

AN ABSTRACT OF THE THESIS OF

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Title: HETEROISIS AND INBREEDING IN THE PROGENY OF  
GENETICALLY DIVERSE PARENTAL CLONES OF FESTUCA  
ARUNDINACEA SCHREB.

Abstract approved: Redacted for privacy  
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The response of maturity, vigor, plant spread, plant height, three forage harvest yields, and total forage yield to heterosis and inbreeding was studied in tall fescue. Parent clones selected for diverse anthesis date, origin, and morphology were separated into two groups based on anthesis date, those having early maturity and those having late maturity. Parents, single-cross (SX), and first generation selfed ( $S_1$ ) progeny were field evaluated.

Parents,  $S_1$ , and SX progeny were space planted on a .914 x 1.219 meter basis at the Hyslop Agronomy Field Laboratory, Corvallis, Oregon, in September, 1969. A randomized block design having four blocks and 14 plant rows as entries was used. Data were collected during the spring, summer, and fall of 1972.

Single-cross progeny had a mean performance better than their

midparents' mean performance for all characteristics, with all differences significant except for plant height and third harvest forage yield. Single-cross progeny averaged 7.03, 13.18, 13.50, 3.89, 42.93, 51.72, 15.14, and 37.12 percent better than their midparents for maturity rating, vigor rating, plant spread, plant height, first, second, and third harvest forage yield, and forage yield, respectively.

There was a greater frequency of individual single-crosses that exhibited significant heterosis in the early x late group than in either the early x early or late x late groups. In addition the average heterotic response of the early x late group was consistently greater than that of either of the other two groups. Thus it appears significant heterosis is more likely to occur, and is likely to be of a greater magnitude, in the progeny of parents having maturity differences, and presumably, greater genetic differences.

Significant variation occurred among the single-cross maturity group means for all characteristics with the early x early single-crosses most often being the better performers. Consequently the additional heterosis observed in the early x late group was usually insufficient to bring performance of this group up to that of the higher performing but less heterotic early x early single-crosses. This suggests heterosis may be of little practical importance.

Inbreeding depression of  $S_1$  progeny was significant for all characteristics. The inbreeding depression was of the greatest

magnitude in the progeny of the early parents. Performance of early parents and early  $S_1$  progeny was generally better than that of their late counterparts.

Heritability estimates were high, particularly those obtained by regressing single-cross progeny on midparents, although two did not differ significantly from zero. The coefficients of determination for the same associations were likewise high, with over 70 percent of progeny variation being explained by linear association with parents for most characteristics. As superior progeny came from superior parents, this high degree of association suggests clonal evaluation may be an effective screening method in tall fescue.

There was strong association among the characteristics of maturity rating, plant spread, plant height, first and third forage yield, and total forage yield, with the lowest of these coefficients of determination,  $R^2 = .6031$ , occurring between maturity rating and plant spread. Vigor rating, second harvest yield, seedling vigor index, and panicle number showed little association among themselves or among the other characteristics, with the highest association,  $R^2 = .3599$ , occurring between panicle number and third harvest yield. Seed yield was moderately associated with forage characteristics, with  $R^2$  values of about .5000, but showed no association with panicle number.

Heterosis and Inbreeding in the Progeny of  
Genetically Diverse Parental Clones of  
Festuca arundinacea Schreb.

by

Blaine Earl Johnson

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HETEROSIS AND INBREEDING IN THE PROGENY OF  
GENETICALLY DIVERSE PARENTAL CLONES OF  
FESTUCA ARUNDINACEA SCHREB.

INTRODUCTION

Heterosis, the increased vigor or performance of single-cross progeny relative to the average of the parents, is a phenomenon that might be utilized by forage breeders for increasing forage production. Not only does it offer a possible direct route via use of superior single-crosses, it helps to define genetic relationships that may exist in a species, so a plant breeder can better manipulate his plant material for variety improvement.

It has been observed in many crop species that larger genetic differences increase the heterotic response. While it is logical to assume the same is true for forage species, there has been little evidence collected either in support of or against such relationships in the grasses. Consequently this study was undertaken in tall fescue, Festuca arundinacea Schreb., to provide such information, and more generally, to gain a better understanding of parent-progeny relationships in the species.

The primary objectives were:

1. To examine the relationship between genetic diversity and heterotic response by studying plant maturity, vigor,

spread, height, and forage yield, and to study inbreeding of the same parents.

2. To study the relationships between parent and progeny performance.
3. To study the relationships that occur among forage characteristics, seedling vigor, and seed yield characteristics.

## LITERATURE REVIEW

Effective use of heterosis requires that the plant breeder understand the character and the relative magnitude of the heterotic response expected from various parent materials. As early as 1912 East and Hayes (East, 1936) expressed the opinion that heterosis in maize increased with increased genetic differences between the parents. Since then, workers have carried out studies in maize, sorghum, wheat and other crops (Pateriani and Lonquist, 1963; Moll et al., 1965; Neihaus and Pickett, 1966; Grant and McKenzie, 1970) in an effort to better understand the relationship between heterosis and genetic diversity.

Lonquist and Gardner (1961) worked with intervarietal crosses in maize. They utilized 12 open pollinated lines, which represented a broad range of genetic diversity, in making a complete diallel. The parent varieties, their 66 intervarietal crosses, and an  $F_1$  double cross hybrid which served as a check were then evaluated for yield performance during two years at two locations. Average heterosis of the  $F_1$  yield was 108.5 percent relative to the midparent and 102.8 percent relative to the high parent. A comparison of all crosses showed 92.4 percent of the crosses exceeded the midparent for yield. The additive effects of the varieties were found to be more important than the non-additive effects; however, the authors noted there were

some important non-additive effects which could be considered in planning a breeding program.

Pateriani and Lonquist (1963) used representative collections of 12 races of corn and  $F_1$  crosses among them in a study of heterosis in interracial crosses of corn. Several morphological types were used, representing well defined races from different parts of Central and South America. Sufficient seed for testing was obtained from 62 crosses among the races.

The 12 races, 62 intercrosses, and 5 check varieties were grown in three yield trials at three different locations and evaluated for grain yield. The mean relative heterosis of the  $F_1$ 's averaged 133 percent of the midparent, and 114 percent of the high parent. Of the 62 crosses, 61 exceeded the midparent yields and 48 exceeded the high parent in yield. Yields of the parental varieties were associated with yields of the  $F_1$  crosses with correlation of midparent versus  $F_1$  cross being  $r = 0.677$ .

Moll, Salhauna and Robinson (1962) reported results from a study of heterosis and genetic diversity in varietal crosses of maize. They made reference to Gilbert (1960) who stated increased heterozygosity might be detrimental rather than advantageous. Moll and his associates used six varieties in their study, two from midwestern U.S., two from southeastern U.S., and two from Puerto Rico. The varieties were crossed in all combinations with one interregional cross failing to

produce seed. The smallest heterosis was found in crosses involving varieties from the same region; heterosis of the southeastern x mid-western crosses tended to be intermediate, with the greatest heterosis being found in crosses involving U. S. varieties and Puerto Rican varieties. It was postulated the U. S. (both southeastern and mid-western) x Puerto Rican variety crosses represented the greatest genetic diversity. The Puerto Rican parents were the lowest yielding varieties, yet were involved in crosses producing the highest yielding progeny. It was concluded that genetic diversity of the parent varieties is associated with greater heterosis in the variety crosses of maize.

The six varieties used by Moll et al. (1962) along with two additional Mexican varieties were used by Moll et al. (1965) in an experiment initiated to determine if heterosis in maize increases with increasing genetic divergence of the parent populations throughout the entire range of diversity of the species. Whereas the earlier study was carried out in one region, the later study was conducted in all three areas from which the plant material originated in order to balance effects due to differences in adaptation. Eight levels of genetic divergence were postulated on the basis of ancestral relationships and differences in adaptation. Genetic divergence of the crosses ranged from within variety crosses having the least to the U. S. and Puerto Rican x Mexican corns showing the most. The plant material evaluated consisted of the eight populations, the 28  $F_1$  crosses among them, and

the corresponding 28  $F_2$  populations. It was found by analysis of variance, variation for yield, ear number, and days to tasseling among levels was 8, 2, and 7, respectively, times greater than variation within levels. Heterosis expressed as the difference between the  $F_1$  mean and the average of the parental varieties increased with increased genetic divergence up to a level and then decreased with further increases in divergence. Moll and his co-workers concluded there is an optimum degree of genetic divergence for maximum expression of heterosis in maize, and that the optimum occurs within a range of divergence that is narrow enough that incompatibility barriers are not apparent.

Niehaus and Pickett (1966) made a complete diallel cross in Sorghum vulgare using eight inbred lines. Three of the lines were from relatively new introductions which differed in height and maturity from the other five lines. All  $F_1$ 's exceeded midparents for yield with those  $F_1$ 's having one of the three recent introductions as a parent performing exceptionally well. Analysis of the  $F_1$  and  $F_2$  showed non-additive effects were significant at the one percent level in the  $F_1$  but were of less importance in the  $F_2$ . The authors concluded genetic diversity is the key to hybrid vigor in sorghum and noted that even though the three introductions varied considerably in height and maturity, they consistently gave very tall and late maturing hybrids.

Grant and McKenzie (1970) selected three spring wheat cultivars and three winter wheat cultivars on the basis of their differences in genetic background. Crosses were made between the two types and then the progeny grown in yield trials on irrigated and non-irrigated soils. Yields up to 40 percent higher than those of the spring wheat parents were attributed to heterosis resulting from hybridization of the two genetically different parental types. Other workers (Nettevich, 1968; Walton, 1971) have also emphasized the importance of genetic diversity among parents used in wheat hybrids.

Jenkins (1969) selected three varieties of Avena byzantina originating in California, Australia, and South Africa, along with a Dutch variety of A. sativa to study heterosis and combining ability in oats. In the  $F_1$  trial there was heterosis for grain yield with the  $F_1$  average being 109 percent of the high parent average. Individual cross means varied from 68 percent to 139 percent of the high parent. Heterosis was greater in the sativa x byzantina crosses than in the sativa x sativa crosses.

Heterosis for lint yield and yield components in intra- and interspecific crosses among varieties of Gossypium hirsutum L. and G. barbadense L. was estimated by Marani (1963). Three varieties of each of the two species were inbred via selfing for two generations and then used to make a complete diallel cross. The 15 crosses and the six parents were field evaluated during two seasons. Heterosis

for lint yield was higher in the interspecific crosses than in the intraspecific crosses. This increase was largely due to an increase in the number of bolls produced. No heterosis for boll size was observed in interspecific crosses, while boll size did increase in the intraspecific crosses. While additive type variation was the main component of genetic variation, Marani noted some crosses exhibited persistent non-additive effects.

In 1961 and 1962 Marani (1967) did further work involving inter- and intraspecific crosses of cotton using four varieties of Gossypium hirsutum L. and four varieties of G. barbadense L. The average magnitude of heterosis for lint yield was 24.5 percent and 21.6 percent increase over the midparent for the intraspecific crosses of G. hirsutum and G. barbadense, respectively, compared with a 72.8 percent increase in the interspecific crosses. Combining all inter- and intraspecific crosses made by Marani (1968) the intraspecific crosses involving hirsutum showed significant increases over the midparent for lint yield in two out of four trials, for the barbadense intraspecific crosses the increase was significant in three out of four trials, and for the interspecific crosses the increase was significant in all four trials. Only the interspecific crosses showed consistent significant increases in lint yield over the high parent.

In a study of genetic diversity and heterosis in tobacco, Vandenberg and Matzinger (1970) made crosses between adapted U. S.

flue-cured varieties and introduction material of native and primitive strains. Comparing the results of this study with earlier studies (Matzinger and Wernsman, 1967, 1968), it was found heterosis for most characters was greatest in  $F_1$  progeny obtained from crossing flue-cured varieties to progenitor species, less heterosis was obtained from crosses involving flue-cured varieties and introduction material from the presumed center of origin of the species, and crosses between flue-cured varieties and Oriental varieties, with the least heterosis being observed in crosses among flue-cured varieties. The number of characters having significant non-additive genetic variation was greater in the flue-cured x introduction crosses than normally found in flue-cured variety intercrosses.

Foster (1971) studied heterosis in Lolium perenne under non-competitive conditions. Six established varieties with similar anthesis date were chosen as parent populations. Based on the assumption that geographically separated populations are usually genetically dissimilar, an attempt was made to select unrelated populations. Each of the 15 intervarietal crosses was made in two ways. In the first, equal proportions of seed of the two parental populations of each pair were bulked, sown in a solid stand, and harvested to provide an  $F_1$  hybrid seed mixture, H50, which theoretically contained approximately 50 percent intervarietal  $F_1$  hybrids. The second method consisted of bagging together the paired panicles of parent plants. Based on

sterility studies this second method produced virtually pure  $F_1$  inter-varietal hybrid seed, H100. The 15 H50 populations, the 15 H100 populations, and the parents were then field evaluated for two years utilizing four randomized blocks with a 2 x 2 foot plant spacing.

During the first year the H50 hybrids were inferior in forage yield to their parents, but showed a 5.9 percent (relative to mean of parents) average heterosis in the second year. Only in the last harvest of the second year did the H50 hybrids show statistically significant (5 percent level) heterosis. Over the two-year harvest period the H50 hybrids produced only 1.1 percent more forage than their parents. The H100 hybrids exhibited much more heterosis than the H50 hybrids. Average heterosis over the period was 14.7 percent and was slightly higher in the second year. In six of the seven harvests the H100 hybrids averaged significantly (5 percent level) more forage than the parents. The H100 group also significantly outyielded the H50 in six of the seven harvests.

Wilsie (1958) studying genetic diversity and heterosis in alfalfa crossed a tall, erect, coarse-stemmed clone and tall, erect, fine-stemmed clone with a prostrate, viny, low yielding, wild type selection.  $F_1$  progeny were evaluated along with the parents for forage yield per plant. The  $F_1$  plants from the two crosses yielded 81 percent and 43 percent above the higher yielding parent. A high degree of variability was noted in the  $F_1$  progenies.

Sriwatanapongse and Wilsie (1968) compared the expression of heterosis in interspecific, intervariety, and intravariety crosses. Two varieties of Medicago sativa and one variety of M. falcata were used to make 60 crosses and reciprocal crosses among and within three populations. The  $F_1$  progenies along with three parental check varieties were field evaluated for forage yield and associated agronomic characters. The interspecific crosses resulted in the highest degree of heterosis for yield, with the within variety crosses showing the least heterosis. This was not true for rate of recovery or persistence where the intra-sativa crosses recovered faster and showed a higher level of persistence than either the intra-falcata crosses or the interspecific crosses.

Brown, Thomas and Kalton (1969) investigated potential heterosis in alfalfa hybrids. Using Flemish and Vernal parental clones, Flemish x Flemish, Vernal x Vernal, and Flemish x Vernal hybrid seed was produced by hand crossing. The hybrids along with several check varieties were evaluated for forage yields under solid planted competitive conditions. In three out of four tests the Flemish x Vernal hybrids produced more forage than either the Flemish x Flemish and the Vernal x Vernal hybrids. The mean yields of the check varieties were exceeded by the yield of the Flemish x Flemish hybrids in two trials, by the Vernal x Vernal hybrids in three trials, and by the Flemish x Vernal hybrids in all four trials. The workers concluded

there is considerable heterosis for yield in crosses between alfalfa clones of diverse genotype, and the more diverse the germ plasm of the parents the more the hybrid vigor exhibited. It was also noted hybrid vigor showed up as early as the seedling year.

Moutray (1971) studied the effects of genetic diversity on response of heterosis in tall fescue, Festuca arundinacea Schreb. Nine parental clones of diverse morphology, anthesis date, and origin were used to produce first generation selfed ( $S_1$ ) seed and single cross (SX) seed. Three types of single crosses were made with respect to anthesis date, these being early x early, late x late, and early x late. Parents,  $S_1$ , and SX were evaluated in the field in a space planted nursery to determine whether or not heterosis occurred for plant height, anthesis date, panicle number, seed yield, and fall vigor rating. Single crosses averaged 15.4, 2.6, 28.2, 24.8, and 23.0 percent above the midparent for height, early anthesis date, panicle number, seed yield, and fall vigor rating respectively. Crosses between maturity groups resulted in the greatest expression of heterosis above the midparent for all characteristics and also exceeded the high parent for panicle number. Early x early had the most vegetative vigor and were tallest. Moutray concluded crosses between parents of diverse morphology and origin result in greater expression of heterosis than crosses among similar parents.

Moutray (1971) utilized the above plant materials in a study of

vigor and vigor characteristics in single cross and first generation selfed seed and seedlings. Respiration, germination, root and shoot growth, rate of growth, and unit growth were measured. The early x late SX group of crosses was found to be intermediate between early x early and late x late groups for seedling vigor characteristics. Early  $S_1$  and early x early SX groups were the more vigorous groups. Little difference was detected between the total  $S_1$ 's and the total SX with the average performance of both groups being very similar for most characteristics.

## MATERIALS AND METHODS

Plant Material

Nine parental clones having differences in morphology, anthesis date, and origin were selected from a plant introduction nursery for this study. A description of the parents is given in Table 1. The parents were separated into two groups with regard to anthesis date; "earlies" and "lates." While there was considerable variation within each of the two groups, the early parents tended to be taller, wider, and have narrower leaves than the late parents; thus, it was assumed there was greater genetic diversity between the two groups than within either group.

During the winter of 1968, crosses were made by bagging together panicles of the parent plants. Single cross (SX) seed was produced by three early x early crosses, three late x late crosses, and three early x late crosses. First generation selfed ( $S_1$ ) seed was produced at the same time by bagging panicles of individual parents prior to anthesis.  $S_1$  seed was obtained from five of the early parents and three of the late parents. Seedlings were placed in peat pots 6 cm square after germination and held in the greenhouse until field establishment. Vegetative propagations of the parent clones were made at the same time the SX and  $S_1$  seed was germinated and handled in a manner similar to the progeny seedlings. The crossing,

Table 1. Description<sup>1</sup> of parental clones used in heterosis and inbreeding study.

Clone	Origin	P.I. number	Anthesis date <sup>2</sup>	Self-fertility <sup>3</sup>	Plant height <sup>4</sup>	Leaf width <sup>4</sup>	Plant width <sup>4</sup>	Panicle number <sup>4</sup>
<u>Early</u>								
P <sub>1</sub>	Switzerland	234-906	May 15	45.00	1	8	2	2
P <sub>2</sub>	Yugoslavia	251-583	May 18	45.80	4	5	5	2
P <sub>3</sub>	Spain	234-047	May 21	9.05	3	5	4	4
P <sub>4</sub>	Greece	199-249	May 27	29.43	3	5	4	5
P <sub>5</sub>	Uruguay	203-728	May 29	29.68	2	5	3	7
<u>Late</u>								
P <sub>7</sub>	Poland	274-617	June 10	14.30	3	4	5	6
P <sub>8</sub>	Yugoslavia	253-311	June 15	21.05	7	2	9	5
P <sub>9</sub>	Turkey	174-209	June 28	3.63	7	9	10	10
P <sub>10</sub>	Switzerland	234-885	June 28	29.33	8	5	8	5

<sup>1</sup>Moutray, J. 1971. An examination of seedling vigor and the effects of genetic diversity on response to heterosis in tall fescue (*Festuca arundinacea* Schreb.). Ph.D. thesis. Corvallis, Oregon State University. 103 numb. leaves.

<sup>2</sup>1967

<sup>3</sup>Weight of selfed seed from three five-panicle samples divided by seed weight of 15 open-pollinated panicles.

<sup>4</sup>Phenotypic rating 1-10 June 4, 1969. 1 represents tallest plant, finest leaves, widest plant, most panicles.

germination, and establishment was done by Moutray (1971) for an earlier study.

### Establishment and Maintenance

The nine parents, nine single-crosses, eight  $S_1$ 's, and the variety Fawn were space planted on a .914 x 1.219 meter basis at the Hyslop Agronomy Field Laboratory, Corvallis, Oregon, on September 23, 1969. The nursery was planted in a randomized block design using four blocks and 14 plant rows as entries. There were not enough seedlings of the selfed generation of parent seven for establishment in all blocks and consequently were not used in this study. Extra plants of the check variety, Fawn, were used as border plants.

The plants were irrigated via the farm water wagon in 1969 prior to the fall rain, received no irrigation during 1970 or 1971, and were irrigated with the farm sprinkling system during the summer of 1972 on June 28, July 21, August 8, and September 14. Fertilizer was applied at the rate of 67.26 kg/ha of 45-0-0 on November 29, 1969, 44.84 kg/ha each of 45-0-0 and 16-20-0 on April 1, 1970; N at 89.68 kg/ha on October 26, 1971, and 44.84 kg/ha of 45-0-0 on May 5, 1972. Weeds were controlled by frequent hoeing during the spring and summer months, along with diuron applications at the rate of 3.363 kg/ha during November of 1970 and 1971.

## Measurements

Maturity rating - Each plant was rated on a scale 1-9, with 1 equaling earliest (most panicles) and 9 equaling latest (no panicles), on April 14, 1972.

Plant vigor - Two weeks after the first forage harvest, each plant was visually rated on a 1-9 scale, 1 equaling most vigor and 9 equaling least vigor. Ratings were made on May 11 for blocks 1 and 2, May 18 for blocks 3 and 4.

Height - Each plant was measured to the nearest centimeter from ground level to the highest growing point on April 18.

Spread - Each plant was measured to the nearest centimeter across its widest part. Data were collected on May 6 for blocks 1 and 2, May 13 for blocks 3 and 4, one week following the first forage harvest.

For maturity, height, spread, and vigor, each plant was measured or given a rating. A mean value was then calculated for each entry in each block, with this mean value being used in the statistical analysis.

Forage yield - Three forage harvests were made during 1972. The first harvest was completed during two days; blocks 1 and 2 on April 27 and blocks 3 and 4 on May 4. The second and third harvests were completed in single days, June 27 for the former and October 4 for the latter. For each harvest the total yield of each entry in each

block was placed in burlap bags and oven dried at 50 C for 48 hours, then weighed on a Toledo scale to the nearest gram. The total weight was then divided by the number of plants per entry to give a mean yield in grams per plant for each entry in each block. A total forage yield was also calculated for each entry in each block by adding the per plant yield of each entry at all three harvests.

### Statistical Analysis

A midparent value for each single-cross in each block was found by calculating the mean value of the two parents involved. The midparents (MP's) and their single-cross progeny (SX's) then served as entries in a two factor analysis of variance. Comparisons were made between each midparent and its single-cross progeny; between the midparent mean and their single-cross progeny mean grouped for early x early, late x late, and early x late crosses; and between the mean of all midparents and the mean of all single-crosses.  $S_1$  progeny were likewise grouped with their  $S_0$  parents for a two factor analysis of variance. Linear comparisons were then made between each  $S_1$  and its parent, the mean of each group of  $S_1$ 's and the respective group mean of parents, and the mean of all  $S_1$ 's and the mean of all parents. An example of the comparisons is shown in Appendix B.

The mean square from the parent-progeny comparison is a measure of the difference between the parent mean and the progeny and

consequently, as the single-cross progeny show increasing amounts of heterosis, the parent-progeny mean square will increase, and likewise as the  $S_1$  progeny show increasingly greater inbreeding depressions the parent-progeny mean square will increase. Thus simple "F" tests allow tests for significant heterosis and for significant inbreeding depression. All individual parent-progeny comparisons are orthogonal in both the MP-SX population and in the  $S_0$ - $S_1$  population. Likewise orthogonality exists among all three comparisons between midparents and single-cross for maturity group means and between both comparisons of  $S_0$  parent and  $S_1$  progeny for maturity group means. Thus, comparisons made among orthogonal parent-progeny mean squares give an indication of the relative magnitude of heterosis, or inbreeding depression for the various individual crosses or self's, or groups of crosses or self's.

Estimates of heritability were calculated by regression of SX on MP's and  $S_1$  on parents. The regression coefficient is an estimate of heritability in the narrow sense (Lush, 1948) expressing the fraction of the phenotypic differences between parents which one expects to recover in the offspring (Hanson, 1963). Heritability estimates and coefficients of determination were calculated for each group of parents and progeny.

All possible simple coefficients of determination between characters were calculated using the characters measured in this study

plus the vigor index, panicle number, and seed yield as measured by Moutray (1971). Moutray defines vigor index as equaling

$$\begin{aligned} & \frac{\text{Number seed germinated to day 4}}{4} \\ + & \frac{\text{Number additional seeds germinated by day 7}}{7} \\ + & \frac{\text{Number additional seeds germinated by day 9}}{9} \end{aligned}$$

Panicle number was the number of panicles on each plant two to four days before the plant was harvested for seed. Seed yield was the total seed yield in grams per plant of each entry. Only  $S_1$  and SX data were used in calculating these coefficients.

## RESULTS AND DISCUSSION

Heterosis and Inbreeding Results

Parents,  $S_1$ , and SX progeny were field evaluated to see if increased diversity between parents for morphology, anthesis date, and geographic origin results in increased heterosis for maturity, vigor, plant spread, plant height, and forage yield.

Mean values for midparents (MP) and their single-cross progeny (SX), for parents ( $S_0$ ) and their first generation selfed progeny ( $S_1$ ) for each of the characters measured are presented in Tables 2-10, along with progeny means expressed as percent of parent means and mean squares from parent-progeny comparisons. Mean squares from analysis of variance for all characters are presented in Appendix Tables 1 and 2.

Maturity Rating (Table 2). The average maturity rating of all MP's was significantly higher than the average rating of all SX's. Although significant heterosis for earlier maturity, i. e., a lower rating, was observed in two of the three early x early (E x E) crosses, and in one of three crosses of both the late x late (L x L) and the early x late (E x L) groups, only the E x L SX's as a group were rated significantly earlier than MP's. The parent-progeny mean square of the E x L group was approximately twice that observed for either the E x E group or the L x L group. However, this was due primarily to

Table 2. Maturity ratings.<sup>1</sup> Parent and progeny means, progeny as percent of parent, and mean square associated with linear comparison between progeny and parent.

Identification	Parent mean	Progeny mean	Progeny as % parent	Mean square
	<u>Midparent</u>	<u>SX</u>		
1 x 2	4.41	3.41	77.32	1.9801*
2 x 3	3.38	4.08	120.71	1.001ns
4 x 5	5.70	4.82	84.56	1.5576*
7 x 8	8.15	7.17	87.98	1.9013*
8 x 9	8.00	7.75	96.88	.1176ns
9 x 10	8.25	8.39	101.70	.0392ns
1 x 9	5.02	4.34	86.45	.9248ns
2 x 10	7.21	5.84	81.00	3.7538**
3 x 8	4.61	5.00	108.46	.3042ns
All early x early crosses	4.50	4.11	91.33	.9126ns
All late x late crosses	8.13	7.77	95.57	.7740ns
All early x late crosses	5.61	5.06	90.20	1.8371**
All crosses	6.08	5.65	92.93	<u>3.3930**</u>
			error =	.3399 with 51 df
	<u>Parent</u>	<u>S<sub>1</sub></u>		
1	3.09	3.77	122.01	.9248ns
2	5.72	7.94	138.81	9.9235**
3	1.04	4.08	392.31	18.4832**
4	5.98	6.85	114.55	1.4965ns
5	5.43	7.01	129.10	4.9770**
8	8.18	8.74	106.85	.6105ns
10	8.66	8.64	99.77	.0003ns
All early self's	4.25	5.93	139.53	28.1568**
All late self's	8.42	8.69	103.21	.5995ns
All self's	5.44	6.72	123.53	<u>22.8225**</u>
			error =	.6796 with 39 df

Mean maturity rating check variety Fawn = 2.89.

<sup>1</sup>Rated from 1 to 9 with 1 equaling earliest plants, thus percentages less than 100 indicate progeny having earlier maturity than parents.

\*, \*\* Indicates significance at the 5 and 1 percent level of probability, respectively.

the higher heterotic  $SX_{2.10}$ . There were significant differences among the means within each group of SX's and MP's with the exception of the L x L MP group. The variations observed among the MP groups and among the SX groups, however, were much smaller than the variation among either the SX group means or among the MP group means.

Inbreeding resulted in a later mean maturity rating for all  $S_1$ 's, as compared to all  $S_0$ 's. All five of the early  $S_1$ 's were rated later than their respective  $S_0$ 's, three of them significantly later. One late  $S_1$  was rated slightly earlier than its  $S_0$  and the other  $S_1$  was rated later than its  $S_0$ ; however, in neither case was the difference significant. The parent-progeny mean square for the late group was quite small and non-significant while that of the early group was relatively large and significant. The mean rating of the early  $S_0$ 's was significantly earlier than the mean rating of the late  $S_0$ 's, and there were significant differences among the early  $S_0$ 's but not between the late  $S_0$ 's. The same pattern was true for the  $S_1$ 's, where the mean rating of early  $S_1$ 's was significantly earlier than the mean of late  $S_1$ 's, and there were significant differences among early  $S_1$  means, but not between the late  $S_1$  means.

Vigor Rating (Table 3). Although seven of the nine SX's had lower vigor ratings than their respective MP's, indicating heterosis for more vigor, only one  $SX_{2.10}$  was rated significantly lower than its MP. Largely because of this one SX the E x L SX's had a lower mean

Table 3. Vigor ratings.<sup>1</sup> Parent and progeny means, progeny as percent of parent, and mean square associated with linear comparison between progeny and parents.

Identification	Parent mean	Progeny mean	Progeny as % parent	Mean square
	<u>Midparent</u>	<u>SX</u>		
1 x 2	7.22	8.28	114.68	2.2791ns
2 x 3	7.43	6.82	91.79	.7442ns
4 x 5	5.07	3.94	77.71	2.5538ns
7 x 8	3.45	2.61	75.65	1.4281ns
8 x 9	3.71	2.80	75.47	1.6562ns
9 x 10	3.85	3.91	101.56	.0066ns
1 x 9	6.36	6.19	97.33	.0545ns
2 x 10	4.71	2.31	49.04	11.5200**
3 x 8	4.66	3.48	74.68	2.7495ns
All early x early crosses	6.57	6.35	96.65	.3015ns
All late x late crosses	3.67	3.11	84.74	1.9212ns
All early x late crosses	5.24	3.99	76.15	9.3126**
All crosses	5.16	4.48	86.82	<u>8.2892**</u>
			error =	.9536 with 51 df
	<u>Parent</u>	<u>S<sub>1</sub></u>		
1	7.04	8.48	120.45	4.1905ns
2	7.39	8.46	114.48	2.2578ns
3	7.47	7.79	104.28	.2080ns
4	3.98	7.43	186.68	23.7016**
5	6.16	7.75	125.81	5.0403*
8	1.74	4.41	253.45	14.2311**
10	2.02	2.95	146.04	1.7298ns
All early self's	6.41	7.98	124.49	24.7276**
All late self's	1.88	3.68	195.74	12.9420**
All self's	5.11	6.75	132.09	<u>37.6420**</u>
			error =	1.0384 with 39 df

Mean vigor rating check variety Fawn = 4.79.

<sup>1</sup> Rated from 1 to 9 with 1 equaling most vigorous plants, thus percentages less than 100 indicate progeny with more vigor than parents.

\*, \*\* Indicates significance at the 5 and 1 percent level of probability, respectively.

rating than the mean of the E x L MP group. The mean rating of all SX's was significantly lower than the mean rating of all MP's. There were significant differences among the MP group means and among the SX group means. Significant variation was also observed among the E x E means and among the E x L means of both MP's and SX's.

Selfing resulted in S<sub>1</sub> progeny having less vigor than their respective S<sub>0</sub>'s in all seven self's, with three of the differences being significant. While the differences between S<sub>0</sub>'s and S<sub>1</sub>'s was significant for both the early means and the late means, the parent-progeny mean square for the early self's was nearly twice that of the late self's indicating inbreeding had a greater effect in reducing vigor in the early self's than in the late self's. The early S<sub>0</sub>'s were rated significantly less vigorous than the late S<sub>0</sub>'s, with the same being true of the S<sub>1</sub>'s. Significant variation was observed among the early S<sub>0</sub> means and between the late S<sub>1</sub> means, with variation between late S<sub>0</sub>'s and among early S<sub>1</sub>'s being non-significant.

Plant Spread (Table 4). SX progeny averaged a significant 3.78 centimeters wider than their MP's, with individual SX's ranging from 103.66 to 124.91 percent of their respective MP. One E x E SX, two L x L SX, and all three E x L SX's were significantly wider than their midparents. Although all three groups of SX's were significantly wider than their respective MP's, parent-progeny mean square was

Table 4. Plant spread (cm). Parent and progeny means, progeny as percent of parent, and mean square associated with linear comparison between parent and progeny.

Identification	Parent mean	Progeny mean	Progeny as % parent	Mean square
	<u>Midparent</u>	<u>SX</u>		
1 x 2	35.62	37.84	106.23	9.8346*
2 x 3	32.24	33.29	103.26	2.2366ns
4 x 5	35.26	37.28	105.71	8.1003ns
7 x 8	21.72	25.82	118.88	33.7431**
8 x 9	20.91	23.95	114.53	18.4225**
9 x 10	22.08	24.17	109.47	8.7153ns
1 x 9	29.81	35.75	119.93	70.5672**
2 x 10	27.89	34.84	124.91	96.6745**
3 x 8	26.43	32.11	121.49	70.3298**
All early x early crosses	34.37	36.14	105.15	18.6384**
All late x late crosses	21.57	24.65	114.28	56.7953**
All early x late crosses	28.04	34.57	123.29	255.3885**
All crosses	28.00	31.78	113.50	<u>258.2886**</u>
			error =	2.1090 with 51 df
	<u>Parent</u>	<u>S<sub>1</sub></u>		
1	38.72	35.12	90.71	25.8840**
2	32.52	25.94	79.76	86.6586**
3	31.94	25.39	79.49	85.8705**
4	31.18	28.60	91.71	13.3645*
5	39.34	33.58	85.36	66.3552**
8	20.91	18.19	86.98	14.8240*
10	23.25	20.76	89.31	12.3505*
All early self's	34.74	29.53	85.00	251.5524**
All late self's	22.08	19.48	88.20	27.1181**
All self's	31.12	26.80	86.12	<u>262.0518**</u>
			error =	2.4680 with 39 df

Mean spread check variety Fawn = 35.69.

\*, \*\* Indicates significance at the 5 and 1 percent level of probability, respectively.

much greater in the E x L group than in either of the other two groups, indicating more heterosis for this group.

Significant variation occurred among the group means of both the SX's and the MP's. Significant variation also occurred among the E x E means and among the E x L means for both MP's and SX's. No significant variation was detected among the L x L means of either the SX's or the MP's.

Plant spread of  $S_1$  plants was reduced considerably compared to  $S_0$  parents. Each  $S_1$  was significantly narrower than its  $S_0$ , and overall the  $S_1$ 's averaged 4.32 centimeters narrower than their  $S_0$ 's. The parent-progeny mean square for the early group was over nine times that of the late group. The early  $S_0$  plants were significantly wider than the late  $S_0$ , and there was significant variation among the early  $S_0$  means, and between the late  $S_0$  means. The same was true of the  $S_1$ 's where the early  $S_1$ 's were significantly wider than the late  $S_1$ 's, there was significant variation among the early  $S_1$  means and between the late  $S_1$  means.

Plant Height (Table 5). Although six of the nine SX's were taller than their respective MP's, only one,  $SX_{1.9}$ , was significantly taller. While this resulted in the E x L group having a mean height significantly higher than the MP mean, the mean of all SX's was not significantly greater than the mean of all MP's. Significant variation was observed among SX group means and among MP group means.

Table 5. Plant height (cm). Parent and progeny means, progeny as percent of parent, and mean square associated with linear comparison between progeny and parent.

Identification	Parent mean	Progeny mean	Progeny as % parent	Mean square
	<u>Midparent</u>	<u>SX</u>		
1 x 2	69.47	70.46	101.43	2.5313ns
2 x 3	69.60	65.28	93.79	37.2816ns
4 x 5	55.71	62.25	111.74	85.4778ns
7 x 8	41.25	42.58	103.23	.3528ns
8 x 9	39.10	38.67	98.90	3.5778ns
9 x 10	29.83	30.25	101.42	.3655ns
1 x 9	53.23	61.47	115.48	135.9601*
2 x 10	46.07	51.88	112.63	67.6866ns
3 x 8	59.51	88.93	99.03	.6786ns
All early x early crosses	64.93	66.00	101.65	101.6405ns
All late x late crosses	36.73	37.17	101.20	1.1793ns
All early x late crosses	52.94	57.43	108.48	121.1403*
All crosses	51.53	57.43	103.89	<u>72.1809ns</u>
			error =	28.7904 with 51 df
	<u>Parent</u>	<u>S<sub>1</sub></u>		
1	73.52	66.86	90.94	88.7112ns
2	65.42	39.35	60.15	1359.0291**
3	73.77	61.26	83.05	312.8751*
4	53.78	43.29	80.49	220.0802*
5	57.64	49.94	86.62	118.9653ns
8	45.25	32.15	71.05	343.2200**
10	26.72	26.82	100.36	.0190ns
All early self's	64.83	52.14	80.43	1609.7266**
All late self's	35.98	29.48	81.95	169.0650ns
All self's	56.59	45.67	80.71	<u>1669.4496**</u>
			error =	45.6563 with 39 df

Mean height check variety Fawn = 74.67.

\*, \*\* Indicates significance at 5 and 1 percent level of probability, respectively.

Variation was less but significant among the means within each of the three groups for both MP's and SX's with the exception of the E x E SX means, where the variation was non-significant.

$S_1$  progeny averaged a significant 10.92 centimeters shorter than their parents. Individual  $S_1$ 's ranged from 60.12 to 100.36 percent of their respective  $S_0$ 's, with three of the five early  $S_1$ 's and one of the two late  $S_1$ 's being significantly shorter than their respective  $S_0$ 's. The mean of early  $S_1$ 's was significantly shorter than the early  $S_0$ 's, but there was no significant difference between the mean of the late  $S_1$ 's and the mean of the late  $S_0$ 's. There was significant variation among the means of the early  $S_0$ 's and among the means of the early  $S_1$ 's. The early  $S_0$ 's were significantly taller than the late  $S_0$ 's, with the same being true for the two groups of  $S_1$ 's. The difference between the two late  $S_0$ 's was significant, but that between the two late  $S_1$ 's was not. Variation among the early means was significant for both  $S_0$ 's and  $S_1$ 's.

First Harvest Forage Yield (Table 6). The yield of single-cross progeny for the first harvest averaged 142.93 percent of MP yield. The mean yield of each of three maturity groups of the SX's significantly exceeded the mean yield of their respective MP's, with the parent-progeny mean square of the E x L group being over twice that of the E x E group and over 10 times as large as that of the L x L group. All individual SX's had a significantly higher yield than their MP's with the exception of two L x L SX's.

Table 6. Forage yield first harvest (g/plant). Parent and progeny means, progeny as percent of parent, and mean square associated with linear comparison between progeny and parent.

Identification	Parent mean	Progeny mean	Progeny as % parent	Mean square
	<u>Midparent</u>	<u>SX</u>		
1 x 2	364.66	470.07	128.91	22292.1613**
2 x 3	329.95	391.72	118.72	7631.0658*
4 x 5	280.48	384.43	137.06	21614.3236**
7 x 8	80.24	143.12	178.37	7909.0465*
8 x 9	60.71	93.09	153.34	2096.9288ns
9 x 10	49.39	65.82	133.26	466.3458ns
1 x 9	242.81	364.68	150.19	29707.0313**
2 x 10	171.24	333.37	194.68	52577.1378**
3 x 8	219.67	325.16	148.02	22259.4450**
All early x early crosses	325.03	415.41	127.81	49013.0740**
All late x late crosses	63.45	100.68	158.68	8145.3242*
All early x late crosses	211.29	341.07	161.46	101145.3601**
All crosses	199.90	285.72	142.93	<u>132560.1469**</u>
			error =	1386.9110 with 51 df
	<u>Parent</u>	<u>S<sub>1</sub></u>		
1	436.46	346.16	79.31	16308.1800**
2	292.84	99.89	34.11	74457.4755**
3	367.95	182.26	49.53	68298.3841**
4	248.98	150.08	60.28	19561.4310**
5	311.96	172.95	55.44	38651.7306**
8	72.27	35.79	49.52	2665.5951ns
10	49.63	46.93	94.56	18.8805ns
All early self's	331.64	190.27	57.37	200056.9792**
All late self's	60.25	41.17	68.33	1564.7958ns
All self's	254.17	147.67	58.10	<u>158797.8901**</u>
			error =	1683.6761 with 39 df

Mean yield check variety Fawn = 425.59.

\*, \*\* Indicates significance at the 5 and 1 percent level of probability, respectively.

There was significant variation among maturity groups for both MP's and SX's. The E x E group had the highest yield for both SX's and MP's with E x L group yielding slightly less, and the L x L group being the poorest producers. Significant variation was observed among the E x E SX means and MP means, among the L x L SX means and among the E x L MP means.

The mean yield at first harvest of the  $S_1$  progeny was 106.55 g/plant less than the parental mean yield. All early  $S_1$ 's produced significantly less forage than their respective  $S_0$ 's while neither late  $S_1$ 's differed in yield significantly from its parent. Consequently the parent-progeny mean square of the early maturity group was quite large compared to the variation of the late group.

Early  $S_0$ 's averaged 271.39 g/plant more forage than late  $S_0$ 's. Variation among early  $S_0$  means was significant while difference between the two late  $S_0$ 's was non-significant. The same pattern was true for the  $S_1$  means with the early  $S_1$  group yielding significantly more than the late  $S_1$  group. This difference was not, however, as great as it was between the  $S_0$  groups. Significant variation occurred among the early  $S_1$  means, but not between the two late  $S_1$  means.

Second Harvest Forage Yield (Table 7). Significant heterosis for forage yield at the second harvest was observed in both the L x L and the E x L maturity groups and for all SX's as a group. One SX in the E x E group significantly out-yielded its MP, but the mean yield of the

Table 7. Forage yield second harvest (g/plant). Parent and progeny means, progeny as percent of parent, and mean square associated with linear comparison between progeny and parent.

Identification	Parent mean	Progeny mean	Progeny as % parent	Mean square
	<u>Midparent</u>	<u>SX</u>		
1 x 2	63.53	67.79	106.71	36.2101ns
2 x 3	50.48	45.91	90.95	41.7241ns
4 x 5	75.08	105.88	141.02	1897.2800*
7 x 8	80.41	126.04	156.75	4165.5628**
8 x 9	71.32	106.05	148.70	2413.0405**
9 x 10	66.42	91.86	138.30	1294.1328*
1 x 9	70.86	103.59	146.19	2142.8331**
2 x 10	59.09	147.75	250.04	15722.9645**
3 x 8	70.51	127.07	180.22	9816.8072**
All early x early crosses	63.03	73.19	116.12	619.6584ns
All late x late crosses	72.71	107.98	148.51	8446.5024**
All early x late crosses	68.82	126.14	183.29	21112.5812**
All crosses	67.52	102.44	151.72	<u>21945.8233**</u>
			error =	268.6476 with 51 df
	<u>Parent</u>	<u>S<sub>1</sub></u>		
1	83.11	52.62	63.31	1859.2802*
2	43.95	10.24	23.30	2273.0653**
3	57.00	19.31	33.88	2841.4491**
4	71.38	30.09	42.15	3408.4896**
5	78.77	48.52	61.60	1830.1250*
8	84.02	35.78	42.59	4654.1952**
10	74.22	40.71	54.85	2246.5105**
Early self's	66.84	32.15	48.10	12030.8391**
Late self's	79.12	38.24	48.33	6683.8800**
All self's	70.35	33.89	48.18	<u>18605.1738**</u>
			error =	266.7052 with 39 df

Mean yield check variety Fawn = 86.25.

\*, \*\* Indicates significance at the 5 and 1 percent level of probability, respectively.

E x E SX's was not significantly different from the MP. The parent-progeny mean square was greatest in the E x L group with that of the E x E group being the least. Individual SX's had yields ranging from 90.95 to 250.04 percent of their respective MP.

There was no significant variation among MP means, either among maturity group means or among means within any of the maturity groups. Significant differences did occur among the SX maturity group means with the E x L mean being the highest, followed by the L x L mean, and the E x E mean being the lowest. Significant variation also occurred among the SX means in each of the three maturity groups.

$S_1$  progeny averaged less than one-half the yield of the  $S_0$  average, with all  $S_1$ 's producing significantly less forage at the second harvest than their respective  $S_0$ 's. The yield of the  $S_1$ 's ranged from 23.30 to 63.61 percent of their  $S_0$ 's. While the parent-progeny mean square was significant in both the early and late group of self's, that of the early group was 1.8 times that of the late group.

There was no significant difference between the early group mean and the late group mean for either  $S_0$ 's or  $S_1$ 's. Likewise, the difference between the two late  $S_0$ 's or the two late  $S_1$ 's was not significant. Significant variation did occur among the early means for both  $S_0$ 's and  $S_1$ 's.

Third Harvest Forage Yield (Table 8). Seven of the nine SX's

Table 8. Forage yield third harvest (g/plant). Parent and progeny means, progeny as percent of parent, and mean square associated with linear comparison between progeny and parent.

Identification	Parent mean	Progeny mean	Progeny as % parent	Mean square
	<u>Midparent</u>	<u>SX</u>		
1 x 2	89.19	95.08	106.60	69.2076ns
2 x 3	83.38	97.13	116.49	377.9875ns
4 x 5	100.93	98.65	97.74	10.4882ns
7 x 8	42.12	54.79	130.08	320.9311ns
8 x 9	33.78	32.17	95.23	5.1681ns
9 x 10	26.82	30.11	112.27	21.6153ns
1 x 9	63.50	69.36	109.23	68.7965ns
2 x 10	52.52	79.45	151.10	1450.4498ns
3 x 8	68.85	89.29	129.69	835.9961ns
All early x early crosses	91.17	96.95	106.34	200.7395ns
All late x late crosses	34.24	39.02	113.96	137.2338ns
All early x late crosses	61.62	79.37	128.81	1889.6651ns
All crosses	62.34	71.78	115.14	<u>1603.2897ns</u>
			error =	639.6029 with 51 df
	<u>Parent</u>	<u>S<sub>1</sub></u>		
1	104.38	78.69	75.39	1319.9522ns
2	74.01	22.88	30.91	5227.5313**
3	92.75	38.23	41.22	5945.9513**
4	106.51	33.14	31.11	10764.8465**
5	95.34	51.95	54.49	3765.3842*
8	44.93	17.02	37.88	1558.7736ns
10	31.03	29.69	96.68	3.5912ns
All early self's	94.60	44.98	47.55	24620.4516**
All late self's	37.98	23.35	61.48	856.0013ns
All self's	78.42	38.80	49.48	<u>21978.4027**</u>
			error =	557.1616 with 39 df

Mean yield check variety Fawn = 118.20.

\*, \*\* Indicates significance at the 5 and 1 percent level of probability, respectively.

produced more forage on a per plant basis than their respective MP's with the mean yield of all SX's being 9.44 g/plant greater than the mean yield of all MP's. There were no significant differences between MP's and SX's. Although non-significant, the parent-progeny mean square of the E x L group of crosses was over nine times that of the E x E group and over 13 times that of the L x L group. Variation among the yields of maturity groups was significant for both MP's and SX's with the E x E group being the highest yielder for both MP's and SX's. Variation among means within maturity groups was non-significant for both MP's and SX's.

Inbreeding resulted in significantly lower yielding progeny for the early  $S_0$ 's, but not for the late  $S_0$ 's. Four of the five early  $S_1$ 's yielded significantly less than their respective  $S_0$ 's while neither late  $S_1$  produced significantly less than its respective  $S_0$ . Overall the yield of the  $S_1$ 's averaged 49.48 percent of the  $S_0$ 's. Early  $S_0$ 's were significantly higher yielding than late  $S_0$ 's but there was no significant variation among the means within either group. Early  $S_1$ 's produced significantly more forage than did the late  $S_1$ 's, and there was significant variation among early  $S_1$  means, but not between the two late  $S_1$  means.

Total Forage Yield (Table 9). Heterosis for total forage yield was significant for the average of all SX's and for the average of each maturity group of SX's. All SX's exceeded their respective MP for

Table 9. Total forage yield (g/plant). Parent and progeny means, progeny as percent of parent, and mean square associated with linear comparison between progeny and parent.

Identification	Parent mean	Progeny mean	Progeny as % parent	Mean square
	<u>Midparent</u>	<u>SX</u>		
1 x 2	517.38	587.98	113.65	9956.7216ns
2 x 3	445.45	534.76	120.05	15950.7661*
4 x 5	456.47	563.96	123.55	23104.9756**
7 x 8	202.83	323.96	159.72	29341.3200**
8 x 9	165.80	231.31	139.51	8583.7753ns
9 x 10	142.56	187.78	131.72	4090.1490ns
1 x 9	377.16	537.63	142.55	51506.0560**
2 x 10	282.84	535.57	189.35	127749.9605**
3 x 8	359.02	541.53	150.84	66617.9751**
All early x early crosses	473.10	562.21	118.84	47648.8994**
All late x late crosses	170.40	247.68	145.35	35838.6002**
All early x late crosses	339.67	538.24	158.46	242582.9123**
All crosses	327.72	449.38	137.12	<u>266412.2847**</u>
			error =	2687.0328 with 51 df
	<u>Parent</u>	<u>S<sub>1</sub></u>		
1	623.95	477.47	76.52	42912.7808**
2	410.79	133.01	32.38	154329.0125**
3	516.80	239.79	46.40	153471.8503**
4	426.86	213.32	49.97	91202.9341**
5	486.08	273.42	56.25	90446.4246**
8	201.23	88.59	44.02	25376.6656**
10	154.88	116.95	75.51	2876.9905ns
All early self's	492.90	267.40	54.25	508484.4602**
All late self's	178.05	102.77	57.72	22671.3249**
All self's	402.94	220.36	54.69	<u>466689.0864**</u>
			error =	2629.3940 with 39 df

Mean total yield check variety Fawn = 630.04.

\*, \*\* Indicates significance at 5 and 1 percent level of probability, respectively.

yield with this difference being significant for all three of the E x L SX's, two of the E x E SX's and one of the L x L SX's. The individual SX's ranged from 113.65 to 189.35 percent of their respective MP's. Maturity groups were in the order of E x L, E x E, and L x L when ranked according to decreasing magnitude of parent-progeny mean square.

There was significant variation among maturity group means for both MP's and SX's. For both midparents and progeny the E x E group averaged the most forage, followed in order by the E x L, and the L x L groups. Significant variation was observed among the E x L group of MP means and among the L x L group of SX means. Variation was non-significant among the E x E MP means, among the L x L MP means, among the E x E SX means, and the E x L SX means.

Relative to their respective parent, there was a significant reduction in total forage yield in six of the seven  $S_1$ 's. All five early  $S_1$ 's produced significantly less than their parent, with one late  $S_1$  producing significantly less than its parent. Yields of individual  $S_1$ 's ranged from a low of 32.88 to a high of 76.52 percent of their respective  $S_0$ 's. Overall the  $S_1$ 's averaged 182.58 g/plant less forage than did their parents. The parent-progeny mean square was significant only for the early group, with the mean square of this group being over 22 times that of the late group.

Early parents significantly outyielded the late parents with the

early  $S_0$  group averaging 314.85 g/plant above the average yield of the late  $S_0$  group. The early  $S_1$  group likewise averaged significantly above the late  $S_1$  group; however, the difference was much less, being 164.63 g/plant. Variation among both  $S_0$  early means and  $S_1$  early means was significant, but non-significant between both the late  $S_0$  means and the late  $S_1$  means.

### Heterosis and Inbreeding Discussion

In this study the average of all SX's significantly exceeded the average of all mid-parents for earlier maturity, more vigor, wider plants, first and second harvest forage yield, and total forage yield. The SX average also exceeded mid-parent average for plant height and third harvest forage yield; however, these differences were not significant. In most instances the early x late SX's contributed most to the overall heterosis of the total SX population, with the parent-progeny mean square of this group exceeding that of the other two groups for all characteristics. Considering all crosses and all characteristics, heterotic effects were significant in 44.4 percent of the individual SX's. Of this 44.4 percent, 20.8 came from early x late SX's, 12.5 from early x early single-crosses, and 11.1 from late x late single-crosses.

Inbreeding resulted in  $S_1$  progeny that were significantly later in maturity, less vigorous, narrower, shorter, produced less forage at

all three harvests, and less total forage. The early parents appeared most sensitive to inbreeding as the parent-progeny mean square of this group was significant and exceeded that of the late group for all characteristics. The parent-progeny mean square of the late group was significant for four of the eight characteristics.

Quantitative characteristics such as those examined in this study are generally believed to be controlled by two types of gene action, that which is additive in nature, and that which deviates from the additive scheme (Robinson, Comstock and Harvey, 1949). The additive portion of the gene system is the average genetic effects and remains fixed from one generation to another, while the non-additive portion is effects conditioned by some type of dominance (Gardner and Lonquist, 1959) and/or various types of epistasis (Bauman, 1959). Under a strictly additive scheme, single-cross progeny would be expected to equal the parental average, or midparent, in performance, and likewise,  $S_1$  progeny would be expected to equal  $S_0$  parents in performance. When heterosis is exhibited by SX progeny exceeding the midparent in performance, this must be the result of some type of intra- and interallelic complementation, that is dominance and epistasis, which causes deviation from the additive scheme. Likewise when an inbreeding depression is observed as poor performance of the  $S_1$  progeny relative to the  $S_0$  parent, this must be due to a loss through increasing homozygosity of the allelic complementation that existed in the parent plant.

As the parent clones of this out-crossed species are actually single-crosses themselves and largely heterozygous, the inbreeding depressions observed were not unexpected. Likewise these largely heterozygous parents would not be expected to produce heterotic progeny unless new combinations of complementing alleles were brought together. The result was that in crosses between genetically similar parents non-additive effects were not apparent, but as the parents became increasingly different genetically, there was increasing possibility of new allelic combinations conditioning non-additive effects, or heterosis.

Specific evidence for such a concept was observed in the three harvests and total forage yields of parents 1, 2, and 10 and  $SX_{1.2}$  and  $SX_{2.10}$ . Inbreeding depression of parents 1 and 2 was, in most instances, significant and of considerable magnitude while that of parent 10 was less. Parent 1, which was the top yielding parent, combined with parent 2 to produce  $SX_{1.2}$  which was high yielding, but failed to exhibit significant non-additive effects except at the first harvest. Parent 2 combined with a genetically less similar parent, parent 10, to produce  $SX_{2.10}$  which produced less forage but had far greater heterotic effects than  $SX_{1.2}$ .

Although crosses between genetically diverse parents gave the greatest heterotic response, this additional response may be of little economic value. The average total yield of early x late SX's was

538.24 g/plant approaching the average total yield of the early x early SX, 562.21. Yet two of the three early x early SX's exceeded all three early x late single-crosses for total forage yield. Heterosis of the early x late SX was sufficient to bring yield up near, or in instances in excess of, the level of its high yielding early parent, but it was not sufficient to bring yield up to the level of SX progeny from two high yielding early parents.

The two characteristics of vigor and second harvest forage yield and their relationship to the relative performance of parents and progeny is particularly interesting. These were the only characteristics in which the performance of the late  $S_0$ 's and the late x late MP's and their respective progenies exceeded that of the parent and progeny groups. The low vigor rating, indicating superior vigor, of the late  $S_0$ 's and  $S_1$ 's and the late x late MP's and SX's was undoubtedly partially due to their shorter growth habit which allowed them to be more tolerant of cutting. Consequently these plants appeared more vigorous following the first harvest when the ratings were made. The tolerance to clipping plus the more pronounced growth of late  $S_0$ 's and  $S_1$ 's and late x late MP's and SX's during the latter part of the spring would at least partially account for the improved relative performance of these plants at second harvest.

This points out the importance of considering environmental effects when examining heterosis and inbreeding. Environmental

effects on the performance of parents or progeny can greatly influence the magnitude of heterosis or inbreeding depression. Heterosis as estimated by parent-progeny mean square for first, second, and third harvest yield of  $SX_{1.2}$  was 22292.16\*\*, 36.21 n. s. , and 69.21 n. s. , respectively, while that of  $SX_{9.10}$  was 466.35 n. s. , 1294.13\*, and 21.62 n. s. , respectively. Likewise inbreeding depression as estimated by parent-progeny mean square for the first, second, and third harvest yield of  $S_1 1$  was 16308.18\*\*, 1859.28\*, and 1319.95 n. s. , respectively, while that of  $S_1 10$  was 18.88 n. s. , 2246.51\*\*, and 3.5912 n. s. , respectively. This indicates an interaction of heterotic response and inbreeding depression with harvest date, or more generally, an interaction between the environment and genotype. An analysis for genotype x harvest interaction would have been particularly enlightening; however, this was prevented by significant differences among the error mean squares for the three harvests.

It is noteworthy that the difference between the means of early and late parental groups was significant for all characters but one. This supports the assumption that separation of the parents into two groups on the basis of anthesis date resulted in genetically distinct groups.

The use of linear contrasts between parents and progeny offered much versatility in examining heterosis and inbreeding. It gave not only a means of testing for significant differences between

parents and progeny, which could have been done via an L. S. D., but in addition the mean square from the contrast offered a measure of that difference. The orthogonality of group mean squares allowed comparisons of the relative magnitude of the heterosis or inbreeding depression of the various groups with the same being true of individual parent-progeny mean squares. Thus the various individual crosses or self's, or groups of crosses or self's that most contributed to overall heterosis or inbreeding depression were identified.

The use of linear contrast mean squares also helped circumvent problems created when data were collected as ratings. The problem occurred when one parent-progeny pair was described by low ratings while another was described by higher ratings. A small difference between the first parent-progeny pair resulted in a greatly inflated or reduced percentage as compared to the second parent-progeny pair.

In this study when progeny mean vigor rating was expressed as percent of the parent mean rating, the percentages were 125.81 and 146.04 for  $S_1 5$  and  $S_1 10$ , respectively. The respective parent-progeny variations were 5.0403 and 1.7298, the first significant, the second non-significant. Thus, while the percentage values gave an indication as to whether progeny were rated lower or higher than parents, the mean square offered an indication as to the magnitude and significance of parent-progeny differences. Caution is always required

in examining any analysis of ratings, as they are not quantitative measurements and should not be interpreted as such.

#### Heritability and the Relationship Between Parent and Progeny Performance

Heritability estimates were computed for all eight characteristics studied in both the MP-SX and the  $S_0$ - $S_1$  populations. The heritability estimates, as presented in Table 10 along with the coefficients of determination, were obtained by regression of progeny on parent, and each is the estimated regression coefficient,  $b$ , along with the standard error of the coefficient. Such regression coefficients are narrow sense heritability estimates expressing the fraction of phenotypic differences of parents that might be expected to be recovered in their progeny (Lush, 1948). They are more commonly referred to as the ratio of additive genetic variation to total phenotypic variation (Briggs and Knowles, 1967).

For the most part the estimates are quite high, with those from the MP-SX population ranging from a high of 1.8112 for second harvest yield to a low of .8730 for maturity rating, and those from the  $S_0$ - $S_1$  population ranging from a high of .9372 for second harvest yield to a low of .4348 for third harvest yield. The MP-SX second harvest yield estimate and the  $S_0$ - $S_1$  third harvest yield estimate did not differ significantly from zero.

Table 10. Heritability estimates<sup>1</sup> and coefficients of determination obtained by regression of progeny on parents.

Character	Midparents and single-cross progeny		Parents and S <sub>1</sub> progeny	
	Heritability estimate	Coefficient of determination	Heritability estimate	Coefficient of determination
Maturity rating	.8730 ± .1376	.8519	.7112 ± .1220	.8717
Vigor rating	1.2804 ± .2164	.8334	.7836 ± .1656	.8174
Plant spread	.9135 ± .1367	.8645	.8545 ± .1186	.9121
Plant height	.9513 ± .1102	.9141	.7684 ± .1873	.7710
Forage yield one	1.1812 ± .1302	.9217	.6404 ± .1518	.7806
Forage yield two	1.8112 ± 1.1275 <sup>2</sup>	.2693	.9372 ± .1948	.8224
Forage yield three	.9825 ± .1450	.8677	.4348 ± .2446 <sup>2</sup>	.3872
Total forage yield	1.0401 ± .1838	.8205	.6692 ± .1823	.7316

<sup>1</sup>Heritability estimate equals regression coefficient plus or minus its standard error.

<sup>2</sup>Insufficient evidence to reject H<sub>0</sub>: β = 0.

Figure 1, which shows the theoretical influence of non-additive effects on the slope of parent-progeny regression lines, offers a partial explanation as to why the estimated values from the SX-MP population were so high. As heterosis is performance of SX progeny above the midparent due to non-additive genetic effects such as dominance and epistasis, regression line one,  $L_1$ , is the expected regression line when SX progeny show no heterosis, while regression lines two and three,  $L_2$  and  $L_3$ , show two different situations in which SX progeny performance exceeds midparent performance due to non-additive effects, assuming equal environmental effects on both parents and progeny.

In a situation such as shown by  $L_1$  where no heterosis is exhibited, there would always be a 1:1 relationship between MP and SX, the SX would always be 100 percent of the midparent, the non-additive effects would always be zero, and the slope equal to 1.0. If heterosis was exhibited, as shown by  $L_2$ ,  $MP_1$  and  $MP_2$  might equal 1.0 and 2.0 respectively, and produce  $SX_1$  and  $SX_2$  which equal 2.0 and 4.0, respectively. In this instance the SX progeny would always equal 200 percent of the MP, but the non-additive effects, indicated by the differences between the  $L_1$  and  $L_2$  at  $MP_1$  and  $MP_2$ , would be 1.0 and 2.0 for  $SX_1$  and  $SX_2$ , respectively. Consequently  $L_2$  would have a slope of 2.0. The situation shown by  $L_3$  may also exist where  $MP_1$  and  $MP_2$  again equal 1.0 and 2.0 respectively, but their heterotic

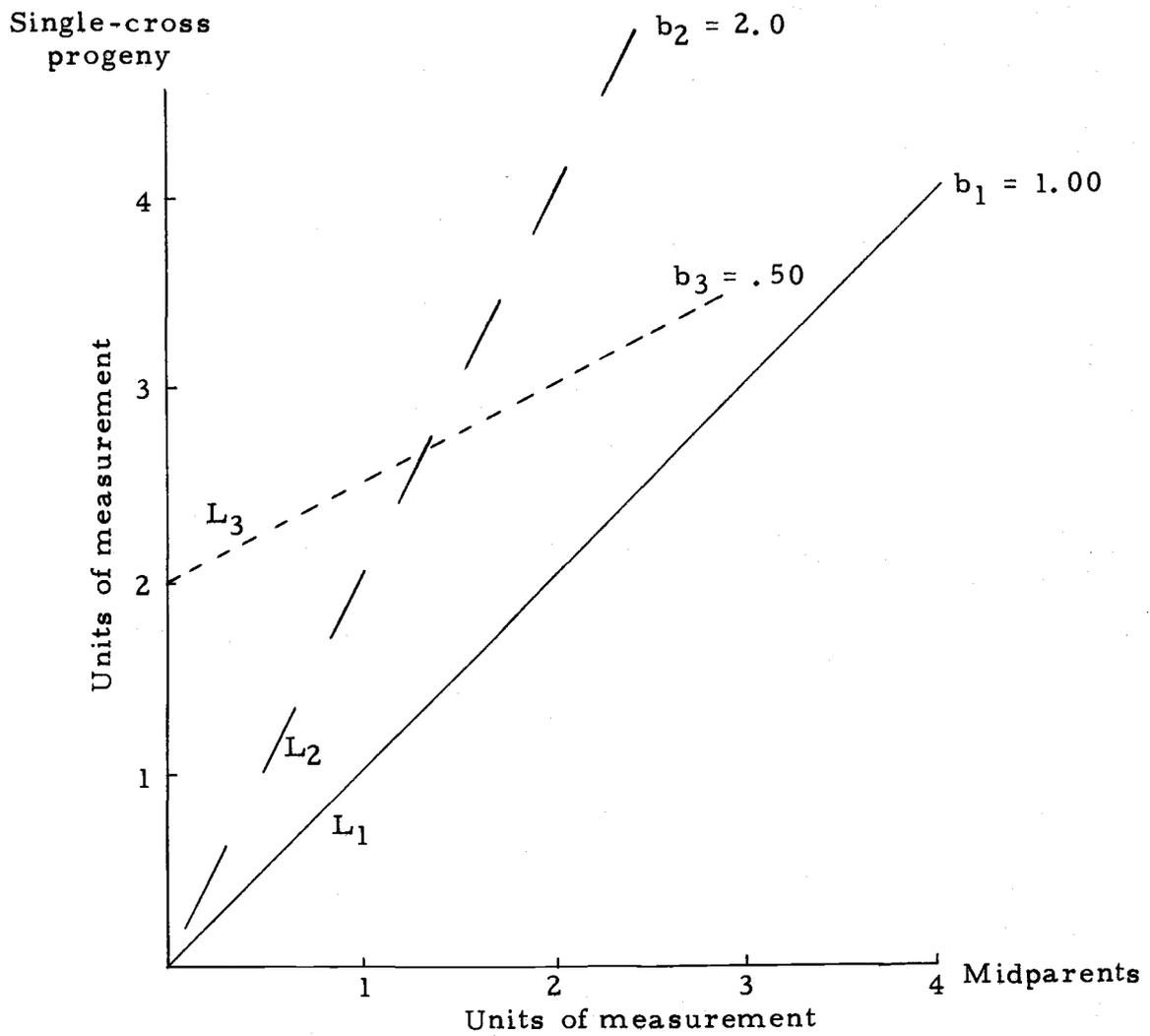


Figure 1. Theoretical influence of non-additive effects on the slope of parent-progeny regression lines.

progeny,  $SX_1$  and  $SX_2$ , equal 2.5 and 3.0, respectively. In this situation  $SX_1$  is 250 percent of  $MP_1$ ,  $SX_2$  is 150 percent of  $MP_2$ , and their respective non-additive effects, indicated by the differences between  $L_1$  and  $L_3$  at  $MP_1$  and  $MP_2$ , are 1.5 and 1.0, and the regression line,  $L_3$ , has a slope of .50. Thus, if estimated regression coefficients are used as heritability estimates and the progeny coming from increasingly higher performing midparents show increasingly greater non-additive effects, the resulting narrow sense heritability estimates will be inflated.

This appears to be happening in the MP-SX population of this study. Evidence for this is found in Figure 2, which shows individual single-cross progeny means plotted against midparent means for total forage yield. For total yield the three late x late MP's and their SX's were much lower yielders than were the early x early and early x late SX's. At the same time the late x late SX's were showing considerably less heterotic effects than the others. The result was the "clustering effect" observed in the plots of the first harvest yield, the low yielding late x late group of plots being "clustered" away from the much higher yielding and more heterotic early x early and early x late group. Due to the extreme differences in heterotic effects and the differences in yield, the slope of the regression line was shifted upward, and consequently, the regression coefficient gave an inflated

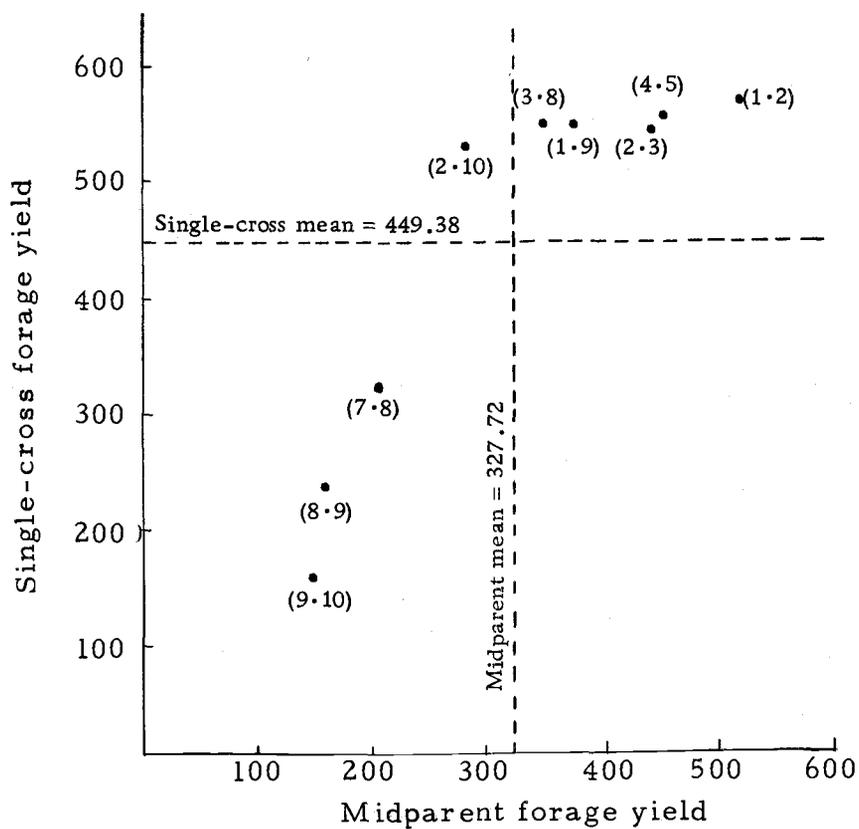


Figure 2. Plot of single-cross means against their respective midparent means for three harvest total forage yields (g/plant).

heritability estimate of first harvest yield. The same effect was observed for first harvest yield, and, to a lesser extent, in the third harvest yield.

In situations such as in the MP-SX population of this study where the regression coefficients are so high they become meaningless as narrow sense heritability estimates, the coefficients of determination,  $R^2$  values, are of greater practical use. The  $R^2$  values express the proportion of progeny variation that can be explained by linear association with parents, and thus, while not giving a quantitative estimate of progeny performance, they do indicate the ability to predict progeny performance based on parent performance.

All  $R^2$  values were quite high with the exception of the two instances where the heritability estimates were not found to differ significantly from zero. It is evident that the better performing parents consistently produced the better performing progeny in both the MP-SX and  $S_0$ - $S_1$  populations. This indicates there would be little practical value in utilizing  $S_1$  or SX progeny tests for parent selection. The same conclusion was reached by Bean (1971) and Thomas and Frakes (1967) who found clonal evaluation to be an effective selection method in tall fescue.

#### Relationships Among Eleven Characteristics in $S_1$ and SX Plants

All possible 55 coefficients of determination,  $R^2$  values, were

calculated among the eight forage characteristics examined in this study plus three characteristics measured by Moutray (1971) and are presented in Table 11.

Six of the forage characteristics, maturity rating, plant spread, plant height, first and third forage yield, and total forage yield, showed strong associations with each other. The  $R^2$  values for these ranged from a low of .6031 for maturity rating and plant spread to a high of .9440 for third harvest yield and total forage yield. A seventh characteristic, seed yield, showed moderate association with the above mentioned characteristics, being most highly associated with plant spread,  $R^2 = .6408$ . The remaining four characteristics, vigor rating, second harvest yield, seedling vigor, and panicle number, showed little association among themselves or with the other seven characteristics, with  $R^2$  values generally being less than .25, except for the association of panicle number and third harvest yield,  $R^2 = .3599$ , and the association of panicle number and total forage yield,  $R^2 = .3205$ .

The lack of association between seedling vigor index and mature plant characteristics is disappointing in that screening seedlings for vigor index could be a quick and early selection method. Seedling vigor apparently is not a good indicator of mature plant performance, however, and selection for superior vigor index would not be expected

Table 11. Coefficients of determination among 11 characteristics in S<sub>1</sub> and SX plants.

	Vigor rating	Plant spread	Plant height	First harvest forage yield	Second harvest forage yield	Third harvest forage yield	Total forage yield	Seedling vigor index <sup>1</sup>	Panicle number <sup>1</sup>	Seed yield <sup>1</sup>
Maturity rating	.2186	.6031	.9010	.8046	.0683	.6239	.6765	.0866	.1132	.4575
Vigor rating		.0914	.2123	.0743	.0678	.0036	.0021	.1282	.1323	.1832
Plant spread			.6698	.8402	.1406	.7735	.8141	.1751	.1610	.6408
Plant height				.8400	.0533	.7217	.7208	.1756	.1296	.5268
First harvest forage yield					.1300	.8934	.9330	.1084	.2213	.5994
Second harvest forage yield						.0904	.2207	.0652	.0004	.0012
Third harvest forage yield							.9440	.1179	.3599	.5461
Total forage yield								.0630	.3205	.4754
Vigor rating									.0890	.1462
Panicle number										.0684

<sup>1</sup>Moutray, J. 1971. An examination of seedling vigor and the effects of genetic diversity on response to heterosis in tall fescue (*Festuca arundinacea* Schreb.). Ph.D. thesis. Corvallis, Oregon State University.

to affect the performance of the mature plant. The same conclusion was reached by Moutray (1971) who studied the same plant material.

It is interesting to note seed yield exhibited a stronger relationship with most forage characteristics, with most  $R^2$  values ranging from about .45 to .65, than it did with panicle number,  $R^2 = .0684$ , which is generally considered a component of seed yield. Apparently selection for increased panicle number is going to have little effect on seed yield. The relationships between seed yield and the various forage characteristics, particularly forage yields, would be of primary importance in a breeding program where increasing seed yield while maintaining forage production is the objective. These relationships should be examined with caution, however, as there was a two-year difference between the collecting of the seed yield data and the forage data and consequently the  $R^2$  values may have been affected by environmental differences.

The strong relationships among most of the forage characteristics are much as would be expected. Maturity rating was made prior to the first harvest, and was largely a function of total spring growth at that time. Consequently maturity was most highly associated with plant height,  $R^2 = .9010$ , which was also measured prior to the first harvest, and with the first harvest,  $R^2 = .8046$ . Plant spread and plant height are two components of forage yield and their strong associations with the forage yields are as would be expected.

The two characteristics of vigor rating and second harvest yield, which failed to exhibit association with the other characteristics, are of interest in that for these two characteristics the performance of late  $S_1$ 's and the late x late SX's was better relative to the other  $S_1$  and SX group than it was for the other characteristics. Evidently this increase in performance of those plants which were usually poor performers was sufficient to destroy any linear relationship that these characteristics may have had with the other characteristics.

## SUMMARY

Heterosis and Inbreeding

Single-cross (SX) progeny and first generation selfed progeny ( $S_1$ ) of parents selected for diversity of anthesis date, morphology, and origin were examined for heterotic response and inbreeding depression. Data on maturity, vigor, plant spread, plant height, first, second, and third harvest forage yield, and total forage yield were collected from the parents,  $S_1$  and SX progeny. A randomized block design having four blocks was used with each experimental plot consisting of 14 plants space planted on .914 x 1.219 meter centers. Establishment was in September, 1969, at the Hyslop Agronomy Farm, Corvallis, Oregon (Moutray, 1971).

A midparent value for all characters was calculated for each single-cross by finding the mean value of the parents involved. For statistical analysis two separate populations were then created, one consisting of the SX progeny and their midparents, MP's, the other consisting of the  $S_1$  progeny and their  $S_0$  parents. Single-cross progeny and their midparents were classified as to the anthesis date of the original parents according to early x early, late x late, and early x late, and the  $S_0$  and  $S_1$  likewise classified as to the parent's anthesis data according to early and late.

Single-crosses as a group exhibited significant heterosis for all characteristics except for plant height and third harvest forage yield. Average heterosis expressed as SX in percent of MP was 92.93 and 86.32 for maturity and vigor rating (percentages less than 100 equal earlier or more vigorous progeny), and 113.50, 103.89, 142.93, 151.72, 115.14, and 137.12 percent for plant spread, plant height, first, second, and third harvest yield, and total forage yield, respectively.

In most instances the heterotic response of the early x late single-crosses was more pronounced than that of either the early x early or the late x late single-crosses. Likewise there was a greater frequency of individual late x late SX progeny that exhibited significant heterosis than there was of either the early x early or late x late single-crosses. Crosses between genetically diverse parents apparently offer greater opportunity for new combinations of the necessary alleles required for the dominance and epistasis that gives the needed non-additive effect for heterosis.

Although the greatest heterotic response was consistently observed in the early x late SX progeny, significant variation existed among SX maturity group means for most characters, and the early x early SX progeny were usually the best performers, particularly for forage yield. This suggests selection of parents on the basis of genetic diversity may not be of primary importance where performance rather than heterotic response is the desired result.

In all instances the  $S_1$  progeny as a group performed significantly poorer than their  $S_0$  parents.  $S_1$  expressed as percent of  $S_0$  was 123.53 and 132.09 percent for maturity and vigor (percentages above 100 percent indicate later and less vigorous progeny) and 86.12, 80.71, 48.18, 49.48, and 54.69 percent for plant spread, plant height, first, second, and third harvest forage yield, and total forage yield. The inbreeding depression of the early  $S_1$  as a group was also significant for all characteristics studied and that of the late  $S_1$  as a group significant for four of the characteristics.

Both early  $S_0$  and early  $S_1$  consistently performed better than their late counterparts. The fact that the early  $S_0$  mean performance was significantly different from the late  $S_0$  mean performance for all but third harvest yield supports the assumption that the parents were separated into two genetically different groups based on differences of anthesis date.

#### Heritability and Parent-Progeny Relationships

Heritability estimates and coefficients of determination were calculated by regression of  $S_1$  progeny on  $S_0$  parents and SX progeny on midparents. The heritability estimates were quite high, particularly those from the SX-MP population. Two estimates, that for MP-SX second harvest yield, and that for  $S_0$ - $S_1$  third harvest yield were found to not differ significantly from zero.

It was observed that increasing heterotic response of SX progeny of high yielding midparents combined with low heterotic response of SX progeny of low yielding midparents would probably result in an inflated heritability estimate. This is believed to be the reason for the high estimates from the MP-SX population where the low yielding late x late SX progeny tended to show little heterosis relative to the high yielding and more heterotic early x early and early x late SX progeny.

Most coefficients of variation were quite high and indicate the better performing progeny came from the better performing parents in both the MP-SX population and in the  $S_0$ - $S_1$  population. Thus this study, as well as others (Thomas and Frakes, 1967; Bean, 1971), indicates that parent evaluation may be an effective method of selecting parents that produce superior progeny in tall fescue.

#### Relationships Among Characteristics

Data from  $S_1$  and SX progeny were used to calculate coefficients of determination among the forage characteristics measured in this study and seedling vigor, panicle number, and seed yield measured by Moutray (1971).

There were strong associations among most forage characteristics with the exception of vigor rating and second harvest yield which showed virtually no association between themselves or with the other

characteristics. Seedling vigor and panicle number likewise showed little association with the other characteristics. Seed yield showed moderate association with most forage characteristics, but showed little association with panicle number generally believed to be a component of seed yield.

The lack of relationship between seed yield and panicle number,  $R^2 = .0684$ , suggests seed yield may not be greatly influenced by selection for superior panicle number. Likewise the lack of association of seedling vigor with seed and forage characteristics indicates screening seedlings for vigor will not greatly affect mature plant performance.

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## APPENDICES

APPENDIX A

Appendix Table 1. Mean squares from analysis of variance for nine characteristics of nine midparents (MP's) and their nine single-cross (SX) progeny.

Source of variation	d.f.	Maturity rating	Vigor rating	Plant spread	Plant height	First harvest forage yield	Second harvest forage yield	Third harvest forage yield	Total forage yield
Error	51	.3399	.9536	2.1090	28.7905	1386.9110	268.6476	639.6029	2687.0328
Between MP, SX	1	3.3930**	8.2892**	258.2886**	72.1809 <sub>ns</sub>	132560.1469**	21945.8233**	1603.2897 <sub>ns</sub>	266412.2847**
Among MP groups	2	41.5950**	25.3001**	491.7324**	2403.8245**	206429.5404**	285.8666 <sub>ns</sub>	9726.6234**	276174.3613**
Among early x early MP's	2	5.4532**	6.7962**	13.8345**	254.7189**	7158.9409**	605.9201 <sub>ns</sub>	319.8627 <sub>ns</sub>	6002.5438 <sub>ns</sub>
Among late x late MP's	2	.0657 <sub>ns</sub>	.1631 <sub>ns</sub>	1.4320 <sub>ns</sub>	147.1315**	974.1632 <sub>ns</sub>	201.5092 <sub>ns</sub>	234.7387 <sub>ns</sub>	3696.5557 <sub>ns</sub>
Among early x late MP's	2	7.7684**	3.7492*	11.5157**	180.9146**	5335.4596*	179.5324 <sub>ns</sub>	277.0713 <sub>ns</sub>	10018.7681*
Among SX groups	2	43.3980**	33.6901**	465.6244**	2630.1161**	324743.9897**	8687.4122**	10585.1689**	367864.7701**
Among early x early SX's	2	1.9967**	19.5031**	24.5559**	68.9896 <sub>ns</sub>	9017.8579**	3683.7161**	12.8591 <sub>ns</sub>	2836.9380 <sub>ns</sub>
Among late x late SX's	2	1.4894*	1.9661 <sub>ns</sub>	4.1925 <sub>ns</sub>	158.7940**	6149.0842**	1173.9888**	750.0755 <sub>ns</sub>	19347.8888**
Among early x late SX's	2	2.4750**	15.8787**	7.2029*	98.6223*	1739.4643 <sub>ns</sub>	1952.7283**	397.1257 <sub>ns</sub>	36.5517 <sub>ns</sub>

\*, \*\* Indicates significance at the 5 and 1 percent level of probability, respectively.

Appendix Table 2. Mean squares from analysis of variance for nine characteristics of seven parents ( $S_0$ 's) and their seven first generation selfed ( $S_1$ ) progeny.

Source of variation	d.f.	Maturity rating	Vigor rating	Plant spread	Plant height	First harvest forage yield	Second harvest forage yield	Third harvest forage yield	Total forage yield
Error	39	.6796	1.0384	2.4680	45.6563	1683.6761	26.7053	577.1616	2629.3940
Between $S_0$ , $S_1$	1	22.7414**	37.6420**	262.0518**	1669.4496**	158797.8901**	18605.1738**	21978.4027**	466689.0864**
Between $S_0$ groups	1	99.2699**	117.2623**	915.7882**	4752.0081**	418144.3105**	862.0912ns	18316.2466**	566432.2423**
Among early $S_0$ 's	4	18.2075**	8.4230**	62.3858**	329.5592**	20967.1667**	1048.3231**	665.4960ns	28895.0161**
Between late $S_0$ 's	1	.4512ns	.1512ns	10.9512*	686.7218**	1025.3656ns	192.1780ns	386.5590ns	4296.1815ns
Between $S_1$ groups	1	43.6475**	105.8415**	600.0936**	2931.8807**	12027.2362**	21.9843ns	2672.3557*	154876.8485**
Among early $S_1$ 's	4	14.1496**	.8761ns	78.3517**	546.6598**	34450.8988**	1336.2058**	1859.1717*	65914.8602**
Between late $S_1$ 's	1	.0190ns	4.2778*	13.2870*	56.8711ns	231.9858ns	48.4620ns	321.3112ns	1609.4301ns

\*, \*\* Indicates significance at the 5 and 1 percent level of probability, respectively.

Appendix Table 3. Mean values for eight characteristics in nine parents, seven S<sub>1</sub> progeny, nine SX progeny, and the check variety, Fawn.

Identification	Maturity rating <sup>1</sup>	Vigor rating <sup>1</sup>	Plant spread <sup>2</sup>	Plant height <sup>2</sup>	First harvest yield <sup>3</sup>	Second harvest yield <sup>3</sup>	Third harvest yield <sup>3</sup>	Total forage yield <sup>3</sup>
P <sub>1</sub>	3.09	7.04	38.72	73.52	436.46	83.11	104.38	623.95
P <sub>2</sub>	5.72	7.39	32.52	65.42	292.84	43.95	74.01	410.79
P <sub>3</sub>	1.04	7.47	31.94	73.77	367.95	57.00	92.75	516.80
P <sub>4</sub>	5.98	3.98	31.18	53.78	248.98	71.38	106.51	426.86
P <sub>5</sub>	5.43	6.16	39.34	57.64	311.96	78.77	95.34	486.08
P <sub>7</sub>	8.11	5.61	22.52	37.23	88.17	76.79	39.43	204.39
P <sub>8</sub>	8.18	1.74	20.91	45.25	72.27	84.02	44.93	201.23
P <sub>9</sub>	7.81	5.68	20.91	32.94	49.14	58.61	22.61	130.36
P <sub>10</sub>	8.66	2.02	23.25	26.72	49.63	74.22	31.03	154.88
S <sub>1</sub> <sup>1</sup>	3.77	8.48	35.12	66.86	346.16	52.62	78.69	477.47
S <sub>1</sub> <sup>2</sup>	7.94	8.46	25.94	39.85	99.89	10.24	22.88	133.01
S <sub>1</sub> <sup>3</sup>	4.08	7.79	25.39	61.26	182.26	19.31	38.23	239.79
S <sub>1</sub> <sup>4</sup>	6.85	7.43	28.60	43.29	150.08	30.09	33.14	213.32
S <sub>1</sub> <sup>5</sup>	7.01	7.75	33.58	49.94	172.95	48.52	51.95	273.42
S <sub>1</sub> <sup>8</sup>	8.74	4.41	18.19	32.15	35.79	35.78	17.02	88.59
S <sub>1</sub> <sup>10</sup>	8.64	2.95	20.76	26.82	46.93	40.71	29.69	116.95
SX <sub>1.2</sub>	3.41	8.28	37.84	70.46	470.07	67.79	95.08	587.98
SX <sub>2.3</sub>	4.08	6.82	33.29	65.28	391.72	45.91	97.13	534.76
SX <sub>4.5</sub>	4.82	3.94	37.28	62.25	384.43	105.88	98.65	563.96
SX <sub>7.8</sub>	7.17	2.61	25.82	42.58	143.12	126.04	54.79	323.96
SX <sub>8.9</sub>	7.75	2.80	23.95	38.67	93.09	106.05	32.17	231.31
SX <sub>9.10</sub>	8.39	3.91	24.17	30.25	65.82	91.86	30.11	187.78
SX <sub>1.9</sub>	4.34	6.19	35.75	61.47	364.68	103.59	69.36	537.63
SX <sub>2.10</sub>	5.84	2.31	34.84	51.88	333.37	147.75	79.45	535.57
SX <sub>3.8</sub>	5.00	3.48	32.11	58.93	325.16	127.07	89.29	541.53
Fawn	2.89	4.79	35.69	74.67	425.59	86.25	118.20	630.04

<sup>1</sup>Rated one to nine with one equaling earliest and most vigorous plants.

<sup>2</sup>Centimeters

<sup>3</sup>g/plant

## APPENDIX B

Numerical Example Showing Linear Comparison Between  
Parent Mean and Progeny Mean Along With  
Its Associated Mean Square

A linear function (Cochran and Cox, 1957)

$$L_j = k_1 t_1 + k_2 t_2 + k_i t_i + \dots + k_p t_p$$

is a contrast among totals when

$$k_1 + k_2 + \dots + k_p = 0$$

and  $t_i$  = total for the measured character of the  $i^{\text{th}}$  classification.

A sum of squares associated with  $L_j$  is

$$s_j^2 = \frac{L_j^2}{D_j} \quad \text{with 1 degree of freedom}$$

where

$$D_j = n(k_1^2 + k_2^2 + \dots + k_p^2) \quad \text{and } n_1 = n_2 = \dots = n_p = n.$$

Example: A linear contrast between  $SX_{1.2}$  and  $MP_{1.2}$  for first harvest forage yield.

Block	Forage yield (g/plant)				Total
	I	II	III	IV	
$SX_{1.2}$	421.43	480.79	542.36	435.71	1880.92
$MP_{1.2}$	298.07	365.29	332.72	462.54	1458.62

Then  $L_j$  is a linear contrast between the midparent and its SX progeny where

$$L_j = k_1 t_1 + k_2 t_2$$

$$\begin{array}{ll} \text{and} & k_1 = +1 & t_1 = 1880.92 \\ & k_2 = -1 & t_2 = 1458.62 \end{array}$$

$$\begin{array}{l} \text{Then} & L_j = 422.30, \\ & D_j = 4(1^2 + 1^2) = 8, \end{array}$$

$$\text{and} \quad s_j^2 = \frac{L_j^2}{D_j} = \frac{(422.30)^2}{8} = 22292.1613.$$

This sum of squares is a component of the entry sum of squares for first harvest forage yield, Appendix Table 1. An "F" test for significant difference between the means of  $MP_{1,2}$  and  $SX_{1,2}$  is made by dividing the contrast mean square by the block x entry mean square, an estimate of the random error.

$$F = \frac{22292.1613}{1386.9110} = 16.0733**$$

This F value indicates yield of  $SX_{1,2}$  was significantly greater than the yield of  $MP_{1,2}$  at the one percent level of probability.