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I am submitting herewith a dissertation written by Syrus Abd-Mishani entitled "Evaluation of Mass Selection for Yield in Corn as Measured by Random S_1 Lines and Their Testcrosses." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Plant and Soil Science.

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EVALUATION OF MASS SELECTION FOR YIELD IN CORN AS MEASURED BY RANDOM S_1 LINES AND THEIR TESTCROSSES

A Dissertation

Presented for the

Doctor of Philosophy

Degree

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Syrus Abd-Mishani

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To the memory of my father

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ABSTRACT

A mass selected corn population (MS 13), and the parent variety Jellicorse (Je) were evaluated at Knoxville and Crossville using random S_1 lines per se and S_0 lines topcrossed to an unrelated single cross. The selected population (MS 13) had undergone thirteen generations of mass selection for ear corn yield.

S_1 lines and their testcrosses of MS 13 did not demonstrate statistically significant average yielding superiority over lines of Je at either Knoxville or Crossville, or the two locations combined. Both S_1 and testcross progenies of MS 13 were greater in yield than Je at Crossville (14.3 percent and 7.9 percent) where more favorable environmental conditions existed for the tests. Indications are that frequencies of favorable yield genes were greater in progenies of MS 13 than in corresponding progenies of Je. Differences are attributable to the effect of mass selection on the parent variety but the unfavorable conditions of the test locations did not allow the selected plants to express maximum yield potential.

The top yielding S_1 and testcross progenies of the study came from the selected population.

Correlations between S_1 and testcross yields for Je and MS 13 were + 0.40** and + 0.48**, respectively.

Genotypes of MS 13 produced more ears/plant with greater nubbin weights, produced taller plants with higher ear placement, and produced more lodged plants. Genotypes of MS 13 flowered later but they

produce grain having slightly less moisture at harvest than genotypes of Je. However, differences in all measured traits were not great and generally nonsignificant at the .05 level of probability.

Variance estimates show that genetic variability among S_1's exceeded that among testcrosses for most traits, as expected, and that S_1 and testcross progenies of Je had less genetic variability in yield and yield related traits than S_1 and testcross progenies of the corresponding MS 13. The results suggest that mass selection increased genetic variance and particularly additively genetic variance of MS 13 relative to Je. The significant yield variability in MS 13 genotypes indicates that continued yield improvement is possible in the selected population from further cycles of mass selection under favorable environmental conditions.

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CHAPTER I

INTRODUCTION

Mass selection is the simplest and oldest method of corn improvement. It has been used as a procedure in the domestication of corn and in the improvement of corn populations. Mass selection consists of selecting phenotypically desirable plants and planting the seeds en masse. A modification of mass selection for yield is progeny evaluation of the selected plants and bulking the seeds of the best yielding plants.

Up to the first quarter of this century mass selection was not considered to be effective in improving the yield of adapted varieties.

The successful development of hybrid corn through inbreeding and hybridization resulted in a temporary abandonment of population improvement. Most of the open-pollinated varieties of corn were developed by a mass selection procedure, and these populations have been utilized by plant breeders as sources of inbred lines to produce hybrids.

Thus, critical evaluations of mass selection were not available prior to 1961. All the efforts were concentrated on developing, improving, and hybridizing potential inbred lines. Although plant breeders have been successful in developing better yielding hybrids, progress has been slow in recent years; consequently, the need for superior populations of corn as a source of inbred lines has been felt by many plant breeders. It is obvious that the best combining lines are those with higher frequencies of favorable genes. The probability of fixing a larger number of favorable genes by inbreeding is largely

dependent upon the comparative frequencies of desirable alleles in parent plants. If undesirable alleles exist in high frequencies in base populations, then the chances of developing highly prepotent inbred genotypes are limited. It follows that selection which increases frequencies of favorable alleles in base populations should augment the chances of extracting superior hybrids.

Fourteen generations of mass selection for yield were conducted in corn in the variety Jellicorse in Tennessee by Josephson and Kincer (1976). A maximum increase in yield of 13.1 percent over the variety was obtained over the 14 generations of selection with no further increases obtained beyond the 10th generation. Moisture in the grain at harvest increased slightly, total number of ears produced per plant increased 22.1 percent, and ear height increased 21.6 percent over the 14 generations of selection.

The main objective of the investigation presented herein was to measure the performance of S_0 lines from the 13th cycle of mass selection and their testcrosses in comparison with the Jellicorse variety: to determine (1) whether mass selection for yield increased the frequency of favorable yield genes and (2) whether mass selection for yield reduced genetic variability.

CHAPTER II

LITERATURE REVIEW

During the first quarter of this century, it was generally concluded that mass selection was not effective for improving yields of adapted corn varieties. Thus, the majority of plant breeders abandoned mass selection. According to Sprague (1955), mass selection for the improvement of corn dates back to the domestication of corn. He further pointed out that no critical evaluation of this breeding method was available from the early literature, but there is considerable indirect evidence that mass selection may have been reasonably effective in improving the yield of corn populations. Most of the open-pollinated varieties in the United States were developed by mass selection. A modification of mass selection called ear-to-row breeding utilizing progeny testing was initiated by Hopkins at the Illinois Experiment Station in 1896 to modify chemical composition and other agronomic factors in corn (Dudley et al., 1974). The earlier results appeared to be very promising, and the procedure was applied by many breeders; but the results with respect to yield proved to be rather disappointing. Montgomery (1909) reported a gain of 9 bushels per acre from the first few years (1903-1907) of ear-to-row breeding at the Nebraska Station, but data for the years 1911 to 1917 reported by Kiesselbach (1922) showed no difference between the parent population, Hogue's Yellow Dent, and the selected population. Williams and Welton (1915) of the Ohio Experiment Station found that 18 of 20 selected

strains yielded more than the parent stock. Increases ranged from 1 1/2 bushels to 11 bushels per acre. Noll (1916), Richey (1922), Hayes and Alexander (1924), and Smith and Brunson (1925) found that ear-to-row selection for yield was not effective. Richey (1922) summarized reports on ear-to-row selection and concluded:

> In view of the expense, the uncertainty with which greater yields have been obtained, and the small increases secured during a series of years in the most favorable cases, so far there appears to be little to recommend ear-to-row breeding as a practical method of corn improvement.

With the striking yield increases obtained with hybrid corn in the 1920's, more conventional selection methods were deserted in favor of inbreeding and hybridization programs. Thus, breeders for a time abandoned mass selection coupled with natural selection in providing the varietal sources from which all inbreds and their hybrid crosses were derived.

Effectiveness of selection for yield improvement in corn populations is dependent upon the presence of additively genetic variance of yield. Hull (1952) attributed the failure of mass selection and ear-to-row selection for yield improvement of corn to the lack of sufficient additively genetic variance because of continued past selection for yield. He concluded that the genetic variance present was largely nonadditive and, therefore, not subject to utilization in mass selection. Gardner (1961) discussed previous reports and stated:

> If overdominance exists, as suggested by Hull, the heterozygote is favored and the effect of selection is toward an equilibrium point with respect to gene frequencies. Both alleles remain in the population and contribute to genetic variation, but selection becomes ineffective when the equilibrium point has been reached.

The successful improvement of corn varieties through recurrent selection procedures (Lonnquist, 1949), where selection was based upon testcross progeny performance, showed the effectiveness of intravarietal selection in improving the yield of corn and, consequently, the existence of genetic variance. Opinions about the types of gene action involved in heterosis of grain yield of corn are divided into the overdominance theory supported earlier by Bruce (1910), Keeble (1910), and Crow (1948). The overdominance (a term coined by Hull) theory of heterosis implies that dominance genetic variance of yield would normally exceed additively genetic variance, whereas, the dominance theory regards the greater portion of genetic variance to be additive. Subsequently, the use of more sophisticated statistical genetic procedures revealed considerable additively genetic variance of yield in open-pollinated varieties of corn and that progress from mass selection would appear worthwhile.

Comstock and Robinson (1948) showed that additive and dominance genetic variance of yield and other traits in corn could be estimated utilizing certain mating designs and assuming no epistasis and equilibrium with respect to segregation of linked genes. Robinson, Comstock, and Harvey (1955) utilized the Comstock and Robinson (1948) mating designs to estimate the genetic variance component and thereby determine the relative importance of additive and dominance genetic variances in three southern varieties of corn. They concluded that additively genetic variance of grain yield and other traits was considerably greater than dominance variance and that overdominant loci were not the single important source of genetic variability in the varieties studied. However, later studies by Lindsey, Lonnquist, and

Gardner (1962); Lonnquist, Cota, and Gardner (1966); Williams, Penny, and Sprague (1965); Compton, Gardner, and Lonnquist (1955); and Goodman (1965) to estimate additive and dominance genetic variances of grain yield and other traits revealed considerable additively genetic variance for yield and further supported the belief that simple additive gene action predominates in corn.

Jenkins (1940) recommended the use of recurrent selection as a method for developing improved varietal populations of corn. The selection was based on the testcross progeny performance (or the combining ability) of S_0 plants or inbred lines of the parent variety. He reported that grain yield was controlled by a large number of dominant genes having approximately equal effects.

Sprague and Tatum (1942) defined general and specific combining ability as follows:

> The term "general combining ability" is used to designate the average performance of a line in hybrid combination. . . . The term "specific combining ability" is used to designate those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved.

Lonnquist (1961) pointed out that the tester choice depends upon the breeder's objectives. A tester providing a broad genetic base is used if selection is for general combining ability; while a tester providing a narrow genetic base, such as an inbred line or a single cross, is employed if selection is for specific combining ability. As is the case with mass selection, the effectiveness of recurrent selection for general combining ability is dependent upon the presence of additively genetic variance for grain yield in the material under selection.

Lonnquist (1949) formed a synthetic population of the cornbelt variety Krug Yellow Dent by combining random S_1 lines selected for their general combining ability. His synthetic population significantly exceeded the parent variety in yield, thereby substantiating the importance of additive gene effects with respect to grain yield. Lonnquist advocated the utility of selection for general combining ability as follows:

> The method should provide a means of increasing the frequency of desired yield genes with continued improvement in yield. Inbreeding in such a population should then permit extraction of inbred lines with far greater numbers of favorable yield genes and consequently of higher combining ability than lines now in use. Thus, the method appears to have value, not only as an end in itself (the commercial use of synthetics), but also as a means to an end, . . . the development of germplasm reservoirs highly suitable for the extraction of superior inbred lines.

Lonnquist (1964) believed that the main weaknesses associated with the early methods of corn improvement were lack of parentage control, poor plot techniques, and reduced intensity of selection for yield because of too much attention being given to show card traits. The most obvious limitation of mass selection as a method of population improvement is that it is based upon phenotypic selection of plants in a single location planting. The observed yield of a plant in such a planting is usually thought of simply as $P_i = \mu + G_i + e_i$ when the genotype X environment interactions and measurement error are included in e. A more realistic model would be:

$$P_{ijk} = \mu + G_i + L_j + Y_k + GL_{ij} + GY_{ik} + LY_{jk} + GLY_{ijk} + e_{ijk}$$

where

μ = Population mean.

G_i = Genotypic value of ith genotype.

L_j = Effect of jth location.

Y_k = Effect of kth year.

GL_{ij} = Interaction of ith genotype with j^{th} location.

GY_{ik} = Interaction of ith genotype and k^{th} year.

LY_{jk} = Interaction of jth location and k^{th} year.

GLY_{ijk} = Interaction of ith genotype, j^{th} location and k^{th} year.

e_{ijk} = Effect of unexplained random influences encountered during the particular growing season.

The genetic effect (G_i) is made up of additive, dominance, and epistatic gene complexes. Progress from mass selection is based mainly on the additive portion of the genetic variance. The location effect (L_j), although treated as a major influence, may be considered also to consist of a complex of submacroenvironmental effects at a given location. Some control over the latter variations can be realized by subdividing the area into a series of subblocks and practicing selection within each unit.

The phenotypic differences on which selections are made are likely to be the result of interaction effects of environment with the particular genotypes selected as much as they result from genetic differences of the type and degree sought. In other words, phenotypic differences are no guarantee of genotypic differences. This would be particularly true after a few generations of effective selection or in a population where additively genetic variance is somewhat limited. The problems associated with differentiation of genotypic differences can be overcome in varying degrees depending partly on the breeder's willingness

to lengthen the generation interval through the use of progeny evaluation procedures (Lonnquist, 1964).

Hallauer and Sears (1969) conducted mass selection for yield in Krug and Iowa Ideal open-pollinated varieties of corn. The plot techniques used were patterned after those suggested by Gardner (1961). They made yield evaluations of the original and six cycles of selection in Krug, and five cycles in Iowa Ideal. They did not find significant improvement of yield in either variety by mass selection. They state:

> The lack of significant progress in Iowa Ideal and Krug after five and six cycles of mass selection, respectively, may be due to one or more of the following: (1) a paucity of additive genetic variance in the varieties, (2) imprecise plot techniques to minimize the confounding effects of the environment, (3) insufficient testing to detect the small differences and to estimate the true value for the different cycles of selection, particularly in the later cycles, (4) a low intensity of selection due to the exclusion of stalk-lodged plants in the basic units of selection, and (5) plant density too high in the plots under selection, a factor which prevented the phenotypic expression of yield for individual plant genotypes that could be selected visually.

Gardner (1961) believed that faulty techniques is the reason for the ineffectiveness of mass selection for yield. He initiated a refined mass selection study for grain yield in 1955 in the Hays' Golden Variety. One sample of seed received thermal neutron radiation. The other untreated sample resulted in a control selected population. Beginning in 1956 the selection nursery was stratified into small areas of 40 plants each, and seed of the highest yielding 10 percent of the plants in each stratum was saved to produce the next generation. Thus each population was advanced in isolated fields each generation. Each generation of selection and the original variety was compared to a yield trial each year. The results indicated that mass selection resulted in a 3.9 percent

gain per year over the original variety. Gardner (1969) continued the study for thirteen generations of selection, and the results showed that the selected population outyielded the parent variety by 38 percent, his selection having resulted in yield gains averaging slightly less than 3 percent per cycle for thirteen cycles of selection in the control and irradiated populations. There is no evidence that a plateau was reached in the mass selection program. He suggested that his refined mass selection technique could be effective for (1) improving yield in other corn varieties and (2) increasing the frequency of favorable genes in varieties before inbreeding and hybridization. Gardner (1969) reported that mass selection not only increased grain yield, but also resulted in important correlated responses such as greater prolificacy, less barrenness, less lodging, later maturity, and taller plants. He pointed out also that mass selection can be used in developing a high yielding, high lysine variety where genes contributing to high lysine have been introduced into a population.

Johnson (1963) reported increases of 33 percent in the grain yields of two Mexican varieties by applying the refined mass selection technique for three cycles.

Lonnquist (1967) reported a 6.28 percent average gain in yield per cycle over the first five cycles of mass selection for prolificacy in Hays' Golden. Grain moisture increased 3.2 percent, and tillering increased in the selected population.

Harris et al. (1972) in a 2-year study using random S_1 lines and their testcrosses of original and improved populations (C9 from nonirridated and I9 from irridated generation) of Gardner's mass

selections, concluded that S_1 lines of the selected populations per se and in testcrosses yielded 27.5 percent and 7.5 percent more than the corresponding groups of the parent variety in 1969 and 1970, respectively. The unfavorable growing conditions of 1970 was responsible for the lower increase. The testcrosses of the two selected populations produced similar yields. The selected populations produced similar germ plasm reservoirs which would be much more suitable for the extraction of superior lines than would the parent variety. Selection also reduced genetic variability in yield and combining ability. Prolificacy resulting from selection for yield was evident in S_1 lines but not in the testcrosses. Both selected populations were higher in shelling percentage and moisture content of seeds, were later in flowering, and produced taller plants with higher ear placement.

Genter (1976) applied mass selection to incorporate desirable traits from 25 Mexican races of corn into a single population with early maturity and plant type that would be useful to temperate zone corn breeders. Ten cycles of selection have been completed. He reported that over the 10 cycles, yield increased 171 percent, days to mid-silk decreased 11 days, and moisture at harvest decreased 7.7 percentage points. The ratio of plant-to-ear height decreased; in C10, ear height averaged 115 cm i.e., 50 percent of plant height. Average time between pollen shed and silk emergence decreased from 9.1 to 7.0 days. Selection had little effect on root lodging, but stalk lodging increased.

It is apparent that the results of many corn investigations conducted in the past two decades tend to support the dominance hypothesis of hybrid vigor and likewise the belief that additive gene

action plays a major role in affecting the grain yield of corn. If additive gene effects on yield truly predominate in corn, then intravarietal selection techniques such as mass selection and recurrent selection for general combining ability should be successful in raising the frequency of favorable yield genes in selected populations above that of their parental varieties. Furthermore, inbred lines extracted from the improved populations should exhibit better yield performance, higher combining ability, and could be expected to produce better hybrids than lines from unselected parental varieties.

Critical information concerning comparison of the combining ability of inbreds extracted from improved varietal populations with the combining ability of inbreds from either less advanced populations or the unselected parental varieties is almost completely lacking in the literature. However, there are some studies comparing the combining ability of S_0 plants of the original population and that of the advanced population.

Penny (1968) studied the differences in yield and combining ability of five synthetic strains of maize, all developed from the same parent variety, Iowa Stiff Stalk Synthetic (BSSS). He reported only small improvements in the general combining ability for yield of BSSS by four methods of selection.

Burton et al. (1971) evaluated the effectiveness of half-sib selection with a double cross tester and S_1 selection <u>per se</u> following four cycles of selection in BSK (The Krug Hi I syn. 3 strain of 'Krug Yellow dent'). Their study showed that the mean yield and the general

combining ability of BSK were significantly improved over the original population by four cycles of selection.

Eberhart et al. (1973) studied the progress from five cycles of reciprocal recurrent selection in the BSSS and BSCB1 (Iowa Corn Borer synthetic #1) maize populations. The results showed significant improvement in the combining ability of advanced populations over the original populations.

Genter and Eberhart (1974) in a dialled-cross study over 16 locations compared the general combining ability of 6 original maize populations and their advanced populations derived from mass selection or recurrent selection procedures. They concluded that four of the advanced populations showed greater general combining ability than the original populations. (BSK(S) and BSSS (HT) (two advanced populations) in their study did not show progress where previous evaluation in Iowa (Burton et al., 1971; Eberhart et al., 1973)) had shown much improvement in general combining ability of the advanced populations. One of the original populations under study was Gardner's mass selection material. They compared C12 from the non-irradiated control with the original (CO) and reported that C12 averaged 12.3 percent higher in yield than CO.

Evaluation of inbred lines can be determined by hybrid performance. The use of testcrosses provides an efficient method for preliminary evaluation of inbred lines. Many investigators have reported on the relation between various plant and ear characters of inbred lines and their testcrosses.

Jugenheimer (1958) found that grain yield, standability, and maturity of three-way crosses were correlated positively and significantly with

the same characters of the S_1 inbred lines. Correlation for grain yield was + 0.589.

Some breeders advocate S_1 line per se performance as an effective evaluation of the yield prepotency of new lines. Lonnquist and Rumbaugh (1958) utilized an unrelated single cross and the parental population as testers for S_1 lines of the Krug variety. They reported a significant correlation of 0.54 for testcross yield; however, the relative yields of the lines per se as determined by the two types of testers were not ranked accurately or similarly. Koble and Rinke (1963) tested random lines from a synthetic corn variety as S_1 lines and topcrosses to a related and unrelated tester. They reported that the relationship between S_1 line per se performance and either testcross was generally as high as or higher than the relationship between the two testcrosses and recommended that selection based on S_1 line per se performance might be used to replace the more expensive and time consuming testcross method. Comstock (1964) concluded on theoretical grounds that, in the absence of overdominance in a population, S_1 testing provides for more rapid genetic advance than the testcross method. Genter and Alexander (1966), in a study of recurrent selection, based selection of lines to be intercrossed on line per se performance by one method and on testcross performance by the second method and succeeded in improving mean S_1 yields by 31.4 percent with two cycles of the line per se evaluation method and 17.9 percent with two cycles of the testcross evaluation method. They observed that although more productive S_1 lines tended to produce the more productive crosses, the correlation between S_1 and testcross yield decreased with each cycle of selection. They concluded from their

results that only progenies in the upper 50 percent in S_1 yield should be retained for further inbreeding and suggested that visual selection for desirable traits plus S_1 line per se yield evaluation offers a greater opportunity for effective early generation selection than testcross methods now generally in use. Lonnquist and Lindsey (1964) evaluated S_1 lines of a third cycle Krug synthetic population as (1) lines per se, (2) in topcrosses to an unrelated synthetic tester, and (3) in topcrosses to parental population. They reported that phenotypic correlations for yield between evaluation procedures were low. Harris et al. (1972) in a mass selection study reported that the phenotypic correlations between S_1 and testcross yield were too low to be of much predictive value. Burton et al. (1971) and Genter (1973) presented experimental evidence showing the testcross method to be less effective in increasing population yield than S_1 progeny testing over four and two selection cycles, respectively. Goulas and Lonnquist (1976) in a study of recurrent selection for intra population improvement in corn using combined testcross and S_1 evaluation method reported that this method can be effectively employed in a recurrent selection program.

It is reasonable to expect that S_1 progeny performance should reflect mainly additively genetic effects while testcross performance should reflect some nonadditive effects as well as dominance or epistatic relationships between the evaluated parent and the tester.

CHAPTER III

MATERIALS AND METHODS

A mass selection study with the prolific Jellicorse variety (Je) utilizing Gardner's stratified method (Gardner, 1961) was started by Josephson and Kincer (1976) in 1961 at Tennessee, for the purpose of evaluating this method of breeding with a prolific variety, and to determine if this breeding method is effective in increasing yield. Jellicorse, originally known as Jellicorse Twin, is a white corn, obtained from continued selection for prolificacy by Reggie Jellicorse, Elmwood, Smith County, Tennessee. The ears are of medium size, with 12 to 16 rows, and are well covered with husk. The grain is sound and of excellent quality. The variety was maintained at the West Tennessee Experiment Station at Jackson until the experiments on mass selection were begun.

The 13th generation of mass selection (MS 13) for yield in the variety Jellicorse and the original variety (Je) were the basic materials used in the investigation presented herein.

In order to evaluate the selected population (MS 13) as a source of superior inbred lines in relation to the parent variety Jellicorse (Je), approximately 100 random plants were self-pollinated in the Jellicorse variety (Je), and 100 plants in the selected population (MS 13). The same S_0 plants were crossed on the unrelated single cross hybrid, Ga209 X Mo18W, to provide the corresponding testcrosses. The experimental materials were prepared in the 1974 nursery at the Plant

Science Field Laboratory, Knoxville, Tennessee. Seventy plants of each population with adequate seed for testing were selected for the studies.

The two sets of 70 S_1 lines, and the corresponding testcrosses along with the original variety, the selected population, and two check hybrids (T115 X Till and Tenn. 505) comprised the entries for the study described herein. They were evaluated at two locations, the Plant Science Field Laboratory at Knoxville, and the Plateau Experiment Station at Crossville in 1975. The two types of progenies (S_1 lines and testcrosses) were tested in a field arrangement of two intermixed 12 X 12 simple lattices with two replications. The experimental entries representing each of the 140 S_1 lines, and the four checks were randomly assigned to blocks of the first lattice. Entries representing each of the 140 testcrosses and the four checks were grouped into blocks of an adjacent second lattice. Grouping of entries into blocks of the second lattice was restricted so that the adjacent block of testcrosses had the corresponding S_1's which comprised a block of the first lattice. Intermixing of the two lattices allowed planting of a block of S_1 lines adjacent to a block containing the corresponding testcrosses thereby permitting extended precision in comparing S_1 lines and their corresponding testcrosses. Two replications were planted at Knoxville as X_1 and Y_1 and two replications of the same entries were planted at Crossville as X_2 and Y_2. The planting plan of block 1 of each lattice in one replication involving two simple lattice designs is shown in Figure 1. The field arrangement of the entries at Knoxville and Crossville are presented in Appendix tables 1 and 2, respectively. Experimental entries within blocks and blocks were randomized at both locations. The

Block #1 of lattice #1 Twelve plots, each plot representing one S_1 line
border
Block #1 of lattice #2 Twelve plots, each plot representing the testcross of one S_1 line in block #1 of lattice #1

Figure 1. Planting plan of block #1 of each lattice in one replication involving two simple lattice designs.

experimental design and methods were the same at Knoxville and Crossville.

The test area at Knoxville was previously planted to soybeans and was fertilized with 1000 pounds per acre of 6-12-12, broadcast and disked in. The test area at Crossville also was in soybeans previously and was fertilized with 250 pounds of 0-26-26 and 112 pounds of nitrogen per acre broadcast and disked in. One hundred pounds of 7-28-28 fertilizer per acre was applied in the row at the time of planting. The experiments were subjected to uniform agronomic practices including a preemergence application of one and one half pounds of Atrazine and one and one half pounds of Lasso per acre for weed control. The test was planted at Knoxville on April 29, 1975 and at Crossville on May 6, 1975. Each plot consisted of two 9-foot rows spaced 40 inches apart. Three-foot alleys separated the blocks. The seed was hand planted every 6 inches and subsequently thinned in the five-to six-leaf stage of growth to 10 plants per row on June 2 at Knoxville and on June 9 at Crossville. The resulting plant density was approximately 13,068 plants per acre. Missing plants were replanted to a purple marker stock and border rows on each side of the experiment were planted to the Jellicorse variety to provide competition for the experimental material. The plots were sidedressed with 100 pounds per acre of nitrogen on May 28 at Knoxville and on June 16 at Crossville.

Measured agronomic variables included ear corn yield, number of ears, number of nubbins, yield of nubbins, percent grain moisture at harvest, days to mid-shed, and mid-silk, ear height, plant height, root lodging, and stalk lodging. Plant height and lodging were not measured

in the experiment at Crossville. The flowering dates of each plot were recorded as the date when 50 percent of the plants in the plot were shedding pollen and silks were emerged on 50 percent of the plants. Plant and ear height means were determined by averaging measurements obtained on ten competitive plants in each plot. The tests were harvested manually on October 6-8 at Knoxville, and on October 15 and 20 at Crossville. Ear corn weights were adjusted to 15.5 percent moisture and a full stand on a plot basis.

The intermixed lattices were analyzed as two distinct experiments in each location with respect to each of the ten measured traits. The Knoxville and Crossville data were first analyzed separately as a simple lattice design, and then the two locations combined were analyzed as a four replicate lattice design. Finally the data were analyzed over locations as a randomized complete block design to obtain the genotype X location component of variance. The data were analyzed utilizing the IBM 360/65 computer at the University of Tennessee Computing Center. The lattice design is based on the following linear model (Cochran and Cox, 1957; Federer, 1955) for observation of each plot:

$$Y_{ijq} = \mu + P_i + B_{ij} + T_q + e_{ijq}$$

Where:

Y_{ijq} = the observation on the qth genotype in the jth block in the ith replicate.

μ = the general mean of the experiment.

P_i = the effect of the ith replicate; $i = 1,2, \ldots, r$.

B_{ij} = the effect of the jth block in the ith replicate; $j = 1,2, \ldots, k$.

T_q = the effect of the qth genotype; $q = 1,2, \ldots, k^2$.

e_{ijq} = the intra-block residual or error, assumed to be normally and independently distributed with mean zero and variance σ^2.

The form of analysis of variance of the simple lattice design utilized for each of the two experiments is presented in Table 1.

The differences between adjusted or unadjusted genotype means of each population were compared with the L.S.D. The form of analysis of variance of the randomized complete block design utilized for estimates of genetic variance ($\sigma^2_{G'}$) of each population (Je and MS 13) for S_1 per se and testcross experiments in each location.

Estimates of genetic variance ($\sigma^2_{G'}$) in each location were obtained by the following formula:

$$\hat{\sigma}^2_{G'} = (\sigma^2 + r\sigma^2_{G'}) - \sigma^2/r$$

Where:

r = number of replications = 2

$\sigma^2_{G'}$ = variance of a genotype

$\sigma^2_G + \sigma^2_{GL} + \sigma^2_{GY} + \sigma^2_{GLY}$

σ^2_G = variance due to genetic differences among genotypes.

σ^2_{GL} = variance due to interactions of genotype with locations.

σ^2_{GY} = variance due to interactions of genotype with year.

σ^2_{GLY} = variance due to interactions of genotype, location, and year.

σ^2 = error variance.

A method described by Snedecor and Cochran (1967) was utilized to compute standard errors for this and all subsequent estimates of variance.

Table 1. Form of analysis of variance of the simple lattice design utilized for the S_1 lines per se, and testcross experiments at each location.

Source of Variation	Degrees of freedom	Mean square	
		Observed	Expected
Replications	r-1	MS_P	$\sigma^2 + k\ {}^2_B + k^2\sigma_P^2$
Genotypes (unadjusted)	k^2-1	MS_T	$\sigma^2 + \frac{k}{k+1}\sigma_B^2 + r\sigma_T^2$
Blocks (adjusted)	r(k-1)	E_b	$\sigma^2 + \frac{k}{r}\sigma_B^2$
Intra-block error	(k-1)(rk-k-1)	E_e	σ^2
Totals	rk^2-1		

k^2 = number of genotypes = 144

k = number of genotypes/block = 12
r =
r = number of replicates = 2

E_b = mean square for "Blocks (adjusted)".

E_e = "Intra-block error" mean square.

P_i, B_{ij}, T_q, and e_{ijq} are assumed to be normally distributed independent random variables from population with mean zero and variance $\sigma_P^2 = E(P_i^2)$, $\sigma_B^2 = E(B_{ij}^2)$, $\sigma_T^2 = E(T_q^2)$, and $\sigma^2 = E(e_{ijq}^2)$ respectively.

Estimates of genotypic correlation ($r_{G'}$), and phenotypic correlation (r_p) between S_1 lines and testcross progenies for each population in each location were obtained utilizing covariance analysis of randomized complete block designs and the following formula described by Becker (1974):

$$r_{G'} = \hat{Cov}_{G'}/(\hat{\sigma}^2_{G'X} - \hat{\sigma}^2_{G'Y})^{1/2} \text{ and}$$

$$r_p = (\hat{Cov}_{G'} + \hat{Cov}_e)/[(\hat{\sigma}^2_{eX} + \hat{\sigma}^2_{G'X})(\hat{\sigma}^2_{eY} + \hat{\sigma}^2_{G'Y})]^{1/2}$$

Where:

X = the trait of S_1 lines.

Y = the trait of testcross progeny.

Estimates of the "genotype X location" component of variance (σ^2_{GL}) and genetic variance over location ($\sigma^2_{G''}$) were obtained by the following formulae:

$$\sigma^2_{GL} = (MS_{GL} - E')/r \quad \text{and}$$

$$\hat{\sigma}^2_{G''} = (MS_G - MS_{GL})/rl$$

Where:

l = number of location = 2

$\sigma^2_{G''} = \sigma^2_G + \sigma^2_{GY} + \sigma^2_{GYL}$ (σ^2_{GL} removed)

E' = an estimate of σ^2_e obtained by pooling the appropriate error variances of each location.

The combined data were analyzed according to procedures given in Cochran and Cox (1957).

CHAPTER IV

RESULTS

Analysis of variance results for ear corn yield are presented in Tables 2, 3, and 4. Analysis of variance results for other measured traits except grain moisture are presented in the Appendix (Tables A3 through A14). The tables include relative efficiencies and coefficients of variation which describe the relative variation among traits and progeny types. The data show that the lattice design was much more efficient at Crossville than at Knoxville.

The analysis of variance over locations for ear corn yield (Table 4) shows that a significant interaction between genotypes and locations occurred.

Mean ear corn yields of S_1 and testcross progeny of the parental population, selected population, and check entries are presented in Table 5. The mean ear corn yield for each progeny type of the selected populations exceeded the mean for the corresponding progeny type of the parent variety at each location, but the differences were not statistically significant at the .05 level of probability.

The top 10 percent of the individual S_1 entries of each parental population are ranked by their ear corn yield means at each location and combined locations means in Tables 6 to 8. Most of the top yielding entries came from the selected population (MS 13). Certain MS 13 S_1 progenies i.e. 19, 51, and 48, and Je S_1 progeny i.e. 64 ranked high as S_1 <u>per se</u> and also in testcrosses at both locations.

Table 2. Analysis of variance of ear corn yield (lb/plot) in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus check entries. Knoxville and Crossville, Tennessee.

		Mean squares			
		S_1 lines		Testcrosses	
Source	D.F.	Knoxville	Crossville	Knoxville	Crossville
Replications	1	0.45	22.20	0.75	6.68
Genotypes (unadjusted)	143	10.23	11.60	2.62	5.32
Blocks (adjusted)	22	2.26	7.96	2.97	10.36
Intra-block error	121	1.49	1.68	1.01	1.31
Total	287	5.90	7.20	1.96	4.02
Relative efficienty (%)		102.58	140.31	117.91	181.53
Coefficient of variation		22.10	16.38	9.24	7.75

Table 3. Combined analysis of variance over location (four-replicate lattice) of ear corn yield (lb/plot) in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus check entries. Knoxville and Crossville, Tennessee.

Source	D.F.	Mean squares	
		S_1 lines	Testcrosses
Replications	3	237.55	740.75
Genotypes (unadjusted)	143	18.16	4.52
Blocks (adjusted)	44	6.26	10.52
Intra-block error	385	2.23	4.52
Total	575	7.73	6.84
Relative efficiency (%)		109.33	141.61
Coefficient of variation		21.86	9.73

Table 4. Analysis of variance over location of ear corn yield (lb/plot) in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus check entries. Knoxville and Crossville, Tennessee.

Source	D.F.	Mean squares	
		S_1 lines	Testcrosses
Locations (L)	1	684.99	2214.80
Genotypes (G)	143	18.77**	4.53*
Genotypes X location (G X L)	143	3.67**	3.43**
Pooled error	286	2.13	2.00

*, ** Significant at the .05 and .01 level of probability, respectively.

Table 5. Mean ear corn yield in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus five experimental check entries. Knoxville and Crossville, Tennessee.

Experimental material		Ear corn yield (lb/plot)			% of increase over corresponding Je progeny type		
Progeny type	Population	Knoxville	Crossville	Combined mean	Knoxville	Crossville	Combined mean
S_1 lines	Je	5.51	7.30	6.32	-	-	-
	MS 13	5.54	8.34	6.87	.54	14.25	8.27
Checks	Je open-pollinated	13.03	13.12	13.08			
	MS 13 open-pollinated	12.42	15.06	13.74			
	T115 X T111	14.20	14.09	14.15			
	Tenn. 505	13.98	12.05	13.02			
L.S.D. (.01)		3.27	3.34	2.72			
L.S.D. (.05)		2.49	2.54	2.07			
Testcrosses	Je	10.82	14.25	12.53	-	-	-
	MS 13	10.95	15.38	13.17	1.20	7.93	5.02
Checks	Je open-pollinated	11.95	13.27	12.61			
	MS 13 open-pollinated	13.34	15.12	14.25			
	Ga209 X Mo18W	9.21	11.88	10.55			
	Tenn. 505	12.01	14.19	13.10			
L.S.D. (.01)		2.59	2.95	2.28			
L.S.D. (.05)		1.97	2.25	1.73			

Table 6. Top 10 percent of 70 random S_1 lines and testcrosses from selected population (MS 13) and the parent variety Jellicorse (Je) ranked by their ear corn yield (lb/plot). Knoxville, Tennessee

Rank	S_1			Test cross		
	Pop.	Entry	Yield	Pop.	Entry	Yield
1	MS 13	19	11.68	MS 13	19	13.95
2	MS 13	51	11.29	Je	34	13.31
3	MS 13	17	9.40	MS 13	51	13.25
4	MS 13	48	9.33	MS 13	71	13.10
5	Je	64	9.11	MS 13	137	12.96
6	Je	14	9.02	MS 13	67	12.87
7	Je	60	8.72	Je	7	12.56
8	MS 13	105	8.49	Je	61	12.47
9	MS 13	42	8.39	Je	40	12.46
10	MS 13	66	8.36	Je	24	12.44
11	Je	39	8.32	Je	14	12.36
12	Je	131	8.16	MS 13	105	12.29
13	Je	111	8.02	MS 13	47	12.27
14	Je	144	7.64	Je	21	12.25
Mean of all entries			5.52			10.89
L.S.D. (.01)			3.27			2.59
L.S.D. (.05)			2.49			1.97

Table 7. Top 10 percent of 70 random S_1 lines and testcrosses from selected population (MS 13) and the parent variety Jellicorse (Je) ranked by their ear corn yield (lb/plot). Crossville, Tennessee.

	S_1			Testcross		
Rank	Pop.	Entry	Yield	Pop.	Entry	Yield
1	MS 13	19	13.73	MS 13	67	18.22
2	MS 13	42	12.92	MS 13	94	17.99
3	Je	64	12.10	MS 13	114	17.56
4	MS 13	48	11.97	MS 13	90	17.53
5	MS 13	51	11.94	MS 13	69	17.30
6	MS 13	105	11.38	MS 13	51	17.27
7	MS 13	94	11.38	MS 13	75	17.26
8	MS 13	113	11.13	Je	131	16.55
9	Je	142	10.78	Je	9	16.51
10	Je	6	10.15	Je	32	16.22
11	Je	131	10.05	Je	60	16.16
12	Je	144	9.98	Je	89	15.56
13	Je	123	9.82	Je	112	15.50
14	Je	103	9.22	Je	64	15.24
Mean of all entries			7.82			14.82
L.S.D. (.01)			3.34			2.95
L.S.D. (.05)			2.54			2.25

Table 8. Top 10 percent of 70 random S_1 lines and testcrosses from selected population (MS 13) and the parent variety Jellicorse (Je) ranked by their two-location ear corn yield means (lb/plot). Knoxville and Crossville, Tennessee.

	S_1			Testcross		
Rank	Pop.	Entry	Combined location yield	Pop.	Entry	Combined location yield
1	MS 13	19	12.40	MS 13	67	15.50
2	MS 13	51	11.42	MS 13	51	15.25
3	MS 13	48	10.85	MS 13	19	15.23
4	Je	64	10.80	MS 13	137	15.04
5	MS 13	42	10.76	MS 13	75	15.03
6	MS 13	105	9.74	MS 13	114	14.77
7	MS 13	17	9.66	MS 13	90	14.63
8	Je	131	9.36	Je	7	13.96
9	Je	142	9.16	Je	34	13.86
10	MS 13	69	9.08	Je	131	13.84
11	Je	60	9.03	Je	40	13.63
12	Je	14	8.97	Je	88	13.60
13	Je	72	8.52	Je	9	13.54
14	Je	138	8.41	Je	55	13.47
Mean of all entries			6.68			12.86
L.S.D. (.01)			2.72			2.28
L.S.D. (.05)			2.07			1.73

Representations of the ear corn yield distributions of Je and MS 13 S_1 and testcross progenies are presented graphically in Figures 2 to 5. The frequency curves illustrate that the lower (except for combined location and testcrosses) and upper tails of the MS 13 distribution lie outside the lower and upper tails of the Je distribution. These results show that the highest yielding lines and testcrosses should come from MS 13.

The mean maximum temperature, mean minimum temperature and precipitation at the test locations for the months April through October in 1975 are shown in Table 9. The growing conditions at Knoxville and at Crossville were somewhat different. It appears that drought produced a hindrance to normal plant development and reduced the vigor and productive capacity of all experimental material at Knoxville. Conditions during the growing period at Crossville were more nearly ideal than at Knoxville. As a consequence of the unfavorable environmental conditions at Knoxville, mean ear corn yields for all progeny types and check entries were lower than at Crossville. Yields at Crossville exceeded those at Knoxville by 32.5 percent for the Je S_1 lines, 50.5 percent for the MS 13 S_1 lines, 31.7 percent for the Je testcrosses, and 40.5 percent for the MS 13 testcrosses (Table 5, p. 28).

The progeny types of Je were better able to compensate for the unfavorable environmental conditions than were the corresponding progeny types of MS 13. This is shown by the reduced average superiority of MS 13 progenies at Knoxville over corresponding Je as compared to that observed in the Crossville experiments. Yield means at Knoxville show an average superiority for MS 13 S_1 progeny of 0.54 percent, and a superiority of

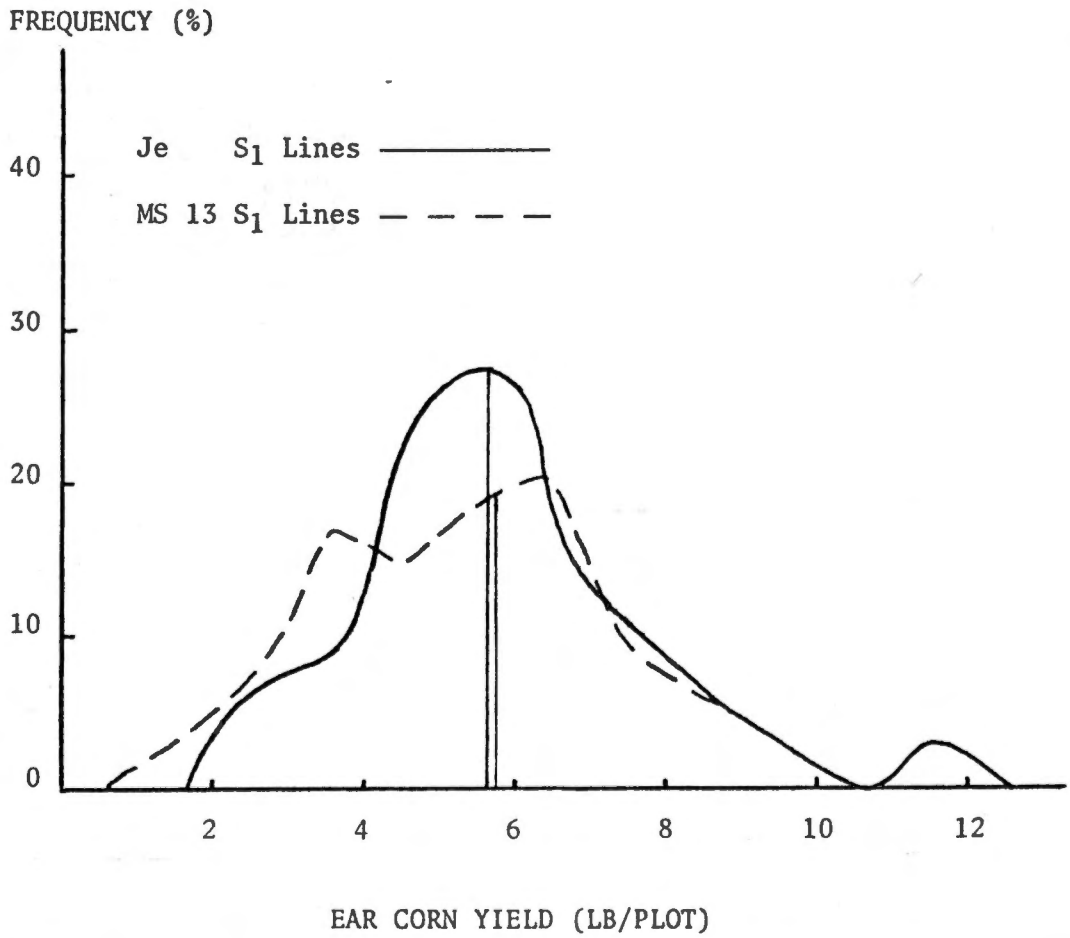

Figure 2. Ear corn yield distributions of random S_1 lines from the parent variety Jellicorse (Je) and the selected population (MS 13) utilizing 1 lb/plot class intervals. Knoxville, Tennessee.

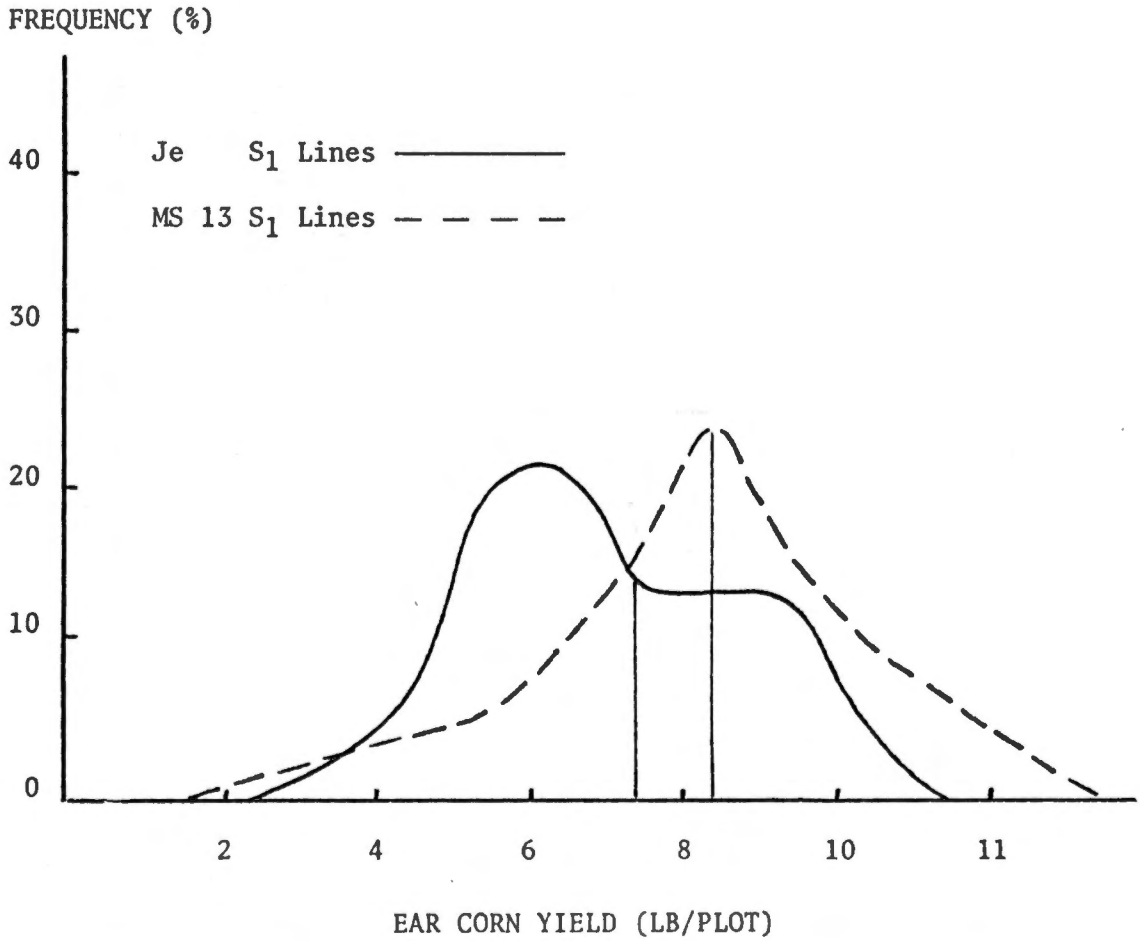

Figure 3. Ear corn yield distributions of random S_1 lines from the parent variety Jellicorse (Je) and the selected population (MS 13) utilizing 1 lb/plot class intervals. Crossville, Tennessee.

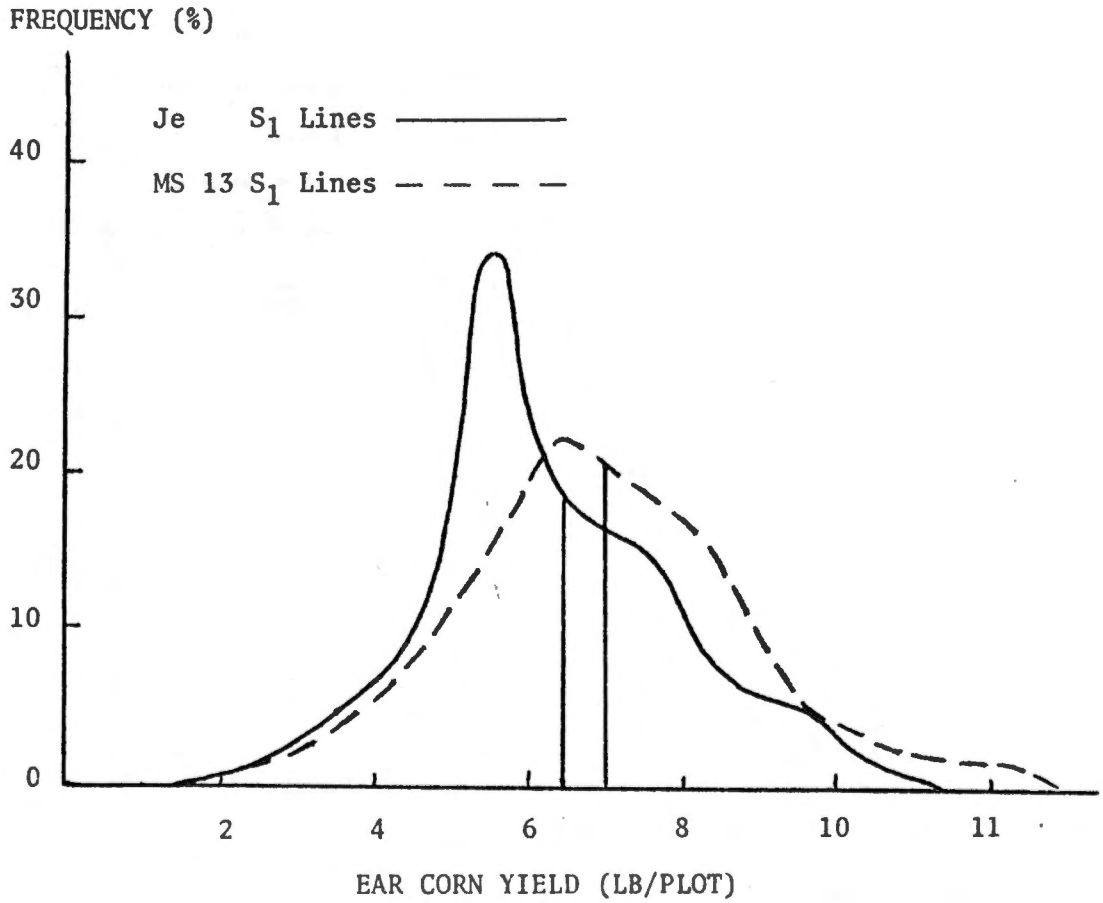

Figure 4. Ear corn yield distributions of random S_1 lines from the parent variety Jellicorse (Je) and the selected population (MS 13) utilizing 1 lb/plot class intervals. Knoxville and Crossville, Tennessee.

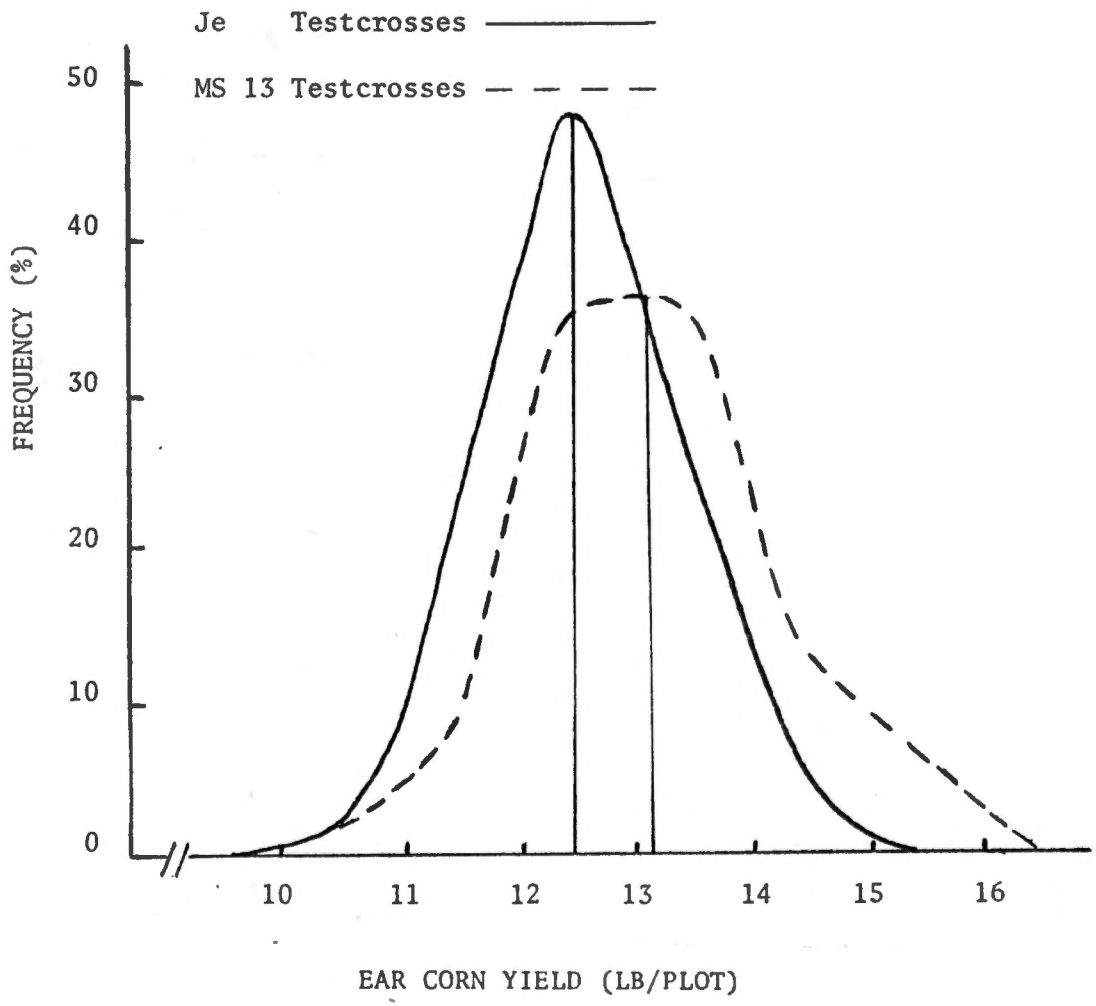

Figure 5. Ear corn yield distributions of testcrosses from the parent variety Jellicorse (Je) and the selected population (MS 13) utilizing 1 lb/plot class intervals. Knoxville and Crossville, Tennessee.

Table 9. The mean maximum temperature, mean minimum temperature and precipitation at the test locations for the months April through October in 1975. Knoxville and Crossville, Tennessee.

	April	May	June	July	August	Sept.	Oct.
				Temperature, °F			
Knoxville	67.3						
Maximum	67.3	*	*	87.8	88.3	77.2	70.7
Minimum	46.5	*	*	68.0	70.1	61.0	51.0
Crossville							
Maximum	63.1	75.5	79.1	81.7	82.4	72.2	68.0
Minimum	40.8	54.5	57.9	61.3	63.3	53.0	46.4
				Precipitation, inches			
Knoxville							
Total	1.86	*	*	1.69	4.23	3.82	4.25
Days rained	7	*	*	10	13	10	10
Crossville							
Total	2.96	4.70	3.88	4.08	2.57	8.34	5.75
Days rained	11	14	9	14	11	14	10

*Data not obtained.

1.2 percent for their testcross progeny. In contrast, the Crossville data show an average superiority of 14.3 percent for the MS 13 S_1 progeny, and 7.9 percent for their testcross progeny.

An evaluation of the mass selected open-pollinated population and the original open-pollinated variety by Josephson and Kincer (1976) showed that a maximum increase of 13.1 percent in yield over the variety was obtained over the 14 generations of selection with no further increases obtained beyond the 10th generation. This superiority of the selected population over the parental variety in this study was statistically significant at the 0.05 level of probability at Crossville but not at Knoxville.

Inbreeding depressions in yield of the S_1 plant due to selfing was measured from the check means S_0 populations for the parental population at each location. The results are shown in Table 10. Under the better environmental conditions at Crossville relative to that of Knoxville, average reductions were not as great for MS 13 and Je. Je showed a slightly lower reduction at Knoxville; however, this was probably due in part to the low yield of the Je open-pollinated variety.

The mean number of ears per plant for the various progeny types and check entries are presented in Table 11. The data were not adjusted for barren or unproductive plants. The MS 13 S_1 progeny mean showed an increase of 17.4 percent over the Je progeny mean at Knoxville, a non significant increase. The superiority of the mass selected population over the parent variety is also evident in the testcrosses.

The S_1 progenies of the selected population produced 29.6 percent more ears than the corresponding progeny type of the parent variety at

Table 10. Estimate of inbreeding depression in ear corn yield due to one generation of selfing the parent variety Jellicorse (Je) and the selected population (MS 13). Knoxville and Crossville, Tennessee.

Population	% reduction in population mean		
	Knoxville	Crossville	Combined
Je	55.9	44.7	50.3
MS 13	57.0	44.7	50.9

Table 11. Mean number of ears per plant in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus five experimental check entries. Knoxville and Crossville, Tennessee.

Experimental material		Ears/plant			% of increase over corresponding Je progeny type		
Progeny type	Population	Knoxville	Crossville	Combined mean	Knoxville	Crossville	Combined mean
S_1 lines	Je	1.38	1.25	1.32	-	-	-
	MS 13	1.62	1.62	1.62	17.39	29.60	22.73
Checks	Je open-pollinated	1.85	1.68	1.77			
	MS 13 open-pollinated	1.87	2.00	1.94			
	T115 X T111	2.05	2.00	2.03			
	Tenn. 505	1.68	1.69	1.69			
L.S.D. (.01)		.70	.49	.45			
L.S.D. (.05)		.53	.38	.36			
Testcrosses	Je	1.49	1.42	1.43	-	-	-
	MS 13	1.66	1.70	1.72	11.41	19.72	20.28
Checks	Je open-pollinated	1.94	1.43	1.69			
	MS 13 open-pollinated	2.02	2.03	2.02			
	Ga209 X Mo18W	1.70	1.48	1.59			
	Tenn. 505	1.66	1.62	1.64			
L.S.D. (.01)		.36	.38	.28			
L.S.D. (.05)		.28	.29	.22			

Crossville. The low number of ears produced in the S_1 progeny of both populations is undoubtedly due to inbreeding depression. This is evidenced by the greater number of ears produced in the testcrosses, since the tester parent is not highly prolific.

Distributions of the number of ears of the Je and MS 13 S_1 progeny is graphically presented in Figure 6. The frequency curves illustrate that the greater proportion of S_1 lines with the highest number of ears would be expected to come from the mass selected population.

Mean number of nubbins are shown in Table 12. The MS 13 mean is higher than the Je mean for both progeny types of both locations, illustrating that the greater number of ears produced in the selected population (Table 11, p. 40) was largely due to nubbin ears.

Mean yield of nubbins for the progeny types of the parental populations and check entries are presented in Table 13. Mean yield of nubbins of each progeny type of the selected population exceeded the mean of the corresponding progeny type of the parent variety at both locations, but the differences were not statistically significant at the .05 level of probability. In terms of size of ears, selection slightly decreased the mean ear weight of top ears at both locations except for nubbins of the testcrosses at Crossville.

Mean grain moisture percentages are shown in Table 14. Percentages were slightly higher in the Je progenies at Crossville but were similar at Knoxville. Distributions of grain moisture of the Je, and MS 13 S_1 progenies are presented graphically in Figure 7. The frequency curves illustrate that the greater proportion of S_1 lines with highest grain

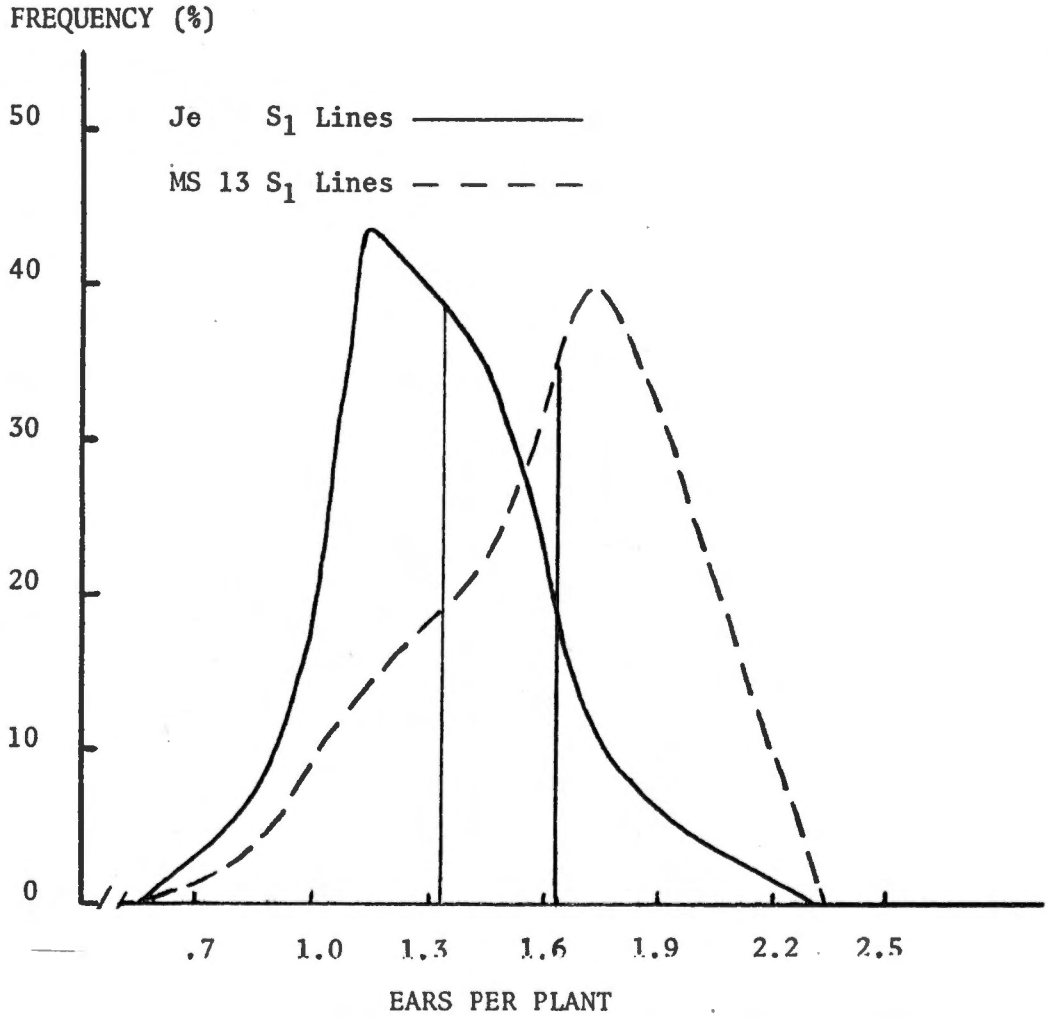

Figure 6. Number of ears per plant distributions of random S_1 lines from the parent variety Jellicorse (Je) and the selected population (MS 13) utilizing 0.3 unit class intervals. Knoxville and Crossville, Tennessee.

Table 12. Mean number of nubbins per plant of S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus five experimental check entries. Knoxville and Crossville, Tennessee.

Experimental material		Nubbins/plant			% of increase over corresponding Je progeny type		
Progeny type	Population	Knoxville	Crossville	Combined mean	Knoxville	Crossville	Combined mean
S_1 lines	Je	0.84	0.62	0.73	-	-	-
	MS 13	1.04	0.82	0.93	18.18	32.26	27.40
Checks	Je open-pollinated	0.53	0.63	0.58			
	MS 13 open-pollinated	0.67	0.59	0.50			
	T115 X T111	0.33	0.36	0.35			
	Tenn. 505	0.58	0.40	0.49			
L.S.D. (.01)		0.63	0.54	0.43			
L.S.D. (.05)		0.48	0.41	0.33			
Testcrosses	Je	0.47	0.36	0.47	-	-	-
	MS 13	0.68	0.42	0.55	19.30	16.67	17.02
Checks	Je open-pollinated	0.65	0.32	0.49			
	MS 13 open-pollinated	1.02	0.65	0.84			
	Ga209 X Mo18W	0.99	0.58	0.79			
	Tenn. 505	0.72	0.51	0.62			
L.S.D. (.01)		0.37	0.32	0.27			
L.S.D. (.05)		0.28	0.25	0.20			

Table 13. Mean yield of nubbins of S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus five experimental check entries. Knoxville and Crossville, Tennessee.

Experimental material		Yield of nubbins (lb/plot)			% of increase over corresponding Je progeny type		
Progeny type	Population	Knoxville	Crossville	Combined mean	Knoxville	Crossville	Combined mean
S_1 lines	Je	2.16	2.55	2.36	-	-	-
	MS 13	2.35	3.27	2.81	8.80	28.24	19.07
Checks	Je open-pollinated	1.36	3.65	2.51			
	MS 13 open-pollinated	2.44	2.90	2.67			
	T115 X T111	1.19	2.05	1.22			
	Tenn. 505	1.56	1.55	1.56			
L.S.D. (.01)		1.98	2.38	1.73			
L.S.D. (.05)		1.50	1.81	1.32			
Testcrosses	Je	1.97	1.68	1.83	-	-	-
	MS 13	2.33	2.07	2.20	18.27	23.21	20.20
Checks	Je open-pollinated	2.65	1.70	2.18			
	MS 13 open-pollinated	3.45	3.15	3.30			
	Ga209 X Mo18W	3.80	2.55	3.18			
	Tenn. 505	2.40	2.20	2.30			
L.S.D. (.01)		1.99	1.56	1.33			
L.S.D. (.05)		1.51	1.19	1.01			

Table 14. Mean grain moisture percentages of S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus five experimental check entries. Knoxville and Crossville, Tennessee.

Experimental material		Grain moisture (%)			% of increase over corresponding Je progeny type		
Progeny type	Population	Knoxville	Crossville	Combined mean	Knoxville	Crossville	Combined mean
S_1 lines	Je	19.3	26.9	23.1	-	-	-
	MS 13	19.3	25.7	22.5	-4.5	-4.5	-2.6
Checks	Je open-pollinated	17.9	26.7	22.3			
	MS 13 open-pollinated	17.7	25.7	21.7			
	T115 X T111	16.2	24.8	20.5			
	Tenn. 505	20.1	24.9	22.5			
Testcrosses	Je	20.3	26.3	23.3	-	-	-
	MS 13	20.3	25.7	23.0	0.0	-2.3	-1.3
Checks	Je open-pollinated	20.3	27.1	23.7			
	MS 13 open-pollinated	19.0	24.4	21.7			
	Ga209 X Mo18W	20.7	23.9	22.3			
	Tenn. 505	19.7	25.5	22.6			

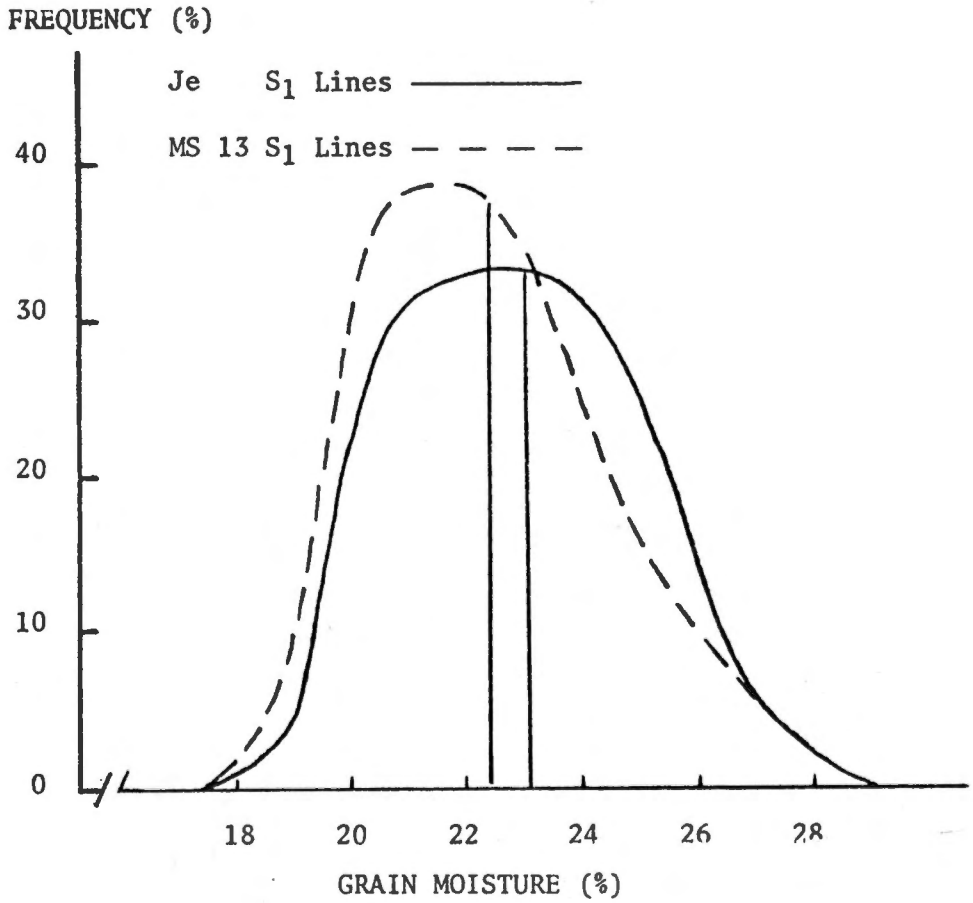

Figure 7. Grain moisture distribution of random S_1 lines from the parent variety Jellicorse (Je) and the selected population (MS 13) utilizing 2.0 percent class intervals. Knoxville and Crossville, Tennessee.

moisture percentage would be expected to come from the original population.

Mean days to mid shed and silk for progeny types and check entries are presented in Table 15. Differences between progeny types were not significant in either location, but the MS 13 progenies were 1 to 2 days later in shedding and silking. The plants were later in flowering at Crossville, and the S_1 progeny were later than the testcross progeny.

Mean ear and plant heights are presented in Table 16. The data show that both ear and plant height were greater in the selected population; however, the differences were not significant. As expected, ear and plant heights were greater in the selected population, indicating that selection for yield increased plant and ear height. Distributions of ear height of Je and Ms 13 S_1 progenies is graphically presented in Figure 8. The frequency curves illustrate that the upper tail of MS 13 distribution lies outside the upper tail of the Je distribution. This result shows that the S_1 lines with the highest ear height came from the mass selected population.

Mean stalk lodging at Knoxville is presented in Table 17. The selected population lodged more than the parent variety both as S_1's and in the testcrosses. However, the differences were not statistically significant.

Estimates of genetic variance ($\sigma^2_{G'}$) for some of the measured traits in S_1 and testcross progenies of Je and MS 13 at each location are presented in Table 18. Standard errors of the estimates are included in the tables. All estimates of genetic variance in the S_1 lines of each population are greater than zero at both locations. Also, most estimates

Table 15. Mean days to mid-shed and mid-silk of S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus five experimental check entries. Knoxville and Crossville, Tennessee.

Experimental material		Days to mid-shed			Days to mid-silk		
Progeny type	Population	Knoxville	Crossville	Combined mean	Knoxville	Crossville	Combined mean
S_1 lines	Je	71.1	81.1	74.8	75.8	81.1	78.5
	MS 13	73.4(3.3)[1]	82.4(1.5)	76.9(2.8)	77.2(1.9)	82.4(1.5)	79.8(1.7)
Checks	Je open-pollinated	66.7	77.9	71.7	69.7	77.9	74.0
	MS 13 open-pollinated	67.0	81.8	74.3	73.0	81.8	77.8
	T115 X T111	66.0	77.7	71.1	67.7	77.7	72.8
	Tenn. 505	69.6	78.0	73.4	71.7	78.0	75.0
L.S.D. (.01)		4.2	3.1	2.9	5.8	2.8	3.5
L.S.D. (.05)		3.2	2.4	2.2	4.4	2.2	2.7
Testcrosses	Je	69.2	77.4	73.3	73.0	79.2	76.1
	MS 13	70.3(1.5)	77.9(.6)	74.1	73.9(1.2)	79.7(.6)	76.7(.8)
Checks	Je open-pollinated	67.5	77.0	72.3	69.7	77.8	74.9
	MS 13 open-pollinated	71.0	76.5	73.8	73.0	78.3	75.9
	Ga209 X Mo18W	69.5	77.0	73.3	74.0	79.7	76.8
	Tenn. 505	69.0	77.0	73.0	71.6	78.1	74.8
L.S.D. (.01)		3.2	2.5	2.2	3.5	2.3	2.3
L.S.D. (.05)		2.5	1.9	1.7	2.7	1.8	1.7

[1]% delay

Table 16. Mean ear heights and plant heights of S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus five experimental check entries. Knoxville and Crossville, Tennessee.

Experimental material		Ear height (inch)			Plant height (inch)
Progeny type	Population	Knoxville	Crossville	Combined mean	Knoxville
S_1 lines	Je	51.3	52.2	52.7	109.2
	MS 13	61.2 (19.3)[1]	61.0 (16.9)	61.1 (15.9)	119.4 (9.3)
Checks	Je open-pollinated	57.0	56.5	56.8	119.4
	MS 13 open-pollinated	66.3	63.5	64.9	135.0
	T115 X T111	53.0	47.0	50.0	107.4
	Tenn. 505	55.7	50.0	52.9	118.2
L.S.D. (.01)		10.5	14.5	9.5	17.2
L.S.D. (.05)		8.0	11.0	7.2	13.1
Testcrosses	Je	58.6	56.5	57.6	120.5
	MS 13	62.7 (7.0)	61.9 (9.6)	62.4 (8.3)	125.8 (4.4)
Checks	Je open-pollinated	61.2	53.6	57.4	126.4
	MS 13 open-pollinated	71.0	70.0	70.5	124.0
	Ga209 X Mo18W	53.8	48.9	51.3	113.8
	Tenn. 505	53.9	51.1	52.4	118.1
L.S.D. (.01)		7.1	9.2	5.6	11.7
L.S.D. (.05)		5.4	7.0	4.2	8.9

[1]% of increase over corresponding Je progeny type.

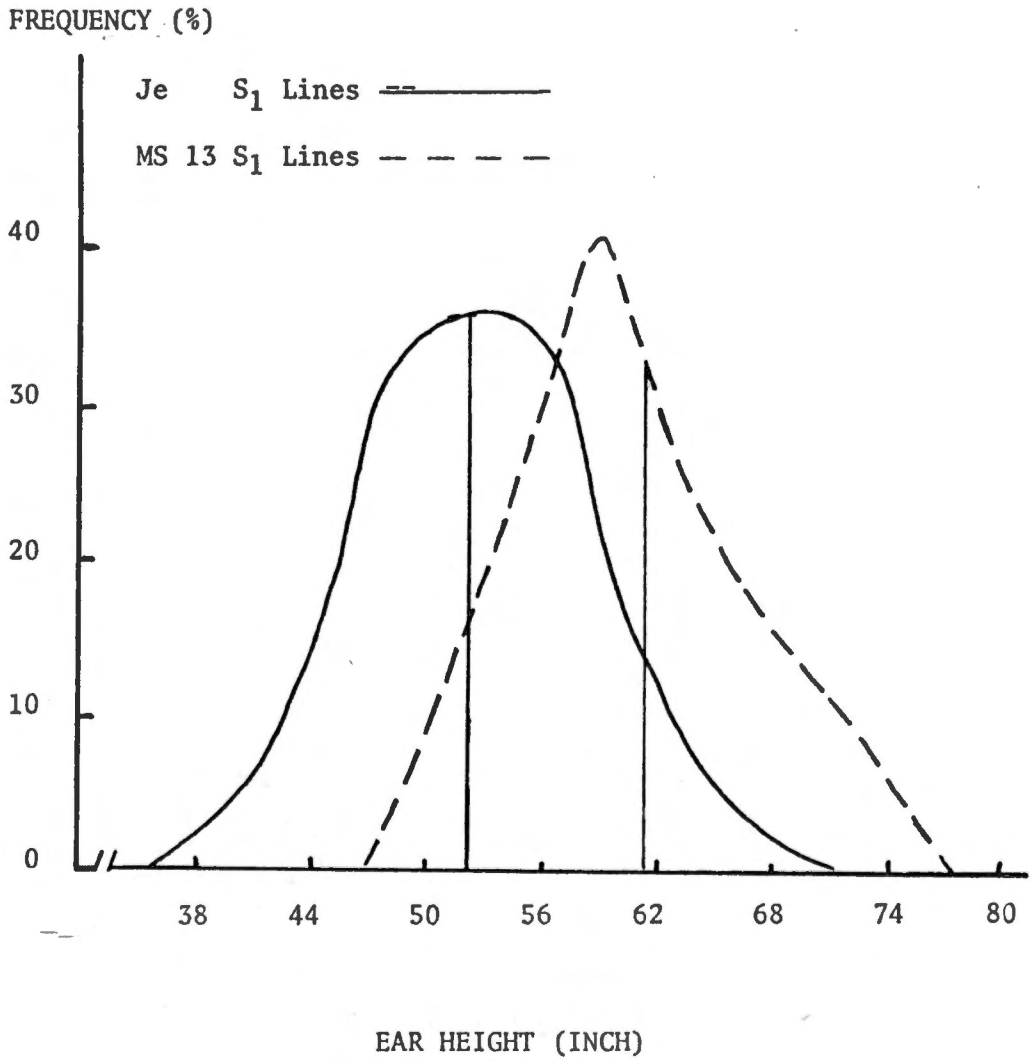

Figure 8. Ear height distributions of random S_1 lines from the parent variety Jellicorse (Je) and the selected population (MS 13) utilizing 6 inch class intervals. Knoxville and Crossville, Tennessee.

Table 17. Mean stalk lodging of S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selection population (MS 13), plus five experimental check entries. Knoxville, Tennessee.

Experimental material			Stalk lodging (%)		% of increase over corresponding progeny type
Progeny type		Population	Mean	Range	
				Knoxville	
S_1 lines		Je	29.4	5.0-80.0	-
		MS 13	33.2	2.8-82.0	12.9
Checks	Je open-pollinated		22.5		
	MS 13 open-pollinated		31.1		
	T115 X T111		7.6		
	Tenn. 505		0.0		
L.S.D. (.01)			33.9		
L.S.D. (.05)			25.8		
Testcrosses		Je	10.6	0.0-35.0	-
		MS 13	11.4	0.0-31.6	7.5
Checks	Je open-pollinated		26.6		
	MS 13 open-pollinated		20.4		
	Ga209 X Mo18W		0.0		
	Tenn. 505		0.0		
L.S.D. (.01)			22.1		
L.S.D. (.05)			16.8		

Table 18. Estimates of genetic variance ($\sigma^2_{G'}$)† and standard error(s) of various traits in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13) at each location, Knoxville and Crossville, Tennessee.

Progeny type	Knoxville		Crossville	
	Je	MS 13	Je	MS 13
		Ear corn yield (lb/plot)		
S_1 lines	1.960* ± .330	3.460* ± .590	3.100 ± .530	3.700 ± .630
Testcrosses	.490* ± .083	.800* ± .136	.577* ± .099	1.110* ± .190
		Ears/plant (no.)		
S_1 lines	.077 ± .013	.096 ± .016	.062* ± .011	.089* ± .015
Testcrosses	.019 ± .003	.017 ± .003	.018 ± .003	.013 ± .002
		Nubbins/plant (no.)		
S_1 lines	.011* ± .002	.052* ± .009	.037* ± .006	.063* ± .011
Testcrosses	.013 ± .002	.010 ± .002	.007 ± .001	.006 ± .000
		Nubbin yield (lb/plot)		
S_1 lines	.019* ± .003	.542* ± .092	.745 ± .130	.880 ± .150
Testcrosses	.083* ± .014	.218* ± .037	.214 ± .037	.205 ± .035

Table 18 (continued)

Progeny type	Knoxville		Crossville	
	Je	MS 13	Je	MS 13
		Days to mid-shed (no.)		
S_1 lines	4.22 ± .72	4.84 ± .82	2.530 ± .430	2.660 ± .450
Testcrosses	1.73 ± .29	1.15 ± .19	.282* ± .048	.416* ± .071
		Days to mid-silk (no.)		
S_1 lines	3.71* ± .45	9.12* ± 1.55	2.650 ± .450	2.270 ± .390
Testcrosses	2.69 ± .46	1.89 ± .32	.567 ± .096	.540 ± .092
		Ear height (inch)		
S_1 lines	27.03 ± 4.60	26.26 ± 4.47	32.14 ± 5.47	34.88 ± 5.94
Testcrosses	7.02 ± 1.20	7.62 ± 1.30	7.70* ± 1.31	10.86* ± 1.85
		Plant height (inch)		
S_1 lines	45.39 ± 7.73	39.51 ± 6.73	-	-
Testcrosses	17.76* ± 3.02	11.52* ± 1.96	-	-
		Stalk lodging (%)		
S_1 lines	226.99 ± 38.65	247.28 ± 42.01	-	-
Testcrosses	7.68* ± 1.30	45.79* ± 7.80	-	-

*Je and MS 13 variances are different at the .05 level of probability.

†$\sigma^2_{G'} = \sigma^2_G + \sigma^2_{GL} + \sigma^2_{GY} + \sigma^2_{GLY}$ (terms defined in page 21).

of variance of the selected population and the parental population of the two progeny types exhibited significant differences on the basis of the χ^2 test. However, genetic variability of each trait measured in the topcross progeny groups were lower than the variability of the same trait measured in corresponding groups of parental S_1 lines at the same location. With the exception of the S_1 lines at Crossville, S_1 and testcross groups of MS 13 exhibited significantly greater genetic variability in ear corn yield than the corresponding S_1 and testcross group of Je at both locations.

Ear corn yield variability in the MS 13 S_1 progeny was slightly greater than in the Je S_1 progeny at Crossville but it was not statistically significant at the .05 level. All progeny groups displayed less genetic variability in ear corn yield at Knoxville than they did at Crossville.

Estimates of genotype X location components of genetic variance (σ^2_{GL}) are presented in Table 19. The genotype X location component estimates for ear corn yield and days to mid-shed of MS 13 and Je S_1 lines were similar. All MS 13 S_1 lines exceeded the Je S_1 lines with respect to the other traits except ear height.

Components estimated for the S_1 lines exceeded the components for the testcross progeny for all traits in MS 13, and for nubbins/plant, days to mid-shed, and ear height in Je.

The genotype X location component estimated for the measured traits and progeny types (Table 19) in most cases is smaller than the combined estimates of genetic variance ($\sigma^2_{G''}$) for the same traits and progeny type (Table 20). This indicates that genotype X location interaction did

Table 19. Estimates of genotype X location components of genetic variance (σ^2_{GL})† with standard errors for various traits in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13). Knoxville and Crossville, Tennessee.

Progeny type	Je	MS 13
	Ear corn yield (lb/plot)	
S_1 lines	.599 ± .099	.740 ± .130
Test crosses	.580 ± .100	.471 ± .080
	Ears/plant (no.)	
S_1 lines	.000* ± .000	.024* ± .004
Testcrosses	.005 ± .000	.001 ± .000
	Nubbins/plant (no.)	
S_1 lines	.050* ± .008	.004* ± .001
Testcrosses	.005* ± .000	.000* ± .000
	Nubbin yield (lb/plot)	
S_1 lines	.107* ± .018	.210* ± .040
Testcrosses	.140* ± .020	.080* ± .014
	Days to mid-shed (no.)	
S_1 lines	.579 ± .99	.630 ± .090
Testcrosses	.352* ± .060	.086* ± .015
	Days to mid-silk (no.)	
S_1 lines	.000* ± .000	1.630* ± .280
Testcrosses	.411* ± .070	.249* ± .042
	Ear height (inch)	
S_1 lines	5.010* ± .850	.350* ± .060
Testcrosses	.000 ± .000	.000 ± .000

†Terms defined in page 21.

*Je and MS 13 variances are different at the .05 level of probability.

Table 20. Combined estimates of genetic variance ($\sigma^2_{G''}$)† with standard error(s) for various traits in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13). Knoxville and Crossville, Tennessee.

Progeny type	Je	MS 13
	Ear corn yield (lb/plot)	
S_1 lines	1.960* ± .330	2.840* ± .480
Testcrosses	.000* ± .000	.488* ± .083
	Ears/plant (no.)	
S_1 lines	.059 ± .010	.069 ± .012
Testcrosses	.014 ± .002	.014 ± .002
	Nubbins/plant (no.)	
S_1 lines	.025* ± .004	.054* ± .009
Testcrosses	.004* ± .000	.008* ± .001
	Nubbin yield (lb/plot)	
S_1 lines	.280* ± .050	.500* ± .090
Testcrosses	.010* ± .002	.130* ± .020
	Days to mid-shed (no.)	
S_1 lines	2.80 ± .48	3.12 ± .53
Testcrosses	.64 ± .110	.70 ± .12
	Days to mid-silk (no.)	
S_1 lines	3.35 ± .57	4.07 ± .69
Testcrosses	1.22 ± .21	.97 ± .16
	Ear height (inch)	
S_1 lines	24.58 ± 4.18	30.23 ± 5.15
Testcrosses	8.81 ± 1.50	10.87 ± 1.85

*Je and Ms 13 variances are different at the .05 level of probability.

†$\sigma^2_{G''} = \sigma^2_G + \sigma^2_{GY} + \sigma^2_{GLY}$ (terms defined in page 21).

not play a major role in determining the genetic variability of the traits studied in this experiment.

The results indicated by the combined estimates of genetic variance in Table 20 show that (1) S_1 genetic variability in all cases exceeded the testcrosses variability for the traits studied and (2) MS 13 S_1 and testcross variability in most traits exceeded that of Je.

Phenotypic correlations between ear corn yield and other measured traits in the S_1 and testcross progenies of Je and MS 13 are presented in Table 21. A correlation coefficient when squared indicates that proportion of the variance in ear corn yield which can be explained by its linear association with the other trait. The data yielded a significant positive correlation between ear corn yield and ear number in all progeny groups at both locations and a significant negative correlation between ear corn yield and flowering, except for days to mid-shed in the testcrosses at Crossville. A significant positive correlation of ear corn yield with ear height was observed in all progeny groups except Je S_1 at Crossville and with plant height at Knoxville except in MS 13 S_1.

Phenotypic and genotypic correlations between ear corn yield of S_1 and testcrosses are presented in Table 22. The data indicate a positive phenotypic correlation between ear corn yields of S_1 line and their testcrosses. Higher correlations were observed for the selected population than for the parent population.

Table 21. Phenotypic correlations between ear corn yield and other traits in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13). Knoxville and Crossville, Tennessee.

Progeny type and source		Correlation coefficients[1]										
		Ears/plant		Days to mid-shed		Days to mid-silk		Ear height		Plant height	% stalk lodging	% root lodging
		Knox.	Cross.	Knox.	Cross.	Knox.	Cross.	Knox.	Cross.	Knox.	Knox.	Knox.
S_1 lines	Je	.69	.75	-.38	-.30	-.48	-.35	.16	.09	.24	-.01	.07
	MS 13	.76	.80	-.49	-.29	-.59	-.39	.10	.20	.10	.15	.06
Testcrosses	Je	.76	.65	-.31	-.06	-.46	-.24	.18	.32	.32	-.16	-.11
	MS 13	.82	.68	-.29	-.14	-.36	-.26	.14	.41	.32	.07	.13

[1]Coefficients greater than 0.17 and 0.22 are significant at the .05 and .01 levels of probability.

Table 22. Phenotypic and genotypic correlations between ear corn yields of S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13). Knoxville and Crossville, Tennessee

Population	Knoxville	Crossville
Je	0.37** (0.75)†	0.40** (0.60)
MS 13	0.45** (0.84)	0.48** (0.62)

** Significant at the .01 level of probability.

† Genotypic correlations are in parentheses and were not tested for significance.

CHAPTER V

DISCUSSION

Mass selection for yield, which consists simply of the propagation of the individuals most desirable, on the basis of their phenotype and the mean performance of their progenies, is the least complex and least expensive procedure for improving the yield of corn populations. The superiority of the selected population is presumably due to an increase in the frequencies of favorable yield influencing genes or gene combinations. Logically, selection which increases the frequencies of favorable yield influencing genes in a population should enhance the chances of extracting genetically better lines from that population. Such lines should also combine with other lines to produce superior hybrids. However, this depends to a great extent on the type of gene action which induces yield superiority in the selected population.

Alleles may act in several different ways. Consider one gene locus which controls one function and which may be occupied by two different alleles. Let's assume that the locus homozygous for one allele produces a superior functional level to that produced by the locus homozygous for the other allele. The functional levels produced by the heterozygous combination might be placed into five major categories. The level might be above that produced by the better homozygous combination, below that produced by the poorer homozygous combination, equivalent to that produced by one or the other of the homozygous combinations, or better than the levels produced by one or

the other of the homozygous combinations. The situation in which the alleles complement each other and produce a better functional level than the better homozygous combination is called overdominance; the situation in which the alleles hinder each other and produce a functional level below that produced by the poorer homozygote is referred to as underdominance; the situation in which the heterozygote produces a level equivalent to one of the homozygotes (usually the better one) is called complete dominance; and situation in which the heterozygote produces a level half way between those of the two homozygotes is called additive gene action and, if more than half way, partial dominance. Thus overdominance, underdominance, complete dominance, additivity, and partial dominance categorize the basic actions possible between two different alleles at one locus relative to the functional levels produced by the two homozygous combinations of those alleles. Interactions of the nature just described are also possible between alleles or allelic combinations at different loci, and this is called epistasis. In addition, pleiotropic effects of heterozygous allelic combinations may be subject to the types of interactions described.

Gene control which is not dependent upon allelic interaction is appropriately termed additive gene action. Various methods have been devised to determine the relative importance of the types of gene action in their influence on certain measurable traits in corn (Comstock and Robinson, 1948; Griffing, 1956). Such methods allow partitioning of genetic variability into additive and dominance components under the assumption of no epistasis. Additive genetic variance is that portion which is due to the average effects of alleles measured over all allelic

combinations in which they appear and dominance genetic variance is the residual which arises due to intralocus interaction. Genetic variance studies of the past two decades have indicated that the additive effects of alleles are extremely important in influencing grain yield of open pollinated corn varieties (Robinson et al., 1954; Lindsey et al., 1962). These studies have encouraged plant breeders to utilize mass selection in which selected genotypes are randomly mated to produce the next generation. The reason for this is that plant breeders are necessarily faced with the task of selecting genotypes whose allelic combinations direct superior grain producing functions and at the same time are heritable. Random mating tends to break up allelic combinations and produce new ones. Thus, if a superior function is dependent upon the additive effect of an allele, then both the allele and its effect would tend to be heritable under random mating. However, if a superior function were dependent upon the interaction effect of an allelic combination, then the effect would not tend to be heritable under random mating since random mating recombination would be apt to produce a different allelic combination in progeny genotypes and likewise a different interaction effect. Selection based on phenotype and in which selected genotypes are randomly mated could be expected to be most sucdessful if the traits for which selection is practiced were the result of additive allelic effects as opposed to interaction effects. If selection is effective, one would expect to increase the frequencies of favorable additive yield genes, thus making the selection population a better germ plasm reservoir for the extraction of genetically superior inbred lines than the parent variety. In other words, if the frequency

of favorable genes can be substantially increased by mass selection before inbreeding, then the probability of obtaining good lines which will produce superior hybrids is greatly increased.

The means in Table 5 (p. 28) show that the MS 13 S_1 and testcross progenies produced better average yields than the corresponding Je progenies at Knoxville, but the differences were not significant. However, the average yield of the MS 13 S_1 and testcross progenies over the corresponding Je at Crossville were greater than the corresponding differences at Knoxville. It demonstrates the not uncommon results of selected genotypes outperforming unselected genotypes considerably more in a relatively better environment than they do in an unfavorable environment. The results of one year's evaluation of MS 13 open-pollinated and Je open-pollinated by Josephson and Kincer (1974)[1] are in good agreement with this view. Results of this type are to be expected since genotypes selected to perform in a favorable environment would necessarily not be expected to perform particularly well in an unfavorable environment. Conditions under which the yearly selections were made were not the same as in 1974. In some years drought affected the selections. Hence, in one year drought tolerant parents may have been selected and in a favorable year the drought tolerant quality of the parents may have been partially eliminated from the selected plants. The best confirming evidence is fluctuations in the performance of the selections of different generations in the one year evaluation experiment

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[1]Josephson, L. M., and H. C. Kincer, (Annual unpublished Rep. of Corn Breeding Project, Univ. of Tennessee, 1974).

by Josephson and Kincer (1974). It seems that under unfavorable conditions the plants of the selected population could not express their maximum yield potential.

Inbreeding depression is thought to be a consequence of directional dominance. According to Falconer (1960),

> If the genes that increase the value of a character are dominant over their alleles that reduce the value, then inbreeding will result in a reduction of the population mean.

Falconer further states

> The contribution of each locus depends upon its gene frequencies, those with intermediate frequencies (for the dominant and recessive allele) having the greatest effect on the change of mean values.

If selection is increasing heterozygosity in the selected population (as shown by the higher genotypic variance of MS 13) by elevating the frequencies of favorable yield genes which are dominant over their less favorable alleles, then MS 13 should show more inbreeding depression for yield than would Je. Results presented in Table 10 (p. 39) show that MS 13 experienced only slightly more inbreeding depression than Je. This would indicate a small increase in the heterozygosity of MS over that of Je. Perhaps selection is operating on dominant favorable yield genes which were already at low frequencies in the parent variety.

The average yields of S_1 lines from Je and MS 13 are excellent indicators of the magnitudes of population means relative to one another since the genetic constitution of each group of S_1 lines represents the genetic constitution of its parental population. However, if MS 13 were subjected to less inbreeding depression than Je, then the S_1 mean

should exemplify greater superiority for MS 13 than does the population mean.

Josephson's one year evaluation in 1974 showed the MS 13 population mean exceeded the Je population mean at Knoxville and Crossville by 4.05 percent and 6.5 percent, respectively. The difference was not statistically significant at the .05 level of probability at Knoxville. This is further evidence that selection (1) increased the frequencies of particular dominant yield influencing genes which were at low frequencies in Je, (2) slowly elevated the overall level of heterozygosity at gene loci of the advanced population, and (3) under the adverse conditions (drought) at Knoxville, the plants of the selected population could not express themselves. However, the frequency curves of ear corn yield in Figures 2, 3, 4, and 5 (pp. 33-36) illustrate that very few plants of the MS 13 genotypes lay beyond the upper tail of the corresponding distribution of Je genotypes. The curves illustrate that the probability of selecting good lines from the upper portion of MS 13 is somewhat better than the probability of obtaining equally good lines from the corresponding Je population. Indications are that selection formulated a population which is more suitable for the extraction of superior inbred lines than the parent variety, but the environmental conditions (drought) of the test location did not allow the plants of the selected population to express maximum yield potential.

As shown in Table 11 (p. 40), Je and MS 13 both exhibited inbreeding depression in ear number at both test locations. This result may not support the conclusion of Harris et al. (1972), and Hallaeur (1974) indicating that prolificacy is influenced by recessive genes which exert

themselves only in the homozygous state. Harris and Hallauer worked with populations generally not prolific while Jellicorse is highly prolific. However, according to the study by Hallauer (1974), prolificacy acts like a threshold character.

Mean ear numbers produced by all progeny types at Crossville were lower than the corresponding values at Knoxville except for MS 13 S_1 and MS 13 testcross progenies.

Other trait means presented in Tables 12 through 17 (pp. 43, 44, 45, 48, 49, 51) indicate that the selected progenies (1) produced a greater number of nubbins, (2) greater nubbin weight, (3) later flowering, (4) taller plants with higher ear placement, and (5) more lodging than did Je genotypes. However, differences in all measured traits exhibited by Je and MS 13 genotypes were not great but were significant at the .05 level of probability with respect to ear height of S_1 progenies at Knoxville.

Horner et al. (1969) and Harris et al. (1972) presented evidence showing that the expected variance due to additive effects of genes is much larger among selfed progenies than among testcross progenies. This is in agreement with the results shown in Tables 18, 19 and 20 (pp. 52, 55, 56) since S_1 variability exceeds testcross variability in most measured traits. The reduced variation exhibited by testcross progenies of each group is not surprising inasmuch as half their germ plasm came from a genetically uniform tester.

Jellicorse S_1 and testcross groups exhibited less genetic variability in yield and yield related traits than did the corresponding MS 13 S_1 and testcross groups. Evidently, selection increased the

overall genetic variance and, likewise, the additively genetic variance of the selected population. However, instances have been reported in which variance decreased after selection (Hallauer, 1970; da silva and Lonnquist, 1968; Harris et al., 1972). It is possible that genetic variances may increase by selection if the initial frequencies of favorable alleles are low. The results demonstrate that there is no limitation of variability to limit rate of response in later selection cycles. It is anticipated that in complex traits, such as those that are influenced by many loci with small effects (e.g., yield), genetic variances would change very slowly with selection. The results show approximately equal additively genetic variance in the selected population and Je at Crossville but greater genetic variance in the selected population at Knoxville.

The results in Table 21 (p. 58) show that yield was positively correlated with ear number. The correlations reported in Table 22 (p. 59) between yields of S_1 lines and their testcrosses are in agreement with results obtained by many other investigators. In general, it would appear that S_1 line performance can be used to predict S_1 testcross performance, and vice versa.

CHAPTER VI

SUMMARY AND CONCLUSIONS

Up to the first quarter of this century mass selection was not considered to be effective in improving the yield of adapted varieties of corn.

The successful development of hybrid corn in the 1920's resulted in a temporary abandonment of population improvement. However, progress in developing better yielding hybrids has been slow in recent years; consequently, the need for superior populations of corn from which inbred lines can be extracted has been felt by many plant breeders.

A mass selected corn population (MS 13), and the parent variety Jellicorse (Je) were evaluated at Knoxville and Crossville using random S_1 lines per se and S_0 lines topcrossed to an unrelated single cross. The selected population (MS 13) had undergone thirteen generations of mass selection for ear corn yield.

Evaluation of fourteen generations of mass selection for yield in corn by Josephson and Kincer (1976) has shown a maximum gain of 13.1 percent over the parent variety Jellicorse.

S_1 lines and their testcrosses of MS 13 did not demonstrate statistically significant average yielding superiority over lines of Je in this study. However, S_1 and testcross progenies of MS 13 were greater in yield than Je at Crossville (14.3 percent and 7.9 percent) where more favorable environmental conditions existed for the tests. Indications are that frequencies of favorable yield influencing genes

were greater in progenies of MS 13 than in corresponding progenies of Je. Differences were attributed to the effect of mass selection on the parent variety. The unfavorable conditions for evaluation at Knoxville did not allow the selected plants to truly express their yield capabilities.

The top yielding S_1 and testcross progenies of the study came from the selected population. This shows that the probability of selecting superior yielding lines from MS 13 is greater than in the corresponding Je population. Indications are that selection has increased the frequencies of allels that contribute to yield improvement. When severe stress conditions occur, the yield advantage of the selected population is reduced.

In order to adequately evaluate mass selection for yield, stress of drought should be removed by irrigating the selection nursery and the test plots used for evaluation.

Je and MS 13 both exhibited inbreeding depression in ear number at both test-locations. MS 13 showed slightly more inbreeding depression in ear number than Je at Knoxville.

Genotypes of MS 13 produced more ears/plant with greater nubbin weights, produced taller plants with higher ear placement, and produced more lodged plants. Genotypes of MS 13 flowered later but they produced grain having slightly less moisture at harvest than genotypes of Je. However, differences in all measured traits (except ear height of S_1 progenies at Knoxville) were not great and generally nonsignificant at the .05 level of probability.

The data yielded a significant positive correlation between ear corn yield and ear number in all progeny groups at both locations

and in most cases a significant negative correlation between ear corn yield and flowering.

Correlations between S_1 and testcross yields for Je and MS 13 were + 0.40** and +0.48**, respectively. The highly significant correlation coefficients show that S_1 testcross performance can be used to predict S_1 line performance, and vice versa.

Variance estimates show that genetic variability among S_1's exceed that among testcrosses for most traits, as expected, and that S_1 and testcross progenies of Je had less genetic variability in yield and yield related traits than progenies of MS 13. The results suggest that mass selection increased genetic variance and particularly additively genetic variance of MS 13 relative to Je.

The genotype X location components of genetic variance (σ^2_{GL}) estimated for measured traits in most cases is smaller than the combined estimates of genetic variance ($\sigma^2_{G''}$). This indicates that genotype X interaction did not play a major role in determining the genetic variability of the traits studied in this experiment.

The significant yield variability in MS 13 genotypes indicates that continued yield improvement is possible in the selected population from further cycles of mass selection under favorable environmental conditions.

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APPENDIX

Table A1. Field arrangement of entries at Knoxville, Tennessee.

Plot	100	200	300	400	500	600	700	800	900	1000	1100	1200
1	118	114	318	314	90	96	290	296	26	28	226	228
2	116	119	316	319	88	93	288	293	36	31	236	231
3	112	115	312	315	87	85	287	285	25	30	225	230
4	117	110	317	310	95	89	295	289	29	27	229	227
5	120	113	320	313	94	91	294	291	33	32	233	232
6	111	109	311	309	92	86	292	286	35	34	235	234
7	77	81	277	281	7	3	207	203	136	137	336	337
8	84	76	284	276	10	2	210	202	134	135	334	335
9	75	78	275	278	6	12	206	212	143	140	343	340
10	79	74	279	274	9	5	209	205	133	138	333	338
11	80	82	280	282	11	1	211	201	139	141	339	341
12	73	83	273	283	8	4	208	204	144	142	344	342
13	47	42	247	242	69	68	269	268	23	20	223	220
14	44	41	244	241	72	66	272	266	21	19	221	219
15	45	39	245	239	61	67	261	267	24	17	224	217
16	46	43	246	243	70	65	270	265	14	22	214	222
17	48	40	248	240	71	64	271	264	15	16	215	216
18	37	38	237	238	62	63	262	263	13	18	213	218
19	121	132	321	332	104	97	304	297	49	53	249	253
20	122	123	322	323	98	101	298	301	50	57	250	257
21	127	129	327	329	105	99	305	299	54	60	254	260
22	124	130	324	330	103	107	303	307	56	59	256	259
23	128	131	328	331	108	100	308	300	51	58	251	258
24	126	125	326	325	106	102	306	302	52	55	252	255
	B1-S1		B1-TC1		B5-S1		B5-TC1		B9-S1		B9-TC1	
	B2-S1		B2-TC1		B6-S1		B6-TC1		B10-S1		B10-TC1	
	B3-S1		B3-TC1		B7-S1		B7-TC1		B11-S1		B11-TC1	
	B4-S1		B4-TC1		B8-S1		B8-TC1		B12-S1		B12-TC1	

Table A1 (continued)

Plot	1300	1400	1500	1600	1700	1800	1900	2000	2100	2200	2300	2400
1	133	73	333	273	34	46	234	246	64	16	264	216
2	25	13	225	213	22	70	222	270	112	88	312	288
3	121	85	321	285	10	94	210	294	76	124	276	324
4	109	49	309	249	130	106	330	306	4	136	204	336
5	37	61	237	261	142	118	342	318	40	100	240	300
6	1	97	201	297	82	58	282	258	52	28	252	228
7	32	92	232	292	129	9	329	209	131	143	331	343
8	80	56	280	256	21	57	221	257	47	107	247	307
9	20	128	220	328	33	81	233	281	95	71	295	271
10	44	104	244	304	69	45	269	245	11	35	211	235
11	8	116	208	316	93	117	293	317	83	59	283	259
12	140	68	340	268	141	105	341	305	23	119	223	319
13	98	134	298	334	135	99	335	299	96	132	296	332
14	74	14	274	214	27	15	227	215	12	36	212	236
15	38	50	238	250	3	75	203	275	72	60	272	260
16	110	86	310	386	39	87	239	287	108	120	308	320
17	2	62	202	262	51	123	251	323	24	144	224	344
18	26	122	226	322	63	111	263	311	48	84	248	284
19	89	125	289	325	126	102	326	302	139	115	339	315
20	29	17	229	217	18	138	218	338	103	31	303	231
21	53	65	253	265	6	90	206	290	43	19	243	219
22	41	77	241	277	30	54	230	254	7	79	207	279
23	137	5	337	205	114	42	314	242	55	127	255	327
24	101	113	301	313	78	66	278	266	91	67	291	267
	B13-S2		B13-TC2		B17-S2		B17-TC2		B21-S2		B21-TC2	
	B14-S2		B14-TC2		B18-S2		B18-TC2		B22-S2		B22-TC2	
	B15-S2		B15-TC2		B19-S2		B19-TC2		B23-S2		B23-TC2	
	B16-S2		B16-TC2		B20-S2		B20-TC2		B24-S2		B24-TC2	

Table A2. Field arrangement of entries at Crossville, Tennessee.

Plot	100	200	300	400	500	600	700	800	900	1000	1100	1200
1	70	61	270	261	117	115	317	315	133	143	333	343
2	64	65	264	265	113	109	313	309	141	138	341	338
3	72	62	272	262	116	111	316	311	134	144	334	344
4	67	69	267	269	112	114	312	314	140	136	340	336
5	63	66	263	266	110	119	310	319	142	135	342	335
6	71	68	271	268	120	118	320	318	139	137	339	337
	B25-S3		B25-TC3		B29-S3		B29-TC3		B33-S3		B33-TC3	
7	14	24	214	224	9	6	209	206	79	75	279	275
8	16	22	216	222	1	5	201	205	82	74	282	274
9	21	13	221	213	10	8	210	208	84	73	284	273
10	17	23	217	223	12	7	212	207	78	77	278	277
11	18	19	218	219	4	2	204	202	83	76	283	276
12	15	20	215	220	11	3	211	203	80	81	280	281
	B26-S3		B26-TC3		B30-S3		B30-TC3		B34-S3		B34-TC3	
13	103	105	303	305	124	127	324	327	56	54	256	254
14	100	107	300	307	131	130	331	330	58	59	258	259
15	98	106	298	306	122	126	322	326	50	52	250	252
16	99	104	299	304	129	121	329	321	60	49	260	249
17	102	101	302	301	125	123	325	323	55	57	255	257
18	108	97	308	297	128	132	328	332	51	53	251	253
	B27-S3		B27-TC3		B31-S3		B31-TC3		B35-S3		B35-TC3	
19	95	87	295	287	46	45	246	245	29	25	229	225
20	91	89	291	289	40	43	240	243	32	27	232	227
21	88	92	288	292	44	37	244	237	36	35	236	235
22	85	90	285	290	39	47	239	247	30	26	230	226
23	86	93	286	293	38	41	238	241	34	31	234	231
24	94	96	294	296	48	42	248	242	33	28	233	228
	B28-S3		B28-TC3		B32-S3		B32-TC3		B36-S3		B36-TC3	

Table A2 (continued)

Plot	1300	1400	1500	1600	1700	1800	1900	2000	2100	2200	2300	2400
1	108	144	308	344	11	59	211	259	39	123	239	323
2	60	36	260	236	71	107	271	307	75	15	275	215
3	120	24	320	224	35	83	235	283	87	51	287	251
4	84	12	284	212	119	47	319	247	111	27	311	227
5	96	132	296	332	131	143	331	343	135	99	335	299
6	48	72	248	272	23	95	223	295	63	3	263	203
7	41	5	241	205	30	42	230	242	130	118	330	318
8	65	17	265	217	90	138	290	338	94	70	294	270
9	77	137	277	337	54	114	254	314	106	142	306	342
10	113	29	313	229	66	18	266	218	58	22	258	222
11	89	125	289	325	126	102	326	302	34	46	234	246
12	101	53	301	253	78	6	278	206	82	10	282	210
13	44	116	244	316	69	117	269	317	4	100	204	300
14	128	56	328	256	81	57	281	257	124	88	324	288
15	104	8	304	208	45	93	245	293	136	40	336	240
16	68	80	268	280	105	21	305	221	28	112	228	312
17	32	92	232	292	129	9	329	209	64	16	264	216
18	140	20	340	220	141	33	341	233	52	76	252	276
19	7	127	207	327	109	61	309	261	98	62	298	262
20	19	31	219	231	85	13	285	218	50	14	250	214
21	79	55	279	255	49	37	249	237	86	2	286	202
22	67	103	267	303	97	25	297	225	122	74	322	274
23	139	115	339	315	133	73	333	273	110	134	310	334
24	91	43	291	243	1	121	201	321	26	38	226	238
	B37-S4		B37-TC4		B41-S4		B41-TC4		B45-S4		B45-TC4	
	B38-S4		B38-TC4		B42-S4		B42-TC4		B46-S4		B46-TC4	
	B39-S4		B39-TC4		B43-S4		B43-TC4		B47-S4		B47-TC4	
	B40-S4		B40-TC4		B44-S4		B44-TC4		B48-S4		B48-TC4	

Table A3. Analysis of variance of number of ears per plant in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus check entries at each location. Knoxville and Crossville, Tennessee.

		Mean squares			
		S_1 lines		Testcrosses	
Source	D.F.	Knoxville	Crossville	Knoxville	Crossville
Replications	1	0.97	0.09	1.15	0.02
Genotypes (unadjusted)	143	0.26	0.26	0.07	0.10
Blocks (adjusted)	22	0.11	0.07	0.04	0.05
Intra-block error	121	0.07	0.04	0.02	0.02
Total	287	0.17	0.15	0.05	0.06
Relative efficiency, %		103.51	105.13	109.17	112.82
Coefficient of variation, %		17.91	13.25	8.97	9.34

Table A4. Analysis of variance of number of nubbins per plant in S_1 and testcross progenies of the parent variety Jellicorse (Je), and the selected population (MS 13), plus check entries at each location. Knoxville and Crossville, Tennessee.

		Mean squares			
		S_1 lines		Testcrosses	
Source	D.F.	Knoxville	Crossville	Knoxville	Crossville
Replications	1	7.93	0.06	0.80	0.06
Genotypes (unadjusted)	143	0.16	0.16	0.05	0.03
Blocks (adjusted)	22	0.11	0.03	0.05	0.02
Intra-block error	121	0.06	0.04	0.02	0.02
Total	287	0.14	0.10	0.04	0.02
Relative efficiency, %		105.84	101.34	109.82	100.65
Coefficient of variation, %		26.34	29.12	23.07	32.07

Table A5. Analysis of variance of nubbin yield (lb/plot) in S_1 and testcross progenies of the parent variety Jellicorse (Je), and the selected population (MS 13), plus check entries at each location. Knoxville and Crossville, Tennessee.

		Mean squares			
		S_1 lines		Testcrosses	
Source	D.F.	Knoxville	Crossville	Knoxville	Crossville
Replications	1	93.96	1.95	3.71	5.80
Genotypes (unadjusted)	143	1.26	2.71	0.93	0.85
Blocks (adjusted)	22	1.33	1.18	0.89	0.25
Intra-block error	121	0.59	0.79	0.54	0.39
Total	287	1.31	1.78	0.77	0.63
Relative efficiency, %		109.92	102.34	103.54	103.00
Coefficient of variation, %		34.24	31.85	35.57	32.04

Table A6. Analysis of variance of days to mid-shed in S_1 and testcross progenies of the parent variety Jellicorse (Je), and the selected population (MS 13), plus check entries at each location. Knoxville and Crossville, Tennessee.

		Mean squares			
		S_1 lines		Testcrosses	
Source	D.F.	Knoxville	Crossville	Knoxville	Crossville
Replications	1	64.00	3.00	34.00	1.00
Genotypes (unadjusted)	143	15.52	8.71	4.99	1.70
Blocks (adjusted)	22	5.33	3.50	2.15	1.49
Intra-block error	121	2.64	1.48	1.49	0.86
Total	287	9.48	5.24	3.40	1.33
Relative efficiency, %		107.30	111.25	101.97	104.41
Coefficient of variation, %		2.25	1.53	1.81	1.26

Table A7. Analysis of variance of days to mid-silk in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus check entries at each location. Knoxville and Crossville, Tennessee.

		Mean squares			
		S_1 lines		Testcrosses	
Source	D.F.	Knoxville	Crossville	Knoxville	Crossville
Replications	1	64.00	7.00	76.00	30.00
Genotypes (unadjusted)	143	15.52	7.55	7.06	2.29
Blocks (adjusted)	22	5.33	2.59	4.13	2.25
Intra-block error	121	2.64	1.21	1.84	0.82
Total	287	9.48	4.49	4.88	1.76
Relative efficiency, %		107.30	108.71	109.75	115.36
Coefficient of variation, %		2.25	1.34	1.85	1.14

Table A8. Analysis of variance of ear height in S_1 and testcross progenies of the parent variety Jellicorse (Je), and the selected population (MS 13), plus check entries at each location. Knoxville and Crossville, Tennessee.

		Mean squares			
		S_1 lines		Testcrosses	
Source	D.F.	Knoxville	Crossville	Knoxville	Crossville
Replications	1	33.94	20.50	74.00	177.31
Genotypes (unadjusted)	143	115.52	136.32	37.13	53.23
Blocks (adjusted)	22	32.79	47.07	32.29	32.50
Intra-block error	12	16.58	28.67	7.71	12.86
Total	287	67.18	83.69	24.48	35.05
Relative efficiency, %		106.91	103.64	133.42	113.00
Coefficient of variation, %		7.17	9.93	4.58	6.07

Table A9. Analysis of variance of plant height in S_1 and testcross progenies of the parent variety Jellicorse (Je), and the selected population (MS 13), plus check entries. Knoxville, Tennessee.

Source	D.F.	Mean squares	
		S_1 Lines	Testcrosses
Replications	1	416.00	817.00
Genotypes (unadjusted)	143	183.58	66.69
Blocks (adjusted)	22	50.46	58.14
Intra-block	121	43.68	20.82
Total	287	115.20	49.31
Relative efficiency, %		100.31	116.12
Coefficient of variation, %		5.84	3.71

Table A10. Analysis of variance of stalk lodging in S_1 and testcross progenies of the parent variety Jellicorse (Je), and the selected population (MS 13), plus check entries. Knoxville, Tennessee.

Source	D.F.	Mean squares	
		S_1 lines	Testcrosses
Replications	1	144.69	334.48
Genotypes (unadjusted)	143	653.50	131.62
Blocks (adjusted)	22	182.15	103.76
Intra-block	121	171.66	68.37
Total	287	412.45	103.53
Relative efficiency, %		100.05	102.58
Coefficient of variation, %		42.72	72.20

Table A11. Combined analysis of variance over location (four-replicate lattice) of number of ears per plant, number of nubbins per plant, and yield of nubbins in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus check entries. Knoxville and Crossville, Tennessee

Source	D.F.	Ears/plant Mean squares		Nubbins/plant Mean squares		Yield of nubbins (lb/plot) Mean squares	
		S_1	Testcrosses	S_1	Testcrosses	S_1	Testcrosses
Replications	3	0.56	0.39	4.88	2.67	52.77	7.05
Genotypes (unadjusted)	143	0.43	0.14	0.26	0.06	2.81	1.14
Blocks (adjusted)	44	0.09	0.06	0.08	0.03	1.36	0.79
Intra-block error	385	0.06	0.02	0.05	0.02	0.85	0.51
Total	575	0.16	0.06	0.13	0.04	1.65	0.72
Relative efficiency, %		101.18	106.73	101.06	102.33	101.67	101.45
Coefficient of variation, %		17.41	9.96	28.89	29.16	36.99	36.04

Table A12. Combined analysis of variance over location (four-replicate lattice) of days to mid-shed and mid-silk, and ear height in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus check entries. Knoxville and Crossville, Tennessee.

Source	D.F.	Days to mid-shed (no.) Mean squares		Days to mid-silk (no.) Mean squares		Ear height (inch) Mean squares	
		S_1	Testcrosses	S_1	Testcrosses	S_1	Testcrosses
Replications	3	2576.00	2993.00	150.67	1727.33	20.33	194.33
Genotypes (unadjusted)	143	20.49	4.89	24.09	7.04	221.38	79.24
Blocks (adjusted)	44	6.06	2.46	8.18	4.40	47.54	42.79
Intra-block error	385	2.50	1.34	3.73	1.56	24.66	9.40
Total	575	20.67	17.92	16.99	12.14	75.32	30.29
Relative efficiency, %		106.60	102.94	105.07	109.50	103.43	123.10
Coefficient of variation, %		2.09	1.64	2.45	1.63	9.18	5.12

Table A13. Analysis of variance over location of number of ears per plant, number of nubbins per plant, and yield of nubbins in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus check entries. Knoxville and Crossville, Tennessee.

Source	D.F.	Ears/plant Mean squares		Nubbins/plant Mean squares		Yield of nubbins (lb/plot) Mean squares	
		S_1	Testcrosses	S_1	Testcrosses	S_1	Testcrosses
Location (L)	1	0.63	0.004	6.65	7.16	64.41	11.62
Genotype (G)	143	0.43**	0.137**	0.26**	0.06**	2.81**	1.14**
Genotype X Location (GXL)	143	0.08**	0.034**	0.06	0.02	1.16**	0.64*
Pooled error	286	0.06	0.025	0.06	0.02	0.78	0.48

*, ** Significant at the .05 and .01 levels of probability, respectively.

Table A14. Analysis of variance over location of days to mid-shed, and mid-silk, and ear height in S_1 and testcross progenies of the parent variety Jellicorse (Je) and the selected population (MS 13), plus check entries. Knoxville and Crossville, Tennessee.

Source	D.F.	Days to mid-shed (no.) Mean squares		Days to mid-silk (no.) Mean squares		Ear height (inch) Mean squares	
		S_1	Testcrosses	S_1	Testcrosses	S_1	Testcrosses
Location (L)	1	7663.54	8946.01	4450.00	5076.56	6.48	332.15
Genotype (G)	143	20.49**	4.90**	24.09**	7.04**	221.51**	79.36**
Genotype X Location (GXL)	143	3.73**	1.80**	5.32**	2.30**	30.47	11.16
Pooled error	286	2.42	1.27	3.61	1.62	25.22	13.60

*, ** Significant at the .05 and .01 levels of probability, respectively.

VITA

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