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Summary

Competition between plants interferes with the selection process: (1) by reducing genotypic differentiation and therefore progress through selection, (2) by imposing a limit on the number of environments and replicates when testing in early generations, both directly by reducing the number of seeds produced per plant, and indirectly through the establishment of field plots as experimental units, and (3) by making single-plant selection for yield unreliable, since competitive ability is usually negatively correlated with yielding ability. The detrimental effects of competition are overcome effectively by using wide spacings (i.e. 90 cm in wheat, 125 cm in maize) and the honeycomb field designs. With such designs a multisite and multireplicate screening of potential crosses and exceptional genotypes or families can be carried out in early generations. In this way annual progress will be maximized and the time needed to develop a new cultivar can be halved. Genes for adaptation and stability will be incorporated early in the programmes and both individual buffering and monoculture performance will be improved. Finally the scheme ensures a constant improvement of the cultivar, and paves the way for mechanizing and computerizing selection for yield.

Descriptors: honeycomb selection, competition, genotypic differentiation, yield, selection efficiency, early generation selection

Results from studies over fifteen years on the role of competition in selection can be summarized into three main effects and a general conclusion.

Effect 1 Competition between plants reduces genotypic differentiation and therefore progress through selection.

When sugar-beet and cotton varieties were tested in the presence and absence of competition, genotypic differentiation for sugar content in sugar beets, and mean number of days to maturity in cotton were reduced under competition by 57 and 49%, respectively. Competition also reduced yield differentiation when seven maize hybrids were tested in the presence and absence of competition, without any change in hybrid rank (Fasoulas, 1981). Similar reduction in the range of yield with increase in plant density was noticed by Baker & Briggs (1982) in barley, and Mitchell et al. (1982) in durum wheat, suggesting that single-plant selection would be most effective at low densities. In fact, Gogas (1983) obtained 40% progress in 4 years of mass honeycomb selection in the F₂ of a single maize hybrid when 0.7 plants were grown per square metre. Gardner (1978), using 2 plants per square metre and mass grid selection, needed 13 years

to obtain 40% progress, whereas Hallauer & Sears (1969) with 4 plants per square metre and grid selection, would have needed 26 years for the same progress. Although these results refer to different source populations, they are comparable, as the existence of additive genetic variance cannot be doubted, especially for the material used by Hallauer & Sears (1969), where studies have shown that 78 to 86% of the total genetic variance for individual-plant yield was due to additive genetic variance. Among the additional factors contributing to the superiority of honeycomb selection for population improvement and extraction of high-yielding inbred lines, should be mentioned the higher intensity of selection (2.5 against 10%) and the moving against the stable grid. In wheat, results from single-plant mass honeycomb selection with 1.4 plants per square metre showed the same gain as in maize (10.4%). This suggests that mass selection is equally effective in inbreeders as in outbreeders, if competition between plants is eliminated.

Effect 2 Competition between plants reduces the number of seeds produced per plant and indirectly establishes field plots as experimental units. This imposes a limit on the possible number of environments and replicates for all methods of family selection and prevents multisite and multireplicate screening for adaptability, yielding ability and stability in early generations.

With the honeycomb selection method plants are grown at 90 cm spacing in wheat and 125 cm in maize. Under such conditions the number of grains produced per selected plant is greater than 5000. This number is enough for progenies to be tested at more than 20 sites, with 100 plants per site, and two seeds per hill thinned later to a single plant. Thus, when evaluation is done in isolation, selection can be practised for high yield stability over many years and sites at an early stage. In this way, genes for adaptation and stability, instead of being irretrievably lost, are incorporated early in the programme. This makes regional tests unnecessary and halves the time needed to develop a new cultivar. Another important aspect of isolation is that it paves the way for mechanizing and computerizing selection for yield. Mechanization is transforming plant breeding techniques by increasing efficiency and by reducing labor, time and cost.

Effect 3 Competition between plants makes single-plant selection for yield unreliable, because competitive ability is usually correlated negatively to yielding ability.

Kawano & Thung (1982) and Kawano et al. (1982), studied the effects of intergenotypic competition in cassava on the efficiency of yield selection under different plant spacings. They found that intergenotypic competition was the major factor responsible for the low predictability of yield in a large plot from yield of a single plant. Because of the negative correlation between competitive ability and root yield in monoculture, they recommended that strong competitors should be eliminated from segregating populations in selecting high-yielding genotypes potentially adapted to productive environments.

Results presented in Table 1 from single-plant honeycomb selection for grain yield in the F_2 of two wheat crosses and two selection methods under two plant spacings (competition: 30 cm; isolation: 90 cm) substantiate the existence of the negative correlation (Fasoulas, 1978). The two F_2 wheat crosses were selected from a total of 83, for contrasting levels of heterosis in F_1 and yield in F_2 . Relative genetic gain was assessed in F_3 and in isolation (90 cm), and is expressed as per cent of the F_2 . For mass selection, the

Table 1. Relative genetic gain (in per cent over F_2) regarding grain yield in F_3 (plant spacing 90 cm) from single-plant honeycomb selection in F_2 of two wheat crosses, with two selection methods and at two plant spacings.

Selection method	Plant spacing (cm)	Sonora 64 × Farnese	Siete Cerros × Resistente
mass selection	30	-2 %	-9 %
	90	22 %*	2 %
best-family descent	30	27 %*	10 %
	90	79 %*	23 %*

* Significant at 5 % level.

average gain from selection under competition was -5.5% while that from selection in isolation was 12%. For the other selection scheme: the best-family descent (the pedigree scheme based on the best performing family and selection of individual plants within the best family only) the average progress under competition was 18.5% and in isolation 51%. Since comparisons were made in isolation (90 cm), verification under dense sowing in F_4 , using as control the initial F_2 , was indispensable. In this test (Table 2), the best four families from the high-yielding cross Siete Cerros × Resistente, two selected in isolation (I) and two in competition (C), were compared. Only the two families selected in isolation outyielded significantly (i.e. 12 and 14%) the F_2 . After this verification, selection was continued in isolation up to the F_6 . From mass honeycomb selection in the high-yielding cross Siete Cerros × Resistente, the variety Lesvos was derived, and from selection in the low-yielding cross Sonora 64 × Farnese the variety Cyprus. Although progress was much higher in the low-yielding cross (Table 1), the derived variety Cyprus was significantly inferior compared with Lesvos and with the leading Mexican variety

Table 2. Performance with dense sowing of four F_3 families of the wheat cross Siete Cerros × Resistente, two selected in isolation (I) and two in competition (C), and relative genetic gain (in per cent over F_2).

Best F_3 families	Yield ¹ (kg/ha)	Genetic gain (%)
I ₁ (90 cm)	6777 ^a	14*
I ₂ (90 cm)	6653 ^{ab}	12*
C ₁ (30 cm)	6173 ^{bc}	
C ₂ (30 cm)	5460 ^d	
Check F_2	5859 ^{cd}	

1. Different letters indicate significant differences.

* Significant at 5 % level.

Table 3. Performance with dense sowing of the wheat varieties Mykonos and Lesvos derived from mass honeycomb selection in isolation, in comparison with the best common parent Siete Cerros and the leading variety Yecora.

Variety	Yield ¹ (kg/ha)	Improvement over Siete Cerros (%)
Mykonos	7350 ^a	178
Lesvos	7088 ^a	172
Yecora	5002 ^b	121
Siete Cerros	4123 ^b	100

1. Different letters indicate significant differences.

Yecora. To eliminate this defect, Cyprus was crossed with both Yecora and Siete Cerros. The cross Cyprus × Yecora showed up hybrid vigour and gave lines far inferior to the lines derived from the highly heterotic Cyprus × Siete Cerros. From the latter cross the variety Mykonos has resulted. In Table 3, results are given from a randomized complete-experiment established in 1981-1982, where the two varieties Mykonos and Lesvos, both derived from heterotic crosses and from mass honeycomb selection in isolation, were compared with the leading variety Yecora and the best parent Siete Cerros. Due to outstanding performance, the two varieties were submitted to National List Trials. The results indicate three important things: (1) single-plant selection for yield is effective only when plants are grown in isolation; (2) the ideal cross to start selection is the one exhibiting the highest heterosis in F₁ and yielding ability in F₂; (3) the best-family descent is a very promising selection scheme. This method, applied in maize across sites to accumulate favourable adaptation and stability genes through a less restrictive form of inbreeding, may become a profitable way of obtaining highly productive and stable inbred lines.

Conclusions Because competitive ability is usually correlated negatively with yielding ability, the right condition to select for superior yielding performance in early generations is isolation. Direct selection for yield in isolation allows for all effects of competition and improves individual buffering and monoculture performance by improving various components of yield traits in a balanced way.

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