

AN ABSTRACT OF THE THESIS OF

Keith Isom Matheson for the Ph. D. in Farm Crops
(Name) (Degree) (Major)

Date thesis is presented Dec. 16, 1964

Title THE BREEDING BEHAVIOR OF FORAGE YIELD IN TWO
POPULATIONS OF TALL FESCUE, (FESTUCA ARUNDINACEA,
SCHREB.)

Redacted for Privacy

Abstract approved _____
(Major professor)

The single-cross and most F_2 progenies of 19 genotypes of tall fescue (Festuca arundinacea, Schreb.) were used to study the breeding behavior of forage yield. Parental genotypes were selected for high self-sterility, high chromogen and high crude protein. These were studied in two groups of nine intermediate and ten late-flowering genotypes.

Progenies were grown on the Hyslop Agronomy Farm, Corvallis, Oregon as plants spaced one foot apart with three feet between rows. Ten plants of each cross for each generation were arranged in a randomized block design with four replications. Variables measured were plant width, natural plant height, plant spread, leaf length, total plant height of regrowth tissue, plant density and forage yield. The collected data were converted to plant means.

Broad- and narrow-sense estimates of heritability were

obtained from expected mean squares according to Griffing's analysis (random model, method four) and compared with estimates of heritability obtained by F_2 -single-cross regression. General and specific combining ability effects were observed and the single-cross- F_2 inbreeding depressions were studied. The F_2 families were obtained by the self-pollination of five single-cross plants.

General combining ability mean squares averaged from two to nine times greater than the mean squares for specific combining ability, with the largest difference being 54.7 times greater. The two populations responded similarly for the variables measured except for total plant height and plant spread. Greater progress from selection could be expected in the late-maturing group with the exception of these two traits.

In most cases, single-cross progenies performed better than their corresponding F_2 progenies. The average of all single-crosses differed from the average of all F_2 progenies in 12 of 20 analyses in 1963, but in only 2 of 12 in 1964. The inbreeding characteristic was most pronounced for forage yield. High-performing single-crosses for the traits studied tended to produce high-performing F_2 progenies. Little or no heterosis was expressed and the expression of inbreeding depression appeared to be influenced greatly by the environment.

Heritability estimates indicated that most traits could be studied more effectively after the second year of plant establishment.

The environmental influence appeared to be less pronounced at that time. Where the coefficient of determination was high between the single-cross and F_2 generations, traits were less influenced by the environment and the disparity between the estimates of heritability was less. When used on cross-pollinated polyploid grasses, the method of diallel analysis proposed by Griffing does not appear to remove all environmental influence and thus overestimates heritability.

Forage yield in the two populations of tall fescue studied was governed principally by additive gene action. Heterosis expressed was mostly in crosses involving low-performing parents.

THE BREEDING BEHAVIOR OF FORAGE YIELD IN TWO
POPULATIONS OF TALL FESCUE,
(FESTUCA ARUNDINACEA, SCHREB.)

by

KEITH ISOM MATHESON

A THESIS

submitted to

OREGON STATE UNIVERSITY

in partial fulfillment of
the requirements for the
degree of

DOCTOR OF PHILOSOPHY

June 1965

APPROVED:

Redacted for Privacy

Associate Professor of Farm Crops

In Charge of Major

Redacted for Privacy

Head of Farm Crops Department

Redacted for Privacy

Dean of Graduate School

Date thesis is presented December 18, 1964

Typed by Carol Baker

ACKNOWLEDGMENTS

The author wishes to express deep gratitude to Dr. R. V. Frakes for his continued assistance, challenge and encouragement throughout the course of the study.

Many thanks are given to Dr. Ralph Bogart for helpful criticism of the manuscript; to Drs. J. Ritchie Cowan and W. W. Chilcote for their interest and advice; and to the Department of Farm Crops for availability and use of facilities. Appreciation is also extended to the many others who directly or indirectly aided in this work.

TABLE OF CONTENTS

	Page
INTRODUCTION	1
REVIEW OF LITERATURE	3
General and Specific Combining Ability	3
Improvement Potential	4
The Diallel Analysis	5
Use of the Diallel Analysis for Heterozygous Polyploid Species	7
Influence of Selection on Results Obtained from the Diallel Analysis	8
The Prediction of Forage Yield Based on General and Specific Combining Ability	10
The Use of Regression as an Estimate of Genetic Potential	11
Heritability Estimates	12
Influence of Environment on Estimates of Genetic Potential	14
Inbreeding Depression	14
Gene Action in Tall Fescue	15
MATERIAL AND METHODS	18
Source Material	18
Nursery Establishment	22
Nursery Maintenance	22
Measurements and Collection of Data	23
Plant Width	24
Natural Plant Height	24
Plant Spread	24
Leaf Length	25
Total Plant Height	25
Plant Density	26
Forage Yield per Plant	26
Analysis of Data	27

TABLE OF CONTENTS (Continued)

	Page
EXPERIMENTAL RESULTS	31
Plant Width	31
Natural Plant Height	34
Plant Spread	36
Leaf Length	40
Total Plant Height	44
Plant Density	47
Forage Yield per Plant	48
DISCUSSION	54
General and Specific Combining Ability	54
Comparison of Groups I and L	56
Inbreeding Depression	57
Heritability Estimates	62
Breeding Behavior	65
SUMMARY AND CONCLUSIONS	67
BIBLIOGRAPHY	72
APPENDIX	76

LIST OF TABLES

Table	Page
1. Identification of parental genotypes of Group I (intermediate maturity), May 21 to 25.	19
2. Identification of parental genotypes of Group L (late maturity), May 26 to 29.	20
3. Expected mean squares in the analysis of variance for general (GCA) and specific (SCA) combining ability, random model.	28
4. Genetic constants for plant width (cm.) in two groups of tall fescue; April 24-28, 1963.	32
5. Genetic constants for natural plant height (cm.) in two groups of tall fescue; April 24-28, 1963.	34
6. Genetic constants for plant spread (cm.) in two groups of tall fescue; May 28-31 and Sept. 26-27, 1963; April 28-29, 1964.	36
7. Genetic constants for leaf length (cm.) in two groups of tall fescue; June 13-17, 1963; June 2-4, 1964.	41
8. Genetic constants for total plant height (cm.) in two groups of tall fescue; June 13-17, 1963; June 2-4, 1964.	44
9. Total plant height and leaf length (cm.) in two groups of tall fescue; parents and single-cross progenies; 1963 and 1964.	45
10. Genetic constants for plant density (rated 1-9) in two groups of tall fescue; June 5, 1964.	47
11. Genetic constants for yield per plant (gm. dry matter) of tall fescue; Group I, 1963 and 1964.	49
12. Genetic constants for yield per plant (gm. dry matter) of tall fescue; Group L, 1963 and 1964.	49

LIST OF TABLES (Continued)

Table	Page
13. Forage yield in grams per plant of Groups I and L, parents and single-cross progenies. Four harvests in 1963 and two in 1964.	50
Appendix Table	
1. Means of forage yield and five other variables; tall fescue, Group I, 1963.	76
2. Means of forage yield and five other variables; tall fescue, Group L, 1963.	79
3. Means of forage yield and four other variables; tall fescue, Group I, 1964.	82
4. Means of forage yield and four other variables; tall fescue, Group L, 1964.	85
5. Mean squares and levels of significance of forage yield and five other variables; tall fescue, Group I, 1963.	88
6. Mean squares and levels of significance of forage yield and five other variables; tall fescue, Group L, 1963.	89
7. Mean squares and levels of significance of forage yield and four other variables; tall fescue, Group I, 1964.	90
8. Mean squares and levels of significance of forage yield and four other variables; tall fescue, Group L, 1964.	91
9. List of mean squares for single-crosses, general combining ability (GCA) and specific combining ability (SCA) of forage yield and five other variables; tall fescue, Group I, 1963.	92

LIST OF TABLES (Continued)

Appendix Table	Page
10. List of mean squares for single-crosses, general combining ability (GCA) and specific combining ability (SCA) of forage yield and five other variables; tall fescue, Group L, 1963.	92
11. List of mean squares for single-crosses, general combining ability (GCA) and specific combining ability (SCA) of forage yield and four other variables; tall fescue, Group I, 1964.	93
12. List of mean squares for single-crosses, general combining ability (GCA) and specific combining ability (SCA) of forage yield and four other variables; tall fescue, Group L, 1964.	93
13. Numerical example for the combining ability analysis and derivation of broad- and narrow-sense heritability estimates from expected mean squares for plant width; Group I, 1963.	94

THE BREEDING BEHAVIOR OF FORAGE YIELD
IN TWO POPULATIONS OF TALL FESCUE,
(FESTUCA ARUNDINACEA, SCHREB.)

INTRODUCTION

The forage breeder is charged with the responsibility of improving quantitatively-inherited characteristics such as forage yield and quality. There is need for more productive forage varieties adapted to specialized ecological conditions. To achieve these aims, a good understanding of the genetic variation in forage crop species is required.

Sound estimates of genetic constants in the cross-pollinated forage species are difficult to obtain because of the inherent environmental variation. Analytical methods for separating the phenotypic variation into variation due to environment and that due to genetic differences have been used by animal breeders and similar methods may be useful for obtaining genetic constants in forage species. Selection pressure may not be effective without estimates of genetic constants. An understanding of the breeding behavior of forage characteristics is necessary to reach the desired objective.

The study of progeny performance of parental material is a logical approach to determine breeding behavior. Diallel analyses have been used to obtain general and specific combining ability estimates from single-cross data. The effectiveness of this technique

has not been proven for cross-pollinated forage species.

Tall fescue (Festuca arundinacea, Schreb.), was used in this study in an effort to supply information to the forage breeder about the breeding behavior of forage yield and the effectiveness of different methods used to develop estimates of genetic constants.

The objectives were:

1. To investigate the breeding behavior of forage yield by studying such variables as plant width, natural plant height, plant spread, leaf length, total plant height and plant density.
2. To compare estimates of genetic constants for two populations.
3. To compare estimates of genetic constants obtained by three analytical methods: diallel analysis, F_2 -single-cross regression and observed inbreeding depression.

REVIEW OF LITERATURE

To effect improvement of a quantitatively-inherited characteristic in a plant population it is essential that part of the variation of that characteristic be due to genetic influence. Complex characters such as yield take the form of continuous rather than discontinuous variation and are influenced profoundly by the environment. There is a need for some method by which the variation due to genetic control and that due to environmental influence can be separated. Combining ability analysis is one method of determining the improvement that might be made in a selected population.

General and Specific Combining Ability

Johnson (1952), in expressing the need for information concerning the relationship of general combining ability to the ultimate yield of synthetic forage varieties, recognized the value of controlled F_1 crosses. Burton (1952) indicated that in breeding of forage crops the effects of individual genes controlling quantitative characters had been assumed or were shown to be additive in their action. General combining ability, summarized by Johnson (1952), is due primarily to additive gene action and specific combining ability is due primarily to deviation from the additive scheme. A definition of combining ability useful to forage breeders is that given by Sprague and Tatum

(1942), where general combining ability is the average performance of a line in hybrid combinations. Cases in which certain crosses perform better or worse than expected on the basis of the average performance of the lines involved due to dominance or epistasis are the result of specific combining ability.

Bolton (1948) found, when studying both inbred and open-pollinated parental sources of alfalfa, that differences in combining ability existed. It was advocated that heterozygous parental lines should be used in breeding because of less problems involved in obtaining seed.

Improvement Potential

The lack of information about quantitative character inheritance in the polyploid forage grasses is discussed by Smith (1956). There is limited understanding of their breeding behavior. Pertinent information on combining ability in forage grasses is reviewed by Hanson and Carnahan (1956). Cowan (1956), in a three-year study, observed a wide range of variability of forage characteristics in tall fescue and found that no correlation existed for the performance of plants in March, August or October. It was concluded that selection for performance in one season would not necessarily be a reliable index of the performance in another season. This would indicate that yield for each growth period was independent of the others and that

selection for more uniform growth throughout the summer period may be possible. The fact that greater improvement has not been made stands as mute testimony of the complexity of the problem.

The Diallel Analysis

The diallel cross has been used and found an effective means of evaluating materials in order to facilitate selection, but hardly proven for grass improvement. Hayman (1960) summarized the various aims of diallel cross experiments and interrelated the design and methods as given by Griffing (1956), Hayman (1954, 1957, 1958), Jinks (1954, 1956), and Kempthorne (1956). These analyses differ in three respects: in the material ultimately under investigation; in the postulated underlying genetic mechanisms; and in the method of estimation of the genetic mechanisms. Which method of analysis the breeder uses is dependent upon his objectives.

Hayman (1960) indicated that inbred and crossbred parents commonly have different error variance, but that a diallel cross containing ten parents would supply useful estimates of six parameters as long as the estimates of the error variances of diagonal and non-diagonal means are relatively accurate. The only time fewer parents could be evaluated in such a cross would be when they and their single-crosses comprised the whole population. The assumptions underlying the diallel analysis are presented by Kempthorne (1956), who stated that

to have homozygous parents was not essential as long as the inbreeding coefficient of them was the same. Dickinson and Jinks (1956), by extending the method of Jinks and Hayman to crosses involving parental heterozygosity, tried to carry the concept further in order that processes of diallel analysis might prove to be more useful. For the analysis to be valid it was necessary that the parents contribute equal samples of gametes to each family. It is understandable that the larger the number of offspring contributing to each family mean, the more likely this stipulation would be fulfilled. The conclusion from this work was that certain conditions such as epistasis were confounded in the statistics but that the technique would be useful for plants which could act as male or female. The method would be less useful to self-incompatible or monoecious plants. It was inferred by Kempthorne (1956) that the analysis of variance for the diallel cross analysis had little use unless epistacy could be ignored.

Griffing (1956) formulated a method and was able to give unbiased estimates of the population additive genetic and non-additive genetic variance by using his method four, model two, providing that epistatic effects were absent. The assumptions made by Griffing for his method are that the parental inbred lines are a random set of lines from a hypothetical population of inbred lines which can be obtained from the original random mating population by some system of breeding acting in the absence of forces which change gene frequencies.

In order that an unbiased estimate of the genetic parameters might be obtained, it was necessary to have the parents excluded from the analysis. Since the calculations would involve data from hybrid combinations and since most forage crop species are essentially hybrid, then by extension of the assumptions, information of gene action governing forage crop yield and other quantitatively-inherited characteristics should be obtained.

Use of the Diallel Analysis for Heterozygous Polyploid Species

Carnahan et al. (1960) studied seedling vigor and fall growth habit in partially-allopoloid alfalfa using the analysis proposed by Griffing. Seven assumptions were given, four of which are: 1) the population was randomly mating and in equilibrium; 2) the parental clones were a random sample of the population with an over-all gene frequency equal to the population; 3) each clone was equally heterozygous and non-inbred and 4) the statistical techniques developed for diploid organisms may be useful for partially-allopoloid species. The remaining assumptions dealt with differential mortality and competition. The result of not meeting the assumptions in their entirety and the effect upon the analyses were uncertain. The conclusions from this study were that general combining ability effects were more important than specific combining ability for both seedling vigor and fall growth habit. There was a significant general and specific

combining ability by location interaction from which it was concluded that genotype by location interactions for breeding materials should receive as much or more attention than that given to specific combining ability. Later, an unanticipated self-pollination problem was found to be involved in the crosses (Hanson et al., 1964).

A study of an eight-clone diallel cross of early maturing tall fescue was made by Echeverri (1964, p. 87) who found that discrepancies occurred between the diallel analyses and the data from other methods of progeny testing. Based on the data, it was thought that tall fescue as a genetic material might not have met the assumptions underlying the diallel analyses. Theurer and Elling (1964) indicated that a satisfactory prediction of synthetic yield could not be made from a five-clone diallel study and indicated that some other method of predicting forage yield might be more useful. Wilcox and Wilsie (1964) concluded that from a nine-clone diallel study selection of classes could be made that may be useful in hybrid combination as well as for synthetic varieties.

Influence of Selection on Results Obtained from the Diallel Analysis

When selfing or other maternal effects were not considered in Griffing's analysis, Dudley (1963) concluded that the general combining ability would be over-distorted in relation to the specific combining ability effects. Similar information was given by Rojas and

Sprague (1952). Information on specific combining ability would be less accurately predicted than general combining ability because of the influence of the genotype by environmental interaction. The specific combining ability variance contained not only non-additive deviation due to dominance and epistasis but also the environmental influence.

When selected lines of corn were tested for combining ability, it was shown by Sprague and Tatum (1942) that the specific combining ability components for yield of corn were high, while a preponderance of general combining ability effects were indicated for unselected material. Kehr (1961) found that specific combining ability was more important than general combining ability for spring growth habit and forage yield in alfalfa. General combining ability effects were slightly larger than the specific component for fall growth habit and rate of recovery after harvest in a diallel series using six previously selected clones based on general combining ability for forage yield.

A hybrid of falcata with common alfalfa showed a larger specific combining ability component than general combining ability (Wilcox and Wilsie, 1964). Heterosis effects were greater in interspecific crosses of cotton than intraspecific crosses according to Marani (1963) and in crosses involving low yielding lines of upland cotton (Miller and Marani, 1963). A hybrid of two clones showing the highest general combining ability for bacterial wilt resistance and forage yield in alfalfa showed, by an

appreciable margin, the smallest amount of specific combining ability (Theurer and Elling, 1963, 1964).

The Prediction of Forage Yield Based on General and Specific Combining Ability

The breeding behavior of yield and related variables among four selected clones of alfalfa were studied by Frakes, Davis and Patterson (1961). The mean square ratio of general combining ability to specific combining ability for forage yield was intermediate to the mean square ratio of the variables of natural height, long stem length (both of which responded to high general combining ability) and natural width and stem number, which were influenced more by specific combining ability. The four variables in partial regression accounted for 93 percent of the variation in yield. From these relationships these workers were confident that it was possible to predict forage yield from the measurable variables. It was also indicated that more emphasis should be placed on non-additive gene action when undertaking a forage breeding program. This concept was in agreement with Kehr (1961) and Bolton (1948).

The relationship between the comparative performance of five elite clones of alfalfa in a diallel cross and the related second generation synthetics was studied for bacterial wilt resistance (Theurer and Elling, 1963) and forage yield (1964). The single-crosses were

studied as spaced plants and the synthetics were studied as spaced plants and in drilled rows. The general combining ability mean squares for wilt resistance were seven and one-half and for yield, three times the magnitude of the specific combining ability mean squares. Both components were considered significant. The two-clone synthetic response followed closely to the expected response on the basis of general combining ability, if yield was evaluated by space-planted synthetics. Forage yield of the two-clone synthetics in solid stand were inconsistent between years, however the mean yield of the synthetic involving the two clones high in general combining ability, according to their data, was among the highest yield of the synthetics.

The Use of Regression as an Estimate of Genetic Potential

The methods of estimating heritability were reviewed by Warner (1952), who classified them into three main categories: 1) parent-offspring regressions; 2) variance components from an analysis of variance and 3) approximation of non-heritable variance from genetically uniform populations to estimate total genetic variance. None of these methods was considered to be completely satisfactory for the breeder who, upon observing the F_2 population, might be interested in knowing the effectiveness of selection. Panse (1940) regressed the F_3 on the F_2 generation to obtain an estimate of the additive genetic fraction of the total F_2 variance for staple-length

measurements in three strains of Indian cotton. When the progeny was grown in replicated plots, selection of individuals from the progeny could be made on the basis of a higher performance than that of the plot as a whole. In this way the environmental influence would be minimized. Burton (1952) indicated that parent-progeny correlations for such characteristics as yield would show some degree of significance if suitable techniques of measurement were found. Kneebone (1958) suggested that squared correlations are a direct measure of probable effectiveness from selection. Estimates of heritability were obtained by McDonald, Kalton and Weiss (1952) by the regressing of open-pollinated progeny on selected brome grass clones. The values obtained were 32.9, 32.3 and 43.3 percent for yield, plant spread at ground level after harvest, and plant height, respectively. The same technique was used by Kneebone (1958), who studied plant height, diameter, and leafiness in sand bluestem. Heritability estimates agreed reasonably well when determined from variance components of clonal data or open-pollinated progeny and compared to twice the parent-progeny regression value.

Heritability Estimates

Variance components were used by Burton (1952) and Burton and DeVane (1958) to arrive at the estimate of heritability in the broad-sense, defined as the total variance due to total genetic effect,

which would estimate the sum of the following variances: 1) additive genetic variance; 2) variance due to dominance deviations from the additive scheme; 3) variance due to the interaction on non-allelic genes and 4) variance due to the interaction of the genotypes and the environment. Formulas for deriving the estimates were:

$$\frac{V_{F_2} - V_{F_1}}{V_{F_2}} \text{ in pearl millet or from propagules of a clone as}$$

$$\frac{V_{S_1} - V_C}{V_{S_1}} \text{ and clonal tall fescue as } \frac{V_G}{V_G + V_e} \times 100 \text{ where } V \text{ is}$$

the variance of the population designated by subscript F_1 and F_2 for generations, S_1 for first-selfed generation, C for the variance within clones, G due to variance of the genotypes and e for the variance among propagules of the same genotype due to the environment.

Estimates of heritability for forage yield were derived from expected mean squares by Thomas and Kernkamp (1954) from the analysis of variance of the polycross progeny of smooth brome grass. If the genotypic variance of the parental clones were associated with the phenotypic variance of their progeny, then these authors indicated that a narrow-sense heritability estimate could be thought of as r^2 . For this trial the heritability of forage yield was 20 percent and the squared association value of parental clones and polycross progeny

was 15 percent. It was found that environmental stress could influence the ratios.

Influence of Environment on Estimates of Genetic Potential

Frakes (1955, p. 53) studied the effect of management on the broad sense estimates of heritability for yield and crude protein among 20 genotypes of tall fescue. When the genotypes were allowed to express themselves, differences were found among them. However, when management stress was more severe, an apparent equilibrium was reached and no differences resulted.

Genotype-environmental interactions in Nicotiana rustica were studied in a diallel cross by Allard (1956). It was found that non-allelic interaction was important in the genetic control of flowering date. Additive effects were apparently stable but the dominance effects were quite unstable for this trait. A complimentary type of non-allelic interaction was found for height, which component was quite stable in different environments. The dominance effects of genes controlling height were changed considerably with environmental changes. Such interactions could certainly account for the disparity of results among various workers in the field.

Inbreeding Depression

Should the procedures for estimating the potential genetic

advance within a population be true predictions, then it would seem that a constant and a reliable estimate of heritability should be obtained by any or all of the procedures used. Matzinger, Mann and Cockerham (1962), working with common tobacco, found that the F_1 hybrids yielded more, were taller and the leaves wider than the mid-parent. All characters studied showed a significant inbreeding depression which in most cases was more evident than the heterotic effect. A fair agreement was found between heterosis and the inbreeding depression. An interesting point of this study was that diallel analyses conducted on the F_1 and F_2 data showed significant general combining ability effects but specific combining ability effects were not significant. In both instances estimates for general combining ability were comparable. Miller and Marani (1963) found an inbreeding depression from the F_1 to the F_2 generation, but the values of the F_2 generation for all traits studied tended to be intermediate between the midparent and the corresponding F_1 progenies. These authors considered the small heterotic effects not to be useful, which was in agreement with Marani (1963), Matzinger, Mann and Cockerham (1962), and Theurer and Elling (1964). This would indicate that breeding of complex traits could be based on additive gene action for the most economical gain.

Gene Action in Tall Fescue

Very limited information on the nature of gene action is

available for tall fescue. Burton and DeVane (1958) indicated a potential improvement of 62 to 72 percent for forage yield. These percentages were based on broad-sense estimates of heritability. On a diallel series of nine intermediate flowering genotypes, Caceres (1963, p. 33-36) found that maturity and selfed-seed yield per panicle were controlled primarily by additive gene action based on general combining ability analyses. A narrow-sense estimate of heritability for selfed-seed yield was 46 percent and for maturity, 19 percent. For this intermediate and a late flowering population of single-cross progenies, an association at the one percent level was found between plant height, plant width, maturity of inflorescence formation and forage yield. Eight parents of an early maturing nature and their open-pollinated, polycross, self-one and single-cross progenies were studied by Echeverri (1964, p. 63-92). Forage yield as a measure of plant recovery after seed harvest showed an inbreeding depression from 32.8 grams per plant for the parents to 27.6 grams per plant for the first-selfed generation. Yield of the single cross progeny was positively correlated ($r = 0.72^{**}$) with the midparent as well as with the low and the tall parent where $n = 28$. Conclusions were that forage yield seemed to respond to additive gene action, however the lowest heritability estimates based on combining ability analyses for the characters studied were for forage yield. Broad- and narrow-sense heritability estimates were 30.9 and 24.4, respectively. Since the

smallest parent produced the best progenies, it was thought that non-additive gene action might be involved.

MATERIAL AND METHODS

Source Material

Twenty-seven genotypes of tall fescue were selected for high self-sterility, high chromogen and high crude protein content from a large, space-planted breeding nursery. These plants were separated into three groups of eight early, nine intermediate and ten late flowering genotypes, based on average anthesis date.

The intermediate maturity group (Group I) and the late maturity group (Group L) were used to study the breeding behavior of forage yield. Description of the parental genotypes of Group I is given in Table 1 and of Group L in Table 2.

The experiment consisted of two nurseries involving the parents of Groups I and L and their open-pollinated progenies, polycross progenies, first-selfed generation, all possible single-crosses for each group and most of the F_2 progenies. These were planted at the Hyslop Agronomy Farm, Corvallis, Oregon in October 1962. Seed to establish the first-selfed generation (S_1), the single-cross (S_x) and the F_2 progenies was obtained under 4 x 4 x 17 inch parchment paper bags. An eyelet and fine malleable wire, which was used to tie the bags to metal stakes, were attached to the top of the bag. The bottom of the bag was tied around the culms and to the metal stake after the

Table 1. Identification* of parental genotypes of Group I (intermediate maturity), May 21 to 25.

Parental Genotypes	Date of Flowering May <u>1/</u>	Chromogen <u>2/</u>	% Crude Protein <u>2/</u>	Grams Seed Yield <u>3/</u>	Forage Appearance <u>4/</u>	% Self Fertility <u>5/</u>	Origin
296	24	132	10.52	3.53	5, 4, 5	15.5	Alta
298	22	132	10.05	3.44	5, 4, 6	2.1	Alta
299	22	162	9.98	4.42	4, 3, 5	9.5	Alta
311	23	151	8.70	3.35	6, 3, 5	5.5	K-31
329	23	135	9.05	3.00	4, 4, 4	4.6	K-31
359	24	127	10.30	3.04	4, 4, 4	7.6	Mo. #1
366	25	147	11.49	2.60	4, 4, 5	5.6	Mo. #2
368	22	125	8.99	4.04	5, 4, 7	7.4	Mo. #3
374	23	138	8.76	2.18	5, 3, 4	7.5	Mo. #3

* Forage breeding project report, p. 51, 1960, Farm Crops Department, Oregon State University.

1/ 1957-58 Average

2/ Clippings made 7-10 through 7-24-57 at similar stage of maturity

3/ Five-panicle samples, 1955

4/ Phenotypic rating 1-7, made early, intermediate and late in summer; 7 is not desirable.

5/ Comparison of open- vs. self-pollinated seed set

Table 2. Identification* of parental genotypes of Group L (late maturity), May 26 to 29.

Parental Genotypes	Date of Flowering May <u>1/</u>	Chromogen <u>2/</u>	% Crude Protein <u>2/</u>	Grams Seed Yield <u>3/</u>	Forage Appearance <u>4/</u>	% Self Fertility <u>5/</u>	Origin
309	26	139	12.06	3.53	3, 4, 5	7.8	Ky. -31
310	28	137	9.50	2.97	6, 3, 5	8.3	Ky. -31
326	28	145	10.16	3.11	3, 2, 4	7.7	Ky. -31
327	27	123	10.28	2.41	4, 3, 4	4.8	Ky. -31
331	29	144	9.58	2.66	4, 2, 4	3.0	Ky. -31
364	28	155	11.29	1.78	5, 3, 4	3.5	Mo. #2
370	26	136	9.98	3.33	4, 3, 4	1.7	Mo. #3
372	26	125	9.59	2.56	4, 4, 5	7.6	Mo. #3
379	27	133	9.72	1.43	5, 4, 4	19.5	Mo. #4
380	29	142	9.51	1.43	6, 4, 5	1.4	Mo. #4

* Forage breeding project report, p. 51, 1960, Farm Crops Department, Oregon State University.

1/ 1957-58 average

2/ Clippings made 7-10 through 7-24-57 at similar stage of maturity

3/ Five-panicle samples, 1955

4/ Phenotypic rating 1-7, made early, intermediate and late in summer; 7 is not desirable.

5/ Comparison of open- vs. self-pollinated seed set

bag had been placed over a predetermined number of panicles by a wire tie tag used to identify the material. At harvest the panicles were cut well up into the bag and the metal stake pulled, leaving the tag attached to the bag for identification. During the thrashing each bag was clipped above the wire and the contents run through a self-cleaning spike tooth thrasher. The seed was then cleaned in a South Dakota blower using a four inch tube and a number 18 air exhaust top opening.

Panicles of two parental clones were bagged together without emasculation to obtain single-cross seed. Five randomly selected single-cross plants were self-pollinated and equal amounts of seed from each plant were bulked for the F_2 populations.

Seed for the open-pollinated progenies came from the same nurseries for the respective groups as the single-cross seed except that only the maternal parentage could be identified. The polycross progenies were obtained from isolated polycross nurseries for the respective groups.

The seed was planted in flats in number two perlite, was watered, vernalized (one week at 38° F.) and germinated in the greenhouse. Seedlings were transplanted into 2 x 2 x 3 inch plant bands filled with a sandy loam river bottom soil mixed with peat moss. The parent plants were cloned and propagules placed in the same plant bands. All plants were fertilized periodically with a complete

fertilizer.

Nursery Establishment

From October 6 through 23, 1962 the established seedlings and parent propagules were moved to the field and hand-transplanted after removal of the plant bands. The experimental field had been prepared by marking, fertilizing (30 pounds of nitrogen per acre), irrigation and cultivation after having been fallowed the previous summer as a weed control measure.

Each nursery was organized into ranges and rows. There were 45 rows per range plus a border row on each end of the range. Rows were three feet apart. Ten plants per row planted one foot apart in each range constituted one plot. In this way plots could be identified by range and row and plants by number, range and row. Two orchardgrass plants per row were used to identify the ranges and to offset border effects.

Nursery Maintenance

On March 13, 1963 a National sickle-mower was used to clip the nurseries to a two-inch height to remove the effect of any variation in forage yield as a result of transplanting. The nurseries were maintained periodically by hand hoeing and tillage between rows with a rotary tiller during the spring and summer.

In addition to the nitrogen applied at establishment, 30 pounds of nitrogen were applied on May 20 after the first harvest and 33 pounds in December of 1963. Karmex (Diuron) was applied at the rate of three pounds of active material as a weed control measure on November 12, 1963. The experiment was irrigated twice during 1963, but did not receive water during the data collecting period of 1964. The nurseries were irrigated on May 29 after the first harvest at the rate of one and one-half inches and after the second harvest on August 13 at the rate of two and one-half inches. This was in addition to the normal annual rainfall of 35 inches, occurring from September 25 to May 15. Little or no moisture fell during the summer period.

After each harvest the nurseries were cut to a uniform three inches with a rotary mower. Because of the large number of plants, some regrowth could be noticed on replications one and two of Group I before the final replications of Group L could be harvested.

Measurements and Collection of Data

Measuring and harvesting generally proceeded from range one row one consecutively through the range. Any break in continuity of measuring due to inclement weather or other cause was at the beginning of a replication. All measurements taken were in centimeters (cm.) and weights in grams (gm.). Measurements were taken on individual plants and the data analysed on a mean plant basis. Plot

weights were taken for plants collectively and converted to average plant weight. The same data were taken on each group. Some changes in the variables measured occurred between years. Means of the ten variables for 1963 and six variables for 1964 by progeny groups are found in the Appendix (Tables 1 to 4).

Plant Width. Plant width measures the widest diameter of foliar growth. This measurement was taken approximately three weeks prior to the first harvest and the data should indicate growth habit. Plant width measurements were made on April 24 for Group I and April 28 for Group L during 1963 only.

Natural Plant Height. Natural plant height was measured from the ground level to the average of the highest growing points of the plant. This measurement for vegetative growth would be influenced by growth habit because of the manner in which the measurements were made. Plants with a lax growth habit would have wider and shorter measurements than plants of more erect nature. Measuring dates were the same as for the measuring of plant width.

Plant Spread. Plant spread as measured gives an indication of the ability of the plant to increase in basal diameter. Measurements were taken across the widest diameter of the plant after forage harvest. The measurements were taken on May 28 and 31 after

the first harvest and on September 26 and 27 after the fourth harvest for Groups I and L, respectively, during 1963. In 1964 the measurements were taken on April 28 and 29 after the first harvest.

Some plants of Group L had ability to creep. This creeping, although measured as spread, was different from the normal growth expressed by the majority of the plants in the two nurseries.

Leaf Length. This measurement was taken by placing the meter stick in the center of the plant and extending the leaf tissue up the rule until the bulk of the foliar tissue would relax to its normal position. Aftermath following the first harvest was measured. A plant having exceptionally long leaves would sometimes far exceed its natural height, since this same plant would tend to be quite a decumbent one. Other plants produced mostly stems with short leaves or lacked leaves altogether. For most plants the measurement would follow closely to the natural height if such a measurement had been made on plant regrowth following the first harvest. Leaf length measurements were made on June 13 for Group I and on June 17 for Group L during 1963 and on June 2 and 4 in 1964 for these two groups, respectively.

Total Plant Height. Many plants had a tendency to produce panicles after the first harvest. If no seed stalks were produced, this measurement was the same value as leaf length. Where panicles

had emerged, this measurement was from the ground to the highest point of the plant. Dates of measurement correspond to those for leaf length.

Plant Density. Plant density was given a phenotypic rating of one to nine on regrowth before the second harvest of 1964. The whole plot was rated. Stemmy plants with little leaf tissue were given a rating of one. A nine rating was given plants having dense foliage growth and with very few short to no-forming panicles. Gradation between these two extremes was grouped into three classes: three, five and seven. Although ratings were intended to be independent of other measurements, they were influenced by growth characteristics. The amount of foliage influenced the rating, since plants producing little top growth were rated lower than where growth was more luxuriant. Both nurseries were rated on June 13, 1964.

Forage Yield per Plant. The first three harvests in 1963 were by hand. Plants were harvested to a height of three inches using a rice knife (sickle). A Toro 25 whirlwind lawn mower was used for the fourth harvest and plants were clipped to a height of three inches. This same harvester was used for the second harvest in 1964. A Simplicity sickle mower with an attached conveying draper was used to harvest the first growth. Herbage was placed in burlap bags with a drawstring and dried in a forced air oven at 160-180° F. Dried

material was removed from the oven and weighed to the nearest gram on a Toledo scale. The bags were emptied and the bag weights recorded.

Harvest dates for 1963 were May 15, June 17, July 30 and September 19 for Group I and May 17, June 18, July 31 and September 20 for Group L. The first harvest date in 1964 for both groups was April 21 and the final harvest was on June 15 and 16.

Analysis of Data

The experimental nurseries were planted in a randomized block design with four replications. Group I consisted of 100 plot entries of ten plants per plot and Group L of 119. There were, then, 8,760 plants in the experiment exclusive of the border row plants, the orchardgrass plants and plants of the check variety Alta. Each variable measured was analyzed separately for each group and for each year by ordinary statistical procedures. A combined analysis of progeny groups was conducted. Mean squares and levels of significance for the ten variables measured during 1963 and for the six variables of 1964 are presented in the Appendix (Tables 5 to 8).

Only the single-cross and the available F_2 data are included in the present work. The random model of experimental method four of the diallel analysis proposed by Griffing (1956) was used to test for general and specific combining ability (Table 3). A numerical

Table 3. Expected mean squares in the analysis of variance for general (GCA) and specific (SCA) combining ability, random model.

Source of Variation	D. F.	Expected Mean Squares
GCA	p-1	$\sigma_e^2 + \sigma_s^2 + (p-2)\sigma_g^2$
SCA	p(p-3)/2	$\sigma_e^2 + \sigma_s^2$
Error	m	σ_e^2

Where p = No. of parents

σ_g^2 = Variance for general combining ability

σ_s^2 = Variance for specific combining ability

σ_e^2 = Error mean square

m = Degrees of freedom for experimental error

example occurs in Appendix Table 13. Since the additive genetic variance is equal to double the variance for general combining ability and the non-additive genetic variance is equal to the specific combining ability variance, it is possible to arrive at both narrow- and broad-sense estimates of heritability (H_n and H_b , respectively) using the expected mean squares listed in Table 3 according to the formulae:

$$H_n = \frac{2\sigma_g^2}{2\sigma_g^2 + \sigma_s^2 + \sigma_e^2} \quad \text{is a ratio of}$$

the additive genetic variance estimate to the estimate of the phenotypic variance.

$$H_b = \frac{2\sigma_g^2 + \sigma_s^2}{2\sigma_g^2 + \sigma_s^2 + \sigma_e^2} \quad \text{is a ratio of}$$

the total genetic variance estimate to the phenotypic variance. This approach assumes that statistical methods developed for diploid organisms are useful in providing information about this allohexiploid species; that the parents studied are equally heterozygous and are a random sample of intermediate and late maturing tall fescue. The parents used were not selected for the variables measured.

The F_2 data regressed on single-cross means as a measure of the amount of change in the F_2 population due to a unit of change in the single-cross population and thus an estimate of narrow-sense heritability, should be a means of evaluating those estimates based on the diallel analysis. The regression value should also be supported by the coefficient of determination (r^2) as an indication of the percentage of variation in the F_2 population that can be accounted for by variation in the single-cross population.

The significance of inbreeding depression from the single-cross data to F_2 mean values for the variables measured was determined by use of the Duncan multiple range test. The significant range was obtained by multiplying the standard error of the mean ($s_{\bar{y}}$)

by the tabular value for the five and one percent levels of significance. The tabular value used was obtained by considering a constant number of 100 means for Group I and 119 means for Group L associated with infinity degrees of freedom, since the degrees of freedom associated with the error term were large. With this level of significance chance variation should be removed and true inbreeding depression indicated.

EXPERIMENTAL RESULTS

Differences occurred among the single-cross progenies of Groups I and L for all variables studied in both 1963 and 1964 with one exception, plant spread in Group L for September, 1963. General combining ability (GCA) and specific combining ability (SCA) mean squares for all variables measured appear in the Appendix, Tables 9 to 12.

Ranges of variables for parents and single-cross progenies referred to in the text are derived from the Appendix, Tables 1 to 4. Numbers of crosses showing heterosis or inbreeding depression relationships are also derived from these tables.

Plant Width

The GCA mean square for plant width in Group I was not significant, while that for SCA was significant (one percent level). In Group L the mean square for GCA was significant at the one percent level and SCA at the five percent level. The ratios of GCA to SCA for plant width of Groups I and L were 1.2:1 and 5.2:1, respectively (Table 4).

Inbreeding depression agreed well with the results obtained from the combining ability analyses. As the percentage of inbreeding depression increased the ratio of GCA to SCA decreased and the significance level of SCA increased. The significance level of inbreeding

Table 4. Genetic constants for plant width (cm.) in two groups of tall fescue; April 24-28, 1963.

Genetic $\frac{1}{2}$ Constants	Group I	Group L
b	. 33	. 31
r^2	. 10	. 08
H_n	. 04	. 52
H_b	. 56	. 72
In	**	NS
In%	79	23
GCA:SCA	1. 2:1**	5. 2*:1*

$\frac{1}{2}$ b = F_2 - Sx regression coefficient

r^2 = F_2 - Sx coefficient of determination

H_n and H_b = narrow- and broad-sense heritability estimates based on expected mean squares from the diallel analysis of variance for single-crosses

In = level of significance between mean of all single-crosses and mean of F_2 's

In% = percent of single-crosses that exhibited a significant inbreeding depression

GCA:SCA = mean square ratio for general to specific combining ability

NS = No significant difference

* = Significant at the 5% level

** = Significant at the 1% level

Note: Significance levels indicated for GCA:SCA refer to levels of significance of mean squares of general combining ability and specific combining ability. Significance for In indicates the average of all single-crosses was significantly different from the average of all corresponding F_2 's.

depression between the mean of all single-crosses and that of the F_2 progenies showed a similar relationship; for Group I a one percent level was indicated, while no significance was shown for Group L.

The parents of Group I ranged in width from 19.4 to 23.8 cm. and their single-cross progenies from 16.1 to 20.9 cm. The same ranges for Group L were 12.5 to 25.4 and 17.9 to 23.6 cm., respectively. Twenty-two of the 28 single-crosses having corresponding F_2 progenies in Group I showed a significant inbreeding depression for plant width, while in Group L only ten of the 34 single-crosses having F_2 progeny showed inbreeding depression. Only one of the 28 single-crosses for which F_2 progeny means were available in Group I was wider than its wider parent. Nine approximately equaled the midparent, with the remainder having widths below the smaller parent. A similar relationship held for Group L (Appendix, Tables 1 to 4).

Based on expected mean squares (Table 3) of the combining ability analysis for plant spread, the broad- and narrow-sense heritability estimates for Group I agreed with inbreeding depression. The same was true for Group L (Table 4). Heritability estimates based on parent-offspring regression (F_2 on single-crosses) were similar for both populations, i. e., 0.33 for Group I compared to 0.31 for Group L. The values of r^2 , which is an estimate of the amount of variation in the F_2 generation accounted for by variation in the

single-cross generation, were 0.10 and 0.08, respectively. The two genetic constants for Groups I and L obtained by regression did not show the same relationship to inbreeding depression as did the other five constants.

Natural Plant Height

The mean squares of GCA and SCA for Group I and for Group L were significant at the one percent level (Table 5). The ratio of GCA

Table 5. Genetic constants for natural plant height (cm.) in two groups of tall fescue; April 24-28, 1963.

Genetic 1/ Constants	Group I	Group L
b	.34	.60
r^2	.11	.69
H_n	.48	.93
H_b	.82	.96
In	*	NS
In%	46	53
GCA:SCA	4.3**:1**	54.7**:1**

1/ See footnote, Table 4, page 32.

to SCA mean squares for Group L was considerably larger than for Group I (54.7:1 compared to 4.3:1). The parents of the latter group ranged in natural height from 15.9 to 26.0 cm., while Group L ranged

from 10.3 to 42.5 cm. The single-cross progeny of Group I ranged in natural height from 16.8 to 24.4 cm., with the mean single-cross being 0.9 cm. higher than the mean parent height. The single-cross means of Group L ranged from 13.2 to 38.1 cm. and had a mean single-cross value of 24.6 cm., compared to the mean parent height of 20.3 cm.

Forty-six percent of the single-cross progenies of Group I and 53 percent of those of Group L showed a significant inbreeding depression as observed in Table 5. Seven single-cross progenies from Group I showed a small amount of heterosis, and were taller than their taller parent. In instances where heterosis was observed, the crosses involved the shorter parents of both groups. The mean F_2 progeny height equaled exactly that of the mean parent. This relationship was shown in the narrow- and broad-sense heritability estimates for Group L, where 0.93 and 0.96, respectively, were indicated. Additive gene action is primarily responsible for natural plant height. The regression value of 0.60 and r^2 of 0.69 support this observation. The demarcation between additive and non-additive gene action was not so evident for Group I. The narrow-sense heritability estimate based on expected mean squares (0.48) and that obtained by regression (0.34) may be quite similar. The r^2 value indicates that 11 percent of the F_2 variance was accounted for by variance in the single-cross generation. A broad-sense heritability estimate of 0.82 (slightly less than twice

the narrow-sense estimate) might indicate that non-additive gene action could be involved for natural plant height in Group I, particularly since this estimate was fairly comparable to the same estimate for Group L.

Plant Spread

Plant spread data were recorded twice for the 1963 season; in May following the first harvest and again, after a four-month growing period. GCA and SCA mean square levels of significance for Groups I and L are listed in Table 6. The GCA effect for Group I

Table 6. Genetic constants for plant spread (cm.) in two groups of tall fescue; May 28-31 and Sept. 26-27, 1963; April 28-29, 1964.

Genetic 1/ Constants	Group I			Group L		
	1963		1964	1963		1964
	May 28	Sept. 26	April 28	May 31	Sept. 27	April 29
b	. 26	. 52	. 45	. 00	. 18	. 00
r^2	. 09	. 21	. 16	. 00	. 02	. 00
H_n	. 32	. 34	. 34	. 03	. 32	. 48
H_b	. 55	. 64	. 50	. 36	. 32	. 75
In	NS	NS	NS	NS	NS	NS
In%	29	21	43	44	26	35
GCA:SCA	2. 7*:1	2. 8*:1*	2. 8*:1	2. 7:1	2. 8:1	4. 6**:1**

1/ See footnote, Table 4, page 32.

was significant at the five percent level in May. The GCA and SCA effects were significant for the September measurement. Eleven months after the first measuring date, plant spread of Group I was measured for the third time. The mean square ratio for GCA and SCA for 1964 was similar to that for the same measurement the previous year. The ratio of GCA to SCA was 2.7:1 in May and 2.8:1 in September of 1963; and 2.8:1 in April of 1964.

The GCA and SCA mean squares for Group L were not significant at the five percent level for either date of measurement in 1963 (Table 6), but were highly significant for the 1964 data. The ratios of GCA to SCA for plant spread of Group L (May and September of 1963) were 2.7:1 and 2.8:1, respectively, but was 4.6:1 for April of 1964. The mean square ratios, with the exception of the April 29, 1964 measurement of Group L, compared exceptionally well. The levels of significance for the two groups did not compare as favorably, but for Group I the levels of significance for the various measuring dates agreed reasonably well.

Plant spread measurements of Group I parents ranged from 11.0 to 14.0 cm. in May and 18.8 to 24.1 cm. in September of 1963. They varied from 25.7 to 33.3 cm. for April of 1964. No apparent consistency occurred in this measurement on the various dates of measurement. There appeared to be more consistency among the parents for the two spring measurements of different years than for

the two measurements taken the same year. Plant spread of the mean single-cross equaled that of the mean of the parents for the 1964 data. Plant spread of single-cross plants of Group I for that year ranged from 26.2 to 32.0 cm. and thus reached neither extreme of the parents. During 1963 the single-cross progenies of Group I did not exceed the parent having the wider spread. The same general trend was shown by Group L, except that the parents ranged from 8.4 to 17.4 cm. and 15.2 to 24.0 cm. on the two dates of measurements in 1963 and from 24.6 to 38.8 cm. for 1964. The single-cross plant spread for 1964 ranged from 25.6 to 32.0 cm. Spread of the mean parent exceeded that of the single-cross mean for that year by 2.0 cm.

A significant inbreeding depression for plant spread did not occur in either group or for either year (Table 6). Only four single-crosses and their F_2 progenies in Group I showed a consistent inbreeding depression over all dates of measurement even though from 21 to 44 percent of the crosses showed inbreeding depressions. This is despite the fact that ten single-cross progenies and their corresponding F_2 families showed an inbreeding depression at either the five or one percent level of significance in May of 1963, six in September of 1963 and 12 in April of 1964. This same relationship was observed for four of the crosses of Group L. Fifteen single-crosses in May of 1963, nine in September of 1963 and 12 in April of 1964 showed inbreeding depressions significant at either the five or one percent

level.

Heritability estimates based on expected mean squares in Group I were quite comparable for all dates measured. The narrow-sense estimates averaged 33 percent, while the broad-sense estimates averaged 56 percent. Based on progeny-parent regression (F_2 -Sx), the narrow-sense estimates for heritability of plant spread at the various dates of measurement were more variable (Table 6). For May, the b value 0.26 was obtained, with the squared association value of 0.09, while for September the corresponding values were 0.52 and 0.21, respectively. The estimate of heritability in 1964 for plant spread based on regression was 0.45 with r^2 equal to 0.16. With the exception of the spring measurement in 1963, heritability of plant spread based on regression exceeded the narrow-sense estimates based on expected mean squares. For Group L the relationship between heritabilities based on regression and expected mean squares was not as consistent because the narrow-sense heritability estimate for May of 1963 was 0.03, for September of 1963 was 0.32 and for April of 1964 was 0.48. The broad-sense estimates for the same periods were 0.36, 0.32 and 0.75. The regression values of F_2 on single-crosses gave small negative values for both spring dates of measurement and are thus considered to be zero. The data for plant spread measurements in September of 1963 indicated a b value of 0.18 with r^2 equal to 0.02. This was true even though one parent (379) exhibited a

rather strong creeping tendency.

More plants in Group L showed creeping tendency than in Group I. It is entirely possible that the same gene systems were not responsible for the creeping tendency as for initiating plant spread, and it would be possible that the interaction of the two systems would lead to a low prediction of progress. The comparable narrow- and broad-sense estimates from single-cross data for the September 1963 date did not disprove this hypothesis, inasmuch as summer growing conditions in Corvallis do not facilitate spreading as do conditions during winter and early spring.

Leaf Length

Leaf length differences occurred among the single-cross progenies in both groups. GCA and SCA effects were significant in both groups in both years (Table 7). The ratio of GCA to SCA indicated that the GCA effects were the most important for leaf length in Group L.

Foliar tissue length of the parents in Group I ranged from 25.7 to 35.9 cm. in 1963 and from 27.6 to 36.0 cm. in 1964. The parent which produced the longer leaves in 1963 was identified as the one producing longer leaves in 1964, however no clear pattern emerged for the short ranging parent. Single-cross progenies of Group I ranged from 28.7 to 37.9 cm. in leaf length in 1963 and from 25.3 to

Table 7. Genetic constants for leaf length (cm.) in two groups of tall fescue; June 13-17, 1963; June 2-4, 1964.

Genetic 1/ Constants	Group I		Group L	
	1963	1964	1963	1964
b	. 30	. 34	. 71	. 77
r ²	. 07	. 12	. 62	. 64
H _n	. 44	. 50	. 86	. 82
H _b	. 71	. 75	. 93	. 88
In	*	NS	*	NS
In%	54	18	62	9
GCA:SCA	3. 7**:1*	4. 5**:1*	34. 1**:1**	19. 9**:1*

1/ See footnote, Table 4, page 32.

34. 4 cm. in 1964. Again, the cross producing the longer leaf tissue was easily identified in both years and the shorter extreme was more nearly comparable from year to year than were the parents. The parents of Group L were very consistent in this respect for the two-year period, while their single-cross progenies were less consistent. In both cases the extremes in Group L could be grouped. In 1963 the parents of Group L ranged from 15. 6 to 45. 1 cm. in leaf length and in 1964 from 18. 4 to 46. 6 cm. For the same periods, single-cross progenies ranged from 27. 4 to 48. 0 cm. and from 26. 5 to 41. 8 cm., respectively. In 1964 the mean of the single-crosses of Group L exceeded the mean of the parents by 0. 8 cm., however in 1963 this difference was nearly ten times greater. In Group I the relationship was similar, however the mean of the parents exceeded

the mean of the single-crosses by six cm. in 1963, contrasted to the opposite relationship for Group L.

Specific combining ability for leaf length in Table 7 was of less magnitude than for many of the other traits measured, yet the expression of heterosis (exceeding the midparent) by the single-cross progenies as shown for leaf length was more pronounced than for most of the traits measured (Appendix, Tables 1 to 4). This was particularly true for the 1963 data of Group I and the 1963 and 1964 data of Group L. Two crosses of Group I (359 x 299 and 311 x 299) were significantly shorter in 1964 (five percent and one percent level, respectively) than their midparents. This relationship did not hold the following year, where heterosis was relatively small. Four single-crosses of Group L showed a significant increase in leaf length over their midparents in 1964. These progenies did not show an inbreeding depression that year, but did in 1963.

Fifty-four percent of the 28 single-cross progenies of Group I for which there were available F_2 progenies showed a significant inbreeding depression in 1963. Only 18 percent of the same progenies showed an inbreeding depression in 1964. In most instances where an inbreeding depression was shown, the F_2 mean held a closer relationship to the midparent than did that of its corresponding single-cross. The 34 single-cross progenies in Group L which had corresponding F_2 progenies showed a significant inbreeding depression for

62 percent of the progenies in the year following establishment. Only nine percent of the progenies showed inbreeding depression for a comparable period in 1964.

The difference in the broad- and narrow-sense estimates of heritability based on expected mean squares for Group I leaf length obtained in 1963 indicated that approximately 25 percent of the genetic variation was due to deviation from the additive scheme. The narrow-sense estimate of 0.44 and broad-sense estimate of 0.71 for leaf length in Group I was indicated for 1963 data. In 1964, these estimates were 0.50 and 0.75, respectively. Based on regression, the narrow-sense estimates for 1963 and 1964 were 0.30 and 0.34, respectively, with the associated r^2 values for the same period being 0.07 and 0.12.

Estimates of heritability for leaf length in Group L by use of expected mean squares and regression of F_2 on single-cross means were more nearly comparable than for Group I, with less spread between the broad- and narrow-sense estimates. The narrow-sense estimates for Group L were 0.86 (1963) and 0.82 (1964) when determined from variance components and 0.71 (1963) and 0.77 (1964) when estimated by regression. The broad-sense heritability estimates for Group L were 0.93 (1963) and 0.88 (1964). Sixty-two percent of the F_2 variation in Group L in 1963 and 64 percent in 1964 can be accounted for by the variation in the single-cross progenies.

Total Plant Height

General combining ability for plant height in Group I was significant (one percent level) for the two years of measurement (Table 8).

Table 8. Genetic constants for total plant height (cm.) in two groups of tall fescue; June 13-17, 1963; June 2-4, 1964.

Genetic Constants	Group I		Group L	
	1963	1964	1963	1964
b	. 62	. 31	. 52	. 10
r ²	. 26	. 14	. 21	. 01
H _n	. 73	. 62	. 59	. 36
H _b	. 80	. 66	. 84	. 53
In	NS	NS	NS	NS
In%	57	4	38	6
GCA:SCA	10. 4**:1	6. 6**:1	6. 9**:1**	3. 3**:1

1/ See footnote, Table 4, page 32.

Specific combining ability was not significant. The ratio of GCA to SCA was 10. 4:1 in 1963 and 6. 6:1 in 1964. The ratios for leaf length for the same periods were 3. 7:1 and 4. 5:1 (Table 7).

In Group L both GCA and SCA for total plant height was significant (one percent level) in 1963 but only the GCA mean square was significant for 1964 data. The ratios of GCA to SCA (Table 8) were 6. 9:1 and 3. 3:1. The respective ratios for leaf length were 34. 1:1

and 19. 9:1 (Table 7).

The leaf length and total plant height ranges of parents and single-cross progenies are shown in Table 9. Leaf length of the longer-leafed plants in Group L was greater than in Group I. With respect to total plant height, the groups were nearly comparable.

Table 9. Total plant height and leaf length (cm.) in two groups of tall fescue; parents and single-cross progenies; 1963 and 1964.

	Parents			Single-cross Progenies		
	Low	High	Mean	Low	High	Mean
<u>Total plant height</u>						
Group I						
1963	40. 9	70. 2	57. 2	45. 1	66. 2	54. 8
1964	42. 7	64. 8	55. 7	42. 4	64. 5	53. 2
Group L						
1963	37. 3	69. 9	60. 0	39. 6	64. 4	56. 1
1964	43. 6	69. 4	58. 6	51. 4	67. 5	59. 2
<u>Leaf length</u>						
Group I						
1963	25. 7	35. 9	30. 8	28. 7	37. 9	33. 2
1964	27. 6	36. 0	31. 6	25. 3	34. 4	30. 9
Group L						
1963	15. 6	45. 1	29. 7	27. 4	47. 7	35. 6
1964	18. 4	46. 6	30. 4	26. 5	41. 8	31. 2

The relationship between total plant height and leaf length is best shown by heritability (H_n) estimates (Table 8). Based on heritability estimates from variance components, leaf length would likely

be less susceptible to selection pressure in Group I than in Group L (Tables 7 and 8). A reverse relationship would likely occur for total plant height. Heritability estimates in the narrow-sense for total plant height determined by regression for Group I were 0.62 for 1963 and 0.31 for 1964. The corresponding values of r^2 equaled 0.26 and 0.14. For Group L, these same r^2 values were 0.21 and 0.01, with the associated regression values of 0.52 for 1963 and 0.10 for 1964. There was reasonable agreement between the narrow-sense estimates based on regression and those obtained from the variance components. For Group I these narrow- and broad-sense estimates were 0.73 and 0.80 (1963) and 0.62 and 0.66 (1964). These same estimates for Group L were 0.59 and 0.84 (1963) and 0.36 and 0.53 (1964).

It would appear that the high heritability of leaf length and a lower heritability of total plant height for Group L (while a reverse relationship was indicated for Group I) were products of the growth characteristics of the two populations. Group I had a tendency to carry foliar tissue up on the tillers and thus was able to show full expression of heritability as the plants matured. Group L had a greater tendency to produce basal foliar tissue. The production of stem material would have no effect on a true expression of leaf length heritabilities. Maturity date may be involved in the relationship. Good agreement was found for inbreeding depression with the estimates of heritability for total plant height.

The inbreeding depression for total plant height in Groups I and L was comparable to previous variables as shown in Table 8. In the 1964 data, four percent of the crosses in Group I showed a significant inbreeding depression and six percent in Group L.

Plant Density

Differences were found among single-cross and F_2 progenies in density ratings for both groups. The GCA and SCA mean squares were significant at the five percent level for Group I (Table 10), with a ratio of GCA to SCA of 2.9:1. For Group L only the GCA mean square was significant (one percent level) with a ratio of GCA to SCA of 5.8:1.

Table 10. Genetic constants for plant density (rated 1-9) in two groups of tall fescue; June 5, 1964.

Genetic 1/ Constants	Group I	Group L
b	.26	.32
r^2	.16	.09
H_n	.35	.54
H_b	.65	.56
In	NS	NS
In%	29	9
GCA:SCA	2.9*:1*	5.8**:1

1/ See footnote, Table 4, page 32.

Good agreement existed between inbreeding depression and combining ability estimates. This relationship can be observed by comparing the GCA:SCA ratio with the inbreeding depression percentages in Groups I and L. Nine percent of the crosses of Group L showed an inbreeding depression, with three times that number occurring in Group I. There is also good agreement of inbreeding depression with heritability estimates based on expected mean squares. The b values showed some relationship to the other constants, but r^2 values showed an opposite relationship to that of the combining ability analysis.

Forage Yield per Plant

The single-cross progenies of both groups differed with respect to forage yield per plant in each year of harvest. Specific combining ability was more important than GCA in the 1963 early harvests of Group I (Table 11). A significant GCA was noted in the later harvests. In 1964, SCA effects were not significant in the second harvest. In Group L (1964), the GCA and SCA mean squares were significant at the five percent level for the final harvest. The SCA component was not significant for the third harvest of 1963, however for the remaining harvests, both SCA and GCA components were significant at the one percent level (Table 12).

The ratios of GCA to SCA by harvest date and by year for both

Table 11. Genetic constants for yield per plant (gm. dry matter) of tall fescue; Group I, 1963 and 1964.

Genetic $\frac{1}{\text{Constants}}$	1963				1964	
	May 15	June 17	July 30	Sept. 19	April 21	June 15
b	.08	.04	.00	.05	.30	.25
r^2	.02	.00	.00	.00	.13	.06
H_n	.19	.16	.58	.37	.60	.33
H_b	.74	.57	.76	.74	.78	.39
In	*	**	**	*	**	NS
In%	61	79	82	64	86	18
GCA:SCA	1.8:1**	1.7:1**	5.8**: 1^*	3.1*: 1^{**}	6.3**: 1^*	2.8*: 1

$\frac{1}{\text{See footnote, Table 4, page 32.}}$

Table 12. Genetic constants for yield per plant (gm. dry matter) of tall fescue; Group L, 1963 and 1964.

Genetic $\frac{1}{\text{Constants}}$	1963				1964	
	May 17	June 18	July 31	Sept. 20	April 21	June 16
b	.21	.19	.34	.44	.69	.21
r^2	.16	.04	.31	.43	.64	.07
H_n	.69	.37	.84	.63	.86	.32
H_b	.91	.72	.88	.82	.92	.57
In	**	**	**	*	**	NS
In%	74	79	82	56	65	26
GCA:SCA	1.1**: 1^{**}	34.1**: 1^{**}	6.9**: 1	9.8**: 1^{**}	25.6**: 1^{**}	2.9*: 1^*

$\frac{1}{\text{See footnote, Table 4, page 32.}}$

groups are presented in Tables 11 and 12. In general, this ratio was greater in Group L than in Group I by a considerable margin. The ratio appeared to be influenced by harvest date and was not consistent from harvest to harvest within each group.

The range of forage yield in the parents and their single-cross progenies is listed in Table 13. A close relationship existed between

Table 13. Forage yield in grams per plant of Groups I and L, parents and single-cross progenies. Four harvests in 1963 and two in 1964.

	Parents			Single-crosses		
	Low	High	Mean	Low	High	Mean
Group I - 1963						
May 15	25.2	45.0	31.3	16.4	34.9	25.1
June 17	14.9	22.4	18.8	14.2	23.2	18.8
July 30	22.4	43.5	32.7	23.1	43.8	34.7
Sept. 19	13.5	36.1	25.9	19.9	38.2	28.3
Group I - 1964						
April 21	94.9	223.9	145.8	108.0	197.4	152.0
June 15	22.3	41.9	32.4	24.8	42.1	32.2
Group L - 1963						
May 17	2.2	63.4	31.8	10.9	50.9	31.7
June 18	1.6	22.1	17.3	12.2	24.7	19.5
July 31	6.3	66.5	38.6	23.1	59.4	39.9
Sept. 20	4.2	32.4	22.0	11.8	49.0	27.2
Group L - 1964						
April 21	11.3	284.6	145.4	81.4	233.4	150.3
June 16	11.2	45.6	33.7	20.2	45.3	34.3

the yield of the high parent and the high single-crosses. Differences between the mean yield of the parents and of their single-crosses were not great. The larger difference occurred between the low parent and low single-cross. This relationship was more noticeable in Group L than in Group I. It is understandable, inasmuch as one parent of Group L (364) was lower yielding than the remaining nine parents. The other parents, when crossed to this low performer, based on additivity, would elevate the mean yield of that cross. The yield of the low-yielding single-crosses of Group I compared to the yield of the midparents was not out of line, when taking into consideration the variation encountered in the other data.

The 28 single-cross progenies for which corresponding F_2 progenies were available in Group I, showed an average of 71 percent inbreeding depression for the four harvests of 1963 (Table 11). Eighty-six percent of crosses in the first harvest of 1964 showed inbreeding depression and 18 percent showed this phenomenon in the second harvest.

Thirty-four single-crosses in Group L could be compared to F_2 progeny. An average of 78 percent of the crosses showed an inbreeding depression for the first three harvest periods of 1963 and 56 percent showed it for the final harvest (Table 12). For the two harvest periods of 1964, 65 and 26 percent, respectively, showed an inbreeding depression. In most instances, the same crosses

showed this phenomenon across harvest periods, however, in a few cases the inbreeding depression was indicated for the later harvests and not for the earlier ones.

In Group I, seven single-crosses were lower yielding than their calculated midparents for the first harvest in 1963 and one showed significant heterosis based on the shortest significant range at the five percent level used to determine inbreeding depression (Appendix, Tables 1 to 4). In 1964, one single-cross showed a lower and one a higher yield than their corresponding midparents. Two crosses showed a slight depression of single-cross yield compared to their midparents in Group L (1963) and in 1963 and 1964 three single-crosses showed heterosis (greater than their midparent). These three crosses showing heterotic effects were consistent for the two years and involved parent 364. With very few exceptions, F_2 progenies were lower in yield than the corresponding single-crosses from which they were derived.

The number of crosses which showed an inbreeding depression for forage yield appeared to be associated with heritability estimates for forage yield based on expected mean squares. In both Groups I and L the number of crosses which showed inbreeding depression in 1963 increased up to the third harvest (Tables 11 and 12). The significance levels of SCA mean squares tended to decrease while the estimates of heritability remained relatively constant or showed a slight

increase. Narrow-sense estimates of heritability were relatively large for the first harvests of both groups in 1964, while the number of crosses which showed inbreeding depression was numerous and, as the heritability estimates decreased, the number of crosses which showed inbreeding depression decreased for the second harvest.

DISCUSSION

The single-cross and F_2 progenies of an intermediate and of a late-maturing group of genotypes of tall fescue were studied to arrive at an understanding of the breeding behavior of the parent populations from which they were derived. The experimental results are discussed under a sequence of five headings: general and specific combining ability, comparison of Groups I and L, inbreeding depression, heritability estimates and breeding behavior.

General and Specific Combining Ability

The single-cross and F_2 progenies of both groups differed among themselves in most of the five variables and forage yield measured in the two years of the experiment (Appendix, Tables 5 to 8). This is in agreement with Caceres (1963, p. 1-57), who studied a different group of single-cross families derived from the same parents used in the present work. The single-cross families used in Caceres' study differed in mean variance for only two of the characteristics measured as determined in a combined analysis of Groups I and L. In both cases, the significance level for Group L was greater than for Group I.

The traits of the single-cross progenies in the present work showed, with the one exception of plant spread in Group L in 1963

on two dates of measurement, significant (five or one percent level) GCA or SCA effects (Tables 4 to 8 and 10 to 12). Not all variables were studied in both years. The variables; leaf length, total plant height, plant spread (spring measurement), and forage yield (two spring harvests), showed excellent agreement within each group (I and L) for the two years.

Nineteen of the 32 diallel analyses conducted indicate that both the GCA and SCA effects were important. The ratio of GCA to SCA with SCA effects set as unity in all cases showed greater than a 1:1 ratio for GCA effects, and in some cases this difference was large. The ratio of GCA to SCA was in most instances larger in 1964 than in 1963. The level of significance was lower for the SCA effects in 1964 than 1963. Exceptions to this were the ratios of total plant height of Group I; and leaf length and total plant height of Group L. These discrepancies appeared to be a result of a narrower range of the single-cross means in 1964 than in the previous year.

If a gene system can correctly be applied to information obtained from combining ability analyses, the results would indicate that additive gene action is relatively more important than gene action which deviates from the additive scheme. This would be in agreement with Caceres (1963, p. 1-57), who used the diallel analysis to study maturity and self-seed yield of Group I, and Echeverri (1964, p. 1-97), who studied an early-maturing group of tall fescue.

Comparison of Groups I and L

Most of the variables measured showed reasonable agreement between Groups I and L. It is impossible to make direct comparison of mean squares, inasmuch as the nurseries of the two groups were planted separately; however, where the mean squares in one population were large with a high level of significance, the trend followed in the other population. A more reliable comparison of the variables measured can be made when comparing Group I with Group L by use of the heritability estimates (Tables 4 to 8 and 10 to 13). The two exceptions where greater progress from selection could be expected in Group I based on additive gene action are with plant spread and total plant height.

Total plant height is a measure of the height of inflorescence tissue which has been initiated after the first harvest and is not altogether a desirable characteristic in forage quality. In Group I this variable would appear to have some relationship to leaf length, inasmuch as foliar tissue had a tendency to be carried high on the culms. Leaf tissue of Group L had a tendency to be more basal. This may account for the greater expression of genetic constants of plant height in Group I than Group L and may indicate why genetic constants for leaf length seem to be influenced by total plant height.

Plant spread is another variable for which it would appear

that greater progress might be made in Group I than Group L. Some plants of Group L showed a tendency to creep, while few plants in Group I showed this tendency. Despite this fact, based on narrow-sense heritability estimates as an estimate of additive gene action, the greater progress in plant spread might be made in Group I (Table 6). It would appear that different sets of gene systems may govern spreading ability and creeping habit. If the variables measured are independent of one another it is not unreasonable to expect some variables to be more responsive in one population than another; a high level of significance for all traits should not be found in the same population.

Inbreeding Depression

All of the characters studied showed an inbreeding depression from the single-cross to the F_2 families, which were obtained by the self-pollination of five randomly selected single-cross plants from each cross. In only a few instances were the means of all single-crosses and the means of all F_2 progenies significantly different from each other. These cases involved plant width, natural plant height, and leaf length in Group I in 1963 and leaf length in Group L in 1963. Forage yield for both groups showed this inbreeding depression for all harvests in 1963 and the first spring harvest in 1964 (Tables 4, 5, 7, 11 and 12). The percentage of crosses showing inbreeding

depression varied from four percent for total plant height in Group I and six percent in Group L in 1964 to 86 percent for forage yield in the first harvest of Group I in 1964. The percentage of crosses which showed inbreeding depression was lower in 1964 than in 1963 with the exception of forage yield of Group I in the first harvest and plant spread of Group I. The narrow-sense heritability estimates for these traits during the same period increased.

The significance level shown for comparison of means would be influenced by environment if the single-cross and F_2 progenies reacted differently. The F_2 progenies would likely show a decline in performance in relation to the single-cross progenies. Since the variation of both progenies was taken into account in determining the shortest significant range, this was probably not a factor. The significance level would be a result of better than 50 percent of the crosses showing inbreeding depression or the result of large differences between the F_2 and single-cross mean for crosses which showed inbreeding depression. The latter effect, if sufficiently great, would still cause a significant inbreeding depression for the average of all single-crosses compared to the average of their corresponding F_2 progenies.

Those traits which responded to heterosis should be the ones for which a greater inbreeding depression was observed. The present study showed that 18 of the 32 measurements for which inbreeding

depression was determined had single-cross values falling between the values of the high and low parents. Six had single-cross values below the low parent and eight above the high parent. The amount of heterosis shown for variables of the latter eight measurements was very small and involved leaf length in Groups I and L only in 1963 and forage yield in Group I of the second through fourth harvests only in 1963 (Appendix, Tables 1 and 2). From four to all 28 of the F_2 progenies performed below the low-performing parent for the six variables showing this characteristic.

Since the populations studied were naturally cross-pollinated, it was anticipated that an inbreeding depression would occur. Miller and Marani (1963) found that in cotton the F_2 progenies tended to perform between the performance of the single-crosses and their mid-parents. Matzinger, Mann and Cockerham (1962) found in their study of common tobacco that an inbreeding depression occurred for all traits studied, which in most instances was more pronounced than any heterosis shown in the F_1 generation following the parental crosses.

The performance of F_2 progenies of Group L in the present study fell between that of the parental extremes. In this group, however, one parent at each extreme of the measurements taken tended to be out of line with the performance of the remaining parents. Many F_2 progenies of Group I for most traits studied (with the

exception of total plant height) performed below the low parent. Statements concerning generalized trends which may exist in both groups are difficult to make without an exception occurring, however, high-performing single-crosses tended to give high-yielding F_2 progeny and the low-performing single-crosses tended to produce low-performing F_2 progeny. The same was true for parents which, when crossed, tended to give single-cross values intermediate to that of the two parents crossed. In those crosses which showed heterosis (above the midparent), the parents were generally low performers. This was consistent with the findings of Miller and Marani (1963).

The expression of inbreeding depression for traits which can be compared in both seasons was shown for fewer crosses in 1964 than in 1963. This would suggest that the environmental influence was less pronounced during the second year after plant establishment, or that the plants had reached an equilibrium and were therefore less subject to environmental influence. If this is true, then some traits would be more accurately studied under conditions of little environmental influence, and the breeder would have a better opportunity for obtaining a more nearly correct estimate of gene action from plants which had become well established. Furthermore, it would appear, from comparison of leaf length, total plant height, plant spread and forage yield of Groups I and L in 1963 and 1964, that for maximum expression of genetic potential for any characteristic measured, traits

could best be studied at a particular stage of plant development.

The relationship of plant response to the environment can best be shown by the comparison of heritability estimates. The heritability estimate for plant spread of Group I (Table 6) was greater for the September 1963 data than for the May 1963 data and was almost the same as that for April 1964 data. The leaf length heritability estimate (Table 7) was greater and total plant height estimate (Table 8) smaller for Group I in 1964 than in 1963. These estimates for Group L (Tables 7 and 8) were greater in 1963 than in 1964. This difference is thought to be due to the growth characteristics of the plant populations and possibly the earlier harvest date in 1964.

Heritability estimates were greater for forage yield of the first, third and fourth harvests of 1963 and for both harvests of 1964 than for the second harvest of 1963. This lower estimate for the second harvest appeared to result from an insufficient growing period for maximum expression and coincides with the finding of Frakes (1955, p. 1-76), who showed a decrease in broad-sense heritability estimates for the yield of 20 genotypes of tall fescue when compared under severe management conditions. These results would indicate that selection of high-combining parents, based on the variables measured, could best be made during a period when environmental influence is the least pronounced. Such variables as leaf length and natural plant height could be selected for relatively early after

plants were well established. Forage yield and plant spread measurements could be more effectively obtained after the plant population had reached an equilibrium. Those characteristics showing the greatest inbreeding depression are influenced more by environment and may be controlled more by a non-additive gene system. It is thought that the inbreeding depression demonstrated in the present study was a manifestation of environmental stress upon genes which were segregating toward homozygosity. The expression of non-additive gene action, if any, was mostly toward deterioration in performance rather than toward useful heterosis.

Heritability Estimates

Should the concept be correct that the traits studied in the present work are governed primarily by additive gene action, then the estimates of heritability determined from the variance components (Table 3) of the diallel analysis of single-cross data and those obtained by the regression of F_2 on single-cross data should be comparable for each trait studied, if the diallel analysis can appropriately be used to test significance of GCA and SCA in tall fescue. Narrow-sense estimates of heritability determined by regression were larger than those determined from expected mean squares in only three instances (Group I) and involved plant spread in 1963 and 1964 and plant width in 1963. The differences between the two narrow-sense estimates for

the 32 analyses conducted varied from three to 58 percent, with an average difference of 21 percent. The larger differences occurred for forage yield of the third harvest (both groups) and plant spread of Group L in 1964. There was also a 21 percent difference between the narrow- and broad-sense heritability estimates for the 32 diallel analyses conducted. The differences between estimates were less in 1964 than in 1963 and appeared to be associated with the same environmental stresses that influenced the other measurements.

An additional generation was used in this study for the estimation of heritability based on regression and because of this, the estimates obtained by this method would appear to be more indicative of the probable progress that can be made through breeding than by use of those estimates based on the diallel analysis. Where the association (r^2) between the F_2 and single-cross generation was high, as in the case of leaf length of plants in Group L, the disparity between the two narrow-sense estimates was smallest as was the difference between heritability estimates in the broad- and narrow-sense based on expected mean squares. In instances where the difference between the broad- and narrow-sense estimates was great, the narrow-sense heritability estimates obtained from regression tended to be low with the percentage of association between the two generations small. It is suggested because of this that heritability estimates in the broad-sense contained a portion of environmental influences which was not

removed by diallel analysis. If the parents had been inbred one generation, it might have been possible for the two heritability estimates in the narrow-sense to be more nearly comparable.

It is visualized that both methods of obtaining narrow-sense heritability estimates may have advantages. The regression method is more reliable because an additional generation is involved, but to obtain that F_2 generation a minimum of one additional season is required with additional expense. Since an average difference of 21 percent occurred between the narrow-sense heritability estimates obtained by regression and those obtained by the diallel analysis and the same difference occurred between the broad- and narrow-sense estimates obtained by diallel analysis, it would appear that approximately the same heritability might be derived for the two methods. It would remain to the discretion of the breeder to evaluate the methods and decide, on the basis of experimental objectives, which is used. The obtaining of all possible single-cross progenies from a group of parents is necessary to use the diallel analysis, and can sometimes be a difficult procedure. The regression procedure does not require all single-crosses. The results obtained by regression of F_2 on single-crosses should be more indicative of the progress that could be expected through selection than the results obtained from diallel analysis.

Breeding Behavior

Based on the differences in heritability estimates discussed above, the comparison of single-cross means with their midparents, the ratio of GCA to SCA, the close association of single-cross means to their corresponding F_2 progeny means, and the decrease in the expression of inbreeding depression in 1964, it appears that all characteristics studied were governed primarily by additive gene action. Some traits such as plant spread and plant width were influenced more by environment than were others, or were not sufficiently heritable for these parents to expect much improvement without the introduction of new germ plasm. Most heritability estimates, however, were sufficiently high for these traits that improvement based on additive gene action is possible.

The groups of parents in this study showed no useful heterosis. Some gene action other than additive may have had importance in the case of creeping ability in Group L, which would counteract the expression of plant spread. The increase in performance of progenies involving some low-performing parents above that which would be expected based on additive gene action, may indicate the presence of genes other than those which were expressed additively. Because of the small amount of heterosis, if expressed, the development of varieties based on the synthetic breeding approach would be more logical.

This is not to indicate that a breeding program should not be based on components of yield, but that superior parents should produce superior progenies.

SUMMARY AND CONCLUSIONS

The single-cross and most F_2 progenies of 19 genotypes of tall fescue were used to study the breeding behavior of the variables; plant width, natural plant height, plant spread, leaf length, total plant height of regrowth tissue, plant density and forage yield. Parents were separated into two groups of nine intermediate and ten late-flowering genotypes based on mean flowering date, and the progenies were studied as Groups I and L. Parents had been selected from a large, space-planted population. Selection was based on high self-sterility, high chromogen, high crude protein and a rating for seed or forage potential.

Progenies of each group were grown in separate nurseries as spaced plants one foot apart on the Hyslop Agronomy Farm, Corvallis, Oregon. Ten plants of each cross were planted in rows three feet apart arranged in a randomized block design with four replications. Individual plant measurements of the six variables and forage yield were recorded and converted to plant means.

Griffing's (1956) random model, method four was used to estimate general and specific combining ability from single-cross variance. Expected mean squares from this analysis were used to arrive at the estimates of heritability in the broad- and narrow-sense, where the broad-sense estimate is a ratio of the total genetic

potential to the total phenotypic variation and the narrow-sense estimate is a ratio of the additive genetic variance to the total phenotypic variation. The F_2 data were regressed on the single-cross data to arrive at a reliable estimate of narrow-sense heritability as a means of elucidating the effect of the diallel analysis when used on this allohexiploid cross-pollinated species.

Inbreeding performance of the single-cross to F_2 generation was observed. F_2 progenies were obtained by the self-pollination of five randomly selected single-cross plants from each cross. Significance of the inbreeding depression was determined by use of the Duncan multiple range test.

Of the 32 analyses conducted (ten each on Groups I and L in 1963 and six each in 1964), 27 were significant (five or one percent level) for GCA and 22 for SCA. Only 19 of the 32 analyses indicated that both GCA and SCA effects were important at either the five or one percent level of significance. Plant spread was the only variable measured which showed no GCA or SCA effects (1963 only, Group L). The ratios of GCA to SCA with SCA mean squares set at unity were generally greater for 1964 than 1963 and greater for Group L than for Group I; however, Group L did not show the larger ratio in total plant height and plant spread.

The two populations responded similarly for the variables measured except for total plant height and plant spread. Group I tended to

produce leaf tissue on the culms, while Group L tended to produce long, basal leaf tissue. Creeping tendency was noted in some Group L plants and this was thought to be controlled by some gene action, leading to a low, narrow-sense estimate of heritability. A relatively high estimate (H_n) was found for plant spread in Group I. With the exception of plant spread and total plant height, the greater progress from selection could likely be made with Group L.

The expression of inbreeding depression appeared to be influenced by the environment. Fewer crosses showed inbreeding depression in 1964 than in 1963. More single-crosses showed heterosis in 1963 than in 1964 and the greatest amount of heterosis was shown for leaf length, a trait which had a high narrow-sense heritability estimate. This was not to be expected, unless much of the inbreeding depression and heterosis shown was a result of chance variation due to environment. The performance of single-cross progenies tended to be intermediate when compared with the performance of parents. High-performing parents produced high-performing single-crosses, which in turn produced high-performing F_2 progenies, although the variation for all traits was great and F_2 progenies performed less well than their single-cross parents. The greater amount of heterosis generally involved the low-performing parents.

Those variables which could be compared for two years showed excellent agreement but an increase in magnitude of

heritability estimates was shown for most traits in 1964. Exceptions were leaf length and total plant height in Group L and total plant height in Group I. It was concluded that for each trait a particular stage in plant development could be reached for maximum genetic expression. For most traits that stage would be at plant maturity. Some traits, as natural plant height and leaf length, could be selected for on the basis of first year performance. Traits such as yield were more subject to environmental stress; consequently, estimates of genetic potential would be more effectively obtained when that influence was least, or after the plants were well-established.

Heritability estimates in the narrow-sense were of similar magnitude when derived from regression of F_2 progeny means on single-cross means or as the narrow-sense heritability estimates from expected mean squares. The latter was an average of 21 per cent higher. For traits such as natural plant height and leaf length in Group L, where the percentage of association (r^2) between the F_2 and single-cross generation was high, the difference between the broad- and narrow-sense estimates was small. The difference between the regression and variance component narrow-sense estimates was also small. In instances where the difference between the broad- and narrow-sense estimates of heritability obtained from expected mean squares was great, the heritability estimate obtained by regression was small, with little association between the single-cross

and F_2 generations. It is thought that the broad-sense heritability contains a portion of environmental influence which is not removed by diallel analysis but that, by keeping in mind the 21 percent difference, both the diallel and regression analyses may be used to arrive at an estimate of heritability. The accuracy of the regression method to obtain an estimate of heritability is superior to the diallel analysis because an additional generation is involved. The results obtained from the regression method should be more indicative of the progress to be expected through breeding than the results from the diallel analysis.

It is concluded that the traits studied are governed primarily by additive gene action. Little or no useful heterosis existed for the traits in the two populations of tall fescue studied.

BIBLIOGRAPHY

1. Allard, R. W. The analysis of genetic-environmental interactions by means of diallel cross. *Genetics* 41:305-318. 1956.
2. Bolton, J. L. A study of combining ability of alfalfa in relation to certain methods of selection. *Scientific Agriculture* 28:97-126. 1948.
3. Burton, Glenn W. Quantitative inheritance in grasses. Sixth International Grassland Congress, Proceedings 6:277-283. 1952.
4. Burton, Glenn W. and E. H. DeVane. Estimating heritability in tall fescue (Festuca arundinacea) from replicated clonal material. *Agronomy Journal* 45:478-481. 1958.
5. Caceres, Oscar. Single cross progeny evaluation in tall fescue, Festuca arundinacea, Schreb. Master's thesis. Corvallis, Oregon State University, 1963. 57 numb. leaves.
6. Carnahan, H. L. et al. General vs. specific combining ability in alfalfa for seedling vigor and fall growth habit in the year of establishment. *Agronomy Journal* 52:511-516. 1960.
7. Cowan, J. Ritchie. Tall fescue. *Advances in Agronomy* 8:283-302. 1956.
8. Dickinson, A. G. and J. L. Jinks. A generalized analysis of diallel crosses. *Genetics* 41:65-78. 1956.
9. Dudley, John W. Effects of accidental selfing on estimates of general and specific combining ability in alfalfa. *Crop Science* 3:517-519. 1963.
10. Echeverri, Silvio. A comparison of progeny testing methods and estimates of combining ability for seed yield and associated variables in tall fescue (Festuca arundinacea, Schreb.). Ph. D. thesis. Corvallis, Oregon State University, 1964. 97 numb. leaves.

11. Frakes, R.V. Dry matter and protein heritability estimates in tall fescue (Festuca arundinacea, Schreb.). Master's thesis. Corvallis, Oregon State College, 1955. 76 numb. leaves.
12. Frakes, R.V., R. L. Davis and F. L. Patterson. The breeding behavior of yield and related variables in alfalfa. III. General and specific combining ability. Crop Science 1:210-212. 1961.
13. Griffing, B. Concept of general and specific combining ability in relation to diallel crossing systems. Australian Journal of Biological Science 9:463-493. 1956.
14. Hayman, B.I. The theory and analysis of diallel crosses. Genetics 39:789-809. 1954.
15. Hayman, B.I. Interaction, heterosis and diallel crosses. Genetics 42:336-355. 1957.
16. Hayman, B.I. The theory and analysis of diallel crosses. II. Genetics 43:63-85. 1958.
17. Hayman, B.I. The theory and analysis of diallel crosses. III. Genetics 45:155-172. 1960.
18. Hanson, A. A. and H. L. Carnahan. Breeding perennial forage grasses. Washington, 1956. 116 p. (U. S. Dept. of Agriculture. Technical Bulletin no. 1145)
19. Hanson, C. H. et al. Performance of two-clone crosses in alfalfa and an unanticipated self-pollination problem. Washington, 1964. 46 p. (U. S. Dept. of Agriculture. Technical Bulletin no. 1300)
20. Jinks, J. L. The analysis of continuous variation in a diallel cross of Nicotiana rustica varieties. Genetics 39:766-788. 1954.
21. Jinks, J. L. The F_2 and backcross generations from a diallel cross of Nicotiana rustica varieties. Heredity 10:1-30. 1956.
22. Johnson, I. J. Evaluating breeding material for combining ability. Sixth International Grassland Congress, Proceedings 6:327-334. 1952.

23. Kehr, W.R. General and specific combining ability for four agronomic traits in a diallel series among six alfalfa clones. *Crop Science* 1:53-55. 1961.
24. Kempthorne, Oscar. The theory of the diallel cross. *Genetics* 41:451-459. 1956.
25. Kneebone, William R. Heritabilities in sand bluestem (Andropogon hallii, Hack.) as estimated from parental clones and their open-pollinated progenies. *Agronomy Journal* 50: 459-461. 1958.
26. Marani, A. Heterosis and combining ability and components of yield in a diallel cross of two species of cotton. *Crop Science* 3:552-555. 1963.
27. Matzinger, D. F., T. J. Mann and C. C. Cockerham. Diallel crosses in Nicotiana tabacum. *Crop Science* 2:382-386. 1962.
28. McDonald, E. D., R. R. Kalton and M. G. Weiss. Interrelationships and relative variability among S_1 and open-pollination progenies of selected brome grass clones. *Agronomy Journal* 44:20-25. 1952.
29. Miller, P. A. and A. Marani. Heterosis and combining ability in diallel crosses of upland cotton Gossypium hirsutum L. *Crop Science* 3:441-444. 1963.
30. Panse, V. G. Application of genetics to plant breeding. II. The inheritance of quantitative characters and plant breeding. *Journal of Genetics* 40:283-299. 1940.
31. Rojas, Basilio A. and G. F. Sprague. A comparison of variance components in corn yield trials. III. General and specific combining ability and their interaction with location and years. *Agronomy Journal* 44:462-466. 1952.
32. Smith, D. C. Progress in grass breeding. *Advances in Agronomy* 8:127-162. 1956.
33. Sprague, G. F. and Loyd A. Tatum. General vs. specific combining ability in single crosses of corn. *Journal of the American Society of Agronomy* 34:923-932. 1942.

34. Theurer, J. C. and L. J. Elling. Comparative performance of diallel crosses and related second generation synthetics of alfalfa. I. Bacterial wilt resistance. *Crop Science* 3:50-53. 1963.
35. Theurer, J. C. and L. J. Elling. Comparative performance of diallel crosses and related second generation synthetics of alfalfa, Medicago sativa L. III. Forage yield. *Crop Science* 4:25-28. 1964.
36. Thomas, H. L. and M. F. Kernkamp. The use of heritability ratios and correlation coefficients for measuring combining ability with smooth brome grass Bromus inermis, Leyss. *Agronomy Journal* 46:553-556. 1954.
37. Warner, John N. A method for estimating heritability. *Agronomy Journal* 44:427-430. 1952.
38. Wilcox, J. B. and C. P. Wilsie. Estimated general and specific combining ability effects and reciprocal effects in crosses among nine clones of alfalfa, Medicago sativa L. *Crop Science* 4:375-377. 1964.

APPENDIX

Appendix Table 1. Means of forage yield and five other variables; tall fescue, Group I, 1963.

		Natural				Total		Yield per Plant			
		Plant Width (cm.)	Plant Height (cm.)	Plant Spread (cm.)	Leaf Length (cm.)	Plant Height (cm.)		(gm.)			
		April 24	April 24	May 28	Sept. 26	June 13	June 13	May 15	June 17	July 30	Sept. 19
Parents	296	21.7	19.6	13.0	24.1	27.2	55.3	29.4	18.8	35.9	24.8
	298	20.2	15.9	12.4	19.8	25.7	51.0	29.8	17.2	25.2	18.0
	299	21.2	26.0	11.2	19.8	32.4	61.8	31.9	16.2	35.6	29.2
	311	23.8	23.8	14.0	23.1	35.0	45.4	45.0	22.4	43.5	36.1
	329	19.5	18.1	11.0	21.3	31.8	64.0	25.2	17.1	33.1	20.1
	359	21.6	19.6	12.4	19.9	35.9	70.2	29.1	21.2	34.3	22.2
	366	20.2	20.0	13.2	22.1	30.7	59.7	33.7	20.9	26.3	30.8
	368	19.4	20.3	12.5	18.8	29.8	40.9	28.4	14.9	22.4	13.5
	374	20.7	18.2	14.0	21.0	29.0	66.0	29.5	20.5	38.3	28.9
Average		20.9	20.2	12.6	21.1	30.8	57.2	31.3	18.8	32.7	25.9
S1 Progeny											
	296	23.0	20.5	11.5	22.6	32.9	43.8	37.2	21.8	42.7	30.1
	298	22.6	25.9	12.8	21.0	36.9	60.6	53.3	24.2	42.7	31.6
	299	20.9	23.5	10.5	18.1	30.7	53.2	34.1	19.2	30.9	22.7
	311	21.1	23.6	10.7	19.1	29.9	34.5	25.1	11.8	21.1	17.4
	329	19.2	19.7	11.4	20.3	31.2	50.6	31.2	18.0	30.2	21.6
	359	19.6	21.7	10.8	19.2	35.7	57.1	24.0	16.8	28.7	22.4
	366	18.3	16.4	10.6	20.2	26.4	53.5	20.2	14.9	24.4	22.5
	368	18.0	21.0	10.0	17.4	31.6	39.6	24.4	14.7	28.8	21.0
	374	19.7	20.1	10.6	19.6	34.2	63.8	28.0	22.4	39.9	28.8
Average		20.3	21.4	11.0	19.7	32.2	50.7	30.8	18.2	32.2	24.2
Open-pollinated											
Progeny	296	22.6	20.8	11.8	22.6	34.1	51.4	39.2	24.6	38.4	33.6
	298	24.0	25.4	12.0	21.1	34.8	57.0	50.0	24.5	43.1	29.2
	299	21.4	28.8	11.8	20.3	37.0	59.2	51.7	22.7	42.2	34.5
	311	23.1	23.4	12.2	21.5	33.2	46.8	44.8	23.4	40.2	35.5
	329	20.5	21.1	11.2	21.8	31.0	49.3	30.6	17.6	35.8	29.2
	359	21.7	26.6	11.3	20.3	37.3	58.0	45.2	23.9	40.6	34.5
	366	20.0	20.8	11.0	21.2	31.0	54.6	35.0	19.3	36.0	34.0
	368	21.0	32.2	11.0	21.6	34.3	47.4	37.9	20.4	39.0	33.6
	374	21.7	22.4	11.9	20.5	31.2	55.7	39.1	19.8	35.2	28.6
Average		21.8	23.6	11.6	21.2	33.8	53.3	41.5	21.9	39.0	32.5
Polycross											
Progeny	296	21.6	22.0	12.4	22.3	32.1	52.4	42.5	22.0	39.2	33.9
	298	22.2	24.9	12.6	21.6	35.0	57.8	45.2	23.2	33.8	28.6
	299	24.1	27.4	11.6	22.7	32.6	53.8	51.4	23.6	42.0	38.4
	311	23.4	23.9	11.5	22.0	34.4	50.8	45.2	21.4	36.7	30.4
	329	23.7	23.8	12.5	22.6	33.3	54.7	47.2	22.8	44.7	32.0
	359	23.6	24.3	13.1	21.8	35.4	58.9	46.6	23.7	43.8	35.6
	366	23.2	23.1	12.0	22.0	31.6	54.8	44.2	20.4	39.5	32.4
	368	23.4	25.1	12.1	22.9	34.2	45.4	46.2	20.1	37.9	35.4
	374	21.7	21.7	12.7	21.8	30.8	57.4	42.8	23.4	40.2	27.0
Average		23.0	24.0	12.3	22.0	33.3	54.0	45.7	22.3	39.8	32.6

Appendix Table 1. (Continued)

		Natural				Total		Yield per Plant			
		Plant	Plant	Plant	Spread	Leaf	Plant				
		Width	Height	Plant	Spread	Length	Height				
		(cm.)	(cm.)	(cm.)	(cm.)	(cm.)	(cm.)	(gm.)			
		April	April	May	Sept.	June	June	May	June	July	Sept.
		24	24	28	26	13	13	15	17	30	17
Single-cross	298 x 296*	20.2	23.4	12.1	21.4	32.7	61.2	25.4	19.7	31.7	26.6
	299 x 296	20.0	23.6	11.6	20.2	37.0	54.8	27.6	21.3	43.8	36.7
Progeny	299 x 298	18.7	23.6	10.7	20.2	34.7	62.2	23.3	19.0	31.6	25.4
	311 x 296*	21.0	22.6	12.4	23.9	34.2	45.2	23.1	20.9	38.8	33.2
	311 x 298*	18.9	23.1	11.0	21.2	35.6	60.4	19.8	16.6	28.3	21.6
	311 x 299	20.6	24.2	11.2	21.6	34.1	53.0	25.7	19.0	40.5	33.3
	329 x 296	18.4	16.8	11.2	20.6	31.9	48.9	21.1	18.7	37.0	26.1
	329 x 298*	21.1	22.8	13.3	23.4	34.4	66.2	31.1	22.8	37.0	28.4
	329 x 299	20.4	22.1	11.2	21.4	32.9	54.8	33.2	20.9	40.5	27.5
	329 x 311	19.6	20.6	10.8	20.0	33.0	45.1	21.4	16.0	30.3	19.9
	359 x 296	18.3	19.7	11.1	20.1	34.2	49.0	23.5	18.2	31.3	25.1
	359 x 298	16.1	18.0	9.9	17.7	32.0	56.4	16.4	14.2	23.1	21.4
	359 x 299	21.1	21.5	9.5	19.8	32.0	57.6	24.4	18.0	35.9	28.3
	359 x 311	19.4	22.2	10.2	20.6	37.9	55.9	20.0	18.4	35.8	25.8
	359 x 329	20.8	21.8	11.7	20.1	35.4	55.0	27.4	18.1	35.9	23.8
	366 x 296	19.2	19.0	11.4	22.3	31.2	53.2	18.8	20.2	38.2	34.2
	366 x 298*	18.8	23.2	11.4	19.1	33.4	62.5	21.6	19.2	24.4	22.8
	366 x 299	20.3	24.3	11.9	20.2	34.5	61.0	31.0	20.4	40.3	35.2
	366 x 311	18.2	19.9	10.1	20.4	31.6	50.0	19.4	16.0	34.1	34.6
	366 x 329	20.1	21.0	11.0	21.2	33.8	55.8	25.0	19.2	34.6	35.4
	366 x 359	17.9	20.2	10.2	20.0	30.2	55.2	19.5	15.5	26.4	21.4
	368 x 296*	18.8	18.8	11.4	20.6	33.8	49.0	25.2	19.4	38.5	26.9
	368 x 298*	20.3	24.4	11.2	20.2	36.7	59.1	27.5	19.2	32.9	25.6
	368 x 299	20.0	22.6	9.8	19.8	34.6	48.6	30.2	18.4	36.2	32.5
	368 x 311*	21.9	23.9	11.6	20.6	37.4	44.3	34.7	21.8	41.0	38.2
	368 x 329	18.7	19.3	10.8	22.2	32.1	50.0	22.0	18.0	35.9	27.4
	368 x 359	20.7	23.6	10.6	18.5	35.9	48.6	34.9	18.5	37.6	30.3
	368 x 366	19.4	19.1	11.0	20.3	30.9	53.1	23.0	17.8	35.0	32.8
	374 x 296	19.0	19.8	11.5	21.5	31.2	50.2	27.0	19.5	34.6	27.6
	374 x 298	20.9	21.4	12.0	20.8	33.4	65.1	29.0	23.2	32.7	26.1
	374 x 299	19.3	20.8	10.3	20.5	29.0	55.1	32.5	18.5	34.5	30.0
	374 x 311	21.4	21.2	11.0	20.3	32.2	55.2	33.8	20.2	34.2	27.4
	374 x 329	19.0	17.6	11.0	21.3	30.2	62.8	25.1	21.4	35.4	26.5
	374 x 359	17.1	19.1	10.7	20.0	33.2	61.6	19.0	15.4	31.4	28.4
	374 x 366	18.0	18.0	11.2	19.6	28.7	54.4	18.0	17.4	31.2	23.1
	374 x 368	19.2	17.4	10.8	20.2	29.8	54.5	23.9	17.2	37.5	28.7
	Average	19.5	21.1	11.1	20.6	33.2	54.9	25.1	18.8	34.7	28.3

Appendix Table 1. (Continued)

		Natural				Total		Yield per Plant			
		Plant	Plant	Plant Spread		Leaf	Plant				
		Width	Height			Length	Height				
		(cm.)	(cm.)	(cm.)		(cm.)	(cm.)	(gm.)			
		April	April	May	Sept.	June	June	May	June	July	Sept.
		24	24	28	26	13	13	15	17	30	17
F ₂	299 x 296	15.6	18.4	9.0	16.8	29.3	38.6	13.4	11.7	21.4	24.7
Progeny	299 x 298	14.8	20.5	9.2	17.6	30.9	5.13	13.2	13.2	20.0	17.8
	311 x 299	14.0	14.4	9.3	17.9	26.1	42.0	10.8	10.2	19.8	16.8
	329 x 296	14.1	15.0	9.1	17.4	27.1	37.0	10.2	11.8	23.4	25.3
	329 x 299	13.2	13.8	8.8	18.1	26.1	42.8	9.2	10.7	19.2	11.6
	329 x 311	17.5	17.3	9.9	19.7	31.2	49.3	19.3	16.0	28.8	21.1
	359 x 296	13.8	14.4	9.6	18.2	26.1	39.0	11.1	10.6	22.7	13.9
	359 x 298	14.0	17.3	9.4	17.2	26.9	47.1	11.0	10.6	18.4	14.3
	359 x 299	17.1	21.1	9.3	17.9	33.9	55.1	19.2	15.1	26.4	24.2
	359 x 311	15.4	16.7	9.8	20.0	29.7	49.8	11.0	11.5	21.6	24.2
	359 x 329	15.2	15.4	9.8	17.8	29.0	51.2	11.5	12.3	19.6	15.3
	366 x 296	14.5	14.6	10.4	19.9	26.0	41.4	10.1	11.1	18.2	14.4
	366 x 299	14.4	15.7	9.3	17.5	26.2	50.5	11.6	12.4	21.0	15.2
	366 x 311	16.0	16.4	9.2	19.4	28.2	40.2	16.0	12.5	22.0	15.6
	366 x 329	17.6	15.6	9.9	20.3	29.2	57.0	16.1	15.1	27.2	19.9
	366 x 359	15.6	14.7	9.6	17.8	25.6	45.4	9.7	9.7	18.7	17.2
	368 x 299	16.2	19.6	9.4	17.4	30.8	46.8	15.9	12.8	23.2	15.9
	369 x 329	14.6	16.1	10.0	17.5	26.2	42.8	11.2	10.8	20.6	16.9
	368 x 359	14.1	13.5	8.2	16.2	25.6	40.8	9.8	9.6	17.2	10.6
	368 x 366	13.2	14.5	9.3	17.7	23.0	37.2	7.9	8.6	17.2	14.5
	374 x 296	15.4	13.3	9.9	19.6	24.2	37.6	12.4	11.2	18.6	14.5
	374 x 298	15.4	17.8	10.2	18.4	25.8	47.1	12.6	11.4	18.1	16.5
	374 x 299	15.0	19.7	8.2	17.5	30.6	51.9	13.2	12.7	21.0	20.0
	374 x 311	17.6	18.2	9.7	20.4	28.8	52.0	18.0	14.2	27.5	19.6
	374 x 329	13.0	13.6	10.1	18.6	26.0	5.28	9.4	11.0	18.0	13.2
	374 x 359	15.1	15.6	9.2	17.8	25.3	47.7	12.2	11.8	20.3	15.6
	374 x 366	14.1	14.3	9.8	17.4	24.6	47.8	10.0	9.3	17.6	14.1
	374 x 368	14.4	15.5	8.8	17.4	28.2	40.0	13.3	10.3	18.8	14.4
	Average	15.0	16.2	9.4	18.2	27.5	45.8	12.5	11.7	21.0	16.8
General Mean		19.0	20.2	10.9	20.1	31.4	51.9	26.0	17.4	31.3	25.3
Alta		23.1	26.7	11.4	20.5	36.7	50.8	37.8	22.4	41.0	35.1
$s_{\bar{y}}$		0.880	1.149	0.485	0.747	1.327	2.597	2.823	1.353	2.256	2.579
C. V.		.09	.11	.09	.07	.08	.10	.22	.16	.14	.20
SSR 5%		3.2	4.2	1.8	2.7	4.9	9.5	10.4	5.0	8.3	9.5
SSR 1%		4.1	5.4	2.3	3.5	6.2	12.2	13.2	6.3	10.6	12.1

* Corresponding F₂ means missing

SSR = Shortest significant range for determining inbreeding depression

Appendix Table 2. Means of forage yield and five other variables; tall fescue, Group L, 1963.

		Natural				Total		Yield per Plant			
		Plant	Plant	Plant	Spread	Leaf	Plant				
		Width	Height	Plant	Spread	Length	Height				
		(cm.)	(cm.)	(cm.)	(cm.)	(cm.)	(cm.)	(gm.)			
		April	April	May	Sept.	June	June	May	June	July	Sept.
		28	28	31	27	17	17	17	18	31	20
Parents	309	23.8	17.0	13.2	22.5	29.3	69.9	32.6	20.8	47.8	18.4
	310	19.2	18.6	11.7	19.9	22.4	51.4	26.9	11.6	30.9	22.1
	326	21.5	12.2	12.3	24.0	30.0	64.6	31.2	23.7	48.1	22.1
	327	21.0	18.5	13.5	23.2	27.7	55.3	34.0	21.2	40.4	24.8
	331	25.4	42.5	12.5	20.8	45.1	68.3	63.4	20.0	66.5	32.4
	364	12.5	10.3	8.4	15.2	15.6	37.3	2.2	1.6	6.3	4.2
	370	20.0	21.1	13.0	21.3	30.9	68.1	20.4	14.1	22.4	23.3
	372	23.0	29.6	13.2	20.0	38.9	59.8	37.6	22.1	29.6	21.4
	379	24.9	17.8	17.4	22.4	29.2	66.3	37.9	20.6	51.4	25.4
	380	21.0	15.6	13.7	22.9	28.0	58.9	31.5	17.8	42.7	26.2
	Average	21.2	20.3	12.9	21.2	29.7	60.0	31.8	17.3	38.6	22.0
S ₁ Progeny	309	19.2	22.9	11.5	19.2	33.1	58.5	25.6	19.6	30.8	18.2
	310	20.2	29.0	11.0	19.5	33.0	45.8	32.4	16.7	32.2	23.6
	326	20.7	16.8	11.2	19.7	32.3	54.2	28.8	18.7	37.2	19.3
	327	20.8	23.2	12.5	19.7	30.0	39.9	34.0	20.3	34.5	25.2
	331	22.0	36.9	12.5	20.7	43.2	57.9	42.7	18.1	42.3	32.4
	364	23.2	35.2	12.6	20.9	40.5	59.7	58.8	21.1	51.6	31.5
	370	20.6	24.4	13.6	19.4	33.0	59.0	33.1	19.2	33.8	22.3
	372	19.8	24.0	10.7	19.0	34.2	47.2	26.1	15.9	24.8	19.6
	379	22.7	32.4	13.5	20.2	40.5	59.9	41.5	17.5	44.1	31.6
	380	20.1	20.4	11.5	19.8	29.1	50.1	28.8	16.5	33.2	17.6
	Average	20.9	26.5	12.0	19.8	34.9	53.2	34.9	18.4	36.5	24.1
Open-pollinated Progeny	309	20.5	22.2	11.7	21.0	35.3	61.5	33.2	22.0	44.8	24.5
	310	21.2	29.2	12.2	20.5	38.4	60.6	44.5	20.4	42.4	35.1
	326	22.7	21.8	12.9	22.6	36.1	59.7	44.4	25.5	50.4	28.8
	327	22.7	26.5	12.4	21.6	34.6	57.0	45.2	24.0	47.0	33.2
	331	24.7	40.2	13.1	20.1	48.0	63.4	62.2	23.4	57.6	36.9
	364	19.8	25.0	12.5	20.4	32.9	61.2	35.8	19.4	33.2	19.8
	370	21.5	31.8	13.1	19.1	39.6	59.5	46.0	22.3	38.3	30.9
	372	23.2	35.7	13.2	20.2	45.4	58.1	50.9	23.6	48.6	40.8
	379	23.4	27.0	13.8	21.8	36.3	56.2	44.4	22.0	48.8	32.7
	380	21.0	23.0	11.9	20.4	33.7	57.8	44.5	19.4	44.2	25.4
	Average	22.0	28.2	12.7	20.8	38.0	59.5	45.1	22.2	45.5	30.8
Polycross Progeny	309	20.1	24.0	12.6	20.9	35.2	63.8	34.1	24.2	41.4	26.4
	310	20.9	24.8	11.7	20.2	33.6	54.1	39.2	18.6	44.4	29.8
	326	22.3	20.4	12.7	21.4	32.2	57.8	46.7	24.2	52.9	30.9
	327	22.6	26.5	12.6	20.6	35.4	53.4	42.4	23.0	42.2	32.5
	331	23.6	29.8	12.4	19.8	40.8	67.4	51.2	24.1	49.0	34.5
	364	22.4	25.4	11.8	19.5	32.4	55.6	39.1	18.2	35.4	21.9
	370	20.5	25.8	12.2	20.5	34.6	56.4	33.8	18.8	36.8	29.2
	372	22.8	29.6	13.0	19.6	38.9	60.1	42.6	23.6	41.2	36.2
	379	22.0	24.4	14.4	21.1	33.6	55.4	41.1	20.8	43.1	29.2
	380	21.4	22.2	12.0	20.1	33.5	59.2	38.7	20.7	42.8	24.2
	Average	21.9	25.3	12.5	20.4	35.0	58.3	40.9	21.6	42.9	29.5

Appendix Table 2. (Continued)

		Natural				Total		Yield per Plant			
		Plant	Plant	Plant Spread	Leaf Length	Plant	Height				
		Width	Height			Height		(gm.)			
		(cm.)	(cm.)	(cm.)	(cm.)	(cm.)	(cm.)	May	June	July	Sept.
		April	April	May	Sept.	June	June	May	June	July	Sept.
		28	28	31	27	17	17	17	18	31	20
Single-	310 x 309	20.1	23.7	12.0	19.6	32.4	58.9	30.2	17.2	32.0	21.7
Cross	326 x 309	20.9	17.4	11.6	21.8	31.9	61.5	26.2	20.5	40.2	24.1
Progeny	326 x 310	20.5	20.8	11.5	20.6	36.4	57.2	29.0	21.2	45.1	25.2
	327 x 309	20.2	25.0	12.2	20.5	32.8	62.3	34.0	23.7	43.0	27.9
	327 x 310*	21.2	25.2	12.0	19.9	33.4	43.0	38.0	21.8	42.6	25.7
	327 x 326*	21.8	18.2	12.0	22.0	30.5	45.6	29.2	21.3	46.4	27.0
	331 x 309	22.7	33.0	11.1	20.9	42.0	64.4	44.7	22.2	53.4	29.4
	331 x 310	23.6	36.9	13.4	20.9	44.7	54.0	50.9	20.5	59.4	42.8
	331 x 326	22.1	29.8	11.9	20.9	40.4	62.7	35.8	20.4	50.3	30.4
	331 x 327*	21.8	32.4	12.2	20.9	41.9	55.1	47.2	24.7	55.5	49.0
	364 x 309*	21.4	22.3	11.4	20.1	33.6	62.2	29.2	19.8	34.0	20.6
	364 x 310	20.8	26.4	13.0	21.0	33.7	58.8	38.2	20.7	46.5	30.9
	364 x 326	18.2	13.2	11.9	19.8	27.4	48.3	10.9	12.2	23.1	11.8
	364 x 327	20.2	21.2	12.3	21.2	31.6	51.3	28.5	20.0	38.5	23.4
	364 x 331*	20.5	34.4	11.0	19.3	44.5	56.7	32.8	16.9	38.1	29.9
	370 x 309	20.1	24.6	11.9	19.5	36.7	62.3	29.8	18.9	39.2	23.7
	370 x 310	21.4	30.1	11.8	20.1	37.6	58.0	42.6	19.9	43.4	37.9
	370 x 326	20.0	17.2	12.0	21.4	32.9	58.1	24.6	19.6	31.7	24.7
	370 x 327*	17.6	20.3	11.8	19.1	30.4	39.6	21.4	16.9	29.4	22.3
	370 x 331	21.5	34.6	11.7	20.4	44.0	59.6	35.8	17.5	41.7	30.9
	370 x 364	20.4	25.8	12.8	19.8	35.5	62.0	30.0	18.0	30.8	26.5
	372 x 309	20.2	24.4	11.3	20.2	37.3	63.9	29.9	22.7	40.5	28.8
	372 x 310	19.6	27.9	11.2	19.2	35.5	47.9	33.9	17.3	36.4	26.4
	372 x 326	20.8	17.5	11.1	19.6	34.5	54.2	29.6	21.4	37.1	28.2
	372 x 327	20.3	26.7	12.0	20.0	37.2	52.2	32.2	20.8	41.0	28.6
	372 x 331	22.8	38.1	12.2	20.6	48.0	59.5	41.2	21.2	48.9	43.7
	372 x 364	20.4	23.8	11.3	19.6	33.0	56.7	26.6	16.4	30.0	18.4
	372 x 370*	20.1	26.7	11.2	19.4	35.0	51.8	25.7	15.4	27.1	25.6
	379 x 309	20.5	22.0	12.4	20.2	33.0	62.4	34.6	21.8	40.7	22.1
	379 x 310	21.8	26.1	11.5	20.2	35.6	55.0	39.6	20.4	42.6	24.0
	379 x 326*	20.8	15.1	12.0	20.9	31.4	53.4	24.9	18.4	34.8	23.0
	379 x 327	21.1	23.7	12.0	21.2	35.8	53.4	32.6	21.7	41.4	30.2
	379 x 331	23.2	32.5	11.3	20.5	43.4	60.0	40.7	20.8	48.2	34.7
	379 x 364*	18.6	21.8	11.0	18.5	33.2	54.0	22.6	15.4	30.8	23.2
	379 x 370*	20.5	22.2	11.2	20.0	33.8	58.8	28.7	18.5	36.0	27.2
	379 x 372	21.4	25.4	12.2	20.2	37.6	55.7	33.8	19.9	36.5	29.7
	380 x 309*	20.2	19.0	11.3	20.7	30.5	60.6	27.0	19.4	38.9	20.8
	380 x 310	19.7	24.3	11.2	20.0	31.5	54.4	24.2	17.6	39.8	26.1
	380 x 326	19.5	16.6	11.8	21.5	31.3	55.1	24.3	20.3	43.1	25.2
	380 x 327	19.4	17.8	11.4	20.9	28.3	49.7	27.2	17.4	34.7	20.6
	380 x 331	22.6	33.2	12.4	20.5	47.7	58.3	45.4	23.3	54.8	41.6
	380 x 364	17.9	18.5	11.1	19.3	30.1	50.3	17.5	13.4	28.8	15.2
	380 x 370	20.8	23.8	11.1	21.1	32.8	61.8	33.6	19.6	34.5	25.4
	380 x 372	21.2	23.3	10.9	20.4	37.8	57.2	32.9	21.8	39.2	25.8
	380 x 379	21.1	22.4	12.2	20.4	33.4	58.4	30.3	19.2	44.8	25.0
	Average	20.7	24.6	11.8	20.3	35.6	56.1	31.7	19.5	39.9	27.2

Appendix Table 2. (Continued)

		Natural				Total					
		Plant	Plant			Leaf	Plant				
		Width	Height	Plant	Spread	Length	Height	Yield per Plant			
		(cm.)	(cm.)	(cm.)		(cm.)	(cm.)	(gm.)			
		April	April	May	Sept.	June	June	May	June	July	Sept.
		28	28	31	27	17	17	17	18	31	20
F ₂	310 x 309	17.3	18.4	9.8	18.2	26.3	51.6	17.2	12.2	23.6	16.2
Progeny	326 x 309	17.8	14.3	9.8	19.8	28.6	54.7	13.8	14.6	23.9	13.3
	326 x 310	17.0	17.2	10.8	18.2	26.6	47.3	13.5	11.7	24.0	14.7
	327 x 309	16.6	15.4	10.0	19.0	27.4	46.3	11.9	15.0	23.1	16.0
	331 x 309	20.5	29.0	10.2	19.8	38.3	55.9	25.4	15.6	33.2	23.6
	331 x 310	19.4	28.0	10.2	18.6	39.4	49.1	21.2	14.1	30.5	25.5
	331 x 326	18.8	20.8	10.0	18.8	33.6	42.4	16.1	12.6	24.7	13.9
	364 x 310	16.2	18.1	9.8	16.5	24.8	40.6	12.0	9.1	15.7	14.4
	364 x 326	18.8	15.6	10.6	18.4	24.8	47.6	13.7	12.3	18.6	10.0
	364 x 327	19.2	19.1	10.3	18.8	22.5	42.3	25.5	11.4	21.2	11.6
	370 x 309	17.9	20.5	10.5	18.7	30.7	46.3	18.2	13.8	27.8	19.0
	370 x 310	17.4	25.8	10.1	18.0	31.5	50.5	16.9	11.5	21.6	16.9
	370 x 326	16.9	14.5	10.4	18.5	27.0	53.3	12.6	12.8	20.6	15.1
	370 x 331	19.6	29.0	10.6	18.4	38.0	59.7	26.4	16.2	30.8	29.2
	370 x 364	19.0	19.7	10.9	19.0	26.4	50.2	17.4	11.5	18.3	13.2
	372 x 309	16.5	18.4	9.6	18.2	27.3	57.5	11.8	13.0	20.5	14.3
	372 x 310	17.2	22.9	9.3	17.6	33.6	41.2	15.0	12.1	23.4	17.4
	372 x 326	17.0	17.5	9.4	19.0	29.0	49.7	16.8	13.6	25.5	15.2
	372 x 327	18.1	19.0	9.9	18.9	28.9	40.7	18.0	14.4	20.4	13.6
	372 x 331	19.1	28.8	10.0	19.5	38.9	47.2	27.4	16.1	28.2	25.2
	372 x 364	18.0	21.3	10.2	17.1	30.0	49.9	20.4	13.2	22.2	11.8
	379 x 309	16.1	13.6	9.1	17.4	26.2	46.2	7.8	10.9	18.2	8.1
	379 x 310	17.4	20.0	9.5	16.8	33.1	49.0	20.6	14.2	24.3	17.7
	379 x 327	15.8	17.2	10.5	17.7	28.2	40.7	18.2	12.8	24.7	18.8
	379 x 331	18.8	25.1	11.0	19.5	36.0	52.4	25.4	16.2	33.7	25.8
	379 x 372	18.0	20.6	9.9	18.5	31.1	52.4	20.7	13.4	24.3	16.6
	380 x 310	19.4	18.6	10.8	19.4	26.7	48.4	21.1	12.4	26.2	14.6
	380 x 326	19.1	22.2	10.9	18.7	33.2	51.9	23.6	16.7	29.0	17.9
	380 x 327	17.6	17.6	10.7	18.8	26.0	39.4	19.4	14.8	25.9	14.8
	380 x 331	21.8	26.6	11.1	20.4	36.2	49.1	30.8	15.1	36.1	19.2
	380 x 364	19.3	17.2	10.9	18.8	31.9	52.6	22.2	14.1	25.8	13.3
	380 x 370	17.3	19.6	10.1	17.4	30.3	51.3	17.3	11.4	19.9	13.6
	380 x 372	19.9	22.8	10.7	18.5	35.2	56.0	24.9	16.1	30.2	19.8
	380 x 379	17.6	17.6	10.1	17.6	25.1	47.2	16.0	11.0	25.1	12.9
	Average	18.1	20.4	10.2	18.5	30.4	49.0	18.8	13.4	24.7	15.6
General Mean		20.2	23.5	11.6	19.9	33.7	54.6	30.2	17.9	35.9	24.0
Alta		22.3	31.2	12.8	20.2	40.8	57.4	51.2	22.9	53.1	33.8
s \bar{y}		0.960	1.304	0.504	0.654	1.451	2.437	2.657	1.271	2.731	2.902
C. V.		.09	.11	.09	.07	.09	.09	.18	.14	.15	.24
SSR 5%		3.5	4.9	1.8	2.4	5.3	9.5	9.8	4.7	10.0	10.6
SSR 1%		4.5	6.1	2.4	3.1	6.8	11.4	12.4	6.0	12.8	13.6

* Corresponding F₂ means missing

SSR = Shortest significant range for determining inbreeding depression

Appendix Table 3. Means of forage yield and four other variables; tall fescue, Group I, 1964.

		Plant	Leaf	Total	Plant	Yield per Plant	
		Spread	Length	Plant	Density		
		(cm.)	(cm.)	Height	Rated(1-9)	(gm.)	
		April 28	June 2	June 2	June 5	April 21	June 15
Parents	296	31.6	30.0	50.0	7.0	180.6	33.5
	298	27.2	31.3	52.8	5.5	134.0	41.9
	299	25.7	34.3	60.5	4.0	153.7	33.2
	311	33.3	32.4	42.7	6.0	223.9	32.4
	329	29.2	32.3	56.3	7.0	120.8	32.7
	359	27.8	36.0	62.6	4.5	118.3	29.5
	366	30.4	27.6	58.4	3.5	135.5	34.1
	368	27.9	30.5	53.4	4.5	94.9	22.3
	374	27.7	29.7	64.8	5.5	150.5	32.2
	Average	29.0	31.6	55.7	5.3	145.8	32.4
S ₁							
Progeny	296	29.8	30.5	52.6	7.0	161.2	40.0
	298	29.8	34.6	58.6	5.5	152.4	39.5
	299	23.6	30.4	55.8	3.5	154.2	26.1
	311	27.0	25.0	42.0	4.0	131.7	21.2
	329	27.4	30.0	48.7	6.0	128.8	30.0
	359	25.4	30.6	49.4	3.5	110.5	16.4
	366	27.6	24.3	53.3	2.0	107.9	23.6
	368	26.3	26.8	43.1	4.0	98.7	21.7
	374	28.2	29.3	57.5	6.5	153.5	31.4
	Average	27.2	29.1	51.2	4.7	133.2	27.7
Open-pollinated							
Progeny	296	30.5	31.4	51.9	6.0	166.8	33.4
	298	29.8	32.1	56.7	5.5	176.7	32.3
	299	26.9	35.0	59.0	5.5	177.8	33.8
	311	29.6	31.2	48.2	6.0	187.6	37.3
	329	29.8	28.2	52.2	6.0	162.8	37.7
	359	29.2	35.2	62.3	6.5	150.0	36.2
	366	28.7	26.1	50.0	4.5	141.0	31.8
	368	30.4	31.4	50.2	5.5	143.0	36.9
	374	29.8	29.9	56.6	5.0	150.4	34.2
	Average	29.4	31.2	54.1	5.6	161.8	34.9
Polycross							
Progeny	296	30.5	31.7	55.7	6.0	163.6	36.8
	298	31.4	33.4	58.9	7.0	151.5	39.2
	299	29.4	30.4	48.4	5.5	193.6	32.8
	311	30.9	31.3	54.6	5.5	162.9	32.9
	329	29.4	30.1	52.3	6.0	170.7	30.5
	359	29.1	32.1	54.3	5.5	166.3	28.1
	366	30.0	28.2	54.5	4.0	159.7	32.6
	368	29.8	28.6	47.8	5.0	158.6	31.7
	374	30.9	31.8	63.0	4.5	140.9	38.6
	Average	30.2	30.8	54.4	5.4	163.1	33.7

Appendix Table 3. (Continued)

	Plant Spread (cm.) April 28	Leaf Length (cm.) June 2	Total Plant Height (cm.) June 2	Plant Density Rated(1-9) June 5	Yield per Plant (gm.) April 21 June 15	
Single-cross Progeny						
298 x 296*	29.0	32.8	52.6	6.0	167.6	30.4
299 x 296	27.6	34.4	55.9	5.0	165.7	33.0
299 x 298	27.6	32.4	54.2	6.0	163.1	26.5
311 x 296*	30.2	32.1	43.4	6.5	178.3	30.3
311 x 298*	28.4	31.2	54.8	6.0	154.1	29.9
311 x 299	30.2	28.0	42.4	6.0	197.4	27.7
329 x 296	30.4	33.0	54.7	7.5	146.6	37.6
329 x 298*	31.8	33.0	60.1	7.0	152.8	39.1
329 x 299	28.6	30.1	48.6	6.0	160.3	26.7
329 x 211	28.5	31.2	48.2	5.0	132.6	24.8
359 x 296	29.4	31.4	56.1	5.0	151.9	35.2
359 x 298	26.2	31.5	57.3	4.0	108.0	29.5
359 x 299	28.3	28.5	48.5	4.5	177.9	25.2
359 x 311	28.6	31.9	49.1	5.0	162.8	27.7
359 x 329	28.2	33.6	56.6	5.5	124.4	27.5
366 x 296	29.3	30.0	53.1	6.5	170.8	35.4
366 x 298*	28.3	30.4	58.6	6.0	159.5	36.4
366 x 299	27.2	30.3	53.8	5.5	167.2	28.9
366 x 311	30.7	25.3	48.2	5.0	172.8	29.0
366 x 329	28.8	31.8	50.5	5.0	154.4	30.7
366 x 359	26.9	28.2	52.0	4.5	109.1	29.3
368 x 296*	29.5	30.6	48.5	5.5	152.4	28.6
368 x 298*	29.4	34.3	55.6	7.0	147.7	36.0
368 x 299	26.2	31.8	51.0	4.0	154.2	27.8
368 x 311*	32.0	31.0	47.0	8.0	181.7	39.4
368 x 329	29.2	31.5	53.4	7.0	126.7	37.8
368 x 359	29.2	33.4	54.5	5.5	137.3	29.7
368 x 366	30.9	28.3	50.0	4.5	145.6	32.5
374 x 296	28.4	31.2	54.8	6.5	157.8	34.4
374 x 298	29.4	33.6	64.5	5.0	140.0	42.1
374 x 299	27.8	28.2	54.1	4.0	166.2	35.4
374 x 311	30.0	28.8	60.0	6.0	158.2	36.6
374 x 329	29.7	30.4	56.0	7.5	146.1	38.8
374 x 359	27.8	32.1	57.3	5.0	123.5	3.1
374 x 366	29.4	27.0	54.2	4.5	125.4	36.2
374 x 368	29.2	27.3	54.2	6.0	130.0	29.4
Average	28.7	30.6	53.3	5.4	149.2	31.7

Appendix Table 3. (Continued)

	Plant Spread (cm.) April 28	Leaf Length (cm.) June 2	Total Plant Height (cm.) June 2	Plant Density Rated (1-9) June 5	Yield per Plant (gm.) April 21 June 15	
F ₂ progeny						
299 x 296	23.5	31.4	50.6	4.0	99.1	22.9
299 x 298	23.1	30.7	54.0	4.0	104.4	30.2
311 x 299	23.8	25.6	49.7	3.0	81.1	16.4
329 x 296	24.6	30.4	55.7	5.5	97.8	28.7
329 x 299	23.6	26.4	52.6	3.5	73.2	21.6
329 x 311	26.7	26.8	50.4	4.5	120.4	22.0
359 x 296	25.0	30.7	52.2	4.5	101.2	26.0
359 x 298	32.7	27.5	53.1	3.0	74.0	23.2
359 x 299	26.1	30.7	55.4	3.5	115.7	21.1
359 x 311	26.6	26.0	45.3	4.0	100.6	24.0
359 x 329	25.7	27.1	54.7	3.5	74.8	24.1
366 x 296	27.6	29.2	54.1	3.5	83.1	25.8
366 x 299	25.4	23.7	54.0	2.0	79.7	23.6
366 x 311	27.8	23.9	41.8	4.0	112.0	19.5
366 x 329	27.8	27.1	59.2	3.5	102.0	37.3
366 x 359	25.8	26.0	50.9	3.0	87.3	29.6
368 x 299	24.5	28.6	47.8	2.5	89.9	18.6
368 x 329	24.7	27.4	55.6	3.5	66.0	22.2
368 x 359	26.1	24.0	54.1	3.0	53.4	15.7
368 x 366	27.2	24.6	49.8	2.0	73.6	18.2
374 x 296	27.0	27.0	49.9	3.5	86.0	29.6
374 x 298	26.4	25.8	52.5	3.0	104.9	24.2
374 x 299	23.2	28.2	54.1	4.0	91.2	21.9
374 x 311	26.1	26.6	56.5	4.5	119.0	30.4
374 x 329	24.6	26.8	54.6	3.5	72.3	25.3
374 x 359	24.6	23.7	53.3	3.5	85.2	21.8
374 x 366	25.2	25.6	52.7	3.5	69.6	21.5
374 x 368	25.9	25.0	48.4	4.0	67.6	17.9
Average	25.4	27.0	52.2	3.6	88.8	23.7
General Mean	28.0	29.7	53.2	4.9	133.9	29.8
Alta	27.4	37.6	59.5	7.0	167.2	32.9
s _y	0.996	1.332	3.069	0.664	10.401	3.703
C. V.	.07	.09	.11	.27	.16	.25
SSR 5%	3.6	4.9	11.3	2.4	38.2	13.6
SSR 1%	4.7	6.2	14.4	3.1	48.7	17.3

* Corresponding F₂ means missing

SSR = Shortest significant range for determining inbreeding depression

Appendix Table 4. Means of forage yield and four other variables; tall fescue, Group L, 1964.

		Plant	Leaf	Total	Plant	Yield per Plant	
		Spread	Length	Plant	Density	(gm.)	
		(cm.)	(cm.)	Height	Rated(1-9)		
		April 29	June 4	June 4	June 5	April 21	June 16
Parents	309	34.2	29.0	57.2	8.0	137.5	33.4
	310	28.9	24.6	52.0	6.0	131.5	34.1
	326	32.1	34.5	57.4	6.0	149.4	28.6
	327	36.5	27.5	62.2	5.5	123.8	45.6
	331	28.8	46.6	69.4	8.5	284.6	43.7
	364	24.6	18.4	43.6	4.0	11.3	11.2
	370	28.6	28.6	63.0	3.5	121.6	29.6
	372	28.4	33.5	60.2	7.5	160.0	35.3
	379	38.8	31.0	59.4	6.5	173.5	31.5
	380	30.2	29.8	61.1	7.5	156.1	44.3
	Average	31.1	30.4	58.6	6.3	145.4	33.7
S1							
Progeny	309	28.7	32.8	60.3	5.5	99.3	36.9
	310	26.9	27.9	56.7	5.0	108.5	29.5
	326	28.8	28.4	48.9	4.0	123.5	25.0
	327	27.1	25.9	52.6	5.0	120.4	34.5
	331	29.1	42.2	66.7	4.5	210.4	38.3
	364	28.8	38.4	62.3	6.5	220.8	41.3
	370	27.5	28.8	60.2	4.5	130.2	29.9
	372	26.3	26.6	54.1	6.0	119.3	27.8
	379	27.7	34.8	59.9	4.5	195.1	27.3
	380	28.6	29.4	57.6	4.0	98.0	33.4
	Average	27.9	31.5	57.9	5.0	142.6	32.4
Open-pollinated							
Progeny	309	29.8	31.5	56.7	6.5	153.2	34.7
	310	29.5	32.5	59.6	5.5	172.2	41.6
	326	31.6	34.4	61.4	5.5	181.4	42.4
	327	31.9	35.1	64.3	6.0	165.3	40.7
	331	27.2	39.7	62.2	6.5	227.3	35.3
	364	30.7	28.4	62.6	4.5	115.3	33.1
	370	28.6	29.5	54.8	5.5	174.5	32.7
	372	28.8	38.8	59.8	5.0	234.5	40.2
	379	32.9	34.2	59.0	5.0	179.1	39.0
	380	28.0	30.1	61.6	6.0	143.8	38.7
	Average	29.9	33.6	60.2	5.6	174.7	37.8
Polycross							
Progeny	309	29.0	29.2	54.0	7.5	147.7	36.6
	310	29.4	29.9	56.6	5.0	155.8	34.6
	326	32.5	32.4	59.7	7.0	182.4	40.1
	327	30.5	30.8	60.3	6.0	153.1	36.8
	331	28.0	35.0	65.3	5.5	165.4	44.2
	364	27.4	29.6	57.6	4.5	131.6	25.8
	370	28.0	28.2	57.4	4.5	143.5	31.1
	372	28.9	31.0	60.3	7.0	177.2	40.5
	379	30.9	30.8	56.4	5.0	142.3	32.8

Appendix Table 4. (Continued)

		Plant	Leaf	Total	Plant	Yield per Plant	
		Spread	Length	Plant	Density		
		(cm.)	(cm.)	Height	Rated (1-9)	(gm.)	
		April 29	June 4	June 4	June 5	April 21	June 16
Polycross							
Progeny	380	29.6	27.6	59.2	5.5	137.8	33.8
(cont.)	Average	29.4	30.4	58.7	5.8	153.7	35.6
Single-cross Progeny							
310 x 309		29.2	27.1	60.9	5.0	102.8	42.0
326 x 309		30.8	28.0	55.3	6.5	142.1	37.6
326 x 310		29.2	30.6	60.0	5.0	160.0	31.8
327 x 309		30.0	28.0	59.8	6.5	159.0	38.6
327 x 310*		29.4	27.9	53.1	5.0	162.8	36.3
327 x 326*		31.8	28.3	53.8	4.0	168.0	36.3
331 x 309		30.1	36.4	62.9	7.0	202.9	36.0
331 x 310		28.9	35.1	54.0	6.5	228.0	37.1
331 x 326		28.3	38.2	59.2	6.5	218.2	33.3
331 x 327*		28.5	36.5	60.8	6.5	233.4	44.1
364 x 309*		29.4	32.3	63.1	6.0	118.1	39.4
364 x 310		31.0	27.8	57.6	4.5	142.4	41.8
364 x 326		27.0	29.1	54.0	4.0	81.4	20.2
364 x 327		31.8	28.2	58.7	5.0	145.0	41.7
364 x 331*		25.6	41.8	64.2	5.5	190.6	30.1
370 x 309		26.9	30.2	59.8	6.0	117.2	33.3
370 x 310		29.0	33.1	59.6	5.5	148.0	34.6
370 x 326		28.6	30.4	57.6	5.5	132.4	26.8
370 x 327*		27.6	26.5	54.0	5.0	122.1	35.1
370 x 331		26.9	37.4	62.1	5.0	197.1	30.8
370 x 364		27.4	32.6	63.2	4.5	138.1	38.5
372 x 309		28.0	30.9	59.4	8.5	150.4	42.5
372 x 310		27.8	30.8	56.4	6.0	147.8	36.7
372 x 326		27.0	31.1	56.9	6.0	133.4	30.1
372 x 327		28.8	31.4	59.7	6.5	146.3	37.0
372 x 331		28.1	39.0	64.9	6.5	210.8	37.7
372 x 364		28.9	29.2	59.0	5.0	116.8	31.9
372 x 370*		27.5	29.0	58.6	5.5	154.8	31.4
379 x 309		30.7	31.6	62.6	5.5	127.0	30.0
379 x 310		31.3	30.0	63.3	5.0	135.8	30.4
379 x 326*		29.6	29.7	51.4	6.5	134.7	28.3
379 x 327		32.0	29.4	62.0	5.5	154.1	38.8
379 x 331		29.0	36.8	62.6	6.0	223.4	31.0
379 x 364*		28.6	28.4	60.1	3.5	114.1	31.2
379 x 370*		30.8	28.2	61.0	5.5	141.4	28.4
379 x 372		31.0	29.8	59.3	5.0	131.5	29.8
380 x 309*		29.6	30.0	60.4	7.5	114.0	41.1
380 x 310		28.6	26.9	54.1	4.0	128.0	29.6
380 x 326		30.5	30.4	60.0	5.5	130.8	34.8
380 x 327		29.9	26.7	53.0	6.5	131.5	26.5
380 x 331		27.3	39.0	67.5	5.5	217.6	34.0
380 x 364		28.6	28.8	59.2	5.0	97.5	30.7
380 x 370		28.1	28.3	62.1	4.5	129.3	35.0
380 x 372		28.7	32.0	59.4	6.5	156.7	45.3
380 x 379		30.7	30.2	58.2	5.0	125.6	27.4
Average		29.1	31.3	59.5	5.6	149.6	34.2

Appendix Table 4. (Continued)

Appendix Table 4. (Continued)

	Plant Spread (cm.) April 29	Leaf Length (cm.) June 4	Total Plant Height (cm.) June 4	Plant Density Rated (1-9) June 5	Yield per Plant (gm.) April 21 June 16	
F ₂ Progeny						
310 x 309	26.4	26.0	49.2	4.5	81.5	35.2
326 x 309	26.7	29.8	57.9	3.5	73.7	28.6
326 x 310	27.8	26.2	58.2	2.5	81.5	31.3
327 x 309	27.9	26.0	55.2	4.5	70.8	34.8
331 x 309	25.4	37.4	60.7	4.5	168.1	28.2
331 x 310	25.2	32.3	54.6	6.0	158.9	27.1
331 x 326	26.1	32.8	46.6	3.5	120.8	30.4
364 x 310	24.0	23.1	52.4	3.5	49.8	29.2
364 x 326	28.4	26.0	61.6	2.5	64.4	22.6
364 x 327	29.6	22.7	52.3	5.5	80.9	24.0*
370 x 309	27.3	28.3	55.2	4.5	102.9	34.6
370 x 310	23.7	26.3	52.4	3.5	81.4	27.4
370 x 326	28.1	27.8	63.7	4.0	81.4	27.6
370 x 331	26.0	32.8	60.2	5.5	131.9	30.5
370 x 364	26.2	25.4	56.4	4.0	70.8	28.7
372 x 309	25.8	27.0	57.0	3.5	67.7	29.6
372 x 310	26.6	28.8	56.6	5.0	82.9	29.7
372 x 326	26.6	30.2	55.0	4.5	108.7	27.4
372 x 327	24.0	26.2	52.2	4.5	87.6	25.8
372 x 331	24.2	33.0	55.5	6.0	147.8	30.8
372 x 364	26.3	25.2	60.8	5.0	74.4	26.7
379 x 309	26.1	26.6	52.7	4.0	67.2	26.4
379 x 310	26.4	25.0	57.3	3.0	63.8	23.4
379 x 327	25.1	24.5	52.9	5.0	93.4	19.8**
379 x 331	26.3	31.4	56.2	5.5	157.3	30.6
379 x 372	31.1	26.3	54.7	3.0	95.0	21.8
380 x 310	29.0	27.0	59.2	4.0	85.7	33.8
380 x 326	26.4	29.7	56.6	6.0	119.1	35.0
380 x 327	25.1	24.2	51.9	4.5	92.0	24.8
380 x 331	28.0	33.8	60.6	5.5	149.7	35.4
380 x 364	27.7	26.1	61.2	4.5	57.9	38.3
380 x 370	26.4	27.0	61.1	2.5	60.4	33.0
380 x 372	27.8	30.6	61.4	5.5	119.7	33.1
380 x 379	25.1	24.5	54.4	3.5	78.0	23.9
Average	26.6	27.9	56.3	4.3	94.9	35.3
General Mean	28.5	30.4	58.2	5.2	135.7	33.0
Alta	29.4	35.0	58.4	7.0	175.3	30.3
s ² y	0.927	1.564	2.833	0.737	10.987	3.832
C. V.	.06	.10	.10	.28	.16	.23
SSR 5%	3.4	5.7	10.4	2.7	40.3	14.1
SSR 1%	4.3	7.3	13.3	3.4	51.4	17.9

* Corresponding F₂ means missing

SSR = Shortest significant range for determining inbreeding depression

Appendix Table 5. Mean squares and levels of significance of forage yield and five other variables; tall fescue, Group I, 1963.

Source of Variation	D.F.	Mean Squares and Levels of Significance									
		Plant Width	Natural Plant Height	Plant Spread	Leaf Length	Total Plant Height	Yield per Plant				
		April 24	April 24	May 28	Sept. 26	June 13	June 13	May 15	June 17	July 30	Sept. 19
Treatments	99	35.3**	50.7**	6.2**	12.0**	49.4**	225.5**	562.4**	76.6**	267.6**	209.5**
Among Groups	5	570.8**	587.4**	86.8**	130.6**	503.5**	1342.7**	9018.2**	1122.5**	3670.7**	2639.0**
Within Groups ^{1/}	94	6.8**	22.2**	2.0**	5.7**	25.3**	166.1**	112.7**	21.0**	86.6**	80.3**
Among Parents	8	7.5*	37.0**	4.5**	12.2**	45.3**	382.8**	127.2**	27.0**	186.7**	198.4**
Among S ₁	8	12.3**	30.3**	2.6**	9.6**	40.2**	378.6**	398.3**	66.8**	246.0**	91.3**
Among OP	8	6.5*	31.6**	.8	2.4	23.4**	87.3**	192.8**	27.6**	33.0	29.1
Among PX	8	3.4	11.6*	1.1	1.2	10.2	69.1*	28.5	7.6	47.4*	53.1
Among SX	35	6.4**	19.6**	2.3*	5.5**	21.2**	131.5**	103.5**	16.8**	83.7**	88.6**
Among F ₂	27	6.7**	19.1**	1.2	5.0**	25.2**	135.6**	36.8	12.6*	41.1**	54.4**
Reps	3	122.0**	5.8	19.0**	32.3**	492.1**	920.4**	2883.1**	509.4**	1407.7**	442.6**
Error	297	3.1	5.3	.9	2.2	7.0	27.0	31.9	7.3	20.4	26.6
Total	399										

^{1/} Mean squares of within groups used to test significance of among groups

** Significant at 1% level

* Significant at 5% level

Appendix Table 6. Mean squares and levels of significance of forage yield and five other variables; tall fescue, Group L, 1963.

		Mean Squares and Levels of Significance									
Source of Variation	D. F.	Natural		Plant		Leaf	Total	Yield per Plant			
		Width	Height	Plant	Spread	Length	Plant				
		April 28	April 28	May 31	Sept. 27	June 17	June 17	May 17	June 18	July 31	Sept. 20
Treatments	118	18.0**	156.3**	6.5**	7.7**	128.9**	191.4**	524.0**	69.7**	463.4**	251.3**
Among Groups	5	185.8**	668.0**	83.9**	83.1**	733.0**	1473.4**	6800.4**	904.9**	5162.4**	2521.5**
Within Groups 1/	113	10.6**	133.6**	3.1**	4.4**	102.2**	134.6**	246.3**	32.7**	255.5**	150.8**
Among Parents	9	54.2**	352.6**	19.6**	25.3**	259.3**	403.3**	936.4**	177.7**	1147.9**	210.6**
Among S ₁	9	6.7	171.8**	4.1**	1.5	91.4**	200.3**	352.3**	11.7	236.2**	129.3**
Among OP	9	8.4*	147.9**	1.7	3.9*	101.0**	20.4	246.4**	15.9*	181.6**	159.6**
Among PX	9	4.9	34.2**	2.4**	1.7	30.9**	79.1**	112.4**	24.6**	105.6**	78.3*
Among SX	44	6.5**	141.9**	1.4	2.3	100.5**	122.0**	244.4**	26.7**	246.7**	202.1**
Among F ₂	33	7.4**	75.7**	1.1	3.1**	84.2**	106.6**	68.2**	13.8**	90.0**	89.5**
Reps	3	18.8**	899.6**	10.4**	95.9**	187.3**	169.8**	528.4**	133.7**	45.8	293.4**
Error	354	3.7	6.8	1.0	1.7	8.4	23.8	28.2	6.5	29.8	33.7
Total	475										

^{1/} Mean squares of within groups used to test significance of among groups

** Significant at 1% level

* Significant at 5% level

Appendix Table 7. Mean squares and levels of significance of forage yield and four other variables; tall fescue, Group I, 1964.

Source of Variation	D. F.	Mean Squares and Levels of Significance					
		Plant Spread	Leaf Length	Total Plant Height	Plant Density	Yield per Plant	
		April 28	June 2	June 2	June 5	April 21	June 15
Treatments	99	20.2**	34.2**	91.1**	7.0**	5135.2**	163.9**
Among Groups	5	233.1**	252.1**	110.2	64.1**	67,648.1**	1425.9**
Within Groups 1/	94	8.9**	22.6**	90.1**	4.0**	1810.0**	96.8**
Among Parents	8	23.1**	25.5**	188.2**	6.3**	5806.3**	109.4*
Among S ₁	8	15.6**	41.2**	140.3**	11.0**	2186.1**	2752.1**
Among OP	8	4.7	34.0**	90.1*	1.4	1112.0*	19.6
Among PX	8	2.5	11.6	89.6*	3.1	828.2	56.6
Among SX	35	7.3**	19.2**	86.1**	4.3*	1650.3**	83.7*
Among F ₂	27	7.9**	20.6**	51.6	1.7	1219.4**	93.7*
Reps	3	50.4**	570.1**	370.7**	33.8**	16,213.5**	115.4
Error	297	4.0	7.1	37.7	1.8	432.7	54.8
Total	399						

1/ Mean squares of within groups used to test significance of among groups

** Significant at 1% level

* Significant at 5% level

Appendix Table 8. Mean squares and levels of significance of forage yield and four other variables; tall fescue, Group L, 1964.

Source of Variation	D.F.	Mean Squares and Levels of Significance					
		Plant Spread	Leaf Length	Total Plant Height	Plant Density	Yield per Plant	
		April 29	June 4	June 4	June 5	April 21	June 16
Treatments	118	22.3**	77.2**	71.8**	5.9**	8589.8**	147.3**
Among Groups	5	193.9**	277.5**	171.2*	40.0**	68,821.7**	727.1**
Within Groups ^{1/}	113	14.7**	68.3**	67.4**	4.4**	5924.6**	121.7**
Among Parents	9	73.4**	214.0**	191.5**	10.9**	17,598.8**	404.9**
Among S ₁	9	3.8	117.4**	105.8**	2.8	8910.9**	114.7*
Among OP	9	13.5**	55.5**	32.5	.8	5086.9**	51.6
Among PS	9	9.7**	18.5	37.9	4.7*	1124.5*	111.5
Among SX	44	9.1**	56.9**	50.8*	3.9**	5415.8**	113.7**
Among F ₂	33	10.8**	47.4**	62.4**	4.2**	4143.8**	78.8
Reps	3	3.6	1452.3**	1438.7**	.4	1172.5	154.1
Error	354	3.4	9.8	32.1	2.2	482.8	58.7
Total	475						

^{1/} Mean squares of within groups used to test significance of among groups

** Significant at 1% level

* Significant at 5% level

Appendix Table 9. List of mean squares for single-crosses, general combining ability (GCA) and specific combining ability (SCA) of forage yield and five other variables; tall fescue, Group I, 1963.

Source of Variation	D.F.	Natural		Plant Spread		Leaf Length	Total Plant Height	Yield per Plant			
		Plant Width	Plant Height					May 15	June 17	July 30	Sept. 19
		April 24	April 24	May 28	Sept. 26	June 13	June 13				
Single-crosses	35	6.36**	19.59**	2.26**	5.52**	21.55**	131.53**	103.49**	16.83**	83.74**	88.62**
GCA	8	7.08	47.84**	4.36*	10.88*	48.56**	434.08**	159.80	24.52	232.24**	184.84*
SCA	27	6.15**	11.20**	1.64	3.92*	13.04*	41.88	86.80**	14.56**	39.72*	60.12**
Error	105	2.82	3.89	1.07	2.16	6.72	30.74	28.24	7.41	22.29	24.51

** Significant at 1% level

* Significant at 5% level

Appendix Table 10. List of mean squares for single-crosses, general combining ability (GCA) and specific combining ability (SCA) of forage yield and five other variables; tall fescue, Group L, 1963.

Source of Variation	D.F.	Natural		Plant Spread		Leaf Length	Total Plant Height	Yield per Plant			
		Plant Width	Plant Height					May 17	June 18	July 30	Sept. 20
		April 28	April 28	May 31	Sept. 27	June 17	June 17				
Single-crosses	44	6.50**	141.90**	1.43*	2.33	100.50**	122.02**	244.35**	26.68**	246.74**	202.06**
GCA	9	18.28**	647.72**	1.56	4.88	427.08**	380.76**	857.00**	60.06**	1026.60**	659.88**
SCA	35	3.48*	11.84**	1.40	1.68	12.52**	55.48**	87.52**	18.08**	46.20	84.32**
Error	132	2.00	6.14	.90	1.67	7.78	26.03	24.22	7.88	34.84	41.38

** Significant at 1% level

* Significant at 5% level

Table 11. List of mean squares for single-crosses, general combining ability (GCA) and specific combining ability (SCA) of forage yield and four other variables; tall fescue, Group I, 1964.

Source of Variation	D.F.	Plant Spread	Leaf Length	Total Plant Height	Plant Density	Yield per Plant	
		April 28	June 2	June 2	June 5	April 21	June 15
Single-crosses	35	7.30*	19.24**	86.04**	4.33**	1650.32**	83.69*
GCA	8	14.42*	48.27**	249.40**	8.79*	4702.57**	164.70*
SCA	27	5.19	10.64*	37.69	3.01*	745.96*	59.69
Error	105	3.93	5.41	32.88	1.61	415.36	54.85 <u>1/</u>

1/ General error from combined analysis

** Significant at 1% level

* Significant at 5% level

Table 12. List of mean squares for single-crosses, general combining ability (GCA) and specific combining ability (SCA) of forage yield and four other variables; tall fescue, Group I, 1964.

Source of Variation	D.F.	Plant Spread	Leaf Length	Total Plant Height	Plant Density	Yield per Plant	
		April 29	June 4	June 4	June 5	April 21	June 16
Single-crosses	44	9.06**	56.93**	50.77**	3.88**	5414.76**	113.75**
GCA	9	24.04**	232.76**	113.60**	11.31**	22,976.99**	236.01*
SCA	35	5.20**	11.72*	34.61	1.96	898.76**	82.31*
Error	132	2.46	7.69	25.58	1.89	481.27	51.52

** Significant at 1% level

* Significant at 5% level

Appendix Table 13. Numerical example for the combining ability analysis and derivation of broad- and narrow-sense heritability estimates from expected mean squares for plant width; Group I, 1963. 1/

From Griffing (1956, p. 478)

$$GCA\ SS = \frac{1}{p-2} \sum_i X_{i.}^2 - \frac{4}{p(p-2)} X_{..}^2$$

$$SCA\ SS = \sum_{i < j} \sum X_{ij}^2 - \frac{1}{p-2} \sum_i X_{i.}^2 + \frac{2}{(p-1)(p-2)} X_{..}^2$$

where p = number of parents and SS = sum of squares

Single-cross means in diallel table

Parents	298	299	311	329	359	366	368	374	Total
1. 296	20.2	20.0	21.0	18.4	18.3	19.2	18.8	19.0	154.9
2. 298		18.7	18.9	21.1	16.1	18.8	20.3	20.9	155.0
3. 299			20.6	20.4	21.1	20.3	20.0	19.3	160.4
4. 311				19.6	19.4	18.2	21.9	21.4	161.0
5. 329					20.8	20.1	18.7	19.0	158.1
6. 359						17.9	20.7	17.1	151.4
7. 366							19.4	18.0	151.9
8. 368								19.2	159.0
9. 374									153.9
									1405.6
Total									702.8

Example:

$$\sum_i X_{i.}^2 = (154.9)^2 + (155.0)^2 + \dots + (153.9)^2 = 219,625.56$$

$$X_{..}^2 = (702.4)^2 = 493,365.76$$

$$\sum_{i < j} \sum X_{ij}^2 = (20.2)^2 + (20.0)^2 + \dots + (19.2)^2 = 13,776.52$$

$$\text{GCA SS} = 1/7 (219,625.56) - 4/63 (493,927.84) = 14.58$$

$$\text{SCA SS} = 13,776.52 - 1/7 (219,625.56) + 2/56 (493,927.84) = 41.72$$

Analysis of variance table

Source of Variation	Degrees of Freedom	SS	MS	Expected Mean Squares
Single-Cross	(S _x -1)	35	56.30	1.61**
GCA	p-1	8	14.58	1.82
SCA	p(p-3)/2	27	41.72	1.54**
Error	m	105	74.09	0.71

m = Degrees of freedom for experimental error.

Error mean square used to test significance of single-crosses and SCA.

SCA mean square used to test significance of GCA.

Heritability Estimates:

$$\sigma_s^2 = 1.54 - 0.71 = 0.83$$

$$\sigma_g^2 = (1.82 - 1.54)/p-2 = 0.04$$

$$\text{Total variation} = 2\sigma_g^2 + \sigma_s^2 + \sigma_e^2$$

$$\text{Genetic variance} = 2\sigma_g^2 + \sigma_s^2$$

$$\text{Additive genetic variance} = 2\sigma_g^2$$

$$\text{Genetic variation due to deviation from the additive scheme} = \sigma_s^2$$

$$H_b = \frac{2\sigma_g^2 + \sigma_s^2}{2\sigma_g^2 + \sigma_s^2 + \sigma_e^2} = \frac{2(0.04) + 0.83}{2(0.04) + 0.83 + 0.71} = \frac{0.91}{1.62} = .56$$

$$H_n = \frac{2\sigma_g^2}{2\sigma_g^2 + \sigma_s^2 + \sigma_e^2} = \frac{2(0.04)}{2(0.04) + 0.83 + 0.71} = \frac{0.08}{1.62} = .05$$

1/ Calculated from means instead of from treatment totals as Appendix Tables 5 to 12.