

Effects of intergenotypic competition on selection

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Summary

A quantitative analysis of intergenotypic competition and its effects on selection is given with a stochastic model and with a simple eco-physiological approach. The principles are illustrated with cereals.

In the stochastic model, expressions are derived for the components of variance in mixture and for the expected response to selection. Selection in a mixture of genotypes is considered to be an indirect way of selection for monoculture performance. Rules of thumb based on the model are developed for the expected response after single-plant selection and after progeny testing with different types of microplots.

On the basis of a simple crop growth model, a concept for the growth of genotypes in a mixed population is developed. In many cases, the relative differences among the genotypes remain about the same during their growth in mixture. Then, the competitive ability of a genotype can largely be explained by its starting position. This is confirmed by the results of an experiment with 12 wheat varieties grown in mixture.

Descriptors: competition, selection, breeding method, model, experimental design, cereals, wheat, *Triticum aestivum*

Introduction

In plant breeding, effects of intergenotypic competition are studied empirically. Often a genotype is grown in monoculture as well as in a mixture with other genotypes. The yield of the genotype in mixture differs from its yield in monoculture. Thus it is concluded that intergenotypic competition may bias the outcome of selection. But how large is that bias? Is it worth developing a method to reduce this bias? To arrive at answers we need to know how intergenotypic competition lowers the selection response, and what plant characters determine competitive ability.

This paper presents a theory about the effect of intergenotypic competition on the yields of genotypes in a mixed population and on the result of artificial selection. We will follow step by step the path by which selection of single plants or progenies leads to a certain response. This is examined with an empirical, stochastic model. To gain insight into the causal factors of competitive ability of a genotype in mixture, a simple model is presented that is based on principles of crop physiology. From both models, techniques are derived to reduce the competition bias, with the effectiveness of the techniques being quantified. The principles of the competition effects are illustrated with cereals.

An empirical, stochastic approach for the selection response

The central question is: to what extent is the response to selection affected by competition between the genotypes in the population to which the selection is applied? Let us consider selection for yield. As the farmer grows his crops in genetically uniform monocultures, the yield of a genotype in mixture should be related to its yield in monoculture. Thus selection response should be measured by the progress made for yield in monoculture.

If we assume an expression for the expected yield of a genotype in mixture as a function of its yield in monoculture, we can then derive how the components of variance for yield alter with intergenotypic competition. We need to know that in order to derive an expression for the response of yield in monoculture to selection for yield in mixture.

The approach has been described fully in Spitters (1979). There the model was tested with the results of trials on single-plant selection and progeny testing in barley.

The stochastic model

Expected yield in mixture As genotypes are selected for their performance in monoculture, we express the yield of a genotype in mixture as a function of its yield in monoculture.

Many experiments show that competition is not additive but multiplicative, a conclusion supported by the physiological approach. This means that in a mixture of two genotypes, the percentage gain in yield per plant by a genotype equals the percentage loss in yield per plant by the other genotype, with gain and loss being expressed relative to their respective yields in monoculture. This proportionality between the expected yield of a genotype i in any mixture and its yield in monoculture is given by

$$Y_{i, \text{mix}} = b_i Y_{i, \text{mono}} \quad (1)$$

The proportionality factor b is a measure of the competitive ability of the genotype in the mixture and is estimated empirically by dividing its yield per plant in mixture by its yield per plant in monoculture.

Equation 1 implies that the yield of a plant depends on the genetic make-up of the entire population rather than on the genetic composition of its nearest neighbours. In cereals, this situation is approximated by individual plants where each plant affects to a considerable degree the plants that are farther than the nearest neighbours (diffuse competition). On the other hand, a row of plants influences only its adjacent rows (nearest-neighbour competition). Only diffuse competition among single plants is considered here. Corresponding expressions for nearest-neighbour competition, i.e. for testing of progenies in row plots were described in Spitters (1979, p. 57, 66-68).

Components of variance The yield of a plant in a population is a stochastic quantity, a function of the two random variables genotype and environment. The observed yield of a plant, its phenotype, is represented by the linear function

$$p = \mu + g + e$$

where \underline{g} is the deviation from the population mean μ due to genotype and \underline{e} is the deviation from the population mean due to environmental and other uncontrolled factors. (Stochastic variables are underlined in the text.)

From Equation 1, we may derive yield of a plant in mixture

$$\underline{p} = \underline{b}(\mu + \underline{g}) + \underline{e} \quad (2)$$

The aggregate environmental effect \underline{e} is taken as additive in accordance with the usual approach in genetics.

For a normally distributed variable, the distribution can be characterized by the mean (the expected value) and the variance. Expressions for the components of variance may be derived from Equation 2. Due to the multiplicative form, only approximate results can be obtained (Spitters, 1979, p. 51-53, 68-69).

For the phenotypic variance in mixture, i.e. the variance among the single plants in the mixture, we obtain

$$\text{var } \underline{p}_{\text{mix}} \approx \text{var } \underline{g}_{\text{mono}} + 2\mu \text{cov}(\underline{b}, \underline{g}_{\text{mono}}) + \mu^2 \text{var } \underline{b} + \text{var } \underline{e}_{\text{mono}} \quad (3)$$

where μ is the population mean of the monocultures. This phenotypic variance in mixture can be partitioned into the variance among genotype means in the mixture, the genetic variance

$$\text{var } \underline{g}_{\text{mix}} \approx \text{var } \underline{g}_{\text{mono}} + 2\mu \text{cov}(\underline{b}, \underline{g}_{\text{mono}}) + \mu^2 \text{var } \underline{b} \quad (4)$$

and the environmental variance

$$\text{var } \underline{e}_{\text{mix}} = \text{var } \underline{e}_{\text{mono}} \quad (5)$$

Response to selection The ultimate interest of the breeder is the progress to be expected with selection for yield. That progress is the progress for monoculture yield when selection is for yield in a mixed population. Let us distinguish two independent steps (Figure 1): (1) the extent to which the selected plants are the genotypes with the highest yield in the particular environment, i.e. in that particular mixture; (2) the extent to which the genotypes with the highest yield in the mixture, yield most in monoculture.

The first step measures the accuracy of yield testing and is represented in the right-hand quadrant of Figure 1. The selected plants have a mean phenotypic yield of \bar{p}_s . The difference between this mean and the population mean \bar{p} is called the selection differential S_{mix} . If the regression of genotype on phenotype is rectilinear the response to selection is

$$R_{\text{mix}} = rc_{R,S} S_{\text{mix}}$$

where rc is the slope of the linear regression. Substitution of the statistical definition of the regression coefficient gives

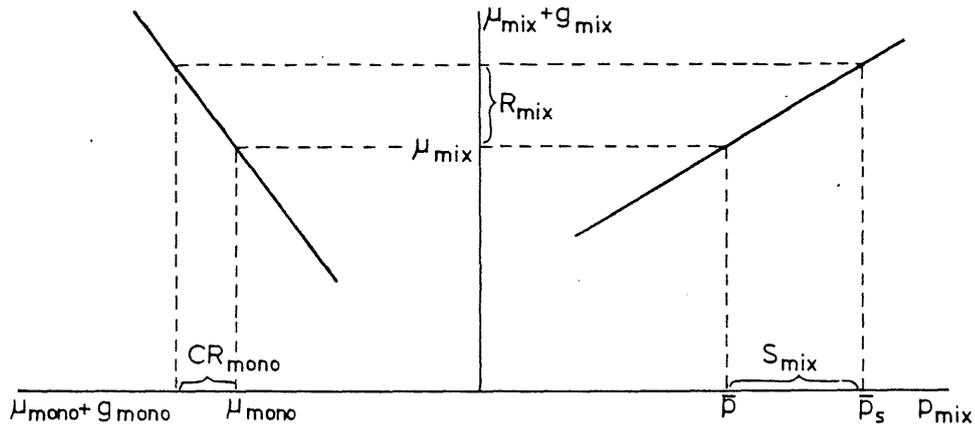


Fig. 1. Correlated response for yield in monoculture due to selection for yield in mixture. Right: Accuracy of yield testing represented by the regression of genotype on phenotype in mixture, showing the selection differential S_{mix} and the selection response R_{mix} for yield in mixture. Left: Interaction between genotype and competition environment represented by the regression of genotype in monoculture on genotype in mixture showing the relation between selection response for yield in mixture (R_{mix}) and correlated response for yield in monoculture (CR_{mono}).

$$R_{mix} = \frac{\text{cov}(g_{mix}, p_{mix})}{\text{var } p_{mix}} \quad S_{mix} = \frac{\text{var } g_{mix}}{\text{var } p_{mix}} S_{mix} = h_{mix}^2 S_{mix}$$

The heritability h_{mix}^2 measures that part of the total phenotypic variation which can be ascribed to genetic differences between plants.

Division of the selection differential S_{mix} by the phenotypic standard deviation transforms S_{mix} into a dimensionless parameter called 'intensity of selection': $i_{mix} = S_{mix} / \sqrt{\text{var } p_{mix}}$. Falconer (1960, p. 194) showed that, with a normal distribution of the measurements, i_{mix} is a simple function of the percentage of individuals selected.

The response to selection can now be extended to

$$R_{mix} = h_{mix}^2 S_{mix} = i_{mix} \sqrt{h_{mix}^2 \text{var } g_{mix}} \quad (6)$$

The response R_{mix} represents the progress in yielding ability in that particular mixture, a character of no interest to the breeder. For this reason we need a second step: the correlated progress in yield in monoculture due to selection in mixture. This is represented in the left-hand quadrant of Figure 1. The correlated response for yield in monoculture is

$$CR_{mono} = r_{c_{mono}, mix} R_{mix} \quad (7)$$

After elaboration of the regression coefficient and substitution of Equation 6, we obtain

$$CR_{mono} = R_{mix} r_g \sqrt{\text{var } g_{mono} / \text{var } g_{mix}} = i_{mix} r_g \sqrt{h_{mix}^2 \text{var } g_{mono}} \quad (8)$$

where r_g is the correlation between the yield of a genotype in monoculture and its yield in mixture.

By extending Figure 1 with a third quadrant, allowance can be made for the drop in response from the generation of selection to the next generation due to the genotypes not being true to seed. With a fourth quadrant allowance can be made for the genotype \times environment interaction arising from the deviation of the growing conditions (husbandry, location, year) where selection has been practised from average farm conditions.

To compare trials with different yield levels, the equations should be formulated in terms of dimensionless variables that are expressed relative to the yield level. This is achieved by expressing variances in terms of coefficients of variation with the coefficient of variation being the standard deviation divided by the population mean μ :

$$CV_e = \sqrt{\text{var } e} / \mu \text{ and } CV_g = \sqrt{\text{var } g} / \mu$$

The responses R_{mix} and CR_{mono} are also divided by the population mean μ . This approach with dimensionless quantities is adopted below. Table 1 summarizes the relevant quantities and equations. The symbols R_{mix} and CR_{mono} are also used for the relative responses.

Illustration of the model and order of magnitude of the competitive bias

The theoretical model was developed to elucidate the lines along which intergenotypic competition biases the outcome of selection. General principles will now be illustrated and an order of magnitude for the effects will be indicated.

Table 1. Coefficients of variation and predicted responses for selection on the basis of grain yield of single plants, 1-row plots, the centre row and all three rows of 3-row plots, and field plots 10 metres square. The values are computed according to Spitters (1979, p. 61, 57, 67, 69, 222). Inputs were $CV_{g, \text{mono}} = 0.05$, $\sqrt{\text{var } b} = 0.20$, $r_{b, g} = 0$, $i = 1.75$ (10% selected), $CV_{e, \text{mono}} = 0.40, 0.20, 0.12, 0.06$ for single plants, single rows, 3-row plots and field plots, respectively. $CV_{e, \text{mono}}$ is the CV_e in absence of intergenotypic competition. The values are considered to be representative for small-grain cereals. The row plots are 2 m long with rows 20 cm apart.

	Single plant	1-row plot	3-row plot		Field plot
			centre	3 rows	
CV_g	0.21	0.11	0.05	0.06	0.05
CV_e	0.40	0.21	0.20	0.12	0.06
$CV_p = \sqrt{(CV_g^2 + CV_e^2)}$	0.45	0.24	0.21	0.13	0.08
$h^2 = CV_g^2 / CV_p^2$	0.21	0.22	0.06	0.20	0.41
$R = i \cdot CV_g \cdot \sqrt{h^2}$	0.17	0.09	0.02	0.05	0.06
$CV_{g, \text{mono}} / CV_{g, \text{mix}}$	0.24	0.45	1.00	0.83	1.00
r_g	0.24	0.45	1.00	0.83	1.00
$CR_{\text{mono}} = R_{\text{mix}} \cdot r_g \cdot CV_{g, \text{mono}} / CV_{g, \text{mix}}$	0.010	0.018	0.021	0.033	0.056

Justification of the applied approach Results of experiments with barley have been used to illustrate the model (Spitters, 1979, p. 163-165, 213-218, 237-245). Any experiment, however, involves only one out of an infinite number of combinations of the population parameter values, which makes it hard to arrive in such an empirical way at rules of thumb about the orders of magnitude of the competition effects. Let us therefore discuss the output from the model, generated with input values that are considered to be realistic averages.

Order of magnitude of the input variables and calculation procedure Input values are given in the caption of Table 1. These estimates are mainly from five years of experiments with barley and spring wheat on sandy clay-loam at Wageningen (Spitters, 1979; Kramer et al., 1982).

The coefficient of genetic variation (CV_g) was that among F_5 or F_6 lines grown in pure stand. A range of 2 to 12% seems quite normal for CV_g . The values for the coefficient of the environmental variation (CV_e) were derived from trials where all the studied types of plot were present. Their ratios will have more general application than their absolute values. The standard deviation of the competitive ability $\sqrt{(\text{var } b)}$ is in the order of 20%. In other words, for 95% of the genotypes yield in mixture deviates less than 40% ($=100 \times 1.96 \sqrt{(\text{var } b)}$) from yield in monoculture. On the whole, there is little relation between the competitive ability of a genotype and its yield in monoculture ($r_{bg} \approx 0$).

From these input values, the components of variance and the response to selection were estimated with the model for several methods of yield testing: single-plant selection and progeny testing with different types of plot (Table 1). The estimates for single plants were obtained from Equations 4-8. As mentioned already, dimensionless variants of these equations were used. The computations for the other situations were based on equations presented in Spitters (1979, p. 57, 61, 67, 222).

To interpret the results, bear in mind that 'interplot' competition is most severe among single plants; it is smaller between 1-row plots; it is slight between 3-row plots and it is negligible between the centre rows of neighbouring 3-row plots and between large field plots. Not only effects of intergenotypic competition are involved but also effects of sample size. A larger plot size implies a greater sample size which reduces CV_e .

Genetic and environmental variance in mixture The genetic variance in mixture is greater than that in monoculture, provided that the correlation between competitive ability and monoculture yield is not too strongly negative (Equation 4). For the parameter values used in Table 1, the genetic variance CV_g^2 in the single-plant mixture was more than 17 times as large as that in monoculture.

On the other hand, the environmental variance, i.e. the variance among entries having the same genotype, is not affected by the diffuse intergenotypic competition among single plants and only very little by the nearest-neighbour competition between rows (compare CV_e for 1-row plots with that for the centre rows of 3-row plots in Table 1). The other differences in CV_e in Table 1 were caused by differences in sample size.

Response to selection As the genetic variance is enhanced while the environmental variance remains practically unchanged, the share of the genetic variation in the total phenotypic variation increases due to intergenotypic competition. Because of this increased heritability, together with the increased genetic variation, the direct response to selection will be greater in presence of intergenotypic competition than in absence of it (Equation 6; contrast 1-row plots with centre rows). The effect of competition may be such that selection of single plants in mixture results in even greater response than selection based on complete field plots with monocultures: 17% against 6% (R in Table 1). Thus discrimination among genotypes for yielding capacity is easier with than without intergenotypic competition.

However yielding capacity in mixture is of no interest because varieties are grown in pure stand. We have to deal with the correlated response for yield in monoculture CR_{mono} , which is the result of the selection for yield in mixture. This correlated response is smaller than the direct response for yield in mixture because the yields in the two environments do not perfectly correspond ($r_g < 1$) and because the useful genetic variation is smaller than that in the selection environment ($CV_{g,mono}/CV_{g,mix} < 1$). The more intense the competition, the greater the reduction from R_{mix} to CR_{mono} (Table 1). Thus, although competition acts as a magnifying glass (increased genetic variation), that glass has severe spherical aberration (correlation coefficient less than one).

The optimum type of plot for yield testing The progress after selection is measured by the correlated response for yield in monoculture CR_{mono} . The field plots show the greatest progress, followed by 3-row plots, single rows and single plants, in that order (Table 1).

A breeder aims to maximize his profits, i.e. the difference between the output (response) and the input (costs) of the selection process. Response and costs should be expressed in the same dimension, e.g. both in monetary values. Now the problem arises how the yield response, calculated with the model, has to be converted into a financial response. The relation between financial and yield response seems S-shaped, rather than linear. With small yield responses, the chance of identifying a genotype that produces a successful variety seems disproportionately small. With high yield responses the law of the diminishing returns will hold. This S-shaped relation is allowed for in an extreme way by assuming that at least the yield response attained with the unreplicated field plots is required to get any financial return. This approach will be worked out now, the more as some principles emerge.

The correlated responses of the different types of plot relate to each other as 0.18 : 0.32 : 0.38 : 0.58 : 1.00, respectively (CR_{mono} in Table 1). To achieve the same response as with the field plots, the response of the microplots should be enhanced. Equation 8 shows that this can be done by increasing $\sqrt{(h^2)}$ or i , that is (1) by testing each entry with a greater number of replicates, which reduces CV_c and consequently enhances the heritability or (2) by increasing the number of entries, which makes it possible to increase the selection intensity i .

For single plants and 1-row plots, $\sqrt{(h^2)}$ should be increased by a factor 5.6 and 3.1, respectively (Equation 8) to level the difference from field plots. Table 1 then shows that the heritability should be increased to more than one, an impossibility since genetic variance never exceeds phenotypic variance. Hence, these plot types are inferior to field

plots, given the input values studied in the model. Harvesting only the centre row of a 3-row plot is also inferior as it will be hardly cheaper than harvesting all three rows, and as it yields a substantial lower response.

To bring the response after selection for yield of all three rows of the 3-row plots to the level in field plots, either i or $\sqrt{(h^2)}$ should be enhanced with a factor 1.7. So, $\sqrt{(h^2)}$ should be magnified to 0.77. Given the CV_g of 0.06, this needs a decrease of CV_e from 0.12 to 0.05, which is achieved with 6 replicates of each entry. As an alternative, i may be increased by the factor 1.7 to a value of 3.0, which corresponds with a selection intensity of 0.4%. Compared to the 10% selection imposed on the field plots, it means a 25-fold increase in population size.

With respect to increase in number of replicates and with respect to stiffer selection, the law of the diminishing returns holds. So there is an optimum for the combination of the two parameters where the number of plots to be tested is minimal. Under the conditions studied, trial and error showed that the optimum was an increase in the number of entries to be tested by 35% and replicating each entry 4 times. Therefore, when the costs of using $1.35 \times 4 (= 5.4)$ 3-row plots are less than of one field plot, yield testing on the basis of 3-row plots would be more profitable. Values for a greater genetic variation in pure stand and for stiffer selection on the field plots are given in Table 2.

The above also suggests that it would be more profitable to evaluate a moderate number of (promising) entries accurately in replicated plots than to test many entries without replication. This trend is stronger, the smaller the heritability and the greater the selection intensity. Bos (1983) has worked out this balance between replication and intensity of selection in more detail.

Table 1 needs some comment. It is claimed that the values substituted for the input parameters were sufficiently accurate to generalize the conclusions. These conclusions were supported by experimental evidence (Spitters, 1979, p. 237-245; Kramer et al., 1982). Nevertheless, there will be situations where some of the findings become modified

Table 2. Increase in the number of replicates r and the number of entries to be tested by a factor n in 3-row plots to achieve the same response as in unreplicated field plots ($r = 1, n = 1$). Given is that combination of r and n that fulfils this requirement with the smallest increase in the total number of 3-row plots. The total number increases by the factor N . Calculations are for two levels for genetic variation of yield in monoculture and for intensity of selection in the field plots.

$CV_{g, mono}$	$i = 1.75$ (10 %)		$i = 2.06$ (5 %)	
	$r \times n$	$= N$	$r \times n$	$= N$
0.05	4×1.35	$= 5.4$	6×0.96	$= 5.8$
0.10	2×1.85	$= 3.7$	3×1.50	$= 4.5$

as there is a substantial variation in the parameters among populations and selection nurseries. Moreover, the prospects of selection on microplots will be somewhat overestimated if agricultural practice in the breeding nursery differs more widely from that in commercial farming. If lack of seed or shortage of land impose restrictions on the larger plot types, yield testing based on single plants or 1-row plots might become useful.

The major drawback, however, concerns the break-even ratio of the costs of a microplot compared to the costs of a field plot. This ratio was calculated on the assumption that at least the yield response attained with the unreplicated field plots was required to get any financial return from yield testing. This is an arbitrary assumption and only illustrates a way of thinking. It emphasizes that choice of optimum plot type will be achieved only when economic aspects are integrated into research on field plot technique.

A causal physiological approach for the characters determining competitive ability

In the preceding, yield in mixture was related to yield in monoculture in an empirical way (Equation 1). Such an empirical relation does not clarify the causal factors determining that relation. Understanding of the processes in a system is, however, prerequisite to intervene in that system in an effective and reliable way.

A simple model is presented below for the growth of a genotype in monoculture and in mixture. The model will be used to derive which characteristics give a high yield in mixture and which give a high yield in monoculture. Subsequently, measures are derived to reduce the bias due to intergenotypic competition. We recently elaborated on this approach (Spitters & Aerts, 1983; Spitters, 1984).

Simple model for growth in mixture

Growth in monoculture In the early stages after emergence, a plant increases almost exponentially in weight. This exponential increment results from an exponential increase of the growth rate, attributable to an exponential rise in the amount of light intercepted (Figure 2). When the canopy closes, plants start hindering each other in the extension of their light interception. Exponential growth ends and competition for light begins. From the time that the canopy has closed, the crop intercepts a constant maximum fraction of the incident light. If light is the main limiting factor, the daily growth rate becomes approximately constant so that the total dry weight increases almost linearly with time (Figure 2).

Growth in mixture We may extend the approach for monocultures to a mixture of two genotypes (Figure 3). Initially, there is no interplant competition. The plants grow almost exponentially, as in monoculture. Once the canopy has closed, nearly all the incident light is intercepted. The light is distributed over the genotypes according to their share in the total leaf area. If the genotypes produce an equal area of new leaf for each unit of absorbed light energy, their shares in the total canopy remain constant (horizontal lines in Figure 3 right). As growth rate is related linearly to the amount of intercepted light, growth in mixture proceeds linearly with time, but for each genotype at a different rate. Owing to these differences in growth rate, the differences between the genotypes

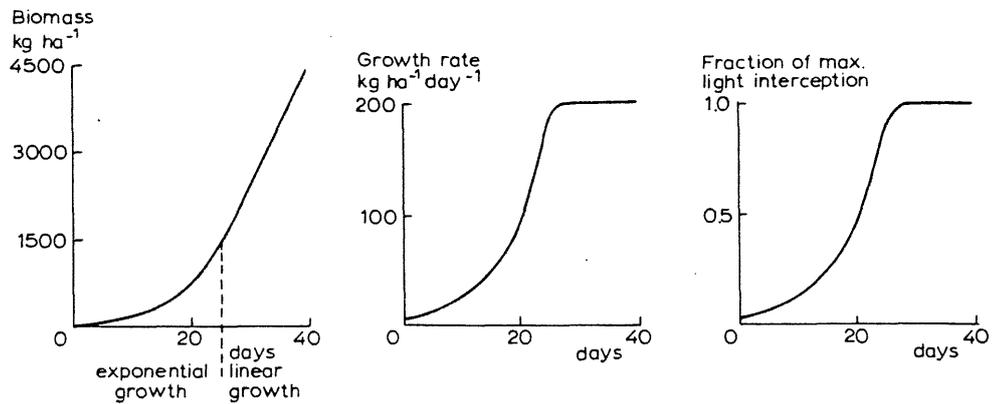


Fig. 2. Progression in time after emergence of total biomass, of daily growth rate, and of fraction of maximum light interception. Schematic example for a spring-sown cereal, illustrating the transition of exponential into linear growth.

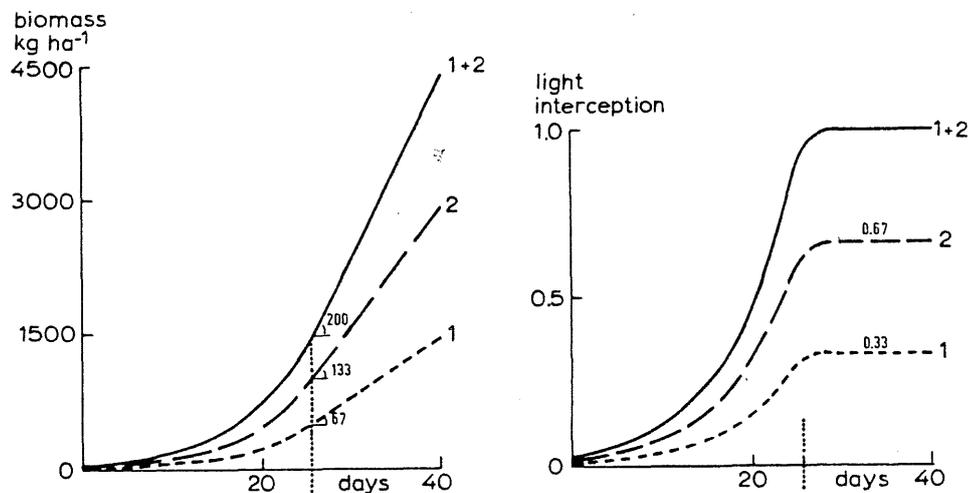


Fig. 3. Progression in time after emergence of biomass and of light interception of two genotypes in a mixed crop. Their totals are identical to those in Figure 2. The initial weight of Genotype 2 was supposed to be twice that of Genotype 1. The slope of the biomass curves represents the growth rate expressed in $\text{kg ha}^{-1} \text{day}^{-1}$.

increase with time (Figure 3 left).

If the share of a genotype in the total canopy remains constant, then this portion equals the share the genotype has at the time the crop is closing. When the genotypes grow at an equal percentage per day during the exponential phase, i.e. when they have the same relative growth rate (RGR), their shares can be fully predicted from their initial weights. This is so in Figure 3 where Genotype 2 possesses twice as heavy seedlings as

Genotype 1. Because the genotypes have the same RGR during their exponential growth (parallel lines on a logarithmic scale), the relative differences are maintained and Genotype 2 acquires twice as large a portion of the canopy. That enables it to grow in the linear phase at twice the rate.

Although the absolute differences between the genotypes in the mixture swell up with time, their relative differences remain constant. The double final biomass of Genotype 2 is fully explained by its seedlings being twice as heavy. This principle holds also when other factors than light limit growth.

Characters determining the competitive ability of a genotype

Deductions from the growth model From the previous concept, one may deduce the strategy a genotype leads to produce a large biomass in mixture. We may loosely define this as a high competitive ability.

The initial status appeared to be critical. A favourable initial status is achieved with a high initial biomass per m², which is attained either at many seedlings per m² or with heavy seedlings. Heavier seedlings are obtained from larger seeds and with earlier emergence.

The relative differences among the genotypes in mixture are, by definition, only maintained if they have the same relative growth rate in course of time, in the exponential as well as in the linear growth stage. This was supposed in Figure 3. However the 'space' may be redistributed in the mixture in favour of the genotypes with the higher relative growth rate. Dry matter increment per unit biomass per unit time (relative growth rate, RGR) can be partitioned into dry matter increment per unit leaf area per unit time (net assimilation rate, NAR) and amount of leaf area formed per unit biomass (leaf area ratio, LAR). Thus, when light is the main growth limiting factor, a genotype will improve its share in the total canopy when it produces more dry matter per unit absorbed light (higher NAR), when it forms a greater leaf area per unit dry weight (greater LAR), or when its leaves are more favourably placed through a greater plant height (higher NAR). When factors other than light are limiting, the process of redistribution of the space becomes somewhat more complex, although a great leafiness is mostly advantageous. If space is redistributed, the relative differences between genotypes in mixture do not remain constant but change with time. This becomes more important the more prolonged competition is, as in perennials.

The characters that determine the competitive ability of a genotype are summarized in Table 3.

The dominating effect of initial status An experiment with 12 wheat varieties grown in mixture at 5 × 5 cm² plant⁻¹ confirmed that genetic differences in biomass production in mixture can be largely ascribed to differences in initial status, expressed as seedling weight ($r^2 = 0.71$, Figure 4). Thus, the simple approach of Figure 3 appears to be useful in the field too.

Differences in seedling weight were partly due to differences in seed weight ($r^2 = 0.64$) and partly to differences in earliness of emergence ($r^2 = 0.54$). Seedling weights predicted from both, by means of the exponential growth function with an RGR of 0.16 d⁻¹, fully

Table 3. Characters determining the biomass production of a genotype in mixture and with that also its competitive ability.

Initial status	<div style="display: flex; align-items: center;"> <div style="margin-right: 10px;"> \swarrow \searrow </div> <div style="text-align: center;"> weight per seedling number of plants per m² </div> <div style="margin-left: 10px;"> <div style="display: flex; flex-direction: column; align-items: center;"> <div style="margin-bottom: 5px;">\swarrow</div> <div style="margin-bottom: 5px;">\searrow</div> </div> <div style="display: flex; flex-direction: column; align-items: center;"> <div style="margin-bottom: 5px;">weight per seed</div> <div>earliness of emergence</div> </div> </div> </div>
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RGR in exponential phase

Redistribution of 'space'

- biomass produced per unit of limiting resource absorbed
- absorption capacity formed per unit biomass
- spatial position with respect to absorption of the limiting resource ('priority')

Length of (vegetative) growing period

explained the differences in weights of seedlings ($r^2 = 1.01$; Figure 4). (These correlations were obtained after adjustment for the error variation of the variety means.)

The genetic variation for initial status was very small: 10% for the genetic coefficient of variation for seed weight and 9 h for the genetic standard deviation of time of emergence. It is remarkable that such small initial differences between genotypes have such a strong influence on their final biomass in mixture. It was noted already that, with certain assumptions, the relative differences are maintained in mixture. On the strength of these assumptions a doubling of final biomass of a genotype in mixture (a 100% yield advantage) is gained with twice as heavy a seedling, either with seeds twice as large or with emergence 4.6 days earlier (RGR = 0.15 d⁻¹).

Many authors have tried to relate competitive ability to morphological characteristics. They often failed, as is illustrated with the finding of Sakai (1961) that 'competitive

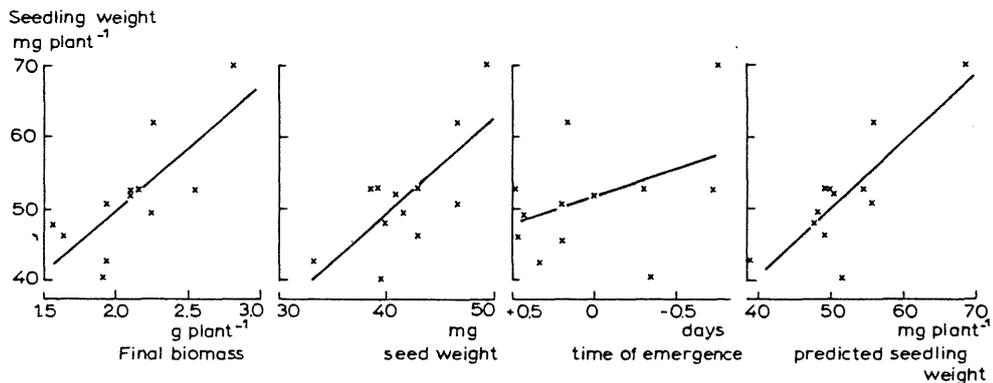


Fig. 4. The final biomass of 12 wheat varieties in mixture in relation to their seedling weights on day 22. The varietal differences in seedling weight are explained by differences in seed weight, time of emergence and the combination of both ($\hat{w}_{22} = w_0 \exp(0.16 \times 22)$). The genetic correlation, i.e. the correlation after adjustment for the error variation of the varietal means, is 0.84, 0.80, 0.73, and 1.00 respectively.

ability was not associated with morphological traits which might be supposed to favour competition'. This is quite understandable from the model.

Effect of competition on marketable yield and relation between yield in mixture and monoculture

Competition among genotypes for growth limiting factors is expressed in their biomass. That is why the previous approach deals with biomass. The farmer, however, is concerned with yield of some desired plant parts rather than with biomass. So the influence of competition on yield will be partitioned into its effects on total dry matter (biomass) and its effects on the allocation of the dry matter within the plant. The degree of correspondence between the yield of a genotype in mixture and its yield in pure stand will receive special attention in the discussion.

Biomass The supply of the growth limiting factors is the same for each monoculture, provided that the genotypes have a similar growing period. Moreover, there is little variation in the efficiency with which the genotypes harness the limiting resources for their dry matter production. Thus, genetic variation for biomass in monoculture is small in general, as often confirmed in the literature.

However in mixture, the genotypes have to draw on the same stock of limiting resources, they compete for the same 'space'. The unequal distribution of these resources between genotypes gives rise to different rates of dry matter production, which is the major cause of the biomass differences in mixture. So genetic differences in mixture will exceed those in monoculture (CV_g in Table 1). In the empirical approach, the competitive ability of a genotype was defined as the ratio between its production in mixture and its production in monoculture (Equation 1). This ratio measures the ability of a genotype to acquire the limiting resources in the mixture, to occupy 'space', with genetic differences in efficiency of utilization being removed from this measure. As a consequence, the competitive ability b of a genotype is proportional to the surface underneath the curve for its fraction of the available resources acquired (the curve for light interception in Figure 3).

Differences in the ability to monopolize the resources are attributable mainly to differences in starting position (Figure 4). If these differences affect monoculture production, their influence is small and in no proportion to their significance for competitive ability. That gives a rationale behind the finding that there is on the whole no relation between competitive ability and pure stand performance, $r_{b,g} \approx 0$.

Under this condition, the genetic correlation between productivity in monoculture and mixture (Spitters, 1979, Equation 4.57) simplifies to

$$r_g = \sqrt{\frac{CV_{g,mono}^2}{CV_{g,mono}^2 + \text{var } \underline{b}}} \quad (9)$$

Hence, the smaller the genetic variation for monoculture biomass relative to that for competitive ability, the worse the relation between the biomass of a genotype in monoculture and its biomass in mixture. Nevertheless, a positive correlation is expected because the genetic differences in yield in monoculture tend to be maintained in mixture.

Harvest index That fraction of the biomass that is located in the agronomically desired plant organs is called the 'harvest index' (HI). In most crop species, HI appears to be little affected by intergenotypic competition (Spitters, 1979, p. 189-191). Thus, the HI of a genotype in monoculture and its HI in mixture will generally show a correlation close to unity.

Marketable yield Yield is the product of biomass and harvest index. As competition little affects HI, the competitive ability of a genotype, as estimated by b in Equation 1, will be about the same, irrespective of whether the estimate is for yield or for biomass. Therefore, the competition variance is also about the same for both traits.

On the other hand, the genetic variance for monoculture performance will be greater for yield than for biomass as there is substantial genetic variation in HI. For example, in cereals, the progress in yield due to breeding is associated with an increase in HI, with little change in biomass (e.g. Riggs et al., 1981).

Given the larger $CV_{g,mono}^2$ of grain yield and the equal competition variance, Equation 9 shows that the genetic correlation between performance in monoculture and mixture is greater for yield than for biomass. For the same reasons, $CV_{g,mono}/CV_{g,mix}$ is greater for yield too. The coefficient of the regression of monoculture performance on mixture performance, the product of the two quantities (Equation 8), is therefore larger for yield. So selection for yield of some plant parts will in general be less biased by intergenotypic competition than selection for biomass itself.

Consequences for breeding practice

As we have seen, the ranking of the genotypes in mixture differs from that in monoculture. This genotype \times population interaction is the mechanism by which intergenotypic competition biases the outcome of selection. The difference between the yield of a genotype in mixture and its monoculture yield is brought about by the unequal distribution of the growth limiting factors between the genotypes constituting the mixture. The share that a genotype gains in mixture is closely related to its initial status, its starting position.

Because initial differences between genotypes bear little relation to yield in monoculture, minimizing the initial differences seems to be an effective method in reducing competition bias. Table 3 indicates how initial differences may be minimized:

- Differences in seed size are reduced by grading the seeds and sowing large and small seeds in separate plots. Grading seeds in order to decrease competition bias is a technique advocated by several authors.
- Simultaneous emergence and establishment is promoted at one hand by favourable germination conditions, especially a fine seed-bed, and at the other hand by uniform drilling, especially in sowing depth.
- Differences in the numbers of plants with which the genotypes are present in the population are of importance when the unit of selection consists of several plants. That holds for progeny testing where progenies of plants selected in a previous year are evaluated in small plots. The number of plants within a plot strongly affects the ability of such plot to compete with its neighbours.

Minimizing variation in initial status not only reduces intergenotypic competition, but

also reduces the intragenotypic competition brought about by non-genetic variation in initial status. And this reduces environmental variation.

Several other methods of reducing the competition bias were proposed for single-plant selection as well as for progeny testing in microplots (Spitters, 1979, p. 176-192, 225-232). The effect of plant spacing was worked out further in a recent paper (Spitters, 1984).

Plant breeding literature on field-plot technique is dominated by numerous papers presenting results of experiments where selection was practised according to various methods in segregating populations. Every time the results were different, leading to conflicting recommendations. The efforts would have been employed more efficiently, if some principles of technological research had been recognized. These start with the definition of a conscientious working hypothesis on the basis of a coherent theory. The hypothesis should be falsified or verified in a reductionistic way with experiments in which the studied methods differ in a minimum number of factors. Use of known pure lines, families or clones will be more fruitful in breeding research than use of unknown irreproducible genotypes of segregating populations. Apart from that, summarizing and quantitating a theory by a mathematical model facilitates the detection of conditions for which the results hold. In that way one comes to 'if . . . , then . . .' statements rather than to the empirical conclusions that 'sometimes method A is better than B and sometimes B is better than A'. Experiments may supply the orders of magnitude for the parameters needed as input in the model (Table 1). Experiments are also required to falsify the theory and are helpful in sharpening and extending the theory. The models presented in this paper are simple. They serve to clarify the broad lines of the effects of intergenotypic competition as well as to provide a frame for further research.

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