

RECURRENT SELECTION AND INBREEDING
FOR MATURITY IN MAIZE

Thesis for the Degree of Ph. D.
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Alain Francois Corcos
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RECURRENT COLLECTION AND IMBEDDING FOR VARIETY IN TIME

by

ALAIN FRANÇOIS CORCOS

AN ABSTRACT

Submitted to the School of Graduate Studies of Michigan
State University of Agriculture and Applied Science

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Approved

E. L. Roseman

The relative effectiveness of continuous inbreeding with selection compared to three cycles of recurrent selection for corn maturity as measured by silking date was studied in populations derived from two double-cross hybrids and four single-cross hybrids.

Direct comparison in the nursery between recurrent and inbred series was difficult due to inbreeding depression which masked the effectiveness of the breeding methods. Decline in fertility and vigor and delayed maturity were among the general effects of inbreeding and are referred to as inbreeding depression.

Inbreeding depression affected the inbred series more than the recurrent selection series. In recurrent selection only one plant in each row was selected in order to maintain inbreeding pressure at a minimum. With inbreeding and selection, plants were selected within and among rows.

To overcome the effects of inbreeding depression, it was suggested that the recurrent selections should be inbred (without selection pressure for maturity) and compared with the inbred selections.

Nursery results indicated that both methods had been very effective in dividing the original F_2 material into two maturity groups and that fixation of genes was rapid. Fixation was very rapid in a population from an early-x-early single cross (1a.153 x W25) and less rapid in a population from an early-x-late single cross (MS24A x L317).

In a corn breeding program, the ultimate objective is to utilize inbred lines in hybrid combination. Thus, evaluation of lines for maturity in testcrosses is important. Comparing inbred and recurrent lines in testcrosses is possibly the best method to overcome the inbreeding depression effects which masked the effectiveness of the breeding methods when compared in the nursery.

Testcross results indicated that the early inbred series were earlier than recurrent series in two of the three cases, and the late inbred series were later than the recurrent series. However, the differences between the two series were very small indicating that the two methods were equally effective. Very rapid fixation of genes and equal effectiveness of the two breeding methods indicated that few genes for maturity were involved.

Lines that were both earlier and later in maturity than the parental lines of the original crosses were obtained in both recurrent and inbred series.

In all the testcross experiments there was a wide range for yield among the selections within a maturity group, indicating that selection for combining ability could be effective within the maturity groups.

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INTRODUCTION

In northern areas of the United States, pre-mature killing frosts are a hazard to successful corn production. Corn is considered mature when the moisture content of the grain is about 35%. Losses in yield and quality result when frost occurs before maturity. The best way to avoid these losses is to grow early-maturing hybrids that will consistently mature ahead of frosts. Due to early frost in the North, these hybrids will usually yield as well as or better than late-maturing hybrids. Early-maturing hybrids are ready for harvest earlier in the fall when weather is usually more favorable for harvest and harvest losses are lower. Mature corn makes better quality feed than immature corn. Lower moisture content permits safer storage.

Developing inbred lines that transmit early maturity, high combining ability, and lodging resistance in double-cross hybrids is a major objective of corn breeding programs in the northern areas of the United States. Early-maturing inbred lines as a group generally possess a lower level of combining ability and lodging resistance than later-maturing inbreds. Inbreeding and selection in heterozygous populations of early X late parents is an effective method to improve combining ability and lodging resistance of early-maturing inbreds.

Inbreeding with selection is necessary in corn improvement to fix desirable characteristics in a line, so that it

will transmit these characteristics in hybrid combinations each time seed is produced. Rapid fixation of genes occurs with inbreeding. This seriously restricts the effectiveness of selection that can be practiced. Recurrent selection is a breeding scheme that offers some opportunity to minimize this disadvantage. Plants from a heterozygous source are evaluated for the desired attribute. Selfed seed of the small sample exhibiting superior performance is then planted ear-to-row. All possible intercrosses are then made by hand, or some type of bulk pollination may be used. The intercrossed population serves as the source material for the next cycle of selection. Opportunity is afforded for cumulative selection.

Four types of recurrent selection are recognized: (1) recurrent selection for characteristics that can be evaluated accurately phenotypically as described above without testcrosses required for (2), (3), and (4); (2) recurrent selection for general combining ability; (3) recurrent selection for specific combining ability; and (4) reciprocal recurrent selection using two heterozygous populations with reciprocal self-pollination and testcrossing, $A \times B$ and $B \times A$.

With corn, recurrent selection has been applied for oil content, tryptophan and lysine amino-acid content in grain, disease and insect resistance, popping expansion of popcorn, and specific combining ability (7, 18, 19, 20, 23). The method has been applied to sweet clover (12, 13, 14), to birdsfoot trefoil (21) and cotton (6).

Silking date is a good criterion of corn maturity, is easily determined, and can be evaluated phenotypically without testcrosses in a recurrent selection scheme. Selected plants

can be pollinated the same generation the characteristic is measured.

The objective of this study was to determine the relative effectiveness of continuous inbreeding with selection compared to three cycles of recurrent selection for corn maturity, as measured by silking date. Theoretically, three generations of selfing in a F_2 population should reduce heterozygosity to 6.25% while three cycles of recurrent selection should leave 35% heterozygosity.

This value 35% is obtained in the following manner:

The gametes produced by N monoecious individuals unite wholly at random. Therefore, the gametes have a chance $1/N$ of coming from the same individual and of $N-1/N$ of coming from different individuals. The loss in heterozygosity is then $1/2N$ or, since ten plants were used in this study, $1/20$ per generation. After three cycles of recurrent selection, it would be possible to continue a selection program.

REVIEW OF LITERATURE

Early maturity in corn is frequently dominant in crosses between early and late inbred lines (5). The F_1 hybrid was earlier than either of the two parental inbred lines which were approximately equal in maturity (28). Jones (15) investigated the inheritance of corn maturity in six crosses of early-late inbred lines. Either complete phenotypic dominance or slight heterosis for earliness was indicated in all crosses. Complete genic dominance for early silking, partial-to-complete genic dominance for lower ear moisture at a uniform time from planting, and variations from none to complete genic dominance for lower ear moisture fifty days after silking were indicated for the different crosses.

Jones (15) was not able to conclude whether gene action was following either arithmetic or geometric schemes. He suggested that both types of gene action might be involved. Using the formula for calculating gene number given to Burton by Wright (1,2), the calculated number of genes was 5 to 19 for silking date, 2 to 11 for moisture content of ears harvested at a uniform period from planting, and 1 to 54 for moisture content of ears harvested fifty days after silking depending on the particular cross involved. Yang (28), in a study of the nature of genes controlling hybrid vigor as they affect silking time in corn, concluded that there were probably 2 or 3 pairs of genes involved. These genes were independently inherited with effects of comparable magnitude.

Heritability values which denote additive genetic variance in per cent of the total variance are useful to the plant breeder because they indicate the extent to which desired characters are transmitted from superior plants to their progenies. The additive genetic variance reflects the degree to which the progeny are likely to resemble the parents. Jones (15) calculated heritability for silking date and moisture content according to Wright's formula (27); which includes both additive and non-additive variance:

$$\frac{\text{Variance } F_2 - \text{Variance } F_1}{\text{Variance } F_2}$$

Heritability values ranged from 11 to 41 per cent for silking date, 36 to 58 per cent for moisture content of ears harvested at a uniform period from planting, and 22 to 83 per cent for moisture content of ears harvested fifty days after silking for the various crosses studied.

Warner (28) obtained a heritability value of 32 per cent using the formula:

$$\text{Heritability} = \frac{(\frac{1}{2}) D}{VF_2} \quad \text{where}$$

$(\frac{1}{2}) D$ = the additive genetic component of variance of F_2 and

VF_2 = total within variance of F_2

and $(\frac{1}{2}) D = 2(VF_2) - (VB_1 + VB_2)$ where

VB_1 and VB_2 are the total within variance of the backcrosses of the F_1 to the respective parents.

The general procedure employed in recurrent selection, which has been effective in improving agronomic characters in corn, cotton and forage crops, was an outgrowth of the suggestion made by Jenkins in 1935 (9) to select among early generation inbreds on the basis of general combining ability. The essential steps were outlined by him in 1940 (10):

(1) the isolation of one generation selfed lines; (2) testing of these lines in top crosses for yield and other characters to determine the relative endowments with respect to genes affecting these characters; and (3) intercrossing of the better endowed selfed lines to produce a synthetic variety; (4) repetition of the above process at intervals after each synthetic variety has had a generation or two of mixing, possibly with inclusion of lines from unrelated sources.

Sprague and Brimhall (23) showed that one cycle of recurrent selection for yielding ability resulted in a mean increase of 7 bushels per acre relative to the tester. Lonnquist (18) produced a high and low yield synthetic, using S_1 lines from Krug yellow dent, an open pollinated variety. After two generations of random mating, S_0 plants were selfed and crossed to (Wf9 x M14) as the tester. The mean of the tester crosses from the high yielding synthetic was 2.7 bushels less than the tester and 6.4 bushels more than the tester crosses of the S_1 lines used to form the synthetic. Tester crosses from the low yielding synthetic averaged 14.5 bushels less than tester. Thus after one cycle, two distinct groups with respect to combining ability had been separated from the original Krug population. McGill and Lonnquist (20) crossed

S₀ plants from Krug and three synthetic varieties developed from Krug by two cycles of recurrent selection to Wf9 x M14 as a tester. They concluded that recurrent selection had been effective in modifying combining ability and that the high yielding synthetics were better sources of new lines than Krug. In a more recent paper (19), they showed that advanced generations of the synthetics maintained their improved productivity through normal mass selection procedures. Visual selection of better plants from synthetic 2 to synthetic 4 resulted in a slight improvement in yield; but the plants were later in maturity.

A modification of recurrent selection for combining ability was suggested by Hull (7), who advanced reasons for believing that genes conditioning corn yield exhibit overdominance. Under this assumption the heterozygote is superior to the best homozygote at loci at which overdominance is operative. Hull's method, called recurrent selection for specific combining ability, involved the use of a stable inbred line as the tester. Sprague (24) reported that "unpublished data indicate that in each of two open pollinated varieties, using inbred 19 as tester, yield increases of approximately 5 bushels per acre were obtained with a single cycle of selection."

Comstock, Robinson, and Harvey (3) proposed a breeding procedure to make maximum use of both general and specific combining ability regardless of overdominance. They designated

their method "reciprocal recurrent selection". Two unrelated stocks are used as source material. S_0 plants of a source A are self-pollinated and crossed to plants of source B as the tester. Selection is based upon experimental comparisons of testcross progenies. Selected plants are intercrossed the third year by use of selfed seed from S_0 plants. Another cycle of selfing and crossing is initiated the fourth year. Plants from source B are tested against plants from source A as the tester in the same way. From theoretical considerations they concluded that "reciprocal recurrent selection" would be superior to selection for general combining ability for loci where overdominance existed and was superior to selection for specific combining ability for loci where partial dominance existed.

Sprague and Brimhall (23) found that recurrent selection for oil percentage in the corn kernel was 2.6 times more efficient than selection during inbreeding. Considerable genetic variability remained in the recurrent series, while genetic variability was exhausted after five generations of inbreeding.

Frey et al. (8) reported results from one cycle of recurrent selection for low zein and high tryptophan in two populations of intercrosses among F_3 progenies of Hy x I 198. One set of F_3 progenies had been selected for low ratio of zein to total protein, and the second set had been selected for high tryptophan content of the grain. No improvement

was realized in the population selected for low zein-protein ratio. An increase of 12.7% of the mean of the F_2 population was obtained in the population selected for high tryptophan percentage.

Jenkins et al. (11) reported on experiments designed to measure the efficiency of recurrent selection in concentrating genes for resistance to leaf blight of corn caused by Helminthosporium turcicum. Nine single-crosses between resistant and susceptible lines were used. The materials used were two-generation-backcrosses to the susceptible parent. Three cycles of recurrent selection were completed for each of the nine progeny groups, providing a total of 27 comparisons. In 24 of these comparisons the differences between successive cycles were positive indicating an increase in resistance; in 19 out of 24, these differences were significant. In three cases the differences were negative, indicating an increase in susceptibility. Jenkins concluded that two cycles of recurrent selection would be warranted in most of the groups studied. The effectiveness of the third cycle appeared to be related to progress in the previous cycles. If the gain has been substantial, little progress was achieved.

Henderson (6) found that recurrent selection in cotton was effective for increasing the frequency of superior gene combinations for length and strength of fiber, weight of seed, and weight of fiber per amount of surface area on the

seed considerably above that found in the F_2 . After one cycle the frequency of plants above the average was 23 per cent. He remarked: ". . . the fifteen intercrosses differed greatly in relative frequency, the lowest progeny having no superior plants, while the highest intercross progeny had 43 per cent of plants above the parent average in all characteristics."

Johnson reported results of one cycle (12) and two cycles (13) of recurrent selection for general combining ability in sweet clover. In both the first and second cycles of the population means slightly exceeded the means of the 10 plants whose S_1 progenies were used to produce the next cycle. The open pollinated progeny test mean of the 10 selected Madrid plants was 116% of Madrid and the first-cycle population was 121% of Madrid. The mean of the 10 plants chosen from the first cycle as parental lines for the second cycle was 146% and the second-cycle population mean was 152% of Madrid. Four successive cycles of phenotypic recurrent selection of biennial sweet clover for first year growth were effective in improving uniformity of growth type and plant vigor according to Johnson and El Banna (14) who measured the change per cycle in terms of variance and population means. The changes were smaller for a plant characteristic with low heritability value such as plant weight than for a plant characteristic with high heritability value such as growth habit. The mean plant yield in the highest vigor group was

increased 88% over the original population by repeatedly choosing and recombining ten plants in the upper portion of the Syn. 1 population.

Peacock and Wilsie (21) reported that one cycle of recurrent selection for shattering resistance reduced seed pod dehiscence of birdsfoot trefoil 17 per cent. The variability among the synthetics produced appeared to be great enough to allow further progress in shattering resistance through additional cycles of recurrent selection.

MATERIALS AND METHODS

F₂ populations of 500 plants each for two double-cross hybrids and four single-cross hybrids were planted in 1954. The two double-crosses were Michigan 51B (W9 x M13) (Ia 153 x W25) and Michigan 20D (Oh 51A x M14) (Oh 40B x W10). The four parental lines for Michigan 51B were classified as relatively early-maturing lines. The parental inbreds Oh 51A and M14 for Michigan 20D are classified as medium in maturity while Oh 40B and W10 are classified as relatively late in maturity. The single-cross hybrids were: one single-cross of two early inbreds (Ia 153 x W25) and three early x late single-crosses, (K53 x 38-11), (MS24A x 38-11), and (MS24A x L317).

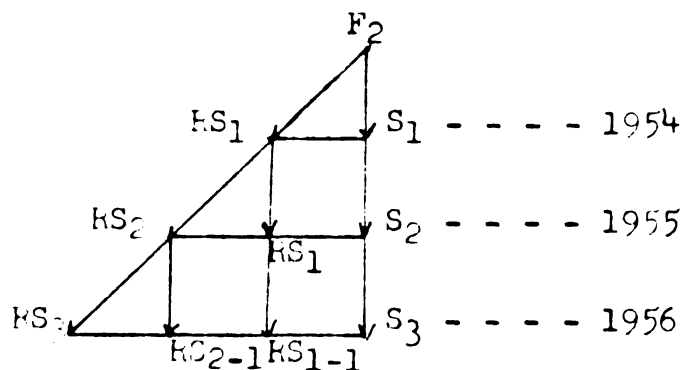
The 20 earliest silking plants were selected in each of the six populations. Ten of these were chosen at random and self-pollinated for the inbreeding series. Equal amounts of pollen from the other ten were bulked and used to pollinate these plants for the recurrent selection series.

The 20 latest silking plants of each population were selected and divided into two groups of ten plants each. One group of 10 was self-pollinated for the late-maturing inbreeding series. The other group of 10 plants was inter-crossed by bulking equal amounts of pollen and constituted the late-maturing recurrent selection series.

For each population in 1955, 50 seeds of each selected ear were planted ear-to-row, making a recurrent selected and an inbred series of twenty rows each. In the inbreeding series, the ten earliest silking plants and the ten latest silking plants were again self-pollinated. The selected plants in five of the populations were crossed to the single cross (Ch 43 x A158) as a tester for combining ability. In the recurrent selected block the earliest plant or two in each row was selected and the pollen of ten of these plants was bulked and applied to the silks of these ten plants. The same procedure was followed for the late silking selections.

Due to heterotic effects, the recurrent selected series would be expected to be earlier than the inbred series. To compare inbreeding more effectively with recurrent selection, 10 of the early silking plants and 10 of the late silking plants were selfed in each recurrent selected block. All plants of the recurrent selection series were crossed to the tester (Ch 43 x A158).

The same procedures were followed in 1956 to provide 9 breeding groups as illustrated below for each population.



- (RS)₁ = Recurrent selected one cycle
- (RS)₂ = Recurrent selected two cycles
- (RS)₃ = Recurrent selected three cycles
- (S)₁ = Inbred with selection one generation
- (S)₂ = Inbred with selection two generations
- (S)₃ = Inbred with selection three generations
- RS-1 = Recurrent selected one cycle, then inbred
with selection one generation
- RS-1-1 = Recurrent selected one cycle, then inbred
with selection two generations
- (RS)₂-1 = Recurrent selected two cycles, then inbred
with selection one generation

These nine breeding groups for each of the six populations were evaluated for maturity in 1957 in an experiment with two replications of 15 plants for each ear-to-row. In each population, the early and late maturity groups were planted in separate blocks. Within each maturity group, each of the nine breeding groups consisted of 10 ear-to-rows of 15 plants in each replication. Some poor stands were obtained in the late maturity groups of the (1a 153 x W25) population.

Silking date and moisture content of ears at harvest were determined for each plant in two populations, Michigan 51B and (H53 x 38-11). For the other four populations, only silking date for each plant was recorded. Silking date was recorded when the silk was exposed about $\frac{1}{2}$ inch. Average days from planting to silking, percentage of moisture content, variance and covariance were calculated for each row.

Analyses of variance for each population were made for each maturity block. Degrees of freedom for each block were as follows:

<u>Source of Variation</u>	<u>Degrees of Freedom</u>
Total	179
Replications	1
Strains	89
Groups	8
Within	9
Interaction	72
Error	89

Degrees of freedom for each breeding group:

<u>Source of Variation</u>	<u>Degrees of Freedom</u>
Total	299
Between	9
Within (estimated from row variance)	290
Parents	n

The ultimate objective in a corn breeding program is to put inbred lines into hybrid combinations. Therefore it is necessary to evaluate the lines for yield and maturity as testcrosses. S₁ and HS₁ selections of four populations were testcrossed to (Oh43 x A158). These testcrosses were evaluated for yield and maturity in four experiments in 1955 as follows:

Table 1. Experiment number, population, and design of the 1955 testcross experiments.

<u>Experiment Number</u>	<u>Population</u>	<u>Design</u>
55-902	(MS24A x 38-11)	6 x 6 simple lattice 4 replicates
55-903	(R53 x 38-11)	6 x 7 rectangular lattice, 4 replicates
55-904	(MS24A x L317)	5 x 6 rectangular lattice, 4 replicates
55-905	(Michigan 20D)	5 x 5 simple lattice 4 replicates

The date when about half the plants had silked in each plot was recorded.

S₂, HS₂ and HS-1 selections of 5 populations were evaluated in testcrosses to (Oh43 x A158) in 1956 as follows:

Table 2. Experiment number, population, and design of the 1956 testcross experiments.

<u>Experiment Number</u>	<u>Population</u>	<u>Design</u>
56-901	Michigan 51B	8 x 8 simple lattice 4 replicates
56-902	Michigan 20D	7 x 7 simple lattice 4 replicates
56-903	R53 x 38-11)	8 x 8 simple lattice 4 replicates

Table 2. Continued

<u>Experiment Number</u>	<u>Population</u>	<u>Design</u>
56-904	(MS24A x L317)	7 x 7 simple lattice 4 replicates
56-905	(MS24A x 38-11)	8 x 8 simple lattice 4 replicates

S₃, HS₃, HS-1-1 and HS₂-1 selections from the third cycle of breeding were evaluated as testcrosses with (Ch43 x A158) in three experiments in 1957 (Table 3). Silking date was recorded for each plant.

Table 3. Experiment number, population, and design of the 1957 testcross experiments.

<u>Experiment Number</u>	<u>Population</u>	<u>Design</u>
57-911	(H53 x 38-11)	10 x 10 triple lattice 3 replicates
57-912	Michigan 51B	10 x 10 triple lattice 3 replicates
57-913	(MS24A x L317)	9 x 9 triple lattice 3 replicates

RESULTS NURSERY RESULTS

Days from Planting to Silking

General Considerations

The first cycle of breeding by either method was effective in dividing the original F_2 material into two maturity groups (Table 4). Although some strains from the early maturity groups were as late as some strains from the late maturity groups, no early-maturity breeding group mean was greater than any late maturity breeding group mean. The F_2 value for each population was intermediate between early and late maturity series.

The greatest progress towards early and late maturity seemed to have been made with the first cycle of breeding as shown in figures 1, 2, 3, 4, 5, 6, Appendix, where values for parental lines F_1 , F_2 , and breeding groups have been graphed.

Differences among breeding groups are highly significant in all cases (Table 5) indicating a difference in progress from the different breeding methods. No significant difference within value means indicated that genetic variance was exhausted after three cycles of breeding.

Comparison between breeding groups in the early maturity series

The mean values of each breeding group are ranked in Table 6. Values within a bracket are not significantly different according to Duncan's multiple range test (4).

Since the objective was to compare the effectiveness of continuous inbreeding (selfing) with selection and the

Table 4. Range and mean days from planting to silking of nine breeding groups from six populations.

	Early Maturity		Late Maturity	
	Range	Mean	Range	Mean
<u>Michigan 51B</u>				
RS	59.0-62.5 = 3.5	60.4	62.5-72.0 = 9.5	66.5
S	61.5-67.0 = 5.5	63.8	68.0-74.0 = 6.0	70.6
RS2	58.0-65.0 = 7.0	60.6	67.0-71.5 = 4.5	68.9
RS-1	59.5-66.5 = 7.0	62.7	65.0-77.5 = 12.5	72.1
S2	60.0-68.5 = 8.5	62.7	71.0-84.0 = 13.0	76.6
RS3	58.0-64.0 = 6.0	60.2	64.5-76.0 = 11.5	71.1
RS2-1	60.5-64.0 = 3.5	61.7	69.0-78.0 = 9.0	73.8
RS-1-1	60.5-69.0 = 8.5	62.6	69.0-77.0 = 8.0	74.2
S3	60.0-65.5 = 5.5	63.0	73.5-86.0 = 12.5	81.5
L.S.D.	1. strains-----3.4		-----7.0	
	2. groups-----1.6		-----4.9	
Michigan 51B F ₁ = 63.0				
F ₂ = 67.0				
<u>K53. x 28-11</u>				
	Range	Mean	Range	Mean
RS	64.5-69.0 = 4.5	66.6	76.0-82.0 = 6.0	79.2
S	63.5-70.5 = 7.0	68.2	73.2-83.0 = 9.8	78.2
RS2	60.5-66.0 = 5.5	64.1	69.5-81.5 = 12.0	77.8
RS-1	63.5-67.5 = 4.0	65.8	78.0-88.0 = 10.0	84.3
S2	64.0-70.0 = 6.0	67.3	80.0-90.5 = 10.5	84.3
RS3	60.5-65.5 = 5.0	63.5	77.5-87.0 = 9.5	80.6
RS2-1	62.5-69.0 = 6.5	65.5	77.0-86.5 = 9.5	82.4
RS-1-1	63.0-72.5 = 9.5	67.0	85.0-90.0 = 5.0	87.1
S3	64.0-67.5 = 3.5	65.2	73.5-86.5 = 13.0	81.6
L.S.D.	1. strains-----4.4		-----7.0	
	2. groups-----1.7		-----3.5	

Table 4. (Continued)

R53 x 38-11		F ₁ = 72.0	R53 = 66.0	
		F ₂ = 74.0	38-11 = 76.0	
		Early Maturity	Late Maturity	
<u>Michigan 20D</u>				
RS	Range	Mean	Range	Mean
S	68.0-73.5	70.3	76.0-80.0 = 4.0	78.2
RS2-1	70.0-76.0	73.6	77.5-89.0 = 11.5	82.6
S2	67.5-71.5	69.6	77.5-84.5 = 7.0	80.0
RS3	68.5-75.0	71.2	83.5-96.0 = 12.5	88.8
RS2-1	69.5-74.0	71.4	76.5-95.0 = 4.5	80.3
RS-1-1	64.0-69.5	67.2	82.5-88.5 = 6.0	85.0
S3	65.5-70.5	68.7	81.5-96.0 = 14.5	89.0
	67.0-75.0	70.1	89.0-98.5 = 9.5	94.0
	67.0-72.5	70.3	89.0-97.1 = 8.1	92.2
		70.3		86.7
L.S.D.	1. strains-----4.5		-----5.3	
	2. groups	-----3.2		-----3.6
Michigan 20D	F ₁ = 71.0			
	F ₂ = 72.0			
			Parental lines	
			M14 = 72.0	
			51A = 79.0	
			Ch.40B = 86.0	
			W10 = 92.0	
<u>MS24A x 38-11</u>				
RS	Range	Mean	Range	Mean
S	70.0-75.5	73.0	81.5-85.5 = 5.5	82.2
RS2	69.0-73.5	72.2	78.5-82.0 = 3.5	80.0
FC-1	67.0-70.0	66.3	80.5-83.5 = 3.0	81.5
	69.0-73.5	71.6	81.5-88.5 = 7.0	83.3

Table 4. (Continued)

<u>MS24A x 38-11</u>	Early Maturity		Late Maturity	
	<u>Range</u>	<u>Mean</u>	<u>Range</u>	<u>Mean</u>
S ₂	67.5-74.5	71.1	83.0-94.0 =	11.0
RS ₃	67.0-73.0	69.9	84.5-89.5 =	5.0
RS ₂₋₁	67.5-73.0	72.2	84.5-93.5 =	9.0
RS-1-1	62.0-72.5	67.3	84.0-92.5 =	8.5
S ₃	68.0-72.0	70.1	81.0-94.0 =	13.0
		<u>70.4</u>		<u>35.1</u>
L.S.D.	1. strains-----3.4	-----2.0	-----5.0	-----2.4
	2. groups			
Parental lines				
MS24A x 38-11	F ₁ = 78.0		MS24A =	69.5
	F ₂ = 77.0		38-11 =	77.2
<u>Ia.153 x W25</u>	<u>Range</u>	<u>Mean</u>	<u>Range</u>	<u>Mean</u>
RS	61.0-65.0	62.8	68.5-75.0 =	6.5
S	60.5-64.5	64.5	69.0-77.5 =	8.5
RS ₂	61.0-64.0	62.3	72.0-77.5 =	5.5
RS-1	63.0-67.5	64.5	73.5-80.0 =	6.5
S ₂	62.0-68.0	64.7	69.5-76.0 =	6.5
RS ₃	59.0-63.5	61.2	72.0-78.5 =	6.5
RS ₂₋₁	60.0-62.5	62.8	74.5-84.5 =	12.0
RS-1-1	60.0-67.0	63.7	74.5-79.0 =	4.5
S ₃	63.0-68.5	<u>65.1</u>	74.5-76.5 =	2.0
		<u>63.5</u>		<u>75.0</u>
L.S.D.	1. strains-----3.3	-----1.3	-----7.2	-----6.0
	2. groups			

Table 4. (Continued)

Ia. 153 x W25		F ₁ = 64.0	Parental lines		Ia.153 = 75.0
		F ₂ = 69.0			W25 = 76.0
NS24A x L317		Early Maturity	Late Maturity		
		Range		Range	Mean
RS	71.5-77.0	= 5.5	76.0-83.0	= 7.0	79.1
S	73.5-78.0	= 4.5	79.5-90.5	= 11.0	85.6
RS2	70.0-74.5	= 4.5	77.0-86.5	= 9.5	82.3
RS-1	71.6-75.0	= 3.4	71.0-81.0	= 10.0	76.6
S ₁	68.5-76.0	= 7.5	83.0-93.0	= 10.0	87.4
RS3	68.0-73.0	= 5.0	81.5-87.5	= 6.5	84.5
RS2-1	75.0-78.0	= 3.0	82.5-89.0	= 6.5	85.8
RS-1-1	67.5-78.5	= 11.0	84.5-91.0	= 6.5	87.8
S ₃	65.5-75.0	= 8.5	89.0-94.0	= 5.0	92.2
					<u>84.0</u>
L.S.D.	1. strains-----	5.2			
	2. br. groups	-----3.7			
					-----8.4
NS24A x L317		F ₁ = 77.5	Parental lines		NS24A = 69.5
		F ₂ = 81.0			L317 = 97.0

Table 5. Analyses of variance for days from planting to silking in different breeding groups from six different crosses.

Source	D.F.	Early Breeding Groups		Late Breeding Groups	
		S.S.	M.S.	S.S.	M.S.
<u>Michigan 51B</u>					
Total	179	1137		6037	
Repl.	1	0	0.0	14	14.0
Strains	89	875	9.8**	4294	58.3**
Breed. groups	8				
Within	9				
276			34.6**	3297	412.9*
Interaction	72				
553			5.1	420	44.6
Error	89	262	2.9	787	10.9
				1099	12.3
<u>Michigan 20D</u>					
Total	179	1508		7728	
Repl.	1	8	8.0	36	36.0
Strains	89	1039	11.6**	7051	79.2**
Breed. groups	8				
Within	9				
508			63.5**	4858	619.7**
Interaction	72				
178			19.7	221	24.5
353			4.9	1872	26.0**
Error	89	421	5.1	641	7.2
<u>E53 x 38-11</u>					
Total	179	1405		4137	
Repl.	1	14	14.0	43	43.0
Strains	89	977	10.9**	2984	33.5**
Breed. groups	8				
Within	9				
370			42.2**	1593	189.2**
Interaction	72				
49			5.4	219	24.3
558			7.7*	1172	16.2
Error	89	414	4.6	1110	12.4

* Significant at the 5 percent level.

** Significant at the 1 percent level.

Table 5. (Continued):

Source	Early Breeding Groups		Late Breeding Groups	
	D.F.	S.S.	D.F.	S.S.
<u>MS24A x 38-11</u>				
Total	179	1405		3248
Repl.	1	11	11.0	8
Strains	89	1135	12.7**	2658
Breed. Groups	8			1580
Within	9		65.1**	207
Interaction	72		8.1	871
Error	89	259	7.5**	582
			2.9	
<u>MS24A x L317</u>				
Total	179	2028		6473
Repl.	1	28	28.0	350
Strains	89	1386	15.5**	4578
Breed. Groups	8			3549
Within	9		83.5**	1214
Interaction	72		25.5	185
Error	89	614	6.7	1545
			6.9	
<u>1a.153 x W25</u>				
Total	179	960		3247
Repl.	1	5	5.0	40
Strains	89	712	8.0**	2036
Breed. groups	8			1248
Within	9		35.1**	619
Interaction	72		3.4	169
Error	89	243	5.5**	1171
			2.7	
				40.0
				22.8**
				156.0**
				68.7
				2.3
				13.1

* Significant at the 5 per cent level.

** Significant at the 1 per cent level.

effectiveness of recurrent selection, breeding groups within a cycle can be compared (Table 6a).

In 9 of 18 cases, recurrent selected breeding groups were earlier than the inbred groups. After three cycles of breeding, in 2 of 6 cases, the recurrent selected groups were earlier than the inbred groups. However, the differences between the recurrent selected and inbred groups were small. These results indicate that there is very little difference between the two breeding methods.

Table 6A. Comparison for early maturity between inbred and recurrent selected groups within a breeding cycle.

<u>Population</u>	<u>First Cycle</u>		<u>Second Cycle</u>		<u>Third Cycle</u>	
Michigan 51B	S > RS		S ₂ > RS ₂		S ₃ > RS ₃	
	63.8	60.4	62.7	60.6	63.0	60.2
Michigan 20D	S > RS		S ₂ = RS ₂		S ₃ = RS ₃	
	73.6	70.3	71.4	69.6	70.3	67.2
RS3 x 38-11	S = RS		S ₂ > RS ₂		S ₃ = RS ₃	
	68.2	66.6	67.3	64.1	65.2	63.5
MS24A x 38-11	S = RS		S ₂ > RS ₂		S ₃ = RS ₃	
	72.2	73.0	71.1	68.3	70.2	68.9
1a.153 x W25	S > RS		S ₂ > RS ₂		S ₃ > RS ₃	
	64.5	62.8	64.7	62.3	64.7	61.2
MS24A x L317	S = RS		S ₂ < RS ₂		S ₃ = RS ₃	
	75.0	73.0	71.7	76.2	70.5	68.8

1. > later than
2. = not later than

Table 6. Ranked mean days to silking for the nine breeding groups in the early maturity series from six crosses.

Michigan 51B

RS ₃	RS	RS ₂	RS ₂ -1	RS-1-1	RS-1	S ₂	S ₃	S	F ₂ mean
60.2	60.4	60.6	61.7	62.6	62.7	62.7	63.0	62.8	67.0

RS3 x 38-11

RS ₃	RS ₂	S ₃	RS ₂ -1	RS-1	RS	RS-1-1	S ₂	S	F ₂ mean
63.5	64.1	65.2	65.5	65.8	66.6	67.0	67.3	68.2	74.0

MS24A x 38-11

RS-1-1	RS ₂	RS ₃	RS ₂ -1	S ₃	S ₂	RS-1	S	RS	F ₂ mean
67.3	68.3	69.9	70.2	70.2	71.1	71.6	72.2	73.0	77.0

Table 6. (Continued)

One of the theoretical advantages of recurrent selection over selfing with selection is the slower decrease in heterozygosity from one cycle to the next. A study of the loss of variability with each cycle and of expected and actual gains is important. The form of analysis of variance for each breeding group is given in Table 7. The within variance was estimated from the average row variance which was obtained according to the following formula:

$$\frac{n_1 s_1^2 + \dots + n_{10} s_{10}^2}{N-10}$$

where n and s^2 are respectively the number of plants and the variance of the row, N the number of plants in the 10 rows.

Table 7. Form of analysis of variance for each breeding group within each maturity group.

<u>Source</u>	<u>D.F.</u>	<u>Expected mean square</u>
Total	299	
Among	9	
Within (estimated from row variance)	290	$\sigma^2 + \sigma_e^2$ within
Parents	n	σ^2

The expected gains were calculated after Lerner (16). Selection differentials were expressed in standard deviations ($\bar{i}$) and in absolute units of measurements (i). Expected gains, Δg , from a generation of selection can be computed. The gains are equal to the product of heritability (h_2) and the selection differential expressed in actual units (i). The heritability

values were calculated in the following manner:

The coefficient of heritability for the F_2 population was calculated according to the following formula:

$$H_2 = \frac{\text{Variance } F_2 - \text{Variance } F_1}{\text{Variance } F_2},$$

which includes the non-additive portion of the genetic variance.

The coefficients of heritability for the various breeding groups were calculated from separate analyses of variance (Table 7).

$$H_2 = \frac{\sigma_e^2 \text{ within}}{\sigma^2 + \sigma_e^2 \text{ within}}$$

In the three early-x-late crosses (MS24A x 38-11), (MS24A x L317), and (R53 x 38-11) (Table 7B) the variances for the late maturing parents were greater than the variances for the early maturing parents. This indicates that the late inbred lines were influenced more by the environment than early inbred lines. Thus, the variance of the early inbred parents was taken as an estimate of environmental variance in the early-maturing groups. Likewise, the variance of the late inbred parent was taken as an estimate of the environmental variance in the late maturing groups. In the cases of the other crosses, Michigan 51B, Michigan 20D, and Ia. 153 x W25, the average variance for the parental lines was used as an estimation of the environmental variance.

Table 7A. Within and among variances in the inbred and recurrent series from the early and late maturity groups.

<u>NS24A x 38-11</u>						
	<u>Early Maturity</u>			<u>Late Maturity</u>		
	<u>Within</u>	<u>Among</u>	<u>F.</u>	<u>Within</u>	<u>Among</u>	<u>F.</u>
RS	13.0	5.8	2.2	26.6	7.8	4.6
RS ₂	14.4	2.1	6.8	23.0	3.6	6.3
RS ₃	15.0	5.4	2.7	29.5	0.5	59.0
S	8.8	5.1	1.7	21.7	7.9	2.6
S ₂	9.4	9.6	0.9	34.3	24.2	1.3
S ₃	12.7	4.4	2.8	26.3	24.4	1.0
<u>1a.153 x W25</u>						
RS	4.1	3.7	1.1	13.2	5.9	2.4
RS ₂	8.5	1.4	6.0	16.4	3.6	4.5
RS ₃	5.7	3.0	1.9	16.2	8.0	2.0
S	7.8	7.9	0.9	14.5	20.2	0.7
S ₂	6.8	5.1	1.2	23.9	15.5	1.6
S ₃	5.5	8.5	0.6	15.5	0.0	-
<u>R53 x 38-11</u>						
RS	15.4	5.1	3.0	31.7	10.7	2.9
RS ₂	17.7	3.2	5.5	29.2	21.3	1.3
RS ₃	16.7	6.2	2.7	31.2	16.7	2.4
S	15.3	13.0	1.1	27.2	19.6	1.3
S ₂	12.6	8.4	1.5	27.9	20.0	1.4
S ₃	20.4	3.6	5.6	45.4	37.3	1.2

Table 7A. (Continued)

Michigan 51B

	<u>Early Maturity</u>		<u>Late Maturity</u>	
	<u>Within</u>	<u>Average</u>	<u>Within</u>	<u>Average</u>
RS	19.2	4.2	19.7	14.3
RS2	26.0	7.2	18.5	6.3
RS3	24.0	6.6	29.4	22.5
S	10.5	8.3	24.3	6.6
S2	7.8	9.0	43.6	26.4
S3	13.5	7.3	36.5	38.2

MS24A x L317

RS	13.6	6.6	22.7	25.4	0.9
RS2	15.7	4.6	38.1	38.2	0.7
RS3	14.3	7.7	11.4	30.6	0.3
S	17.2	5.2	24.8	26.8	0.9
S2	15.5	8.9	25.2	22.6	1.1
S3	16.3	11.6	10.7	15.7	0.7

Michigan 20D

RS	17.0	23.4	25.0	3.6	6.9
RS2	15.7	3.3	26.6	3.9	3.9
RS3	13.0	7.4	30.4	5.9	5.7
S	20.1	5.2	33.1	35.8	0.9
S2	16.4	4.6	27.3	22.4	0.3
S3	11.6	5.6	19.9	24.1	0.3

Table 7B. Average row variance of the inbred and recurrent series from the early and late maturing groups.

<u>MS24A x 38-11</u>		<u>Ia. 153 x W25</u>	
	<u>Early</u>	<u>Late</u>	
RS	13.0	36.6	4.1
RS ₂	14.4	23.0	8.5
RS ₃	15.0	29.5	5.7
S	8.8	21.7	7.8
S ₂	9.4	24.3	6.8
S ₃	12.7	26.3	5.5
MS24A.....	12.0		Ia.153.....16.3
38-11.....	27.4		W25.....16.2
F ₁	10.5		F ₁18.3
F ₂	29.5		F ₂43.3
<u>R53 x 38-11</u>		<u>MS24A x L317</u>	
RS	15.4	31.7	13.6
RS ₂	17.7	29.2	15.7
RS ₃	16.7	31.2	14.3
S	15.3	27.2	17.2
S ₂	12.6	27.9	15.5
S ₃	20.4	45.4	16.3
R53.....	13.3		MS24A.....12.0
38-11.....	27.4		L317.....14.0
F ₁	15.2		F ₁4.0
F ₂	24.5		F ₂29.8
<u>Michigan 51B</u>		<u>Michigan 20D</u>	
RS	19.2	19.6	17.0
RS ₂	26.0	18.5	15.7
RS ₃	24.0	29.4	13.0
S	10.5	8.3	20.1
S ₂	7.8	9.0	16.4
S ₃	13.5	7.3	11.6
Ia. 153.....	16.3		Oh.40B.....22.2
W25.....	16.2		Oh.51A.....44.4
W9.....	8.2		M14.....36.2
M13.....	6.5		W10.....22.9
F ₁	4.0		F ₁5.2
F ₂	12.85		F ₂40.1

Table 8. Selection differential, heritability (h^2), expected (ih^2) and actual gains in the early maturity series of six populations.

<u>Michigan 51B</u>					
	$\bar{I}$	$\bar{i}$	h^2	ih^2	<u>actual gain</u>
F ₂	1.6	10.1	75%	7.5	6.6
RS	0.3	1.2	38%	0.4	-0.2
RS ₂	0.9	0.3	54%	2.3	0.4
				<u>10.2</u>	<u>6.8</u>
F ₂	1.6	10.1	75%	7.5	3.2
S	1.5	4.8	0%	0.0	1.1
S ₂	1.8	5.0	0%	0.0	-0.3
				<u>7.5</u>	<u>4.0</u>
<u>Michigan 20D</u>					
F ₂	1.0	5.2	75%	3.9	1.7
RS	2.0	8.2	0%	0.0	0.7
RS ₂	1.7	6.4	0%	0.0	2.4
				<u>3.9</u>	<u>4.8</u>
F ₂	1.0	5.2	76%	3.9	-1.6
S	2.5	11.2	0%	0.0	0.6
S ₂	1.6	6.5	0%	0.0	1.7
				<u>3.9</u>	<u>0.7</u>
<u>NS24A x L317</u>					
F ₂	2.0	13.1	75%	9.8	8.0
RS	1.6	4.1	4%	0.16	-3.2
RS ₂	1.8	2.4	17%	0.43	2.4
				<u>10.39</u>	<u>11.2</u>
F ₂	2.0	13.1	75%	9.8	6.0
S	1.9	5.6	28%	1.6	3.3*
S ₂	1.6	6.2	14%	1.0	1.2*
				<u>12.4</u>	<u>10.5</u>

* Significantly different from zero

Table 8. (Continued)

Ia.153 x W25

	<u>I</u>	<u>I</u>	<u>h²</u>	<u>ih²</u>	<u>actual gain</u>
F ₃	1.6	5.7	57%	2.0	6.2
RS	1.8	4.0	0%	0.0	-0.5
RS ₂	1.6	5.0	0%	0.0	1.1
				2.0	7.8
F ₂	1.6	5.7	57%	2.0	4.5
S	2.5	7.2	0%	0.0	-0.2
S ₂	1.5	3.9	0%	0.0	0.0
				2.0	4.3
<u>R53 x 38-11</u>					
F ₂	1.5	7.4	38%	2.6	7.4
RS	2.0	7.0	13%	0.9	2.5*
RS ₂	1.7	6.8	25%	1.7	0.6
				5.4	10.5
F ₂	1.5	7.4	38%	2.6	5.8
S	2.0	7.8	0%	0.0	0.9
S ₂	1.7	5.9	0%	0.0	2.1*
				2.6	8.9
<u>MS24A x 38-11</u>					
F ₃	1.9	11.9	74%	8.8	4.0
RS	1.7	6.1	7%	0.4	4.7*
RS ₂	1.0	3.8	20%	0.8	-1.6
				2.7	7.1
F ₂	1.9	11.9	74%	8.8	4.8
S	1.7	4.3	0%	0.0	1.1
S ₂	1.6	4.8	0%	0.0	0.0
				2.0	6.8

* Significantly different from zero

Genetical variability was exhausted after one or two cycles of breeding. This conclusion was reached from the following:

(1) The within variance representing the variability between plants did not decrease (Table 7B) from one cycle to the next as expected, had genetical variability been present.

(2) The F ratios between within and among variances (Table 7A) were not significant. There was less variability among strains than within rows.

(3) The variances of the early-maturing groups (Table 7B) were close to the values of the earliest parents.

(4) The F_2 heritability values (Table 8A) were high and expected gains were realized. The heritability values were much reduced after the first cycle of breeding, and progress, if any, was much less.

In Table 9 actual gains were considered null if the differences between cycles were non-significant. No progress toward early silking date was made after the first breeding cycle in either the recurrent series or inbred series of the double cross Michigan 51B, the early single cross (Ia.153 x W25), and the double cross Michigan 20D where the parental lines are similar in maturity. On the contrary, some progress toward early silking was made after the first breeding cycle in the recurrent series of the three early-x-late single crosses (MS24A x 38-11), (R53 x 38-11), and (MS24A x L3.7), and in the inbred series of the single cross (MS24A x L317).

Table 9. Expected and actual gains in the early-maturing series of six populations.

Groups	Expected Gains	Actual gains	Expected Gains	Actual Gains
<u>Michigan 51B</u>			<u>Ia.153 x W25</u>	
F ₂	7.5	6.6	2.0	6.2
RS	0.4	0.1	0.0	0.0
RS ₂	2.3	0.0	0.0	0.0
F ₂	7.5	3.2	2.0	4.5
S ₂	0.0	0.0	0.0	0.0
S ₂	0.0	0.0	0.0	0.0
<u>Michigan 20D</u>			<u>R53 x 28-11</u>	
F ₂	3.9	1.7	2.8	7.4
RS	0.0	0.0	0.9	2.4
RS ₂	0.0	0.0	1.7	0.0
F ₂	3.9	-1.6	2.8	5.8
S ₂	0.0	0.0	0.0	2.1
S ₂	0.0	0.0	0.0	0.0
<u>MS24A x L317</u>			<u>MS24A x 33-11</u>	
F ₂	9.8	8.0	8.8	4.0
RS	0.1	0.0	0.4	4.7
RS ₂	0.4	6.4	0.8	0.0
F ₂	9.8	6.0	8.8	4.8
S ₂	1.6	3.3	0.0	0.0
S ₂	1.0	1.2	0.0	0.0

It is concluded that fixation of genes for early silking date was very rapid. Very little improvement can be made after the first cycle of breeding. Progress seemed to be greater with more diverse crosses of early-x-late lines such as MS24A x L317.

COMPARISON BETWEEN BREEDING GROUPS IN
THE LATE MATURITY SERIES

The mean values of each breeding group are ranked in Table 10. Values within a bracket are not significantly different according to Duncan's multiple range test (4). Breeding groups within a cycle can be compared (Table 10A).

Table 10A. Comparison between inbred and recurrent selected groups within a breeding cycle for late maturity.

Population	First cycle	Second cycle	Third cycle
Michigan 51B	S = RS 70.6 66.5	S ₂ > RS ₂ 76.2 68.9	S ₃ > RS ₃ 81.5 71.1
Michigan 20D	S > RS 86.6 78.2	S ₂ > RS ₂ 89.3 80.0	S ₃ > RS ₃ 93.2 85.0
R53 x 38-11	S = RS 78.2 79.2	S ₂ > RS ₂ 84.3 77.8	S ₃ = RS ₃ 81.6 80.6
MS24A x 38-11	S = RS 80.9 82.2	S ₂ > RS ₂ 86.6 81.5	S ₃ = RS ₃ 88.1 86.4
Ia. 153 x W25	S = RS 72.1 71.4	S ₂ = RS ₂ 74.0 74.8	S ₃ = RS ₃ 76.0 75.1
MS24A x L317	S = RS 85.6 79.2	S ₂ = RS ₂ 87.4 82.3	S ₃ = RS ₃ 92.2 84.5

> later than
 = equal in maturity

Though the results differed somewhat for each population, the inbred series tended to be later than the recurrent series. However, after three cycles of breeding, the differences between the recurrent and the inbred series were small and non-significant.

Table 10. Ranked mean days to silking for the nine breeding groups in the late maturity series from six crosses.

Michigan 51B

F2	KS	KS2	S	KS3	KS-1	KS2-1	KS-1-1	S2	S3
67.0	66.5	68.9	70.6	71.1	72.1	73.8	76.2	76.2	81.5

RS3 x 38-11

F2	RS2	S	RS	KS3	S3	KS2-1	S2	KS-1	KS-1-1
74.0	77.8	78.2	79.2	80.6	81.6	83.4	84.3	84.3	87.1

MS24A x 38-11

F2	S	KS2	KS	KS-1	KS3	S2	S3	KS2-1	KS-1-1
77.0	80.9	81.5	82.2	83.3	86.4	86.6	88.1	88.1	88.9

Table 10. (Continued)

Michigan 20D

F2	RS	RS2	S	RS3	RS-1	RS2-1	S2	S3	RS-1-1
72.0	78.2	80.0	82.6	85.0	88.8	89.0	89.3	93.2	94.0

Ia. 153 x W25

F2	RS	S	S2	RS2	RS3	RS-1	S3	RS-1-1	RS2-1
69.0	71.4	72.1	74.0	74.8	75.1	75.6	76.0	77.6	80.5

NS24A x L317

F2	RS-1	RS	RS2	RS3	S	RS2-1	S2	RS-1-1	S3
81.0	76.6	79.2	82.3	84.5	85.6	85.8	87.4	87.8	92.2

Observation in the field led to believe that inbreeding depression affected the inbred series more than the recurrent series, making the comparison very difficult.

Table 7B indicates that variances for the late maturity groups were close to the late maturity inbred parent variance and those variances did not decrease from one cycle to the next except in the inbred series from the cross (MS24A x L317) and Michigan 20D. This indicates that the genetic variability was usually exhausted after the first breeding cycle.

In Table 11A actual gains were considered null if the differences between cycles were non-significant. Gains could have been expected in the recurrent series in only three crosses, Michigan 51B, (MS24A x L317), and (MS24A x 38-11). In general, there was considerable gain when none was expected. These gains must be interpreted as effects of inbreeding depression.

These results indicate that fixation of late maturity genes was very rapid by either breeding method.

Table 11. Selection differential, heritability (h^2), expected (ih^2) and actual gains in the late maturity series of six populations.

Michigan 51B

	<u>I</u>	<u>i</u>	<u>h^2</u>	<u>ih^2</u>	<u>Actual Gain</u>
F2	1.7	6.1	75%	4.5	- 1.5
RS	3.6	15.4	19%	2.9	2.4
RS2	1.2	6.5	12%	1.9	2.2
				<u>9.3</u>	<u>4.1</u>
F2	1.7	6.1	75%	4.5	3.6
S	2.0	5.6	0%	0.0	6.0 *
S2	1.4	3.7	0%	0.0	4.9
				<u>4.5</u>	<u>14.5</u>

Michigan 20D

F2	1.8	11.3	76%	8.5	6.2
RS	1.3	6.5	0%	0.0	8.0
RS2	2.2	11.2	0%	0.0	13.0 *
				<u>8.5</u>	<u>27.2</u>

F2	1.8	11.3	76%	8.5	10.6
S	1.3	3.7	0%	0.0	6.7 *
S2	1.4	4.2	0%	0.0	2.9 *
				<u>8.5</u>	<u>21.2</u>

MS24A x 38-11

F2	1.4	7.6	74%	5.6	5.2
RS	2.0	12.0	24%	2.9	- 0.7
RS2	1.3	6.2	0%	0.0	4.9 *
				<u>8.5</u>	<u>9.4</u>

* Significantly different from zero at the 5% level.
Reference point is the F2 value.

Table 11. (Continued)

MS 24A x 38-11

✓

	<u>I</u>	<u>I</u>	<u>r²</u>	<u>1r²</u>	<u>Actual Gain</u>
F2	1.4	7.6	74%	5.6	3.9
S	2.0	9.2	0%	0.0	5.7 *
S2	1.6	7.8	0%	0.0	1.5
				<u>5.6</u>	<u>11.1</u>

Ia.153 x W25

F2	2.0	13.2	57%	7.5	2.4
RS	1.3	3.2	0%	0.0	3.4
RS2	1.5	6.0	0%	0.0	0.3
				<u>7.5</u>	<u>6.1</u>

F2	2.0	13.2	57%	7.5	2.1
S	1.3	4.9	0%	0.0	1.9
S2	2.3	8.9	0%	0.0	2.0
				<u>7.5</u>	<u>6.0</u>

MS24A x L317

F2	1.7	14.5	75%	10.8	- 1.8
RS	1.3	10.8	38%	4.1	3.1
RS2	1.5	6.5	50%	4.0	2.2
				<u>18.9</u>	<u>3.5</u>

F2	1.7	14.5	75%	10.8	4.6
S	2.0	9.8	43%	8.5	1.8
S2	1.1	5.5	43%	6.6	4.8
				<u>25.9</u>	<u>11.2</u>

* Significantly different from zero at the 5% level.
Reference point is the F₂ value.

✓

Table 11. (Continued)

<u>R53 x 38-11</u>		<u>I</u>	<u>I</u>	<u>h²</u>	<u>1h²</u>	<u>Actual Gain</u>
F2 RS KS2		1.5	7.3	38%	2.7	5.2
		1.7	9.5	0%	0.0	- 1.4
		1.6	8.6	0%	0.0	<u>2.8</u> 6.6
F2 S S2		1.5	7.3	38%	2.7	4.2
		1.7	8.1	0%	0.0	6.1 *
		2.6	13.5	0%	<u>0.0</u> 2.7	- <u>2.7</u> 7.6

* Significantly different from zero at the 5% level.
Reference point is the F₂ value.

Table 11A. Expected and actual gains in the late-maturing series of six populations.

Groups	Expected Gains	Actual Gains	Expected Gains	Actual Gains
<u>Michigan 51B</u>			<u>Ia.153 x W25</u>	
F ₂	4.5	- 1.5	7.5	2.4
RS	2.9	0.0	0.0	0.0
RS ₂	1.9	0.0	0.0	0.0
F ₂	4.5	0.0	7.5	2.1
S	0.0	6.0	0.0	0.0
S ₂	0.0	4.9	0.0	0.0
<u>Michigan 20D</u>			<u>R53 x 38-11</u>	
F ₂	8.5	6.2	2.7	5.2
RS	0.0	0.0	0.0	0.0
RS ₂	0.0	13.0	0.0	0.0
F ₂	8.5	10.6	2.7	4.2
S	0.0	6.7	0.0	6.1
S ₂	0.0	3.9	0.0	0.0
<u>MS24A x L317</u>			<u>MS24A x 38-11</u>	
F ₂	10.8	- 1.8	5.6	5.2
RS	4.1	0.0	2.9	0.0
RS ₂	4.0	0.0	0.0	4.9
F ₂	10.8	0.0	5.6	3.9
S	8.5	0.0	0.0	5.7
S ₂	6.6	0.0	0.0	0.0

MOISTURE CONTENT AT HARVEST

As another measure of maturity, moisture content of ears at harvest was determined for each plant in two populations, Michigan 51B and (R53 x 38-11), harvested September 22 and October 5 respectively. Some plants of the Michigan 51B population silked as late as the first week of September, and some of the (R53 x 38-11) population silked as late as the second week of September. Thus, many ears were immature.

Results of moisture content measurements at harvest were similar to those measurements from planting date to silking.

Fixation of genes for low and high moisture content was very rapid. The greatest progress towards early and late maturity seemed to have been made with the first cycle of breeding, as shown in figures 7 and 8, where values for parental lines, F₁, F₂ and breeding group means have been graphed. Though a few strains from the early-maturing (Table 12) were as high in moisture content as some strains from the late-maturing series, none of the breeding group means from the early-maturing series was greater than any breeding group mean from the late-maturing series.

Analyses of variance (Table 13) indicated that there were differences among early breeding groups of the two crosses and among the late breeding groups of the Michigan 51B cross.

Table 12. Range and mean for ear moisture content at harvest of 9 breeding groups from two populations.

<u>K53 x 38-11</u>	Early Maturity		Late Maturity	
	Range	Mean	Range	Mean
RS	31.8-41.6 = 9.8	37.6	51.8-62.1 = 10.3	56.7
S	29.3-45.9 = 16.6	39.7	44.2-67.2 = 11.0	58.3
RS2	20.6-34.5 = 13.9	32.4	43.9-62.6 = 18.7	53.3
RS-1	28.0-38.7 = 10.7	34.4	52.6-73.2 = 20.6	64.9
S2	26.2-44.2 = 16.0	35.8	51.1-79.3 = 28.2	64.0
RS3	24.9-35.3 = 10.4	32.2	53.9-69.4 = 16.5	58.0
RS2-1	26.1-37.5 = 11.4	30.8	58.1-75.0 = 16.9	63.5
RS-1-1	26.2-46.0 = 9.8	35.3	64.1-74.8 = 10.7	69.4
S3	28.0-41.5 = 13.5	33.4	55.5-68.9 = 13.4	62.2
		<u>34.6</u>		<u>61.1</u>
L.S.D.				
1. strains.....	8.6			16.4
2. groups.....	4.9			12.5
Parental lines				
	K53:	39.3	F1:	51.9
	38-11:	59.7	F2:	49.4

Table 12. (Continued)

<u>Michigan 51B</u>	<u>Early Maturity</u>	<u>Mean</u>	<u>Late Maturity</u>	<u>Mean</u>
	<u>Range</u>		<u>Range</u>	
RS	33.2-43.2 = 10.0	37.9	43.6-53.5 = 9.9	47.8
S	37.5-52.5 = 15.0	42.5	45.7-53.7 = 8.0	52.2
RS	36.0-43.2 = 7.2	36.5	46.5-55.8 = 9.3	50.8
RS-1	35.1-46.3 = 11.2	40.1	47.0-64.6 = 16.7	55.5
S2	32.4-45.4 = 13.0	42.9	56.5-72.2 = 15.7	62.3
RS3	27.0-36.4 = 8.5	34.3	45.6-58.5 = 12.9	54.4
RS2-1	36.6-40.5 = 3.9	39.3	50.3-62.3 = 12.0	59.1
RS-1-1	29.1-45.4 = 16.3	36.5	48.5-72.4 = 13.9	62.7
S3	31.5-48.5 = 17.0	38.7	67.5-77.9 = 10.4	70.3
		39.2		51.5
L.S.D.	1. strains.....6.6		9.5	
	2. groups.....6.2		7.3	
	Parental lines			
	1. Ia. 153 = 57.0		F ₁ = 43.0	
	2. W25 = 57.7			
	3. W9 = 57.7		F ₂ = 44.0	
	4. M13 = 66.4			

Table 13. Analyses of variance for moisture content in different breeding groups from two different crosses.

<u>RH53 x 38-11</u>				<u>Early maturity groups</u>		<u>Late maturity groups</u>	
Source	D.F.	S.S.	M.S.	S.S.	M.S.		
Total	179	6115.13		12,088.76			
Repl.	1	138.95	138.95	0.10	0.1		
Strains	89	4311.24	48.44	6,075.80	68.2		
Breed. groups	8						
Within	9	1251.25	138.95	1727.70	21.5		
Interaction	72	414.37	48.44	2671.09	24.6		
Error	89	2645.62	36.72	1677.01	22.3		
		1664.94	18.70	6,012.86	67.5		
<u>Michigan 51B</u>							
Total	179	5414.26		13,835.33			
Repl.	1	394.80	394.80	44.60	44.60		
Strains	89	4036.31	45.35	11,778.10	132.3		
Breed. groups	8						
Within	9	930.91	116.36	7993.0	999.1		
Interaction	72	650.90	72.32	769.0	98.5		
Error	89	2454.40	34.0	3106.1	43.1		
		983.15	11.04	2,012.63	22.61		

COMPARISON BETWEEN BREEDING GROUPS IN THE EARLY MATURITY SERIES

The mean values of each breeding group are ranked in Table 14. Values within a bracket are not significantly different according to Duncan's multiple range test (4). Breeding groups within a cycle can be compared, Table 14A.

Table 14. Ranked means for ear moisture content at harvest of nine breeding groups from two crosses, Michigan 51B and R53 x 38-11.

<u>R53 x 38-11</u>									
RS ₂ -1	RS ₃	RS ₂	S ₃	RS-1	RS-1-1	S ₂	RS	S	F ₂
30.8	32.2	32.4	33.4	34.4	35.3	35.8	37.6	38.7	40.4
<u>Michigan 51B</u>									
RS ₃	RS	RS ₂	RS-1-1	S ₃	RS ₂ -1	RS ₁	S	S ₂	F ₂
34.3	37.0	38.5	38.5	38.7	39.3	40.1	42.4	42.9	44.0

Table 14A. Comparison between inbred and recurrent selected series within a breeding cycle for early maturity.

<u>Population</u>	<u>First cycle</u>		<u>Second cycle</u>		<u>Third cycle</u>	
R53 x 38-11	S	= RS	S ₂	= RS ₂	S ₃	= RS ₃
	39.7	37.6	35.8	32.4	33.4	32.2
Michigan 51B	S	= RS	S ₂	= RS ₂	S ₃	= RS ₃
	42.5	37.9	42.9	38.5	38.7	34.3

The recurrent series tended to be lower in moisture content than the inbred series but the differences between them were non-significant. These results agreed with those obtained from days to silking where the differences were also small.

Row variance for the nine early breeding groups (Table 15) gives an indication of the variability in the series. Variability in the early recurrent series of the cross (R53 x 38-11) was similar to the variance of the early inbred parent, R53, indicating that genetic variability was about exhausted. Variability in the early inbred series of the (R53 x 38-11) cross decreased when compared with the R53 value, indicating that after three cycles of selfing very little variability existed for moisture content.

The variances of Ia.153 and W25 were considerably greater than the variances of M13 and W9 and should be taken as an estimate of the environment. The variances of the early series tended to increase, but not to the extent of the latest parental line value, W25. It is safe to assume that the variability in these series was exhausted.

Table 15. Average row variance for the inbred and recurrent series of the early and late Michigan 51B and R53 x 38-11 maturity groups.

<u>R53 x 38-11</u>			<u>Michigan 51B</u>	
	<u>Early</u>	<u>Late</u>	<u>Early</u>	<u>Late</u>
RS	50.2	67.4	48.2	36.4
RS ₂	43.6	91.5	57.9	50.0
RS ₃	65.6	81.3	86.2	81.4
S	99.1	125.0	38.7	81.6
S ₂	79.2	75.3	90.9	94.6
S ₃	51.5	86.7	74.8	72.8
R53	50.6		Ia.153	66.0
38-11	79.0		W25	99.0
			M13	15.4
F ₁	46.8		W9	8.2
F ₂	114.0		F ₁	5.4
			F ₂	32.9

Table 16. Ranked means for ear moisture content at harvest for the nine breeding groups from two crosses.

<u>R53 x 38-11</u>									
F ₂	RS ₂	RS	RS ₃	S	S ₃	RS ₂ -1	S ₂	RS-1	RS-1-1
49.4	53.3	56.7	58.0	58.3	62.2	63.5	64.0	64.9	60.4

<u>Michigan 51B</u>									
F ₂	RS	RS ₂	S	RS ₃	RS-1	RS ₂ -1	RS-1-1	S ₂	S ₃
44.0	47.8	50.8	52.2	54.4	55.5	58.1	62.7	62.9	70.3

COMPARISON BETWEEN BREEDING GROUPS IN THE LATE MATURITY SERIES

The mean values of each breeding group are ranked in Table 16. Values within a bracket were not significantly different according to Duncan's multiple range test (4). There were no significant differences among the breeding groups of the R53 x 38-11 population. However, the inbred series in the Michigan 51B population were very high in moisture content when compared to the recurrent series, Table 16A. These increases in moisture content in the inbred series should be attributed to inbreeding depression since, referring to Table 15, the variance in the late inbred groups did not decrease from one cycle to the next, and was inferior to the latest parental line, W25. This indicates that very little genetical variability remained after the first cycle of breeding.

Table 16A. Comparison between inbred and recurrent series in the double cross Michigan 51B.

<u>First cycle</u>		<u>Second cycle</u>		<u>Third cycle</u>	
RS	< S	RS ₂	< S ₂	RS ₃	< S ₃
47.8	52.2	50.8	62.9	54.4	70.3

TEST CROSS EXPERIMENT RESULTS

General Considerations

The objective of the yield trials was to measure the differences in maturity between breeding groups when the lines were in hybrid combinations.

Results show that the most important differences were between early and late maturity groups. Differences between recurrent selected and inbred groups were very small, and when significant did not indicate any trend. Cycle gains were very small, indicating that genetical variability was exhausted after three cycles of breeding.

There were significant differences among the selections for days to silking in all the experiments, Table 17, except 55-904 and 55-905 which tested the populations of the single-cross (MS24A x L317) and the double cross Michigan 202. There were significant differences among the selections for ear moisture content in all the experiments.

The correlation coefficients for silking date with moisture content were all positively significant (Table 18), indicating that the early-silking selections were lower in moisture content than the late silking selections. In general there were no positive correlations between yield and moisture content in the 1955 testcross experiments (Table 18). In 4 of 5 experiments in 1956 the high yielding selections were the late-maturing selections. In 1957 the high-yielding selections from two early-x-late single crosses, (MS24A x L317) and (K53 x 38-11) were the early-maturing selections which had time to ripen

Table 17. "F" values, coefficients of variability of experiments conducted in 1955, 1956, and 1957 as to days from planting to silking, moisture content at harvest and yield.

Population	Exp. No.	Silking Days		Moisture		Yield	
		F.	Coef.	F.	Coef.	F.	Coef.
NS24A x 38-11	55-902	2.45**	2.0%	5.11**	8.4%	2.37**	12.8%
	56-905	2.80**	2.6%	2.95**	6.8%	2.29**	13.7%
Michigan 20D	55-905	1.30	4.4%	5.05**	9.7%	0.45	16.4%
	56-902	5.40**	1.6%	2.57**	7.3%	2.12**	11.7%
R53 x 38-11	55-903	5.00**	2.1%	5.36**	12.3%	1.39	13.1%
	56-903	10.3**	2.0%	6.71**	6.6%	3.34**	12.8%
	57-911	21.9**	2.6%	7.68**	8.2%	14.9**	15.0%
(NS24A x L3.7)	55-904	0.9	4.43%	5.55**	9.4%	3.18**	13.8%
	56-904	5.3**	1.70%	5.65**	6.0%	2.18**	15.8%
	57-913	3.8**	3.50%	4.26**	9.4%	6.20**	20.3%
Michigan 51B	56-901	5.8**	2.30%	7.66**	4.7%	2.81**	15.5%
	57-912	15.9**	1.96%	8.91**	5.1%	4.60**	17.6%

** Significant at the 1 per cent level.

before killing frost on September 20. The parental lines of the double-cross Michigan 51B are considered early-maturing lines, and all the selections from this double-cross population had time to ripen before killing frost.

Table 18. Correlation coefficients between days to silking and ear moisture content at harvest, and between moisture content and yield in the 1955, 1956 and 1957 testcross experiments.

<u>Population</u>	<u>Experiment Number</u>	<u>Silking date x Moisture:</u>	<u>Moisture x Yield</u>
(MS24A x 38-11)	55-902	0.757**	0.140
(MS24A x 38-11)	56-905	0.543**	0.488**
Michigan 20D	55-905	0.345**	-0.150
Michigan 20D	56-902	0.456**	0.463**
Michigan 51B	56-901	0.828**	0.671**
Michigan 51B	57-912	0.975**	0.794**
(R53 x 38-11)	55-903	0.680**	0.653**
(R53 x 38-11)	56-903	0.738**	0.707**
(R53 x 38-11)	57-911	0.892**	-0.196
(MS24A x L317)	55-904	0.777**	0.200
(MS24A x L317)	56-904	0.659**	0.563**
(MS24A x L317)	57-913	0.720**	-0.268

** Significant at the 1 per cent level.

Differences between breeding groups.

The means of RS₃, S₃, RS₂ and S₂ breeding groups for days to silking and ear moisture content have been ranked in Table 19. Values within a bracket were not significant according to the following test:

$$t = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{S_p / 1/n (N_1 + N_2)}}$$

where $\bar{x}_1$ and $\bar{x}_2$ are the means of the breeding groups, S_p the square root of the error mean square given in the analysis of variance, N_1 and N_2 the number of selections in each breeding group, and n the number of replicates.

In one population (R53 x 38-11) there were no differences in date of silking or moisture content between the S₃ and RS₃ breeding groups in either the early or the late maturing groups. Similar results were obtained by both breeding methods. In the other two populations the early inbred selections were earlier in maturity than the recurrent selections, and in the Michigan 51B population the late inbred selections were later in maturity than the recurrent selections. The differences between those breeding groups were very small.

In Table 20 actual gain cycles were considered null if the differences between cycles were non-significant. Actual gains though small seemed to have been made for early silking

date in all the crosses and for lower moisture content in the Michigan 51B and MS24A x L317 crosses. Very small gain seemed to have been made for late maturity in the Michigan 51B and MS24A x L317 crosses.

Table 19. Days to silking and ear moisture content of S_3 , RS_3 , S_2 and RS_2 breeding groups in three 1957 testcross experiments.

<u>DAYS TO SILKING</u>				<u>MOISTURE CONTENT</u>			
<u>Early Maturity</u>		<u>Late Maturity</u>		<u>Early Maturity</u>		<u>Late Maturity</u>	
<u>Michigan 51B</u>							
S ₃	RS ₃	RS ₃	S ₃	S ₃	RS ₃	RS ₃	S ₃
59.1	60.4	64.7	68.1	27.4	29.8	38.5	42.1
S ₂	RS ₂	RS ₂	S ₂	S ₂	RS ₂	RS ₂	S ₂
61.0	61.4	64.3	67.3	32.4	32.0	37.1	40.0
<u>RS3 x 38-11</u>							
S ₃	RS ₃	RS ₃	S ₃	S ₃	RS ₃	RS ₃	S ₃
63.1	63.4	73.6	73.4	33.9	35.4	44.5	44.6
S ₂	RS ₂	RS ₂	S ₂	S ₂	RS ₂	RS ₂	S ₂
65.1	64.7	72.5	73.5	34.4	33.8	44.9	46.9
<u>MS24A x L317</u>							
S ₃	RS ₃	RS ₃	S ₃	S ₃	RS ₃	RS ₃	S ₃
66.4	68.5	72.9	73.2	35.0	37.1	42.3	43.6
S ₂	RS ₂	RS ₂	S ₂	S ₂	RS ₂	RS ₂	S ₂
68.1	69.8	71.4	73.1	37.0	38.1	41.9	42.0

Table 20. Cycle gains in days to silking and ear percent moisture content in three populations tested in 1957.

<u>Population</u>		<u>EARLY MATURITY</u>		<u>LATE MATURITY</u>	
		<u>Days</u>	<u>Moisture</u>	<u>Days</u>	<u>Moisture</u>
Michigan 51B	Inbred	1.9	5.0	0.0	2.1
	Recur.	1.0	2.2	0.0	1.4
R53 x 38-11	Inbred	2.0	0.0	0.0	0.0
	Recur.	1.3	0.0	0.0	0.0
MS24A x L317	Inbred	1.7	2.0	0.0	1.6
	Recur.	1.3	1.0	1.5	0.4

These results indicate that recurrent selection was no more effective than continuous inbreeding with selection.

This conclusion is important. First, inbred lines are used to transmit early or late maturity in hybrid combinations; second, inbreeding depression in the nursery made very difficult a direct comparison between inbred and recurrent selected lines. Therefore, testcrossing lines for maturity may be the only way to measure the relative effectiveness of the two breeding methods.

One important point was demonstrated in experiment 57-911. It was possible to obtain earlier and later lines than the parental lines from an early-x-late cross, Table 21. The parental lines R53 and 38-11 testcrossed to (oh43 x A158) were included. One line of the recurrent selected series (HSL3-RSL105-RSL110) and one line of the inbred series (121-2-2) were later in date of silking and higher moisture content than

the parental line, 38-11. Two lines of the S_2 breeding groups were higher in moisture content than the parental line 38-11. One of these lines (L21-2) gave rise to two lines which were higher in moisture content than the parental line 38-11. One line of the recurrent selected series (RSE20-RSE1-RSE4) and one line of the inbred series (E2-2-4) were earlier in date of silking than the early parental line R53.

Table 21. Range, mean ear moisture content, and mean days to silking for early and late RS₃, S₃, RS₂, and S₂ breeding groups of three 1957 testcross experiments.

DAYS TO SILKING						
Population		Early Maturity		I.S.D.	Late Maturity	
		Range	Mean		Range	Mean
R53 x 38-11	RS ₃	61.3-65.6	63.4	4.0	71.0-76.0	73.5
	S ₃	61.6-64.3	63.1	4.0	72.3-75.3	73.4
	RS ₂	62.0-67.6	65.1	4.0	70.3-73.6	72.5
	S ₂	64.3-65.3	64.7	4.0	72.0-75.0	73.5
NS24A x L317	RS ₃	66.0-69.6	68.5	7.0	71.3-76.0	72.9
	S ₃	64.3-70.0	66.4	7.0	73.0-75.0	73.8
	RS ₂	68.3-71.0	69.8	7.0	69.9-72.9	71.4
	S ₂	66.3-70.0	68.1	7.0	72.0-76.0	73.1
Michigan 51B	RS ₃	58.3-62.0	60.4	3.0	63.3-65.6	64.7
	S ₃	58.0-60.0	59.1	3.0	66.3-69.3	68.1
	RS ₂	59.3-64.3	61.4	3.0	62.6-65.6	64.3
	S ₂	59.3-63.0	61.0	3.0	67.3-68.3	67.3

Parental lines included R53 66 days $\bar{x}$ 2.8
38-11 71 days $\bar{x}$ 2.8

* Significant at the 5 per cent level.
** Significant at the 1 per cent level.

Table 21. (Continued)

MOISTURE CONTENT						
Population		Early Maturity		L.S.D.	Late Maturity	
		Range	Mean		Range	Mean
H53 x 38-11	RS ₃	32.6-41.1	35.4	7.0	40.7-48.1	44.0
	S ₃	33.1-35.0	33.9	7.0	42.8-47.8	44.5
	RS ₂	26.2-36.7	33.8	7.0	42.4-50.1	44.9
	S ₂	31.4-38.8	34.4	7.0	45.0-48.2	46.9
MS24A x L317	RS ₃	28.3-40.4	37.1	7.5	38.6-45.4	42.3
	S ₃	29.6-41.6	35.0	7.5	42.1-46.8	44.2
	RS ₂	36.6-41.3	38.1	7.5	40.3-43.5	41.9
	S ₂	34.3-39.8	37.0	7.5	39.0-45.4	42.0
Michigan 51B	RS ₃	28.1-32.2	29.8	3.0	36.5-40.3	38.5
	S ₃	27.8-36.0	31.4	3.0	39.1-45.4	42.1
	RS ₂	27.9-36.2	32.0	3.0	33.6-38.7	37.1
	S ₂	29.2-36.2	32.4	3.0	37.5-42.5	40.0

Parental lines included H53 38-11 5%
 36.3 40.4 5%
 * Significant at the 5 per cent level.
 ** Significant at the 1 per cent level.

YIELD RESULTS

Selection was directed toward maturity and not combining ability. Hence variability for yield should be expected within maturity groups. The only trend that could be expected was that late-maturing selections should yield more than early-maturing selections in a year with a long growing season.

In two 1955 test cross experiments (Table 22) evaluating selected F₂'s of the MS24A x 38-11 and MS24A x L317 populations, the yield ranges within maturity groups were greater than the L.S.D. indicating high and low yielding selections within the groups. Though the differences between early and late selections were significant, the yield ranges overlapped indicating that some early selections yielded as much as some late selections. The same conclusions can be drawn from the 1956 testcross experiments (Table 23). Less variability for yield seemed to exist within maturity groups of the 1957 testcross experiments (Table 24), since the yield ranges were smaller in many cases than the L.S.D. and when they were greater the differences were small. Selections within a maturity group tended to be similar in nature. However, since there was a very great overlapping for yield among the maturity groups, it would be possible to select for combining ability in early and late-maturing lines.

In the R53 x 38-11 population, the parental lines

R53 and 38-11 were included. Four lines from the early-maturity groups yielded more than the early-parental line R53. No late maturing line yielded more than 38-11.

Table 22. Range and mean for yields of early and late selected F₂ in the 1955 testcross experiments.

Population	<u>EARLY MATURITY</u>		<u>LATE MATURITY</u>		Difference	L.S.D.
	Range	Mean	Range	Mean		
MS24A x 38-11	72.2-114.4	96.6	88.7-115.1	103.5	6.9*	17.8
MS24A x L317	87.4-111.0	94.7	61.8-120.4	99.2	4.5*	18.8
R53 x 38-11	78.0-93.7	86.2	75.9-96.2	86.1	0.1	-
Michigan 20D	87.6-89.1	88.6	82.9-96.3	87.3	1.3	-

* Significant at the 5 per cent level.

- No differences among the selections.

Table 23. Range and Mean for yields of RS₂ and S₂ breeding in five 1956 testcross experiments.

Population	<u>EARLY</u>		<u>LATE</u>		Difference	I.S.D.
	Range	Mean	Range	Mean		
Michigan 51B RS ₂	47.3-69.2	60.7	58.8-77.5	69.8	9.1*	14.2
S ₂	55.6-72.8	62.7	64.5-80.1	72.1	9.4*	14.2
Michigan 20D RS ₂	67.5-88.1	72.3	72.1-79.9	74.4	2.1	10.8
S ₂	65.4-82.4	74.0	54.1-82.4	69.3	-4.7	10.8
RS3 x 38-11 RS ₂	62.4-76.8	68.7	63.5-92.7	83.8	15.1*	13.4
S ₂	54.4-77.3	68.8	68.1-91.1	80.4	11.6*	13.4
NS24A x L317 RS ₂	74.0-83.6	80.0	73.5-82.1	77.0	-3.0	14.7
S ₂	54.7-77.0	68.7	79.1-90.2	84.2	15.5*	14.7
MS24A x 38-11 RS ₂	62.8-79.6	71.1	67.7-85.5	77.2	6.1*	13.8
S ₂	56.4-74.2	64.3	61.8-84.5	73.8	9.5*	13.8

* Significant at the 5 per cent level.

Table 24. Range and mean for yields of RS₃, S₃ and RS-1-1 breeding groups in the 1957 testcross experiments.

Population		<u>EARLY MATURITY</u>		<u>LATE MATURITY</u>		Mean Difference	L.S.D.		
		range	mean	range	mean				
Nichigan 51B	RS ₃	41.6-56.2:	14.6	48.8	60.7-75.4:	14.7	65.9	17.1*	25.0
	S ₃	55.6-72.8:	17.2	62.7	64.5-80.1:	15.6	72.1	12.9*	25.0
MS24A x L317	RS ₃	60.3-82.4:	22.1	67.8	41.0-66.8:	25.8	58.1	-9.7*	28.0
	S ₃	51.5-74.5:	23.0	57.7	58.3-70.1:	11.8	63.4	45.7*	28.0
R53 x 38-11	RS ₃	53.7-72.0:	18.3	61.2	56.0-68.3:	12.3	61.6	0.4	17.0
	S ₃	50.0-68.8:	18.8	60.3	47.3-64.6:	17.3	57.5	-2.8	17.0

* Significant at the 5 per cent level.

DISCUSSION

The objective was to study the effectiveness of continuous inbreeding (selfing) with selection compared to three cycles of recurrent selection. Direct comparison in the nursery between recurrent series and inbred series was difficult due to inbreeding depression which masked the effectiveness of the breeding methods.

Results with testcrosses indicated that recurrent selection was no more effective than continuous inbreeding with selection. These results were not in agreement with those obtained by others to improve yield, oil content, and leaf blight resistance in corn. Recurrent selection was more effective than continuous inbreeding with selection.

Self-fertilization leads to a rapid increase in homozygosity: F_2 , 50%; S_1 , 75%; S_2 , 87.5%; S_3 , 93.7%. Rapid fixation of genes occurs with such a method. Any breeding scheme which involves a rapid fixation of genes imposes very definite restrictions upon the effectiveness of any selection which may be practiced (22). These limitations are: (1) large number of genes, (2) masking effects of environment, (3) complicated system of gene interaction, (4) inadequate methods of isolating and evaluating lines.

Recurrent selection is a breeding scheme that offers some opportunity to minimize the rapid increase in homozygosity which is led by self-fertilization. The basis of recurrent

selection is to intercross selected plants, or bulked pollen from the selected plants is used to pollinate them, and the intercrossed populations serve as a source of material for the next cycle of selection. Theoretically, genes for the desired characteristic should be more concentrated in the recurrent selected population.

The following reasons are proposed to explain why recurrent selection was not more effective than inbreeding with selection to improve maturity, taking the silking date as a criterion.

Selection in the recurrent selected series was at a disadvantage compared to continuous inbreeding because of the necessity for the ten earliest and ten latest maturing plants to flower at the same time in order to effect the intercross. In the recurrent selection program only one plant in each row was selected to maintain inbreeding pressure at a minimum. Therefore, a few of the earliest plants in a particular row shed pollen at a time when there were no plants in other rows with receptive silks. These early plants were lost from the population. In the continuous inbreeding program, such plants were saved. Recurrent selection for late maturity presented a similar problem. Bulking pollen of the ten latest plants required that there be ten plants in flower at the same time. Therefore, slightly earlier plants were chosen in the recurrent selection series than in the inbreeding series.

Rapid fixation of genes and equal effectiveness of the two breeding methods tend to indicate that few genes for maturity were involved. Jones (15) using the formula for calculating gene number given to Burton by Wright (2) found that the gene number for silking date ranged from 5 to 19. Mohamed* in a recent article estimated the number of genes for the same characteristic at three. Such few genes could be isolated very rapidly with any breeding scheme.

Decline in fertility and vigor and delay in maturity are among the general effects of inbreeding and are referred to as inbreeding depression.

In the recurrent selection program only one plant in each row was selected in order to maintain inbreeding pressure at a minimum. Therefore, inbreeding depression would be expected to affect the recurrent series less than the inbred series and render their comparison very difficult. This was confirmed by visual observation in the field.

One method to overcome the effects of inbreeding depression would have been to inbreed the recurrent selections (without any selection pressure for maturity) and compare them with the inbred selections (figure A).

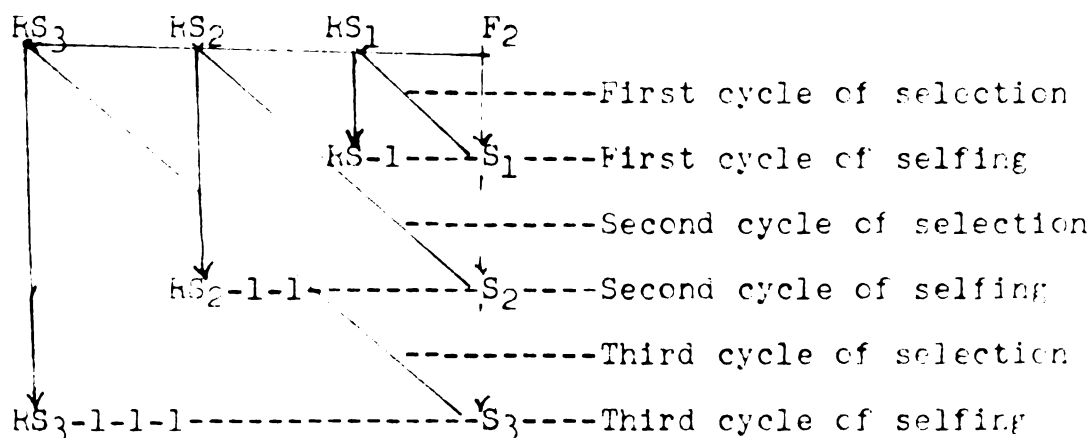
This would have required self-pollinating the KS_1 selections once, the KS_2 selections twice, the KS_3 selections three times, and then comparing the $KS-1$, KS_2-1-1 and the

* Mohamed, Ali. Inheritance of quantitative characters in Zea Mays. 1. Estimation of the number of genes controlling the time of maturity. Genetics. 713-724, 1959.

KS₃-1-1-1 groups with the S₁, S₂ and S₃ breeding groups.

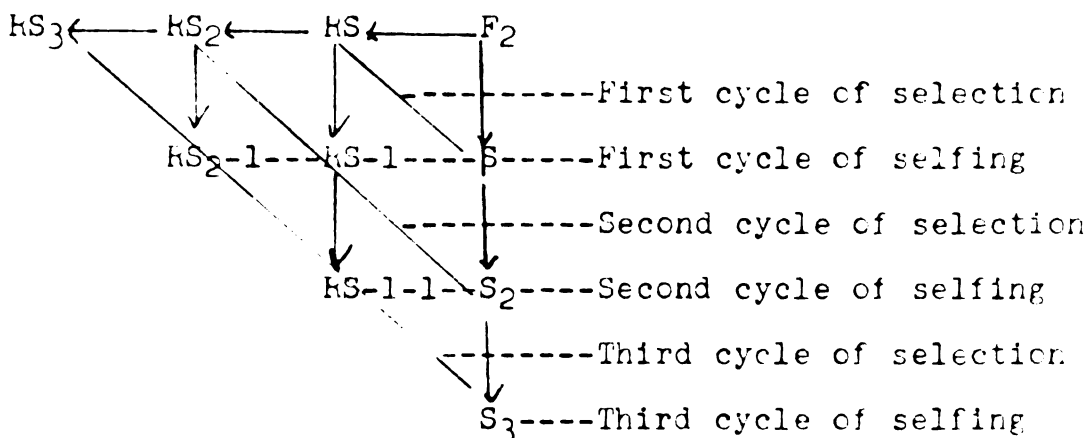
This selfing of the recurrent selected groups could have been done in winter in the greenhouse or in Florida since no selection was involved.

Figure A. Breeding diagram that should have been used to compare recurrent selected and inbred series.



In this study, selection pressure and inbreeding pressure (selfing) were applied at the same time, (figure B) and their effects could not be separated.

Figure B. Breeding diagram that was used to compare recurrent selected and inbred series. This was the procedure that was used.



Comparing inbred and recurrent lines in testcross is possibly the best method to overcome the effects of inbreeding depression. Furthermore, since the ultimate objective is to utilize inbred lines in hybrid combinations, their evaluation for maturity is of primary importance.

Study of ear-to-row variance for days to silking (Table 7B) and for ear moisture content at harvest (Table 15) indicated that gene frequency was at equilibrium after one or two cycles of breeding. Such an equilibrium occurs in the two following situations:

(1) When the homozygote has an advantage over the heterozygote as in the case of selection for late-maturity, the only stable equilibrium is at the point of fixation of the preferred allele. Thus, if the expression for the rate of change in allelic frequency per generation

$$q : \frac{sq(1-q)^2}{1 - s(1-q)^2} \text{ is set equal to zero, it can}$$

readily be seen that for values of s other than zero, the only roots of q are zero or 1.

(2) On the contrary, when the heterozygote is preferred over either homozygote, as possibly in the case of early recurrent series, the equilibrium value of q is determined in the following manner (16):

Box 1. Gene frequencies when heterozygote is favored over both homozygotes.

Genotype	AA	Aa	aa	Total
Initial frequency	q^2	$2q(1-q)$	$1-q^2$	1
Selective value	$1-S_A$	1	$1-S_a$	
Parents selected	$q^2(1-S_A)$	$2q(1-q)$	$(1-q^2)(1-s_a)$	$1-S_A q^2 - S_a(1-q)^2$

The change in q in successive generations is then

$$q: \frac{q(1-q) \quad S_a(1-q) - S_A q}{1-S_A q^2 - S_a (1-q)^2}$$

When this expression is equated to zero, the equilibrium value of the frequency of A is

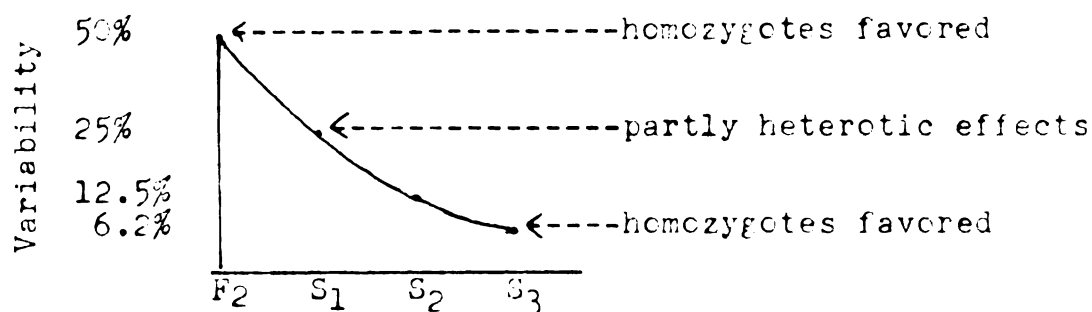
$$q_A = \frac{S_a}{S_A + S_a}$$

and that of a is

$$q_a = \frac{S_A}{S_A + S_a}$$

If there is only slight heterocsis, variability would decrease slowly and some progress would be expected, Figure C.

Figure C. Decrease in variability when homozygotes, heterozygotes are favored.

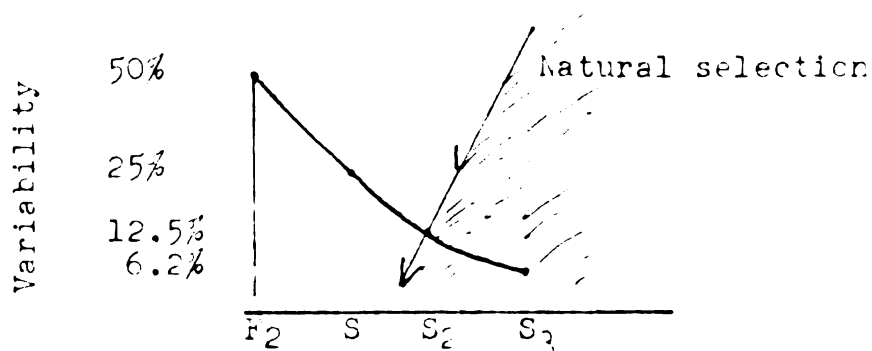


No progress for early silking date (Table 9) was made after the first breeding cycle in either the recurrent series or inbred series from the double-cross Michigan 51E. Row variance in the early recurrent series (Table 7B) attained an equilibrium at a higher value than that for the inbred series or than that of the parental lines. It might be assumed that progress for early maturity in this population ceased, not because of lack of variability, but because the heterozygotes were favored. The only way to overcome heterotic effects would be to resort to testcrossing.

In the other populations, row variance in the early breeding groups equated the variance of the early parental lines (Table 7B), indicating that variability was exhausted.

In the late-maturity groups the recessive homozygote was favored regardless of heterosis. After three cycles of selfing, no variability would remain unless natural selection played a role in removing the unfit homozygote from the population (Figure D).

Figure D. Variability of the late inbred series as affected by natural selection which removes the unfit homozygotes.



Natural selection played such a role in the 1a.153 x W25 population. Progress toward late-maturity ceased. Many plants died or did not reproduce. These degenerative aspects of inbreeding also affected late populations of the early-x-late crosses. Lethal factors which may have been present in the original population or caused by mutation were brought to the recessive condition by selection for late maturity.

SUMMARY

The relative effectiveness of continuous inbreeding with selection compared to three cycles of recurrent selection for corn maturity as measured by silking date was studied in populations derived from two double-cross hybrids and four single-cross hybrids.

Direct comparison in the nursery between recurrent and inbred series was difficult due to inbreeding depression which masked the effectiveness of the breeding methods. Decline in fertility and vigor and delayed maturity were among the general effects of inbreeding and are referred to as inbreeding depression.

Inbreeding depression affected the inbred series more than the recurrent selection series. In recurrent selection only one plant in each row was selected in order to maintain inbreeding pressure at a minimum. With inbreeding and selection, plants were selected within and among rows.

To overcome the effects of inbreeding depression, it was suggested that the recurrent selections should be inbred (without selection pressure for maturity) and compared with the inbred selections.

Nursery results indicated that both methods had been very effective in dividing the original F_2 material into two maturity groups and that fixation of genes was rapid. Fixation of genes was very rapid in a population from an early-x-early

single cross (Ia.153 x W25) and less rapid in a population from an early-x-late single cross (M324A x L317).

In a corn breeding program, the ultimate objective is to utilize inbred lines in hybrid combination. Thus, evaluation of lines for maturity in testcrosses is important. Comparing inbred and recurrent lines in testcrosses is possibly the best method to overcome the inbreeding depression effects which masked the effectiveness of the breeding methods when compared in the nursery.

Testcross results indicated that the early inbred series were earlier than recurrent series in two of the three cases, and the late inbred series were later than the recurrent series in one of the three cases. However, the differences between the two series were very small, indicating that the two methods were equally effective. Very rapid fixation of genes and equal effectiveness of the two breeding methods indicated that few genes for maturity were involved.

Lines that were both earlier and later in maturity than the parental lines of the original crosses were obtained in both recurrent and inbred series.

In all the testcross experiments there was a wide range for yield among the selections within a maturity group, indicating that selection for combining ability could be effective within the maturity groups.

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APPENDIX

Figure 1. Mean days to silking for the four parental lines, F₁, F₂ and the nine inbred and recurrent selection breeding groups in the early and late maturity series from Michigan 51B.

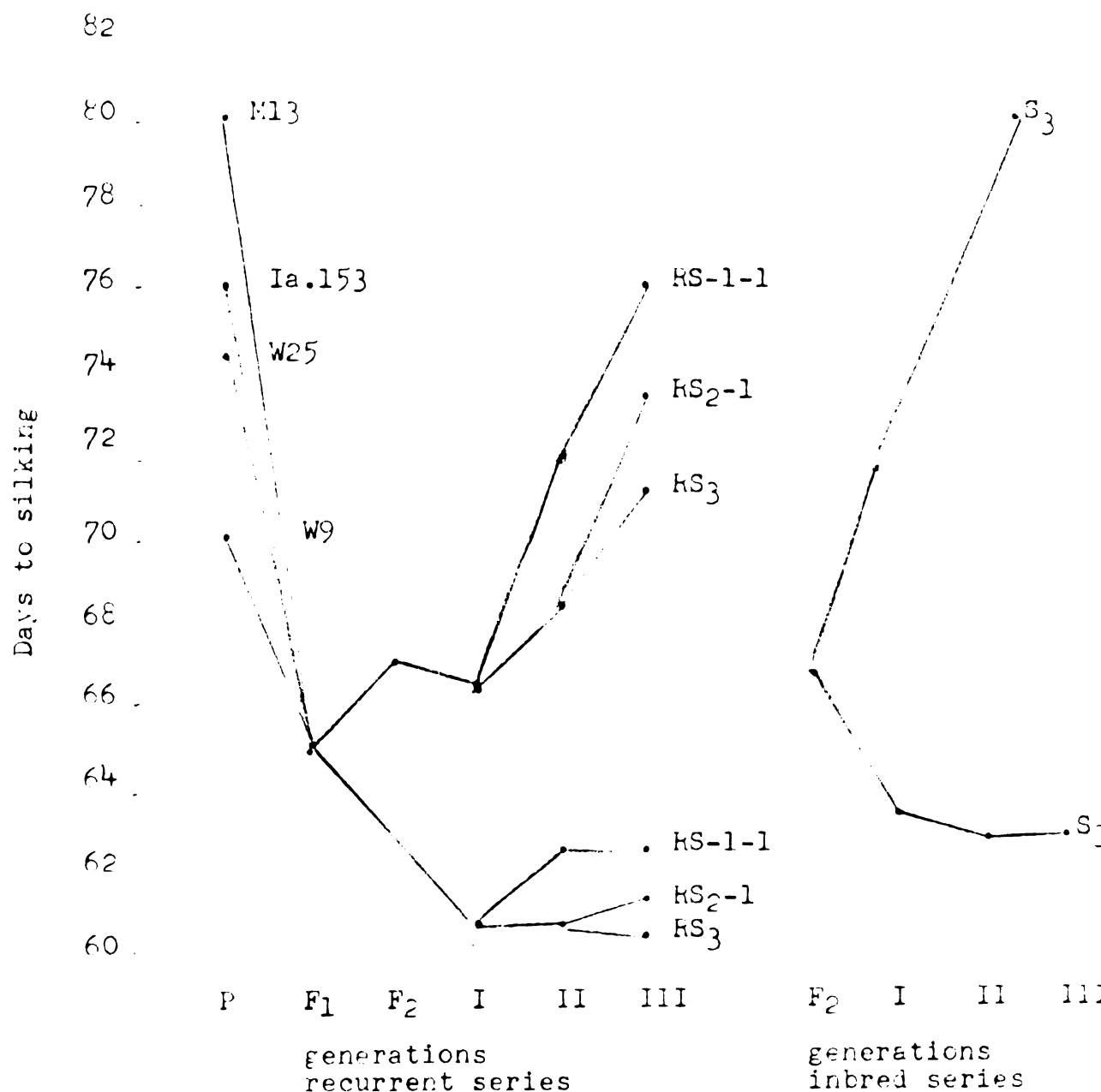


Figure 2. Mean days to silking for the two parental lines, F₁, F₂ and inbred and recurrent selection breeding groups in the early and the late maturity series from (H53 x 38-11).

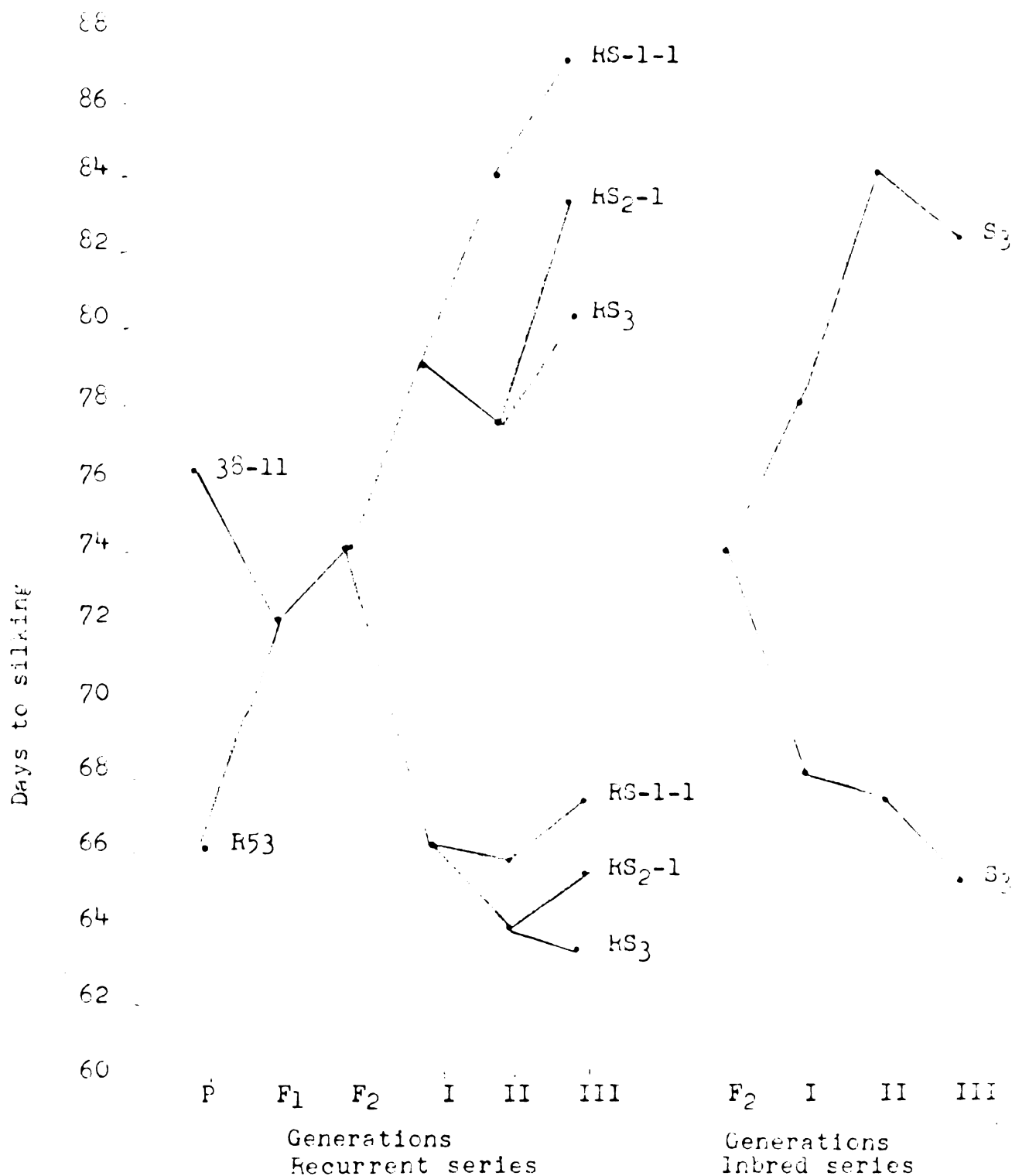


Figure 3. Mean days to silking for the two parental lines, F_1 , F_2 and the nine inbred and recurrent selection breeding groups in the early and late maturity series from (MS24A x 38-11).

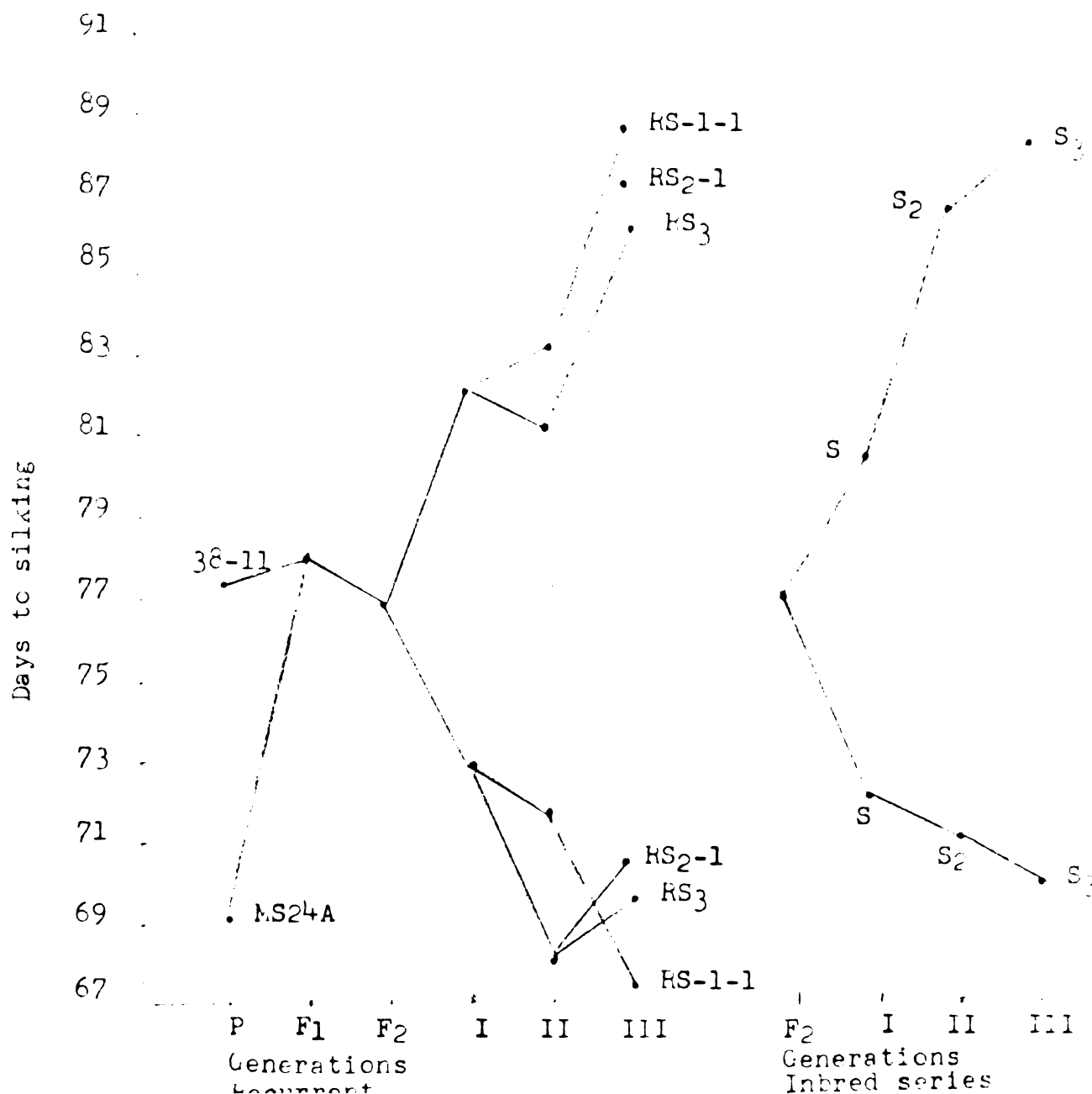


Figure 4. Mean days to silking for the four parental lines, F_1 , F_2 and the nine inbred and recurrent selection breeding groups in the early and late maturity series from Michigan 20D.

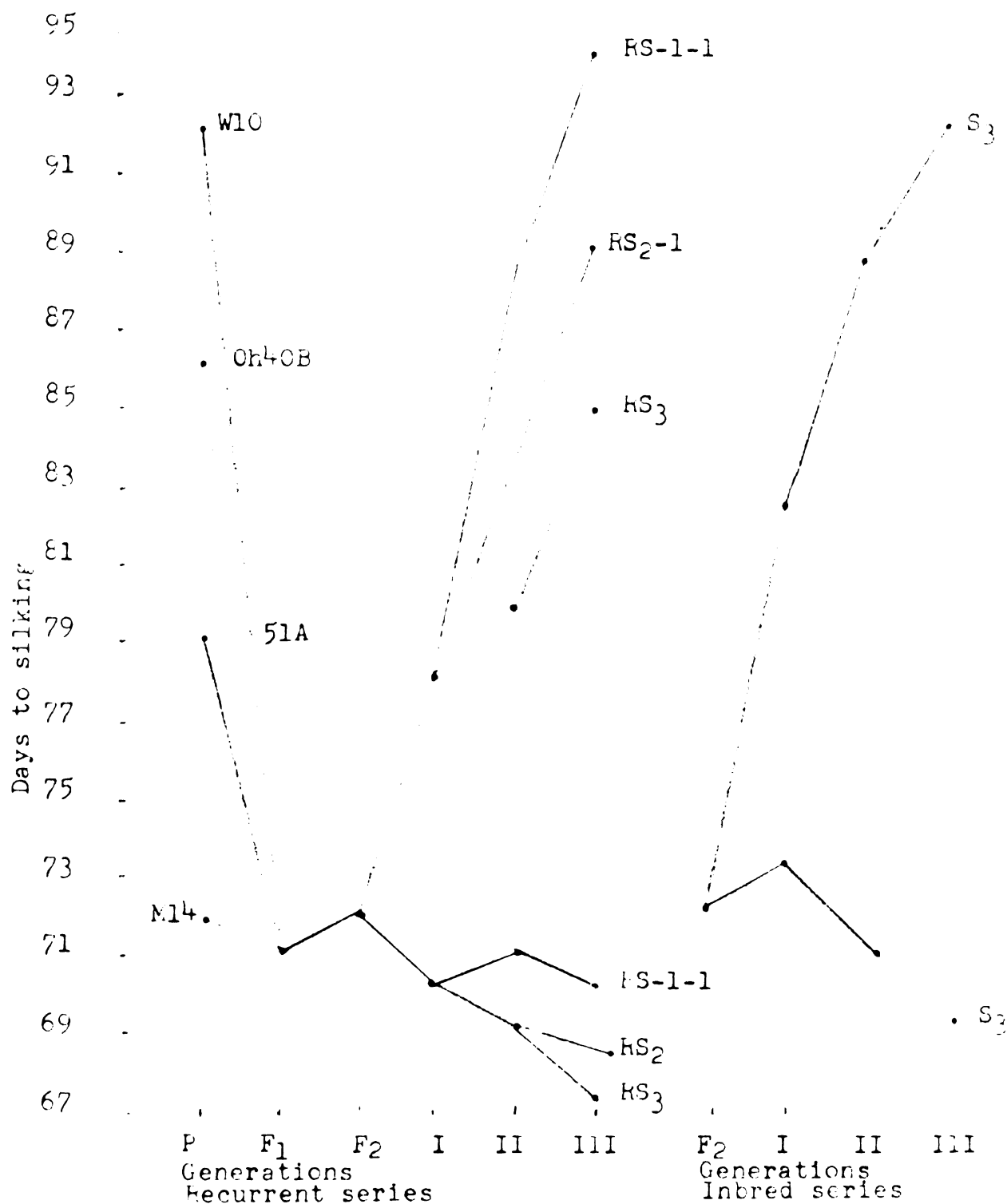


Figure 5. Mean days to silking for the two parental lines, F_1 , F_2 and the nine inbred and recurrent selection breeding groups in the early and late maturity series from (Ia.153 x W25).

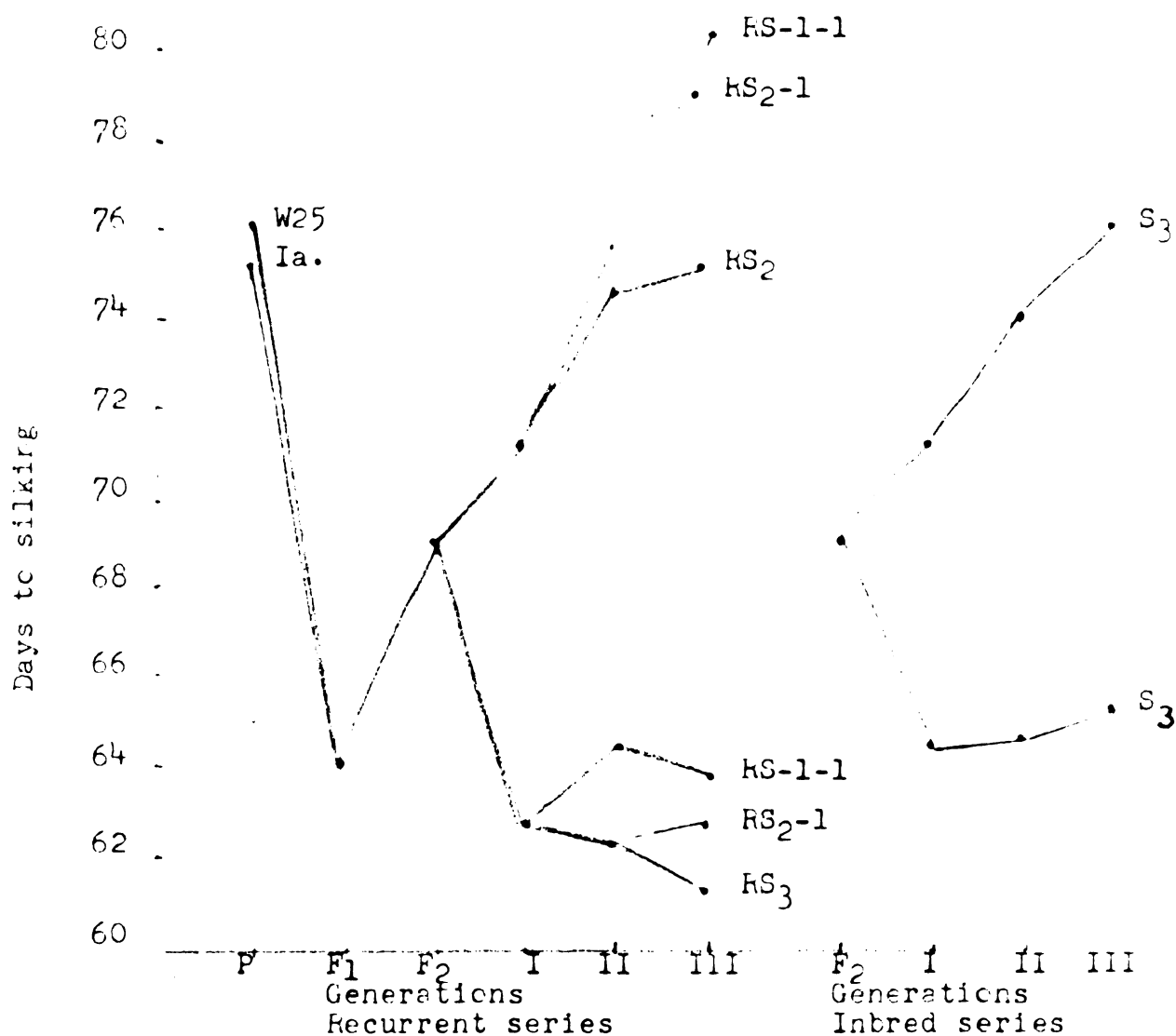


Figure 6. Mean days to silking for the two parental lines, F₁, F₂ and the nine inbred and recurrent selections breeding groups in the early and the late maturity series from (MS24A x L317).

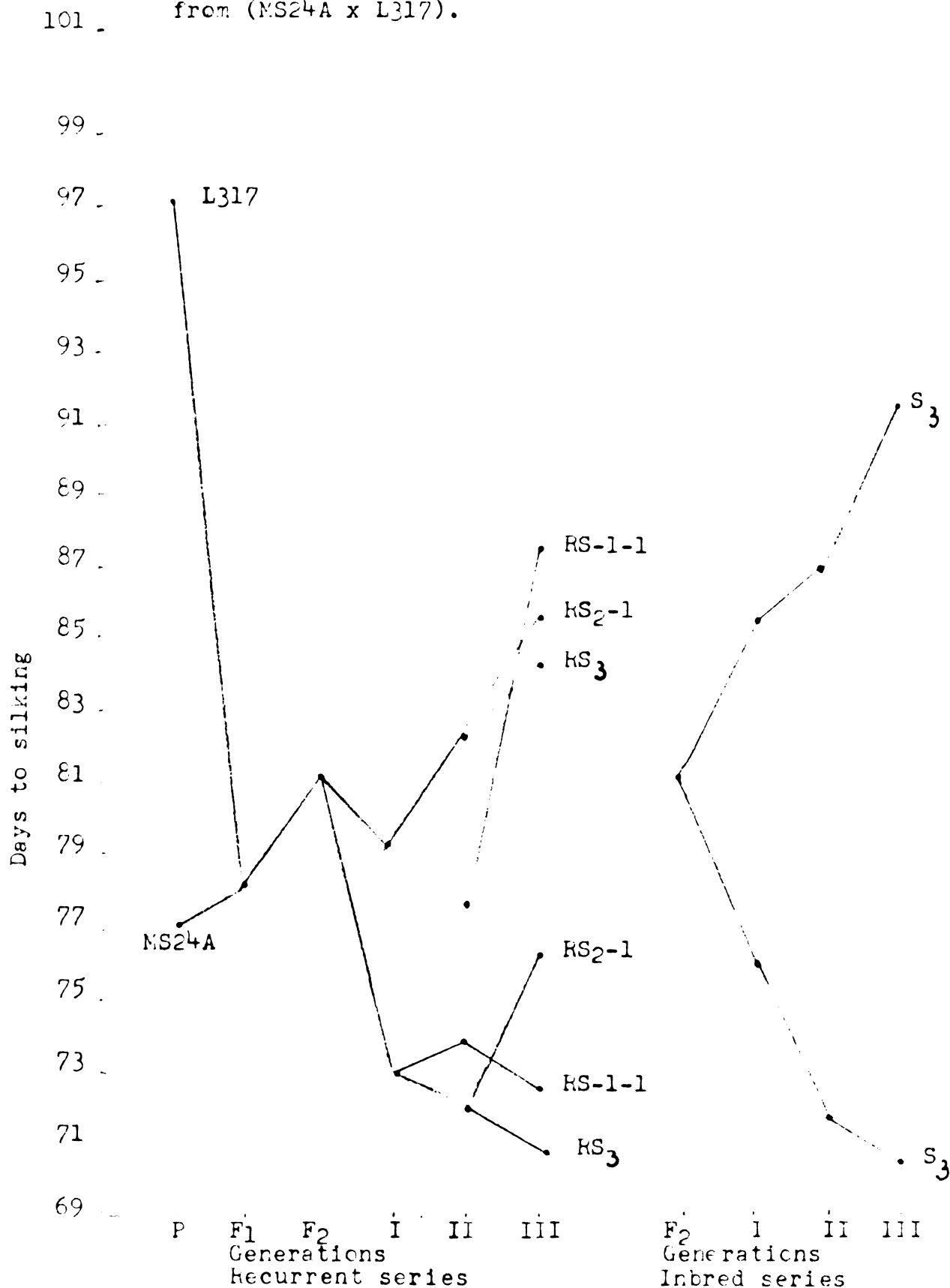


Figure 7. Mean moisture content for the four parental lines F₁, F₂ and the nine recurrent selections and inbred breeding groups of the early and the late maturity series from Michigan 51B.

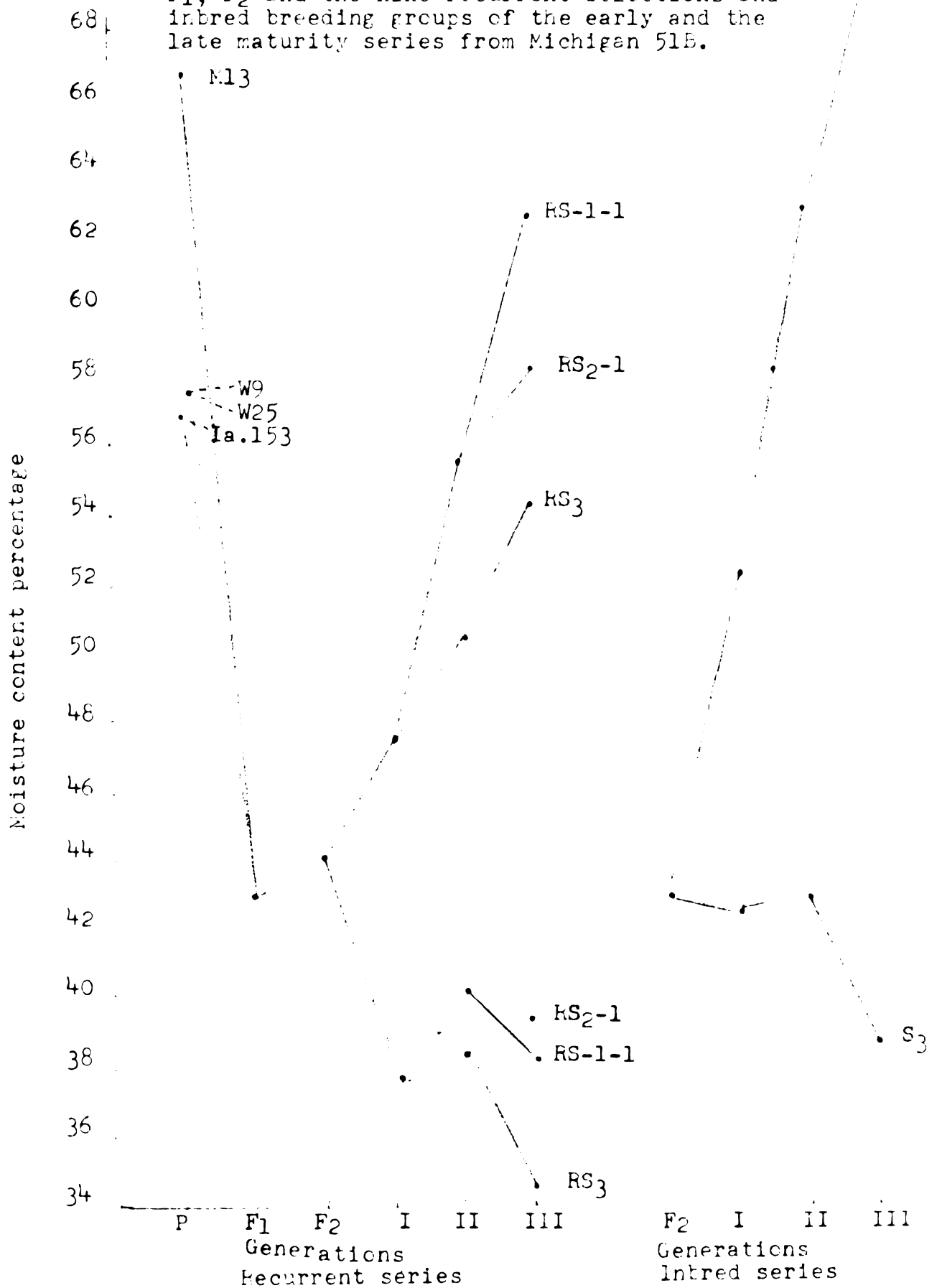
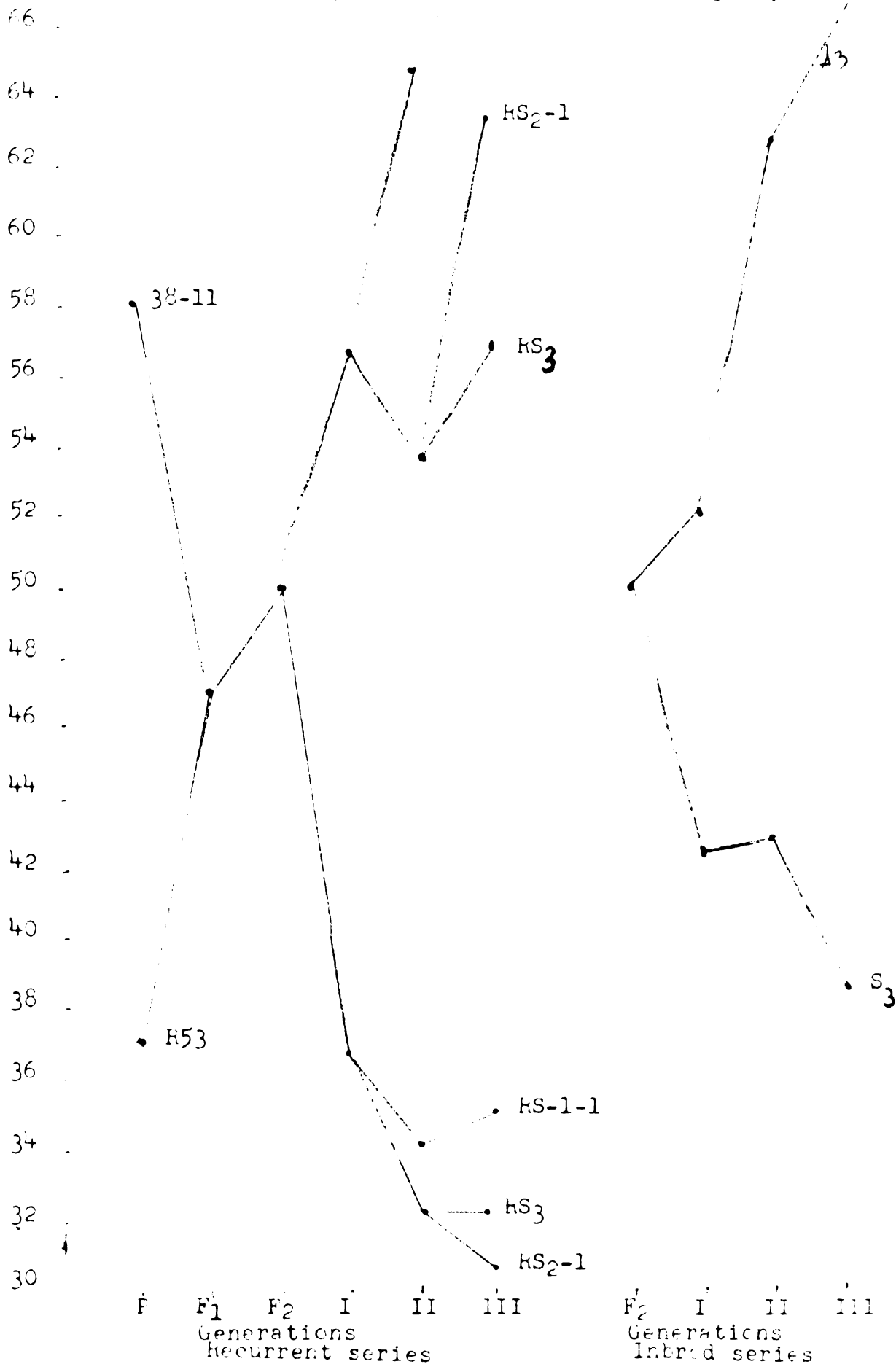


Figure 8. Mean moisture content of lines, F_1 , F_2 and the and inbred breeding and late maturity

the two parental nine recurrent selections groups of the early series from (R53 x 38-11)

Moisture content percentage



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