Euphytica 34 (1985) 883–895

EFFECTS OF COMPETITION AND SELECTION PRESSURE ON YIELD RESPONSE IN WINTER RYE (*SECALE CEREALE* L.)[1]

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Received 2 October 1984

INDEX WORDS

Secale cereale, rye, family-individual selection index, selection efficiency, honeycomb selection, natural selection, positive skewness.

SUMMARY

Three intensities of mass honeycomb selection (14.3,5.3 and 1.6%) applied to an unselected rye population gave respectively an annual yield response of 0.28, –3.69 and –5.20% at 15 cm spacing, and of 4.07, 5.39 and 8.99% at 90 cm spacing. The negative response with competition was explained by strong negative correlation between competing and yielding ability which causes positive skewness because of transposition of low yielders and strong competitors from the left to the right tail of the distribution. The positive response in the absence of competition was mainly due to the increased genotypic differentiation which allowed effective discrimination between high and low yielding genotypes. The efficiency of the selection in the absence of competition was further improved by using the honeycomb designs which adjust soil heterogeneity and application of very high family and individual selection pressures.

Two cycles of mass honeycomb selection increased the population yield by 29.4%, one cycle of mass plus one cycle of pedigree honeycomb selection did so by 34.5%. The results are discussed in relation to the selection response and to the efficiency of various breeding schemes.

INTRODUCTION

The literature on the effects of competition in the selection process was summarized by SPITTERS (1979) separately for each stage of a breeding program, namely unselected bulk propagation, single plant selection, and progeny selection. A conclusion was that when bulk propagation is practiced there is a considerable chance for natural selection to cause a dilution or even loss of desirable genes as a result of crowding. The literature is no unanimous about the degree to which intergenotypic competition accounts for the inefficiency of single plant selection for yield. In the case of progeny selection, it is generally stated that competition may or will seriously complicate selection for yield in single rows. Generally, the numerous findings of significant competition effects show that competition between genetically different plants and rows may confound selection for yield and decrease its reliability.

FASOULAS (1973) and FASOULAS & TSAFTARIS (1975) on the basis of positive yield response from honeycomb selection without competition, suggested selection in the

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[1] Part of senior author's doctoral thesis

absense of competition. Later, FASOULAS (1978) comparing materials selected at 30 and 90 cm spacing by honeycomb selection, arrived at the conclusion that competition may completely erase response, thus rendering it compulsory to select without competition. Recently, FASOULAS (1984) summarized results from studies over fifteen years on the role of competition in selection and concluded that the negative correlation between competing ability and yielding ability makes isolation the proper condition to select in early generations for superior yielding performance. Bos (1981) studied in winterrye the relative efficiency of honeycomb selection and other procedures of mass selection. Three generations of continued honeycomb selection reduced culm length by 6.1% and increased kernel yield by 4.3%. When the effect of density on the result of honeycomb selection was considered, he offered experimental support of FASOULAS (1973) and FASOULAS & TSAFTARIS (1975) suggestion for selection without competition (BOS, 1981, section 8.5). SPITTERS (1979, sections 5.6, 8.3.3) on the other hand, on the strength of general considerations arrived at the conclusion that selection should be done at high plant densities. Apparently, concerning the effect of competition in the selection process experimental results give conflicting answers and opinions about the extent to which intergenotypic competition affects the efficiency of selection.

The main aim of the present investigation was to find out how competition biases efficiency of selection for yield, by studying the relation between selection pressure and response to selection both with and without competition. This was made possible only after developing reliable criteria for adjusting selection pressure (FASOULAS, 1981).

MATERIALS AND METHODS

An unselected rye population which was bulk propagated at the University farm for more than 20 years, was purposely chosen as the selection material. Thus, apart from the expected large genetic variation, the crucial problem about the extent to which natural selection favors genes controlling competing and yielding ability could also be ascertained. The investigations was carried out at the University Farm in the growing seasons 1981–82, 1982–83 and 1983–84 in seven experiments.

In the first growing season 1981–82, two unreplicated honeycomb experiments were established side by side. Experiment 1 had 2160 plants of the source population out of 2.232 positions spaced 15 cm to represent competitive conditions, and experiment 2 had 2127 plants of the same population out of 2226 positions spaced 90 cm to represent absence of competition. In both experiments border plants were also included. The purpose of the experiments was to apply three selection pressures namely 14.3, 5.3 and 1.6% for studying the relation between selection intensity and competition. The three selection pressures were applied to both experiments using moving hexagonal grids containing 7, 19 and 61 plants respectively (FASOULAS, 1981). For each of the two experiments 3 separate seed mixtures were formed from kernels produced by the plants selected by the respective selection pressures. Plants selected by the 1.6% selection pressure were not included in the mixture of 5.3% intensity, and in its turn these plants were not included in the mixture of 14.3% intensity. Thus the best plants which in fact belong to the 5.3% group were not included in the actual mixture and also the best plants which in fact belong to the 14.3% group were not included in the actual mixture. This yields biased results for the 14.3% and 5.3% mixtures. Widely spaced plants in experiment 2 were threshed individually while for the closely spaced plants of experiment 1 the weight of the ears was recorded as yield given the high correlation (r = 0.997) between kernel yield and weight of the ears found by Bos (1981).

In the second growing season 1982–83, four experiments were estaslished, namely experiments 3, 4, 5 and 6. Experiment 3 was a randomized complete block design with seven entries in six replicates. Plots consisted of five rows, 4 m long, spaced 25 cm apart, and from which only the central three rows were harvested. The seven entries were the three mixtures representing the three selection pressures of experiment 1, the three mixtures representing the same selection pressures of experiment 2, and the source population. The purpose of the experiment was to see how efficiency is affected by competition and no competition under various selection pressures.

Experiment 4 had three entries, the mixture of 1.6% intensity from experiment 1 (M1) the mixture of 1.6% intensity from experiment 2 (M2), and the source population (P). The two mixtures were grown in competition and in alternate rows with the source population in continuous single-rows plots, 4 m long, spaced 25 cm apart and replicated 10 times in the following arrangement: P-M1-P-M2-P-M1-P-M2-P- and so on. The purpose of the experiment was to study the fate of genes controlling competing and yielding ability when selection is practised with and without competition.

Experiment 5 had 31 entries: the source population (P) and the 30 halfsib families (F1 to F30) selected by the 1.6% selection pressure in experiment 2. The half-sib families were grown in competition with the source population (P) in continuous single-row plots, 4 m long, spaced 25 cm apart, without replication in the following arrangement: P-F1-P-F2-P-F3-P- ... -P-F30-P. The purpose of the experiment was to study how genes controlling competing ability are distributed among the 30 families whose mothers were selected for high yielding ability without competition. In experiments 4 and 5 border rows were also included.

Experiment 6 was a replicated-49 honeycomb trial with 90 replicates and plants spaced 90 cm. In this trail 25 half-sib families selected by 1.6% selection pressure in experiment 2 were yield tested to apply the second cycle of mass selection and the first cycle of pedigree selection. By using duplicate samples, twenty-four families were assigned two code numbers each while the twenty-fifth family had only one, thus constituiting the 49 entries required in the design. These 25 HS-families belonged to the 30 included in experiment 5.

In the third growing season 1983–84, the multipurpose experiment 7 was established in a randomized complete block design with six replicates. Plots consisted of five rows, 4 m long, spaced 25 cm apart, and from which only the three central rows were harvested. The entries involved in this experiment were the source population and 9 seed mixtures derived from experiment 6 as follows: 1) one single-seed-descent (SSD) mixture from all plants belonging to the 25 HS-families mentioned in Table 3; 2) one mixture from 30 plants mass selected by 1.6% selection pressure; and 3) seven separate pedigree mixtures from various numbers of plants belonging to 4 families selected on the basis of yielding and/or competing ability. The seven pedigree mixtures (see also Tables 3 and 4) were composited as follows. Mixtures 2 and 4 were from family C which ranked first on the basis of yielding ability but was less competitive than the source population. Mixture 2 was from an equal number of seeds of the best 4 plants and mixture 4 from all 77 plants. Family 3F, which ranked second on the basis of yielding ability but showed higher competing ability than the source population, contributed another two analogous mixtures, numbers 1 and 3. Family 1G, which yielded similarly to family 3F but had a competing ability similar to the source population, contributed one mixture, number 7, of seeds produced by all 81 plants. Family 7F, which ranked low on the basis of yielding ability but was first on the basis of competing ability, contributed one mixture, i.e. number 5, derived from all 70 plants. The seventh mixture, number 6, was composed from the 298 plants of the 4 families. For each of the six replicates a separate SSD mixture from 1780 plants was prepared to serve two purposes: (1) to verify for a second time the maximizing progress of the first selection cycle, and (2) to assess progress by the second selection cycle performed in Exp. 6.

Total rainfall in the tree critical months, namely March, April and May in the years 1982, 1983 and 1984 was 151, 56 and 163 mm respectively. In the unusually dry season of 1983 one sprinkle irrigation was applied.

RESULTS AND DISCUSSION

Figure 1 presents the two yield histograms of the source population, one from Exp. 1 with competition and the other from Exp. 2 without competition. Comparing the two histograms belonging to the same population grown with and without competition, the following differences become evident: (1) The frequency distribution is normal without competition and skewed with competition. (2) The coefficient of variation increases with competition. According to YAMANE (1973, p. 79) CV measures the reliability of the estimate of the standard deviation and tends to be large when the data have a very skew distrubution. YAMANE suggests that in such cases a large amount of data becomes necessary to get a reliable estimate of the standard deviation. Yet, in the case of the population with competition, although the sample size is large, the distribution is skewed meaning that skewness not due to sampling error but to biological causes, which have to be ascertained. (3) The phenotypic standard deviation and the overall mean yield per plant are about 5 and 7.5 times larger without than with competition, respectively. According to FALCONER, (1981, p. 175) increasing phenotypic standard deviation constitutes a means of increasing response to selection. Another thing of importance to observe in the two histograms is the position of plants selected by 1.6% intensity. The use of moving hexagonal grids for controlling soil heterogeneity resulted in selecting plants that would have been excluded by truncation selection.

Table 1 shows yield response to mass honeycomb selection when selection was practiced at 90 and 15 cm, by applying three selection pressures, 14.3, 5.3 and 1.6%. As selection pressure increased, response to selection increased positively at 90 cm and negatively at 15 cm. These results could only be interpreted by the existence of a strong negative correlation between competing and yielding ability, which in the presence of competition favours selection of strong competitors (symbolized by CC) and low yielders (y) but in the absence of competition selection of high yielders (Y). This is confirmed by the results of experiment 4 shown in Table 2. Mixture 6 gave in pure

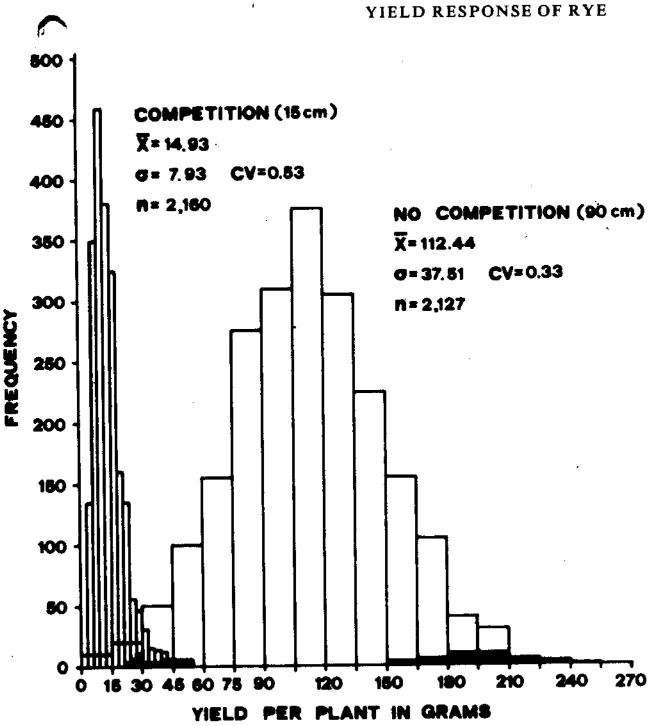

Fig. 1. The distribution of yield of the unselected rye population with and without competition. Competition causes positive skewness. In comparison to absence of competition it reduces the phenotypic standard deviation, and increases the coefficient of variation (CV). In absence of competition the distribution is normal. The shaded area depicts plants selected by the 1.6% selection pressure.

Table 1. Average yield per plot of six mixtures obtained after mass honeycomb selection and response to selection relative to the source population (Exp. 3).

Selection procedures			Mean yield per plot (g)	One year response (%)
mixture number	interplant distance (cm)	selection intensity (%)		
1	90	1.6	1152	8.99
2	90	5.3	1114	5.39
3	90	14.3	1100	4.07
4	15	14.3	1060	0.28
5	15	5.3	1018	-3.69
6	15	1.6	1002	-5.20
7	Source population		1057	0.00

culture a progress of -5.2% (Table 1), but the same mixture in competition with the source population gave a significant positive progress of 20.1%. This indicates that genotypes involved in mixture 6 are for the greater part low yielders (y) and very strong competitors (CC), i.e. (yCC). This could mean that the phenotypes of (yCC)

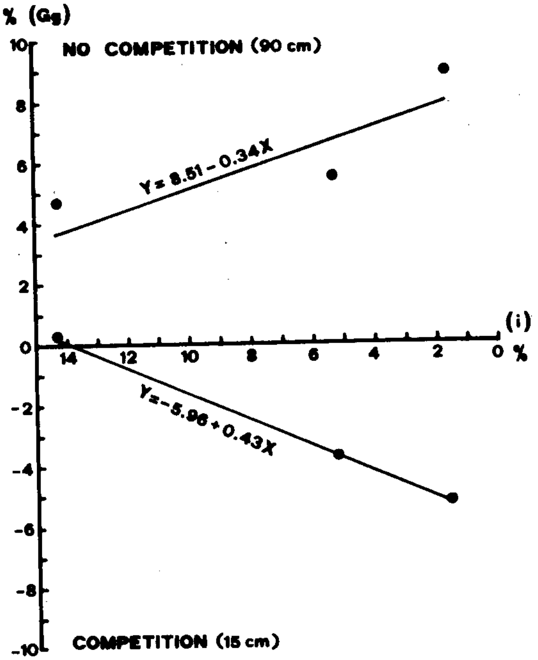

Fig. 2. The observed relation between response to selection and selection pressure with and without competition. The gain per generation (Gg) is plotted against selection intensity (i).

genotypes are, under competition, transposed from the left to the right tail of the distribution and will be preferentially selected. This hypothesis explains that the positive skewness of populations in equilibrium and competition is due to transposition of low yielders and strong competitors (yCC) from the left to the right tail of the distribution, and of high yielders and weak competitors (Yc) in the opposite direction. It could also explain why increased selection pressure in the presence of competition often leads to disappointing results.

Figure 2 despicts the observed positive and negative relation between response to selection and intensity of selection in the two conditions of competition. This relation gives an answer to why WIEBE et al. (1963) suggested to save from an advanced hybrid population the poorest plants when yield is the criterion of selection. The same authors made the plausible remark that if this is a universal phenomenon then it may explain

Table 2. Average yield per row and response to selection when mixtures 1 and 6 from Table 1 grew in competition with the source population (Exp. 4).

Treatment	Mean yield per row (g)	One year response %
Mixture 1 (90 cm)	316.9 n.s.	11.4
Mixture 6 (15 cm)	341.5*	20.1
Source population	284.4	00.0

*P = 0.05–0.01; n.s. = nonsignificant.

why breeding for increased yield has progressed so slowly. Similar results were obtained in cassava by KAWANO & THUNG (1982), and KAWANO et al. (1982), who recommended that strong competitors should be eliminated from segregating populations in selecting high yielding genotypes potentially adapted to productive environments.

On the other hand, mixture 1, which in pure culture gave a progress of 8.99% (Table 1), slightly improved its performance to 11.4% when grown in competition with the source population (Table 2). Obviously, mixture 1 contains genotypes combining high yielding with fair competing ability (YC). The types of plants occurring in mixture 1 are revealed by the results of experiment 5 given in the last column of Table 3. In this column the yield of 25 out of the 30 families of experiment 5 is given as a percentage of the average yield of the two adjacent rows of the source population. These results reveal that selection without competition favours two kinds of genotypes, namely, high yielders-fair competitors (YC), and high yielders-weak competitors (Yc). Genotypes of the composition (yc) are always at a selective disadvantage.

The increased negative response to selection with increase in selection pressure under competition (Table 1) combined with the results of Table 2, indicates that under competition plants of the yCC type occupy the far end of the right tail and are relatively more often selected by higher selection pressures than plants of the YC type falling behind in the distribution.

Included also in Table 3 are the results from experiment 6 aiming to assess the performance of 25 families which were obtained from mothers selected by 1.6% selection pressure at 90 cm and were subsequently tested at the same spacing. Family performance in experiment 6 was assessed by two indexes, performance index 'P' giving the percentage of family means which a particular family exceeds significantly (FASOULAS, 1983), and the combined family-individual selection index 'FI' giving the number of mass selected plants per family at a certain selection pressure and reflecting the capacity of families to yield exceptional genotypes. The combined index 'FI' cannot be evaluated by conventional designs because by using field plots as testing units these designs lay families in the field separately so that individual selection is based on comparisons between plants of the same family and not between plants of different families as in the case of honeycomb designs. In the replicated honeycomb designs families are allocated into moving replicates, which ensures that every progeny plant is in the center of a complete replicate and means that there are as many moving replicates as there are plants in the field (border plants excluded). On the basis of the two indexes, two families namely families 3F and 6C, showed exceptional performance. Family 3F showed higher competing abibility than the source population (170%) while family 6C was less competitive (72%). Two more families, 1G and 7F, were considered; the first for similar competing ability with the source population (95%) and the second for very strong competing ability (294%).

The correlation between columns 'P' and '%' of Table 3 reflecting respectively yielding ability in absence of competition and competing ability of 25 families was significant and negative, $r = -0.47$. This means that inspite of the removal of low yielders and strong competitors (yCC) which were not preferentially selected in Exp. 2, correlation between yielding and competing ability still remains negative. This might be due to the fact that in Exp. 2 both Yc and YC plants were selected.

Figure 3 gives the yield histogram of 1780 offspring plants belonging to the 25 fami-

Table 3. Mean yield ($\bar{X}$) per plant in grams, performance index (P), and family-individual selection index (FI) of 25 families obtained from mothers selected by 1.6% selection pressure in experiment 2, and tested at 90 cm spacing in experiment 6. The last column gives the results of experiment 5 where the 25 families grew in competition with the source population and their yield is expressed in % of the average yield of the 2 adjacent source population rows. n: actual number of plants.

Family code	$\bar{X}$	n	P	FI	%
6C	157.7	77	63	4	72
3F	153.9	70	38	4	170
1A	150.4	70	38	2	128
5B	150.4	77	38	1	110
1G	150.3	81	38	1	95
1D	148.5	71	29	2	147
3E	147.6	36	29	0	82
7A	146.4	80	21	0	66
3D	144.7	78	17	1	69
3B	142.8	68	13	2	98
7D	141.4	79	13	1	242
4G	140.6	72	13	1	117
7B	140.2	83	13	2	147
2C	140.1	65	13	1	95
2B	139.6	76	13	2	97
4A	138.5	50	13	0	119
1B	133.9	81	4	2	161
2E	133.1	86	0	1	107
7C	132.7	69	0	1	158
5G	132.4	72	0	1	185
5A	131.0	69	0	1	114
7F	130.4	70	0	0	294
1C	122.4	67	0	0	149
6B	118.8	66	0	0	67
2D	118.5	67	0	1	189

P = percentage of family means which a particular family exceeds significantly.
FI = number of selected plants per family at 1.6% selection pressure.

lies of Table 3, whose mothers were selected by 1.6% intensity at 90 cm in 1982 and tested in 1982–83 in experiment 6 at the same spacing. Although the progenies were grown without competition, the histogram is still positively skewed as was shown by the chi-square test for normality. This case of positive skewness manifested in the absence of competition is a desirable condition since it is not due to transposition of low yielding plants from the left to the right tail of the curve but to the elimination from the left tail of such plants by efficient selection. Thus, for populations not in linkage equilibrium and grown in absence of competition the magnitude of postive skewness reflects the magnitude of selection efficiency. By contrast, for populations in equilibrium and grown in the presence of competition, the magnitude of positive skewness reflects the magnitude of the negative correlation between yielding and competing ability. In the histogram the position of the 30 mass selected plants by 1.6% intensity (shaded area) are indicated as well as the position of 4 plants from family 3F reflecting a selection pressure of about 0.2% (arrows).

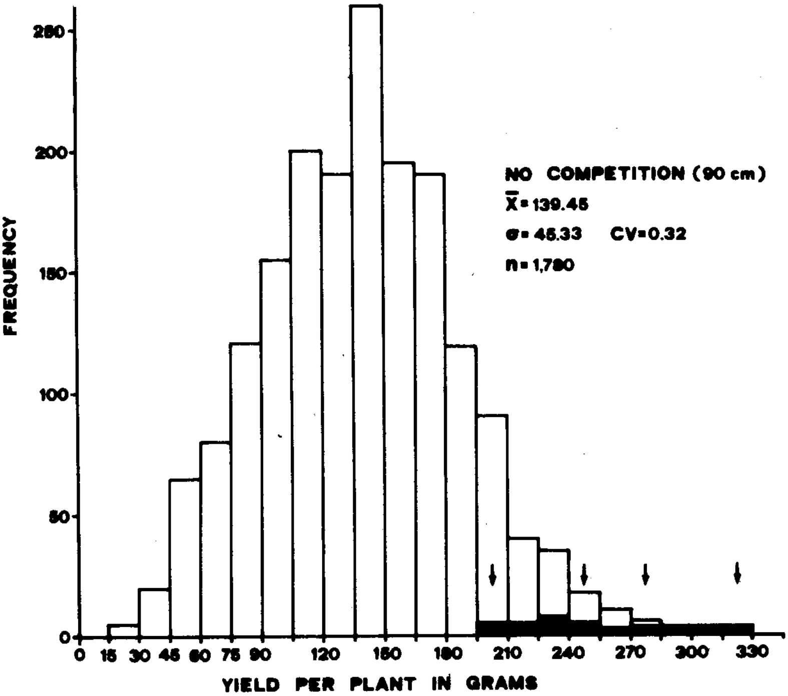

Fig. 3. The distribution of yield of the population resulting from 1.6% selection pressure in the absence of competition. Significant positive skewness was detected. The shaded area depicts the position of plants selected by 1.6% intensity. The arrows indicate the position of four plants from family 3F selected by 0.2% selection pressure.

The results of experiment 7, where nine mixtures were tested against the source population to assess advance through selection, are presented in Table 4. The SSD mixture gave a 12.9% advance, whereas plants from which this mixture was derived gave a 8.99% advance in the previous year. This difference in progress as assessed in the two years may be attributed to the genotype × year interaction caused by the difference in weather conditions in the two years of testing. Progress of eight mixtures relative to the SSD mixture is given in column 7 of Table 4. It is interesting to notice that progress is mainly determined by the intensity of individual selection. Thus, in mixtures 1 and 3 where offspring of plants selected in family 3F were involved, progress was 19.1% for 0.2% selection pressure and 14.1% for 3.9% selection pressure. Similarly, in mixtures 2 and 4 where similar offspring of family 6C were involved, progress was 15.4 and 5.8% for 0.2 and 4.3% selection pressures respectively. These results indicate that efficient increase of individual selection pressure to such high levels is possible by pedigree honeycomb selection, which offers the possibility of isolating by objective criteria the best family or families and of appling very efficient individual selection both among and within families. They also point out that the two phases of pedigree selection i.e. family and individual selection are almost of equal importance in maximizing efficiency. Families 7F and 1G, which on the basis of 'P' and 'FI' values were inferior to families 3F and 6C, remained so in their response to selection.

Table 4. Average yield per plot of nine mixtures: seven pedigree, one mass, and one single-seed-descent (Exp. 7). Response to selection is given for one generation relative to the SSD mixture, and for two generations relative to the source population.

Mixture characteristics					Mean yield per plot (g)	One year response (%)	Two year response
number	parental families	number of parental plants	family selection pressure (%)	individual selection pressure (%)			
1	3F	4	4	0.2	1513a*	19.1	34.5
2	6C	4	4	0.2	1465a	15.4	30.2
3	3F	70	4	3.9	1449a	14.1	28.8
4	6C	77	4	4.3	1344b	5.8	19.5
5	7F	70	4	3.9	1308bc	3.0	16.3
6	3F, 6C, 7F, 1G	298	16	16.7	1211d	–4.6	7.6
7	1G	81	4	4.5	1153e	–9.6	2.5
8	Mass	30		1.6	1456a	14.6	29.4
9	SSD	1,780			1270cd	00.00	12.9
10	Population				1125e		00.0

* Means followed by the same letter are not significantly different at the 5% level.

The mass selection mixture from 1.6% intensity gave an annual response of 14.6%. These results, where increase in selection pressure is accompanied by analogous response to selection, is the outcome of selection in the absence of competition and of the development of objective and reliable criteria for individual and family selection. Reliability of family and individual selection is expected to increase considerably if instead of 'P' of 'FI' values per se their average values across sites, 'Ps' and 'FIs' are used in order to account for genotype × environment interaction (FASOULAS, 1983).

The high gains in the absence of competition have also an important impact upon the relation between predicted and realized response to selection. Predicted response based on an average heritability value is an inaccurate estimate because it disregards that heritabilities differ from family to family and from plant to plant within the same family. Comparing the responses obtained from families 3F and 6C at the two selection pressures, it becomes evident that family 3F inspite of its lower performance (P = 38) than 6C in the previous year (Table 3), showed higher gain than family 6C. This simply denotes how important it is to develop reliable criteria for family evaluation. Indexes 'Ps' and 'FIs', which can only be obtained through across site screening, offer such criteria. Response to selectmion differs also within families according to the intensity of individual selection. The higher the selection pressure the better the responses. In family 6C for example, the selection of 4 plants representing a selection pressure of about 0.2% gave an annual response of 15.4% and the offspring of the 77 plants of the same family representing a selection pressure of 4.3% a 5.8% response. Apparently, once selection criteria for identifying the few exceptional plants are developed, then any information about the inheritance of quantitative characters matters little. The development of such criteria depends upon the efficient control of the confounding effects of competition, soil heterogeneity, and genotype × environment interaction. The first is accomplished by selecting in the absence of competition, the second by using moving hexagonal grids of various sizes, and the third by using the replicated honeycomb designs allowing multisite screening (FASOULAS, 1981).

Given that the realized response to selection within the same family depends on the intensity of selection or else on the ability to isolate the few exceptional plants, it turns out that all conventional pedigree schemes which use eye assessment for individual selection within families, will have reduced efficiency. This is also true for formal recurrent selection schemes, like full-sib, S_1, S_2, testcross and reciprocal, where use of controlled pollination imposes eye assessment before plants reach maturity and where progeny testing and recombination add generations without selection.

The results in Table 4 show further that efficient selection in the absence of competition may recover cultivars of two types, type YC exemplified by family 3F, and type Yc by family 6C (Exp. 5, Table 3). Comparing now the results in Tables 3 and 4 it can be seen that under wide stand $3F < 6C$ (Exp. 6, Table 3) and under solid stand $3F > 6C$ (Exp. 7, Table 4). In other words, under solid stand Family 3F of the YC type displayed better performnce than family 6C of the Yc type. The same also happened with family 7F of the YCC type in comparison with family 1G of the Yc type. If this is not due to coincidence or the genotype × year interaction then it may suggest that genotypes of the YC or YCC type might be more advantageous than genotypes of the Yc type when comparison is made under solid stand. This may also offer a logical explanation why some authors (JENSEN & FEDERER, 1965; KANNENBERG & HUNTER, 1972; and BLIJENBURG & SNEEP, 1975) demonstrated a good agreement between the ability of a genotype to compete well in mixture and its yield in pure culture.

On the other hand, reports of a negative correlation between yielding ability in pure culture and competitive ability (MONTGOMERY, 1912; CHRISTIAN & GRAY, 1941; SMITH et al., 1970; KHALIFA & QUALSET, 1974; HAMBLIN & ROWELL, 1975; among others) are justifiable, on the assumption that cultivars of the Yc type will be inferior in mixture although they show good performance in pure culture.

In the last column of Table 4 the rates of improvement in two years are presented. It can be noticed, that individual and family selection in the absence of competition increased yielding and reduced competing ability. Selection under competition however (Table 1 and 2) did exactly the opposite because natural selection establishes a negative correlation between competing and yielding ability. The impact of this is that under bulk propagation natural selection will considerably reduce efficiency of subsequent selection pressures.

CONCLUSIONS

Interplant competition may render single plant selection for yield ineffective irrespective of the magnitude of the additive genetic variance present in the population, the intensity of selection applied, and the efficiency of the experimental design.This is because under competition (1) genotypic expression and differentiation are reduced and (2) plants of low yielding and strong competing ability are preferentially selected because of their transposition from the left to the right tail area of the distribution which causes positive skewness and negative response to selection.

Positive skewness is of two kinds, one caused by competition because natural selection establishes a strong negative correlation between yielding and competing ability, and the other caused by efficient artificial selection which preserves high yielding genotypes and eliminates low yielding ones.

Selection efficiency in each cycle depends on the magnitude of genetic variation and on the ability to identify phenotypically the few exceptional genotypes. Phenotypic identification of exceptional genotypes is possible by practising selection in the absence of competition and by applying very high selection pressures. Increased individual selection pressure improves efficiency up to a certain point by using moving hexagonal grids of various size. Efficiency is further improved through progeny testing and application of high family selection pressures. This can only be accomplished by the replicated honeycomb designs which combine the following advantages:

(1) Ensure efficient soil heterogeneity control by using many moving replicates and by allocating families uniformly across the selection site.

(2) Allow to isolate families yielding exceptional genotypes by offering the possibility of applying individual selection among and within families.

(3) Make possible selection at several sites to effectively exploit genotype × environment interaction early in the program which renders regional tests unnecessary and cuts in half the time required to release a cultivar.

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