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Convergent-Divergent Selection for Area Improvement in Maize[1]

J. H. Lonnquist, W. A. Compton, J. L. Geadelmann, F. A. Loeffel, Boyd Shank, and A. F. Troyer[2]

ABSTRACT

The development of basic breeding populations that are adapted to a wide area and have at least some resistance to crop hazards in a region is important to breeders. A program designed to develop such a population of maize (*Zea mays* L.) for the northern Cornbelt is described. Six breeders in the area contributed germplasm samples (convergence) which were intercrossed. Samples of the resulting population were sent to each collaborator (divergence) who practiced mass selection for healthy, productive plants. In subsequent years, harvested samples (balanced composites) sent to Wisconsin (the convergent phase) were subdivided and redistributed (divergence) in such a way that seed for each location did not include seed harvested from that location the previous year.

Results from the first four cycles of selection were evaluated in performance trials at all locations over a 2-year period. Significant increases in productivity (grain yield) and reduction in grain moisture at harvest were obtained. Evidence of increased stability was noted over the four cycles of selection.

Additional index words: **Population improvement, Mass selection, Cooperative breeding, Stabilizing selection, *Zea mays* L.**

A common practice in many plant breeding programs is to select within and among families of various types at some convenient nursery site for several years. Screening for resistance to certain diseases or insects may be done in special nurseries during the initial generations of selection. Subsequently selected stocks are increased and included in performance trials over widely dispersed sites in a search for strains superior over a wide area. On the other hand, inbred lines of maize (*Zea mays* L.) selected at a given site are often used commercially in cross combination with lines developed in other areas giving hybrids which may demonstrate wide area adaptation.

The development of maize populations having wide adaptation and relatively high tolerance to common crop hazards (insects, diseases, drought, etc.) characteristic of a region is a worthwhile objective in breeding. Such populations would serve as desirable sources for new inbred lines. Extracted lines may be expected to produce hybrid combinations that are fairly resistant to crop hazards characteristic of the region and have broad adaptability. This paper describes an area improvement procedure conceived as a cooperative venture by breeders located at various sites within the northern U.S. Corn Belt. It is patterned somewhat after a suggestion of Wright (3).

The cooperative mass selection program provides selection pressures against a wide array of crop hazards which may occur differentially in separate parts of the region from time to time. While perhaps less effective than family selection in achieving such a goal, the procedure is less costly. Selection progress realized at any one of the sites contributes to overall population improvement while increasing adaptation to a somewhat broader area than would occur if continued selection were confined to a single site. The program has been underway in the northern Corn Belt since 1970.

The objectives of the area improvement scheme are: (i) development of an improved population as a source of parent lines having a) a wide area adaptation and b) moderate levels of resistance to important crop hazards occurring in the region; (ii) to provide a basis for strengthening cooperative research activities among interested breeders in the region at minimum cost. The current report presents evidence obtained from a 2-year evaluation of the first four cycles of selection.

MATERIALS AND METHODS

The procedure was conceived as a system involving the convergence of separate units of germplasm from a broad area followed by intercrossing and then dispersal to a set of locations in the area. Following mass selection, samples of the harvested seed would be returned (convergence) to a central location for inter-mixing prior to divergence to the cooperating locations for continued selection. Five collaborators in the northern U.S.

[1] A contribution from the Dep. of Agronomy, Univ. of Wisconsin, Madison; Dep. of Agronomy, Univ. of Nebraska, Lincoln; Dep. of Agronomy and Plant Genetics, Univ. of Minnesota, St. Paul; Northrup King and Co., Stanton, Minn.; the Dep. of Plant Sciences, South Dakota State Univ., Brookings; Pioneer Hybrid International, Mankato, Minn. Received 9 Oct. 1978.

[2] Department of Agronomy, Univ. of Wisconsin, Madison; Dep. of Agronomy, Univ. of Nebraska, Lincoln; Dep. of Agronomy and Plant Genetics, Univ. of Minnesota, St. Paul; formerly of Northrup King and Co., Stanton, Minn., currently NAPB, Brookston, Ind.; Dep. of Plant Sciences, South Dakota State Univ., Brookings; formerly of Pioneer Hi Bred International, Mankato, Minn., currently Pfizer Genetics, St. Louis, Mo.

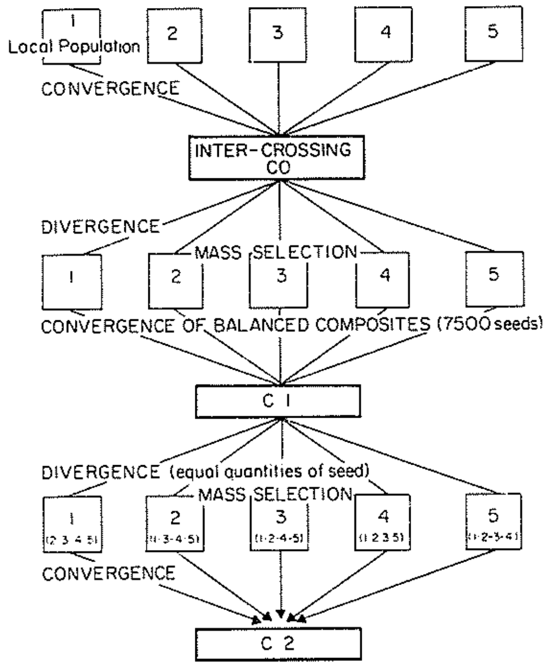

Fig. 1. Area improvement in maize through convergent-divergent selection.

Corn Belt contributed seed of some 30 cultivars and/or synthetics that were used to form the initial composite (CO) for the program (convergence). Included were early cultivars, cultivar composites, early × tropical composites, and synthetics formed from early inbred lines. These materials provided an extremely broad genetic background.

In the initial synthesis of the CO population, the 30 components were planted in an isolated crossing block using single rows of 250 seeds of each as female rows. These were detasseled. The male rows were planted with a mechanical mixture of equal numbers of seeds of each of the 30 components. The male rows were planted at three 10-day intervals with the females being planted at the time of the second male planting. This was done to maximize intercrossing of components with varying flowering dates.

At harvest, the 25 to 50 earliest, most prolific, healthy, and otherwise desirable plants were selected within each female row. A balanced composite of seed was formed from selected plants in each female row. Subsequently, a sample of 2,550 seeds was formed using equal numbers of seeds from each of these 30 balanced "female" composites. This seed was planted and intermated in Hawaii during the winter of 1970. The resulting harvest was dried and shelled. A total of eight samples (balanced composites) of 7,500 seeds each were formed from this crop, and these were considered the original "Area Improvement Composite" designated (AI CO). Three samples were placed in cold storage. The remaining five samples were distributed to the collaborators in the program (divergence) who planted the seed in isolated blocks for mass selection. The area was initially that represented by locations in northeastern Nebraska, northern and southern Minnesota, northern Iowa, and south central Wisconsin. A sixth location, southeastern South Dakota, was added in 1973. Each isolation was approximately ¼ ha. Care was used to assure plant densities of approximately 53,300 plants/ha. Moderate densities were deemed advantageous in early stages of selection since extremely diverse materials, including subtropical, were included in the initial composite. At harvest, healthy plants exhibiting earliness, prolificacy, above average productivity, and other desirable attributes were chosen. Selection intensity was approximately 5%.

The harvested seed (selected sample) at each location was dried and used in making up a balanced composite of 7,500+ seeds. Each harvested plant was represented equally in the composite. The composites were sent to Madison, Wis. (convergence) where new balanced composites were formed for planting the following season. Following the formation of CO, the

Table 1. Summary of performance of Area Improvement AI C0 to C4 and two check hybrids grown in 10 locations 1975–76.

Identity	Grain yield: Mean	Low density†	High density†	Moisture in grain at harvest
	quintals/ha			%
Hybrid checks				
A619•A632	79.6	76.8	82.5	21.7
A654•W182B	56.0	54.9	57.2	16.1
Area improvement				
C0	52.9	53.4	52.4	22.5
C1	53.1	52.6	53.4	20.4
C2	55.9	57.1	54.7	20.9
C3	55.7	56.4	55.0	20.2
C4	56.8	54.9	58.7	19.6
L.S.D. (0.05)	2.9			0.8

† Low = 35,600 plants/ha; High = 53,300 plants/ha.

convergent and divergent stages were mechanical in nature and were carried out each year as was the selection procedure (see Fig. 1). During the first 2 years with five locations involved, the seed sample from each location was divided into $l - 1 = 4$ equal lots (7,500/4 = 1,875 seeds). Seed to be returned to location 1 (divergence) for next year's planting and selection was made up of one-fourth part of the previous year's sample sent in from locations 2, 3, 4, and 5 (4 × 1,875 = 7,500s). Seed for location 2 would likewise consist of one-fourth parts of that received from locations 1, 3, 4, 5, etc. with the addition of a sixth location in 1973, $l = 6$ giving $l - 1 = 5$ subsamples of 7,500/5 = 1,500 seeds each. The makeup of the seed lots of 7,500 seeds returned to each cooperator was formed as before. Thus seed from plants selected in a specific location in 1 year was not included in the sample planted at that location the following year. In this way chances of fixation of genotypes particularly well adapted to a given site were minmized.

A test to measure progress realized through selection cycles (C0-C4) was carried out in 1976 and 1977 at each of the six locations involved in the selection program. The seven entries in the tests included two hybrid checks, A632 × A619 and A654 × W182B. The populations were planted in a split plot arrangement of two densities (35,500 and 53,300 plants/ha) with three replications using 2- × 8-m plots with hills spaced 75 cm. Plots were overplanted and thinned in the seedling stage to the desired stands.

RESULTS AND DISCUSSION

The hybrid checks averaged significantly higher yield and lower grain moisture at harvest than the area improvement cycles (Table 1). Also, hybrids showed significantly higher yields with increased planting densities, whereas the area improvement populations did not. Cycles of selection were highly significant for both yield and moisture in grain at harvest. The linear regression was highly significant for both traits (see Fig. 2).

We used the method proposed by Plaisted and Peterson (1) to evaluate the ability of selections to yield consistently in different test locations. The mean estimates of variety × location variance components ($\hat{\sigma}^2_{VL}$) are shown in Table 2. In the northern Corn Belt, the area represented by the trials conducted in this study, the hybrid checks do relatively well. They provided a point of reference for the measurement of progress realized by the selection scheme involved. Perhaps, not surprisingly, the greatest contribution to σ^2_{VL} was shown by the two single cross hybrids, especially since relatively higher yields were involved. The more variable populations (area improvement composites) contributed less variation, with the C4

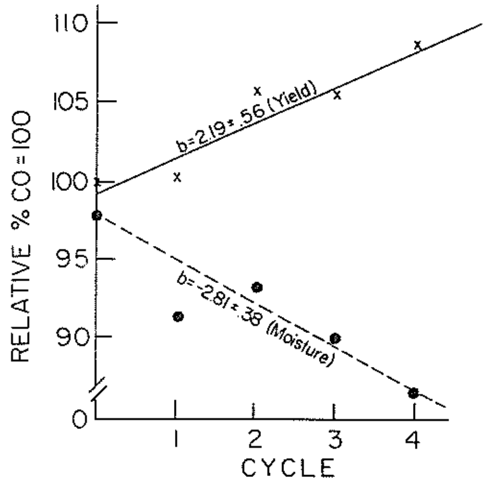

Fig. 2. Response from convergent-divergent selection in the northern U.S. cornbelt.

population showing least. These results reflect the hoped for trend in the apparent greater stability obtained from the type of selection practiced and the generally lesser stability of the single-cross hybrids. While the trend in contribution to σ^2_{VL} is in the hoped for direction, it is doubtful whether rapid changes should be expected to occur. Nevertheless, changes as they do occur may later be reflected in performance of parent inbred lines extracted from these populations.

The average relative changes in population performance from the four cycles of selection were 2.19 ± 0.56% for yield and −2.81 ± 0.38% for moisture at harvest (Fig. 2). The combination of increased yields with earlier maturity is a highly desirable trend for the crop in this region.

Although selection emphasis was for healthy, early maturing, prolific, standing plants, there has been no apparent change in stalk quality. Perhaps marking desirable plants at a time when early maturity is detectable but delaying harvest until differences in stalk quality are more pronounced would contribute to greater progress in this important trait. The lack of apparent change in stalk quality could be considered a gain since yield increased and moisture in grain at harvest decreased (an indication of early maturity) and one might expect increased lodging with earlier, higher yielding plants.

Area improvement is conceived as stabilizing selection with respect to some large area or region as compared wtih that more commonly expected from continued mass selection in a specific locale. This seems contrary to the concept of Tigerstedt (2) who regards stabilizing as well as diversifying selection to possibly result in genetic heterogeneity and polymorphism in populations. Stabilizing selection was generally considered as selection for optimum adaptation to a particular locale. The program outlined herein is diversifying (disruptive) selection in one sense, but we expect that continued selection within a changing population at a series of locations will result in stabilizing selection relative to the larger area, in this case the northern U.S. Corn Belt. From the standpoint of population improvement, adversities likely to surface within a relatively broad area are not likely to occur in epidemic proportions throughout the region each year. Yet, some serious adversity may well characterize certain portions of the region in any 1 year. In the area improvement scheme, any opportunity to select for resistance to a particular problem in a particular locale will contribute some gain in resistance to that problem in the population as a whole. Net gain in a population undergoing area improvement should exceed that accomplished by selection at any single site and result in improved stability of the population or its derivatives (lines or hybrids) over the region.

Average performance over the region gave evidence that the selection practiced resulted in improved yield and earlier maturity. Continued selection should lead to further improvement of the germplasm resource for breeding programs in the northern U.S. Corn Belt.

Table 2. Estimates of relative contribution of two hybrid checks and five cycles of selection from an Area Improvement scheme to the mean cultivar × location interaction component of variance.

Population (hybrid or cycle)	$\hat{\sigma}^2_{VL}$
A619 × A632	173.72
A654 × W182B	249.25
AI C0	68.47
AI C1	53.81
AI C3	53.12
AI C2	52.79
AI C4	49.42
Mean	100.08

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