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Genetic Studies in an Exotic Population of Corn (*Zea mays* L.) Grown under two Plant Densities

II. Choice of a Density Environment for Selection[1]

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Summary. Design II progenies from an exotic population of corn (*Zea mays* L.) were evaluated in a randomized incomplete block design with two replications at two plant-population densities (17,222 plants/ha and 68,888 plants/ha) in 1970 and 1971, at Lincoln, Nebraska. Five traits were studied, i.e., grain weight, number of ears, days to flower, plant height, and ear height.

It was suggested that a trait such as grain weight should be expressed on a unit area basis in the following situations:

1. when genetic parameters (except for correlation and the ratio between two values) obtained from experiments with different plant-population densities are to be compared, and
2. when combined analyses of variance of data from experiments involving different plant-population densities are to be performed to test the significance of genotype by density effects.

The estimates of genetic parameters were used to compute the expected direct and indirect genetic changes in grain weight and other traits from selection for grain weight. Three selection schemes were compared, i.e. mass selection (M.S.), full-sib (F.S.) selection, and half-sib (H.S.) selection in which S_1 seeds from the selected male parents are used for recombination. A ten year selection program was considered. F.S. selection appears to be the most promising of the three, if there are no practical limitations and if costs are disregarded. A high-density selection environment appears to be a little better than a low density one for family selection. Mass selection at low density may result in good gains when measured at higher densities.

From a long term point of view, it is possible that selection at low densities could allow response to continue for a longer period of time and perhaps reach a higher selection limit than selection at higher densities. Long term selection studies are necessary to compare response to high and low density-selection.

Introduction

The first part of the study dealt with estimates of genetic parameters and the effect of different plant-population densities on the estimates. It was found that even with a large difference such as that between the two plant-population densities used in this study the differences between the estimates of genetic parameters were not significant. Which plant-population density, then, should be chosen as the environment in which to conduct a selection program? Tentative suggestions are made in this paper.

Materials and Methods

The maize (*Zea mays* L.) population (Gaspé × Colombian) and the experimental procedures used to estimate genetic parameters were described in detail in the first paper (Subandi and Compton, 1974). The Design II progenies were evaluated in a randomized incomplete block design with two replications at two plant-population densities (17,222 plants/ha and 68,888 plants/ha) in 1970 and 1971, at Lincoln, Nebraska. The five traits studied were grain weight (g/plant and kg/plot), number of ears per plant and per plot, days to flower, plant height (cm) and ear height (cm).

To test the genotype × density interaction, an analysis of variance combined over years and densities was performed for each trait. A portion of the analysis of variance is presented in Table 1. A complex F test for the variance components was approximated by a method given by Cochran (1951).

Three selection schemes, i.e., mass selection (M.S.), full-sib selection (F.S.) and half-sib selection (H.S.) in which S_1 seeds from the selected male parents are used for recombination, were compared. In the mass selection scheme considered here, grid size as described by Gardner (1961), is equal to our individual plot size. Thus, one grid would contain 10 and 40 plants at the low and the high plant-population densities, respectively. Two hundred grids and fifty grids are used for the respective densities to provide 200 selected ears for the next generation.

In the F.S. and H.S. selection, S_0 plants are used to produce the F.S. progenies. In the H.S. selection each S_0 male parent is selfed and crossed to three randomly selected S_0 female parents, and equal quantities of seeds from each F.S. family with a common male parent are then bulked to produce H.S. families. In both F.S. and H.S. selection, 200 families are evaluated in one year using the same plot size as used in this study, with 2 replications. The selection intensity would be 10% for all selection schemes.

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Table 1. *Portion of the analysis of variance for data of progenies produced in a Design II mating system grown at two plant-population densities in two years*

Source of variation	d.f.	M.S.	Expectation of mean squares
Males & Females (Z) × Densities (Ds)/Blocks (B)	$b\,(m+f-2)\,(d-1)$	M_{17}	$\sigma^2 + r\,\sigma^2_{MFDsY} + r\,n\,\sigma^2_{ZDsY} + r\,y\,\sigma^2_{MFDs} + r\,n\,y\,\sigma^2_{ZDs}$
Males (M) × Ds/B	$b\,(m-1)\,(d-1)$	M_{18}	$\sigma^2 + r\,\sigma^2_{MFDsY} + r\,f\,\sigma^2_{MDsY} + r\,y\,\sigma^2_{MFDs} + r\,f\,y\,\sigma^2_{MDs}$
Females (F) × Ds/B	$b\,(f-1)\,(d-1)$	M_{19}	$\sigma^2 + r\,\sigma^2_{MFDsY} + r\,m\,\sigma^2_{FDsY} + r\,y\,\sigma^2_{MFDs} + r\,m\,y\,\sigma^2_{FDs}$
M × F × Ds/B	$b\,(m-1)\,(f-1)\,(d-1)$	M_{20}	$\sigma^2 + r\,\sigma^2_{MFDsY} + r\,y\,\sigma^2_{MFDs}$
Z × Ds × Y (Years)/B	$b\,(m+f-2)\,(d-1)\,(y-1)$	M_{21}	$\sigma^2 + r\,\sigma^2_{MFDsY} + r\,n\,\sigma^2_{ZDsY}$
M × Ds × Y/B	$b\,(m-1)\,(d-1)\,(y-1)$	M_{22}	$\sigma^2 + r\,\sigma^2_{MFDsY} + r\,f\,\sigma^2_{MDsY}$
F × Ds × Y/B	$b\,(f-1)\,(d-1)\,(y-1)$	M_{23}	$\sigma^2 + r\,\sigma^2_{MFDsY} + r\,m\,\sigma^2_{FDsY}$
M × F × Ds × Y/B	$b\,(m-1)\,(f-1)\,(d-1)\,(y-1)$	M_{24}	$\sigma^2 + r\,\sigma^2_{MFDsY}$
Error	$b\,d\,y\,(m\,f-1)\,(r-1)$	M_{25}	σ^2
Plants within plots	$\Sigma\,(w_i-1)$	M_{26}	σ^2_W

b, m, f, d, y, r = number of blocks, males per block, females per block, plant-population densities, year, and replications, respectively. $n = m = f$ in this experiment. w_i = number of plants in the i^{th} plot in which individual plant data were taken. M_i = the value of the i^{th} mean square. σ^2_{MDs} and σ^2_{FDs} = variances due to interaction of males and densities and females and densities, respectively. σ^2_{ZDs} = the pool of σ^2_{MDs} and σ^2_{FDs}. σ^2_{MFDs} = variance due to interaction of males, females and densities. σ^2_{MDsY} and σ^2_{FDsY} = variances due to interaction of males, densities and year, and of females, densities and years, respectively. σ^2_{ZDsY} = the pool of σ^2_{MDsY} and σ^2_{FDsY}. σ^2_{MFDsY} = variance due to interaction of males, females, densities, and years.

One, two, and three years/cycle are required for Mass, F.S. and H.S. selection, respectively. The estimates of genetic parameters reported in the first paper were used to compute the expected genetic changes in the five traits from selection for grain weight. The formula for the expected genetic change per year in the j^{th} trait from selection for the i^{th} trait is:

$$\Delta_{G(j)} = \frac{1/2\,k\,r_{A(ij)}\,\hat{\sigma}_{A(i)}\,\hat{\sigma}_{A(j)}}{n\sqrt{\hat{\sigma}^2_{P(i)}}}$$

where: $\Delta_{G(j)}$ = expected genetic change in the j^{th} trait; k = standardized selection differential which is equal to 1.539, 1.694, and 1.742 for M.S. at the low density, M.S. at the high density, and both F.S. and H.S. selection, respectively (Table 2 in Becker, 1967); $r_{A(ij)}$ = the estimate of the additive genetic correlation coefficient between the i^{th} and the j^{th} traits; $\hat{\sigma}_{A(i)}$ and $\hat{\sigma}_{A(j)}$ = the additive standard deviation estimates for the i^{th} and the j^{th} traits, respectively; n = number of years per cycle of selection; and $\hat{\sigma}^2_{P(i)}$ = the phenotypic variance estimate for the i^{th} trait, which was grain weight in this case.

The phenotypic variance for each selection scheme was estimated with the following formulae (since the criterion for selection in the present study was yield only, the i subscript was not shown in the formulae to reduce their complexity):

Mass Selection: $\hat{\sigma}^2_P = \hat{\sigma}^2_A + \hat{\sigma}^2_{AY} + \hat{\sigma}^2_D + \hat{\sigma}^2_{DY} + \hat{\sigma}^2_{We}$

F.S. Selection:

$$\hat{\sigma}_{\bar{P}(\text{F.S.})} = \frac{1}{2}(\hat{\sigma}^2_A + \hat{\sigma}^2_{AY}) + \frac{1}{4}(\hat{\sigma}^2_D + \hat{\sigma}^2_{DY}) + \frac{\hat{\sigma}^2_{P_1} + \dfrac{\left[\frac{1}{2}(\hat{\sigma}^2_A + \hat{\sigma}^2_{AY}) + \frac{3}{4}(\hat{\sigma}^2_D + \hat{\sigma}^2_{DY})\right] + \hat{\sigma}^2_{We}}{w}}{r}$$

H.S. Selection in which S_1 progenies from the selected male parents are recombined:

$$\hat{\sigma}^2_{\bar{P}(\text{H.S.})} = \frac{1}{4}(\hat{\sigma}^2_A + \hat{\sigma}^2_{AY}) + \frac{1}{4f}(\hat{\sigma}^2_A + \hat{\sigma}^2_{AY} + \hat{\sigma}^2_D + \hat{\sigma}^2_{DY}) + \frac{\hat{\sigma}^2_{P_1} + \dfrac{\left[\left(\frac{3}{4} - \frac{1}{4f}\right)(\hat{\sigma}^2_A + \hat{\sigma}^2_{AY}) + \left(1 - \frac{1}{4f}\right)(\hat{\sigma}^2_D + \hat{\sigma}^2_{DY})\right] + \hat{\sigma}^2_{We}}{w}}{r}$$

where: $\hat{\sigma}^2_P$, $\hat{\sigma}^2_{\bar{P}(\text{F.S.})}$, and $\hat{\sigma}^2_{\bar{P}(\text{H.S.})}$ = estimates of phenotypic variances among individual plants, among F.S. family means, and among H.S. family means, respectively. $\hat{\sigma}^2_A$, $\hat{\sigma}^2_{AY}$, $\hat{\sigma}^2_D$, and $\hat{\sigma}^2_{DY}$ = estimates of additive, additive × year interaction, dominance, and dominance × year interaction variances, respectively; $\sigma^2_{P_1}$ = the estimate of the plot component of error variance; σ^2_{We} = the estimate of the within plot component due to environmental effects; w = number of plants in each plot; and r = number of replications.

Grain weight measured at the two plant-population densities was treated as two different traits. The additive genetic correlation between these two traits was estimated and used in the formulae for expected genetic change to compute expected correlated response in one density from selection at another density.

Experimental Results

A portion of the analysis of variance combined over years and densities is presented in Table 2. The pooled mean squares for males × densities and females × densities were significant at $P = .01$ for grain weight and number of years. The mean squares for males and females × densities were significant at $P = .05$ for number of years and plant height.

The expected genetic changes per year in all traits from selection for grain weight at each density are

Table 2. *Portion of the analysis of variance of five traits in Gaspé × Colombian combined over two years and two plant-populations densities*

Source of variation	d.f.	Grain weight (kg/plot)	No of ears per plot	Days to flower	Plant height (cm)	Ear height (cm)
Males & Females (Z) × Densities (Ds)/Blocks (B)	128	0.5108**	42.53**	1.968	91.83	56.61
Males (M) × Ds/B	64	0.4206	36.70*	1.851	85.01	62.60
Females (F) × Ds/B	64	0.6009**	48.36**	2.085	98.65	50.62
M × F × Ds/B	128	0.2207	20.00*	1.578	77.01*	42.00
Z × Ds × Y (Years)/B	128	0.2351	17.10	1.288	102.97**	55.98**
M × Ds × Y/B	64	0.2564*	17.89	1.465	127.22**	70.98**
F × Ds × Y/B	64	0.2138	16.30	1.111	78.71	40.98
M × F × Ds × Y/B	128	0.1762	14.77	1.307	55.69	40.78
Error	1024	0.1877	15.58	1.582	82.69	52.35

* Significant at the .05 level of probability.
** Significant at the .01 level of probability.

Table 3. *Expected genetic change per year in five traits from selection on grain weight in Gaspé × Colombian at the low and the high plant-population densities**

Selection scheme	Density	Grain weight		Number of ears		Days to flower		Plant height		Ear height	
		q/ha	% of mean	per plot	% of mean	days	% of mean	cm	% of mean	cm	% of mean
Mass	Low	3.30	7.77	1.62	6.92	0.24	0.32	1.60	0.69	1.49	1.61
	High	1.80	2.76	0.56	1.41	−0.08	−0.11	0.26	0.10	−0.16	−0.14
Full-Sib	Low	3.98	9.36	1.95	8.33	0.29	0.39	1.93	0.83	1.80	1.95
	High	3.49	5.34	1.04	2.63	−0.15	−0.20	0.50	0.20	−0.31	−0.28
Half-sib	Low	3.13	7.35	1.53	6.55	0.23	0.30	1.52	0.65	1.41	1.53
	High	2.68	2.83	0.80	2.02	−0.11	−0.15	0.39	0.15	−0.23	−0.21

* 200 grids of 10 plants each and 50 grids of 40 plants each are used in mass selection at the low and the high density, respectively. 200 full-sib and 200 half-sib families are evaluated in the F.S. and H.S. selection, respectively. Selection intensity is 10% in all selection schemes.

presented in Table 3. At the low density, F.S. selection gave the highest expected genetic changes in all traits, followed by mass selection and H.S. selection. At the high density, F.S. selection also gave the highest expected genetic changes in all traits followed by H.S. and mass selection, in that order. Selection at the high density would have been expected to slightly reduce days to flower and ear height. In all selection schemes selection at the low density consistently gave higher expected genetic change than at the high density.

Table 4. *Expected direct and correlated response to selection per year in Gaspé × Colombian*

Selection scheme	Response/year (q/ha)		
	Density	Direct	Correlated*
Mass selection	Low	3.30	2.33
	High	1.80	1.36
F.S. selection	Low	3.90	2.81
	High	3.49	2.63
H.S. selection	Low	3.13	2.20
	High	2.68	2.03

* Selection performed at density shown and the selected population is grown at the alternate density indicated on the other line.

The expected correlated and direct responses to selection are presented in Table 4. The direct response was consistently greater at the lower density. The expected correlated responses were consistently greater when selection was practiced at the low density than when done at the high density. In mass selection, the expected correlated response from selection at the low density was higher than the expected direct response at the high density. In F.S. and H.S. selection, the expected correlated responses from selection at the low density were close to the expected direct responses at the high density.

Discussion

Differences in units of measure for estimates of genetic variance and their interaction with environments create two problems which need to be examined and understood. The first arises when genetic variance estimates obtained from experiments with different plant-population densities are to be compared. The second occurs when experiments involving different plant-population densities are to be combined. The first problem was discussed in our first paper (Subandi and Compton, 1974). The following discussion pertains to the second problem.

In an analysis of variance of data collected from one density, the results are readily converted from a plant to a unit area basis, or vice versa, since the coding factor is the same for all sources of variation. The results of F tests will remain unchanged. The difficulty occurs when experiments with different densities are combined. The conversion factor from a plant to a unit area basis is different for different sources of variation, so the F values will change unequally. The degrees of freedom associated with the simple F test remain unchanged but those associated with the complex F test may change. Therefore, the results of an F test for the same effect can be different depending on whether the trait is measured on a plant or a unit area basis. Different units of measure could lead the experimenter to arrive at different decisions for the same problem.

Since genetic and genotype × environment interaction variances are estimated as a function of different mean squares, the conversion factors from a plant to a unit area basis for the variance estimates are not necessarily the same as those for the mean squares involved in the function. Appropriate conversion factors have not been determined. We suggest that the easiest way to accomplish this is to convert the data to a unit area basis before the analysis is performed.

Estimates of additive genetic variance at the two densities were not significantly different for any traits observed (Subandi and Compton, 1974). However, the additive × density interaction was important for grain weight and number of ears as shown by the significance of the mean squares for $Z \times Ds$ (Table 2). This indicates that selection would be expected to give higher gain when conducted at a particular density and is justification for estimating the genetic parameters at separate densities as reported in the first paper.

If the response to selection is assumed to be linear, the number of years required before the population means at each density reach the same level, will be 15, 46 and 50 years which would allow 15, 23, and 17 cycles of mass, F.S. and H.S. selection, respectively. In mass selection, the linear response over such long periods of time may be possible but it could be questioned for F.S. and H.S. selection. Kojima and Kelleher (1963) concluded that, regardless of the kinds of organisms, traits, and the method of selection, the total response in population mean continues to change linearly in the direction of selection during the early 10 to 15 cycles of selection on the average. However, for grain yield in corn, the longest term selection experiment to date in which there was agreement between realized and expected gain from selection based on estimates of genetic variance has only been reported through 10 generations of mass selection (Gardner, 1968). Satisfactory agreement between *realized* and expected gain from F.S. selection was reported for 6 to 7 cycles (Moll and Robinson, 1967; Moll and Stuber, 1971).

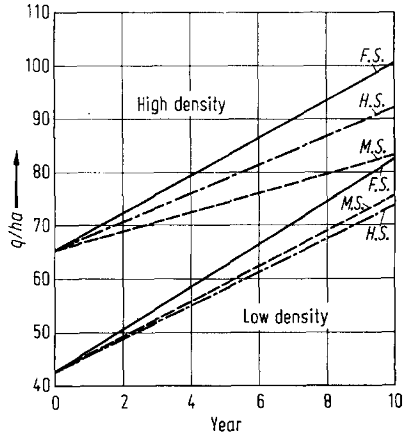

Figure 1. Expected population means in Gaspé × Colombian following 10 years of selection at low and high plant-population densities

We assume that, in this study, the response to selection will be linear for 10 years, which means 10, 5 and 3 cycles for mass, F.S. and H.S. selection, respectively. The expected population means following 10 years of selection are indicated in Fig. 1. The mean level for F.S. selection at the low density would approach the mean level for mass selection at the high density but the rank of the means would remain the same as the rank of the expected gains from selection. Full-sib selection appears to be the most attractive of the three selection schemes at both densities.

Frahm and Kojima (1966) studied mass selection for light and heavy body weight in *D. pseudoobscura.* During early cycles of selection there was some indication that, for the best performance under both densities, selection should be conducted at the low density for heavy weight and at the high density for light weight. This seems to be in agreement with the results of our study. The authors concluded that the results of selection under two different larval densities were similar and one environmental condition served almost as well as the other.

Data reported by Arboleda and Compton (1974) indicate that selection in good and in poor cropping seasons gave better direct than indirect gain in yield. Selection in each season tended to give the same total gain when averaged over both cropping seasons. Most of the experimental evidence to date seems to indicate that selection under more environmental stress will provide material that performs well under both more and less environmental stress. Falconer (1960), basing his conclusions on the results of a selection experiment with mice for growth on high and low planes of nutrition, suggested that if good performance under a variety of conditions is desired, selection should be conducted under conditions that are least

Table 5. *Expected population means (q/ha) after 10 years of selection for grain weight in Gaspe × Colombian*

Selection scheme	Density	Expected	
		population*	means †
Mass selection	Low	75.52	88.53
	High	83.23	56.12
F.S. selection	Low	82.32	93.33
	High	100.13	68.82
H.S. selection	Low	73.82	87.23
	High	92.03	62.82

* Selection is performed at density shown and the selected population is grown at the same density.

† Selection is performed at density shown and the selected population is grown at the alternate density indicated on the other line.

favorable for the desired expression of the character. Kojima and Kelleher (1963), reviewing selection studies on growth rates of mice and some farm animals, stated that the results of experiments tend to indicate that slightly restricted nutritional levels are better environments for selection than fully sufficient levels. In corn, selection based on testcross performance at high density was more effective in improving hybrid yields than selection at low density when the same testers used in selection were used also for comparisons (Russell and Teich, 1967; Russell, 1969).

In our study, the differences between the expected population means at the high density following 10-years of projected selection at high and low density are not very large, except possibly in the case of F.S. selection (Table 5). This further supports the possibility that, within limits of a 10-year selection period, selection at the low density may produce material that performs well under both high and low densities, particularly with mass selection, if the assumption of linearity of direct and correlated response is true. However, Bohren *et al.* (1966) pointed out that the estimates of additive genetic variances and covariances are expected to be valid for prediction over a shorter period for correlated response than for direct response. In a study with mice, Falconer (1960) found that the observed responses to selection in one environment, when tested in another environment, were in good agreement with the theory of selection for correlated characters for only the first four generations of selection.

In comparing the three selection schemes several other factors besides the expected gain from selection need to be considered. Four hundred plots are needed for family evaluation in both F.S. and H.S. selection but only 200 plots at low and 50 plots at high density are needed in mass selection. If three females/male are used, six hundred successful crosses and 200 successful selfs are required in the H.S. selection; only 200 successful crosses are required in the F.S. scheme and none for mass selection. On the other hand, mass selection requires isolation. The number of parents selected in each cycle would be 20, 40, and 200 in the H.S., F.S. and mass selection, respectively. This should, at least in the long run, produce detectable differences in the gain from selection. In H.S. selection, linkage may influence the expected gain from selection with only one generation of recombination in each cycle. Therefore, taking into account the practicality and the expected gains from selection. F.S. or mass selection seem to offer more promise than the type of H.S. selection discussed here.

The choice of a plant population density in which to practice selection should be examined in relation to two different time-objectives. Consider a ten-year period of a selection program. Since the high density used in the present study is close to that recommended to farmers and since the expected direct response to selection at the high density is higher than the expected correlated response from selection at the low density when grown at the high density, selection at the high-density environment should be better in the short run. In mass selection, a low-density environment is a more convenient environment in which to work. It may be more effective than a high-density environment as indicated by a slightly higher value of the expected correlated response from selection at the low density than direct response from selection at the high density. Therefore, in the case of mass selection, a low density selection environment may be better.

Consider long term selection. It is not yet known how long response to selection for grain yield will continue. In the authors opinions. it is *possible* that response to selection in low density environments will continue longer and reach higher selection limits than selection practiced at high densities. It does not seem completely logical for corn breeders tc concentrate all their attention on selection at higher densities, even though much evidence exists that present corn varieties and hybrids usually yield more at higher densities. The authors feel that evidence from the study reported here suggests the possibility of gains from selection at lower densities that would compare favorably with gains at higher densities. Much better evidence, of course, would be provided by observed results of long term recurrent selection studies at different densities.

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