and j, i is the 'growing' and j the 'non-growing' genotype. The yield of i in mixture with 'empty space', that is with the non-growing j, is derived from Eqn 4.6a as

$$O'_{ie} = \frac{k_{ie}Z_i}{k_{ie}Z_i + Z_e} M'_i$$

where $k_{ie}$ is the relative crowding coefficient of i against empty space. The total number of grains, either viable or dead, per $cm^2$ $Z_t = Z_i + Z_e$ remains constant over all densities. Substitution of $Z_e = Z_t - Z_i$ provides

$$O'_{ie} = \frac{k_{ie}Z_i}{(k_{ie}-1)Z_i + Z_t} M'_i = \frac{\beta_i Z_i}{\beta_i Z_i + 1} \Omega'_i$$

with

$$\beta_i = \frac{k_{ie}-1}{Z_t} \text{ and } \Omega'_i = \frac{k_{ie}}{k_{ie}-1} M'_i$$

Replacing $O'_{ie}$ by $M'$ and omitting the subscripts i, give for the yield at a density of Z plants $cm^{-2}$

$$M' = \frac{\beta Z}{\beta Z + 1} \Omega' \qquad (5.1)$$

The equation describes a hyperbola with horizontal asymptote $\Omega'$ and initial slope $\beta\Omega'$ (Fig. 20). The expression can be recast into the linear regression form

$$\frac{1}{M'} = \frac{1}{\beta\Omega'} \frac{1}{Z} + \frac{1}{\Omega'} \qquad (5.2)$$

Therefore, when the reciprocals $1/M'$ and $1/Z$ are plotted against each other, the intersections of the regression line with the axes are $1/\Omega'$ and $\beta$, respectively (Fig. 20)

The meaning of $\beta$ and $\Omega'$ can be understood as follows. The density-response curve has $\Omega$ as its horizontal asymptote. Thus, $\Omega'$ is the extrapolated yield at infinite density. When the crop uses the total available space, its yield reaches the maximum value $\Omega'$. At lower densities, the crop occupies a relative space equal to $M'/\Omega'$ (see Eqn 4.3). The space confiscated per plant is derived from Eqn 5.1 as

$$\frac{M'}{Z\Omega'} = \frac{\beta}{\beta Z+1} \qquad (5.3)$$

The theoretical area arrested by an isolated plant is $\beta$, which is found by letting Z approach zero in Eqn 5.3. The yield of the isolated plant is $\beta\Omega'$. This is found by, at first, expressing Eqn 5.1 per plant by dividing by Z and, secondly, in the resulting expression letting Z approach zero.

A general picture of the density response in barley can be drawn from published spacing experiments. Dry matter production of grains is related to kernels per $m^2$ sown (Table 8, Fig. 21). Some authors gave the yield as fresh weight and the seed dressing in kg $ha^{-1}$. When no conversion factors were recorded, it is assumed that the harvested grains are at 15% moisture and the thousand-kernel weight amounts to 40 g. Data from supra-optimal densities are discarded, because the model does not take into account the fall of yield at these rates.

Table 8. Relation between dry matter yield of grains and density in barley. The relation is characterized by the theoretically maximal yield $\Omega$ and the space occupied by a single-growing plant $\beta$. Data from densities where the yield declines with increasing seed rate are discarded. The number and the range of densities refer to the densities used in the calculation. The number of series of densities is the product of years, sites, fertilizer levels, sowing time and genotypes.

| Reference | Country | Number of series | Densities | | $\Omega'$ | $\beta$ |
|---|---|---|---|---|---|---|
| | | | nr. | range $cm^2 kernel^{-1}$ | $g\ m^{-2}$ | $m^2\ plant^{-1}$ |
| Moës (1954) | Belgium | 2 | 3 | 27 - 44 | 396 | 0.0149 |
| Jackson & Page (1957) | GB | 28 | 4 | 12 - 31 | 346 | 0.0844 |
| de Wit (1960, Fig. 32) | Neth. | 1 | 2 | 31 - 310 | 454 | 0.0591 |
| Holm & Pedersen (1962) | Denmark | 5 | 4 | 25 - 164 | 424 | 0.0559 |
| Bengtsson & Ohlsson (1966) | Sweden | 71 | 6 | 17 - 100 | 350 | 0.0281 |
| Sakai & Tyama (1966) | Japan | 12 | 5 | 4 - 1024 | 768 | 0.0140 |
| Kirby (1967) | GB | 4 | 2 | 50 - 100 | 488 | 0.0569 |
| de Wit (1968) | Neth. | 1 | 7 | 4 - 267 | 479 | 0.0462 |
| Severson & Rasmusson (1968) | USA | 26 | 4 | 76 - 686 | 504 | 0.0417 |
| Kirby (1969) | GB | 6 | 4 | 29 - 278 | 440 | 0.0500 |
| Kirby (1970) | GB | 1 | 3 | 50 - 200 | 725 | 0.0208 |
| Sandfaer (1970) | Denmark | 2 | 3 | 32 - 578 | 417 | 0.2420 |
| Willey & Holliday (1971) | GB | 1 | 3 | 42 - 909 | 553 | 0.1413 |
| Kirby (cited by Evans, 1972) | GB | 1 | 3 | 50 - 200 | 548 | 0.0684 |
| Maddens (1974b) | Belgium | 16 | 5 | 29 - 67 | 609 | 0.0681 |
| Pedersen & Jørgensen (1976) | Denmark | 39 | 3 | 25 - 400 | 420 | 0.3500 |
| Hamblin et al. (1978) | Australia | | 3 | 16 - 1600 | 426 | 0.1439 |
| median | | | | | 454 | 0.0569 |

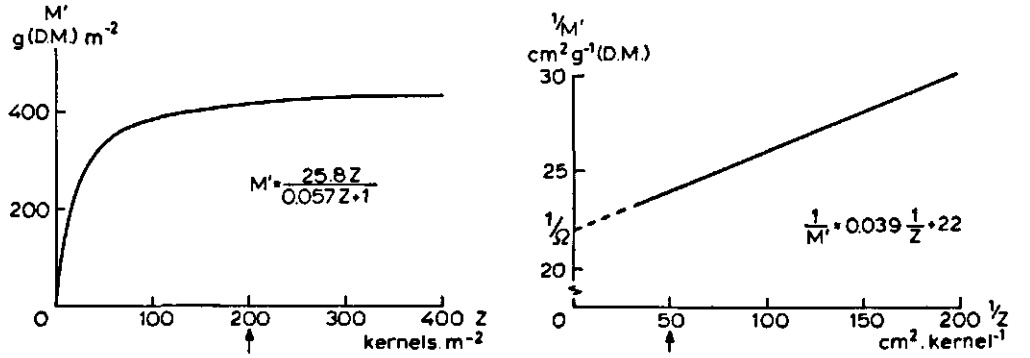


Fig. 21. Relation between grain yield M' and density Z in barley. Curves are based on the medians of Ω' and β derived from Table 8.

For each of the references, the inverses of yield and density are regressed against each other according to Eqn 5.2. No account is taken of a heterogeneity of errors of the yield reciprocals among densities. The estimates of $\Omega'$ and $\beta$ are given in Table 8. The medians of $\Omega'$ and $\beta$ are recorded rather than some weighted means because the error structure of the experiments is unknown. When we substitute the medians into Eqn 5.1, the relation between the grain yield M in g dry matter per $m^2$ and the density Z in kernels per $m^2$ becomes

$$M' = \frac{25.8\ Z}{0.057\ Z+1}$$

or in linear form

$$\frac{1}{M'} = 0.039\ \frac{1}{Z} + 0.0022$$

Both are presented in Fig. 21. Most of the studies are carried out in Western Europe, so the equations give an impression of the yield-density relation in barley reasonably supplied with water and nutrients.

An indication as to how far the model fits the data of density experiments can be gained from the proportion of the variation among the average yields at different densities, that is 'explained' by the linear equation 5.2. This proportion is given by the squared coefficient of the correlation between 1/M' and 1/Z. The most extensive study, that of Bengtsson & Ohlsson (1966) with 71 trials of six divergent densities each, supplies the value of 0.986. The experiment of Sakai & Iyama (1966) with 12 cultivars at five spacings ranging from 4 to 1024 $cm^2\ plant^{-1}$ provides 0.989. Obviously, the proportions are high, partly due to the wide range of densities used. It is concluded that, in barley, Eqns 5.1 and 5.2 describe properly the yield density relation, if indeed a yield depression at high densities does not occur or when these densities are discarded.

The effect of competition at various spacings can be described by adapting Eqn 4.10. Suppose that one of the (m+1) genotypes does not grow at all; this genotype re-

presents the empty space. Then the yield of genotype i in mixture becomes

$$O_i' = \frac{b_i z_i}{b_1 z_1 + \ldots + b_n z_n + b_e z_e} M_i' \qquad (5.4)$$

Varying the relative frequency of the empty space $z_e$, and with that the other relative frequencies, provides the outcome of competition over a range of spacings.

Equation 5.4 can be expressed in $\beta$ and $\Omega'$. Division by $b_e$ and use of the absolute number of plants $cm^{-2}$ results in

$$O_i' = \frac{k_{ie} Z_i}{k_{1e} Z_1 + \ldots + k_{ne} Z_n + Z_e} M_i' \qquad (5.5)$$

Let $Z_t$ plant places $cm^{-2}$ correspond with m $cm^2$ plant $place^{-1}$, so $m = 1/Z_t$ with $Z_t = Z_1 + \ldots + Z_n + Z_e$. Note that a plant place can be empty. Now we can derive from the expression $\beta = (k_{ie}-1)Z_t$ that

$$k_{ie} = (\beta_i + m)/m \qquad (5.6)$$

Substitution of $Z_t = 1/m$ into Eqn 5.1 supplies

$$M_i' = \frac{\beta_i}{\beta_i + m} \Omega_i' \qquad (5.7)$$

When we substitute Eqns 5.6 and 5.7, together with $m = 1/(Z_1 + \ldots + Z_n + Z_e)$ into Eqn 5.5, we arrive at

$$O_i' = \frac{\beta_i Z_i}{\beta_1 Z_1 + \ldots + \beta_n Z_n + 1} \Omega_i' \qquad (5.8)$$

Given the monoculture yields of the genotypes at two strongly different spacings, then for each genotype i, $\beta_i$ and $\Omega_i'$ can be solved from Eqn 5.1. Substitution of the values of $\beta$ and $\Omega'$ into Eqn 5.8 provides the yield of a genotype in mixture at a density of $(Z_1 + \ldots + Z_n)$ plants $cm^{-2}$. On the other hand, given the yields of the genotypes in monoculture and mixture at a certain spacing and given an estimate of $b_e$, the yields of the genotypes in monoculture as well as in mixture can be predicted for any density.

Torssel & Nicholls (1976) described a model that they claimed was an alternative for the model of de Wit (1970), who simulated competition throughout the growth period using successive harvests in density experiments. However, their model can only be compared with the simple model of de Wit (1960) and can be transformed to Eqn 5.8 with the only difference that each $\beta_j Z_j$ in the denominator is multiplied by $\Omega_j'/MAX$, where MAX is the yield at infinite density in the mixture. There is no argument for this 'weighting factor'. Furthermore, several other objections can be made against their approach and experimental testing. So their model has to be rejected.

The de Wit (1960) model, to predict the yield of genotypes in mixture from their monoculture yields at different densities, is based on the assumptions that:

(1) The genotypes compete for the same resources (Section 4.1). In general, this will be true if the competing genotypes belong to the same species (Sections 3.3 and 6.3.1).

(2) The growth curves of single-growing plants are similar, that is the course curves of the $\beta$s are the same apart from a multiplication factor on the $\beta$ axis (de Wit, 1960; Baeumer & de Wit, 1968). Hence, the assumption is violated when the growth curve of a genotype is shifted in time compared with the growth curve of another genotype.

An example may clarify the prerequisite of similar growth curves. Suppose two isogenic lines, that differ only with respect to the time of emergence and do not differ in monoculture yield at final harvest. So, both genotypes produce the same estimates of $\beta$ and $\Omega'$ at the time of harvest (Eqn 5.1) and, thus, they are expected to be equally competitive. From Eqn 5.8 it is then expected that they produce the same yield in a mixture. However, when they are really grown in a mixture, the rapid emerging genotype claims the available space at an earlier stage. Therefore, it produces the higher yield in the mixture and is the stronger competitor. The assumption of similar growth curves may be a serious limitation in the applicability of Eqn 5.8.

(3) The genotypes have the same plant height. Taller plants may have a competitive advantage over shorter plants. Like the above-mentioned non-similarity of the growth curves, differences in plant height do not necessarily reflect themselves in differences in monoculture yields at various spacings. Baeumer & de Wit (1968) defined the assumption that the genotypes 'cannot encroach upon the light space once occupied by the other'. In my experiments with barley cultivars, there were large differences among the cultivars in plant height. However, these differences were not associated with differences in competitive ability (Section 8.3.1). Therefore, it is concluded that differences in height between genotypes do not seriously bias the applicability of Eqn 5.8.

The first assumption was already made for the basic competition model (Section 4.1). The second and third assumptions are required to predict the competitive ability of the genotypes in mixture from a spacing experiment with the genotypes grown in monoculture and harvested at only one time. This will be explained by means of Figs 22 and 23. The available space is distributed among the genotypes in accordance with their $\beta$ curves. The space acquired by a genotype determines its competitive ability (Eqn 4.1). Simulation studies and experiments showed that the distribution of the space at an early time has a very great influence on the outcome of competition. In the model, however, the distribution of the space is read off from the $\beta$ at final harvest. The $\beta$ at final harvest reflects the entire course curve of $\beta$ only when the curves are similar (Figs 22a and 23a). This explains the assumption of similarity of the $\beta$ curves. The bias originating from deviations from this assumption can be understood from the other situations presented in Figs 22 and 23.

Similarity of the $\beta$ curves is a real situation. It occurs when the genotypes differ in time of emergence, but have the same relative growth rate of $\beta$ in time and end their exponential increase of $\beta$ at the same time due to photoperiodicity. Under the assumption of similar $\beta$ curves, the influence of competition and density of stand on the response to selection are worked out in detail in Sections 5.3 and 5.4. This provides the reference with which the other situations are compared in Section 5.6.

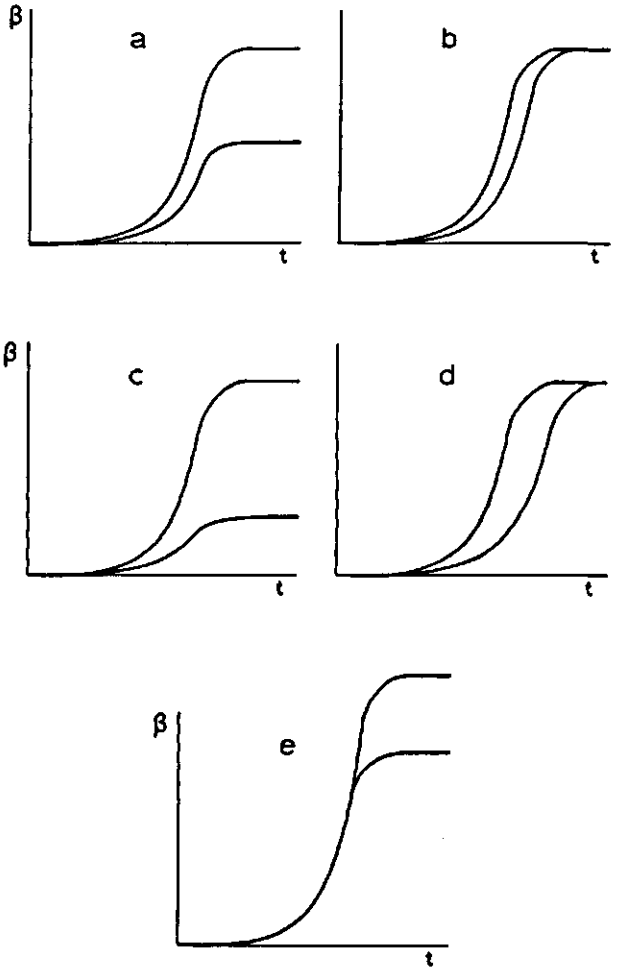


Fig. 22. The increase of β, the space occupied by a single freely grown plant, in time plotted for two genotypes. The genotypes differ in their initial value of β (a and b), in their relative growth rate of β (c and d), or in their maximum value of β (e). The genotypes finish their exponential increase at the same time (a and c) or they reach the same maximum value of β (b and d).

Baeumer & de Wit (1968), de Wit (1970) and de Wit & Goudriaan (1974) presented a dynamic model to predict the biomass yields of genotypes in a mixture in course of time by means of parameters derived from a spacing experiment with the genotypes grown in monoculture at divergent densities, harvested at intervals. Their model accounts for non-similarity of the growth curves and for differences of growth in height. However, their approach is not used in Sections 5.3 and 5.4 because, for breeding, it is too time-consuming to collect the required data. Moreover, the simple model provides an analytical approach and facilitates understanding.

*Summary* The model of de Wit (1960) to describe the density-response curve is explained in full. His extension, to estimate the yield of genotypes in a mixture from their mono-

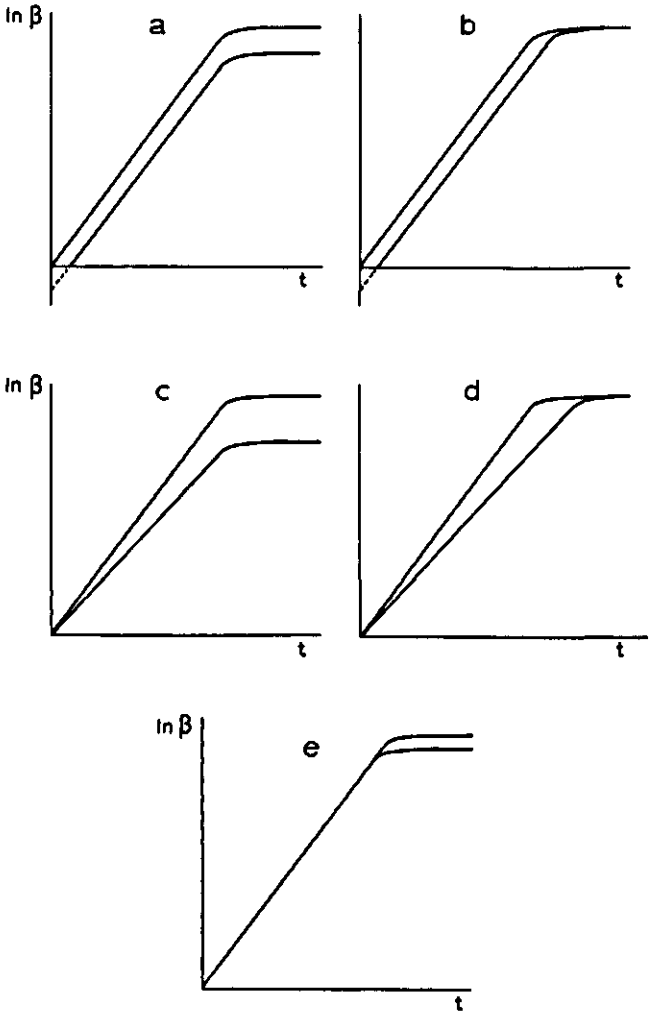


Fig. 23. Similar to Fig. 22 but β plotted on a logarithmic scale.

culture yields at divergent densities, is also discussed. This extension holds when (1) the genotypes compete for the same space, (2) the genotypes have similar growth curves of single-growing plants, (3) the genotypes have the same height in course of time. In applying the method to segregating populations, the assumption of similar growth curves will be, sometimes, seriously violated.

## 5.3 SELECTION OF SINGLE PLANTS IN MIXTURE AT WIDE STAND (DIFFUSE COMPETITION)

In the foregoing, the expected yield of a genotype was related to the density of stand and the genetic composition of the mixture. Of primary importance for a breeder is, however, the progress that is made when selection is in a segregating population, i.e. in a mixture at a certain density. Already in Section 4.4, expressions were derived for

the response to selection in mixture. In what follows, a similar procedure is applied to express the response to selection in mixture in relation to density. Just as in Section 4.4, two kinds of competitive interference are distinguished: (1) when the yield of an experimental unit is determined by the relative frequencies of the genotypes in the mixture (diffuse competition, Section 5.3), (2) when competition is only between adjacent neighbours (nearest-neighbour competition, Section 5.4). The first type occurs when single plants are the units of selection and the second type occurs with single rows.

*5.3.1 Components of variance*

The aim is to select genotypes that yield high when they are grown in monoculture at a commercial density of say m $cm^2$ $plant^{-1}$. However, early selection occurs in a segregating population, that is in a mixed stand, at a wide spacing of say s times m $cm^2$ $plant^{-1}$. These arrangements can be represented by

| | |
|---|---|
| monoculture of i at m $cm^2$ $plant^{-1}$ | i i i i i i i i i |
| mixture at 3 m $cm^2$ $plant^{-1}$ | e e h e e i e e j |

where each letter represents a plant except 'e' that denotes an empty place.

The genotypic yield of a random genotype i in a mixture at a spacing of sm $cm^2$ $plant^{-1}$ is given by Eqn 5.4. When the yields are expressed per plant instead of per unit area, we arrive at

$$O_{i,sm} = \frac{b_i}{b_1 z_1 + \ldots + b_n z_n + b_e z_e} M_{i,m} \qquad (5.9)$$

the spacing is denoted by a subscript. The crowding coefficients refer to a spacing of m $cm^2$ $plant^{-1}$ (Section 5.3.5). At this spacing $z_e = 0$.

The yield $O_{i,sm}$ of a random genotype i in a mixture at a spacing of sm $cm^2$ $plant^{-1}$ relative to the yield $O_{j,sm}$ of a random genotype j in that mixture at that spacing is found from Eqn 5.9 to be

$$\frac{O_{i,sm}}{O_{j,sm}} = \frac{b_i}{b_j} \frac{M_{i,m}}{M_{j,m}}$$

This ratio is independent of s and is, therefore, independent of the spacing at which the mixture is grown. In conclusion, the rank of the genotypes in a mixture is not affected by the spacing at which the mixture is grown.

Equation 5.9 can be worked out further. At m $cm^2$ $plant^{-1}$, the relative frequency of empty space is $z_e = 0$, so that at sm $cm^2$ $plant^{-1}$ $z_e = (s-1)/s$. Therefore, at sm $cm^2$ $plant^{-1}$ there remains $1-z_e = 1/s$ for the other genotypes. We assume that in a selection field any plant has a unique genotype. Hence, when there are n plants in the selection field, then $z_1 = \ldots = z_n = 1/sn$. For the crowding coefficients b of the n genotypes, an arbitrary level may be chosen, for example $\epsilon\underline{b} = 1$ (Section 6.2.1). When we substitute $\epsilon\underline{b} = 1$, $z_e = (s-1)/s$ and $z_1 = \ldots = z_n = 1/sn$ into Eqn 5.9, we obtain

$$O_{i,sm} = \frac{b_i}{\frac{1}{s} + \frac{s-1}{s} b_e} M_{i,m} = \frac{sb_i}{1 + (s-1)b_e} M_{i,m} \qquad (5.10)$$

For convenience, we replace

$$t = (s-1)b_e \qquad (5.11)$$

Hence, we have for the genotypic yield of genotype i in the mixture at sm $cm^2$ $plant^{-1}$

$$O_{i,sm} = \frac{s}{1+t} b_i M_{i,m} \qquad (5.12)$$

With Eqn 4.14:

$$O_i = b_i M_i$$

this gives:

$$O_{i,sm} = \frac{s}{1+t} O_{i,m} \qquad (5.13)$$

The multiplication factor s/(1+t) is a function of s and $b_e$ and, therefore, depends on the spacing but is not affected by the genotypes involved.

To derive expressions for the components of the variance among plants, we adopt the stochastic approach of Section 4.3. The phenotypic yield of a plant of a random genotype i in mixture is given by Eqn 4.50 as

$$\underline{p}_i = \underline{c}_i (\mu + \underline{g}_i) + \underline{e}_i \qquad (4.50)$$

where $\mu$ the mean of the monocultures, $\underline{g}_i$ the deviation of the monoculture yield of i from $\mu$, $\underline{c}$ a multiplication factor describing the effect of intergenotypic competition, and $\underline{e}$ the residual error (Section 4.3.1.1). From Eqn 5.12, we see that

$$\underline{c}_i = \frac{s}{1+t} \underline{b}_i \qquad (5.14)$$

The genetic variance is the variance among the expected (genotypic) yields of the genotypes. From Eqn 5.13, we obtain for the genetic variance in mixture at sm $cm^2$ $plant^{-1}$

$$\text{var } g_{mix,sm} = \text{var } \underline{O}_{sm} = \frac{s^2}{(1+t)^2} \text{ var } \underline{O}_m = \frac{s^2}{(1+t)^2} \text{ var } g_{mix,m}$$

An elaborated expression for the genetic variance in mixture was given by Eqn 4.52. Hence, we have

$$\text{var } g_{mix,sm} \approx \frac{s^2}{(1+t)^2} (\text{var } \underline{g} + 2\mu \text{ cov}(\underline{b}, \underline{g}) + \mu^2 \text{ var } \underline{b}) \qquad (5.15)$$

Note that the parameters on the right side are at m $cm^2$ $plant^{-1}$ and in monoculture.

With wider spacing, the yields of single plants increase considerably. Consequently, the error or environmental variance of individual plants increase too. The ratio between the standard error $\sqrt{\text{var } \underline{e}}$ and the population mean $\mu$ is called the coefficient of variation. In Section 5.3.2, arguments are given for the supposition that the coefficient of variation is constant over densities. There it is also shown that this leads to

$$\text{var } \underline{e}_{\text{mono,sm}} \approx \frac{s^2}{(1+t)^2} \text{ var } \underline{e}_{\text{mono,m}} \tag{5.19}$$

For single plants, the environmental variation in mixture is equal to that in monoculture (Eqn 4.53). Consequently,

$$\text{var } \underline{e}_{\text{mix,sm}} \approx \frac{s^2}{(1+t)^2} \text{ var } \underline{e} \tag{5.16}$$

The phenotypic variance is the sum of the genetic and environmental variance. For the phenotypic variance in mixture, we obtain from Eqns 5.15 and 5.16

$$\text{var } \underline{p}_{\text{mix,sm}} \approx \frac{s^2}{(1+t)^2} (\text{var } \underline{g} + 2\mu \text{ cov}(\underline{b},\underline{g}) + \mu^2 \text{ var } \underline{b} + \text{var } \underline{e}) \tag{5.17}$$

Note that the parameters on the right side are at m $cm^2$ $plant^{-1}$ and in monoculture.

*Summary* Under certain assumptions, the rank of the genotypes in a mixture is not affected by the spacing at which the mixture is grown. The phenotypic, genetic and environmental variances in a mixture, grown at a wide stand of s times m $cm^2$ $plant^{-1}$, are expressed as function of the components of variance in monoculture at m $cm^2$ $plant^{-1}$.

### *5.3.2 Density dependence and normality of the environmental error*

When the spacing becomes wider, single-plant yields rise considerably. Consequently, the error or environmental variance of individual plants increases too. With respect to the present model, it is necessary to account for the increased environmental variation at wider spacings. When different experiments are compared, it is often found that the random variation in an experiment is proportional to the yield level of that experiment. Hence, the ratio between the standard error and the population mean, called the coefficient of variation CV, remains constant over a wide range of yield levels, especially when the trials, like density experiments, are at the same location and in the same year.

When the CV is constant over densities, we may write for the two densities of m and sm $cm^2$ $plant^{-1}$

$$\frac{\sqrt{\text{var } \underline{e}_{\text{mono,m}}}}{\mu_{\text{mono,m}}} = \frac{\sqrt{\text{var } \underline{e}_{\text{mono,sm}}}}{\mu_{\text{mono,sm}}}$$

Hence,

$$\text{var } \underline{e}_{\text{mono,sm}} = \frac{\mu^2_{\text{mono,sm}}}{\mu^2_{\text{mono,m}}} \text{ var } \underline{e}_{\text{mono,m}}$$

In a monoculture of a random genotype i, grown at sm $cm^2$ $plant^{-1}$, is $z_i = 1/s$ and $z_e = (s-1)/s$. From Eqn 4.11, we derive for the monoculture at sm $cm^2$ $plant^{-1}$

$$\underline{M}_{i,sm} = \frac{s\ \underline{b}_i}{\underline{b}_i + (s-1)b_e} \underline{M}_{i,m} = \frac{s\ \underline{b}_i}{\underline{b}_i + t}\ \underline{M}_{i,m} \qquad (5.18)$$

For convenience, $(s-1)b_e$ is replaced by t (Eqn 5.11).
This produces

$$\mu_{\text{mono,sm}} = \epsilon\underline{M}_{sm} = \frac{s}{1+t}\ \mu_{\text{mono,m}} \qquad (5.18a)$$

Therefore

$$\text{var } \underline{e}_{\text{mono,sm}} = \frac{s^2}{(1+t)^2}\ \text{var } \underline{e}_{\text{mono,m}} \qquad (5.19)$$

Eqn 5.18 will be used in the present model to account for the heterogeneity of error variances among spacings. However, we do not aim at supplying each plant at a given density with an error term proportional to the yield of the plant. Indeed, this would assume a log-normal distribution of single-plant yields.

Is the assumption of a constant CV over different densities justified? Skorpík (1976) found for three wheat varieties grown in 3 years and on two sites, that the coefficient of variation of grain yield per plant remained fairly stable over the six spacings which ranged from 22 to 450 $cm^2$ $plant^{-1}$. Pedersen & Jørgensen (1976), in barley, observed that the grain yield per plant increased from 4.2 to 8.3 g going from 100 to 200 $cm^2$ $plant^{-1}$ while the CV only changed from 34.6% to 26.9%.

In crops other than small cereals, constancy of the CV over densities is frequently observed for biomass (e.g. Kira et al., 1953; Hozumi et al., 1956). In general, the CV increases with time during the ontogeny (Kira et al., 1953; Stern, 1965). Care has to be taken in cross-fertilizing species where the CV is affected by intergenotypic competition.

In the present study, the Exps 77-1a and e (Section 2.1.4) provide an estimate of the CV at 125 and 3120 $cm^2$ $plant^{-1}$, respectively. Indeed, the latter arrangement is a mixture, but the spacing is so wide that interplant competition can be neglected. In Exp. 77-1a, the 50 plants of each of the 48 monoculture plots are divided into two groups according to odd and even plant numbers in order to exclude the correlation between adjacent plants from the interplant variance. The interplant variance per plot is obtained as the average of the interplant variances of both groups of 25 plants per plot. The CV is estimated for biomass and total weight of ears per plant. Going to a larger spacing, the yield increased considerably, whereas the CV did not change much (Table 9). The somewhat lower CV at the wider spacing suggests a hyperbolic rather than a linear relation between the standard error and $\mu$. A hyperbolic trend can also be derived from the barley data of Hamblin et al., (1978) and for biomass in the turnip data reported by Hozumi et

Table 9. Mean (g plant$^{-1}$) and coefficient of variation (CV) of plants in monoculture at two spacings. The coefficient of variation refers to a surface occupied by 50 plants.

| Spacing (cm$^2$ plant$^{-1}$) | Aboveground biomass | | Total ear weight | |
|---|---|---|---|---|
| | mean | CV | mean | CV |
| 125 | 11.0 | 0.47 | 6.4 | 0.48 |
| 3120 | 88.1 | 0.31 | 45.5 | 0.33 |

al. (1956, Fig. 3). In both experiments a mixture of genotypes is involved instead of a monoculture: Hamblin et al. (1978) used a segregating population and Hozumi et al. (1956) used a cross-fertilizing crop. These methods may have influenced the CV at different spacings differently.

There are several aspects in the relation between the density and the CV. When spacings are wider:

(1) The CV decreases because non-genetic interplant competition, as source of a magnified variance, decreases. In a monoculture, differences between the plants with respect to biomass arise from non-genetic factors. These differences cause differences in competitive ability between the plants. In monoculture, the competitive ability of a plant will be closely correlated with its biomass. Therefore, interplant competition magnifies the differences in biomass and, therefore, the variance among the plants (compare with the increased genetic variance due to intergenotypic competition; Eqn 4.52). As a monoculture is involved, the increased interplant variance denotes an increased environmental variance. Hence, going to wider spacings, interplant competition decreases and with that the environmental variance arisen from non-genetic competition decreases relatively.

(2) The CV may decrease because of the larger supply of growth factors available per plant. For, it is general experience that the CV of field plots is lower at very high yield levels than at moderate or normal yield levels. Moreover, soil heterogeneity in the field expresses itself more clearly in the yield of field plots when there is nutrient shortage and drought. So, under the latter conditions the environmental variance is increased whereas the yield level is decreased.

(3) The CV increases because the field area, on which a certain number of plants is grown, increases with the spacing. For, the larger the field, the larger the variance among plants within the field. This increase of CV may be obviated by adjusting the estimate of the interplant variance for the area by means of the empirical law of Smith (1938) (Section 8.1).

The joint effect of these factors on the CV will vary from trial to trial. In a homogeneous field, the third factor is relatively unimportant. There the CV decreases the wider the spacing. In a heterogeneous field, the reverse may be true. As a first approach, I assume the CV to be constant over different densities. Moreover, the range of spacings, which a breeder considers for selection, is relatively small.

A better understanding of the relation between the CV and the density is achieved by considering the shape of the frequency distribution at each density. Koyama & Kira (1956) showed for a large number of crops that the frequency distribution of biomass per plant is normal in the early stages of growth, but becomes more skew with time. Then a relative small proportion of the plants develops vigorously and a large fraction remains small. An increased plant density promotes the change towards this positive skewness. They concluded from their exponential growth model that the distribution of weight per plant would become log-normal. Therefore the authors suggested a logarithmic transformation of the data. Also Aikman & Watkinson (1979) gave a theoretical model for frequency distributions of weight per plant.

Skewness of the distribution of biomass per plant was also reported in fiber flax by Obeid et al. (1967), and in lucerne by Rotili & Zannone (1971). They also noted that the higher the density the more skew the distribution. When the seeds are drilled rather than accurately spaced by hand, the distribution of the area per plant tends to be log-normal (Mead, 1966). Ford (1975) studied frequency distributions of weights per plant in populations in relation to mortality.

The skewness of yield per plant, as reported in the above-mentioned literature, can be explained by the present competition model. In a segregating population, where each plant has a unique genotype, the yield of a genotype follows Eqn 4.10 with $z_1 = \ldots\ldots = z_n = \frac{1}{n}$ where n the number of genotypes. When the expectation value of the crowding coefficient b is set to unity and M is expressed per plant, the yield per plant in mixture is $O_i = b_i M_i$ (Eqn 4.14). We may imagine a monoculture, analogous to this genotype mixture, where each individual has a unique position with respect to the environmental and random effects. In absence of competition the phenotypic performance of a random plant i is

$$p_i = \mu + \underline{e}_i$$

However, in the field the plants interfere with each other, and the inequality of the $\underline{p}$s gives rise to differences in competitive ability. This is characterized by the competition coefficient $\underline{c}$ according to

$$p_i = \underline{c}_i \, (\mu + \underline{e}_i)$$

Note that in this equation $\underline{c}$ describes the competiton among plants having the same genotype but a different phenotype. The expression may also be written as $\underline{O}_i = \underline{b}_i \, \underline{M}_i$ where the parameters denote environmental instead of genetic effects.

The literature discussed previously, shows that in situations without interplant competition, that is in the early stages of growth and also later at very wide spacings, the distribution of single-plant yields is normal or practically normal. Hence, we may assume the distribution of $\underline{M}$ to be normal. On the other hand, $\underline{b}$ shows a ln-normal distribution (Section 6.2.1). The distribution of the actual yield $\underline{O}$ will lay between both types. At moderate competition it will be close to normal, whereas when competition is severe it will tend to ln-normal. This holds the more as the competitive ability, with

respect to non-genetic competition, of a plant will be closely related to its biomass. The explanation will hold for biomass and probably for grain yield too. For other characters already the distribution of M may deviate from normal and also the assumptions underlying the competition model (Section 4.1) will be less certain.

When the frequency distribution of yield per plant is near ln-normal, the logarithmic transformed data must be used in statistical testing. However, in the previous literature (e.g. Koyama & Kira, 1956) in many of the populations studied the distribution remained near normal and no transformation was necessary. Apparently, in those populations the growth period was too short or the spacing too wide to give skewness.

The distribution of yield per plant is studied in Exp. 76-1a (Section 2.1.4). As already mentioned in this section, the 50 plants of each of the 48 monoculture plots were divided into two groups according to odd and even plant numbers in order to exclude the correlation between adjacent plants. Of each of the 96 groups of 25 plants the coefficient of skewness was computed. Only two varieties, 'L98' and 'Titan', showed a significant coefficient of skewness for biomass and total weight of ears: +0.56 and +0.55, respectively (n=374, $P < 0.01$ one-tailed). The coefficients of skewness for the other varieties averaged +0.06 (n=1981, $P > 0.05$ one-tailed) for biomass and +0.11 (n=1981, $0.01 < P < 0.05$ one tailed) for total weight of ears. The two former cultivars deviated from the others by a slow, irregular and relatively poor emergence. This resulted in some refilled places and a few open places which influenced the non-discarded neighbour plants. Especially the irregular emergence will have caused a large variation in initial plant size and with that a great variation in competitive ability among the plants. This accounts for skewness. The low coefficient of skewness for the other varieties will have been promoted by the sparse stand (5x25 $cm^2$ $plant^{-1}$) and the practice of sowing two seeds per hole and singling the plants after emergence which stimulates uniformity of the seedlings. Also the accurate spacing of the plants may have contributed to the low coefficient of skewness.

The skewness for yield per row was studied in the uniformity trials where each row was sown with the variety 'Varunda'. The coefficient of skewness was computed per strip of rows and, thereafter, averaged over strips. In Exp. 76-3e, the coefficient of skewness was +0.38 and +0.30 (n=1080, $P < 0.01$) for biomass and grain yield, respectively. In Exp. 77-2e, the coefficient of skewness was +0.02 and +0.01 (n=576, $P > 0.05$) for biomass and grain yield, respectively. Hence, in the former experiment, there was a slight positive skewness for yield per row, whereas in the latter experiment no skewness of the frequency distribution of yield per row was detected.

The rows were sown with a 6-row drill. In Exp. 76-3, the two outside rows of the sowing round yielded sometimes very high (Section 9.4.3), which accounted for the positive skewness. When only the four centre rows were considered in Exp. 76-3e, the coefficient of skewness for grain yield reduced to +0.09 (n=720, $P > 0.05$).

*Summary* It is concluded that the distribution of yield per plant changes from normal to ln-normal in course of time and with increased planting rate. The conclusion is supported by experimental data and a theoretical model. When interplant competition is relatively weak and the growing period short, the trend to skewness is so small that the distribution

of yields per plant is nearly normal, as in my barley experiment. It probably holds also for other experiments with small cereals, especially when the plants are accurately spaced in a sparse stand. With respect to the present competition model, it seems reasonable to assume that the coefficient of variation, that is the ratio between the standard error and the population mean, is constant over densities. This assumption is used to adjust the environmental variance for the density of stand.

*5.3.3 Response to selection in mixture at wide stand*

The main interest of breeders is the response to selection. Therefore, the bias due to intergenotypic competition and wide spacing will be expressed in terms of a change in the response to selection. This will be done in a way similar to that followed in Section 4.4 where the effect of competition alone on the selection response was discussed.

In Section 4.4, selection in a segregating population was considered to be comparable with indirect selection for a primary character by means of a secondary character. Here, the primary character is the yield in monoculture at a commercial spacing of say m $cm^2$ $plant^{-1}$, because the selected genotypes ultimately have to perform in monoculture at that spacing. However, selection for yield is applied in a segregating population, that is in a mixture, at wider stands of say s times m $cm^2$ $plant^{-1}$. When we select for yield in a mixture at sm $cm^2$ $plant^{-1}$, a correlated response for yield in monoculture at m $cm^2$ $plant^{-1}$ will be the result. The expression for the correlated response is obtained from the definition (Eqn 4.36) as

$$CR_{mono,m} = i_{mix,sm} \frac{cov(g_{mix,sm}, g_{mono,m})}{\sqrt{var\ p_{mix,sm}}} \qquad (5.20)$$

where the spacing is indicated by the subscripts.

The covariance between genotypic yield in mixture at sm $cm^2$ $plant^{-1}$ and genotypic yield in monoculture at m $cm^2$ $plant^{-1}$ is

$$cov(\underline{O}_{sm}, \underline{M}_{m}) = cov(g_{mix,sm}, g_{mono,m})$$

From Eqn 5.13, we see that

$$cov(\underline{O}_{sm}, \underline{M}_{m}) = \frac{s}{1+t}\ cov(\underline{O}_{m}, \underline{M}_{m})$$

The latter covariance was already given in Eqn 4.54. Hence, we arrive at

$$cov(g_{mix,sm}, g_{mono,m}) = \frac{s}{1+t}\ (var\ \underline{g} + \mu\ cov(\underline{b}, \underline{g})) \qquad (5.21)$$

where the parameters at the right-hand side refer to a monoculture at m $cm^2$ $plant^{-1}$.

Substitution of Eqns 5.21 and 5.17 into 5.20 gives for the correlated response for yield in monoculture at m $cm^2$ $plant^{-1}$, brought about by selection for yield in

mixture at sm $cm^2$ $plant^{-1}$,

$$CR_{mono,m} = i_{mix,sm} \frac{\text{var } \underline{g} + \mu \text{ cov}(\underline{b},\underline{g})}{\sqrt{\text{var } \underline{g} + 2 \mu \text{ cov}(\underline{b},\underline{g}) + \mu^2 \text{var } \underline{b} + \text{var } \underline{e}}} \qquad (5.22)$$

Eqns 5.22 and 4.55 are equal because the expected rank of the genotypes in mixture is not affected by the density of stand. It is true, the yield per plant increases with wider spacings, but the multiplication factor is the same for all genotypes. This was shown in Section 5.3.1.

The bias due to intergenotypic competition and wide spacing is defined by the ratio of the correlated response of monoculture yield at m $cm^2$ $plant^{-1}$, when selection is for yield in mixture at sm $cm^2$ $plant^{-1}$, to the response in a hypothetical mixture at m $cm^2$ $plant^{-1}$ where intergenotypic competition is absent (see Eqn 4.38). This is expressed as

$$\text{degree of bias} = \frac{CR_{mono,m}}{R_{mono,m}} \qquad (5.23)$$

The degree of bias is found by division of Eqn 5.22 by Eqn 4.38.

With the bias expressed as a function of dimensionless parameters one can gain a better idea about the spurious effect of competition on selection (Section 4.4.4). The expression of Eqn 5.23 in terms of the dimensionless parameters is identical to that for the bias solely due to intergenotypic competition (Eqn 4.56). Also the equations of the constituents of CR/R, the coefficient $r_g$ of the genetic correlation between $\underline{O}_{sm}$ and $\underline{M}_m$ (Eqn 4.57), and the square root of the ratio between the heritability in mixture at sm $cm^2$ $plant^{-1}$ and the heritability in monoculture at m $cm^2$ $plant^{-1}$ (Eqn 4.58) are the same.

In conclusion, the bias brought about by selection in a mixture is not affected by the spacing at which the mixture is grown. With wider spacings, the bias due to inter-plant competition is replaced entirely by the bias due to competition against empty space. The latter stands for a different response of the genotypes to varying spacings. Therefore, growing of segregating populations at wide stands does not remove the biasing effect of competition on selection.

However, it must be kept in mind that the model is based on:

- The de Wit model that relates the yield of a genotype in mixture and monoculture to the density of stand. The assumptions underlying this model were given in Section 5.2 and are discussed in Section 5.6.
- A diffuse nature of competition. In barley, competition between individual plants can be reasonably characterized as diffuse competition (Section 4.2.2). The experiments dealt only with one spacing, namely 5 x 25 $cm^2$ $plant^{-1}$.
- Constancy of the CV over densities (Section 5.3.2), which was assumed to attune the environmental variance to the spacing.

*Summary* In this section, the progress due to selection in a segregating population, that is in a mixture, grown at wide stand is quantified. The progress is measured by the

correlated response for yield in monoculture at m $cm^2$ $plant^{-1}$, brought about by selection for yield in mixture at s times m $cm^2$ $plant^{-1}$. The bias in selection which arises from intergenotypic competition and wide spacing is defined as the ratio between this correlated response and the response in a hypothetic mixture at m $cm^2$ $plant^{-1}$ where intergenotypic competition is absent. The correlated response and the bias brought about by selection in mixture are unaffected by the spacing. Therefore, selection at wide spacings does not remove the spurious effect of competition on selection. With wider spacings, the bias due to interplant competition is entirely replaced by the bias due to competition against empty space.

*5.3.4 Bias due to differential response of the genotypes to spacing*

The joint effect of density response and interplant competition was studied. Now the bias solely accounted for by differential response to spacing, which also occurs in pure stand, is quantified. Hence, the effects of intergenotypic competition will be removed from the foregoing equations.

We have seen that genotypes may react differently to various spacings. Mostly, this reaction is measured by the genotype x density interaction in an analysis of variance (Section 5.1.1). The regression of yield on spacing, as applied by Sakai & Iyama (1966) measures the contribution of each genotype to the interaction. However, the present model provides a more rational, direct and powerful approach (see the advantages of the de Wit model mentioned in Section 3.3).

The genotypic yield per plant of a random genotype i in monoculture at sm $cm^2$ $plant^{-1}$ is given by Eqn 5.18 as

$$\underline{M}_{i,sm} = \frac{sb_i}{\underline{b}_i + t} \; \underline{M}_{i,m} \tag{5.18}$$

The phenotypic yield of i in monoculture at sm $cm^2$ $plant^{-1}$ can be presented in analogy to Eqn 4.50 as

$$\underline{P}_i = \underline{c}_i \; (\mu + \underline{g}_i) + \underline{e}_i \tag{5.24}$$

From Eqn 5.18, we see that

$$\underline{c}_i = \frac{s\underline{b}_i}{\underline{b}_i + t} \tag{5.25}$$

The phenotypic variance is found from Eqn 5.24 to be

$$\begin{aligned} \text{var } \underline{P}_{mono,sm} &= \text{var}(\underline{c}(\mu + \underline{g}) + \underline{e}) \\ &= \mu^2 \text{ var } \underline{c} + \text{var}(\underline{c}\,\underline{g}) + 2\mu \text{ cov}(\underline{c},\underline{c}\,\underline{g}) + \text{var } \underline{e} \end{aligned} \tag{5.26}$$

Allowance has yet to be made for the density dependence of the error variance (Eqn 5.19). Substitution of Eqns 5.19 and 5.25 and, thereafter, repeated use of the

differential method results in

$$\text{var } \underline{p}_{\text{mono,sm}} \approx \frac{s^2}{(1+t)^2} \text{ var } \underline{g} + \frac{2\mu ts^2}{(1+t)^3} \text{cov}(\underline{b},\underline{g}) + \frac{\mu^2 s^2 t^2}{(1+t)^4} \text{ var } \underline{b} +$$

$$+ \frac{s^2}{(1+t)^2} \text{ var } \underline{e} \qquad (5.27)$$

The total, phenotypic variance can be partitioned into the variance among the genotypic yields, that is the genetic variance

$$\text{var } \underline{g}_{\text{mono,sm}} \approx \frac{s^2}{(1+t)^2} \text{ var } \underline{g} + \frac{2\mu ts^2}{(1+t)^3} \text{cov}(\underline{b},\underline{g}) + \frac{\mu^2 s^2 t^2}{(1+t)^4} \text{ var } \underline{b} \qquad (5.28)$$

and the environmental variance

$$\text{var } \underline{e}_{\text{mono,sm}} \approx \frac{s^2}{(1+t)^2} \text{ var } \underline{e} \qquad (5.29)$$

The variances on the left side of the equations hold for single plants grown in monoculture at sm $cm^2$ $plant^{-1}$. When plot means of genotypes are considered, instead of yields of individual plants, the environmental variance must be that belonging to the means.

When selection is applied at wide stands, the direct response for yield at wide spacing brings about a simultaneous correlated response for monoculture yield in commercial stands. This correlated response is defined in Eqn 4.36. From this, we can write

$$CR_{\text{mono,m}} = i_{\text{mono,sm}} \frac{\text{cov}(\underline{g}_{\text{mono,sm}},\underline{g}_{\text{mono,m}})}{\sqrt{\text{var } \underline{p}_{\text{mono,sm}}}} \qquad (5.30)$$

The phenotypic variance was already expressed in Eqn 5.27. The covariance can be recast as

$$\text{cov}(\underline{g}_{\text{mono,sm}},\underline{g}_{\text{mono,m}}) = \text{cov}(\underline{M}_{i,\text{sm}},\underline{M}_{i,\text{m}})$$

$$= \text{cov}(\underline{c}_i(\mu + \underline{g}_i), (\mu + \underline{g}_i))$$

$$= \mu \text{ cov}(\underline{c}_i,\underline{g}_i) + \text{cov}(\underline{c}_i \underline{g}_i,\underline{g}_i)$$

After substitution of Eqn 5.25 for $\underline{c}_i$, the differential approximates become

$$\text{cov}(\underline{c}_i,\underline{g}_i) \approx \frac{st}{(1+t)^2} \text{ cov}(\underline{b}_i,\underline{g}_i)$$

$$\text{cov}(\underline{c}\ \underline{g}_i,\underline{g}_i) \approx \frac{s}{1+t} \text{ var } \underline{g}_i$$

Therefore

$$\mathrm{cov}(g_{\mathrm{mono},sm},\ g_{\mathrm{mono},m}) = \frac{s}{1+t}\ \mathrm{var}\ \underline{g} + \frac{\mu s t}{(1+t)^2}\ \mathrm{cov}(\underline{b},\underline{g}) \tag{5.31}$$

The correlated response for monoculture yield at m $cm^2$ $plant^{-1}$, brought about by selection for yield in a monoculture at sm $cm^2$ $plant^{-1}$, is obtained by substitution of Eqns 5.27 and 5.31 into Eqn 5.30 as

$$CR_{\mathrm{mono},m} = i_{\mathrm{mono},sm}\ \frac{\mathrm{var}\ \underline{g} + \frac{\mu t}{1+t}\ \mathrm{cov}(\underline{b},\underline{g})}{\sqrt{\mathrm{var}\ \underline{g} + \frac{2\mu t}{1+t}\ \mathrm{cov}(\underline{b},\underline{g}) + \frac{\mu^2 t^2}{(1+t)^2}\ \mathrm{var}\ \underline{b} + \mathrm{var}\ \underline{e}}} \tag{5.32}$$

Similar to Eqn 5.23, the bias due to selection at a deviating spacing is defined by the ratio of the correlated response of monoculture yield at m $cm^2$ $plant^{-1}$, when selection is for yield in a monoculture at sm $cm^2$ $plant^{-1}$, to the response of direct selection in monoculture at m $cm^2$ $plant^{-1}$.

With the bias CR/R expressed in terms of dimensionless parameters one can gain a better idea of the spurious effect of competition on selection. It can be derived that

$$\frac{CR}{R} = \frac{i_{\mathrm{mono},sm}}{i_{\mathrm{mono},m}}\ \frac{t + 1 + (t + \tfrac{1}{2})r_{bg}\sqrt{\gamma}}{\sqrt{(2t+1)(t+1)r_{bg}h^2\sqrt{\gamma} + (t^2+t+3/8)h^2\gamma + (t+1)^2}} \tag{5.33}$$

where $h^2$ the heritability in monoculture at m $cm^2$ $plant^{-1}$, $r_{bg}$ the coefficient of the correlation between $\underline{b}$ and $\underline{g}$ and $\gamma = \mu^2 \mathrm{var}\ \underline{b}/\mathrm{var}\ \underline{g}$ the competitive stress.

In analogy to Eqn 4.40, the bias CR/R can be partioned into the coefficient $r_g$ of the genetic correlation between $\underline{M}_{sm}$ and $\underline{M}_m$ and the square root of the ratio between the heritability in monoculture at sm $cm^2$ $plant^{-1}$ and that in monoculture at m $cm^2$ $plant^{-1}$:

$$\frac{CR}{R} = \frac{i_{\mathrm{mono},sm}}{i_{\mathrm{mono},m}}\ r_g\ \frac{h_{\mathrm{mono},sm}}{h_{\mathrm{mono},m}}$$

We can derive

$$r_g = \frac{t+1 + (t+\tfrac{1}{2})\ r_{bg}\sqrt{\gamma}}{\sqrt{(t+1)^2 + (2t+1)(t+1)r_{bg}\sqrt{\gamma} + (t+\tfrac{1}{2})^2\gamma}} \tag{5.34}$$

$$\frac{h_{\mathrm{mono},sm}}{h_{\mathrm{mono},m}} = \sqrt{\frac{(t+1)^2 + (2t+1)(t+1)\ r_{bg}\sqrt{\gamma} + (t+\tfrac{1}{2})^2\gamma}{(2t+1)(t+1)r_{bg}h^2\sqrt{\gamma} + (t^2+t+3/8)h^2\gamma + (t+1)^2}} \tag{5.35}$$

With wider spacings, the interplant competition decreases. Hence, at increased spacings the expected yield of the genotypes in mixture approaches their expected yield in monoculture. Consequently, the above equations for monocultures approach their counterparts for mixtures which were given in Section 5.3.3. An illustration is given in Fig. 24.

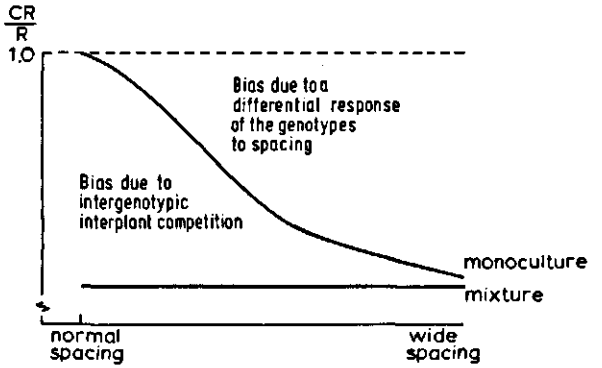


Fig. 24. Effect of plant spacing on the ratio of the correlated response CR brought about by selection at a certain spacing in monoculture or mixture, and the direct response to selection R in monoculture at a normal spacing.

When genotypes are tested in monoculture, it is useful to know what the optimal spacing for yield testing is. In particular, it may be questioned whether a sparse stand is more efficient for selection than a normal stand. Information can be obtained from Eqn 5.33 by taking the first derivative to s. This shows that the ratio of the correlated and the direct response to selection (Eqn 5.33) has a maximum at the optimal spacing $s_{opt}$ x m $cm^2$ $plant^{-1}$ with

$$s_{opt} = 1 + \frac{1}{b_e} \frac{r_{bg}\,(1-h^2)}{h^2\,(1-r^2_{bg})\,\sqrt{\gamma} - r_{bg}\,(1-h^2)} \qquad (5.36)$$

*Summary* The components of variance and the response to selection are expressed as function of the spacing. Effects of intergenotypic competition are excluded. Hence, the equations define the effect of spacing in absence of intergenotypic competition, that is in monoculture.

### *5.3.5 The crowding coefficient as function of the spacing*

The crowding coefficient in the preceding sections holds for a population at m $cm^2$ $plant^{-1}$. We have seen that the strength of interplant competition diminishes with increased density. Hence, the density of stand affects the magnitude of the crowding coefficient. It is useful to quantify the density dependence of the crowding coefficient.

The genotypic yield per plant of genotype i in a mixture where all genotypes are at equal frequencies and at sm $cm^2$ $plant^{-1}$ is given by Eqn 4.14 as

$$O_{i,sm} = b_{i,sm} M_{i,sm}$$

In Eqn 5.12, the genotypic yield in mixture at sm $cm^2$ $plant^{-1}$ is related to the genotypic yield in monoculture at m $cm^2$ $plant^{-1}$ as

$$O_{i,sm} = \frac{s}{1+t} \; b_{i,m} \; M_{i,m}$$

Combining both equations results in

$$\frac{s}{1+t} \; b_{i,m} M_{i,m} = b_{i,sm} M_{i,sm} \tag{5.37}$$

According to Eqn 5.18, the genotypic monoculture yields of genotype i at two spacings relate to each other as

$$M_{i,sm} = \frac{s \; b_{i,m}}{b_{i,m} + t} \; M_{i,m}$$

Substitution of this expression for $M_{i,sm}$ into Eqn 5.37 and omitting the subscript i supplies

$$b_{sm} = \frac{b_m + t}{1 + t} = \frac{b_m + (s-1)b_{e,m}}{1 + (s-1)b_{e,m}} \tag{5.38}$$

For the variance we find

$$\text{var } \underset{\sim}{b}_{sm} = \frac{1}{(1+t)^2} \; \text{var } \underset{\sim}{b}_m \tag{5.39}$$

Starting from a population of m $cm^2$ $plant^{-1}$, when the spacing becomes wider, s increases and with that t. Hence, var $\underset{\sim}{b}_{sm}$ declines from var $\underset{\sim}{b}_m$ to zero. This can easily be understood. When the plants are spaced wider, the interplant and intergenotypic competition decreases and, consequently, the crowding coefficients draw to unity and their variance reduces. At very scanty stands the plants do not interfere, so their yield in mixture equals that in pure stand and the crowding coefficients are all unity.

In the preceding sections, a model was presented to quantify the effect of spacing on the components of variance (Section 5.3.1) and the response to selection (Sections 5.3.3 and 5.3.4). The input variables are at a reference spacing of m $cm^2$ $plant^{-1}$. However the input variables are dependent on density. More insight into the model is obtained by quantifying the density dependence of the input variables whereby quantities estimated at a certain spacing can be transformed to the reference spacing of m $cm^2$ $plant^{-1}$

The relation between the average monoculture yield at sm $cm^2$ $plant^{-1}$ and that at m $cm^2$ $plant^{-1}$ can be derived from Eqn 5.18a to be

$$\mu_{sm} = \frac{s}{1+t} \; \mu_m \tag{5.40}$$

Eqn 5.18 for the genotypic monoculture yield at sm $cm^2$ $plant^{-1}$ can be rewritten to

$$\underset{\sim}{g}_{sm} = \frac{s \; \underset{\sim}{b}_m}{\underset{\sim}{b}_m + t} \; (\mu_m + \underset{\sim}{g}_m) - \mu_{sm} \tag{5.41}$$

The relation between $\underset{\sim}{b}_{sm}$ and $\underset{\sim}{b}_m$ was already presented by Eqn 5.38. The environmental variance in monoculture at sm $cm^2$ $plant^{-1}$ is given by Eqn 5.19 as

$$\text{var } \underline{e}_{sm} = \frac{s^2}{(1+t)^2} \text{ var } \underline{e}_m \qquad (5.42)$$

Substitution of the foregoing equations into the expressions for the variances and for the response to selection in mixture, as these were described in Sections 4.3 and 4.4, produces the correponding expressions of Sections 5.3.1 and 5.3.3 which take account of the spacing effect. For example, substitution of Eqns 5.38, 5.40, 5.41 and 5.42 into Eqn 4.51 for the phenotypic variance in mixture results in Eqn 5.17.

It can be shown that the coefficient of the correlation between $\underline{b}$ and $\underline{g}_{mono}$ depends on the spacing, that is

$$r_{\underline{b}_{sm}\underline{g}_{sm}} \neq r_{\underline{b}_m\underline{g}_m}$$

Substitution of Eqns 5.39, 5.40 and 5.41 into the definition of the competitive stress $\gamma = \mu^2 \text{ var } \underline{b}/\text{var } \underline{g}$ shows that, in general, the competitive stress decreases the wider the spacing. That is, in general,

$$\gamma_{sm} < \gamma_m$$

*Summary* The density dependence of the crowding coefficient b and of the other input variables of the present competition and density model is quantified.

## 5.4 PROGENY TESTING IN SINGLE ROWS IN MIXTURE AT WIDE STAND (NEAREST-NEIGHBOUR COMPETITION)

In Section 5.3, the influence of spacing and intergenotypic competition on the components of variance and on the response to selection is defined for single plants as unit of selection. The yield of a single plant seems to be affected by the relative frequencies of the genotypes in the mixture, whereas the genotype of the direct neighbours has no influence as such (diffuse competition, Section 4.2.2). On the other hand, in barley, the competitive influence of a row was restricted to its adjacent neighbours (Section 4.2.2). Therefore, when rows are the unit of selection, a model is required that somewhat deviates from the model for single plants (Section 4.2.1). The procedure that will be applied in this section runs parallel to that used in Section 5.3 for single plants. Details are therefore not repeated.

Breeders aim at selecting genotypes that yield high when they are grown in monoculture at a commercial row spacing. However, the progenies of selected plants are tested in rows. Each progeny in a single row. As the progenies differ from each other with respect to their genetic composition, progeny testing is biased by intergenotypic competition between the rows. Many authors suggested to grow the rows far apart in order to decrease the interrow competition. Then progeny testing occurs in a mixture at a wide row distance. However, it was shown in Section 5.3 that, under certain assumptions, at a wide stand no competitional bias is removed. Although, the model for interrow competition somewhat deviates from the model used in Section 5.3, it will be shown again that the competitional bias is hardly changed by growing the rows further apart.

5.4.1.1 Expected yield in mixture at wide stand

Breeders aim to select those progenies that yield high in monoculture at a commercial row spacing of say m cm row$^{-1}$. However, selection is supposed to occur in a mixed stand at a wide row spacing of say s times m cm row$^{-1}$. This can be presented by

monoculture of i at m cm row$^{-1}$ i i i i i i i i i (Arr. 5.1)

monoculture at 3 m cm row$^{-1}$ e e h e e i e e j (Arr. 5.2)

where each letter denotes a single row and 'e' is an empty row. The sowing density within a row in the selection nursery is supposed to be equal to that under farmers' practice.

To derive the expected (genotypic) yield of the random genotype i, situated between the random genotypes h and j, a procedure is followed similar to that described in Section 4.2.1. At first, we consider a 1:1 mixture of h and i. At a spacing of 3 m cm row$^{-1}$ this can be presented by

i e e h e e i e e h e e i e e h e e (Arr. 5.3).

The genotypic yield per row of h, in the 1:1 mixture with i, at sm cm row$^{-1}$ can be derived from Eqn 5.9 to be

$$O_{h,sm} = \frac{2sb_h}{b_i + b_h + 2(s-1)b_e} M_{h,m} = \frac{2sb_h}{b_i + b_h + 2t} M_{h,m} \qquad (5.43)$$

where, for convenience, we have used the notation $t = (s-1)b_e$. The genotypic yield per row of h in monoculture at sm cm row$^{-1}$ is given by Eqn 5.18 as

$$M_{h,sm} = \frac{sb_h}{b_h + t} M_{h,m}$$

Substitution into Eqn 5.43 produces

$$O_{h,sm} = \frac{2b_h + 2t}{b_i + b_h + 2t} M_{h,sm} \qquad (5.44)$$

When we replace in the 1:1 mixture of Arrangement 5.3 every second h row by a j row, we obtain

i e e h e e i e e j e e i e e h e e (Arr. 5.4).

We assume that a row, sown with a progeny, is only affected by its adjacently sown neighbour rows. Hence, a row is fully protected by its neighbour rows against competition from rows that are further away. On the other hand, we assume that an empty row gives no protection at all against the competitive influence of other rows. Then, the yield of h in Arrangement 5.4 equals the yield of h in the alternated 1:1 mixture of h and i (Arr. 5.3). Thus the genotypic yield of h in Arrangement 5.4 is given by Eqn 5.44. Similarly, the genotypic yield of j in this mixture is

$$O_{j,sm} = \frac{2b_j + 2t}{b_i + b_j + 2t} M_{j,sm}$$

We write for the genotypic yield of i in Arrangement 5.4

$$O_{i,sm} = xM_{i,sm}$$

Then, in Arrangement 5.4, the weighted sum of the relative yields $O'_{sm}/M'_{sm}$ equals

$$RYT = \tfrac{1}{2}x + \tfrac{1}{4}\frac{2b_h + 2t}{b_i + b_h + 2t} + \tfrac{1}{4}\frac{2b_j + 2t}{b_i + b_j + 2t}$$

RYT = 1 when the genotypes compete for the same space (Section 4.2.1). Now, x can be solved and substituted into $O_{i,sm} = xM_{i,sm}$. Now we find for the genotypic yield of i situated between h and j

$$O_{i,sm} = \left(\left(1 - \frac{b_h + t}{b_i + b_h + 2t}\right) + \left(1 - \frac{b_j + t}{b_i + b_j + 2t}\right)\right) M_{i,sm} \qquad (5.45)$$

Substitution of Eqn 5.18 for the monoculture yield at sm cm row$^{-1}$ gives

$$O_{i,sm} = \frac{sb_i(2b_i + b_h + b_j + 4t)}{(b_i + b_h + 2t)(b_i + b_j + 2t)} M_{i,m} \qquad (5.46)$$

When we replace in Arrangement 5.4 all sown rows, except one row of i and both its neighbour rows h and j, by rows with a different genetic composition, we obtain an arrangement that is characteristic for a selection nursery. For, in a selection nursery, each row will have a unique genetic composition. Under the assumption that the effect of second and higher-order neighbours is negligible, the expected yield of i, situated between h and j, will satisfy Eqn 5.46, whatever the genotype of its second and higher-order neighbours.

5.4.1.2 Phenotypic variance

To express the components of the variance among rows, an approach similar to that of Section 4.3 is used. The phenotypic performance of a row of a random genotype i situated between rows with the random genotypes h and j, respectively, is given by the stochastic expression

$$\underline{p}_{i,hj} = \underline{c}_{i,hj}(\mu + \underline{g}_i) + \underline{e}_i \qquad (4.21)$$

where $\mu$ the mean of the monocultures, $\underline{g}_i$ the deviation of the monoculture yield of i from $\mu$, $\underline{c}$ a multiplication factor describing the effect of intergenotypic competition, and $\underline{e}$ the environmental error (Section 4.3.1.1). The expectations are $\varepsilon\underline{g} = 0$ and $\varepsilon\underline{e} = 0$. Eqn 5.46 supplies

$$\underline{c}_{i,hj} = \frac{sb_i(2\underline{b}_i + \underline{b}_h + \underline{b}_j + 4t)}{(\underline{b}_i + \underline{b}_h + 2t)(\underline{b}_i + \underline{b}_j + 2t)} \qquad (5.47)$$

Since the bs are set to an expectation value of unity, the expectation of $\underline{c}$ approximates

$$\varepsilon \underline{c} \approx \frac{s}{1+t} \tag{5.48}$$

The phenotypic variance can be broken down according to Eqn 4.21 as

$$\text{var } \underline{p} = \text{var}(\underline{c}\mu + \underline{c}\,\underline{g} + \underline{e}) = \text{var } (\underline{c}\mu + \underline{c}\,\underline{g}) + 2\,\text{cov}((\underline{c}\mu + \underline{c}\,\underline{g}), \underline{e}) + \text{var } \underline{e}$$

When the genotypes are randomly distributed across the field, the genetic effects, $\underline{g}$ as well as $\underline{b}$, are not correlated with the environmental effects. As $\underline{b}$ and $\underline{e}$ are uncorrelated, $\underline{c}$ and $\underline{e}$ are also uncorrelated. Hence,

$$\text{cov}((\underline{c}\mu + \underline{c}\,\underline{g}), \underline{e}) = 0$$

The phenotypic variance appears in the form

$$\text{var } \underline{p} = \mu^2 \text{ var } \underline{c} + \text{var } (\underline{c}\,\underline{g}) + 2\mu \text{ cov}(\underline{c}, \underline{c}\,\underline{g}) + \text{var } \underline{e} \tag{5.49}$$

Use of the method of statistical differentials (Section 4.3.1.2) provides

$$\text{var}(\underline{c}\,\underline{g}) \approx (\varepsilon\,\underline{c})^2 \text{ var } \underline{g} + 2(\varepsilon\,\underline{c})(\varepsilon\,\underline{g}) \text{ cov}(\underline{c}, \underline{g}) + (\varepsilon\,\underline{g})^2 \text{ var } \underline{c}$$

$$= \left(\frac{s}{1+t}\right)^2 \text{var } \underline{g}$$

$$\text{cov}(\underline{c}, \underline{c}\,\underline{g}) \approx (\varepsilon\,\underline{g}) \text{ var } \underline{c} + (\varepsilon\,\underline{c}) \text{ cov}(\underline{c}, \underline{g}) = \frac{s}{1+t} \text{ cov}(\underline{c}, \underline{g})$$

So we obtain for the phenotypic variance

$$\text{var } \underline{p} \approx \frac{s^2}{(1+t)^2} \text{ var } \underline{g} + 2\mu \frac{s}{1+t} \text{ cov}(\underline{c},\underline{g}) + \mu^2 \text{ var } \underline{c} + \text{var } \underline{e} \tag{5.50}$$

According to Eqn 5.47 the competitional variance is

$$\text{var } \underline{c}_{i,hj} = \text{var } \frac{s\underline{b}_i(2\underline{b}_i + \underline{b}_h + \underline{b}_j + 4t)}{(\underline{b}_i + \underline{b}_h + 2t)(\underline{b}_i + \underline{b}_j + 2t)}$$

The bs are set to an expectation value of unity, they are uncorrelated and have variance var $\underline{b}$. Worked out according to the method of statistical differentials, the competitional variance becomes

$$\text{var } \underline{c} \approx \frac{s^2\,(t^2+t+3/8)}{(1+t)^4} \text{ var } \underline{b} \tag{5.51}$$

The covariance between the competition coefficient $\underline{c}_{i,hj}$ and the genotypic performance in monoculture $\underline{g}_i$ can, according to Eqn 5.47, be developed as

$$\text{cov}(\underline{c}_{i,hj},\underline{g}_i) \approx \frac{s(t+1)}{(1+t)^2} \text{ cov}(\underline{b},\underline{g}) \tag{5.52}$$

Substitution of Eqns 5.51 and 5.52 into Eqn 5.50 supplies the phenotypic variance in

mixture at a spacing of sm cm row$^{-1}$

$$\text{var } \underline{p} = \frac{s^2}{(1+t)^2} \text{ var } \underline{g} + \frac{\mu s^2(2t+1)}{(1+t)^3} \text{ cov}(\underline{b},\underline{g}) + \frac{\mu^2 s^2(t^2+t+3/8)}{(1+t)^4} \text{ var } \underline{b} + \\ + \text{var } \underline{e} \qquad (5.53)$$

where $t=(s-1)b_e$. Note that the parameters on the right side are for monocultures at m cm row$^{-1}$.

When the mixture is grown at the same row distance as the monoculture, s=1 and with that t=0. Substitution of these values reduces Eqn 5.53 to Eqn 4.28.

With wider spacing, the yields of single rows increase considerably. Consequently, the environmental variance of individual rows increases too. It was assumed that the coefficient of variation is constant over densities (Section 5.3.2). According to Eqn 5.19, this assumption gives

$$\text{var } \underline{e}_{sm} = \frac{s^2}{(1+t)^2} \text{ var } \underline{e}_m \qquad (5.54)$$

Although this derivation was done for single plants as unit of selection, it holds for single rows too. For, in monocultures, the competition model for single rows is equivalent to that for single plants (Section 5.4.3). Substitution of Eqn 5.54 into Eqn 5.53 gives for the phenotypic variance in mixture at sm cm row$^{-1}$

$$\text{var } \underline{p} = \frac{s^2}{(1+t)^2} \text{ var } \underline{g} + \frac{\mu s^2(2t+1)}{(1+t)^3} \text{ cov}(\underline{b},\underline{g}) + \frac{\mu^2 s^2(t^2+t+3/8)}{(1+t)^4} \text{ var } \underline{b} + \\ + \frac{s^2}{(1+t)^2} \text{ var } \underline{e} \qquad (5.55)$$

5.4.1.3 Genetic and environmental variance

The effects of intergenotypic competition on the phenotypic variance can be split up into (a) the change of the variance between genotypes and (b) the increase of the environmental variation. The same approach can be used as in Section 4.3.1.4. Again the population to be selected is imagined to be made up of genotypes replicated throughout the nursery.

The expected yield of i in mixture is provided by

$$\varepsilon \underline{O}_i = (\varepsilon \underline{c}_{i,hj})(\mu + g_i)$$

with, according to Eqn 5.47, the expected competition effects on i are

$$\varepsilon \underline{c}_{i,hj} = \varepsilon \left( \frac{s b_i (2b_i + \underline{b}_h + \underline{b}_j + 4t)}{(b_i + \underline{b}_h + 2t)(b_i + \underline{b}_j + 2t)} \right)$$

where i is fixed. The genotypes are allotted to each other at random, so $\varepsilon \underline{b}_h = \varepsilon \underline{b}_j = 1$ and we find

$$\epsilon \underline{c}_i \simeq \frac{2sb_i}{b_i+1+2t}$$

so

$$\epsilon \underline{O}_i \simeq \frac{2sb_i}{b_i+1+2t} \quad (\mu + g_i)$$

The variance among the expected yields of the genotypes in mixture is

$$\text{var } \underline{O} = \text{var } \left(\left(\frac{2s\underline{b}}{\underline{b}+1+2t}\right) (\mu + \underline{g})\right)$$

$$= 4\mu^2 s^2 \text{ var } \left(\frac{\underline{b}}{\underline{b}+1+2t}\right) + 4s^2 \text{ var } \left(\frac{\underline{b}\ \underline{g}}{\underline{b}+1+2t}\right) + 8\mu s^2 \text{ cov } \left(\frac{\underline{b}}{\underline{b}+1+2t} , \frac{\underline{b}\ \underline{g}}{\underline{b}+1+2t}\right)$$

This Equation can be simplified by using the differential method and substituting $\epsilon \underline{b}=1$ and $\epsilon \underline{g}=0$. Adoption of the notation var $\underline{g}_{mix,sm}$ = var $\underline{O}$ for the genetic variance in mixture at sm cm row$^{-1}$ gives

$$\text{var } \underline{g}_{mix,sm} \simeq \frac{s^2}{(1+t)^2} \text{ var } \underline{g} + \frac{\mu s^2(2t+1)}{(1+t)^3} \text{ cov } (\underline{b},\underline{g}) + \frac{\mu^2 s^2(t^2+t+\frac{1}{4})}{(1+t)^4} \text{ var } \underline{b} \qquad (5.56)$$

where the parameters on the right side are for monocultures at m cm row$^{-1}$.

The phenotypic variance between rows belonging to genotype i, with random neighbours h and j, is expressed in accordance with Eqn 4.21 as

$$\text{var } \underline{p}_{i,hj} = \text{var } (\underline{c}_{i,hj}(\mu + g_i)) + \text{var } \underline{e}_i$$

As i is fixed, we have

$$\text{var } \underline{p}_{i,hj} = (\mu + g_i)^2 \text{ var } \underline{c}_{i,hj} + \text{var } \underline{e}_i$$

It can be derived from Eqn 5.47 by means of the method of statistical differentials that, when $b_i$ is fixed

$$\text{var } \underline{c}_{i,hj} \simeq \frac{2s^2 b^2_i}{(b_i+1+2t)^4} \text{ var } \underline{b}$$

So we have for the environmental variance within genotype i in mixed stand

$$\text{var } \underline{p}_{i,hj} \simeq \frac{2s^2 b^2_i (\mu+g_i)^2}{(b_i+1+2t)^4} \text{ var } \underline{b} + \text{var } \underline{e}_i$$

For this expression we use the notation var $\underline{e}_{i,mix,sm}$. The expected environmental variance within a genotype in mixed stand at sm cm row$^{-1}$ is

$$\text{var } \underline{e}_{mix,sm} = \epsilon \text{ var } \underline{e}_{i,mix,sm} \simeq \frac{\frac{1}{8}\mu^2 s^2}{(1+t)^4} \text{ var } \underline{b} + \text{var } \underline{e}$$

where var $\underline{e}$ in monoculture at m cm row$^{-1}$. Taking into account the density dependence of the error variance, expressed by Eqn 5.54, we get

$$\text{var } \underline{e}_{mix,sm} \approx \frac{\frac{1}{8}\mu^2 s^2}{(1+t)^4} \text{ var } \underline{b} + \frac{s^2}{(1+t)^2} \text{ var } \underline{e} \qquad (5.57)$$

The phenotypic variance in mixture is

$$\text{var } p_{mix} = \text{var } g_{mix} + \text{var } \underline{e}_{mix}$$

Substitution of Eqns 5.56 and 5.57 gives

$$\text{var } p_{mix,sm} \approx \frac{s^2}{(1+t)^2} \text{ var } g + \frac{\mu s^2(2t+1)}{(1+t)^3} \text{ cov } (\underline{b},g) + \frac{\mu^2 s^2(t^2+t+3/8)}{(1+t)^4} \text{ var } \underline{b}$$

$$+ \frac{s^2}{(1+t)^2} \text{ var } \underline{e} \qquad (5.58)$$

where the parameters on the right side are at m cm$^2$ plant$^{-1}$ and in monoculture. Evidently, Eqn 5.58 is identical to Eqn 5.55.

When the row spacing becomes extremely wide, s approaches infinity and with that $t = (s-1)b_e$ approaches infinity. The limits of the phenotypic variance (Eqn 5.58), the genetic variance (Eqn 5.56) and the environmental variance (Eqn 5.57) for s approaching infinity, can be proved to be equal to the correponding equations for the interplant-competition model (Eqns 5.17, 5.15 and 5.16, respectively). This is obvious as, at very wide spacings, interrow competition is absent and, therefore, the assumption that competition is only between adjacent neighbours is no longer necessary. The plant and the row competition model differ from each other with respect to this assumption. Hence, the wider the spacing the smaller the difference between both models.

*Summary* A model is introduced that defines the effect of row spacing and intergenotypic interrow competition on the expected yield per row and on the phenotypic, genetic and environmental variance among rows. The model will be of value for progeny testing in rows. The model is developed in analogy to that for single plants (Section 5.3). Unlike the interplant-competition model (diffuse competition), the interrow-competition model is based on the assumption that the competitive influence of an experimental unit is restricted to its adjacent neighbours (nearest-neighbour competition).

### *5.4.2 Response to selection in mixture at wide stand*

As the main interest of breeders is the response to selection, the bias due to intergenotypic interrow competition and wide row spacing is defined in terms of a change in the response to selection. Again the procedure is similar to that for single plants (Section 5.3.3). When selection is for yield in a mixture at a spacing of sm cm row$^{-1}$, a correlated response for yield in monoculture at m cm row$^{-1}$ is the result. The expression for the correlated response is given by Eqn 5.20 as

$$CR_{mono,m} = i_{mix,sm} \frac{cov(g_{mix,sm} , g_{mono,m})}{\sqrt{var\ p_{mix,sm}}} \qquad (5.20)$$

The covariance between the expected yield in mixture at sm cm row$^{-1}$ and the expected yield in monoculture at m cm row$^{-1}$ can be expanded to

$$cov(\varepsilon\underline{O}_{i,sm} , \varepsilon\underline{M}_{i,m}) = cov(\underline{g}_{mix,sm} , \underline{g}_{mono,m})$$

$$= cov(\underline{c}_i (\mu + \underline{g}_i) , (\mu + \underline{g}_i))$$

$$= \mu\ cov(\underline{c}_i , \underline{g}_i) + cov(\underline{c}_i\underline{g}_i , \underline{g}_i)$$

As the expectations $\varepsilon\underline{O}_i$ and $\varepsilon\underline{M}_i$ are involved, in Eqn 5.47 for $\underline{c}_{i,hj}$, $\underline{b}_h$ and $\underline{b}_j$ are replaced by their expectation values that equal unity. This gives

$$\underline{c}_i = \frac{2s\underline{b}_i}{\underline{b}_i+1+2t}$$

Substitution of this quantity in the covariances and employment of the statistical differentials give

$$cov(\underline{c}_i,\underline{g}_i) \simeq \frac{s(\frac{1}{2}+t)}{(1+t)^2}\ cov(\underline{b}_i,\underline{g}_i)$$

$$cov(\underline{c}_i\underline{g}_i,\underline{g}_i) \simeq \frac{s}{1+t}\ var\ \underline{g}_i$$

Now we obtain

$$cov(\underline{g}_{mix,sm} , \underline{g}_{mono,m}) \simeq \frac{s}{1+t}\ var\ \underline{g} + \frac{\mu s(\frac{1}{2}+t)}{(1+t)^2}\ cov(\underline{b},\underline{g}) \qquad (5.59)$$

The correlated response can be elaborated by substitution of Eqns 5.58 and 5.59 into Eqn 5.20. This gives

$$CR_{mono,m} \simeq i_{mix,sm} \frac{var\ \underline{g} + \frac{\mu(\frac{1}{2}+t)}{1+t}\ cov\ (\underline{b},\underline{g})}{\sqrt{var\ \underline{g} + \frac{\mu(2t+1)}{1+t}\ cov\ (\underline{b},\underline{g}) + \frac{\mu^2(t^2+t+3/8)}{(1+t)^2}\ var\ \underline{b} + var\ \underline{e}}} \qquad (5.60)$$

The bias due to intergenotypic competition and wide spacing is defined by the ratio of the correlated response of monoculture yield at m cm row$^{-1}$, when selection is for yield in mixture at sm cm row$^{-1}$, to the response in a hypothetic mixture at m cm row$^{-1}$ where intergenotypic competition is absent (see Eqns 4.38 and 5.23). The degree of bias CR/R is found by division of Eqn 5.60 by Eqn 4.38.

To gain more insight of the bias, the approach of Section 4.4. with dimensionless parameters is used. The degree of bias is presented analogously to Eqn 4.40 by

$$\frac{CR}{R} = \frac{i_{mix,sm}}{i_{mono,m}} \; r_g \; \frac{h_{mix,sm}}{h_{mono,m}} \qquad (5.61)$$

*It can be worked out, after substitution of Eqns 5.56 and 5.59 into Eqn 4.37, that the* coefficient of the genetic correlation between $\varepsilon O_{sm}$ and $\varepsilon M_{sm}$ is

$$r_g = \frac{t+1+(t+\frac{1}{2})\; r_{bg}\sqrt{\gamma}}{\sqrt{(t+1)^2 + (2t+1)(t+1)\; r_{bg}\sqrt{\gamma} + (t+\frac{1}{2})^2\,\gamma}} \qquad (5.62)$$

and, after substitution of Eqns 5.56 and 5.58 into Eqn 4.41, that the square root of the ratio of the heritabilities satisfies

$$\frac{h_{mix,sm}}{h_{mono,m}} = \sqrt{\frac{(t+1)^2 + (2t+1)(t+1)\; r_{bg}\sqrt{\gamma} + (t+\frac{1}{2})^2\,\gamma}{(2t+1)(t+1) r_{bg} h^2\sqrt{\gamma} + (t^2+t+3/8)h^2\,\gamma + (t+1)^2}} \qquad (5.63)$$

Substitution of Eqns 5.62 and 5.63 into Eqn 5.61 gives for the degree of bias

$$\frac{CR}{R} = \frac{i_{mix,sm}}{i_{mono,m}} \; \frac{t+1+(t+\frac{1}{2})\; r_{bg}\sqrt{\gamma}}{\sqrt{(2t+1)(t+1)\; r_{bg}\, h^2\sqrt{\gamma} + (t^2+t+3/8)\, h^2\,\gamma + (t+1)^2}} \qquad (5.64)$$

where $h^2$ the heritability in monoculture at m cm row$^{-1}$, $r_{bg}$ the coefficient of the correlation between $\underline{b}$ and $\underline{g}$ and $\gamma = \mu^2$ var $\underline{b}$/var $\underline{g}$ the competitive stress.

The first derivatives to s show that the correlation between yield in mixture at sm cm row$^{-1}$ and yield in pure culture at m cm row$^{-1}$ (Eqn 5.62) consistently decreases with increasing s, that the ratio of the heritabilities (Eqn 5.63) has a minimum at

$$s = 1 - \frac{1}{b_e}\,\frac{r_{bg} + \frac{1}{2}\sqrt{\gamma}}{r_{bg} + \sqrt{\gamma}}$$

and that the ratio of the correlated and the direct response to selection (Eqn 5.64) has a maximum at

$$s_{opt} = 1 + \frac{1}{b_e}\,\frac{h^2\sqrt{\gamma}\,(2r_{bg}^2 - 1 + r_{bg}\sqrt{\gamma}) + 4r_{bg}\,(1-h^2)}{4h^2\sqrt{\gamma}\,(1-r_{bg}^2) - 4r_{bg}\,(1-h^2)} \qquad (5.65)$$

where $b_e$ the crowding coefficient of empty space.

The breeder aims to select genotypes that produce the highest yield in monoculture at a commercial stand of m cm row$^{-1}$. Selection occurs necessarily in a mixture and can be done, from a theoretical point of view, optimally at a row spacing of $s_{opt}$ times m cm row$^{-1}$. The optimal value of s is given by Eqn 5.65. However, the numerator and the denominator of Eqn 5.64 differ relatively little. Substitution of different, but realistic, values of t, $r_{bg}$, $h^2$ and $\gamma$ into Eqn 5.64 shows that the degree to which competition

disturbs the outcome of selection is hardly affected by the row spacing (Fig. 46). Hence, contrary to general opinion, hardly any competitional bias is removed by growing the rows at a wider spacing. Indeed interrow competition decreases, but this type of competition is replaced by competition against empty space. An illustration can be found in Fig. 24. From the model for competitional bias in single-plant selection it was already expected that the effect of row spacing on the competitional bias would be small. The assumptions underlying the competition-density model are discussed in Sections 5.3.3 and 5.6.

*Summary* The progress due to selection in a mixture of single rows grown at a wide row distance is quantified. The progress is measured by the correlated response for yield in monoculture at m cm row$^{-1}$, brought about by selection for yield in mixture at s times m cm row$^{-1}$. The correlated response was hardly affected by the row spacing. Hence, hardly any competitional bias can be removed by selection in rows grown at a wide row distance.

### *5.4.3 Bias due to differential response of the genotypes to spacing*

Selection in a mixture of rows is inflated by intergenotypic competition between the rows. With wider row distance, the bias due to interrow competition is largely replaced by the bias due to a differential response of the genotypes to spacing. In Sections 5.4.1 and 5.4.2 the total effect of density response and interrow competition was defined. The effect solely due to the differential response to spacing can be separated, as was already done for single plants as unit of selection in Section 5.3.4. The equations given there also hold for rows as unit of selection, because without competition between the experimental units and in monoculture the interrow-competition model is equivalent to the interplant-competition model. Both models differ only with respect to how many neighbours an experimental unit extends its competitive influence. In the model for interrow competition, it is assumed that only the adjacent neighbours are affected. On the other hand, in the model for interplant competition, it is assumed that also second and higher order neighbours are considerably influenced. When competition between experimental units is absent, the difference between both models disappears. The same holds for monocultures because then all experimental units have the same genotype.

In conclusion, the outcome of selection at wide stand is biased by the differential response of the genotypes to spacing. For a quantification of the effects solely due to the differential response to spacing, the reader is referred to Section 5.3.4. For, in this situation, the interplant and the interrow-competition model are equivalent.

### *5.4.4 The crowding coefficient as function of the spacing*

The crowding coefficient depends on the density of stand. The crowding coefficient referred to in the preceding sections is that at m cm row$^{-1}$. In this section the density dependence of the crowding coefficient is worked out.

The expected per-row yield of genotype i in a mixture where all genotypes are at equal frequencies and at sm cm row$^{-1}$ is given by Eqn 4.15 as

$$O_{i,sm} \simeq \frac{2b_{i,sm}}{b_{i,sm}^{+1}} M_{i,sm}$$

The relation between the expected yield of i in mixture at sm cm row$^{-1}$ and the expected yield of i in monoculture at m cm row$^{-1}$ can be derived from Eqn 5.46 by replacing $b_h$ and $b_j$ by their expectation values that equal unity. This gives

$$O_{i,sm} \simeq \frac{2sb_{i,m}}{b_{i,m}^{+1+2t}} M_{i,m}$$

Combination of both expressions for $O_{i,sm}$ gives

$$\frac{2sb_{i,m}}{b_{i,m}^{+1+2t}} M_{i,m} \simeq \frac{2b_{i,sm}}{b_{i,sm}^{+1}} M_{i,sm} \qquad (5.66)$$

The expected monoculture yield of i is given by Eqn 5.18 as

$$M_{i,sm} = \frac{sb_{i,m}}{b_{i,m}^{+t}} M_{i,m}$$

Substitution of $M_{i,sm}$ into Eqn 5.66 and omission of the subscript i gives for the crowding coefficient

$$b_{sm} = \frac{b_m^{+t}}{1+t} = \frac{b_m+(s-1)b_{e,m}}{1+(s-1)b_{e,m}} \qquad (5.67)$$

For the variance we find

$$\text{var } \underline{b}_{sm} = \frac{1}{(1+t)^2} \text{ var } \underline{b}_m \qquad (5.68)$$

## 5.5 NUMERICAL EXAMPLE

A numerical example illustrates the bias due to selection in a widely spaced segregating population. We apply the same dimensionless input and output parameters as used in Section 4.5. The following values, based on Tables 17 and 18 are realistic for plant selection:

heritability $h^2 = \text{var } \underline{g}/(\text{var } \underline{g} + \text{var } \underline{e}) = 0.10$

competitive stress $\gamma = \mu^2 \text{ var } \underline{b}/\text{var } \underline{g} = 5$

coefficient of correlation between competitive ability and monoculture yield

$$r_{bg} = \text{cov}(\underline{b},\underline{g})/\sqrt{\text{var } \underline{b} \text{ var } \underline{g}} = 0.2$$

All parameters are at m cm$^2$ plant$^{-1}$ and in monoculture.

The density experiments, reviewed in Table 20, supply an estimate of the crowding coefficient of empty space $b_e$. The area occupied by a single freely-grown barley plant will be about $\beta$=569 cm$^2$. The seeding rate used by farmers in Western-Europe is 80 to 100 kg seed ha$^{-1}$, which is about 200 plants m$^{-2}$. Therefore we take m=50 cm$^2$ plant$^{-1}$ as

the spacing to which we bred the varieties. The crowding coefficient of a random genotype i with respect to empty space is

$$\underline{k}_{ie} = \underline{b}_i/b_e = (\underline{\beta}_i + m)/m \qquad (5.6)$$

Suppose that the varieties involved in Table 20 are a random sample from a population. In this population, we set $\varepsilon\underline{b}_i = 1$ and $\varepsilon\underline{\beta}_i = \beta$. This gives

$$b_e = m/(\beta+m)$$

Substitution of $\beta$=569 cm$^2$ plant$^{-1}$ and m=50 cm$^2$ plant$^{-1}$ results in $b_e$=0.081.

Plant selection for yield, whenever adequate, occurs in stands where s times m roughly amounts to 100 to 500 cm$^2$ plant$^{-1}$. Therefore, the output of the model is given for s in the range of 1 to 10. When s=1 the density of the population conforms with that in commercial practice. When s approaches infinity, the spacing is so wide that interplant competition does not occur and the results in mixture coincide with those in monoculture.

In each of Figs 25a, b, c, two curves are drawn: one for a population with intergenotypic competition ('mixture') and the other for a hypothetic population without intergenotypic competition ('monoculture'). The latter shows the bias due to a differential response of the genotypes to spacing and the former adds the effects of intergenotypic competition. With wider spacings the bias that arises from the presence of intergenotypic interplant competition is progressively replaced by the bias that arises from the differential response of the genotypes to spacing (Figs 24 and 25).

It was derived that, under certain assumptions, the expected yields of the genotypes, relative to each other, in a mixture are not affected by the spacing at which the mixture is grown (Section 5.3.1). As a consequence, in mixture, the heritability, the correlation with monoculture yield at m cm$^2$ plant$^{-1}$, and the response to selection are not affected by the density of stand (Section 5.3.3). This accounts for the horizontal lines drawn for the mixed stand in Fig. 25. Without intergenotypic competition, that is in monoculture, the quantities equal unity at the reference spacing (s=1). This will be evident as the effects were expressed relative to a monoculture at s=1. At very wide stands (s=$\infty$), the yields in monoculture equal those in mixture. Hence, with wider spacings, the curves for the monocultures approach those for a mixture. In reality, the curves coincide at a spacing of roughly 1500 to 3000 cm$^2$ plant$^{-1}$. However, this is not accounted for by the model where the density response is described by a hyperbolic function.

In the numerical example, at any spacing, $CR_{mono,m}$ is in mixture greater than in monoculture (Fig. 25c). Hence, selection in mixture here more efficiently raises the monoculture yield than selection among monocultures. As density response is a special case of intergenotypic competition, here selection among monocultures more efficiently raises the monoculture yield at m cm$^2$ plant$^{-1}$ when it is done at wider spacings (Fig. 25c). The ratio $h_{mono,sm}/h_{mono,m}$ increases with a wider spacing (Fig. 25a). As the denominator is a constant, it involves that the heritability $h^2_{mono,sm}$ increases, showing that the portion of the total variation among monocultures that is attributed to genetic differ-

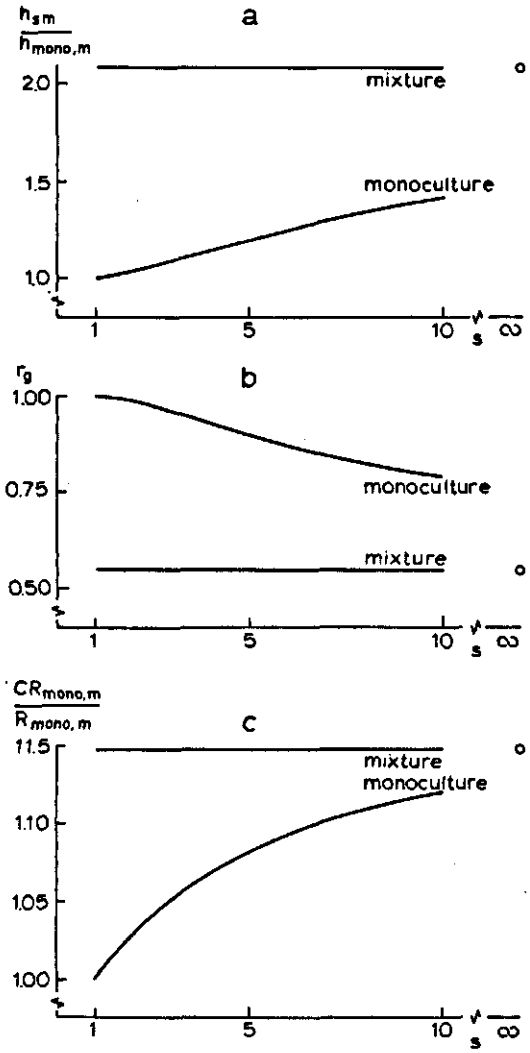


Fig. 25. Effect of plant spacing on (a) the heritability ratio $h_{sm}/h_{mono,m}$, (b) the correlation coefficient $r_g$ of yield at sm cm$^2$ plant$^{-1}$ and monoculture yield at m cm$^2$ plant$^{-1}$, and (c) the ratio of the correlated response CR for monoculture yield at m cm$^2$ plant$^{-1}$ brought about by selection at sm cm$^2$ plant$^{-1}$ and the direct response to selection R in monoculture at m cm$^2$ plant$^{-1}$. Open circles denote values at infinite spacing.

ences increases the wider the spacing. The ratio $h_{mono,sm}/h_{mono,m}$ exceeds unity (Fig. 25a). denoting that the genetic differences among monocultures become clearer at wider stands. The correlation between the monoculture yield at sm cm$^2$ plant$^{-1}$ and that at m cm$^2$ plant$^{-1}$ however, decreases the wider the stand (Fig. 25b). The increase in heritability has a greater effect than the decline of the correlation so that selection among monocultures becomes more efficient the sparser the stand (Fig. 25c). The findings only hold for the example given. So, the higher selection response at mixed growing and that for monocultures at wider spacings are not general rules.

When selection is for yield per row, the effect of spacing on the outcome of selection is more complicated than when selection is for yield per plant. Then, in mixture, the above-mentioned quantities are affected by the spacing too (Section 5.4.2), the competitive effect of a row, in contrast to that of a plant, being restricted to its adjacent neighbours.

The model is based on certain assumptions which are discussed in Section 5.6.

## 5.6 DEVIATIONS FROM THE ASSUMPTIONS UNDERLYING THE MODEL

Under certain assumptions, the rank of the genotypes in a mixture is not affected by the spacing at which the mixture is grown (Section 5.3.1). This implies that all genotypes have one and the same value for the ratio $O_{narrow}/O_{wide}$ of their yield in mixture at narrow stand and their yield in mixture at wide stand (Eqn 5.13). Hence, when for each genotype $O_{narrow}/O_{wide}$ is plotted against the crowding coefficient, a vertical line is the result (Fig. 26). This illustrates that no effect of intergenotypic competition can be removed by selection at a wide stand.

In the model, it is assumed that the genotypes have similar β curves (Section 5.2). Only then does the β observed at final harvest ($\beta_{max}$) reflect the entire course curve of β (Figs 22a and 23a). For in the model, the competitive ability of a genotype is read from its β at final harvest whereas, in reality, its competitive ability is the resul-

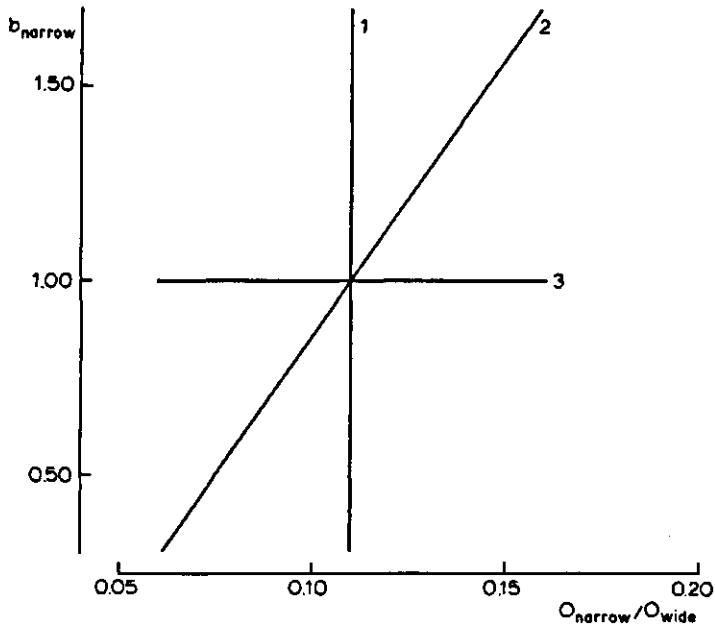


Fig. 26. Relation between the crowding coefficient b at narrow stand and the ratio $O_{narrow}/O_{wide}$ of the yield in mixture at narrow stand and that at wide stand. The relations hold for (1) genotypes that have similar β curves, (2) genotypes that differ only in their initial value of β, and (3) genotypes that differ only in their $\beta_{max}$. $Z_{narrow}$ = 80 plants $m^{-2}$, $Z_{wide}$ = 3.2 plants $m^{-2}$, $\beta_{max}$ = 0.1590 $m^2$ $plant^{-1}$.

tant of its β during the exponential stage. The β is the area occupied by a single, freely grown plant.

Which types are favoured in selection at wide stand, compared with selection at narrow stand, when the assumption of similarity of the β curves is violated? For that purpose, the influence of the parameters determining the β curve on the relation between the crowding coefficient and $O_{narrow}/O_{wide}$ is discussed. The β curve is determined by (a) the initial value at time t=0, (b) the relative growth rate (RGR), that is the slope of the line when β is on a logarithmic scale (Fig. 23), and (c) the β at final harvest ($\beta_{max}$).

Let the genotypes be differentiated only by their β at time t=0 (Figs 22b and 23b). Types with a small initial value of β are those that grow from small seeds and those that emerge late. A late emergence is interpreted by a low value of β at time t=0, i.e. at the time of emergence of the earliest genotype (Fig. 23a, b).

The relative space occupied by a genotype i at time t is derived from Eqn 5.8 as

$$RS_{i,t} = \frac{O_i'}{\Omega_i'} = \frac{\beta_{i,t} Z_i}{\beta_{1,t} Z_1 + \ldots + \beta_{n,t} Z_n + 1} \qquad (5.69)$$

When t=0 is

$$RS_{i,0} = \frac{\beta_{i,0} Z_i}{\beta_{1,0} Z_1 + \ldots + \beta_{n,0} Z_n + 1}$$

At time t=0, the area occupied by all plants is $\beta_{1,0} Z_1 + \ldots + \beta_{n,0} Z_n \ll 1$. Hence at time t=0 is

$$RS_{i,0} = \beta_{i,0} Z_i$$

In a segregating population where the n genotypes are unreplicated,

$$Z_1 = \ldots = Z_n = \frac{1}{n} Z$$

so that

$$RS_{i,0} = \frac{1}{n} \beta_{i,0} Z \qquad (5.70)$$

As the genotypes have the same RGR, their β curves are similar in the exponential phase. In this phase the competitive relations are established. Baeumer & de Wit (1968, p. 108) showed that for similar β curves

$$RS_{i,t} = \frac{\beta_{i,t}}{(\beta_{i,t} - \beta_{i,0}) \sum_{j=1}^{n} RS_{j,0} + \beta_{i,0}} RS_{i,0}$$

Given that $\beta_{1,t} = \ldots = \beta_{n,t} = \beta_t = \beta_{max}$ and that $\beta_{i,0} \ll \beta_{i,t}$, we reach at

$$RS_{i,t} = \frac{\beta_t}{b_t \sum_{j=1}^{n} RS_{j,0} + \beta_{i,0}} \; RS_{i,0}$$

Substitution of Eqn 5.70 for $RS_{i,0}$ gives

$$RS_{i,t} = \frac{\beta_t Z \beta_{i,0}}{\beta_t Z \sum_{j=1}^{n} \beta_{j,0} + n\beta_{i,0}} \tag{5.71}$$

The ratio between the yield per plant in mixture at narrow stand and that at wide stand is

$$\frac{O_{i,n}}{O_{i,w}} = \frac{O'_{i,n}}{O'_{i,w}} \frac{Z_{i,w}}{Z_{i,n}} = \frac{RS_{i,n}}{RS_{i,w}} \frac{Z_w}{Z_n} \tag{5.72}$$

Substitution of Eqn 5.71 gives

$$\frac{O_{i,n}}{O_{i,w}} = \frac{\beta_t Z_w \sum_{j=1}^{n} \beta_{j,0} + n\beta_{i,0}}{\beta_t Z_n \sum_{j=1}^{n} \beta_{j,0} + n\beta_{i,0}} \tag{5.73}$$

The relative crowding coefficient of i to j is at $z_1 = \ldots = z_n = \frac{1}{n}$

$$k_{i,j} = \frac{O_i}{O_j} \frac{M_j}{M_i}$$

As the genotypes are supposed to be differentiated only by their initial value of $\beta$, $M_i = M_j$ and $\Omega'_i = \Omega'_j$ and hence

$$k_{ij} = \frac{O_i}{O_j} = \frac{RS_i}{RS_j}$$

Setting $\varepsilon b = 1$ (Section 6.2.1) and substitution of Eqn 5.71 for the relative space gives for the crowding coefficient of genotype i at narrow stand

$$b_i = \frac{n\beta_t Z_n \beta_{i,0} + n\beta_{i,0}}{\beta_t Z_n \sum_{j=1}^{n} \beta_{j,0} + n\beta_{i,0}} \tag{5.74}$$

When $\underline{b}_i$ is plotted against $\underline{O}_{i,n}/\underline{O}_{i,w}$ (Eqn 5.74 against Eqn 5.73), we obtain a regression line with slope $\delta\underline{b}_i/\delta(\underline{O}_{i,n}/\underline{O}_{i,w})$ that passes through the point $(\varepsilon\underline{b}, \varepsilon(\underline{O}_n/\underline{O}_w))$. When this is elaborated, we find for the regression line

$$\underline{b}_i = \frac{Z_n(\beta_t Z_n + 1)}{Z_n - Z_w} \quad \frac{\underline{O}_{i,n}}{\underline{O}_{i,w}} - \frac{Z_w(\beta_t Z_n + 1)}{Z_n - Z_w} \tag{5.75}$$

In conclusion, when the genotypes are only differentiated by their initial value of

$\beta$ (Figs 22b and 23b), the crowding coefficient b at narrow stand and the ratio $O_{narrow}/O_{wide}$ are linearly related. The regression line is fixed by the value of $\beta$ at final harvest and by the two sowing densities. Because the slope of the line is positive, the types having a low initial value of $\beta$ are favoured by selection in mixture at wide stand (Fig. 26). The types with a low initial value of $\beta$ are those growing from small seeds and those with a retarded emergence.

In situation c of Figs 22 and 23, the genotypes differ in RGR, while they finish their exponential growth at the same time. When the crowding coefficient of the weak competitor relative to that of the strong competitor equals that in situation a, the weak competitor in c has a smaller $\beta_{max}$ than the weak competitor in a. Due to its smaller $\beta_{max}$, it has a lower $O_{wide}$. Because $O_{narrow}$ is for both weak competitors the same, the weak competitor in c has a greater value of $O_{narrow}/O_{wide}$. Hence, in situation c, the relation between $O_{narrow}/O_{wide}$ and b has a negative slope. The curve has as horizontal asymptote the crowding coefficient $b_e$ of a non-growing genotype. In conclusion, in situation c, selection at a wide stand favours the types having a high RGR.

The situation where the genotypes differ in RGR but have the same $\beta_{max}$ (Figs 22d and 23d) was simulated by the dynamic model of Baeumer & de Wit (1968). It appeared that the relation between the crowding coefficient and the ratio $O_{narrow}/O_{wide}$ is linear and is not very different from that given by Eqn 5.75. Hence, in situation d, selection at a wide stand favours the types having a low RGR.

In Figs 22e and 23e, the genotypes differ only with respect to their value of $\beta_{max}$. As the competitive relations are established during the exponential increase of $\beta$, the genotypes will hardly differ in competitive ability. That is, the crowding coefficient of all genotypes is about one. Given an equal $\Omega'$, all genotypes produce about the same yield in mixture at narrow stand so that $O_{narrow}$ is approximately constant.

Because the yield of an isolated plant is $\beta\Omega$, the genotype with the highest $\beta_{max}$ has the highest yield at a wide stand. That is, this genotype has the smallest value of $O_{narrow}/O_{wide}$. Hence, the competitive situation of Fig. 22e results in a horizontal line in Fig. 26. Selection at a wide stand favours therefore the genotypes with the highest $\beta_{max}$. These are the types with a prolonged exponential increase of $\beta$.

In barley, $\beta$ increases exponentially in time until ear emergence. In oats, the exponential increase carries on even for a longer time (de Wit, 1970, Fig. 10). Therefore, at least in barley, selection at a wide stand favours types with a late ear emergence.

In the model used in Sections 5.3 and 5.4, it was assumed that space once occupied cannot be released (Section 5.2). Types that may lose once occupied space are the short-straw types and probably also the shallow-rooting types. Selection at wide stand would favour these types compared with selection at narrow stand. In Section 8.3.1, it is shown, however, that the genotypes may differ strongly in height without their competitive ability being significantly affected, indicating that application of the model is not being markedly biased. Therefore, short-straw types do not markedly benefit from selection at a wide stand.

By selection at a wide stand, the bias that originates from the competition effects of type a (Figs 22 and 23) is replaced by the bias due to the differential reaction of the genotypes to spacing. On the other hand, the bias that arises from the competition effects of type b and d is removed by selection at a wide stand. Then the types with a later emergence, the types growing from small seeds and those with a small RGR are favoured compared with selection at narrow stand. However, these types with a slow juvenile growth are, in general, inferior in agronomical practice. Exceptions may be found in crops growing on a limited supply of stored water (Passioura, 1976, 1977; Hall et al., 1979; but see also Hurd, 1974) and in winter cereals where a slower juvenile growth may give a better winter hardiness. Selection at a wide stand increases the bias that arises from the competition effects of type c and it introduces the bias that originates from the competition effects of type e. The latter implies that, at least in barley, types with a late ear emergence are favoured.

*Summary* It is concluded that selection in mixture can be done best at a normal, narrow spacing.

# 6 Competitive relations among barley varieties and their estimation

## 6.1 OBJECTIVES

In this chapter, I intend:
- to introduce methods of estimation and statistical testing of competition effects for several arrangements of plants and rows (Section 6.2);
- to test the assumption of competition for the same resources (Section 6.3.1);
- to give a general impression of the competition effects among the barley varieties used (Section 6.3.2);
- to estimate the parameters required as input for the competition model (Sections 6.3.2 and 6.4).

Data of the experiments mentioned in Chapter 2 are used along with results from some barley mixtures described in the literature. The characters studied are grain yield as the economic yield and aboveground biomass as measure of primary production.

## 6.2 METHODS OF ANALYSIS OF MIXTURE EXPERIMENTS

### *6.2.1 Basic principles*

To quantify competition effects, the model of de Wit (1960) is used (Section 4.1). In this model, the competitive ability of a genotype is measured by its crowding coefficient b. This quantity does not stand on its own, for only ratios of bs have significance. Only their relative values are important and an arbitrary level may be chosen. In the present study, for each trial the median of the b values is taken as one.

The effects of competition can also be characterized by the relative crowding coefficient k, that is the ratio of two crowding coefficients (Eqn 4.4). The k values are distributed around expectation unity, but the distribution is non-normal, as zero and infinity are the limits. Since $k_{ij} = b_i/b_j$ and $k_{ji} = b_j/b_i$, the probability of $k_{ij}$ equals the probability of its reciprocal:

$$P(k_{ij}) = P(k_{ji}) = P(1/k_{ij})$$

Using logarithmic values, we have

$$P(\ln k_{ij}) = P(-\ln k_{ij})$$

Therefore, a logarithmic transformation results in ln k values which are symmetrically distributed around expectation zero and which have plus and minus infinity as their

limits. Therefore, ln k values probably better fit a normal distribution than do the untransformed k values. Ln-transformed k values have certain advantages in computation, which will appear in the following sections. Moreover, in the ordinary statistical tests of significance, it is assumed that the variables show a normal distribution. When k is lognormal, then b is also lognormal. Hence, statistical testing of varieties for their ln b values implies testing of their ratios of b values. To average k values or b values, the geometric mean, i.e. the antilog of the arithmetic mean of the logs has to be taken.

In estimating var $\underline{b}$ and cov($\underline{b}$,$\underline{g}$), which are required as input parameters in the competition model, the untransformed b values are used because the variances of the yields are based on untransformed yields.

In some experiments, the mixtures are grown separately from the monocultures. Then, the estimate of k according to Eqn 4.5 will still be the same as when the mixtures and pure cultures were randomized. However, the estimate of the relative yield total RYT will be biased in such an arrangement. This is shown by supposing that the fertility level of the mixture part of the field is x times that of the monoculture section. When genotype x environment interaction is absent, Eqn 4.5 becomes

$$k_{ij} = \frac{xO_i/M_i}{xO_j/M_j} \frac{z_j}{z_i} = \frac{O_i/M_i}{O_j/M_j} \frac{z_j}{z_i}$$

Hence, $k_{ij}$ is not affected.

The relative yield total, however, changes to

$$RYT = \frac{xO_i}{M_i} + \frac{xO_j}{M_j} = x\left(\frac{O_i}{M_i} + \frac{O_j}{M_j}\right)$$

Hence, in such an experimental layout the test on its deviation from unity has to be interpreted with caution.

The relative yield total also has a skew frequency distribution with one as expectation value and zero and infinity as the limits. Therefore, use of ln-transformed values may be preferred, especially when the RYT values show a large standard deviation.

### *6.2.2 Binary mixtures with one or more testers*

In Exps 76-1 and 77-2a, the varieties were grown in binary mixtures with 'Varunda' as common associate. Each mixture plot was situated between the two corresponding monoculture plots. Such a 3-plot unit gives estimates of monoculture yields $M_i$ and $M_s$ and mixture yields $O_i$ and $O_s$ of the studied genotype i and the standard variety s at relative seed frequencies of $z_i = z_s = \frac{1}{2}$. The relative crowding coefficient of i with respect to s is estimated according to Eqn 4.5 as

$$k_{is} = \frac{O_i/M_i}{O_s/M_s}$$

The experiments were laid out as randomized block designs with the 3-plot cells as basic units. The logarithms of the k-values, which are supposed to be normally distributed, were subjected to an analysis of variance. Since $k_{is} = b_i/b_s$, the logarithm can

be written as

$$\ln k_{is} = \ln b_i - \ln b_s$$

Because all varieties are tested against the standard, $\ln b_s$ is a constant. Hence, the statistical test is done on disparity of ln bs and with it on relative differences between the varieties in their competitive ability.

Each 3-plot unit also gives an estimate of the relative yield total. Since we have a replicated design, it can be tested whether a particular genotype and the standard compete for the same resources. From each 3-plot unit, a RYT value was computed. The RYT-values were subjected to an analysis of variance of a randomized block design to estimate the error variance of the RYTs. The error variance was used in a two-tailed simultaneous t-test (Section 6.3.1).

### *6.2.3 Competition diallel*

In competition diallels the components are grown in all pairwise, 1:1 binary mixtures together with the pure cultures. The additive models for this design were reviewed in Section 3.2.1. In the following, a shortcut analysis based on the de Wit model is introduced.

The relative crowding coefficient is estimated according to Eqn 4.5. The logarithmic value is set into a diallel arrangement and the array means are considered (Table 10). When n is the number of genotypes in the diallel, the array mean for genotype j is

$$\ln b_j - \frac{1}{n} \sum_{i=1}^{n} \ln b_i$$

All array means have the latter part of the expression in common. Therefore, the competitive ability of a genotype is measured by its array mean in the diallel table. It follows that the difference between the array mean of a random genotype g and the array mean for another random genotype h is

Table 10. Logarithms of relative crowding coefficient, expressed as $\ln k_{ij} = \ln b_i - \ln b_j$, arranged into a 3x3 diallel, which can be produced by mixing the entries in all pairwise combinations.

| | Associate | | | Array mean |
|---|---|---|---|---|
| | 1 | 2 | 3 | |
| Producer 1 | $\ln b_1 - \ln b_1$ | $\ln b_1 - \ln b_2$ | $\ln b_1 - \ln b_3$ | $\ln b_1 - 1/3 \sum_{i=1}^{3} \ln b_i$ |
| 2 | $\ln b_2 - \ln b_1$ | $\ln b_2 - \ln b_2$ | $\ln b_2 - \ln b_3$ | $\ln b_2 - 1/3 \sum_{i=1}^{3} \ln b_i$ |
| 3 | $\ln b_3 - \ln b_1$ | $\ln b_3 - \ln b_2$ | $\ln b_3 - \ln b_3$ | $\ln b_3 - 1/3 \sum_{i=1}^{3} \ln b_i$ |

$$\ln b_g - \ln b_h = \ln (b_g/b_h) = \ln k_{gh}$$

which is the logarithm of the relative crowding coefficient of g with respect to h.

The method has some disadvantages:

- the monocultures are superrepresented into the estimation of the ln bs;
- the ln b estimates are correlated with each other, which hampers statistical testing.

To avoid the correlation structure, parameters representing either the differences or the sums of the component scores per plot should be analysed. This technique was used by Williams (1962) for his additive competition model. A least-square or a maximum-likelihood procedure should remove the superappraisal of the contribution of the monoculture plots and estimates the crowding coefficients as well as the monoculture performances. However, algebraic and statistical treatment becomes cumbersome.

The present study makes only limited use of competition diallels, therefore the shortcut method is considered to be satisfactory. Moreover, the difference between the two methods with respect to the parameter estimates can be shown to be small.

*6.2.4 Border effects in multi-row plots*

Competition studies often deal with multi-row plots. From the central rows an estimate of pure-culture performance is obtained, while from the outer rows yield under competitive conditions is estimated. Under the assumption that only the first neighbour row is influenced by competition, 3-row plots are the smallest units for such a study.

The 3-row plot of genotype i bordered with a plot of genotype j can be represented by

i i i j j j (Arr. 6.1)

where each row is represented by a letter denoting the genotype sown in that row. The expected yield of the outside row of i is derived from Eqn 4.13:

$$O_{i,ij} = \frac{3b_i+b_j}{2b_i+2b_j} M_i = \frac{3k_{ij}+1}{2k_{ij}+2} M_i \qquad (6.1)$$

The relative crowding coefficient of i with respect to j is calculated as

$$k_{ij} = \frac{2 O_{i,ij}-M_i}{3M_i-2 O_{i,ij}} \qquad (6.2)$$

From the expected yield of the outside row of the adjacent 3-row plot of j it is derived that

$$k_{ji} = \frac{2 O_{j,ji}-M_j}{3M_j-2 O_{j,ji}}$$

which gives a second estimate of $k_{ij}=1/k_{ji}$ as

$$k_{ij} = \frac{3M_j-2 O_{j,ji}}{2 O_{j,ji}-M_j} \qquad (6.3)$$

Both estimates (Eqns 6.2 and 6.3) are correlated with each other because they originate from adjacent rows, which are at about the same location. Therefore, their geometric mean is entered into an analysis instead of two individual values. The geometric means derived from different units of two 3-row plots are uncorrelated.

The following procedure can be used to estimate the crowding coefficient b. When we have n genotypes, each ln k can be written in the multiple regression form

$$y = a_1x_1 + a_2x_2 + ..... + a_nx_n$$

where the regression coefficients $a_i$ denote the ln $b_i$ values and $x_i$ the presence or absence of genotype i in the two 3-row plots. When a genotype is present in a unit of two 3-row plots, x=+1 or -1 for that genotype in that unit. When the genotype is absent, x=0. For instance, the relative crowding coefficient of i with respect to j is given by

$$\ln k_{ij} = 0 \cdot \ln b_1 + .... + 1. \ln b_i + .... (-1) \cdot \ln b_j + .... 0 \cdot \ln b_n$$

This agrees with the general equation

$$\ln k_{ij} = \ln b_i - \ln b_j$$

When the genotypes are replicated throughout the trial, the equations can be solved simultaneously, giving estimates of ln $b_i$ (i=1, .... n). The technique is essentially a least-squares method. An average of zero is chosen as an arbitrary level for the ln b values. These values, estimated as the regression coefficients, are subjected to a multiple range test together with their standard deviation. In this way, it is tested to what extent the b values differ from each other.

In the present experiments, trials of 3-row plots were arranged in strips (Section 2.1). The varieties were repeated several times in each strip and the strips were also replicated. To account for a strip effect, which is supposed to be small, the multiple regression equations were extended with an orthogonal polynomial.

We have seen that the 3-row plots are arranged in 6-row units as in Arr. 6.1. Hence, except for the center row, only one border row of each 3-row plot is involved in the estimation procedure. To consider the other border row too, the first 3-row plot of the nursery strip (Fig. 4) is skipped to obtain parallel series of 6-row units. In this way a second set of ln b estimates is obtained. The two sets of ln b estimates are correlated, because they have the yield of the central rows of the 3-row plots in common. To allow for the correlation $(n_1+n_2)2/3$ degrees of freedom are used in the joint test, where $n_1$ and $n_2$ are the degrees of freedom of the error variance in set 1 and 2, respectively.

The method, described in this section, is generally applicable in the estimation and testing of the crowding coefficients from border effects in multi-row plots. It became clear that many replications of the variety plots are required to obtain reliable estimates of the crowding coefficients of the varieties.

*6.2.5 Alternated standards*

Sometimes the test rows are alternated with rows of a standard variety. The arrangement is

i s j s k s l s (Arr. 6.2)

where each row is represented by a letter denoting the genotype sown in that row. Neglecting the effects of second neighbours, the expected yield of genotype i can be derived from Eqn 4.13 to be

$$O_{i,ss} = \frac{2b_i'}{b_i+b_s} M_i = \frac{2k_{is}}{k_{is}+1} M_i$$

This gives for the relative crowding coefficient

$$k_{is} = \frac{O_{i,ss}}{2M_i - O_{i,ss}}$$

An estimate of M is derived from neighbouring trials with monocultures. Evidently, the nearer the monoculture plots to the alternated check trial, the smaller the error. A monoculture trial was assigned to an alternated check trial; uncorrelated replicates were made because there were independent sets of both. The logarithms of the relative crowding coefficients are used in an analysis of variance.

The previous method was used, although additional information could be obtained from the yield of the standards. However, this additional information was considered not sufficient to justify the statistical trouble required in the analysis of the yields of the standards.

Since the estimates of $O_{i,ss}$ and $M_i$ originate from different trials, the disparity between their fertility levels reflects itself in the relative yield total (Section 6.2.1). Hence, deviations of RYT from unity are confounded by the fertility differences and care has to be taken in the interpretation of RYT.

The method, described above, is based upon Eqn 4.13. In this equation, it is assumed that the effects of second and higher neighbours can be neglected (Section 4.2.1). For single rows as experimental unit, this assumption was valid. However, when individual plants are the unit of experimentation, this is not true (Section 4.2.2). For individual plants, the original de Wit model based on diffuse competition seems more appropriate (Section 4.2.2) and with that Eqn 4.10. When n plants, each of a different genotype, are alternately grown with n standard plants, the expected yield of a plant of a genotype i can be derived from Eqn 4.10. Substitution of $z_s = \frac{1}{2}$ and $z_1 = \ldots\ldots = z_n = \frac{1}{2}n$ gives

$$O_i' = \frac{b_i/2n}{\frac{1}{2}b_s+(b_1+\ldots\ldots+b_n)/2n} M_i'$$

Making $\frac{1}{n}\sum_{j=1}^{n} b_j = 1$ and expressing the yield per plant instead of per unit area, then the equation simplifies to

$$O_i = \frac{2b_i}{b_s+1} M_i$$

Hence, the crowding coefficient is estimated as

$$\ln b_i = \ln(O_i/M_i) + \ln(\tfrac{1}{2}b_s + \tfrac{1}{2})$$

The estimates of the ln b values are used in an analysis of variance, followed by statistical testing on differences among the varieties in their crowding coefficients b. Note that the term $\ln(\frac{1}{2}b_s + \frac{1}{2})$ is a constant so that this statistical analysis is justified.

*6.2.6 Multicomponent or global mixtures*

It is common in competition studies to mix seeds of a number of varieties in equal proportions and to grow the bulk population as a unit. A similar type of mixture, called a multicomponent or global mixture, is obtained when plants of the varieties are randomized and accurately spaced by hand (Exps 76-2a, 77-1b, d, e). Single-row plots, each with a different variety also belong to this category of mixtures (Exps 76-3a, 77-2b). The varieties may be completely randomized or grouped into a randomized block design.

In the multicomponent mixtures we can apply two approaches. When single rows form the experimental units, the nearest-neighbour concept holds. But when individual plants are considered, the de Wit model for diffuse competition is more appropriate (Section 4.2.2).

In the nearest-neighbour concept, it is supposed that competition effects are restricted to the direct neighbours. The expected yield of i in the mixture is then given by

$$O_i = \frac{2b_i}{b_i+1} M_i \qquad (4.15)$$

From this equation the crowding coefficients b can be estimated after substitution of O, the yield in the multicomponent mixture, and M, the yield in the monoculture. On the other hand, the equation enables us to estimate the yields in the multicomponent mixture after substitution of M and b. The bs may be estimated from 1:1 mixtures by the procedure given in Section 6.2.2. However, the two genotypes in the 1:1 mixtures have to be alternately placed, as the bs used in the equations of the nearest-neighbour approach refer to such an arrangement (Section 4.2.3). Random 1:1 mixtures give rise to deviating estimates of the bs.

De Wit (1960) assumed in his model that the yield of a genotype in a mixture is not influenced by the planting pattern (Section 4.2.3). That is, the relative seed frequencies rather than the arrangement of the genotypes in the mixture are of importance. When this is the case, the yield of i in the multicomponent mixture is described by Eqn 4.14 as

$$O_i = b_i M_i \qquad (4.14)$$

When the b value is estimated from 1:1 mixtures, it makes no difference whether the genotypes in the 1:1 mixtures are grown alternately or at random. For, when the assumption of de Wit holds, both arrangements produce similar yields.

When the Eqn 4.14 or 4.15 is used to estimate b values from the multicomponent mixture, the log transformed b values are used in an analysis of variance.

Again, a difference in fertility level between the monoculture plots at one side and the mixture at the other does not inflate the estimates of the crowding coefficients. However, the relative yield total is affected (Section 6.2.1).

## 6.3 EXPERIMENTS

### *6.3.1 Test on competition for the same resources*

In the models presented in Chapters 4 and 5, it was assumed that competition was for the same resources. The assumption was operationally defined by a relative yield total (RYT) of unity (Section 3.3 and 4.1). So, the assumption can be verified by testing whether the RYTs deviate from unity.

In Exps 76-1 and 77-2a, each variety was grown in monoculture and in 1:1 mixture with Varunda. For any combination of a variety and Varunda, a RYT was calculated. Since the trials were replicated, the RYTs could be tested. The other experiments did not allow a sufficiently accurate test of RYT.

The RYT values, averaged over varieties, were close to their expectation (Table 11). The F tests did not reveal significant differences ($P > 0.10$). The simultaneous 99% confidence interval given in Table 11 was constructed by means of the two-tailed simultaneous t-test (Miller, 1966, p. 242). The values of the single varieties with Varunda were all within the confidence limits. It is noted that, given the size of the confidence intervals, small departures of RYT from unity cannot be identified.

Hence, in these experiments, the RYTs did not deviate significantly from unity. Moreover, RYTs in the barley mixtures, described in the literature, were also close to unity (Section 3.4). It is therefore concluded that, in general, genotypes of barley compete for the same resources.

**Table 11. Relative yield total (RYT) averaged over varieties within experiments, and simultaneous 99% confidence intervals around the expected value of RYT when competition is for the same resources. The values between brackets give the observed range.**

| Experiment | Average | | Confidence interval | |
|---|---|---|---|---|
| | grain yield | biomass | grain yield | biomass |
| 76-1 | 0.995(0.95-1.06) | 1.001(0.94-1.07) | 1 ± 0.13 | 1 ± 0.10 |
| 77-2a | 0.996(0.92-1.09) | 0.997(0.91-1.06) | 1 ± 0.11 | 1 ± 0.12 |

Table 12. Performance in monoculture ($M_i$) and binary mixture with the standard 'Varunda' as common associate ($O_{is}$) in g $m^{-2}$. $O_{si}$ is the mixture yield of the standard and $k_{is}$ is the relative crowding coefficient of the tested variety with respect to the standard. Exp. 76-1.

| Variety | Grain yield | | | | Aboveground biomass | | | |
|---|---|---|---|---|---|---|---|---|
| | $M_i$ | $O_{is}$ | $O_{si}$ | $k_{is}$ | $M_i$ | $O_{is}$ | $O_{si}$ | $k_{is}$ |
| Golden Promise | 443 a* | 316 | 518 | 0.54 e | 838 a | 642 | 1098 | 0.58 e |
| Minerva | 415 ab | 432 | 336 | 1.22 b | 858 a | 890 | 760 | 1.12 b |
| Julia | 400 ab | 352 | 404 | 0.86 bcd | 844 a | 768 | 826 | 0.91 bc |
| Belfor | 398 ab | 386 | 364 | 1.05 bc | 843 a | 832 | 732 | 1.12 b |
| Piccolo | 398 ab | 342 | 432 | 0.78 cde | 834 a | 758 | 934 | 0.80 cde |
| Balder | 397 ab | 322 | 478 | 0.67 de | 842 a | 674 | 1020 | 0.65 de |
| Camilla | 395 ab | 372 | 418 | 0.88 bcd | 856 a | 796 | 884 | 0.87 bcd |
| v.d. Have 198-71 | 379 ab | 290 | 448 | 0.66 de | 826 a | 634 | 994 | 0.63 de |
| Proctor | 339 bc | 246 | 506 | 0.57 de | 810 a | 594 | 1064 | 0.57 e |
| Titan | 305 c | 252 | 470 | 0.69 de | 824 a | 636 | 1004 | 0.64 de |
| Bigo | 292 c | 366 | 296 | 1.69 a | 848 a | 992 | 648 | 1.49 a |
| Uniculm | 199 d | 152 | 526 | 0.58 de | 638 b | 504 | 1118 | 0.58 e |
| Varunda (standard) | 395 | *395* | *395* | *1.00* | 825 | *825* | *825* | *1.00* |

* Values followed by the same letter are not significantly different in the Student-Newman-Keuls test at $P \leq 0.05$.

Table 13. Performance in monoculture ($M_i$) and binary mixture with the standard 'Varunda' as common associate ($O_{is}$) in g $row^{-1}$. $O_{si}$ is the mixture score of the standard and $k_{is}$ the relative crowding coefficient of the tested variety with respect to the standard. Exp. 77-2, 0.20 x 1.70 $m^2$ $row^{-1}$.

| Variety | Grain yield | | | | Aboveground biomass | | | |
|---|---|---|---|---|---|---|---|---|
| | $M_i$ | $O_{is}$ | $O_{si}$ | $k_{is}$ | $M_i$ | $O_{is}$ | $O_{si}$ | $k_{is}$ |
| Varunda | 157 | 141 | 165 | 0.81 b* | 303 | 274 | 319 | 0.83 b |
| Tamara | 163 | 178 | 140 | 1.17 ab | 325 | 357 | 270 | 1.19 ab |
| Belfor | 163 | 155 | 158 | 0.90 b | 311 | 304 | 310 | 0.94 ab |
| Aramir | 149 | 166 | 149 | 1.14 ab | 295 | 331 | 288 | 1.16 ab |
| Camilla | 163 | 174 | 136 | 1.18 ab | 294 | 322 | 270 | 1.21 ab |
| Golden Promise | 140 | 124 | 156 | 0.86 b | 279 | 246 | 308 | 0.85 b |
| Balder | 147 | 168 | 155 | 1.12 ab | 300 | 334 | 296 | 1.12 ab |
| WZ 704068-14 | 152 | 142 | 149 | 0.93 b | 267 | 258 | 289 | 0.97 ab |
| Goudgerst | 127 | 159 | 128 | 1.47 a | 282 | 344 | 253 | 1.43 a |
| L 98 | 107 | 75 | 172 | 0.60 c | 255 | 168 | 382 | 0.57 c |
| Titan | 98 | 57 | 201 | 0.42 d | 248 | 143 | 440 | 0.40 d |
| Bigo | 159 | 142 | 152 | 0.88 b | 376 | 359 | 330 | 0.95 ab |
| Varunda (standard) | 150 | *150* | *150* | *1.00* | 297 | *297* | *297* | *1.00* |

* Values followed by the same letter are not significantly different in the Student-Newman-Keuls test at $P \leq 0.05$.

*6.3.2 Competition effects*

Competition effects are well demonstrated by the difference in yield of a genotype when that genotype is grown in a pure and a mixed stand. Tables 12 and 13 show that these differences may be large. In the experiments, the varieties were grown in monoculture and in binary mixture with a standard variety. The competitive ability of a variety was therefore characterized by its relative crowding coefficient with respect to the standard, and calculated by Eqn 4.5.

In Table 14, the yield in a multicomponent plant mixture and that in adjacent monocultures are given. The former was averaged over a rectangular and a triangular planting pattern, both at 125 $cm^2$ $plant^{-1}$. This was allowed because in the joint analysis of variance, significant variety x stand interaction did not occur ($P > 0.10$). The competition effects were measured by the crowding coefficient, expressed on a relative scale. In the triangular design 1/7th of the plants were standards. However, addition of a new genotype to a multicomponent mixture does not change the relative crowding coefficients $k_{ij} = RY_i/RY_j$, which can easily be understood from Eqn 4.10. The yields in the mixture were, however, influenced due to the insertion of the standard, but the influence was very small. In the present experiment, where the standard was Varunda with a crowding coefficient of 1.14 and 1.12 for grain yield and biomass, respectively, the mixture yields recorded in Table 14 were 0.99 times those expected if no checks were inserted.

In the line-selection field, several arrangements of the rows enabled a quantification

Table 14. Performance in monoculture ($M_i$) and multicomponent mixture ($O_i$) in g $plant^{-1}$ and the crowding coefficient $b_i$. The mixture yield is averaged over the mixture at 5x25 $cm^2$ $plant^{-1}$ (Exp. 77-1b) and that at 10.4 x 12 $cm^2$ $plant^{-1}$ (Exp. 77-1d).

| Variety | Grain yield | | | Aboveground biomass | | |
|---|---|---|---|---|---|---|
| | $M_i$ | $O_i$ | $b_i$ | $M_i$ | $O_i$ | $b_i$ |
| Varunda | 5.3 abc* | 5.1 | 1.08 bcd | 11.1 ab | 10.4 | 1.06 bcd |
| Tamara | 5.7 abc | 6.8 | 1.34 b | 11.8 ab | 14.0 | 1.36 b |
| Belfor | 5.3 abc | 5.6 | 1.18 bc | 11.5 ab | 11.5 | 1.14 bc |
| Aramir | 6.1 a | 4.6 | 0.83 de | 12.6 a | 9.6 | 0.85 d |
| Camilla | 5.0 abc | 5.2 | 1.15 bc | 10.0 ab | 10.4 | 1.16 bc |
| Golden Promise | 4.5 c | 4.7 | 1.17 bc | 9.3 b | 9.4 | 1.17 bc |
| Balder | 4.8 bc | 4.9 | 1.10 bcd | 10.5 ab | 10.0 | 1.05 bcd |
| WZ 704068-14 | 5.5 abc | 4.4 | 0.92 cd | 9.9 ab | 8.0 | 0.93 cd |
| Goudgerst | 4.7 c | 7.4 | 1.74 a | 10.6 ab | 16.9 | 1.77 a |
| L 98 | 6.0 ab | 3.7 | 0.69 e | 12.3 a | 7.3 | 0.68 e |
| Titan | 4.6 c | 1.8 | 0.44 f | 10.5 ab | 4.2 | 0.46 f |
| Bigo | 5.6 abc | 5.0 | 0.99 bcd | 12.3 a | 10.7 | 0.97 cd |

* Values followed by the same letter are not signigicantly different in the Student-Newman-Keuls test at $P \leq 0.05$.

of the competition phenomena (Section 6.2). Since the methods gave similar estimates of the crowding coefficients, the estimates were pooled when several arrangements were available (Tables 15 and 16).

In the rest of this section, only noteworthy features of the experiments are mentioned. In Chapters 8 and 9 the results are discussed in more detail and interpreted in terms of the models of Chapters 4 and 5.

The rank of the varieties with respect to their monoculture performance often deviated from that in commercial practice and fluctuated among the experiments. See for example the position of Bigo in Tables 6, 12 and 13. The very different growing conditions of 1976 and 1977 partly accounted for the large variety x year interaction. The disparity between experiments also originated from differences in soil type and density of stand. The relatively low percentage of emergence of L98 and Titan affected their yields in the line-selection field, but hardly influenced their yields in the singled plant-selection nursery. The discrepancy with the 'commercial' yield may partly be traced back to the prevention of mildew, the main disease, and the fact that lodging did not bias the experiments. It is remarkable that the differences between the cultivars for monoculture yield were mostly small, especially among the high yielding entries. It seemed that the better the environment was controlled, the smaller the differences in monoculture yield among the varieties. The experiments were accurate as can be seen from the variation coefficient which was only 2.8% for the grain yields in Table 15 as well as for those in Table 16.

The varieties differed in competitive ability as measured by the crowding coefficient. The competitive relations changed considerably from experiment to experiment. The explanation for this strong fluctuation may be similar to that for the inconsistency of monoculture performance. The results for aboveground biomass and those for grain yield ran parallel.

Bigo had a remarkable behaviour. On sand in the dry year, it showed a low grain

Table 15. Monoculture performance $M_i$ in g row$^{-1}$ estimated from the six central rows of 8-row plots and from the central row of 3-row plots and the crowding coefficient $b_i$, estimated from border effects in 3-row plots and from rows alternated with rows of a standard variety. Exp. 76-3, 0.20 x 1.80 m$^2$ row$^{-1}$.

| Variety | Grain yield | | Aboveground biomass | |
|---|---|---|---|---|
| | $M_i$ | $b_i$ | $M_i$ | $b_i$ |
| Minerva | 193 a* | 1.07 ab | 385 a | 1.04 ab |
| Julia | 188 ab | 0.98 ab | 385 a | 0.98 ab |
| Belfor | 185 ab | 1.19 a | 377 a | 1.16 a |
| Camilla | 176 b | 1.07 ab | 344 b | 1.09 a |
| Golden Promise | 151 c | 0.82 b | 306 c | 0.81 b |
| Uniculm | 70 d | 0.87 b | 226 d | 0.92 ab |

* Values followed by the same letter are not significantly different in the Student-Newman-Keuls test at $P \leq 0.05$.

Table 16. Monoculture performance $M_i$ in g row$^{-1}$ estimated from (i) four central rows of 6-row plots, and (ii) central row of 3-row plots. The crowding coefficient $b_i$ is estimated from (i) binary mixtures with 'Varunda' as common associate, (ii) border effects in 3-row plots, and (iii) alternated standard trial. Exp. 77-2, 0.20 x 1.70 m$^2$ row$^{-1}$.

| Variety | Grain yield | | Aboveground biomass | |
|---|---|---|---|---|
| | $M_i$ | $b_i$ | $M_i$ | $b_i$ |
| Varunda | 150 a | 0.96 d | 292 bcd | 0.95 cd |
| Tamara | 165 a | 1.19 b | 325 b | 1.20 b |
| Belfor | 161 a | 1.02 cd | 314 b | 1.06 bc |
| Aramir | 154 a | 1.15 bc | 302 bc | 1.19 b |
| Camilla | 165 a | 1.06 bcd | 303 bc | 1.09 bc |
| Golden Promise | 132 b | 0.91 d | 265 de | 0.87 d |
| Balder | 156 a | 1.03 cd | 318 b | 1.02 c |
| WZ 704068-14 | 151 a | 1.01 cd | 267 de | 1.04 c |
| Goudgerst | 131 b | 1.50 a | 291 bcd | 1.47 a |
| L 98 | 106 c | 0.72 e | 253 e | 0.68 e |
| Titan | 109 c | 0.49 f | 274 cde | 0.46 f |
| Bigo | 156 a | 0.97 d | 380 a | 0.97 cd |

x Values followed by the same letter are not significantly different in the Student-Newman-Keuls test at $P \leq 0.05$.

yield but a strong aggressiveness (Table 12). On the other hand, on loam in the wet year it demonstrated a high grain yield associated with an extremely high biomass, but only a moderate competitive ability (Table 16). So its monoculture performance in relation to other varieties was favoured by the last conditions, which agrees with the experience of farmers that Bigo is a variety for clay and loam soils (Rassenlijst, IVRO, Wageningen). Since under these circumstances its competitive ability was lowered, there was no apparent relation between agronomic and ecological adaptiveness.

In the models presented in Chapters 4 and 5, the effect of competition on the outcome of selection is described by the change in the selection response. The quantities, needed as input in the equations, are the population mean, variances and covariances. As these may differ strongly from experiment to experiment, their ratios are preferred to obtain a general impression (Section 4.4.4). These dimensionless quantities are given in Table 17 with the average monoculture yield as scaling factor. The estimates of the variances were derived from analyses of variances. The analysis of variance takes account of the error of the varietal means and thus the estimates are unbiased. In Exp. 76-2, the quantities were estimated per main plot because of the highly significant variety x main plot interaction ($P < 0.01$). The estimates, presented in Table 17, were the averages of the two main plots.

Table 17. The general mean of the monocultures $\mu_{mono}$, the heritability in monoculture $h^2_{mono}$, the genetic correlation $r_{b,g_{mono}}$ between the crowding coefficient and the performance in monoculture, and the competitive stress $\gamma$.

| Experiment | Spacing | Grain yield | | | |
|---|---|---|---|---|---|
| | | $\mu_{mono}$ | $h^2_{mono}$ | $r_{b,g_{mono}}$ | $\gamma$ |
| 76-1 | 11.5 cm row$^{-1}$ | 363. | 0.81 | -0.03 | 4.37 |
| 76-2a,d; Plot 1 | 6x25 cm$^{-2}$plant$^{-1}$ | 3.93 | 0.30 | -0.49 | 1.08 |
| 76-2a,d; Plot 2 | 6x25 cm$^2$plant$^{-1}$ | 4.14 | 0.28 | -0.18 | 0.35 |
| 76-3b,c,f | 20 cm row$^{-1}$ | 161. | 0.76 | +0.65 | 0.15 |
| 77-1a,b | 5x25 cm$^2$plant$^{-1}$ | 5.24 | 0.03 | -0.17 | 12.65 |
| 77-2a,c,d | 20 cm row$^{-1}$ | 145. | 0.33 | +0.54 | 3.09 |
| | | Aboveground biomass | | | |
| | | $\mu_{mono}$ | $h^2_{mono}$ | $r_{b,g_{mono}}$ | $\gamma$ |
| 76-1 | 11.5 cm row$^{-1}$ | 822. | 0.40 | +0.41 | 32.68 |
| 76-2a,d; Plot 1 | 6x25 cm$^2$plant$^{-1}$ | 9.71 | 0.21 | -0.32 | 1.92 |
| 76-2a,d; Plot 2 | 6x25 cm$^2$plant$^{-1}$ | 9.37 | 0.16 | -0.09 | 2.18 |
| 76-3b,c,f | 20 cm row$^{-1}$ | 337. | 0.60 | +0.59 | 0.32 |
| 77-1a,b | 5x25 cm$^2$plant$^{-1}$ | 11.03 | 0.03 | -0.16 | 18.01 |
| 77-2a,c,d | 20 cm row$^{-1}$ | 299. | 0.23 | +0.34 | 5.22 |

The heritabilities were based on plot yields (Exp. 76-1), single-plant yields (Exps 76-2, 77-1) or single-row yields (Exps 76-3, 77-2). The heritabilities referred to an area of a replicate (Exp. 76-1), a mixture plot (Exps 76-2, 77-1) or a strip (Exps 76-3, 77-2). In Exp. 76-2, the heritability for single plants was relatively high. This result may be due to the practice of raising the plants in peat pots in the glasshouse and planting the plants in the peat pots in the field. Also the heritability in Exp. 77-1a, may even have been overestimated due to the practice of sowing two kernels per plant place and singling the emerged plants. The kernels were accurately spaced by hand. The results suggest that the heritability for single-plant yields is extremely low. On the other hand, the heritability observed for the yields of individual rows was promising. It is emphasized that variety mixtures rather than segregating population, were involved. This may have inflated the estimates.

The competitive stress $\gamma = \mu^2_{mono}$ var $\underline{b}$/var $g_{mono}$ differed strongly among the experiments. For biomass, $\gamma$ was relatively high in Exp. 76-1. This was promoted by the small differences among the varieties with respect to biomass production in monoculture (Table 12). Comparison of Exp. 76-2 with Exp. 77-1 suggested that the planting out of the plants in peat pots (Exp. 76-2) had greatly reduced the differences between the varieties in competitive ability. The experiments dealt with varieties, so the genetic variance as well as the variance of the crowding coefficients will be inflated. Therefore, care has to be taken in the interpretation of $\gamma$.

## 6.4 CORRELATION BETWEEN COMPETITIVE ABILITY AND MONOCULTURE YIELD

A fundamental question is: are the genotypes with the highest yield in monoculture also the strongest competitors? That is, are monoculture yield and competitive ability positively correlated? The relation between both quantities is defined by the coefficient $r_{bg}$ of the correlation between the crowding coefficient $\underline{b}$ and the genetic value of the monoculture yield $\underline{g}$. The correlation coefficient is one of the input parameters of the model presented in Chapters 4 and 5. As was shown in Section 4.5, an estimate of its magnitude is required to gain a general idea about the spurious effect of competition on selection. In this section, information about the correlation coefficient is derived from my experiments as well as from experiments described in the literature.

In the literature, many experiments were reported where genotypes were grown in monoculture and mixture. I restrict myself to barley. The correlation coefficients $r_{bg}$ estimated from published results of barley mixtures are surveyed in Table 18. Only experiments with four or more entries were involved. The correlation found by Stadler (1921) was based on his own 'coefficient of competition' which approximates the crowding coefficient b. Sakai & Gotoh (1955) grew five varieties and their $F_1$s in monocultures and mixtures. The results of the $F_1$s were discarded because the deviating way of production of $F_1$ seed will have influenced strongly the competitive ability of the $F_1$s but hardly their monoculture yield (Section 7.4). No grain yield data were given by Sakai & Gotoh (1955). The correlation coefficient given in Table 18 under the head grain yield being that for weight of the ears.

The correlation coefficients estimated from my experiments are given in Table 17. The most extensive trials with other small grains were those from Stadler (1921). He found positive correlations of 0.48 and 0.37 averaged over three experiments in wheat and oats, respectively. In wheat 218 and in oats 71 entries were involved of which the border effects in row plots were evaluated.

Table 18. Genetic correlation between the crowding coefficient b and the performance in monoculture $g_{mono}$ for grain yield and biomass, calculated from published results of barley mixtures.

| Reference | Nr. of entries | Character | | Experimental design |
|---|---|---|---|---|
| | | grain yield | biomass | |
| Stadler (1921) | 27 | +0.44 | | border effects in row plots |
| Suneson & Wiebe (1942) | 4 | -0.52 | | bulk-propagated mixture |
| Sakai (1955, Fig. 5) | 14 | | -0.38 | binary mixtures with tester |
| Sakai & Gotoh (1955) | 5 | +0.12 | +0.00 | binary mixtures with testers |
| Sakai & Iyama (1966) | 12 | -0.08 | +0.42 | binary mixtures with tester |
| Norrington-Davies (1967) | 5 | | +0.67 | competition diallel |
| Sandfaer (1970) | 4 | -0.69 | | competition diallel |
| Blijenburg & Sneep (1975) | 8 | +0.80 | | bulk-propagated mixture |

In conclusion, there is a wide range in the estimates of the correlation coefficient $r_{bg}$, either derived from the literature (Table 18) or from my experiments (Table 17). The median of $r_{bg}$ is probably close to zero and may be slightly positive, but frequently negative values were found. The large variation of $r_{bg}$ suggests that the correlation strongly depends on the population and probably also on the environment in which it is studied. However, it may be promoted by the small number of varieties involved in each experiment.

Because mixtures of varieties were used rather than segregating populations, the findings have to be interpreted with caution. (1) Only a small number of varieties was studied in each experiment, so that the correlation coefficient estimated in an experiment had a few degrees of freedom and with that a wide confidence interval. One deviating variety, out of a set of varieties, has a strong influence on the correlation coefficient in that set of varieties. When this variety is removed, the correlation coefficient will change considerably. For example, when Titan and L98 were eliminated in Exp. 77-2, the correlation coefficient $r_{bg}$ for grain yield changed from +0.54 to -0.27. (2) Varieties are selected genotypes. The breeder selects the varieties from segregating populations. Moreover, the researcher usually selects from an assortment of varieties those varieties that he expects will show distinct effects. Consequently, varieties are not representative for the genotypes in a segregating population. In this way, a correlation coefficient for varieties may fundamentally differ from the corresponding correlation coefficient for genotypes in a segregating population. (3) The differences among varieties are larger than those among the genotypes in a segregating population. Enlarged differences inflate the correlation coefficient. (4) Varieties are homozygous genotypes, whereas in segregating populations a high degree of heterozygosity occurs. The competitive ability of heterozygotes may be different from that of the corresponding homozygotes (Section 7.4) and with it $r_{bg}$. Moreover the heterozygotes are not true to seed.

The correlation coefficients, derived from different references, could not be compared unconditionally as they were estimated from experiments that differ strongly in husbandry and growing conditions.

# 7 Bulk propagation

## 7.1 INTRODUCTION

After a cross has been made, the population is mostly propagated as bulk for some generations before plant selection and progeny testing are applied. During bulk propagation no selection is applied by the breeder. Nevertheless, there is natural selection in favour of the 'fittest' individuals. The fittest plants are those which produce the largest number of viable seeds that give rise to fertile plants. In the literature, the term 'fitness' is used in various ways. To avoid confusion the term 'reproductive rate' is preferred here. The reproductive rate of a genotype is defined as the number of seeds harvested divided by the number of seeds sown of that genotype.

The main question is whether the types with the highest reproductive rate are also the agronomically desired ones. Here, we assume that yield in pure stand measures the agronomic value. Frequently, the problem is studied by growing a mixture of several varieties for some years and by studying which varieties survive in the mixture. The literature, reviewed in Section 1.3.1, shows that any relation between survival in mixture and pure-stand yield is possible: positive as well as negative values of the correlation coefficient are found. Hence with bulk propagation, there is a considerable chance that natural selection brings about a dilution or even loss of desirable alleles or allele-combinations as a result of crowding.

The effects of natural selection on bulk breeding should be quantified. A model that defines the effects, requires an approach different from that presented in Chapters 4 and 5 for plant selection and progeny testing. It has to allow for heterozygosity of a number of genotypes and segregation in their offspring. Such a model falls outside the scope of this study. However, my experiments, where varieties were grown in monoculture and mixture, illustrate what may happen when bulk propagation is practised for some generations. Therefore, I will discuss some results of these experiments and of several experiments described in the literature.

Crowding in variety mixtures has already been modelled by de Wit (1960). His model will be used. It is desirable to supplement it with an expression for the correlation between reproductive rate in mixture and yield in monoculture.

Mixtures of varieties are of limited value in the simulation of segregating populations. In self-fertilizing species, the varieties are homozygous and thus 'true to seed' when they are propagated. However the genotypes in a segregating population are partly heterozygous which gives rise to the segregation in the next generation. Furthermore, heterozygotes show a higher monoculture yield than the corresponding homozygotes. The question is whether this hybrid vigour expresses itself also in mixture. When this

is the case, the shift to homozygosity with advancing generations is retarded compared with the situation where no difference exists between heterozygotes and homozygotes in their reproductive rate. Some experiments on this field are reported in the literature. These are reviewed and interpreted in the de Wit terminology.

In this chapter it is aimed:
- to discuss, based on experimental results, the effect of crowding in variety mixtures with special reference to the relation between reproductive rate in mixture and yield in monoculture (Section 7.3);
- to study the reproductive rate of heterozygotes relative to the corresponding homozygotes (Section 7.4);
- to discuss the consequences of natural selection on bulk propagation of a segregating population (Section 7.5).

## 7.2 A MODEL FOR CROWDING IN VARIETY MIXTURES

A mathematical approach of crowding among varieties in mixture was given by de Wit (1960, pp. 4-6, 16, 55-58). His competition model was outlined in Section 4.1. In this section, those aspects which deal with crowding in variety mixtures are summarized.

The 'reproductive rate' of a genotype i in a mixture is defined as

$$a_i = \frac{O_i'}{Z_i} \tag{7.1}$$

where $O'$ the number of grains harvested and Z the number of grains sown, both per unit area. The 'relative reproductive rate' of genotype i with respect to j is

$$\alpha_{ij} = \frac{a_i}{a_j} = \frac{O_i' Z_j}{O_j' Z_i} \tag{7.2}$$

After substitution of Eqn 4.6 for $O'$, this becomes

$$\alpha_{ij} = \frac{b_i M_i'}{b_j M_j'} = k_{ij} \frac{M_i'}{M_j'} \tag{7.3}$$

Thus $\alpha_{ij}$ does not depend on the relative seed frequencies and, therefore, it does not depend on the composition of the mixture.

The ratio of i to j in the harvested seed is derived from Eqn 7.2 to be

$$\frac{O_i'}{O_j'} = \alpha_{ij} \frac{Z_i}{Z_j} \tag{7.4}$$

When a sample from the harvest is sown next year, i and j are sown in the ratio $O_i' : O_j'$. Evidently, when the mixture is sown again and again under the same conditions, in the tth year the ratio of i to j in the seed sown is

$$\left(\frac{O_i'}{O_j}\right)_t = \alpha_{ij}^{t-1} \frac{Z_i}{Z_j} \qquad (7.5)$$

Substitution of Eqn 4.10 for the yield of i and j in a mixture of n genotypes into Eqn 7.2 shows that $\alpha_{ij}$ is unaffected by the presence of other genotypes. Hence, the fraction of i in the mixture relative to the fraction of j in the mixture is independent from the presence of other genotypes in the mixture.

Substitution of Eqn 5.8 for the yield of i and j in a mixture of n genotypes at arbitrary spacings into Eqn 7.2 shows that $\alpha_{ij}$ is also independent of the sowing density. Therefore, the outcome of crowding in a mixture is density independent. However, Eqn 5.8 is based on the assumption that isolated plants of the genotypes show similar growth curves. That is, the growth curves differ only by a multiplication factor on the biomass axis (section 5.2). When there are marked deviations from this assumption, the outcome of growing a mixture for several generations will be density dependent. Late-establishing types are more rapidly crowded out in a dense stand than in a sparse stand (Section 5.6).

The relative reproductive rate of each of the genotypes in a mixture can be computed by Eqn 7.2 with respect to an arbitrary reference variety j. That need be done only once; the changes in the composition of the mixture with advancing generations can then be predicted by Eqn 7.5 under the assumption that there is no $\alpha$ x year interaction.

When the yield in mixture is expressed per plant instead of per unit area, the relative reproductive rate can be derived from equation 7.2 to be $\alpha_{ij} = O_i/O_j$. In population biology and population genetics, the terms relative fitness, survival, selective and adaptive value are used for this quantity.

In conclusion, de Wit (1960): (a) quantified crowding in variety mixtures; (b) divided the ability of a variety to survive in mixture into its competitive ability b and its ability to produce kernels in monoculture $M'$ (Eqn 7.3); (c) supplied a prediction of the changes in the composition of the mixture with advancing generations based on results from only one year.

When a population is propagated as bulk for several generations, certain types will become dominant. Do the dominating types tend to produce the highest yield in pure stand? A measure of this tendency is the coefficient of correlation between $\alpha_{ij}$, the reproductive rate of a genotype i relative to a reference genotype j, and $M_i$, its yield in monoculture. The latter is proportional to the number of grains per unit area when there are no differences in weight per seed among the genotypes. For reasons mentioned in Section 7.1, the approach is restricted to a population of homozygous genotypes. It is assumed that in the first generation studied, the genotypes are sown with equal frequencies.

The coefficient of correlation between $\alpha_{ij}$ and $M_i'$ is, by definition,

$$r_{\underline{\alpha}_{ij}\underline{M}_i'} = \frac{\mathrm{cov}(\underline{\alpha}_{ij}, \underline{M}_i')}{\sqrt{\mathrm{var}\ \underline{M}_i'\ \mathrm{var}\ \underline{\alpha}_{ij}}}$$

Substitution of Eqn 7.3 gives

$$r_{\underline{\alpha}_{ij}\underline{M}_i'} = \frac{\mathrm{cov}((\underline{b}_i\underline{M}_i'/b_jM_j'),\ \underline{M}_i')}{\sqrt{\mathrm{var}\ \underline{M}_i'\ \mathrm{var}\ (\underline{b}_i\underline{M}_i'/b_jM_j')}} = \frac{\mathrm{cov}(\underline{b}_i\underline{M}_i',\underline{M}_i')}{\sqrt{\mathrm{var}\ \underline{M}_i'\ \mathrm{var}(\underline{b}_i\ M_i')}}$$

Note that j, the reference genotype, is fixed. Approximations of the covariance and the variance were found by the method of statistical differentials (Section 4.3.1.2). Then in the resulting expression we substitute: the yield level $\varepsilon\underline{M}=\mu$, the expectation of the $\underline{b}$s $\varepsilon\underline{b}=1$ (Section 6.2.1), and the variance among genotypes var $\underline{M}$=var $\underline{g}$. This gives

$$r_{\underline{\alpha}_{ij}\underline{M}_i'} = \frac{\mathrm{var}\ \underline{g} + \mu\ \mathrm{cov}\ (\underline{b},\underline{g})}{\sqrt{\mathrm{var}\ \underline{g}(\mathrm{var}\ \underline{g} + 2\mu\ \mathrm{cov}\ (\underline{b},\underline{g})+\mu^2\ \mathrm{var}\ \underline{b})}} \qquad (7.6)$$

Evidently, the correlation coefficient is not affected by the arbitrary choice of the reference genotype j.

The expression is useful for computation of the correlation coefficient when the components of variance are given. However, the insight is improved and derivation of general conclusions is facilitated by use of dimensionless parameters. Suitable dimensionless parameters are the coefficient $r_{bg}$ of the correlation between the crowding coefficient $\underline{b}$ and grain production in monoculture $\underline{g}$, and the 'competitive stress' $\gamma=\mu^2$ var $\underline{b}$/ var $\underline{g}$. These parameters were introduced in Section 4.4.4, where their significance also was discussed. After elaboration of Eqn 7.6, we have

$$r_{\underline{\alpha}_{ij}\underline{M}_i'} = \frac{r_{bg}\sqrt{\gamma} + 1}{\sqrt{\gamma + 2r_{bg}\sqrt{\gamma} + 1}} \qquad (7.7)$$

*Summary* An outline is given of the de Wit (1960) model for crowding in variety mixtures. Concurrently, the question is raised whether in a population of homozygous genotypes, the types which become dominating in the population after some generations are those with the highest yield in monoculture. The relation is quantified by an expression for the correlation between reproductive rate in mixture and grain production in monoculture.

## 7.3 EXPERIMENTS WITH VARIETY MIXTURES

### *7.3.1 Introduction and experimental design*

The effect of natural selection in populations of homozygous genotypes of a self-fertilizing species is discussed. To simulate such populations, mixtures of barley varieties were grown. Four mixtures, each with 12 varieties, were sown and the number of kernels produced per variety was counted.

In Exp. 76-2a, the varieties were sown on 30 March in peat pots in the glasshouse. When the plants were in the second-leaf stage, they were placed in a garden frame. On 4 May, the plants in the peat pots were planted out in the field at 6x25 $cm^2$ $plant^{-1}$ according to the arrangement described in Section 2.1.2. The experiment was laid out in

two adjacent main plots. Since the drought stress of the main plots was very different, they were considered as two treatments. Drought was more severe in main plot 1 and thus that plot was harvested 14 days earlier than main plot 2.

In Exp. 77-1b, the varieties were sown directly in place. The seeds were accurately spaced by hand, two kernels being sown at each place and the plants being singled after emergence. The density of stand was 5x25 $cm^2 plant^{-1}$. The planting was described in Section 2.1.4. In 1977, on 30 March, a mixture of 12 varieties was sown in the glasshouse, in a way similar to the field experiment 77-1b. The glasshouse trial consisted of 20 replicates. Each replicate had 12 plants, i.e. one per variety.

### *7.3.2 Reproductive rates*

The reproductive rate of a variety is defined in Eqn 7.1 as the ratio of the number of kernels harvested and the number of kernels sown. In the experiments, all varieties were sown at the same frequency. Therefore, the reproductive rate was proportional to the number of kernels harvested. The differences between the varieties with respect to the number of kernels produced in the mixtures were highly significant and therefore the differences in reproductive rates were also highly significant (Table 19).

The coefficient of correlation between the two main plots of Exp. 76-2a with respect to the number of kernels produced per variety was +0.79, that between the field and the glasshouse experiment of 1977 was -0.38. The poor agreement between both experiments can mainly be ascribed to the behaviour of L98 and Titan. These cultivars produced fewest grains in the field but most grains in the glasshouse. Also in Exp. 76-2a the reproductive rate of Titan was relatively high, while L98 was not included in those mixtures . In the experiments sown with a drill, both varieties had a small monoculture yield and a very low competitive ability (Tables 12, 13 and 16) which point to a low reproductive rate in the drill sowings.

At first sight, the results seemed contradictory. However in the field, L98 and Titan emerged late whereas in the glasshouse their rate of emergence did not differ from that of the other varieties. Temperature is probably the main cause of the paradox. In Exp. 76-2a, where the plants were raised for some weeks in the glasshouse, and in the glasshouse experiment in 1977, the temperature during germination and early growth was relatively high. On the contrary, in Exp. 77-1b and the drilled trials, the germination and early growth took place at the low, fluctuating field temperatures of March and early April. A time-lag at emergence causes a poor position in the competition for the available space. L98 and Titan had a time-lag in the field but not in the glasshouse and this explains the differences in their behaviour in the different experiments.

There is considerable evidence that species and genotypes which establish first have a competitive advantage (Harper, 1965). Advantage of early emergence in sunflower was illustrated by D'Yakov & Dragavtzev (1975). They used two seed samples of the same cultivar. In 'mixture' plots the grains of one sample were sown and some days later the grains of the other sample were sown between them. Within each 'monoculture' plot, the grains were sown simultaneously. A difference in sowing time brought about a corresponding difference in time of emergence. In mixture, there was a large difference in yield

Table 19. Number of grains produced per plant in mixtures where 12 varieties were grown at the same frequency. In 1976 the spacing was 6x25 $cm^2$ $plant^{-1}$ and in 1977 it was 5x25 $cm^2$ $plant^{-1}$. Exps 76-2a, 77-1b and a glasshouse experiment.

| Variety | 76-2a | | 77 | |
|---|---|---|---|---|
| | Plot 1 | Plot 2 | field(77-1b) | glasshouse |
| Varunda | | | 124 c | 73 bc |
| Tamara | | | 188 a | 88 abc |
| Belfor | 111 cde | 156 b | 126 c | 65 c |
| Aramir | | | 127 c | 81 abc |
| Camilla | 120 cde | 142 b | 133 c | 43 d |
| Golden Promise | 135 bc | 139 b | 158 abc | 38 d |
| Balder | 93 ef | 113 cd | 135 c | 67 c |
| WZ 704068-14 | | | 159 abc | 81 abc |
| Goudgerst | | | 175 ab | 79 abc |
| L98 | | | 85 d | 103 a |
| Titan | 153 ab | 136 bc | 42 e | 97 ab |
| Bigo | 164 a | 182 a | 142 bc | 80 abc |
| Piccolo | 106 de | 149 b | | |
| Julia | 131 bcd | 83 e | | |
| Minerva | 107 de | 99 de | | |
| v.d. Have 198-71 | 98 ef | 114 cd | | |
| Proctor | 76 f | 98 de | | |
| Uniculm | 23 g | 22 f | | |

Values followed by the same letter are not significantly different in the Student-Newman-Keuls test at $P \leq 0.05$.

between both samples. However the monocultures sown at different times had about the same yield. Thus, a difference in emergence of a few days resulted in a relatively great difference in competitive ability. Similar experiments with similar results were published by Kiesselbach (1923) with rows of maize as experimental units and by Oka & Morishima (1975) with plants of rice. Also the results of experiments with different sowing times of a species in stands of another species, point to a competitive advantage of the component that is established first (Harper, 1961; Rerkasem, 1978; Elberse & de Kruyf, 1979). These data support the view that the poor competitive ability and the low reproductive rate of L98 and Titan in the field was caused by their retarded emergence.

The conditions in the field during March and early April were sub-optimal for emergence, while the conditions in the glasshouse with a rather homogeneous environment and high temperatures were near-optimal. A slow, irregular emergence and a reduced number of established plants at sub-optimal conditions, in contrast to a normal emergence in near-optimal situations, is characteristic for reduced seed vigour. Apparently, seeds of L98 and Titan had a reduced vigour. Remarkably, L98 and Titan were the only varieties involved

in the experiments without a West-European origin (Table 6). The different origin may account for the reduced vigour of the seeds. Titan has naked seeds, a characteristic that is considered to be unfavourable under Dutch conditions, especially for field emergence.

Harlan & Martini (1938), Blijenburg & Sneep (1975) and others reported that the varieties with a geographical origin very different from the location where the mixture is grown, are rapidly crowded out. An explanation for this phenomenon may be a slow development of the deviating types early in the season, as a result of late or reduced emergence or retarded early growth.

*Summary* Large differences were found between the varieties in their reproductive rate in mixture. The extremely low reproductive rate of two of the varieties in the field could be traced back to their retarded emergence. The late emergence was ascribed to reduced seed vigour. Both these varieties were the only ones without a West-European origin. Late establishment may be an important reason for the frequently reported phenomenon that types with a geographical origin very different from the location where the mixture is grown, are rapidly eliminated from the mixture.

### *7.3.3 Relation between reproductive rate in mixture and yield in monoculture*

The ability of a genotype to survive in mixture is characterized by its reproductive rate relative to that of a reference genotype. In the mixtures all varieties were grown at the same frequency. Therefore the relative reproductive rate of a variety was proportional to the number of grains produced by that variety in mixture. The relative reproductive rate of a genotype is determined by its competitive ability and by its number of grains produced in monoculture, relative to a reference genotype (Eqn 7.3).

*Experiment 77-1* The reproductive rate of a genotype in mixture was defined in Eqn 7.1 as $O_i'/Z_i$ where $O_i'$ the number of grains harvested and Z the number of grains sown, both per unit area. In a mixture, where the genotypes are grown in equal frequencies, the reproductive rate equals the number of grains produced per plant $O_i$. For such a mixture $O_i=b_iM_i$ (Eqn 4.14) with $b_i$ the crowding coefficient and $M_i$ the grain production per plant in monoculture. Hence, in a mixture where the genotypes are grown in equal frequencies, the reproductive rate of a genotype i is $b_iM_i$. Such a mixture was laid out in Exp. 77-1b. In this way, the reproductive rate in mixture can be partitioned into (1) the grain production in monoculture and (2) the competitive ability (Fig. 27). The monoculture data were derived from Exp. 77-1a and the crowding coefficient was estimated from Exp. 77-1a (monocultures) and Exp. 77-1d (mixture). For Exp. 77-1d, the number of grains per plant, which was not recorded, was estimated from the ear weight per plant of a variety by means of its weight ratio grain:ear and its weight per grain. The weight ratio and the weight per grain were observed in the monocultures. Hence, no information is used that is obtained from the mixture of Exp. 77-1b itself.

In this experiment, 48% of the variation among genotypes in the number of kernels produced in mixture could be ascribed to variation in the estimated crowding coefficients and only 9% to the observed differences in grain production in monoculture (Fig. 27).

The remaining variation was mainly attributable to random error and differences between mixture and monoculture with respect to conversion factors of ear weight per plant. In conclusion, in this experiment, the reproductive rate of a genotype was mainly determined by its competitive ability and only slightly by its number of grains produced in monoculture. Because the plants were grown at 5x25 $cm^2$ $plant^{-1}$, the observed trend would be even more pronounced at normal seed rates. However, it should be noted that in this experiment, the differences among the varieties in monoculture were small.

The relation between the reproductive rate in mixture and the grain weight per plant (grain yield) in monoculture (r=0.03) was even weaker than the relation between the reproductive rate in mixture and the number of grains produced in monoculture (r=0.30). This was partly due to the relatively low correlation between grain number and grain weight per plant in monoculture (r=0.47, Fig. 27). Hence, the differences between the varieties in monoculture arose mainly from differences in weight per kernel rather than from differences in number of kernels. In the other experiments, with monocultures as well as with mixtures, the range in variety yields was much larger. It appeared that the wider the range, the higher the correlation coefficient of grain number and grain weight per plant.

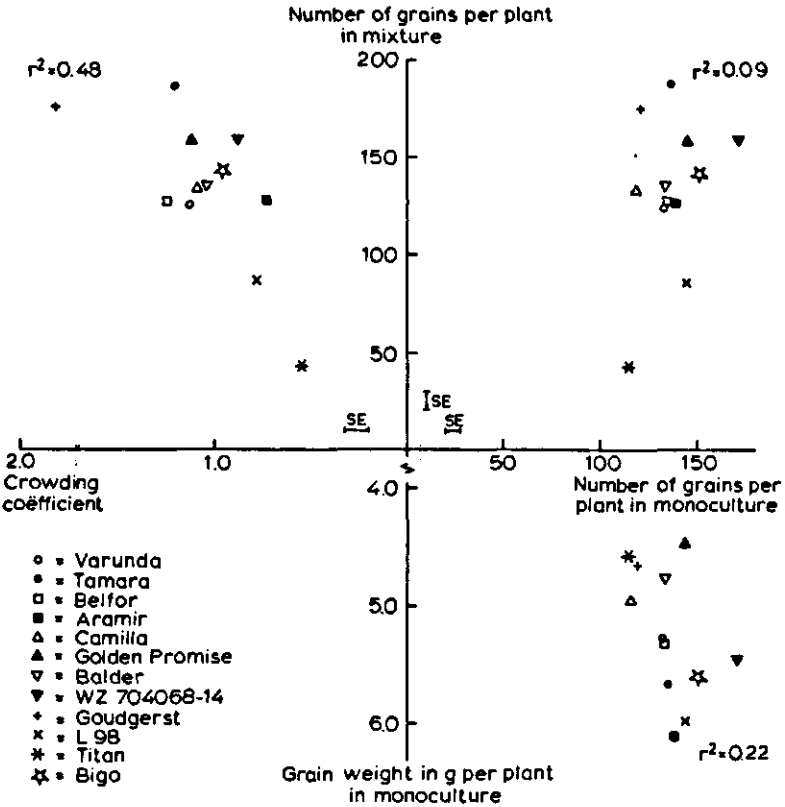


Fig. 27. The reproductive rate in mixture of each of 12 varieties, split into the crowding coefficient and the number of grains produced per plant in monoculture. The reproductive rate is measured by the number of grains produced in the mixture as the varieties were sown in equal frequencies. The relation with the grain yield in monoculture is also given. Exp. 77-1.

When monoculture yield was measured by the relative yield in national variety trials (Table 6), the relation between reproductive rate in mixture and grain yield in monoculture was considerably improved (r=0.58). The relation was even slightly better than that between monoculture yield in microplots (Exp. 77-1a) and the relative yield in national variety trials (r=0.44). In my opinion, however, it is going too far to support Suneson & Stevens (1953) who asked 'whether superiority based on comparative testing (in monoculture) is a better measure of superior variety than is survival capacity.'

*Experiment 76-2* In this experiment, the varieties were grown in mixtures as spaced plants and, adjacent to the mixtures, in monocultures in field plots. The coefficient of correlation between number of grains produced in mixture (Table 19) and monoculture yield in field plots (Table 12) was 0.39 and 0.42 for Plot 1 and 2, respectively. It is emphasized that the plants in the multicomponent mixture were planted out in peat pots in the field at 6x25 $cm^2$ $plant^{-1}$, in contrast to the drilled sowing with higher seed rates which was used in the field plots. Thus the comparison between the mixture and the field plots may be confused by the variety x method interaction.

In Exp. 76-2d, the varieties were planted out in monoculture in peat pots at 6x25 $cm^2$ $plant^{-1}$. Hence, they were treated like their counterparts in the mixture. Because only two replicates were laid out, the individual variety means have little significance and are, therefore, not given. Pooled over the two main plots, the correlation between number of grains produced in mixture (Exp. 76-2a) and number of grains produced in monoculture at the same spacing (Exp. 76-2d) was 0.72. The correlation between number of grains produced in mixture and grainweight per plant in monoculture at the same spacing was 0.65.

*Glasshouse experiment 1977* The correlation between number of grains produced in mixture in the glasshouse experiment (Table 19) and the relative yield in national variety trials (Table 6) was -0.33. Probably the negative correlation can be largely ascribed to differences in monoculture yield in the glasshouse and in the field. Thus selection for yield has to take place in an environment which is similar to that where the varieties ultimately have to perform.

Care has to be taken in extrapolating the correlation coefficient of reproductive rates of varieties in mixture and their yield in monoculture, to segregating bulks. (See also Section 6.4 for the interpretation of correlation coefficients estimated from variety mixtures). The differences between varieties are larger than those between genotypes in a segregating population. Thus the correlation coefficients, reported in this section, tend to be higher than the corresponding correlation coefficients for genotypes in a segregating population. Varieties are selected on their agronomic value so that they might give fundamentally different correlations than random genotypes do. The heterozygosity of the genotypes in a segregating bulk complicates the interpretation of the correlation between reproductive rate and monoculture yield as pure line. In my experiments, the comparisons of mixtures with monocultures in field plots were complicated by differences in husbandry and often by differences in year and location too.

*Summary* In the mixture studied, the differences in reproductive rate among the varieties were mainly due to their differences in competitive ability. Differences in number of grains produced in monoculture were found to have little effect on reproductive rate. In field experiments, the genetic correlation between reproductive rate in mixture and grain yield (i.e. grain weight) in monoculture ranged from 0.03 to 0.65. Hence, the correlation was always positive. Extrapolation of correlation coefficients obtained in variety mixtures to segregating bulks is discussed.

### *7.3.4 Shift in genotypic frequencies under bulk propagation*

De Wit (1960) introduced a method to predict the shifts in the composition of a mixture when this mixture is sown and resown year after year under constant environmental conditions. The method, described in Section 7.2, is applied to the data of Exp. 77-1b. As was found by Harlan & Martini (1938), Pal et al. (1960) and Blijenburg & Sneep (1975), there is one 'winning' variety that gains each year, there are losing varieties that lose each year and there are intermediate varieties. The intermediate ones gain first at the cost of the losers, but subsequently lose because later they have to compete predominantly against the winner. The computed share in the mixture is given in Fig. 28 for three representative cultivars for a period of 8 years. After 20 years, 75% of the plants would belong to the cultivar Tamara. Ultimately, Tamara would be the only one that survives.

At the moment, mixtures of varieties are in fashion whatever the supposed advantages. Fig. 28 illustrates what may happen when a farmer multiplies his own seed. The mixture dissociates rapidly so that the claimed advantages of the mixture are partly lost. It also emphasizes that the commercial seed must be manufactured by mechanical blending of seed from the monocultures of the constituent varieties.

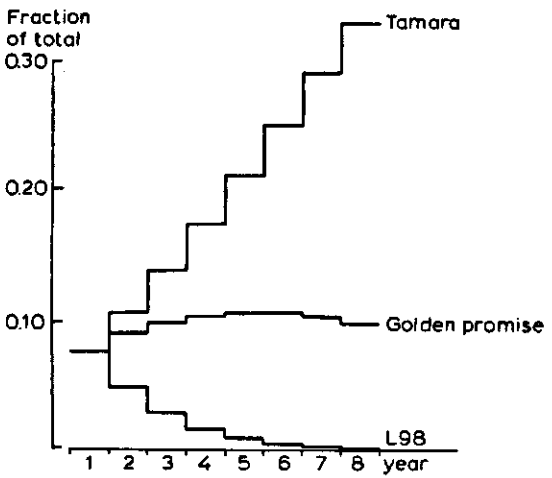


Fig. 28. Simulated relative frequencies of three varieties out of a mixture of 12 varieties when the mixture is grown for 8 years under constant environmental conditions. The simulation is based on the reproductive rates of varieties measured in one year. Exp. 77-1b.

*Summary* The shift in the composition of variety mixtures grown for several generations is illustrated by the data from a mixture of 12 varieties. Consequences for seed production of commercial mixtures are discussed.

### *7.3.5 Changes in mean and genetic variance of yield under bulk propagation*

With respect to yield, the value of a population for a breeder is determined by the level and the variance of the 'yield capacity' of the present genotypes. The yield level must be high enough and there must be sufficient genetic variation available for selection to be justified. So it seems convenient to express the effect of natural selection on bulk propagation with advancing generations in terms of changes in the yield level $\mu$ and the genetic variance var g.

We assume a population with genotypes that are true to seed. Hence, we exclude heterozygosity and cross fertilization. A variety mixture of a strictly self-fertilizing species satisfies this assumption. Because the varieties are intended to be grown in monoculture, the 'yield capacity' of a genotype refers to its yield in monoculture at a normal crop density. Evidently, the yield in the mixture does not measure the agronomic value: it only measures the ability to yield high in that particular mixture. The average 'yield capacity' of a mixture is therefore defined as the average of the monoculture yields, weighted according to the relative seed frequencies in that mixture:

$$\mu_{mono} = z_1M_1 + .... + z_nM_n$$

and the genetic variance is

$$\text{var } g_{mono} = \text{var } \underline{M} = z_1M_1^2 + .... + z_nM_n^2 - (z_1M_1 + .... + z_nM_n)^2$$

where M the monoculture yield and z the relative seed frequency of the subscripted genotype in mixture. When intergenotypic competition is absent in the mixture, $\mu_{mono}=\mu_{mix}$ and var $g_{mono}$=var $g_{mix}$.

De Wit (1960) introduced a method to predict the shifts in the frequencies of the varieties grown in a mixture for several generations (Section 7.2). Given the monoculture yields and the initial frequencies, this method enables us to estimate the changes of $\mu_{mono}$ and var $g_{mono}$ over the course of generations in bulk propagation. It is assumed that the environmental conditions are constant from year to year. As was shown in Section 7.2, under certain assumptions, the density of stand does not affect the shifts in the composition of the mixture. Then the density does not affect the changes in time of $\mu_{mono}$ and var $g_{mono}$.

As an example, the method is applied to a mixture where 12 varieties were sown at the same frequency at 5x25 $cm^2$ $plant^{-1}$ (Exp. 77-1b). The yield capacity of the varieties is measured either by their yield in adjacent monocultures at 5x25 $cm^2$ $plant^{-1}$ (Fig. 29) or by their relative yield in national variety trials (Fig. 30). It is claimed that the latter measures the yield under 'average' farm conditions, i.e. the yield in the 'average' environment where the varieties ultimately have to grow. We see, that there is not neces-

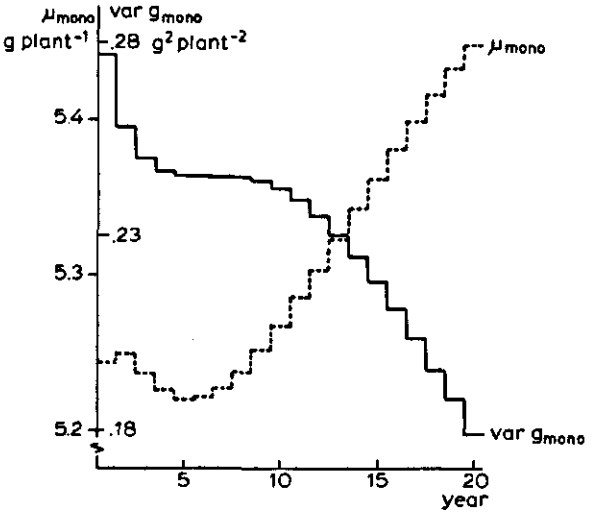


Fig. 29. Simulated changes in yield level $\mu_{mono}$ and genetic variance var $g_{mono}$ in a mixture of 12 varieties grown for 20 years. The initial frequency of the varieties equals 1/12. The simulation is based on the reproductive rates of the varieties measured in mixture in one year (Exp. 77-1b). The yield level and the genetic variance are expressed with respect to monoculture yield, measured in microplots at 5x25 $cm^2$ $plant^{-1}$ (Exp. 77-1a).

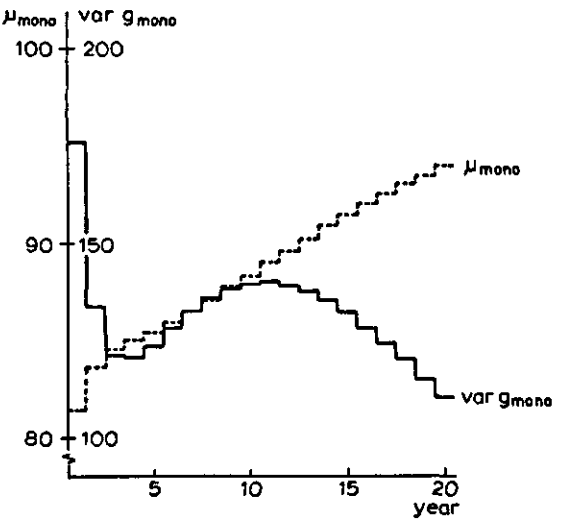


Fig. 30. Similar to Fig. 29, except that the monoculture yield is measured by the relative yield in national variety trials (Table 6).

sarily either a steady increase or steady decrease of $\mu_{mono}$ and var $g_{mono}$. The course curves show both rises and declines. On the whole, the yield level of this population increased because the winning cultivar, Tamara, yielded best in monoculture (Tables 6 and 14). The path of the curve for var $g_{mono}$ in Fig. 30 can be understood from the

reproductive rates (Table 19) and the monoculture yields (Table 6). At first, there was a rapid decline of var $g_{mono}$ because two extremes, L98 and Titan, were eliminated. Subsequently, the genetic variance increased as varieties with medium yields were crowded out while two extremes, the high-yielding Tamara and the low-yielding Goudgerst, were favoured. Finally, Tamara was the winner and, thus, the genetic variance approached zero.

In a barley composite population, Jain (1961) and Allard & Jain (1962) found that with 18 cycles of bulk propagation the plant to plant variation decreased. They ascribed the decrease to the elimination of 'unadapted' types. In *Phaseolus vulgaris*, Hamblin (1977) studied four single-cross populations until the F6 generation. The mean seed yield of the two high-yielding crosses did not alter, but there was a steady increase in the mean seed yield of the two low-yielding crosses with subsequent generations. According to the author, this was probably due to a larger frequency of 'poorly adapted' genotypes in the low-yielding crosses. There were no differences in interplant variation between the generations within the crosses. Later generations than F6 were not involved because in breeding practice, bulk propagation is mostly not prolonged after the F6. The decrease in heterozygosity with subsequent generations interferes with the trends in the population mean and the interplant variance. It should be noted that the interplant variation measured by Jain (1961) and Allard & Jain (1962) was in mixture at wide stands and that measured by Hamblin (1977) was in mixture at normal densities. However, of interest to the breeder is the genetic variance for monoculture yield at a commercial seed rate and not the yield under the conditions considered by those authors. As is shown in Chapters 4, 5 and 8, the genetic variance in monoculture at a commercial stand may greatly differ from the genetic variance in mixture and from that at wide stands.

Figs 29 and 30 are of little use for deriving general conclusions about the consequences of bulk breeding. They only illustrate a method of analysing the breeding perspective of a population and the consequences of propagating the population for several generations. The results are restricted to the varieties involved as grown under the prevailing conditions. The monoculture yields refer to those in microplots at a somewhat wide spacing (Fig. 29) or to the relative yield in field plots but in a set of environments (Fig. 30). Moreover, the variety mixture consists of a few, homozygous genotypes, whereas a segregating population is characterized by many genotypes and some degree of heterozygosity. In a variety mixture, the genetic variance is a population parameter for the fixed set of involved varieties and thus is of little relevance for segregating populations.

In quantitative genetics, the conventional model is based on absence of differential viability for the genotypes of the character studied (Mather & Jinks, 1972, p. 127). However, for most quantitative traits, especially seed yield, there is always differential viability. Some genotypes show a high reproductive rate while others are poorly reproductive. Several models which account for a differential reproductive rate have already been developed by population geneticists (review by Li, 1976; Wright, 1969 and 1977). These models deal with the effect of natural selection in mixture, which effect can be charaterized by the relative reproductive rates of the genotypes. No reference is made to the monoculture yield of the genotypes which is of little interest to the population geneticists. In breeding, however, monoculture yield is the crucial quantity. Monoculture

performance is one of the quantities in the expression for the relative reproductive rate, introduced by de Wit (1960). Therefore, it is useful to combine his agro-ecological approach with the conventional genetic model. The procedure of Section 4.3 is a first step. Attention has to be paid to the feature that the de Wit model is proportional, while the genetic model is additive. Additivity of genetic effects can be criticized (Rasmusson, 1933) as well as additivity of genetic and environmental effects, since deviations from additivity appear to be the rule.

*Summary* The value of a population for a breeder is expressed in terms of the mean and the genetic variance for yield. Yield is referred to yield in monoculture since ultimately, the genotypes have to perform in monoculture. An example is given of the changes in the mean and the genetic variance when a mixture is grown for several generations. It is recommended that the competition model of de Wit (1960) be combined with the conventional genetic model in order to account for the competition-dependent changes in gene frequencies and variances with advancing generations and to interpret these changes in a population in terms of monoculture yield of the genotypes.

## 7.4 REPRODUCTIVE RATE OF HETEROZYGOTES RELATIVE TO HOMOZYGOTES

In breeding, a segregating population is usually created by intercrossing two genotypes. In self-fertilizing species, the parents are homozygous and the resulting $F_1$ is therefore heterozygous for those loci for which the parents differ. Often, the heterozygous $F_1$ surpasses both its parents in yield. This phenomenon is called 'hybrid vigour' or 'heterosis'. In general, it is supposed that heterosis for yield accompanies heterosis for competitive ability and reproductiveness in mixture. When this is true, the growth towards homozygosity with advancing generations of self fertilization is slower than would be expected when there is no difference in reproductive rate between homozygotes and heterozygotes. Moreover, when single plants are selected for yield, predominantly heterozygotes are chosen as these produce the highest yield in mixture. Now we will examine whether, in self-fertilizing cereals, heterosis for yield, competitive ability, and reproductive rate is the rule.

For the small cereals, there is extensive literature to show that $F_1$ often outyields both its parents. A review of the early literature on heterosis in wheat is given by Briggle (1963). In most experiments only a small number of $F_1$s are grown together with their parents and then at a wide stand. However, for a general view on the heterosis effect, an extensive trial seems better than a number of small, selected experiments. A comprehensive test was reported by Zeven (1972). Fifty-seven winter wheat and 50 spring wheat $F_1$s and their parents were grown in the field at a relatively wide density of 67 plants $m^{-2}$ in unreplicated plots of 50 plants. The $F_1$ plots were bordered with rows sown with the parents. The unpublished results (Zeven, pers. commun.) showed that, in winter wheat, 52 $F_1$s outyielded both their parents, 5 $F_1$s were intermediate and none of them had a lower yield than both their parents. In spring wheat, these numbers were 38, 6 and 6, respectively. In winter wheat, the mean yield of the $F_1$s was 626 g $m^{-2}$ and that of their parents was 407 g $m^{-2}$. In spring wheat, the $F_1$s yielded 413 g $m^{-2}$ and the parents

318 g $m^{-2}$. The choice of the parents was not fully at random. For example, combinations were avoided in which it was expected that the $F_1$ would show hybrid necrosis. However, the populations used by breeders are also derived from selected crosses. Probably, the crosses involved in this trial are representative for a large part of the crosses used in breeding programmes.

In conclusion, the monoculture yield of heterozygotes is considerably higher than that of the corresponding homozygotes. This will also hold for the number of grains produced in monoculture.

The competitive ability of heterozygotes in relation to homozygotes can be measured by the relative crowding coefficient $k_{het.hom} = b_{het}/b_{hom}$. Reliable estimates could not be derived from experiments, reported in the literature, where both are grown in monoculture and mixture. In barley, Sakai & Gotoh (1955) studied five varieties and their 10 $F_1$ hybrids in pure culture and in mixtures with two tester varieties at 12x50 $cm^2$ $plant^{-1}$. They found that all the $F_1$s had a higher plant weight and eight of them had also a higher weight of the ears than their midparent value. There were marked heterotic effects: the $F_1$s outyielded the parents by 36% and 28% for plant weight and ear weight per plant, respectively. However, only one of the $F_1$s was superior in competitive ability to its midparent with respect to plant weight. For ear weight, two of the 10 $F_1$s had a higher competitive ability compared with the midparent. On the other hand, in a similar study in rice, Sakai & Utiyamada (1957) found that for five crosses the $F_1$ was more competitive than both its parents, for one cross the $F_1$ was intermediate, and in none of the crosses was the $F_1$ weaker than both its parents. In barley, Suneson (1962) sowed three $F_1$s and three parents in monoculture and in a mixture at a commercial rate. In monoculture, there was a large heterosis effect for yield. From his results, it can be derived that the $F_1$s had a higher competitive ability than either of the parents. Suneson observed that the hybrids germinated faster, grew taller and headed earlier than either parent. In wheat, Phung & Rathjen (1977) found an $F_1$ intermediate in competitive ability compared with the parents at 6.7 x 6.7 $cm^2$ $plant^{-1}$. It is unknown whether there was heterosis for yield as monocultures were not grown.

Density experiments are an extreme form of competition experiments, as was shown by de Wit (1960). He introduced a method to estimate the competitive relations among genotypes solely from monocultures grown at various densities. I applied that procedure of de Wit (1960, p. 59) to published data of grain yields in experiments where $F_1$s and their parents were grown in field plots at several seed rates. Data from supra-optimal densities were discarded (Section 5.2). It is emphasized that the estimation is based on similarity of the growth curves of isolated growing plants. The crowding coefficient of heterozygotes relative to their homozygous counterparts was estimated to be 1.32 for the barley data of Severson & Rasmusson (1968), 0.70 for the spring wheat data of Briggle et al. (1967), and 1.02 for the winter wheat data of Zeven (1972). The estimates refer to a population grown at 50 $cm^2$ $plant^{-1}$. The authors studied five, one, and six hybrids at four, five, and four spacings, respectively. In all studies, there was a prominent heterosis for yield in pure stand.

The experiments where $F_1$s and their parents were grown in monoculture and mixture

as well as the experiments where they were raised in monocultures at different densities, do not provide a consistent picture of the competitive ability of heterozygotes relative to homozygotes. The median of the relative crowding coefficient $k_{het.hom}$ is probably close to unity, i.e. there is on the whole no competitive advantage of the heterozygotes over the homozygotes. However, only a few experiments were involved. Moreover, the homozygotes were cultivars or breeder lines and so they did not constitute a random sample from the homozygotes that occur in a segregating population. Furthermore, $F_1$ seed and parental seed were obtained in different ways. $F_1$ seed was produced by artificial pollination of emasculated ears, which were probably enveloped while parental seed was produced with natural self-fertilization. It may be that in some experiments $F_1$ seed was produced in the glasshouse while seed of the parents was harvested on the field. On the other hand, Suneson (1962) and Severson & Rasmusson (1968) made crosses on male-sterile plants.

The difference in the manner of seed production may have caused differences in size and vigour of $F_1$ seeds and parental seeds. In spring wheat, Hellingman (1977) emasculated about 100 ears of each of three varieties. Each of these ears was enveloped together with one non-emasculated ear of the same variety, of a similar size and of a similar developmental stage as the emasculated ear. Pollination was promoted by shaking the envelopes several times for some days. Due to the smaller number of kernels per ear on the emasculated ears (average of 10 kernels/ear) than on the non-emasculated ears (average of 25 kernels/ear), the former kernels were larger in size. Besides the enveloped ears, ears where seed set occurred in a natural manner, were harvested. The kernels produced by these ears were larger in size than those from both types of enveloped ears. Hellingman (1977) suggested that the smaller size of kernels from enveloped ears may be due to a higher temperature and more aphids inside the envelope than outside. Shading of ears by the envelope may have been of importance too. The kernels from enveloped ears were perhaps also less vigorous.

In cereals, plants originating from small seeds give about the same yield in pure stand but a lower yield in mixture than plants from larger seeds (Montgomery, 1912; Kiesselbach, 1918; Christian & Gray, 1941; Kaufmann & McFadden, 1960; Helgason & Chebib, 1963; Sandfaer, 1970; Roy, 1973; and others). This is explained by the slower early growth of plants from smaller seeds due to fewer reserves in the endosperm. Slowness in the early stages of growth brings about a competitive disadvantage as has been shown in experiments (Harper, 1965) and simulation studies (de Wit, 1970).On the other hand, in monoculture, plants from small seeds compete against plants of the same seed-size origin. Then their genetic potential can express itself fully, and their monoculture yield nearly equals that of plants from large seeds.

$F_1$ seeds may be less vigorous than the parental seeds because of the manipulations required for their production. Just as with smallness of seeds, that vigour will hardly affect the pure stand performance. However, reduced vigour of seeds will markedly decrease their competitive ability (Section 7.3.2). The experiments of Suneson (1962) and Severson & Rasmusson (1968) showed clear competitive advantage of heterozygotes. Remarkably, in these experiments, $F_1$ seed was produced on male-sterile plants, that is with a minimum of human manipulation.

In conclusion, $F_1$ seed and parental seed is produced in different ways. This leads

to differences in seed size and, perhaps, also to differences in seed vigour between both groups. The differences are more pronounced in mixture than in pure stand. Therefore, the estimates of the relative crowding coefficient $k_{het.hom}$, from the previous experiments reported in the literature, are greatly biased. In future experiments, seeds of the parents should be produced in the same way as seeds of their $F_1$.

The reproductive rate of heterozygotes relative to homozygotes is a function of their grain production in monoculture and their competitive ability (Eqn 7.3). When we consider the conservative estimate of $k_{het.hom} = 1$ and the higher grain production of heterozygotes to homozygotes in monoculture, we see from Eqn 7.3 that the relative reproductive rate $\alpha_{het.hom}$ is larger than unity. Hence from the monoculture yields, it is expected that heterozygotes have a higher reproductive rate than the corresponding homozygotes. Experimental evidence on this point can be derived from the literature. The reproductive rate of heterozygotes to homozygotes may be estimated from the changes in their frequencies in hybrid populations. In barley, Jain & Allard (1960) studied the changes in frequency of homozygotes and heterozygotes at eight loci occurring over 18 generations. Because of linkage, the hereditary units in consideration here are not single loci but chromosome segments marked by the loci studied. The authors observed a higher reproductive rate of the heterozygote than either of the corresponding homozygotes for five loci, an intermediate reproductive rate for two loci, and a lower one for only one locus. Averaged over eight loci, the reproductive rate of the heterozygotes relative to the corresponding homozygotes was 1.22. In similar studies, a reproductive rate of heterozygotes compared with that of both their corresponding homozygotes was higher in *Phaseolus lunatus* for three loci (Allard & Hansche, 1964; see also Harding et al., 1966) and in wild oats for two loci (Imam & Allard, 1965).

*Summary* From the literature on self-fertilizing cereals, an attempt was made to derive a general conclusion about the position of heterozygotes relative to their corresponding homozygotes with respect to reproductive rate and its components: the monoculture yield and the competitive ability. In general, heterozygotes substantially outyield the homozygotes. On the other hand, no clear conclusion about their competitive ability can be given because in all experiments, reported in the literature, $F_1$ seed and parental seed were obtained differently. This leads to differences in seed size and perhaps also to differences in seed vigour between both groups. It is argued that these differences hardly influence the monoculture yields, but greatly bias the estimates of the competitive ability. In general, the reproductive rate in mixture was higher for heterozygotes than for homozygotes.

## 7.5 BULK PROPAGATION AS PART OF A BREEDING PROGRAMME

In breeding practice, a segregating population is, in general, propagated as bulk for some generations before single plants are selected from it. Starting artificial selection just after some generations of bulk propagation, was compared in Section 1.3.1 with starting artificial selection already in $F_2$ or $F_3$. The choice is mainly determined

by the expected influence of natural selection and by that of the increase of homozygosity with advancing generations.

In this section, the ways in which intergenotypic competition and natural selection affect the outcome of bulk propagation are surveyed.

For most breeders the increased homozygosity is the main reason for multiplying a population for several generations before selecting single plants from it. In Section 7.4, it was concluded that heterozygotes have, in general, a higher reproductive rate than the corresponding homozygotes. Therefore, the growth to homozygosity will be slower than expected from the genetic models that assume that the genotypes have identical reproductive rates. Also the small percentage of cross fertilization that occurs in self-fertilizing crops contributes to this delay. In my opinion these effects on the degree of homozygosity are too small to influence the choice between starting artificial selection in late generations or in early generations.

Natural selection favours those genotypes that produce the largest number of viable kernels giving rise to fertile plants. These approximate the genotypes with the highest reproductive rate in mixture. The reproductive rate of a genotype i relative to a reference genotype j is a function of its grain production in monoculture and of its crowding ability in mixture (Eqn 7.3). Therefore, nature favours strong competitors but also genotypes that produce many grains in monoculture. The latter genotypes are those with the highest monoculture yield, if indeed the differences in monoculture yield between the genotypes are explained by differences in grain number rather than by differences in weight per grain. The effect of differences in weight per grain is levelled because the higher reproductive rate of genotypes with smaller grains due to more grains per gram is opposed by a lower reproductive rate due to the competitive disadvantage of smallness of the seeds.

The coefficient of the correlation between the reproductive rate of a genotype in mixture and its grain production in monoculture $r_{\alpha M'}$ determines the degree to which types that yield best in pure stand are favoured by natural selection. Information about the magnitude and the sign of $r_{\alpha M'}$ can be derived from variety mixtures and segregating populations and they can also be obtained from a theoretical model.

The literature on survival of barley varieties in mixtures grown for several generations was reviewed in Section 1.3.1. There was a tendency that varieties preferred by local farmers become dominant in the mixture or are crowded out only in late generations. On the other hand, varieties with a geographical origin very different from the location where the mixture is grown tend to be rapidly crowded out. The findings for variety mixtures suggest a positive sign of the correlation of $\alpha$ and $M'$. In my field experiments with mixtures of 12 barley varieties, $r_{\alpha M'}$ appeared to be always positive. Its value ranged from 0.03 to 0.65 (Section 7.3.3). In the field, the two varieties without a West-European origin had an extremely low reproductive rate.

Correlation coefficients found in variety mixtures cannot automatically be extended to segregating populations (Section 7.3.3). Composite crosses, which are obtained by mixing $F_1$ or $F_2$ seed of many single crosses, approach more closely populations derived

from simple crosses. In this way, composite crosses give additional information about the size of the correlation coefficient $r_{\alpha M}'$ that can be expected in populations from simple crosses. In what follows, only composites of barley are involved.

Rasmusson et al. (1967) produced a composite by blending seed of 6000 entries of a world collection of barley. Hence, the population was not a composite cross but a mixture of many pure lines. The yield of the population increased by 57% during the 6 years that the mixture was grown. The large increase may be due to rapid elimination of poor lines. Suneson & Stevens (1953) and Suneson (1956, 1964) found that the yield of their composite crosses increased with generations when the yield was expressed as a percentage of the yield of a standard variety. However, the yield of the standard declined in the course of years and the absolute yields of the composites showed a less clear picture. In the composite cross studied by Jain & Suneson (1966), the $F_{22}$ yielded more than the $F_6$. On the other hand, Singh & Johnson (1969, 1970) and Baltjes (1975) did not find a consistent yield increase of their composite crosses with advancing generations.

In conclusion, some authors have found a steady increase of the yield of barley composites in course of generations whereas others found no consistent yield increase, but no author has observed a significant decrease in yield. At first glance, these results suggest that reproductive rate in mixture and grain yield in monoculture are positively correlated. However, the yield of a mixture $\mu_{mix}$ does not equal the mean monoculture yield of its components $\mu_{mono}$. In Section 4.4.5, it was derived that

$$\mu_{mix} = \mu_{mono} + cov(\underline{b},\underline{g})$$

where $\underline{b}$ the crowding coefficient and $\underline{g}$ the monoculture yield. Therefore, a certain yield increase in the composite gives the same increase of the average monoculture yield of its components, only if $cov(\underline{b},\underline{g})$ remains constant. These conditions will not be met, but mostly the bias is not large. As heterozygotes have a higher yield than homozygotes, the increase of homozygosity with generations oppose a yield increase caused by natural selection. This also complicates the interpretation of the yield trend in composites. A conservative conclusion, that can be derived from the yield trend in composite crosses, is that $\mu_{mono}$ does not decrease in time, i.e. $r_{\alpha M}'$ is zero or slightly positive. The suggestion of a positive correlation is supported by the study of Suneson (1956). He made selections from different generations of a barley composite cross and found that high-yielding selections made up a greater proportion of the composite as the number of generations advanced.

The results of composite crosses cannot be automatically transferred to populations from single crosses. In a composite, there will be a large number of low-yielding and poorly adapted types because of the widely different parents used. These types are eliminated rapidly from the population, which partly explains a yield increase of the composite in course of time. This kind of elimination probably holds for single-cross populations also, when one of the parents is a low-yielding and poorly adapted type. However, in breeding, most populations are from single crosses between two high-yielding parents. There is some literature on crowding in single-cross populations. In wheat, Khalifa & Qualset (1975) studied a bulk from a cross between a short and a tall variety. They

observed that the yield of the bulk, as well as the mean yield of the derived lines, tended to increase with advanced generations. On the other hand, in rice, the findings of Jennings & Herrera (1968), already described in Section 1.3.1, point to a negative association between reproductive rate in mixture and monoculture yield in their population from a cross between a dwarf and a tall cultivar.

We obtain a better idea about the relation between the reproductive rate in mixture and the yield in monoculture from the model of de Wit (1960). He expressed the relative reproductive rate of a genotype i as the product of its crowding coefficient $b_i$ and its grain production in monoculture $M_i'$ relative to $b_j$ and $M_j'$ of a reference genotype j (Eqn 7.3). As the monoculture production is a constituent of the relative reproductive rate, the relative reproductive rate of a genotype tends to be positively correlated with its grain production in monoculture. The positive relation is stronger (a) the larger the influence of the monoculture production on the relative reproductive rate, that is the less severe competition is, and (b) the more the crowding coefficient b and the monoculture production M' operate in the same direction, that is the higher the correlation coefficient of b and M'. In Eqn 7.8, the correlation coefficient $r_{aM'}$ is expressed in terms of the competitive stress $\gamma$ and the coefficient $r_{bg}$ of the correlation between b and g. The correlation coefficient $r_{bM'}$ equals $r_{bg}$. The graphical presentation of Eqn 7.7 in Fig. 31 confirms the conclusion that the lower $\gamma$ and the higher $r_{bg}$, the higher $r_{aM'}$. It shows that, even when the correlation between competitive ability and monoculture production is slightly negative, $r_{aM'}$ is still positive.

A general statement about the size of $r_{aM'}$, based on the existing data, is difficult to give. (a) There is much diversity in the estimates of $r_{bg}$, whether derived from the literature (Section 6.4, Table 18) or from my experiments (Table 17). The median of $r_{bg}$

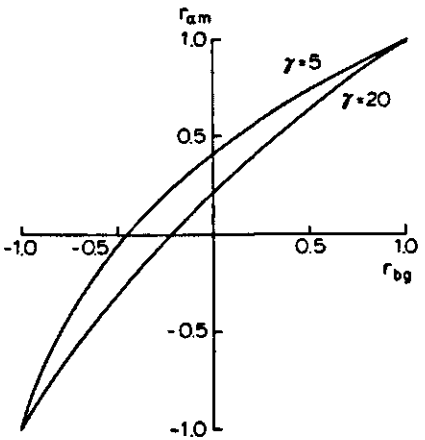


Fig. 31. The coefficient $r_{aM'}$ of the correlation between the relative reproductive rate in mixture and the number of grains produced in monoculture, expressed as function of the coefficient $r_{bg}$ of the correlation between the crowding coefficient b and the genetic value of the number of grains produced in monoculture g. The relation, mathematically expressed by Eqn 7.7, is plotted at two levels of the competitive stress $\gamma$.

is close to zero and probably slightly positive, but it has a large standard deviation. Estimates of $r_{bg}$ are derived from variety experiments, which approach is subject to criticism (Sections 6.4 and 7.3.3). (b) No information about the competitive stress could be derived from the literature. From Exp. 77-1, where 12 varieties were sown in mixture and monoculture at 5x25 $cm^2$ $plant^{-1}$, $\gamma$ was estimated to be 12.2 for the number of grains produced per plant. In bulk propagation, the spacing is closer and, hence, the competitive stress larger. In populations from single crosses, the genetic variances, var g as well as var b, are probably smaller than those in the variety mixture and this affects $\gamma=\mu^2$ var b/var g. (c) M' is expressed here in number of grains, but in production agriculture only the yield in tonnes $ha^{-1}$ is relevant. When the differences between the genotypes in monoculture yield can largely be ascribed to differences in number of grains produced and only slightly to differences in weight per grain, M' for number of grains is approximately proportional to M' for grain yield.

From the previous discussion on variety mixtures and composites as well as on theoretical grounds, it is suggested that the coefficient $r_{\alpha M}'$ for the correlation between the reproductive rate in mixture and the yield in monoculture is positive. However, the evidence is not strong and in some populations the correlation coefficient is negative (see for example Jennings & Herrera, 1968).

When a cross is propagated in bulk, it is generally only for three to six generations. Given the information about $r_{\alpha M}'$ it is not likely that natural selection causes a significant decline in 'yield capacity' of the population in this small number of generations. The 'yield capacity' of a population is the weighted average monoculture yield of the genotypes that constitute the population (Section 7.3.5). No account is made in this definition for the heterozygosity which cannot be used in pure-line breeding. In general, a slight increase in the yield capacity is expected because of the positive sign of $r_{\alpha M}'$, especially for crosses between a low-yielding, poorly adapted parent and a high-yielding parent. The low-yielding, poorly adapted segregants are rapidly crowded out from the population (Section 7.3.2).

The value of a population for breeding is determined not only by its yield level but also by the present genetic variance. The latter also is affected by natural selection as was discussed in Section 7.3.5.

Whatever the sign and the magnitude of the correlation coefficient $r_{\alpha M}'$, some valuable alleles will be diluted or even lost from the population. However, the breeder does not have to worry about a few favourable alleles lost because of natural selection. He will lose a by far larger number of favourable alleles due to the mediocre discrimination in plant selection and progeny testing. Moreover he has to reckon with an overall response to selection. Furthermore, a breeder does not chose single plants at random from a population, but he tries to select the desired types. In this way, he may partly counterbalance the adverse effects of natural selection. He can also apply alternative methods for or modifications of bulk breeding (Section 1.3.1).

In conclusion, delaying selection for yield until late generations is not handicapped by intergenotypic competition and natural selection. However this is no reason to start selection and yield testing only in late generations. Early generation selection was dis-

cussed in Section 1.2. There, it was concluded that starting yield testing in early generations is unrealistic, but that visual selection, on the other hand, has to begin as early as possible.

My experiments were concerned with yield testing in relation to intergenotypic competition. Experiments directed towards the effect of competition on selection over several generations require another experimental design. To connect these to breeding practice, populations originating from simple crosses have to be studied. From these populations, the correlation coefficient $r_{bg}$ and the competitive stress $\gamma$ may be estimated. This permits an interpretation in terms of the approach presented in this chapter, especially in Section 7.3.5. Account has yet to be made for heterozygosity.

*Summary* The correlation between the reproductive rate in mixture and the yield in monoculture will, in general, be positive. Especially low-yielding and poorly adapted types are rapidly crowded out from a population. This conclusion is based on the results of variety mixtures and composites as well as on theoretical grounds. The final conclusion is that delaying selection for yield until late generations is not handicapped by intergenotypic competition and natural selection.

# 8 Selection of single plants

In the literature, the response to selection of single plants for yield was mostly disappointing (Section 1.3.2). This poor response is ascribed to several factors, among others intergenotypic competition. However, the way in which intergenotypic competition biases the outcome of selection is not well understood. Moreover, the complicating effect of intergenotypic competition on selection is poorly quantified (Section 1.4). The model introduced in Chapter 4 provides a better understanding of the bias from intergenotypic competition and also quantifies this bias. In the present chapter, the model is illustrated and tested by experiments with variety mixtures.

Many authors have suggested the selection of single plants at a wide stand in order to eliminate competition between the plants. However, the genotypes differ in their response to spacing. In Chapter 5, a model was introduced to describe the effect of interplant competition as well as the effect of a differential response of the genotypes to spacing on the outcome of selection. The model is discussed in combination with the results of experiments with variety mixtures grown at different densities. Special attention is paid to the assumptions on which the model is based.

In the literature, several other methods were proposed to reduce the effects of intergenotypic competition. In this chapter these methods are worked out and evaluated.

Competition effects become more apparent when the large environmental error, which is characteristic for single-plant yields, is reduced. Some methods to cope with the environmental error are discussed and the influence of competition on the efficiency of the methods is pointed out.

## 8.1 ESTIMATION OF THE VARIANCES

In this section, the way that the components of the variance among plants were estimated is described. The variances are required as input in the model of Chapters 4 and 5. Moreover, they are needed to quantify the success of a selection method and to compare the selection methods with each other.

In the experiments, varieties were used to simulate the genotypes of a segregating population. This approach was discussed in Section 2.4. The varieties were grown in mixtures and in their monocultures (Exps 76-2 and 77-1; Section 2.1). This chapter deals mainly with Exp. 77-1. Therefore, the analyses discussed in this section are concerned with this experiment.

*Variances in monoculture* In Exp. 77-1a, the varieties were grown in monoculture plots of which 50 plants were harvested per plot. The variety plots were laid out in a four-times replicated randomized block design (Section 2.1.4). The effects of plots and

replicates were approximately random. The varieties were fixed but since they were used to simulate the random genotypes of a segregating population, they were treated as random in the analyses.

The yield of a plant can be described by

$$Y_{ikl} = \mu + g_k + s_i + b_{ik} + e_{l(ik)}$$

with the genotypes k=1, ....K, the replicates i = 1, ....I, and per plot the plants l=1, .... L. The variances of the stochastic effects are $\sigma_g^2$, $\sigma_s^2$, $\sigma_b^2$ and $\sigma_e^2$, respectively. The variances $\sigma_g^2$, $\sigma_s^2$ and $\sigma_b^2$ were estimated from the analysis of variance of plot means from the randomized block design. The interplant, within-plot variance $\sigma_e^2$ is estimated per plot. For this, the 50 plants per plot were divided into two groups according to odd and even plant numbers. The interplant variance per plot was obtained as the average of the interplant variances of both groups of 25 plants per plot. In this way, the covariance between adjacent plants was excluded from the interplant variance. The analysis of the monoculture in Exp. 76-2d was done similarly.

*Variances in mixture* The design of the variety mixture of Exp. 77-1b was given in Section 2.1.4 and Figs 2 and 3. The field was partitioned into 15 plots. Of these plots, five were grown with the variety mixture of Exp. 77-1b. Within each plot, there were eight replicates consisting of 12 plants each, one plant of each of the 12 varieties. The varieties were randomized within a replicate. The plot effect was random, the replicate effect was approximately random and the variety effect was considered to be random. The yield of a plant can be described by

$$Y_{ijk} = \mu + g_k + s_i + gs_{ik} + r_{j(i)} + e_{ijk}$$

with the genotypes k=1, ....K, the plots i=1, ....I, and per plot the replicates j=1, ....J. The variances of the stochastic effects are $\sigma_g^2$, $\sigma_s^2$, $\sigma_{gs}^2$, $\sigma_r^2$ and $\sigma_e^2$, respectively. Table 20 shows the analysis of variance. The estimates of the variances were derived from this table.

The other arrangements with mixtures in Exps 77-1 and 76-2 were analysed in a similar way.

*The environmental variance as function of the plot size* When the plot area becomes larger, the environmental variance among the plants within the plot almost always increases. In the experiment, the area of the monoculture plots differed from that of the mixture plots. Therefore, the estimates of the environmental variances in both types of plots could not be compared directly with each other. In the following, a method is presented to adjust the variance to the plot area.

Smith (1938) described the relation between the interplant variance and the plot size by

$$V_{\bar{N}} = V_1/N^f$$

Table 20. Analysis of variance of the variety mixtures where K genotypes are randomized as single plants within replicates. J replicates are nested within I plots.

| Source of variation | df | SS | $\varepsilon(\underline{MS})$ |
|---|---|---|---|
| Mean | 1 | $Y_N^2 = (Y...)^2/IJK$ | |
| Genotypes | K-1 | $Y_G^2* = \sum_k (Y_{..k})^2/IJ - Y_N^2$ | $\sigma_e^2 + J\sigma_{gs}^2 + IJ\sigma_g^2$ |
| Plots | I-1 | $Y_S^2* = \sum_i (Y_{i..})^2/JK - Y_N^2$ | $\sigma_e^2 + K\sigma_r^2 + JK\sigma_s^2$ |
| Genotype x plot | (I-1)(K-1) | $Y_{G\times S}^2* = \sum\sum_{ik} (Y_{i.k})^2/J - Y_N^2 - Y_G^2* - Y_S^2*$ | $\sigma_e^2 + J\sigma_{gs}^2$ |
| Replicates within plots | I(J-1) | $Y_R^2* = \sum\sum_{ij} (Y_{ij.})^2/K - Y_S^2$ | $\sigma_e^2 + K\sigma_r^2$ |
| Error | I(J-1)(K-1) | by difference | $\sigma_e^2$ |
| Total | IJK | $\sum\sum\sum_{ijk} (Y_{ijk})^2$ | |

where $V_{\bar{N}}$ is the variance of mean yields per plant with N plants per plot, i.e. the variance among plot means. $V_1$ is the variance among single plants and f is the index of environmental heterogeneity. The parameter f must be estimated empirically. The value of the index indicates the degree of correlation between adjacent plots. The larger its value, the lower the correlation between adjacent plots. The lower limit of the index is zero and its upper limit is, in general, unity. As was mentioned by Federer (1955), f may exceed unity when interplant competition is operative.

We may avoid the covariance between adjacent plants by the procedure that was proposed earlier in this section. Then, the interplant variance within a plot of N plants is

$$V_N = N \times V_{\bar{N}} = V_1 \times N^{1-f}$$

or expressed in logarithmic form, suitable for linear regression:

$$\ln V_N = \ln V_1 + (1-f) \ln N$$

By computing the interplot variance $V_{\bar{N}}$ for plots of different sizes, a set of equations is achieved with which $V_1$ and f can be computed. Then, the interplant variance $V_N$ can be estimated for plots with any number of plants.

It was found that, in Exp. 76-2d, f=0.906 for grain yield and f=0.924 for biomass. Exp. 77-1a supplied f=0.989 for grain yield and f=0.988 for biomass. The values of f were close to unity, which pointed to lack of fertility and other gradients in the field. Hence, the adjustments of the variance for a larger plot area were small.

*Summary* The analyses, used in the estimation of the appropriate variances, were described. A method was presented to adjust the environmental variance, estimated for a certain plot size, to a larger or smaller plot size.

## 8.2 COMPETITIONAL BIAS IN SINGLE-PLANT SELECTION, AN APPLICATION OF THE MODEL

In this section, the influence of intergenotypic competition on single-plant selection is explained. The central question is formulated and is illustrated by the results of Exp. 77-1. The effect of competition on single-plant selection is interpreted in terms of the competition model by applying the model to the experiments where varieties were grown in mixtures and monocultures. The confrontation of the model with actual experiments illustrates the model and tests its adequacy.

### *8.2.1 The central question*

The central question is: to what extent are the results of single-plant selection for yield biased by intergenotypic competition among the plants? Selection is for phenotype in order to save the best genotypes from a population. Hence, the question is: to what extent are the highest-yielding genotypes chosen when selection is for the phenotypes with the highest yield in presence of competition? Plant selection occurs necessarily in presence of competition as a segregating population is a mixture of genotypes. However, a farmer grows his varieties in monocultures. Therefore, we must reformulate the question as: to what extent are the genotypes with the highest yield in monoculture chosen when selection is for the phenotypes that yield most in a mixture?

### *8.2.2 Response to selection*

The central question is illustrated by considering the results of actual selection in a variety mixture (Exp. 77-1b). The variety mixture simulates a segregating population. The extent to what the conventional prediction of the response agrees with the realized response to selection is studied. The consequences of neglecting competition when applying the conventional procedure of predicting the response are emphasized.

In plant breeding, it is desirable to have an idea about the progress that can be made by selection in a certain population. The progress depends on (1) the degree to which the genotypically highest yielding plants are chosen when selection is done for the plants with the highest phenotypic yield, and (2) the degree to which the genotype of a selected plant is maintained in the next generation. Furthermore, the progress is affected by genotype x year, genotype x location and genotype x husbandry interactions. My study is restricted to the first point: the reliability of yield testing and the influence of intergenotypic competition on it. In this situation, the homozygosity of the varieties does not limit the simulation of the partly heterozygous genotypes (Section 4.4.3).

The heritability gives an indication of the reliability of yield testing as it measures the part of the total, phenotypic variation that can be ascribed to genetic differences. From the estimate of the heritability and from the observed phenotypic variance, the response to selection is predicted by

Table 21. The result of selection for single-plant yield in variety mixtures, expressed in terms of the response for mixture yield and the correlated response for monoculture yield. The proportion selected is either 0.05 or 0.10. The grain yield is expressed in g plant$^{-1}$. Exps 77-1a, b and 76-2a,d.

| Character | Notation | 77-1a,b | | 76-2a,d plot 1 | | 76-2a,d plot 2 | |
|---|---|---|---|---|---|---|---|
| | | 0.05 | 0.10 | 0.05 | 0.10 | 0.05 | 0.10 |
| Population mean in mixture | $\bar{P}_{unsel} = \bar{O}_{unsel}$ | 5.14 | 5.14 | 3.80 | 3.80 | 4.10 | 4.10 |
| Mean yield of selected plants | $\bar{P}_{sel}$ | 11.80 | 10.50 | 8.67 | 7.75 | 8.98 | 8.22 |
| Mean expected yield in mixture of the selected genotypes | $\bar{O}_{sel}$ | 6.65 | 6.49 | 5.43 | 5.15 | 5.74 | 5.56 |
| Realized response for yield in mixture | $R_{mix} = \bar{O}_{sel} - \bar{O}_{unsel}$ | 1.51 | 1.35 | 1.63 | 1.35 | 1.64 | 1.46 |
| Predicted response for yield in mixture | $\hat{R}_{mix} = ih^2_{mix} \sqrt{var\ P_{mix}}$ | 1.78 | 1.51 | 1.75 | 1.49 | 2.18 | 1.85 |
| Population mean of the monocultures | $\bar{M}_{unsel}$ | 5.24 | 5.24 | 3.93 | 3.93 | 4.14 | 4.14 |
| Mean expected monoculture yield of the selected genotypes | $\bar{M}_{sel}$ | 5.24 | 5.25 | 3.67 | 3.78 | 4.24 | 4.46 |
| Realized correlated response for monoculture yield | $CR_{mono} = \bar{M}_{sel} - \bar{M}_{unsel}$ | 0.00 | 0.01 | -0.26 | -0.15 | 0.10 | 0.32 |

$$\hat{R} = i\, h^2 \sqrt{\text{var } p} \qquad (4.33)$$

where i is the intensity of selection.

Eqn 4.33 was applied to the variety mixture of Exp. 77-1b which gave the predicted response $\hat{R}_{mix}$ (Table 21). The response was the difference between the expected genotypic yield of the selected plants and the genotypic yield of all plants.

By actual selection in the variety mixture, mainly 'Goudgerst' and 'Aramir' were chosen (Fig. 32). The results of a selection percentage of 5% differed little from those at 10%. The mean yields of the varieties in mixture 0 (Table 22) were used in calculating the realized response to selection,

$$R_{mix} = z_1 O_1 + \ldots + z_{12} O_{12} - \frac{1}{12}(O_1 + \ldots + O_{12})$$

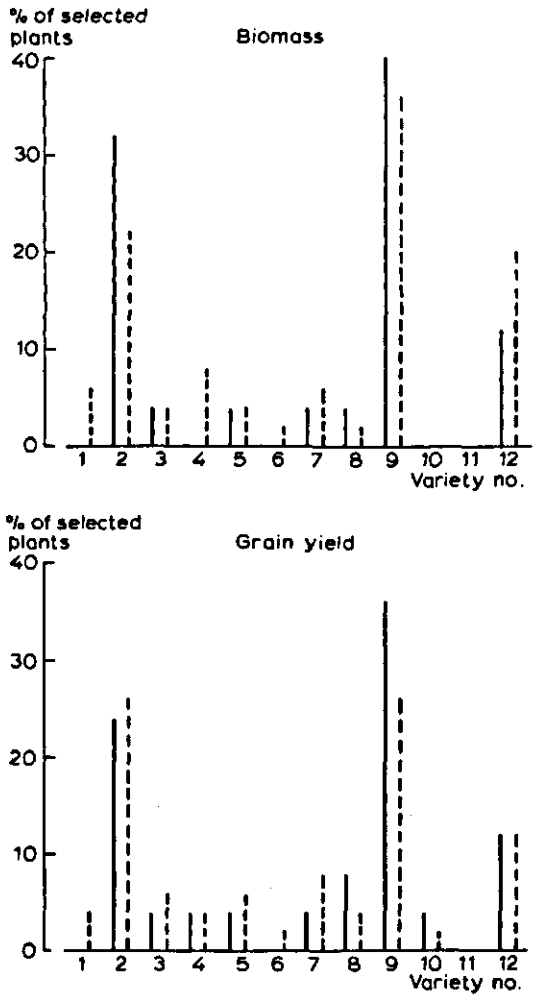


Fig. 32. Plants selected for biomass and plants selected for grain yield from a mixture of 480 plants belonging to 12 different varieties. The selected plants were grouped according to variety. The variety numbers correspond with those in Table 22. The percentages selected were 5% (solid lines) and 10% (broken lines). Exp. 77-1b.

Table 22. Grain yield in g plant$^{-1}$ in monoculture (Exp. 77-1a) and mixture (Exp. 77-1b). The crowding coefficient b is estimated from the monocultures and the mixture of Exp. 77-1b as well as from the monocultures and the mixture of Exp. 77-1d.

| Variety | | M | O | b | |
|---|---|---|---|---|---|
| | | | | 77-1a,b | 77-1a,d |
| 1 | Varunda | 5.3 | 5.1 | 0.96 | 1.09 |
| 2 | Tamara | 5.7 | 7.8 | 1.40 | 1.16 |
| 3 | Belfor | 5.3 | 5.4 | 1.06 | 1.19 |
| 4 | Aramir | 6.1 | 5.3 | 0.89 | 0.68 |
| 5 | Camilla | 5.0 | 5.4 | 1.11 | 1.06 |
| 6 | Golden Promise | 4.5 | 4.9 | 1.13 | 1.09 |
| 7 | Balder | 4.8 | 5.1 | 1.07 | 1.03 |
| 8 | WZ 704068-14 | 5.5 | 4.8 | 0.91 | 0.83 |
| 9 | Goudgerst | 4.7 | 7.7 | 1.59 | 1.73 |
| 10 | L98 | 6.0 | 3.5 | 0.59 | 0.72 |
| 11 | Titan | 4.6 | 1.6 | 0.34 | 0.49 |
| 12 | Bigo | 5.6 | 5.3 | 0.95 | 0.93 |
| | $S.E._{mean}$ | 0.28 | 0.39 | 0.079 | 0.124 |

where z is the frequency of the subscripted variety in the selected group. In the mixture, all varieties were sown at the same frequency of 1/12. The realized response agreed reasonably well with the predicted response (Table 21).

At first sight, one would conclude that the conventional approach is adequate. However, the response measures the progress with respect to yielding ability in the environment studied, i.e. in that particular mixture. However, the breeder aims at selecting genotypes that give the highest yields in monoculture. Comparing the composition of the selected group (Fig. 32) with the yields of the varieties in monoculture (Table 22) showed that some of the varieties with a high monoculture yield were rarely selected. The crowding coefficients indicate that these varieties were the poor competitors. On the other hand, the predominantly chosen variety 'Goudgerst' had a low monoculture yield in the present experiment (Table 22) as well as in the Dutch national variety trials (Table 6).

What is the progress made for yielding ability in monoculture? In other words, what is the correlated response for monoculture yield brought about by selection for yield in the mixture? The correlated response was calculated by

$$CR_{mono} = z_1M_1 + .... + z_{12}M_{12} - \frac{1}{12}(M_1 + .... + M_{12})$$

where z is the frequency of the subscripted variety in the selected group and M the monoculture yield of the subscripted variety. In this experiment, the correlated response was about zero (Table 21). Hence, selection for yield in the mixture did not result in

any progress for monoculture yield. Note that the conventional procedure predicted a response of 35% at a selection percentage of 5% and a response of 29% at a selection percentage of 10% (Table 21).

*Summary* The conventional procedure to predict the response to selection does not account for intergenotypic competition so that the predicted response is the response for yield in the particular mixture. However the breeder aims at selecting genotypes that give the highest yields in monoculture. The correlated response for monoculture yield, brought about by selection for yield in a mixture, is lower than the direct response for mixture yield. In the experiment discussed, the difference was considerable. Consequently, the conventional procedure provides a much too optimistic picture of the progress that can be achieved by selection. Given its wrong results in presence of competition, the conventional procedure to predict the response to selection is useless when yield is the character studied.

### *8.2.3 Application of the model*

It was concluded that, with intergenotypic competition, the conventional procedure to predict the response to selection is useless. Therefore an alternative model was introduced in Chapter 4 to predict the response for monoculture yield when selection is done for yield in a mixture. In this section, the model is tested experimentally and the influence of competition on selection is illustrated by the experiments.

*Comparison of the realized values in Exp. 77-1 and the values predicted by the model*
The model was used to predict the variances and the response to selection in the mixture (Exp. 77-1b). The parameters, required as input in the model, were partly estimated from the monocultures (Exp. 77-1a): the population mean $\mu_{mono}$, the genetic variance var $g_{mono}$ and the environmental variance var $e_{mono}$. By the procedure described in Section 8.1, the environmental variance was adjusted to an area equal to the area of a mixture plot, i.e. an area of 1.30 $m^2$. The variance of the crowding coefficient var $\underline{b}$ and the covariance between the crowding coefficient and the monoculture yield cov($\underline{b}$,$g_{mono}$) were estimated from the monocultures (Exp. 77-1a) and mixtures. The mixture at 5x25 $cm^2$ $plant^{-1}$ (Exp. 77-1b) and the mixture at 10.4x12 $cm^2$ $plant^{-1}$ (Exp. 77-1d) each provided an estimate.

Substituting the parameters into the appropriate equations of Section 4.4.5 provided the expectations of the variances and the selection response in a mixture. The expected values, those based on Exps 77-1a and 1b as well as those based on Exps 77-1a and 1d, agreed well with the observed values in the mixture of Exp. 77-1b (Table 23). The agreement was partitioned in:

(1) The agreement between the observations and the expectations based on Exps 77-1a and 1b. The similarity of both showed (a) the goodness of fit of the Taylor-series approximations used in the derivation of the equations of the variances and the responses from the basic Eqn 4.14, and (b) the similarity in yield level and environmental variance between the monoculture plots and the mixture plots.

(2) The agreement between the expectations based on Exps 77-1a and 1b and the ex-

pectations based on Exps 77-1a and 1d. The correspondence between both was good, i.e. the yields of the varieties were similar for the two mixtures. This was also shown by the absence of variety x experiment interaction in a joint analysis of variance of the two experiments ($P > 0.10$). The good agreement between the results of both mixtures supported the accuracy and repeatability of the observed variety yields in the mixtures.

The good agreement between expectations and observations indicated that, at least for this experiment, the Taylor-series approximations were adequate and that the values of the input parameters showed a satisfactory accuracy and repeatability.

*Variances and selection responses in monoculture and mixture* The effect of intergenotypic competition on selection can be understood from the variances as they were observed in monoculture and in mixture (Table 23). The genetic variance, i.e. the variance among variety means, was more than 10 times as large in mixture as in monoculture. Hence competition acted as a magnifying-glass (Fig. 33). The genetic variance increased in spite of the negative correlation between competitive ability and monoculture yield ($r_{bg} = -0.17$).

Table 23. Mean, variances and derived quantities in monoculture and mixture. The expectations for the mixture are computed, with the model, from the input parameters $\mu_{mono}$ = 5.24 g plant$^{-1}$, var $\underline{e}_{mono}$ = 6.35 g$^2$ plant$^{-2}$, var $\underline{g}_{mono}$ = 0.224 g$^2$ plant$^{-2}$, var $\underline{b}$ = 0.103 (Exp. 77-1a,b) and 0.083 (Exp. 77-1a,d), cov($\underline{b}$,$\underline{g}_{mono}$) = -0.0251 g plant$^{-1}$ (Exp. 77-1a,b) and -0.0458 g plant$^{-1}$ (Exp. 77-1a,d). The values observed in the mixture (Exp. 77-1b) are also given. The responses in the column '$mix_{obs}$' are the responses predicted from the variances observed in the mixture. The character under selection is grain yield in g plant$^{-1}$.

| | Mono | $Mix_{obs}$ | $Mix_{exp}$ | |
|---|---|---|---|---|
| | 77-1a | 77-1b | 77-1a,b | 77-1a,d |
| $\mu$ | 5.24 | 5.14 | 5.22 | 5.19 |
| var $\underline{g}$ | 0.22 | 2.54 | 2.90 | 2.47 |
| var $\underline{e}$ | 6.35 | 6.09 | 6.35 | 6.35 |
| var $\underline{p}$ | 6.57 | 8.63 | 9.25 | 8.82 |
| $h^2$ | 0.03 | 0.29 | 0.31 | 0.28 |
| CV | 0.48 | 0.48 | 0.48 | 0.49 |
| $h_{mix}/h_{mono}$ | | 2.94 | 3.04 | 2.87 |
| $r_{g_{mono,mix}}$ | | 0.11 | 0.11 | -0.02 |
| R/i | 0.09 | 0.86 | 0.95 | 0.83 |
| $CR_{mono}/i_{mix}$ | | 0.03 | 0.03 | -0.01 |
| $CR_{mono}/R_{mix}$ | | 0.03 | 0.03 | -0.01 |
| $CR_{mono}/R_{mono}$ | | 0.32 | 0.35 | -0.06 |

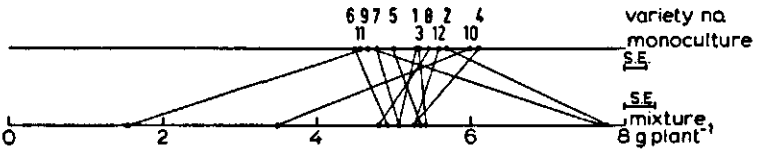


Fig. 33. Grain yield in monoculture and mixture. The variety numbers correspond with those in Table 22. Exp. 77-1a,b.

On the other hand, the environmental variance was not changed by mixed growing ($F_{185}^{33}$=1.043, P < 0.01) which was in accordance with the model. As the genetic variance was enhanced and the environmental variance remained unchanged, the phenotypic variance and the heritability in mixture exceeded those in monoculture. Consequently, the expected direct response for yield in the mixture (Eqn 4.33) was substantially greater than the direct response in 'monoculture'. This 'monoculture' has to be seen as a population without intergenotypic competition or with all genotypes equally competitive.

However, the breeder aims to select genotypes that yield most in monoculture. By definition, the correlated response for monoculture yield is smaller than the direct response for yield in a mixture. In this experiment, the genetic correlation between monoculture yield and mixture yield was low ($r_g$ = 0.11) so that the correlated response was also low. Hence, in this mixture, selection for yield was not successful.

To what extent did intergenotypic competition bias the outcome of selection? $R_{mono}$ is the direct response for monoculture yield in a population without intergenotypic competition and $CR_{mono}$ measures the correlated response for monoculture yield when selection is in a mixture. The ratio $CR_{mono}/R_{mono}$ defines the bias that originates from intergenotypic competition. In this experiment, the ratio was 0.32. Hence, if there were no intergenotypic competition, the response to selection would have been three times as large.

Selection of single plants for yield is of questionable value, not only because intergenotypic competition may seriously bias the outcome of selection, but especially because the heritability for single-plant yield is very low and because many plants can already be discarded on visual grounds.

*Response to selection in Exp. 76-2* Main plot 1 of Exp. 76-2 had a more severe drought stress than main plot 2 so that main plot 1 was harvested two weeks earlier. The difference between both main plots expressed itself in a highly significant variety x main plot interaction (P < 0.01) in the joint analysis of variance of the two main plots in Exp. 76-2a. Therefore, the plots were analysed separately.

In selection of single plants for yield, some varieties were preferentially chosen (Fig. 34). In main plot 1, 'Titan' dominated the mixture, whereas in monoculture this variety had a low yield. The difference between the yield of 'Titan' in mixture and monoculture was the main cause of the negative response for monoculture yield $CR_{mono}$ when selection was for yield in mixture (Table 21). However, according to the conventional procedure to predict the response to selection, selection was expected to give a yield increase of 40%. This illustrates the uselessness of the conventional method.

In main plot 2, the variety composition in the selected group and the monoculture

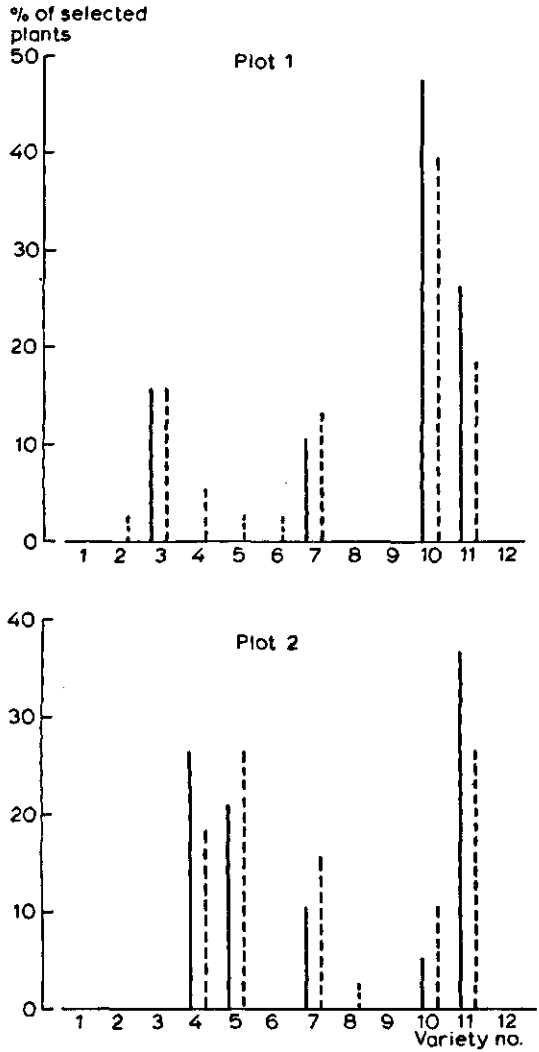


Fig. 34. Plants selected for grain yield from mixtures of 384 plants per plot. The selected plants were grouped according to variety. The variety numbers refer to the rank of the varieties in Table 12. The percentages selected were 5% (solid lines) and 10% (broken lines). Exp. 76-2a.

yields differed from those in main plot 1. Selection in main plot 2 resulted in a moderate correlated response for monoculture yield.

The estimates of the heritability in monoculture, the competitive stress $\gamma$ and the coefficient $r_{bg}$ of the correlation between the crowding coefficient b and the genotypic yield in monoculture $g_{mono}$ were given in Table 17. The practice of raising the plants in peat pots in the greenhouse and planting them out in the peat pots in the field promoted a high heritability and a low $\gamma$. The heritability for grain yield increased due to mixed growing: in main plot 1 from 0.30 in monoculture to 0.46 in mixture and in main plot 2 from 0.28 in monoculture to 0.49 in mixture.

*Summary* The competition model was applied to experimental data. The predictions derived from the model agreed well with the observations. Therefore, it was concluded that the Taylor-series approximations used in the model were valid and that the estimates of the input parameters were satisfactory accurate and repeatable. It was shown that the procedure, which is generally applied in the literature to predict the response to selection, is of no value as it does not account for intergenotypic competition.

## 8.3 SELECTION AT WIDE SPACING

Selection at wide spacing has often been advocated in order to decrease or to exclude the influence of interplant competition. However the genotypes differ in their response to spacing. The effect of interplant competition as well as the effect of a differential response of the genotypes to spacing on the outcome of selection was described in a model (Chapter 5). It was shown that, under certain assumptions, the rank of the genotypes in a mixture is not affected by the spacing at which the mixture is grown. Consequently, with wider spacings, the bias due to interplant competition is entirely replaced by the bias arisen from a differential response of the genotypes to spacing (Section 5.3.3, Fig. 24). In this section, it is studied whether the conclusions are confirmed by experimental results. Furthermore, the assumptions underlying the model are tested. The experimental testing gives a better understanding of the model and shows its limitations.

### *8.3.1 Yield at wide stand predicted from the yield at narrow stand*

Under the assumptions made in Section 5.2, it was derived that the rank of the genotypes in a mixture is not influenced by the spacing at which the mixture is grown. True enough, the yield per plant increases with wider spacings but the yield of the genotypes, relative to each other, would remain constant. Hence, the yield of a genotype in mixture at wide stand is estimated by multiplying the yield of that genotype in the same mixture at narrow stand with a constant. The constant is given by Eqn 5.13.

We can test the model with the data of Exp. 77-1 where a variety mixture was grown at a spacing of 10.4x12 $cm^2$ $plant^{-1}$ (Exp. 77-1d) and at a spacing of 52x60 $cm^2$ $plant^{-1}$ (Exp. 77-1e). The variety means for biomass and ear weight per plant at the wide stand was plotted against the corresponding variety means at the narrow stand (Fig. 35). The relation, expected according to the model, was represented by a broken line. The trend for biomass was similar to that for ear weight. The yield of 'Goudgerst' at wide stand was strongly overestimated by the model, whereas the yield of 'Titan' was very much underestimated. The yields of 'WZ 704068-14', 'Aramir' and 'L 98' at wide stand were also underestimated, but to a lesser degree.

In conclusion, the experimental results differed from what was expected according to the model so that in the variety mixture studied, one or more of the assumptions, underlying the model, were violated. The assumptions, on which the model is based, are: (a) the genotypes compete for the same resources, which assumption was demonstrated to be valid (Section 6.3.1); and (b) the competitive ability of genotypes in mixture can

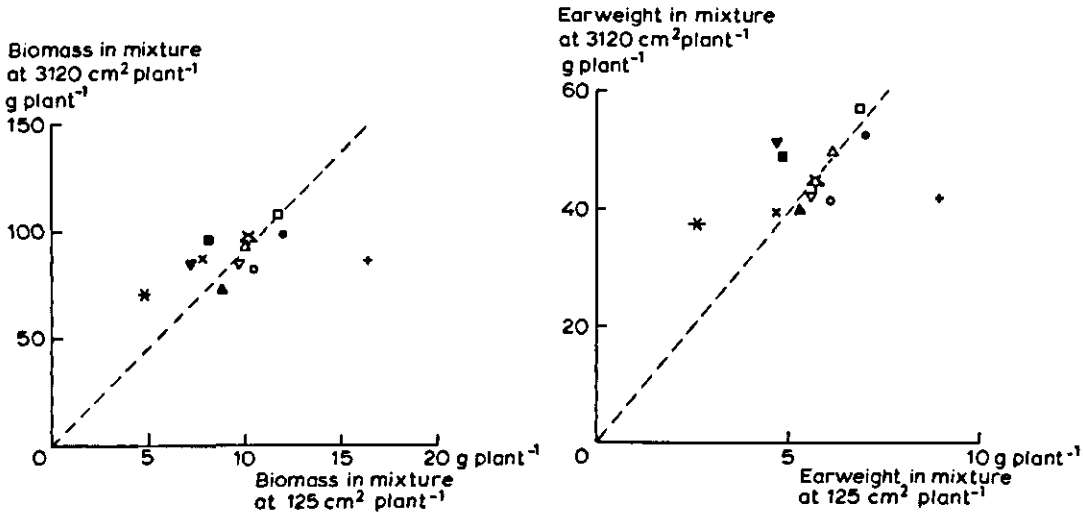


Fig. 35. Variety means for biomass and ear weight in mixture at 3120 $cm^2$ $plant^{-1}$ (Exp. 77-1e) plotted against the corresponding variety means in mixture at 125 $cm^2$ $plant^{-1}$ (Exp. 77-1d). The broken lines give the relation that was expected according to the model. For explanation of the variety symbols see Fig. 27.

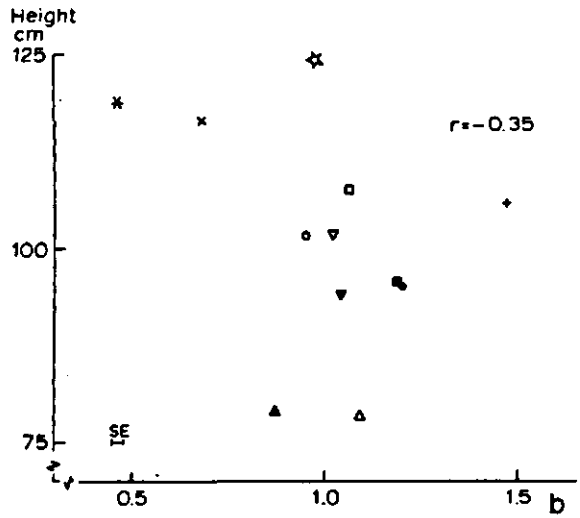


Fig. 36. Relation between the height of a variety in monoculture and its crowding coefficient for biomass. The height is the maximum height of the crop, which was attained during the growth period on 28 June. For explanation of the variety symbols see Fig. 27. Exp. 77-2, drilled rows.

be explained from their response to spacing when they are grown in monocultures at different spacings and harvested at only one time. The second assumption implies that the growth curves of single-growing plants of the genotypes are similar and that the genotypes have the same height in course of time.

The crop height in course of time was followed in the monocultures that were sown

in drilled rows (Exp. 77-2a). There was no relation between the shape of the curve for the height of a variety and its competitive ability (unpublished data). In none of the experiments was there a clear relation between the height of a variety and the crowding coefficient of the variety (Figs 36-39). One might expect a good relation between plant height and crowding coefficient in Exp. 76-2a because the varieties were not planted out

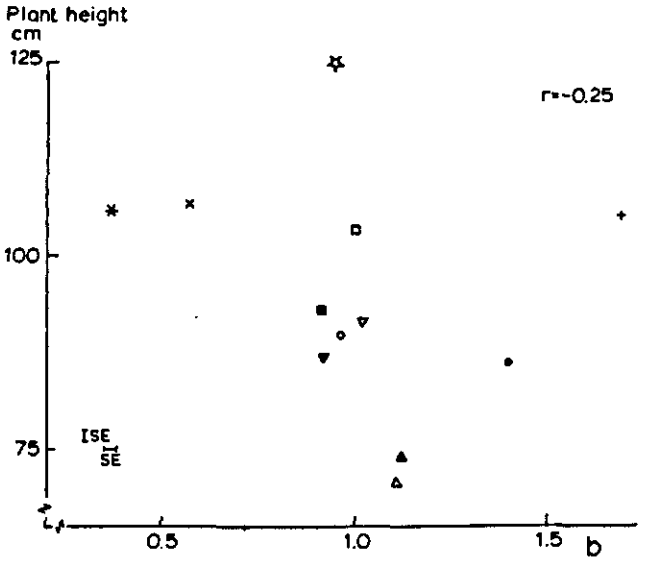


Fig. 37. Relation between the plant height of a variety in monoculture and its crowding coefficient for biomass. For explanation of the variety symbols see Fig. 27. Exp. 77-1a,b; 5 x 25 $cm^2$ $plant^{-1}$.

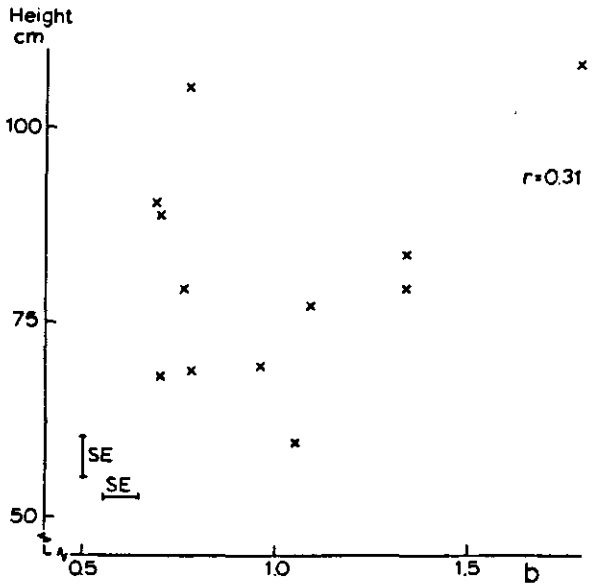


Fig. 38. Relation between the height of a variety in monoculture and its crowding coefficient for biomass. Each cross denotes a variety. Exp. 76-1, field plots.

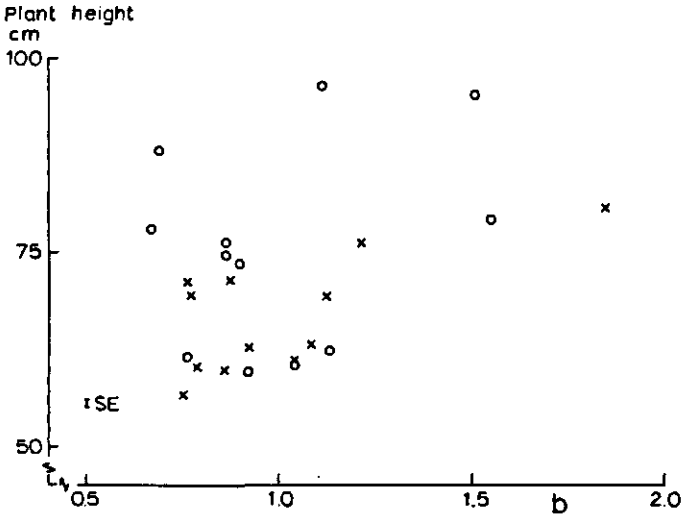


Fig. 39. Relation between the plant height of a variety in monoculture and its crowding coefficient for biomass. Each cross marks a variety in Plot 1, and each open circle denotes a variety in Plot 2. The correlation coefficients are 0.66 for Plot 1 and 0.30 for Plot 2. Exp. 76-2a,d; 6 x 25 $cm^2$ $plant^{-1}$.

in peat pots in the field until 3 and 4 May so that differences among the varieties in juvenile growth could not influence the outcome of competition. However, also in this experiment the relation between plant height and competitive ability was poor (Fig. 39). The correlation coefficient in main plot 1 declined to 0.37 when the strong competitor 'Titan' was removed.

Consequently, in my experiments plant height was, in relation to other causes of competition, unimportant. Hence, although the assumption that the genotypes have the same height in course of time was not met, it was not the reason for the deviations from what was expected according to the model.

According to the model, all varieties would give the same value of $O_{narrow}/O_{wide}$. However, this was not true (Fig. 40). The deviations from what was expected according to the model were due to non-similarity of the growth curves. This is explained in the following. The deviation in yield of a variety at wide stand was associated with its competitive ability at narrow stand. The yield at wide stand of a strong competitor was underestimated by the model, i.e. its ratio $O_{narrow}/O_{wide}$ was high. On the other hand, the yield at wide stand of a weak competitor was overestimated, i.e. its ratio $O_{narrow}/O_{wide}$ was low. The values of $O_{narrow}/O_{wide}$ came from Exps 77-1d and e, whereas the crowding coefficients were estimated from Exps 77-1a and b. Hence, both quantities were derived from independent experiments. The random variation in the points was probably large as two yield ratios were plotted against each other.

The broken line in Fig. 40 represents the relation expected if the $\beta$ curves of the varieties were similar (Fig. 22a), whereas the solid line reflects the relation expected if the varieties differed only in their initial value of $\beta$ but had the same $\beta_{max}$ (Fig.

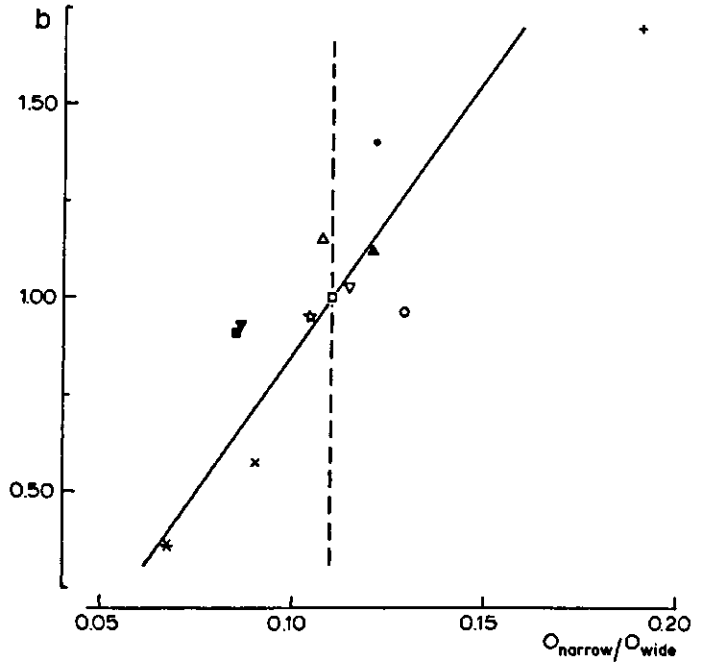


Fig. 40. The crowding coefficient b of the varieties at narrow stand plotted against the ratio of their biomass in mixture at narrow stand (Exp. 77-1d) and their biomass at wide stand (Exp. 77-1e). The crowding coefficient is estimated for biomass from Exp. 77-1a and b. For the variety symbols see Fig. 27.

22b) (Section 5.6). Situation 22b fitted the observations better than did situation 22a. Situation 22b is found when the varieties differ in time of emergence and differ in the size of the seeds from which they are grown. A result similar to that of situation 22b is achieved by situation 22d where the varieties differ in the relative growth rates of single-growing plants, i.e. in the relative growth rate of early growth (Section 5.6).

The variety characteristics support that, in the present variety mixture, probably situation b and d of non-similarity of the $\beta$ curves accounted for the deviations from what was expected according to the simple model. In the field, the late and slow emergence of the varieties 'Titan' and 'L 98' was very striking (Section 7.3.2). 'WZ 704068-14' had a much lower weight of the kernels that were sown (Table 27). Probably, these characteristics were the reason for the low competitive ability of these varieties in mixture at narrow stand. At the very wide stand, these characteristics gave no yield disadvantage which is confirmed by the underestimation of their yield at that spacing (Fig. 35). It is tempting to ascribe the position of 'Goudgerst' to a relatively rapid emergence and early growth of this North-West European variety at the low temperatures of end March and begin of April. However, this was not studied. In the Dutch national list of varieties (Rassenlijst 1978, RIVRO, Wageningen), 'Aramir' was characterized by a somewhat slow development, whereas 'Tamara' was marked by a rather quick early development.

In conclusion, the results indicated that in the mixture of barley varieties, competition could be explained by the course curve of $\beta$ as given in Fig. 22 b and d. That

the varieties tended to attain the same $\beta_{max}$ (Fig. 22 b and d), rather than that the exponential growth of single-growing plants was finished for all varieties at the same time (Fig. 22 a and c), is probably because barley is only slightly sensitive to daylength.

The findings cannot be automatically transposed to breeders' populations. In those segregating populations, the genotypes are less divergent than the varieties involved in the experiments. Further research is required to study which type of intergenotypic competition is predominant in breeders' population.

*Summary* It was expected from the model introduced in Section 5.3, that, under certain assumptions, the rank of the genotypes in a mixture does not depend on the density at which the mixture is grown. In the variety mixture studied, this expectation was not met. The deviation from the model was ascribed to the violation of the assumption that the growth curves of single-growing plants of the varieties are similar. The variety mixture was an extreme population, grown at extreme densities. This facilitated the illustration and discussion of the assumptions. However, breeders are concerned with far less extreme situations. Further research is required to study which type of intergenotypic competition is predominant in their populations.

The differences between the varieties in their crowding coefficients were mainly due to the non-similarity of the growth curves of single-growing plants of the varieties.

### *8.3.2 Response to selection*

In the population at wide stand, selection was practised for ear weight per plant. This character was supposed to measure grain yield which was not recorded independently. In Exp. 77-1a, the environmental correlation between ear weight and grain yield was 0.995, the genetic correlation was 0.983 and the phenotypic correlation was 0.994.

When selection was for ear weight at the wide stand, mainly plants of the varieties 'Belfor', 'Camilla', 'WZ 704068-14' and 'Tamara' were chosen (Fig. 41). On the other hand, at the dense stand mainly 'Goudgerst, 'Belfor' and 'Tamara' were selected (Fig. 42). Hence, the variety composition in the selected group differed between the wide stand and the dense stand. However, according to the model, it was expected that the result of selection in a mixture is independent of the density at which the mixture is grown. The discrepancy between the expectation and the observation was caused by a serious violation of one of the assumptions on which the model is based (Section 8.3.1).

In Table 24, the realized responses and some other quantities were summarized. The response for mixture yield at wide stand was greater than that at narrow stand. This larger response resulted from the higher yield level at the wide stand because when the response was adjusted for the yield level by dividing it by the phenotypic standard deviation, this standardized response at wide stand was smaller than that at narrow stand. The smaller standardized response at wide spacing was due to a lower heritability in the mixture at that spacing. The heritability decreased with wider spacings because the relative decrease of the genetic variance ($\sqrt{\text{var } \underline{g}}/\mu$) with wider spacings had a greater influence on the heritability than had the relative decrease of the environmental variance ($\sqrt{\text{var } \underline{e}}/\mu$) with wider spacings. The relatively high genetic variance in mixture at narrow

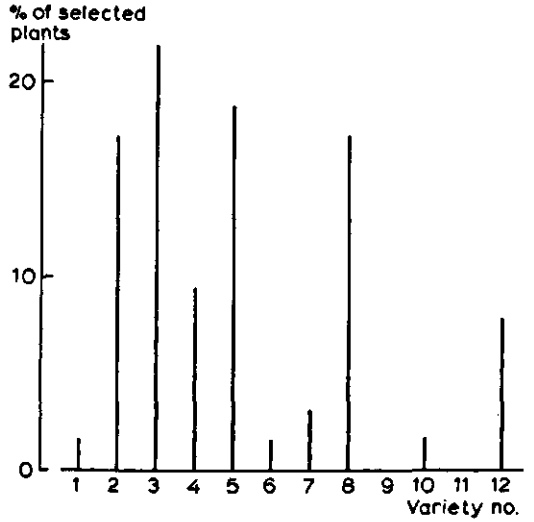


Fig. 41. Variety composition in the selected group when selection was for ear weight per plant from a mixture of 624 plants grown at 3120 $cm^2$ $plant^{-1}$. The percentage selected was 10%. The variety numbers refer to the rank of the varieties in Table 22. Exp. 77-1e.

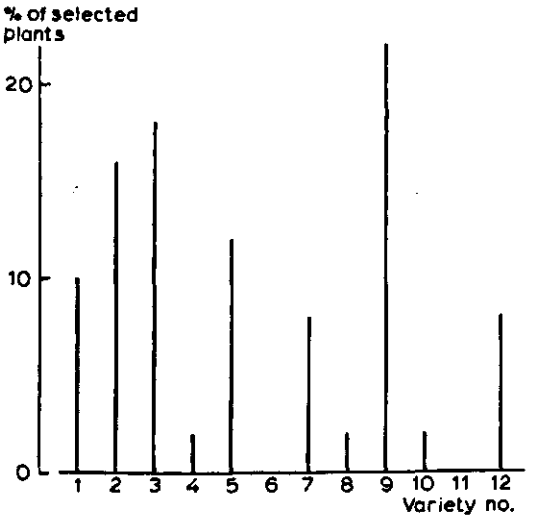


Fig. 42. Variety composition in the selected group when selection was for ear weight per plant from a mixture of 480 plants grown at 125 $cm^2$ $plant^{-1}$. The percentage selected was 10%. The variety numbers refer to the rank of the varieties in Table 22. Exp. 77-1d.

stand could be mainly ascribed to the varieties 'Titan', 'L 98' and 'Goudgerst' which had, due to their extreme low or strong competitive ability, an extremely low or high yield in the mixture at narrow stand. These extreme competition effects were not accounted for by the differential response of the varieties to spacing (Fig. 40, Section 8.3.1). Therefore, these varieties showed less extreme yields at the wide stand, which explained the reduced genetic variance at the wide stand.

Table 24. Mean, variances and realized responses to selection with respect to ear weight per plant. The correlated response is for ear weight in monoculture at the narrow stand. The selection percentage was 10%. Ear weight is recorded in g plant$^{-1}$. Exps 77-1a,d,e.

| | Monoculture narrow | Mixture narrow | Mixture wide |
|---|---|---|---|
| $\mu$ | 6.39 | 5.69 | 45.5 |
| var $\underline{g}$ | 0.22 | 2.04 | 33.5 |
| var $\underline{e}$ | 9.28 | 8.96 | 231.6 |
| var $\underline{p}$ | 9.50 | 11.00 | 265.1 |
| $\sqrt{\text{var } \underline{g}}/\mu$ | 0.07 | 0.25 | 0.13 |
| $\sqrt{\text{var } \underline{e}}/\mu$ | 0.48 | 0.53 | 0.33 |
| $h^2$ | 0.02 | 0.19 | 0.13 |
| $R_{mix}$ | | 1.16 | 5.34 |
| $R_{mix}/\sqrt{\text{var } \underline{p}}$ | | 0.35 | 0.33 |
| $r_g$ | | -0.11 | 0.39 |
| $CR_{mono}$ | | -0.05 | 0.18 |

Despite the lower direct standardized reponse for mixture yield, the correlated response for monoculture yield at dense stand, brought about by selection for mixture yield, was higher at wide stand than at narrow stand (Table 24). This could be traced to the genetic correlation with monoculture yield at narrow spacing, which was higher for the wide stand. In both stands, the final correlated response to selection was negligible: 3% for the wide stand and -1% for the narrow stand. This was caused by the small differences among the varieties in monoculture yield.

Substitution of the observed heritabilities and genetic correlations (Table 24) in the expression for $CR_{mono}/R_{mono}$ (Eqn 4.40) gave 0.91 for the wide stand and -0.31 for the narrow stand. Hence, the correlated response for yield in monoculture at narrow spacing, gained by selection in mixture at wide stand, was estimated to be close to the direct response gained by selection among monocultures grown at narrow spacing. The difference in $CR_{mono}/R_{mono}$ between the wide and the narrow stand is so large because the competition effects at the narrow stand could mainly be ascribed to the non-similarity of growth curves as given in Fig. 22 b and d. The competition effects that arise from these types of nonsimilarity are removed by growing the plants at a wide spacing.

The correlated response for grain yield in monoculture in drilled rows (Exp.77-2) was also greater when selection was for ear weight per plant in mixture at wide stand (9%) than when it was in mixture at narrow stand (5%).

The competition effects in the present mixture were mainly of the type given in Fig. 22 b and d. The bias that arises from this type of intergenotypic competition is removed by selection at a wide stand (Section 5.6). Therefore, the genetic variance was relatively smaller and the genetic correlation with monoculture yield at a dense stand

was higher when the spacing became wider.

At the wide stand, the environmental variance decreased relatively. As was shown by the lower coefficient of variation (CV) (Table 24). In Section 5.3.2, it was pointed out that the CV is influenced by the spacing in three ways. The CV increases because the field area, on which a certain number of plants is grown, increases with the spacing. On the other hand, the CV decreases because non-genetic interplant competition, as source of increased environmental variation, is removed. Furthermore, an increased supply of growth factors per plant may reduce the CV.

In Exp. 77-1, the fertility gradient in the field was extremely low. Therefore, standardized to a field area occupied by 182 plants, the CV increased only from 0.481 at 125 $cm^2$ $plant^{-1}$ to 0.488 at 3120 $cm^2$ $plant^{-1}$. The values were obtained from the environmental variance for ear weight in monoculture by the method described in Section 8.1. The larger CV at the narrow stand was due to non-genetic interplant competition and a reduced supply of growth factors per plant at that narrow stand.

The realized responses to selection and the observed variances only hold for the present experiment. The experimental data were used to illustrate the discussion of selection at wide stand. For a general view on the applicability of selection at wide stands, many segregating populations must be studied.

*Summary* In the variety mixture studied, the heritability in mixture at wide stand was smaller than that in mixture at narrow stand. This contributed to the smaller standardized selection response for mixture yield at the wide stand. The correlated response for yield in monoculture at narrow stand, brought about by selection in mixture, was larger when the mixture was grown at wide stand. This result was ascribed to the higher genetic correlation with monoculture yield for the wide spacing.

### *8.3.3 Consequences for breeding practice*

In this section, some practical consequences of selection in mixture at a wide stand are compared with those of selection in mixture at a narrow stand.

(1) Which types are favoured by growing a mixture at a wide stand? This question was already discussed in Section 5.6.

(2) Environmental variation. The environmental variance relative to the population mean, i.e. the CV, is influenced by the density of stand (Section 5.3.2). On one hand, the CV is smaller with wider stands because non-genetic interplant competition, as source of a magnified variance, decreases. Furthermore, the larger supply of growth factors available per plant, may also reduce the CV. On the other hand, the CV increases because the area of the field increases. Moreover, differences in husbandry between a wide and a narrow stand may influence the CV. The joint effect of these factors on the CV will vary from trial to trial.

(3) Visual selection. A breeder selects individual plants visually. Visual selection at wide stand is complicated by the fact that the habit of a plant is greatly influenced by the density of stand. Among others, selection for lodging resistance is hampered. On

the other hand, at wide stand, individual plants can be easily recognized and, during the growing season, negative mass selection may be applied by removing undesired plants.

(4) Husbandry. A wider stand requires a larger field area to screen the same number of plants which increases the costs. Due to the open stand at a wide spacing, weeds are a problem during the entire growth period. Late in the season, hoeing by hand, instead of spraying with herbicides, may then be necessary. Open stands of awned barley are damaged by birds more than closed crop surfaces are. Also hares prefer an open stand where they graze selectively on leafy types.

(5) Seed yield per plant. A high seed production per plant is required when the progenies of the selected plants are tested for yield in microplots of reasonable size. The wider the stand, the higher the seed yield per plant. At the wide stand of Exps 77-1e and f, plants with more than 100 fertile ears were frequently found. But the seeds formed at the wide stand differ greatly in quality with that of the late developed ears being relatively poor.

*Summary* Advantages and disadvantages of selection at wide stands are pointed out. The choice of the optimal density depends on the objectives of the breeder. I suggest that in selection for yield, close spacings are preferable. In visual selection, somewhat wider spacings may be preferred especially when a large seed production per plant is desired for progeny testing.

## 8.4 REDUCING THE BIAS FROM COMPETITION

In the literature, several methods were proposed to diminish or to remove the biasing effect of intergenotypic competition on the outcome of selection (Section 1.3.2). These methods were: (1) selection at wide spacings, (2) grading the seeds to size or weight and sowing only seeds of about the same size together in one selection plot, (3) alternating the plants from the segregating population with plants of a standard variety, (4) indirect selection for monoculture yield, (5) mathematical correction for competition. In this section, the utility of the methods in controlling the bias of intergenotypic competition on selection is discussed.

### *8.4.1 Wide spacing*

Many authors have advocated the use of wide spacing in order to remove interplant competition. However, selection at wide spacing introduces a bias that arises from the differential response of the genotypes to spacing. For a discussion, see Section 8.3.

### *8.4.2 Grading of the seeds*

Plants growing from large seeds show a competitive advantage over those from small seeds (Section 7.4). When large and small seeds are sown in separate plots, these differences in seed size are eliminated as source of competition. In this way, one removes (a) that part of intergenotypic competition that is related to differences in seed size

among the genotypes and (b) that part of the intragenotypic competition that is caused by non-genetic differences among the plants in seed size. The method is most effective when both competition effects are equivalent, i.e. when the competitive ability of large seeds of small-seeded genotypes equals that of small seeds of large-seeded genotypes having the same size as the former.

The importance of the non-genetic differences in seed size as biasing factor in selection was demonstrated by McMillan (1935). He found with a pure line of wheat grown at 15 x 15 $cm^2$ $plant^{-1}$, that 24% of the variance among the plants for yield was accounted for by the correlated variation in early growth and weight of the seeds sown. The simple correlations between the weight of a seed and the yield of the plant that grew from it, averaged 0.39. Chebib et al. (1973) partitioned wheat seed into three groups: small, large and unsorted. The interplant variance for yield in the plots sown with small or large seeds was less than that in the plots sown with unsorted seeds. The spacing averaged 10 x 30 $cm^2$ $plant^{-1}$.

For each of three spring wheat cultivars, Austenson & Walton (1970) weighed about 900 seeds individually and sowed them at 15 x 15 $cm^2$ $plant^{-1}$. Averaged over the cultivars, the correlation between the weight of a seed and the yield of the plant grown from it was 0.19. Bhatt & Derera (1973) found, averaged over four wheat varieties, a correlation coefficient of 0.12 between the weight of the seeds and the yield of the plants raised. The spacing was 8 x 50 $cm^2$ $plant^{-1}$.

The density of stand in these experiments was relatively wide. In a selection plot, where the spacing is less and so interplant competition more severe, the contribution of the variation in initial seed weight to the variation in yield per plant is greater.

With segregating populations, a breeder may prefer to sow only the large seeds. In this manner, he selects for large-seededness and probably for seeds from less diseased mother plants. The latter effect was found by McFadden et al. (1960) for *Ustilago nuda* in barley, but see also their discussion on the consequences for selection on resistance against seed-borne diseases. Given the variation in grain size found among the successful varieties, it may be preferable to sow not only the large seeds but also the seeds of intermediate size. Frey (1967) and Bhatt & Derera (1973) discussed the correlated changes in other plant characters brought about by mass selection on seed size.

In conclusion, grading of the seeds and sowing only seeds of about the same size together in one selection plot is an effective and cheap method to reduce the disturbing effects of interplant competition. The efficiency is greater, the greater the density of stand.

### *8.4.3 Plants from the segregating population alternated with standard plants*

In this system, the plants from the segregating population are alternated within a row with plants of a standard variety. Hence, both neighbours of each plant from the segregating population belong to the standard. It is hoped for that (a) the competitional bias is smaller because the competing neighbours are genetically the same for all plants, and that (b) a correction can be made for the competitive situation by comparing the

observed yield of a plant with that of its neighbouring standard plants. However, the competitive influence of a plant reaches farther than its adjacent neighbour (Section 4.2.2). For a discussion of the situation where competiton is restricted to the adjacent neighbours see Section 9.2.2.

The expected yield of a random genotype i in the mixture is defined by Eqn 4.10. This equation shows that the yield of i depends on the frequency at which the standard occurs in the mixture but that the yield of i, relative to that of another genotype j, is independent of the frequency of the standard. Hence, the yields of the genotypes, relative to each other, are expected not to change when a new genotype is introduced in the mixture. We saw this already for the effect of plant spacing on yield (Section 5.3.1) where the introduced genotype was a non-growing genotype that represented the empty space. As in Section 5.3, it can be derived that inserting plants of a standard variety in a population is expected not to influence the outcome of selection.

Alternating the plants with plants of the standard variety doubles the plot size. This enlarges the environmental variance, which enlargement was not considered in the model. Therefore, the method will even depress the response to selection.

As the competitive influence of a plant extends farther than its nearest neighbour, the yield of a standard plant does not reflect the competitive ability of its adjacent neighbours. Moreover, the heritability of single-plant yield is low. Therefore correction for the competitive ability of a plant by means of the yield of its neighbour plants will not work.

In Exps 76-2b and 77-1c, plants of the studied varieties were alternated with plants of the standard 'Varunda' (Fig. 3c). The yields of the varieties in Exp. 77-1c differed from the yields of the same varieties in the mixtures without inserted standards (Table 25). The competition effects seemed to be decreased by the insertion of the standard. This was shown by the correlation between the crowding coefficient b and the ratio $O_{normal}/O_{alternated}$ for the yield in the normal mixture (Exp. 77-1b) and the yield in the mixture with the alternated standard (Exp. 77-1c). The crowding coefficient was estimated from Exps 77-1a and 1d. The correlation coefficient was 0.76 for ear weight and 0.70 for biomass. Hence, the yield of strongly competing varieties tended to be higher in the normal mixture than in the alternated mixture. Vice versa, the poorly competitive varieties tended to have a lower yield in the normal mixture than in the alternated mixture.

In Exp. 76-2 the correlation between b and $O_{normal}/O_{alternated}$ was, in main plot 1, -0.21 and -0.23 for grain yield and biomass, respectively. In main plot 2, the corresponding correlations were -0.13 and -0.01. So, in Exp. 76-2, the abovementioned tendency did not occur. This suggests that the deviating yield in the alternated mixture of Exp. 77-1c may have been due to random error.

In conclusion, alternating the plants of a segregating population with plants of a standard variety is useless for making allowance for competition.

Table 25. Ear weight in g plant$^{-1}$ in monoculture, in a normal mixture, in a mixture with alternated standard plants, in a mixture at a triangular spacing of 125 cm$^2$ plant$^{-1}$, and in a mixture at a triangular spacing of 3120 cm$^2$ plant$^{-1}$. Exps 77-1a to e.

| Variety | Monoculture | Normal mixture | Alternated mixture | Triangular mixture, dense | Triangular mixture, wide |
|---|---|---|---|---|---|
| Varunda | 6.3 ab* | 6.0 b | 6.5 abc | 6.1 bc | 41 de |
| Tamara | 6.9 ab | 9.4 a | 8.3 a | 7.0 b | 53 ab |
| Belfor | 6.4 ab | 6.4 b | 5.7 abcd | 6.8 b | 57 a |
| Aramir | 7.4 a | 6.3 b | 5.8 abcd | 4.8 c | 49 bcd |
| Camilla | 6.2 ab | 6.5 b | 7.7 ab | 6.1 bc | 50 abcd |
| Golden Promise | 5.5 b | 5.9 b | 5.8 abcd | 5.2 bc | 40 e |
| Balder | 5.9 ab | 6.1 b | 5.0 bcd | 5.6 bc | 42 de |
| WZ 704068-14 | 6.5 ab | 5.6 b | 5.8 abcd | 4.7 c | 51 abc |
| Goudgerst | 5.8 ab | 9.6 a | 7.1 abc | 8.9 a | 42 de |
| L 98 | 7.1 ab | 4.0 c | 4.3 cd | 4.7 c | 40 e |
| Titan | 5.9 ab | 2.0 d | 3.2 d | 2.6 d | 37 e |
| Bigo | 6.9 ab | 6.3 b | 6.3 abc | 5.7 bc | 45 cde |

* Values followed by the same letter are not significantly different in the Student-Newman-Keuls test at $P \leq 0.05$.

### 8.4.4 *Indirect selection for monoculture yield*

Monoculture yield is the 'target character' of selection. Necessarily, individual plants are selected from a mixture. Selection in the mixture is an indirect selection for monoculture yield.

The most obvious character to select for in the mixture is yield. Selection for this 'auxiliary character' results in a correlated response for monoculture yield (Section 4.4.2). Are there auxiliary traits that give a higher correlated response than mixture yield gives? The utility of a trait as auxiliary trait is measured by the correlated response for monoculture yield, brought about by selection for the auxiliary trait:

$$CR_{mono} = i_{mix}\, r_g\, h_{mix} \sqrt{\text{var } g_{mono}} \qquad (4.36)$$

where $r_g$ is the genetic correlation between the auxiliary and the target character, and $h_{mix}$ is the square root of the heritability of the auxiliary character in mixture. The genetic variance for monoculture yield var $g_{mono}$ and the selection intensity $i_{mix}$ can be considered to be constant. Hence, the utility of a character as auxiliary character is determined by the product $r_g\, h_{mix}$.

In the mixture of Exp. 77-1b, the heritability and the correlation coefficient with monoculture yield were computed for several characters (Table 26). Distinguished were monocultures in hand-sown plantings of 5 x 25 cm$^2$ plant$^{-1}$ and monocultures in drilled rows. The agreement between both type of monocultures is poor (Tables 14 and 16, $r = 0.20$).

Table 26. Heritability of some characters measured in mixture at 5 x 25 $cm^2$ $plant^{-1}$ (Exp. 77-1b) and genetic correlation of these characters with grain yield in monoculture. Monoculture yield is measured in hand-sown plots at 5 x 25 $cm^2$ $plant^{-1}$ (Exp. 77-1a) and in drilled rows (Exp. 77-2).

| Character | $h^2_{mix}$ | Hand-sown monoculture | | Drilled-row monoculture | |
|---|---|---|---|---|---|
| | | $r_g$ | $r_g h_{mix}$ | $r_g$ | $r_g h_{mix}$ |
| Grain yield per plant | 0.29 | 0.11 | 0.059 | 0.60 | 0.325 |
| Ears per plant | 0.49 | -0.14 | -0.095 | 0.56 | 0.389 |
| Grains per ear | 0.67 | 0.43 | 0.353 | -0.18 | -0.150 |
| Weight per grain | 0.36 | 0.24 | 0.143 | 0.05 | 0.032 |
| Biomass per plant | 0.33 | 0.05 | 0.026 | 0.52 | 0.300 |
| Harvest index | 0.25 | 0.48 | 0.241 | 0.38 | 0.190 |
| Ear weight per plant | 0.30 | 0.08 | 0.041 | 0.58 | 0.317 |
| Grains per plant | 0.28 | 0.03 | 0.017 | 0.61 | 0.324 |
| Grain yield per tiller | 0.57 | 0.52 | 0.390 | -0.20 | -0.148 |
| Biomass per tiller | 0.62 | 0.43 | 0.338 | -0.24 | -0.190 |
| Plant height | 0.69 | 0.25 | 0.209 | -0.07 | -0.055 |

This may be ascribed to the differences in density of stand and in husbandry. In the hand-sown plantings, the seeds were accurately spaced by hand, two seeds were sown per place and the emerged plants were singled. This procedure favoured 'Titan' and 'L 98' because they showed a lower percentage of emergence than the other varieties. Also the small differences between the varieties in monoculture yield contributed to the low correlation between both types of monocultures.

The monoculture yield in drilled rows (Table 16) was probably the best estimator of the monoculture yields of the varieties. It agrees better with agronomic practice and it was stronger correlated with the relative yield in national variety trials (r=0.74 vs 0.44). The disadvantage was that the comparison of the mixture yields at 5 x 25 $cm^2$ $plant^{-1}$ (Exp. 77-1b) with the monoculture yields in drilled rows was confused by differences in density of stand and in husbandry.

Grain yield per plant showed a relatively high value of the product $r_g h_{mix}$ when the drilled monocultures were the reference (Table 26). Other characters with a high value were number of ears, ear weight, number of grains and biomass per plant. In mixture, they were all strongly correlated with grain yield per plant (Table 32). These results suggest that, in this mixture, selection for yield per plant was as good as or better than selection for any of the other characters in improving the monoculture yield.

Indirect selection was not studied more extensively because variety mixtures were involved instead of segregating populations. The choice of the varieties affects strongly the magnitude of the genetic correlation and the heritability (Section 2.4). For example, the 4-rowed and 6-rowed varieties had, compared with the 2-rowed varieties, heavy tillers with a large number and a large weight of grains per tiller (Table 27) but their yield

in the drilled monocultures was low. These characteristics accounted for the negative correlations in the fifth column of Table 26.

It is general experience that genetic correlations and heritabilities differ strongly from population to population. Hence, for each population the characters suitable for indirect selection may differ.

Instead of selection for one character, selection may be done for several characters. The characters can be selected independently ('independent-culling levels'), simultaneously ('index selection'), or sequentially ('tandem selection'). Indirect selection for a target trait by means of one or more auxiliary traits is well known. The method is mainly applied in animal breeding where the units of selection are expensive. However, single plants are cheap, the heritability of most single-plant traits is very low and any measurement on a plant is relatively time-consuming. For instance, for the measurements required for Table 27, the capacity per man was about 100 plants per day. Moreover, in the early generations, many plants can be discarded visually (Section 1.2). So, it may be questioned whether any method of single-plant selection which requires the measurement of several traits per plant, will ever be economically realistic in small grains. Most breeders even consider selection of single plants for yield on a quantitative base, impracticable.

One aspect of the utility of a trait for indirect selection is its sensitivity to competition. The degree to which the expression of a certain genotype for a character is modified by competition is measured by the crowding coefficient of the genotype with respect to that character. The crowding coefficient given in Table 29 was estimated from the performance in monoculture (Table 27) and that in mixture (Table 28) by the procedure described in Section 6.2.6. It is noted that the crowding coefficients for characters other than yield tend to be fortuitous because the model of de Wit (1960) was developed primarily for biomass yields.

The competitive sensitivity of a character may be measured by its variance for the crowding coefficient b. One may also express the variance for the crowding coefficient relative to the genetic variation by the parameter $\gamma = \mu^2_{mono}$ var $\underline{b}$/var $g_{mono}$, where the population mean $\mu_{mono}$ is used as scaling factor (Section 4.4.4). The values of var $\underline{b}$ and $\gamma$ showed about the same trend (Table 30).

Biomass, ear weight and grain yield per plant were affected most by competition while the number of grains per plant was also sensitive to competition. In mixture, all these characters were higly correlated with grain yield (Table 31) and with each other. The number of ears per plant was influenced to a somewhat lower degree while the other characters were hardly affected by competition. The stronger a character was influenced by intergenotypic competition, the lower its heritability tended to be in monoculture (Table 30) . An explanation may be that a character which is strongly affected by intergenotypic competition is also influenced strongly by intragenotypic competition between the plants. In general, the latter increases the environmental variance and, therefore, lowers the heritability in monoculture (Section 5.3.2).

The competitive ability of a variety, measured by its crowding coefficient for biomass, was not clearly related to any of the traits observed in the monoculture of

Table 27. Performance of the varieties in monoculture at 5 x 25 $cm^2$ $plant^{-1}$ Exp. 77-1a.

| Variety | Grain yield g per plant | Ears per plant | Grains per ear | Grain weight g per grain | Biomass g per plant | Harvest index | Ear weight g per plant |
|---|---|---|---|---|---|---|---|
| Varunda | 5.3 abc* | 5.6 bc | 24 e | 0.040 bcd | 11.1 ab | 0.48 bcd | 6.3 ab |
| Tamara | 5.7 abc | 6.3 ab | 22 ef | 0.042 abc | 11.8 ab | 0.48 bc | 6.9 ab |
| Belfor | 5.3 abc | 5.8 bc | 23 e | 0.040 cd | 11.5 ab | 0.46 cde | 6.4 ab |
| Aramir | 6.1 a | 6.3 ab | 22 ef | 0.044 a | 12.6 a | 0.49 b | 7.4 a |
| Camilla | 5.0 abc | 5.8 bc | 20 f | 0.043 ab | 10.0 ab | 0.50 b | 6.2 ab |
| Golden Promise | 4.5 c | 7.1 a | 20 f | 0.031 f | 9.3 b | 0.48 bc | 5.5 b |
| Balder | 4.8 bc | 6.8 a | 20 f | 0.036 e | 10.5 ab | 0.46 def | 5.9 ab |
| WZ 704068-14 | 5.5 abc | 4.6 d | 37 c | 0.032 f | 9.9 ab | 0.55 a | 6.5 ab |
| Goudgerst | 4.7 c | 5.4 c | 22 ef | 0.039 cd | 10.6 ab | 0.44 ef | 5.8 ab |
| L 98 | 6.0 ab | 3.1 e | 47 b | 0.041 abc | 12.3 a | 0.49 b | 7.1 ab |
| Titan | 4.6 c | 3.6 e | 32 d | 0.040 bcd | 10.5 ab | 0.44 f | 5.9 ab |
| Bigo | 5.6 abc | 3.0 e | 51 a | 0.037 de | 12.3 a | 0.46 def | 6.9 ab |

* Values followed by the same letter are not significantly different in the Student-Newman-Keuls

Table 28. Performance of the varieties in mixture at 5 x 25 $cm^2$ $plant^{-1}$. Exp. 77-1b.

| Variety | Grain yield g per plant | Ears per plant | Grains per ear | Grain weight g per grain | Biomass g per plant | Harvest index | Ear weight g per plant |
|---|---|---|---|---|---|---|---|
| Varunda | 5.1 b* | 5.3 d | 23 d | 0.040 bcd | 10.3 b | 0.49 b | 6.0 b |
| Tamara | 7.8 a | 9.0 a | 21 d | 0.041 bc | 16.0 a | 0.49 b | 9.4 a |
| Belfor | 5.4 b | 5.2 d | 24 d | 0.043 ab | 11.1 b | 0.48 b | 6.4 b |
| Aramir | 5.3 b | 6.0 cd | 21 d | 0.041 bc | 11.1 b | 0.48 b | 6.3 b |
| Camilla | 5.4 b | 5.8 cd | 23 d | 0.040 bcd | 10.7 b | 0.49 b | 6.5 b |
| Golden Promise | 4.9 b | 6.9 bc | 23 d | 0.031 f | 10.1 b | 0.48 b | 5.9 b |
| Balder | 5.1 b | 6.1 cd | 21 d | 0.036 e | 10.4 b | 0.49 b | 6.1 b |
| WZ 704068-14 | 4.8 b | 4.8 d | 33 c | 0.030 f | 8.8 bc | 0.55 a | 5.6 b |
| Goudgerst | 7.7 a | 7.7 b | 23 d | 0.044 a | 17.4 a | 0.44 c | 9.6 a |
| L 98 | 3.5 c | 2.0 ef | 41 b | 0.040 bcd | 6.8 c | 0.51 b | 4.0 c |
| Titan | 1.6 d | 1.7 f | 22 d | 0.038 cde | 3.7 d | 0.41 d | 2.0 d |
| Bigo | 5.3 b | 3.0 e | 50 a | 0.037 de | 11.2 b | 0.48 b | 6.3 b |

* Values followed by the same letter are not significantly different in the Student-Newman-Keuls

| Grains per plant | Biomass g per tiller | Weight (g) of the seed sown | Number of rows in ear |
|---|---|---|---|
| 133 bc | 1.92 def | 0.047 | 2 |
| 136 bc | 1.82 ef | 0.047 | 2 |
| 134 bc | 2.00 de | 0.046 | 2 |
| 139 bc | 1.96 de | 0.045 | 2 |
| 116 c | 1.74 f | 0.047 | 2 |
| 144 abc | 1.33 g | 0.043 | 2 |
| 134 bc | 1.47 g | 0.042 | 2 |
| 172 a | 2.16 d | 0.032 | 4 |
| 120 bc | 1.98 de | 0.047 | 2 |
| 145 abc | 3.82 b | 0.045 | 6 |
| 115 c | 2.66 c | 0.045 | 4 |
| 151 ab | 4.12 a | 0.044 | 4 |

:est at P ≤ 0.05.

| Grains per plant | Grain yield g per tiller | Biomass g per tiller | Height cm |
|---|---|---|---|
| 124 c | 0.93 cd | 1.89 de | 90 d |
| 188 a | 0.86 cde | 1.76 de | 89 d |
| 126 c | 1.02 c | 2.11 cd | 99 c |
| 127 c | 0.87 cde | 1.81 de | 90 d |
| 133 c | 0.90 cde | 1.84 de | 78 f |
| 158 abc | 0.71 e | 1.46 f | 75 f |
| 135 c | 0.78 de | 1.61 ef | 92 d |
| 159 abc | 0.98 c | 1.80 de | 82 e |
| 175 ab | 0.99 c | 2.23 c | 108 b |
| 85 d | 1.70 b | 3.33 b | 98 c |
| 42 e | 0.82 cde | 1.97 cde | 88 d |
| 142 bc | 1.86 a | 3.90 a | 115 a |

test at P ≤ 0.05.

Table 29. Crowding coefficients of the varieties estimated from the variety means in mixture and monoculture.Exps 77-1a,b.

| Variety | Grain yield per plant | Ears per plant | Grains per ear | Weight per grain | Biomass per plant | Harvest index | Ear weight per plant | Grains per plant | Biomass per tiller | Plant height |
|---|---|---|---|---|---|---|---|---|---|---|
| Varunda | 0.97 c* | 0.98 b | 0.99 ab | 1.02 ab | 0.96 c | 1.01 a | 0.97 c | 0.96 b | 1.00 abc | 1.02 bcd |
| Tamara | 1.39 ab | 1.47 a | 0.98 ab | 0.98 ab | 1.40 ab | 0.99 ab | 1.40 ab | 1.42 a | 0.97 abc | 1.06 b |
| Belfor | 1.04 bc | 0.93 b | 1.04 ab | 1.09 ab | 1.00 c | 1.04 a | 1.03 bc | 0.96 b | 1.10 ab | 0.98 bcd |
| Aramir | 0.87 c | 0.97 b | 0.97 ab | 0.94 b | 0.91 c | 0.96 ab | 0.89 c | 0.94 b | 0.95 bcd | 0.99 bcd |
| Camilla | 1.09 bc | 1.04 b | 1.15 a | 0.93 b | 1.11 bc | 0.99 ab | 1.07 bc | 1.18 ab | 1.07 ab | 1.13 a |
| Golden Promise | 1.11 bc | 1.00 b | 1.13 a | 1.00 ab | 1.12 bc | 1.00 ab | 1.10 bc | 1.13 ab | 1.14 ab | 1.04 b |
| Balder | 1.08 bc | 0.92 b | 1.14 a | 1.05 ab | 1.02 c | 1.05 a | 1.06 bc | 1.03 b | 1.13 ab | 1.03 bc |
| WZ 704068-14 | 0.90 c | 1.08 b | 0.89 b | 0.95 ab | 0.92 c | 0.98 ab | 0.90 c | 0.95 b | 0.86 de | 0.97 cd |
| Goudgerst | 1.67 a | 1.47 a | 1.03 ab | 1.12 a | 1.70 a | 0.99 ab | 1.71 a | 1.50 a | 1.18 a | 1.05 b |
| L 98 | 0.59 d | 0.66 c | 0.92 b | 0.99 ab | 0.57 d | 1.03 a | 0.58 d | 0.60 c | 0.88 cd | 0.94 d |
| Titan | 0.34 e | 0.47 d | 0.80 c | 0.93 b | 0.36 e | 0.95 b | 0.36 e | 0.37 d | 0.79 e | 0.86 e |
| Bigo | 0.95 c | 1.02 b | 0.96 ab | 0.99 ab | 0.94 c | 1.01 a | 0.95 c | 0.96 b | 0.95 bcd | 0.95 d |

* Values followed by the same letter are not significantly different in the Student-Newman-Keuls test at $P \leq 0.05$.

Table 30. General mean, variances and derived quantities for characters measured in monoculture at 5 x 25 $cm^2$ $plant^{-1}$ (Exp. 77-1a). The crowding coefficient b, involved in $r_{bg}$, is that for biomass.

| Character | μ | var g | var e | $h^2$ | var b | γ | $r_{bg}$ |
|---|---|---|---|---|---|---|---|
| Grain yield per plant (g) | 5.24 | 0.22 | 6.28 | 0.03 | 0.111 | 13.58 | -0.18 |
| Ears per plant | 5.27 | 1.92 | 4.59 | 0.29 | 0.074 | 1.08 | 0.54 |
| Grains per ear | 28.3 | 118.6 | 39.9 | 0.75 | 0.010 | 0.07 | -0.50 |
| Weight per grain (mg) | 38.8 | 16.1 | 24.1 | 0.40 | 0.002 | 0.22 | -0.04 |
| Biomass per plant (g) | 11.03 | 0.76 | 26.77 | 0.03 | 0.112 | 18.02 | -0.16 |
| Harvest index | 0.476 | 0.00085 | 0.00314 | 0.21 | 0.001 | 0.17 | -0.03 |
| Ear weight per plant (g) | 6.39 | 0.22 | 9.28 | 0.02 | 0.113 | 20.97 | -0.22 |
| Grains per plant | 136. | 201. | 3484. | 0.05 | 0.090 | 8.36 | -0.12 |
| Biomass per tiller (g) | 2.25 | 0.75 | 0.30 | 0.71 | 0.014 | 0.09 | -0.47 |
| Plant height (cm) | 94.7 | 227. | 43. | 0.84 | 0.004 | 0.18 | -0.25 |

Table 31. General mean, variances, heritability and genetic correlation with grain yield per plant for characters measured in mixture at 5 x 25 $cm^2$ $plant^{-1}$. Exp. 77-1b.

| Character | μ | var g | var e | $h^2$ | $r_g$ |
|---|---|---|---|---|---|
| Grain yield per plant (g) | 5.14 | 2.54 | 6.09 | 0.29 | 1.00 |
| Ears per plant | 5.27 | 4.68 | 4.97 | 0.49 | 0.86 |
| Grains per ear | 26.9 | 87.1 | 42.6 | 0.67 | -0.20 |
| Weight per grain (mg) | 38.6 | 17.5 | 30.8 | 0.36 | 0.34 |
| Biomass per plant (g) | 10.6 | 12.34 | 24.98 | 0.33 | 0.99 |
| Harvest index | 0.482 | 0.00097 | 0.00293 | 0.25 | 0.17 |
| Ear weight per plant (g) | 6.16 | 3.80 | 8.72 | 0.30 | 1.00 |
| Grains per plant | 133. | 1457. | 3731. | 0.28 | 0.91 |
| Biomass per tiller | 2.14 | 0.52 | 0.31 | 0.62 | -0.13 |
| Plant height (cm) | 91.9 | 134. | 59. | 0.69 | 0.21 |

the variety ($r_{bg}$ in Table 30). In the literature, this problem has often been met. For example, Sakai (1961) concluded from his experiments that 'competitive ability was not associated with morphological traits which might be supposed to favour competition'.

In Exp. 77-2 with drilled rows, 'Bigo' was the tallest variety (124 cm), had the highest biomass production in monoculture (380 g $row^{-1}$), and an early ear emergence. On the other hand, 'Camilla' was the shortest variety (78 cm), had a moderate biomass production in monoculture (303 g $row^{-1}$), and a very late ear emergence. Nevertheless, 'Camilla' was a stronger competitor than 'Bigo' (Table 16). This was also true in the plant mixtures (Table 14).

Many authors have related competitive ability to various morphological characters

Table 32. Relative crowding coefficients of the varieties with respect to Varunda estimated from binary mixtures with Varunda as common associate. Exp. 76-1.

| Variety | Grain yield | Ears per plant | Grains per ear | Weight per grain |
|---|---|---|---|---|
| Golden Promise | 0.54 e* | 0.67 bcd | 0.91 a | 0.90 ab |
| Minerva | 1.22 b | 1.14 ab | 1.03 a | 1.02 ab |
| Julia | 0.86 bcd | 0.93 bc | 0.96 a | 0.97 ab |
| Belfor | 1.05 bc | 0.95 bc | 1.00 a | 1.05 a |
| Piccolo | 0.78 cde | 0.78 bcd | 0.99 a | 1.00 ab |
| Balder | 0.67 de | 0.78 bcd | 0.94 a | 0.91 ab |
| Camilla | 0.88 bcd | 0.82 bcd | 1.03 a | 1.03 ab |
| v.d. Have 198-71 | 0.66 de | 0.55 cd | 1.33 a | 0.92 ab |
| Proctor | 0.57 de | 0.49 d | 1.27 a | 0.92 ab |
| Titan | 0.69 de | 0.78 bcd | 0.95 a | 0.93 ab |
| Bigo | 1.69 a | 1.58 a | 1.06 a | 1.05 a |
| Uniculm | 0.58 de | 0.58 cd | 1.14 a | 0.89 b |

* Values followed by the same letter are not significantly different in the Student-Newman-Keuls test at $P \leq 0.05$.

based on an observed correlation with those characters. This approach must be criticized: (1) Correlations obtained from experiments with varieties are of limited value and have to be interpreted with care (Sections 2.4 and 6.4). For example, the relatively strong correlations for ears per plant, grains per ear and biomass per tiller in Table 30, could largely be ascribed to the deviating scores of the extreme poor competitors, the 6-rowed 'L 98' and the 4-rowed 'Titan', for these characters. (2) An approach based on ecophysiological grounds is always preferable to an empirical approach with correlation coefficients.

In Section 8.3.1 it was shown that, in my experiments, differences in competitive ability between the varieties could mainly be ascribed to differences in juvenile growth. This agreed with the observation that the number of ears per plant was most strongly affected by competition, whereas the number of grains per ear was slightly affected and the weight per grain was hardly affected by competition (Tables 29 and 32). In Table 32, the relative crowding coefficients for the number of grains per ear had a wide confidence interval because this character was not measured directly but derived from grain yield and number of ears per $m^2$ and from weight per grain. The dominance of juvenile growth among the factors that determined the outcome of competition, holds probably for many other experiments. Hence, relating competitive ability to characters, that express themselves late in the development, is often doomed to fail.

*Summary* The degree to which a character is influenced by intergenotypic competition was measured by its variance for the crowding coefficients. Especially yield per plant was strongly affected by competition. Of the yield components, competition affected

strongly the number of ears per plant, slightly the number of grains per ear, and hardly the weight per grain. In the literature, competitive ability was often related to morphological traits based on correlation coefficients observed in variety mixtures. This approach was criticized. In my experiments, differences in competitive ability between the varieties could mainly be ascribed to differences in juvenile growth.

In the studied variety mixture, selection for grain yield per plant was as efficient as or more efficient than selection for any of the other traits in order to raise monoculture yield in drilled plots.

*8.4.5 Mathematical correction for competitive ability, selection for harvest index*

If it were possible to determine the competitive ability of a plant in the mixture, adjustment of the yield of the plant for the effects of competition could be applied. Alternating the plants with plants of a standard variety was already discussed in Section 8.4.3. It was concluded that this method is useless in making allowance for competition.

The competitive ability of a plant is strongly affected by its juvenile growth. Measuring the rate of juvenile growth of each plant is impracticable but visual rating of the plants to juvenile growth may be of value. Differences in juvenile growth and, therefore, competition effects are reduced by sowing only seeds of about the same size in one selection plot (Section 8.4.2).

The competitive ability of a plant may be read off from its score for a certain character. The character should be highly sensitive for competition, whereas, when grown in monoculture, the genotypes should differ only slightly for this character. Hence, var $\underline{b}$ should be large and var $g_{mono}$ should be small. That is, $\gamma = \mu^2_{mono}$ var $\underline{b}$/var $g_{mono}$ should be high. The competitive influence on this character should run parallel to that on grain yield, i.e. the correlation between the crowding coefficient for that character and the crowding coefficient for grain yield should be close to unity.

Grain yield per plant, itself, seemed to satisfy the prerequisites (Table 30). Also ear weight per plant met the requirements due to its high correlation with grain yield. However, in selection for grain yield, grain yield itself or closely related characters are not suitable in the correction for competition. Biomass demonstrates also a high $\gamma$ (Table 30) and the crowding coefficients for biomass were strongly correlated with the crowding coefficients for grain yield (Tables 12-16). Moreover, in small grains, the progress in yield due to breeding is associated with an increase in grain yield/biomass ratio with little change in biomass (van Dobben, 1962, 1966; Sims, 1963; Aufhammer & Fischbeck, 1964; Sandfaer et al, 1965; Donald & Hamblin, 1976, p. 367). Therefore, the biomass of a plant seems a suitable character for adjusting the grain yield of the plant for competition.

The yield of a plant of a random genotype i in a mixture where all genotypes are at the same frequency was defined by

$$O_i = b_i M_i \qquad (4.14)$$

It is assumed that in monoculture all genotypes have the same biomass. Thus

$$M_{i,biom} = \bar{M}_{biom} = \bar{O}_{biom}$$

where $\bar{O}_{biom}$ is the mean biomass per plant in the mixture. The crowding coefficient of i for biomass is estimated as

$$b_{i,biom} = O_{i,biom} / M_{i,biom} = O_{i,biom} / \bar{O}_{biom}$$

The crowding coefficient of a genotype for grain yield equaled its crowding coefficient for biomass (Tables 12-16). Therefore,

$$b_{i,grain} = b_{i,biom} = O_{i,biom} / \bar{O}_{biom}$$

The expected monoculture yield of i is derived from Eqn 4.14 as

$$M_{i,grain} = \frac{O_{i,grain}}{b_{i,grain}} = \frac{O_{i,grain}}{O_{i,biom}} \bar{O}_{biom}$$

Note that $O_{i,grain}/O_{i,biom}$ is the harvest index of a plant and $\bar{O}_{biom}$ is a constant. Hence, selection after adjusting the grain yield of a plant for competition by way of its biomass, means selection for harvest index. The method is especially effective when in mixture the differences between the plants with respect to biomass originate mainly from genetic differences in competitive ability, i.e. the heritability for biomass in mixture is high. However, also a part of the non-genetic interplant variance is eliminated by selection for harvest index which also accounts for competition that arises from non-genetic causes (see Section 5.3.2 where this type of competition is defined).

In small grains, selection for harvest index has often been suggested (review by Donald & Hamblin, 1976). However the effect of competition on the harvest index and its consequences for selection, has not been studied well and in no case well understood. In what follows, the assumptions on which the above-mentioned correction for competition is based, are discussed and the effect of competition on the harvest index is pointed out.

In the method which allowed for the competitive ability of a plant by means of selection for its harvest index, it was assumed that:

(1) Biomass production of a plant should be strongly affected by competition. My experiments as well as the results reported in the literature, showed that biomass is highly sensitive to competition.

(2) In monoculture, the differences in biomass among the genotypes should be small compared with the differences in grain yield. This tendency should express itself in (a) the coefficient of genetic variation in monoculture, which should be substantially lower for biomass than for grain yield, and (b) a stronger genetic correlation in monoculture between grain yield and harvest index than between grain yield and biomass. As was reported earlier in this section, the progress in yield of varieties due to breeding

Table 33. Coefficient of genetic variation ($\sqrt{var\ g}$ / $\mu$) and genetic correlation coefficient, both in monoculture. In the data of Exp. 76-1, the standard 'Varunda' is included also. For Exp. 76-1, the values are given with and without the strongly deviating variety 'Uniculm'.

| Experiment | Coefficient of genetic variation | | Genetic correlation coefficient | | |
|---|---|---|---|---|---|
| | biomass | grain yield | grain yield vs HI | grain yield vs biomass | biomass vs HI |
| 76-1 incl. Uniculm | 0.055 | 0.173 | 0.97 | 0.79 | 0.63 |
| 76-1 exl. Uniculm | 0 | 0.107 | 0.98 | 0.33 | 0.14 |
| 77-1a | 0.079 | 0.090 | 0.41 | 0.83 | -0.17 |
| 77-2 | 0.111 | 0.139 | 0.69 | 0.65 | -0.10 |

is associated with an increase of the harvest index with little change in biomass. Consequently, the genetic correlations between grain yield and harvest index were high (review by Donald & Hamblin, 1976, p. 365). In my experiments, the assumption was less satisfactory (Table 33). These experiments as well as those reported in the literature, dealt with varieties. When the assumption that the genotypes with the highest monoculture yield have also the highest harvest index holds for varieties, this does not include, however, that this trend holds also for genotypes of a segregating population. Especially short-straw types, such as WZ 704068-14 (Table 16, 27), may fail to connect a high harvest index to a high grain yield because their biomass production is low. Further research is required to study whether a strong correlation between harvest index and monoculture yield holds for genotypes of segregating populations.

(3) The competitive change in biomass should run parallel to that in grain yield. That is, the crowding coefficient for biomass is closely correlated with that for grain yield. In all my experiments, the agreement was nearly perfect (Tables 12-16).

In conclusion, selection for havest index, as a method to take account of competition, seems worth further consideration. In any case, this method is a new point in favour of selection for harvest index.

Because the biomass and the grain yield of a plant are affected by competition in a similar way, their ratio, the harvest index, is not influenced by competition. This expressed itself in the crowding coefficients for harvest index, that were all close to unity (Table 29). Apparently, the distribution of dry matter in the plant between grains and straw does not depend on the competitive ability of the plant. Thus the harvest index is probably not influenced by competition that originates from non-genetic causes. This can be studied in monocultures. The competitive ability of a plant in monoculture is likely to be related to its biomass production so that in monoculture, the harvest index of a plant would be independent of its biomass.

In the monocultures of Exp. 77-1a, the grain yield and biomass per plant were measured on 18 random plants per plot. From these data, the correlation between harvest index and biomass was calculated per plot. There were no significant differences between the varieties with respect to the correlation coefficients. The correlation coefficients

averaged 0.015 (n=864). which confirmed the expectation of independency of harvest index and biomass of individual plants in monoculture. For illustration, the distribution of the variety 'Tamara' was given (Fig. 43). A few plants had a low harvest index which might be ascribed to losses due to threshing. The relation between harvest index per tiller and biomass per tiller was asymptotic: the harvest index per tiller increased with the biomass per tiller, but at greater tiller biomass with a lower rate. Because most of the tillers had a large biomass and thus about the same harvest index, the harvest index per plant did not significantly depend on the biomass per plant.

In conclusion, the harvest index of a plant was not influenced significantly by competition, irrespective of whether the competition originated from either genetic or non-genetic causes. The conclusion agrees with the statement of de Wit (1968) that plants with a determinate growth can stand miniaturization without reduction of the fraction of seeds. He based this upon the finding that the grain yield and the biomass of determinate crops reacted similarly to changes in density of stand.

Harvest index was not influenced by competition in any of my experiments. The experiments were laid out on different soils in two contrasting years (Section 2.2). Single rows as well as single plants were used as experimental unit. Therefore, the observed inertia of harvest index for competition holds probably for many other experiments.

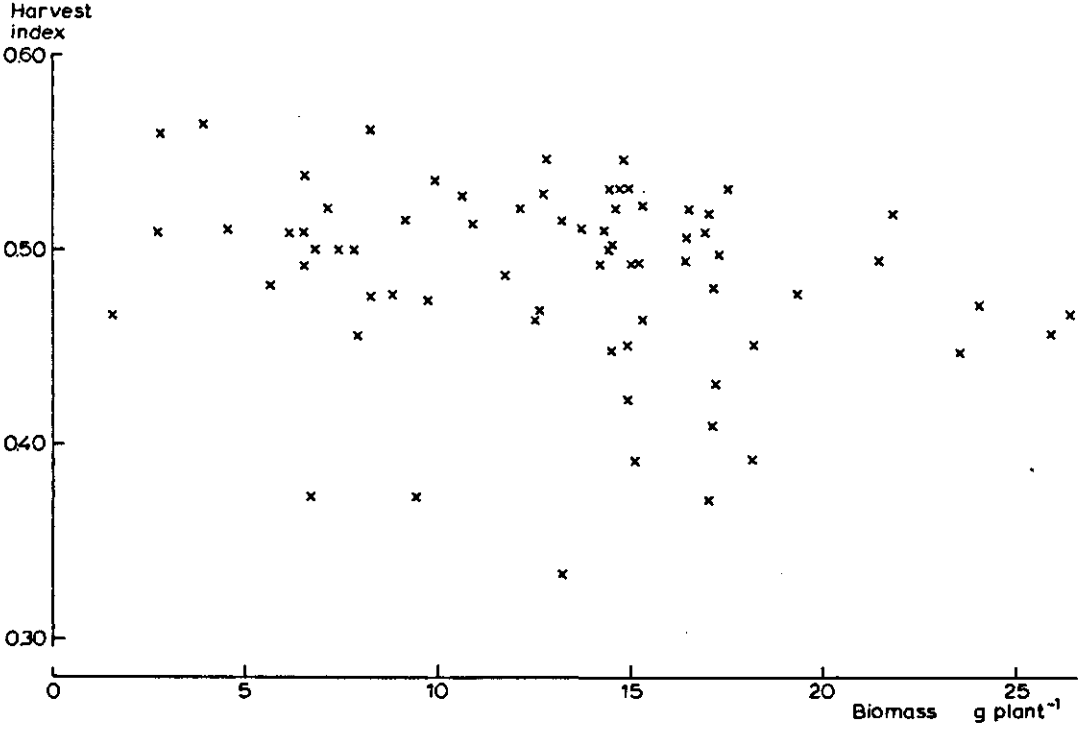


Fig. 43. Relation between harvest index and biomass of single plants in a monoculture of the variety 'Tamara'. Exp. 77-1a; 5 x 25 cm$^2$ plant$^{-1}$.

Table 34. Correlations between some characters with respect to the genetic, environmental, phenotypic and intergenotypic-competition effects in monoculture as well as in mixture. The environmental correlation in mixture is supposed to equal that in monoculture (compare Eqn 4.53). Exps 77-1a,b; 5 x 25 $cm^2$ $plant^{-1}$.

| Effects involved in the correlation | Grain yield vs HI | Grain yield vs biomass | Biomass vs HI |
|---|---|---|---|
| $g_{mono}$ | 0.41 | 0.83 | -0.17 |
| $g_{mix}$ | 0.17 | 0.99 | 0.01 |
| $e_{mono} = e_{mix}$ | 0.23 | 0.98 | 0.02 |
| $p_{mono}$ | 0.23 | 0.97 | 0.00 |
| $p_{mix}$ | 0.21 | 0.98 | 0.01 |
| $b$ | 0.17 | 1.00 | 0.09 |

In a monoculture, the plants of a variety that differ in their biomass do not differ systematically in their harvest index (Fig. 43). Consequently, the environmental correlation between biomass and grain yield is close to unity. The genetic correlations between biomass, grain yield and harvest index are variable. As yield differences among genotypes are mostly increased due to competition, whereas the harvest index remains unchanged, the genetic correlation between biomass and grain yield is generally greater with intergenotypic competition (mixture) than without intergenotypic competition (monoculture). Single-plant yields are characterized by a low heritability. Therefore, the phenotypic correlation is close to the environmental correlation and, therefore, close to unity. The heritability in monoculture is mostly smaller than in mixture. Hence, in monoculture, the phenotypic correlation is relatively closer to the environmental correlation than is the case in mixture. These trends were illustrated with the data of Exps 77-1a and b (Table 34).

In a barley $F_3$, Hamblin (1971, cited by Donald & Hamblin, 1976) recorded correlations between grain yield and biomass that were close to unity. From these results, Donald & Hamblin (1976, p. 366) stated that 'a strong positive relationship of biological yield and grain yield may be characteristic of genotypes competing in mixtures'. The authors mean probably the phenotypic correlation since the correlation among $F_3$ plants is a correlation among phenotypes. However, the previous considerations show that a phenotypic correlation between grain yield and biomass that is found to be close to unity has nothing to do with intergenotypic competition but is the result of the low heritability of single-plant yields.

*Summary* It was suggested that selection for harvest index would adjust the yield of a plant in mixture for its competitive ability. The mathematical foundation of this method was based on the assumptions that (1) the biomass production of a plant is strongly affected by competition, (2) in monoculture, the differences in biomass among the genotypes are small compared with the genotypic differences in grain yield, and (3) the competitive effect on biomass runs parallel to that on grain yield. The second assumption was not always valid.

Harvest index was found not to be influenced by competition, neither by intergenotypic nor by intragenotypic competition. The genotypes had in monoculture the same harvest index as they had in mixture. The harvest index of plants within a monoculture was independent of biomass.

## 8.5 REDUCING THE BIAS FROM ENVIRONMENTAL VARIATION

There is an extensive literature on methods that allow for soil heterogeneity in order to reduce the bias from environmental variation. These methods are discussed here because (1) the effect of competition on the efficiency of these methods is neglected, and (2) competition effects come more to the fore when the environmental variation is smaller.

### *8.5.1 Inventory of methods*

There are several methods for coping with soil heterogeneity. The following classification may be made.

(1) Grids. A selection plot is divided into subplots, the 'grids'. Plants are selected within the grids. For example, at a selection percentage of 10%, within each grid the 10% highest yielding plants are chosen. Grid selection was introduced by Gardner (1961). Skorda (1973) and Verhalen et al. (1975) evaluated the method experimentally and discussed its use. Grid selection is comparable with 'stratified sampling' (Snedecor & Cochran, 1967, p. 520).

For each plant the grid may be shifted so that the plant is the centre of the grid. Such a moving grid provides a better allowance for soil heterogeneity than the fixed grids, but requires more computation work, requires that the position of each plant in the field is recorded and is impracticable for the plants at the border of the field.

(2) Moving mean. The yield level of the habitat of a plant in the field is estimated by the mean yield of its neighbour plants. It is this successive estimation of the mean yield levels that is the origin of the term 'moving mean'.

The adjusted yield of the plant at place i was calculated as

$$p_i^a = p_i - \tfrac{1}{4}\,(p_{i-2} + p_{i-1} + p_{i+1} + p_{i+2}) \qquad (8.1)$$

where $p^a$ the adjusted yield and p the unadjusted yield. The subscript indicates the rank of the plants within a row. A proportional adjustment, by expressing the yield of a plant as a percentage of the yield of its neighbours, would have been better than the subtractive adjustment because $\sqrt{\text{var } g}$ and $\sqrt{\text{var } e}$ tend to be proportional to the yield level rather than independent of it.

Several related alternatives are possible. For example, neighbours of third and higher order also may be incorporated in the moving mean; nearby neighbours may receive a higher weight than neighbours at a larger distance; the trend in the field may be fitted by a polynomial response surface for single-plant yields (Kendall, 1976; Hamblin

et al. 1978) or may be eye fitted; an analysis of covariance may be applied with the moving means acting as the independent covariable (Townley-Smith & Hurd, 1973; Mak et al., 1978). An analysis of covariance would avoid overadjustment (Yates, 1936; Baker & McKenzie, 1967). As the genetic differences for biomass are mostly smaller than those for grain yield, biomass per plant may be preferable as covariate in the adjustment.

Moving means were employed for single plants by Hamblin et al. (1978). Knott (1972), Townley-Smith & Hurd (1973) and Mak et al. (1978) applied the method on row plots.

The disadvantage of moving means is that the yield of all plants has to be measured, notwithstanding that many plants can be discarded visually.

(3) Inserted plants belonging to a standard variety. The plants from the segregating population are alternated with plants of a standard variety (Fig. 3). Hence, every plant from the segregating population has only plants of the standard variety as adjacent neighbours.

The adjusted yield of a plant at place i was calculated by

$$p_i^a = p_i - \tfrac{1}{2}(s_{i-1} + s_{i+1}) \qquad (8.2)$$

where s is the yield of a standard plant at the place denoted by the subscript.

Some of the alternatives mentioned for the moving mean, may be useful for the adjustment by means of inserted standards. Compared with the moving mean, this method has the advantage that the genotype of the plants, by which the yield is adjusted, is always the same. Moreover, it is not necessary to measure the yield of all plants in the field. A disadvantage is that the selection plot is two times larger because half of the plants belong to the standard. This increases the amount of work. Moreover, a larger field area results almost always in an enhanced environmental variance. This was illustrated by the difference in $\hat{\sigma}_e^2$ between Exp. 77-1c on the one hand and Exps 77-1b and 1d on the other hand (Table 35).

(4) Adjustment at a triangular spacing (Fasoulas, 1973; Fasoulas & Tsaftaris, 1975).

(4a) Moving mean. At a triangular spacing, any plant can be considered to be the centre of a hexagon with its six neighbours as the angular points of the hexagon (Fig. 3). The adjusted yield of a plant in row j at place i is computed from the yield of the six surrounding plants as

$$p_{j,i}^a = p_{j,i} - \tfrac{1}{6}(p_{j-1,i-\frac{1}{2}} + p_{j-1,i+\frac{1}{2}} + p_{j,i-1} + p_{j,i+1} + p_{j+1,i-\frac{1}{2}} + p_{j+1,i+\frac{1}{2}}) \qquad (8.3)$$

As the six neighbours are all at an equal distance from the central plant, the adjustment is more balanced than that by a corresponding moving mean in a rectangular spacing. The alternatives mentioned for the latter, may be useful here also.

(4b) Standard triangle. In the field, plants of a standard variety are inserted in a systematic way (Fig. 3). In the neighbourhood of any plant, there are three plants of the standard variety. These three standard plants constitute a triangle so that any plant is situated within a standard triangle. The adjusted yield of a plant is

Table 35. Effect of adjustment for soil heterogeneity on variances, heritability and realized responses to selection. Selection was for ear weight in g plant$^{-1}$ at a selection percentage of 10% within plots. The monoculture yield is the grain yield in g row$^{-1}$ in monocultures of drilled rows (Table 16). The response for mixture yield is, for the adjustments, the correlated response for the unadjusted mixture yields, brought about by selection for the adjusted yields. For explanation of the variances see Table 20. Exps 77-1b, c, d, e.

| Method | $\hat{\sigma}^2_g$ | $\hat{\sigma}^2_e$ | $\hat{\sigma}^2_r$ | $\hat{\sigma}^2_s$ | $\hat{\sigma}^2_{gs}$ | $h^2_{mix}$ | $R_{mix}$ | $CR_{mono}$ |
|---|---|---|---|---|---|---|---|---|
| Multicomponent mixture | | | | | | | | |
| unadjusted | 3.80 | 8.72 | 0 | 0.09 | 0 | .30 | 1.88 | 5.0 |
| moving mean | 4.71 | 11.81 | 0 | 0 | 0 | .29 | 1.87 | 4.2 |
| Alternated standard | | | | | | | | |
| unadjusted | 1.14 | 10.28 | 0.16 | 0 | 1.60 | .10 | 0.56 | -2.2 |
| adjusted via standards | 2.00 | 13.49 | 0.24 | 0 | 1.25 | .13 | 0.59 | 4.2 |
| Honeycomb design, narrow | | | | | | | | |
| unadjusted | 2.04 | 8.88 | 0.08 | 0 | 0.61 | .19 | 1.16 | 7.5 |
| moving mean | 2.60 | 11.38 | 0 | 0 | 0.75 | .19 | 1.16 | 6.5 |
| standard triangle | 2.45 | 10.81 | 0.53 | 0.77 | 0.66 | .18 | 1.26 | 5.6 |
| moving grid | | | | | | | 1.39 | 3.6 |
| Honeycomb design, wide | | | | | | | | |
| unadjusted | 33.5 | 220.3 | 11.4 | 24.8 | 0 | .13 | 5.34 | 13.3 |
| moving mean | 35.6 | 278.4 | 0 | 0 | 0 | .11 | 5.09 | 11.6 |
| moving grid | | | | | | | 4.87 | 11.9 |

$$p^a = p - \tfrac{1}{3}(s_1 + s_2 + s_3) \qquad (8.4)$$

where $s_1$, $s_2$ and $s_3$ are the yields of the standard plants.

(4c) Selecting only the plants that yield higher than all of their six neighbours. Any plant is considered to be the centre of a hexagon and is compared with its six neighbours at the angular points of the hexagon. The plant is only saved when it yields more than all of its six neighbours. The method may be considered to be a 'moving grid'. By this method, in Exp. 77-1d, 13.2% and, in Exp. 77-1e, 11.8% of the total number of plants was selected. The percentage of selected plants was reduced to 10% by removing from the groups of selected plants those plants with the lowest yield. Method 4c is slightly inferior to method 4a because in method 4c it is assumed that there is no fertility gradient within a hexagon. The advantage of method 4a over method 4c is that of a moving mean within a hexagon.

Compared with a rectangular spacing, a triangular spacing is less convenient in sowing. The methods 4a and 4c imply that the yield of all plants has to be measured.

The hexagonal arrangement was used in competition studies by Kira et al. (1953), Sakai (1955, 1957), Mead (1967), Martin (1973), Tauer (1975), Veevers & Boffey (1975), and Boffey & Veevers (1977).

*8.5.2 Grid selection*

The selection field was partitioned into grids. The grids were chosen to be the plots (Fig. 2). In the mixtures at the narrow stand, the area of a grid was 1.0 x 1.3 $m^2$ and in the mixtures at the wide stand, the area was 8.7 x 6.8 $m^2$.

Selection within plots removes the variance between plots, $\sigma_s^2$, from the environmental variance. In my experiments, this variance was low, compared with the environmental variance within a plot, $\sigma_e^2 + \sigma_r^2$ (Table 35). Nevertheless, in the multicomponent mixture, the realized response $R_{mix}$ for ear weight per plant in mixture increased from 1.70 g $plant^{-1}$ to 1.88 g $plant^{-1}$ by the use of grids. In grid selection, 10 plants were chosen from each plot of 96 plants. On the other hand, from the five plots of Exp. 77-1b, 8, 12, 16, 10 and 4 plants were chosen respectively, when the plants with the highest yield were selected from the entire field of 3.0 x 22.5 $m^2$. This result suggested that the plots differed little in their yield level. This was observed also from the mean yield per plot: 6.5, 5.9, 6.6, 6.2 and 5.6 g $plant^{-1}$ for the five plots, respectively. In conclusion, in Exp. 77-1b, the differences between the grids were small. Therefore, selection within grids gave only a small gain over selection without grids.

Compared with selection without grids, grid selection requires no additional work, while it gives always a profit provided that the number of plants within a grid is high enough to give an accurate estimate of the yield level of the grid. Therefore, grid selection was applied in all experiments. In plant selection, the plots were chosen to be the grids. In selection based on yield per row, strips of adjacent rows were considered to be the grids (Fig. 4). All actual data, published in this report, on results of selection were obtained by selection within grids. If not mentioned otherwise, the estimates of variances were those within grids.

An arbitrary size was chosen for the grids. The smaller the grids, the larger the environmental variance between grids and the smaller the environmental variance within grids. As selection within grids avoids the environmental variance between grids, this would suggest that the smaller the grids the more efficient is selection. However, in small grids, non-representativeness of genotypic composition and random error in the plant yields lead to overadjustment (Eqn 8.15). Hence there is an optimal grid size. The choice of size and shape of grids is also affected by practical reasons and by the observed fertility patterns in the field.

In conclusion, partitioning the selection plot into grids and selecting the best plants within grids is an effective, cheap and simple method to reduce the environmental variance.

*8.5.3 Correlation between adjacent neighbours*

The yield of a plant or of a row of plants is adjusted for soil heterogeneity by means of the yield of its neighbours. So, it is assumed that the yield level of the place in the field where the studied entry stands is measured by the yield of the neighbours. Hence, the critical issue is: to what extent are the yields of adjacent neighbours correlated with each other.

In the literature, the usefulness of moving means and inserted checks was studied mainly for selection based on the yields of row plots. Therefore, the correlation between neighbours is discussed for row plots also.

A method is often evaluated in a uniformity trial, i.e. an experiment where all rows are sown with the same variety. Here it is shown that the correlation between adjacent neighbours in a line-selection field may be markedly different from that in a uniformity trial. Hence, the results obtained from uniformity trials are of limited value for line selection.

8.5.3.1 Correlation between adjacent rows

The coefficient of the correlation between the yield of a row at place i and the yield of its neighbour row at place i + 1 is, by definition

$$r_p = \frac{\mathrm{cov}(\underline{p}_i, \underline{p}_{i+1})}{\mathrm{var}\ \underline{p}} \qquad (8.5)$$

The subscript p indicates that the correlation is between phenotypes.

*Uniformity trial* In a uniformity trial, all rows are sown with the same variety so that therefore the phenotypic correlation between neighbour rows equals the environmental correlation. The environmental correlation is, by definition,

$$r_e = \frac{\mathrm{cov}(\underline{e}_i, \underline{e}_{i+1})}{\mathrm{var}\ \underline{e}} \qquad (8.6)$$

The soil conditions for two neighbour rows will be more alike than those for two rows chosen at random on the field. Therefore, the correlation between neighbours tends to be positive. On the other hand, competition between neighbour rows forces the correlation towards minus one. This may be explained as follows. If in a monoculture, a row grows more rapidly than its neighbour rows, it produces more biomass and is also a stronger competitor than its neighbours. Due to this competitive adavantage of rows with a greater biomass, the biomass differences between neighbour rows are enlarged which leads to a negative trend in the correlation between neighbours.

*Line-selection field* In a line-selection field with 1-row plots, the genetic constitution is different for each row. The phenotypic correlation between the rows can be expanded to

$$r_p = \frac{\text{cov}(\underline{p}_{i,mix},\underline{p}_{i+1,mix})}{\text{var } \underline{p}_{mix}} = \frac{\text{cov}(\underline{e}_i,\underline{e}_{i+1}) + \text{cov}(\underline{g}_{i,mix},\underline{g}_{i+1,mix})}{\text{var } \underline{e}_{mix} + \text{var } \underline{g}_{mix}} \qquad (8.7)$$

Likely the environmental covariance in mixture is about equal to that in monoculture. The correlation between rows in a line-selection field differs from that in a uniformity trial (Eqn 8.6) in that the denominator is increased, especially with the genetic variance, and that the numerator is supplemented with the genetic covariance between rows. More specifically, adjacent rows of a mixture are less alike than those in a monoculture because they differ in genotype, and, therefore, their phenotypic correlation is lower. The phenotypic variance, and consequently the denominator of Eqn 8.7, is increased by intergenotypic competition also because in mixture, the environmental variance and, in general, the genetic variance are larger than in monoculture (Section 4.5).

The genetic covariance between rows can be derived as follows. Suppose that the arrangement of single rows is

v w x y

where a letter denotes the genotype sown in the row. We may write the genetic covariance between the row of w and the row of x as $\text{cov}(\underline{O}_{w,vx}, \underline{O}_{x,wy})$. Substitution of Eqn 4.13 and extending the expression by the method of statistical differentials gives

$$\text{cov}(\underline{g}_{i,mix},\underline{g}_{i+1,mix}) = \text{cov}(\underline{O}_{w,vx},\underline{O}_{x,wy}) \simeq -\tfrac{1}{4}\mu^2 \text{ var } \underline{b} - \tfrac{1}{2}\mu \text{ cov}(\underline{b},\underline{g}_{mono}) \qquad (8.8)$$

Hence, although the genotypes are allotted to each at random, there is a genetic correlation for their yield in mixture. Since this genetic correlation is generally negative (Eqn 8.8), the phenotypic correlation between the rows (Eqn 8.7) is forced to minus one.

The genetic correlation between rows can be understood as follows. The yield of a row is partly determined by the competitive ability of its neighbour rows. When the neighbours of a row are strong competitors, the yield of the row is depressed. On the other hand, the yield of the neighbours is enhanced when they are located adjacent to a poor competitor. This tends to correlate the yield of adjacent rows negatively. As intergenotypic competition between the rows is genetically determined, the correlation is a genetic one.

Substitution of Eqns 8.8, 4.29 and 4.30 into Eqn 8.7 provides for the phenotypic correlation between rows in a mixed stand

$$r_p = \frac{\text{cov}(\underline{e}_i,\underline{e}_{i+1}) + \text{cov}(\underline{g}_{i,mix}\underline{g}_{i+1,mix})}{\text{var } \underline{p}_{mix}}$$

$$\simeq \frac{\text{cov}(\underline{e}_i,\underline{e}_{i+1}) - \tfrac{1}{4}\mu^2 \text{ var } \underline{b} - \tfrac{1}{2}\mu \text{ cov}(\underline{b},\underline{g}_{mono})}{\text{var } \underline{g}_{mono} + \mu \text{ cov}(\underline{b},\underline{g}_{mono}) + \tfrac{3}{8}\mu^2 \text{ var } \underline{b} + \text{var } \underline{e}_{mono}} \qquad (8.9)$$

In summary, the correlation between rows in a line-selection field is, compared with that in a uniformity trial,

(1) closer to zero, because
- neighbour rows are less alike because they differ genetically,
- the phenotypic variation among rows is also in general increased by intergenotypic competition;

(2) forced to minus one because intergenotypic competition tends to result in a negative genetic correlation between adjacent rows.

As a consequence, the correlation between rows in a uniformity trial is almost always an overestimation of that in a line-selection field. Hence, correlations estimated from a uniformity trial give a too optimistic view of the opportunities of moving means in the adjustment for soil heterogeneity in a line-selection field.

In contrast to the lines in a line-selection field, all standard plots have the same genotype. This suggests that the environmental correlation measured in a uniformity trial indicates well the efficiency of adjustment by inserted standard plots. However, this correlation gives a slight overestimation of this efficiency because (i) the standard plots are affected differently by intergenotypic competition as the neighbouring lines are different for each standard plot, and (ii) the standard and the lines may react differently to the fertility gradient in the field.

*Actual data* In the uniformity trial of Exp. 76-3e, the correlation between adjacent rows was positive, whereas in the uniformity trial of Exp. 77-2e the correlation was negative (Table 36). Apparently, in the latter experiment, the effects of interrow competition overshadowed the effects of soil heterogeneity.

The correlations in the line-selection field were compared with those in the uniformity trial, shifted towards minus one. This shift was expected according to the previous-described theoretical considerations. The trend towards negative values was reinforced in my experiments because the varieties were laid out in randomized block designs. Thus within a replicate, a row of a variety never meets a row of the same variety as its neighbour. This gives an additional negative genetic covariance between neighbour rows. Hence, a completely randomized design would have been more suitable for comparisons of correlations.

The correlation between adjacent neighbours is forced to plus one when the field area is increased, i.e. when the group of rows is extended within which the correlation is computed (Table 36). From the theory on within and between group correlations (Li, 1975, p. 310), it can be derived that the total correlation between rows is

$$r_t = \frac{\mathrm{cov}(p_i, p_{i+1})_w + \mathrm{var}\ p_b}{\mathrm{var}\ p_w + \mathrm{var}\ p_b} = \frac{r_w\ \mathrm{var}\ p_w + \mathrm{var}\ p_b}{\mathrm{var}\ p_w + \mathrm{var}\ p_b}$$

where the subscript w denotes the within-group variables and the subscript b the between-group variables. When the variance between groups is small compared with that within groups, i.e. when the fertility gradient in the field is small, the correlation between rows increases only slightly with an increased field area.

In the literature, the correlation between neighbour plots was estimated by Harris (1920), Hayes (1925), Garber et al. (1926), Griffee (1928), Wiebe (1935), Briggs &

Table 36. Correlation between adjacent neighbours with respect to grain yield and biomass. The correlation mentioned in Exp. 77-1e under grain yield is that for ear weight per plant. The area is the area on the field wherein the correlation is estimated and n is the number of experimental units on which the correlation is based.

| Experiment | Spacing | n | Area $m^2$ | Correlation coefficient | |
|---|---|---|---|---|---|
| | | | | grain yield | biomass |
| 76-2a | 150 $cm^2$ $plant^{-1}$ | 768 | 1.0 x 5.8 | +0.14 | +0.12 |
| 77-1b | 125 $cm^2$ $plant^{-1}$ | 480 | 1.0 x 1.3 | +0.02 | +0.01 |
| 77-1e | 3120 $cm^2$ $plant^{-1}$ | 624 | 8.7 x 6.8 | +0.07 | +0.07 |
| 76-3a | 20 cm $row^{-1}$ | 288 | 1.8 x 19.2 | -0.14 | -0.14 |
| 76-3a | 20 cm $row^{-1}$ | 288 | 46.8 x 36.0 | -0.08 | -0.04 |
| 76-3e | 20 cm $row^{-1}$ | 576 | 1.8 x 19.2 | +0.29 | +0.31 |
| 76-3e | 20 cm $row^{-1}$ | 1080 | 1.8 x 36.0 | +0.33 | +0.35 |
| 76-3e | 20 cm $row^{-1}$ | 1080 | 46.8 x 36.0 | +0.49 | +0.50 |
| 77-2b | 20 cm $row^{-1}$ | 480 | 1.7 x 28.8 | -0.23 | -0.25 |
| 77-2b | 20 cm $row^{-1}$ | 480 | 142.0 x 28.8 | -0.22 | -0.25 |
| 77-2e | 20 cm $row^{-1}$ | 576 | 1.7 x 28.8 | -0.09 | -0.10 |
| 77-2e | 20 cm $row^{-1}$ | 576 | 142.0 x 28.8 | -0.05 | -0.04 |

Shebeski (1968), Townley-Smith & Hurd (1973) and Hadjichristodoulou & Della (1976). Most correlations were much higher than those observed in my experiments. A negative correlation was never reported. A very high correlation of 0.82 was found by Wiebe (1935) in spring wheat for a uniformity trial with 1-row plots spaced 30 cm apart. High correlations also were obtained by Briggs & Shebeski (1968) in spring wheat nurseries of 3-row plots with 60 cm between the plots and 15 cm between the rows within a plot. Every third plot was sown with a check variety. The correlations between contiguous check plots was 0.63, 0.88 and 0.87 for three trials studied.

Higher values of the correlation indicate a greater soil heterogeneity within the field. However, such comparisons must be made with caution since the correlation depends not only on the pattern of soil heterogeneity but also on the size and shape of the plots and the size and the shape of the experimental field, and on the genetic variation in the population. Compared with that in 1-row plots, the correlation between adjacent multi-row plots tends to be higher because (1) the area needed to test the same number of entries is larger, (2) intergenotypic interplot competition is less severe, and (3) the plot error variance is reduced because of an increased sample size. On the other hand, the reduced similarity in soil condition of the plots, because of an increased plot width, decreases the correlation. Going from 1-row to 3-row plots, in the uniformity trials the correlation between grain yield of neighbour plots increased from +0.33 to +0.46 (Exp. 76-3e) and from -0.09 to + 0.36 (Exp. 77-2e).

*Consequences for adjustment for soil heterogeneity* The best results of allowance for soil heterogeneity by means of neighbour plots are expected when the correlation between neighbour plots is high. For adjustment by moving means the phenotypic correlation should be high, whereas for adjustment by inserted checks the environmental correlation should be high.

The environmental correlation is high when the environmental covariance between the plots is large but, at the same time, the environmental variance is small (Eqn 8.6). A large environmental covariance is attained when the soil heterogeneity occurs in a heavy, coarse-grained pattern because only then are nearby plots more strongly related than random plots. A small environmental variance is secured by an appropriate plot technique and slight small-grained soil heterogeneity. Hence, adjustment by inserted standard plots is most effective with a good plot technique on a heterogeneous experimental field. In addition, for adjustment by inserted standards, the effects of intergenotypic competition should be small and the standard and the lines should react similarly to the fertility gradient in the field.

A high phenotypic correlation requires, in addition, a small genetic variance and a value of the genetic covariance, as little negative as possible (Eqn 8.7). This is achieved when there is little genetic variation in the population and intergenotypic interplot competition is low. In particular, the genetic variance and genetic covariance should be low relative to the environmental covariance. The probability for this condition tends to be greater the lower the heritability. Hence, adjustment by moving means is most effective in a genetically narrow population in a trial with a good plot technique, little intergenotypic competition between the plots and grown on a heterogeneous field.

### 8.5.3.2 Correlation between adjacent plants

In contrast to the competition effect of a row, which is restricted to its adjacent neighbours, a single plant has a considerable influence on neighbours of higher order (Section 4.2.2). In the limit situation, where the competition effect of a plant on its nearest neighbour is as large as on a random plant in the field, the genetic covariance between neighbour plants is zero. Substitution of $\text{cov}(\underline{g}_i,\underline{g}_{i+1}) = 0$ and of the expression of var $\underline{p}_{mix}$ (Eqn 4.51) into Eqn 8.7, supplies for the correlation between neighbour plants

$$r_p = \frac{\text{cov}(\underline{e}_i,\underline{e}_{i+1})}{\text{var } \underline{p}_{mix}} \approx \frac{\text{cov}(\underline{e}_i,\underline{e}_{i+1})}{\text{var } \underline{g}_{mono} + 2\,\mu\,\text{cov}(\underline{b},\underline{g}_{mono}) + \mu^2\,\text{var } \underline{b} + \text{var } \underline{e}_{mono}} \qquad (8.10)$$

Actually, a plant will be influenced somewhat more by its nearest neighbours than by random plants so that the real expression of the correlation between adjacent plants is slightly shifted from Eqn 8.10 to Eqn 8.9.

In my experiments, the correlation between neighbour plants was low (Table 36). The low correlation was promoted due to growing the varieties in a randomized block design instead of in a completely randomized design (Section 8.5.3.1).

*8.5.4 The principles of adjustment*

Other workers have generally measured the efficiency of a method in coping with soil heterogeneity by the reduction of the environmental variance or variation coefficient which is brought about by the adjustment. However, in such an experimental evaluation, it is not considered how the adjustment comes about. In the literature, the theoretical approach is poor, especially as the adjustment is affected by competition. In this section its principles are illustrated by a simple example.

8.5.4.1 Single plants

Let the yield of a plant be adjusted by the yield of its two nearest neighbours. The adjusted yield of a plant at place i is

$$p_i^a = p_i - \tfrac{1}{2}(p_{i-1} + p_{i+1}) \tag{8.11}$$

The variance of the adjusted yields can be expanded as

$$\text{var } \underline{p}^a = \tfrac{3}{2} \text{ var } \underline{p} - 2 \text{ cov}(\underline{p}_i, \underline{p}_{i+1}) + \tfrac{1}{2} \text{ cov}(\underline{p}_{i-1}, \underline{p}_{i+1}) \tag{8.12}$$

In a stand where all of the plants have the same genotype, and in a stand where the neighbour plants at places i-1 and i+1 are of a standard genotype, we may write the variance of the adjusted yields

$$\text{var } \underline{e}^a = \tfrac{3}{2} \text{ var } \underline{e} - 2 \text{ cov}(\underline{e}_i, \underline{e}_{i+1}) + \tfrac{1}{2} \text{ cov}(\underline{e}_{i-1}, \underline{e}_{i+1}) \tag{8.13}$$

Hence, the adjustment leads to (1) an increase in environmental variance because in the adjusted yield of a plant the error variation of its neighbours is introduced as well as the covariance among the neighbours, and (2) a decrease in environmental variance because the yield of a plant is correlated with that of its adjacent neighbours. The correlation tends to be positive because neighbours have about the same soil conditions. As a plant extends its competitive influence to remote plants also, interplant competition hardly deflates the correlation. The adjustment reduces the environmental variance when the covariance between plants cancels out the introduced error variation of the neighbours (Eqn 8.13). If this is not the case, the environmental variance is even enhanced by the adjustment. For avoiding over-adjustment see Section 8.5.1.

In a segregating population, the phenotypic variance of the adjusted yields (Eqn 8.12) can be partitioned in a genetic and in an environmental variance. Employing the approach, used in Section 4.3.1.4, gives the genetic variance after adjustment

$$\text{var } g_{mix}^a = \text{var } g_{mix} \tag{8.14}$$

and the environmental variance

$$\text{var } \underline{e}^{a}_{mix} = \frac{3}{2} \text{ var } \underline{e}_{mix} + \tfrac{1}{2} \text{ var } \underline{g}_{mix} - 2 \text{ cov}(\underline{e}_i, \underline{e}_{i+1}) + \tfrac{1}{2} \text{ cov}(\underline{e}_{i-1}, \underline{e}_{i+1}) \qquad (8.15)$$

Hence, the genetic variance does not change due to adjustment (Eqn 8.14). Comparison of Eqns 8.13 and 8.15 shows that the environmental variance after adjustment in a segregating population is increased by a genetic component. This genetic component accounts for the bias in the moving mean which arises from the genetic variation of the plants that constitute the moving mean.

A covariance between plants, which would be in monoculture just high enough to reduce the environmental variance, does not suffice in a mixture (Eqns 8.13 and 8.15). Hence, results of genetically uniform stands overestimate the opportunities of adjustment by moving means in segregating populations.

The environmental variance is reduced by the adjustment when var $\underline{e}^{a}$ < var $\underline{e}$. When the adjustment is by alternated standard plants, we can derive from Eqn 8.13 that the environmental variance is reduced when

$$r_{e_{i,i+1}} - \tfrac{1}{4} r_{e_{i-1,i+1}} > \tfrac{1}{4}$$

When the adjustment is by a moving mean, we can derive from Eqn 8.15 that the environmental variance is reduced when

$$r_{p_{i,i+1}} - \tfrac{1}{4} r_{p_{i-1,i+1}} > \tfrac{1}{4}$$

These results illustrate that the success of adjustment by standard plants is determined by the environmental correlation between neighbours, whereas the success of adjustment by a moving mean is determined by the phenotypic correlation between neighbours.

### 8.5.4.2 Single-row plots

Suppose in a selection nursery that the progenies are sown in rows. In each row a single progeny is sown. The yield of a row is adjusted for soil heterogeneity by the yield of its two nearest neighbour rows. The phenotypic variance of the adjusted yields is given by Eqn 8.12 to be

$$\text{var } \underline{p}^{a}_{mix} = \frac{3}{2} \text{ var } \underline{p}_{mix} - 2 \text{ cov}(\underline{p}_{i,mix}, \underline{p}_{i+1,mix}) + \tfrac{1}{2} \text{ cov}(\underline{p}_{i-1,mix}, \underline{p}_{i+1,mix}) \qquad (8.16)$$

Applying an approach similar to that used in Section 4.3.1.4, gives the genetic variance

$$\text{var } \underline{g}^{a}_{mix} = \text{var } \underline{g}_{mix} - \text{cov}(\underline{g}_{i,mix}, \underline{g}_{i+1,mix}) + \text{cov}(\underline{g}_{i-1,mix}, \underline{g}_{i+1,mix}) \qquad (8.17)$$

and the environmental variance

$$\text{var } \underline{e}^{a}_{mix} = \tfrac{1}{2} \text{ var } \underline{g}_{mix} - \text{cov}(\underline{g}_{i,mix}, \underline{g}_{i+1,mix}) - \tfrac{1}{2} \text{ cov}(\underline{g}_{i-1,mix}, \underline{g}_{i+1,mix}) +$$

$$+ \frac{3}{2} \text{ var } \underline{e}_{mix} - 2 \text{ cov}(\underline{e}_i, \underline{e}_{i+1}) + \tfrac{1}{2} \text{ cov}(\underline{e}_{i-1}, \underline{e}_{i+1}) \qquad (8.18)$$

Evidently, Eqn 8.16 is the sum of Eqns 8.17 and 8.18.

The previous equations can be worked out by substitution of the expressions for the quantities given on the right side.

The genetic and environmental variance in mixture were given by Eqns 4.29 and 4.30, respectively. The genetic covariance between adjacent neighbours in mixture was expressed by Eqn 8.8. It was explained there that, although the genotypes are allotted to each other at random, their yields in mixture are genetically correlated. From Eqn 4.13, it can be derived that the covariance between neighbours of second order is

$$\mathrm{cov}(g_{i-1,mix}, g_{i+1,mix}) = \frac{1}{16}\mu^2 \,\mathrm{var}\, \underline{b} \qquad (8.19)$$

The rows at place i-1 and i+1 are positively correlated because they have row i as a common neighbour.

Eqn 8.17 shows that the adjustment affects the genetic variance. Substitution of Eqns 8.8 and 8.19 into Eqn 8.17 and adopting the dimensionless parameters $r_{bg}$ and $\gamma$ (Section 4.4.4), shows that var $g^a_{mix}$ > var $g_{mix}$ when $r_{bg} > -\frac{5}{8}\sqrt{\gamma}$. Therefore, the adjustment mostly increases the genetic variance in mixture. This may be explained as follows. In the allowance for soil heterogeneity, it is assumed that the yield level of a place in the field where a row stands, is measured by the yield of the neighbour rows. When a row is sown with a strong competitor, the yield of its neighbours is depressed due to intergenotypic competition. That is the yield level of the habitat of the row is underestimated. Consequently, the adjustment of a strong competitor is biased upwards. Vice versa, the adjustment of a weak competitor is biased downwards. This results in an increased genetic variance after adjustment. Theoretically, a decrease in genetic variance may occur when the strong competitors are, in monoculture, low-yielding types (negative $r_{bg}$) and, when at the same time, the competition effects are small (low $\gamma$).

In contrast to line selection, for plant selection no change in the genetic variance after adjustment was expected (Eqn 8.14) because the interplant-competition model is based on diffuse competition, i.e. the yield of a plant is determined by its competitive ability relative to that of all other genotypes in the mixture rather than just to that of its adjacent neighbours. Actually, this prerequisite is only approximate so that the expressions for plant-selection are expected to be shifted slightly to the corresponding equations for line selection.

Because the adjustment affects the rank of the genotypes in mixture, it influences the genetic covariance between yield in mixture and yield in monoculture also. The genetic covariance is

$$\mathrm{cov}(g^a_{mix}, g_{mono}) = \mathrm{cov}((g_{i,mix} - \tfrac{1}{2} g_{i-1,mix} - \tfrac{1}{2} g_{i+1,mix}), g_{mono})$$

After substitution of Eqn 4.13, the genetic covariance can be extended to

$$\mathrm{cov}(g^a_{mix}, g_{mono}) = \mathrm{cov}(g_{mix}, g_{mono}) + \tfrac{1}{4}\mu\, \mathrm{cov}(\underline{b}, g_{mono}) \qquad (8.20)$$

Thus when the strong competitors tend to be the genotypes with the highest monoculture

yield ($cov(\underline{b},\underline{g}_{mono}) > 0$), the adjustment increases the genetic covariance between yield in mixture and yield in monoculture.

The progress made by selection in mixture was expressed by the correlated response for monoculture yield brought about by selection for yield in a mixture (Section 4.4.2). Substitution of Eqn 4.43 into Eqn 8.20 and of Eqns 8.17 and 8.18 into Eqn 8.16 and, thereafter, substitution of Eqns 8.20 and 8.16 into Eqn 4.36 gives an expression for the expected progress that can be made by selection after adjustment.

The equations serve only to illustrate the effect of intergenotypic interrow competition on the allowance made for soil heterogeneity. They are restricted to the example where the yield of a row is adjusted by the yield of its two adjacent neighbours. When more neighbours are involved in the moving mean, the effects of competition are reduced. When an analysis of covariance is used in the adjustment, this analysis is biased by interrow competition because its assumption is violated that the variable and the covariable are independent.

*Summary* Intergenotypic competition between the rows affects the outcome of adjustments for soil heterogeneity. Due to intergenotypic competition, the adjustments influence the rank of the genotypes in the mixture. Strong competitors are favoured whereas weak competitors are adversely affected so that the genetic variance is generally increased after adjustment. Also the environmental variance after adjustment is biased upwards. When the strong competitiors tend to be the genotypes with the highest monoculture yield, the adjustments increase the genetic covariance between yield in mixture and yield in monoculture. Consequently, the correlated response for monoculture yield, brought about by selection for yield in mixture, is affected by adjusting the yields in mixture for soil heterogeneity.

### *8.5.5 Experimental evaluation in plant selection*

In this section, some methods to account for soil heterogeneity in plant selection are evaluated experimentally. Selection was done for ear weight per plant in Exp. 77-1. Adjustment for soil heterogeneity was made within grids whereby a grid consisted of a plot (Figs 2 and 3). In any selection method, 10% of the plants was selected from the population.

Within an experiment, the genotypic composition of the selected group was hardly affected by the adjustments (Table 37). Consequently, the realized response for mixture yield as well as the realized correlated response for monoculture yield, brought about by selection in mixture, were hardly affected by the adjustments (Table 35). Therefore, in my experiments, these methods were of no use in coping with soil heterogeneity. The lack of success was caused by the low correlation between neighbour plants (Table 36). The low correlation indicates that the environmental variance among plants was hardly explained by a coarse-grained pattern of soil heterogeneity.

The adjustments for soil heterogeneity were compared with grid selection because these methods are of practical value only when their additional costs are cancelled out by their additional gain over grid selection (Section 8.5.6). Selection of the 10%

Table 37. Effect of adjustment for soil heterogeneity on the percentage of each variety in the selected group. Selection was for ear weight per plant at a selection percentage of 10% within plots. The number of selected plants was 50, 25, 50 and 64 plants in Exps 77-1b, 1c, 1d and 1e, respectively. The numbering of the adjustments refers to the numbering used in Section 8.5.1.

| Variety | Multicomponent mixture | | Alternated standard | | Honeycomb design narrow | | | | Honeycomb design wide | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | unadj. | adj.2 | unadj. | adj.3 | unadj. | adj.4a | adj.4b | adj.4c | unadj. | adj.4a | adj.4c |
| Varunda | 4 | 6 | 6 | 4 | 10 | 6 | 8 | 2 | 2 | 2 | 2 |
| Tamara | 28 | 23 | 20 | 18 | 16 | 18 | 12 | 20 | 17 | 19 | 16 |
| Belfor | 4 | 8 | 12 | 13 | 18 | 16 | 16 | 12 | 22 | 22 | 25 |
| Aramir | 4 | 4 | 0 | 5 | 2 | 2 | 2 | 4 | 9 | 9 | 11 |
| Camilla | 5 | 6 | 4 | 16 | 12 | 14 | 12 | 12 | 19 | 12 | 9 |
| Golden Promise | 2 | 0 | 4 | 12 | 0 | 0 | 0 | 0 | 2 | 2 | 5 |
| Balder | 7 | 6 | 0 | 8 | 8 | 4 | 10 | 4 | 3 | 5 | 6 |
| WZ 704068-14 | 4 | 3 | 2 | 0 | 2 | 2 | 2 | 0 | 17 | 16 | 19 |
| Goudgerst | 30 | 34 | 28 | 14 | 22 | 24 | 28 | 32 | 0 | 1 | 0 |
| L 98 | 2 | 2 | 12 | 8 | 2 | 2 | 2 | 6 | 2 | 2 | 2 |
| Titan | 0 | 0 | 4 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 |
| Bigo | 10 | 8 | 8 | 2 | 8 | 10 | 8 | 8 | 8 | 9 | 6 |

highest yielding plants from the entire field, i.e. selection without grids, gave a realized response $R_{mix}$ of 1.70 g plant$^{-1}$ and a correlated response for grain yield in monoculture in drilled rows of 5.1 g row$^{-1}$. Hence grid selection and the other methods for coping with soil heterogeneity gave only a slight advantage over conventional selection or were even inferior (Table 35) because there was hardly any fertility gradient in the field.

The environmental and genetic variance were consistently and substantially increased by the adjustments. An increase of the environmental variance can be understood from Eqn 8.15. On the other hand, according to the model, it was expected that the genetic variance would not be influenced by the adjustments (Eqn 8.14). The observed increase of the genetic variance was partly accounted for by the randomized block design used. Due to this design, a plant of a genotype never had a plant of the same genotype as neighbour within a replicate so that the genetic correlation between neighbour plants was negative. This results in an increased genetic variance after adjustment (Eqn 8.17). The increase of the genetic variance in the honeycomb designs is smaller than that in the multicomponent mixture (Table 35) because of the position of the replicates (Fig. 3d) and the applied adjustment.

It can be calculated that the use of a randomized block design only partly accounted for the increase of the genetic variance. Furthermore, in the experiment where the plants were alternated with plants of a standard variety, the block design would not bias the adjustment. Nevertheless, also in the latter experiment an increase in genetic variance was observed. An increase is expected when competition is preferentially between adjacent neighbours (Eqn 8.17), as was apparently the case in my experiments. This conclusion was supported by the finding with the honeycomb design at a wide spacing where there was no interplant competition, that the increase of the genetic variance was relatively much smaller than that in the correponding design at a narrow stand. This increase of the genetic variance at the wide stand may be accounted for by the randomized block design used.

The equations given for adjustment of single-plant yields and those for adjustment of single-row yields (Section 8.5.4) represent both limits of the real situation (Section 4.2.3). It was concluded that, in my experiments, the yields of rows satisfied one limit, whereas the yields of plants approached the other limit (Section 4.2.2).

We can compute under which conditions the method, proposed by Fasoulas & Tsaftaris (1975), gives a reduction of the environmental variance. From Eqn 8.3, it can be seen that the phenotypic variance after adjustment is

$$\text{var } \underline{p}^a = \text{var}(\underline{p}_{j,i} - \tfrac{1}{6}(\underline{p}_{j-1,i-\frac{1}{2}} + \underline{p}_{j-1,i+\frac{1}{2}} + \underline{p}_{j,i-1} + \underline{p}_{j,i+1} + \underline{p}_{j+1,i-\frac{1}{2}} + \underline{p}_{j+1,i+\frac{1}{2}}))$$

The central plant is equidistant from each of its six neighbours, and the distances between the plants in a hexagon differ relatively little (Fig. 3). Therefore, as a simplification the covariances are supposed to be equal to each other, say $\text{cov}(\underline{p}_i, \underline{p}_{i+1})$. According to Section 8.5.4.1, the phenotypic covariance equals the environmental covariance $\text{cov}(\underline{e}_i, \underline{e}_{i+1})$. Now the phenotypic variance can be expanded to

$$\text{var } \underline{p}^{a}_{mix} = \frac{7}{6} \text{ var } \underline{p}_{mix} - \frac{7}{6} \text{ cov}(\underline{e}_i, \underline{e}_{i+1})$$

$$= \frac{7}{6} \text{ var } \underline{g}_{mix} + \frac{7}{6} \text{ var } \underline{e}_{mix} - \frac{7}{6} \text{ cov}(\underline{e}_i, \underline{e}_{i+1}) \qquad (8.21)$$

The genetic variance is not influenced by the adjustment (Eqn 8.14), so that

$$\text{var } \underline{g}^{a}_{mix} = \text{var } \underline{g}_{mix} \qquad (8.22)$$

and

$$\text{var } \underline{e}^{a}_{mix} = \frac{7}{6} \text{ var } \underline{e}_{mix} + \frac{1}{6} \text{ var } \underline{g}_{mix} - \frac{7}{6} \text{ cov}(\underline{e}_i, \underline{e}_{i+1}) \qquad (8.23)$$

The environmental variance is reduced by the adjustment for soil heterogeneity when var $\underline{e}^{a}_{mix}$ < var $\underline{e}_{mix}$. From Eqn 8.23, we see that then the coefficient of the phenotypic correlation between neighbour plants

$$r_p = \frac{\text{cov}(\underline{p}_i, \underline{p}_{i+1})}{\text{var } \underline{p}} > \frac{1}{7}$$

Slight deviations of the threshold value from 1/7 occur when interplant competition is not exactly diffuse and when the covariances for the plants within a hexagon are not all equal. Expressing the yield of the central plant as a percentage of the mean yield of its neighbours, instead of subtracting the mean yield of the neighbours from the yield of the central plant, does not change this result.

In Exp. 77-1e, the phenotypic correlation was smaller than 1/7 (Table 36) so that the environmental variance increased after the adjustment (Table 35) and the adjustment had even a detrimental effect. Given the low heritability for single-plant yields and, consequently, the low phenotypic correlation between adjacent plants, the adjustment proposed by Fasoulas & Tsaftaris (1975) is not only a waste of time but will often lead to a decline in the response to selection.

Rather than to adjust the yield of a central plant by taking the difference between the yield of that plant and the yield of its six neighbours, and risk overadjusting, the yield of the six neighbours may be used as a covariable in an analysis of covariance. Analysis of covariance was recommended by Yates (1936) and Baker & McKenzie (1967) for adjusting the yield of field plots by the yield of systematically inserted control plots.

### *8.5.6 Usefulness of adjusting for soil heterogeneity in plant selection*

The methods which allow for soil heterogeneity in single-plant selection were reviewed in Section 8.5.1. The methods 2, 4a and 4c, where the yield of every plant has to be measured, are likely not useful because many plants can be discarded visually. Determining the yield of the inferior plants is a waste of time.

In the methods 3 and 4b, where adjustment is by plants of a standard variety, only the yield of the visually selected plants and their surrounding standard plants has to

be measured. As mostly two standard plants are used in the adjustment of the yield of a plant, the number of yield determinations is about three times as large as when no adjustment is applied. Hence, adjustment by standards brings about much additional work and also an increased field area. A larger field almost always means a larger environmental variance. In conclusion, adjustment by inserted standard plants is not useful.

Furthermore, the above-mentioned methods are only efficient when the correlation between neighbour plants is high. However, a high correlation is doubtful.

Partitioning the selection field into grids and selecting the best plants within grids was concluded to be effective, cheap and simple (Section 8.5.2). The other methods for coping with soil heterogeneity are of practical value only when their additional costs are cancelled out by their additional gain over grid selection. It is unlikely that this is so because the correlation between neighbour plants is very small within grids, i.e. within relatively small areas of the field.

In conclusion, in selection of single plants for yield, grid selection should be applied.

# 9 Progeny testing

In breeding practice, the progenies of selected plants are screened visually. Yield testing is done in field plots in later generations with a small number of promising lines (Sections 1.1 and 1.2). If yield testing were done in microplots, a considerably larger number of lines could be screened for yield. Moreover, also the progenies of single plants may then be selected for yield.

However, yield testing in microplots is biased by intergenotypic competition between the plots. In the literature, the effect of competition on the outcome of selection is not well understood and hardly quantified. Therefore, a model was developed to quantify the effect of intergenotypic competition on yield testing in single rows (Sections 4.3 and 4.4). In the present chapter, the model will be illustrated and tested with data of experiments with varieties grown in rows, each variety in a single row.

The effects of intergenotypic competition are reduced by using more rows per plot. A larger plot size increases the sample size and, therefore, reduces the environmental variance. The amount of work to test a fixed number of lines, however, mostly increases as more rows per plot are used. It may also be questioned whether the efficiency of selection is higher for n replicates of single-row plots than for unreplicated n-row plots. The effects of plot size and replication on intergenotypic competition between the plots and on the environmental variance will be described with a model.

Testing in microplots introduces a large experimental error. The possibilities for reducing this error will be discussed. Several methods which reduce the experimental error also affect the bias due to intergenotypic competition and, on the other hand, some methods, of which it is claimed that they reduce the competitional bias, influence the experimental error. These effects will be quantified in terms of the competition model. In the experiments, varieties were sown in rows according to different arrangements of the rows so that the methods of which it is claimed that they reduce the experimental error or the bias due to intergenotypic competition could be evaluated experimentally. Moreover, the experimental results are used to illustrate the models.

## 9.1 COMPETITIONAL BIAS IN YIELD TESTING IN 1-ROW PLOTS, AN APPLICATION OF THE MODEL

In this section, the effect of intergenotypic competition on selection among 1-row plots is discussed. This is done by applying the model of Sections 4.3 and 4.4 to the results of Exps 76-3 and 77-2 where varieties were grown in 1-row plots. The 1-row plots simulate a line-selection field, i.e. a mixture with rows as experimental unit. The aim of selection is to save the genotypes that yield most in monoculture. Therefore, monoculture plots of the varieties are used as reference.

*9.1.1 Experiment 77-2*

*Experimental design* Twelve varieties were sown in rows in mixtures and monocultures (Section 2.1.5). In each row only one variety was sown. The monoculture yield of the varieties was estimated by the yield of the four central rows of 6-row plots (Exp. 77-2a) and by the yield of the central row of 3-row plots (Exp. 77-2c). The crowding coefficient of the varieties was estimated from binary mixtures with a standard variety (Exp. 77-2a, Section 6.2.2), from border effects in 3-row plots (Exp. 77-2c, Section 6.2.4), and from an arrangement where the rows were alternated with rows of a standard variety (Exp. 77-2d, Section 6.2.5).

From the estimates of the monoculture yields and of the crowding coefficients, the components of the variance and the response to selection in 1-row plots (Exp. 77-2b) were predicted by means of the model. Hence, in the prediction no information is used that came from Exp. 77-2b itself.

Each arrangement was grown as a strip of rows (Fig. 4). Within an arrangement, the varieties were sown according to a randomized block design. The arrangements were laid out together in a four-times replicated randomized block design (Fig. 4). The effect of the strips is random and the effect of the replicates within a strip is approximately random. The variety effect is treated as random since the varieties were used to simulate the random lines of a line-selection field.

The yield of a plot is described by

$$Y_{ijk} = \mu + g_k + s_i + gs_{ik} + r_{j(i)} + e_{ijk}$$

with the genotypes $k = 1, \ldots K$, the strips $i = 1, \ldots I$, and per strip the replicates $j = 1, \ldots J$. The variances of the stochastic effects are $\sigma^2_g$, $\sigma^2_s$, $\sigma^2_{gs}$, $\sigma^2_r$ and $\sigma^2_e$, respectively. The analysis of variance is similar to that given in Table 20 for single plants. The variances were estimated from this analysis.

*Response to selection* The implications of intergenotypic competition for line selection are illustrated by the results of actual selection in the 1-row plots. It is shown which errors arise in the traditional approach where intergenotypic competition is neglected. For a more extensive discussion of the problem see Section 8.2.2 where a similar approach was applied for plant selection.

The response to selection is predicted from the heritability and the phenotypic variance by

$$R = i\, h^2 \sqrt{\text{var } p} \qquad (4.33)$$

where i is the selection intensity (Section 4.4.2). In this equation, it is assumed that the regression of genotype on phenotype is linear. However, in the variety mixture of Exp. 77-2b, the regression deviated seriously from linearity because of the skewness of the frequency distribution of the genotypes. This was met by removing the data of the low-yielding varieties 'Titan' and 'L 98 whereafter the equation of the response could

be applied (Section 9.1.3).

Actual selection for grain yield per row gave the picture as presented in Fig. 44 From the frequency of the varieties in the selected group (Fig. 44) and their mean yield in the mixture (Table 38), the realized response to selection was calculated. The realized and the predicted response agreed well (Table 39) so that the traditional approach seemed suitable.

The response measures the progress made for yield in the environment where selection was applied, that is in that particular mixture. However, the varietites are bred to perform in monoculture. Comparison of the composition of the selected group (Fig. 44) and the yields of the varieties in monoculture (Table 38) shows that the variety 'Camilla', which had the highest yield in monoculture, was not selected from the mixture. On the other hand, one of the lowest-yielding varieties in monoculture, 'Goudgerst', was frequently found in the selected group.

What progress was made for monoculture yield? In other words, what is the correlated response for yield in monoculture, brought about by selection for yield in mixture? From the frequency of the varieties in the selected group (Fig. 44) and their average yield in monoculture (Table 38), the realized correlated response for monoculture yield was obtained. That correlated response was less than one-half of the direct response for mixture yield (Table 39).

As the traditional approach to predict the response to selection does not account for intergenotypic competition, it predicts the direct response for yield in a mixture of the same composition as the mixture in which selection was applied. However, the breeder is concerned with the progress for yield in monoculture. This progress, measured by the correlated response for monoculture yield, is substantially lower. In the present

Table 38. Grain yield in g $row^{-1}$ in monoculture, M (Exp. 77-2a,c) and in a mixture of 1-row plots, O (Exp. 77-2b).

| Variety | | M | O |
|---|---|---|---|
| 1 | Varunda | 150 a* | 143 cd |
| 2 | Tamara | 165 a | 175 a |
| 3 | Belfor | 161 a | 146 cd |
| 4 | Aramir | 154 a | 165 ab |
| 5 | Camilla | 165 a | 143 cd |
| 6 | Golden Promise | 132 b | 120 e |
| 7 | Balder | 156 a | 159 abc |
| 8 | WZ 704068-14 | 151 a | 133 de |
| 9 | Goudgerst | 131 b | 153 bc |
| 10 | L 98 | 106 c | 86 f |
| 11 | Titan | 109 c | 65 g |
| 12 | Bigo | 156 a | 163 ab |

* Values followed by the same letter are not significantly different in the Student-Newman-Keuls test at $P \leq 0.05$.

Table 39. The result of selection for yield of 1-row plots, expressed in terms of the response for mixture yield and the correlated response for monoculture yield. The proportion selected is either 0.05 or 0.10. In the predicted response, account has been taken of the skew distribution of the yields. The grain yield is expressed in g row$^{-1}$. Exp. 77-2.

| Character | Notation | 0.05 | 0.10 |
|---|---|---|---|
| Population mean in mixture | $\bar{P}_{unsel} = \bar{O}_{unsel}$ | 137.5 | 137.5 |
| Mean yield of selected rows | $\bar{P}_{sel}$ | 215.9 | 207.2 |
| Mean expected yield in mixture of the selected genotypes | $\bar{O}_{sel}$ | 161.1 | 160.7 |
| Realized response for yield in mixture | $R_{mix} = \bar{O}_{sel} - \bar{O}_{unsel}$ | 23.6 | 23.2 |
| Predicted response for yield in mixture | $\hat{R}_{mix} = i\, h^2_{mix} \sqrt{var\, p_{mix}}$ | 26.2 | 24.0 |
| Population mean of the monocultures | $\bar{M}_{unsel}$ | 144.7 | 144.7 |
| Mean expected monoculture yield of the selected genotypes | $\bar{M}_{sel}$ | 155.9 | 156.1 |
| Realized correlated response for monoculture yield | $CR_{mono} = \bar{M}_{sel} - \bar{M}_{unsel}$ | 11.2 | 11.4 |

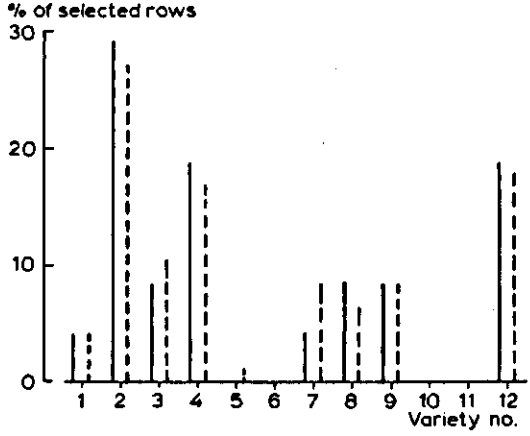


Fig. 44. Variety composition in the group of rows with the largest grain yield in the population of 1-row plots. The variety numbers correspond with those in Table 38 . The percentages selected were 5% (solid lines) and 10% (broken lines). Exp. 77-2b.

experiment, the direct response for mixture yield was 17%, while the correlated response for monoculture yield was only 8% (Table 38).

*Summary* The traditional approach to predict the response to selection overestimates considerably the possibilities of selection and is therefore of no value when intergenotypic competition operates between the rows.

*Application of the model* As the traditional procedure is of no use when intergenotypic

competition is operative, a procedure that accounts for intergenotypic competition was developed (Sections 4.3 and 4.4). In the present section, the model is illustrated by experimental data.

The parameters needed as input in the model, were estimated from several arrangements in which the varieties were grown. The population mean in monoculture and the genetic variance in monoculture were estimated from the four central rows of 6-row plots (Exp. 77-2a) and from the central row of 3-row plots (Exp. 77-2c). The environmental variance in monoculture was obtained from the variance among the central rows of the 3-row plots containing the same variety and from the variance among the central parts of the 6-row plots containing the same variety. The crowding coefficients were estimated from binary mixtures with a standard variety (Exp. 77-2a), from border effects in 3-row plots (Exp. 77-2c), and from single rows that were alternated with rows of a standard variety (Exp. 77-2d). From these data the variance among the crowding coefficients and the covariance between the crowding coefficient and the monoculture yield were also estimated.

By substituting the estimates in the appropriate equations of the competition model, the components of the variance among rows and the response to selection were predicted for an arrangement where the varieties are grown in 1-row plots. As the arrangement of 1-row plots was actually grown (Exp. 77-2b), the predicted values could be compared with the realized values.

The monoculture and the mixture differed greatly with respect to the variances and the derived quantities (Table 40). The values expected from the model and those observed agreed very well, especially as none of the information used came from Exp. 77-2b itself. Furthermore, it should be kept in mind that estimates of variances, and even more so their derived quantities, show a large random variation.

We see that the genetic variance in mixture was 2.5 times as large as the genetic variance in monoculture. Hence, in this population, intergenotypic competition magnified the differences between the genotypes (Fig. 45).

The environmental variance was increased by mixed growing as was reflected by a higher coefficient of variation. This increase is because in monoculture all rows have an identical genetic environment, whereas in mixture the genetic make-up of the neighbourhood differs from row to row. Since adjacent rows compete with each other, the

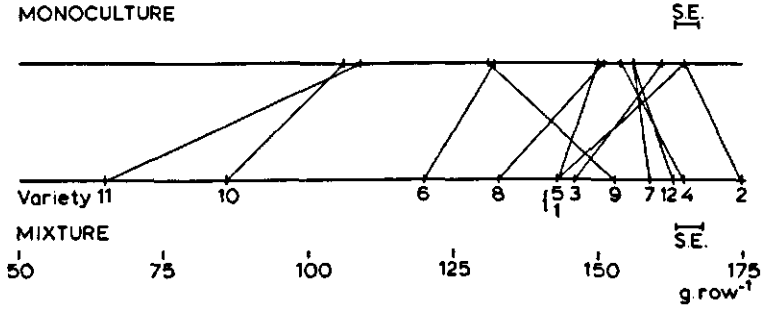


Fig. 45. Grain yield in monoculture and mixture. The variety numbers correspond with those in Table 38. Exp. 77-2.

Table 40. Mean, variances and derived quantities in monoculture and mixture. The expectations for the mixture are computed, with the model, from the input parameters $\mu_{mono}$ = 144.7 g row$^{-1}$, var $g_{mono}$ = 403 g$^2$ row$^{-2}$, var $e_{mono}$ = 835 g$^2$ row$^{-2}$, var $b$ = 0.0594, and cov($b$,$g_{mono}$) = 2.646 g row$^{-1}$ (Exp. 77-2a,c,d). The observed values in mixture are those in 1-row plots (Exp. 77-2b). The responses in the column of the observed values in mixture are the responses predicted from the variances observed in the mixture. The character under selection is grain yield in g row$^{-1}$.

| | Monoculture | Mixture | |
|---|---|---|---|
| | | expected | observed |
| $\mu$ | 145 | 144 | 138 |
| var $g$ | 403 | 1097 | 1044 |
| var $e$ | 835 | 991 | 905 |
| var $p$ | 1238 | 2088 | 1949 |
| $h^2$ | 0.33 | 0.53 | 0.54 |
| CV | 0.200 | 0.218 | 0.219 |
| $h_{mix}/h_{mono}$ | | 1.27 | 1.28 |
| $r_{g_{mono},mix}$ | | 0.89 | 0.86 |
| R/i | 11.5 | 24.0 | 23.6 |
| $CR_{mono}/i_{mix}$ | | 13.0 | 12.7 |
| $CR_{mono}/R_{mix}$ | | 0.54 | 0.54 |
| $CR_{mono}/R_{mono}$ | | 1.14 | 1.11 |

variation in genetic environment enhances the environmental variance in mixture (Eqn 4.30). The probability of demonstrating a statistically significant increase of the environmental variance is not large, even in extensive trials, since the expected increase is relatively small.

As the genetic variance was enhanced relatively more than the environmental variance, the heritability in mixture exceeded the heritability in monoculture. Since both the genetic variance and the heritability were larger in mixture than in monoculture, the expected direct response to selection for yield in the mixture was much (2 x) higher than that if selection were without intergenotypic competition, i.e. in a 'monoculture' (Eqn 4.33).

However, a breeder aims at selecting those genotypes that yield highest in monoculture. The correlated response for monoculture yield, brought about by selection for yield in mixture, is, by definition, smaller than the direct response for mixture yield. In this experiment, the correlated response for monoculture yield was about half of the direct response for mixture yield. Nevertheless, this correlated response was expected

Table 41. Selection responses estimated by the model and responses obtained by actual selection among single-row plots ($R_{mix}$ and $CR_{mono}$) and among the centre row of 3-row plots ($R_{mono}$). Selection was for grain yield, in g row$^{-1}$, at a selection percentage of 10%. Exp. 77-2.

| | Estimated | Observed |
|---|---|---|
| $R_{mix}$ | 22.4 | 23.2 |
| $CR_{mono}$ | 12.0 | 11.4 |
| $R_{mono}$ | 14.3 | 13.5 |
| $CR_{mono}/R_{mix}$ | 0.53 | 0.49 |
| $CR_{mono}/R_{mono}$ | 0.84 | 0.84 |

to be higher than the direct response for monoculture yield in a population without intergenotypic competition. Hence, in this experiment, intergenotypic competition would have had a positive effect on the progress made by selection. The differences between the genotypes were increased so much due to competition that this increase more than outweighed the bias due to the differential reaction of the genotypes to mixed growing.

The estimated response may be compared with the realized response. However, the yields showed a skew frequency distribution due to the presence of two extremely low-yielding varieties. Omitting the data of these varieties resulted in an approximately normal frequency distribution for the yields of the remaining 10 varieties. In the population of the 10 varieties is $\mu_{mono}$ = 152 g row$^{-1}$, var $g_{mono}$ = 128 g$^2$ row$^{-2}$, var $e_{mono}$ = 835 g$^2$ row$^{-2}$, var $b$ = 0.0246 and cov($b$,$g_{mono}$) = -0.481 g row$^{-1}$. From these quantities the selection responses were predicted by means of the model. The results were transposed to the mixture of 12 varieties according to the procedure described in Section 9.1.3. The estimated responses are given in Table 41.

The observed direct response for mixture yield and the observed correlated response for monoculture yield, brought about by selection for yield in mixture, were obtained by actual selection among the single-row plots. The observed direct response for monoculture yield was found by selection among the central rows of 3-row plots. In fact, this response was not exactly a direct response because the monoculture yield was measured by both the yield of the central row of the 3-row plots and the yield of the four central rows of the 6-row plots.

The responses estimated by the model agreed well with the responses obtained by actual selection (Table 41). The progress for monoculture yield attained by selection with intergenotypic competition was 84% of the progress made by selection without intergenotypic competition.

### *9.1.2 Experiment 76-3*

The competition model was applied also to Exp. 76-3. This experiment was smaller than Exp. 77-2 but otherwise similar.

The monoculture yields of the six varieties were estimated from the six central

rows of the 8-row plots (Exp. 76-3f) and the central row of the 3-row plots (Exp. 76-3b). The environmental variance in monoculture was derived from the variance of the yields of the central rows of the 3-row plots containing the same variety. These rows were always the second or fifth row of a 6-row sowing pass. In the uniformity strips (Exp. 76-3e), the variance among all rows of the sowing passes was 1.3 times the variance among the second and fifth rows (Section 9.4.3). Therefore, the environmental variance in monoculture was estimated to be 1.3 times the environmental variance of the central rows of the 3-row plots. The crowding coefficients were estimated from the border effects in 3-row plots (Exp. 76-3b) and from the arrangement where the rows were alternated with rows of a standard variety (Exp. 76-3c).

By feeding the information about the monoculture yields and the crowding coefficients into the model, estimates were obtained of the variances and of some derived quantities in single-row plots. As this arrangement was actually grown (Exp. 76-3a), we may compare the expected values with the observed values. Note that for the expected values no information was used that came from Exp. 76-3a itself.

The values expected according to the model agreed well with the observed values

Table 42. Mean, variances and derived quantities in monoculture and mixture. The expectations for the mixture are computed with the model from the input parameters $\mu_{mono}$ = 160.5 g row$^{-1}$, var $\underline{g}_{mono}$ = 2186 g$^2$ row$^{-2}$, var $\underline{e}_{mono}$ = 674 g$^2$ row$^{-2}$, var $\underline{b}$ = 0.0129, and cov($\underline{b}$,$\underline{g}_{mono}$) = 3.44 g row$^{-1}$ (Exp. 76-3b,c,f). The observed values in mixture are those in 1-row plots (Exp. 76-3a). The responses in the column of the observed values in mixture are the responses predicted with the variances observed in the mixture. The character under selection is grain yield in g row$^{-1}$.

| | Monoculture | Mixture | |
|---|---|---|---|
| | | expected | observed |
| $\mu$ | 161 | 162 | 169 |
| var $\underline{g}$ | 2186 | 2820 | 3168 |
| var $\underline{e}$ | 674 | 715 | 716 |
| var $\underline{p}$ | 2860 | 3536 | 3784 |
| $h^2$ | 0.76 | 0.80 | 0.84 |
| CV | 0.162 | 0.165 | 0.158 |
| $h_{mix}/h_{mono}$ | | 1.02 | 1.02 |
| $r_{g_{mono},mix}$ | | 0.99 | 0.98 |
| R/i | 40.9 | 47.4 | 51.5 |
| $CR_{mono}/i_{mix}$ | | 41.4 | 41.9 |
| $CR_{mono}/R_{mix}$ | | 0.87 | 0.81 |
| $CR_{mono}/R_{mono}$ | | 1.01 | 1.02 |

(Table 42). However, the genetic variance in mixture was underestimated by the model because the varieties were laid out in a randomized block design. Within a replicate of a block design, a row has never a row of the same variety as its neighbour so that the genetic correlation is negative. Therefore the effects of intergenotypic competition and, consequently, the genetic variance in mixture increases. The model takes no account of this type of genetic correlation because this does not occur in selection nurseries. This complication of using a randomized block design hardly affected the genetic variance in Exp. 77-2 because there (i) twice as many varieties were involved and (ii) the varieties sown in the last row of a replicate and the first row of the next replicate were preferentially chosen to be the same.

In Exp. 76-3, the genetic variance increased due to intergenotypic competition. As was expected, the environmental variance also increased. Because the relative increase of the genetic variance was larger than that of the environmental variance, the heritability was increased by mixed growing.

As in the mixture both the genetic variance and the heritability were larger than in monoculture, the direct response for yield in mixture was expected to exceed the direct response without intergenotypic competition. The correlated response for monoculture yield, brought about by selection for yield in mixture, was lower than the direct response for mixture yield. Nevertheless, intergenotypic competition was expected not to have reduced the progress for monoculture yield as the ratio $CR_{mono}/R_{mono}$ was about unity. This was accounted for by the higher heritability in mixture than in monoculture ($h_{mix}/h_{mono} > 1$) and the high correlation between the yield of a genotype in mixture and that genotype in monoculture ($r_g$ was high). The high genetic correlation resulted from the high correlation between competitive ability and monoculture yield ($r_{bg} = 0.65$) and from the relatively small differences in competitive ability between the varieties. The latter followed from the variance of the crowding coefficients which was only 1/5 of that in Exp. 77-2.

The selection responses that were predicted from the variety composition of the group of actually selected rows deviated from the responses presented in Table 42 because of the skewness of the frequency distribution of the genotypic yields (Section 9.1.3). However, this deviation is not detrimental to the illustrative character of this table.

### *9.1.3 Influence of skewness on the predicted response to selection*

The response to selection is predicted by Eqn 4.32. This equation is based on linearity of the regression of the genotypic on the phenotypic yields (Section 4.4.2). This regression is linear when the genotypic as well as the environmental effects follow a normal frequency distribution and when the environmental variance within genotypes is constant for each genotype (homogeneity of environmental variance). Then, the phenotypic yields also show a normal distribution. For non-normal frequency distributions, the regression generally deviates from linearity. In the experiments, some varieties gave extremely low yields which gave rise to skewed frequency distributions. In the following, the consequences of skewness are discussed and a procedure to account for this is described.

Suppose that for each genotype the environmental effects are normally distributed and that there is homogeneity of the environmental variances over genotypes. When the genotypic yields show negative skewness, the curve of the regression of genotype on phenotype (Fig. 10) is convex. Then, the slope of the section where the selection differential S is projected on the genotype axis is lower than the average slope of the curve for the entire population. The regression coefficient for the entire curve equals the heritability of the population (Section 4.4.2). Hence when negative skewness occurs the regression coefficients

$$b_{R.S} < b_{g.p} = h^2$$

Therefore, the estimation of the response to selection by $R = h^2S$ is biased upwards when negative skewness occurs. This appeared in Exp. 77-2b where the direct response, at a selection percentage of 10%, was predicted to be 27%, whereas the realized response was only 17%. This upward bias appeared also in Exp. 76-3a where the predicted direct response was 53% and the realized response only 23%.

When the data of the two extremely low-yielding varieties were removed from the population of 12 varieties in Exp. 77-2b, the frequency distribution of the genotypic yields was approximately normal. As the environmental effects were also approximately normally distributed and as there was homogeneity of the environmental variances over the varieties, the regression of genotype on phenotype was approximately linear so that the equation for the selection response could be applied. The genetic and environmental variance were estimated for the limited population of 10 varieties. Based on these estimates the response to selection in the group of 12 varieties was predicted, which was a response adjusted for skewness. The adjusted response was 17% which was identical to the realized response.

The procedure is explained now in more detail. In the limited population, the mixture of 10 varieties, $h^2_{mix} = 0.20$ and var $p_{mix} = 1137$ g$^2$ row$^{-2}$. From the original population of 12 varieties, 10% of the rows was selected. This corresponded with selection of 12% of the rows from the limited population of 10 varieties. Hence, for the selection intensity i a value was chosen that agreed with a selection percentage of 12%, that is $i = 1.67$. Eqn 4.33 gave then for the predicted response 11.5 g row$^{-1}$. This is the response made with respect to the mean yield of 150.0 g row$^{-1}$ of the population of 10 varieties. In the population of 12 varieties, the mean yield was 137.5 g row$^{-1}$, so that the predicted response, transposed to the original population, became 11.5 + (150.0 - 137.5) = 24.0 g row$^{-1}$.

In this experiment, the exclusion of the data of the two varieties was allowed because no rows of these varieties were present in the group of rows with a high yield and selection occurred only among the rows showing a high yield.

Previous workers have applied Eqn 4.33 to predict the response in generation t + 1 brought about by selection in generation t. In general, the equation has used without regard to the shape of the frequency distributions. However, the previous example demonstrated the necessity to take account of the shape of the distributions prior to the application of the equation. It was shown that the bias in the predicted response can

be serious when the distributions are skewed.

Linearity of the regression is also assumed in the prediction of the correlated response for monoculture yield (Eqn 4.35). In Exps 76-3 and 77-2, the frequency distribution of the genotypic yield in mixture and that of the genotypic yield in monoculture were skewed. Nevertheless, the regression was approximately linear which may be accounted for by the high correlation between both variables and the multiplicativity of the competition model.

Because the crowding coefficient shows a log-normal distribution, the frequency distribution of the genotypic yields in mixture tends to be shifted to positive skewness when compared with the frequency distribution of the genotypic yields in monoculture. Eqn 4.35 for the correlated response may be extended to allow for this effect.

*Summary* In the prediction of the response to selection, it is assumed that the regression of the genotypic yield on the phenotypic yield is linear. However, when the frequency distributions of the genotypic and the phenotypic yield are skewed, the regression deviates, in general, from linearity. The effect of skewness on the prediction of the response to selection was discussed. A method was described which took account of skewness in the present experiments.

## 9.2 COMPETITIVE RELATIONS IN N-ROW PLOTS AND IN ROWS BORDERED WITH ROWS OF A STANDARD

In a line-selection field, the lines are grown in rows, each line in a separate row. The rows may be arranged according to different designs. Up to now, only single-row plots have been discussed. To reduce the effects of intergenotypic competition, many authors have suggested growing the lines in n-row plots or bordering all lines with a common variety. The effect of these arrangements on the bias due to intergenotypic competition will be quantified in a way similar to that introduced in Sections 4.3 and 4.4 for single-row plots.

### *9.2.1 n-row plots*

All n rows of a n-row plot are sown with the same variety. Only the two outside rows are affected by intergenotypic competition because the competitive influence of a row is restricted to its adjacent neighbour rows (Section 4.2.2.2). The n-2 central rows constitute a monoculture.

Suppose the arrangement is

$$h_1\ h_2 \cdots h_{n-1}\ h_n\ i_1\ i_2 \cdots i_{n-1}\ i_n\ j_1\ j_2 \cdots j_{n-1}\ j_n$$

where each letter represents a row and the subscripts denote the position of the row in the field. The letter stands for the genotype sown in the row.

The genotypic yield of the two outside rows of a plot, sown with the random genotype i, is derived from Eqn 4.13 to be

$$\underline{O}_{i,ih} = \frac{3\underline{b}_i + \underline{b}_h}{2\underline{b}_i + 2\underline{b}_h} \quad M_i$$

and

$$\underline{O}_{i,ij} = \frac{3\underline{b}_i + \underline{b}_j}{2\underline{b}_i + 2\underline{b}_j} \quad \underline{M}_i$$

The genotypic yield of the n-2 central rows is

$$\underline{O}_{i,ii} = \underline{M}_i$$

Hence, the genotypic yield per row of a n-row plot is

$$\underline{O}_i = \left(\frac{3\underline{b}_i + \underline{b}_h}{2n\underline{b}_i + 2n\underline{b}_h} + \frac{n-2}{n} + \frac{3\underline{b}_i + \underline{b}_j}{2n\underline{b}_i + 2n\underline{b}_j}\right) \underline{M}_i \qquad (9.1)$$

This is written in genetic terms by representing the part between brackets by $\underline{c}_{i,hj}$ and $\underline{M}_i$ by $\mu + \underline{g}_i$. Thus

$$\underline{O}_i = \underline{c}_{i,hj} \ (\mu + \underline{g}_i) \qquad (4.19)$$

The mean phenotypic yield per row of a n-row plot of a random genotype i, situated between a plot sown with a random genotype h and a plot sown with a random genotype j, is

$$\underline{p}_{i,hj} = \underline{c}_{i,hj} \ (\mu + \underline{g}_i) + \underline{e}_i \qquad (4.21)$$

The phenotypic variance for the mean yield per row among n-row plots is

$$\text{var } \underline{p}_{mix} = \text{var } (\underline{c}\mu + \underline{c}\underline{g}_{mono}) + \text{var } \underline{e}_{mono} \qquad (4.22)$$

Without intergenotypic competition between the plots, the environmental variance for the mean yield per row of n-row plots is

$$\text{var } \underline{e}_{mean} = \text{var } \frac{1}{n} (\underline{p}_1 + \ldots + \underline{p}_n) = \text{var } \frac{1}{n} (\underline{e}_1 + \ldots + \underline{e}_n)$$

A simplified expression is obtained under the assumption that the covariances between two rows of the same plot are all equal, i.e.

$$\text{cov}(\underline{p}_1, \underline{p}_2) = \text{cov}(\underline{p}_1, \underline{p}_3) = \ldots = \text{cov}(\underline{p}_1, \underline{p}_n)$$

Then, without intergenotypic competition, the environmental variance for the mean yield per row of n-row plots is

$$\text{var } \underline{e}_{\text{mean,mono}} = \frac{1}{n} \text{ var } \underline{e}_{\text{mono}} + \frac{n-1}{n} \text{ cov}(\underline{e}_1, \underline{e}_2) \qquad (9.2)$$

where var $\underline{e}_{\text{mono}}$ the environmental variance of single rows in monoculture.

Substitution of Eqns 9.1 and 9.2 into Eqn 4.22 and expanding the resulting expression by the method of statistical differentials (Section 4.3.1.2) gives

$$\text{var } \underline{p}_{\text{mix}} = \text{var } \underline{g}_{\text{mono}} + \frac{\mu}{n} \text{ cov}(\underline{b}, \underline{g}_{\text{mono}}) + \frac{3}{8} \frac{\mu^2}{n^2} \text{ var } \underline{b} + \frac{1}{n} \text{ var } \underline{e}_{\text{mono}} + \\ + \frac{n-1}{n} \text{ cov}(\underline{e}_1, \underline{e}_2) \qquad (9.3)$$

As in Section 4.3.1.4, the phenotypic variance can be partitioned into the variance between genotypes

$$\text{var } \underline{g}_{\text{mix}} = \text{var } \underline{g}_{\text{mono}} + \frac{\mu}{n} \text{ cov}(\underline{b}, \underline{g}_{\text{mono}}) + \frac{1}{4} \frac{\mu^2}{n^2} \text{ var } \underline{b} \qquad (9.4)$$

and the variance for the mean yield per row between plots sown with the same genotype

$$\text{var } \underline{e}_{\text{mix}} = \frac{1}{n} \text{ var } \underline{e}_{\text{mono}} + \frac{n-1}{n} \text{ cov}(\underline{e}_1, \underline{e}_2) + \frac{1}{8} \frac{\mu^2}{n^2} \text{ var } \underline{b} \qquad (9.5)$$

The covariance between the genotypic yield of a genotype in mixture and the genotypic yield of that genotype in monoculture can be derived from Eqn 9.1 in the same way as was done for single-row plots in Eqn 4.43. The genetic covariance is found to be

$$\text{cov}(\underline{g}_{\text{mix}}, \underline{g}_{\text{mono}}) = \text{var } \underline{g}_{\text{mono}} + \frac{1}{2} \frac{\mu}{n} \text{ cov}(\underline{b}, \underline{g}_{\text{mono}}) \qquad (9.6)$$

The expressions for the direct response for mixture yield and the correlated response for monoculture yield, brought about by selection for yield in mixture, are found by substitution of the appropriate equations into Eqns 4.33 and 4.36, respectively.

In the model, the total field area was kept constant for all plot types. However the larger the plot, the smaller the number of lines that can be tested on a given area. To compare the plot types with respect to a constant number of lines, var $\underline{e}_{\text{mono,mean}}$ must be adjusted for the differences in field area between the plot types. This may be done by the coefficient of soil heterogeneity introduced by Smith (1938) (Section 8.1).

Substitution of n=1 reduces the equations to the corresponding equations for 1-row plots which were given in Sections 4.3 and 4.4.

Substitution of n=2 supplies the equations for the mean yield per row of 2-row plots:

$$\text{var } \underline{p}_{\text{mix}} = \text{var } \underline{g}_{\text{mono}} + \frac{1}{2} \mu \text{ cov}(\underline{b}, \underline{g}_{\text{mono}}) + \frac{3}{32} \mu^2 \text{ var } \underline{b} + \frac{1}{2} \text{ var } \underline{e}_{\text{mono}} + \\ + \frac{1}{2} \text{ cov}(\underline{e}_1, \underline{e}_2) \qquad (9.7)$$

$$\text{var } \underline{g}_{mix} = \text{var } \underline{g}_{mono} + \frac{1}{2}\mu \text{ cov}(\underline{b},\underline{g}_{mono}) + \frac{1}{16}\mu^2 \text{ var } \underline{b} \tag{9.8}$$

$$\text{var } \underline{e}_{mix} = \frac{1}{2} \text{var } \underline{e}_{mono} + \frac{1}{2} \text{cov}(\underline{e}_1,\underline{e}_2) + \frac{1}{32}\mu^2 \text{ var } \underline{b} \tag{9.9}$$

$$\text{cov}(\underline{g}_{mix},\underline{g}_{mono}) = \text{var } \underline{g}_{mono} + \frac{1}{4}\mu \text{ cov}(\underline{b},\underline{g}_{mono}) \tag{9.10}$$

The equations for the mean yield per row of 3-row plots are found, after substitution of n=3, to be

$$\text{var } \underline{p}_{mix} = \text{var } \underline{g}_{mono} + \frac{1}{3}\mu \text{ cov}(\underline{b},\underline{g}_{mono}) + \frac{3}{72}\mu^2 \text{ var } \underline{b} + \frac{1}{3} \text{var } \underline{e}_{mono} + \\ + \frac{4}{9} \text{cov}(\underline{e}_1,\underline{e}_2) + \frac{2}{9} \text{cov}(\underline{e}_1,\underline{e}_3) \tag{9.11}$$

$$\text{var } \underline{g}_{mix} = \text{var } \underline{g}_{mono} + \frac{1}{3}\mu \text{ cov}(\underline{b},\underline{g}_{mono}) + \frac{1}{36}\mu^2 \text{ var } \underline{b} \tag{9.12}$$

$$\text{var } \underline{e}_{mix} = \frac{1}{3} \text{var } \underline{e}_{mono} + \frac{4}{9} \text{cov}(\underline{e}_1,\underline{e}_2) + \frac{2}{9} \text{cov}(\underline{e}_1,\underline{e}_3) + \frac{1}{72}\mu^2 \text{ var } \underline{b} \tag{9.13}$$

$$\text{cov}(\underline{g}_{mix},\underline{g}_{mono}) = \text{var } \underline{g}_{mono} + \frac{1}{6}\mu \text{ cov}(\underline{b},\underline{g}_{mono}) \tag{9.14}$$

In Section 9.5, the model is illustrated with experimental data and the use of plots of 1, 2 and 3 rows is discussed.

*Summary* Equations were derived for the phenotypic, genotypic and environmental variance for mean yield per row of n-row plots in relation to intergenotypic competition between the plots. Also an expression for the genetic covariance of the yield of n-row plots in a line-selection field and the yield of n-row plots in monoculture was worked out. Based on these equations, the response to selection can be predicted. From the general equations for n-row plots, the correponding equations for 2-row and 3-row plots were derived.

### *9.2.2 Rows alternated with rows of a standard variety*

To reduce the bias due to intergenotypic competition between rows, several authors have recommended bordering all plots with rows sown with a common variety. The common border should be an intermediate competitor (Section 1.3.3). However, the consequences of this method have not yet been quantified in a model. In this section, expressions are derived for the variances and for the response to selection for an arrangement where single-row plots are alternated with rows of a standard variety. The arrangement of the rows may be represented by

g s h s i s j s

where each letter stands for a row. The letter s denotes a row sown with the standard variety.

The genotypic yield of a row sown with a random genotype i is derived from Eqn 4.12 to be

$$\underline{O}_{i,ss} = \frac{2\underline{b}_i}{\underline{b}_i+b_s}\ \underline{M}_i \tag{9.15}$$

The standard s is fixed.

Written in genetic terms, the phenotypic yield of i is

$$\underline{P}_{i,ss} = \frac{2\underline{b}_i}{\underline{b}_i+b_s}\ (\mu + \underline{g}_i) + \underline{e}_i$$

The mean yield of all lines is

$$\varepsilon\underline{P} = \frac{2}{1+b_s}\ \mu$$

Hence, trials that differ from each other with respect to the standard, differ in their yield level. For trials that differ in yield level, it is assumed that the environmental variance within a trial is proportional to the yield level of that trial (Section 5.3.2), so that the coefficient of variation is constant over trials. Therefore, the phenotypic yield of a row of a random genotype i is written as

$$\underline{P}_{i,ss} = \frac{2\underline{b}_i}{\underline{b}_i+b_s}\ (\mu + \underline{g}_i) + \frac{2}{1+b_s}\ \underline{e}_i \tag{9.16}$$

The phenotypic variance can be expanded by the method of statistical differentials to be

$$\text{var}\ \underline{P}_{mix} \approx \frac{4}{(1+b_s)^2}\ \text{var}\ \underline{g}_{mono} + \frac{8b_s}{(1+b_s)^3}\ \mu\ \text{cov}(\underline{b},\underline{g}_{mono}) + \\ + \frac{4b_s^2}{(1+b_s)^4}\ \mu^2\ \text{var}\ \underline{b} + \frac{4}{(1+b_s)^2}\ \text{var}\ \underline{e}_{mono} \tag{9.17}$$

As in Section 4.3.1.4, we may split the phenotypic variance into the variance between genotypes

$$\text{var}\ \underline{g}_{mix} \approx \frac{4}{(1+b_s)^2}\ \text{var}\ \underline{g}_{mono} + \frac{8b_s}{(1+b_s)^3}\ \mu\ \text{cov}(\underline{b},\underline{g}_{mono}) + \frac{4b_s^2}{(1+b_s)^4}\ \mu^2\ \text{var}\ \underline{b} \tag{9.18}$$

and the environmental variance

$$\text{var}\ \underline{e}_{mix} = \frac{4}{(1+b_s)^2}\ \text{var}\ \underline{e}_{mono} \tag{9.19}$$

The covariance of the genotypic yield of a genotype in mixture and the genotypic yield of that genotype in monoculture is

$$\text{cov}(g_{mix}, g_{mono}) = \text{cov}(\underline{O}_i, \underline{M}_i) = \frac{2}{1+b_s} \text{ var } g_{mono} + \frac{2\mu b_s}{(1+b_s)^2} \text{ cov}(\underline{b}, g_{mono}) \qquad (9.20)$$

The expressions of the direct response for mixture yield and the correlated response for monoculture yield, brought about by selection for yield in mixture, are obtained after substitution of the appropriate equations into Eqns 4.33 and 4.36, respectively.

What is the effect of bordering all rows with rows of a standard variety? Let the standard variety be an intermediate competitor so that $b_s = 1$. After substitution of $b_s = 1$ into Eqns 9.18 and 9.20, these equations equal the corresponding Eqns 4.29 and 4.43 for a line-selection field without inserted standard. Hence, introduction of an intermediate competitive standard does not affect the genetic variance and genetic covariance of the lines because the expected yield in mixture remains unchanged for each of the genotypes. This can be seen from the equality of Eqn 9.15, after substitution of $b_s = 1$, to Eqn 4.15.

On the other hand, comparison of Eqn 9.19 and Eqn 4.30 for the environmental variance in mixture shows that the genetic component of the environmental variance is removed by alternating the rows with rows of a standard. This can be explained as follows. In a line-selection field, the genetic constitution of the neighbourhood differs from row to row so that the environmental variance increases by a genetic component (Section 4.5). When the rows are alternated with rows of one standard variety, the genetic environment becomes constant for all rows so that the genetic component of the environmental variance is eliminated.

Most authors, who have recommended alternating with a standard, have not realized that, in the monocultures, each genotype competes against a different competitor. A strongly competitive genotype stands in its monoculture in an environment of strong competitors. Conversely, a weakly competitive genotype grows in its monoculture among weak competitors. This feature causes the difference between the expected yield of a genotype in mixture and the expected yield of that genotype in monoculture. Bordering all rows in mixture with rows of an intermediate standard does not remove this discrepancy between monoculture and mixture.

In conclusion, the only effect of bordering all rows with rows of a common intermediate competitor is that the environmental variance is no longer inflated by intergenotypic competition. However, this advantage is small since var $\underline{e}_{mix}$ - var $\underline{e}_{mono}$ is small (Eqn 4.30, Tables 40 and 42). Furthermore, alternation with a standard doubles the field area which enhances the environmental variance. The latter effect was not included in Eqn 9.19 but may be introduced by the coefficient of soil heterogeneity of Smith (Section 8.1). When there is a heavy, coarse-grained pattern of soil heterogeneity, insertion of a standard may even result in a net increase of the environmental variance. Considering also the additional work due to the inserted rows, the method is always useless.

What is the effect of the competitive ability of the standard variety? The poorer a competitor the standard variety is, the higher the yield of all other genotypes (Eqn 9.15). Because the increase of the yield of a genotype in the mixture is proportional to the yield of that genotype in monoculture, the genetic variance also is enhanced (Eqn 9.18). Due to the assumed proportionality of the environmental variance and the yield level, the environmental variance also is increased (Eqn 9.19).

It may be derived from Eqn 4.44 that the correlated response for monoculture yield depends only slightly on the competitive ability of the standard. Whether a higher competitive ability of the standard results in either a small increase or a small decrease of the correlated response depends on the size of $h^2$, $r_{bg}$ and $\gamma$ (Eqn 4.47).

In a mixture of single plants, the response to selection is expected not to change when a new genotype is introduced in the mixture (Section 8.4.3). The difference between mixtures of rows and those of single plants is that in single-plant mixtures the yields are determined by the relative frequencies of the genotypes rather than by their mutual arrangement. The effect of a doubled field area, due to the insertion of the standards, on the environmental variance was not included in the equations of the response to selection.

The weakest competitor which can be imagined is an empty row. When an empty row is used as common neighbour, the arrangement becomes an arrangement where the rows are sown at twice the normal spacing. For such a weakly competitive common neighbour, the assumption that the competitive influence of a row is restricted to its adjacent neighbours is violated. The model for the influence of the row distance on the outcome of selection assumes that an empty row gives no protection at all against the competitive influence of other rows (Section 5.4.1.1).

*Summary* Expressions were derived for the variances and the response to selection when the rows are alternated with rows of a standard variety. When the standard is an intermediate competitor, only the environmental variance is reduced whereas the genetic variance and the genetic covariance with monoculture yield remain unchanged. The reduction of the environmental variance due to a common genetic environment of all rows is small. It is questionable whether this reduction cancels out the increase of the environmental variance due to a doubled field area.

When the standard variety is not an intermediate competitor, all of the variances and their derived quantities are affected. However, the response to selection is modified only slightly and not necessarily in a favourable direction. Considering also the additional amount of work, it is concluded that alternating the rows with rows of a standard variety is useless in reducing the bias that arises from intergenotypic competition between the rows.

## 9.3 REDUCING THE COMPETITIONAL BIAS

In this section, the possibilities of reducing the bias that arises from interrow competition are discussed. The literature on this subject was reviewed in Section 1.3.3.

*(1) n-Row plots* A row is only influenced by its nearest neighbour rows. Hence, the n-2 central rows of a n-row plot constitute a monoculture. The two outside rows are affected by intergenotypic competition, but to a lesser degree than single-row plots because one of their neighbours is always of their own genotype. When the number of rows per plot increases (i) the mean yield of the plot approaches the monoculture yield, and (ii) the sample size increases so that the environmental variance decreases. The effects were quantified in Section 9.2.1.

The effect of plot size on the environmental variance is discussed in more detail in Section 9.4 together with the practical implications. In Section 9.5, different plot sizes are evaluated experimentally.

*(2) Bordered plots* Discarding the border rows of a plot eliminates the bias that arises from competition between the plots. One row at each side is sufficient as a row is only influenced by its adjacent neighbour rows. My study is directed towards yield testing in microplots. The maximum plot size was chosen to be three rows. Hence, discarding the borders implies selection for the central row of 3-row plots.

Does selection for the yield of the central row of a 3-row plot result in a higher response than selection for the yield of the entire 3-row plot? This question may be asked because the environmental variance of a single row is substantially larger than the environmental variance of the mean of three rows. In other words the question becomes: is the direct response to selection for yield of single rows in monoculture greater than the correlated response for monoculture yield, brought about by selection for the yield of 3-row plots in a mixed stand? By combining Eqns 4.32, 4.36, 9.3 and 9.6, we can derive that selection for the yield of the entire 3-row plot is superior when

$$6 + r_{bg}\sqrt{\gamma} > \sqrt{12\, r_{bg} h^2 \sqrt{\gamma} + \tfrac{3}{2} h^2 \gamma + 12 + 24\, h^2 + 24\, r_e (1-h^2)}$$

where $r_e$ is the correlation between the rows within a plot. In general, the left side of the expression exceeds the right side, which can be understood from the magnitude of the values found for the variables (Table 17). In my experiments, selection for the yield of all three rows was much better than selection for the yield of only the central row (Tables 54-57).

Selection for the yield of all three rows may be preferable on practical grounds also: (i) mechanical harvesting is done more convenient for all three rows than for only the central row, and (ii) a larger amount of seed per line is obtained from three rows than from only one row. Harvesting the rows of a 3-row plot separately and allocating the central row for selection and seed production and the border rows only for seed production is too time-consuming.

In conclusion, selection for the yield of all three rows of a 3-row plot gives, in general, a higher response than selection for only the central row. Hence the gain from an increased sample size more than outweighs the detrimental effect of the bias due to intergenotypic competition between the plots.

*(3) A wide distance between the rows* Many authors have claimed that the bias from intergenotypic competition is eliminated by growing the rows at a wide spacing. However, in Chapter 5 it was proved with wider spacings that the bias due to intergenotypic competition between the experimental units is replaced by the bias due to a differential response of the genotypes to spacing. In plant selection, where the frequency of the genotypes in the mixture is important rather than their arrangement, the bias replacement is complete provided that certain assumptions are satisfied. In line selection, where only the genotype of the nearest neighbours is of influence, small deviations from complete bias replacement occur (Section 5.4).

The effect of the row spacing on the response to selection is illustrated in Fig. 46 for some situations which are thought to be realistic for line selection. The curves were computed with the density model of Section 5.4. The crowding coefficient $b_e$ was calculated from Exp. 76-3, by the method given in Section 5.5, from the monoculture yield at 20 cm row$^{-1}$ and the yield at 60 cm row$^{-1}$. As the direct response in monoculture at 20 cm row$^{-1}$ R is constant for all situations, Fig. 46 presents the expected progress for monoculture yield brought about by selection in mixture at different row spacings. As was already shown in Section 5.4.2, the progress is affected only slightly by the spacing between the rows.

In the model, it was assumed that the competitive ability of the genotypes in mixture can be predicted from their response to spacing in a density experiment with the genotypes grown in monocultures and harvested at only one time (Section 5.2). The consequences of violation of this assumption were discussed in Section 5.6.

The consequences of wide spacing were discussed in more detail in Section 8.3 with respect to plant selection. The implications for breeding practice were given in Section 8.3.3. The advantage of a wide spacing that individual plants may be recognized more easily, is of no importance for rows as visual selection of individual rows may conveniently be done at normal row spacings. If we also consider the other points of the dis-

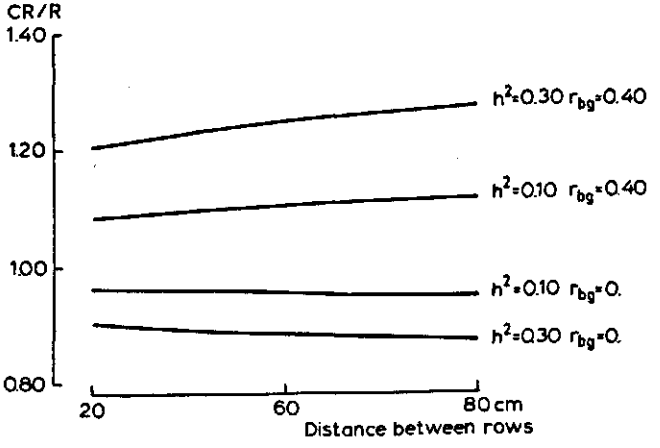


Fig. 46. The ratio between the correlated response for monoculture yield at 20 cm row$^{-1}$, brought about by selection for yield in mixture at various row spacings, and the direct response to selection without intergenotypic competition at 20 cm row$^{-1}$. The values were calculated with the density model from $b_e = 0.14$ and $\gamma = 2$.

cussion about the effect of wide spacing on plant selection, it can be concluded that selection of rows has to take place at a row spacing equal to that used by the farmer.

*(4) Bordering all plots with rows of one common variety* The effect of alternating single-row plots with rows of a standard variety was quantified in Section 9.2.2. It was shown that, when the standard is an intermediate competitor, only the environmental variance is reduced, whereas the genetic variance in mixture and the genetic covariance between mixture and monoculture yield remain unchanged. The environmental variance is reduced to the level of the environmental variance in monoculture because in alternating the rows with a standard, each row has an identical genetic environment as in a monoculture. However, this reduction of the environmental variance is small and it is questionable whether it cancels out the increase of the environmental variance due to a doubling of the field area brought about by the inserted standards.

When the standard variety is not an intermediate competitor, all variables are influenced but the response to selection is modified only to a small degree.

In conclusion, the response to selection is little affected by bordering all plots with rows of one common variety. Moreover, the response is not necessarily enhanced by this method. Furthermore, the amount of work increases considerably due to the insertion of the common variety. Therefore the method is useless for reducing the bias due to intergenotypic competition.

*(5) Mathematical correction for competitive ability* If it were possible to determine the competitive ability of a row in the selection field, the yield of the row could be adjusted for the effects of competition. The competitive ability of a row may be read (a) from the yield of its neighbour rows when these are sown with a known variety and (b) from its score for a certain character. Method 5a involves that the rows are alternated with rows of a standard variety. Method 5b implies selection for harvest index (Section 8.4.5).

(5a) Alternating the rows with rows of a standard variety. In Exps 76-3c and 77-2d, the rows were sown according to

$$s\ s_1\ s_2\ a\ s_3\ b\ s_4\ c\ s_5\ d\ s_6\ e\ s_7\ f\ s_8\ s_9\ s$$

The letters a to f represent rows of the genotypes to be tested while s stands for rows of a standard variety. The subscript denotes the position of the standard rows in the field. The rows $s_1$ and $s_9$ supply an estimate of the monoculture yield of the standard. The rows $s_2$ to $s_8$ and a to f are rows of the respective genotypes in a mixture and their expected yield is derived from Eqn 4.13. Hence, 13 equations are obtained with 12 unknown variables: the six monoculture yields of the genotypes a to f and the six crowding coefficients of these genotypes relative to the standard. The equations are solved simultaneously, which results in estimates of the monoculture yields of the six genotypes.

The method is based on the assumption that the yield of a row differs from the monoculture yield of the genotype sown in that row, mainly due to intergenotypic compe-

tition with the neighbour rows. However the yield of a single row is subject to environmental and random variation, whose effects may be substantially larger than the effects of intergenotypic competition. Therefore it is not surprising that application of method 5a to Exp. 76-3c resulted in nonsense estimates of the monoculture yields. Hence, the yield of a row of a standard variety is not a good measure of the intergenotypic-competitive ability of its neighbour rows.

(5b) The harvest index of a genotype in a mixture equals the harvest index of that genotype in monoculture (Section 8.4.5). Furthermore, within the same genotype, the harvest index is independent of the plant size (Fig. 43). Therefore, the harvest index is not affected by either intergenotypic or intragenotypic competition. The literature showed that the progress in yield due to breeding is associated with an increase in harvest index with little change of biomass (Section 8.4.5). Hence in monoculture the varieties with the highest harvest index tend to yield most as well. When this trend holds also for the genotypes of segregating populations, then this suggests that in selection for harvest index in mixture preferentially the genotypes with the highest monoculture yield will be chosen because of the harvest index's independency of competition. In other words, selection for harvest index implies adjustment of the yield of a phenotype for competition (Section 8.4.5). Selection for harvest index, as a method to take account of competition, seems worth further consideration.

*(6) Grouping lines that are similar to each other* When competitive ability is related to a certain plant character, the lines may be grouped according to competitive ability by that character. Plant height, date of ear emergence and date of maturity are frequently mentioned for this purpose. However, the correlations, reported in the literature, between these characters and competitive ability are variable. This is not surprising as competitive ability was associated with juvenile growth rather than with morphological characters that express themselves later on during ontogeny (Section 8.3.1 and 8.4.4). Hence, grouping the lines according to these morphological characters is hardly useful in reducing intergenotypic competition. Moreover, especially for first-year lines it is cumbersome to gain the foreknowledge about these morphological characters.

It is also impracticable to gain for each line foreknowledge about the growth curve in the juvenile phase. However, the size and the quality of the seed affect the juvenile growth. Plants growing from large seeds show a competitive advantage over those from small seeds (Section 7.4). When large-seeded and small-seeded lines are sown separately, these differences in seed size are eliminated as source of competition (Section 8.4.2). It may be more convenient to sieve the seed so that the seed of all lines is about the same size. However, this technique requires a large initial seed stock of each line.

In breeding practice, the lines are already partly grouped according to similarity because lines that originate from the same cross are grown together. Also the visual selection of mother plants for a particular, desired habit promotes the similarity among the lines.

*(7) Equal number of kernels per row* When a row is sown with more kernels, its competitive ability is enhanced (Kiesselbach, 1918, 1919, 1923).

The results in Tables 43 and 44 and in Fig. 47 are from an experiment with 6-row plots which were all sown with the variety 'Varunda'. In the 'monoculture' plots, all rows were sown with a same number of kernels per row. In the 'mixture' plots, three rows sown with a certain number of kernels per row, were alternated with three rows with another number of kernels. Each mixture plot was situated between both their corresponding monoculture plots. A competition diallel of three sowing densities within the row was laid out in a three-times replicated randomized block design. For technical details see Exp. 77-2a (Section 2.2). The crowding coefficients were estimated by the method described in Section 6.2.3.

The differences in competitive ability between the rows of different seed rates may be understood as follows. Each plant tries to acquire its part of the available space. All plants are of the same genotype. Hence, when the planting arrangement does not affect the partitioning of the space among the plants, it is expected that the space confiscated by a row of 100 kernels, a row of 50 kernels and a row of 25 kernels is in the ratio 100:50:25. When the rows of different seed rates occur at the same frequency, the ratio of the crowding coefficient is derived from Eqn 4.9 to be

$$b_{100} : b_{50} : b_{25} = 100 : 50 : 25$$

The ratio of the crowding coefficients of the rows of 50 and 25 kernels was indeed 50:25 (Table 44). However, the crowding coefficient of the rows of 100 kernels was lower than

Table 43. Biomass and grain yield in monocultures and in rows alternated with rows sown with either 100, 50 or 25 kernels $row^{-1}$.

| | | Biomass (g $row^{-1}$) | | | Grain yield (g $row^{-1}$) | | |
|---|---|---|---|---|---|---|---|
| | | Associate | | | Associate | | |
| | | 100 | 50 | 25 | 100 | 50 | 25 |
| Producer | 100 | 281 | 312 | 441 | 140 | 153 | 214 |
| | 50 | 229 | 283 | 355 | 111 | 138 | 164 |
| | 25 | 112 | 166 | 249 | 52 | 79 | 119 |

Table 44. Relative crowding coefficients for biomass and grain yield of rows sown with either 100, 50 or 25 kernels $row^{-1}$.

| | | Biomass | | | | Grain yield | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Associate | | | | Associate | | | |
| | | 100 | 50 | 25 | $b_i/b_{100}$ | 100 | 50 | 25 | $b_i/b_{100}$ |
| Producer | 100 | | 1.48 | 3.64 | 1 | | 1.44 | 3.60 | 1 |
| | 50 | 0.68 | | 1.91 | 0.62 | 0.69 | | 1.80 | 0.62 |
| | 25 | 0.27 | 0.52 | | 0.30 | 0.28 | 0.56 | | 0.31 |

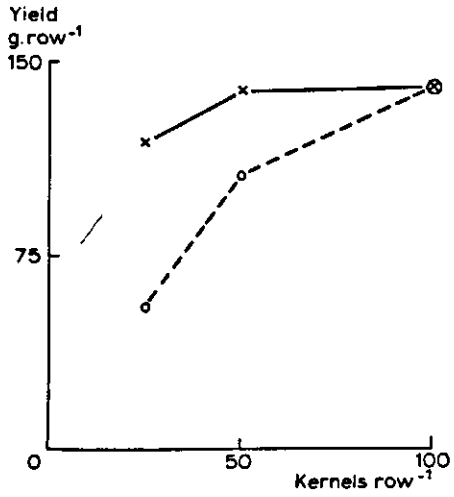


Fig. 47. Grain yield in monoculture (x), and in rows alternated with rows of 100 kernels row$^{-1}$ (0) for rows sown with different numbers of kernels per row.

was expected. Apparently, at this high seed rate the intra-row spacing was so much smaller than the interrow spacing that the arrangement of the plants affected the outcome of competition. At a high seed rate within the row, the plants of the same row competed more against each other than that they competed against plants from adjacent rows.

In conclusion, to minimize differences between the rows with respect to competitive ability it is of utmost importance to sow the same number of kernels in all rows.

*(8) Minimization of alleys* The plants at the ends of a row benefit from the empty space offered by alleys. When the genotypes differ in their response to empty space, the alley effect biases the outcome of selection. This effect is comparable with that of the sowing density and row spacing.

In my experiments, only the central part of a row was harvested for yield (Fig. 4) so that the effect of a differential response of the varieties to the alleys was largely avoided. However, in mechanical harvesting, it is too time-consuming to discard the ends of the rows. Therefore, the alleys should be as narrow as possible.

The alley effect is important particularly in miniature row plots and in hill plots. The advantage of miniature row plots is that only a small amount of seed per plot is required. Therefore replicates may be laid out and the plots may consist of several rows. The latter reduces the effect of intergenotypic competition between the plots. However, it may be questioned whether the decreased effect of intergenotypic competition in miniature multi-row plots, compared with the conventional single-row plots, cancels out the increased alley effect. Problems of mechanical sowing and harvesting of miniature plots limit their use. In oats, Jensen & Robson (1969) obtained good results with yield testing in miniature row plots, when compared with those in conventional row plots, provided that the miniature plots were replicated frequently.

In the small grains, hill plots are usually sown 30 cm apart with 30 seeds per hill.

Hill plots were compared with row plots by Bonnett & Bever (1947), Ross & Miller (1955), Jellum et al. (1963), Lessman & Atkins (1963), Frey (1965), Smith et al. (1970), Khadr et al. (1970) and Baker & Leisle (1970). The comparisons were based mostly on the variation coefficient and the correlation between both plot types. The general opinion was that hill plots are useful in preliminary screening for yield in order to eliminate the inferior genotypes. But it was recommended that final evaluation of the lines be done in field plots. The consequences of using hill plots may be quantified in terms of the present competition model. This gives a better understanding of the effects of the wide spacing between the hills and of competition between the hills and permits a theoretical comparison with row plots.

Considering the discussion about the use of wide row spacings, conventional row plots seem preferable to miniature plots and hill plots.

*Summary* To minimize the effects of competition the same number of kernels should be sown in all rows using seed of the same size and comparable quality with the distance between rows equal to that used by farmers, and with the alleys as narrow as possible. Selection for harvest index, as a method for adjusting for competition, is worth further consideration. Grouping the lines according to morphological character is difficult and, moreover, is hardly of use in reducing intergenotypic competition. On the other hand, grouping the lines according to the cross from which they are derived and to seed size is effective. Bordering all plots with rows of one common variety is useless for reducing the effects of intergenotypic competition.

## 9.4 REDUCING ENVIRONMENTAL VARIATION

Methods for minimizing the environmental variation in line selection are reviewed.

### *9.4.1 Replication*

When a line is replicated throughout the nursery, the yield of that line can be estimated more precisely. The variance of a mean of n replicates is

$$\text{var } \underline{e}_{\text{mean}} = (\text{var } \underline{e})/n \qquad (9.21)$$

where var $\underline{e}$ is the environmental variance of unreplicated plot yields.

Replication of the lines enables us to estimate the environmental variance and, consequently, provides a reliability estimate of the yield of the lines.

### *9.4.2 Blocking*

Blocking refers to the assignment of a group of lines to a block of land. By blocking, the variance among the blocks is eliminated from the environmental variance.

In many experiments, complete block designs are used. In these designs all treatments appear in each block so that a replicate coincides with a block. In a line-selec-

tion field, the number of treatments, i.e. the number of lines, is large. A large number of treatments increase the size of the blocks and, therefore, the environmental variance within a block. To accommodate for the increased block size, incomplete block designs were developed. In these designs, the number of blocks is no longer equal to the number of replicates but a replication is further subdivided into smaller blocks to which only a part of the total number of lines is allotted. The blocks are so constructed that the variance between the blocks can still be removed from the total environmental variance. The incomplete block designs were introduced by Yates (1936) for variety trials and were reviewed by Cochran & Cox (1957).

Also in unreplicated trials, the field may be divided into blocks. From each block the best lines are selected, which is called 'grid selection' (Section 8.5.2). In my experiments, the strips of rows were chosen as grids (Fig. 4). The results of selection presented in this report were obtained by selection within grids.

### *9.4.3 Plot size*

In this section, the considerations which determine the choice of the plot size are reviewed. Only those differences in plot size are discussed which originate from differences in the number of rows per plot. Unreplicated n-row plots are compared with n times replicated 1-row plots.

*(1) Sample size and environmental variance* A larger number of rows per plot increase the sample size and, therefore, reduce the environmental variance. The environmental variance of the mean yield per row of a plot of n rows is derived from Eqn 9.2 as

$$\text{var } \underline{e}_{\text{mean}} = \left(\frac{1}{n} + \frac{n-1}{n} r_e\right) \text{var } \underline{e} \qquad (9.22)$$

where $r_e$ is the correlation between the rows of a plot and var $\underline{e}$ is the environmental variance of single rows. This simplified equation holds when the correlations between any two rows of the same plot are all equal and when the outside rows of the plot are not influenced by intergenotypic competition from the adjacent plots (Section 8.5.3.1).

Unreplicated n-row plots may be compared with n times replicated 1-row plots with respect to their environmental variance. The smaller $r_e$, the closer the environmental variance of n-row plots approaches the environmental variance of n times replicated 1-row plots (Eqns 9.21 and 9.22). Hence, when $r_e = 0$, grouping the rows in one plot is as efficient as replication in minimizing the environmental variance. The correlation between neighbour rows is low when the soil heterogeneity is small or when it occurs in a fine-grained pattern (Section 8.5.3.1), or when the field area is small. Therefore, $r_e$ is smaller when computed within blocks than when computed over the entire field.

Grouping of the rows was compared with replication of the rows in the uniformity trials where all rows were sown with the variety 'Varunda'. In Exp. 76-3e, the correlation of the biomass yields of adjacent rows was +0.35. Therefore, in this experiment, the environmental variance was reduced more by replication than by an increase of the number of rows per plot (Fig. 48).

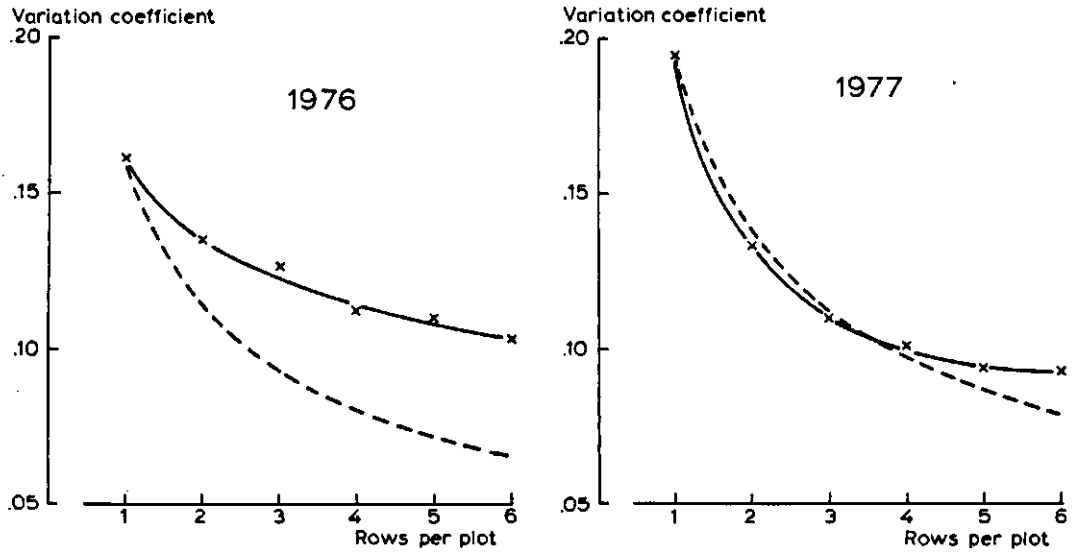


Fig. 48. Effect of the plot size on the variation coefficient for biomass per plot (solid lines). The broken lines give the expected values when the rows are replicated throughout the field instead of grouped adjacent to each other. Exps 76-3e and 77-2e.

In Exp. 77-2e, the biomass yields of adjacent rows were negatively correlated ($r_e$ = -0.10) as interrow competition affected the correlation more than did soil heterogeneity (Section 8.5.3.1). In accordance with Eqn 9.22, grouping the rows gave a somewhat lower environmental variance than did replication (Fig. 48). This held for 2-row plots and for 3-row plots. With larger plots, replication became more efficient. In the plots of more than three rows, the environmental variance of the plot mean was determined more by the correlations between second and higher-order neighbours than by the correlation between adjacent neighbours. Second and higher-order neighbours did not compete with each other so that their mutual correlations were positive because of soil heterogeneity. Then replication became superior to grouping of the rows (Eqns 9.21 vs 9.22).

The difference between Exps 76-3 and 77-2 for the effect of plot size on environmental variance, as was observed in the uniformity trials, was also found in the experiments where different varieties were grown in 1-row plots and in 3-row plots (Tables 54 and 55).

As we have seen, in contrast to general opinion, the environmental variance may be reduced more by grouping of n rows in one n-row plot than by making n replicates of single-row plots. In Exp. 77-2e, this higher reduction resulted from the relatively large effects of non-genetic competition between the rows which caused a negative correlation between the rows. However, there are other mechanisms that may lead to superiority of grouping rows: (i) when the number of rows per plot increases, the effect of intergenotypic competition reduces and, therefore, the environmental variance decreases (Eqn 9.5); (ii) the rows of a sowing pass often differ systematically in their yield, which may be accommodated by using multi-row plots (point 3 of this section); (iii) an increased plot size facilitates mechanization which often leads to a reduced environmental variance.

*(2) Field area required to test a certain number of lines* An increase of the plot size enlarges the area of the field that is needed to grow a certain number of lines. An enlarged area means additional work and, almost always, a larger environmental variance. In my experiments, the increase of the environmental variance with an increased area was small. For example, in Exp. 76-3e, going from a strip of 96 rows to a strip of 180 rows, the environmental variance among single rows increased only from 898 to 901 $g^2$ $row^{-2}$.

*(3) Systematic differences in yield between the rows of a sowing pass* The rows were sown with a 6-row drill. In Exp 76-3, the two outside rows of a sowing pass yielded more than the four central rows (Table 45). The environmental variance among all rows was 1.3 times higher than the environmental variance among the central rows. Moreover, 67% of the 10% highest-yielding rows in the variety mixture were outside rows. Without systematic differences in yield between the rows of a sowing pass, it is expected that only 33% of the selected rows would be outside rows.

The higher yield of the outside rows may be caused by (i) a wider distance between sowing passes than between rows within sowing passes, and (ii) a better water supply of the outside rows due to soil compaction in the wheel track of the sowing drill.

Account may be taken of the higher yield of the outside rows by using 3-row and 6-row plots in such a way that the plots do not differ in their number of outside rows and in their number of central rows of the sowing passes. Then the environmental variance between the plots is reduced because (i) the systematic effect of the outside rows of the sowing passes is equal for all plots, and (ii) the effect of variations in spacing between the passes is levelled off.

In Exp. 77-2, the previous difference between outside and central rows was absent (Table 45). The reason may be that (i) in the wet year 1977, in contrast to the extremely dry year 1976, the soil compaction was of no advantage, and that (ii) the distance between the sowing passes (22.2 cm $\pm$ 2.7 cm) approached more closely the distance between the rows within a sowing pass (20.0 cm $\pm$ 0.8 cm). Remarkably, in each strip, the sixth row had a consistently lower yield than the other rows, which may have accounted for the somewhat higher yield of its neighbours: the first and fifth rows (Table 45). It might be that the coulter of the sixth row was set a little deeper or that the harvested central part of the row received less kernels. A deeper sowing results in a later emergence and, consequently, a competitive disadvantage and a lower yield.

In the variety mixture (Exp. 77-2b), 32% of the 10% highest-yielding rows were outside rows. This result agrees with the expectation when the outside rows have the same

Table 45. Grain yield in g $row^{-1}$ of the consecutive rows of a 6-row sowing pass in the uniformity trials. The column, denoted by n, gives the number of rows involved in the experiments.

| Experiment | n | 1 | 2 | 3 | 4 | 5 | 6 | S.E. |
|---|---|---|---|---|---|---|---|---|
| 76-3e | 1080 | 201.4 | 174.5 | 175.0 | 176.1 | 171.9 | 196.2 | 0.42 |
| 77-2e | 576 | 152.4 | 149.3 | 146.2 | 149.0 | 157.5 | 135.6 | 2.84 |

yield as the central rows.

In conclusion, the rows of a sowing pass may systematically differ in their yield. Frequently, the outside rows of the sowing pass have a higher yield than the central rows. This difference may be accounted for by using 3-row or 6-row plots.

*(4) Intergenotypic interplot competition* Increasing the number of rows per plot decreases the bias that arises from interplot competition. These competition effects were discussed and defined in a model in Section 9.2.1.

*(5) Visual selection* When the plots are larger, the lines can be selected more easily for their characteristics as crop. Then, unreplicated 3-row plots may be preferred over three replicates of single-row plots.

*(6) Disease* In a line-selection field, the lines differ in susceptibility for a disease. The plots, each containing a single line, influence one another with respect to the percentage disease. The error from this type of interplot interference was discussed by van der Plank (1963, pp. 285-310). Additional research on parts of the problem was done by James & Shih (1973), James et a. (1973), Parleviet & van Ommeren (1975), and Patanothai et al. (1975).

Van der Plank (1963, p. 287) described methods to reduce this type of error. One of the methods is an increase in plot size. As most diseases spread fast and far, it is questionable whether increasing the plot size from a single row to three rows per plot gives any reduction of the error.

On the other hand, when a disease tends to form foci in the field, then three replicates of single-row plots may give a more reliable screening for resistance than unreplicated 3-row plots.

*(7) Other considerations* When first-year progenies are tested, the seed supply of each progeny is limited. In barley, a seed supply of 300 kernels per progeny is possible when the mother plants are grown at a wide stand. Then of each progeny three rows of 100 seeds each can be sown. Therefore, the present discussion was restricted to plots of 1, 2 and 3 rows.

To harvest 300 kernels per plant, the plants must be grown at a wide stand. A wider stand requires a larger field area and brings about additional work and additional problems (Section 8.3.3). When single-plant progenies are concerned in yield testing, the previous is in favour of unreplicated 1-row plots in the comparison with replicated plots and 3-row plots.

By using unreplicated 1-row plots instead of unreplicated 3-row plots, three times as many lines can be tested in a given field area. Thus, in unreplicated 1-row plots, the intensity of selection may be higher which enhances the response to selection (Eqn 4.32).

Larger plots facilitate mechanization. Three-row plots can be harvested with the present nursery combines, whereas mechanical harvesting of single-row plots is cumbersome. Mechanization saves work and may also reduce the environmental variance.

Instead of growing the lines in single-row plots in three replicates in one location, the lines may be grown in three different locations in unreplicated single-row plots.

Unreplicated 3-row plots require less work in harvesting, in preparing sowing and in administration than three replicates of 1-row plots.

### *9.4.4 Adjustment for soil heterogeneity*

The yields of the plots may be adjusted for soil heterogeneity by a moving mean and by systematically arranged standard plots.

In small grains, the efficiency of adjustment by standard plots in reducing the environmental variance was studied in uniformity trials by Kiesselbach (1918), Stadler (1921), and Mak et al. (1978) and in variety trials and line-selection nurseries by Griffee (1928), Baker & McKenzie (1967), Briggs (1969), Knott (1972), and Townley-Smith & Hurd (1973). The results were mostly disappointing, i.e. the environmental variance hardly decreased or sometimes even enhanced when the adjusted yields were used. Moreover, a decrease in environmental variance because of the adjustment, has to offset an increase of the environmental variance that originates from the larger field area brought about by the insertion of standard plots. Furthermore, standard plots give additional work. Because of all these things, Baker & McKenzie (1967) concluded that systematically arranged control plots are of questionable value.

When the yield of all plots is measured, one may try to reduce the environmental variance by a moving mean. Care has to be taken for overadjustment (Section 8.5.4.2), which can be avoided by an analysis of covariance.

For a further discussion about the use of moving means and standard plots, see Section 8.5.

## 9.5 EXPERIMENTAL EVALUATION OF PLOT TYPES

The effects of plot type on the bias due to interplot competition and on the environmental variance were discussed in Sections 9.3 and 9.4. Models for the influence of plot type on the outcome of selection were given in Section 9.2. In the present section, different plot types are evaluated experimentally by means of variety mixtures. The models are illustrated with experimental data.

The grain yield and biomass of the varieties in the different plot types are presented in Tables 46-49. The variances are given in Tables 50-53. From these, the heritabilities and the variation coefficients were derived (Tables 54 and 55).

The environmental variance was obtained as $\hat{\sigma}^2_e + \hat{\sigma}^2_r$ and refers, therefore, to an area occupied by a strip of rows (Fig. 4). In Exp. 77-2, all strips contained the same number of rows, whereas in Exp. 76-3, the strips of the different arrangements of the rows contained different numbers of rows. In Exp. 76-3a, b and c, the strips consisted of 96, 126 and 122 rows, respectively. However, the differences in the number of rows per strip had hardly any effect on the environmental variance. This can be seen from

Table 46. Grain yield in g row$^{-1}$ in single-row and 3-row plots, in single rows alternated with rows of the standard variety 'Varunda', and in the four central rows of 6-row plots. For the 3-row plots, mean row yields for all three rows, the central row, and the two border rows are presented. Exp. 77-2.

| Variety | 1-row plots | 3-row plots | | | Alternated standard | Central rows 6-row plots |
|---|---|---|---|---|---|---|
| | | 3 rows | centre | border | | |
| Varunda | 143 cd* | 151 b | 148 ab | 152 b | 153 a | 150 ab |
| Tamara | 175 a | 178 a | 166 a | 184 a | 166 a | 163 a |
| Belfor | 146 cd | 159 b | 162 ab | 158 b | 163 a | 159 a |
| Aramir | 165 ab | 164 ab | 169 a | 161 b | 157 a | 145 ab |
| Camilla | 143 cd | 165 ab | 171 a | 162 b | 160 a | 160 a |
| Golden Promise | 120 e | 129 c | 132 bc | 128 c | 117 b | 132 bc |
| Balder | 159 abc | 167 ab | 173 a | 163 b | 146 a | 146 ab |
| WZ 704068-14 | 133 de | 154 b | 146 ab | 158 b | 147 a | 152 ab |
| Goudgerst | 153 bc | 154 b | 142 ab | 160 b | 161 a | 124 c |
| L 98 | 86 f | 100 d | 102 d | 100 d | 84 c | 107 d |
| Titan | 65 g | 99 d | 111 cd | 92 d | 60 d | 107 d |
| Bigo | 163 ab | 166 ab | 160 ab | 168 b | 151 a | 152 ab |

* Values followed by the same letter are not significantly different in the Student-Newman-Keuls test at $P \leq 0.05$.

Table 47. Biomass in g row$^{-1}$ in single-row and 3-row plots, in single rows alternated with rows of the standard variety 'Varunda', and in the four central rows of 6-row plots. For the 3-row plots, mean row yields for all three rows, the central row, and the two border rows are presented. Exp. 77-2.

| Variety | 1-row plots | 3-row plots | | | Alternated standard | Central rows 6-row plots |
|---|---|---|---|---|---|---|
| | | 3 rows | centre | border | | |
| Varunda | 290 c* | 299 de | 291 bcde | 303 d | 305 bc | 290 bcd |
| Tamara | 350 b | 353 b | 329 bcd | 364 b | 329 ab | 321 b |
| Belfor | 299 c | 322 bcd | 324 bcd | 321 cd | 317 ab | 307 bc |
| Aramir | 341 b | 325 bcd | 333 bc | 320 cd | 320 ab | 285 bcd |
| Camilla | 278 c | 313 cd | 319 bcd | 310 d | 300 bc | 294 bcd |
| Golden Promise | 243 d | 260 fg | 267 cde | 256 e | 235 d | 263 cd |
| Balder | 334 b | 338 bc | 348 b | 332 bcd | 300 bc | 301 bc |
| WZ 704068-14 | 247 d | 282 ef | 263 de | 291 d | 267 cd | 268 cd |
| Goudgerst | 354 b | 344 bc | 316 bcd | 359 bc | 351 ab | 277 cd |
| L 98 | 199 e | 249 g | 251 e | 248 e | 198 e | 253 d |
| Titan | 165 f | 257 fg | 287 bcde | 242 e | 148 f | 266 cd |
| Bigo | 399 a | 414 a | 397 a | 423 a | 365 a | 369 a |

* Values followed by the same letter are not significantly different in the Student-Newman-Keuls test at $P \leq 0.05$.

Table 48. Grain yield in g $row^{-1}$ in single-row and 3-row plots, in single rows alternated with rows of the standard variety 'Varunda', in the six central rows of 8-row plots, all 20 cm apart, and in single-row plots 60cm apart. For the 3-row plots, mean row yields for all three rows, the central row, and the two border rows are presented. Exp. 76-3.

| Variety | 1-row plots | 3-row plots | | | Alternated standard | Central rows 8-row plots | 1-row plots 60 cm apart |
|---|---|---|---|---|---|---|---|
| | | 3-rows | centre | border | | | |
| Minerva | 217 a* | 204 a | 191 a | 211 a | 200 a | 194 a | 473 a |
| Julia | 194 b | 193 ab | 179 a | 200 ab | 188 a | 197 a | 435 ab |
| Belfor | 209 a | 197 ab | 178 a | 206 ab | 194 a | 193 a | 468 ab |
| Camilla | 190 b | 189 b | 180 a | 194 b | 185 a | 172 ab | 430 b |
| Golden Promise | 139 c | 147 c | 146 b | 148 c | 135 b | 157 b | 332 c |
| Uniculm | 68 d | 70 d | 72 c | 69 d | 69 c | 67 c | 69 d |

* Values followed by the same letter are not significantly different in the Student-Newman-Keuls test at $P \leq 0.05$.

Table 49. Biomass in g $row^{-1}$ in single-row and 3-row plots, in single rows alternated with rows of the standard variety 'Varunda', in the six central rows of 8-row plots, all 20 cm apart, and in single-row plots 60 cm apart. For the 3-row plots, mean row biomass for all three rows, the central row, and the two border rows are presented. Exp. 76-3.

| Variety | 1-row plots | 3-row plots | | | Alternated standard | Central rows 8-row plots | 1-row plots 60 cm apart |
|---|---|---|---|---|---|---|---|
| | | 3-rows | centre | border | | | |
| Minerva | 429 a* | 403 a | 372 a | 418 a | 393 a | 397 a | 954 a |
| Julia | 397 b | 392 ab | 360 a | 407 a | 376 a | 411 a | 950 a |
| Belfor | 421 a | 393 ab | 354 a | 413 a | 389 a | 399 a | 979 a |
| Camilla | 376 c | 373 b | 352 a | 383 b | 362 a | 336 b | 912 a |
| Golden Promise | 279 d | 295 c | 288 b | 299 c | 269 b | 325 b | 720 b |
| Uniculm | 221 e | 227 d | 225 c | 228 d | 220 c | 227 c | 307 c |

* Values followed by the same letter are not significantly different in the Student-Newman-Keuls test at $P \leq 0.05$.

Table 50. Effect of the arrangement of the rows on mean and variances for grain yield in g row$^{-1}$. For explanation of the variances see Table 20. Exp. 77-2.

| Arrangement | mean | $\hat{\sigma}^2_g$ | $\hat{\sigma}^2_e$ | $\hat{\sigma}^2_r$ | $\hat{\sigma}^2_s$ | $\hat{\sigma}^2_{gs}$ |
|---|---|---|---|---|---|---|
| 1-row plots | 138 | 1044 | 894 | 11 | 0 | 25 |
| 3-row plots: 3 rows | 149 | 650 | 266 | 16 | 54 | 0 |
| central row | 149 | 494 | 885 | 0 | 17 | 0 |
| border rows | 149 | 745 | 432 | 8 | 74 | 0 |
| rows alternated with standard | 139 | 1128 | 728 | 25 | 13 | 14 |

Table 51. Effect of the arrangement of the rows on mean and variances for biomass in g row$^{-1}$. For explanation of the variances see Table 20. Exp. 77-2.

| Arrangement | mean | $\hat{\sigma}^2_g$ | $\hat{\sigma}^2_e$ | $\hat{\sigma}^2_r$ | $\hat{\sigma}^2_s$ | $\hat{\sigma}^2_{gs}$ |
|---|---|---|---|---|---|---|
| 1-row plots | 292 | 4620 | 3968 | 34 | 0 | 69 |
| 3-row plots: 3 rows | 313 | 2185 | 1191 | 61 | 547 | 0 |
| central row | 311 | 1450 | 3923 | 169 | 277 | 0 |
| border rows | 314 | 2640 | 1915 | 5 | 690 | 0 |
| rows alternated with standard | 286 | 3906 | 3004 | 140 | 63 | 92 |

Table 52. Effect of the arrangement of the rows on mean and variances for grain yield in g row$^{-1}$. For explanation of the variances see Table 20. Exp. 76-3.

| Arrangement | mean | $\hat{\sigma}^2_g$ | $\hat{\sigma}^2_e$ | $\hat{\sigma}^2_r$ | $\hat{\sigma}^2_s$ | $\hat{\sigma}^2_{gs}$ |
|---|---|---|---|---|---|---|
| 1-row plots | 169 | 3168 | 610 | 106 | 211 | 19 |
| 3-row plots: 3 rows | 167 | 2613 | 255 | 71 | 591 | 76 |
| central row | 158 | 1945 | 491 | 22 | 532 | 86 |
| border rows | 171 | 2978 | 408 | 88 | 621 | 80 |
| rows alternated with standard | 162 | 2512 | 541 | 91 | 226 | 180 |
| rows 60 cm apart | 368 | 23920 | 2367 | 1296 | 0 | 0 |

Table 53. Effect of the arrangement of the rows on mean and variances for biomass in g row$^{-1}$. For explanation of the variances see Table 20. Exp. 76-3.

| Arrangement | mean | $\hat{\sigma}^2_g$ | $\hat{\sigma}^2_e$ | $\hat{\sigma}^2_r$ | $\hat{\sigma}^2_s$ | $\hat{\sigma}^2_{gs}$ |
|---|---|---|---|---|---|---|
| 1-row plots | 354 | 7106 | 2461 | 482 | 1004 | 78 |
| 3-row plots: 3 rows | 347 | 4922 | 854 | 338 | 2615 | 121 |
| central row | 325 | 3171 | 1852 | 138 | 2274 | 115 |
| border rows | 358 | 5894 | 1327 | 355 | 2801 | 171 |
| rows alternated with standard | 335 | 5000 | 2084 | 470 | 1119 | 607 |
| rows 60 cm apart | 804 | 67447 | 10388 | 8054 | 0 | 0 |

Table 54. Effect of arrangement of the rows on mean, genetic variance, environmental variance, heritability and variation coefficient for grain yield. Grain yield is expressed in g row$^{-1}$. Exp. 77-2.

| Arrangement | | mean | var $\underline{g}$ | var $\underline{e}$ | $h^2$ | CV |
|---|---|---|---|---|---|---|
| 1-row plots: | unreplicated | 138 | 1044 | 905 | 0.54 | 0.22 |
| | 3 replicates | 138 | 1044 | 302 | 0.78 | 0.13 |
| 3-row plots: | 3 rows | 149 | 650 | 282 | 0.70 | 0.11 |
| | central row | 149 | 494 | 885 | 0.36 | 0.20 |
| | border rows | 149 | 745 | 440 | 0.63 | 0.14 |
| rows alternated with standard | | 139 | 1128 | 753 | 0.60 | 0.20 |

Table 55. Effect of arrangement of the rows on mean, genetic variance, environmental variance, heritability and variation coefficient for grain yield. Grain yield is expressed in g row$^{-1}$. Exp. 76-3.

| Arrangement | | mean | var $\underline{g}$ | var $\underline{e}$ | $h^2$ | CV |
|---|---|---|---|---|---|---|
| 1-row plots: | unreplicated | 169 | 3168 | 716 | 0.82 | 0.16 |
| | 3 replicates | 169 | 3168 | 239 | 0.93 | 0.09 |
| 3-row plots: | 3 rows | 167 | 2613 | 326 | 0.89 | 0.11 |
| | central row | 158 | 1945 | 513 | 0.79 | 0.14 |
| | border rows | 171 | 2978 | 496 | 0.86 | 0.13 |
| rows alternated with standard | | 162 | 2512 | 632 | 0.80 | 0.16 |
| rows 60 cm apart | | 368 | 23920 | 3663 | 0.87 | 0.17 |

the uniformity trial (Exp. 76-3e), where an increase of the strip from 96 rows to 180 rows, resulted in an increase of the environmental variance of only from 898 to 901 $g^2$ row$^{-2}$.

Grain yield and biomass were affected in a similar way by intergenotypic competition (Section 8.4.5), so that, in what follows, only grain yield is considered. Exp. 77-2 was more comprehensive than Exp. 76-3 so that mainly the former experiment is discussed.

The competition model that defines the influence of plot type on the outcome of selection, was applied to Exp. 77-2. The input parameters were estimated according to Section 9.1.1 and are given in the heading of Table 40. For the predictions in the 2-row and 3-row plots, the covariance between adjacent rows and the covariance between second-neighbour rows are also required as input. These covariances were $cov(\underline{e}_1,\underline{e}_2) = -78$ g row$^{-1}$ and $cov(\underline{e}_1,\underline{e}_3) = -18$ g row$^{-1}$, respectively. The covariances were derived from the corresponding correlations which were estimated from the uniformity trial to be -0.09 and -0.02, respectively. The crowding coefficient of the standard variety 'Varunda', which is required for the arrangement where the rows were alternated with rows of a standard, was read from Table 16 to be 0.955.

Table 56. Mean, variances and derived quantities predicted with the competition model for different arrangements of rows. The studied character is grain yield in g row$^{-1}$. Exp. 77-2.

| | 1-row plots | | 3-row plots | | 2-row plots | Alternated standard |
|---|---|---|---|---|---|---|
| | unreplicated | 3 replicates | 3 rows | centre | | |
| $\mu$ | 144 | 144 | 145 | 145 | 144 | 147 |
| var $\underline{g}$ | 1097 | 1097 | 565 | 403 | 672 | 1124 |
| var $\underline{e}$ | 991 | 330 | 257 | 835 | 417 | 874 |
| $h^2$ | 0.53 | 0.77 | 0.69 | 0.33 | 0.62 | 0.56 |
| CV | 0.22 | 0.13 | 0.11 | 0.20 | 0.14 | 0.20 |
| $h_{mix}/h_{mono}$ | 1.27 | 1.54 | 1.45 | 1 | 1.38 | 1.31 |
| $r_{g_{mono,mix}}$ | 0.89 | 0.89 | 0.98 | 1 | 0.96 | 0.90 |
| $R_{mix}/i_{mix}$ | 24.0 | 29.0 | 19.7 | 11.5 | 20.4 | 25.2 |
| $CR_{mono}/i_{mix}$ | 13.0 | 15.7 | 16.3 | 11.5 | 15.1 | 13.5 |
| $CR_{mono}/R_{mono}$ | 1.14 | 1.37 | 1.42 | 1 | 1.32 | 1.18 |

The results of the computations are given in Table 56. The predicted values agreed well with the observed values reported in Table 54 as seen from the dimensionless quantities: the heritability and the variation coefficient. The two border rows of a 3-row plot (Table 54) are equivalent to a 2-row plot (Table 56). The predictions and observations were not always completely independent of each other. Their dependency may be derived from the description of the estimation of the input parameters.

The following arrangements of the rows are now considered (Table 56):

*Replicated vs unreplicated 1-row plots* Replication reduces the environmental variance and therefore increases the heritability. This enhances the direct response for yield in mixture and also the correlated response for yield in monoculture as the genetic correlation between yield in mixture and yield in monoculture is not affected by replication.

*Bordered vs unbordered plots* The two outside rows of a 3-row plot protect the central row against the competitive influences exerted by the adjacent plots. Hence, the yield of the central row represents the yield in a monoculture. Given the uniform genetic constitution of its neighbourhood, the environmental variance of the central rows of 3-row plots is smaller than the environmental variance of 1-row plots (Section 4.5).

An additional reduction of the environmental variance is obtained by using 3-row plots when the outside rows of a sowing pass systematically outyield the central rows of the sowing pass, as in Exp. 76-3 (Table 45). When only the central rows of the sowing passes were considered in the uniformity trial, the variance among the rows was 0.76 times that when all rows were considered because the central rows were more alike in

their yield than all rows (Table 45). This effect accounts for the large difference between the actual environmental variance of the central rows of 3-row plots and the actual environmental variance of 1-row plots (Table 55). A central row of a 3-row plot was always the second or fifth row of a sowing pass.

In Exp. 77-2, intergenotypic competition magnified the differences in yield between the genotypes. Therefore, the genetic variance was lower in the bordered than in the unbordered rows. In spite of the reduced environmental variance, this resulted in a lower heritability for the bordered rows and, therefore, in a lower direct response to selection. This was not cancelled out by the fact that bordered rows represent monocultures ($r_g = 1$). Therefore, in this experiment, more progress was predicted for yield in monoculture when selection for yield was done with unbordered rows than with bordered rows. This predicted advantage would be even higher since bordered rows require a three times larger field area to test the same number of lines.

A more detailed discussion was given in Section 9.1.1.

*Bordering all plots with rows of one common variety* The rows that were alternated with rows of the standard variety 'Varunda' may be compared with the single-row plots. The standard variety was a weak competitor ($b_s < 1$), which tended to increase the genetic variance and the environmental variance due to a scaling effect (Section 9.2.2). However, the increase in environmental variance was offset by a decrease due to the homogeneous genetic constitution of the neighbour rows so that overall environmental variance was reduced. The greater genetic variance and the smaller environmental variance gave a higher heritability which accounted for a higher direct response to selection in the arrangement with an alternated standard. Because of this somewhat higher direct response and the minor differences between both arrangements in the genetic correlation with monoculture yield, the correlated response for monoculture yield was somewhat higher where the rows were alternated with a standard than with single-row plots.

The use of the alternating arrangement was discussed more extensively in Section 9.2.2.

*Number of rows per plot* In Table 56, plots with 1, 2 and 3 rows may be compared. A larger number of rows per plot give a smaller environmental variance and a genetic variance closer to that without intergenotypic competition between the plots. As in this experiment the genetic variance in monoculture was smaller than in mixture, the genetic variance became smaller as the number of rows per plot increased. When the plot size was larger, the heritability increased because the decrease of the environmental variance had a larger effect on the heritability than the decrease of the genetic variance. However, the direct response to selection was reduced because the decrease in genetic variance was of relatively more importance than was the increase in heritability. In larger plots, the effects of interplot competition are less severe so that their yields are more closely correlated with the yield in monoculture. This higher genetic correlation cancelled out the lower direct response so that the correlated response for monoculture yield increased with the number of rows per plot.

The increase of the response with more rows per plot was substantially accounted

for by the reduction of the environmental variance due to an increased sample size. This can be understood from the predicted environmental variance which in bordered plots without intergenotypic competition was: 835, 379 and 240 $g^2$ $row^{-2}$ for plots with 1, 2 and 3 rows, respectively. Consequently, the heritability was 0.33, 0.52 and 0.63 and the response for monoculture yield $R_{mono}/i$ was 11.5, 14.4 and 15.9 g $row^{-1}$ for plots with 1, 2 and 3 rows, respectively. The plot types were compared to a fixed field area.

Considerations involved in the choice of the plot size were discussed in Section 9.4.3.

*Unreplicated 3-row plots vs three times replicated 1-row plots* In this experiment, the environmental variance was reduced more by grouping the rows adjacent to each other than by replicating the rows throughout the field. This higher reduction was accounted for by (i) a negative environmental correlation between adjacent rows and by (ii) the decrease of intergenotypic competition with increased plot size (Eqn 9.5). Due to the reduced interplot competition, the differences between the genotypes and, consequently, the genetic variance, were smaller in 3-row plots. This resulted in a lower heritability and in a lower direct response to selection. However, the yield in 3-row plots is more closely correlated with yield in monoculture. This higher genetic correlation cancelled out the lower direct response so that the correlated response for monoculture yield was higher in unreplicated 3-row plots than in three times replicated 1-row plots.

The practical aspects of yield testing in 3-row and 1-row plots were discussed in Section 9.4.3.

The predicted variances and heritabilities agreed well with the observed values (Tables 54 and 56). On the other hand, the agreement between the predicted response and the realized response was poor because of the strongly skewed frequency distribution of the genotypic yields in this variety experiment (Section 9.1.3). However, this does not detract from the illustrative character of Table 56. When allowance was made for the skewed distributions (Section 9.1.3), the correlated responses presented in Table 57 were obtained. The realized correlated responses for monoculture yield were derived

Table 57. Expected and observed correlated responses for yield in monoculture brought about by selection in different arrangements of rows. The selection percentage was 10%. The response is expressed in g $row^{-1}$. Exp. 77-2.

| Arrangement | Correlated response | |
|---|---|---|
| | expected | observed |
| 3-row plots | 17.5 | 14.6 |
| 2-row plots | 15.4 | 13.9 |
| central rows of 3-row plots | 14.3 | 13.5 |
| three times replicated 1-row plots | 14.2 | |
| rows alternated with rows of a standard | 12.2 | 12.4 |
| unreplicated 1-row plots | 12.0 | 11.4 |

from the group of varieties in the upper 10% for plot yield (Table 58) and the yield of those varieties in monoculture (Table 39).

The rank of the arrangements was identical for the expected responses and the observed responses (Table 57) in spite of the wide confidence intervals of the responses. However, the observed responses were, in general, lower because in the experimental evaluation, the correlation between variety means in mixture and monoculture was involved. This correlation is phenotypic as the variety means are subject to random variation. The phenotypic correlation is lower than the genetic correlation which the model deals with. In selection nurseries we are concerned also with genetic correlations so that the correlated responses obtained in experiments with variety mixtures are underestimates, whereas the model provides the correct estimates.

In the experiments and in the model, the arrangements were compared to a fixed field area. However, the area required to test a certain number of lines in 1-row plots is 1/3 of the area needed to test the same number of lines in 3-row plots. The smaller the area, the smaller the environmental variance and, therefore, the greater the response to selection. However, in the present experiment, the reduction of the environmental variance by a smaller field area was insignificant.

From Table 57, it can be shown that the response per unit area, i.e. for a fixed number of lines to be tested, was highest when selection was for yield of 1-row plots. As a smaller area reduces the amount of work, this would suggest that unreplicated 1-row plots were most efficient in making progress with monoculture yield. However, 3-row plots are more convenient for mechanization and may give, therefore, a higher response per unit of cost. Moreover, 3-row plots are a better guard against the capricious effects of intergenotypic competition.

Table 58. The portion of the varieties in the selected group, when selection was for grain yield in different arrangements of the rows at a selection percentage of 10%. Exp. 77-2.

| Variety | 1-row plot | 3-row plot | | | Alternated standard |
|---|---|---|---|---|---|
| | | 3-rows | centre | border | |
| Varunda | .04 | .00 | .00 | .05 | .12 |
| Tamara | .27 | .30 | .10 | .42 | .21 |
| Belfor | .10 | .05 | .15 | .05 | .17 |
| Aramir | .17 | .00 | .20 | .08 | .04 |
| Camilla | .01 | .20 | .10 | .05 | .17 |
| Golden Promise | .00 | .00 | .00 | .00 | .00 |
| Balder | .08 | .20 | .35 | .15 | .04 |
| WZ 704068-14 | .06 | .05 | .00 | .05 | .04 |
| Goudgerst | .08 | .05 | .00 | .05 | .08 |
| L 98 | .00 | .00 | .00 | .00 | .00 |
| Titan | .00 | .00 | .00 | .00 | .00 |
| Bigo | .18 | .15 | .10 | .10 | .13 |

The outcome of selection depends on the population, the field, and the field plot technique. When other estimates are used as input for the model, the rank of the arrangements for the response to selection may be changed.

When yield testing in microplots is useful, then, given the present nursery equipment, I recommend the use of 3-row plots with all three rows considered in selection for yield.

The last sections have shown that an integrated model is necessary to indicate which method of yield testing is optimal for which population and for which fields. Account has to be taken of the costs of each method. Optimalization techniques are required to choose the most convenient method of yield testing for each situation.

The advantages of such a model building are that the knowledge about different aspects of the problem may be integrated, that the relations between the various aspects become more apparent and are made explicit, that gaps in the present knowledge are defined, that the importance of each parameter and aspect within the problem may be estimated, and that the outcome of untried situations can be predicted.

# Summary

Breeders aim at selecting from a population genotypes whose agronomic performance is superior. In the self-fertilizing cereals, the selected genotypes, the varieties, are grown by the farmer in monoculture. Therefore, we must select those types from a genetically heterogeneous population which perform best in a genetically homogeneous monoculture. In the heterogeneous population, genotypes interfere because they compete for limited resources. Some genotypes, the strong competitors, yield better in mixture than in monoculture while poor competitors, have a lower yield in mixture than in monoculture. As intergenotypic competition results in different yields of a genotype in mixture and in monoculture, it complicates selection.

The aim of the present study is to explain and to quantify the influence of competition on the subsequent stages of breeding programmes. For this, a mathematical model is introduced that defines the influence of intergenotypic competition on the response to selection (Chapters 4 and 5). The model is tested with the results of experiments where varieties of barley were grown in mixtures and monocultures. Here, the variety mixtures simulate segregating populations.

By means of the model and illustrated with experimental data, the effect of competition is discussed for bulk propagation (Chapter 7) and selection of individual plants (Chapter 8) and progenies (Chapter 9). Methods are discussed to reduce the biasing effect of competition.

In the literature, many different models are used to analyse competition effects. The model of de Wit (1960) is superior for the present purpose and is chosen as the basic model (Chapter 3). This model gives an expression of the yield of a genotype in a mixture, averaged over all individuals of that genotype in the mixture. However, selection is for individual units. In plant selection, a single plant is the unit of selection. In line selection, a row of plants all belonging to the same line is generally the unit of selection.

Competition between the units of selection falls within two limits (Section 4.2). In one limit, all units of the population compete with each other to the same degree ('diffuse competition'). Thus the yield of a unit depends on the genotypic composition of the entire population. In the other limit, only the nearest neighbours compete with each other ('nearest-neighbour competition'). Then, the yield of a unit depends on the genotype of its nearest neighbours and is, therefore, independent of the genotypic composition of the entire population.

The original model of de Wit describes diffuse competition. From this model, another model is developed that defines the competition between nearest neighbours (Section 4.2.1).

In small grains, the competition between individual plants is characterized reasonably as diffuse competition. On the other hand, a row only competes against its nearest neighbours (Section 4.2.2).

Both competition models describe the yield of a genotype in a mixture without considering the variation in the yield of that genotype in the mixture. These models are deterministic. On the other hand, in genetics, the effects of genotype and environment are represented by a stochastic expression. In both competition models, the effects are taken to be multiplicative, whereas the genetic model is based on additivity of genotypic and environmental effects. An expression is derived for the phenotypic performance of a random genotype in a segregating population, that is in a mixture, by combining the deterministic, multiplicative competition models with the stochastic, additive genetic model (Section 4.3.1.1).

In this combined model, the phenotypic, genotypic and environmental variance in mixture are expressed as functions of the corresponding variances in monoculture. This is done for rows as unit of selection (nearest-neighbour competition, Section 4.3.1) as well as for single plants (diffuse competition, Section 4.4.5). Then the following appears: When the correlation between competitive ability and monoculture yield is not too strongly negative, the genotypic variance in mixture is greater than that in monoculture. Hence, in general, intergenotypic competition enhances the differences between the genotypes. In line selection, where competition is restricted to nearest neighbour rows, the expected environmental variance in mixture is larger than that in monoculture. In plant selection, however, where competition is diffuse, the expected environmental variance in mixture equals that in monoculture (Section 4.5).

The influence of intergenotypic competition on selection is expressed by its influence on the response to selection. In genetics, the response is understood by the progress made in generation t+1 by selection in generation t. Selection occurs in a heterogeneous population; one tries to choose the genotypes that perform best in monoculture. Therefore, the central question is: to what extent are the genotypes with the highest yield in monoculture in generation t+1 chosen when selection is for the phenotypes yielding highest in a mixture in generation t? The central question is split into three:

(1) To what extent are the highest yielding phenotypes in the mixture in generation t also the highest yielding genotypes in that mixture in that generation?

(2) To what extent are the genotypes that give the highest yield in the mixture in generation t also the genotypes yielding highest in monoculture in that generation?

(3) To what extent do the genotypes selected in generation t maintain their expected monoculture yield in generation t+1? (Sections 4.4.1 and 4.4.3).

The first question refers to the degree to which the genotypes with the highest yield in the mixture are identified by selection in that mixture. The progress that is made for yielding ability in that mixture is called the direct response to selection. The second question defines the effect of intergenotypic competition on the outcome of selection. Selection for yield in the mixture leads to a correlated response for mono-

culture yield. The third question concerns the effect of heterozygosity and mode of proportions (Section 6.2).

In *bulk propagation* of a segregating population (Chapter 7), the gene frequencies in the population change because of natural selection. To what extent does the change occur in the direction desired by the breeder? In other words, in how far are the types favoured by natural selection also the types yielding most in monoculture? Natural selection favours the types with the greatest reproductive rate. Therefore, the correlation between the reproductive rate in mixture and the yield in monoculture is the central issue. This correlation is expressed in terms of the competition model of de Wit (Section 7.2).

The reproductive rate of a genotype is the product of its competitive ability in mixture and its grain production in monoculture. This definition already suggests a tendency to a positive correlation between reproductive rate and monoculture yield. In the experiments with barley varieties, this correlation was always positive (Section 7.3.3). Also the literature on variety mixtures and composite crosses points to a usually positive relation between reproductive rate and monoculture yield (Section 7.5). Partly based on this relation, the conclusion is that delaying selection for yield until the late generations of a segregating population is not handicapped by intergenotypic competition and natural selection.

The value of a population for a breeder is measured by the mean and the variance for yield. The yield refers to the yield in monoculture because that, and not the yield in the particular mixture, is the goal of the breeder. The shift in the mean and the variance for monoculture yield in subsequent generations of bulk propagation is illustrated by data of a variety mixture (Section 7.3.5).

In the self-fertilizing small grains, the monoculture yield of heterozygotes is mostly substantially higher than that of the corresponding homozygotes. However, no clear conclusion can be drawn from the literature on the competitive ability of heterozygotes relative to that of homozygotes. On the other hand, the reproductive rate of heterozygotes is, in general, greater than that of the corresponding homozygotes (Section 7.4).

The effect of intergenotypic competition on the outcome of *selection of individual plants* (Chapter 8) is quantified by means of the competition model of Chapter 4. This model is discussed and tested with data from experiments where barley varieties were grown in mixtures and monocultures. The predictions obtained by the model, of the response to selection and of the intermediate variables, agree very well with the values observed in the mixtures (Section 8.2.3).

The influence of competition on the outcome of selection is reduced in an inexpensive and effective way by grading the seed and sowing only seeds of about equal size in one plot (Section 8.4.2). The grain/biomass ratio is not influenced by competition. If also in monoculture the genotypes with the highest grain/biomass ratio yield most as well, then selection for grain/biomass ratio adjusts the yield of the plants for their competitive ability (Section 8.4.5).

A wide spacing does not reduce the effect of intergenotypic competition because,

with wider spacing, the effect of intergenotypic interplant competition on the response reproduction on the outcome of selection (Fig. 12). The present study is restricted to the first two questions.

The conventional genetic models do not account for intergenotypic competition and thus give rise to wrong conclusions in the genetic analysis of yield (Section 4.4.3).

Expressions are derived for the direct response for mixture yield as well as for the correlated response for monoculture yield brought about by selection for yield in mixture (Section 4.4). The expressions are not influenced by heterozygosity and mode of reproduction, which come under the third question.

Intergenotypic competition will reduce the response to selection more, the higher the heritability in absence of intergenotypic competition and the lower the correlation between competitive ability and monoculture yield. Competitive stress, the third effective parameter, has a variable influence. The effects are illustrated by the results of numerical simulation. The effect of intergenotypic competition on the response to selection is not necessarily negative; it sometimes increases the response.

It has often been suggested that the influence of intergenotypic competition can be eliminated by selection at a wide stand. However, competition between the plants or between the rows is indeed removed by the wide stand, but an effect of differences between the genotypes in their reaction to the wide stand is introduced (genotype x density interaction).

The model for the influence of intergenotypic competition on the response to selection (Chapter 4) is extended to allow for the effect of density on the response to selection (Chapter 5). Continuity of the approach is achieved by interpreting the reaction to the wide stand as competition against hypothetic genotypes that do not grow at all.

When single plants are selected at a wider stand, the effect of intergenotypic interplant competition on the response to selection is completely replaced by the effect of the differential reaction of the genotypes to the wide stand. Then, the density of stand does not affect the outcome of selection in the mixed population. This is traced back to the phenomenon that the rank of the genotypes in a mixture is not influenced by the density at which the mixture is grown. The conclusions hold for diffuse competition. In line selection, however, competition is restricted to nearest neighbour rows. According to the model, density then has a small effect on the outcome of selection.

The density model is based on the assumption that the growth curves of separately grown plants of the genotypes are similar (Section 5.2) and that the variation coefficient is constant over the range of densities (Section 5.3.2). Similarity of the growth curves means that the growth curves are the same except for a multiplication factor on the yield axis. When the growth curves are not similar, especially genotypes with a retarded juvenile development tend to be favoured by selection at a wide stand (Section 5.6).

Methods are developed to estimate competition effects in various types of mixtures of single plants and of rows. The methods deal with binary mixtures with a tester variety, binary mixtures constituted according to a diallel design, border effects in multi-row plots, mixtures where plants or rows of the genotypes are alternated with

plants or rows of a standard variety, mixtures where all genotypes are sown in equal to selection is replaced by the effect of the different reaction of the genotypes to the wider spacing (Section 8.3). Neither is there any reduction in competitional bias when the plants of a segregating population are alternated with plants of a standard variety (Section 8.4.3).

The differences in competitive ability among the barley varieties used in these experiments were mainly due to differences in juvenile growth (Section 8.3.1).

The detrimental effect of soil heterogeneity on the response to selection can be reduced by grid selection and by adjustment via inserted standards or via a moving mean. The methods are evaluated, mainly by a theoretical approach. In plant selection, both latter methods have a low efficiency and present practical problems. On the other hand, dividing the selection field into grids and selecting the best plants from each grid is effective and cheap (Section 8.5).

The effect of intergenotypic competition on *yield testing of progenies* in rows (Chapter 9) is quantified by means of the competition model of Chapter 4. This model is illustrated and tested with the experiments where barley varieties were grown in rows, each variety in a single row. The model predicted the competition effects very well (Section 9.1).

The influence of intergenotypic competition is reduced by growing the progenies in multi-row plots. Therefore, the competition model is extended to describe the effect of plot size on the response to selection (Section 9.2.1).

The theoretical and practical aspects of methods that diminish the bias due to intergenotypic competition are discussed. The same number of kernels should be sown in all rows using seed of the same size and comparable quality with the distance between rows equal to that used by farmers, and with the alleys as narrow as possible. Selection for the grain/biomass ratio, as a method for adjusting for competition, is worth further consideration. Grouping the progenies according to morphological characters is hardly of use in reducing intergenotypic competition and is, moreover, difficult to realize. On the other hand, grouping the progenies according to the cross from which they are derived and to seed size will be effective. Alternating all rows with rows of a standard variety is, however, of no use in reducing the effects of competition.

Yield testing in microplots brings about a large environmental variation or error variation. This can be reduced by replication, use of block designs, grid selection, use of larger plots, and adjustment for soil heterogeneity. The latter method is, however, of questionable value.

The influence of competition on the response to selection is discussed for several plot types with the competition model. The effects are illustrated with the results of variety experiments. Given the present nursery equipment, 3-row plots with all three rows considered in selection for yield, seem the most suitable type of microplot (Section 9.5).

# Samenvatting

In de veredeling beoogt men die genotypen uit een populatie te selecteren die zich, in landbouwkundig gunstige zin, onderscheiden van de andere aanwezige genotypen. Bij de zelfbevruchtende graangewassen worden de geselecteerde genotypen, de rassen, door de boer in monocultuur geteeld. Dus men tracht die typen uit een genetisch heterogene populatie te selecteren die het goed doen in een genetisch homogene monocultuur. In de heterogene populatie beïnvloeden de genotypen elkaar in hun expressie omdat zij concurreren om in beperkte mate aanwezige groeifactoren. Sommige genotypen, de sterke concurrenten, brengen in mengsel meer op dan wanneer ze zouden worden geteeld in monocultuur. Andere genotypen, de zwakke concurrenten, vertonen daarentegen een lagere opbrengst in mengsel dan in monocultuur. Omdat intergenotypische concurrentie resulteert in verschillende opbrengsten van een genotype in mengsel en in monocultuur vertroebelt het de selectie.

Het doel van dit onderzoek is de invloed van concurrentie op de verschillende fasen van veredelingsprogramma's uiteen te zetten en te kwantificeren. Hiertoe is een mathematisch model geïntroduceerd dat de invloed van intergenotypische concurrentie op de selectierespons beschrijft (hoofdstuk 4 en 5). Dit model is getoetst met resultaten van proeven waar gerstrassen geteeld zijn in mengsels en monocultures. De rassenmengsels bootsen hier splitsende populaties na.

Aan de hand van het model en geïllustreerd met de experimentele gegevens is de invloed beschreven van concurrentie op massale vermeerdering (hoofdstuk 7), selectie van individuele planten (hoofdstuk 8) en selectie van nakomelingschappen (hoofdstuk 9). Methoden worden besproken om de verstorende invloed van concurrentie te verminderen.

In de literatuur worden vele, verschillende modellen gebruikt om concurrentie-effecten te analyseren. Het model van De Wit (1960) is voor het gestelde doel superieur en is dan ook als basismodel gekozen (hoofdstuk 3). Dit model levert een expressie voor de opbrengst van een genotype in een mengsel, gemiddeld over alle individuele eenheden. Bij plantselectie is een individuele plant de eenheid van selectie. Bij lijnselectie is meestal een rijtje van planten, alle behorende tot dezelfde lijn, de eenheid van selectie.

Concurrentie tussen de eenheden van selectie is te karakteriseren binnen twee limietsituaties (sectie 4.2). In de ene limietsituatie concurreren alle eenheden in de populatie in gelijke mate met elkaar ('diffuse concurrentie'). Dientengevolge is de opbrengst van een eenheid afhankelijk van de genotypische samenstelling van de gehele populatie. In de andere limietsituatie concurreren slechts de naaste buren met elkaar ('naaste-buur-concurrentie'). In deze situatie is de opbrengst van een eenheid afhankelijk van het genotype van zijn naaste buren en dus onafhankelijk van de genotypische samenstelling

van de gehele populatie.

Het oorspronkelijke model van De Wit beschrijft diffuse concurrentie. Daaruit is een ander model ontwikkeld dat de concurrentie tussen naaste buren beschrijft (sectie 4.2.1). Bij de kleine granen is de concurrentie tussen individuele planten redelijk te karakteriseren als diffuse concurrentie. Daarentegen blijkt een rij slechts te concurreren tegen zijn naaste buren (sectie 4.2.2).

Beide concurrentiemodellen geven een uitdrukking voor de opbrengst van een bepaald genotype in een mengsel en beschouwen niet de toevalsvariatie in de opbrengst van dat genotype in het mengsel. Het zijn deterministische modellen. Daarentegen worden de effecten van genotype en milieu in de genetica in een stochastische vorm geschreven. In beide concurrentiemodellen worden de effecten multiplicatief beschouwd terwijl het genetische model gebaseerd is op additiviteit van genotypische effecten en milieu-effecten. Een uitdrukking is afgeleid voor de genotypische prestatie van een willekeurig genotype in een splitsende populatie, d.w.z. in een mengsel, door de deterministische, multiplicatieve concurrentiemodellen te combineren met het stochastische, additieve genetische model (sectie 4.3.1.1).

In het gecombineerde model worden de fenotypische variantie, genotypische variantie en milieuvariantie in mengsel uitgedrukt als functies van de overeenkomstige varianties in monocultuur. Dit is gedaan voor zowel rijtjes als eenheid van selectie (naaste-buur-concurrentie) (sectie 4.3.1) als voor individuele planten als eenheid van selectie (diffuse concurrentie) (sectie 4.4.5). Het volgende blijkt dan: Indien concurrentievermogen en monocultuuropbrengst niet al te sterk negatief gecorreleerd zijn, is de genotypische variantie in mengsel groter dan die in monocultuur. Dus in het algemeen vergroot intergenotypische concurrentie de verschillen tussen de genotypen. Bij lijnselectie, waar concurrentie beperkt is tot naaste buurrijen, is de verwachte milieuvariantie in mengsel groter dan die in monocultuur. Bij plantselectie, waar concurrentie diffuus is, is daarentegen de verwachte milieuvariantie in mengsel gelijk aan die in monocultuur (sectie 4.5).

De invloed van intergenotypische concurrentie op selectie is uitgedrukt door zijn invloed op de selectierespons. In de genetica wordt onder de respons verstaan de vooruitgang die geboekt wordt in generatie t+1 door selectie in generatie t. Selectie vindt plaats in een heterogene populatie met als doel de genotypen te selecteren die het best voldoen in monocultuur. De centrale vraag luidt dus: in welke mate worden de genotypen gekozen met de hoogste opbrengst in monocultuur in generatie t+1 indien men de fenotypen selecteert met de hoogste opbrengst in een mengsel in generatie t? De centrale vraag is opgesplitst in drie subvragen:

(1) In hoeverre zijn de hoogst opbrengende fenotypen in het mengsel in generatie t tevens de hoogst opbrengende genotypen in dat mengsel in die generatie?

(2) In hoeverre zijn de genotypen met de hoogste opbrengst in het mengsel in generatie t tevens de genotypen met de hoogste opbrengst in monocultuur in die generatie?

(3) In hoeverre handhaven de genotypen die geselecteerd zijn in generatie t hun verwachte monocultuuropbrengst in generatie t+1? (secties 4.4.1 en 4.4.3).

De eerste subvraag refereert naar de mate waarin de genotypen met de hoogste op-

brengst in het mengsel geïdentificeerd worden bij selectie in dat mengsel. De vooruitgang die gemaakt wordt voor opbrengstvermogen in dat mengsel wordt de directe respons voor selectie genoemd. De tweede subvraag definieert de invloed van intergenotypische concurrentie op het selectieresultaat. Selectie voor opbrengst in het mengsel leidt tot een gecorreleerde respons voor monocultuuropbrengst. De derde subvraag betreft het effect van heterozygotie en reproductiewijze op het selectieresultaat (Fig. 12). Deze studie beperkt zich tot de twee eerste subvragen.

De conventionele genetische modellen houden geen rekening met intergenotypische concurrentie en leiden daarom tot onjuiste conclusies bij de genetische analyse van opbrengst (sectie 4.4.3).

Voor zowel de directe respons voor mengselopbrengst als voor de gecorreleerde respons voor monocultuuropbrengst, teweeg gebracht door selectie op opbrengst in mengsel, zijn uitdrukkingen afgeleid (sectie 4.4). De uitdrukkingen gelden ongeacht of de genotypen heterozygoot dan wel homozygoot zijn en ongeacht of men te doen heeft met een zelfbevruchtend dan wel met een kruisbevruchtend gewas; deze effecten komen pas bij de derde subvraag aan de orde.

Intergenotypische concurrentie reduceert de selectierespons sterker naarmate de erfelijkheidsgraad in afwezigheid van intergenotypische concurrentie groter is en naarmate de correlatie tussen concurrentievermogen en monocultuuropbrengst lager is. De sterkte van de concurrentie, de derde bepalende parameter, heeft een wisselende invloed. De effecten zijn geïllustreerd met de resultaten van numerieke simulatie. Intergenotypische concurrentie heeft niet noodzakelijkerwijs een negatieve invloed op de selectierespons maar verhoogt in sommige gevallen de respons.

Er is vaak voorgesteld de invloed van intergenotypische concurrentie uit te sluiten door in een wijde stand te selecteren. Echter, door de wijde stand elimineert men weliswaar de concurrentie tussen planten of tussen rijen, maar men introduceert het effect van de verschillen tussen de genotypen in hun reactie op de wijde stand (genotype x dichtheids interactie).

Het model voor de invloed van intergenotypische concurrentie op de selectierespons (hoofdstuk 4) is uitgebreid met het effect van de standdichtheid op de selectierespons (hoofdstuk 5). Continuïteit in de beschouwing is verkregen door de reactie op de wijde stand te beschouwen als concurrentie tegen hypothetische genotypen die in het geheel niet groeien.

Indien men individuele planten bij een ruime stand selecteert, wordt het effect van intergenotypische interplant concurrentie op de selectierespons volledig vervangen door het effect van de verschillende reactie van de genotypen op de ruime stand. De standdichtheid heeft dan geen invloed op het resultaat van selectie in een mengsel. Dit is terug te voeren op het verschijnsel dat de volgorde van de genotypen in een mengsel niet wordt beïnvloed door de dichtheid waarbij dat mengsel wordt geteeld. De conclusies gelden voor diffuse concurrentie. Indien concurrentie beperkt is tot naaste buren, zoals bij lijnselectie, heeft de standdichtheid een, overigens gering, effect op het selectieresultaat.

Het dichtheidsmodel is gebaseerd op de veronderstelling dat de groeicurven van geïsoleerd groeiende planten van de genotypen gelijkvormig zijn (sectie 5.2) en dat de

variatiecoëffiënt constant is over de reeks van dichtheden (sectie 5.3.2). Gelijkvormigheid van groeicurven houdt in dat de groeicurven gelijk zijn afgezien van een vermenigvuldigingsfactor op de opbrengst-as. Indien de groeicurven ongelijkvormig zijn tenderen met name de genotypen met een vertraagde juveniele ontwikkeling bevoordeeld te worden door selectie in een wijde stand (sectie 5.6).

Voor uiteenlopende typen van mengsels van individuele planten en van rijen zijn methoden ontwikkeld om de concurrentie-effecten te schatten. Het betreft hier binaire mengsels met een toetsras, binaire mengsels samengesteld volgens een diallele opzet, randeffecten in veldjes die bestaan uit meerdere rijen, mengsels waarin planten of rijen van de genotypen zijn gealterneerd met planten of rijen van een standaardras, mengsels waar alle genotypen in een gelijke verhouding zijn uitgezaaid (sectie 6.2).

Bij *massale vermeerdering* van een kruisingspopulatie (hoofdstuk 7) veranderen de genfrequenties in de populatie tengevolge van natuurlijke selectie. In hoeverre vindt de verandering plaats in de door de kweker gewenste richting? D.w.z., in hoeverre zijn de typen die bevoordeeld worden door natuurlijke selectie tevens de typen met de hoogste opbrengst in monocultuur? Natuurlijke selectie bevoordeelt de typen met de grootste reproduktiesnelheid. Centraal staat dus de correlatie tussen de reproduktiesnelheid in mengsel en de opbrengst in monocultuur. Deze correlatie is uitgedrukt in termen van het concurrentiemodel van De Wit (sectie 7.2).

De reproduktiesnelheid van een genotype is het produkt van zijn concurrentievermogen in mengsel en zijn korrelproduktie in monocultuur. Deze definitie suggereert reeds een tendens naar een positieve correlatie tussen reproduktiesnelheid en monocultuuropbrengst. In de experimenten met gerstrassen was deze correlatie steeds positief (sectie 7.3.3). Ook de literatuur over rassenmengsels en 'composite crosses' wijst op een, in het algemeen, positief verband tussen reproduktiesnelheid en monocultuuropbrengst (sectie 7.5). Mede op basis van deze relatie is geconcludeerd dat natuurlijke selectie en concurrentie geen hinderpaal vormen voor het uitstellen van selectie op opbrengst tot de late generaties van een kruisingspopulatie.

De waarde van een populatie voor een kweker wordt gemeten door het gemiddelde en de variantie voor opbrengst. De opbrengst verwijst naar de opbrengst in monocultuur aangezien deze, en niet de opbrengst in het bepaalde mengsel, van belang is voor de kweker. De verschuiving van het gemiddelde en de variantie van monocultuuropbrengst in opeenvolgende generaties van massale vermeerdering is geïllustreerd met gegevens van een rassenmengsel (sectie 7.3.5).

De monocultuuropbrengst van heterozygoten is bij de zelfbevruchtende granen meestal beduidend groter dan die van de overeenkomstige homozygoten. Omtrent het concurrentievermogen van heterozygoten ten opzichte van homozygoten kan op basis van literatuurgegevens geen duidelijke uitspraak worden gedaan aangezien de in de literatuur beschreven experimenten inadequaat zijn opgezet. De reproduktiesnelheid van heterozygoten is in het algemeen groter dan die van de overeenkomstige homozygoten (sectie 7.4).

De invloed van intergenotypische concurrentie op het resultaat van *selectie van individuele planten* (hoofdstuk 8) is gekwantificeerd met behulp van het concurrentiemodel van hoofdstuk 4. Dit model is toegelicht en getoetst aan experimenten waar gerstrassen zijn geteeld in mengsels en monocultures. De voorspellingen, verkregen uit het model, van de selectierespons en de intermediaire parameters kwamen goed overeen met de waarden waargenomen in de mengsels (sectie 8.2.3).

De invloed van concurrentie op het selectieresultaat wordt op een goedkope en effectieve wijze gereduceerd door het zaad te zeven naar grootte en slechts zaden van ongeveer dezelfde grootte in één veldje uit te zaaien (sectie 8.4.2). De korrel/biomassa-verhouding wordt niet door concurrentie beïnvloed. Indien tevens in monocultuur de genotypen met de hoogste korrel/biomassa-verhouding ook het meeste opbrengen, dan corrigeert men door selectie op korrel/biomassa-verhouding de opbrengst van de planten voor hun concurrentievermogen (sectie 8.4.5).

Een ruime stand reduceert niet het effect van intergenotypische concurrentie omdat, gaande naar een wijdere stand, het effect van intergenotypische interplantconcurrentie op de selectierespons wordt vervangen door het effect van de verschillende reactie van de genotypen op de ruimere stand (sectie 8.3). Ook het alterneren van de planten van een splitsende populatie met planten van een standaardras vermindert niet het effect van intergenotypische concurrentie op de selectierespons (sectie 8.4.3).

De verschillen tussen de gerstrassen in concurrentievermogen berustten vooral op verschillen in juveniele groei (sectie 8.3.1).

Het verstorend effect van bodemheterogeniteit op de selectierespons kan gereduceerd worden door vakselectie en door correctie via ingelaste standaarden of via een schuivend gemiddelde. De methoden zijn vooral theoretisch geëvalueerd. In plantselectie zijn de beide laatstgenoemde methoden weinig efficiënt en stuiten bovendien op praktische bezwaren. Het verdelen van het selectieveld in vakken en het selecteren van de beste planten binnen ieder vak is daarentegen effectief en goedkoop (sectie 8.5).

De invloed van intergenotypische concurrentie op *opbrengsttoetsing van nakomelingschappen* in rijtjes (hoofdstuk 9) is gekwantificeerd met behulp van het concurrentiemodel van hoofdstuk 4. Dit model is toegelicht en getoetst aan de experimenten waar gerstrassen geteeld werden in rijtjes, ieder ras in een enkele rij. Het model gaf een goede voorspelling van de concurrentie-effecten (sectie 9.1).

De invloed van intergenotypische concurrentie wordt gereduceerd door de nakomelingschappen te telen in veldjes die bestaan uit meerdere rijen. Daarom is het concurrentiemodel uitgebreid met de beschrijving van het effect van veldjesgrootte op het selectieresultaat (sectie 9.2.1).

De theoretische en praktische aspecten van methoden om de invloed van intergenotypische concurrentie te reduceren zijn besproken. Het is aanbevolen om in alle rijen hetzelfde aantal korrels te zaaien, slechts zaad te gebruiken van gelijke grootte en vergelijkbare kwaliteit, een rijafstand te gebruiken die gelijk is aan die toegepast wordt door de boer en de paden zo smal mogelijk te maken. Selectie op korrel/biomassa-verhouding lijkt waardevol om nader bestudeerd te worden als methode om te corrigeren voor concurrentie. Groepering van nakomelingschappen naar morfologische eigenschappen is weinig

effectief in het reduceren van concurrentie en bovendien moeilijk te realiseren. Groepering van nakomelingschappen naar de kruising waarvan zij zijn afgeleid en naar zaadgrootte zal effectief zijn. Het alterneren van de rijen met rijen van een standaardras heeft daarentegen geen nut in het verminderen van de concurrentie-effecten.

Opbrengsttoetsing in microveldjes brengt een grote milieu- of toevalsvariatie met zich mee. Deze is te reduceren door het uitleggen van parallellen, het gebruik van blokkenproeven, vakselectie, het gebruik van grotere veldjes en correcties op bodemheterogeniteit (sectie 9.4).

De invloed van concurrentie op de selectierespons bij de diverse typen van veldjes is toegelicht aan de hand van het concurrentiemodel en geïllustreerd met de resultaten van de rassenproeven. Uitgaande van de huidige proefveld-outillage lijken veldjes van 3 rijen, waarvan alle drie de rijen gebruikt worden voor de opbrengstbepaling, de meest geschikte vorm van microveldjes (sectie 9.5).

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