1 THE ROLE OF MASS SELECTION AND MUTAGENIC TREATMENT
2 IN MODERN CORN BREEDING¹

3 C. O. Gardner²

4 University of Nebraska, Lincoln, Nebraska

5 INTRODUCTION

6
7
8 Mass selection certainly is not a new technique for corn
9 improvement. On the contrary, it is undoubtedly the oldest and
10 simplest of all breeding schemes, but toward the end of the first
11 quarter of this century, a widespread belief arose that the method was
12 ineffective. Consequently, it was abandoned and corn breeders
13 concentrated their efforts on hybridization programs. Yet, a thorough
14 search of the literature has failed to uncover any critical evidence to
15 justify the viewpoint. Techniques used could easily account for all
16 failures recorded.

17 By 1955 enough evidence had accumulated to suggest that the
18 magnitude of additive genetic variance in open-pollinated varieties of
19

20 ¹ Contribution from the Department of Agronomy, University of Nebraska.
21 Published with the approval of the Director as Paper No. 2754
22 Journal Series, Nebraska Agricultural Experiment Station and as
23 Atomic Energy Commission Technical Information Document C00-1512-18.

24
25 ² Professor of Agronomy, University of Nebraska.

DISTRIBUTION OF THIS DOCUMENT IS UNLIMITED

TO TYPISTS—Begin typing flush with the left-hand marginal line, and end typing so the average length of lines corresponds with the right-hand marginal line

DISCLAIMER

This report was prepared as an account of work sponsored by an agency of the United States Government. Neither the United States Government nor any agency Thereof, nor any of their employees, makes any warranty, express or implied, or assumes any legal liability or responsibility for the accuracy, completeness, or usefulness of any information, apparatus, product, or process disclosed, or represents that its use would not infringe privately owned rights. Reference herein to any specific commercial product, process, or service by trade name, trademark, manufacturer, or otherwise does not necessarily constitute or imply its endorsement, recommendation, or favoring by the United States Government or any agency thereof. The views and opinions of authors expressed herein do not necessarily state or reflect those of the United States Government or any agency thereof.

DISCLAIMER

Portions of this document may be illegible in electronic image products. Images are produced from the best available original document.

1 corn was sufficiently great to permit effective mass selection.
2 Consequently, a program was initiated at the University of Nebraska
3 that year. Because of my interest in the effects of irradiation on
4 quantitative traits, mutation breeding was incorporated into the
5 experiment. It seemed logical to me that if mutation breeding was to
6 be effective for quantitative traits such as grain yield, the breeding
7 procedure had to involve recurrent selection and recombination along
8 with mutagenic treatment. Mass selection with seed irradiation seemed
9 the best procedure to use.

10 EXPERIMENTAL PROCEDURE

11 The variety chosen for this experiment was Hays Golden, which was
12 believed to be fairly well adapted to most of the corn-growing regions
13 of Nebraska; however the variety was possibly too early in maturity to
14 make full use of the growing season in southeastern Nebraska. One
15 sample of seed received thermal neutron irradiation (1.28×10^{13} $N_{th}/$
16 cm^2) at the beginning of the experiment and again (9.81×10^{12} N_{th}/cm^2)
17 two generations later to give rise to the Irradiated Selected
18 population. An untreated sample gave rise to the Control Selected
19 population.

20 Each population is grown in isolation each year and normal cross
21 pollination occurs. At harvest time, 10% of the plants are selected
22 based on yield phenotype. Each selected plant contributes equally to
23 the seed used to plant the next generation. In 1961, we lost the
24 Control Selected population due to failure to apply chemicals for corn
25 rootworm control. The plot lodged early and selection at harvest time
was impossible. Remnant seed was used to replant generation 6 in 1962.

1 An annual yield trial is grown to evaluate response to selection.
2 At first every generation available was included, but as seed became
3 old we noted a decline in yield due to age of seed. Now, each
4 generation of selection is tested over a three-year period. In 1969 we
5 tested generations 11, 12 and 13 of the Control and generations 12, 13
6 and 14 of the Irradiated population. Plant density in yield trials has
7 varied from approximately 8,000 plants per acre in the first trial to
8 approximately 21,000 plants per acre in current trials. A minimum of
9 ten replications has been used, with the parent variety Hays Golden
10 duplicated in each replication. To maintain good viable seed of Hays
11 Golden, 3000 to 4000 plants are grown in isolation every three years
12 and a random sample of 300 to 500 plants is harvested to represent the
13 variety. A check hybrid, Nebr. 501D, has been included in the annual
14 yield trial since 1960.

15 We have made important modifications in the mass selection
16 procedure, which we believe have contributed substantially to its
17 success. These are as follows: (1) Each population has been grown in
18 isolation away from other corn to avoid contamination and to take full
19 advantage of the selection differential. (2) We have used a low rate
20 of planting of 7,841 plants per acre to permit near maximum expression
21 of the genotype and to minimize competitive effects between plants.
22 (3) We have made every effort to minimize environmental sources of
23 variation by using a double rate of planting and thinning plants to a
24 near perfect stand, by avoiding severe moisture stress through the use
25 of timely irrigation, and by using the grid system in making our
selections at harvest time.

1 The grid system simply involves subdividing the isolated nursery
2 into approximately square plots of 40 plants each (see Figure 1)
3 leaving an unharvested border around the field. The obviously highest-
4 yielding five to eight plants in each plot are harvested and kept
5 separate. They are dried to a constant moisture level before shelling
6 and weighing. The four highest-yielding plants are then chosen from
7 each plot to contribute equal numbers of seeds to the next generation.
8 They also contribute equal numbers of seeds to the bulk sample used in
9 yield trials to evaluate the effectiveness of the mass selection
10 procedure.

12 RESULTS AND DISCUSSION

13 The results obtained in our research have amazed many corn
14 breeders including me, yet they are completely consistent with
15 theoretical expectations based upon extensive knowledge accumulated on
16 the variety Hays Golden and some selected generations. Previous reports
17 of this research may be found in several publications (1, 2, 3, 5).

18 A summary of the annual yield trials involving the first thirteen
19 generations of the Control Selected population tested over a fourteen-
20 year period is presented in Figure 2. The generation means indicate a
21 remarkably linear trend, so the linear relationship between grain yield
22 and generation of selection has been used as the measure of progress.
23 A gain of 2.93% per generation has been realized, and 85% of the
24 variation in generation means can be explained by the linear model.
25 There is no evidence that we are approaching a plateau in our mass

5
1 selection program. The estimated total gain of 38% is very close to
2 the yield of the check hybrid, Nebr. 501D, which has averaged 41.4%
3 more than Hays Golden over the last ten years.

4 Results from the Irradiated Selected population shown in Figure 3
5 are equally interesting. Irradiation decreased yields and the effects
6 were barely offset by selection during the first three generations. If
7 we conclude that no progress was made until the irradiation treatment
8 was discontinued and that the response was linear thereafter, these
9 data suggest a gain of 4.38% per generation. A good fit to the
10 straight line shown in Figure 3 is indicated by the fact that 88% of
11 the variation in generation means is explained by the linear
12 relationship. If the irradiation treatment increases additive genetic
13 variance, greater gains in that population compared to the Control
14 seem reasonable.

15 When we compare the responses of the two selected populations on
16 the same graph as in Figure 4, we note that they follow one another
17 quite closely, particularly from generation four through thirteen. If
18 greater progress is being made in the Irradiated population, it is not
19 clearly evident from this graph. Although the Irradiated population
20 may be gaining at a faster rate than the Control, the 4.38% gain
21 suggested by Figure 3 may be an overestimate.

22 Genetic variance studies were conducted at the 6th and 10th
23 generations of selection (3, 5) using the nested mating design (Design
24 I). Additive genetic variance estimates for grain yield are reported
25 in Table 1 and those for number of ears per plant in Table 2.

1 After six generations of selection, there was no evidence of a
2 decline in additive genetic variance for grain yield in the Control
3 Selected population, and greater additive genetic variance appeared to
4 exist in the Irradiated Selected one. After ten generations of
5 selection, the additive genetic variances estimated from the first
6 year's data followed exactly the same pattern as generation six data.
7 However, the second year was a less productive one and a pronounced
8 population x environment interaction occurred. The second ears
9 commonly found on plants of the two selected populations failed to
10 develop. The net result was reflected in the overall analysis as
11 reduced additive genetic variance for selected populations relative to
12 Hays Golden. Estimates indicate that the Irradiated Selected
13 population was approximately equal to Hays Golden in additive genetic
14 variance, but the Control Selected one was substantially lower.

15 Much of the increased additive genetic variance in grain yield
16 observed in generation six and again the first year in generation ten
17 is related to one of the major yield components, number of ears per
18 plant or prolificacy. Increased prolificacy appeared substantially
19 earlier in the Irradiated population but has also occurred in the
20 Control. At generation six, the Irradiated population was substantially
21 higher in additive genetic variance for prolificacy than either Hays
22 Golden or the Control, which did not differ. At generation ten, the
23 Irradiated population still had much more additive genetic variance for
24 prolificacy than either of the others, but the Control also had
25 significantly more than Hays Golden.

1 Since expected gains from selection are a function of additive
2 genetic variance, it seems reasonable to believe that we should be
3 making more progress in the Irradiated population than in the Control.
4 Predicted gains, based on genetic variance studies of Hays Golden and
5 of generations six and ten of selected populations, are presented in
6 Table 3. Realized gains (Figures 2 and 3) are in excellent agreement
7 with expectation. Theoretically, we should make faster progress in the
8 Irradiated population and ultimately reach a higher selection limit.
9 Although we need more years of selection to clearly establish the value
10 of mutation breeding, the higher estimates of additive genetic variance
11 and predicted gains from mass selection in an irradiated population are
12 encouraging. Perhaps the method of measuring response in Figure 2
13 gives a slight overestimate; however, it is in reasonably good
14 agreement with expected gains.

15 Mass selection has not only increased grain yield, but has also
16 resulted in important correlated responses such as greater prolificacy,
17 less barrenness, less lodging, later maturity and taller plants. Hays
18 Golden is predominantly a single-eared variety, but the Control
19 Selected now has 45 to 50% multiple-eared plants and the Irradiated
20 Selected 65 to 70% in the isolated nurseries. Of the prolific plants
21 in the Irradiated population this year, 92% had two or more ears on
22 the main stalk; in the Control, only 65% had two or more ears on the
23 main stalk. Barrenness was 3.6% in the Control and only 0.8% in the
24 Irradiated population. We must keep in mind that the two selected
25 populations are grown in separate isolations and field effects cannot

1 be separated from population effects.

2 In days to flower, the Control Selected population tends to be
3 four to five days later and the Irradiated Selected one three to four
4 days later than Hays Golden. At harvest time, the moisture in the
5 grain is about two percentage points higher than Hays Golden in the
6 Control and about one percentage point higher in the Irradiated
7 population. Both selected populations tend to be 10 to 12 inches
8 taller than the parent variety with correspondingly higher ear
9 placement.

10 SUMMARY AND CONCLUSIONS

11 Although we have had excellent success using mass selection to
12 increase grain yield in the Hays Golden variety, I do not believe that
13 improved varieties are likely to replace hybrids in American
14 Agriculture. However, I do believe that mass selection can play a
15 vital role in the improvement of populations from which superior lines
16 can be extracted to produce better hybrids.

17 Mass selection also offers an excellent way to utilize corn germ
18 plasm from other parts of the world. In the Corn Belt, we have made
19 use of only a very small fraction of the total germ plasm available,
20 and there must be many favorable genes not present in our populations
21 that would be quite useful when incorporated into adapted material.

22 At the University of Nebraska, Dr. W. A. Compton is making extensive
23 use of mass selection in crosses between exotic varieties and in
24 crosses between exotic varieties and Corn Belt varieties or composites
25

1 Some hybrid corn companies are also utilizing exotic materials and some
2 are using mass selection techniques.

3 In many of the developing countries of the world where corn is an
4 important human food and education of the masses is lacking, mass
5 selection should be an excellent way to increase yields of local
6 varieties or of varietal crosses. In Mexico, Johnson (4) obtained a
7 yield increase of 33% in three cycles of mass selection in a tropical
8 variety. Where genes contributing to high lysine have been introduced
9 into a population, mass selection can be used in developing a high-
10 yielding, high-lysine variety.

11 Mass selection also seems to be an ideal procedure for a mutation
12 breeding program. Unfavorable genes, chromosomal changes resulting in
13 partial sterility and any other deleterious effects can be rapidly
14 screened from the population, leaving reasonably normal plants,
15 hopefully possessing some desirable genetic changes. Recombination
16 and selection would increase the frequency of any favorable changes.

17 The value of mutation breeding for corn improvement must remain
18 somewhat questionable until we have further evidence. Nevertheless,
19 the research reported here and other research work done at Nebraska (2)
20 are encouraging. At the present time, our Irradiated Selected
21 population seems superior in some respects to the Control Selected one
22 even though a yield superiority cannot be demonstrated. We do think
23 that additive genetic variance for grain yield can be increased by
24 mutagenic treatment, but the same thing can be accomplished by
25 crossing to exotic varieties. In both cases the mean is also

1 generally reduced. Since corn breeders have not been limited by
2 genetic variability and because of the vast amount of corn germ plasm
3 available in world collections, I doubt that any hybrid corn companies
4 will be making extensive use of mutagenic agents in the near future.

5 In closing I would like to remind you that mass selection has
6 several important advantages that make it a useful scheme to improve
7 segregating populations no matter what the source of variation. Mass
8 selection is simple to operate and is a very inexpensive procedure.
9 Inbreeding can be held to a very low level even when the selection
10 intensity is quite high, and the method has been shown to be effective
11 in increasing grain yield. I think that in commercial breeding work,
12 attention needs to be given to traits other than yield even though
13 yield itself is a composite of many traits including resistance to
14 diseases and insects. Excessive ear height and too much delay in
15 maturity need to be guarded against. I believe that this can be done
16 and that substantial improvement in yield can still be realized using
17 the mass selection procedure which we have followed.

LEGAL NOTICE

This report was prepared as an account of work sponsored by the United States Government. Neither the United States nor the United States Atomic Energy Commission, nor any of their employees, nor any of their contractors, subcontractors, or their employees, makes any warranty, express or implied, or assumes any legal liability or responsibility for the accuracy, completeness or usefulness of any information, apparatus, product or process disclosed, or represents that its use would not infringe privately owned rights.

LITERATURE CITED

1. Gardner, C. O. 1961. An evaluation of effects of mass selection and seed irradiation with thermal neutrons on yield of corn. *Crop Science* 1:241-245.
2. Gardner, C. O. 1968. Mutation studies involving quantitative traits. In The Present State of Mutation Breeding, Gamma Field Symposia No. 7, pp. 57-77.
3. Gardner, C. O. 1969. Genetic variation in irradiated and control populations of corn after ten cycles of mass selection for high grain yield. In Nature, Induction and Utilization of Mutations in Plants. International Atomic Energy Agency and Food and Agriculture Organization of the United Nations Publication.
4. Johnson, E. C. 1963. Mass selection for yield in a tropical corn variety. *Amer. Soc. Agron. Abst.* p. 82.
5. Lonquist, J. H., O. Cota, and C. O. Gardner. 1966. Effect of mass selection and thermal neutron irradiation on genetic variances in a variety of corn. *Crop Science* 6:330-332.

Table 1. Additive genetic variance estimated for grain yield (grams per plant) in Hays Golden and two selected populations after six and ten generations of selection.

Population	Additive genetic variance	
	Generation 6	Generation 10
Hays Golden	308	723
Control Selected	420	214
Irradiated Selected	811	646

Table 2. Additive genetic variance estimated for number of ears per plant in Hays Golden and two selected populations after six and ten generations of selection.

Population	Additive genetic variance $\times 10^2$	
	Generation 6	Generation 10
Hays Golden	1.68	.43
Control Selected	.88	2.23
Irradiated Selected	5.96	5.18

Table 3. Expected gains from selection based on genetic variance studies conducted on Hays Golden and generations six and ten of two selected populations.

Population	Expected gain (% of population mean)		
	8 experiments combined	1963-64 experiments	1967-68 experiments
Hays Golden	3.16	2.42	4.79
Control Selected-6		1.81	
Irradiated Selected-6		3.92	
Control Selected-10			1.13
Irradiated Selected-10			3.65

FIGURE 1. ILLUSTRATION OF THE GRID SYSTEM USED TO SUBDIVIDE THE ISOLATED NURSERY TO MAKE SELECTIONS AT HARVEST TIME. EACH DOT REPRESENTS ONE PLANT.

Figure 2. Response of the Control Selected Population to generations of selection.

Figure 3. Response of the Irradiated Selected Population to generations of selection.