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SELECTION FOR MODIFIER GENES TO IMPROVE PERFORMANCE OF OPAQUE-2 GENOTYPES*

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The discovery by Mertz, Nelson and Bates (1) in 1964 stimulated considerable breeding effort to develop opaque-2 hybrids with improved protein quality and eventually quantities of protein.

The initial approach has involved finding the best performing hybrid combinations among standard inbreds converted to opaque-2 by backcrossing. Such hybrids or varieties are now grown on a limited scale in a number of countries. They generally are lower yielding because of reduced kernel weight, and have poorer grain quality. There are definite genotype interactions with the opaque-2 gene. However, limited genetic variation in continuous backcrossing programs places severe limitations on selection for modifiers.

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Our studies on expression of the opaque-2 phenotype in diverse genotypes revealed a wide range of expression. The data in Table 1 are from a diallel among 15 S_1 lines from a synthetic. The percentages refer to the number of F_1 ears, by families, in which the opaque-2 kernel weight was 90% or more of the normal kernel weight on the same ear. The data are based on approximately 132 heterozygous F_1 ears per family. Variation among families was considerable. For example, in family 803 only 18% of the ears had opaque-2 kernels weighing 90% or more of normal on the same ear. In families 799 and 817 the frequency of such ears was 50%. This illustrates even with S_1 lines from a synthetic that there are heritable modifiers or gene interactions that do affect the opaque-2 kernel weight when compared to normal kernels on the same ear.

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TABLE 1

Diallel of S_1 families—Percentage of F_1 ears by families in which the opaque-2 kernel weight was 90% or more of the normal kernel weight on the same ear (25 kernel samples).[a]

Family	%	Family	%
789	31	805	38
791	46	807	37
793	24	809	43
795	39	811	42
797	30	813	40
799	52	815	26
801	42	817	50
803	18		

[a] Based on approximately 132 F_1 ears per family.

In Table 2 are correlation coefficients calculated from data for these 562 segregating F_1 ears. The weight of normal kernels was highly correlated (r = .88) with opaque-2 kernel weight on the same ear. Weight of normal correlated with difference between weight of opaque gave r = .73, while weight of opaque when correlated with the difference gave r = .32. This indicates it was largely the variation weight of normal kernels that was influencing the differences in kernel weight on the same ear.

TABLE 2

Correlations between normal and opaque-2 kernel (25) weights on 562 segregating ears from a synthetic.

	Wt. of normal	Wt. of opaque	Difference (nor.—o₂)	o₂ as % of normal
Wt. of normal	—	.882**	.726**	—.555**
Wt. of opaque-2		—	.316**	—.109
Difference			—	—.960**
Means	6.91	5.98	.93	87.1

** Significant at the 1% level.

In the last column of Table 2 opaque-2 kernel weight expressed as % of normal when correlated with weight of normal gave r = —.56. This same characteristic correlated with weight of opaque was not significant (r = —.11). Therefore, it was the variation in weight of normal kernels that largely determined the relationships of opaque-2 compared to normal on the same segregating ears.

The means for the 562 ears for 25 kernel weight were 6.91 and 5.98 grams for the normal and opaque, respectively. The opaque weight expressed as % of normal on the same ear averaged 87.1. This is a fairly representative figure for unselected germplasm we have studied.

Figure 1 shows the frequency distributions of 25 kernel weights for the 562 F_1 ears from this diallel. The distribution for the opaque-2 kernel weights was not as variable as that for the normal kernel weights.

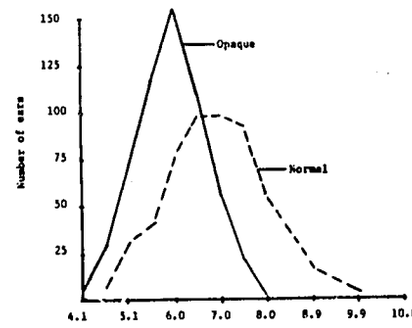

FIGURE 1

Frequency distribution of opaque-2 and normal kernel weights on segregating ears from a synthetic.

Another approach to improve the kernel weight of opaque has involved a recurrent selection program. On about 200 segregating ears from a synthetic, 50 kernel samples of opaque and normal were weighted. Fifteen ears which showed the least difference in kernel weight between normal and opaque were selected. Normal kernels (to maintain a segregating population) were planted and the resulting plants intercrossed. Plants from the intercrosses were selfed and the opaque and normal kernels from segregating ears were weighed and fifteen ears showing least difference were selected. For comparison purposes a control population was handled in a similar manner but with no selection.

Results after three cycles of selection for the select and control populations are given in Table 3. These data are based on five replications with approximately 15 segregating ears per replication. For the select population the opaque-2 kernel weight expressed as % of normal on the same ear was 94.6 compared to 88.5 for the control. This is a significant improvement. However, it is somewhat disappointing to note that the reason for this improvement was due primarily to reduced normal kernel weight in the select compared to the control (12.82 vs. 13.69 grams). The increase in opaque kernel weight compared to control was small and not significant. It should be emphasized that little selection for kernel weight per se was practiced, but was mainly concerned with the weight difference between normal and opaque on the same ear to eliminate environmental effects. A more practical selection program would probably involve selection for both weight per se and least difference (normal—opaque). We still may have made some progress here but this must be determined by a yield test of these populations.

Specific gravities have been determined on kernels from these populations and the select population does have a significantly greater density than the control population.

Percent protein of the select and control populations was 11.97 and

TABLE 3

Kernel weight, protein and lysine content of normal and opaque-2 after three cycles of recurrent selection for weight of opaque-2 as expressed in percent of normal kernel weight.

	50 Kernel weight			% Protein of o_2	Lysine as % of protein
	+	o_2	o_2 as % of normal		
Select	12.82	12.09	94.6	11.97	4.17
Control	13.69	11.99	88.5	12.38	4.33
Difference	− .87*	+ .10	+ 6.1*	− .41	− .16

* Indicate significant difference. Data based on five replications with approximately 15 ears per plot.

12.38, respectively. Lysine values expressed as % of protein were 4.17 and 4.33 for the select and control populations, respectively. Even though these lower values for protein and lysine were not statistically significant compared to the control it is still rather disturbing. However, lysine values are still quite good for each population.

We also carried out a similar recurrent selection program in a floury-2 population. Selection is somewhat more difficult because three dose floury kernels cannot be selected with absolute accuracy because of dosage expression involved. Progress has been somewhat similar to the opaque experiment but data on kernel weight comparisons are not yet processed.

Data on protein and lysine of the select and control floury-2 populations (Table 4), again as with opaque, indicate selection reduced protein content. However, lysine expressed as % of protein was nearly equal for both populations.

TABLE 4

Protein and lysine content of floury-2 after three cycles of recurrent selection for weight of floury-2 as expressed in percent of normal kernel weight.[a]

	Percent protein	Lysine as % of protein
Select	10.74	3.33
Control	11.46	3.35

[a] Data based on five replications.

The difference in lysine levels of opaque with an average of 4.25 and for floury-2 with 3.34 is fairly representative of the hybrids and populations we have tested. The opaque-2 gene, therefore, offers a somewhat better potential for improved protein quality in corn.

Another promising approach to modifying opaque-2 phenotype involves visual selection of more specific modifiers in segregating families during selfing. This appears promising and the modified opaque expressions (Figure 2) may be classified under the following categories:

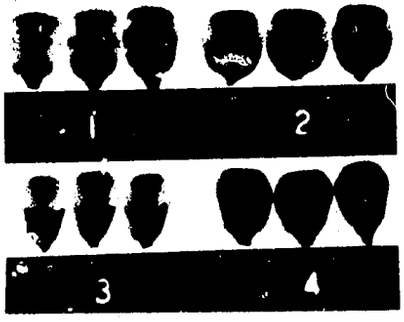

FIGURE 2

Light transmission with modified opaque-2 types (1) diffuse, (2) saddle, (3) ½:½, and (4) normal opaque.

1. Kernels with ½:½ phenotype as described by Zuber (2), with top or crown part normal or vitroeous endosperm and the base part opaque. On the ear these give a normal phenotypic appearance. This type occurs rather frequently and lysine values are good ranging from 3.6 to over 4.0 as a % of protein.
2. A saddle pattern where the soft or opaque starch is limited to the center of the abgerminal side of the kernel. These types are not numerous but one family gave a lysine value of 3.9.

3. A sectored or diffuse type where the soft starch is distributed irregularly in otherwise vitroeous endosperm starch. This type is rather rare and heritability is erratic.
4. A plump, dense type that is generally free of kernel rot but still has a definite opaque phenotype. Most of these have a bright yellow appearance as opposed to the "faded" appearance of many opaques. Lysine levels are generally quite satisfactory.

These modifier genes acting on these expression of opaque-2 are definitely heritable, involve more than one gene, and in the case of the first three categories are probably recessive.

Another breeding approach that may merit consideration is selection for large germ size (by oil analyses) in opaque genotypes. Sreeramulu, Bauman and Roth (3) showed that in some cases opaques compensate for reduced endosperm yield with germs that are larger than those of their normal counterparts. This compensation might be enhanced by high oil genotypes. Also, the germ has a relatively large percentage of high quality protein. Some very preliminary data in Table 5 show results of analyses on a composite from ten ears in each of high oil (7.9%) and normal oil (4.3%) from samples from a synthetic. The two composites did not differ in percent protein. However, the high oil and normal oil composites had 4.33 and 3.86 lysine expressed as percent of protein, respectively. This is an advantage of .47 for the high oil selection and indicates such selection may be valuable in increasing protein quality and caloric value.

TABLE 5

Protein and lysine content of high and low oil composites from an opaque-2 synthetic.*

	% Oil	% Protein	Lysine as % of protein
High oil	7.92	12.2	4.33
Low oil	4.28	12.2	3.86

* Composites of 10 ears and duplicate analyses.

Research has indicated the presence of many modifier genes and interactions that may improve the performance of opaque-2 genotypes. However, detail testing, genetic studies and protein and lysine analyses will be required to achieve this improvement.

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