

ANALYSES OF SEED AND FORAGE PRODUCTION
TRAITS IN BIG BLUESTEM,
ANDROPOGON GERARDII
VITMAN

By

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ANALYSES OF SEED AND FORAGE PRODUCTION

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ANDROPOGON GERARDII

VITMAN

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PREFACE

I have considered my research of native plant species a labor of love rather than work. Finding new and interesting facts about often neglected species has always been rewarding and exciting to me, and my studies of big bluestem are no exception to that rule. A series of field and laboratory experiments were conducted on big bluestem characterizing its vegetative and reproductive traits. The results of those investigations are contained herein and are presented in five parts. Part I, "Pollen Size and Pollen Viability in Big Bluestem as Related to Spikelet Type," was published in the 1989 November-December issue of Crop Science; Part V, "Occurrence of Conioscinella nuda (Diptera: Chloropidae) in Native and Introduced Bluestem," was published in the 1989 July issue of the Journal of the Kansas Entomological Society. Parts II, III, and IV are to be submitted as individual papers to Crop Science.

Thanks are extended to the Agronomy Department of Oklahoma State University and to the United States Department of Agriculture, Agricultural Research Service, Plant Science & Water Conservation Laboratory, Stillwater, for the use of their facilities and equipment and for the opportunity to conduct these studies. Thanks also go to Dr. C. M. Taliaferro, my major adviser and committee chairman,

for his time, effort, and moral support. Likewise, appreciation is expressed to Dr. R. W. McNew, Dr. L. G. Morrill, Dr. R. J. Tyrl, and Dr. L. M. Verhalen, my graduate committee, for their help, advice, and criticism during this research project. I appreciate very much the time and effort Mr. W. L. (Bill) Richardson spent on making the big bluestem crosses used in these studies. Without his help, these studies would not have been possible.

Special thanks go to Dr. R. M. Ahring for the wealth of knowledge he taught me about forage seed production and seed technology, his encouragement throughout this project, and last of all for his friendship. Finally, thanks without end are given to my wife Merry and to my parents Betty A. and George W. Springer for their love and encouragement over all these years.

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PART I

POLLEN SIZE AND POLLEN VIABILITY IN BIG
BLUESTEM AS RELATED TO SPIKELET TYPE

ABSTRACT

The utilization of big bluestem, Andropogon gerardii Vitman, for revegetation is limited by seed availability. Although several factors influence seed production in cross-pollinated species, effective pollination is essential for seed set. Objectives of this study were to compare pollen grain size and viability from pedicellate and sessile spikelets of six big bluestem accessions in each of 2 years. Coulter Counter measurements of mean pollen diameter varied significantly with spikelet type and year. The mode pollen diameter varied with accession, spikelet type, and year. Mean and mode pollen diameters were consistently larger in sessile than pedicellate spikelets. Differences in pollen viability were attributable to accession, spikelet type, and an accession by spikelet interaction. Among accessions, pedicellate-spikelet pollen viability varied from 4 to 78% averaged over years, and in two accessions was nearly as high as the sessile spikelet. Phenotypic variation in pedicellate-spikelet pollen viability suggests that selection for this trait should be effective, assuming heritable variation of sufficient magnitude.

INTRODUCTION

Big bluestem, a perennial warm-season grass indigenous to much of North America, is considered the most important warm-season forage grass in the tall-grass prairie regions of the continent (Gould and Shaw, 1983). Big bluestem is cross-pollinated, individual plants typically are highly heterozygous, and the species is highly heterogeneous (Law and Anderson, 1940). In spite of widespread occurrence, the species is an unpredictable seed producer (Cornelius, 1950), which limits available seed for revegetation.

The inflorescence of big bluestem has paired spikelets. The pedicellate spikelet floret is either bisexual, staminate, or neuter, while the sessile spikelet floret is bisexual. Boe et al. (1983) found highly significant differences in pedicellate-spikelet seed yield among big bluestem accessions from different sites in eastern South Dakota. In their study, pedicellate-spikelet seed yield was correlated positively with total seed yield, and they considered it feasible to increase seed yield potential by selecting for increased seed set in pedicellate spikelets. They found that caryopses from pedicellate spikelets were smaller than those from sessile spikelets.

Because effective pollination is essential for seed set in big bluestem, it is of interest to know if differences exist in the size and/or viability of pollen from the pedicellate and sessile spikelets. Pollen size affects distance of travel via wind dissemination, and may be related to viability. We report here the results of a study to determine the size and viability of pollen from pedicellate and sessile spikelets of selected big bluestem accessions.

MATERIALS AND METHODS

Size and viability of pollen from the pedicellate and sessile spikelets of six big bluestem accessions were measured in 1986 and 1987. Accession origin, pollen origin, total number of pollen grains sized for determination of mean and mode diameter, and total number of pollen grains tested for viability estimates of each accession are given in Table 1. Pollen grain size was measured with a Coulter Counter model Z_{B1} and Coulter Channelyzer unit, interfaced with an IBM-PC microcomputer. While the Coulter Counter is primarily used in medicine for counting and sizing blood cells, it also can be used for counting and sizing minute particles such as fungal spores and pollen grains (Brotherton, 1969). As particles are sucked through the aperture of the Coulter Counter, a resistance forms between the internal and external aperture electrodes. The resistance is caused by the particle as it displaces the

electrolyte solution. The resultant voltage drop is proportional to the size (volume) of the particle. Regular and irregular shaped particles can be counted and sized with the Coulter Counter. Pollen grains of big bluestem are spherical without much sculpturing, which simplifies determination of their diameters from volumetric measurements. The instrument was calibrated using 22.5- μm polystyrene reference particles.

Pollen samples were from plants in a field nursery established in 1985 by planting two ramets of each accession in a completely random design. In 1986 and 1987, five inflorescences, 1 to 2 days from anthesis, were collected from each plant of each accession. The same two plants of each accession were studied both years. Undehisced anthers were dissected from the pedicellate and sessile spikelets of each plant of each accession, and respectively placed into 35-mL Coulter Accuvette II sample vials. Approximately 20 mL of Coulter Isoton II balanced electrolyte solution was added to each vial. Vials were sonicated 4 to 5 min using a 455-mL ultrasonic cleaner to release pollen grains from the anthers. Empty anthers and anther fragments were removed from the pollen-anther solution using a dropper pipette. Purified pollen samples were sonified for 10 to 20 sec prior to analysis to disperse the grains.

Viability was estimated for each pollen sample. Prior to adding the isoton solution, five anthers were selected from each vial and squashed on a microscope slide in a drop

of aniline blue in lactophenol (Radford et al., 1974). Approximately 150 to 200 pollen grains were scored for viability based on stainability.

Data collected from the Coulter Counter were converted into a pollen-size frequency distribution. The mean and mode pollen diameters were determined for each distribution. Data were analyzed using PROC ANOVA (SAS Institute, 1985). The model was a split-split plot design with accession as the main plot factor, year as the subplot factor, and spikelet as the sub-subplot factor (Table 2).

RESULTS

Pollen Size

Differences in mean pollen diameter were attributed to spikelet type and year, while differences in mode pollen diameter were due to accession, spikelet type, and year (Table 2). Mean and mode pollen diameter averaged over accessions, spikelet types, and years were 32.4 and 32.8 μm , respectively (Table 3). Pollen diameter was greater in 1986 than in 1987. Sessile spikelets consistently contained larger pollen grains than pedicellate spikelets. Accession 1836, compared with other accessions, had a smaller mode pollen diameter. Otherwise, pollen size among accessions averaged across spikelet types and years did not differ.

Pollen Viability

Accession, spikelet type, and an accession by spikelet-type interaction accounted for significant variation for pollen viability (Table 2). Average pollen viability in sessile spikelets was 2.3 times greater than those in pedicellate spikelets (Table 3). Pollen viability in sessile spikelets range from 78% in accession 1947 to 93% in accession 1843 (Fig. 1). Among accessions, pedicellate-spikelet pollen viability ranged from 4% in accession 2397 to 78% in accession 1843.

DISCUSSION

Differences in size and viability of pollen in pedicellate and sessile spikelets of big bluestem may be induced during floral development. With one exception, the veins that form the vascular tissues of the two spikelet types are independent (Maze, 1977). According to Maze, the vascular bundles that serve the sessile spikelets descends farther down the culm than do those of the pedicellate spikelets. The vein common to both spikelets is a large central vein primarily serving the sessile spikelet.

Small pollen grain size per se may not be detrimental to reproductive potential. According to McCubbin (1944), particle size is related to distance traveled via wind dissemination. Small pollen grains tend to travel farther than large ones. Consequently, small viable grains are

capable of pollinating plants farther removed from the source plant and of potentially greater genetic difference.

Boe et al. (1983) reported significant variation in pedicellate-spikelet fertility (seed set) among big bluestem accessions. They indicated that selection for increased fertility from pedicellate spikelets should be possible. The phenotypic variation in pedicellate-pollen viability among accessions in our study suggests that selection for this trait should be effective, assuming heritable variation of sufficient magnitude. Thus, accessions 1843 and 1952, with high pedicellate- and high sessile-spikelet pollen viability, may have a higher reproductive potential than accessions 1836 and 2397, with high sessile- and low pedicellate-spikelet pollen viability.

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TABLE 1

Accession Number and Origin, Pollen Origin, Total Number of Pollen
Grains Sized for Determination of Mean and Mode Diameter, and
Total Number of Grains Viewed for Percent Pollen Viability
Estimates of Six Big Bluestem Accessions

| Accession number | Accession origin | Spikelet | Total pollen grains | |
|---------------------|---------------------|-------------|---------------------|-----------|
| | | | Sized | Viability |
| | | | ----- no. ----- | |
| 1836 | Hughes Co., OK | Pedicellate | 80 951 | 814 |
| | | Sessile | 108 016 | 859 |
| 1843 | Nowata Co., OK | Pedicellate | 66 365 | 811 |
| | | Sessile | 54 487 | 791 |
| 1947 | Parker Co., TX | Pedicellate | 76 488 | 606 |
| | | Sessile | 95 334 | 610 |
| 1952 | Bell Co., TX | Pedicellate | 100 709 | 754 |
| | | Sessile | 109 414 | 741 |
| 2397 | Nueces Co., TX | Pedicellate | 49 537 | 834 |
| | | Sessile | 104 156 | 854 |
| 2675 | Victoria Co., TX | Pedicellate | 92 421 | 805 |
| | | Sessile | 118 612 | 803 |

TABLE 2

Mean Squares in the Analyses of Variance for Percent Pollen Viability,
Mode Pollen Diameter, and Mean Pollen Diameter of Big Bluestem

| Source | df | Mean squares | | |
|--------------------------------|----|--------------|----------|----------|
| | | Viability | Mode | Mean |
| Accession | 5 | 1 744.54* | 36.69* | 7.77 |
| Plant(Accession) | 6 | 305.19 | 6.46 | 3.81 |
| Year | 1 | 0.00 | 44.89** | 10.34** |
| Year*Accession | 5 | 361.89 | 3.21 | 2.25 |
| Year*Plant(Accession) | 6 | 328.75 | 4.05 | 1.64 |
| Spikelet | 1 | 27 420.95** | 277.45** | 142.13** |
| Accession*Spikelet | 5 | 1 158.81** | 10.72 | 0.45 |
| Spikelet*Plant(Accession) | 6 | 141.06 | 7.39 | 2.34 |
| Year*Spikelet | 1 | 41.84 | 0.26 | 0.05 |
| Year*Accession*Spikelet | 5 | 29.24 | 7.85 | 2.99 |
| Year*Spikelet*Plant(Accession) | 6 | 160.81 | 9.73 | 3.95 |

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

TABLE 3

Mean Main Effects for Percent Pollen Viability, Mode Pollen Diameter, and Mean Pollen Diameter of Big Bluestem

| Variable | Level | Viability | Diameter | |
|-----------|-------------|-----------|---------------------------|-------|
| | | | Mode | Mean |
| | | -- % -- | ----- μm ----- | |
| Year | 1986 | 59.8a* | 33.4a | 33.3a |
| | 1987 | 59.8a | 31.5b | 32.4b |
| Spikelet | Pedicellate | 35.9a | 30.0a | 31.1a |
| | Sessile | 83.7b | 34.8b | 34.6b |
| Accession | 1836 | 51.1ab | 28.5a | 32.1a |
| | 1843 | 85.4c | 32.6b | 32.7a |
| | 1947 | 52.3ab | 32.0b | 31.6a |
| | 1952 | 66.0bc | 33.0b | 32.7a |
| | 2397 | 42.9a | 33.9b | 33.7a |
| | 2675 | 60.1ab | 34.6b | 34.3a |

* Means for each variable followed by the same letter are not significantly different at $P < 0.05$ (LSD test).

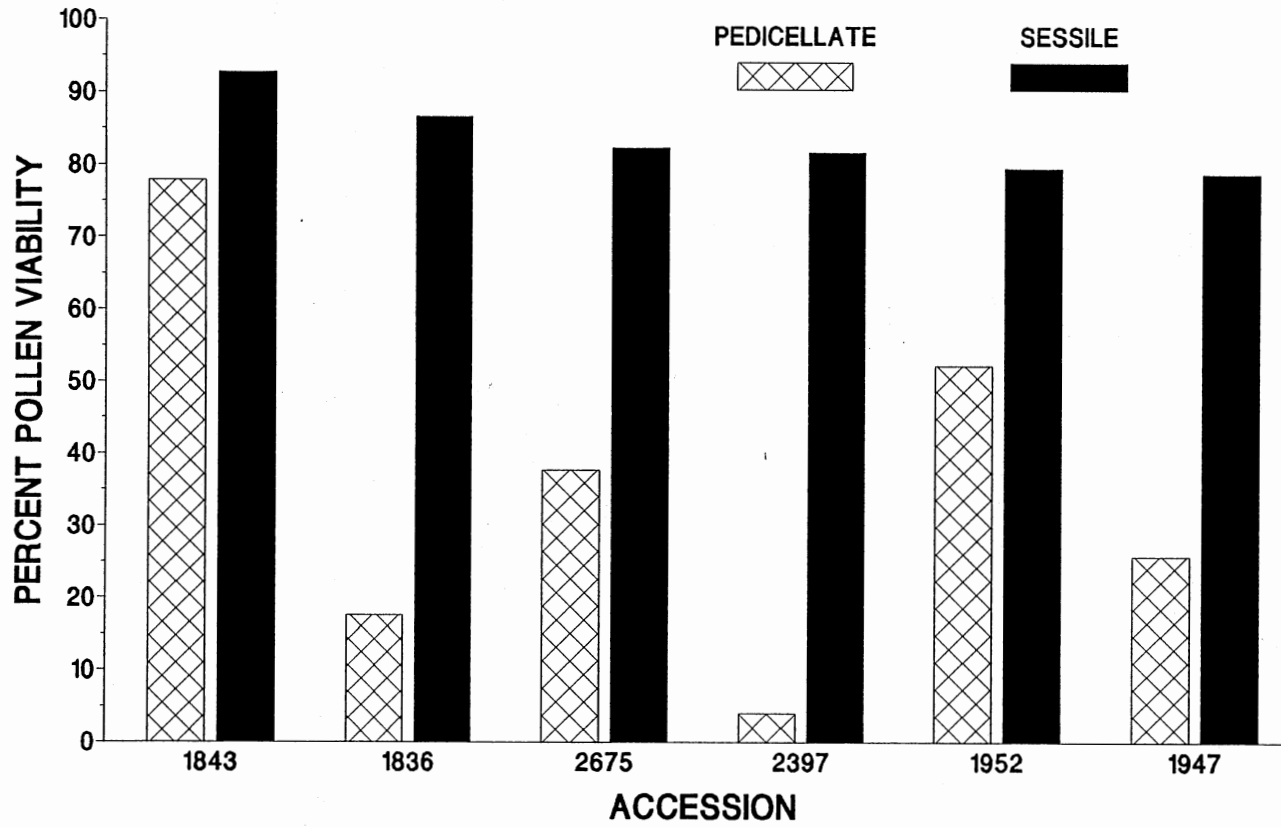


Figure 1. Mean percent pollen viability estimates from pedicellate and sessile spikelets of six big bluestem accessions averaged across 2 years.

PART II

POLLEN SIZE, POLLEN VIABILITY, AND COMBINING
ABILITY IN BIG BLUESTEM

ABSTRACT

Seed production in big bluestem, Andropogon gerardii Vitman, is limited by several factors including ineffective pollination. Pollen grain size may affect both the distance and duration of flight as well as viability. The objectives of our study were to compare the size and viability of pollen grains from pedicellate and sessile spikelets of parents and hybrid plants produced from a diallel cross among six diverse big bluestem accessions and to estimate the general and specific combining ability of pollen characteristics. Differences in pollen size were attributed to spikelet type and year. Mean pollen diameters averaged 30.5 and 32.9 μm for pedicellate and sessile spikelets, respectively. Similarly, mode pollen diameters averaged 29.3 and 32.7 μm for pedicellate and sessile spikelets. Differences among F_1 (SCA effects) crosses occurred in the sessile spikelet for mode pollen diameter, and differences between reciprocal F_1 (REC effects) crosses occurred for both sessile spikelet mean and mode pollen diameters. No statistical differences were observed in pedicellate spikelets for either mean or mode pollen diameter. Differences in pollen viability were attributed to spikelet type. Pollen viability averaged 43.3 and 75.1% for

pedicellate and sessile spikelets, respectively. Approximately one-third of the genotypes had pollen viabilities of 50% or greater in both pedicellate and sessile spikelets. Significant GCA effects occurred for both pedicellate and sessile spikelets. The magnitude of phenotypic variation among genotypes for pedicellate pollen viability suggests that selection for this trait should be effective assuming at least a moderate narrow-sense heritability. Phenotypic correlations between pollen fertility and pollen size were all positive and, except for one trait combination, were all significant.

INTRODUCTION

Big bluestem is adapted for growth throughout most of North America and is one of the most valued warm-season forage species of the central Great Plains mixed and tallgrass prairie regions (Gould and Shaw, 1983). This multipurpose species produces a high quality forage that is grazed by all classes of livestock; it produces a high quality hay when cut before seed stalk formation, and it is an excellent conservation species (Hoover et al., 1948). The usefulness of big bluestem for revegetating pastures or rangelands, unfortunately, is limited by seed availability. In spite of its widespread occurrence, it is an unpredictable seed producer (Cornelius, 1950). Seed production in cross-pollinated species, such as big bluestem, is limited by several factors including ineffective pollination.

The inflorescence of big bluestem consists of many paired spikelets. The floret of the pedicellate spikelet is either bisexual, staminate, or neuter, while the floret of the sessile spikelet is always bisexual. Boe et al. (1983) found significant seed set differences in pedicellate spikelets of big bluestem accessions collected from different sites in eastern South Dakota. In their study,

pedicellate spikelet seed yield was correlated positively with total seed yield. They considered it feasible to increase the seed yield potential of this species by selecting for increased seed set in pedicellate spikelets.

Pollen grain size may affect both the distance and duration of pollen flight (McCubbin, 1944), as well as pollen viability (Jones and Newell, 1946). Small viable pollen grains may have a dispersive advantage over large viable grains in that they may travel greater distances. The objectives of this study were to compare pollen size and pollen viability from pedicellate and sessile spikelets of parent and hybrid plants produced from a diallel cross among six diverse big bluestem accessions and to estimate the general and specific combining ability of pollen characteristics.

MATERIALS AND METHODS

Size and viability of pollen from pedicellate and sessile spikelets of six big bluestem (parental) accessions and their reciprocal F_1 progeny were determined in 1986 and 1987. Big bluestem accessions used as parents were clonally propagated lines originally collected and maintained by the USDA-Soil Conservation Service, Plant Material Centers at Knox City, Texas, and Manhattan, Kansas. The accession number, origin, and the average flowering date of the six parent accessions were:

1. 1836; Hughes County, Oklahoma; 8 August.
2. 1843; Nowata County, Oklahoma; 18 July.
3. 1947; Parker County, Texas; 20 July.
4. 1952; Bell County, Texas; 5 August.
5. 2397; Nueces County, Texas; 5 October.
6. 2675; Victoria County, Texas; 17 September.

Pollen grain size was measured with a Coulter Counter model Z_{B1} and Coulter Channelyzer unit, interfaced with an IBM-PC microcomputer. While the Coulter Counter is used primarily in medicine for counting and sizing blood cells, it also can be used for counting and sizing minute particles such as fungal spores and pollen grains (Brotherton, 1969). As particles are sucked through the aperture of the Coulter Counter, a resistance forms between the internal and external aperture electrodes. The resistance is caused by the particle as it displaces the electrolyte solution. The resultant voltage drop is proportional to the size (volume) of the particle. Both regular and irregular shaped particles can be counted and sized with the Coulter Counter. Pollen grains of big bluestem are spherical without much sculpturing, which simplifies determination of their diameters from volumetric measurements. The instrument was calibrated using a 22.5- μ m polystyrene reference particle.

Pollen samples were from plants growing in a field nursery which was established in 1985 by planting two ramets of each parental accession and four F₁ progeny plants from each cross in a completely random design. The four progeny

plants consisted of two plants each from reciprocal matings. In 1986 and 1987, five inflorescences, 1 to 2 days from anthesis, were collected from each plant. The same two plants were studied both years. Undehisced anthers were dissected from the pedicellate and sessile spikelets of each plant, and placed into separate 35-mL Coulter Accuvette II sample vials. Approximately 20 mL of Coulter Isoton II balanced electrolyte solution was added to each vial. Vials were sonicated 4 to 5 min using a 455-mL ultrasonic cleaner to release pollen grains from the anthers. Empty anthers and anther fragments were removed from the pollen-anther solution using a dropper pipette. Purified pollen samples were sonified for 10 to 20 sec prior to analysis to disperse the grains.

Viability was estimated for each pollen sample. Prior to adding the isoton solution, five anthers were selected from each vial and squashed on a microscope slide in a drop of aniline blue in lactophenol (Radford et al., 1974). Approximately 150 to 200 pollen grains were scored for viability based on stainability.

Data collected using the Coulter Counter were converted into a pollen-size frequency distribution. The mean and mode pollen diameters were determined for each distribution. Data were analyzed using PROC ANOVA (SAS Institute, 1985). The model was a split-split plot design with cross as the main plot factor, year as the subplot factor, and spikelet as the sub-subplot factor. Data for each spikelet type were

also subjected to diallel analyses using Griffing's (1956) Method 1, Model I procedure and PROC GLM (SAS Institute, 1985). Phenotypic correlation coefficients were calculated for pedicellate and sessile spikelet pollen fertility, mean pollen diameter, and mode pollen diameter using PROC CORR (SAS Institute, 1982).

RESULTS AND DISCUSSION

Pollen Viability

Differences in pollen viability were attributed only to spikelet type (Table 1). Pollen viability averaged 43.3 and 75.1% for pedicellate and sessile spikelets, respectively. Approximately one-third of the genotypes studied possessed pollen viabilities of 50% or greater in both pedicellate and sessile spikelets.

Significant GCA effects also occurred for these data (Table 1). In general, lines 1, 5, and 6 reduced while lines 2 and 3 increased pollen viability in pedicellate and sessile spikelets (Table 2). Pollen viability in the sessile spikelets, on the average, was greater than 50% and ranged from 41.3 to 92.8%. Only one hybrid, s₁₅, had significantly less than 50% viable pollen. In contrast, pollen viability in pedicellate spikelets ranged from 4.0 to 80.0%. Similarly, Boe et al. (1983) reported significant variation in pedicellate spikelet seed set among big bluestem accessions. They indicated that selection for

increased seed set from pedicellate spikelets should be possible. The magnitude of phenotypic variation in pedicellate pollen viability among genotypes in our study also suggests that selection for this trait should be effective assuming it has at least a moderate narrow-sense heritability. Thus, genotypes with high pedicellate- and high sessile-spikelet pollen viability may have a greater reproductive advantage over genotypes with low pedicellate- and high sessile-spikelet pollen viability.

Phenotypic correlation coefficients between pollen fertility and pollen size were all positive and, except for one trait combination, were all significant (Table 4). This suggests that selection for increased pollen fertility should result in an increase in pollen grain size. Correspondingly, selection for increased pollen grain size should result in increased pollen fertility.

Pollen Size

Differences in mean and mode pollen sizes were attributed to spikelet type and year (Table 1). The mean pollen diameter averaged 30.5 and 32.9 μm for pedicellate and sessile spikelets, respectively. Similarly, the mode pollen diameter averaged 29.3 and 32.7 μm for pedicellate and sessile spikelets, respectively. Differences between pedicellate and sessile spikelet pollen size may be partially explained by difference in spikelet vascularization. Maze (1977) found that with only one

exception, the vascular bundles which serve the pedicellate and sessile spikelets of big bluestem are independent. He further found that vascular tissues serving sessile spikelets descended further down the culm than those serving pedicellate spikelets, and that the vein common to both spikelets is a large central vein primarily serving the sessile spikelet.

The mean pollen diameter in 1986 averaged 32.3 μm compared to 31.2 μm in 1987. Similarly, the mode pollen diameter in 1986 averaged 31.5 μm compared to 30.5 μm in 1987. Yearly differences in pollen size may be expected due to seasonal differences in temperature, rainfall, and other factors impact the general plant growth and plant condition. If plants are not capable of maintaining steady growth, physiological processes during pollen formation may be altered, and thus affect pollen diameter. Because pollen was sampled from undehisced anthers of unopened spikelets, desiccation due to hot dry winds should not have been a factor affecting pollen size.

Differences between reciprocal F_1 (REC effects) crosses occurred between spikelet types for the mean pollen diameter (Table 1). No statistical differences were observed in pedicellate spikelets for either the mean or the mode pollen diameters. In general, the sign and magnitude of GCA, SCA, and reciprocal effect estimates are similar between pedicellate and sessile spikelets for both the mean and mode pollen diameters (Table 2). This suggests that factors

influencing pollen size act similarly upon both spikelet types. In several species, reciprocal difference in pollen size and viability has been shown to be caused by genetic differences, non-genetic differences, or interactions between the two (Wright, 1969). Pollen size in big bluestem lines 1, 2, and 3 appeared to be conditioned by nuclear gene(s). Reciprocal crosses between these lines produced F_1 's with relatively similar pollen sizes (Table 3). Reciprocal crosses between lines 1 and 5 suggested pollen size to be strongly influenced by cytoplasmic inheritance. Large reciprocal differences in pollen size from crossing lines 3 and 6, and 4 and 6 may possibly be caused by interactions between nuclear and cytoplasmic genes.

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TABLE 1
 Mean Squares from the Analyses of Variance for Percent
 Viability, Mode Diameter, and Mean Diameter
 of Big Bluestem Pollen Grains

| Source | df | Mean squares | | |
|------------------|----|--------------|---------|---------|
| | | Viability | Mean | Mode |
| Genotype (G) | 35 | 1 618.3 | 17.8 | 29.3 |
| GCA | 5 | 3 386.0* | 16.8 | 30.7 |
| SCA | 15 | 1 090.6 | 17.4 | 29.5 |
| REC | 15 | 1 556.9 | 18.5 | 28.7 |
| Plant(G) | 36 | 1 480.4 | 16.9 | 21.7 |
| Year (Y) | 1 | 616.3 | 85.5** | 82.3* |
| Y X G | 35 | 442.6 | 8.3 | 12.7 |
| Y X GCA | 5 | 343.3 | 1.9 | 4.2 |
| Y X SCA | 15 | 586.0 | 7.7 | 12.2 |
| Y X REC | 15 | 332.3 | 11.0 | 16.0 |
| Y X Plant(G) | 36 | 361.3 | 7.6 | 15.4 |
| Spikelet (S) | 1 | 73 221.1** | 411.7** | 800.9** |
| S X G | 35 | 786.8 | 4.5 | 8.1 |
| S X GCA | 5 | 217.3 | 2.0 | 9.1 |
| S X SCA | 15 | 1 029.1 | 2.9 | 5.7 |
| S X REC | 15 | 734.4 | 7.0* | 10.3 |
| S X Plant(G) | 36 | 605.4 | 3.2 | 7.2 |
| Y X S | 1 | 132.0 | 3.3 | 14.6 |
| Y X S X G | 35 | 341.7 | 1.9 | 5.1 |
| Y X S X GCA | 5 | 220.5 | 1.9 | 2.0 |
| Y X S X SCA | 15 | 311.3 | 2.7 | 6.8 |
| Y X S X REC | 15 | 412.5 | 1.0 | 4.4 |
| Y X S X Plant(G) | 36 | 258.0 | 3.0 | 7.9 |
| Mean | | 59.2 | 31.7 | 31.0 |

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

TABLE 2

Estimates of General (g_j) and Specific Combining Ability (s_{ij}) and
 Reciprocal Effects (r_{ij}) for Pedicellate and Sessile Spikelet
 Pollen Viability, Mean Pollen Diameter, and Mode Pollen
 Diameter of Big Bluestem †

| Effect | Pollen viability | | Mean pollen diameter | | Mode pollen diameter | |
|----------|------------------|---------|---------------------------|---------|----------------------|---------|
| | Pedicellate | Sessile | Pedicellate | Sessile | Pedicellate | Sessile |
| | ----- % ----- | | ----- μm ----- | | | |
| g_1 | -5.3 | -4.9 | 0.3 | 0.0 | 0.0 | -0.9 |
| g_2 | 13.0** | 8.0** | 0.2 | 0.0 | -0.2 | 0.4 |
| g_3 | 3.1 | 1.6 | -0.7 | -0.8* | -0.7 | -0.9 |
| g_4 | -1.1 | 2.2 | 0.3 | 0.3 | 0.8 | 0.4 |
| g_5 | -5.2 | -2.4 | -0.2 | -0.2 | 0.0 | 0.1 |
| g_6 | -4.5 | -4.4 | 0.1 | 0.6 | 0.2 | 1.0* |
| s_{11} | -15.1 | 21.4** | -0.8 | 1.0 | -1.3 | -1.7 |
| s_{12} | 7.2 | 1.3 | -0.1 | -0.9 | 0.2 | -0.5 |
| s_{13} | 2.6 | -10.2 | 0.9 | -0.2 | 1.0 | 0.9 |
| s_{14} | 12.5 | -1.2 | 0.8 | 0.7 | 0.6 | 1.8 |
| s_{15} | 3.6 | -7.9 | -1.1 | -1.1 | -0.5 | -0.3 |
| s_{16} | -10.8 | -3.4 | 0.3 | 0.5 | 0.0 | -0.1 |
| s_{22} | 8.7 | 1.7 | -0.2 | 1.6 | 0.1 | 2.8 |
| s_{23} | 16.0 | -4.1 | -0.5 | -0.6 | -1.1 | -1.4 |
| s_{24} | 17.9 | 0.8 | 0.8 | -0.2 | 1.4 | -0.6 |
| s_{25} | 0.9 | 0.6 | -1.2 | -0.6 | -1.5 | -1.5 |
| s_{26} | 17.2 | -0.4 | 1.2 | 0.8 | 0.9 | 1.3 |

TABLE 2. cont.

| Effect | Pollen viability | | Mean pollen diameter | | Mode pollen diameter | |
|-----------------|------------------|---------|---------------------------|---------|----------------------|---------|
| | Pedicellate | Sessile | Pedicellate | Sessile | Pedicellate | Sessile |
| | ----- % ----- | | ----- μm ----- | | | |
| ^s 33 | -23.5 | 0.4 | 0.9 | 2.0 | 2.0 | 3.1 |
| ^s 34 | 6.7 | 3.9 | 0.7 | 0.2 | 0.1 | -0.2 |
| ^s 35 | 28.3** | 9.7 | 0.3 | 0.1 | -0.3 | -0.7 |
| ^s 36 | 1.9 | 0.1 | -2.3** | -1.4 | -1.8 | -1.8 |
| ^s 44 | 11.3 | 0.1 | -0.1 | 0.9 | 0.1 | 1.7 |
| ^s 45 | -2.4 | -2.6 | -0.8 | -0.2 | -1.0 | -0.3 |
| ^s 46 | -10.3 | -1.0 | -1.4 | -1.4 | -1.2 | -2.4* |
| ^s 55 | -28.9 | 11.6 | 2.2 | 2.4 | 2.2 | 3.4* |
| ^s 56 | -1.5 | -11.5 | 0.6 | -0.6 | 1.0 | -0.7 |
| ^s 66 | 3.4 | 16.1 | 1.6 | 2.1 | 1.1 | 3.7* |
| ^r 12 | -14.7 | 4.7 | 0.3 | 0.0 | -0.9 | -0.1 |
| ^r 13 | 9.3 | -11.9 | 0.6 | -0.5 | -0.2 | -0.4 |
| ^r 14 | -21.8 | -8.0 | -1.7 | -1.0 | -3.1** | -1.6 |
| ^r 15 | 28.3* | 18.6** | 2.0 | 3.0** | 2.1 | 3.7** |
| ^r 16 | -16.7 | 1.7 | -2.0 | -1.4 | -1.5 | -1.8 |
| ^r 23 | 23.0 | 7.1 | -0.7 | 1.6 | -1.6 | 0.8 |
| ^r 24 | 3.0 | -6.0 | -0.8 | -0.1 | -1.1 | 0.1 |
| ^r 25 | 14.6 | 0.9 | 0.7 | 0.1 | -0.2 | -0.3 |
| ^r 26 | 11.1 | -1.9 | 0.6 | 0.4 | 1.3 | 0.7 |

TABLE 2. cont.

| Effect | Pollen viability | | Mean pollen diameter | | Mode pollen diameter | |
|-----------------|------------------|---------|---------------------------|---------|----------------------|---------|
| | Pedicellate | Sessile | Pedicellate | Sessile | Pedicellate | Sessile |
| | ----- % ----- | | ----- μm ----- | | | |
| r ₃₄ | 11.3 | -8.0 | 1.1 | 1.3 | 0.1 | 2.6 |
| r ₃₅ | 6.9 | 0.0 | 0.3 | 1.0 | 0.1 | 1.8 |
| r ₃₆ | 6.6 | 5.1 | 1.2 | -2.4** | 1.0 | -2.8* |
| r ₄₅ | -12.5 | -13.2 | 0.2 | 0.2 | 0.4 | 0.3 |
| r ₄₆ | 0.6 | -13.1 | -0.8 | -2.7** | -1.5 | -2.7* |
| r ₅₆ | -5.5 | -6.9 | -0.4 | -0.3 | 0.0 | -0.8 |

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

† Standard errors for:

| | | | | | | |
|---|-------|-------|------|------|------|------|
| g _i | 5.15 | 3.11 | 0.41 | 0.42 | 0.47 | 0.53 |
| s _{ii} | 16.29 | 9.83 | 1.31 | 1.33 | 1.48 | 1.63 |
| s _{ij} (i≠j) | 11.75 | 7.09 | 0.95 | 0.95 | 1.07 | 1.21 |
| r _{ij} (i≠j) | 13.82 | 8.34 | 1.11 | 1.12 | 1.25 | 1.43 |
| g _i -g _j (i≠j) | 8.00 | 4.81 | 0.64 | 0.65 | 0.72 | 0.80 |
| s _{ii} -s _{jj} (i≠j) | 22.58 | 13.62 | 1.82 | 1.84 | 2.05 | 2.33 |
| s _{ii} -s _{ij} (i≠j) | 22.58 | 13.62 | 1.82 | 1.84 | 2.05 | 2.33 |
| s _{ii} -s _{jk} (i≠j,k; j≠k) | 19.55 | 11.80 | 1.57 | 1.60 | 1.77 | 2.02 |
| s _{ij} -s _{ik} (i≠j,k; j≠k) | 17.85 | 10.77 | 1.44 | 1.46 | 1.62 | 1.84 |
| s _{ij} -s _{kl} (i≠j,k,l; j≠k,l; k≠l) | 15.96 | 9.63 | 1.28 | 1.30 | 1.45 | 1.65 |
| r _{ij} -r _{kl} (i≠j; k≠l) | 19.55 | 11.80 | 1.57 | 1.60 | 1.77 | 2.02 |

TABLE 3
 Parents, Crosses, and Reciprocal Means by Spikelet Type for Pollen
 Viability, Mean Pollen Diameter, and Mode Pollen Diameter
 Combined Over Years

| Parent or Progeny | Pollen viability | | Mean pollen diameter | | Mode pollen diameter | |
|-------------------|------------------|---------|----------------------|---------|----------------------|---------|
| | Pedicellate | Sessile | Pedicellate | Sessile | Pedicellate | Sessile |
| | ----- % ----- | | ----- μ m ----- | | | |
| s ₁₁ | 17.6 | 86.6 | 30.3 | 33.9 | 27.9 | 29.1 |
| s ₁₂ | 72.8 | 74.8 | 30.6 | 32.1 | 30.2 | 31.7 |
| s ₁₃ | 34.4 | 73.6 | 30.3 | 32.4 | 29.8 | 32.1 |
| s ₁₄ | 71.2 | 79.2 | 33.6 | 34.9 | 33.8 | 35.5 |
| s ₁₅ | 8.0 | 41.3 | 27.5 | 28.7 | 26.6 | 27.9 |
| s ₁₆ | 39.4 | 60.6 | 33.2 | 35.5 | 31.1 | 34.4 |
| s ₂₂ | 77.9 | 92.8 | 30.8 | 34.6 | 29.0 | 36.2 |
| s ₂₃ | 20.3 | 73.6 | 30.3 | 29.9 | 28.9 | 30.0 |
| s ₂₄ | 34.2 | 92.1 | 32.7 | 33.1 | 32.4 | 32.7 |
| s ₂₅ | 37.3 | 80.5 | 28.7 | 32.0 | 27.9 | 32.0 |
| s ₂₆ | 57.7 | 80.2 | 31.5 | 33.9 | 29.0 | 34.6 |
| s ₃₃ | 25.8 | 78.8 | 30.0 | 33.3 | 29.9 | 34.0 |
| s ₃₄ | 40.6 | 90.9 | 29.6 | 31.3 | 29.4 | 29.4 |
| s ₃₅ | 62.6 | 84.1 | 29.6 | 31.3 | 28.2 | 29.3 |
| s ₃₆ | 37.1 | 67.4 | 26.4 | 33.7 | 26.0 | 33.8 |
| s ₄₄ | 52.3 | 79.6 | 31.0 | 34.4 | 30.9 | 35.1 |
| s ₄₅ | 47.1 | 85.6 | 29.7 | 32.6 | 28.7 | 32.5 |
| s ₄₆ | 26.7 | 85.0 | 30.3 | 35.1 | 30.5 | 34.4 |

TABLE 3. cont.

| Parent or Progeny | Pollen viability | | Mean pollen diameter | | Mode pollen diameter | |
|-------------------|------------------|---------|---------------------------|---------|----------------------|---------|
| | Pedicellate | Sessile | Pedicellate | Sessile | Pedicellate | Sessile |
| | ----- % ----- | | ----- μm ----- | | | |
| ^s 55 | 4.0 | 81.9 | 32.3 | 34.9 | 31.4 | 36.3 |
| ^s 56 | 37.5 | 63.7 | 31.4 | 33.1 | 30.6 | 33.9 |
| ^s 66 | 37.7 | 82.4 | 32.4 | 36.3 | 30.9 | 38.4 |
| r ₁₂ | 43.5 | 84.2 | 31.3 | 32.0 | 28.4 | 31.5 |
| r ₁₃ | 53.0 | 49.6 | 31.6 | 31.4 | 29.4 | 31.4 |
| r ₁₄ | 27.5 | 63.1 | 30.2 | 32.9 | 27.6 | 32.3 |
| r ₁₅ | 64.7 | 78.5 | 31.5 | 34.7 | 30.9 | 35.2 |
| r ₁₆ | 6.0 | 64.0 | 29.2 | 32.7 | 28.0 | 30.8 |
| r ₂₃ | 66.2 | 87.8 | 28.9 | 33.1 | 25.7 | 31.5 |
| r ₂₄ | 40.3 | 80.1 | 31.0 | 32.9 | 30.3 | 32.8 |
| r ₂₅ | 66.5 | 82.3 | 30.0 | 32.2 | 27.4 | 31.3 |
| r ₂₆ | 80.0 | 76.5 | 32.7 | 34.7 | 31.6 | 36.0 |
| r ₃₄ | 63.2 | 74.8 | 31.9 | 34.0 | 29.6 | 34.6 |
| r ₃₅ | 76.4 | 84.0 | 30.2 | 33.0 | 28.4 | 33.0 |
| r ₃₆ | 50.3 | 77.5 | 28.8 | 28.9 | 28.0 | 28.2 |
| r ₄₅ | 22.1 | 59.1 | 30.0 | 33.0 | 29.5 | 33.2 |
| r ₄₆ | 28.0 | 58.8 | 28.7 | 29.8 | 27.6 | 28.9 |
| r ₅₆ | 26.6 | 49.9 | 30.5 | 32.5 | 30.5 | 32.3 |

TABLE 4
Phenotypic Correlations Between Pollen Fertility and Pollen Size,
Based on 72 Observations Each Year

| Pollen character | Pollen viability | | Mean pollen diameter | | Mode pollen diameter | |
|-----------------------------|------------------|-------------|----------------------|-------------|----------------------|-------------|
| | Sessile | Pedicellate | Sessile | Pedicellate | Sessile | Pedicellate |
| | ----- % ----- | | ----- μ m ----- | | | |
| <u>Pollen viability</u> | | | | | | |
| Pedicellate | 0.37** | 0.28** | 0.23** | 0.14 | 0.21* | |
| Sessile | | 0.20* | 0.30** | 0.18* | 0.26** | |
| <u>Mean pollen diameter</u> | | | | | | |
| Pedicellate | | | 0.61** | 0.83** | 0.56** | |
| Sessile | | | | 0.50** | 0.90** | |
| <u>Mode pollen diameter</u> | | | | | | |
| Pedicellate | | | | | | 0.48** |

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

PART III

COMBINING ABILITY FOR VEGETATIVE CHARACTERISTICS
IN BIG BLUESTEM

ABSTRACT

Big bluestem, Andropogon gerardii Vitman, is an important forage species grazed by all classes of livestock. Because leaves are the primary plant part consumed, the ratio of leaf to total plant biomass (leafiness) is considered the most important forage character in the selection of superior big bluestem cultivars. The objectives of our study were to estimate the general (GCA) and specific (SCA) combining abilities of vegetative yield components (number of culms plant⁻¹, number of leaves culm⁻¹, and leaf area) using hybrid plants produced from a diallel cross among six diverse big bluestem accessions. Differences in number of culms plant⁻¹ were attributed to year, GCA effects, SCA effects, and reciprocal (REC) effects. The number of culms plant⁻¹ were related to growth habit, with sod-forming types tending to have more culms plant⁻¹. Differences in number of leaves culm⁻¹ were attributed to GCA effects, and the data suggest that as plant height increased the number of leaves culm⁻¹ increased. Differences in total leaf area plant⁻¹ were attributed to year, GCA effects, SCA effects, and REC effects. Significant positive phenotypic correlations were measured for total leaf area culm⁻¹ vs. total leaf area plant⁻¹ and

total culms plant⁻¹ vs. total leaf area plant⁻¹. Thus, increasing total leaf area plant⁻¹ via selection may be accomplished by increasing the total leaf area culm⁻¹, increasing the number of culms plant⁻¹, or by increasing both.

INTRODUCTION

Big bluestem is a perennial warm-season tallgrass species distributed throughout most of North America. Similar to other native warm-season tallgrass species of the Great Plains region, big bluestem begins growth in early to mid April and provides excellent forage until the end of June. On rangelands consisting primarily of big bluestem, animal gains of one kg head⁻¹ day⁻¹ from April to June are not uncommon (Owensby and Anderson, 1967). As plants form reproductive tillers, forage becomes less palatable and nutritious; consequently, animal gains decline. This generally occurs in July or August; and by October, dietary supplements are needed to avoid animal weight loss.

Ross et al. (1975) studied forage quality of plant parts (culms and leaves) in big bluestem and concluded that it was feasible to increase whole plant in vitro dry matter digestion (IVDMD) by selecting for increased culm IVDMD. However, they stated that "Since the leaves are almost exclusively grazed, selection for increased IVDMD of the stem would not necessarily result in a more digestible cultivar for grazing." They suggested that the objectives of a big bluestem breeding program should be for maximum forage production and leafiness as well as for high seed

production. Similarly, Law and Anderson (1940) considered leafiness (leaf area) as the single most important character in the selection of superior big bluestem cultivars. Therefore, the objectives of our study were to compare vegetative yield components, i.e., number of culms plant⁻¹, number of leaves culm⁻¹, and leaf area, of parents and hybrid plants produced from a diallel cross among six diverse big bluestem accessions and to estimate the general (GCA) and specific (SCA) combining ability of vegetative characters.

MATERIALS AND METHODS

Vegetative characteristics, i.e., canopy height, number of culms plant⁻¹, number of leaves culm⁻¹, the length and width (cm) of flag, mid-culm, and basal-culm leaves, of six big bluestem accessions and their F₁ progeny were measured in 1986 and 1987. Big bluestem accessions used as parents were from clonally propagated lines originally collected and maintained by the USDA-Soil Conservation Service, Plant Material Centers at Knox City, Texas, and Manhattan, Kansas. The accession number, origin, and the average flowering date of the six parent accessions were:

1. 1836, Hughes County, Oklahoma, 8 August.
2. 1843, Nowata County, Oklahoma, 18 July.
3. 1947, Parker County, Texas, 20 July.
4. 1952, Bell County, Texas, 5 August.
5. 2397, Nueces County, Texas, 5 October.
6. 2675, Victoria County, Texas, 17 September.

In the summer of 1984, paired controlled crosses were made in the greenhouse among the six accessions using a complete diallel mating design. Sessile spikelets of each accession were emasculated and pollinated using the techniques of Richardson (1958). Caryopses for the crosses were germinated during the fall of 1984, and plantlets were established in a field plot in the spring of 1985. The experimental design was a randomized complete block with eight replications. Each block contained one plant each of the six parent accessions and 30 F_1 progeny plants from each cross. The 30 F_1 progeny plants from respective crosses consisted of 15 plants each from reciprocal matings.

In 1986 and 1987, respectively, from a randomly chosen culm of each plant, the flag, mid-culm, and basal-leaf areas were estimated by multiplying their length by their width by 0.681. The conversion factor (0.681) was established and used by Law and Anderson (1940) to correct for over-estimation of leaf areas in big bluestem. Total leaf area culm^{-1} was calculated by averaging the flag, mid-culm, and basal-leaf areas of each culm multiplied by the number of leaves culm^{-1} . Total leaf area plant^{-1} was calculated by multiplying the total leaf area culm^{-1} by the number of culms plant^{-1} . The vegetative canopy height (cm) was measured in the full-leaf stage of growth prior to the formation of reproductive tillers.

Data for each response variable were subjected to diallel analysis using Griffing's (1956) Method 1, Model I

procedure and PROC GLM (SAS Institute, 1985). Phenotypic correlation coefficients were calculated using PROC CORR (SAS Institute, 1985).

RESULTS AND DISCUSSION

Plant Canopy Height

Differences in plant canopy height were attributed to year, GCA effects, year by GCA effects, SCA effects, year by SCA effects, and reciprocal (REC) effects (Table 1). Significant positive GCA estimates occurred for accessions 1 and 5, and a significant negative estimate occurred for accession 6 (Table 2). Mean plant canopy heights for all F₁ crosses were higher than the corresponding mean plant canopy heights of the parents contributing to the hybrid (Table 3). Similarly, significant negative SCA estimates occurred for all parental accessions. Reciprocal differences occurred for crosses between accessions 3 and 4 and between 3 and 5; however, the magnitude of the estimates were about half those of parental accessions. In general, plant canopy height was a function of the plant growth habit. Prior to the elongation of reproductive tillers, accessions 1 and 5 tended to have thickened culms and an erect growth habit. Other accessions tended to have thinner culms and an ascending growth habit.

Culms Per Plant

Differences in numbers of culms plant⁻¹ were attributed to year, GCA effects, SCA effects, and REC effects (Table 1). Significant positive GCA estimates were shown for accessions 2, 4, and 6; and significant negative estimates were obtained for accession 1 (Table 2). Similar to canopy height, mean numbers of culms plant⁻¹ for all F₁ crosses were higher than the corresponding mean number of culms plant⁻¹ of the parents contributing to the hybrid, and significant negative SCA estimates occurred for all parental accessions (Table 3). Reciprocal differences were primarily associated with accession 3. Density of culms was also a function of plant growth habit. Big bluestem has two distinct growth habits: sod-forming or bunch. Ecologically, sod-forming grasses tend to grow in areas of adequate moisture, and bunch grasses in areas of limited moisture (Weaver 1968). Accession 3 tended to be sod-forming with great lateral growth. This habit tended to increase the number of culms plant⁻¹.

Leaves Per Culm

Differences in number of leaves culm⁻¹ were attributed to GCA effects. Significant positive and negative GCA estimates occurred for accessions 1 and 5 and for 2, 3, and 4, respectively. Accessions 1 and 5 tended to be taller than other accessions at maturity. If internode lengths are equal and there is a one-to-one relationship between nodes

and leaves, then number of leaves would increase as the plant height increases.

Leaf Area

The mean leaf area culm^{-1} increased linearly from the flag leaf toward the basal-culm leaf. Differences in flag leaf areas were attributed to both GCA and SCA effects. Significant positive and negative GCA estimates occurred for accessions 5 and 6 and for 2, 3, and 4, respectively. The significant SCA estimates were primarily associated with crosses of accessions 5 and 6.

Significant variation in mid-culm leaf areas was attributed to year, GCA effects, SCA effects, and year by SCA effects (Table 1). Significant positive GCA estimates occurred for accessions 5 and 6, and significant negative estimates were obtained for accessions 2, 3, and 4. Averaged across years, significant negative SCA estimates occurred for crosses s_{25} , s_{35} , and s_{45} (Table 2). A significant positive SCA estimate occurred for s_{55} . The year by SCA interaction showed fluctuations in yearly SCA estimates.

Significant variation in basal-culm leaf areas was attributed to year, GCA effects, and year by GCA effects. Significant positive GCA estimates occurred for accessions 1 and 5, and negative estimates were noted for accession accessions 2, 3, and 4 in both years. The year by GCA interaction is possibly due to accession 5. GCA estimates

for accession 5 were -0.6 and 2.2 for 1986 and 1987, respectively. Other GCA estimates were both similar in magnitude and direction (sign).

Differences in total leaf area culm⁻¹ were attributed to GCA effects, SCA effects, and year by REC effects (Table 1). Significant positive GCA estimates occurred for accessions 1 and 5, and significant negative estimates were calculated for accessions 2, 3, and 4. Significant negative SCA estimates occurred for crosses s₂₅ and s₃₅. Similar to the flag, mid-culm, and the basal-culm leaf areas, a significant positive SCA estimate occurred for s₅₅. Reciprocal differences between years were primarily due to fluctuations in REC estimates. In both years, most REC estimates were not significantly different from zero.

Differences in total leaf area plant⁻¹ were attributed to year, GCA effects, SCA effects, REC effects, and year by GCA effects (Table 1). Significant positive GCA estimates occurred for accessions 5 and 6, and significant negative estimates were obtained for accessions 1, 2, 3, and 4 in each year. Negative SCA estimates occurred for all parental accessions. In general, significant SCA and REC estimates follow the same trend as did number of culms plant⁻¹.

As stated earlier, Law and Anderson (1940) considered leafiness (total leaf area) as the single most important character in the selection of superior big bluestem cultivars. Because of the considerable variation for this trait in big bluestem, selections are feasible. Significant

positive phenotypic correlation coefficients were measured for total leaf area culm⁻¹ vs. total leaf area plant⁻¹ and total culms plant⁻¹ vs. total leaf area plant⁻¹ (Table 4). Thus, increasing the total leaf area plant⁻¹ may be accomplished via selection by increasing the total leaf area culm⁻¹, increasing the number of culms plant⁻¹, or by increasing both. Leaf (IVDMD) forage quality is an important trait in big bluestem; however, improvements in leaf IVDMD only increases the total digestible forage. Increased forage production, as increased total leaf area plant⁻¹, allows for an increased livestock carrying capacity.

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TABLE 1

Mean Squares for Plant Canopy Height, Number Culms Plant⁻¹, Number Leaves Culm⁻¹, Flag Leaf Area, Mid Leaf Area, Basal Leaf Area, Total Leaf Area Culm⁻¹, and Total Leaf Area Plant⁻¹ for Big Bluestem Parents and F₁ Progenies at Stillwater, Oklahoma in 1986 and 1987

| Mean squares | | | | | | | | | |
|--------------|-----|---------------------|-------------------------------|-------------------------------|-----------|------------|------------|--------------------------|---------------------------|
| Source | df | Plant canopy height | No. culms plant ⁻¹ | No. leaves culm ⁻¹ | Leaf area | | | | |
| | | | | | Flag | Mid | Basal | Total culm ⁻¹ | Total plant ⁻¹ |
| Block (B) | 7 | 447.0 | 3 593.9** | 12.8 | 146.3 | 316.5 | 711.5 | 41 726.6 | 463 039 341.7 |
| Year (Y) | 1 | 2 911.5* | 44 644.2** | 10.4 | 147.4 | 1 352.6* | 3 135.2* | 90 029.2 | 5 854 316 798.9 |
| B X Y | 7 | 333.1 | 222.7 | 18.1 | 154.7 | 243.0 | 267.2 | 17 873.9 | 125 258 847.7 |
| Genotype (G) | 35 | 1 171.1** | 8 674.9** | 23.5** | 240.9** | 1 696.5** | 1 657.3** | 203 983.4** | 1 356 019 711.3** |
| GCA | 5 | 2 549.3** | 19 404.0** | 142.4** | 1 207.9** | 10 268.2** | 10 481.6** | 1 254 135.0** | 6 536 493 838.5** |
| SCA | 15 | 1 495.6** | 10 065.3** | 4.8 | 128.1** | 427.0** | 221.8 | 50 400.6** | 673 822 784.8** |
| REC | 15 | 387.1* | 3 708.0** | 2.5 | 31.4 | 108.7 | 151.4 | 7 515.8 | 311 391 928.7* |
| B X G | 245 | 217.8 | 1 468.3 | 3.5 | 44.9 | 144.4 | 222.7 | 15 505.7 | 171 034 557.3 |

TABLE 1. cont.

| Source | df | Mean squares | | | | | | | |
|-----------|-----|---------------------|-------------------------------|-------------------------------|-----------|---------|--------|--------------------------|---------------------------|
| | | Plant canopy height | No. culms plant ⁻¹ | No. leaves culm ⁻¹ | Leaf area | | | | |
| | | | | | Flag | Mid | Basal | Total culm ⁻¹ | Total plant ⁻¹ |
| Y X G | 35 | 191.9** | 150.9 | 2.0 | 35.2 | 108.8** | 121.8 | 6 386.1* | 53 485 548.0 |
| Y*GCA | 5 | 377.7** | 236.3 | 2.1 | 48.8 | 114.0 | 292.8* | 6 905.5 | 146 378 826.1* |
| Y*SCA | 15 | 266.1** | 196.6 | 1.1 | 49.0 | 144.5** | 54.6 | 4 810.4 | 32 213 896.2 |
| Y*REC | 15 | 55.6 | 76.8 | 3.0 | 17.1 | 71.3 | 132.1 | 7 788.8* | 43 792 773.8 |
| B X Y X G | 245 | 47.8 | 194.8 | 1.7 | 43.4 | 63.7 | 111.6 | 4 363.5 | 51 071 590.0 |
| Mean | | 68.2 | 86.6 | 9.0 | 9.9 | 28.0 | 41.3 | 249.7 | 21 049.7 |

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

TABLE 2

Estimates of General (g_i) and Specific Combining Ability (s_{ij}), and Reciprocal Effects (r_{ij}) for Plant Canopy Height, Number Culms Plant⁻¹, Number Leaves Culm⁻¹, Flag Leaf Area, Mid Leaf Area, Basal Leaf Area, Total Leaf Area Culm⁻¹, and Total Leaf Area Plant⁻¹ for Big Bluestem Parents and F₁ Progenies at Stillwater, Oklahoma Averaged Over 1986 and 1987 †

| Effect | Plant canopy height | Culms plant ⁻¹ | Leaves culm ⁻¹ | Leaf area | | | | |
|----------|---------------------|---------------------------|---------------------------|-----------------------------|--------|--------|--------------------------|---------------------------|
| | | | | Flag | Mid | Basal | Total culm ⁻¹ | Total plant ⁻¹ |
| | -- cm -- | ----- no ----- | | ----- cm ² ----- | | | | |
| g_1 | 5.2** | -18.8** | 0.3** | 0.0 | 0.9 | 4.5** | 20.3** | -2 926.7** |
| g_2 | -1.2 | 5.4* | -0.6** | -2.8** | -2.8** | -6.9** | -73.7** | -4 799.1** |
| g_3 | -0.9 | 4.0 | -0.7** | -1.2** | -4.2** | -4.9** | -55.0** | -3 716.1** |
| g_4 | -0.8 | 6.7** | -0.6** | -1.7** | -4.8** | -4.5** | -50.3** | -2 385.6** |
| g_5 | 3.0** | -3.9 | 1.5** | 4.1** | 13.2** | 12.0** | 145.1** | 10 343.3** |
| g_6 | -5.2** | 6.6** | 0.2 | 1.4** | 1.8* | 0.8 | 13.6 | 3 484.2** |
| s_{11} | -16.4** | -32.2** | -0.9* | -1.7 | -3.8 | 2.7 | -32.6 | -10 698.7** |
| s_{12} | 3.0 | -7.9 | 0.4 | 1.0 | 1.6 | -0.1 | 15.9 | 381.6 |
| s_{13} | 2.6 | 14.4** | -0.3 | 1.1 | 0.3 | -1.1 | -9.0 | 3 384.8 |
| s_{14} | 2.1 | 7.8 | 0.6* | 0.0 | 0.6 | 1.3 | 22.1 | 4 268.6* |
| s_{15} | 3.7 | 4.8 | -0.1 | -1.1 | -1.3 | -2.7 | -16.6 | -1 330.3 |

TABLE 2. cont.

| Effect | Plant canopy height | Culms plant ⁻¹ | Leaves culm ⁻¹ | Leaf area | | | | |
|-----------------|---------------------|---------------------------|---------------------------|-----------------------------|--------|-------|--------------------------|---------------------------|
| | | | | Flag | Mid | Basal | Total culm ⁻¹ | Total plant ⁻¹ |
| | -- cm -- | ----- no ----- | | ----- cm ² ----- | | | | |
| s ₁₆ | 4.8* | 13.0* | 0.3 | 0.6 | 2.5 | -0.1 | 20.2 | 3 994.0* |
| s ₂₂ | -15.5** | -39.9** | -0.4 | 0.7 | 0.9 | -1.3 | 5.7 | -5 200.5** |
| s ₂₃ | 2.5 | 19.6** | 0.4 | 0.5 | 1.0 | 0.0 | 20.2 | 3 014.4 |
| s ₂₄ | 3.5 | 10.2 | -0.1 | 1.0 | 2.5 | 2.8 | 21.0 | 2 025.0 |
| s ₂₅ | 3.7 | 11.8* | -0.2 | -2.7** | -3.8* | -0.2 | -50.1** | 751.4 |
| s ₂₆ | 2.8 | 6.0 | 0.0 | -0.6 | -2.3 | -1.1 | -12.8 | -971.8 |
| s ₃₃ | -8.0** | -25.0** | 0.4 | -1.3 | -1.9 | -0.3 | 7.8 | -3 184.0 |
| s ₃₄ | 4.9* | 1.4 | 0.2 | 0.7 | 2.5 | 0.5 | 16.8 | 618.8 |
| s ₃₅ | -0.2 | -10.8 | -0.5 | -1.1 | -3.5* | -3.4 | -59.6** | -5 612.4** |
| s ₃₆ | -1.8 | 0.3 | -0.1 | 0.1 | 1.5 | 4.3* | 23.8 | 1 778.5 |
| s ₄₄ | -14.9** | -29.3** | -0.4 | 0.0 | -2.5 | -6.4* | -28.8 | -7 417.6** |
| s ₄₅ | 2.4 | -1.3 | 0.1 | -0.8 | -4.6** | 0.9 | -23.7 | -251.1 |
| s ₄₆ | 1.9 | 11.2* | -0.3 | -0.9 | 1.4 | 0.8 | -7.3 | 756.2 |
| s ₅₅ | -13.3** | -17.0** | 0.5 | 8.0** | 14.3** | 6.6* | 157.4** | -44.1 |
| s ₅₆ | 3.7 | 12.4* | 0.3 | -2.2* | -1.0 | -1.2 | -7.4 | 6 486.5** |

TABLE 2. cont.

| Effect | Plant canopy height | Culms plant ⁻¹ | Leaves culm ⁻¹ | Leaf area | | | | |
|-----------------|---------------------|---------------------------|---------------------------|-----------------------------|------|-------|--------------------------|---------------------------|
| | | | | Flag | Mid | Basal | Total culm ⁻¹ | Total plant ⁻¹ |
| | -- cm -- | ----- no ----- | | ----- cm ² ----- | | | | |
| s ₆₆ | -11.5** | -43.0** | -0.2 | 2.9* | -2.1 | -2.7 | -16.5 | -12 043.5** |
| r ₁₂ | 1.7 | 0.6 | 0.3 | 0.5 | 1.4 | 0.5 | 15.5 | 1 141.6 |
| r ₁₃ | 2.3 | 1.0 | 0.1 | 0.6 | 2.1 | 2.6 | 15.5 | 1 281.3 |
| r ₁₄ | 0.0 | -6.0 | 0.0 | -1.3 | 0.1 | -3.5 | -13.4 | -2 805.9 |
| r ₁₅ | 1.4 | 3.3 | -0.2 | 1.3 | 2.3 | -0.8 | 3.7 | 1 729.3 |
| r ₁₆ | -2.3 | -0.6 | -0.1 | -1.5 | 0.4 | -0.4 | -10.4 | -551.8 |
| r ₂₃ | -2.6 | -1.8 | -0.2 | -0.3 | -0.2 | -1.8 | -6.7 | -1 231.9 |
| r ₂₄ | -3.7 | 2.7 | 0.2 | -0.4 | -0.2 | -0.6 | -0.5 | 382.0 |
| r ₂₅ | -1.9 | -12.7 | -0.4 | -1.4 | -1.5 | 0.9 | -19.5 | -5 266.1** |
| r ₂₆ | 1.7 | -3.6 | -0.7* | 0.3 | -2.2 | -0.8 | -19.6 | -2 714.9 |
| r ₃₄ | -7.0** | -25.1** | -0.2 | 0.8 | 3.3 | 1.7 | 9.9 | -3 210.0 |
| r ₃₅ | -7.6** | -17.8** | -0.4 | 1.6 | 0.8 | -0.2 | -4.6 | -5 034.9** |
| r ₃₆ | -3.1 | -15.1* | 0.2 | -0.5 | 2.5 | 3.9 | 33.3 | -5.9 |
| r ₄₅ | 3.4 | -0.3 | -0.1 | 0.1 | 1.1 | 4.7* | 17.8 | 846.0 |
| r ₄₆ | 2.2 | -8.6 | 0.0 | 0.1 | -0.6 | 0.6 | 1.4 | -1 835.1 |

TABLE 2. cont.

| Effect | Plant canopy height | Culms, plant ⁻¹ | Leaves culm ⁻¹ | Leaf area | | | | |
|-----------------|---------------------|----------------------------|---------------------------|-----------------------------|-----|-------|--------------------------|---------------------------|
| | | | | Flag | Mid | Basal | Total culm ⁻¹ | Total plant ⁻¹ |
| | -- cm -- | ----- no ----- | | ----- cm ² ----- | | | | |
| r ₅₆ | -1.9 | 15.7* | -0.1 | 1.6 | 3.6 | 2.3 | 19.5 | 7 439.6** |

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

† Standard errors for:

| | | | | | | | | |
|--|------|-------|------|------|------|------|-------|----------|
| g _i | 0.97 | 2.52 | 0.12 | 0.44 | 0.79 | 0.98 | 8.20 | 861.59 |
| s _{ii} | 3.07 | 7.98 | 0.39 | 1.40 | 2.50 | 3.10 | 25.94 | 2 724.59 |
| s _{ij} (i≠j) | 2.21 | 5.76 | 0.28 | 1.00 | 1.81 | 2.24 | 18.71 | 1 964.73 |
| r _{ij} (i≠j) | 2.61 | 6.77 | 0.33 | 1.18 | 2.12 | 2.64 | 22.01 | 2 311.89 |
| g _i -g _j (i≠j) | 1.51 | 3.91 | 0.19 | 0.68 | 1.22 | 1.52 | 12.71 | 1 334.77 |
| s _{ii} -s _{jj} (i≠j) | 4.26 | 11.06 | 0.54 | 1.93 | 3.47 | 4.31 | 35.95 | 3 775.30 |
| s _{ii} -s _{ij} (i≠j) | 4.26 | 11.06 | 0.54 | 1.93 | 3.47 | 4.31 | 35.95 | 3 775.30 |
| s _{ii} -s _{jk} | | | | | | | | |
| (i≠j,k; j≠k) | 3.70 | 9.60 | 0.47 | 1.67 | 3.00 | 3.73 | 31.13 | 3 269.51 |
| s _{ij} -s _{ik} | | | | | | | | |
| (i≠j,k; j≠k) | 3.37 | 8.74 | 0.43 | 1.52 | 2.74 | 3.41 | 28.41 | 2 984.64 |

TABLE 2. cont.

| Effect | Plant canopy height | Culms, plant ⁻¹ | Leaves culm ⁻¹ | Leaf area | | | | |
|---|---------------------|----------------------------|---------------------------|-----------------------------|------|-------|--------------------------|---------------------------|
| | | | | Flag | Mid | Basal | Total culm ⁻¹ | Total plant ⁻¹ |
| | -- cm -- | ----- no ----- | | ----- cm ² ----- | | | | |
| $s_{ij}-s_{kl}$ (i≠j, k, l; j≠k, l; k≠l) | 3.01 | 7.82 | 0.38 | 1.36 | 2.45 | 3.04 | 25.41 | 2 669.54 |
| $r_{ij}-r_{kl}$ (i≠j; k≠l) | 3.70 | 9.58 | 0.47 | 1.68 | 3.00 | 3.73 | 31.13 | 3 269.51 |

TABLE 3

Mean Values for Plant Canopy Height, Number Culms Plant⁻¹, Number Leaves Culm⁻¹, Flag Leaf Area, Mid Leaf Area, Basal Leaf Area, Total Leaf Area Culm⁻¹, and Total Leaf Area Plant⁻¹ for Big Bluestem Parents and F₁ Progenies at Stillwater, Oklahoma
Averaged Over 1986 and 1987

| Parent or Progeny | Plant canopy height | Culms, plant ⁻¹ | Leaves culm ⁻¹ | Leaf area | | | | |
|-------------------|---------------------|----------------------------|---------------------------|-----------------------------|------|-------|--------------------------|---------------------------|
| | | | | Flag | Mid | Basal | Total culm ⁻¹ | Total plant ⁻¹ |
| | -- cm -- | ----- no ----- | | ----- cm ² ----- | | | | |
| s ₁₁ | 62.2 | 16.7 | 8.7 | 8.2 | 26.0 | 53.1 | 257.7 | 4 497.6 |
| s ₁₂ | 73.4 | 64.7 | 8.7 | 7.6 | 22.1 | 37.3 | 196.7 | 12 564.0 |
| s ₁₃ | 72.8 | 85.2 | 8.1 | 9.3 | 22.9 | 37.1 | 190.4 | 16 510.4 |
| s ₁₄ | 74.7 | 88.2 | 9.3 | 9.6 | 24.6 | 46.1 | 255.2 | 22 812.0 |
| s ₁₅ | 78.8 | 65.3 | 10.9 | 11.6 | 38.5 | 56.0 | 394.8 | 25 406.8 |
| s ₁₆ | 75.3 | 88.1 | 10.0 | 13.5 | 32.8 | 46.8 | 314.2 | 26 153.2 |
| s ₂₂ | 50.3 | 57.5 | 7.2 | 5.0 | 15.0 | 24.1 | 107.9 | 6 250.9 |
| s ₂₃ | 71.2 | 117.5 | 8.2 | 6.6 | 18.1 | 30.3 | 147.8 | 16 780.7 |
| s ₂₄ | 73.4 | 106.2 | 7.5 | 6.8 | 18.9 | 32.2 | 147.1 | 15 508.0 |
| s ₂₅ | 75.6 | 112.7 | 10.1 | 9.9 | 31.9 | 44.3 | 290.5 | 32 611.4 |
| s ₂₆ | 62.8 | 108.3 | 9.2 | 7.6 | 22.7 | 33.8 | 196.4 | 21 477.9 |
| s ₃₃ | 58.4 | 69.7 | 7.9 | 6.2 | 17.8 | 31.2 | 147.4 | 10 433.4 |

TABLE 3. cont.

| Parent or Progeny | Plant canopy height | Culms plant ⁻¹ | Leaves culm ⁻¹ | Leaf area | | | | |
|-------------------|---------------------|---------------------------|---------------------------|-----------------------------|------|-------|--------------------------|---------------------------|
| | | | | Flag | Mid | Basal | Total culm ⁻¹ | Total plant ⁻¹ |
| | -- cm -- | ----- no ----- | | ----- cm ² ----- | | | | |
| s ₃₄ | 78.4 | 123.9 | 8.1 | 6.9 | 18.2 | 30.7 | 151.2 | 18 776.8 |
| s ₃₅ | 77.8 | 93.8 | 9.6 | 10.0 | 32.6 | 45.1 | 284.8 | 27 099.3 |
| s ₃₆ | 63.4 | 112.8 | 8.1 | 10.7 | 24.7 | 37.6 | 198.8 | 22 602.2 |
| s ₄₄ | 51.6 | 70.7 | 7.4 | 6.5 | 15.8 | 25.8 | 120.3 | 8 860.9 |
| s ₄₅ | 69.4 | 88.4 | 10.1 | 11.5 | 30.7 | 45.0 | 303.0 | 27 910.3 |
| s ₄₆ | 61.9 | 119.8 | 8.3 | 8.6 | 26.9 | 37.7 | 204.3 | 24 739.7 |
| s ₅₅ | 61.0 | 61.8 | 12.5 | 26.2 | 68.6 | 71.9 | 697.4 | 41 692.2 |
| s ₅₆ | 71.6 | 86.1 | 11.1 | 11.7 | 38.4 | 50.5 | 381.4 | 33 924.1 |
| s ₆₆ | 46.2 | 56.9 | 9.1 | 15.7 | 29.5 | 40.1 | 260.3 | 15 974.7 |
| r ₁₂ | 76.9 | 65.9 | 9.4 | 8.6 | 25.0 | 38.3 | 227.7 | 14 847.1 |
| r ₁₃ | 77.5 | 87.3 | 8.4 | 10.5 | 27.1 | 42.4 | 221.4 | 19 072.9 |
| r ₁₄ | 74.7 | 76.2 | 9.4 | 7.0 | 24.8 | 39.2 | 228.4 | 17 200.2 |
| r ₁₅ | 81.6 | 72.0 | 10.5 | 14.2 | 43.1 | 54.3 | 402.3 | 28 865.3 |
| r ₁₆ | 70.6 | 86.8 | 9.7 | 10.5 | 33.6 | 46.0 | 293.4 | 25 049.5 |
| r ₂₃ | 65.9 | 113.9 | 7.8 | 6.1 | 17.7 | 26.6 | 134.4 | 14 316.9 |

TABLE 3. cont.

| Parent or Progeny | Plant canopy height | Culms plant ⁻¹ | Leaves culm ⁻¹ | Leaf area | | | | |
|-------------------|---------------------|---------------------------|---------------------------|-----------------------------|------|-------|--------------------------|---------------------------|
| | | | | Flag | Mid | Basal | Total culm ⁻¹ | Total plant ⁻¹ |
| | -- cm -- | ----- no ----- | | ----- cm ² ----- | | | | |
| r ₂₄ | 65.9 | 111.6 | 7.9 | 6.0 | 18.5 | 31.0 | 146.1 | 16 272.0 |
| r ₂₅ | 71.9 | 87.2 | 9.2 | 7.1 | 28.9 | 46.0 | 251.4 | 22 079.2 |
| r ₂₆ | 66.2 | 101.1 | 7.9 | 8.3 | 18.4 | 32.2 | 157.1 | 16 048.2 |
| r ₃₄ | 64.4 | 73.6 | 7.6 | 8.5 | 24.8 | 34.1 | 171.0 | 12 356.7 |
| r ₃₅ | 62.5 | 58.2 | 8.9 | 13.4 | 34.3 | 44.8 | 275.6 | 17 029.6 |
| r ₃₆ | 57.2 | 82.5 | 8.5 | 9.7 | 29.7 | 45.3 | 265.3 | 22 590.3 |
| r ₄₅ | 76.2 | 87.8 | 9.9 | 11.6 | 32.8 | 54.4 | 338.5 | 29 602.4 |
| r ₄₆ | 66.2 | 102.5 | 8.3 | 8.8 | 25.8 | 38.9 | 207.0 | 21 069.4 |
| r ₅₆ | 67.8 | 117.6 | 10.9 | 14.8 | 45.5 | 55.2 | 420.6 | 48 803.4 |

TABLE 4

Phenotypic Correlations Between Vegetative Characters in Big Bluestem,
Based on 288 Observations each Year

| Vegetative character | Culms plant ⁻¹ | Leaves culm ⁻¹ | Leaf area | | | | |
|------------------------------------|---------------------------|---------------------------|-----------------------------|--------|--------|--------------------------|---------------------------|
| | | | Flag | Mid | Basal | Total culm ⁻¹ | Total plant ⁻¹ |
| | ----- no ----- | | ----- cm ² ----- | | | | |
| Plant canopy ht. (cm) | 0.31** | 0.19** | -0.03 | 0.13** | 0.23** | 0.17** | 0.31** |
| Culm plant ⁻¹ | | -0.02 | -0.12** | -0.10* | -0.10* | -0.11* | 0.49** |
| Leaves culm ⁻¹ | | | 0.20** | 0.53** | 0.50** | 0.77** | 0.64** |
| Flag leaf area | | | | 0.55** | 0.33** | 0.55** | 0.34** |
| Mid-leaf area | | | | | 0.67** | 0.88** | 0.66** |
| Basal-leaf area | | | | | | 0.82** | 0.62** |
| Total leaf area culm ⁻¹ | | | | | | | 0.75** |

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

PART IV

COMBINING ABILITY FOR REPRODUCTIVE CHARACTERISTICS
IN BIG BLUESTEM

ABSTRACT

Seed production in big bluestem, Andropogon gerardii Vitman, is often poor because of genetic and environmental factors. To enhance seed production in big bluestem, a basic understanding of the genetic variation of traits which affect seed set would be useful. Therefore, the objectives of this study were to compare the flowering dates and seed yield components of parents and hybrids produced from a diallel cross among six diverse big bluestem accessions and to estimate the general (GCA) and specific (SCA) combining abilities for those traits. Significant differences were observed for flowering date among big bluestem parents and crosses. Hybrid plants tended to have a flowering date intermediate between their parents. Differences in number of culms plant⁻¹ were attributed to year, GCA effects, SCA effects, and reciprocal (REC) effects. The number of culms plant⁻¹ were related to growth habit with sod-forming types tending to have more culms plant⁻¹. Significant variation in the number of sessile, pedicellate, and total caryopses culm⁻¹ was attributed to year, GCA effects, year by GCA effects, and SCA effects. Also a significant year by REC and year by SCA interaction occurred for sessile and pedicellate caryopses culm⁻¹, respectively. When comparing

year differences in pedicellate and sessile caryopses culm⁻¹ the percent reduction from 1986 to 1987 was remarkably similar. The reduction in pedicellate and sessile spikelets was 51 and 46%, respectively. This suggests that plant and environmental factors affecting seed set act similarly upon both the pedicellate and sessile spikelets. Significant variation for total number of caryopses plant⁻¹ varied with year, GCA effects, SCA effects, and year by GCA effects. Phenotypic correlation coefficients between flowering date and other yield component characters, except the number of spikelets inflorescence⁻¹, were all significant and negative. Although seed set is important, the number of culms plant⁻¹ tended to have a greater impact on the total seed yield plant⁻¹. Thus, simultaneous selection for increased numbers of caryopses culm⁻¹ and increased numbers of culms plant⁻¹ should offer the most convenient method for increasing seed yield in big bluestem.

INTRODUCTION

The primary objectives of most programs in forage grass breeding are for increased forage yield and quality. Although these traits are certainly important, forage varieties are not necessarily preferred by producers because of them alone. A successful forage variety must be adapted, useful, have good seed production, and have good seedling habits (Harlan, 1960). Typically, a forage species is adapted to areas larger than its own local area of origin. It generally can be used within 480 km north and 240 km south of its origin without problems of winter hardiness, longevity, or disease. East or west movements are affected by changes in elevation and rainfall. A change of 300 m in elevation is approximately equal to a northerly move of 280 km (Source of Native Seeds and Plants, 1987). Seed production in big bluestem is influenced by several yield components, i.e., number of fertile spikelets inflorescence⁻¹, number of fertile spikelets producing a caryopsis (percent seedset), caryopsis weight (seed size), number of inflorescences culm⁻¹, and number of culms unit area⁻¹. The objectives of my study were to compare the flowering dates and selected seed yield components of parental and hybrid plants produced from a diallel cross

among six diverse big bluestem accessions and to estimate the general and specific combining abilities for those traits.

MATERIALS AND METHODS

Reproductive characters, i.e., number of culms plant⁻¹, number of sessile spikelets inflorescence⁻¹ and sessile spikelets culm⁻¹, pedicellate, sessile, and total number of caryopses culm⁻¹, and total number of caryopses plant⁻¹, of six big bluestem parental accessions and their F₁ progeny were measured in 1986 and 1987, respectively. Big bluestem accessions used as parents were from clonally propagated lines originally collected and maintained by the USDA-Soil Conservation Service, Plant Material Centers at Knox City, Texas, and Manhattan, Kansas. The accession number, origin, and the average flowering date of the six parent accessions were:

1. 1836; Hughes County, Oklahoma; 8 August.
2. 1843; Nowata County, Oklahoma; 18 July.
3. 1947; Parker County, Texas; 20 July.
4. 1952; Bell County, Texas; 5 August.
5. 2397; Nueces County, Texas; 5 October.
6. 2675; Victoria County, Texas; 17 September.

In the summer of 1984, controlled paired crosses were made in the greenhouse among the six accessions using a complete diallel mating design. Sessile spikelets of each accession were emasculated and pollinated using the

techniques of Richardson (1958). Caryopses for the crosses were germinated during the fall of 1984, and plantlets were established in a field plot in the spring of 1985. The field plot experimental design was a randomized complete block with eight replications. Each block contained one plant of each of the six parent accessions and 30 F_1 progeny plants from each cross. The 30 F_1 progeny plants from respective crosses consisted of 15 plants each from reciprocal matings.

Data collected from each plant included the flowering date and the number of culms plant⁻¹. The flowering date of each plant was recorded in Julian days when at least five inflorescences were flowering (Law and Anderson, 1940). From a randomly selected culm of each plant, the number of inflorescences at each node was recorded. Similarly, from a randomly selected inflorescence at each node, the number of sessile spikelets inflorescence⁻¹, and the number of pedicellate, sessile, and total number of caryopses inflorescence⁻¹ were recorded. The number of pedicellate caryopses culm⁻¹ were calculated by summing over all nodes the number of pedicellate caryopses inflorescence⁻¹ at a node multiplied by the number of inflorescences node⁻¹. Similarly the number of sessile caryopses culm⁻¹ were calculated by summing over all nodes the number of sessile caryopses inflorescence⁻¹ at a node multiplied by the number of inflorescences node⁻¹. The total number of caryopses culm⁻¹ were calculated by adding the number of pedicellate and

sessile caryopses culm⁻¹. The total number of caryopses plant⁻¹ were calculated by multiplying the total number of caryopses culm⁻¹ times the number of culms plant⁻¹.

Data for each response variable were subjected to diallel analyses using Griffing's (1956) Method 1, Model I procedure and PROC GLM (SAS Institute, 1985). Phenotypic correlation coefficients were calculated using PROC CORR (SAS Institute, 1985).

RESULTS AND DISCUSSION

Flowering Date

To maximize usable forage and seed set in big bluestem, the time of maturity (flowering date) must be controlled. The later a cultivar flowers in the season the longer its forage can be utilized; however, later flowering cultivars may not have enough time to mature a seed crop before frost. McMillan (1959) observed that clones of big bluestem from southern and eastern communities flowered later than clones from northern and western communities, and that time of maturity was conditioned by genetic variation of the species as well as habitat variation associated with differences in day lengths, temperatures, and soil types. I similarly observed that accessions, originally collected from south Texas, flowered significantly later than accessions collected from northern Texas and Oklahoma. Significant variation was observed among the parental clones and progeny

lines for flowering date; however, little variation was observed within each of the parental clones or progeny lines. Differences in plant flowering dates were associated with year, general combining ability (GCA) effects, specific combining ability (SCA) effects, year by GCA effects, and year by SCA effects (Table 1). For individual years except for accession 4 in 1986 and averaged over years, significant negative GCA estimates occurred for accessions 1, 2, 3, and 4, and significant positive GCA estimates occurred for accessions 5 and 6 (Table 2). The year by GCA interaction was possibly caused by accession 3 which showed a reverse trend in GCA estimates when compared to other accession between the two years (Table 2). Similarly, averaged over years, significant SCA estimates occurred for hybrid plant combinations of early maturing types with late maturing types (Table 3). The year by SCA interaction tended to be caused by yearly fluctuations in SCA estimates. Comparing the 21 SCA estimates between years showed that only 5 disagreed in direction (sign), and in general the magnitude of change was similar for the two years. Hybrid plants tended to have flowering dates intermediate to those of their parents (Table 4). Because little variation existed within progeny lines, flowering dates should be relatively easy to predict and select for, given that the flowering dates of the parents are known for any given location.

Culms Per Plant

Differences in numbers of culms plant⁻¹ were attributed to year, GCA effects, SCA effects, and REC effects (Table 1). Significant positive GCA estimates were shown for accessions 2, 4 and 6 and significant negative estimates for accession 1 (Table 2). Similar to the canopy height, mean numbers of culms plant⁻¹ for all F₁ crosses were higher than the corresponding mean numbers of culms plant⁻¹ of the parents contributing to the hybrid, and significant negative SCA estimates occurred for all parental accessions (Table 3). Reciprocal differences were primarily associated with accession 3. A cross with accession 3 as the female parent produced progeny with 25 to 50 more culms than that of the male parent. Density of culms is also a function of plant growth habit. Big bluestem has two distinct growth habits: sod-forming or bunch. Ecologically, sod-forming grasses tend to grow in areas of adequate moisture, and bunch grasses in areas of limited moisture (Weaver 1968). Accession 3 is a sod-forming type with great lateral growth. This habit increases the number of culms plant⁻¹.

Seed Production

The seed yield potential of big bluestem is directly related to the total number of fertile spikelets produced plant⁻¹. The inflorescence of big bluestem consists of paired spikelets. Pedicellate spikelets are either

bisexual, staminate, or neuter, while sessile spikelets are always bisexual. Approximately 75% of the harvested pure seed in our study was from sessile spikelets. Thus, positive selection for number of sessile spikelets plant⁻¹ would increase the seed yield potential of the species. There were significant differences in number of sessile spikelets inflorescence⁻¹ for year, GCA effects, SCA effects, year by GCA effects, and year by SCA effects (Table 1). Excluding accession 1, the GCA estimates in each year were in the same direction (sign), and significant positive GCA estimates occurred only for accession 5 (Table 2). The average number of sessile spikelets inflorescence⁻¹ in 1986 was 55.7 compared to 63.0 in 1987. During June and July in 1986, there may have been inadequate moisture for optimum plant growth and development, thus lowering the number of spikelets inflorescence⁻¹. Averaged over years, parental accession 5 had the highest number of sessile spikelets inflorescence⁻¹ at 99.7. The average number of sessile spikelets inflorescence⁻¹ of other parental accession ranged from 50.0 in accession 3 to 53.6 in accession 1 (Table 4). Growth in big bluestem is indeterminant, and flushes of growth occur when moisture is favorable. In 1987, the average number of inflorescences culm⁻¹ were reduced by drought stress in August. Slowed growth reduced the number of inflorescences culm⁻¹, and decreased the seed yield potential of the species by lowering the total number of spikelets culm⁻¹.

There were significant GCA, SCA, and REC effects for the number of sessile spikelets culm⁻¹ (Table 1). Averaged over years, significant positive GCA estimates occurred for accession 1, and significant negative estimates occurred for accessions 3, 5, and 6 (Table 2). The average number of sessile spikelets culm⁻¹ ranged for 398.9 to 1057.9 for accessions 5 and 1, respectively. In 1987, the mean number of sessile spikelets culm⁻¹ was 595.3 compared to 649.9 in 1986. Based on hybrid populations from crosses between accessions 1 and 3, 2 and 4, and 2 and 5, the number of sessile spikelets culm⁻¹ appears to be controlled by nuclear genes. Reciprocal crosses among these accessions produced F₁'s with relatively similar numbers of spikelets culm⁻¹. However, reciprocal crosses between accessions 1 and 4, 3 and 5, and 2 and 6 suggested that the number of spikelets culm⁻¹ may be strongly influenced by cytoplasmic inheritance (Table 4).

Significant variation in the number of sessile, pedicellate, and total caryopses culm⁻¹ was attributed to year, GCA effects, year by GCA effects, and SCA effects (Table 1). Also a significant year by REC and year by SCA interaction occurred for sessile and pedicellate caryopses culm⁻¹, respectively. When comparing year differences in pedicellate and sessile caryopses culm⁻¹ the percent reduction from 1986 to 1987 was remarkably similar. The reduction in pedicellate and sessile spikelets was 51 and 46%, respectively. This suggests that plant and

environmental factors affecting seed set act equally upon the two spikelet types. Similarly, the reduction from 1986 to 1987 for the total number of caryopses culm⁻¹ (pedicellate plus sessile) was 47%. GCA interactions with years showed that accessions 2 and 3 responded differently in each environment. Although the magnitude of GCA estimates for the other accessions were different for each year, the directions (sign) were the same. The average flowering date for crosses utilizing accessions 2, or 3, or both tends to be earlier and has a smaller variance when compared to other accessions and their crosses. In 1987, drought stress may partially explain the year by GCA, year by SCA, and year by REC interactions. For all three variables averaged over years, there were significant positive GCA estimates for accession 1, and significant negative estimates for accessions 5 and 6. Significant SCA effects also occurred for the three variables, and averaged over years, significant SCA estimates were associated with crosses of accession 1 (Table 2). The highest number of pedicellate and sessile caryopses culm⁻¹ were also observed for s₁₁. These data suggest that seed production in big bluestem is controlled by quantitative characters, which are primarily additive in nature. Thus, crosses with accession 1 tend to vary for the number of caryopses produced culm⁻¹, and depending upon the accession it is crossed with, the effects may be positive or negative (Tables 3 & 4).

The interaction among seed yield components in big bluestem produces plant to plant variations in seed yield. If the total number of caryopses culm⁻¹ are high and the number of culms plant⁻¹ are low, then the relative seed yield will be low. Similarly, if the number of culms plant⁻¹ are high and the number of caryopses culm⁻¹ are low, then the relative seed yield varies with the number of culms plant⁻¹. Thus, the total number of caryopses plant⁻¹ then varies with the number of culms plant⁻¹. Significant variation for total number of caryopses plant⁻¹ varied with year, GCA effects, SCA effects, and year by GCA effects. Year differences were associated with the number of spikelets inflorescence⁻¹ and the number of inflorescence culm⁻¹, and have been previously discussed. Significant positive GCA estimates occurred for accessions 1 and 2, and significant negative estimates occurred for accessions 5 and 6 (Table 2). The year by GCA interaction was associated with accession 3 which showed a reverse trend when compared to other accessions between years (Table 2). Significant SCA estimates primarily occurred for crosses which had a significant increase in the number of culms plant⁻¹ and moderate to high numbers of caryopses culm⁻¹ (Tables 3 & 4). Thus, the total number of caryopses plant⁻¹ was closely allied with the number of culms plant⁻¹.

Phenotypic correlation coefficients between flowering date and other yield component characters, except the number of spikelets inflorescence⁻¹, were all significant and

negative (Table 5). As expected, the number of culms plant⁻¹, caryopses culm⁻¹, and caryopses plant⁻¹, were lower for later flowering types. Similarly, as the number of culms plant⁻¹ increased the number of caryopses culm⁻¹ decreased; however, the number of caryopses plant⁻¹ significantly increased. Thus, positive selection for increased numbers of culms plant⁻¹ would increase seed yield. Correspondingly, positive selection for increased numbers of caryopses culm⁻¹ would significantly increase the seed yield in big bluestem.

Increasing seed yield in big bluestem is a complex task and there are several approaches which have merit. Selecting for pedicellate spikelet fertility has been proposed as a method of increasing the seed yield in the species (Boe, et al. 1983). In their study, pedicellate-spikelet seed yield was correlated positively with total seed yield, and they considered it feasible to increase the seed yield potential by selecting for increased seed set in pedicellate spikelets. Ross, et al. (1975), studied several agronomic characters of big bluestem including seed set. Twenty-three families were selected from open-pollinated parents with good seed and forage potential. They estimated seed production by dividing threshed seed weight by unthreshed weight and converting it to percent. They found no correlations between seed set and forage yield components, and concluded that selection for seed set could be practiced without loss to forage production.

Although seed set is important, the number of culms plant⁻¹ tends to have a greater impact on the total seed yield plant⁻¹. Law and Anderson (1940) stated "... it has been possible to increase the mean number of culms per plant from 57±29 to 148±49 by four generations of selection." Thus, simultaneous selection for increased numbers of caryopses culm⁻¹ and increased numbers of culms plant⁻¹ should offer the fastest and most convenient method for increasing the seed yield in big bluestem.

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TABLE 1

Mean Squares for Flowering Date, Culms Plant⁻¹, Sessile Spikelets Inflorescence⁻¹, Sessile Spikelets Culm⁻¹, Sessile Caryopses Culm⁻¹, Pedicellate Caryopses Culm⁻¹, Total Caryopses Culm⁻¹, and Total Caryopses Plant⁻¹, for Big Bluestem at Stillwater, Oklahoma in 1986 and 1987

| Mean squares | | | | | | | | | |
|--------------|-----|----------------|------------------------------|-----------------------------|--------------------|----------------------------------|-------------|---------------|-------------------------------------|
| Source | df | Flowering date | No. culm plant ⁻¹ | No. sessile spikelets | | No. caryopses culm ⁻¹ | | | Total caryopses plant ⁻¹ |
| | | | | inflorescence ⁻¹ | culm ⁻¹ | sessile | pedicellate | total | |
| Block (B) | 7 | 1 130.6** | 3 593.9** | 1 943.3** | 716 659.9* | 42 545.8 | 3 187.5 | 52 237.4 | 471 024 271.9 |
| Year (Y) | 1 | 2 332.1** | 44 644.2** | 7 709.9** | 429 789.5 | 1 160 108.5** | 69 454.2** | 1 797 275.4** | 4 791 610 293.8** |
| B X Y | 7 | 133.9 | 222.7 | 150.0 | 111 006.7 | 29 692.5 | 5 103.1 | 42 808.7 | 271 547 981.9 |
| Genotype (G) | 35 | 8 751.7** | 8 674.9** | 2 563.8** | 635 768.4** | 78 972.3** | 18 747.3** | 161 010.9** | 490 400 753.7** |
| GCA | 5 | 54 774.8** | 19 404.0** | 12 563.8** | 2 930 411.5** | 447 768.5** | 101 269.5** | 967 015.3** | 1 805 050 154.8** |
| SCA | 15 | 1 503.9** | 10 065.3** | 788.4 | 289 666.5** | 19 516.8* | 8 560.5** | 39 185.1* | 393 454 734.9** |
| REC | 15 | 658.5 | 3 708.0** | 1 005.8 | 216 989.2* | 15 495.7 | 1 426.8 | 14 168.7 | 149 130 305.3 |
| B X G | 245 | 450.4 | 1 468.3 | 619.1 | 139 151.4 | 12 513.6 | 3 702.9 | 24 057.6 | 150 722 267.4 |

TABLE 1. cont.

| Mean squares | | | | | | | | | |
|--------------|-----|----------------|------------------------------|-----------------------------|--------------------|----------------------------------|-------------|-------------|-------------------------------------|
| Source | df | Flowering date | No. culm plant ⁻¹ | No. sessile spikelets | | No. caryopses culm ⁻¹ | | | Total caryopses plant ⁻¹ |
| | | | | inflorescence ⁻¹ | culm ⁻¹ | sessile | pedicellate | total | |
| Y X G | 35 | 193.9** | 150.9 | 647.6** | 108 686.8 | 18 291.4** | 7 184.8** | 37 706.1** | 112 005 323.9* |
| Y*GCA | 5 | 380.2** | 236.3 | 2 607.0** | 90 344.5 | 70 289.5** | 27 998.2** | 183 176.3** | 228 268 731.7** |
| Y*SCA | 15 | 251.1** | 196.6 | 479.4* | 118 468.0 | 5 865.0 | 4 862.2* | 12 405.1 | 86 820 292.8 |
| Y*REC | 15 | 74.7 | 76.8 | 162.6 | 105 019.7 | 13 385.0* | 2 569.6 | 14 517.0 | 98 435 885.6 |
| B X Y X G | 245 | 86.8 | 194.8 | 236.8 | 73 389.8 | 6 778.9 | 2 403.3 | 12 249.0 | 67 166 206.2 |
| Mean | | 229.8 | 28.7 | 59.4 | 622.6 | 121.5 | 33.8 | 155.3 | 11 920.1 |

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

TABLE 2

Estimates of General (g_i) Combining Ability (GCA) Effects for Big Bluestem
at Stillwater, Oklahoma in 1986 and 1987

| Variable | Year | Mean | GCA effects | | | | | |
|---|------|-------|-------------|---------|----------|--------|---------|----------|
| | | | g_1 | g_2 | g_3 | g_4 | g_5 | g_6 |
| Flowering date (day) | 1986 | 231.8 | -7.0** | -20.8** | -8.5** | -1.3 | 23.8** | 13.7** |
| | 1987 | 227.8 | -8.0** | -21.6** | -6.5** | -6.0** | 27.1** | 14.9** |
| | avg. | 229.8 | -7.5** | -21.2** | -7.5** | -3.7** | 25.5** | 14.3** |
| Culms plant ⁻¹ (no) | 1986 | 77.8 | -19.5** | 4.6 | 3.0 | 8.6** | -3.7 | 7.0** |
| | 1987 | 95.4 | -18.2** | 6.2* | 5.1 | 4.7 | -4.1 | 6.3* |
| | avg. | 86.6 | -18.9** | 5.4* | 4.1 | 6.7** | -3.9 | 6.7** |
| Sessile spikelets inflorescence ⁻¹ (no) | 1986 | 55.7 | 1.2 | -1.8 | -0.2 | -4.3** | 9.2** | -4.2** |
| | 1987 | 63.0 | 1.4 | -9.4** | -6.5** | -4.9* | 22.3** | -3.0 |
| | avg. | 59.4 | 1.3 | -5.6** | -3.4* | -4.6** | 15.8** | -3.6* |
| Sessile spikelets culm ⁻¹ (no) | 1986 | 649.9 | 249.0** | 1.2 | -120.7** | 44.6 | -42.7 | -131.3** |
| | 1987 | 595.3 | 196.0* | 15.7 | -67.4* | 31.6 | -84.7** | -91.1** |
| | avg. | 622.6 | 222.5** | 8.5 | -94.1** | 38.1 | -63.7** | -111.2** |

TABLE 2. cont.

| Variable | Year | Mean | GCA effects | | | | | |
|--------------------------|------|----------|----------------|----------------|----------------|----------------|----------------|----------------|
| | | | g ₁ | g ₂ | g ₃ | g ₄ | g ₅ | g ₆ |
| Sessile caryopses | 1986 | 166.3 | 118.5** | 24.2* | -24.5* | -1.9 | -71.7** | -44.6** |
| culm ⁻¹ (no) | 1987 | 76.6 | 55.2** | 0.5 | 0.3 | 0.1 | -29.0** | -26.2** |
| | avg. | 121.5 | 86.9** | 12.4 | -12.1 | -0.9 | -50.5** | -35.4** |
| Pedicellate caryopses | 1986 | 44.8 | 66.1** | 7.2 | -9.8 | -9.6 | -27.3** | -26.5** |
| culm ⁻¹ (no) | 1987 | 22.9 | 22.6** | -4.9 | 1.1 | -3.0 | -9.8** | -6.0* |
| | avg. | 33.9 | 44.4** | 1.1 | -4.4 | -6.3 | -18.6** | -16.2** |
| Total caryopses | 1986 | 211.2 | 184.6** | 31.3* | -34.3* | -11.5 | -99.0** | -71.1** |
| culm ⁻¹ (no) | 1987 | 99.5 | 77.8** | -4.3 | 1.4 | -2.8 | -38.8** | -33.2** |
| | avg. | 155.3 | 131.2** | 13.5 | -16.5 | -7.1 | -68.9** | -52.1** |
| Total caryopses | 1986 | 14 804.4 | 4 385.7** | 2 962.5** | 113.3 | 1 633.2 | -6 701.9** | -2 393.9* |
| plant ⁻¹ (no) | 1987 | 9 035.9 | 2 779.0** | 282.4 | 1 412.0 | 436.8 | -3 576.9** | -1 333.4 |
| | avg. | 11 920.1 | 3 582.4** | 1 623.0* | 762.7 | 1 035.0 | -5 139.4** | -1 863.6* |

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

TABLE 3

Estimates of Specific Combining Ability (s_{ij}) and Reciprocal Effects (r_{ij}) for Flowering Date, Culms Plant⁻¹, Sessile Spikelets Inflorescence⁻¹ and Sessile Spikelets Culm⁻¹, Sessile Caryopses Culm⁻¹, Pedicellate Caryopses Culm⁻¹, Total Caryopses Culm⁻¹, and Total Caryopses Plant⁻¹, for Big Bluestem Parents and F₁ Progenies at Stillwater, Oklahoma Averaged Over 1986 and 1987 †

| Effect | Flowering date | Sessile spikelets | | | Caryopses culm ⁻¹ | | | Total caryopses plant ⁻¹ |
|-----------------|----------------|---------------------------|-----------------------------|--------------------|------------------------------|-------------|---------|-------------------------------------|
| | | Culms plant ⁻¹ | inflorescence ⁻¹ | culm ⁻¹ | sessile | pedicellate | total | |
| | -- day -- | ----- no. ----- | | | | | | |
| s ₁₁ | 5.9 | -32.0** | -8.4* | -9.6 | 51.4** | 62.6** | 114.0** | -11 431.4** |
| s ₁₂ | 1.5 | -7.9 | -3.3 | 76.6 | 20.5 | -4.3 | 16.1 | 759.3 |
| s ₁₃ | 0.3 | 14.4** | -0.9 | -113.3* | -36.5** | -2.1 | -38.6* | 3 152.9* |
| s ₁₄ | -1.4 | 7.8 | 0.2 | 52.9 | -14.4 | -8.3 | -22.7 | 3 647.4* |
| s ₁₅ | 0.6 | 4.8 | 3.9 | 25.3 | -8.1 | -30.8** | -38.9* | 385.2 |
| s ₁₆ | -6.9** | 13.1** | 6.7* | -31.9 | -12.8 | -17.1* | -29.9 | 3 486.6* |
| s ₂₂ | 12.2** | -39.9** | 5.0 | -102.0 | -27.3 | 15.2 | -12.1 | -6 305.5** |
| s ₂₃ | 2.2 | 19.6** | -1.6 | -57.4 | -3.5 | -6.3 | -9.8 | 1 786.1 |
| s ₂₄ | 6.0** | 10.2** | -1.0 | -182.3** | -37.3** | -12.8 | -50.1** | -3 296.2* |
| s ₂₅ | -8.9** | 11.8** | 4.0 | 174.8** | 24.4 | 9.3 | 33.7 | 4 700.0** |
| s ₂₆ | -12.9** | 6.0 | -3.0 | 90.2 | 23.3 | -1.0 | 22.2 | 2 356.2 |

TABLE 3. cont.

| Effect | Flowering date | Culms plant ⁻¹ | Sessile spikelets | | Caryopses culm ⁻¹ | | | Total caryopses plant ⁻¹ |
|-----------------|----------------|---------------------------|-----------------------------|--------------------|------------------------------|-------------|-------|-------------------------------------|
| | | | inflorescence ⁻¹ | culm ⁻¹ | sessile | pedicellate | total | |
| | -- day -- | | ----- no. ----- | | | | | |
| s ₃₃ | -12.8** | -25.0** | -2.6 | 75.0 | 33.8 | 2.3 | 36.1 | -2 274.1 |
| s ₃₄ | -3.5 | 1.4 | 1.0 | 61.1 | -6.3 | 1.7 | -4.6 | -1 328.2 |
| s ₃₅ | 2.8 | -10.8** | -1.4 | 27.1 | 11.1 | 0.5 | 11.6 | -1 214.1 |
| s ₃₆ | 11.0** | 0.3 | 5.5 | 7.5 | 1.5 | 3.9 | 5.5 | -122.5 |
| s ₄₄ | -4.7 | -29.3** | 0.8 | 145.5** | 57.2** | -2.8 | 54.4* | 166.6 |
| s ₄₅ | 2.5 | -1.3 | -4.5 | -56.8 | 3.1 | 14.4 | 17.5 | 110.9 |
| s ₄₆ | 1.1 | 11.2** | 1.7 | -20.5 | -2.3 | 7.7 | 5.4 | 699.4 |
| s ₅₅ | -2.1 | -17.0** | 8.7* | -96.2 | -17.2 | 3.3 | -13.9 | -1 497.0 |
| s ₅₆ | 5.1* | 12.4** | -10.8** | -74.2 | -13.3 | 3.3 | -10.0 | -2 484.9 |
| s ₆₆ | 2.6 | -43.0** | -0.0 | 28.8 | 3.6 | 3.2 | 6.8 | -3 934.9 |
| r ₁₂ | 0.2 | 0.6 | -0.3 | 173.9** | 46.6** | 0.5 | 47.1* | 3 257.9 |
| r ₁₃ | 2.6 | 1.0 | 4.0 | 56.3 | -6.7 | -8.0 | -14.7 | -1 310.0 |
| r ₁₄ | 7.4** | -6.0 | -2.7 | -122.5** | -49.3** | 13.9 | -35.4 | -4 796.7** |
| r ₁₅ | -1.1 | 3.3 | 0.6 | -33.9 | -18.5 | 0.3 | -18.2 | -48.9 |
| r ₁₆ | 0.6 | -0.6 | -0.8 | -28.8 | -7.3 | 5.6 | -1.6 | 8.3 |

TABLE 3. cont.

| Effect | Flowering date | Culms plant ⁻¹ | Sessile spikelets | | Caryopses culm ⁻¹ | | | Total caryopses plant ⁻¹ |
|-----------------|----------------|---------------------------|-----------------------------|--------------------|------------------------------|-------------|-------|-------------------------------------|
| | | | inflorescence ⁻¹ | culm ⁻¹ | sessile | pedicellate | total | |
| | -- day -- | | | | no. | | | |
| r ₂₃ | -1.7 | -1.8 | -2.2 | -5.6 | -19.9 | 8.5 | -11.3 | -1 740.3 |
| r ₂₄ | -0.6 | 2.7 | 5.2 | 75.6 | 9.2 | 8.7 | 18.0 | 2 229.2 |
| r ₂₅ | -3.5 | -12.7** | 0.5 | -68.8 | -12.1 | 10.0 | -2.1 | -1 523.3 |
| r ₂₆ | -1.4 | -3.6 | -2.7 | -114.0** | -20.4 | 2.6 | -17.7 | -2 429.9 |
| r ₃₄ | 7.0** | -25.1** | 8.0* | 2.9 | 11.1 | 5.0 | 16.1 | -2 047.1 |
| r ₃₅ | -2.8 | -17.8** | -14.5** | -123.6** | -5.0 | -2.7 | -7.7 | -1 110.0 |
| r ₃₆ | 11.1** | -15.1** | -5.5 | -83.6 | -16.5 | -2.0 | -18.4 | -2 183.2 |
| r ₄₅ | -5.5* | -0.3 | 7.9* | 64.9 | 13.5 | 9.1 | 22.6 | 1 104.3 |
| r ₄₆ | -3.7 | -8.6 | 3.6 | 27.6 | 24.0 | 2.1 | 26.1 | 2 595.1 |
| r ₅₆ | 1.7 | 15.7** | -5.2 | -24.7 | 0.0 | -0.3 | -0.3 | 444.6 |

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

† Standard errors for:

| | | | | | | | | |
|-----------------|------|------|------|-------|-------|-------|-------|----------|
| g _i | 1.40 | 2.52 | 1.64 | 24.58 | 7.37 | 4.00 | 10.21 | 808.81 |
| s _{ii} | 4.42 | 7.98 | 5.18 | 77.71 | 23.30 | 12.68 | 32.31 | 2 557.69 |

TABLE 3. cont.

| Effect | Flowering date | Culms plant ⁻¹ | Sessile spikelets | | Caryopses culm ⁻¹ | | | Total caryopses plant ⁻¹ |
|--|----------------|---------------------------|-----------------------------|--------------------|------------------------------|-------------|-------|-------------------------------------|
| | | | inflorescence ⁻¹ | culm ⁻¹ | sessile | pedicellate | total | |
| | -- day -- | | ----- no. ----- | | | | | |
| s_{ij} (i≠j) | 3.19 | 5.76 | 3.74 | 56.04 | 16.80 | 9.14 | 23.30 | 1 844.03 |
| r_{ij} (i≠j) | 3.75 | 6.77 | 4.40 | 65.94 | 19.78 | 10.76 | 27.41 | 2 170.27 |
| g_i-g_j (i≠j) | 2.17 | 3.91 | 2.54 | 38.07 | 11.42 | 6.21 | 15.83 | 1 253.01 |
| $s_{ii}-s_{jj}$ (i≠j) | 6.12 | 11.06 | 7.18 | 107.68 | 32.29 | 17.56 | 44.78 | 3 544.03 |
| $s_{ii}-s_{ij}$ (i≠j) | 6.12 | 11.06 | 7.18 | 107.68 | 32.29 | 17.56 | 44.78 | 3 544.03 |
| $s_{ii}-s_{jk}$ (i≠j,k; j≠k) | 5.31 | 9.58 | 6.22 | 93.25 | 27.97 | 15.21 | 38.78 | 3 069.22 |
| $s_{ij}-s_{ik}$ (i≠j,k; j≠k) | 4.84 | 8.75 | 5.67 | 85.13 | 25.52 | 13.89 | 35.40 | 2 801.80 |
| $s_{ij}-s_{kl}$ (i≠j,k,l; j≠k,l; k≠l) | 4.33 | 7.82 | 5.08 | 76.14 | 22.83 | 12.42 | 31.66 | 2 506.01 |
| $r_{ij}-r_{kl}$ (i≠j; k≠l) | 5.31 | 9.60 | 6.22 | 93.26 | 27.97 | 15.21 | 38.78 | 3 069.22 |

TABLE 4

Mean Values for Flowering Date, Culms Plant⁻¹, Sessile Spikelets Inflorescence⁻¹, Sessile Spikelets Culm⁻¹, Sessile Caryopses Culm⁻¹, Pedicellate Caryopses Culm⁻¹, Total Caryopses Culm⁻¹, and Total Caryopses Plant⁻¹, for Big Bluestem Parents and F₁ Progenies at Stillwater, Oklahoma Averaged Over 1986 and 1987

| Parent or progeny | Flowering date | Sessile spikelets | | | Caryopses culm ⁻¹ | | | Total caryopses plant ⁻¹ |
|-------------------|----------------|---------------------------|-----------------------------|--------------------|------------------------------|-------------|-------|-------------------------------------|
| | | Culms plant ⁻¹ | inflorescence ⁻¹ | culm ⁻¹ | sessile | pedicellate | total | |
| | -- day -- | ----- no. ----- | | | | | | |
| s ₁₁ | 220.8 | 16.7 | 53.6 | 1 057.9 | 346.6 | 185.2 | 531.7 | 7 653.4 |
| s ₁₂ | 202.4 | 64.7 | 52.1 | 756.3 | 194.6 | 74.6 | 269.1 | 14 626.9 |
| s ₁₃ | 212.5 | 85.2 | 52.4 | 581.4 | 166.3 | 79.7 | 246.1 | 20 728.0 |
| s ₁₄ | 209.9 | 88.2 | 60.8 | 1 058.6 | 242.3 | 49.7 | 292.0 | 24 981.6 |
| s ₁₅ | 249.6 | 65.3 | 79.8 | 840.5 | 168.4 | 28.5 | 196.9 | 10 797.2 |
| s ₁₆ | 229.1 | 88.1 | 64.6 | 730.8 | 166.9 | 39.2 | 206.1 | 17 117.1 |
| s ₂₂ | 199.6 | 57.5 | 53.1 | 537.6 | 118.9 | 51.3 | 170.2 | 8 860.6 |
| s ₂₃ | 205.1 | 117.5 | 51.0 | 485.1 | 138.1 | 15.7 | 153.8 | 17 832.2 |
| s ₂₄ | 211.6 | 106.2 | 42.9 | 411.2 | 86.4 | 7.2 | 93.6 | 9 052.7 |
| s ₂₅ | 228.7 | 112.7 | 73.1 | 811.0 | 120.0 | 15.7 | 135.7 | 14 627.1 |
| s ₂₆ | 211.4 | 108.3 | 49.9 | 724.0 | 141.6 | 15.1 | 156.7 | 16 465.6 |

TABLE 4. cont.

| Parent or progeny | Flowering date | Culms plant ⁻¹ | Sessile spikelets | | Caryopses culm ⁻¹ | | | Total caryopses plant ⁻¹ | |
|-------------------|----------------|---------------------------|-----------------------------|--------------------|------------------------------|-------------|-------|-------------------------------------|--|
| | | | inflorescence ⁻¹ | culm ⁻¹ | sessile | pedicellate | total | | |
| | -- day -- | | ----- no. ----- | | | | | | |
| s ₃₃ | 202.0 | 69.7 | 50.0 | 509.4 | 131.0 | 27.4 | 158.4 | 11 171.3 | |
| s ₃₄ | 208.1 | 123.9 | 44.5 | 624.8 | 91.0 | 19.9 | 110.9 | 14 436.7 | |
| s ₃₅ | 253.4 | 93.8 | 84.9 | 615.4 | 75.1 | 14.1 | 89.2 | 7 439.3 | |
| s ₃₆ | 236.5 | 112.8 | 63.5 | 508.4 | 91.5 | 19.1 | 110.6 | 12 879.9 | |
| s ₄₄ | 217.7 | 70.7 | 51.1 | 844.2 | 176.9 | 18.4 | 195.4 | 14 156.8 | |
| s ₄₅ | 259.6 | 88.4 | 58.2 | 475.2 | 59.9 | 14.2 | 74.1 | 6 822.3 | |
| s ₄₆ | 245.2 | 119.8 | 49.4 | 501.4 | 58.4 | 16.9 | 75.3 | 9 195.9 | |
| s ₅₅ | 278.6 | 61.8 | 99.7 | 398.9 | 3.6 | 0.0 | 3.6 | 144.4 | |
| s ₅₆ | 272.9 | 86.1 | 66.0 | 398.1 | 22.0 | 2.6 | 24.6 | 1 987.7 | |
| s ₆₆ | 261.0 | 56.9 | 52.2 | 428.9 | 53.3 | 4.6 | 57.9 | 4 258.0 | |
| r ₁₂ | 202.9 | 65.9 | 51.5 | 1 104.1 | 287.7 | 75.5 | 363.2 | 21 142.7 | |
| r ₁₃ | 217.7 | 87.3 | 60.4 | 693.9 | 152.9 | 63.7 | 216.7 | 18 108.1 | |
| r ₁₄ | 224.7 | 76.2 | 55.4 | 813.6 | 143.7 | 77.5 | 221.2 | 15 388.2 | |
| r ₁₅ | 247.3 | 72.0 | 81.1 | 772.7 | 131.3 | 29.2 | 160.5 | 10 699.4 | |
| r ₁₆ | 230.4 | 86.8 | 63.0 | 673.1 | 152.3 | 50.5 | 202.8 | 17 133.8 | |

TABLE 4. cont.

| Parent or progeny | Flowering date | Sessile spikelets | | | Caryopses culm ⁻¹ | | | Total caryopses plant ⁻¹ |
|-------------------|----------------|---------------------------|-----------------------------|--------------------|------------------------------|-------------|-------|-------------------------------------|
| | | Culms plant ⁻¹ | inflorescence ⁻¹ | culm ⁻¹ | sessile | pedicellate | total | |
| | -- day -- | ----- no. ----- | | | | | | |
| r23 | 201.6 | 113.9 | 46.6 | 474.0 | 98.3 | 32.8 | 131.1 | 14 351.6 |
| r24 | 210.3 | 111.6 | 53.4 | 562.4 | 104.9 | 24.6 | 129.5 | 13 511.2 |
| r25 | 221.7 | 87.2 | 74.1 | 673.3 | 95.7 | 35.7 | 131.5 | 11 580.4 |
| r26 | 208.6 | 101.1 | 44.4 | 496.1 | 100.9 | 20.3 | 121.2 | 11 605.8 |
| r34 | 222.1 | 73.6 | 60.5 | 630.6 | 113.3 | 29.9 | 143.2 | 10 342.5 |
| r35 | 247.8 | 58.2 | 55.9 | 368.3 | 65.1 | 8.7 | 73.7 | 5 219.2 |
| r36 | 258.7 | 82.5 | 52.5 | 341.2 | 58.6 | 15.2 | 73.7 | 8 513.4 |
| r45 | 248.6 | 87.8 | 74.0 | 604.9 | 86.9 | 32.4 | 119.4 | 9 031.0 |
| r46 | 237.8 | 102.5 | 56.6 | 556.5 | 106.4 | 21.2 | 127.5 | 14 386.0 |
| r56 | 276.4 | 117.6 | 55.5 | 348.7 | 22.0 | 2.0 | 24.0 | 2 876.8 |

TABLE 5

Phenotypic Correlations Between Reproductive Characters in Big Bluestem,
Based on 288 Observations Each Year

| Reproductive character | Culms plant ⁻¹ | Sessile spikelets | | Caryopses culm ⁻¹ | | | Total caryopses plant ⁻¹ |
|---|---------------------------|-----------------------------|--------------------|------------------------------|-------------|---------|-------------------------------------|
| | | inflorescence ⁻¹ | culm ⁻¹ | sessile | pedicellate | total | |
| | | | | no. | | | |
| Flowering date (Julian day) | -0.14** | 0.24** | -0.30 | -0.36** | -0.22** | -0.35** | -0.41** |
| Culms plant ⁻¹ | | 0.02 | -0.11** | -0.21** | -0.21** | -0.23** | 0.20** |
| Sessile spikelets inflorescence ⁻¹ | | | 0.19** | -0.03 | -0.01 | -0.03 | -0.04 |
| Sessile spikelets culm ⁻¹ | | | | 0.71** | 0.46** | 0.69** | 0.56** |
| Sessile caryopses culm ⁻¹ | | | | | 0.60** | 0.95** | 0.76** |
| Pedicellate caryopses culm ⁻¹ | | | | | | 0.81** | 0.49** |
| Total caryopses culm ⁻¹ | | | | | | | 0.73** |

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

PART V

OCCURRENCE OF CONIOSCINELLA NUDA (DIPTERA:
CHLOROPIDAE) IN NATIVE AND
INTRODUCED BLUESTEM

ABSTRACT

Adult flies of Conioscinella nuda (Adams) were reared from seedheads of Andropogon gerardii Vitman, Schizachyrium scoparium (Michx.) Nash, and Bothriochloa ischaemum (L.) Keng var. ischaemum collected near Stillwater, El Reno, and Sayre, Oklahoma, respectively. Previously, studies on taxonomy had been conducted with this insect, but no information on host range was given. C. nuda could potentially be an economically important pest of native and introduced chaffy-seeded, warm-season grasses grown for seed.

INTRODUCTION

Ahring and Howell (1968) reported the occurrence of Conioscinella nuda (Adams) (Figure 1) in grass seed fields near El Reno, Oklahoma, in 1963. They found the insect associated with experimental seed production blocks of an Asiatic bluestem, Bothriochloa intermedia (R.Br.) A. Camus. However, its effects on seedset and seed production were not determined.

MATERIALS AND METHODS

In August 1986 and 1987, larvae (suspected as being from the Order Diptera) were dissected from big bluestem, Andropogon gerardii Vitman, spikelets collected near Stillwater, Oklahoma. Larvae were observed feeding upon developing ovaries of that species (Figures 1b and 1c). In August 1987, culms of big bluestem and little bluestem, Schizachyrium scoparium (Michx.) Nash, were collected at Stillwater and El Reno, respectively, and placed in 1000 ml Erlenmeyer flasks filled with water. The culms were then caged with clear plastic trash bags having a nylon mesh screen on one side and were maintained at ambient room temperature in the laboratory. Approximately 7 days later, adult flies were collected within the cages and subsequently

identified as C. nuda. C. nuda was the only insect found to emerge from the cages. Identification of C. nuda adults and larvae was made by C. W. Sabrosky, retired Research Entomologist, Systematic Entomology Laboratory, USDA-ARS, Beltsville, Maryland. In July 1987, a sample of seed collected near Sayre, Oklahoma, from a seed production field of 'Plains' Old World bluestem, B. ischaemum (L.) Keng var. ischaemum, was sent to our laboratory in a sealed plastic bag for seedset evaluation. Several dead C. nuda adults were collected from the bag, and spikelets contained larvae essentially identical to those found in big bluestem. Dr. Sabrosky (pers. comm.) suspected these larvae were C. nuda. Voucher specimens of the adult insect and larvae are deposited at the K. C. Emerson Entomology Museum, Oklahoma State University, Stillwater.

RESULTS AND DISCUSSION

Although studies have been performed on the morphology and taxonomy of the adults of C. nuda (Adams, 1905; Stone et al., 1965; Tucker, 1908), information has not been published on its host range and life cycle. Chaffy-seeded, warm-season grasses, such as native and introduced bluestem with their indeterminant growth habits, mature seed continuously thereby providing seed-feeding insects a habitat over the entire growing season. In such grasses seedset and seed yield are often low, and insects play a major role in effecting seedset. Thus, total seed production may be

affected by this species, and C. nuda could potentially be an economically important pest of native and introduced chaffy-seeded, warm-season grasses grown for seed.

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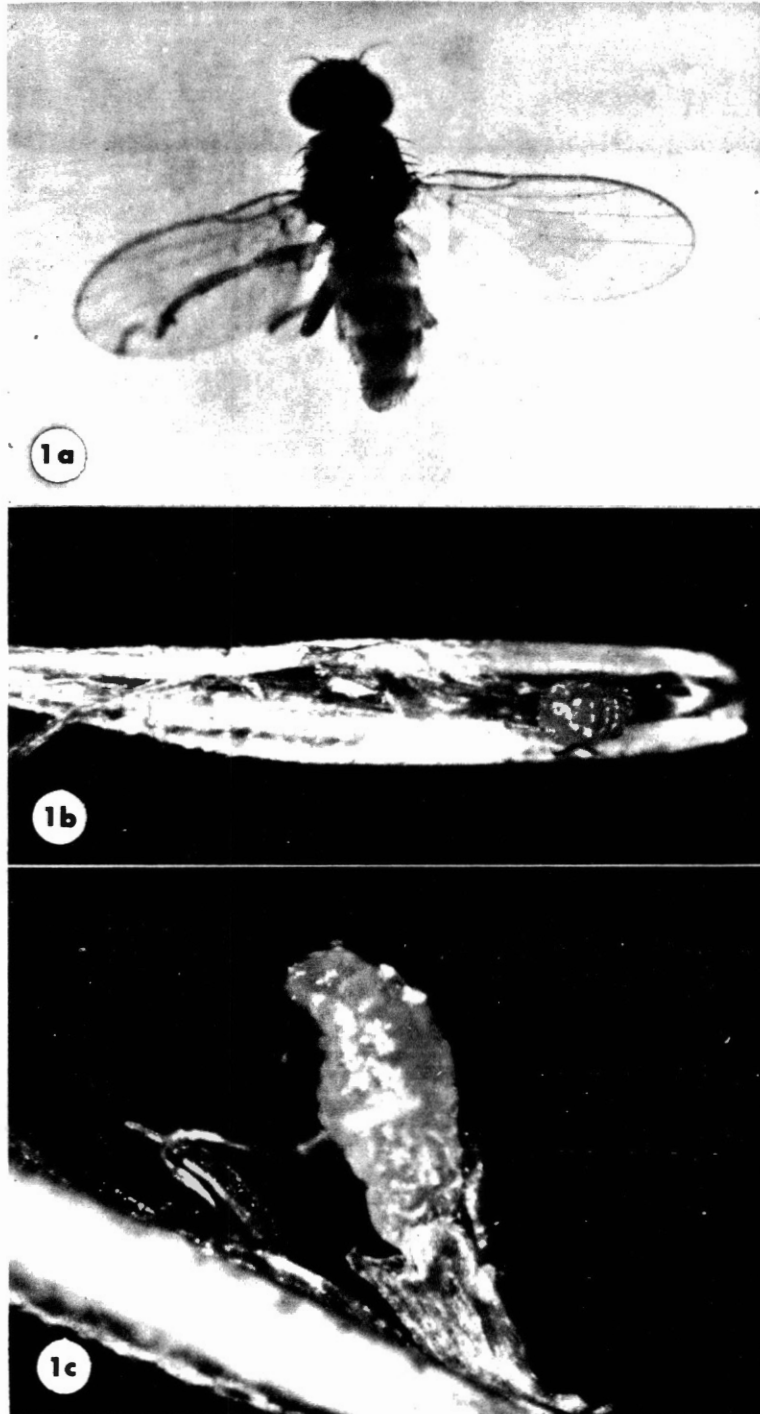


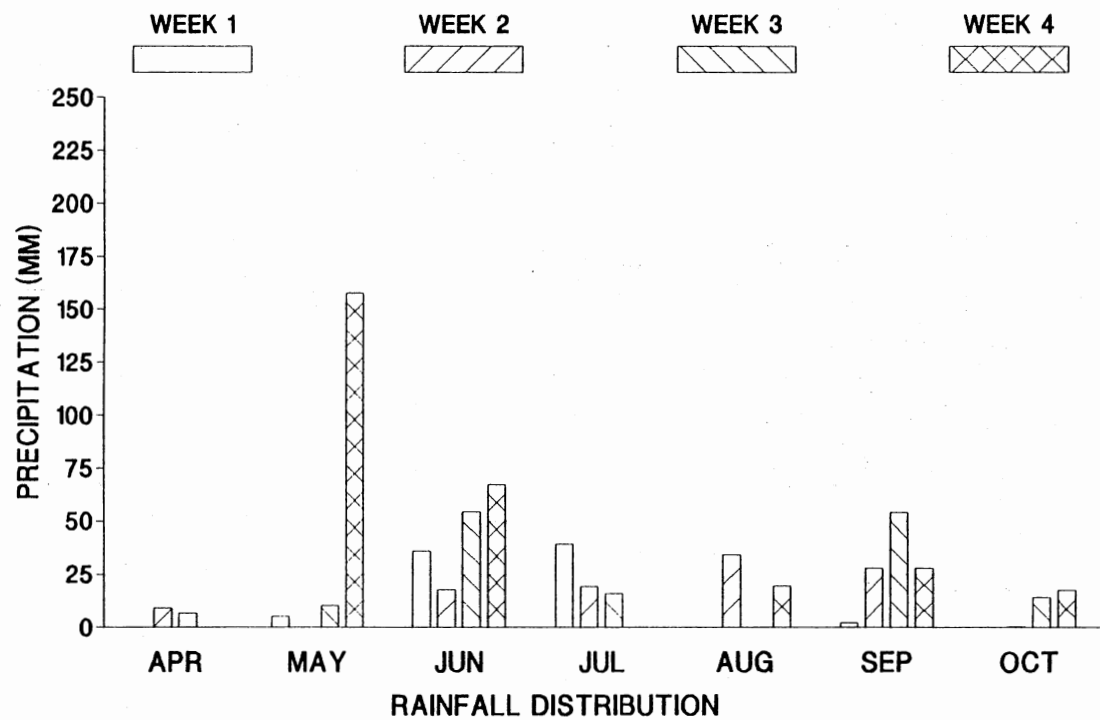
Figure 1. Adult of Conioscinella nuda and larvae found feeding upon the ovary in spikelets of Andropogon gerardii and other bluestems. 1a. Adult (x16). 1b. Larva, facing view (x8). 1c. Larva, side view (x11).

APPENDIX

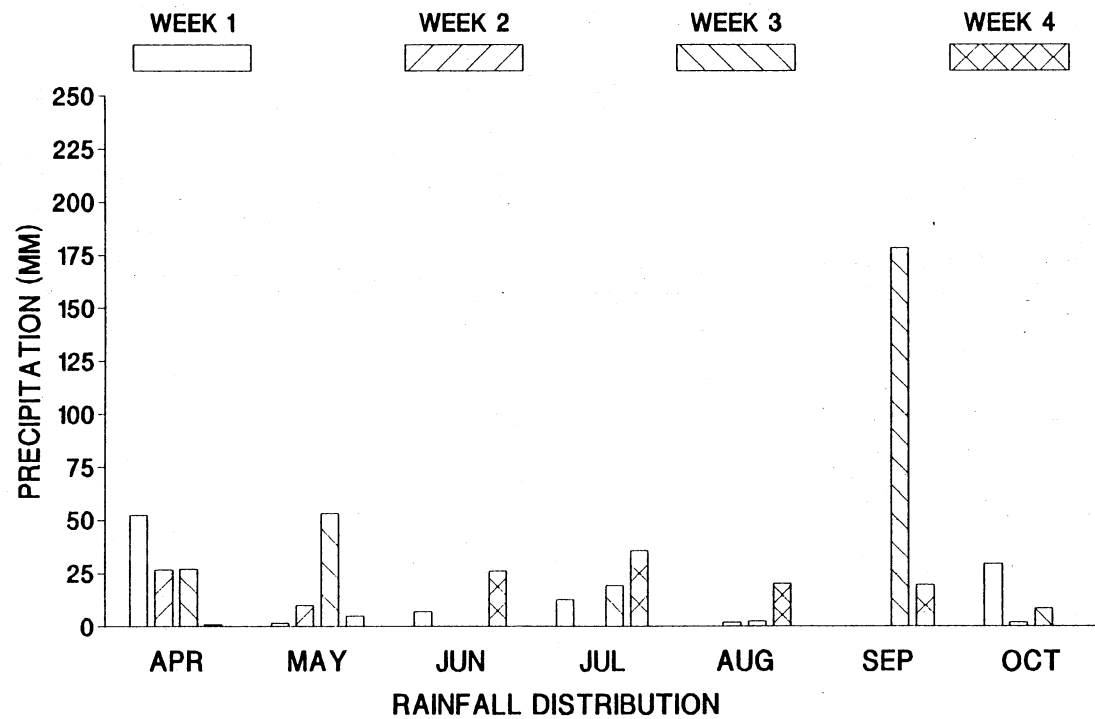
SEASONAL WEATHER DATA FOR STILLWATER, OKLAHOMA

IN 1987 AND 1988

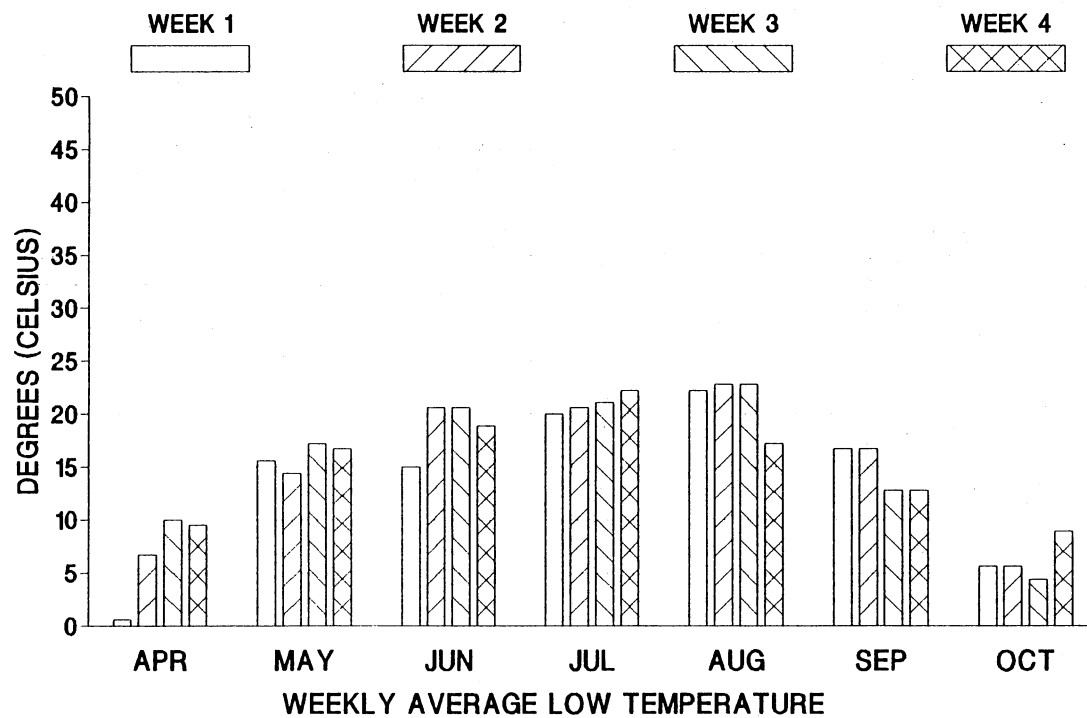
SEASONAL RAINFALL IN 1987 RECEIVED AT STILLWATER, OKLAHOMA



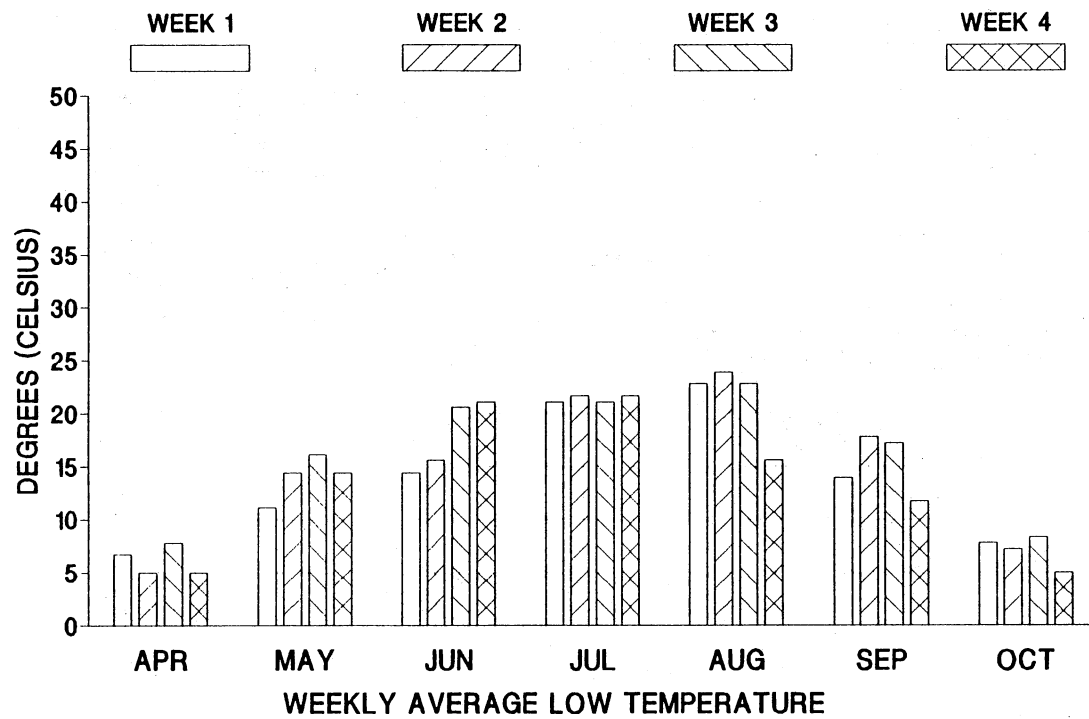
SEASONAL RAINFALL IN 1988 RECEIVED AT STILLWATER, OKLAHOMA



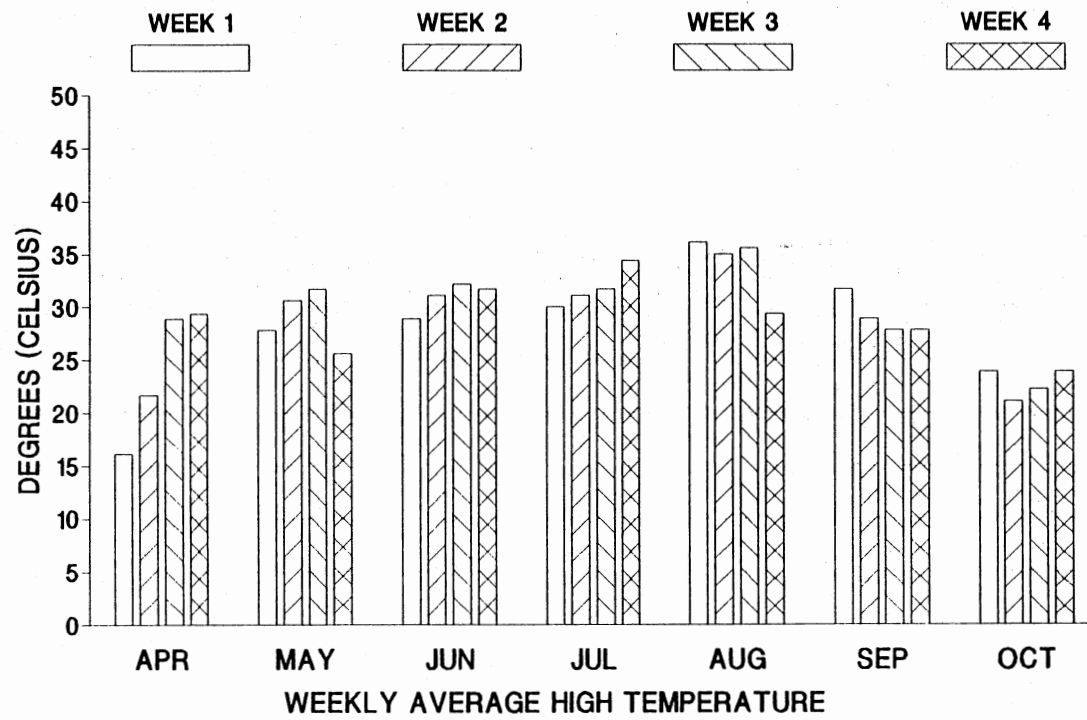
SEASONAL TEMPERATURES IN 1987 AT STILLWATER, OKLAHOMA



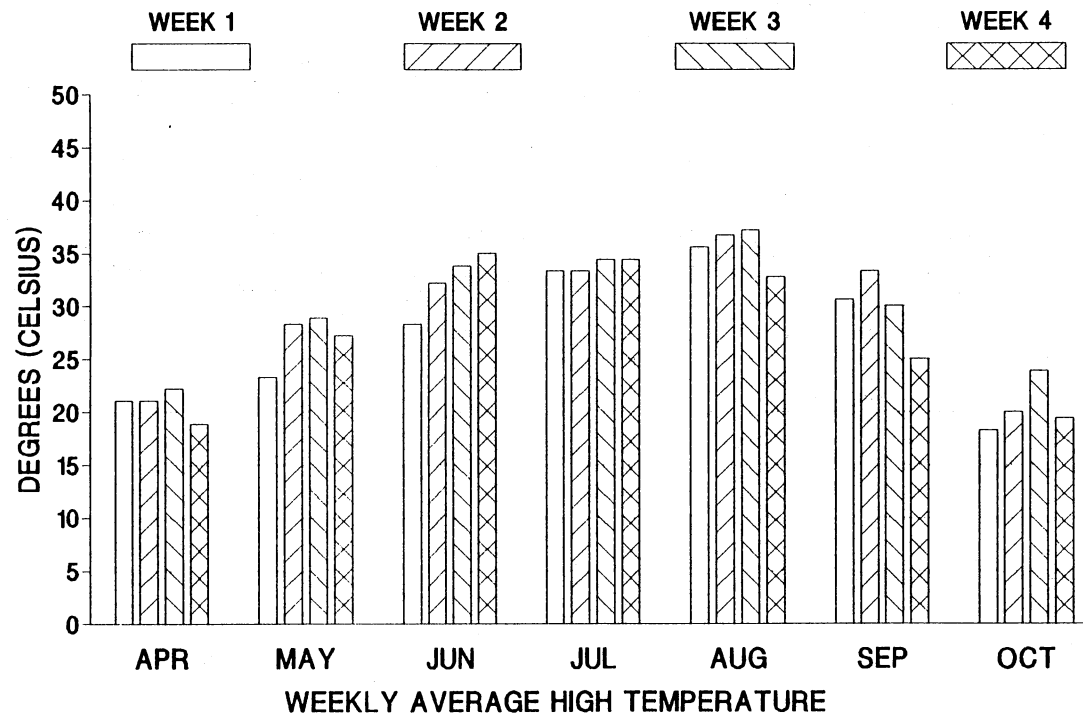
SEASONAL TEMPERATURES IN 1988 AT STILLWATER, OKLAHOMA



SEASONAL TEMPERATURES IN 1987 AT STILLWATER, OKLAHOMA



SEASONAL TEMPERATURES IN 1988 AT STILLWATER, OKLAHOMA



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