POPULATION STUDIES ON VARIABILITY, EFFECTS OF
IRRADIATION AND PROGRESS FROM SELECTION IN
AN OPEN-POLLINATED VARIETY OF CORN

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INTRODUCTION

In the early 1920's a widespread belief arose among corn breeders that no further progress in increasing grain yield in adapted open-pollinated varieties was possible through mass selection or ear-to-row breeding. Richey (1922) in summarizing the status of corn breeding at that time indicated that mass selection for adaptability was effective, but once a variety became adapted, no further progress was possible. He clearly stated, "There appears to be little to recommend ear-to-row breeding as a practical method of corn improvement." Finally, he concluded "The entire evidence from all corn-breeding investigations for the present points to pure-line methods as the only sound basis for real improvement of corn". With such a general attitude among corn breeders, mass selection and ear-to-row breeding methods were quickly abandoned in favor of the development of inbred lines and the hybrid method of breeding.

Hull (1945, 1952) postulated that overdominance was the primary contributing factor to the magnitude of yield heterosis observed in hybrids. If he were

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correct, selection could have shifted gene frequencies in adapted varieties to the equilibrium point. At equilibrium, all genetic variance would be dominance variance and mass or family selection would be ineffective.

A search through the early literature fails to uncover any critical information on the effectiveness of mass selection and ear-to-row breeding. As pointed out by Sprague (1955), it appears that mass selection and ear-to-row breeding to increase yield were discredited as breeding methods, not because of genetic limitations but rather because of inadequate control over environmental variation and generally poor techniques.

By 1955 sufficient evidence had accumulated in North Carolina and Nebraska to suggest that additive genetic variance did exist in adapted open-pollinated varieties. The magnitude was sufficiently great that mass selection should have been effective unless heritability was too low. Consequently, I decided to initiate such a program in the Hays Golden variety in 1955, selecting only for yield. Initial results were reported in 1961. In more recent years, other associated selection programs have been initiated. The purpose of this paper is to discuss results of some of these programs which are summarized in Figure 1.

**MASS SELECTION**

Hays Golden is a variety collected in south central Nebraska which is adapted to the major corn growing areas of the state. One of our most widely used inbred lines N6 came from this variety. Two samples of seed were used to initiate the mass selection program. One was given a dose of $1.28 \times 10^{13}$ thermal
neutrons per square centimeter at the beginning and a smaller dose ($9.64 \times 10^{12}$ $N_{th}/cm^2$ and $9.98 \times 10^{12}$ $N_{th}/cm^2$ on two lots of seed which were then combined) two years later. No additional irradiation has been practiced. Mass selection has been practiced each generation for over 10 years.

Mass selection requires growing a population in isolation. Mating is at random and takes place prior to selection. Highest yielding plants are harvested. Equal numbers of seeds from each selected plant (basically a half-sib family) are composited to form the next generation. Three major changes in technique are believed to be responsible for progress being made. Selection is for grain yield only without regard to other agronomic traits, except that no lodged plants are harvested. Irrigation is used to avoid severe moisture stress and excessive micro-environmental variations. The nursery is divided into approximately square areas (grids) $160'' \times 200''$ containing 40 plants (See Figure 2). The highest yielding plants in each grid are harvested. The ears are dried to a constant moisture level and weighed to choose the top 4 (10%) from each grid. This latter procedure minimizes any micro-environmental variations that exist in the nursery plot of $\frac{1}{3}$ to $\frac{1}{2}$ acre.

Progress from mass selection has been measured each year, always comparing the selected generations against the original variety, which is maintained by growing 3,000 to 4,000 plants in isolation every 2 or 3 years. In recent years a hybrid check has also been included. Now, selected generations are kept in the test for only 3 years to avoid having to use old seed.

The response to mass selection during the first 6 years is indicated in Figure 3. Response has been quite linear and is estimated to be 3.29 percent.
per generation. The effects of thermal neutron irradiation and response to selection are indicated in Figure 4. Reduced yields in generations 1 and 3 as a result of thermal neutron treatment were quickly offset by rapid gains from selection. The linear regression coefficient is not a true measure of response in the treated population.

Genetic variation was evaluated in Hays Golden and the two selected populations after 6 generations of selection. Results are indicated in Table 1. A gain in yield of only 2 percent per generation is indicated for the selected populations. This is, in part, due to the fact that barren plants cannot be mated. They exist in higher frequency in the parent variety. A notable increase in prolificacy (no. of ears/plant) is evident in the irradiated population. Selected populations are slightly later maturing and taller.

No decrease in additive genetic variance in yield resulted from selection. Irradiation seems to have increased additive genetic variance for both yield and prolificacy. No conclusions can be drawn from estimates of dominance variance. Although negative estimates have a high probability of occurring in Design I experiments, the negative estimate for yield of the Irradiated population makes one wonder if additive genetic variance is over estimated.

In Figures 5 and 6, response to selection for 10 generations is indicated. Response is still linear throughout the range and, if anything, is increasing in later generations. A gain of 2.85 percent per generation was realized. A similar response of 2.66 percent was realized in the Irradiated population, but, of course, this is an underestimate due to the early reductions in yield from the thermal neutron treatment.
Another Design I study but on a more extensive scale was conducted to evaluate genetic variation in generation 10. This is shown in Table 2. In general, the conclusions supported those obtained at generation 6. Both selected populations show increased prolificacy, later maturity and taller plants. There is still no evidence of a reduction in additive genetic variance due to selection and irradiation still seems to have increased additive genetic variance. Greater future gain and a higher maximum yield should be possible in the Irradiated population; however, the negative estimate in dominance variance raises some questions.

An examination of a vast amount of data collected on full-sib within half-sib families (Design I mating system) in the variety Hays Golden has been summarized in Tables 3, 4, 5 and 6. Table 3 gives data for experiments run in one environment. Additive genetic variance is indicated to be over 15 times greater than dominance variance. When the experiments are viewed as sets in two environments (Table 4), additive genetic variance is less but still over 4 times greater than dominance variance. Obviously estimates of \( \sigma^2_A \) from individual experiments are biased upward. The same bias is observed in Table 5 for Design II experiments (factorial or cross-classified mating system), but Design II studies are believed to give more reliable estimates of dominance variance. Here \( \sigma^2_A \) is only 1.5 times greater than \( \sigma^2_D \). Comparison of estimates from the two types of studies are made in Table 6, but we must keep in mind that we have much more data on Design I studies. Predicted gain based on extensive Design I studies is 3.03 percent per generation, very close to realized gains. A similar prediction from Design II studies is 3.37 percent per generation.
Generations 2, 4, 6 and 8 of both selected populations and the original variety were crossed in all possible combinations. There was no evidence of heterosis. In Figure 7 the yields of generations 2, 4, 6 and 8 for both selected populations and the yields of the crosses of corresponding generations are shown graphically. Crosses are intermediate to their parents. This graph suggests a yield response of approximately 4 percent per generation. In Figures 8 and 9, the generations of selected populations and their F₁ crosses to the parent variety are shown graphically. In both cases, crosses tend to be intermediate. Previous studies with Krug and Reid varieties and improved populations selected from them by recurrent selection for general combining ability (Lonnquist and Gardner, 1961) had revealed substantial heterosis in excess of the better parent. In that selection system a generation of inbreeding occurred each cycle prior to recombination.

PROLIFIC SELECTION

Since substantial increases resulted in prolificacy from the mass selection for yield study, Lonnquist (1967) initiated in 1961 a program of mass selection for prolificacy only. Remarkable gains in yield were realized in early generations, indicated to be about 6.50 percent per generation in Figure 10, when the linear regression coefficient is used. There is some indication of a plateau having been reached but more data are needed to be conclusive.

HALF-SIB FAMILY SELECTION

In 1962, Lonnquist initiated a half-sib family selection program practicing mass selection within the half-sib family. This is a modified ear to row selection scheme in which selections are made in an isolated nursery based on
yield trials conducted in three environments. A total of 200 families are tested each year and the top yielding 40 (20%) are selected. The best 5 plants in each family are chosen so that 200 half-sib families are available for testing and selecting each year. As in mass selection, mating at random with the entire 200 families occurs each generation prior to making selections.

Response to this selection scheme has also been very great as indicated in Figure 11. A gain of 8.21 percent per generation is suggested by the linear regression coefficient, but the indication of a rapid increase and then a plateau is even more pronounced than in the selection for prolificacy study.

CONCLUSIONS

There is evidence of considerable additive genetic variance in the Hays Golden variety. A gain in yield of 3 percent per generation should be possible by mass selection. An average gain of at least 2.85 percent per generation was realized over a 10-year period. Gain has been quite linear, and no decrease in gain with the advance in generations is evident. Additive genetic variance for yield has not been decreased by selection, and it appears to have been increased by thermal neutron irradiation treatment. Correlated responses to selection include greater prolificacy, later maturity and taller plants. An index approach to hold maturity and plant height to acceptable levels while selecting for yield seems advisable. Selecting for prolificacy alone increased yield faster than selecting for yield alone, but a plateau may have been reached early. Selection based on a modified ear-to-row selection scheme has been the most effective scheme in early generations, but a plateau may have been reached as in selection for prolificacy.
Mass selection is simple to perform, requires minimum effort, holds inbreeding at low levels, and generally shows considerable promise as a method for population improvement. It is believed to be an excellent method for use in varietal improvement in developing countries and should be very useful in our crosses and composites involving Corn Belt varieties and exotic varieties.

If only a 2 percent gain in yield per year could have been realized since 1925, populations would now be 86 percent above their 1925 level. The hybrid system has not done that well.
LITERATURE CITED


New York, N.Y.
Table 1. Results of a genetic variance study at generation 6, 1963-64.
(Nested design known as Design I mating system).

<table>
<thead>
<tr>
<th>Popn.</th>
<th>Grain yield (lbs)</th>
<th>No. of ears</th>
<th>Days to flower</th>
<th>Ear ht. (in.)</th>
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</thead>
<tbody>
<tr>
<td>HG</td>
<td>.654 %</td>
<td>1.10</td>
<td>72.7</td>
<td>37.9</td>
</tr>
<tr>
<td>G6</td>
<td>.737 112.7</td>
<td>1.11</td>
<td>73.5</td>
<td>42.1</td>
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<tr>
<td>I6</td>
<td>.725 110.9</td>
<td>1.28</td>
<td>74.3</td>
<td>44.2</td>
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Mean values

<table>
<thead>
<tr>
<th>Popn.</th>
<th>(x 10^3)</th>
<th>(x 10^2)</th>
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<tbody>
<tr>
<td>HG</td>
<td>2.34 %</td>
<td>1.68</td>
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<td>G6</td>
<td>3.19 136.3</td>
<td>.88</td>
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<td>I6</td>
<td>6.16 263.2</td>
<td>5.96</td>
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Additive genetic variance

<table>
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<tr>
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<td>2.80</td>
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<td>G6</td>
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<td>1.86</td>
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<tr>
<td>I6</td>
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Dominance variance
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<th>0.25</th>
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<td>6.94</td>
<td>5.94</td>
<td>3.94</td>
<td>1.94</td>
<td>0.94</td>
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<td>3.94</td>
<td>4.94</td>
<td>5.94</td>
<td>6.94</td>
<td>7.94</td>
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### Dominance Variance

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<th>38.3</th>
<th>67.0</th>
<th>72.3</th>
<th>71.8</th>
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<td></td>
<td>30.8</td>
<td>31.7</td>
<td>32.5</td>
<td>32.0</td>
<td>31.5</td>
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<td>38.0</td>
<td>28.0</td>
<td>28.5</td>
<td>29.0</td>
<td>29.5</td>
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### Additive Genotype Variance

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<td>107.0</td>
<td>107.0</td>
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<td>95.6</td>
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### Mean Values

- Heterosis (ZH)
- Heterosis (ZH)
- Heterosis (ZH)
- Heterosis (ZH)

<p>| | | | | | |</p>
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</table>

Table 2: Results of a Genotype Variance Study at Generation 10, 1967.

- 12
Table 3. Summary of estimates of components of variance for grain yield from individual experiments involving full-sib within half-sib families (Design I) from the parent variety Hays Golden.

<table>
<thead>
<tr>
<th>Progeny set</th>
<th>Year</th>
<th>Loc.</th>
<th>n</th>
<th>Component x 10^3</th>
<th>( \sigma_m^2 )</th>
<th>( \sigma_f^2 )</th>
<th>( \sigma_e^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>56</td>
<td>1</td>
<td>256</td>
<td>2.238</td>
<td>1.950</td>
<td>2.200</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>56</td>
<td>2</td>
<td>256</td>
<td>2.075</td>
<td>1.650</td>
<td>2.000</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>57</td>
<td>1</td>
<td>256</td>
<td>1.795</td>
<td>1.785</td>
<td>2.570</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>57</td>
<td>3</td>
<td>256</td>
<td>0.513</td>
<td>0.400</td>
<td>3.000</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>60</td>
<td>1</td>
<td>256</td>
<td>2.523</td>
<td>2.102</td>
<td>2.075</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>62</td>
<td>1</td>
<td>256</td>
<td>1.340</td>
<td>1.853</td>
<td>3.186</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>63</td>
<td>1</td>
<td>400</td>
<td>1.366</td>
<td>2.187</td>
<td>2.567</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>64</td>
<td>1</td>
<td>400</td>
<td>0.365</td>
<td>1.391</td>
<td>3.531</td>
<td></td>
</tr>
</tbody>
</table>

**Mean**

\( \sigma_A^2 = 1.552 \)
\( \sigma_D^2 = 1.665 \)
\( \sigma_e^2 = 2.642 \)

**Pooled**

\( \sigma_A^2 = 1.599 \)
\( \sigma_D^2 = 1.703 \)
\( \sigma_e^2 = 2.640 \)
Table 1. Summary of estimates of components of variance for grain yield experiments involving full-sib within half-sib families (Design I) from the parent variety Hays Golden conducted in two environments.

<table>
<thead>
<tr>
<th>Progeny set</th>
<th>Year</th>
<th>Loc</th>
<th>n</th>
<th>Component x 10^3</th>
<th>( \sigma^2_m )</th>
<th>( \sigma^2_f )</th>
<th>( \sigma^2_{ma} )</th>
<th>( \sigma^2_{fe} )</th>
<th>( \sigma^2_e )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>56</td>
<td>1+2</td>
<td>256</td>
<td></td>
<td>1.956</td>
<td>1.750</td>
<td>.200</td>
<td>.050</td>
<td>2.100</td>
</tr>
<tr>
<td>2</td>
<td>57</td>
<td>1+3</td>
<td>256</td>
<td></td>
<td>.358</td>
<td>.625</td>
<td>.798</td>
<td>.480</td>
<td>2.760</td>
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<tr>
<td>3</td>
<td>60+6s</td>
<td>1</td>
<td>256</td>
<td></td>
<td>1.212</td>
<td>1.392</td>
<td>.719</td>
<td>.586</td>
<td>2.630</td>
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<tr>
<td>4</td>
<td>63+6s</td>
<td>1</td>
<td>400</td>
<td></td>
<td>.585</td>
<td>1.286</td>
<td>.382</td>
<td>.498</td>
<td>3.051</td>
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Mean

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th>Component x 10^3</th>
<th>( \sigma^2_m )</th>
<th>( \sigma^2_f )</th>
<th>( \sigma^2_{ma} )</th>
<th>( \sigma^2_{fe} )</th>
<th>( \sigma^2_e )</th>
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<tbody>
<tr>
<td>Pooled</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.028</td>
<td>1.263</td>
<td>.525</td>
<td>.404</td>
<td>2.635</td>
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</tbody>
</table>

From pooled estimate

\[ \sigma^2_A = 4.200 \]
\[ \sigma^2_D = 0.916 \]
\[ \sigma^2_P = 28.176 \]
\[ \sigma^2_A/\sigma^2_P = 0.15 \]
\[ \sigma^2_A = 0.15 \]
\[ \sigma^2_D = 0.03 \]
Table 5. Estimates of components of variance for grain yield from experiments involving full sib and half-sib families from a Design II mating system (Cross-classified or factorial mating design) in the parent variety Hays Golden.

<table>
<thead>
<tr>
<th>Year</th>
<th>n</th>
<th>$\sigma^2_{m}$</th>
<th>$\sigma^2_{mf}$</th>
<th>$\sigma^2_{e}$</th>
<th>$\sigma^2_{w}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1962</td>
<td>250</td>
<td>1.324</td>
<td>.720</td>
<td>3.731</td>
<td>15.508</td>
</tr>
<tr>
<td>1963</td>
<td>250</td>
<td>1.470</td>
<td>.726</td>
<td>2.258</td>
<td>22.335</td>
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</table>

**Combined Analysis**

- $\hat{\sigma}^2_{m} = .972$
- $\hat{\sigma}^2_{mf} = .649$
- $\hat{\sigma}^2_{me} = .245$
- $\hat{\sigma}^2_{mfe} = .083$
- $\hat{\sigma}^2_{e} = 2.978$
- $\hat{\sigma}^2_{w} = 18.511$
- $\hat{\sigma}^2_A = 3.888$
- $\hat{\sigma}^2_D = 2.596$
- $\hat{\sigma}^2_P = 20.460$
- $\hat{\sigma}^2_A/\hat{\sigma}^2_P = .19$
- $\hat{\sigma}^2_S = 3.37\%$
Table 6. Comparison of estimates of components of variance, heritability, and expected gain from selection for grain yield using Design I and Design II families from the parent variety Hays Golden.

<table>
<thead>
<tr>
<th>Variance</th>
<th>Design I</th>
<th>Design II</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \sigma_A^2 )</td>
<td>4.200</td>
<td>3.888</td>
</tr>
<tr>
<td>( \sigma_D^2 )</td>
<td>.916</td>
<td>2.596</td>
</tr>
<tr>
<td>( \sigma_P^2 )</td>
<td>28.176</td>
<td>20.460</td>
</tr>
<tr>
<td>( \sigma_A^2 / \sigma_P^2 )</td>
<td>.15</td>
<td>.19</td>
</tr>
<tr>
<td>G</td>
<td>3.03 %</td>
<td>3.37 %</td>
</tr>
</tbody>
</table>
Fig. 1. Selection program involving the variety Hays Golden. N=thermal neutron irradiation, X = X-radiation.
Fig. 2 Grid system used for mass selection. Each grid is 160" x 200" or 222.2 square feet.
Fig. 3. Response of Control population to mass selection during first 6 generations.
Fig. 4. Response of Irradiated population to mass selection during first 6 generations.
Fig. 5. Response of Control population to mass selection during first 10 generations.
Fig. 6. Response of Irradiated population to mass selection during first 10 generations.
Fig. 7. Results of crossing corresponding generations of selection in the Control and Irradiated populations.
Fig. 8. Results of crossing selected generations of the Control population with the parent variety Hays Golden.
Fig. 9. Results of crossing selected generations of the Irradiated population with the parent variety Hays Golden.
Fig. 10. Grain yield response when selection is for number of ears per plant.
Fig. 11 Grain yield response to ear-to-row selection plus mass selection within rows.
ANDY WYATT: What was the selection history of the Hays Golden variety prior to the initiation of the selection experiment?

GARDNER: The Hays Golden variety of corn was selected at the Agricultural Experiment station in Hays, Kansas, by Mr. A. F. Swanson. The variety has proven to be well adapted in all of the principal corn growing regions of the state and particularly in south central Nebraska, where the strain which we have used was collected. It is shorter in stature than other adapted varieties in eastern Nebraska and is believed to be somewhat more drought tolerant. The particular strain used had been maintained at the Nebraska Experiment Station for several years without selection prior to 1955.

A. B. CHAPMAN: Have you grown hybrids with the mass selected populations in comparative tests?

GARDNER: Yes, one of our best double crosses Nebr. 501D which has as its parents (Wf9 x Hy) x (N6 x N6D) has been grown in our comparative yield trials for several years. The line N6 was developed from the Hays Golden variety. N6D is a related line derived from N6 and a gamete from the Hays Golden variety. In 9 yield trials from 1960 to 1966, Nebr. 501D hybrid has yielded 33.4 percent more than the Hays Golden variety. In three of those trials in 1961, 1962 and 1963, Nebr. 501D yielded only 14.3, 14.5 and 16.7 percent more respectively. Perhaps the Hays Golden variety mean was estimated to be unusually high due to random variations in the environment. Several selected generations were estimated to be lower yielding than Hays Golden in those trials. Beginning in 1964, we have grown twice as many plots of Hays Golden as other populations in order to
estimate that mean more precisely. In 4 such trials, Nebr. 5OLD has averaged
43.7 percent more than Hays Golden. Therefore, I would say that the double
cross hybrid Nebr. 5OLD yields approximately 5 to 10 percent more than our
populations improved by mass selection. We should surpass the hybrid in another
3 or 4 years.

P. R. DAY: In the graphs showing response to selection, were the yields from
different generations always measured in different years?

GARDNER: No, in the beginning and for several years, we grew every selected
generation available along with the Hays Golden variety in the yield trial each
year. Then we realized that some seed was getting too old to give good results.
Now we test only the three most recently selected generations of the Control
selected population and of the Irradiated selected population along with the
Hays Golden variety and the hybrid Nebr. 5OLD. All yields recorded each year
are expressed in percent of Hays Golden.

P. R. DAY: Plant height increased as kernel yield was selected. Was there
also an increase in total plant dry matter production?

GARDNER: Although we have not measured total dry matter production, I am
positive that there has been an increase. We have an experiment planned this
year to measure total dry matter production of the above ground portion of the
plant in the original Hays Golden and in the selected populations.

JACK F. HILL: Isn't the mathematics overestimating the additive genetic
variance and underestimating the dominance variance? If so, why?

GARDNER: In the absence of epistasis, the estimates obtained are believed to
be unbiased; however, the estimates of additive genetic variance and dominance
variance are not independent. If by chance sampling, \( \sigma^2_A \) is overestimated, \( \sigma^2_D \) will
be underestimated. \( \sigma_2^2 = h\sigma_m^2 \) and \( \sigma_D^2 = \frac{1}{4}(\sigma_f^2 - \sigma_m^2) \). If epistasis does exist then

\[
4\sigma_m^2 = \sigma_A^2 + \frac{1}{4}\sigma_A^2 + \frac{1}{16}\sigma_{AAA}^2 + \ldots
\]

\[
4(\sigma_f^2 - \sigma_m^2) = \sigma_D^2 + \frac{1}{2}\sigma_{AA}^2 + \frac{1}{2}\sigma_{AD}^2 + \frac{1}{4}\sigma_{DD}^2 + \frac{3}{8}\sigma_{AAA}^2 + \ldots
\]

in which case dominance variance should be overestimated more than the additive genetic variance.

A. NORDSKOG: If you had started with a commercial hybrid rather than Hays Golden, would you have gotten further?

GARDNER: This is a difficult question to answer. Of course the progress that could be made by mass selection in a segregating population produced from a cross of homozygous lines would depend upon the amount of additive genetic variance present relative to the total variance, i.e. heritability. If hybrid vigor is primarily due to the cumulative action of partially to completely dominant genes coming from the parents, there should be no question of making progress by mass selection. You would expect to be starting at a higher yield level than in the case of a variety, which would be an advantage. On the other hand, you would also be starting in a population with a rather narrow gene base. A single cross would most likely have a higher mean but a narrower gene base than a double cross.

Linkage and number of loci involved would also play a role. Linkage disequilibrium would restrict the genetic combinations available for selection in an \( F_2 \) descended from homozygous lines. Number of loci involved would affect the ultimate ceiling which one might expect to reach. If many loci are segregating for yield in a variety compared to relatively few in an \( F_2 \) of a hybrid, the greatest ultimate progress might well come from selection in the variety. At
North Carolina State University, considerable success has been realized in selecting for increased yield starting with the $F_2$ generation of crosses between homozygous lines. Full-sib families have been tested and selected, but I see no reason to believe that mass selection would not have been equally effective. I know of no case where mass selection has been tried on hybrid material.

If heteroses is primarily due to overdominance or epistasis, then mass selection starting in the $F_2$ generation of a hybrid would not be very effective. Our results suggest that overdominance is not important, but I think epistasis may be of some importance in specific combinations of lines used to produce hybrids. Even so, I would still expect to be able to make some progress by mass selection, because I think most of the heterosis observed results from bringing together different dominant favorable genes in the lines used.

A. NORDSKOG: I don't believe there is a great amount of epistasis.

GARDNER: Significant amounts of epistasis have not generally been detected in open-pollinated varieties, but this does not mean that epistasis does not exist. It can merely be accounted for in terms of additive genetic and dominance effects and variances in such populations. In crosses of specific lines to produce hybrids, epistasis may be extremely important. More information is needed.

G. W. FRIARS: What transformation was used on ear number when estimating variance components?

GARDNER: We have not used any transformation. We analyze plant means per plot based on at least 10 plants. Means of that number should be reasonably normally distributed. Perhaps we should give more thought to this problem, however.

R. GEORGE JAAP: Do you have any theories to explain Lonnquist's heterosis
results from crossing lines developed by intrapopulation selection?

GARDNER: Not unless it is due to inbreeding as a result of small effective population number used to make the synthetic variety, followed by restoration of the vigor in the hybrid from the cross of the parent variety and the improved synthetic.

MOAV: Early selection on the basis of "ear-to-row" probably had the correlated effect of reducing ear number per plant. Thus, the base population had a low frequency of the alleles for increased ear number and they probably were not dominant. Selection for the aggregate trait "yield" could have had its major effect on these loci for increased ear number. This may explain at least partially: (a) the high correlated response of increased ear number, (b) the apparent slight increase in the additive component, and (c) the fact that selection for ear number resulted in higher yield gains than selection directly for yield.

GARDNER: I agree with what you say, but I should emphasize that early selection work was directed toward plants with one large ear for two reasons: (1) One large ear could be picked by hand in half the time required to pick two small ears with the same total yield and (2) considerable emphasis was placed on selection for ears that could compete in corn shows held at county and state fairs. Size of ear was very important in corn show competition.