

South Dakota State University

Open PRAIRIE: Open Public Research Access Institutional Repository and Information Exchange

Electronic Theses and Dissertations

1979

Variability and Breeding Behavior in Big Bluestem Populations from Eastern South Dakota

Arvid A. Boe

Follow this and additional works at: <https://openprairie.sdstate.edu/etd>

Recommended Citation

Boe, Arvid A., "Variability and Breeding Behavior in Big Bluestem Populations from Eastern South Dakota" (1979). *Electronic Theses and Dissertations*. 5626.
<https://openprairie.sdstate.edu/etd/5626>

This Thesis - Open Access is brought to you for free and open access by Open PRAIRIE: Open Public Research Access Institutional Repository and Information Exchange. It has been accepted for inclusion in Electronic Theses and Dissertations by an authorized administrator of Open PRAIRIE: Open Public Research Access Institutional Repository and Information Exchange. For more information, please contact michael.biondo@sdstate.edu.

VARIABILITY AND BREEDING BEHAVIOR IN BIG BLUESTEM
POPULATIONS FROM EASTERN SOUTH DAKOTA

BY

ARVID A. BOE

A thesis submitted
in partial fulfillment of the requirements for the
degree Doctor of Philosophy, Major in
Agronomy, South Dakota
State University
1979

SOUTH DAKOTA STATE UNIVERSITY LIBRARY

VARIABILITY AND BREEDING BEHAVIOR IN BIG BLUESTEM

POPULATIONS FROM EASTERN SOUTH DAKOTA

This thesis is approved as a creditable and independent investigation by a candidate for the degree, Doctor of Philosophy, and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Date

Head, Plant Science Department

Date

ACKNOWLEDGMENTS

I am especially grateful to my major advisor, Dr. James G. Ross, for the innumerable kindnesses and friendship he so freely gave to me during my graduate work and for the unfailing advice he provided during the development and preparation of this dissertation.

Sincere appreciation is extended to Terril Heilman, George Holborn, Rama Kota and the grass crews for assistance in data collection, and to Dr. Lee Tucker for the help with computer programming and data analysis.

Deep gratitude is extended to my wife Shari for her encouragement, understanding and patience all through graduate school and for her timely help with the dissertation rough draft; and to my two daughters Andrea and Miranda thanks for understanding about all of the evenings and weekends I spent working.

To my parents and Shari's parents I express deep appreciation for all the encouragement and help they so unselfishly gave during my graduate work.

Appreciation is expressed to Regional Project NC-7 through the Regional Plant Introduction Station, Iowa State Univ., for funds aiding in the collection of germplasm.

VARIABILITY AND BREEDING BEHAVIOR IN BIG BLUESTEM
POPULATIONS FROM EASTERN SOUTH DAKOTA

Abstract

ARVID A. BOE

Under the supervision of Professor James G. Ross

Three spaced-plant big bluestem (Andropogon gerardii Vit.) nurseries at Brookings, South Dakota were analyzed for their genetic variability and agronomic potential. Unselected native collections, the 1972 nursery, was comprised of 34 strains each representing a site collection from the eastern edge of South Dakota. The first cycle recurrent selection nursery, established in 1977, was comprised of progeny of 19 plants from the 1972 nursery that were exceptional seed producers in the drought year 1976. The second cycle recurrent selection nursery, established in 1976, was comprised of progeny of 33 agronomically desirable plants from open-pollinated nurseries established from different southeastern South Dakota collections. These collections were from selected plants in relict colonies in southeastern South Dakota.

The objectives of this study were to describe the variation in the populations studied, to estimate heritabilities of the agronomically desirable characteristics and to determine the most efficient breeding methods to produce a superior variety.

Highly significant differences for seed yield, vigor, leafiness and plant height were found among strains in the 1972 nursery and among half-sib families in the 1976 and 1977 nurseries. Highly significant differences for seed weight were found among families in the 1976

and 1977 nurseries.

Broad sense heritability estimates for strains were high for plant height, heading date and pollination date in the 1972 nursery.

Narrow sense heritability estimates based on one year's data were extremely high for seed weight, plant height, vigor, leafiness, number of flowering culms and seed yield in the 1977 nursery. Positive assortative mating (like to like) must have been responsible for inflationary effects on the heritability estimates.

Narrow sense heritability estimates based on two years' data were moderately high for vigor, leafiness and plant height in the 1976 nursery. Estimates based on one year's data were moderately high for seed yield and fertility index and very high for seed weight.

Phenotypic and genetic correlations between agronomic characters in the 1976 and 1977 nurseries were generally positive, indicating that simultaneous multitrait selection for forage and seed characters would be profitable.

Multiple regression and path coefficient analysis of seed yield components in the 1977 nursery indicated that number of flowering culms, size and/or number of racemes per culm and fertility index all contributed directly to seed yield. Number of flowering culms was the most important while size and/or number of racemes per culm and fertility index were both considerably more important than seed weight in determining seed yield.

A composite made from open-pollinated seed of plants with heavy seeds (mean 100 seed weight = .26g) from the 1976 nursery produced significantly taller seedlings than a composite comprised of plants selected for forage and seed yield (mean 100 seed weight = .20g) from

the same nursery. As seed weight is highly heritable, mass selection for heavy seed should enhance seedling vigor.

Mass selection should be extremely effective for seed weight and plant height and moderately effective for seed yield, vigor, leafiness, fertility index and number of flowering culms. More precision in selection, however, for these characters would be possible based on progeny test data. No sizable negative genetic correlations between characters were observed, consequently simultaneous multitrait selection should also be effective.

TABLE OF CONTENTS

	Page
INTRODUCTION.....	1
REVIEW OF LITERATURE.....	3
Agronomic evaluations.....	3
Germ plasma collections and breeding.....	4
Seed weight and seedling vigor.....	10
Seed yield.....	13
Chromosome numbers.....	15
MATERIALS AND METHODS.....	18
Unselected native collections 1972 nursery.....	18
First cycle recurrent selection 1977 nursery.....	21
Second cycle recurrent selection 1976 nursery.....	24
Stand establishment of composites with different seed weights..	26
RESULTS AND DISCUSSION.....	28
Unselected native collections 1972 nursery.....	28
First cycle recurrent selection 1977 nursery.....	38
Second cycle recurrent selection 1976 nursery.....	54
Stand establishment of composites with different seed weights..	60
CONCLUSIONS.....	66
LITERATURE CITED.....	68

LIST OF TABLES

Table	Page
1. Estimates of variance components and heritabilities for indicated characters in the unselected native collections nursery.....	29
2. Height, family height and chromosome numbers for each of the 19 plants studied cytologically; plants are arranged in approximate descending order north to south, with Brookings at it's corresponding latitude.....	31
3. Means and ranges of seed weight for the 23 1972 nursery clones harvested in 1976, 1977 and 1979.....	36
4. Analysis of variance for seed weight measured from 23 clones over 3 years.....	37
5. Ranges of 19 family means, means and heritability estimates for indicated characters in the first cycle recurrent selection nursery observed September, 1978.....	39
6. Analysis of variance of repeated measurements of seed weight of 29 clones from the native collections nursery, including the 19 ovule parents of the first cycle recurrent selection nursery.....	43
7. Estimates of parameters characterizing variation in seed weight in the first cycle recurrent selection nursery.....	45
8. Genetic and phenotypic correlations among characters in the first cycle recurrent selection nursery.....	47
9. Phenotypic correlations between seed production characters in the first cycle recurrent selection nursery.....	48
10. Path coefficient analysis of number of culms, seed weight, fertility index and raceme weight per culm upon seed yield in the first cycle recurrent selection nursery.....	53
11. Ranges of 33 family means, means, and heritability estimates for indicated characters in the second cycle recurrent selection nursery.....	55
12. Estimates of variance components for indicated characters in the first and second cycle recurrent selection nurseries.....	57
13. Genetic and phenotypic correlations among characters in the second cycle recurrent selection nursery.....	59

LIST OF TABLES (cont.)

Table	Page
14. Mean seed weights of two 50 seed samples from sessile and pedicellate seed yield fractions of plants in the second cycle recurrent selection nursery.....	61
15. Analysis of variance of seedling heights and numbers of three composites planted in a field test at Brookings, South Dakota June 30, 1979.....	63
16. Mean seed weights, seedling heights and seedling numbers for three composites planted in a field test at Brookings, South Dakota June 30, 1979.....	64

LIST OF FIGURES

Figure	Page
1. Chromosomes during diakinesis, from plant #177-4, $2n = 60$	33
2. Chromosomes during diakinesis, from plant #188-2, $2n = 60 + 12$ or 13 accessory chromosomes.....	33

INTRODUCTION

There is a need over much of the Great Plains for high yielding warm-season domesticated grasses which would provide pasture during the hot months of July and August when the cool-season grasses are dormant. Native warm-season grasses have made only limited contributions to the North American cultivated grassland economy, even though natural selection over the millenia has permitted the survival of only those strains that are adapted to the environmental vagaries of the Great Plains. Big bluestem (*Andropogon gerardii* Vit.) appears to have many of the characteristics of a valuable cultivated warm-season grass and consequently was selected for study of its breeding potential.

This species is a tall, sod-forming, warm-season native grass with short rhizomes. Growth is initiated in late May or early June and continues during July and August. It was once the dominant species over much of the true prairie region and currently in eastern South Dakota is the dominant species in native pastures that are well managed. It provides abundant palatable forage during summer months and will stand extensive grazing if allowed to make an initial growth during the first part of the growing season (Ross and Krueger, 1976). Grazing studies in South Dakota (Krueger and Curtis, 1979) have revealed that a full-season pasture system comprised of separate pastures of cool and warm-season species offers maximum beef production efficiency.

The objectives of this study were: (1) to assess and describe the variability in agronomic forage and seed characters that exist in and among strains of big bluestem from eastern South Dakota,

(2) to determine the heritability of agronomically valuable characteristics, (3) to determine breeding methods that would facilitate the development of a variety possessing qualities superior to present varieties.

REVIEW OF LITERATURE

Agronomic Evaluations

Warnes et al. (1971) pointed out the importance of the perennial warm season prairie grasses as part of the total forage resources which provide grazing in the Plains states, and emphasized the need of revegetation of marginally productive land with adapted varieties of these perennial prairie grasses. Harlan (1962) and Keim and Newell (1962) have described the historical uses of the native grasses for revegetation in the Great Plains. Cornelius (1946) reported that a mixture of warm-season native grasses produced higher yields and better erosion control than introduced cool-season species on thin upland soil of low fertility near Manhattan, Kansas.

Newell (1968) pointed out that strains of native perennial grasses have evolved in the natural vegetation and have persisted through recent fluctuations of climatic conditions attesting to their adaptation to stresses of drought, heat and cold and to their resistance to attacks by insects and disease. He also emphasized the importance of preserving the best of these germ pools of variation and gathering more information on their characteristics.

In the northern Great Plains, forage is generally in short supply during the summer since cool-season grasses predominate in most pastures. Warm-season grasses such as big bluestem (*Andropogon gerardii* Vit.) however, are most productive when temperatures are high during July and August. In South Dakota, Krueger and Curtis (1979) found that big bluestem and switchgrass (*Panicum virgatum* L.)

pastures can be used successfully for beef production in July and August. They reported that a full-season pasture system comprised of separate pastures of cool and warm-season species provided the highest carrying capacity and beef production per hectare when compared with either a short-season pasture system of an alfalfa and cool season grass mixture, or a fair condition cool-season native grass range.

Cornelius (1944) conducted revegetation studies with several warm-season native grasses near Manhattan, Kansas. The land that was planted to native grasses was eroded and much of the top soil had been lost. His studies showed that approximately the same basal cover was obtained the second year after establishment by seeding as in 20 years of natural revegetation on abandoned land. Of the 8 species studied, Cornelius found *Bouteloua curtipendula* (Michx.) Torr., *Sorghastrum nutans* (L.) Nash., *Panicum virgatum* and *Andropogon gerardii* to be the most easily established based on seedlings established per square meter/viable seed planted per square meter.

Because of the breadth of ecotypic differentiation in big bluestem, seed supplies moved too far northward or southward from their points of origin are often unadapted. Yet, as pointed out by Newell (1968), if ecotypes which exhibited desired characteristics were found, these could be incorporated by hybridization to provide broad adaptation.

Germ Plasm Collections and Breeding

From the late 1930's to the present, seed and clones of many of the native grasses have been collected for observation and compari-

son in experimental trials at experiment stations throughout the Great Plains (Ross, 1974). If improvement is to be made, examination of the types and extent of variation of plants from different sources is an important consideration. In fact there still exists opportunity for the collection of strains that have resulted from natural selection in particular environments (Newell, 1968; Ross, 1974).

The drought of the 1930's and the additional stress of overgrazing, seriously depleted the ranges over much of the Great Plains region. Anderson and Aldous (1938) realized that something needed to be done to restore the ranges. They as plant breeders, saw the value of producing superior strains of native grasses that were adapted to the Great Plains for revegetation purposes. Weaver and Fitzpatrick (1932) had described big bluestem and little bluestem (*Andropogon scoparius* Michx.) as the first and second most important species of the prairie. Because of the vegetative cover contributed by little bluestem over a wide range of habitats and its division into definite habitat types, Anderson and Aldous (1938) decided to study the variation and inheritance of agronomic characters in the species. They studied three generations, the original population and two successive recurrent selection populations, and determined that wide variations in agronomic characters were due to genetic differences. Their conclusions were based on observations that progeny from individual plants varied significantly from progeny of other plants.

In 1935 studies of the variability and inheritance of agronomic characters in big bluestem were initiated (Law and Anderson, 1940).

They studied strains from Nebraska, Kansas and Oklahoma and noted the extensive variation both between and within ecotypes. They attributed this great variability to a high degree of cross-pollination and variable chromosome numbers (Church, 1929; Church, 1940; Nielsen, 1939). They found great variability between progeny groups in number of culms, basal diameter, plant height, time of maturity and seed set and highly significant interannual correlations in leafiness, number of culms, basal diameter, plant height and time of maturity.

During the same period, the value of switchgrass for grazing, hay and soil conservation purposes was being realized by some agronomists. Because of these economic uses and also because of its wide range of naturally occurring ecotypes, Nielsen (1944) studied plant variation and chromosome numbers of switchgrass from an area extending from Wisconsin and North Dakota south to Arkansas and Arizona.

Numerous domestic collections of switchgrass were made in Nebraska in 1935. Desirable strains were selected from these collections and the variety Nebraska 28 was released in 1942 (Eberhart and Newell, 1959). In the 1940's a few more collections were made and in 1953 a planned sampling of switchgrass was conducted in Nebraska. Eberhart and Newell (1959) selected clones from approximately 100 of the collections grown in nurseries at Lincoln, Nebraska and conducted an intensive study of plant to plant variation. They emphasized that in evaluating plant material for breeding improved varieties a knowledge of the proportion of the total variance that

is due to genetic variation is desirable. They calculated broad sense heritability estimates for seven agronomic traits in the endemic strains studied. They recommended that improvement of switchgrass should be possible by making large numbers of collections and testing random samples from each collection over at least two years. Further progress could be made by selecting clones within a strain if genetic variation was sufficient.

Kneebone (1958), working in Oklahoma, evaluated 19 sand blue-stem (*Andropogon hallii* Hack.) clones from Kansas and Oklahoma and their open-pollinated progenies. He concluded that selection would be effective for height, plant diameter, leafiness and protein content of leaves. He utilized analyses of variance among parent clones, analyses of variance among their open-pollinated progenies, parent-progeny correlations and regressions, and interannual correlations to estimate the heritability of plant height and plant diameter.

Newell and Eberhart (1961) studied genetic variation among switchgrass clones that had been selected from the better endemic strains grown on the Nebraska Experiment Station from collections made in native populations. They found extensive genetic variance among clones even though the clones had been selected from the better strains. They recorded data for seven characters exhibited by the clones in 1956 and 1957 (crossing blocks were established in fall 1955 and spring 1956) and obtained broad sense heritability estimates adjusted by removal of clone x year interaction from the estimate of genetic variance. In order to secure information on the relative importance

of additive and nonadditive genetic variance, they calculated parent-offspring covariances. Open-pollinated progeny means were regressed on the parental clone means and heritability estimates in the narrow sense were calculated by doubling the regression coefficient. Their heritability estimates indicated that ample additive genetic variance was present among clones of switchgrass and progress could be made by selection of clones within superior strains. They also calculated phenotypic and genotypic correlations among the observed characters and determined that effective simultaneous selection could be made for important characters in the development of superior varieties.

Peters and Newell (1961) found that big bluestem and sand bluestem would hybridize and suggested that improvement might be possible through the hybridization of divergent types.

Newell and Peters (1961) described desirable agronomic features of big bluestem and sand bluestem. Big bluestem is leafy and fine culmed while sand bluestem is less leafy and coarse culmed, but produces much larger caryopses. F_1 hybrids of big bluestem x sand bluestem exceeded the parent types by 31% for forage quality, 20% in height of leaves, 9% in total height of plants and 59% in total plant yield. They pointed out that inasmuch as self-fertilization is deleterious in the bluestems, natural-occurring strains or biotypes or refinements of them by selection should be sought out for supplying the desirable range of variation. These strains would constitute the building blocks from which hybrids or synthetic varieties could be developed. They pointed out that such varieties developed from

native strains of adjacent origin should be especially well adapted in transition zones surrounding areas of sandy soils where large amounts of well-adapted seed for revegetation programs of soil conservation would be valuable.

Ross (1974) expressed deep concern for the tentativeness of the relict colonies of tall grass prairie that exist along the eastern edge of South Dakota. He stressed that as agriculture becomes more intense and roads are improved and widened, the colonies that exist in road ditches and other areas will surely be destroyed. Ross made collections from tall grass prairie colonies ranging from the Cheyenne River in southeastern North Dakota to the confluence of the Big Sioux River with the Missouri River in northeastern Iowa. Seed from these colonies was planted in replicated spaced-plantings at Brookings, South Dakota and observations on agronomic variability and aesthetic qualities were made.

Ross et al. (1975) evaluated agronomic characters in families obtained from open-pollinated parents that were grown from seed collected from outstanding plants in colonies in the valleys of the Big Sioux and Missouri rivers of southeastern South Dakota. Significant differences among 23 families occurred in the factors contributing towards yield (e.g., height, vigor and leafiness). Moderately high heritability estimates were obtained for leaf/total weight, raceme weight, stem weight, stem in vitro dry matter digestibility, total weight and total in vitro dry matter digestibility. Inter-annual correlations for height and vigor measurements were not high,

indicating a strong effect of environment on these traits. Seed production potential was not related to forage yield components, indicating that selection for seed yield could be practiced without sacrificing forage yields. They concluded mass selection for maximum forage yield combined with leafiness should yield progress in a breeding program. Lack of variability for total seed yield in the breeding nursery (heritability = .16, and family means not significantly different) indicated that continued mass selection for that character would not be successful.

Seed Weight and Seedling Vigor

Paramount to the success of the native warm-season grasses in pastures and revegetation programs is the enhancement of seedling vigor. Seedling vigor is especially important in grasses that are seeded under trying environments such as exist in the Great Plains.

Seedling vigor in grasses has been measured by rate of germination, force of growth against resistance, rate of top growth and rate of root system development (Kneebone, 1972).

Numerous studies with several grass species have shown that seed size and weight are extremely important characteristics associated with seedling vigor. Within any given species, seedlings from large seed emerge faster (Kneebone and Cremer, 1955; Rogler, 1954; Tossell, 1960) and grow faster once emerged (Kneebone and Cremer, 1955; Tossell, 1960; Trupp and Carlson, 1967) than seedlings from smaller seed. Kneebone (1972) summarized the data correlating seed size and stand establishment in several forage grass species.

Rogler (1954) studied vigor of crested wheatgrass seedlings produced from eight seed weight classes planted at six depths in both the greenhouse and field. He found high correlations between seed weight and seedling vigor. He determined seedling vigor by measuring rate of emergence and time elapsed until development of second and third leaves, and concluded that selection for large seed size was a direct method of increasing seedling vigor in crested wheatgrass.

Kneebone and Cremer (1955) conducted greenhouse and field seedling vigor studies with buffalograss (*Buchloe dactyloides* (Nutt.) Engel.), indiangrass, sand bluestem, sideoats grama and switchgrass. They hand screened caryopses of different size classes from one seed lot for several strains and obtained data on time of seedling emergence, number of plants emerged, seedling height at various intervals, dry weight per plot and seedling vigor scores. They found the larger the seed within a lot, the more vigorous were the seedlings produced from it. They noted differences in seedling vigor both among species and among strains within species.

Seed size is not only important because of its relationship to seedling vigor but also because of positive correlations in many species with desirable mature plant traits (Kneebone, 1972). Christie and Kalton (1960) found significant positive correlations between seed weight and seed yield per plant, leaf width and vigor in smooth brome grass (*Bromus inermis* Leyss). and indicated that they expected no adverse effects of selection for high seed weight on either seed

or forage production.

Kneebone (1956) found that sand bluestem progenies grown from large seeds tended to be more vigorous not only in early seedling stages, but throughout the first season of growth and beyond.

Lawrence (1963) evaluated twelve clonal lines of Russian wild ryegrass (*Elymus junceus* Fisch.) and their polycross seed for seedling vigor and other traits, and found highly significant correlations between seed size and seed yield (.808) and between seed size and forage yield (.720).

Schaaf et al. (1962) evaluated over 100 crested wheatgrass strains over an 11-year period and found that the average correlation coefficient (.403) between forage yields and seed weights of the strains was significant at the 0.1% level.

Schaaf and Rogler (1963) found little or negative association between seed size and seed yield in crested wheatgrass (*Agropyron desertorum* (Fisch.) Schult.), apparently because in that species low seed set contributes to high seed size. Kneebone (1972) emphasized the importance of knowing the situation in the individual species being studied.

Seed size is highly heritable in many grass species. Wherever progenies have been tested, combinations of high seed weight parents have given progeny with higher seed weights than combinations of low seed weight parents (Kneebone, 1972). With additive variance comprising a large portion of the total genetic variance, rapid progress can be made by simple mass selection of large seeded parents.

Massey (1964) studied seed characteristics and seedling behavior in three bluestem species. In 50 accessions of big bluestem, seed set was significantly correlated with seed weight, laboratory germination, seedling emergence from $\frac{1}{2}$ inch and 5 inch depths. Seed weight was also significantly correlated with laboratory germination and seedling emergence characteristics. Seed weight was also significantly correlated with seedling emergence in sand bluestem and little bluestem. He concluded that in the three species of bluestem he studied, seed weight contributed directly to seedling emergence.

Seed Yield

Most certainly another important aspect of native warm-season grass improvement is the development of varieties possessing good seed yields, since the success of any variety is closely related to the economics of seed production. Cornelius (1950) concluded that, in general, native grasses have a low seed set. He stressed the negative effect of unfavorable weather on seed set but also acknowledged the greater intrinsic ability of certain grasses to overcome unfavorable conditions and produce more caryopses.

Law and Anderson (1940) observed extreme variability in the seed set of big bluestem that was in their estimate influenced by the genetic constitution of the plant.

Eberhart and Newell (1959) found that heritability estimates for seed yield in switchgrass were reduced by large strain x year interactions. However, they were concerned that bias may have been caused by a non-random sample of years as regards seed production.

Newell and Eberhart (1961) reported that seed yield was positively correlated with seed quality and total plant yield in switchgrass. The heritability of seed yield varied depending on the type of switchgrass (small blue-green, medium-tall blue-green or tall green). The range of heritability estimates was 0 to .74.

Ross and Adams (1955) found that differences in seed yield or seed set among 30 smooth brome grass clonal lines and their open-pollinated progenies were highly heritable and the gene action involved was mostly additive.

Knowles (1954), also working with smooth brome grass, reported that regressions of open-pollinated offspring on parent clones indicated that heritability of seed production was lower than either creeping-rooted habit or forage yield.

Nielsen and Kalton (1958) found heritability estimates for seed yield of .32 and an interannual correlation of .68 in smooth brome grass. They also found genetic correlations of .80 and .69 for seed yield with panicle number and .73 and .41 for seed yield with fertility for two successive years.

Tossell (1960) found identical heritability values for seed yield and seed weight in smooth brome grass. Regression coefficients of inbred progenies on their parental clones were .39 for both traits.

Path coefficient analysis was used in crested wheatgrass (Dewey and Lu, 1959) to determine the inter-relationships among several seed, spike and forage characters to establish the relative importance of each as they affected seed yield. Fertility and plant size had strong

influences, direct and indirect, upon seed yield, whereas seed size and spikelets per spike were relatively unimportant.

Similar path coefficient studies of seed yield have been conducted with field beans (Duarte and Adams, 1972), soybeans (Pandey and Torrie, 1973) and rapeseed (Thurling, 1974).

Chromosome Numbers

Early chromosome number reports of $2n = 70$ (Church, 1929; Nielsen, 1939) and $2n = 40$ (Church, 1940) were made for big bluestem, but more recently Gould (1956) has determined that $2n = 60$ is most prevalent. Gould (1956) studied chromosome numbers of big bluestem populations from Wisconsin to Texas and detected irregular meiotic behavior in only one collection, that being from DeKalb, Illinois. He estimated the Illinois collection to have a chromosome number of $n = 42$ or 43 and noted that no viable seed had been produced by this collection grown in Texas for five years. Gould also found collections in the same area exhibiting chromosome numbers of $n = 30$.

Church (1929, 1940) and Nielsen (1939) reported that differences between biotypes of *Andropogon* were correlated with ploidy levels. Fults (1942) and Snyder and Harlan (1953) did not find this type of correlation in *Bouteloua*.

Nielsen (1944) studied plant variation and chromosome numbers of *Panicum virgatum* from an area extending from Wisconsin and North Dakota south to Arkansas and Arizona. A polyploid series of 18, 36, 54, 72, 90 and 108 somatic chromosomes was determined. He found no geographical segregation of races on the basis of chromosome number and pointed out that morphological characteristics differed to a high degree

among plants with the same chromosome number.

McMillan and Weiler (1959) noted from collections of switchgrass in the Great Plains that characteristics such as plant height were extremely variable for plants of the same chromosome number. They found tetraploid plants of short stature in northern areas and taller tetraploids in the southern areas. They found the tetraploid number, $2n = 36$, to be more western and northern to the Central States than the octoploid, $2n = 72$, while populations with a preponderance of 72 chromosome types were found in Kansas. Hexaploid types were found less frequently and only in association with the other types, suggesting their origin by hybridization.

Dewald and Jalal (1974) studied 27 little bluestem and 24 big bluestem clones from four native North Dakota populations. They concluded big bluestem was characterized by a diploid chromosome number of 60 and occasional multivalent associations. They stated that the presence of multivalents in the two species indicated they were segmental allopolyploids with incomplete diploidization. Predominant chromosome aberrations of microsporogenesis in these species were due to homology differences. These were observed as unoriented univalents at metaphase, lagging chromosomes at anaphase I and II, and micronuclei at dyad and quartet stages.

DeSelm (1960) studied big bluestem and little bluestem populations from remnant pristine prairies in Ohio and found only $2n = 60$ and diploid behavior in big bluestem.

Bragg (1964) studied ecotypes of four grasses native to Texas.

Big bluestem plants from eastern Texas were hexaploids (2n = 60), but plants from central Texas as well as plants from the Trans-Pecos area, had meiotic irregularities so counts could not be established.

Collected from following list:

1. ...
2. ...
3. ...
4. ...
5. ...
6. ...
7. ...
8. ...
9. ...
10. ...
11. ...
12. ...
13. ...
14. ...
15. ...
16. ...
17. ...
18. ...

The above list of the above-mentioned plants is

MATERIALS AND METHODS

Three spaced-plant populations of big bluestem at Brookings, South Dakota were studied. These populations originated from systematic seed collections by Dr. James G. Ross from representative as well as agronomically desirable plants from relict colonies in eastern South Dakota and extreme southeastern North Dakota and northwest Iowa.

Unselected Native Collections 1974 Nursery

Unselected native collections, 1972 nursery, were comprised of 29 endemic strains from the eastern edge of South Dakota, four endemic strains from extreme southeastern North Dakota and one endemic strain from extreme northwest Iowa. In the fall of 1971 Dr. James G. Ross collected seed from varying numbers of plants at 34 different sites corresponding to the above strains. In March 1972 the collected seed was planted in the greenhouse and in June 1972 the seedlings were transplanted to a 40 inch center field-spaced-planting at Brookings, South Dakota. A completely randomized design was used. Strains were assigned to experimental units at random. Families of collected plants from each strain were nested within the appropriate strain and progenies were nested within the appropriate families within strains. A total of 4,472 plants were transplanted to the field. Numbers of families within strains ranged from four to 86. In most cases, ten progeny per family were planted but due to differential survival in the field progeny number per family ranged from two to ten.

Data were recorded for eight characters exhibited by the plants as

follows: (1) vigor (scale was from 1 = most vigorous to 5 = least vigorous), 1973 and 1977; (2) leafiness (scale was from 1 = leafiest to 5 = least leafy), 1973 and 1977; (3) height (cm), 1973; (4) heading date, 1975; (5) pollination date, 1975; (6) inflorescence production (scale was from 1 = most flowering culms to 5 = no flowering culms), 1976 and 1977; (7) total unthreshed weight of racemes from five random flowering culms, 1976; (8) total weight of the naked caryopses obtained from five random flowering culms, 1976. Characters 7 and 8 data were recorded only for those plants having a character 6 rating of three or less.

All observations were made and analyzed on an individual plant basis. The data were analyzed as a hierarchal classification with two levels of unbalanced subsampling (Steel and Torrie, 1960). An electronic computer was used to facilitate the speed and accuracy of the derivation of estimates of variance components from analyses of variance.

Heritabilities were estimated by the use of variance components from analyses of variance.

Source	Degrees of freedom	Parameters estimated
Strains	$s - 1$	$\sigma_{iwf}^2 + p\sigma_{fws}^2 + p\sigma_s^2$
Families within strains	$s (f - 1)$	$\sigma_{iwf}^2 + p\sigma_{fws}^2$
Progeny within families within strains	$sf (p - 1)$	σ_{iwf}^2

The letter s denotes the number of strains; f the number of families within a strain; p the number of progeny within a family within a strain. Heritability estimates were calculated by the formula:

$$h^2 = \sigma_s^2 / (\sigma_s^2 + \sigma_{fws}^2 + \sigma_{iwf}^2)$$

Since σ_g^2 is an estimate of total genetic variance, these strain heritability estimates are in a broad sense.

Twenty-three plants from the 1972 nursery that provided more than 100 undamaged caryopses after threshing from the five flowering culms that were harvested in 1976 were reharvested for seed in 1977 and 1979. One hundred seed weights were determined for each plant for each of the 3 years. Six strains and 19 families were represented in the 23-plant sample. The data were analyzed as follows:

Source	df	Parameters estimated
Total	yc - 1	
Years	y - 1	$\sigma_e^2 + c\sigma_y^2$
Clones	c - 1	$\sigma_e^2 + y\sigma_c^2$
Years x Clones	(y - 1)(c - 1)	σ_e^2

Multiple measurements of the same character reduces the variance due to temporary environment. The σ_c^2 is an estimate of total genetic variance plus the variance due to permanent environment. Repeatability (Lush, 1945) was calculated from the variance components as follows:

$$R = \sigma_c^2 / (\sigma_c^2 + \sigma_e^2)$$

The variance and standard errors of variance components and the standard error of the repeatability estimate were determined after Becker (1975) as follows:

$$\text{var}(\sigma_e^2) = \frac{2 MS_e^2}{df_1 + 2}; \text{ S.E.}(\sigma_e^2) = \sqrt{\text{var}(\sigma_e^2)}$$

$$\text{var}(\sigma_c^2) = \frac{2}{(k)^2} \left[\frac{MS_e^2}{df_1 + 2} + \frac{MS_c^2}{df_2 + 2} \right];$$

$$\text{S.E.}(\sigma_c^2) = \sqrt{\text{var}(\sigma_c^2)}$$

$$\text{S.E.}(R) = \sqrt{\frac{2(1-R)^2(1+(K-1)R)^2}{K(K-1)(C-1)}}$$

where,

K = number of measurements/genotype

c = number of clones

df₁ = degrees of freedom associated with σ_e^2

df₂ = degrees of freedom associated with σ_c^2

In July and August of 1977 two plants from each of the 34 strains were randomly chosen for chromosome number analysis. Immature inflorescences were fixed in a 3:1 mixture of absolute alcohol-glacial acetic acid for 24 to 48 hours. Final storage was in 70% alcohol in refrigeration. Aceto-carmin smears were made from anthers and preparations were temporarily sealed with wax and refrigerated.

Chromosome counts were most easily made from pollen mother cells in diakinesis and were made on at least five cells from each plant. It was found possible to make counts on plants from 17 of the 34 strains.

Photomicrographs were taken with a Leitz microscope camera at 1000X.

First Cycle Recurrent Selection 1977 Nursery

First cycle selection 1977 nursery consisted of families of 19 selected individuals from unselected native collections, 1972 nursery. In 1976 total seed production of five random flowering culms was determined for all plants in the 1972 nursery that had an inflorescence production rating of three or less (see description of 1972 nursery above).

Nineteen seventy six was an extremely droughty year and only approximately one fourth of the plants in the 1972 nursery were given an inflorescence production rating ≤ 3 . Seed from nineteen 1972 nursery plants that were the best seed producers in 1976 was planted in the greenhouse in March 1977 and seedling progenies were transplanted to a field 40 inch center spaced-plantings at Brookings, South Dakota in June 1977. A randomized complete block design was used. Ten spaced-plants were replicated four times for twelve of the families but due to paucity of seed five families were replicated three times and two families were replicated only twice. A total of 546 plants were transplanted to the field.

Data were recorded for characters exhibited by plants as follows:

- (1) vigor (scale was from 1 = most vigorous to 5 = least vigorous), 1978;
- (2) leafiness (scale was from 1 = leafiest to 5 = least leafy), 1978;
- (3) height (cm), 1978; (4) total number of flowering culms/plant, 1978;
- (5) total unthreshed weight of all racemes from individual plants, 1978;
- (6) total weight of all spikelets containing seed from individual plants, 1978; (7) weight of 100 seeds (measured to nearest hundredth of a gram) from each plant.

All observations were made and analyzed on an individual plant basis. The data were analyzed as a randomized complete block design with unequal numbers of observations/experimental unit.

Heritabilities based on one year's data were estimated by the use of variance components from analyses of variance.

Source	Degrees of freedom	Parameters estimated
Total	rfp - 1	
Replicates (R)	r - 1	
Families (F)	f - 1	$\sigma_e^2 + p\sigma_{RF}^2 + p\sigma_F^2$
R x F	(f - 1) (r - 1)	$\sigma_e^2 + p\sigma_{RF}^2$
Remainder	rf (p - 1)	σ_e^2

The letter p denotes the number of progenies in a family in each replicate.

All effects were considered to be random. No pollination control was exercised in the initial spaced-plantings. Big bluestem is almost entirely cross pollinated so it was assumed the male parent was a random sample of pollen from the entire spaced-planting and the progeny of each selected plant were half-sibs. The among families component of variance (σ_F^2) is equivalent to the covariance of half-sibs and equals one-fourth the additive genetic variance. The formula for heritability may be expressed as:

$$h^2 = 4\sigma_F^2 / (\sigma_F^2 + \sigma_{RF}^2 + \sigma_e^2)$$

Heritability of seed weight was also estimated by doubling the regression of the mean of family seed weight in the 1977 nursery (1978 data) on the mean of 3 years seed weight data (1976, 1977 and 1979) of the appropriate parent plants from the 1972 nursery.

Phenotypic correlations between the characters studied were made on an individual plant basis. Genetic correlations were calculated as follows (Falconer, 1960):

$$r_g = \frac{\text{cov } xy}{\sqrt{(\text{var } x)(\text{var } y)}}$$

where,

cov xy = covariance between characters x and y

var x = among families component of variance for character x

var y = among families component of variance for character y

Individual plant seed characters data were subjected to a maximum r^2 multiple regression analysis in an effort to determine the relative importance of several seed character variables in total seed production. Seed weight (weight of 100 seeds), number of flowering culms, unthreshed raceme weight/flowering culm and fertile spikelets weight/total unthreshed raceme weight were considered independent variables, while seed yield was considered the dependent variable. Path coefficients were determined from multiple regression analysis and simple correlation coefficients.

Second Cycle Recurrent Selection 1976 Nursery

Second cycle selection 1976 nursery consisted of families of 33 selected plants from previously established open pollinated spaced-plantings. The initial spaced-plantings were comprised of Dr. James G. Ross' germplasm collections from southeastern South Dakota relict populations. Approximately 150 collection sites were represented in the initial spaced-planted populations. Thirty-three outstanding plants from the initial spaced-plantings were selected on the basis of superior vigor, leafiness, height and fertility of the pedicellate spikelet and seed from these plants was harvested in October 1975. In March 1976 the seed was planted in the greenhouse and in June 1976 the seedling progenies of each of the 33 selected plants were transplanted

to the field in a 40 inch spaced-planting at Brookings, South Dakota. Where available, ten spaced-plants of each of the 33 families were replicated four times in a randomized complete block design. However, due to small amounts of seed collected from some of the plants and differential survival of seedlings in the greenhouse and field, family size ranged from six to 37. A total of 868 plants was transplanted to the field.

Data were recorded for characters exhibited by the plants as follows: (1) vigor (scale was from 1 = most vigorous to 5 = least vigorous), 1977 and 1978; (2) leafiness (scale from 1 = leafiest to 5 = least leafy), 1977 and 1978; (3) height (cm), 1977 and 1978; (4) total unthreshed weight of all racemes from individual plants, 1977; (5) total weight of all spikelets containing seed from individual plants, 1977; (6) the ratio of fertile spikelet weight (character 5) to total raceme weight (character 4), 1977; (7) the fraction by weight of total fertile spikelets that were pedicellate spikelets, 1977; (8) the fraction by weight of total fertile spikelets that were sessile spikelets; (9) weight of 50 seeds (measured to the nearest hundredth of a gram) from each plant. The two 50-seed samples were obtained from most of the plants for both sessile and pedicellate fractions. Pedicellate spikelets were separated from sessile spikelets by hand screening. Pedicellate spikelets are awnless and more circular in cross section than sessile spikelets. The seed yield from each plant was subjected to a uniform hand screening procedure to separate fertile pedicellate from fertile sessile spikelets.

All observations were made and analyzed on an individual plant basis. The data were analyzed as a randomized complete block design with unequal numbers of observations/experimental unit.

Heritabilities based on one year's data, phenotypic correlations and genetic correlations were obtained by the same methods applied to the 1977 nursery.

Heritabilities based on two year's data were also estimated by the use of variance components from analyses of variance.

Source	Degrees of Freedom	Parameters Estimated
Total	yrfp - 1	
Year-replicates (RY)	yr - 1	
Families (F)	f - 1	$\sigma_e^2 + p\sigma_{(RY)F}^2 + pyr\sigma_F^2$
RY x F	(f - 1) (yr - 1)	$\sigma_e^2 + p\sigma_{(RY)F}^2$
Remainder	yrf (p - 1)	σ_e^2

σ_{RF}^2 was replaced by $\sigma_{(RY)F}^2$ when two years' data were utilized in calculation of heritability estimates.

Stand Establishment of Composites with Different Seed Weights

On June 30, 1979 a field test to evaluate seedling vigor of a named check variety and three experimental composites was planted at Brookings, South Dakota. The four entries were: (1) Pawnee, a variety released by the Nebraska Agriculture Experimental Station in 1963; (2) SD 44, a 17 plant bulked seed composite of the most outstanding individuals (based on vigor, leafiness, height and total seed production data) from the 1976 nursery; (3) SD 45, a 10 plant bulked seed composite of the largest seeded individuals from the 1976 nursery; (4) SD 43, a second cycle recurrent selection composite of outstanding individuals from southeastern South Dakota relict populations. A randomized complete block design was used and each entry was replicated four times.

Plots were seeded with a four row belt seeder with double disc openers and depth bands. Seed placement was approximately one half inch in depth. Plot dimensions were four feet by 21 feet. Seeding rate was 10g. pure live seed/plot. The weight of 100 seeds of each of the entries was as follows: (1) Pawnee, .21 g., SD 44, .20 g., SD 45, .26 g., and SD 43, .18 g.

On July 10, the number of emerged seedlings/two feet of seedling row were counted for three random two foot sections in the middle two rows of each plot. On August 2, 1979 the height of the seedlings was sampled. A 20 foot transect was divided into ten two foot intervals in the center 20 feet of each of the four seedling rows in each plot. At each two foot interval, the height of the seedling nearest the interval mark was measured. A total of 40 measurements/plot or 160 measurements/entry were collected. The data were analyzed as a randomized complete block design with equal numbers of observations/experimental unit and were subjected to analyses of variance.

RESULTS AND DISCUSSION

Unselected Native Collections 1972 Nursery

Large differences existed among the 34 strains in all characters studied indicating that some strains were superior for particular characters. These differences were significant at the .01 level of probability for all characters (Table 1).

Large differences also existed among families within particular strains, indicating superiority of certain progeny groups when compared with other progeny groups within the same strain. These differences were also highly significant for all characters (Table 1).

Estimates of heritability among strains determined for the measured characters are presented in Table 1. Broad sense heritability estimates for strains when compared to the intraclass correlation $\sigma_{fws}^2 / (\sigma_{fws}^2 + \sigma_{iwf}^2)$ were larger for most characters studied. This indicated that greater phenotypic variations were exhibited among all strains in comparison with variation among families within strains.

Heading date, pollination date and height were highly heritable characters (Table 1), while vigor, leafiness, seed yield and fertility index were lowly heritable. The heritability estimate of number of flowering culms appeared to be affected by strain x year interaction. In 1976, a subnormal moisture year, the heritability estimate was .47, but in 1977, a supranormal moisture year, the heritability estimate was .19. This discrepancy in estimates can be explained by the observation that some of the more mesophytic southeastern strains did not produce flowering culms in 1976 because of the moisture deficiency. The more northern strains, however, were able to produce

Table 1. Estimates of variance components and heritabilities for indicated characters in the unselected native collections nursery.

Character measured	Year measured	No. of sites	No. of families	No. of individuals	σ_s^2	σ_{fws}^2	σ_{iwf}^2	σ_{fws}^2		h^2
								σ_{fws}^2	σ_{iwf}^2 †	
Vigor	1973	33	636	4470	.12825	.07244	.36700	.17		.23
Leafiness	1973	33	633	4417	.12971	.05917	.32115	.16		.25
Height	1973	33	633	4417	357.26213	114.67095	362.59289	.24		.43
Heading date	1975	33	630	3872	108.11522	12.36658	40.49693	.23		.67
Pollination date	1975	33	630	3861	112.74645	13.14054	44.28649	.23		.66
Flowering culm production	1976	33	636	4456	.40807	.10178	.35472	.22		.47
Seed yld of 5 culms	1976	23	234	734	.00096	.00099	.00548	.15		.13
Raceme wt. of 5 culms	1976	23	234	733	.08186	.06182	.23191	.21		.22
Flowering culm production	1977	31	567	3966	.25325	.18005	.89816	.18		.19
Vigor	1977	21	360	2598	.21002	.15259	.91826	.14		.16
Leafiness	1977	21	360	2598	.16742	.11109	.83639	.12		.15
Fertility index	1976	23	234	733	.00038	.00068	.00295	.19		.10

†The intraclass correlation of two random individuals from the same family in the subpopulation consisting of one site.

flowering culms and a large among-strain variation was evident. In 1977 when moisture conditions were favorable, a distinctive differential strain response for flowering culm production was not evident, indicating that in a high moisture year, all the strains could produce flowering culms.

Heading date and pollination date were highly heritable (Table 1). The general trend was for the northernmost strains to flower approximately 1 month before the southernmost strains. Transplant garden studies (McMillan 1956, 1959a, 1959b, 1965) have shown that many of the native North American grass species that exhibit extensive ecotypic differentiation possess general patterns of flowering behavior. The trend is for earlier flowering by strains from northern and western communities and progressively later flowering southward and eastward.

Height was a highly heritable character (Table 1), indicating extensive variation for that character among strains. As was found in this study (Table 2), the general trend for the northern strains to be shorter than the southern strains has previously been observed. McMillan (1964) studied ecotypic differentiation in plant height of big bluestem strains from southern Manitoba to Texas and found the northern ecotypes were shorter than the southern ecotypes.

The results of these comparisons of endemic strains of big bluestem from eastern South Dakota suggest that characters useful in breeding programs may be obtained from general areas of collection. Eberhart and Newell (1959) drew similar conclusions from their study of switchgrass biotypes from Nebraska. Large size was characteristic

Table 2. Height, family height and chromosome numbers for each of the 19 plants studied cytologically; plants are arranged in approximate descending order north to south, with Brookings at its corresponding latitude.

Lat	Plant #	Site #	Height (cm)	Family Ht. (cm)	2n Chrom. #
N	53-8	3	137	142.3	60
	133-9	7	114	102.5	60 + 12 or 13
	177-4	9	130	138.1	60
	188-2	9	124	102.9	60 + 12 or 13
	214-7	11	167	138.3	60
	235-1	12	133	122.6	60
	Brookings				
	271-5	15	106	139.4	60
	308-3	16	141	144.9	60
	324-7	18	127	130.9	60
	349-10	20	191	177.0	60
	378-1	21	148	136.7	60
	430-9	22	124	150.0	60
	461-2	22	147	145.5	60
488-5	23	158	193.5	60	
567-2	28	181	186.7	60	
578-2	29	198	138.7	60	
619-2	32	174	190.5	60	
628-3	33	164	165.1	60	
S	638-4	33	186	185.7	60

of the southern strains while early maturity was characteristic of the northern strains. It appears that the northern strains possess the inherent ability to produce seed under droughty conditions, while the southern strains have greater forage yield potential but lack the ability to produce seed under moisture stress.

The moderate to high heritability estimates for several of the characters indicate that progress may be expected by selection among strains for those characters. However, the heritability estimates obtained are in the broad sense and may be biased upward by non-additive genetic variances, strain x environment interaction and strain x year interaction. The difference in broad sense heritability estimates for number of flowering culms in successive years suggests that heritability estimates made in any single year may be biased upward.

Chromosome number analysis of 19 random plants from 17 strains revealed that 17 of the plants exhibited chromosome numbers of $2n = 60$ (Fig. 1). Two plants exhibited irregular meiotic behavior and chromosome numbers of $2n = 60 + 12$ or 13 (Fig. 2). The 12 or 13 extra chromosomes appeared as univalents in diakinesis and were determined to be accessory chromosomes.

Elliott and Love (1948) stressed the importance of studying the meiotic mechanism in forage grasses. They pointed out that meiotic irregularities may introduce limitations to random recombination of genetic factors in crossbred progenies and encouraged cytological studies be concurrent with agronomic programs in an effort to determine chromosomal constitution effects on breeding behavior.

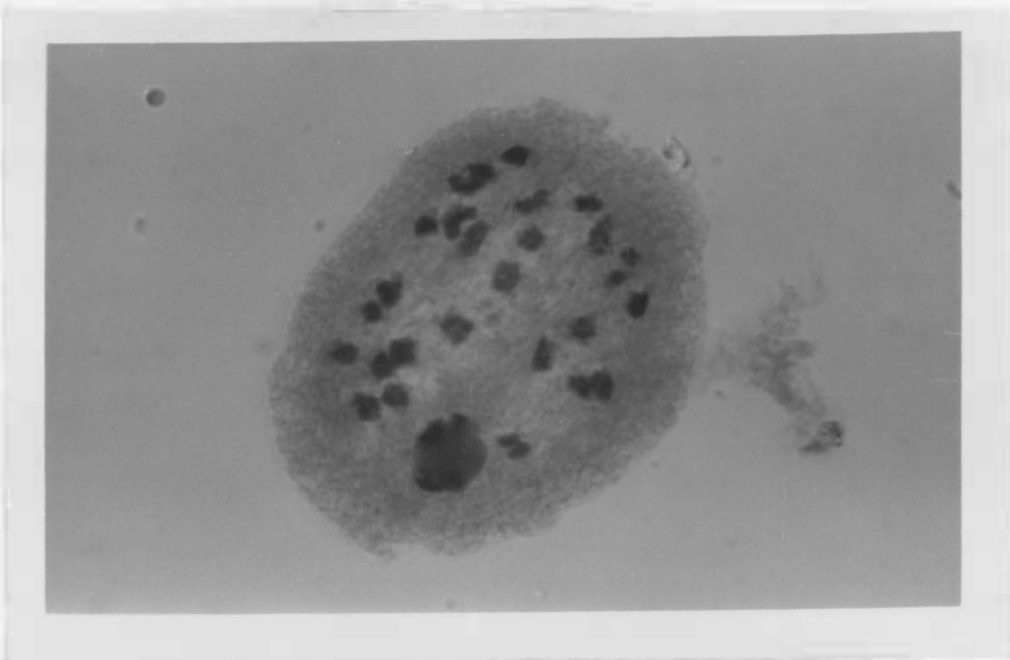


Fig. 1. Chromosomes during diakinesis from plant #177-4, $2n = 60$.

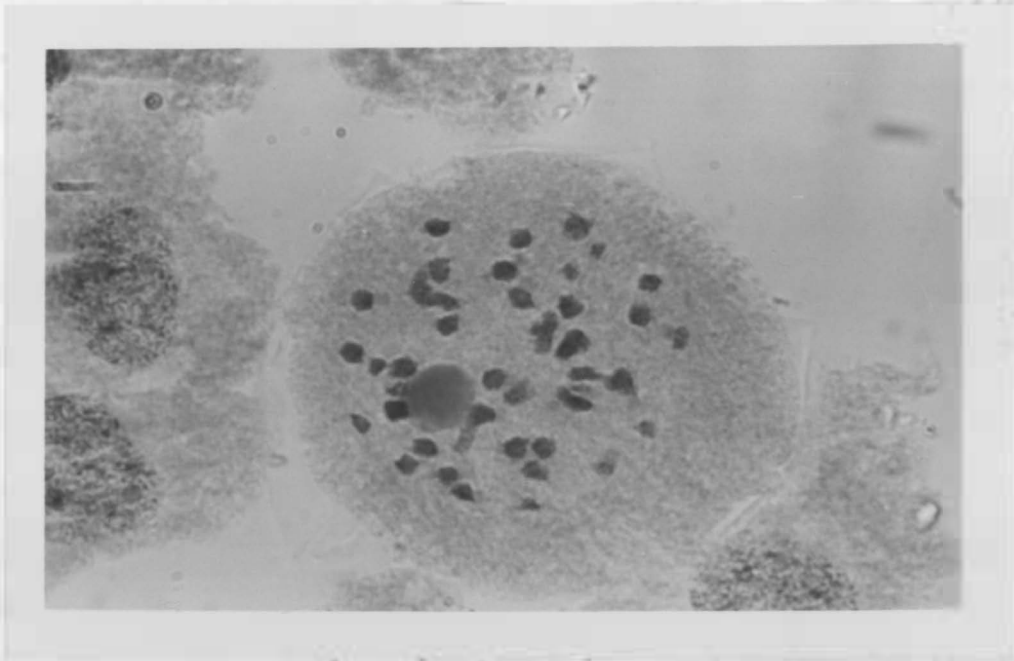


Fig. 2. Chromosomes during diakinesis from plant #188-2,
 $2n = 60 + 12$ or 13 accessory chromosomes.

Table 2 presents chromosome numbers and height measurements for the 19 plants studied cytologically. It appears that the presence of accessory chromosomes may have a deleterious effect on the height of plants possessing them. Plants #177-4 and #188-2 are progeny of plants from the same collection site. Plant #177-4 had a chromosome number of $2n = 60$ and was from a family of ten plants with mean height 138.1 cm. Plant #188-2 had a chromosome number of $2n = 60 + 12$ or 13 and was from a family of ten plants with mean height 102.9 cm. The two families of #133-9 and #188-2 had the shortest mean heights of the 19 families listed in Table 2. cursory examination of two of the sibs of plant #188-2 revealed that they, too, possessed accessory chromosomes. Gould (1956) noted that a big bluestem accession from DeKalb, Illinois with a chromosome number of $n = 42$ or 43 produced no viable seed when grown in Texas for five years, indicating that meiotic irregularity reduced fertility.

Differences in ploidy levels do not appear to exist in the strains sampled in this population. However, accessory chromosomes leading to meiotic irregularities occurred in approximately 10% of the sampled plants. This indicates that accessory chromosomes may be more common in big bluestem than previously thought. However, from a breeding standpoint, plants possessing accessory chromosomes appear to be less vigorous than plants possessing 60 chromosomes, and would most likely be eliminated early in a breeding program because of their lack of agronomic potential. Big bluestem is not vegetatively aggressive and only those plants that can produce large amounts of seed are useful in a breeding program. The plants possessing accessory chromosomes

did not exhibit agronomic potential and thus there appears to be no problem associated with meiotic irregularities and breeding for crop improvement in big bluestem.

As $2n = 60$ was by far the most prevalent chromosome number constitution in the 19 plants studied, representing sampling from 17 strains, there is no indication that ecotypic differentiation present in the population is correlated with ploidy level differences. Big bluestem strains from eastern South Dakota appear to be predominantly hexaploids, but strains possessing accessory chromosomes are present.

Twenty-three clones, representing six strains and 19 families, and including 13 of the ovule parents of the 1977 nursery, were harvested for seed in 1976, 1977 and 1979. Seed weight measurements were made from each plant for each year and analysis of variance was utilized to produce estimates of variance components used in estimating repeatability of seed weight. Table 3 presents means and ranges of seed weight obtained from the 3-year study of seed weight in 23 clones from the 1972 nursery.

Analysis of variance and the repeatability estimate for seed weight are presented in Table 4. The effect of year on overall seed weight was highly significant (Table 4). In a dry year mean seed weight was reduced considerably (Table 3). It is of extreme importance, however, to note that the ranking of the clones did not fluctuate much from year to year. The effect of clone on seed weight was highly significant (Table 4). Multiple measurements remove the effect of temporary environment from the estimate of genetic variance but do not remove that portion of the environmental variance that is peculiar to the individual clone. Repeatability gives an upper estimate of herita-

Table 3. Means and ranges of seed weight for the 23 1972 nursery clones harvested in 1976, 1977 and 1979.

	Precip. (cm) 6/1 - 8/30 Brookings, S.D.	Avg. Max. Temp. (°c) 6/1 - 8/30 Brookings, S.D.	Mean (g)	Range (g)
1976	15.8	29.4	.150	.098 - .196
1977	35.8	26.6	.179	.121 - .224
1979	†	†	.183	.135 - .225

†Collated data not available, but precipitation and temperatures were similar to 1977.

Table 4. Analysis of variance for seed weight measured from 23 clones over 3 years.

Source	df	S.S.	M.S.	E(M.S.)
Total	68	58770.9	-----	-----
Years	2	15160.2	7580.1**	$\sigma_e^2 + 23\sigma_y^2$
Clones	22	37216.9	1691.7**	$\sigma_e^2 + 3\sigma_c^2$
Years x Clones	44	6393.8	145.3	σ_e^2

$$\sigma_c^2 = (1691.7 - 145.3)/3 = 515.5$$

$$\text{S.E. } (\sigma_c^2) = 163.09$$

$$\text{S.E. } (\sigma_e^2) = 30.30$$

$$\text{Repeatability (R)} = 515.5/515.5 + 145.3 = .78 + .07$$

**Significant at the .01 level.

bility, estimating all the genetic variance plus a portion of the environmental variance, and is in most instances an overestimate of genotypic heritability. It's usefulness, besides setting an upper limit to heritability, is as an indicator of the gain in accuracy to be expected from multiple measurements. When repeatability is high, multiple measurements give little gain in accuracy.

The repeatability of seed weight in the sample of clones studied was $.78 \pm .04$ (Table 4). The years in which the sampling was conducted represent high and low extremes of temperature and moisture (Table 3). The magnitude of the repeatability estimate indicates that even though mean seed weight was affected by the environment, all the clones were essentially affected in the same fashion and no substantial changes in order of ranking occurred. This information is extremely useful, because it suggests that in selecting for increased seed weight, it would not be necessary to take measurements for more than one year.

First Cycle Recurrent Selection 1977 Nursery

A large amount of genetic variation was expressed among families in 1978. Analyses of variance for the several characters measured indicated highly significant differences among families for all characters (Table 5).

Heritability estimates calculated from estimates of variance components from analyses of variance were extremely high for all characters studied. Estimates calculated from the performance of the half-sib families ranged from $1.80 \pm .37$ for plant height to $.62 \pm .22$ for total seed yield. Vigor, unthreshed raceme weight and seed weight

Table 5. Ranges of 19 family means, means and heritability estimates for indicated characters in the first cycle recurrent selection nursery observed September, 1978.

Character	No. plants	Range	Mean	h^2
Vigor, 1 to 5	546	1.59 - 3.49	2.64**	1.23 \pm .33
Leafiness, 1 to 5	546	2.55 - 3.91	3.38**	.82 \pm .26
Height (cm)	546	120.72 - 186.04	139.43**	1.80 \pm .37
No. flow. culms	546	7.69 - 32.15	18.92**	.89 \pm .27
Raceme wt. (g)	546	3.76 - 24.38	11.29**	1.09 \pm .31
Seed yld. (g)	546	1.78 - 8.77	4.60**	.62 \pm .22
Seed weight (g)	322	.15 - .23	.18**	1.02 \pm .34

**Family means significantly different at the .01 level.

also appear to be highly heritable characters (Table 5).

Heritability of seed weight was also estimated by doubling the regression of the mean of each of the half-sib families (1978 data) on the mean of 3 years' observations (1976, 1977, 1979) of the appropriate parent clones. The estimate obtained was $.94 \pm .25$, quite close to the estimate provided from variance components from the analysis of variance.

The estimates of heritability were based on data collected at one location for one year, and thus are probably biased upward by genotype x year and genotype x environment interactions (Comstock and Moll, 1963). Eberhart and Newell (1959) observed low strain x year interactions and high heritability estimates for the characters plant height and height of leaves and large strain x year interactions and low heritability estimates for seed yield and plant yield in switchgrass. Newell and Eberhart (1961) found that removal of clone x year interaction from estimates of genetic variance greatly reduced heritability estimates, but the estimates were still moderately high for all characters except seed yield in medium-tall, blue-green switchgrass ecotypes. Ross et al. (1975) found small interannual correlations for height and vigor in a big bluestem population derived from open-pollinated southeastern South Dakota ecotypes, indicating a large genotype x year interaction. Kneebone (1958) obtained heritability estimates for plant height in sand bluestem that greatly exceeded 1.0 in 1956 but did not observe estimates of such inflated magnitude in 1955. He utilized parent-open-pollinated offspring regression for separate years to obtain his estimates.

The extremely high heritability estimates also indicate that positive assortative mating may have occurred in the source population.

This is highly plausible when the extreme diversity of plant type and variation in the date of maximum pollination in the source population are considered. The result of positive assortative mating is a closer association of parent and offspring for a particular character than predicted by random pollination. Newell and Eberhart (1961) reported positive assortative mating-induced upward biases for estimates of heritability in populations of switchgrass.

The most severe type of positive assortive mating is selfing. Failure of random mating could increase the expectation of σ_F^2 from $\frac{1}{2}\sigma_A^2$ to σ_A^2 , where σ_A^2 is the additive genetic variance, if selfing occurred. If maximum bias is assumed, even though big bluestem is quite non-self-fertile (Law and Anderson, 1940; Newell and Peters, 1961), the heritability estimates in Table 5 would be one fourth of their listed magnitude. The σ_F^2 is large relative to σ_{RF}^2 and σ_e^2 providing evidence that substantial amounts of additive genetic variance exist in the population. However, due to inaccurate measurement of the bias produced by positive assortative mating it is extremely difficult to accurately determine heritability estimates for the characters listed in Table 5.

Jain (1979) also pointed out the dangers in assuming random mating. He worked with an insect-pollinated species (Limnanthes alba Hartw.) where flowering occurred over a period of 2 to 3 weeks. He observed that few plant breeders have noted the role of phenotypic assortative mating in the quantitative genetic analysis of variation in outbreeding species. Latter (1965a) developed an assortative mating theory in relation to the estimation of heritability using open-pollinated progenies and Crow and Kimura (1971) discussed the theory

in relation to r = correlation between mates and n = number of loci, such that $f = 4/(2n(1 - r) + 4)$ and h^2 can then be adjusted by $(1 - f)h^2$ as a multiplier.

Latter (1965b) has shown that the covariance between ovule parent and offspring in a population in equilibrium is

$$\frac{1}{2}h^2(1 + \rho)\sigma_p^2$$

where ρ is the degree of assortative mating and σ_p^2 is the phenotypic variance.

Newell and Eberhart (1961) obtained heritability estimates in the narrow sense by doubling the parent-progeny regression b , where $b = \text{Cov parent-offspring}/\sigma_p^2$.

Combining formulae, the ovule parent-offspring correlation expectation becomes $\frac{1}{2}h^2(1 + \rho)$ (Latter, 1965b).

The component of variance among half-sib progeny groups for a character x is $\frac{1}{4}(h_w^2(x) + \rho h^4(x)(2 + \rho))\sigma_p^2(x)$ (Latter, 1965b), where $h_w^2(x)$ denotes the within season heritability of character x . It follows then that the expectation of the correlation between half sibs is

$$\frac{1}{4}(h_w^2(x) + \rho h^4(x)(2 + \rho))$$

Repeated measurements of seed weight in the ovule parents of the 1977 nursery as well as ten random individuals from the 1972 nursery were made in 1976, 1977, and 1979. Five of the ovule parents were measured in two of the three years and one ovule parent was measured only in 1976. The analysis of variance of the repeated measurements is presented in Table 6. The coefficient of σ_c^2 was determined after Becker (1975) as follows:

$$k = \frac{1}{N - 1} (m. - \Sigma m_k^2/m.),$$

Table 6. Analysis of variance of repeated measurements of seed weight of 29 clones from the native collections nursery, including the 19 ovule parents of the first cycle recurrent selection nursery.

Source	df	S.S.	M.S.	E(M.S.)
Total	79	.086696	-----	-----
Years	9	.014548	.007274	
Clones	28	.062915	.002247	$\sigma_e^2 + 2.755\sigma_c^2$
Years x Clones	49	.009233	.000188	σ_e^2

where m . = total number of measurements and N = number of clones. From the analysis of variance the estimates of variance components are,

$$\sigma_e^2 = .0018842$$

$$\sigma_c^2 = (.002247 - .0018842)/2.755 = .000747$$

Repeatability can be calculated from the estimates of variance components as follows,

$$R = .000747/(\.000747 + .0018842) = .80 \pm .06$$

The expectations of three estimates characterizing variation in seed weight, assuming all the genetic variance to be additive are presented in Table 7, where h^2 = narrow sense heritability and h_w^2 = narrow sense heritability for one particular season.

The degree of phenotypic assortative mating in the population can be estimated to be (after Latter, 1965b),

$$\hat{\rho} = 2(.47/.80) - 1 = .175$$

Substitution in the expectation for the half-sib correlation leads to the following estimate of the within season heritability

$$h_w^2 = 4(.254) - .175(2.175)(.80)^2 = .78$$

The estimate of heritability of seed weight after removal of bias from assortative mating is .78. As h_w^2 is approximately equal to h^2 estimated from multiple measurements there is little evidence of variance due to genotype x year interaction. The accuracy of the estimation of within season heritability is dependent on the genetic variance being entirely additive and not biased by permanent environmental effects that would not be removed by multiple measurements.

The character associations investigated and the simple and genetic correlation coefficients obtained are listed in Table 8. Most

Table 7. Estimates of parameters characterizing variation in seed weight in the first cycle recurrent selection nursery.

Parameter	Estimate	Expectation
Repeatability	$.80 \pm .06$	h^2
Ovule parent-offspring correlation	$.47 \pm .12$	$\frac{1}{2}(h^2 (1 + \rho))$
Half-sib correlation	$.25 \pm .08$	$\frac{1}{4}(hw^2 + \rho h^4 (2 + \rho))$

of the agronomic characters measured were significantly correlated. High positive phenotypic correlation coefficients were obtained for the relationship between total seed yield and total unthreshed raceme weight ($r = .837$), between height and vigor ($r = .727$), between vigor and total unthreshed raceme weight ($r = .708$), between leafiness and number of flowering culms ($r = .700$) and between number of flowering culms and total unthreshed raceme weight ($r = .699$).

Genetic correlations tended to be similar to the phenotypic correlations but were slightly larger. High positive genetic correlations occurred between leafiness and vigor, height and vigor, number of flowering culms and leafiness and total seed yield and leafiness. Since no negative genetic correlations of substantial magnitude were observed, simultaneous selection for forage yield and quality and seed production should be possible in this population (Table 8).

Ross et al. (1975) found highly significant correlations between forage yield and total seed yield in big bluestem, indicating that selection for forage yield would not decrease seed production. Newell and Eberhart (1961) found highly significant negative correlations between forage quality index and plant height and seed quality in small blue-green switchgrass biotypes. They concluded that difficulties could be encountered from the simultaneous selection of characters in the development of synthetic varieties.

The relationships of seed characters are shown in Table 9. Number of flowering culms was positively correlated with seed yield ($r = .54$) but negatively correlated with all other variables. Plants that

Table 8. Genetic and phenotypic correlations among characters in the first cycle recurrent selection nursery.

Character	Vigor	Leafiness	Height	No. of flow. culms	Seed yield	Raceme weight	Seed weight
<u>Genetic correlation</u>							
Vigor		.897 (+.063)	.924 (+.082)	.620 (+.190)	.722 (+.154)	.903 (+.100)	-.095 (+.277)
Leafiness	.530**		.666 (+.162)	.833 (+.147)	.932 (+.110)	.984 (+.083)	-.232 (+.276)
Height	.727**	.237**		.274 (+.239)	.561 (+.183)	.722 (+.126)	.143 (+.261)
No. of flow. culms	.572**	.700**	.147**		.841 (+.092)	.809 (+.094)	-.521 (+.258)
Seed yield	.583**	.459**	.357**	.525**		.962 (+.026)	.110 (+.295)
Raceme weight	.708**	.599**	.434**	.699**	.837**		-.084 (+.279)
Seed weight	.126**	-.082	.170**	-.086	.285**	.095*	
<u>Phenotypic correlation</u>							

*,**Phenotypic correlations significant at the .05 and .01 levels, respectively.

Table 9. Phenotypic correlations between seed production characters in the first cycle recurrent selection nursery.

	No. culms	Sd. wt.	Fert. ind.	Rac. wt./culm	Sd. yld.
No. culms		-.11*	-.24**	-.18**	.54**
Sd. wt.			.40**	.22**	.25**
Fert. ind.				-.07	.24**
Rac. wt/culm					.41**
Sd. yld.					

*,**Significant at the .05 and .01 levels, respectively.

produced large numbers of culms tended to produce fewer and/or smaller racemes per culm, smaller seeds, and fewer fertile florets per total number of florets than plants producing fewer culms. Dewey and Lu (1959), working with crested wheatgrass, found plant size to be positively correlated with seed yield, indicating that the seed producing advantage of large plants came from their having more spikes per plant.

Other correlations of interest are between seed weight and fertility index ($r = .40$) and seed weight and raceme weight per culm ($r = .22$). Plants characterized by large seed tended to be more fertile and produced larger and/or greater numbers of racemes per culm than smaller seeded plants but did not produce as many flowering culms as smaller seeded plants (correlation between seed size and number of flowering culms was $-.11$). These relationships indicate that the number of fertile florets per total number of florets decreases as the number of culms increased and that fertility and seed weight increase together. As seed weight and raceme weight per culm are positively correlated there is evidence that number and/or size of racemes per culm does not limit fertility and seed weight but number of flowering culms does. Plants producing few flowering culms tended to produce larger and/or more racemes per culm than many-culmed plants.

Of particular interest and contrary to the findings of Dewey and Lu (1959) is the positive correlation between seed weight and fertility index. Seed set in this study was estimated by the fertility index. This fertility index (Raeber and Kalton, 1956) on an individual plant basis is intended to measure the number of fertile florets per total number of florets. It is determined from the ratio

of threshed (clean seed) weight/unthreshed weight of all racemes from an individual plant. Raeber and Kalton (1956) found a positive correlation ($r = .94$) between fertility index and actual fertility in twenty bromegrass clones. Trupp and Slinkard (1965) found that fertility index as described by Ross and Bullis (1962) and synonymous with the above definition had a positive correlation ($r = .94$) with percent fertile basal florets in intermediate wheatgrass (Agropyron intermedium (Host.) Beauv). Christie and Kalton (1960) found a positive correlation ($r = .58$) between fertility index and seed weight in polycross progenies of seventy-one bromegrass clones. The range in seed weight was from .74 to .94 grams per 300 seeds. Among the seventy-one parent clones the range in seed weight was .71 to 1.30 grams per 300 seeds and the correlation between seed weight and fertility index was positive ($r = .25$). In this study the positive correlation between seed weight and fertility index in the 1977 nursery indicates that plants that were able to fill a large percentage of the total number of florets also produced large seeds. Massey (1964) also found a significant positive correlation between seed weight and seed set in big bluestem. In a good seed producing year such as 1978, when this study's measurements were made, it seems probable that the environment did not limit the percentage of florets that were filled. If the number of filled florets per total number of florets is strongly affected by environment, in a favorable year heavy-seeded plants could also produce high fertility percentage. Heritability of seed weight is high (Table 5) and thus little affected by environmental incongruencies. Seed weight ranged from .10 to .32 grams per 100 seeds. The magnitude of this range could feasibly bias the fertility index causing large-seeded

plants to exhibit a larger fertility index value than would be obtained from actual fertility analysis. However, the findings of Christie and Kalton (1960) and Massey (1964) suggest that a wide range in seed weight did not bias the fertility index in favor of heavy-seeded types.

It appears that in the big bluestem nursery studied, increased seed yields can be realized via two different routes. A many-culmed plant will produce large seed yields but will exhibit poor seed set percentage and light seed weight, so selection for many culms could result in poor quality seed even though the total yield would be increased. The other avenue of increasing seed production may be to select large-racemed plants that produce more seeds per culm and heavier seeds than small-racemed, many-culmed plants. However, the negative correlation between seed weight and number of flowering culms is probably not so formidable that selection for both number of flowering culms and seed weight would give positive results. From the forage value standpoint, increasing the number of culms tends to increase leafiness ($r = .70$) thus, producing a more palatable plant. In breeding a grass for forage use a compromise between seed production and forage quality has to be considered.

Thurling (1974) found a positive correlation between seed weight and number of seeds per pod, and a negative correlation between seeds per pod and pods per plant in Brassica campestris. In the 1977 nursery, large-racemed plants produced the heaviest seeds and it appears they produced more seeds per culm than small-racemed plants. This corresponds with Thurling's observations in B. campestris. Also, in the 1977 nursery, a negative correlation was found between raceme weight per

culm and number of flowering culms, corresponding with Thurling's findings of a negative correlation between pods per plant and seeds per pod.

Table 10 presents a breakdown of the correlation coefficients into their four components. The direct effects point out that number of flowering culms, raceme weight per culm and fertility index all contribute directly to the enhancement of seed yield. Seed weight, however, contributes to seed yield mostly through the indirect effects of raceme weight per culm and fertility index. Looking at simple correlation coefficients only, it appears that seed weight is just as important as fertility index in contributing to total seed yield. Path coefficient analysis, however, revealed that the direct effect of seed weight was small compared to the direct effect of fertility index, raceme weight per culm and number of flowering culms.

It is interesting to note that had it not been for the large negative indirect effect of number of flowering culms, the correlation between fertility index and seed yield would have been high. Conversely, the correlation between number of flowering culms and seed yield was reduced by the negative indirect effects of fertility index and raceme weight per culm. If seed yields are to be increased, it appears that a compromise must be reached in a selection program for the characters number of flowering culms and fertility index. As number of flowering culms is positively correlated with leafiness and only slightly negatively correlated with seed weight, it seems more emphasis should be placed on number of flowering culms rather than fertility index or raceme weight per culm.

Table 10. Path coefficient analysis of number of culms, seed weight, fertility index and raceme weight per culm upon seed yield in the first cycle recurrent selection nursery.

Pathways of association	Coefficients
Seed yield vs no. culms	
Direct effect	.756
Indirect effect via rac. wt./culm	-.105
Indirect effect via fert. index.	-.105
Indirect effect via seed weight	-.003
Total correlation	.542
Seed yield vs raceme weight/culm	
Direct effect	.574
Indirect effect via no. culms	-.139
Indirect effect via fert. index	-.031
Indirect effect via seed weight	.007
Total correlation	.410
Seed yield vs fertility index	
Direct effect	.447
Indirect effect via no. culms	-.178
Indirect effect via rac. wt./culm	-.040
Indirect effect via seed weight	.012
Total correlation	.241
Seed yield vs seed weight	
Direct effect	.030
Indirect effect via no. culms	-.087
Indirect effect via rac. wt./culm	.127
Indirect effect via fert. index	.178
Total correlation	.247

Multiple regression analysis indicated that 76% of the variation in seed yield could be explained by variation in the four independent variables. Big bluestem seed is hard to thresh because of variation in the pubescence of inflorescence structures. When all seed samples are given the same threshing treatment it is possible that the accuracy of measurements of seed yield and fertility index may be reduced by the variability in the morphology of the material.

It must be pointed out that these observations may only be valid when applied to similar spaced-plant populations.

Second Cycle Recurrent Selection 1976 Nursery

Extensive variation was evident among families in 1977 and 1978. Analyses of variance for nine characters indicated highly significant differences among families for eight characters and a significant difference among families for weight of the pedicellate spikelet fraction of seed yield (Table 11). Heritability estimates calculated from estimates of variance components from analyses of variance were moderately high for most characters studied (Table 11), ranging from $.73 \pm .20$ for seed weight to $.19 \pm .10$ for pedicellate spikelet fraction weight.

The computer program used required a full data set (a value for each plant for each of the characters being analyzed). When the seed characters data were analyzed, certain individuals were removed from the analyses because they lacked all or portions of the seed characters data. Estimates of heritability for vigor, leafiness and height were calculated using 712 and 868 individuals for each of the individual years 1977 and 1978, and heritability estimates based on two years'

Table 11. Ranges of 33 family means, means, and heritability estimates for indicated characters in the second cycle recurrent selection nursery.

Character	Date	No. Plants	Range	Mean	h^2
Vigor	10/77	712	1.48 - 2.57	2.02**	.33 + .13
Leafiness, 1 to 5	10/77	712	1.54 - 2.50	1.95**	.33 + .13
Height (cm)	10/77	712	157.41 - 194.67	171.01**	.42 + .15
Raceme wt. (g)	10/77	712	27.99 - 65.06	40.17**	.41 + .14
Seed yld. (g)	10/77	712	11.33 - 29.04	18.26**	.30 + .12
Fertility index	10/77	712	35.73 - 54.44	44.71**	.42 + .14
Seed weight (g)	10/77	712	.07 - .12	.09**	.73 + .20
Sessile fraction (g)	10/77	712	8.84 - 24.83	15.47**	.29 + .12
Pedicellate frac. (g)	10/77	712	1.23 - 4.76	2.88*	.19 + .10
Vigor, 1 to 5	10/77	868	1.42 - 2.59	2.02**	.37 + .13
Leafiness, 1 to 5	10/77	868	1.43 - 2.52	1.92**	.36 + .13
Height (cm)	10/77	868	158.71 - 194.20	171.72**	.43 + .14
Vigor	10/78	868	1.21 - 2.14	1.63**	.29 + .13
Leafiness	10/78	868	1.30 - 2.48	1.76**	.53 + .15
Height (cm)	10/78	868	160.34 - 220.21	196.64**	.67 + .19
Vigor	1977-78	868	-----	-----	.33 + .10
Leafiness	1977-78	868	-----	-----	.37 + .11
Height (cm)	1977-78	868	-----	-----	.54 + .14

*,**Family means significantly different at the .05 and .01 levels, respectively.

data for 868 individuals were obtained for the same three characters. The exclusion of 156 individuals only slightly altered the estimates of heritability for vigor, leafiness and height from 1977 data (Table 11). However, heritability estimates obtained from 1978 data did differ from the 1977 estimate (Table 11). Heritability estimates for vigor, leafiness and height based on combined 1977 and 1978 data were approximately mid way between the individual year estimates (Table 11). Table 12 presents variance components for the nine characters studied. Replication x family interactions were generally of little consequence, except for vigor and height measured in 1978 and the pedicellate seed fraction measured in 1977, indicating very little fluctuation in ranking of families across blocks. When combined years' data were analyzed, the replicate-year x family interaction was highly significant for all three characters for which two years' data were obtained (Table 12). This suggests that families exhibited some oscillation of ranking across replicate-year combinations. When two years' data are available, this interaction can be removed from the numerator of the heritability estimate and thus a more accurate estimate of heritability is obtained.

The families studied were progenies of individuals selected for their vigor, leafiness, height, seed yield and fertility of the pedicellate spikelet. The ovule parents of the 33 families, however, had not been intentionally selected for heavy seed weight. Seed weight was positively correlated with seed yield ($r_g = .352$), so selection for seed yield may have indirectly included mild selection for seed weight.

It is interesting to note that seed weight was more highly heritable than height in the second cycle selection 1976 nursery, while the

Table 12. Estimates of variance components for indicated characters in the first and second cycle recurrent selection nurseries.

Character	Cycle	$\sigma^2_{\sigma^2}$	σ^2_{RF}	$\sigma^2_{(RY)F}$	σ^2_e
Vigor, 1977	2	.04469**	.0022	-----	.435867
Vigor, 1978	2	.041599**	.03864**	-----	.488979
Vigor, 1978	1	.22735**	.006654	-----	.505430
Vigor, 1977-78	2	.04319519**	-----	.0252445**	.461821
Leafiness, 1977	2	.04177**	.01513	-----	.406965
Leafiness, 1978	2	.0942**	.01179	-----	.605527
Leafiness, 1978	1	.09742**	.034612**	-----	.342957
Leafiness, 1977-78	2	.05413265**	-----	.0276386**	.507443
Height, 1977	2	37.29035**	.53925	-----	309.288735
Height, 1978	2	72.4253**	15.331*	-----	348.435
Height, 1978	1	271.92923**	0	-----	339.557105
Height, 1977-78	2	52.3604349**	-----	11.33535**	328.18881
Raceme wt., 1977	2	51.1809496**	4.93972	-----	447.746764
Raceme wt., 1978	1	21.81035**	1.3862373	-----	56.673626
Seed yld., 1977	2	10.540457**	2.41299	-----	125.970501
Seed yld., 1978	1	2.46592**	.795017*	-----	12.767636
Sessile frac., 1977	2	7.71191395**	2.75892	-----	94.836847
Pedicellate frac., 1977	2	.2806488*	.7612032**	-----	4.763822
No. slow culms, 1978	1	31.17418**	1.1369505	-----	108.461785
Seed weight, 1977	2	.0000544*	.0000081	-----	.000236
Seed weight, 1978	1	.000379**	0	-----	.001114
Fertility index, 1977	2	11.806252**	.39034	-----	100.526432

*,**The corresponding mean squares from the analysis of variance were significant at .05 and .01 levels, respectively.

opposite was true for the first cycle selection 1977 nursery. Progenitors of the 1976 nursery had been evaluated for height and thus some of the genetic variation for that character may have been decreased. Also the 1976 nursery was comprised of progenies of agronomically desirable individuals from only southeastern South Dakota strains and as such does not contain the breadth of ecotypic differentiation that abounds in the unselected native collections, 1972 nursery, or the first cycle selection, 1977 nursery.

Relationships between the nine characters studied are presented in Table 13. Vigor was positively correlated with leafiness ($r = .22$), height ($r = .165$), raceme weight ($r = .574$) and seed yield ($r = .489$) and only slightly negatively correlated with fertility index ($r = .016$) and seed weight ($r = .050$). Leafiness was positively correlated with seed yield ($r = .264$) and height was positively correlated with seed yield ($r = .236$). Seed weight was positively correlated with seed yield ($r = .150$) and fertility index ($r = .307$). Positive correlations between characters of agronomic interest indicate that selection for a particular character (s) should not hinder progress in improving another character(s).

Lack of strongly negative correlations between all characters of agronomic interest is desirable from the standpoint of simultaneous multitrait selection. Selection for forage yield and quality simultaneous with selection for seed yield and seed weight should result in progress for all characters in the second cycle recurrent selection 1976 nursery.

Of particular interest in this nursery is fertility of the pedicellate spikelet. Virtually all of the plants yielded some fertile

Table 13. Genetic and phenotypic correlations among characters in the second cycle recurrent selection nursery.

Character measured	Vigor	Leafiness	Height	Raceme weight	Seed yield	Fertility index	Seed weight	Sessile fraction	Pedicellate fraction
<u>Genetic correlation</u>									
Vigor		.309 (+.246)	.022 (+.259)	.631 (+.253)	.494 (+.480)	.391 (+.235)	.436 (+.209)	.517 (+.280)	.359 (+.312)
Leafiness	.222**		-.303 (+.244)	.186 (+.262)	-.013 (+.275)	.391 (+.234)	-.101 (+.237)	-.055 (+.278)	.185 (+.305)
Height	.165**	.008		.484 (+.200)	.617 (+.188)	-.291 (+.234)	.277 (+.218)	.629 (+.187)	.673 (+.218)
Raceme weight	.474**	.319**	.270**		.920 (+.041)	-.162 (+.243)	-.078 (+.230)	.919 (+.044)	.969 (+.081)
Seed yield	-.016	.264**	.236**	.916**		.231 (+.244)	.006 (+.244)	1.004 (+.003)	1.040 (+.056)
Fertility index	-.016	-.013	.010	.133**	.467**		.352 (+.203)	.246 (+.244)	.180 (+.278)
Seed weight	-.050	-.046	-.007	.062	.150**	.307**		-.040 (+.245)	.098 (+.268)
Sessile fraction	.477**	.254**	.240**	.897**	.978**	.453**	.162**		1.068 (+.077)
Pedicellate fraction	.320**	.186**	.118*	.627**	.719**	.379**	.034	.602**	
<u>Phenotypic correlation</u>									

*,** significant at the .05 and .01 levels, respectively.

pedicellate spikelets and a positive correlation was found between seed yield and pedicellate spikelet fraction weight ($r = .719$). There was no correlation between seed weight and pedicellate fraction weight ($r = .034$) although seed weights of pedicellate spikelets were lighter than sessile spikelets (Table 14). The correlation between sessile spikelets seed samples 1 and 2 was .89 and the correlation between pedicellate spikelets seed samples 1 and 2 was .86. The heritability estimate of pedicellate fraction weight was low (Table 11), and the block x family interaction was significant (Table 12), suggesting that the character is influenced strongly by environmental inconsistencies. The pedicellate spikelet is typically staminate or neuter in big bluestem, but Dr. James G. Ross (personal communication) noted that several southeastern South Dakota strains in spaced-plantings at Brookings, South Dakota exhibited high degrees of pedicellate spikelet fertility. As there is a pedicellate spikelet associated with each sessile spikelet, the potential for increased seed production as a consequence of increasing the percentage of pedicellate spikelet fertility is enormous.

Stand Establishment of Composites with Different Seed Weights

Most biologists use the term seedling vigor in its broadest sense to describe a vigorous growth habit that involves a more rapid size increase than that of competing plants of the same age. Prompt seedling growth as soon as conditions become favorable is an obvious advantage toward successful stand establishment. Conditions required for success in grass seedling establishment are: (1) vigorous adapted seedlings, (2) reduced competition, (3) favorable environment (Kneebone, 1972). In the Great Plains, improved strains of native grasses are adapted but the other critical conditions are not often met. The

Table 14. Mean seed weights of two 50 seed samples from sessile and pedicellate seed yield fractions of plants in the second cycle recurrent selection nursery.

Source	Sample no.	No. of plants	Weight (g)	Std. Dev.
Sessile spikelets	1	713	.089	.017
Sessile spikelets	2	708	.090	.018
Pedicellate spikelets	1	593	.078	.017
Pedicellate spikelets	2	581	.078	.017

environments in which strains of native grasses are planted are often unfavorable and only those plants that are able to develop an adequate root system and top growth greater than competing seedlings will survive.

The analysis of variance of seedling height measured in the field at Brookings thirty-three days after planting is presented in Table 15. Seedling numbers and height measurements were not possible for Pawnee because of a poor stand. Seedlings from heavy seeded composites grew at a faster rate than seedlings from lighter seeded ones. SD 45, a bulk composite of the heavy-seeded plants from the second cycle recurrent selection nursery, produced significantly taller seedlings than SD 44, a bulk composite of the most agronomically desirable plants from the same open-pollinated nursery. Table 16 presents mean seed weights, seedling heights and seedling numbers for the three composites planted in a field test at Brookings, South Dakota June 30, 1979. Within the second cycle recurrent selection nursery, the heavy-seeded plants as represented by SD 45 produced the tallest seedlings. Heritability of seed weight in this nursery was $.73 \pm .20$ (Table 11), indicating that in this population increased seedling height could be achieved by mass selection for heavy seed weight.

SD 43, a second cycle recurrent selection composite of agronomically promising plants from southeastern South Dakota strains produced significantly shorter seedlings than second cycle recurrent selection 1976 nursery composites (Table 15). SD 43 was not selected for heavy seed size, so it probably does not contain seed from the heaviest seeded plants of the population from which it was derived. Consequently, it

Table 15. Analysis of variance of seedling heights and numbers of three composites planted in a field test at Brookings, South Dakota June 30, 1979.

Source	Seedling height		Seedling numbers	
	df	M.S.	df	M.S.
Total	479	-----	35	-----
Composites (C)	2		2	
SD 44 vs SD 45	1	7097.03*	1	192.67
SD 43 vs SD 44 & SD 45	1	10355.65*	1	80.22
Blocks (B)	3	696.62	3	22.69
B x C	6	837.93	6	37.33
Error	468	693.92	24	58.94

*Significant at the .05 level.

Table 16. Mean seed weights, seedling heights and seedling numbers for three composites planted in a field test at Brookings, South Dakota June 30, 1979.

Composite	100 seed weight (g)		Seedling height (mm)		Seedling numbers †	
	Mean	Range	Mean	Std. dev.	Mean	Std. dev.
SD 43	.18	-----	53.23	24.12	14.08	8.69
SD 44	.20	.17-.24	58.37	25.87	20.08	6.94
SD 45	.26	.23-.28	67.79	28.71	14.42	5.60

†Number of seedlings/2 ft. of row.

may not represent the seedling height potential of its source population.

Large amounts of variation in seedling height were encountered within experimental plots. The variance of observations within SD 45 was greater than the within composite variances associated with SD 44 and SD 43, indicating that there could be a positive correlation between seedling height means and within composites variances. However, Bartlett's test for homogeneity of variances was not significant and the test of the hypothesis of composite seedling height means being equal is valid.

Seedling numbers counts ten days after planting in three random two-foot sections from the middle two rows of each plot showed no significant differences between composites (Table 15). Under the excellent conditions for stand establishment in this test there apparently was no effect of seed weight as indicated by the composites, on the number of seedlings established at ten days after planting. This would not be expected under less optimum conditions.

The composites with heavier seed, however, did show greater vigor and would be more easily established than lighter seeded composites. Selection for heavier seed therefore, should be an important objective in a breeding program in this species.

CONCLUSIONS

Comparisons among strains, and also among half-sib families in recurrent selection nurseries, demonstrated that extensive phenotypic variations were present in all characters studied. Highly significant differences between strains and families occurred in the factors contributing toward forage (vigor, leafiness and height) and seed (seed weight and fertility index) yield. Heritability studies indicated that a significant portion of this total variation for the above characters was due to genetic differences, although heritabilities appeared to have been biased by positive assortative mating and genotype x environment interactions.

Two cycles of recurrent selection for factors contributing toward forage and seed yield did not exhaust genetic variability for these characters. Heritability estimates were moderately high for these characters in the second cycle nursery, indicating that continued recurrent selection would be effective in the improvement of these characters.

Path coefficient analysis of seed yield components in the first cycle nursery indicated that number of flowering culms, fertility index and raceme weight per culm all contributed directly to seed yield. Seed weight, however, contributed to seed yield mostly through indirect effects via fertility index and raceme weight per culm.

Because a composite of plants with heavy seeds produced significantly taller seedlings than a composite with lighter seeds from the

same population, seed weight appeared to be positively correlated with seedling vigor. Therefore, mass selection for the highly heritable character, seed weight, should improve seedling vigor.

More precision in selection for moderately heritable characters contributing to forage and seed yield would be possible based on progeny test data. Open-pollinated progeny testing in replicated four-row plots would be fairly accurate in identifying superior parent clones. If selected clones were sufficiently superior, they could be established in a synthetic for subsequent testing.

Since no formidable negative genetic correlations between characters were observed, simultaneous multitrait selection should also be effective.

LITERATURE CITED

- Anderson, K. and A. E. Aldous. 1938. Improvement of Andropogon scoparius Michx. by breeding and selection. J. Am. Soc. Agron. 30: 862-869.
- Becker, W. A. 1975. Manual of quantitative genetics. 3rd ed. Students Book Corporation, Pullman, Wa.
- Bragg, L. H. 1964. Variation in four grass taxa in Texas. Diss. Abst. 25:2723.
- Christie, B. R. and R. R. Kalton. 1960. Inheritance of seed weight and associated traits in bromegrass, Bromus inermis Leyss. Can. J. Pl. Sci. 40:353-365.
- Church, G. L. 1929. Meiotic phenomena in certain gramineae. II. Paniceae and Andropogoneae. Bot. Gaz. 88:63-88.
- , 1940. Cytotaxonomic studies in the gramineae Spartina, Andropogon, and Panicum. Amer. Jour. Bot. 27:263-271.
- Comstock, R. E. and R. H. Moll. 1963. Genotype-environment interactions. In W. D. Hanson and H. F. Robinson (ed.) Statistical genetics and plant breeding. Publ. 982 Nat'l. Acad. Sci. - Nat'l. Res. Council. Washington, D. C., p. 164-194.
- Cornelius, D. R. 1944. Revegetation in the tall grass prairie region. J. Am. Soc. Agron. 36:393-400.
- , 1946. Comparison of some soil-conserving grasses. J. Am. Soc. Agron. 38:682-690.
- , 1950. Seed production of native grasses under cultivation in eastern Kansas. Ecol. Mono. 20:3-29.
- Crow, J. F. and M. Kimura. 1970. An introduction to population genetics theory. Harper and Row, New York.
- DeSelm, H. R. 1960. Variation in Andropogon gerardii Vitman and A. scoparius Mx. in two Ohio prairie areas. Diss. Abst. 20:2510-2511.
- Dewald, G. W. and S. M. Jalal. 1974. Meiotic behavior and fertility interrelationship in Andropogon scoparius and A. gerardi. Cytologia 39:215-223.
- Dewey, D. R. and K. H. Lu. 1959. A correlation and path coefficient analysis of components of crested wheatgrass seed production. Agron. J. 51:515-518.

- Duarte, R. A. and M. W. Adams. 1972. A path coefficient analysis of some yield component relationships in field beans (Phaseolus vulgaris L.). *Crop. Sci.* 12:579-582.
- Eberhart, S. A. and L. C. Newell. 1959. Variation in domestic collections of switchgrass, Panicum virgatum L. *Agron. J.* 51:613-616.
- Elliott, F. C. and R. M. Love. 1948. The significance of meiotic chromosome behaviour in breeding smooth brome grass, Bromus inermis Leyss. *J. Amer. Soc. Agron.* 40:335-341.
- Falconer, D. S. 1960. Introduction to quantitative genetics. The Ronald Press, New York.
- Fulst, J. L. 1942. Chromosome complements in *Bouteloua*. *Am. J. Bot.* 29:45-55.
- Gould, F. W. 1956. Chromosome counts and cytotaxonomic notes on grasses of the tribe Andropogoneae. *Am. J. Bot.* 43:395-404.
- Harlan, J. 1962. Hay and pasture seedings for the southern Great Plains and the southwest. Ch. 46. In M. E. Heath, D. S. Metcalfe, R. F. Barnes (ed.). *Forages*. 2nd ed. Iowa State Univ. Press. Ames, Iowa.
- Jain, S. K. 1979. Response to mass selection for flowering time in meadowfoam. *Crop. Sci.* 19:337-339.
- Keim, F. D. and L. C. Newell. 1962. Hay and pasture seedings for the northern Great Plains. Ch. 44. In M. E. Heath, D. S. Metcalfe, R. F. Barnes (eds.). *Forages*. 2nd ed. Iowa State Univ. Press. Ames.
- Kneebone, W. R. 1956. Breeding for seedling vigor in sand bluestem (Andropogon hallii Hack.) and other native grasses. *Agron. J.* 48:37-40.
- , 1958. Heritabilities in sand bluestem (Andropogon hallii Hack.) as estimated from parental clones and their open-pollination progenies. *Agron. J.* 50:459-461.
- , 1972. Breeding for seedling vigor. In: *The biology and utilization of grasses* (V. B. Youngner, C. M. McKell, eds.) pp. 90-100. Academic Press, New York.
- , and C. R. Cremer. 1955. The relationship of seed size to seedling vigor in some native grass species. *Agron. J.* 47:472-477.
- Knowles, R. P. 1955. Testing for combining ability in brome grass. *Agron. J.* 47:15-19.

- Krueger, C. R. and D. C. Curtis. 1979. Evaluation of big bluestem, indiagrass, sideoats grama, and switchgrass pastures with yearling steers. *Agron. J.* 71:480-482.
- Latter, D. B. H. 1965a. Quantitative genetic analysis in Phalaris tuberosa. I. The statistical theory of open-pollinated progeny. *Genet. Res.* 6:360-370.
- , 1965b. Quantitative genetic analysis in Phalaris tuberosa. II. Assortative mating and maternal effects in the inheritance of date of ear emergence, seed weight and seedling growth rate. *Genet. Res.* 6:371-385.
- Law, A. G. and K. L. Anderson. 1940. The effect of selection and inbreeding on the growth of big bluestem (Andropogon furcatus Muhl.) *J. Am. Soc. Agron.* 32:931-944.
- Lawrence, T. 1963. A comparison of methods of evaluating Russian wild ryegrass for seedling vigor. *Can. J. Plant Sci.* 43:307-312.
- Lush, J. L. 1945. Animal breeding plans. 3rd. ed. Iowa State Press, Ames, Ia.
- Massey, G. D. 1964. Seed characteristics and seedling behavior in three bluestem species. *Diss. Abst.* 25:3179-3180.
- McMillan, C. 1956. Nature of the plant community. I. Uniform garden and light period studies of five grass taxa in Nebraska. *Ecology* 37(2): 330-340.
- , 1959a. The role of ecotypic variation in the distribution of the central grassland of North America. *Ecol. Mono.* 29(4):285-308.
- , 1959b. Nature of the plant community. V. Variation within the true prairie community-type. *Am. J. Bot.* 46(6): 418-424.
- , 1964. Ecotypic variation within four North American prairie grasses. I. Morphological variations within transplanted community fractions. *Am. J. Bot.* 51(10):1119-1128.
- , 1965. Ecotypic variation within four North American prairie grasses. II. Behavioral variation within transplanted community fractions. *Am. J. Bot.* 52(1):55-65.
- , and J. Weiler. 1959. Cytogeography of Panicum virgatum in central North America. *Am. J. Bot.* 46:590-593.
- Newell, L. C. 1968. Effects of strain source and management practice on forage yields of two warm-season prairie grasses. *Crop Sci.* 8:205-210.

- , and S. A. Eberhart. 1961. Clone and progeny evaluation in the improvement of switchgrass, Panicum virgatum L. Crop Sci. 1:117-121.
- , and L. V. Peters. 1961. Performance of hybrids between divergent types of big bluestem and sand bluestem in relation to improvement. Crop Sci. 1:370-373.
- Nielsen, E. L. 1939. Grass studies. III. Additional somatic chromosome compliments. Am. J. Bot. 26:366-372.
- , 1944. Analysis of variance of Panicum virgatum Agr. Res. 69:327-353.
- Pandey, J. P. and J. H. Torrie. 1973. Path coefficient analysis of seed yield components in soybeans (Glycine max (L.) Merr.). Crop Sci. 13:505-507.
- Peters, L. V. and L. C. Newell. 1961. Hybridization between divergent types of big bluestem, Andropogon gerardi Vitman, and sand bluestem, Andropogon hallii Hack. Crop Sci. 1:359-363.
- Raeber, J. G. and R. R. Kalton. 1956. Variation and inheritance of fertility and its components in Bromus inermis Leyss. Agron. J. 48:212-216.
- Rogler, G. A. 1954. Seed size and seedling vigor in crested wheatgrass. Agron. J. 46:216-220.
- Ross, J. G. 1974. Preservation of representative plants from relict colonies of tall warm-season grasses in eastern South Dakota and southeastern North Dakota. Proc. S. D. Acad. Sci. 53:299.
- , and M. W. Adams. 1955. The influence of heredity on seed and forage production in smooth brome grass. Proc. S. D. Acad. Sci. 34:16-20.
- , and S. S. Bullis. 1962. Oahe intermediate wheatgrass. South Dakota Agr. Exp. Sta. Bull. 506.
- , and C. R. Krueger. 1976. Grass species and variety of performance in South Dakota. S. D. Ag. Exp. Sta. Bull. 642.
- , R. T. Thaden and W. L. Tucker. 1975. Selection criteria for yield and quality in big bluestem grass. Crop Sci. 5:303-306.
- Schaaf, H. M. and G. A. Rogler. 1963. Breeding crested wheatgrass for seed size and yield. Crop Sci. 3:347-350.
- , G. A. Rogler and R. J. Lorenz. 1962. Importance of variations in forage yield, seed yield, and seed weight to the improvement of crested wheatgrass. Crop Sci. 2:67-71.

- Snyder, L. A. and J. R. Harlan. 1953. A cytological study of Bouteloua gracilis from western Texas and eastern New Mexico. *Am. J. Bot.* 40:702-707.
- Steele, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill, New York.
- Thurling, N. 1974. Morphophysiological determinants of yield in rapeseed (Brassica campestris and Brassica napus). II. Yield components. *Aust. J. Agric. Res.* 25:711-721.
- Tossell, W. E. 1960. Early seedling vigour and seed weight in relation to breeding in smooth brome grass. *Can. J. Pl. Sci.* 40:268-280.
- Trupp, C. F. and I. T. Carlson. 1971. Improvement of seedling vigor of smooth brome grass (Bromus inermis Leyss.) by recurrent selection for high seed weight. *Crop Sci.* 11:225-228.
- , and A. E. Slinkard. 1965. Seedset rating as a measure of fertility in grasses. *Crop Sci.* 13:599-600.
- Warnes, D. D., L. C. Newell and W. J. Moline. 1971. Performance evaluation of some warm-season prairie grasses in Nebraska environments. *Neb. Agr. Exp. Sta. Bull.* 241.
- Weaver, J. E. and T. J. Fitzpatrick. 1932. Ecology and relative importance of the dominants of tall-grass prairie. *Bot. Gaz.* 93:112-150.