

SEED YIELD AND YIELD COMPONENTS OF
SELECTED BERMUDAGRASS CLONES AND
THEIR F₁ AND F₂ GENERATIONS

By

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TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION	1
II. REVIEW OF LITERATURE	3
Heterosis Concept	3
Inbreeding Depression in Cross-Fertilized Crops	9
Combining Ability and Recurrent Selection	11
Mating Schemes of Cross-Fertilized Crops	13
Synthetic Varieties and Inbreeding Depression	
Effects	16
Breeding Better Bermudagrasses	19
III. MATERIALS AND METHODS	26
IV. RESULTS AND DISCUSSION	34
Seed Yield	34
Yield Components	37
Pollen Viability Potential	47
Orthogonal Contrasts	51
LCB Polycross	55
V. SUMMARY AND CONCLUSIONS	56
BIBLIOGRAPHY	59

LIST OF TABLES

Table	Page
I. Origin and Classification of Bermudagrass Parental Clones Used to Derive F_1 and F_2 Generations	27
II. Family Groups	29
III. Analysis of Variance for Seed Yield	35
IV. Seed Yield of Bermudagrass Parental Clones and Their F_1 and F_2 Generations	36
V. Analysis of Variance for Yield Components	39
VI. Seed Yield Components of Open- and Self-Pollinated Bermudagrass Heads of Parental Clones and Their F_1 and F_2 Generations	42
VII. Analysis of Variance for Pollen Viability	49
VIII. Percent Filled, Half-Filled, and Empty Pollen Grains with Regard to Starch for Parental Bermudagrass Clones and Their F_1 and F_2 Generations	50
IX. Orthogonal Contrasts of F_1 and F_2 Generation	53
X. Orthogonal Contrasts of Families I and II	54

LIST OF FIGURES

Figure	Page
1. Histogram of Bermudagrass Seed Yield Estimated from Plot and Subsample Harvest Methods Grouped by Family	38
2. Histogram of Bermudagrass Head Density Grouped by Family	41
3. Histogram of Raceme Number of Bermudagrass Heads Grouped by Family	43
4. Histogram Depicting the Number of Florets on Open- and Self-Pollinated Bermudagrass Heads Grouped by Family	45
5. Histogram Depicting the Number of Seeds per Open-Pollinated Bermudagrass Heads Grouped by Family	46
6. Histogram of Percent Seed Set for Open-Pollinated Bermudagrass Heads Grouped by Family	48
7. Histogram of Percent Filled, Half-Filled, and Empty Pollen Grains with Regard to Starch	52

CHAPTER I

INTRODUCTION

Bermudagrass is a naturally cross-pollinated species and probably the most widely used turf and forage grass in the Southern United States. Hybridization in bermudagrass has combined important agronomic characters such as dry matter digestibility, percent protein, and adaptation to a wide range of climatic conditions. An increase in heterosis also occurs in hybrids however, sterility in many crosses is encountered and the hybrid must be propagated vegetatively. Even though vegetative propagation is practical, most forage producers and homeowners would prefer to establish new varieties by seed. Planting equipment developed for vegetative propagation is also difficult to use in confined areas such as home sites, or on the steep embankments of dams, highway bridges, or roadbanks.

Seeded bermudagrasses are typical of many cross-fertilized species in that seeded varieties are heterogeneous populations. Little is known about how agronomic traits are affected in breeding populations and for this reason, an in-depth review of the literature is presented to focus attention on some of the concepts, methods, and problems related to the improvement of naturally cross-pollinated crops through plant breeding. The development of the heterosis concept and problems with inbreeding are the first two topics of discussion in the literature review. Combining ability, recurrent selection, and mating schemes utilizing these

principles in breeding cross-pollinated crops are also presented using examples primarily from the current knowledge accumulated on maize improvement.

The development of synthetic varieties rather than a single line variety has been useful in breeding cross-pollinated crops. Results from synthetic varieties of alfalfa indicate that a decrease in fertility occurs with advancing generations with even modest levels of inbreeding (Wilse, 1958). The strong self-incompatibility of alfalfa which enforces outcrossing is similar to self-incompatibility reported for bermudagrass by several workers (Burton, 1965; Kneebone, 1967; Burton and Hart, 1969; Richardson, Taliaferro, and Ahring, 1978). Therefore, some of the problems encountered when breeding synthetic varieties of alfalfa are presented in the literature review. Information on bermudagrass and its successful turf and forage hybrids as well as information pertinent to the development of seeded bermudas is also reviewed.

This study was concerned with an investigation of the effect of two levels of inbreeding on the cross-fertility of bermudagrass breeding populations. The primary objective was to evaluate the advanced single cross generations of selected bermudagrass clones adapted to Oklahoma conditions to determine if changes occur in fertility or seed yield. A secondary objective was to look at the plant components responsible for seed yield and draw some inferences as to why seed yield increases or decreases with advancing generations.

CHAPTER II

REVIEW OF LITERATURE

Heterosis Concept

Koelreuter (1766, as cited in Zirkle, 1952) published a great deal about plant hybridization after an intensive investigation of the subject. He described hybrid vigor of interspecific crosses of several genera and observed floral mechanisms which insured cross-pollination. He concluded that nature had designed plants to benefit from cross-breeding. Sprengel (1793, as cited in Zirkle, 1952) illustrated the structure of flowers with great detail and explained how self-pollination was generally avoided. Knight (1799, as cited in Zirkle, 1952) developed his principle of 'anti-breeding' as the natural consequence of crossing.

Darwin (1868, as cited in Zirkle, 1952) depicted the early livestock breeders who used inbreeding to accumulate desirable characters and then cross-breeding to prevent degeneration. Darwin states, ". . . although free crossing is a danger on the one side which everyone can see, too close breeding is a hidden danger on the other (p. 7)." Darwin (1876, as cited in Zirkle, 1952) published his book Cross- and Self-fertilization in the Vegetable Kingdom in which he concluded, "The first and most important conclusion which may be drawn from the observations in this volume is that cross-fertilization is generally beneficial and

self-fertilization injurious (p. 8)."

Beal (1800), influenced by Darwin's work, developed a method insuring hybrid seed in corn. The two parental stocks, grown in isolation for a number of years, were planted together in alternate rows. All of one stock was detasseled rendering it able to produce hybrid seed only. This hybrid seed was planted for the main crop and Beal reported an increased yield of 151 percent using this method.

McCluer (1892) reported the following observations with regard to plant vigor in maize: 1) sterility and deformity often follow selfing, 2) crossing imparts vigor, 3) it is impossible to tell what varieties of corn will produce progeny of increased size when crossed, 4) what appears to be the best ear does not always produce the largest crops, and 5) nearly all of the hybrids grown a second year are smaller than those of the first year. Morrow and Gardiner (1893) reported similar observations with those of McCluer especially with regard to the statement that yield is greater in the F_1 hybrid than the better parent and the F_2 generation will also be greater than the better parent, yet slightly less than the F_1 hybrid.

The rediscovery of Mendel's Laws in 1900 by DeVries, Correns, and Tschermak focused attention on problems of heredity and led to renewed interests in hybrid vigor. Mendel (1865, as cited in Zirkle, 1952) described hybrid vigor in his pea varieties as follows:

The longer of two paternal stems is usually exceeded by the hybrid, a fact which is possibly only attributable to the greater luxuriance which appears in all parts of plants when stems of very different lengths are crossed (p. 8).

Shull (1905, as cited in Shull, 1952) first recognized a case of hybrid vigor in a cross between Russian sunflower and the wild

Helianthus annuus. He found F_1 hybrids much taller than the tallest parent and concluded that the hybrid resulted from the unlikeness in the constitution of uniting gametes. Shull (1906, as cited in Shull, 1952) observed that self-fertilization of maize served to 'purify' the strains and comparisons should not be thought of as cross-fertilization versus self-fertilization. He proposed that comparisons be made between pure strains and their hybrids and moreover, a well-regulated field of maize is a mass of very complex hybrids.

Shull (1912, as cited in Shull, 1952) while in Germany, proposed the word 'heterosis' and later suggested,

The heterosis concept is the interpretation of increased vigor, size, fruitfulness, speed of development, resistance to disease and insect pests, or to climatic rigors of any kind manifested by cross-bred organisms as compared with corresponding inbreds, as the specific results of unlikeness in the constitutions of the uniting gametes (Shull, 1952, p. 48).

Davenport (1908) was the first to point out the now well-recognized fact that in most cases the dominant character is beneficial to the organism possessing it, while the recessive counterpart has a weakening effect. Keeble and Pellew (1910) found that two different dominant factors were responsible for pea hybrids that were taller than either parent. One of the dominant factors resulted in longer internodes while the other increased their number.

Bruce (1910) developed an algebraic model which explained the decrease in the number of homozygous loci in hybrid progeny. He postulated that a correlation should result between the number of recessives and deleterious effects. Bruce designated the frequencies of dominant and recessive alleles as p and q in one line and P and Q in the other. The array of individuals in the two groups would then be $(p^2DD+2pqDR+q^2RR)^n$ and $(P^2DD+2PQDR+Q^2RR)^n$, where D and R are the dominant and

recessive alleles on the n number of factor pairs.

The mean number of homozygous loci that result when the two populations are crossed is nqQ . The average number for the two parent populations is $n(q^2+Q^2)/2$. The first expression is a geometric mean of the two parental recessive genotypic frequencies while the second expression is an arithmetic mean. Bruce pointed out that the geometric mean should always be less than the arithmetic mean and therefore, the number of homozygous recessive loci in the hybrid will be less than the mean number in the two parent populations. Bruce concluded that if either or both parent populations were selfed the decrease of homozygous recessive loci in the hybrid would be greater.

The "dominance hypothesis" supported by Davenport, Keeble, Pellew, and especially Bruce met stiff opposition on two grounds. First, if vigor was not a product of heterozygosity, it should be possible, by selection, to obtain individuals which are homozygous for all beneficial dominant loci and have the same vigor as F_1 hybrids. The second argument concerned the segregating F_2 population of the two inbred lines. Those opposed to the dominance hypothesis believed the F_2 population distribution of the trait being measured should be skewed according to the expansion of a 3:1 dominant to recessive ratio (Crow, 1952).

Jones (1917) removed the first objection by showing that if a detrimental recessive were linked with a favorable dominant allele, the heterozygous chromosome would be superior to both homozygotes and that this linked combination might not break up easily. Collins (1921) dispelled the second objection by illustrating a large number of factors, regardless of linkage, causes a skewed distribution to disappear and the probability of getting all beneficial dominant factors into one

homozygous strain becomes vanishingly small.

East (1936) elaborated on the concept of heterosis by considering a series of alleles at a given locus each having a positive or additive effect. As the alleles become more and more divergent in function, the action becomes more nearly additive in the heterozygote. Hull (1945), however, supported the overdominance concept to explain superior heterozygotes from crosses of two inbred lines. He pointed out that this would not be true with dominant genes acting in an additive manner unless it were assumed a plant with no favorable dominants had a negative yield.

Quinby and Karper (1946) reported a case of single locus heterosis involving a locus free of deleterious alleles. They found certain heterozygous combinations produced in hybrid sorghum plants stimulated greater meristematic growth and cell division which resulted in increased tillering. Crow (1952) found the dominance hypothesis adequate for explaining the deterioration that results from inbreeding and the recovery of vigor after out-crossing. On the other hand, he believed that the theory did not adequately explain how hybrids could greatly exceed in fitness the equilibrium populations from which their parents were derived. Crow concluded that the overdominance hypothesis demands rare gene interactions of a form where two alleles differ qualitatively or each does something that the other fails to do. A small proportion of the loci may be of this type and, though few, are a major factor in the population.

Dobzhansky (1952) described differences between what he called mutation heterosis (dominance) and balanced heterosis (overdominance). He defined mutation heterosis as the result of adaptively superior dominant

alleles sheltering deleterious recessive mutant alleles in populations of sexually reproducing and cross-fertilizing organisms. Balanced heterosis occurred when the heterozygote exceeded both parents in some positive or negative quality. He proposed that mutational heterosis was a protective device of sexual species with a certain population structure against the natural mutation pressure. Balanced heterosis, he proposed, maintains a multiplicity of genotypes that are adaptive in the various ecological niches the population occupies.

Whaley (1952) described heterosis in physiological terms as differences due to fundamental aspects of metabolic processes. Differences of primary importance would concern enzymes, auxins, and other growth substances active in plant growth. The resulting specific gene action which lies at the basis of the physiological advantage or advantages gives rise to hybrid vigor.

Robinson and Cockerham (1961) found the relationship between performance and heterozygosity to be linear for both yield and ear weight in maize hybrids. They concluded that the model of additive and dominant gene effects fit the results satisfactorily. Cornelius and Dudley (1974) and several other workers argue the point that overdominance is a minor factor in heterosis and stress importance on the effects of dominance and linkage.

The heterosis concept has developed into one of the most exciting problems facing plant breeders today. Considering the number of genes involved in heterosis, and the complexity of the interactions known to exist, it is no surprise that a single theory or experiment can not account for all the effects concerning heterosis.

Inbreeding Depression in Cross-Fertilized Crops

Self-fertilization in most naturally cross-fertilized species results in drastic inbreeding depression. Mather (1943), and later Stebbins (1957), suggested that self-fertilized species evolved from cross-fertilized species. If this is true, the development of normally cross-fertilized species into populations tolerant to some degree of inbreeding could be achieved if yield and vigor are maintained as inbreeding occurs (Genter, 1971). Since the transition from cross- to self-fertilized species took place gradually over a great deal of time with varying degrees of selfing and crossing, a continual increase in the frequency of desirable genes would result in a succession of improved populations.

For inbreeding to occur (Good and Hallauer, 1977 and Burton, Stuber, and Moll, 1978) there is a minimum of three conditions which are necessary: 1) a population must have favorable alleles at gene loci which control the character of interest, 2) there must be some degree of dominance among the alleles, and 3) upon inbreeding the loss of heterozygosity must occur in those particular loci.

Inbreeding in normally cross-fertilized species renders many homozygous recessives that would remain sheltered in heterozygotes under normal cross-breeding (Dobzhansky, 1952). These recessives become suddenly exposed to natural or artificial selection and the loss of fitness of inbred lines is the consequence. The existence of inbreeding depression for any character is sufficient evidence for the presence of some degree of dominance at some loci (Cornelius and Dudley, 1974).

Wright (1934) developed a method for computing the degree of inbreeding by the use of path coefficients. The coefficient of inbreeding (F) was proposed to measure the departure from the amount of homozygosity under random mating toward complete homozygosity. Malecot (1948, as cited in Busbice, 1969) has shown how the general coefficients for F , given by the method of path coefficients, can also be demonstrated directly from probability theory. Kempthorne (1957) further expanded the probability method for computing the coefficient of inbreeding of individuals and redefined the term as the probability of two genes picked at random from a locus being identical by descent.

Cornelius and Dudley (1974) reported that inbreeding depression, when significant, was linearly related to the coefficient of inbreeding for most characteristics studied in maize. Their results and the results of the many workers they reviewed, led them to conclude any non-linearity is evidence for epistatic gene action. Stuber and Moll (1969) estimated the amount of total variability that could be attributable to epistasis to be less than 10 percent. Moreover, Stuber and Moll (1974) compared the relative importance of errors caused by genotype by environmental interaction effects. They found yield, ear number, and ear height in maize to have greater discrepancies due to genotype by environmental interaction effects than to epistatic effects.

According to de Leon and Lonnquist (1978) the coincidence of yield depression with increased homozygosity (given by F) for maize agrees with other reports. Burton, Stuber, and Moll (1978) reviewed several previous studies with levels of inbreeding in the range of $F = 0.25$ to $F = 1.0$ in material developed from selfing, sib-mating, or backcrossing. The results have generally shown a linear relationship between perfor-

mance and the level of homozygosity. In addition, evidence concerning epistasis suggests it to be important in some genetic combinations but, apparently does not occur with sufficient frequency or effect to be detectable in variance component studies of random mating populations (Stuber and Moll, 1969, Cornelius and Dudley, 1974, and Stuber and Moll, 1974).

Combining Ability and Recurrent Selection

The concept of combining ability is becoming increasingly important in connection with testing procedures to study and compare the performances of lines in hybrid combinations. The terms general and specific combining ability were originally defined by Sprague and Tatum (1942) when the testing procedure they used was a diallel crossing system. General combining ability measures the average performance of a strain in a series of test crosses. Specific combining ability measures the deviation of the actual performance of a combination from the predicted performance based on the general combining ability (Allard, 1960). Griffing (1956) has prepared a detailed examination of the concept of combining ability in relation to diallel crossing systems. Sprague (1966) reviewed the results of several workers with regard to general and specific combining ability in recurrent selection schemes.

The recurrent selection concept arose from theoretical considerations based on less restrictive forms of inbreeding. Allard (1960, p. 471) defined recurrent selection as,

. . . a method of plant breeding designed to concentrate favorable genes scattered among a number of individuals by selecting in each generation among progeny produced by matings inter se of the selected individuals (or their selfed progeny) of the previous generation.

A decrease in the rate of inbreeding decreases fixation of deleterious genes which occurs in selfing. Selfing also does not allow adequate opportunity for selection since the selfed plant selected in each line imposes a limit on the possibility for further improvement of the line.

Breeding schemes which favored mild inbreeding as opposed to selfing were suggested by Hayes and Garber (1919) and East and Jones (1920); however, critical data were not published in either case. Jenkins (1940) reported a detailed description of how mild inbreeding could be used for early testing of general combining ability in maize. Hull (1945) suggested that selection for several cycles of intercrossing might be useful in improving specific combining ability. This method acquired the term recurrent selection and Hull (1945, p. 134) defined the method

. . . to include reselection generation after generation, with interbreeding of selects to provide for genetic combination. Thus selection among isolates, inbred lines, or clones is not recurrent until selects are interbred and a new cycle of selection initiated.

The advantage of this system is that the performance ceiling is set by the most favorable combinations of genes contained in a group of foundation genotypes rather than by the genotype of a single foundation plant. Four types of selection are recognized and vary by the way in which desirable agronomic characters are identified. These four types include: 1) simple recurrent selection, 2) recurrent selection for general combining ability, 3) recurrent selection for specific combining ability, and 4) reciprocal recurrent selection (Allard, 1960).

Simple recurrent selection is effective for traits with high heritability which can be measured visually or by simple tests. In simple recurrent selection, plants are divided into a group to be discarded

and a group to be advanced based on phenotypic scores of individual plants or their S_1 progeny. Recurrent selection for general combining ability employs test crosses to a broad-based tester (outbred line) (Sprague, 1952). Recurrent selection for specific combining ability utilizes test-crosses to a narrow-based tester (inbred line) (Hull, 1945). Reciprocal recurrent selection uses two heterozygous source populations, A and B, which are simultaneously tested with selected pollen parents from the opposite source (Comstock, Robinson, and Harvey, 1949).

Mating Schemes of Cross-Fertilized Crops

In cross-fertilized crops two general methods of breeding for heterotic response are now widely used. First, selection within a line and between selfed lines and then use of single, three-way, or double-crosses for the commercial crop. Second, breeding desirable clones of perennial crops which are evaluated for combining ability by polycross, or similar methods, and the desirable clones used to produce F_1 crosses, double-crosses, or synthetic varieties (Tysdal, Kiesselbach, and Westover, 1942; Hayes, 1952; and Hallauer, 1972). It should be recognized, however, that in several crops the two separate methods are integrated into one system for simultaneous varietal improvement and development.

Development of maize hybrids from base populations generally has been done in three steps: 1) selection among inbreds based on their phenotypes, 2) selection among remaining inbreds for combining ability with broad-based testers, and 3) selection among F_1 hybrids of the inbred lines which survive the first two steps. It is assumed the first two steps effectively retain lines having the highest frequency of

genes with favorable additive effects. The last step involves primarily non-additive genetic effects (Horner et al., 1973).

Horner et al. (1973) investigated the contribution of the three processes listed above by completing five cycles of recurrent selection where the three steps were represented by: 1) selection for yield of S_2 lines (S_2 Progeny Testing), 2) selection for combining ability with a broad-based source population (Parental Tester Method) and, 3) selection for combining ability with an inbred line (Inbred Tester Method). They found a significant linear increase in general combining ability over cycles for all methods, but the Inbred Tester Method was significantly more effective. They concluded that the Inbred Tester Method allowed for more successful selection of favorable dominant genes than was possible with a broad-based tester. The testing of S_2 progeny showed slow progress for combining ability improvement and suggested it was not effective in fixing favorable dominant alleles.

Comstock, Robinson, and Harvey (1949) concluded on theoretical grounds that in the absence of overdominance, S_1 testing would provide for more rapid genetic advance than half-sib testing. Genter (1971 and 1973) states that selection based on half-sib performance to primarily select for desirable additive and dominant genes, but does not select effectively against deleterious genes since they may be masked by the tester. As inbreeding progresses, potential population improvement that might be provided by an increased frequency of favorable genes may be counterbalanced by an increase in the frequency of homozygous deleterious genes. Selection based on the S_1 inbred performance is effective for selection of additive effects and presents an opportunity for selection against major deleterious recessive genes that become homozygous

with inbreeding. If selection is effective for favorable genes and against unfavorable genes, productivity of advanced populations should increase.

Burton et al. (1971) reported that the evaluation of lines on the basis of S_1 progeny performance identified superior genotypes more rapidly than test-cross evaluation. Less inbreeding depression (difference between population and population selfed) occurred among the populations derived by S_1 selection. They theorized deleterious genes were masked by the tester genotype in test-cross evaluation, and that fewer deleterious genes were eliminated. Their study also found both mean yield and combining ability significantly improved by recurrent selection and that S_1 selection was equal to or better than half-sib selection.

Goulas and Lonquist (1976) suggest S_1 progeny performance reflecting additive genetic effects and half-sib performance reflecting non-additive, dominance, or epistatic genetic effects can be combined and effectively employed in recurrent selection programs. Kenworthy and Brim (1977) reported that selection based on S_1 progeny performance significantly increased seed yield of a base population of soybeans. Moll et al. (1978) found that heterosis for grain yield increased after reciprocal recurrent selection and decreased slightly after full-sib mating. De Leon and Lonquist (1978) found pairing of half-sib families for the production of full-sib crosses to be advantageous over crossing plants at random if either hybrid development or initiation of full-sib recurrent selection are the breeding goals. The advantages they listed are: 1) opportunity to examine half-sib families visually before flowering, 2) opportunity to avoid unnecessary inbreeding, 3) more balanced sampling through making more full-sib matings among a wider

array of half-sib families.

Synthetic Varieties and Inbreeding

Depression Effects

Synthetic varieties are also a means of partial utilization of heterosis. Synthetic varieties are produced by randomly mating several parents so that all possible matings between the parents have equal probability of occurring. The parents are designated as Syn-0 and their progeny are called the Syn-1. The amount of seed of a synthetic is multiplied by successive generations of random mating called the Syn-2, Syn-3, and so on. A synthetic is an expanding population consisting of a few individuals in the Syn-0 and many individuals in the advanced generations. Since the number of parents in the Syn-0 is small, inbreeding will result in advanced generations and eventually effect vigor to some degree (Busbice, 1969).

Synthetic varieties were first suggested by Hayes and Garber (1919) in their work with protein content of maize. MacCaully (1928) proposed a method of 'plot-breeding' where selected plants were grown together to gradually combine all favorable alleles of plants in the plot into a single strain. Kiesselbach (1933) reported yields of Syn-1 and Syn-2 populations in which some of the synthetics were as productive as standard varieties, but none as superior.

Tysdal, Kiesselbach, and Westover (1942) developed a method of selecting for heterosis in vegetatively propagated clonal material of alfalfa by means of polycross progeny testing. Parental clones previously evaluated for agronomic characters were randomly planted together in isolation. Polycross progeny produced by the selected clones were

used for determining combining ability while selfed clonal progeny were used to assess the presence of deleterious recessive genes in the parental clones. They concluded the polycross progeny test was effective in selecting superior plants and that the selfed clonal progeny testing may be unnecessary. Close correlation between the average polycross progeny performance of resulting synthetic varieties in the Syn-1 generation was further evidence for the usefulness of this polycross progeny test method.

Sprague and Jenkins (1943) reported yields of maize synthetics whose component lines were selected for specific characteristics other than combining ability. These synthetics did not differ significantly in yield from standard open-pollinated varieties. Tysdal and Crandal (1948) reported eight different alfalfa Syn-1 and Syn-2 progenies producing about the same forage yield. Lonquist (1949) reported the relative performance of Syn-2 and Syn-3 varieties made from S_1 lines of maize. He found that the low Syn-2 yielded 85 and 88 percent (for year one and two respectively) of the high parent and the high Syn-2 yield 142 and 118 percent of the high parent. The low Syn-3 equaled the high parent and the high Syn-3 yielded 127 percent of the high parent.

Grauman and Matlock (1952) studied Syn-1 through Syn-4 generations of six alfalfa synthetics and observed a slight decline in forage yield from the Syn-1 to the Syn-2 and a slight increase in forage yield from the Syn-2 to the Syn-3. They assumed that synthesis was approaching completion in the Syn-2 and was probably attained in the Syn-3. Carnahan and Miller (1955, as cited in Busbice et al., 1974) outlined possible deficiencies concerning the polycross progeny test: 1) non-random mating, 2) provision of a less sensitive measure for additive inheritance

than evaluation of either clone or its self-progeny, 3) progeny testing for highly heritable characters is unnecessary, and 4) progeny testing before simple phenotypic selection was a waste of effort. Even with these deficiencies they concluded that the polycross progeny test had merit in determining the breeding value of selected clones.

Davis (1955) found significant positive correlation coefficients for forage yield among S_1 and polycross progenies of alfalfa significant when similar methods of planting were used. Carnahan (1960) reported highly significant correlations ($r = 0.77$ and $r = 0.88$) for the Syn-1 and Syn-2 generations of six, two-clone diallel crosses of ladino clover. Pearson and Elling (1961) described a method for predicting synthetic varietal performance in alfalfa using clonal testcross data. The sum of squares for "among clonal crosses" was partitioned into general and specific combining abilities according to the method proposed by Griffing (1956). Busbice (1969) demonstrated a method for computing inbreeding in advanced generations based on the coefficient of inbreeding proposed by Kempthorne (1957). The method he proposed can help in determining the effects of varying the number of parents used to produce a synthetic variety, the amount of inbreeding of parents, and the synthetic generation that should be used for agronomic production.

Hill et al. (1971) found the expected genetic advance made from selection on the basis of polycross progeny test performance to be greatest for alfalfa hay, seed, and chaff yields, but expected genetic advance with individual plant selection was greater for disease resistance. They proposed that the improvement of traits in alfalfa with medium to high heritabilities could be accomplished by phenotypic recurrent selection followed by use of the polycross progeny to select

parents for synthetic varieties. Hill (1973) evaluated six alfalfa clones, their S_1 through S_4 progeny, and their Syn-1 through Syn-4 for spring growth and plant height. Linear regression alone on the coefficient of inbreeding generally did not give a good fit to the observed results and the cubic regression was significant more often than the quadratic.

Bula et al. (1974) studied population characteristics of advanced generations of an alfalfa synthetic increased from selfed, single-cross, or polycross seed. They found geographic location and number of generations of increase to be much more important considerations in the maintenance of cultivar characteristics than the method of producing breeder seed. Lowe, Cleveland, and Hill (1974) found most of the approach to random mating to occur from the Syn-1 to the Syn-2 generations. A single generation of bulk seed increase eliminates performance differences attributable to methods of synthesis in prior generations. They concluded the Syn-1 would need to be the seed generation of commerce for double-cross synthetics before any observed advantage over conventional synthesis is realized.

Busbice et al. (1974) evaluated the effectiveness of polycross and self-progeny performance in increasing the forage yield of alfalfa synthetics. They concluded from available data and theoretical considerations that selection of parents should be based on both their inbred and outcross yield which capitalizes on additive and non-additive gene action.

Breeding Better Bermudagrasses

Bermudagrass, Cynodon dactylon (L.) Pers., is probably the most

widely used turf and forage grass in the Southern United States. The basic chromosome number ($X = 9$) is well established for most Cynodon species. Most bermudagrasses are tetraploids, however, regular diploid meiosis generally occurs (Forbes and Burton, 1963). The high occurrence of trivalent formation in the triploid hybrids indicates homology exists between the genomes of some diploid and tetraploid C. dactylon and C. transvaalensis Burt-Davy.

Bermudagrass was once considered a serious pest until Burton (1943) developed 'Coastal' bermuda ('Tift' X an introduction from Africa). Fertilized Coastal bermuda provided a good source of protein with levels ranging from 12 to 18 percent (Harlan, 1970). The use of bermudagrass as a forage prompted work to increase adaptation and forage quality. Dry matter digestibility is the primary limiting factor and substantial improvement was made by Burton, Hart, and Lowery (1967) with the cultivar 'Coastcross I' (Coastal X PI 255445 from Kenya). Coastcross I had 12.3 percent higher dry matter digestability than Coastal bermuda and in livestock feeding trials this resulted in higher daily intake and daily gains.

Winterhardiness is an important selection factor for bermudagrasses grown in Oklahoma. The cultivar 'Midland' (Coastal X common from Indiana) was derived in Georgia and then named and released cooperatively by the Oklahoma and Georgia Agricultural Experiment Stations and the USDA (Harlan, 1970). Oklan (an F_1 hybrid selected from an abandoned Oklahoma State University nursery) surpasses Midland in forage production, however, is intermediate between Coastal and Midland for winterhardiness (Holt et al., 1978). Hardie bermudagrass develops large rhizomes which contribute to its winterhardiness, however is best adapted

to higher rainfall areas because of poor dry matter production in dry areas (Holt et al., 1978). Tifton 44 (Coastal X an accession from Berlin) has also demonstrated improved agronomic characters and has as much winterhardiness as Midland (Burton and Monson, 1978). Although, some of the winter hardy types yield less than Coastal or Coastcross I, their adaptation allows them to be grown where Coastal and Coastcross I cannot survive the winter.

There are several improved turf-type bermudagrasses most of which are F_1 hybrids of C. transvaalensis and C. dactylon. The varieties 'Tiffine', Tifgreen', and Tifway' have been developed in this manner (Burton, 1965). The variety 'Sunturf' (direct increase of PI 184339) is well adapted to Oklahoma conditions withstanding temperatures as low as 4°F and possessing considerable drought tolerance (Huffine, 1957). The Kansas State Experiment Station improved the degree of winterhardiness and turf quality by screening seedlings from a polycross nursery of African introductions and locally adapted commons (Juska and Hanson, 1964). Keen (1966, personal communication) released 'Midway' bermuda from this polycross nursery and later in 1971 (personal communication) 'Midiron' was released. Both turfs had done well under Oklahoma growing conditions.

Hybridization in bermudagrass has combined important characteristics as well as the increase in heterosis. Sterility is encountered in many Cynodon hybrids, but imposes little limitation on their commercial use because they can be easily propagated vegetatively (Burton, 1965). Vegetative propagation maintains the superiority of the genotype and state certification programs have helped to insure that commercial plantings of these hybrids remain pure. Even though vegetative

propagation is practical, as evidenced by the several million acres planted by this method, some forage producers and homeowners would prefer to establish new varieties by seed.

Seeded bermudas are typical of many cross-fertilized species in that seeded varieties are heterogeneous populations usually derived from non-inbred parents under limited control. Burton (1948) reported controlled hybrids made by careful emasculation of exerted, undehisced anthers. Anthesis was controlled by placing plants in a dark room at 45°F and anthers would not dehisce if plants ready to flower were kept in a constant mist chamber. Richardson (1958) described a method for controlled pollinations made by emasculating florets by hand prior to anthesis.

Burton (1965) found that bermuda heads, ready to flower within 24 hours, will shed pollen and set seed if culms with heads are cut close to ground level and placed immediately in bottles of tap water. These bottles containing heads were isolated, paired, or grouped to produce selfs, singlecrosses, or polycrosses, respectively. He reported the number of crosses obtained was influenced by self-incompatibility of the clones used. This mutual pollination technique saves labor and is particularly useful in making hybrids between clones that set few seed. Burton suggested the high degree of self-incompatibility in selected bermudagrass clones and the ease of vegetative propagation could be used to produce F_1 hybrid seed by planting alternate strips of two self-sterile, cross-fertile clones. He reported forage yields of seed-propagated F_1 hybrids equaled Coastal bermuda.

Kneebone (1967) listed the number of heads per acre and the percentage of florets setting seed as the two primary yield components

affecting seed yield of bermudagrasses. He measured self-pollination by bagging heads before anthesis and later determining seed-set. Kneebond reported selfed seed-set was near zero in experimental plots as well as in several commercial seed production locations. Heads exposed to outside pollen and then bagged set seed as well as unbagged heads. The assurance of outcrossing allows crosses to occur without emasculation of the female parent. He also described how commercial production of hybrids could be accomplished by propagating two or more lines in alternate rows with suitable isolation from other bermudagrasses.

Burton, Hart, and Lowery (1967) investigated the breeding behavior of six superior bermudagrass genotypes to obtain general and specific combining ability estimates for forage yield. They reported specific combining ability effects for yield were nearly three times greater than general combining ability effects. A comparison of the in vivo nylon bag digestibility of four clones and their hybrids demonstrated that the clone with the most digestible forage was a parent of the more digestible F_1 hybrids.

Reid (1967) measured the exhibition of heterosis by 50 bermudagrass hybrids whose parents were from a wide range of geographical areas and represented five different Cyndon species. Hybrid vigor relative to the midparent was expressed in all crosses for plant yield, height, and radius of sod spread. Green and dry weight yield had consistent increases over the high parent as a result of hybridization. He concluded that as genetic divergence increased, the percent heterosis decreased, and conversely, as the genetic divergence decreased, the percent heterosis increased.

Harlan and de Wet (1969) suggested that variability within C.

dactylon is a result of population fragmentation based on chromosomal behavior. Plants within populations interbreed freely producing fertile progeny while crosses between populations yield hybrids with varying degrees of sterility due to the presence of meiotic irregularities. They proposed a classification of the species using six botanical varieties with one variety subdivided into three races.

Ahring, Taliaferro, and Morrison (1974) discovered several well-adapted, winterhardy bermudagrass genotypes (clones) among the several Cynodon accessions collected by Harlan et al. and maintained by the Oklahoma Agricultural Experiment Station. Richardson, Taliaferro, and Ahring (1978) evaluated eight of these bermudagrass clones and their cross- and self-fertilized progeny. They reported significant variability existed among the bermudagrass genotypes for cross- and self-fertility which agrees with the findings of Harlan and de Wet (1969) and tend to substantiate the conclusions of Kneebone (1967) and Burton and Hart (1969) indicating a strong self-incompatibility mechanism enforcing outcrossing.

Strict attention must now be given to inbreeding and its potential effect on cross-compatibility of component plants that might be used in relatively narrow germplasm base seed propagated varieties. The extent to which various levels of inbreeding might reduce fertility in bermudagrass breeding populations is unknown (Richardson, Taliaferro, and Ahring, 1978). Results extrapolated from other crop plants with strong self-incompatibility mechanisms, particularly alfalfa, suggest that significant decreases in fertility might occur with even modest levels of inbreeding (Wilse, 1958). Several workers, however, have found a small advantage in yield of seed and forage from open-pollinated, narrow-based

synthetics produced from only a few clones (Busbice and Gurgis, 1976).

In this study, five cross-compatible, self-incompatible bermudagrass clonal plants, well-adapted to Oklahoma, were polycrossed and also paired in certain combinations to produce singlecross (F_1) seed. The F_1 seed of three of the singlecross combinations (Guymon/9945, Guymon/9959, and SS-17/SS-21) were advanced to the F_2 generation in isolated plantings. The five parental clones, the F_1 and F_2 generation singlecross populations, and the five-clone polycross (Syn-1) were evaluated for seed yield and yield components to determine if changes in fertility or seed production occurred with advancing generations.

CHAPTER III

MATERIALS AND METHODS

The study was conducted on the Agronomy Research Station, Stillwater, Oklahoma in 1980. Plant material used in the study included clonal plants 'Guymon', 9945, 9959, SS-16, and SS-21; F_1 and F_2 populations of Guymon X 9945, Guymon X 9959, and SS-16 X SS-21, and the Syn-1 generation of a five-parent polycross.

Information on the parental clones used to derive the various advance generations is summarized in Table I. The 'Guymon' accession is a "common" bermudagrass collected near the town by that name in northwest Oklahoma. The 9945 and 9959 accessions were introduced from Yugoslavia and Turkey, respectively. The SS-16 and SS-21 plants trace to open-pollinated seed harvested from F_1 plants of the crosses Guymon X 9958 and Guymon X 9945, respectively. The five-parent polycross included a bulk of equal quantities of seed harvested from the clonal plants Guymon, 9959, 10978-b, an F_1 plant of Guymon X 10978-b and an F_1 plant of Guymon X 9959.

The F_1 progenies of the Guymon X 9945, Guymon X 9959, and SS-17 X SS-21 crosses were produced by vegetatively propagating the respective parents in alternating rows in isolation and allowing the self-incompatible plants to cross-pollinate. These isolated plantings were on the Southwest Livestock and Forage Research Station near Ft. Reno, Oklahoma.

TABLE I
 ORIGIN AND CLASSIFICATION OF BERMUDAGRASS PARENTAL
 CLONES USED TO DERIVE F₁ AND F₂ GENERATIONS

Oklahoma Accession No.	Classification	Origin
Guymon	<u>C. dactylon</u> var <u>dactylon</u> Temperate race	Oklahoma
9959	<u>C. dactylon</u> var <u>dactylon</u> Selucidus race	Yugoslavia
9945	<u>C. dactylon</u> var <u>dactylon</u> Selucidus race	Turkey
SS-16	<u>C. dactylon</u>	Open-pollinated seedling from Guymon X 9958 F ₁
SS-21	<u>C. dactylon</u>	Open-pollinated seedling from Guymon X 9945 F ₁
9958	<u>C. dactylon</u> var <u>dactylon</u> Selucidus race	Italy
10978-b	<u>C. dactylon</u> var <u>dactylon</u> Temperate race	Oklahoma

Seed harvested from these plantings were used to establish isolated plantings on the South Central and Southwestern Agronomy Research Stations. The F_2 seed harvested from the individual plantings was used for the F_2 generations in the study. The first generation seed (Syn-1) of the five-parent synthetic was produced under isolation on Agronomy Research land near Lake Carl Blackwell approximately 15 miles west of Stillwater, Oklahoma. The term 'Family Group' was designated in reference to the two parental clones and their F_1 and F_2 populations and is summarized in Table II.

The twelve entries were established at the Agronomy Field Research Station, Stillwater, Oklahoma, April 10, 1978. The field plot design of the test was a randomized complete block with four replications. Individual plots of the five parental clones were established by planting eight potted plants 0.30m (1 ft) apart in a row through the center of each 1.52m X 4.28m (5 ft X 14 ft) plot. The remaining F_1 and F_2 generations and five-parent synthetic were seeded by sowing five 3.65m (12 ft) long rows spaced 0.15m apart. A border row of the five-parent synthetic was seeded along the entire south side of the experiment. The soil is a Kirkland silt loam belonging to the Abruptic Paleustolls and was fertilized prior to planting and each year thereafter according to soil test recommendations. In early March 1980, the plots were burned to remove thatch and allow a uniform starting point for spring growth. At the end of May, the plot was mowed to a height of two inches. Supplemental irrigation was needed during the summer months due to the lack of rainfall and high temperatures.

Seed yield, count data for yield components, and pollen viability were the response variables included in the study. The number of kg/ha

TABLE II
FAMILY GROUPS

Family Group	Parental Clone, F ₁ and F ₂ Generation, or Synthetic
I	Guymon 9945 Guymon X 9945 F ₁ Guymon X 9945 F ₂
II	Guymon 9959 Guymon X 9959 F ₁ Guymon X 9959 F ₂
III	SS-16 SS-21 SS-16 X SS-21 F ₁ SS-16 X SS-21 F ₂
IV	LCB Polycross

of seed produced was estimated using two different harvesting methods: 1) a sample area of 3.10m^2 (33 sq. ft) cut with a Jari mower; and 2) three hand-clipped subsamples of a 0.09m^2 (1 sq. ft) area from each plot. Head density was determined by counting the number of heads within each 0.09m^2 subsample. Yield component data for each plot included: number of racemes per head, number of florets per head, number of seeds per head, and percent seed set determined by the formula:

$$\% \text{ seed set} = \frac{\# \text{ of seeds per head}}{\# \text{ of florets per head}} \times 100.$$

Count data were taken from ten open- and self-pollinated heads subsampled from each plot. Pollen viability was estimated by the number of filled, half-filled, and empty pollen grains with regard to the amount of stained starch granules present in the pollen grains.

The method designed for plot subsampling was a grid system which divided the plot into 70 equal 0.09m^2 (1 sq. ft) units herein referred to as 'quadrats'. The plot dimensions called for five rows (labeled A through E) and fourteen columns (labeled 1 through 14) of quadrats. Each of the quadrats was assigned a three element code based on the row and column coordinates of the quadrat (e.g. B10 would be the quadrat found in the second row, tenth column). All quadrats in the A and E rows along with the quadrats in columns one and fourteen were used as a border around the area from which plot subsamples were taken. Plot subsampling followed a pre-assigned randomized order generated by the computer. Each of the 48 plots within the experiment had a computer print-out of the order quadrats were to be sampled and was closely followed when subsamples were taken.

All quadrat subsamples were located by using a large but lightweight grid constructed of three quarter-inch diameter polyvinyl chloride (PVC) pipe and ten gauge wire. The PVC pipe was used to make a 1.52m X 4.28m rectangular frame which corresponded to plot dimensions. Ten gauge wire was threaded through holes drilled at 0.3m centers along all sides of the large rectangle. The end result was a network of 0.09m^2 quadrats formed by intersections of the regularly-spaced wire running in perpendicular directions. The long and short sides of the grid were labeled to correspond with row and column letters and numerals described above.

In the pollen viability study conducted during July, replications were blocked according to days due to the timing required to obtain adequate amounts of pollen from individual heads. Three heads (emerged from the boot, but not undergoing anthesis) with 40-50 cm of culm attached were collected from each entry of a single replication the afternoon prior to the morning pollen viability was determined. The culm bearing each individual head was placed in a 40ml test tube filled with water. The test tubes containing the heads were kept in the laboratory at an approximately 8 cm spacing and 15 cm away from south-facing windows. The following morning pollen was collected from each raceme of an inflorescence by tapping the raceme and allowing the pollen to fall directly onto a microscope slide with one drop of iodine potassium-iodide (100ml distilled water, 1.0gm potassium iodide). The pollen and stain were mixed thoroughly with a dissecting needle and covered with a cover slip. Pollen counts were made using the microscope at 100X magnification. Starting from the upper left corner, the first 100 pollen grains located within a micro grid (dimensions 1mm X 1mm) were categorized into filled, half-filled, and empty with regard to the amount of stained

starch granules within the pollen grains.

Yield component data were taken from ten open- and self-pollinated heads subsampled from each plot using the grid system described earlier. During the third week of July, heads were self-pollinated (SP) by enclosing them individually in waterproof pollinating bags after they had emerged from the boot but prior to anthesis. The open-pollinated (OP) and SP heads were harvested six weeks later on September 2, 1980. Each OP and SP head was examined for number of racemes and number of florets per raceme. The florets were removed from each individual raceme with a scalpel and were dropped into a petri dish filled with acetone. The specific weight of acetone is 0.78g and quickly separated filled and empty florets. The empty florets were buoyant while those containing a caryopsis sank. All other count data for each head in the yield component study were later calculated.

In September the hand-clipped samples were harvested using the grid system described above. Hand-clipped samples were dried in a large oven at about 50°C for five weeks. Afterwards, head density was determined by counting the heads removed from each sample. Each sample was individually threshed using a hand rub-board and screened with a 1/16-inch round hole screen leaving a sample consisting of florets and some small plant debris. Once screened, samples were weighed and then cleaned using a South Dakota Seed Blower (Ames Powercount, Co., Brookings, South Dakota) which partitioned the sample into florets containing a caryopsis and those florets lacking a caryopsis. The fraction of florets with seed were screened once more, weighed, and this value was used to estimate seed yield.

In September 1980, a 3.10m² area within the plot was harvested by

cutting a 0.92m (3 ft) swath 3.36m (11 ft) through the center of the plot with a Jari mower. The mowed forage was raked and placed into large bags made of a nylon weave. All 48 harvested samples were hung from the ceiling of a greenhouse and allowed to dry for five weeks. Samples were individually threshed using a one-eighth round hole screen within a No. 10 Modern Hammermill (C. S. Bell Co., Hillsboro, Ohio, U.S.A.) powered by a two horsepower (171 rpm) electric motor. Afterwards, samples were screened through the following series of screens: 1/12 inch round hole, 1/16 inch round hole, 6 X 32 mesh, and 26 X 26 mesh. Once screened, each sample was weighed and then cleaned several times with a Bate Laboratory Aspirator (H. T. McGill Co., Houston, Texas, U.S.A.). The sample after this process consisted primarily of florets containing a caryopsis and its weight was used to determine plot seed yield.

Analysis of Variance and Duncan's Multiple Range Test were conducted for all response variables using the procedures outlined in Statistical Analysis System (SAS) 72 and 79 User's Guides (SAS Institute Inc. Box 8000, Cary, North Carolina 27511). Orthogonal contrasts were made using the procedure described in the General Linear Models (GLM) section of the SAS 79 User's Guide to determine if the variation or interaction among F_1 and F_2 generations for all the response variables was significant. Orthogonal contrasts were also made to determine if the variation or interaction among and within families I and II was significant.

CHAPTER IV

RESULTS AND DISCUSSION

The 1980 summer was exceptionally hot and dry. Temperatures exceeding 100°F were recorded for 28 consecutive days during the period from June 26 through August 21, with the remainder of the days having temperatures greater than 90°F. Supplemental irrigation was required to maintain the vigor of the bermudagrass entries in this study. The high temperatures depressed percent seed set and seed yields relative to those reported in previous studies at the Oklahoma Agricultural Research Station. The total effect of the climatic conditions on the differences found for entries in this study is unknown.

Seed Yield

Variation among the entries was highly significant ($P < 0.01$) for seed yield estimated by both harvest methods (Table III). The overall means for the plot and subsample methods were 191.0 and 187.8 kg/ha, respectively (Table IV). The coefficients of variation were 37.48 percent for the plot method and 43.36 percent for the subsample method. The 9959 clone had the highest yield (387.1 kg/ha) for the plot method. The seed yield value of 376.7 kg/ha for the Guymon X 9959 F_1 generation was greatest for the subsample method. The SS-16 X SS-21 F_1 generation had the lowest mean seed yield for the plot and subsample methods with

TABLE III
ANALYSIS OF VARIANCE FOR SEED YIELD

Response Variable	df	Mean Square
Plot Harvest Method		
Entry	11	63.58 **
Error	33	4.924
Subsample Harvest Method		
Entry	11	15.743**
Error	33	1.621

** Significant at the 0.01 level.

TABLE IV
SEED YIELD OF BERMUDAGRASS PARENTAL CLONES
AND THEIR F₁ AND F₂ GENERATIONS^{1/}

Parent or Progeny Population	Seed Yield Estimates	
	Plot Method ^{2/} kg/ha	Subsample Method ^{3/} kg/ha
Guymon	125.8ef	135.5ed
9945	38.7f	24.4e
Guymon X 9945 Syn-1	194.5de	233.3cd
Guymon X 9945 Syn-2	309.0abc	303.3abc
9959	387.1a	346.7ab
Guymon X 9959 Syn-1	354.8ab	376.7a
Guymon X 9959 Syn-2	288.1abcd	236.7bcd
SS-16	48.4f	37.8e
SS-21	203.2cde	212.2cd
SS-16 X SS-21 Syn-1	35.5f	18.9e
SS-16 X SS-21 Syn-2	60.6f	65.6e
LCB Polycross	250.0bcd	246.7bcd
Average	191.0	187.8
Prob > F	0.001	0.001
CV%	37.48	43.36

^{1/} Duncan's Multiple Range Test is also presented. Means with the same letter are not significantly different.

^{2/} Each mean has four seed yield observations from a 3.10m² area.

^{3/} Each mean has 12 seed yield observations from a 0.09m² area.

respective values of 35.5 and 18.9 kg/ha.

The results from both harvest methods indicate there was a decrease in seed yield from the F_1 to the F_2 generation for the Guymon X 9959 family while the Guymon X 9945 and SS-16 X SS-21 families had increased seed yields with advancing generations. The increase in seed yield between the Guymon X 9945 F_1 and F_2 generations with respective means of 194.5 and 309.0 kg/ha for the plot method was significant ($P < 0.05$). The seed yield increase for the Guymon X 9945 F_1 and F_2 generations with mean values of 233.3 and 303.3 kg/ha, respectively, was not significant. The seed yield decrease between the F_1 and F_2 generations of the Guymon X 9959 family, with respective plot harvest means of 354.8 and 288.1 kg/ha, were not significantly different. The seed yield decrease for the subsample method, however, was significant ($P < 0.05$) for the Guymon X 9959 F_1 and F_2 generations with mean values of 367.7 and 236.7 kg/ha, respectively. The seed yield increase between the SS-16 X SS-21 F_1 and F_2 generations was not significant for either harvest method. The estimated mean seed yields for the plot and subsample methods were very closely related (Figure 1).

Yield Components

Variation among entries was significant ($P < 0.01$) for all yield component variables evaluated in the study (Table V). The OP and SP heads differed significantly for percent seed set ($P < 0.01$), number of seeds per head ($P < 0.01$), and the number of florets per head ($P < 0.05$). The first order entry by pollination mode (OP vs SP) interaction was significant ($P < 0.01$) for percent seed set and number of seeds per head. The Guymon clone had the highest mean head density (278.7 heads/0.09m²) and

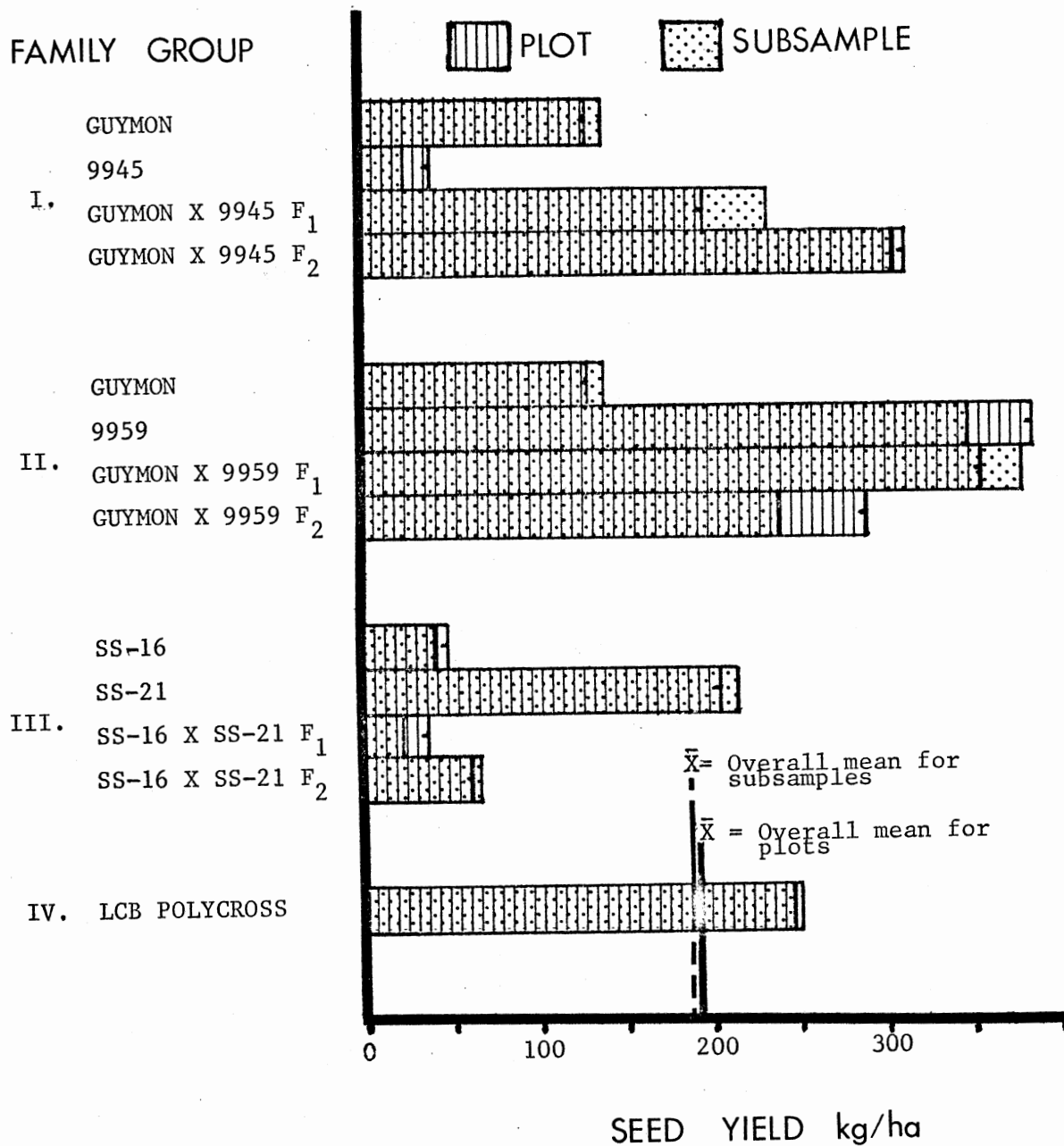


Figure 1. Histogram of Bermudagrass Seed Yield Estimated from Plot and Subsample Harvest Methods Grouped by Family.

TABLE V
ANALYSIS OF VARIANCE FOR YIELD COMPONENTS

Response Variable	df.	Mean Square
Head Density		
Entry	11	43,008.310**
Error	33	2,800.842
Racemes/Head		
Entry	11	16.538**
Pollination mode	1	0.104
Entry * Pollination	11	1.320
Error	69	1.150
Florets/Head		
Entry	11	180,878.283**
Pollination mode	1	68,040.337*
Entry * Pollination	11	6,996.031
Error	69	10,150.307
Seeds/Head		
Entry	11	24,039.312**
Pollination mode	1	460,031.484**
Entry * Pollination	11	18,340.728**
Error	69	1,783.884
Percent Seed Set		
Entry	11	0.594**
Pollination mode	1	9.912**
Entry * Pollination	11	0.432**
Error	69	0.034

** Significant at the 0.01 level.

* Significant at the 0.05 level.

the SS-16 X SS-21 F_1 generation had the lowest mean value (68.8 heads/0.09m²) among the entry means reported in Table VI. The overall mean was 162.5 heads per 0.09m² and the coefficient of variation was 19.14 percent. The slight increase in head density between F_1 and F_2 generations for the Guymon X 9945 and Guymon X 9959 families was not significant. The increase in head density between the SS-16 X SS-21 F_1 and F_2 generations with respective values of 68.8 and 135.2 per 0.09m² was significant ($P < 0.05$). The F_2 generations of the Guymon X 9945 and Guymon X 9959 families with respective means of 212.5 and 194.4 heads per 0.09m² were not significantly different, however, both of these F_2 generations were significantly greater ($P < 0.05$) than the SS-16 X SS-21 F_2 generation which had 135.2 heads per 0.09m² (see also Figure 2).

Mean number of racemes per head varied from 4.05 for the Guymon clone to 6.05 for the SS-16 clone (Table VI). The overall mean was 5.02 racemes per head and the coefficient of variation was 4.32 percent. Differences between the F_1 and F_2 generations for the number of racemes per head within all three families were not significant. The F_2 generations of the Guymon X 9945 and Guymon X 9959 families (with respective mean values of 4.86 and 4.66 racemes/head) had significantly fewer ($P < 0.05$) racemes per head than the SS-16 X SS-21 F_2 generation (5.66 racemes/head) (see also Figure 3).

The high mean value for the number of florets per OP head was 337.52 for the SS-16 clone; the lowest mean number of florets for OP heads was 154.15 for the 9945 clone (Table VI). The overall mean for the number of florets per OP head was 241.22 and the coefficient of variation was 12.24 percent. The highest mean values for the number of florets per SP head were the SS-16 and SS-21 clones at 286.52 and 291.15, respec-

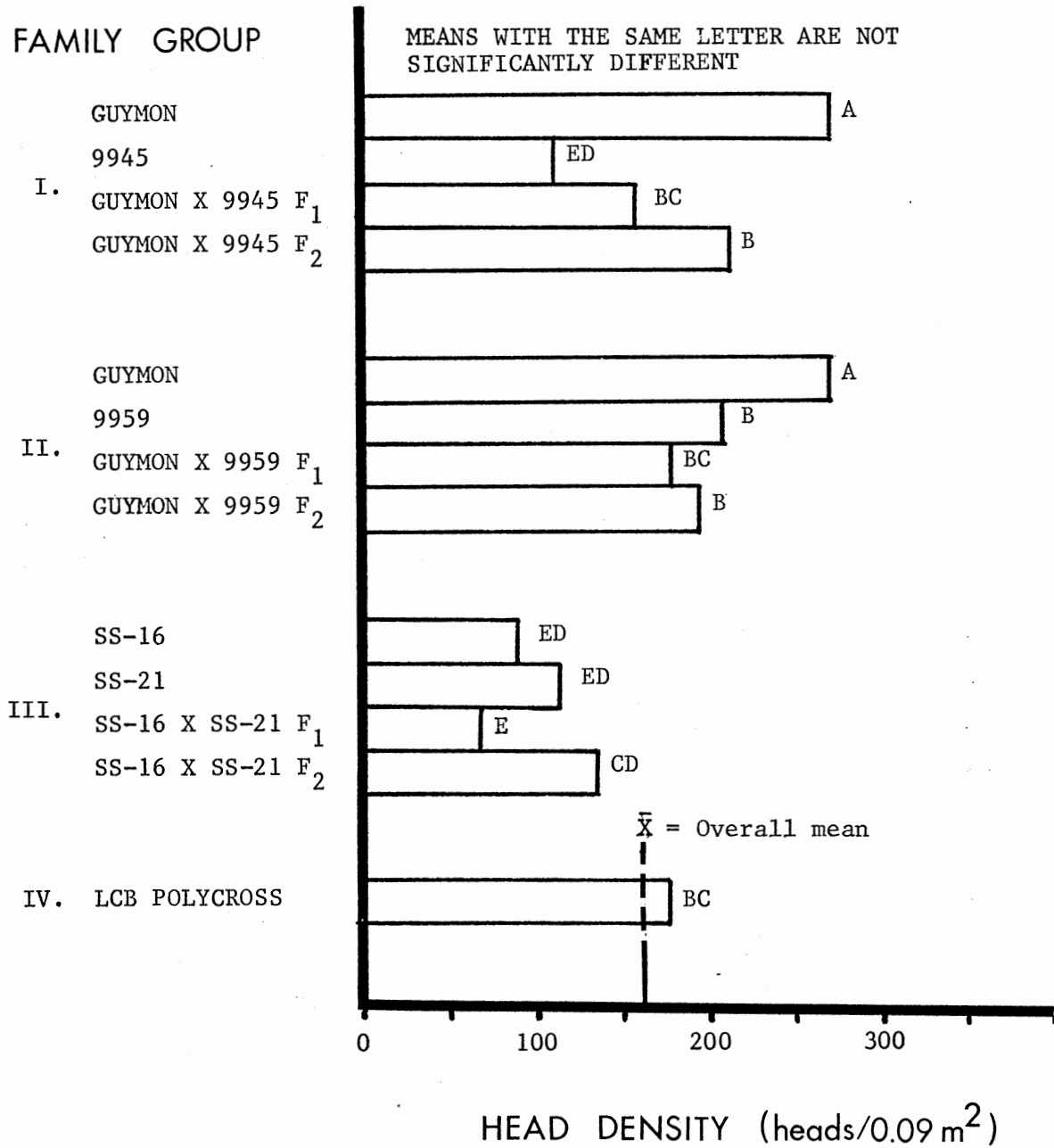


Figure 2. Histogram of Bermudagrass Head Density Grouped by Family.

TABLE VI

SEED YIELD COMPONENTS OF OPEN- AND SELF-POLLINATED BERMUDAGRASS HEADS
OF PARENTAL CLONES AND THEIR F₁ AND F₂ GENERATIONS

Parent or Progeny Population	No. of Heads ^{2/} per 0.09m ²	No. of Racemes ^{3/} per Head	No. of Florets ^{4/} per Head		No. of Seeds ^{4/} per Head		Seed Set ^{4/} 'Percentage	
	OP	OP + SP	SP	OP	SP	OP	SP	OP
Guymon	278.7a	4.74cd	195.0cd	213.9c	0.28b	20.98def	0.13b	10.27ef
9945	111.5ed	5.00c	149.9d	154.2d	0.25b	13.12f	0.14b	8.19ef
Guymon X 9945 Syn-1	159.7bc	4.85c	220.5bc	230.0c	1.42b	42.25cde	0.65b	19.31de
Guymon X 9945 Syn-2	212.5b	4.86c	217.9bc	223.2c	2.90ab	47.08cd	1.11b	22.85cd
9959	210.5b	4.50d	204.8c	209.3c	6.30ab	83.60ab	3.23ab	42.00ab
Guymon X 9959 Syn-1	181.3bc	4.68cd	190.9cd	212.7c	6.78a	93.75a	5.03a	45.57a
Guymon X 9959 Syn-2	194.4b	4.66cd	188.0cd	215.4c	2.05ab	61.85bc	1.46ab	31.28bc
SS-16	91.0ed	6.05a	286.5a	337.5a	1.58b	12.60f	0.46b	4.24f
SS-21	114.0ed	5.01c	291.2a	288.6b	2.10ab	74.85ab	0.80b	26.51cd
SS-16 X SS-21 Syn-1	68.8e	5.39b	266.0ab	304.0ab	0.55b	9.28f	0.20b	2.96f
SS-16 X SS-21 Syn-2	135.2cd	5.66b	260.8ab	297.4ab	4.03ab	15.78ef	1.33b	5.11f
LCB Polycross	175.4bc	4.90c	220.7bc	208.4c	6.75ab	87.22ab	2.75ab	42.88a
Average	162.5	5.02	224.4	241.2	3.08	46.86	1.44	21.76
Prob > F	0.001	<0.001	0.001	0.001	0.118	0.001	0.113	0.001
CV%	19.14	4.32	13.85	12.24	139.78	38.85	158.91	35.13

^{1/} Duncan's Multiple Range Test is also presented. Means with the same letter are not significantly different.

^{2/} Each mean has 12 observations.

^{3/} Each mean has 80 observations.

^{4/} Each mean has 40 observations.

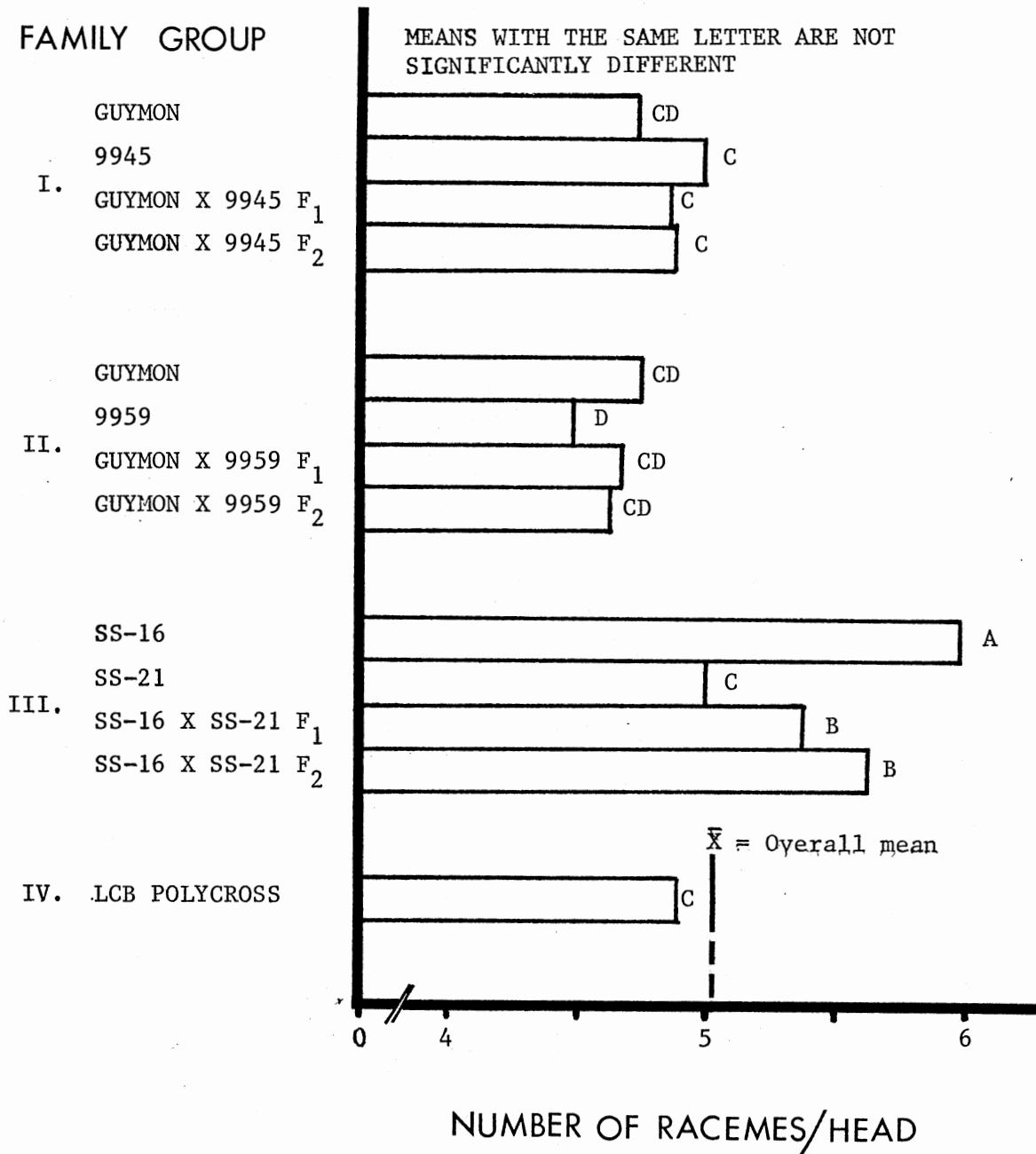


Figure 3. Histogram of Raceme Number of Bermudagrass Heads Grouped by Family.

tively. The low mean was 149.95 florets per SP head for the 9945 clone. The overall mean number of florets per SP head was 224.38 and the coefficient of variation was 13.85 percent. Differences between the F_1 and F_2 generation for number of florets per SP heads within each of the three families were not significant (see also Figure 4).

The overall means for the number of seeds for OP and SP heads were 46.86 and 3.08, respectively. The coefficient of variation for number of seeds per OP head was 38.85 percent while the value for SP heads was extremely high at 139.78 (Table VI). The highest mean number of seeds per OP head was 93.75 for the Guymon X 9959 F_1 generation. The SS-16 X SS-21 F_1 generation had the lowest mean value of 9.28 seeds per OP head. The decrease between the Guymon X 9959 F_1 and F_2 generation means with respective values of 93.75 and 61.85 seeds per head was significant ($P < 0.05$). However, no significant differences were observed between the F_1 and F_2 generations of the Guymon X 9945 and SS-16 X SS-21 families where both had greater values for the F_2 than for the F_1 . The number of seeds per SP heads were much lower than the number of seeds per OP heads. Variation among entries for the number of seeds per SP heads was not significant (Table VI). The highest mean value of 8.78 seeds per SP head recorded for the Guymon X 9959 F_1 generation was nearly equal to the low mean value reported for mean number of seeds per OP head for the SS-16 X SS-21 F_1 generation. The Guymon and 9945 clones, and the SS-16 X SS-21 F_1 generation mean number of seeds per SP head were all below one. Significant differences were absent between the F_1 and F_2 populations in the three families (see also Figure 5).

Percent seed set of OP heads was much higher than the values for SP heads. The overall mean for the OP percent seed set was 21.76 per-

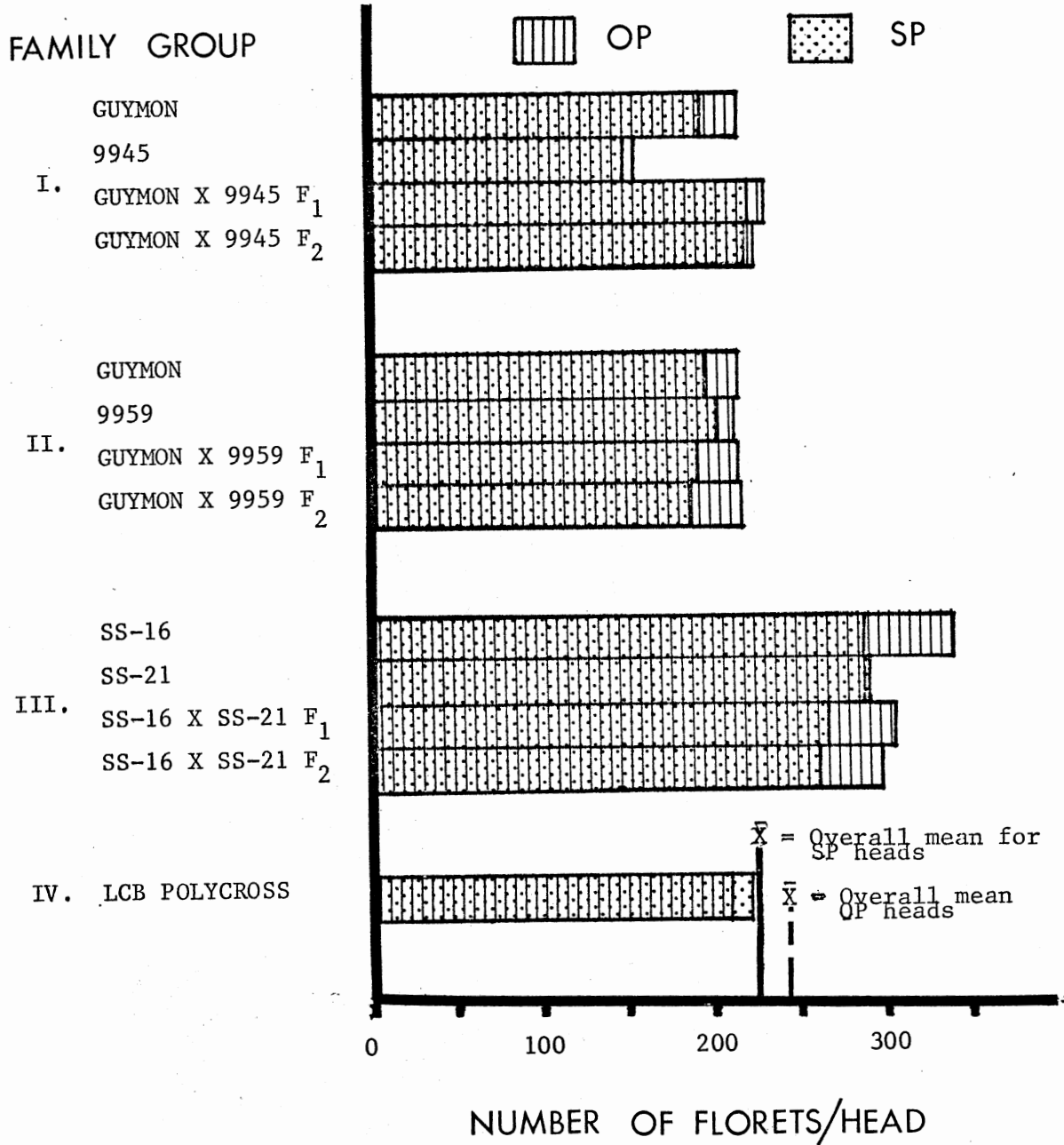


Figure 4. Histogram Depicting the Number of Florets on Open- and Self-Pollinated Bermudagrass Heads Grouped by Family.

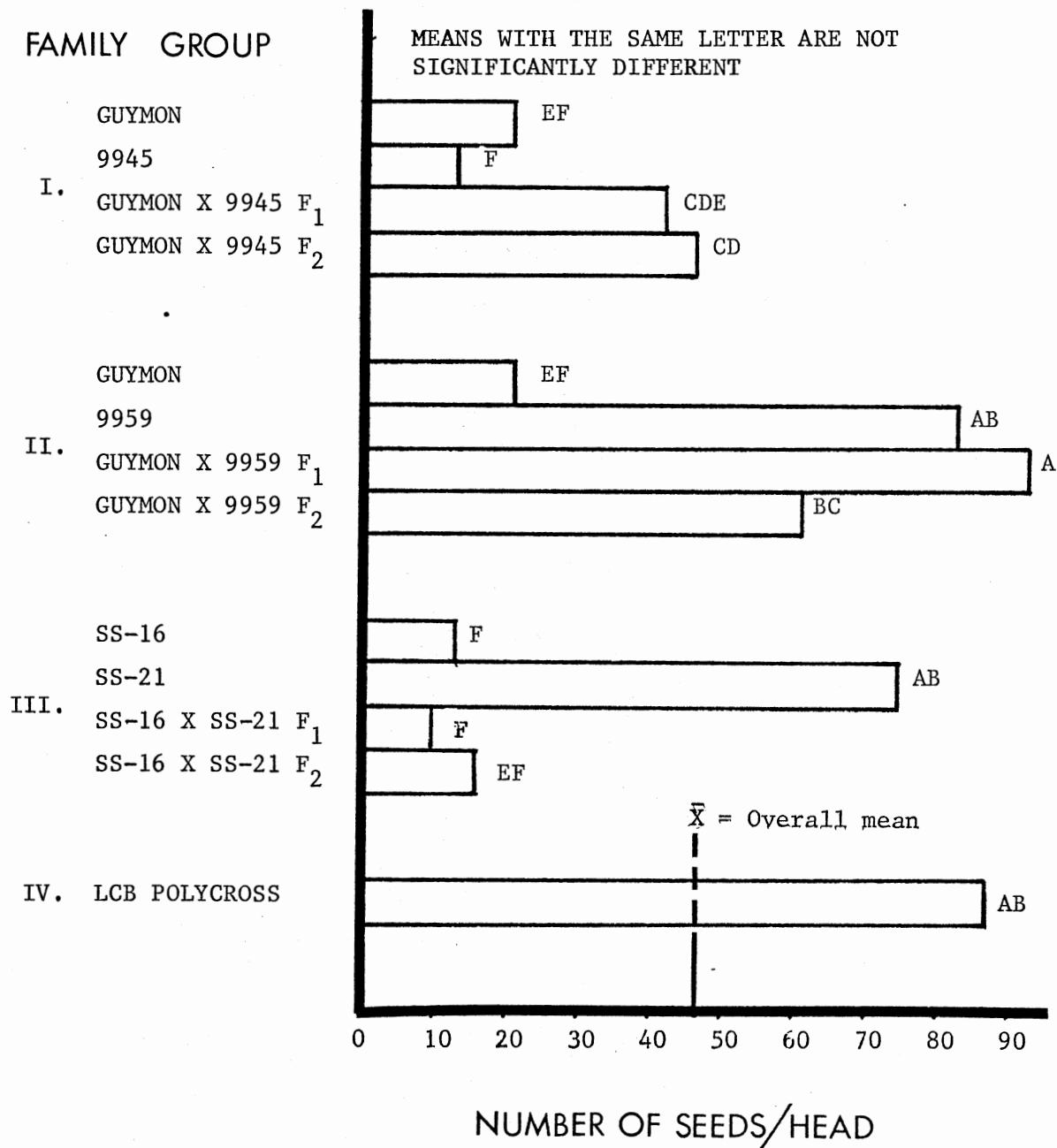


Figure 5. Histogram Depicting the Number of Seeds per Open-Pollinated Bermudagrass Heads Grouped by Family.

cent and the coefficient of variation was 35.13 percent (Table VI). The Guymon X 9959 F_1 generation had the highest mean percent seed set of 45.57 percent and the low mean value was 2.96 percent recorded for the SS-16 X SS-21 F_1 generation. A significant ($P < 0.05$) decrease in percent seed set occurred between the Guymon X 9959 F_1 and F_2 generations with respective values of 45.57 and 31.28. The percent seed set increase between the F_1 and F_2 generations of the Guymon X 9945 and SS-16 X SS-21 families was not significant. Variation among entries for percent seed set of SP heads was not significant but the coefficient of variation was extremely high at 158.91 percent (Table VI). The Guymon X 9959 F_1 generation had the highest mean SP percent seed set of 5.03 percent and six of the entries had mean SP percent seed set values less than one. The overall mean for SP percent seed set was 1.44 percent and no significant differences were found between the means of F_1 and F_2 populations (see also Figure 6).

Pollen Viability Potential

Significant variation among entries was observed for pollen viability as measured by filled, half-filled, and empty pollen grains with regard to the amount of starch present (Table VII). The overall means for filled, half-filled, and empty pollen grains were 41.44, 33.66, and 24.80 percent, respectively. The filled and empty pollen grain categories had respective coefficients of variation of 15.22 and 18.31 percent (Table VIII). The 9959 clone had the highest mean percentage of starch filled pollen grains at 56.75 and the lowest mean percentage of 8.95 empty pollen grains. The SS-16 X SS-21 F_1 population had the highest mean percentage value (49.50) for empty pollen grains and the

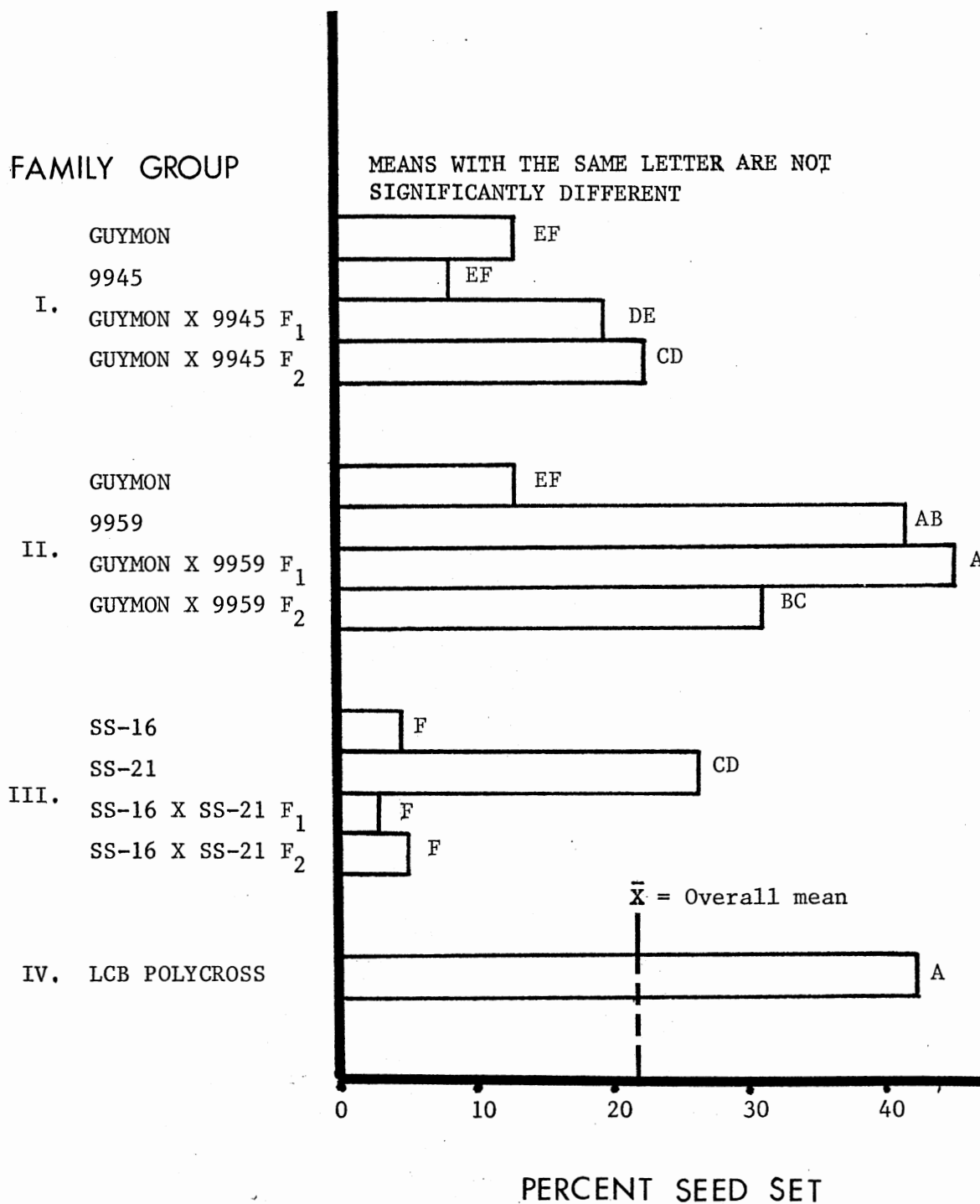


Figure 6. Histogram of Percent Seed Set for Open-Pollinated Bermuda-grass Heads Grouped by Family.

TABLE VII
ANALYSIS OF VARIANCE FOR POLLEN VIABILITY

Response Variable	df	Mean Square
Percent Filled Pollen		
Entry	11	2,079.405**
Error	33	671.977
Percent 1/2-Filled Pollen		
Entry	11	852.180**
Error	33	287.375
Percent Empty Pollen		
Entry	11	4,258.423**
Error	33	971.895

** Significant at the 0.01 level.

TABLE VIII
 PERCENT FILLED, HALF-FILLED, AND EMPTY POLLEN
 GRAINS WITH REGARD TO STARCH FOR PARENTAL
 BERMUDAGRASS CLONES AND THEIR
 F₁ AND F₂ GENERATIONS^{1/}

Parent or Synthetic Progeny	Filled ^{2/}	1/2-Filled ^{2/}	Empty ^{2/}
----- % -----			
Guymon	31.58bcd	34.38abcd	33.58abc
9945	45.46abc	39.12ab	15.29cd
Guymon X 9945 Syn-1	41.42abc	30.17bcd	28.33bcd
Guymon X 9945 Syn-2	41.50abc	24.88d	33.50abc
9959	56.75a	34.25abcd	8.95d
Guymon X 9959 Syn-1	42.92abc	42.04a	15.00cd
Guymon X 9959 Syn-2	48.08ab	36.83abc	15.00cd
SS-16	43.29abc	29.25bcd	27.00bcd
SS-21	45.50abc	40.46ab	14.00cd
SS-16 X SS-21 Syn-1	23.58d	26.62cd	49.50a
SS-16 X SS-21 Syn-2	28.50cd	26.88cd	44.38ab
LCB Polycross	48.71ab	39.04ab	13.04cd
Average	41.44	33.66	24.80
Prob > F	0.006	0.008	0.0007
5% LSD	15.22	9.96	18.31
CV%	25.54	20.56	51.32

^{1/} Duncan's Multiple Range Test is also presented. Means with the same letter are not significantly different.

^{2/} Each mean has 24 observations.

lowest mean percentage (23.58) for filled pollen grains. The coefficient of variation for percent half-filled pollen grains was 9.96 with the Guymon X 9959 F_1 generation having the highest mean percentage value of 42.04. The data for the three pollen categories are superimposed upon each other for each of the twelve entries in the study and graphically presented in Figure 7. The results indicate that as the number of filled pollen grains increases the number of empty pollen grains decreases. The half-filled pollen grains follow a similar pattern to those values plotted for filled pollen grains, however, there was no significant variation or interaction between the pollen categories. The differences between the F_1 and F_2 generations for all three pollen categories were not significant.

Orthogonal Contrasts

Significant variation or interaction between the F_1 and F_2 generations was not observed for: 1) either method of estimating seed yield, 2) any of the yield components with the exception of head density, 3) for the three pollen categories (Table IX). Highly significant variation ($P < 0.01$) was observed between the Guymon X 9945 family (excluding the Guymon clone) and the Guymon X 9959 family (excluding the Guymon clone) for percent seed set of OP and SP heads, number of seeds per OP head, number of racemes per head, and estimated seed yield determined by both harvest methods (Table X). Significant variation ($P < 0.05$) occurred for number of seeds per SP head, head density and the percent half-filled and empty pollen grains. Interaction between the Guymon X 9945 and Guymon X 9959 families was significant ($P < 0.01$) for percent seed set and number of seeds for OP heads, head density, and estimated

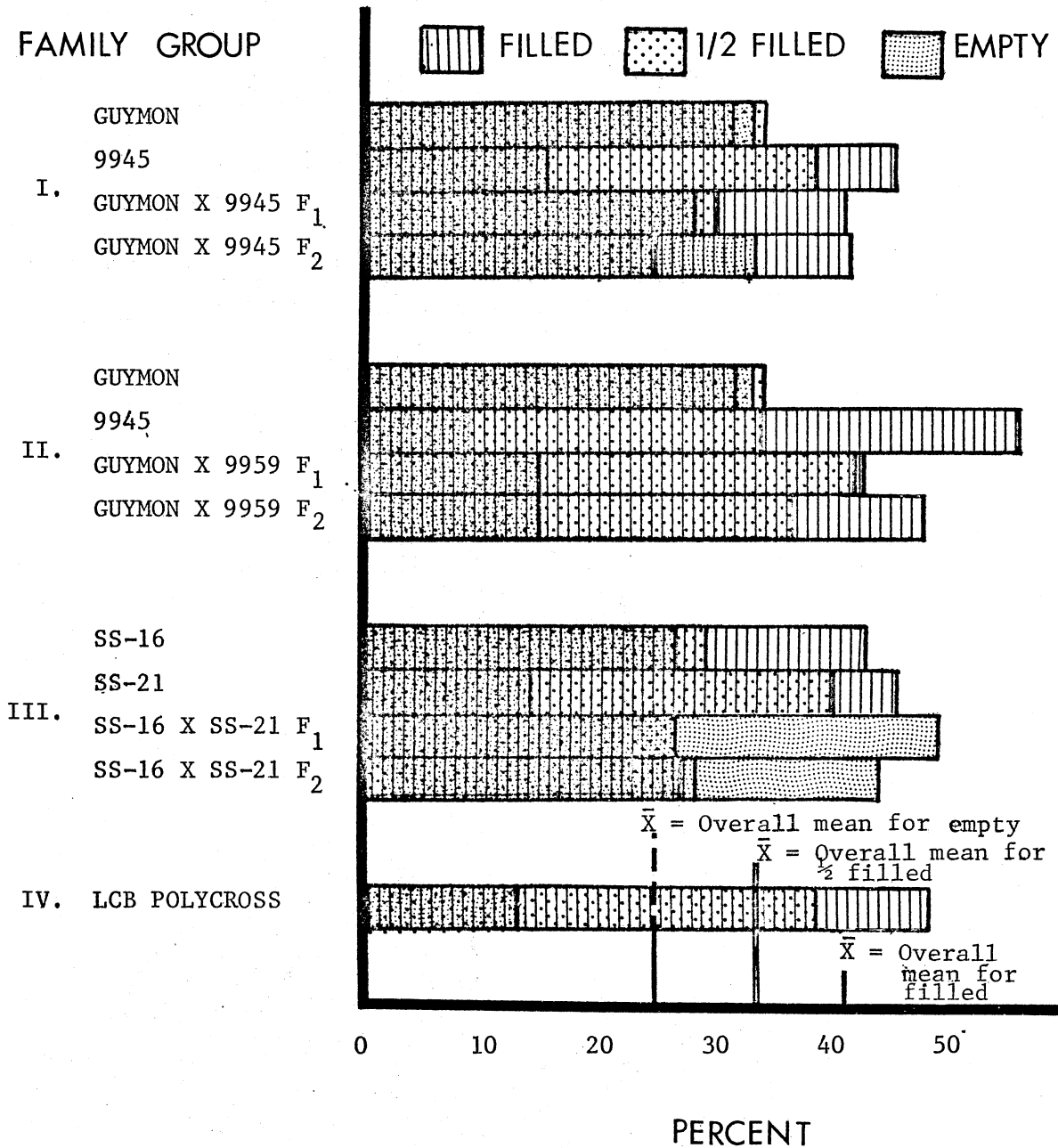


Figure 7. Histogram of Percent Filled, Half-Filled, and Empty Pollen Grains with Regard to Starch.

TABLE IX
 ORTHOGONAL CONTRASTS OF F₁ AND F₂ GENERATION

Response Variable		F ₁ vs F ₂		F ₁ * F ₂ Interaction	
		Mean Square (df = 1)	Prob>F	Mean Square (df = 2)	Prob>F
% Seed Set	OP	0.005	0.365	0.006	0.355
	SP	0.001	0.487	0.001	0.325
Seeds/Head	OP	282.220	0.363	408.778	0.305
	SP	2.100	0.739	25.714	0.263
Florets/Head	OP	75.615	0.781	41.648	0.958
	SP	74.553	0.772	51.460	0.943
Racemes/Head		0.050	0.308	0.076	0.216
Heads/0.09m ²		8791.129	0.005	5583.260	0.007
Seed Yield/0.09m ²		0.077	0.707	0.475	0.422
Seed Yield/3.10m ²		3.450	0.409	1.726	0.707
% Filled Pollen		68.907	0.438	37.955	0.715
% ½-Filled Pollen		70.047	0.235	55.188	0.328
% Empty Pollen		0.001	0.998	39.613	0.784

TABLE X
 ORTHOGONAL CONTRASTS OF FAMILIES I AND II

Response Variable		I vs II		I * II Interaction	
		Mean Square (df = 1)	Prob>F	Mean Square (df = 2)	Prob>F
% Seed Set	OP	0.312	0.009	0.034	0.007
	SP	0.004	0.001	0.001	0.217
Seeds/Head	OP	1267.041	0.001	1603.755	0.014
	SP	104.722	0.024	38.785	0.140
Florets/Head	OP	19.761	0.412	4665.548	0.014
	SP	602.001	0.887	3097.030	0.04
Racemes/Head		0.510	0.002	0.065	0.264
Heads/0.09m ²		4826.115	0.032	7732.310	0.002
Seed Yield/0.09m ²		7.965	0.001	6.151	0.001
Seed Yield/3.10m ²		153.520	0.001	66.430	0.001
% Filled Pollen		250.260	0.144	47.962	0.655
% ½-Filled Pollen		239.612	0.032	187.977	0.030
% Empty Pollen		971.130	0.020	74.574	0.635

seed yield from both harvest methods. The number of seeds per OP head, number of florets per OP and SP heads, and the percent half-filled pollen grains had significant interaction ($P < 0.05$) between the two families. There was no significant interaction observed for percent seed set and number of seeds per SP heads, number of racemes per head, and percent filled and empty pollen grains. No significant variation resulted between the 9959 clone, and Guymon X 9959 F_1 and F_2 generations or the 9945 clone, Guymon X 9945 F_1 and F_2 generations for the yield components with the exceptions of head density and number of florets per SP head. Significant variation ($P < 0.05$) also occurred for seed yield estimated from hand-clipped subsamples. Variation within the two families for seed yield estimated from the plot harvest method and the three pollen categories was not significant.

LCB Polycross

The LCB Polycross seed yield means for both harvest methods were greater than the overall mean, however significantly lower ($P < 0.05$) than the highest yielding entry for both harvesting methods. Mean head density for the LCB Polycross was also greater than the overall mean, yet significantly less ($P < 0.05$) than the best entry. Number of racemes per head was not significantly greater than the entry with the lowest mean number of racemes, however was significantly ($P < 0.05$) less than the highest mean for the number of racemes per head. The LCB Polycross number of florets for OP and SP heads was significantly different ($P < 0.05$) from the highest and lowest entry means. There was no significant differences between the LCB Polycross and the entry for the highest number of seeds and percent seed set for OP and SP heads.

CHAPTER V

SUMMARY AND CONCLUSIONS

The results suggest significant variation exists among the bermudagrass entries for the response variables evaluated in this study with the exceptions of number of seeds and percent seed set for SP heads. The seed yield decreased for the Guymon X 9959 family with advancing generations while it increased for the Guymon X 9945 and SS-16 X SS-21 families. However, a significant decrease was recorded for the Guymon X 9959 family for the subsample method only and a significant increase occurred for the Guymon X 9945 family for the plot harvest method only. The slight increases found for head density between the F_1 and F_2 generations for the Guymon X 9945 and Guymon X 9959 families were not significant. The increase in head density between the SS-16 X SS-21 F_1 and F_2 generations was significant, however, the head density in the F_2 generation was also significantly less than the F_2 generations of the Guymon X 9945 and Guymon X 9959 families which were not significantly different from each other.

Significant differences for number of racemes per head were not observed between the F_1 and F_2 generations within any of the three families. The SS-16 X SS-21 F_2 generation had a significantly greater number of racemes per head than the number of racemes for the Guymon X 9945 and Guymon X 9959 F_2 generation heads. A significant difference between

the F_1 and F_2 generations for the number of florets per head within the three families was not observed. Moreover, the number of florets per head for the SS-16 X SS-21 F_2 generation was not significantly greater than the Guymon X 9945 F_2 generation, however, it was significantly greater than the F_2 generation of the Guymon X 9959 family. The number of seeds per head decreased from the F_1 to the F_2 generations in the Guymon X 9959 family. A slight increase in seeds per head was observed from the F_1 to the F_2 generations of the Guymon X 9945 and SS-16 X SS-21 families, however, this increase was not significant. The results for percent seed set were similar with a significant decrease between the F_1 and F_2 generations for the Guymon X 9959 family while the increases in percent seed set for the Guymon X 9945 and SS-16 X SS-21 F_1 and F_2 generations were not significant. The differences found between the F_1 and F_2 generations in the pollen viability study were not significant in any of the three families.

Variation and interaction for orthogonal contrasts made among the F_1 and F_2 generations was not significant for any of the response variables evaluated with the exception of head density. Variation for contrasts made between the Guymon X 9945 and Guymon X 9959 families were significant for all response variables evaluated with the exceptions of the number of florets per OP and SP heads and percent filled pollen. Interaction between the two families was significant for seed yield estimated by both harvest methods and yield components of OP heads.

The outstanding clone and F_1 population appear to be 9959 and Guymon X 9959, respectively. However, the significant decrease in seed yield for the subsample method, number of seeds per head, and percent

seed set that occurred between the Guymon X 9959 F_1 and F_2 generations may be evidence for the effect of inbreeding depression with regard to seed yield. The increase in seed yield, head density, number of seeds per head, and percent seed set between the F_1 and F_2 generations of the Guymon X 9945 family may be evidence that this singlecross would be a likely candidate for propagation by seed since increase by seed does not decrease key yield components. The LCB polycross did not have outstanding values for the response variables studied, however, it was consistent and this may merit more attention in future studies.

The self-incompatibility of SP bermudagrass heads is in good agreement with the results presented in previous studies (Burton, 1965; Kneebone, 1967; Richardson, Taliaferro, and Ahring, 1978). Work is now needed, however, in the area of the amount of self-pollination that occurs in isolation under natural conditions. The relatively good seed yields under adverse conditions by some of the parental clones and F_1 and F_2 generations during the 1980 summer support data that high seed yields are attainable. Further data are needed to determine the effects of advancing generations on fertility, however, the effects measured in 1980 are far less deleterious than expectations based on the results extrapolated from other cross-pollinated crops. The results from pollen viability estimates shows some correlation with seed yield. A more extensive analysis of these data and similar studies should be completed before any conclusions regarding the significance of good pollen viability and good seed yield can be drawn. The effectiveness of polycross synthetics for bermudagrass varietal improvement also needs additional work.

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