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Date 28 July 1993

COMBINING ABILITY OF MAIZE INBRED LINES FROM FOUR CYCLES OF RECURRENT SELECTION

A Thesis
Presented for the
Master of Science
Degree
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Wesley Neal Denton

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DEDICATION

This thesis is dedicated to my wife, Melissa E. Denton,

and

my parents, Harry C. Denton and Thelma P. Denton.

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ABSTRACT

The goal of recurrent selection is to improve population performance while maintaining genetic variability. In maize (Zea mays L.), this genetic improvement should lead to improved performance of hybrids derived from the improved population. Inbred lines from four cycles (C); C0, C1, C3, and C4 of S_1 and testcross selection for grain yield in a maize population (Tennessee Late Low-ear synthetic) were crossed to three testers to determine whether improvements in population performance resulted in improved performance of lines selected from the population. A minimum of seven lines from each cycle X selection method group was crossed to inbred lines B73, T220, and T165. Hybrids were evaluated at two locations for two years. From S_1 selection, C1 hybrids had significantly better combining ability for grain yield than C0 hybrids (10.01 vs 9.49 Mg ha^{-1}), but yield of C3 and C4 hybrids did not differ from C1. Combining ability for grain yields of hybrids from testcross selection were lower than for S_1 selection in C1 and C3. The C4 hybrids from testcross selection were significantly higher yielding than the C3 hybrids (9.97 vs 9.66 Mg ha^{-1}). There was no difference between selection methods in combining ability of C4 hybrids. In both testcross and S_1 selection grain moisture, erect plants, and plant height decreased from C0 to C4. Ear height increased from C0 to C1 and decreased in C4 of S_1 selection to a lower placement than C0, whereas ear height in C4 of testcross selection had a decrease, but the hybrids still had a higher ear placement than C0. The increase in combining ability of lines was less than the response to selection observed in the random mating population.

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PART I

INTRODUCTION

Genetic improvement of quantitatively inherited traits has been studied more extensively in corn (Zea mays L.) than any other agronomic crop. Many breeding procedures have been proposed and evaluated as methods of attaining genetic improvement of quantitative traits (Hallauer and Miranda, 1981). Comstock (1964) in a review of breeding methods, concluded that recurrent selection offered the greatest potential for long term improvement of quantitative traits in corn.

The goal of recurrent selection is to increase the frequency of favorable alleles in a genetically variable population; however, corn farmers do not grow genetically variable populations. In order to be judged successful, recurrent selection must result in higher performance of hybrids developed from the improved populations. If recurrent selection increases the frequency of favorable alleles, then inbred lines selected from the population should also have a higher frequency of favorable alleles resulting in improved performance levels.

There have been many reports of successful population improvement from recurrent selection since the method was proposed by Hull (1945) and Comstock et al. (1949), but there is little information on the performance of inbred lines extracted from the improved populations. Only one inbred line, B73 (Russell, 1972), resulting from recurrent selection has achieved widespread use in the production of commercial corn hybrids.

In 1972, the University of Tennessee Corn Breeding Project initiated an experiment to compare response to selection based on selfed progeny versus hybrid progeny performance. Burgess (1990) compared response to selection for the two methods through four cycles of selection, and found that population performance was increased by both types of progeny testing. During this selection experiment, inbred lines were extracted from the improved populations.

The objective of this research is to determine whether improvements in population performance result in improved combining ability of the inbred lines derived from the genetically improved population.

PART II

LITERATURE REVIEW

Recurrent selection:

Recurrent selection has become a basic breeding method for improvement of grain yield and other quantitative characters in corn. This breeding method has two broad objectives: (1) an increase in the frequency of favorable alleles and (2) maintenance of genetic variability by intermating superior progenies from each cycle (Hallauer et al., 1988). Three phases are necessary to complete one cycle of recurrent selection. First is the development of progeny from a base population, then evaluation of progeny in replicated trials, and next the recombination of selected progenies to continue selection in future cycles (Hallauer et al., 1988).

Combining ability analysis is often employed to evaluate the contribution recurrent selection has had on a population of corn. Sprague and Tatum (1942) first differentiated general and specific combining ability. They stated that general combining ability (GCA) is used to give the average performance of a line in hybrid combinations. Specific combining ability (SCA), on the other hand, designates specific combinations of inbreds that do relatively better or worse than the average over a group of inbred lines. In inbred development, inbreds showing high GCA make good broad based testers and inbreds having high SCA are used as narrow based testers.

Historically, Hayes and Garber (1919) were the first researchers to use principles of recurrent selection to develop a cultivar. They did not call their system recurrent selection, and only carried out one cycle with the selection procedure, but it included the three phases of recurrent selection (Sprague and Brimhall, 1950). Jenkins (1940) put these principles of selection into the first recurrent cyclical breeding procedure. Although he used a detailed system and carried on work with the population for several generations, his use of half-sib families and emphasis on additive gene effects biased his procedure to evaluate GCA.

Hull (1945) was the first to formally introduce the principle and to use the term recurrent selection in describing a corn breeding method. His scheme was developed to simplify and better identify favorable inbred lines. The method was set up to speed the production of commercial hybrids more so than the existing selection methods. He proposed to use recurrent selection in crossbred populations of corn for high combining ability or yield, and use a single homozygous tester. The homozygous tester was to be maintained through all cycles of selection and become one of the parents for the commercial hybrid. The uniform tester would measure the mean collection of alleles that showed increased favor in specific combinations and thus improve SCA. The use of this technique when evaluating hybrid vigor should be an efficient method of improving corn yield.

Comstock et al. (1949) modified Hull's recurrent selection method and referred to their procedure as reciprocal recurrent selection. Instead of using one population in the scheme, they proposed the improvement of two populations concurrently. Reciprocal recurrent selection uses the two populations as testers for each other, rather than a single homozygous tester. With this system two populations are improved, making maximum used of both GCA and SCA. Comstock et al. (1949) saw this reciprocal selection method as one that could utilize the many kinds of gene actions involved in the production of corn hybrids. The method of recurrent selection described by Hull (1945) does not account for all the possible types of gene actions. This system also has an apparent advantage in that both general and specific combining ability are improved. This allowed several inbreds to be produced for hybrid production, whereas Hull's system only allowed the production of one inbred in the same amount of time.

The methods outlined by Hull (1945) and Comstock et al. (1949) are both used extensively as selection procedures in corn populations. The choice of which system researchers will use is dependant on the specific goals of the breeding program.

Recurrent selection is used in some facet in most corn breeding programs. The benefits of this procedure are widely accepted and much has been reported of its ability to improve maize populations. In 1959, Sprague et al. reported the results of an experiment in which recurrent selection for SCA was used to improve two populations simultaneously. They wished to determine the gene action responsible for the yield heterosis or hybrid vigor in corn. The data collected had a bearing on three problems. First, the effects of successive cycles of recurrent selection for combining ability on yield when looking at a specific tester. Second, the effect of the selection practiced on genetic variability and the yields of the successive cycles as distinct populations. Third, the performance of intravarietal crosses at the same stage of selection. The yields from the experiment after two cycles of selection indicated the effectiveness of recurrent selection for SCA. The genetic variance was reduced somewhat, but some additive genetic variance still persisted after two cycles of selection. The intravarietal crosses between cycle populations showed proportionate increases in yield as the level of selection increased. The gene action involved in yield heterosis in this study was explained best by an additive model with partial to complete dominance.

The selection procedure has been modified often to improve response for certain traits or characteristics. Lonnquist and Rumbaugh (1958) selected two groups of S_1 lines from two cycles of selection. One group was selected for GCA and the other group was selected for superior SCA. The GCA group performed significantly better when evaluated in crosses than did the SCA group. The data substantiated the long held belief in corn breeding that lines should be screened initially for GCA rather than SCA, which allows removal of deleterious gene effects early in selection. The assumption was made that, for early identification of superior lines for hybrid corn production, a broad genetic base is much more desirable. Lonnquist (1951) conducted an experiment to modify combining ability of corn. He used a recurrent selection procedure consisting of taking S_0 plants from cycles of selfing and testcrossing and producing a composite of the highest yielding S_0 plants determined by a testcross procedure. This composite was allowed to intermate randomly for several generations before producing the next cycle. Lonnquist determined that this allowed him to select for greater GCA, which increased the frequency of the favorable genes, resulting in selection of a superior genotype. Horner et al. (1963) reported results from parallel recurrent selection experiments for improved grain yield. A narrow genetic base tester (stable inbred line) was used in one series and a broad genetic base tester was used in the other. Grain yield and combining ability was increased significantly in advanced cycles by the narrow base tester, but not by the broad base tester. Also, the variance components for lines were large and significant in each cycle where the narrow base tester was used. With a broad base tester, the variance decreased to nonsignificant levels in the advanced cycles. Their results indicated that recurrent selection for combining ability with an inbred line tester is more effective than a broad genetic base tester for improving grain yield in corn. In 1973, Russell et al. reported on recurrent selection for specific combining ability for yield in two maize populations. In both maize populations, GCA and SCA were increased through five cycles of selection. They concluded that both additive and nonadditive gene effects were important, but overdominance effects were found to be unimportant in both populations.

Hallauer (1984) reported improvement in SCA over seven cycles of reciprocal recurrent selection in two populations of two-ear synthetics. He found gradual improvement in one of the populations; whereas in the other population the most improvement was achieved in the first cycle of selection. Adequate genetic variability for further improvement existed in both populations after seven cycles. This method would be useful for the development of new inbred lines or for improvement of populations that exhibit important heterotic patterns. Eyherabide and Hallauer (1991) estimated the direct and indirect responses to eight cycles of reciprocal full-sib selection. They found both SCA and GCA were improved significantly in the populations and their crosses. They suggested that reciprocal full-sib recurrent selection seems an efficient procedure to improve yield performance and other agronomic traits, such as standability and prolificacy.

Russell and Eberhart (1975) and Moll and Hanson (1984) reported studies comparing recurrent selection and reciprocal recurrent selection. Russell and Eberhart (1975) evaluated three maize crosses with reciprocal and testcross selection, a form of recurrent selection. They concluded that a modified reciprocal recurrent selection system using an inbred line tester rather than a population would be an efficient method for simultaneously improving populations and developing single cross hybrids. They concluded this, because genetic variance among testcross families can be expected to be approximately twice as large for an inbred tester as for the population tester. Moll and Hanson (1984) followed with a series of experiments that demonstrated similar results when comparing reciprocal recurrent selection and full-sib selection, a form of recurrent selection. Many high yielding crosses were found from inbreds derived from both the reciprocal and full-sib selection, but the greatest gain in combining ability and yield was achieved with reciprocal recurrent selection.

The use of recurrent selection to improve important agronomic traits in maize populations has also been well documented. Stalk and root lodging, disease and insect resistance, and especially yield, have been improved in maize populations by methods employing recurrent selection techniques. In 1983, Mulamba et al. reported the effect recurrent selection had on yield. They compared populations derived from three recurrent selection experiments that differed in the type of progeny on which selection was based. Half-sib and S_1 progeny selection methods were more effective than mass selection for developing improved germplasm. This should not discount the use of mass selection in maize breeding, because the success of this system is purely dependent on the genetic base of the population and the traits selected. Walejko and Russell (1977) conducted five cycles of recurrent selection for SCA for yield of two open-pollinated varieties. Both GCA and SCA increased significantly along with significant gains in yield. Significant associated changes were noted for kernel row number, ear length, ears per plant, kernel weight, shelling percentage, ear height, and plant height. Crosbie and Mock (1980) evaluated five populations from recurrent selection experiments and found that ear sink size increased with increased grain yield, but no significant changes were found to occur in days to 50% silking, ear or plant height. Strangland et al. (1982) examined several agronomic traits including yield in a population produced from seven cycles of reciprocal recurrent selection in two maize synthetics, Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic No.1 (BSCB1). With grain yield increases came increases for grain-filling duration and rate, stay-green period, ear-length and diameter, kernel row number, and kernel weight, and decreases in pollen-silk interval.

Inbred Line per se vs. Testcross Evaluation:

The success of applied breeding program in maize is dependent on the ability to identify superior inbreds for development of superior hybrids. The use of testcrosses to evaluate inbred lines is commonly used in corn breeding. This practice actually reduces the range of trait expression, because a parent line contributes only one-half of the genes observed in the progeny. Even though this is the case, this system of evaluation has been used for two reasons: (1) inbred lines are selected on basis of performance in crosses, because their eventual use depends on combining ability, and (2) testing of inbred lines, which often lack vigor, is difficult because of their greater susceptibility to environmental stresses (Lonnquist and Lindsey, 1964). Hallauer and Lopez-Perez (1979) compared five testers for variability among testcrosses of lines at two levels (S_1 and S_8) of inbreeding. They determined testers can rank lines similarly, and correlated testcross performance with line performance using yield as their major trait for selection. They found that the correlation between the yield of hybrids of S_1 lines and their S_8 derivatives varied from 0.17 to 0.56 depending on the tester. The correlation between the yield of S_7 lines per se and the S_8 hybrids produced by those lines was even lower, ranging from 0.17 to -0.09. They found that using a high-performance inbred line (high GCA) as a tester was as effective as using a low-performance inbred line (low GCA) tester in identifying superior lines; therefore they concluded that an unrelated elite inbred line that is used in producing hybrids would be an appropriate choice as a tester.

There have been many comparisons of S_1 progenies versus testcrosses as the family unit for recurrent selection. Lonnquist and Lindsey (1964) conducted an experiment with a total of 169 S_1 lines from the third cycle of recurrent selection in Krug synthetic. They were evaluated agronomically (1) as lines per se, (2) in topcrosses to an unrelated synthetic tester and (3) in topcrosses to the parental population. The resulting inbred and topcross populations were significantly higher yielding than the parental population and did not significantly differ from each other, indicating that all three procedures were successful. Of the 19 lines selected based on line per se performance, and the 25 lines selected from the two topcross procedures, only 6 were in common. Lonnquist (1968) later took the three highest yielding and three lowest yielding lines from each of three procedures and intermated them. His evaluation of this study led him to state that a low-yield parental tester might be a good choice to evaluate new inbred lines. Duclos and Crane (1968) compared performance of topcrosses and S_1 progeny for improving populations of corn from a synthetic population. In the first cycle of selection, S_1 progeny looked to be the most effective, but in later cycles, topcross selection was more effective in increasing yield and combining ability.

Genter and Alexander (1962) reported S_1 and testcross performance in a recurrent selection project. The S_0 plants from four synthetic corn varieties were selfed and crossed with two single-cross testers. They reported S_1 progeny performance was observed to be less effected by the environment than testcross performance. In addition, S_1 progeny performance was as closely related to testcross performance as the performance of one testcross was to another. In 1973 Genter made a similar comparison after two cycles of recurrent selection in two synthetic varieties. He found testcross selection increased the frequency of genes with dominant effects for yield, but the yield of the advanced population did not improve significantly, indicating that testcross selection did not decrease the frequency of deleterious genes that suppress yield when homozygous. In the final analysis Genter found testcross selection improved heterosis, but S_1 selection increased yield and combining ability. Carangal et al. (1971) made a similar comparison of S_1 and testcross progeny from a 13-line maize synthetic. Genetic variance for yield was greater in the first cycle for the selfed progeny than the testcrosses, but decreased in the second cycle. They found S_1 selection for grain yield gave greater improvement in the population and was equal to testcross selection for improvement of combining ability.

Koble and Rinke (1963) compared random S_1 lines from a synthetic corn variety as S_1 lines and in topcrosses with a related and unrelated tester for yield performance. They found the relationship between the S_1 line performance and either of the testcrosses was as high or higher than the relationship between the two testcrosses themselves. They suggested that S_1 selection may be as effective and simpler than testcross procedures in the evaluation of potential lines.

Burton et al. (1971) compared S_1 line and half-sib testcross evaluation through four cycles of recurrent selection in a synthetic population of maize. Both mean yield and combining ability were significantly improved by both methods of selection, but S_1 selection was equal to or better than half-sib testcross selection in this particular population. Their results supported the argument that S_1 performance identified superior genotypes more quickly and efficiently than testcrosses. They put forth the explanation that testers often mask deleterious genes allowing them to remain in the population at a higher frequency than does the S_1 selection method.

Burgess and West (1993) reported their evaluation of direct and correlated responses (ear height, stalk lodging, grain moisture, silk delay) to S_1 and testcross selection for grain yield in a population that had previously undergone selection for ear height. After four cycles, S_1 selection increased yield 44% and testcross selection increased yield 21% in the population. They stated S_1 selection seemed to be superior for selection in this population.

PART III

MATERIALS AND METHODS

The source population used for this study, Tennessee Late Low-ear (TLLE), is a maize synthetic which was produced by intermating eight inbreds. This population was then subjected to ten cycles of mass selection for low ear placement (Josephson and Kincer, 1977).

Development of Genetic Material:

Recurrent selection for grain yield in TLLE-C10 was described by Burgess (1990). Two selection methods were compared that differed in the type of progeny upon which selection was based. The S_1 selection was based on the evaluation of a family resulting from self-pollination of a single plant. These S_1 families were grown in yield trials and remnant seed of the S_1 families was used to intermate selected progeny. Half-sib testcross selection required that individual plants be self-pollinated (S_1 families produced) and crossed to a tester. The hybrid families (testcrosses) were grown in yield trials and S_1 plants of the selected families were intermated to complete each cycle of selection. In addition to intermating of S_1 progeny to complete each cycle of selection, the selfed progeny could be planted in the nursery for further inbreeding and selection to produce advanced generation inbred lines. The procedures used to extract inbred lines from each cycle of selection varied somewhat over the course of the selection experiment, as described below:

Cycle zero (C0) - To initiate recurrent selection for yield, 100 plants of TLLE-C10 were self-pollinated and crossed to single cross tester. The following year, each of the 100 S_1 progeny were planted in the corn nursery for further inbreeding and selection. Visual selection based on plant and ear characteristics was applied at harvest to advance progeny to the next generation of inbreeding. Seven lines from cycle C0 survived the selection process to reach the 5th generation and were released to the public as T256, T258, T260, T262, T264, T266, and T268.

Cycle one (C1) - Following S_1 and testcross progeny trials, 10 lines were selected for intermating within each method of selection. In C1 and C2 the 10 S_1 progeny from each method were intermated by crossing in a diallel pattern. Seed from the diallel crossing was bulked to form a composite for the initiation of the next cycle of selection. The inbred lines for this study, however, were initiated by planting a row in the nursery from each diallel cross and initiating inbreeding and selection within each of these rows. Inbreeding was advanced further for the C1 lines than for the other cycles of selection. There were 7 lines from recurrent selection based on S_1 progeny trials and 8 lines from selection based on testcross progeny trials. Some of these lines were related as indicated in Table 1.

Cycle Two (C2) - No lines were selected from cycle two of recurrent selection.

Cycle Three(C3)- Beginning with C3, the methods used to intermate selected progeny for recurrent selection and to select lines from the progeny were altered. Intermating of selected lines was accomplished with a chain mating system rather than a diallel system. Progeny selected on the basis of performance in yield trials, were entered into the nursery for inbreeding and further

Table 1. Amount of inbreeding and yield testing of 59 inbred lines derived via either S_1 or testcross (TC) selection in Tennessee Late Low-ear Synthetic.

Selection			Generations	Testers		
Method	Cycle	Line*	Inbred	B73	T165	T220
None	0	1	6	1,2ǂ	1,2	1,2
		2	6	1,2	1,2	1,2
		3	6	1,2	1,2	1,2
		4	6	1,2	1,2	1,2
		5	6	1,2	1,2	1,2
		6	6	1,2	1,2	1,2
		7	6	1,2	1,2	1,2
S_1	1	8	10	1,2	1,2	1,2
		9	10	1,2	1,2	1,2
		10	10	1,2	-,2	1,2
		11	10	1,2	1,2	-,-
		12	10	1,2	-,2	1,2
		13	7	1,2	1,2	1,2
		14	8	1,2	1,2	-,2
TC	1	15	10	1,2	1,2	1,2
		16	10	1,2	1,2	1,2
		17	10	1,2	1,2	1,2
		18	7	1,2	1,2	1,2
		19	7	1,2	1,2	-,2
		20	7	1,2	1,2	1,2
		21	7	1,2	1,2	1,2
		22	10	1,2	1,2	1,2
S_1	3	23	6	1,2	1,2	1,2
		24	6	1,2	1,2	1,2
		25	6	1,2	1,2	1,2
		26	6	1,2	1,2	1,2
		27	6	1,2	1,2	-,2
		28	6	1,2	1,2	1,2
		29	6	1,2	1,2	1,2
		30	6	1,2	1,2	1,2
TC	3	31	6	1,2	1,2	-,2
		32	6	1,2	1,2	-,2
		33	6	1,-	1,2	1,2
		34	6	1,2	1,2	1,2
		35	6	1,2	1,2	1,2
		36	6	1,-	1,2	1,2
		37	6	1,2	1,2	1,2
S_1	4	38	5	1,2	1,2	1,2
		39	5	1,2	1,2	1,2
		40	5	1,2	1,2	-,2
		41	5	1,2	1,2	1,2
		42	5	1,2	1,2	1,2
		43	5	1,2	1,2	1,2
		44	5	1,2	1,2	-,2
		45	5	1,2	1,2	-,2
		46	5	1,2	1,2	1,2

(continued on next page)

Table 1. continued.

Selection			Generations Inbred	Testers		
Method	Cycle	Line*		B73	T165	T220
S_1	4	47	5	1,2	1,2	1,2
		48	5	1,2	1,2	1,2
		49	5	1,2	1,2	1,2
TC	4	50	5	1,2	1,2	1,2
		51	5	1,-	1,2	-,-
		52	5	1,-	1,2	1,2
		53	5	1,2	1,2	1,2
		54	5	1,2	1,2	1,2
		55	5	1,2	1,2	1,2
		56	5	1,2	1,2	1,2
		57	5	1,-	1,2	1,-
		58	5	1,2	1,2	1,2
		59	5	1,2	1,2	1,2
Check		┼60		1,2	1,2	1,2

* During ear-to-row selection and inbreeding some pairs of lines were selected from a common S_1 line. No more than two lines were derived from a single S_1. Pairs of lines that are derived from the same S_1 are: 11-12; 24-25; 28-29; 31-32; 36-37; 45-46; 48-49; 52-53; 54-55.

‡ Years in yield test;
1 = Seed available for yield trial in 1991.
2 = Seed available for yield trial in 1992.
\- = DeKalb variety, DK689.

┼ Check Hybrid;
Check = B73 x Mo17 for B73 tester;
Check = T165 x T167 for T165 tester;
Check = T220 x T232 for T220 tester.

selection. From C3 There were eight lines from the S_1 recurrent selection progeny and seven lines from the testcross recurrent selection project. Some of these lines were related as indicated in Table 1.

Cycle Four(C4) - Inbred lines from C4 were selected in the same manner as described from C3. Twelve lines from the S_1 selection progeny and 10 lines from the testcross selection progeny survived to the S_5 generation. Again, some of the lines were related, as indicated in Table 1.

Three inbred lines were chosen as testers to evaluate combining ability of the lines selected from each cycle of recurrent selection. Tester B73 is a widely used inbred line developed from Stiff Stalk Synthetic (BSSS) at Iowa State University (Russell, 1972). Tester T220 was developed at the University of Tennessee and derived from Neal's Paymaster and Hill's Yellow Dent varieties (Josephson et al., 1982). Tester T165, a white grained line, contains germplasm from Tekoe Yellow and lines derived by the University of Tennessee from the Jellicorse variety (West et al., 1988). These three testers were chosen because they have performed well in hybrid yield trials, have good GCA and SCA, were unrelated to each other, and were productive as inbreds, so that adequate quantities of hybrid seed for yield testing could be obtained by hand pollination.

In 1990, each of the 59 lines from the recurrent selection project was planted in the nursery using two planting dates. Each of the tester lines was planted in a block adjacent to the recurrent selection lines. Hand pollinations were made using the tester lines as female parents. In order to produce sufficient hybrid seed for yield trials, a goal of five pollinated ears for each cross was established. Some crosses did not produce sufficient seed for yield trials, due either to poor synchronization of flowering between the lines and testers, poor pollen production, or poor seed set. An attempt to produce additional seed in a winter nursery was largely unsuccessful, and, as a result, some hybrids were not grown in yield trials in 1991. Since some crosses were missed, and others had only enough seed for 1991 yield trials, hybrids with low seed quantity were made again in the 1991 Knoxville nursery. The 1991 pollinations were again only partly successful, so that some of the hybrids tested in 1991 had insufficient seed for testing in 1992. Table 1 indicates the years of testing for each of the hybrids. Hybrids that were not tested in a year were replaced by a commercial hybrid (DeKalb DK689) in order to simplify the field layout of the experiment. After harvest, data from the commercial hybrid was deleted from the data set, resulting in missing values for some hybrids in 1991 or 1992.

Evaluation Experiments:

The F1 hybrids between the testers and selected inbred lines were grown at the Plant Sciences Field Laboratory, Knoxville, TN and Milan Experiment Station, Milan, TN, for two consecutive years, 1991 and 1992. At Knoxville the soil on which the experiment was conducted was classified as a Sequatchie loam, a fine-loamy siliceous thermic Humic Hapludult. At Milan the soil was classified as a Collins silt loam, a coarse-silty mixed acid thermic Aquic Udifluvent. The hybrids were arranged in a randomized complete block design with four replication. The planting dates were 18 April 1991 and 15 April 1992 at Knoxville and 23 April 1991 and 13 April 1992 at Milan. The harvest dates at Knoxville were 5, 6, 7 Sept. 1991 and 28, 29, 30 Sept. 1992, and at Milan were 2, 3 Sept. 1991 and 23, 24 Sept. 1992. Plot technique was the same at both locations in both years. The two row plots were 6.08 m in length with rows planted 0.762 m apart. All locations were planted at a rate of 80 seeds plot^{-1} both years. In 1991 the experiment was thinned to 56 plants plot^{-1} (60,252 plants ha^{-1}) at Knoxville and 50 plants plot^{-1} (53,797 plants ha^{-1}) at Milan. In 1992 the experiment was thinned to 60 plants plot^{-1} (64,556 plants ha^{-1}) at Knoxville and 64 plants plot^{-1}, (68,860 plants ha^{-1}) at Milan. Atrazine and alachor were applied pre-emergence for weed control at both locations in both years. Nicosulfuron was applied post-emergence for johnsongrass control at Milan. Fertilizer was applied at the rates recommended by the University of Tennessee Soil Testing Lab for a potential yield of 9.07 Mg ha^{-1}. At planting nitrogen fertilizer was applied at a rate of 56 kg ha^{-1} both years at both locations. A sidedress application of nitrogen was applied about six weeks after planting at a rate of 112 kg ha^{-1} at the Milan location. The sidedress applications of nitrogen at Knoxville in 1991 were applied six weeks after planting at a rate of 172.5 kg ha^{-1} and in 1992 at a rate of 123.2 kg ha^{-1}. No phosphorous (P_2O_5) or potassium (K_2O) fertilized was applied at Knoxville in 1991. At Milan in 1991, 107.5 kg ha^{-1} of P_2O_5 and K_2O was applied. In 1992, 56 kg ha^{-1} of P_2O_5 and K_2O were applied at Knoxville and 89.6 kg ha^{-1} of P_2O_5 and K_2O were applied at Milan.

Data collected and conversions performed on the data were as follows:

Number of plants per plot - a count was taken prior to harvest of the number of plants in each plot.

Number of erect plants per plot (%) - a count of stalk and root lodged plants was taken immediately before harvest. The number of stalk plus root lodged plants was then used to calculate percent erect plants.

Plant height (m) - the distance from the soil surface to the flag leaf was measured on several randomly selected plants per plot. The mean plant height of the selected plants was used to represent a plot value. This trait was only measured at Knoxville, TN on two replications.

Ear height (m) - the distance from the soil surface to the top ear node was measured on several randomly selected plants per plot. The mean ear height of the selected plants was used to represent a plot value. This trait was only measured at Knoxville, TN on two replications.

Days to mid-silk (d) - a count of the number of days from planting until 50% of the plants in a plot had silks emerged. This trait was only measured on two replications at Knoxville.

Grain moisture at harvest (g kg^{-1}) - a shelled grain sample was collected in a moisture meter in the combine and moisture was recorded electronically for each plot during harvest.

Grain yield (Mg ha^{-1}) - plots were harvested by a modified plot combine and weight of shelled grain was recorded electronically. Shelled grain weight was converted to grain yield at 155 g kg^{-1} moisture by the following formula:

$$Y = (W * C)(100-H)/84.5$$

Where:

Y = grain yield in Mg ha^{-1}.

W = weight of shelled grain in pounds per plot.

C = .4879 (a constant to convert pounds per plot to Mg ha^{-1}).

H = percent moisture of grain at harvest.

Data Analysis:

Standard analysis of variance techniques were used to evaluate combining abilities of selected inbreds from the four cycles of recurrent selection for grain yield improvement. The computerized statistical package, General Linear Mixed Models (GLMM) (Blouin and Saxton, 1990) was used to analyze the data. The form of the analysis of variance is presented in Table 2. Years and locations were considered a set of four random environments for the statistical analysis. A covariance adjustment for difference in plant stand within each environment was used in the estimation of mean grain yield. The GLMM statistical program differs from the conventional analysis of variance, in that no F statistic for random effects is calculated. The output from the program does however include estimates of the variances for each random component. To complete the analysis of variance table, expected mean squares were used to calculate mean squares for the random components, and F values were calculated by hand computation. These calculated mean squares are correct for the case of balanced data, but as the number of missing values increases, their reliability decreases. The only case where serious bias is thought to occur due to missing values is for the variable days to mid-silk. This variable was measured on only two replications at Knoxville, and had more missing values than any other

Table 2. Form of the analysis of variance for grain yield (Mg ha^{-1}), grain moisture (g kg^{-1}), erect plants (%), plant height (m), ear height (m), and days to mid-silk (d) for hybrid populations.

	Variables	
	Grain Yield, Grain Moisture, and Erect Plants	Plant Height, Ear Height, and Days to Mid-silk
Source of Variation	Degrees of Freedom	
Environments[E]	3	1
Replications[R](Environments)	12	4
Blocks(R(E) X Testers[T])	96	48
T	2	2
Lines [L] [GCA]	59	59
Among Cycle[C]0 L	6	6
C0 vs. Selected Lines[SL]	1	1
Among SL	51	51
Methods[M]	1	1
C(M)	4	4
L(C(M))	46	46
T X L [SCA]	118	118
C0 L X T	12	12
C0 vs. SL X T	1	1
Among SL X T	102	102
M X T	2	2
C(M) X T	8	8
L(C(M)) X T	92	92
E X T	6	2
E X L	177	59
C0 X E	18	6
C0 vs. SL X E	1	1
SL X E	153	51
M X E	3	1
C(M) X E	12	4
L(C(M)) X E	138	46
T X L X E	354	118
C0 X T X E	36	12
C0 vs. SL X T X E	1	1
SL X T X E	306	102
M X E X T	6	2
C(M) X E X T	24	8
L(C(M)) X E X T	276	92
Error	2053	1509

variable. Least significant difference (LSD) values at the 0.05 level of probability were calculated for tables of means. In the calculation of LSD values, the appropriate mean square for interaction of environments with the components of interest was substituted for the error mean square.

The following statistical model was used for the analysis of variance:

$$Y_{ijkl} = u + Y_i + L_j + G_k + YL_{ij} + YG_{ik} + LG_{jk} + YLG_{ijk} + R(Y)_l + E_{ijkl}$$

Where:

Y_{ijkl}	=	yield of the plot containing the kth tester and the jth line in the ith environment in the lth replication.
u	=	population mean.
Y_i	=	random effect of the ith environment.
L_j	=	fixed effect of the jth line, which was subdivided into:
		m = fixed effect of the mth method.
		c = fixed effect of the cth cycle.
G_k	=	fixed effect of the kth tester.
YL_{ij}	=	interaction effect of the ith environment and the jth line.
YG_{ik}	=	interaction effect of the ith environment and the kth tester.
LG_{jk}	=	interaction effect of the jth line and the kth tester.
YLG_{ijk}	=	interaction effect of the ith environment, the jth line, and the kth tester.
$R(Y)_l$	=	random effect of the lth replication within the ith environment.
E_{ijkl}	=	error effect associated with the ith environment, the jth line, the kth tester, and the lth replication.

PART IV

RESULTS

Both 1991 and 1992 were excellent growing seasons for corn in Tennessee. The hybrids from each cycle performed best in 1992, partly due to poor seedling emergence in 1991. Each selected line was crossed to three testers, B73, T165, and T220, to produce three sets of hybrids. In 1991 at Milan, the mean yields of the B73, T165 and T220 hybrid sets were, 8.90, 9.04, and 8.42 Mg ha^{-1}, respectively, with an average across all testers of 8.79 Mg ha^{-1}; whereas at Knoxville the mean yields for the three sets of hybrids were 8.39, 7.76, and 7.83 Mg ha^{-1}, respectively, with an overall mean yield of 8.01 Mg ha^{-1}. In 1992, the B73, T165, and T220 hybrid sets yielded 11.08, 10.88, and 10.89 versus 11.40, 11.98, and 11.50 Mg ha^{-1} at Milan and Knoxville, respectively. The location average were 10.95 versus 11.64 Mg ha^{-1} for Milan and Knoxville, respectively (Table 3). The flowering dates in 1991 were 10 to 15 days earlier than the following year, due to the cooler temperatures during 1992.

The main effects of environment and tester were not significant for grain yield (Table 4). In the comparison of variation due to inbred lines, there were significant differences among C0 lines and the mean for all C0 lines (9.49 Mg ha^{-1}) was significantly lower than the mean for all selected lines (9.89 Mg ha^{-1}) (Table 5). Using single degree of freedom comparisons the mean for all hybrids from S_1 selection and the mean for all hybrids from TC selection were significantly higher than the mean of all C0 hybrids. Comparisons of lines from each selection method revealed that the mean for all hybrids from S_1 selection (9.99 Mg ha^{-1}) was significantly higher than the mean of all hybrids from TC selection (9.79 Mg ha^{-1}) (Table 5). As expected there were significant differences among hybrids within each method and cycle of selection (Table 4).

There was a significant interaction effect between testers and lines, but the comparison of C0 hybrids versus all selected line hybrids by tester was not significant, and the method of selection by tester effect was not significant (Table 4). It appears that most of the tester by line interaction was due to the differences among individual lines

Table 3. The mean grain yield at Knoxville (K) and Milan (M), Tennessee in 1991 and 1992 averaged over hybrid sets produced by crossing inbred lines from Tennessee Late Low-ear Synthetic cycle 0, and cycles 1, 3, 4 of S_1 and testcross selection onto three testers.

Environments		Testers			
Year	Location	B73	T165	T220	Mean
		----------------	Mg ha^{-1}	----------------	
1991	M	8.90	9.04	8.42	8.79
	K	8.39	7.76	7.83	8.01
	Mean	8.65	8.40	8.13	8.40
1992	M	11.08	10.88	10.89	10.95
	K	11.40	11.98	11.50	11.64
	Mean	11.24	11.43	11.20	11.29

Table 4. Results of the analysis of variance for grain yield (Mg ha^{-1}), grain moisture (g kg^{-1}), and erect plants (%), for 59 inbred lines crossed to three testers and grown in four environments.

	Variables		
Source of Variation	Grain Yield	Grain Moisture	Erect Plants
Environments [E]	†ns	ns	s
Replications[R](E)	s	ns	s
Blocks(R(E) X Tester[T])	s	s	s
T	ns	ns	ns
Lines[L] [GCA]	s	s	s
Among Cycle[C]0 L	s	s	ns
C0 vs. Selected Lines[SL]	s	ns	ns
Among SL	s	s	s
Method[M]	s	ns	ns
Cycle[C](M)	ns	s	ns
L(C(M))	s	s	s
T X L [SCA]		s	ss
C0 L X T	s	s	ns
C0 vs. SL X T	ns	s	ns
Among SL X T	s	s	ns
M X T	ns	ns	ns
C(M) X T	s	s	ns
L(C(M)) X T	s	s	ns
E X T	s	s	s
E X L	s	s	s
C0 X E	ns	ns	ns
C0 vs. SL X E	ns	ns	ns
SL X E	s	s	s
M X E	ns	ns	s
C(M) X E	ns	s	ns
L(C(M)) X E	s	s	s
T X L X E	ns	s	s
C0 X T X E	ns	ns	ns
C0 vs SL X T X E	ns	ns	ns
SL X T X E	ns	s	s
M X E X T	ns	ns	ns
C(M) X E X T	ns	s	ns
L(C(M)) X E X T	ns	ns	ns

† ns = nonsignificant; s = significant at $P \leq 0.05$.

Table 5. Mean grain yield of hybrid sets produced by crossing inbred lines from Tennessee Late Low-ear Synthetic cycle 0, and cycles 1, 3, and 4 of S_1 and testcross (TC) selection onto three testers, evaluated at Knoxville and Milan, Tennessee in 1991 and 1992.

Selection		Tester			
Method	Cycle	B73	T165	T220	Mean
		Mg ha^{-1}			
None	0	9.65	9.44	9.40	9.49
S_1	1	10.48	9.67	9.89	10.01
	3	10.15	9.88	9.93	9.99
	4	10.04	9.93	9.90	9.96
	Mean	10.22	9.83	9.91	9.99
TC	1	9.94	9.80	9.47	9.74
	3	9.59	9.67	9.70	9.66
	4	10.21	9.88	9.82	9.97
	Mean	9.91	9.78	9.66	9.79
Check*		10.58	10.62	10.66	10.61
LSD 0.05 (among cycles)		0.30	0.30	0.30	0.24

* Check hybrids are: B73 X Mo17 for B73 tester;
T165 X T167 for T165 tester;
T220 X T232 for T220 tester.

crossed to the three testers. The cycle within method by tester effect was significant, and this effect can be seen in Table 5 by comparing the response of S_1 selected hybrids in C1 and C3 on the three testers. In C1 of S_1 selection the mean for B73 testcrosses was 10.48 Mg ha^{-1}. In C4 of S_1 selection, the mean for B73 hybrids decreased to 10.04 Mg ha^{-1}. For both T165 and T220 hybrids the mean yield of C1 hybrids from S_1 selection was lower than from B73 hybrids, but the means for T165 and T220 hybrids were higher in C4 than C1 (Table A1).

Both environment by line and environment by tester interactions were significant (Table 4). Method of selection by environment and the effect of cycles within method of selection by environment was non-significant. Since the main effects of selection did not interact with environments, means for each line evaluated are presented as an average of the four environments (Table A1). None of the second order interaction among environments, testers, and lines were significant for grain yield (Table 4).

The inbred lines from S_1 selection crossed to B73, T165, and T220 resulted in a gain in combining ability for grain yield of 4.1%, 4.6%, and 5.3% respectively from C0 to C4 with a average gain over all testers of 5.0%. The inbred lines from testcross selection crossed to B73, T165, and T220 resulted in a gain in combining ability for grain yield of 5.8%, 4.7%, and 4.5% respectively from C0 to C4 with an average gain in over all testers of 5.0% (Table 5).

Of the selected lines, the best combining line was 38 (11.05 Mg ha^{-1}) from C4 of S_1 selection and the poorest was 56 (8.99 Mg ha^{-1}) from C4 of testcross selection (Table A1). In C0, the best performing line across the three testers was 3 (10.68 Mg ha^{-1}). The lines from S_1 selection that demonstrated the best hybrid performance and GCA in C1, C3, and C4 were respectively, lines 10 (10.71 Mg ha^{-1}), 27 (10.55 Mg ha^{-1}), and 38 (11.05 Mg ha^{-1}) (Table A1). The lines from S_1 selection with the poorest hybrid performance and GCA in C1, C3, and C4 were 8 (9.52 Mg ha^{-1}), 25 (9.59 Mg ha^{-1}), and 47 (9.10 Mg ha^{-1}). The lines from testcross selection with the best GCA for grain yield in C1, C3, and C4 were 19 (10.52 Mg ha^{-1}), 33 (10.02 Mg ha^{-1}), and 51 (10.41 Mg ha^{-1}). The lines from the testcross selection with the poorest GCA for grain yield in C1, C3, and C4 were 16 (9.15 Mg ha^{-1}), 31 (9.19 Mg ha^{-1}) and 56 (8.99 Mg ha^{-1}) (Table A1).

For comparison purposes 10.00 Mg ha^{-1} was chosen as a reference point to relate a distribution to the means of inbred lines across testers (Figure 1). C0 had 2 hybrids (29%) above and 5 hybrids (71%) below 10 Mg ha^{-1}. From S_1 selection, C1 had 3 lines (43%) above and 4 lines (57%) below, C3 had 3 lines (37%) above and 5 lines (63%) below, and C4 had 5 lines (42%) above and 7 lines (58%), below 10.0 Mg ha^{-1}. From the testcross selection, C1 had 3 lines (38%) above and 5 lines (62%) below, C3 had 1 line (14%) above and 6 lines (86%) below, and C4 had 5 lines (50%) above and 5 lines (50%) below the chosen reference point. With the exception of C3 of testcross selection, each of the selected populations produced a higher frequency of good combining lines for yield than C0 (Figure 1).

From S_1 selection, C1 hybrids had significantly better combining ability for grain yield than C0 hybrids (10.01 vs 9.49 Mg ha^{-1}) but yield of C3 and C4 hybrids did not differ from C1. Yields of hybrids from testcross selection were lower than for S1 selection in C1 and C3 (Table 5). The C4 hybrids from testcross selection were significantly higher yielding than the C3 hybrids (9.97 Mg ha^{-1} vs 9.66 Mg ha^{-1}). There was a significant difference between selection methods in yield of C1 (10.01 Mg ha^{-1} vs 9.74 Mg ha^{-1}) and C3 (9.99 Mg ha^{-1} vs 9.66 Mg ha^{-1}). There was no difference between selection methods in yield of C4 hybrids (Table 5).

In C0 the means among testers did not differ. The mean of hybrids produced with B73 (10.48 Mg ha^{-1}) and inbreds from S_1 selection in C1 was significantly larger than the means of T165 (9.67 Mg ha^{-1}) and T220 (9.89 Mg ha^{-1}); whereas the mean of lines from C1 of testcross selection

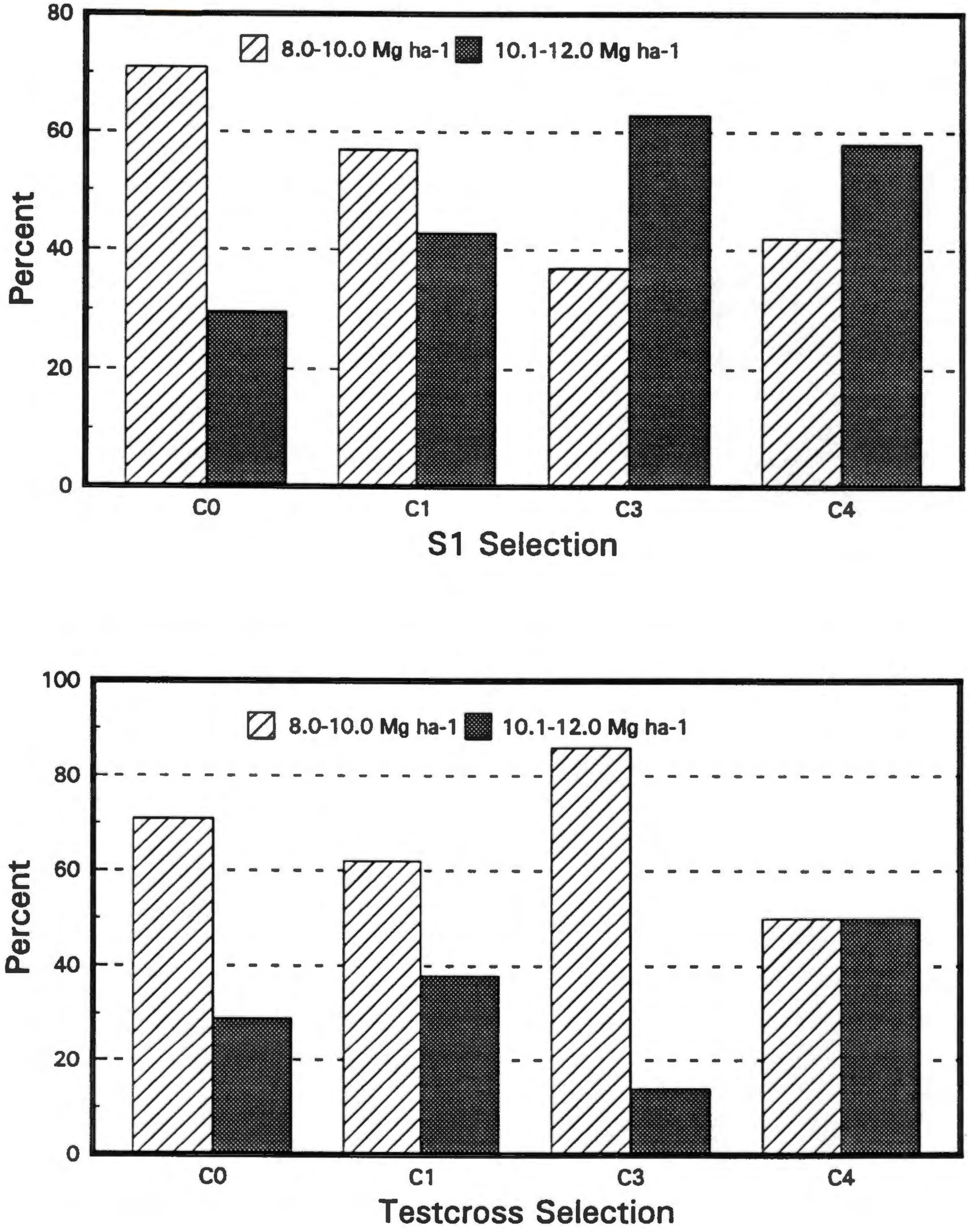

Figure 1. Percentage of hybrid sets that yielded above and below 10 Mg ha^{-1} in cycle 0 and cycles 1, 3, and 4 from S_1 (top) and testcross selection (bottom).

produced with B73 (9.94 Mg ha^{-1}) and T165 (9.80 Mg ha^{-1}) were both significantly larger than T220 (9.47 Mg ha^{-1}) (Table A1). In C3 no differences between testers in either selection method was found. In addition, S_1 selected lines in C4 showed no significant differences between testers, but testcross selected lines crossed to B73 (10.21 Mg ha^{-1}) were significantly higher than T165 (9.88 Mg ha^{-1}) and T220 (9.82 Mg ha^{-1}) (Table A1). The S_1 selected inbred lines showed better hybrid performance than testcross selected inbred lines in C1 and C3, but there was no difference between selection methods in C4 (Table 5).

The analysis of variance for grain moisture (Table 4) produced results similar to the analysis of grain yield. The main effects for environment and tester were not significant. The comparison of C0 versus all selected lines was not significant, nor were the comparison of all S_1 selected hybrids versus all testcross selected hybrids. Cycle of selection had a significant effect on grain moisture, and in Table 6 we can see a decrease in mean grain moisture for each method as selection advances from C0 to C4. Significant tester by line interactions were found for grain moisture at harvest. These interactions appear to be due to differences between B73 and the other two testers. B73 is an early maturing line in Tennessee and the B73 hybrids were consistently lower in grain moisture than the other two testers. The significant cycle within method by tester interaction can be seen in the means for each cycle of testcross selection in Table A2. The mean for C1 and C3 of testcross selection did not change for B73 hybrids, while there was a small decrease in grain moisture between C1 and C3 for both T165 and T220 (Table A2). The environmental interactions of primary interest were the comparison of C0 lines versus selected lines by environment, and method by environment. Both of these components were not significant. From S_1 selection, C3 (199 g kg^{-1}) and C4 (196 g kg^{-1}) differed significantly from C0 (202 g kg^{-1}), in addition C4 (196 g kg^{-1}) differed from C1 (200 g

Table 6. Mean of grain moisture, erect plants, plant height, ear height, and days to mid-silk of hybrids produced by crossing inbred lines from Tennessee Late Low-ear Synthetic cycle 0, and cycles 1, 3, and 4 of S1 and testcross (TC) selection onto three testers, evaluated at Knoxville and Milan, Tennessee in 1991 and 1992.

Selection		Variable				
Method	Cycle	Grain Moisture	Erect Plants	Plant Height	Ear Height	Days to Mid-silk
		$g\ kg^{-1}$	%	m	m	d
None	0	202	98.4	2.76	1.22	76
S_1	1	200	96.1	2.72	1.26	75
	3	199	96.0	2.69	1.28	74
	4	196	95.8	2.72	1.21	75
	Mean	198	96.0	2.71	1.25	75
TC	1	201	97.5	2.80	1.32	76
	3	200	97.1	2.73	1.32	75
	4	197	98.0	2.70	1.26	73
	Mean	199	97.5	2.74	1.30	75
Check*		193	97.5	2.76	1.44	74
LSD 0.05 (cycles)		3	1.4	.02	.02	17

* Check hybrids are: B73 X Mo17 for B73 tester;
T165 X T167 for T165 tester;
T220 X T232 for T220 tester.

kg^{-1}). From testcross selection, C1 (201 g kg^{-1}), and C3 (200 g kg^{-1}) did not statistically differ from C0 (202 g kg^{-1}), however C4 (197 g kg^{-1}) differed statistically from all other cycles (Table 6). From C0 to C4 with S_1 selection there was a decrease in grain moisture in the B73, T165, and T220 hybrids of 5.0%, 2.4%, and 2.0% respectively, with an average decrease over all three testers of 3.0%. From C0 to C4 with testcross selection there was a decrease in grain moisture in the B73, T165, and T220 hybrids of 4.5%, 2.9%, and 0.0% respectively, with an average decrease across all testers of 2.5% (Table A2).

In the other variables, upright plants, plant height, ear height and days to mid-silk the tester interaction effects were not significant as frequently, so the means from these variables were averaged over all three testers (Table 6).

In the analysis of variance for erect plants (Table 4), plant height, ear height and days to silk (Table 7) significant tester by line interaction were found only for ear height. For this variable the tester interactions of primary interest (C0 versus selected lines by tester, and method of selection by tester) were not significant.

In the analysis of percentage erect plants, environments had a significant effect, but tester effect was not significant (table 4). The comparison of all C0 hybrids versus selected hybrids was not significant, but there were differences between selection methods for percentage upright plants. Hybrids produced from testcross selected lines had significantly greater standability (97.2%) than hybrids from S1 selected lines (96.0%) (Table 6).

Percentage upright plants decreased 2.6% from C0 to C4 of S_1 selection. For testcross selection upright plants decreased 1.3% from C0 to C3, but increased 0.9% from C3 to C4 (Table 6). The range of percentage upright plants in C0 was 97.8% to 98.9%. The ranges of S_1 selection in C1, C3, and C4 were 93.2% to 97.6%, 91.6% to 97.0%, and 92.5% to 97.7%. The ranges of testcross selection in C1, C3, and C4 were

Table 7. Results of the analysis of variance for plant height (m), ear height (m), and days to mid-silk (d), for 59 inbred lines crossed to three testers and grown in four environments.

Source of Variation	Plant Height	Ear Height	Days to Mid-silk
	Variables		
Environments [E]	†s	s	ns
Replications[R](E)	ns	ns	ns
Blocks(R(E) X Tester[T])	s	s	s
T	ns	ns	s
Lines[L] [GCA]	s	s	ns
Among Cycle[C]0 L	s	s	ns
C0 vs. Selected Lines[SL]	s	s	ns
Among SL	s	s	ns
Method[M]	ns	ns	ns
C(M)	s	s	s
L(C(M))	s	s	s
T X L [SCA]	s	s	ns
C0 L X T	ns	ns	ns
C0 vs. SL X T	ns	ns	ns
Among SL X T	ns	s	ns
M X T	ns	ns	ns
C(M) X T	ns	ns	ns
L(C(M)) X T	ns	s	ns
E X T	s	s	ns
E X L	s	ns	ns
C0 X E	ns	s	ns
C0 vs. SL X E	ns	ns	s
SL X E	ns	ns	s
M X E	ns	ns	ns
C(M) X E	ns	ns	s
L(C(M)) X E	ns	ns	s
T X L X E	ns	ns	ns
C0 X T X E	ns	ns	s
C0 vs SL X T X E	ns	ns	ns
SL X T X E	ns	ns	s
M X E X T	ns	s	s
C(M) X E X T	ns	ns	ns
L(C(M)) X E X T	ns	ns	ns

† ns = nonsignificant; significant P ≤ 0.05.

95.0% to 99.4%, 95.0% to 99.0%, and 96.6% to 99.7% (Table A3).

In the analysis of variance for plant height (Table 7), environments and line effects were significant, but tester effects were not significant. There was significant variation within C0 and selected line groups, but method of selection did not influence plant height. Plant height decreased in both selection procedures in comparison with C0 line hybrids (Table 6).

The LSD value of .06 displayed differences among many line means (Table A3). The mean plant height of C0 (2.76 m) was significantly taller than the plant heights of the hybrids from S_1 selection in C1 (2.72 m), C3 (2.69 m), and C4 (2.72 m), when using the calculated LSD (.02) (Table 6). Plant height from C0 (2.76 m) was significantly shorter than the plant heights of the lines from testcross selection in C1 (2.80 m), but significantly taller than C3 (2.73 m) and C4 (2.70 m). Across cycles, lines from testcross selection produced taller hybrids than the lines from the S_1 selection (Table 6). The cycle mean from S_1 selection in C1 was significantly larger than the cycle means of S_1 lines in C3. The cycle mean from testcross selection in C1 was significantly larger than C3 and C4, however C3 was also significantly larger than C4. Within each cycle the average of testcross and S_1 selected lines statistically differed from one another (Table 6).

The range in plant height in C0 was 2.57 m to 2.99 m. The ranges for lines from S_1 selection in C1, C3, and C4 were 2.61 m to 2.77 m, 2.46 m to 2.96 m, and 2.46 m. to 2.88 m. The ranges for lines from the testcross selection in C1, C3, and C4 were 2.57 m to 2.95 m, 2.53 m to 3.05 m, and 2.53 m to 2.88 m (Table A3).

Results of the analysis of variance for ear height were similar to results from plant height analysis. Environment and line effects were significant, but tester and method of selection were not significant. Ear height of all selected line hybrids (1.28 m) was significantly higher than the ear height of C0 line hybrids (1.22 m) (Table 6).

Significant differences among lines were found in each cycle across both selection methods using the calculated LSD value of 0.05. The average ear heights of C1 (1.32 m), C3 (1.32 m), and C4 (1.26 m) lines from testcross selection were significantly taller than the average ear heights of C1 (1.26 m), C3 (1.28 m), and C4 (1.21 m) lines from S_1 selection (Table 6). Cycle means from S_1 selection differed significantly between C1, C3, and C4 with an increase from C1 to C3 and decrease from C3 to C4. Ear height did not differ between cycle means of C1 and C3 lines within testcross selection, but C4 was significantly lower than C1 or C3. Ear height over the cycles increased, whereas plant height decreased (Table 6).

The range of the line means within cycle C0 was 1.07 m to 1.35 m. The ranges in C1, C3 and C4 for S_1 selection were 1.16 m to 1.35 m, 1.14 m to 1.45 m., and 1.02 m to 1.37 m, whereas the ranges for testcross selection were 1.26 m to 1.40 m, 1.14 m to 1.58 m, and 1.08 m to 1.43 m (Table A3).

In the analysis of variance for days to mid-silk (Table 7) tester was the only main effect which was significant. As mentioned previously, B73 is an early maturing line in Tennessee and the hybrids of this line flowered in significantly fewer days than T165 and T220. The most positive conclusion that can be drawn from the analysis days to silk is that maturity did not change as a result of selection. Earlier maturity is usually desirable if other factors are equal, and hybrids from the selected lines can be identified that are earlier than the C0 hybrids, such as line 57 from C4 of testcross selection (Table A3).

With the LSD value of 7 for line means the only cycle that had significant differences was C4 testcross selection. The LSD of 17 for cycle means showed that no difference exists between C0 (76 d) and S_1 selection in C1 (75 d), C3 (74 d), or C4 (75 d) and testcross selection in C1 (76 d), C3 (75 d) or C4 (73 d). No differences were determined between the two methods in each cycle (Table 6).

PART V

DISCUSSION

The objective of this research was to determine whether improvements in population performance result in improved combining ability of the inbred lines derived from the genetically improved population. Burgess and West (1993) compared response to selection for the two methods through four cycles of selection, and found that population performance was increased by both S_1 and testcross selection.

The average increase in combining ability for grain yield of the lines from S_1 selection was 5.1% from C0 (9.49 Mg ha^{-1}) to C4 (9.96 Mg ha^{-1}) (Table 5). Burgess and West (1993) found that the yield of the population from S_1 selection increased 44.0% from C0 (3.89 Mg ha^{-1}) to C4 (5.60 Mg ha^{-1}). The average increase in combining ability for grain yield of the hybrids from testcross selection was 5.1% from C0 (9.49 Mg ha^{-1}) to C4 (9.97 Mg ha^{-1}) (Table 5). The grain yield from the testcross selection in the population increased 27.6% from C0 (3.89 Mg ha^{-1}) to C1 (4.96 Mg ha^{-1}) and decreased 12.3% from C1 to C2 (4.38 Mg ha^{-1}), but again increased 8.2% between C3 (4.68 Mg ha^{-1}) and C4 (4.71 Mg ha^{-1}) for a net increase from C0 to C4 of 21.0% (Burgess and West, 1993). The S_1 selection in the population, and the lines from this selection performed similarly with consistent gains from one cycle to the next. The lines from testcross selection and the testcross population behaved similarly in that both decreased in grain yield after C1, however the testcross lines rebounded in C4 producing significantly higher yields than C1.

The response to selection was greater for the random mated population than for hybrids produced by lines selected from those populations. This result is to be expected given that the correlation between line per se performance for grain yield, and hybrid grain yield is low (Lamkey and Hallauer, 1986; Hallauer and Lopez-Perez, 1979). During inbreeding in the nursery, selection is for line per se characteristics. Lines were not tested for hybrid performance during the inbreeding phase of development, so that they are somewhat analogous to a set of random lines concerning their potential for producing good combining, high yielding hybrids. Theoretically, the changes in hybrid performance that occur as selection proceeds are a result of the changes in gene frequency due to selection. The positive and significant changes in hybrid performance observed in this study indicate that recurrent selection which alters population performance can be expected to also alter the performance of hybrids developed from the population.

Although the magnitude of the gains in combining ability from selection were much lower for hybrids than for the population, the entire set of hybrids would not be expected to have commercial potential. In an applied breeding program, the best combining line for grain yield from the tester X line (SCA) group would be selected for further evaluation. Using this basis the highest yielding hybrid with B73 as one parent was line 10 (11.270 Mg ha^{-1}) from C1 of S_1 selection. This hybrid was 3.3% higher yielding than the best B73 hybrid from C0 (line 3, 10.913 Mg ha^{-1}). The highest yielding hybrid with T165 as one parent was line 51 (11.458 Mg ha^{-1}) from C4 of TC selection. This hybrid was 5.8% higher yielding than the best T165 hybrid from C0 (line 3, 10.913 Mg ha^{-1}). The highest yielding hybrid with T220 as one parent was line 38 (11.234 Mg ha^{-1}) from C4 of S_1 selection. This hybrid was 9.0% higher yielding than the best T220 hybrid from C0 (line 3, 10.308 Mg ha^{-1}). The highest yielding hybrid (10) from the B73 group yielded 6.5% better than the B73 X Mo17 check, which has been grown extensively as a commercial hybrid. The highest yielding T165 hybrid (51) performed 7.3% better than the T165 X T167 check. The highest yielding T220 hybrid (38) performed 5.1% better than the T220 X T232 check (Table A1). These results suggest that any of these superior lines could be further evaluated and possibly released for commercial hybrid production.

The average grain moisture from the hybrid groups produced by crossing every S_1 selected line to the three testers, B73, T165, and T220, decreased 2.7% from C0 (202 g kg^{-1}) to C4 (196 g kg^{-1}) and the testcross lines decreased 2.5% from C0 (202 g kg^{-1}) to C4 (197 g kg^{-1}) (Table A2).

Burgess and West (1993) reported the average grain moisture for the S_1 selected population decreased 13.3% from C0 (241 g kg^{-1}) to C4 (209 g kg^{-1}) and the testcross population decreased 10.8% from C0 (241 g kg^{-1}) to C4 (215 g kg^{-1}). The selected lines in hybrid combinations did not decrease as dramatically as the population, but the trend of reduction in grain moisture over sequential cycles of selection was evident. Testcross selection in both incidences had smaller decrease from C0 to C4 (Table 6).

Percentage erect plants was calculated for the selected lines whereas stalk lodging was presented in population study (Burgess and West, 1993). The conversion of stalk lodging to percentage erect plants can be accomplished by simply subtracting percent stalk lodging from 100. Erect plants in the S_1 selected lines significantly decreased 2.6% from C0 (98.4%) to C4 (95.8%) and testcross selected lines group decreased 1.3% from C0 (98.4%) to C3 (97.1%), but then increased slightly by 0.9% in C4 (98.0%) (Table 6). In the random mating population S_1 selection increased stalk lodging 5.0% from C0 (1%) to C4 (6%), but no significant difference was seen between the cycles in testcross selection (West and Burgess, 1993).

The lines taken from S_1 selection in the population and the S_1 population itself showed significant trends for reduction in erect plants over cycles. In addition, lines from testcross selection displayed similar results however the testcross population had no significant differences in upright plants over cycles (Table 6).

Although small increases and decreases did occur between cycles no significant difference in ear height was observed from C0 to C4 of S_1 or testcross selection in the random mating population, (West and Burgess, 1993). The improved lines from testcross selection had a significant increase of 3.3% between C0 (1.22 m) and C4 (1.26 m). The improved lines from S_1 selection increased 4.9% from C0 (1.22 m) to C3 (1.28 m), but then decreased in C4 (1.21 m) so no significant difference was observed between C0 and C4 (Table 6).

In the population study, plant height did not differ significantly between C0 (1.99 m) and C4 (1.99 m) (Burgess and West, 1993), but the average of the S_1 selected lines differed significantly with a 1.4% decrease from C0 (2.76 m) to C4 (2.72 m). The testcross selected lines differed significantly from C0 (2.76 m) to C4 (2.70 m) with a 2.2% increase. The testcross cycles in the population had a slight increase of 2.0% from C0 (1.99 m) to C4 (2.03 m), but it was not significant (Table 6).

The results of this study indicate that recurrent selection can be an effective method for hybrid development in an applied corn breeding program. Grain yield of hybrids produced by inbred lines from the advanced cycles of selection had a higher mean than the lines from the C0 population, and there was a higher frequency of high yielding hybrids from the selected populations than from the C0 cycle. Gains in mean hybrid yields for each cycle of selection were much lower than the gains observed for the population per se (5% versus 44% for C0 versus C4 of S1 selection). This may be due in part to characteristics of the population chosen for this study. D. R. West (1993, personal communication) has extensive experience with Tennessee Late Low-ear Synthetic, and believes that this population has generally low combining ability for the development of hybrids. Choice of a different population that is known to produce lines with good combining ability (i.e. Jellicorse or Neal Paymaster), may have resulted in higher gains in hybrid performance from the advanced cycles of selection.

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APPENDIX

Table A1. Grain yield of hybrid sets produced by crossing inbred lines from Tennessee Late Low-ear Synthetic cycle 0, and cycles 1, 3, and 4 of S_1 and testcross (TC) selection onto three testers, evaluated at Knoxville and Milan, Tennessee in 1991 and 1992.

Selection			Tester			
Method	Cycle	Line	B73	T165	T220	Mean
			------------------Mg ha^{-1}------------------			
None	0	1	9.158	9.362	9.856	9.46
		2	10.468	10.203	9.803	10.16
		3	10.913	10.825	10.308	10.68
		4	9.189	8.818	9.770	9.26
		5	9.858	9.369	8.511	9.25
		6	9.133	9.042	7.728	8.63
		7	8.798	8.479	9.788	9.02
		Mean	9.65	9.44	9.40	9.49
S_1	1	8	10.324	8.787	9.460	9.52
		9	10.610	9.627	8.773	9.67
		10	11.270	10.897	10.169	10.71
		11	10.817	8.969	11.231	10.26
		12	9.568	10.299	10.094	9.91
		13	10.597	9.960	9.628	10.06
		14	10.146	9.590	10.401	9.97
		Mean	10.48	9.67	9.89	10.01
S_1	3	23	10.285	9.854	10.007	10.05
		24	10.289	10.330	10.183	10.27
		25	10.000	9.375	9.381	9.59
		26	9.770	9.690	10.073	9.84
		27	10.759	10.105	11.008	10.55
		28	10.210	10.197	9.219	9.88
		29	9.516	10.010	10.018	9.85
		30	10.363	9.504	9.744	9.87
		Mean	10.15	9.88	9.93	9.99
S_1	4	38	11.120	10.784	11.234	11.05
		39	10.637	10.384	8.888	9.97
		40	9.243	9.390	9.982	9.47
		41	10.513	9.983	10.074	10.19
		42	10.300	9.642	10.387	10.11
		43	9.857	9.987	9.992	9.95
		44	9.737	9.820	9.808	9.72
		45	10.410	9.513	9.684	9.80
		46	10.752	10.701	10.570	10.66
		47	9.607	9.030	8.660	9.10
		48	9.709	10.297	10.212	10.07
		49	8.625	9.579	9.954	9.39
		Mean	10.04	9.93	9.90	9.96

(continued on next page)

Table A1 continued.

Selection			Tester			
Method	Cycle	Line	B73	T165	T220	Mean
			------------------Mg ha^{-1}------------------			
TC	1	15	10.296	9.434	8.890	9.54
		16	9.068	9.414	8.958	9.15
		17	10.567	9.615	9.898	10.03
		18	9.045	9.323	9.282	9.22
		19	10.920	10.621	10.228	10.52
		20	9.497	9.614	9.138	9.42
		21	9.616	10.022	9.227	9.64
		22	10.462	10.337	10.324	10.38
		Mean	9.94	9.80	9.47	9.74
TC	3	31	9.000	8.752	10.050	9.19
		32	9.446	9.095	9.902	9.41
		33	10.294	10.224	9.516	10.02
		34	10.003	10.006	9.906	9.97
		35	8.581	10.373	9.568	9.51
		36	9.497	9.925	9.985	9.81
		37	10.256	9.332	9.426	9.67
		Mean	9.59	9.67	9.70	9.66
TC	4	50	10.161	9.757	10.160	10.03
		51	10.358	11.458	9.674	10.41
		52	10.927	9.292	9.169	9.81
		53	11.056	9.534	9.684	10.09
		54	9.789	9.682	9.774	9.75
		55	10.584	9.620	9.733	9.99
		56	8.385	8.588	9.999	8.99
		57	9.785	10.294	10.387	10.18
		58	10.431	10.056	9.936	10.07
		59	10.071	9.982	9.091	9.71
		Mean	10.21	9.88	9.82	9.97
Check*		60	10.58	10.62	10.66	10.61
LSD 0.05 (among lines)			0.77	0.77	0.77	0.16
LSD 0.05 (among cycles)			0.30	0.30	0.30	0.24

* Check hybrids are: B73 X Mo17 for B73 tester;
T165 X T167 for T165 tester;
T220 X T232 for T220 tester.

Table A2. Grain moisture (g kg^{-1}) of hybrid sets produced by crossing inbred lines from Tennessee Late Low-ear Synthetic cycle 0, and cycles 1, 3, and 4 of S_1 and testcross (TC) selection onto three testers, evaluated at Knoxville and Milan, Tennessee in 1991 and 1992.

Selection			Tester			
Method	Cycle	Line	B73	T165	T220	Mean
			g kg^{-1}			
None	0	1	201	206	205	204
		2	202	199	206	202
		3	206	212	206	208
		4	197	206	209	204
		5	187	198	201	195
		6	195	203	205	201
		7	200	204	206	203
		Mean	198	204	205	202
S_1	1	8	206	209	211	209
		9	193	205	208	202
		10	201	208	207	205
		11	199	204	199	201
		12	190	190	199	193
		13	189	197	199	195
		14	192	202	195	196
		Mean	196	202	203	200
S_1	3	23	191	204	209	201
		24	191	199	200	196
		25	195	198	197	197
		26	195	206	204	202
		27	193	202	199	198
		28	193	200	200	198
		29	187	196	200	194
		30	193	208	207	202
		Mean	192	202	202	199
S_1	4	38	189	199	200	196
		38	184	195	198	192
		40	176	189	195	187
		41	190	194	204	196
		42	190	206	201	199
		43	185	193	200	193
		44	189	200	201	197
		45	193	205	202	200
		46	196	206	207	203
		47	189	201	201	197
		48	191	201	200	197
		49	187	198	201	195
		Mean	188	199	201	196

(continued on next page)

Table A2 continued.

Selection			Tester			
Method	Cycle	Line	B73	T165	T220	Mean
			g kg^{-1}			
TC	1	15	201	212	209	207
		16	192	207	204	201
		17	192	205	203	200
		18	198	213	206	205
		19	192	201	199	197
		20	192	196	202	197
		21	195	208	207	203
		22	188	196	202	196
		Mean	194	205	204	201
TC	3	31	187	195	194	192
		32	195	198	200	198
		33	197	204	209	203
		34	198	200	203	201
		35	189	200	199	196
		36	191	203	200	198
		37	200	212	215	209
		Mean	194	202	203	200
TC	4	50	193	207	210	203
		51	189	193	199	194
		52	196	206	214	205
		53	192	201	210	201
		54	185	194	205	195
		55	186	196	207	196
		56	183	193	194	190
		57	190	192	205	196
		58	188	194	203	195
		59	185	201	203	196
		Mean	189	198	205	197
Check*		60	176	200	204	193
LSD 0.05 (among lines)			2	2	2	5
LSD 0.05 (among cycles)			3	3	3	3

* Check hybrids are: B73 X Mo17 for B73 tester;
T165 X T167 for T165 tester;
T220 X T232 for T220 tester.

Table A3. Erect plants (%), plant height (m), ear height (m), and days to mid-silk (d) of hybrids produced by crossing inbred lines from Tennessee Late Low-ear Synthetic cycle 0, and cycles 1, 3, and 4 of S1 and testcross selection (TC) onto three testers, evaluated at Knoxville and Milan, Tennessee in 1991 and 1992.

Selection			Variable			
Method	Cycle	Line	Erect Plants	Plant Height	Ear Height	Days to Mid-silk
			%	m	m	d
None	0	1	97.8	2.70	1.16	76
		2	97.8	2.72	1.22	75
		3	98.8	2.99	1.35	76
		4	98.4	2.82	1.24	79
		5	98.4	2.77	1.29	76
		6	98.9	2.57	1.07	75
		7	98.4	2.74	1.21	78
		Mean	98.4	2.76	1.22	76
S_1	1	8	96.8	2.67	1.23	74
		9	96.9	2.61	1.16	73
		10	95.1	2.79	1.34	76
		11	96.3	2.74	1.35	72
		12	96.9	2.77	1.26	77
		13	93.2	2.72	1.27	74
		14	97.6	2.76	1.24	76
		Mean	96.1	2.72	1.26	7
S_1	3	23	95.2	2.72	1.32	75
		24	96.3	2.78	1.37	74
		25	96.6	2.46	1.14	73
		26	96.3	2.67	1.25	74
		27	94.5	2.69	1.45	78
		28	97.0	2.54	1.11	73
		29	97.0	2.72	1.19	73
		30	91.6	2.96	1.41	75
		Mean	96.0	2.69	1.28	74
S_1	4	38	95.9	2.80	1.30	74
		39	92.6	2.74	1.27	75
		40	94.8	2.64	1.13	76
		41	97.5	2.76	1.27	73
		42	96.8	2.88	1.37	74
		43	96.2	2.61	1.16	75
		44	96.5	2.74	1.32	77
		45	92.5	2.68	1.24	77
		46	95.6	2.77	1.18	74
		47	95.6	2.46	1.02	76
		48	97.6	2.82	1.17	74
		49	97.7	2.70	1.16	74
		Mean	95.8	2.72	1.21	75

(continued on next page)

Table A3 continued.

Selection			Variable			
Method	Cycle	Line	Erect Plants	Plant Height	Ear Height	Days to Mid-silk
			%	m	m	d
TC	1	15	96.5	2.57	1.26	76
		16	98.5	2.95	1.36	78
		17	95.0	2.85	1.40	76
		18	99.4	2.75	1.25	76
		19	96.3	2.91	1.37	77
		20	97.4	2.72	1.33	75
		21	99.1	2.87	1.29	75
		22	97.9	2.78	1.34	75
		Mean	97.5	2.80	1.32	76
TC	3	31	95.0	2.54	1.20	76
		32	98.2	2.67	1.17	76
		33	99.0	2.69	1.41	74
		34	97.3	2.75	1.34	75
		35	98.0	2.87	1.40	77
		36	96.0	3.05	1.58	74
		37	96.1	2.53	1.14	73
		Mean	97.1	2.73	1.32	75
TC	4	50	98.2	2.81	1.33	74
		51	96.6	2.80	1.43	72
		52	99.7	2.82	1.22	74
		53	98.7	2.77	1.33	76
		54	98.1	2.53	1.21	73
		55	98.8	2.59	1.24	70
		56	98.6	2.54	1.08	75
		57	97.7	2.88	1.35	69
		58	96.6	2.67	1.26	76
		59	96.9	2.60	1.16	74
		Mean	98.0	2.70	1.26	73
	Check*	60	97.5	2.76	1.44	74
LSD 0.05 (line means)			3.0	.06	.05	7
LSD 0.05 (cycle means)			1.4	.02	.02	17

* Check hybrids are: B73 X Mo17 for B73 tester;
T165 X T167 for T165 tester;
T220 X T232 for T220 tester.

VITA

Wesley Neal Denton was born (March 24, 1968) in Cocke County, Tennessee. He was reared on a small dairy and beef cattle farm. He graduated from Cocke County High School in 1986. He attended Berea College, Berea, Kentucky, and received his Bachelor of Arts in Biology, Secondary Education in May, 1991. During Neal's undergraduate career, he married (August 19, 1989) Melissa G. Edlin. In July, 1991 he began his graduate career as a research assistant in the Department of Plant and Soil Science, University of Tennessee, Knoxville. Neal completed his Master's degree in August 1993 and moved to Lexington, Kentucky to begin a Ph.D. program in the Department of Agronomy at the University of Kentucky.