Inheritance of combining ability in bromegrass Bromus inermis Leyss

Dale B. Grissom
Iowa State College

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INHERITANCE OF COMBINING ABILITY IN BROMEGRASS,

BROMUS INERMIS LEYSS.

by

Dale B. Grissom

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of
The Requirements for the Degree of

DOCTOR OF PHILOSOPHY

Major Subject: Crop Breeding

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

Professor in Charge of Farm Crops

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of Graduate College

Iowa State College

1955
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INTRODUCTION

In the improvement of cross-pollinated forage crops by breeding, the major goal is to increase the frequency of desirable gene combinations conditioning important agronomic characters. Prerequisite to progress toward this goal is the need for basic research with respect to the nature of inheritance of important agronomic characteristics. Another requirement is the development of procedures for efficient evaluation of genetic variability and influences of environment on variability. Interrelationships among agronomic characteristics also merit investigation so that simultaneous selection can be judiciously practiced for desired features.

The present study is an attempt to provide information to help clarify some of these problems. For this purpose, topcross progenies of a number of $S_0$ clones of bromegrass and $S_1$ selections from each were evaluated for forage yield, leafiness, disease resistance, and spring vigor in solid stands. Objectives were to determine if combining ability for the various characteristics is inherited, the extent of segregation for combining ability, and the relative degree to which observed variation is inherited. It was also desired to relate previous evaluations of parental $S_0$ and $S_1$ material in a space-planted test and topcross progenies for seedling vigor with mature plant performance in solid seedlings. Other considerations were the effects of inbreeding for one generation
and their relationship to combining ability, and the influences of genetic and environmental factors on extent of intercharacter correlations.

Results which were obtained are presented and discussed in regard to both the aims of the investigation and possible applications to bromegrass breeding.
REVIEW OF PERTINENT LITERATURE

Several good summaries of the literature on the general problems involved in the breeding of naturally cross pollinated forage crops are available. Johnson (12) and Kalton, et al. (15) have given extensive reviews dealing with the importance of evaluation of breeding materials for combining ability. Hawk (6) has presented an extensive review dealing with bromegrass breeding. Consequently, the present review will be limited to pertinent literature dealing with variation in and inheritance of combining ability, relationships among progenies in different tests and years, inbreeding effects, and intercharacter relationships.

Inheritance of Combining Ability

Few studies have been reported on the extent of variation and inheritance of combining ability in perennial forage species seeded in solid stands. Consequently, data from space-planted experiments in forages and from other crops are the major sources of information. Procedures used in studies of combining ability and its inheritance have been developed primarily through research with corn. Results of these investigations provide an insight into what may be expected in forage crops breeding with respect to combining ability.

As early as 1935, Jenkins (10) concluded that combining ability was an inherited characteristic in corn and that it could be determined early
in the inbreeding process. In studies with inbred lines of corn classed as high and low combiners, Johnson and Hayes (13) and Green (2) derived a greater frequency of high combining lines from crosses of high x high than from crosses of either high x low or low x low combiners indicating that combining ability was inherited. Sprague (25) has presented an extensive summary of literature dealing with these and other studies of combining ability and its inheritance in corn.

Differences in combining ability among selections have been noted in many forages. Knowles (17) obtained highly significant differences for forage yield and degree of creeping among 64 strains of bromegrass under space-planted conditions. These differences were evident among single cross, polycross, and open-pollination progenies. Hawk and Wilsie (7) obtained marked differences among yields of open-pollination progenies of S₀, S₁, and S₂ bromegrass plants during three years of study. McDonald, et al. (21) found significant differences in mean performance for yield, height, vigor of growth, and spread among open-pollination progenies of 40 S₀ selections in the same species. In tests of open-pollination progenies of selected S₀ plants, Knowles (18) obtained significant differences for forage yield and seed yield in several of the groups studied in both spaced and solid seeded stands.

In breeding studies with Agropyron intermedium, Heinrichs (8) obtained highly significant differences among clonal lines for all characters studied. Forage yield, seed yield, and winter killing were herit-
able to a lesser extent than vigor and most morphological characters. He concluded that polycross progenies were better than open-pollination progenies for evaluation of general combining ability but open-pollination progeny performance was entirely satisfactory.

Tysdal and Crandall (29) concluded that polycross progeny performance of clones of alfalfa was a good measure of breeding value and was directly related to performance in synthetics. Hoover (9) obtained significant variation in general combining ability among S₀ clones of sweet clover. These and other studies with bromegrass and with other grass and legume crops have demonstrated the existence of variation for combining ability.

Literature dealing with segregation for combining ability during the inbreeding process is not so uniformly agreeable. Jenkins (11) concluded that limited segregation within S₁ populations makes selection within S₁ or later generation inbred lines an undesirable method of isolating new lines of corn. In contrast, Sprague and Bryan (26) reported significant segregation among F₄ lines of corn for combining ability for yield prepotency, lodging, and disease resistance. Lonnquist (19) was successful in altering combining ability during four generations of inbreeding in corn through a recurrent selection program.

The possibilities of improvement through selfing and selection in polyploid species have not been so well defined. Elliott and Love (1) extended this viewpoint following cytological studies with bromegrass
when they stated:

So much segmental interchange, presumably the result of natural selection, decreases the number of potential linkage groups and thus restricts recombination possibilities. ... The meiotic irregularities present in clones of smooth brome grass introduce further limitations in obtaining desirable gene combinations in inbred or cross-bred progenies.

Hawk and Wilsie (7) obtained no significant differences in combining ability between selected S₁ or S₂ clones and their S₀ parents in brome grass.

Knowles (18) found no significant differences in open-pollination progeny performance of 39 inbred selections, nor were the inbred segregates higher in combining ability than selected S₀ plants from commercial varieties. However, Raaher (24) obtained significant differences within seven of 18 S₁ families in topcross performance indicating segregation for combining ability for seedling vigor.

In other forage crops, Hanson, Myers, and Garber (5) presented data which substantiated the fact of significant segregation among inbred lines of orchard grass. Inbred lines were isolated which were better in combining ability than the original selection. They proposed the use of inbred lines as one alternative in an orchard grass improvement program.

Hoover (9) found significant differences among S₁ topcross progenies within two of eight sweet clover families studied. He concluded that the merit of inbreeding depended upon the superiority of the S₁ progenies in comparison with the original population.

The extent to which combining ability is a heritable characteristic
A number of progeny "choses" and 1 to 25 percent for progeny percentage in outcross progeny tests of
the from 0 to 25 percent for early yield, 0 to 15 percent for seed yield.

Heterosis variance ratio, calculated percentages of genetic variance
' (27) in the same study gave a value of 65 percent. Thomas and Kernan
estimated heritability in progenies as about 65 percent. Pecorini under open-pollination

Heterosis (24) estimated heterosis by combining 
progeny's performance, respectively, on the parent of progeny in progeny's

and 84, 100, and 96 percent for degree of breeding from the regression
obtained estimates of heterosis of 12, 14, and 22 percent for yield
various tests of progeny selection. In another study, knowledge of (18) obtained height
applied values ranging from 24 to 65 percent for total production in

heterosis. Observed coxrossed progeny on parent performance, knowledge of (18) observed hetero-

observed generation on parent performance. These is the double regression method, one-

progeny-parent regression method. Using the double regression method, one-

heterosis of yield in progenies in progeny's approximately 22 percent by the

yielding ability of the parent's clone. Modanid, et al. (21) estimated

in outcross progeny yields could be attributed to the differences in
and yields (7) concluded that from 20 to 35 percent of the variance
characters have been somewhat higher. In studies with progeny,

characters have been somewhat higher. In studies with progeny, our

explained heterosis and variance of total, heterosis estimates for yield.

is of great importance in breeding program but little is known re-
In orchardgrass, Kalton and Leffel (14) estimated heritability of general combining ability by the variance ratio method. Spring vigor score, disease score and green forage yield were estimated as 15, 38, and 21 percent, respectively. Values of 53 percent for bloom date and 42 percent for panicle production were also obtained. In crested wheatgrass, Knowles (17) obtained heritabilities ranging from 11 to 20 percent for yield and from 51 to 56 percent for reaction to aphids.

Parent-Progeny and Progeny Test Relationships

Numerous other investigations of parent-progeny and progeny test relationships have been made in forage crops. Hawk and Wilsie (7) and Knowles (17) have given extensive reviews of literature dealing with parent-progeny relationships in bromegrass. The degree of relationship has varied from test to test due to planting method and seasonal interactions. Murphy (22) studied correlation in performance among different types of progenies under different methods of planting for several species of grasses in the same test. All average correlation values were found to be highly significant. He concluded that any of the several planting methods could be used satisfactorily for selection purposes.

Kalton, et al. (15) obtained variable and low correlations for forage yield between parents and outcross progenies in orchardgrass. Correlations were also variable among different types of progenies from the
Group when tested in spaced plants.

was not true, however, for an entire group in broadcast plots or the late

or a late group of clones when tested in broadcast plots. This

when in the greenhouse and subsequent force of outcrossing plot.

Hunsun (25) found a significant correlation between top and

in the investigation. In studies with orchardgrass, otherwise and

results will be correlated with maturity plant yield as expected

obtained were with in clones in combination by seedling

by number (24) in the seedling stage and stembelt variant differences were

Exco selections. Material included in the present study was evaluated

seedling vigor and forage yield by open pollination progeny of clone-

segregates of 0.65 and 0.68 in 1940 but 1947, respectively, between

segment from yield. Hawk and White (7) open pollination co-

few experiments have been reported recently and seedling vigor to sub-

ence for spacing vigor was 0.66.

where there. The correlation between clones and open pollination plots

progeny and clones and open pollination progeny in immediate

iations of 0.91 and 0.98, respectively, between clones and progeny-

Green test procedure. However, the hybrid vigor was highest when means were determined with the

some parents. In general, the correlations in performance among out-

6
respectively. For populations processes of 12 percent of the open-positive
were not selected within the limited situations respectively. They concluded that a range of 100, 99, and 100 percent,
and whistle (7) obtained mean relative yields of 0.9, 0.8, and 2 selections in 
processes have been discussed by several authorities. In tests of open-
relative levels of combining ability under veres non-identical.

Imperative Wences
their $I_4$ progenies. Knowles (17) concluded that non-inbred plants offered greater possibilities as breeding material than inbred plants of Fairway crested wheatgrass.

Only one investigation was noted in forages dealing with inbreeding depression and its relationship to combining ability. Tysdal, et al. (30) obtained a negative but small correlation between yields of inbreds and their hybrids in alfalfa.

Intercharacter Relationships

Relationships between forage yield and factors affecting forage quality have been reported. In bromegrass, Tsiang (28) obtained a significant positive correlation between yield and leaf spot resistance. Grennell (3) reported significant correlations of 0.37 and -0.48 between hay vigor and leaf disease for 161 phenotypically desirable and 48 phenotypically undesirable selections, respectively, in a replicated, space-planted topcross nursery of bromegrass. He also reported correlations of 0.22 and 0.04 between hay vigor and leafiness for the same two groups of material. Leafiness and leaf disease were negatively correlated. The author suggested that the correlation may vary considerably depending upon the population level for the characteristics under study.

Kalton, Smit, and Leffel (16) reported that spring vigor and
leafiness of $S_1$ progenies were strongly associated with first cutting forage yields of orchardgrass in 1950. Kalton, et al. (15) reported disease score and forage yield correlations ranging from low positive to significantly negative in various types of progenies in orchardgrass. Spring vigor score and forage yield were positively correlated. Most of these studies of character relationships have been made under spaced planted conditions. No information on the effect of different planting methods on intercharacter expressions appears available.
MATERIALS AND METHODS

The parental plant material studied in this investigation originated as single plant selections from a space planted nursery of approximately 4500 individuals. This nursery was established in 1944 from seed and consisted of approximately 1500 plants each of the varieties, Fischer, Lincoln, and Achenbach. In the summer of 1946 a total of 252 plants were selected for further evaluation and open-pollinated and selfed seed were collected from each selection. The outcrossed seed from the 252 plants together with four check varieties was seeded in the fall of 1946 in an open-pollination progeny test. The planting was made in a 16 x 16 simple lattice design with two replications. Plots consisted of single 18 foot drilled rows spaced three feet apart. This test will be referred to subsequently as the O.P. progeny row test.

Forage yields were taken in the O.P. progeny row test for three years. Guenther (4) reported results for 1947 and 1948. On the basis of yields in 1948, 40 clones were selected for continuing the study by sampling the range from 21 to 41 pounds and choosing two representatives from each pound increment. In 1949 a new nursery was established consisting of the clonal, open-pollination, and S_1 progenies of the 40 families. The planting plan was a split plot design with families as whole plots. Each whole plot in turn was represented by two S_0 plant propagules, 13 S_1 seedlings, and 13 open-pollination progeny seedlings.
Each whole plot entry was replicated three times. McDonald (20) reported individual plant data from this test for green weight of forage, fall and spring vigor, leafiness, panicle score, height, and spread.

In 1950 a space-planted topcross nursery consisting of 20 of the 40 families studied by McDonald (20) was established by vegetative propagation. Each family in the topcross nursery was represented by the S₀ clone and 20 S₁ selections from each. The S₁ plants were selected in the fall of 1949 from the previous nursery with vigor of growth in the year of establishment as the only criteria of selection. Also included in the topcross nursery were 40 additional S₀ clones which showed promise in previous tests. The topcross nursery was grown in three replications with each replication consisting of spaced single plant plots of each entry. Alternate rows were seeded to the variety, Fischer, which served as the common pollinator. Since the preponderance of pollen available for pollination came from Fischer, it was assumed that the greater portion of seed harvested from individual plants was topcross seed. Equal portions of seed harvested from the three replications of each S₀ and S₁ selection were bulked and served as the seed supply for planting the test presented and discussed herein.

From the 20 families represented in the topcross nursery, topcross progenies of 18 S₀ clones and 10 S₁ selections from each were chosen to be included. The S₁ entries within each family were chosen to represent the entire range of forage yields on an individual plant basis as
recorded by McDonald (20). Two families were discarded because of insufficient topcross seed supplies. In addition, 13 other selected S0 topcross entries and nine named varieties were included to make a total of 220 entries in the test. This test will be referred to hereafter as the topcross progeny test.

The topcross progeny test was arranged in a split-plot design of five replications with families as whole plots and the respective S0 and S1 topcross progenies as subplots. Two additional whole plots contained the 13 extra S0 topcross progenies and the nine named varieties. Replication size was 80 x 110 feet with the exception of the fifth replication which was 55 x 160 feet. Whole plot size averaged 27 1/2 x 16 feet. Individual subplots were 5 x 8 feet with the center 3 x 5 feet harvested for yield. Each subplot was delimited by a single drilled row of alfalfa on all sides of the plot (Figure 1).

The topcross progeny test was seeded in broadcast plots in the spring of 1952 with oats as a companion crop. As a result of an unusually heavy crop of volunteer sweet clover in 1953, the test was kept clipped and no data recorded. Fertilizer was applied in June, 1953, after clipping at the rate of approximately 50 pounds of nitrogen per acre. In March, 1954 the test was fertilized at the rate of approximately 80 pounds of elemental nitrogen per acre. Yield data recorded in 1954 were based on a single cutting made in June of that year. Insufficient moisture made a second harvest impossible. In March, 1955, nitrogen was again applied
Figure 1. A portion of the topcross progeny test showing individual plots surrounded by a single drilled row of alfalfa
at the rate of approximately 80 pounds per acre. Following the first cutting in June, 1955 nitrogen was applied at the rate of 50 pounds per acre and a second harvest was made in August.

All plots were harvested and data recorded for agronomic characters in the following manner:

**Forage yield** - three cuttings were taken, one in 1954 beginning June 22 and two in 1955 beginning June 9 and August 3. Yields were obtained by first removing an 18 inch strip from each end of the plot and then taking a 3 foot cut from the remainder. Green weights were recorded to the nearest 0.1 pounds based on a 15 square foot area.

**Spring vigor** - a composite score based on height, leafiness, and spread taken on May 14, 1954, and ranging from one (little vegetative production) to five (most vegetative production).

**Leafiness** - percentage of total culmage which was leaves. Ten culms with the inflorescence attached were selected at random from the forage harvested from each plot. The leaves were stripped from the culms at the ligule, leaves and culms dried and weighed separately, and leafiness calculated as a percentage of the total weight.

**Leaf disease** - scored as an estimated percent of leaf area killed by disease organisms and recorded at the time of harvest in 1954.
Scores ranged from one (0-10 percent of leaf area dead) to ten (90-100 percent of leaf area dead).\textsuperscript{1}

Analyses of variance of all data were computed according to standard methods. Heritability estimates were obtained by using the progeny-parent regression method of analysis. This method measures the relative degree to which a given characteristic is transmitted from parent to progeny and is defined as heritability in the "narrow sense". It provides a measure of additive genetic variance and is of major importance in segregating populations. To obtain a measure of character relationships, environmental and genetic correlations were calculated using the components of variance method. These correlations were obtained by dividing the appropriate covariances by the geometric mean of the corresponding variances, as outlined by Hoover (9). Performance in the present study also was related to previous results from other tests by use of correlations to provide information on the nature of planting method, seasonal, and progeny test interactions.

\textsuperscript{1}A complex of leaf spotting diseases was present but the major damage appeared to be due to \textit{Pyrenophora bromi} (Died.) Drechsler.
EXPERIMENTAL RESULTS

According to the main objectives set forth for the experiment, the results are presented under four general headings: inheritance of combining ability, combining ability relationships with previous evaluations, effects of inbreeding, and intercharacter relationships. Three topics are discussed under the general heading of inheritance. These consist of $S_0-S_1$ topcross progeny performance, segregation for combining ability, and heritability of combining ability. Two aspects of the effects of inbreeding are considered. The first is the effect of inbreeding on combining ability, and the second is the relationship between inbreeding depression and combining ability. Results pertaining to the other general topics are presented and discussed separately.

Inheritance of Combining Ability

One criterion for determining that combining ability for a given character is inherited is demonstration of significant differences among selections within a heterogenous population when outcrossed to a common tester stock. The type of tester stock used determines the type of combining ability measured. The bromegrass variety, Fischer, which is assumed to be highly heterogenous, was the tester stock for the selections included in this study. Thus, a measure of general combining ability
would be expected.

**S₀-S₁ topcross progeny performance**

As one measure of the inheritance of combining ability for each character studied, individual plot data from topcross progenies of 18 S₀ clones and 10 S₁ selections from each were subjected to standard split-plot analyses of variance. These analyses of variance of forage yield are given individually for each cutting in each year, for total yield in 1955, and for two-year totals on an individual year basis. Analyses of spring vigor scores, leaf disease scores, and leafiness percentage were obtained only for results in 1954. For simplification of presentation, S₀ topcrossed clones and their S₁ topcrossed progenies will be referred to as S₀ clones and S₁ progenies hereafter.

As presented in Tables 1 and 2, analyses of variance of forage yields for individual cuttings, 1955 total, and two-year means show no significant differences among families. On the other hand, in every case highly significant differences were demonstrated among S₁ progenies within families when tested over all families. These results suggest possibly that the range of open-pollination progeny yields of the parental S₀ clones, as reported by Guenther (4), was not a good index of the combining ability of the lines or that the technique used in the topcross progeny test was such that differences could not be detected. Both explanations may have contributed, since family mean yields ranged only from 3.67 to
<table>
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<th>Source of variation</th>
<th>1954</th>
<th>1955</th>
<th>Mean squares</th>
<th>Mean squares</th>
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<tr>
<td></td>
<td></td>
<td></td>
<td>First cutting</td>
<td>Second cutting</td>
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<tr>
<td>Replications</td>
<td>4</td>
<td>30.50**</td>
<td>8.76**</td>
<td>13.49**</td>
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<td>Families</td>
<td>17</td>
<td>3.30</td>
<td>1.44</td>
<td>0.47</td>
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<tr>
<td>Error (a)</td>
<td>68</td>
<td>2.61</td>
<td>1.24</td>
<td>0.53</td>
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<td>S₀ vs. S₁</td>
<td>1</td>
<td>8.03**</td>
<td>0.01</td>
<td>0.44*</td>
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<td>S₁ progenies within families</td>
<td>162</td>
<td>0.37**</td>
<td>0.18**</td>
<td>0.08**</td>
</tr>
<tr>
<td>S₀ vs. S₁ x families</td>
<td>17</td>
<td>0.39*</td>
<td>0.23*</td>
<td>0.05</td>
</tr>
<tr>
<td>Error (b)</td>
<td>720</td>
<td>0.18</td>
<td>0.10</td>
<td>0.03</td>
</tr>
<tr>
<td>S₀ vs. S₁ x replications</td>
<td>4</td>
<td>0.36</td>
<td>0.17</td>
<td>0.04</td>
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<tr>
<td>S₁ progenies within families x replications</td>
<td>648</td>
<td>0.18</td>
<td>0.10</td>
<td>0.03</td>
</tr>
<tr>
<td>S₀ vs. S₁ x families x replications</td>
<td>68</td>
<td>0.19</td>
<td>0.12</td>
<td>0.03</td>
</tr>
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* Significant at the 5% level
** Significant at the 1% level
Table 2. Analysis of variance of two-year forage yields of topcross progenies of 18 S₀ clones of bromegrass and 10 S₁ segregates from each in 1954 and 1955 (single year basis)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>D.F.</th>
<th>Mean square</th>
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<tr>
<td>Total</td>
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<td></td>
</tr>
<tr>
<td>Replications</td>
<td>4</td>
<td>58.00**</td>
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<td>Families</td>
<td>17</td>
<td>4.37</td>
</tr>
<tr>
<td>Error (a)</td>
<td>68</td>
<td>4.63</td>
</tr>
<tr>
<td>S₀ vs. S₁</td>
<td>1</td>
<td>6.41*</td>
</tr>
<tr>
<td>S₁ progenies within families</td>
<td>162</td>
<td>0.38**</td>
</tr>
<tr>
<td>S₀ vs. S₁ x families</td>
<td>17</td>
<td>0.39</td>
</tr>
<tr>
<td>Error (b)</td>
<td>720</td>
<td>0.24</td>
</tr>
<tr>
<td>S₀ vs. S₁ x replications</td>
<td>4</td>
<td>0.39</td>
</tr>
<tr>
<td>S₁ progenies within families x replications</td>
<td>648</td>
<td>0.24</td>
</tr>
<tr>
<td>S₀ vs. S₁ x families x replications</td>
<td>68</td>
<td>0.30</td>
</tr>
<tr>
<td>Years</td>
<td>1</td>
<td>90.58</td>
</tr>
<tr>
<td>Years x replications</td>
<td>4</td>
<td>7.68</td>
</tr>
<tr>
<td>Years x families</td>
<td>17</td>
<td>1.37</td>
</tr>
<tr>
<td>Years x families x replications</td>
<td>68</td>
<td>0.93</td>
</tr>
<tr>
<td>Remainder</td>
<td>900</td>
<td>0.14</td>
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* Significant at the 5% level
** Significant at the 1% level
4.29 pounds per plot when averaged over 55 plots each for two years.

The analysis of variance for spring vigor score appears in Table 3. Highly significant differences were indicated among families for this character. Differences significant at the one percent level were also demonstrated among S₁ progenies when tested over all families. Visual observations among named varieties included in the test indicated the so-called "southern strains" of bromegrass showed more early spring growth than "northern strains". These results suggest that genetic differences in combining ability for early spring growth do exist in bromegrass.

Differences among families and among S₁ progenies within families for leaf disease score were both significant at the one percent level in 1954 (see Table 3). Disease scores were not taken in 1955, since leaf infection was very meager as compared to 1954. Means for leafiness percentage ranged from 15.9 to 21.5 percent for all entries. Mean squares for leafiness percentages are given in Table 3. No significant differences could be shown among families for leafiness; however, differences significant at the one percent level were demonstrated among S₁ progenies when all families were considered.

Analyses of variance of the two additional whole plots included in the topcross progeny test showed no significant differences among S₀ topcrossed clones for forage yield. However, mean forage yields for these additional clones were equal to the mean of the highest yielding
Table 3. Analysis of variance of spring vigor scores, leaf disease scores, and leafiness percentage of topcross progenies of 18 $S_0$ clones of bromegrass and 10 $S_1$ segregates from each in 1954

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>D.F.</th>
<th>Mean squares</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Spring vigor score</td>
</tr>
<tr>
<td>Total</td>
<td>989</td>
<td>3.22*</td>
</tr>
<tr>
<td>Replications</td>
<td>4</td>
<td>3.22*</td>
</tr>
<tr>
<td>Families</td>
<td>17</td>
<td>2.57**</td>
</tr>
<tr>
<td>Error (a)</td>
<td>68</td>
<td>0.99</td>
</tr>
<tr>
<td>$S_0$ vs. $S_1$</td>
<td>1</td>
<td>0.02</td>
</tr>
<tr>
<td>$S_1$ progenies within families</td>
<td>162</td>
<td>0.41**</td>
</tr>
<tr>
<td>$S_0$ vs. $S_1$ x families</td>
<td>17</td>
<td>0.24*</td>
</tr>
<tr>
<td>Error (b)</td>
<td>720</td>
<td>0.14</td>
</tr>
<tr>
<td>$S_0$ vs. $S_1$ x replications</td>
<td>4</td>
<td>0.05</td>
</tr>
<tr>
<td>$S_1$ progenies within families x replications</td>
<td>648</td>
<td>0.14</td>
</tr>
<tr>
<td>$S_0$ vs. $S_1$ x families x replications</td>
<td>68</td>
<td>0.13</td>
</tr>
</tbody>
</table>

* Significant at the 5% level
** Significant at the 1% level
clonal family in the test. Differences in forage yield, significant at the one percent level, were demonstrated among named varieties. Southern strains gave the highest yields. Differences were also demonstrated among entries included as checks for spring vigor, leaf disease, and leafiness percentage. Northern strains gave the lowest spring vigor scores, below average scores for disease reaction, and the lowest leafiness percentages.

**Segregation for combining ability**

Topcrosses of 10 $S_1$ selections within each of the 18 families were studied to determine if segregation for combining ability occurs in bromegrass. Yield data for progenies of the $S_1$ segregates from each family were analyzed for individual cuttings, for total yield in 1955, and for two-year mean yields. $F$ values from these individual analyses of the 18 clonal families are given in Table 4. Six of the 18 families showed significant differences for forage yield among $S_1$ progenies within families in 1954. Three were significant at the five percent level and three at the one percent level. Four other families gave $F$ values approaching the five percent level of significance.

Data from first cutting forage yields in 1955 show significant differences in five of the 18 families studied. Three of the families reached the one percent level of significance. Second cutting forage yields in 1955 followed the same general pattern as first cutting yields
Table 4. F values from analyses of variance of forage yields of topcross progenies of S₁ segregates from 18 individual clonal families

<table>
<thead>
<tr>
<th>Clonal family</th>
<th>1954 First cutting</th>
<th>1955 Second cutting</th>
<th>Total</th>
<th>Two-year mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>391</td>
<td>2.36*</td>
<td>0.78</td>
<td>1.71</td>
<td>0.98</td>
</tr>
<tr>
<td>396</td>
<td>1.17</td>
<td>1.00</td>
<td>0.77</td>
<td>0.75</td>
</tr>
<tr>
<td>401</td>
<td>2.62*</td>
<td>0.40</td>
<td>0.31</td>
<td>0.50</td>
</tr>
<tr>
<td>420</td>
<td>1.83</td>
<td>2.29*</td>
<td>4.60**</td>
<td>2.96**</td>
</tr>
<tr>
<td>450</td>
<td>2.06</td>
<td>5.36**</td>
<td>4.95**</td>
<td>3.58**</td>
</tr>
<tr>
<td>455</td>
<td>0.98</td>
<td>2.99**</td>
<td>0.86</td>
<td>1.33</td>
</tr>
<tr>
<td>478</td>
<td>1.26</td>
<td>2.88*</td>
<td>1.51</td>
<td>2.06</td>
</tr>
<tr>
<td>482</td>
<td>0.58</td>
<td>1.18</td>
<td>2.74*</td>
<td>1.78</td>
</tr>
<tr>
<td>503</td>
<td>1.06</td>
<td>1.51</td>
<td>2.48*</td>
<td>1.59</td>
</tr>
<tr>
<td>505</td>
<td>3.03**</td>
<td>0.36</td>
<td>2.07</td>
<td>0.69</td>
</tr>
<tr>
<td>510</td>
<td>1.40</td>
<td>3.70**</td>
<td>3.22**</td>
<td>2.58*</td>
</tr>
<tr>
<td>526</td>
<td>7.61**</td>
<td>0.29</td>
<td>0.63</td>
<td>0.25</td>
</tr>
<tr>
<td>527</td>
<td>1.21</td>
<td>0.65</td>
<td>0.53</td>
<td>0.48</td>
</tr>
<tr>
<td>529</td>
<td>3.02**</td>
<td>0.63</td>
<td>1.18</td>
<td>0.82</td>
</tr>
<tr>
<td>530</td>
<td>2.19*</td>
<td>1.22</td>
<td>1.04</td>
<td>0.92</td>
</tr>
<tr>
<td>538</td>
<td>2.06</td>
<td>2.00</td>
<td>2.18*</td>
<td>1.42</td>
</tr>
<tr>
<td>567</td>
<td>2.02</td>
<td>1.57</td>
<td>1.10</td>
<td>1.01</td>
</tr>
<tr>
<td>570</td>
<td>1.97</td>
<td>0.80</td>
<td>2.58*</td>
<td>0.42</td>
</tr>
</tbody>
</table>

*Significant at the 5% level  
**Significant at the 1% level
with seven families showing significant differences. Three of these were the same ones showing significant differences in the first cutting. Analyses of variance of 1955 total yields show only three families indicating segregation for combining ability for forage production. The same was true for two-year mean yields. Results indicate that had evaluations been more critical, possibly either by increasing precision of the test or by increasing numbers of \( S_1 \) progenies within families, more definite conclusions could be drawn regarding segregation for combining ability for forage yield.

From the standpoint of genetic advance through selfing, only Family 450 contained \( S_1 \) segregates which were significantly better in combining ability for forage yield than the \( S_0 \) mother clone. Four families showed \( S_1 \) segregates which were significantly poorer in combining ability than the \( S_0 \) mother clone. They were Families 420, 505, 528, and 529.

Table 5 shows \( F \) values calculated from the analyses of individual families for spring vigor score, leaf disease score, and leafiness percentage. Ten of the 18 families studied showed significant differences among \( S_1 \) progenies for spring vigor score. Six of the ten families demonstrated differences significant at the one percent level. A large portion of the variation obtained in leaf disease scores appeared attributable to variation among families. Only one family showed significant differences among \( S_1 \) progenies for this character. Analyses of variance results indicate that at least seven families were segregating for
Table 5. F values from analyses of variance of spring vigor score, leaf disease score and leafiness percent of topcross progenies of S1 segregates from 18 individual clonal families in 1954

<table>
<thead>
<tr>
<th>Clonal family</th>
<th>Spring vigor score</th>
<th>Leaf disease score</th>
<th>Leafiness (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>391</td>
<td>5.67*</td>
<td>1.41</td>
<td>1.29</td>
</tr>
<tr>
<td>396</td>
<td>1.87</td>
<td>0.89</td>
<td>1.73</td>
</tr>
<tr>
<td>401</td>
<td>1.11</td>
<td>1.26</td>
<td>2.85*</td>
</tr>
<tr>
<td>420</td>
<td>1.80</td>
<td>1.74</td>
<td>1.41</td>
</tr>
<tr>
<td>450</td>
<td>10.57**</td>
<td>5.21**</td>
<td>2.06</td>
</tr>
<tr>
<td>455</td>
<td>1.46</td>
<td>1.47</td>
<td>2.61*</td>
</tr>
<tr>
<td>478</td>
<td>1.93</td>
<td>1.28</td>
<td>1.35</td>
</tr>
<tr>
<td>482</td>
<td>3.86**</td>
<td>0.73</td>
<td>5.96**</td>
</tr>
<tr>
<td>503</td>
<td>2.00</td>
<td>1.80</td>
<td>1.83</td>
</tr>
<tr>
<td>505</td>
<td>4.08**</td>
<td>0.67</td>
<td>3.26**</td>
</tr>
<tr>
<td>510</td>
<td>2.16*</td>
<td>1.35</td>
<td>2.08</td>
</tr>
<tr>
<td>526</td>
<td>2.71*</td>
<td>1.22</td>
<td>1.95</td>
</tr>
<tr>
<td>527</td>
<td>3.62**</td>
<td>0.76</td>
<td>0.98</td>
</tr>
<tr>
<td>529</td>
<td>3.14**</td>
<td>1.15</td>
<td>1.41</td>
</tr>
<tr>
<td>530</td>
<td>0.33</td>
<td>0.21</td>
<td>2.44*</td>
</tr>
<tr>
<td>538</td>
<td>2.43*</td>
<td>1.95</td>
<td>2.49*</td>
</tr>
<tr>
<td>567</td>
<td>1.80</td>
<td>0.47</td>
<td>1.65</td>
</tr>
<tr>
<td>570</td>
<td>2.36*</td>
<td>1.60</td>
<td>5.64**</td>
</tr>
</tbody>
</table>

* Significant at the 5% level
** Significant at the 1% level
I suspect that the parent-progeny correlation obtained for forage yield

It was found that the techniques used in the experiment. It was

correlation as to what portion of the correlation

parent-progeny correlation could be shown between parents and

progeny for survival score, mean disease score, and test

versus, no significant correlation were significant at the one percent level. Con-

trary to these results, the disease scores for forage yield were significant at the one percent level in

presented in Table 6. All correlations between 50 clones and 51 progeny

correlation coefficients between parent and progeny means also were

and 15 percent, respectively.

This disease score and test results were very low with values of 16

heritability value of 46 percent for survival score. Estimates for

two-year means. Regression of Si progeny on 50 clones gave a

appear in Table 6. Values ranged from 40 percent in 1984 to 65 percent

heritability estimate. Genetic gains of forage yield

on the mean obtained show the regression on the variety's potential on

is not expected that crosses selected from a common tester would have any effect

heritability estimate on parent expressed as a percentage value. It

by the regression method where heritability equals the regression co-

heritability estimates for the various characters were calculated.

heritability of combining ability

If values approaching the five percent level of significance

combining ability for test scores percentage. Several other characters have
Table 6. Parent-progeny correlations and regression of $S_1$ family means on $S_0$ parents based on topcross progeny performance in 1954 and 1955

<table>
<thead>
<tr>
<th>Character</th>
<th>&quot;r&quot;</th>
<th>&quot;p&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forage yield</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1954</td>
<td>0.60**</td>
<td>0.40</td>
</tr>
<tr>
<td>1955</td>
<td>0.63**</td>
<td>0.47</td>
</tr>
<tr>
<td>two-year mean</td>
<td>0.65**</td>
<td>0.48</td>
</tr>
<tr>
<td>Spring vigor score</td>
<td>0.45</td>
<td>0.46</td>
</tr>
<tr>
<td>Leaf disease score</td>
<td>0.42</td>
<td>0.16</td>
</tr>
<tr>
<td>Leafiness (%)</td>
<td>0.31</td>
<td>0.19</td>
</tr>
</tbody>
</table>

** Significant at the 1% level for 16 D.F.

and spring vigor were influenced to some degree by techniques involved in the use of the split-plot design.

Combining Ability Relationships with Previous Evaluations

In addition to providing information on inheritance of combining ability, the present investigation was designed to compare performance in solid stands with previous evaluations of the parental material in spaced or row plantings. Correlations involving these comparisons are summarized in Table 7. They provide an insight into the problems facing the forage breeder in evaluation of selected parent material, as
Table 7. Correlations of agronomic performance in the present study with previous evaluations of the same clonal families using different planting methods and progeny types

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S₀</em> topcrosses (solid seeded) and:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parental <em>S₀</em> clones (3-foot spacing) 1950</td>
<td>0.16</td>
<td>0.41</td>
<td>0.33</td>
<td>-0.11</td>
<td>-0.24</td>
</tr>
<tr>
<td>Parental <em>S₀</em> clones (tiller bed) 1951</td>
<td>0.14</td>
<td>0.28</td>
<td>0.25</td>
<td>-0.35</td>
<td>0.15</td>
</tr>
<tr>
<td>O.P. progenies (3-foot spacing) 1950</td>
<td>-0.12</td>
<td>0.34</td>
<td>0.08</td>
<td>-0.22</td>
<td>-0.36</td>
</tr>
<tr>
<td>O.P. progenies (3-foot drilled rows) 1947-50 mean</td>
<td>0.45*</td>
<td>-0.28</td>
<td>0.20</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S₁</em> topcrosses (solid seeded) and:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>S₁</em> progenies (3-foot spacing) 1950</td>
<td>0.03</td>
<td>0.05</td>
<td>0.04</td>
<td>0.27</td>
<td>0.10</td>
</tr>
</tbody>
</table>

* Significant at the 5% level for 26 D.F. for *S₀* topcrosses and 16 D.F. for *S₁* topcrosses
Correlations were Generally Low and Variable between Methods of Evaluating Yields of Topcross Progenies in Solid Seedbeds and Open-Pollinated Progeny Rows for Sprouting Yields and Topcross Progenies of 50 Clone Studies. Similar results were Obtained for Yields for All Yields, Total Correlation between Open-Pollinated Progeny Rows and Topcross Progenies of 50 Clone Studies, However, there were no Positive Correlations Obtained between Parent Material from Different Years and Tests.

Correlations Generally were Low and Variable between Methods of Evaluating Yields of Topcross Progenies in Solid Seedbeds and Open-Pollinated Progeny Rows for Sprouting Yields and Topcross Progenies of 50 Clone Studies. Similar results were Obtained for Yields for All Yields, Total Correlation between Open-Pollinated Progeny Rows and Topcross Progenies of 50 Clone Studies, However, there were no Positive Correlations Obtained between Parent Material from Different Years and Tests.
calculated between seedling yields and mature plant yields in an effort to study possibilities of a more rapid method of evaluating parental material for combining ability for forage yield. A highly significant "r" value of 0.25 was obtained when all entries in the test were considered individually. On a family mean basis, a non-significant correlation of 0.19 was obtained. Although a highly significant correlation was obtained in the first instance, the value of seedling yields in predicting mature plant yields appears to be small.

**Inbreeding Effects**

Relative levels of combining ability were studied in the S₀ and S₁ generations of plant selections included in this study to determine the effects of inbreeding for one generation on combining ability. In the analyses of variance for the various characters studied, a mean square was calculated comparing S₀ clones and S₁ progenies on a mean basis.

**Effects of inbreeding on combining ability**

In Tables 1 and 2, significant differences were shown between the mean of all S₀ clones and the mean of all S₁ progenies for forage yield. In each case the mean yield of S₀ clones was significantly higher than that of S₁ progenies. No significant differences could be demonstrated between S₀ and S₁ performance for forage yield for the first cutting in 1955 and for total forage yield the same year. A significant interaction
of families x generations in 1954 indicated that all families did not produce segregates which were significantly poorer in combining ability for forage yield than the mother clones. Individual family means of \( S_0 \) clones and \( S_1 \) progenies for forage yield are presented in Table 8. Families 401, 450, 538, and 570 produced segregates which were somewhat higher in mean forage yield than the \( S_0 \) mother clones. The other 14 families were lower in yield giving a grand mean of \( S_0 \) clones and \( S_1 \) progenies of 4.19 and 3.99 pounds per plot, respectively.

No significant differences were shown between \( S_0 \) clones and \( S_1 \) progenies for spring vigor scores. A significant interaction of families x generations (see Table 3) indicates that all families did not perform the same for early spring growth. The grand means for spring vigor scores of \( S_0 \) clones and \( S_1 \) progenies were 2.94 and 2.93, respectively.

Leaf disease scores of \( S_1 \) progeny means were significantly better than \( S_0 \) clonal means, as shown in Table 8. Here again a significant interaction of families x generations, as presented in Table 3, showed that all families did not perform the same for leaf disease resistance. Families 396, 401, 450, 503, and 567 gave lower disease scores for the \( S_0 \) clones than for means of \( S_1 \) progenies. The grand means for \( S_0 \) clones and \( S_1 \) progenies were 4.18 and 3.93, respectively, for leaf disease score.

No significant difference was indicated between \( S_0 \) clones and \( S_1 \)
Table 8. Mean performance of \( S_0 \) and \( S_1 \) topcross progenies for forage yield, spring vigor score, leaf disease score and leafiness percentage

<table>
<thead>
<tr>
<th>Clonal families</th>
<th>Forage yield two year mean</th>
<th>Spring vigor score</th>
<th>Leaf disease score</th>
<th>Leafiness (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( S_0 )</td>
<td>( S_1 )</td>
<td>( S_0 )</td>
<td>( S_1 )</td>
</tr>
<tr>
<td>391</td>
<td>3.89</td>
<td>3.79</td>
<td>3.0</td>
<td>2.9</td>
</tr>
<tr>
<td>396</td>
<td>3.95</td>
<td>3.65</td>
<td>3.0</td>
<td>2.7</td>
</tr>
<tr>
<td>401</td>
<td>3.81</td>
<td>3.86</td>
<td>3.0</td>
<td>3.1</td>
</tr>
<tr>
<td>420</td>
<td>4.55</td>
<td>4.25</td>
<td>3.2</td>
<td>3.1</td>
</tr>
<tr>
<td>450</td>
<td>4.13</td>
<td>4.16</td>
<td>2.8</td>
<td>3.3</td>
</tr>
<tr>
<td>455</td>
<td>4.57</td>
<td>4.04</td>
<td>3.4</td>
<td>3.1</td>
</tr>
<tr>
<td>478</td>
<td>3.81</td>
<td>3.66</td>
<td>2.6</td>
<td>2.7</td>
</tr>
<tr>
<td>482</td>
<td>3.93</td>
<td>3.86</td>
<td>2.8</td>
<td>2.7</td>
</tr>
<tr>
<td>503</td>
<td>3.97</td>
<td>3.92</td>
<td>3.0</td>
<td>3.0</td>
</tr>
<tr>
<td>505</td>
<td>4.39</td>
<td>4.00</td>
<td>3.0</td>
<td>2.9</td>
</tr>
<tr>
<td>510</td>
<td>4.61</td>
<td>4.25</td>
<td>3.2</td>
<td>2.9</td>
</tr>
<tr>
<td>526</td>
<td>4.35</td>
<td>4.00</td>
<td>2.8</td>
<td>2.8</td>
</tr>
<tr>
<td>527</td>
<td>4.22</td>
<td>3.73</td>
<td>2.8</td>
<td>2.5</td>
</tr>
<tr>
<td>529</td>
<td>4.31</td>
<td>3.96</td>
<td>2.6</td>
<td>2.8</td>
</tr>
<tr>
<td>530</td>
<td>4.31</td>
<td>4.09</td>
<td>3.0</td>
<td>3.0</td>
</tr>
<tr>
<td>538</td>
<td>3.92</td>
<td>4.16</td>
<td>2.8</td>
<td>3.2</td>
</tr>
<tr>
<td>567</td>
<td>4.48</td>
<td>4.24</td>
<td>2.8</td>
<td>2.7</td>
</tr>
<tr>
<td>570</td>
<td>4.18</td>
<td>4.20</td>
<td>3.2</td>
<td>3.2</td>
</tr>
<tr>
<td>Mean</td>
<td>4.19</td>
<td>3.99*</td>
<td>2.94</td>
<td>2.93</td>
</tr>
</tbody>
</table>

* Grand mean of \( S_1 \) differs significantly from mean of \( S_0 \) at the 5% level
progenies for leafiness percentage. Grand means were 18.27 and 18.46 percent, respectively, for \(S_0\) clones and \(S_1\) progenies.

**Inbreeding depression as related to combining ability**

McDonald (20) recorded yields of inbred plants and calculated inbreeding depression for the \(S_1\) progeny selections included in this investigation. Correlations between \(S_1\) plant yields in percent of \(S_0\) plant yields and \(S_0\) topcross yields were all negative, as shown in Table 9. The range was from -0.04 to -0.44, with the latter value significant at the five percent level. Correlations between yield of \(S_1\) plants in percent of open-pollination progeny yields and \(S_0\) topcross yields were somewhat variable with a range from low positive to moderately negative. A correlation of -0.29 was obtained between \(S_1\) in percent of open-pollination progenies and two-year means of topcross yields. Correlations between \(S_1\) plant yields and \(S_0\) topcross yields were also variable but the trend was in the negative direction. None, however, reached a level of statistical significance.

**Intercharacter Relationships**

Interrelationship of characters is an important consideration in an overall selection program in the improvement of plant species. Associations exhibited in solid seedings are of particular importance, since little information is available for such conditions. Environmental,
Table 9. Correlations between yield measurements of inbreeding depression and topcross performance of 28 $S_0$ clones in 1954 and 1955

<table>
<thead>
<tr>
<th>Relationship</th>
<th>1954</th>
<th>1955</th>
<th>1954-55 means</th>
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<tr>
<td>$S_1$ in percent of $S_0$ and:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$S_0$ topcrosses</td>
<td>-0.44*</td>
<td>-0.04</td>
<td>-0.36</td>
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<tr>
<td>$S_1$ in percent of O.P. and:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$S_0$ topcrosses</td>
<td>-0.29</td>
<td>0.06</td>
<td>-0.20</td>
</tr>
<tr>
<td>$S_1$ progenies and:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$S_0$ topcrosses</td>
<td>-0.34</td>
<td>0.17</td>
<td>-0.18</td>
</tr>
</tbody>
</table>

* Significant at the 5% level for 26 D.F.

Phenotypic, and genetic correlations among characters studied herein are presented in Table 10.

A positive genetic correlation was obtained between forage yield and leafiness percentage. However, the environmental correlation showed an offsetting effect giving a phenotypic correlation of about zero. Almost no genetic correlation was evident between forage yield and leaf disease infection. The environmental correlation indicates that conditions which increase forage yield also tend to increase the incidence of leaf disease. Significantly positive environmental and phenotypic correlations were obtained between forage yield and early spring growth. A moderately high
Table 10. Environmental, phenotypic, and genetic correlations among characteristics measured in 1954

<table>
<thead>
<tr>
<th>Characters correlated</th>
<th>Environmental correlation</th>
<th>Phenotypic correlation</th>
<th>Genetic correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forage yield and:</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Leafiness (%)</td>
<td>-0.31**</td>
<td>-0.01</td>
<td>0.28</td>
</tr>
<tr>
<td>Leaf disease score</td>
<td>0.25**</td>
<td>0.13</td>
<td>0.01</td>
</tr>
<tr>
<td>Spring vigor score</td>
<td>0.55**</td>
<td>0.46**</td>
<td>0.41</td>
</tr>
<tr>
<td>Leafiness (%) and:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf disease score</td>
<td>-0.13</td>
<td>-0.18**</td>
<td>-0.24</td>
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<tr>
<td>Spring vigor score</td>
<td>-0.25**</td>
<td>0.09</td>
<td>0.30</td>
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<tr>
<td>Leaf disease score and:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring vigor score</td>
<td>0.16*</td>
<td>0.25**</td>
<td>0.34</td>
</tr>
</tbody>
</table>

* Significant at the 5% level for 218 D.F.
** Significant at the 1% level for 218 D.F.
genetic correlation also was obtained between the same characters.

Leafiness percentage and leaf disease were negatively correlated, indicating that as disease increased the leaf-stem ratio decreased. The genetic correlation between leafiness percent and spring vigor was positive but a negative environmental correlation reduced the phenotypic correlation to a low level. Leaf disease score and spring vigor score were positively correlated. This may have been the result of more favorable moisture conditions for development of disease in those progenies which were actively growing early in the spring.

From the standpoint of genetic advance through selection, the genetic correlation between leaf disease and spring vigor appeared to be the only association of a deleterious nature in a selection program. The genetic correlations between other characters were either of no consequence or in the desired direction.
in the present study.

It appears that only a sample of the possible concepts were examined. Even though the post-test was not designed to measure the extent that the initial evaluation of the concepts for the computer aptitude attitude is influenced, a force of total results, based on family means, suggests that computer instruction percentage, if done not preceded the support of an instructional content on the computer aptitude attitude in demonstrating could be demonstrated among families for force yield and difference in content aptitude over existing deep exact. Although on the other hand, the results were obtained during induction rather than instruction that general agreement to the various character.

In the present investigation, a number of topics were tested in the present investigation at the computer aptitude when proposed tested in the presence of potential value in a prospective improvement program, as—

DISCUSSION
forage yield of individual families were obtained among cuttings. Since 1954 and 1955 were exceedingly dry years, environmental influences may have tended to restrict the expression of the genetic constitution of individual selections thus resulting in smaller differences than would normally be expected.

In the combined analysis of variance for the two-year forage yields, a mean square for years was calculated. There appears to be no valid error term for a test of significance for years. Consequently, only an estimate can be made. It would appear that a significant difference was obtained between years in the topcross progeny test with yields in 1955 below those in 1954. The mean yields were 4.24 and 3.42 pounds per plot for the first and second year, respectively. On an individual entry basis, the correlation between years in the topcross progeny test was highly significant (r = 0.39) but only moderate in predictive value. As a result of the value obtained, somewhat variable yield results would be expected. As stated by Murphy (22), a correlation of unity cannot be obtained as long as experimental error is present. No information is available as to the portion of the value from 0.39 to unity which was due to experimental error and that which was due to interaction of selections x years.

Statistically significant differences also were obtained among progenies within a number of families for spring vigor score, leaf disease score, and leafiness percentage. These results also indicate that
segregation for combining ability occurs in bromegrass.

Another aspect of the present study was to obtain estimates of heritability for combining ability. It was thought that the split-plot arrangement would provide a reasonably precise test of the concept that $S_0$ and mean $S_1$ evaluations of combining ability should be similar for each family. Mean squares for families in the whole plot analysis would indicate that leaf disease and spring vigor scores exhibited a higher heritability in the "broad sense" than leafiness and forage yield. Analyses of individual families indicated that spring vigor and leafiness were more heritable. The interactions of families x generations showed leafiness percentage and forage yield were more influenced by the genetic background. Heritability estimates in the "narrow sense", based on regression of $S_1$ means on $S_0$, showed spring vigor and forage yield to be more heritable than leaf disease or leafiness percentage. These apparent discrepancies may be explained on the basis of differential environmental correlations among entries within whole plots as compared to that among whole plots within a replication. The correlations between $S_0$ topcrossed clones and $S_1$ topcrossed progenies may have been influenced in the same manner. However, no confirming data are available on this subject.

Several possible sources of bias may have been introduced into the determination of leafiness percentage since only culms which possessed an inflorescence were chosen. There may have been a difference in leaf percentages of headed and non-headed culms. There may also have been a
difference in the ratio of headed to non-headed culms among topcrossed selections entered in the test. Variation in maturity and fertility could have affected leaf percentage through its influence on total culm weight. More information should be obtained on these points in the following years when seed setting is studied for this group of selections.

Associations in performance between the present and previous studies were disappointing from a breeding standpoint. The correlations between progenies in space-planted tests and topcrossed progenies in the solid seeded test generally were low and variable. The correlation values would indicate that tests of spaced $S_0$ plants and their open-pollination progenies, either spaced or in cultivated rows, are not reliable indicators of combining ability for the characteristics studied. Consequently, it emphasizes the point that combining ability should be evaluated under conditions as similar as possible to the way in which the crop is normally grown. Because of the heavy volunteer crop of sweet clover the first year after seeding of the topcross test, no yield results were recorded. There may have been a higher correlation between the seedling yields reported by Raebel (24) and first year topcross forage yields than between seedling yields and second and third year yields, as reported in this study.

No information is available as to why the $S_1$ topcross progenies gave forage yields significantly less than $S_0$ topcrossed mother clones in three out of five analyses. A possible explanation may be the presence
of greater amounts of selfed seed in $S_1$ than $S_0$ seed lots used to plant
the topcross progeny test. If outcrossed seedlings did not eliminate all
selfed plants, then a reduction in forage yield would be expected. If
equal amounts of selfed seed were present, then a reduced yield would be
expected on the basis of number of times selfed in the two groups. $S_0$
topcrossed clones showed significantly more leaf disease infection than
$S_1$ topcross progenies. This may be related to the correlation between
leaf disease and forage yield. Since a significantly positive environ-
mental correlation was obtained between the two characters, it would be
expected that disease would increase as forage yield increases.

The results relating inbreeding depression and combining ability
suggest that overdominance may at least be a partial explanation for
heterosis in bromegrass. There was a tendency for the lower yielding
inbred lines to give the better outcross progenies. Lines showing the
greatest inbreeding depression often gave the better topcrosses. This
also may be explained on the basis of overdominance. These results are
in agreement with Knowles (17) who observed that specific combining abil-
ity was more important than general combining ability in studies of
diallel crosses in bromegrass. However, much more data should be col-
lected and studied before definite conclusions can be made on this point.

Genetic correlations between characters measured in the topcross
progeny test were all of no consequence or in the desired direction for
efficient selection except one. A positive genetic correlation was
The formula was:

\[
Y = a + bX
\]

In another whole plot of a split plot design, the formula was:

\[
\left( \frac{2s^2}{\frac{d_2 - d_1}{d_1 - d_2}} + \frac{1}{d_1 - d_2} \right) \frac{sn}{1} = b - \frac{L}{X - L}
\]

In addition to calculating the standard error of the mean difference between the characters measured, a formula was developed for the characters measured before setting up the design. The formula for a number of characters measured before setting up the design was:

\[
Y_{\text{predicted}} = a + bX
\]

For combining ability and population studies through selection and recombinant selection studies, the formula to determine the genetic improvement of characters observed from the results of-3 bits of genetic improvement is needed in the form of crop breeding as to the post-springing vektor, but that correlates with total forage yield. However, the same was true for forage yield and tonnage. Early spring growth was a negative environment correlation. However, the genetic correlation was positive and in the desired direction. The formula that showed a negative environment correlation was:

\[
Y_{\text{predicted}} = a + bX
\]

The formula used was:

\[
Y = a + bX
\]

To be determined to stimulate selection for forage quality, good com-
R = number of replications

D₁ = number of levels of a whole plot treatment which one desires to consider

D₂ = number of levels of another whole plot treatment which one desires to consider

\( \bar{x}_1 \) = mean of levels of whole plot treatment which one desires to consider

\( \bar{x}_2 \) = mean of levels of another whole plot treatment which one desires to consider

With the proper weighting of "t", differences necessary for significance at the five and one percent level were calculated for each character measured in the test. Results of these calculations are given in the footnotes of Appendix Table II.

Considering the practical breeding aspects of this investigation, it seems advisable that all breeding material be evaluated for combining ability. Although segregation for combining ability was indicated, the possibilities of significantly enhancing combining ability through selection following selfing of individual clonal families seem remote. A more desirable method of increasing combining ability would seem to be a reciprocal recurrent selection series, since specific combining ability is indicated to be an important consideration in evaluation of brome-grass selections. With adequate evaluation and rigid selection on a large scale progress should become a reality.

There appears to be no advantage in evaluating combining ability of clonal selections in space-planted nurseries. Rather, evaluations should
performance were exhibited despite the environmental restriction of
the for all characters studied, indicating further that differences in
activity. Significant differences were also obtained among named verte-
brates. Significant differences were also observed for the selected
scores and test scores were also better than the respective
with combining activity on the average. For the average, the scoring
that showed the additional 50 top scored clones included in the test showed
relative merits can be properly determined.
however, this procedure is in need of further investigation before its
where could be established on the basis of tests in the scoring stage.
from indicated are that possibly a small percentage of the low con-
outside under conditions comparable to the way the crop is normally
48
SUMMARY AND CONCLUSIONS

1. Topcross progenies of 18 S₀ clones of bromegrass and 10 S₁ segregates from each along with 13 other S₀ topcrosses and nine named varieties were grown in solid seedings in a split-plot design with five replications. Families made up the whole plots with S₀ and S₁ selections as subplots within each whole plot. All entries were evaluated for forage yield, spring vigor, leaf disease infection, and leafiness percentage in 1954 and for forage yield only in 1955. Dry weather prohibited a second cutting in 1954; however, two cuttings were made in 1955. Forage yields were recorded on a green weight basis from a 15 square-foot area. Spring vigor was evaluated on a 1 (poorest) to 5 (best) basis. Leaf disease was recorded on a numerical basis with 1 (0-10% leaf area killed) to 10 (90-100% leaf area killed). Leaf percentage was calculated as the percentage of the total culmage which was leaves. All data were subjected to standard split-plot analyses to obtain information on the inheritance of combining ability and extent of segregation for combining ability. Estimates of heritability of combining ability were calculated by progeny-parent regressions. Results of the topcross progeny test were correlated with previous evaluations of the parental material in an effort to obtain information on the relationships between space-planted and solid-seeded performance. Other aspects investigated were the effect of inbreeding for one generation on
combining ability and correlations between inbreeding depression and combining ability. Intercharacter relationships, as measured in the topcross progeny test, also were studied to determine selection possibilities on the basis of solid stands.

2. Statistically significant differences were obtained among topcross entries included in the test indicating that combining ability for forage yield, spring vigor score, leaf disease infection, and leafiness percentage is inherited. On a family mean basis, significant differences could be demonstrated only for leaf disease and spring vigor scores. Analyses of S₁ selections on an individual family basis indicated that three of the 18 families appeared to be segregating for combining ability for forage yield on a two-year mean basis. Significant differences among S₁ segregates within families were observed for ten families for spring vigor score, seven families for leafiness percentage, and one family for leaf disease score, indicating that segregation for combining ability also occurs for these characteristics.

3. Heritability estimates, as calculated by the regression method, gave values of 16, 19, 46, and 48 percent, respectively, for leaf disease reaction, leafiness percentage, spring vigor, and forage yield. Correlations between S₀ and S₁ progeny means ranged from 0.31 for leafiness percentage to 0.65 for two-year mean forage yields.

4. Correlations between S₀ topcrosses seeded in solid stands and previous evaluations of the same clonal families were low and variable
with a range of -0.36 for leafiness between $S_0$ topcrosses and O.P. progenies spaced three by three feet to 0.45 for forage yield between $S_0$ topcrosses and O.P. progenies in three-foot drilled rows. In general, correlations between $S_0$ topcross performance and previous evaluations for forage yield were positive but of very low predictive value. $S_0$ topcrosses and previous evaluations of the clonal families showed, in the main, negative associations for spring vigor and leafiness scores. Almost no correlation was obtained between performance of $S_1$ topcrosses in solid seedings and $S_1$ progenies grown in spaced plantings of three by three feet.

5. Analyses of variance of forage yields and leaf disease scores showed topcrosses of $S_0$ clones to be significantly higher, on the average, for these characters than $S_1$ topcross progenies. The mean values for $S_0$ and $S_1$ were 4.19 and 3.99 pounds per plot and 4.18 and 3.93, respectively, for forage yield and leaf disease score. No differences in combining ability could be shown between generations for spring vigor score and leafiness percentage.

6. Inbreeding depression and combining ability for forage yield were positively correlated. There was also a tendency for the lower yielding $S_1$ lines to give the better topcrosses. The correlation was -0.18 between $S_1$ selections and their topcrosses for forage yield on a two-year mean basis.
7. All possible intercharacter correlations were calculated among characters measured in the topcross progeny test. Values obtained were either of no consequence or in the desired direction for efficient selection except one. Positive associations between leaf disease infection and early spring growth were obtained. This appears to be detrimental to simultaneous selection for these two characteristics.

8. It was suggested that a reciprocal recurrent selection series be set up to study further the inheritance of combining ability and the possibilities of genetic advance through selection. It was further suggested that some of the additional S₀ clones tested be included in the series since some of these clones showed high combining ability for the characteristics studied.
LITERATURE CITED


ACKNOWLEDGMENTS

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Table 11. Mean topcross performance of 18 S<sub>0</sub> clones and 10 S<sub>1</sub> segregates from each plus 13 other S<sub>0</sub> topcrosses and 9 named varieties for forage yield, spring vigor score, leaf disease score, and leafiness percentage.

<table>
<thead>
<tr>
<th>Clone</th>
<th>1954-55 Mean forage yield</th>
<th>1954 Spring vigor score</th>
<th>1954 Leaf disease score</th>
<th>1954 Leafiness (%)</th>
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</thead>
<tbody>
<tr>
<td>391</td>
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<td>3.0</td>
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* Significantly better than Fischer at the 5% level
** Significantly better than Fischer at the 1% level

Levels of Significance between the mean of an individual entry in one whole plot and the mean of an individual entry in another whole plot:

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