VARIATION IN ANDROGOGN GERARDI VITIAN AND A. SCOPARIUS Wx. IN TWO OHIO PRAIRIE AREAS

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in the Graduate School of The Ohio State University

By

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Adviser
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INTRODUCTION

One of the most constantly challenging problems of ecological plant geography is the interpretation of vegetation in time and space, especially when that vegetation is disjunctive. Although mapping the distribution of species, floral elements, and vegetation types is a precursor to their complete interpretation, other techniques are helpful.

The problem here lies in genetic differences (infra-specific variation) in *Andropogon Gerardi*¹ and *A. scoparius*, hereinafter referred to as Big and Little Bluestem respectively, which occupy two contrasting prairie habitats in Ohio. These are the edaphic prairies of southern Ohio and the climatic prairies of the drift plains. It will be shown that there are, in both species, small but definite physiological and morphological characteristics which are expressed to different degrees within the species in the two prairie areas.² Whether the differences are greater

¹Nomenclature followed is essentially that of Fernald, 1950.

²The writer uses the term prairie to denote undisturbed grassland communities related floristically and historically to the Tall Grass Prairie Formation of the Middle West as mapped by Transeau and many students. Prairie remnant is used to denote small remnants of these former expanses left after the destructive activities of man. Prairie area refers to a group of prairies (now remnants) formerly centering in Marion and Adams Counties, Ohio (figures 1, 2, and 3).
Figure 1. Map of Ohio showing the two sampling areas. Prairie remnants from which samples were taken are symbolized by solid circles. The drift areas are Illinoian, Ill; Tazewell, T; and Cary, C. (from Goldthwaite, 1952).
or less than those (unmeasured) differences between, for example, the Marion-Urbana prairies or the Marion-Toledo oak openings is not known. However, differences do exist between samples of Big and Little Bluestem from the Marion and Adams county prairie areas of Ohio.

Big and Little Bluestem were used as test plants because of their abundance, indeed their dominance of former Ohio prairies, wide geographical distribution, and known genetic variability.

One of the earliest statements in the literature concerning the northern area is that of Atwater, (1819) who wrote:

"...Sandusky Plains lying on the high ground between the headwaters of the Whetstone [Olentangy] branch of the Scioto River and the waters of streams running into Lake Erie, are still more extensive than those of Pickaway, covered with a coarse, tall grass, intermixed with weeds, with here and there a tree, presenting to the eye a landscape of great extent."

This prairie area occupies part of an undissected Cary till plain except in the north-west one-third where it is transected by the inconspicuous Wabash moraine. Typically it is gently rolling to flat, the latter especially to the north in the Killdeer Plains, where the Toledo silt loam is widespread and well developed. This soil is known to residents as "Jack-wax" and is almost impervious to water (Morrison, et al, 1918). The area is now thoroughly drained and much of the former wet prairie of Spartina pectinata where otherwise undisturbed, has gone over to
the Bluestems. A complete account of these prairies is included in the excellent vegetation survey of the Northern Virginia Military Lands by Dobbins (1937).

Sampling areas, which were mostly along railroad rights of way and little used pastures are indicated in figure 1. Such sampling areas, while showing little disturbance, may contain genetically unstable populations. Comparisons of other populations with these give unreliable results as noted by Wiegand (1935).

The earliest account, known to the writer, of the Adams county prairie area as it formerly existed is that of John Locke (1838), an early geologist and a qualified botanist. He wrote:

"When it is left in conical mound-like outliers, the marl is often barren of trees, and produces some peculiar prairie like plants, as the prairie docks, wild sunflowers, scabish and rudbeckias, etc. These places are called 'bald hills' and 'buffalo beets'. Several occur within a mile of West Union in a northerly direction and would be quite a paradise for the botanist."

The grassland areas of Adams county lie primarily in a discontinuous belt east of and roughly parallel to Ohio Brush Creek. They are best developed and most extensive on slopes underlain by Silurian limestone and dolomite, where soil profiles are shallow and poorly developed, and internal drainage is excessive (Jones, 1945; Taylor et al, 1938). These prairies, largely dominated by Little Blue stem and side-oats grama (Bouteloua curtipendula), have
Figure 2. View of a prairie remnant, northwest of Locust Grove, Adams county, Ohio. August, 1953.

Figure 3. A prairie remnant in southwestern Crawford county, Ohio. In the background is a grove of Quercus macrocarpa. In front of it is an extensive Big Bluestem community. September, 1952.
been studied by Braun (1928 b), and Jones (1944, 1945).

The location of remnants from which grass samples were taken are shown in figure 1. All of those indicated occur over dolomite.

Two kinds of collections were made. Population samples of each species, and sod block transplants were collected at most prairie remnant stations. The latter were replanted and grew to maturity in the greenhouses of the Botany Department at the Ohio State University. Morphological characters of the latter compared with each other and with herbarium material from the prairie center. The results of well over 20,000 measurements of various types are included here. In addition chromosome counts were made, rates of growth measured, and germination experiments executed.

It should be apparent that techniques of this kind could contribute knowledge toward a better understanding of species of interest to the ecologist other than those of the prairie.
The Andropogoneae Presl. of the family Gramineae is a large "natural" tribe abundant in tropical and subtropical grasslands and savannas. It extends into temperate regions in North America (Bews, 1929). In a study of recent by Hartley (1950), it was concluded that it is a group of recent origin with a center of distribution in southeastern Asia.

The tribe contains, according to Pilger (1940), six subtribes. The genus Andropogon L. is contained in the subtribe Andropogoninae Stapf. Andropogon is further divided by Pilger into five sections of which two are native to North America. These are Schizachyrium, and Leptopogon Stapf (Arthrolophias). Amphilophis usually treated as a section of Andropogon is given by Pilger as the genus Botrochloa O. Kuntze. Species with racemes solitary on each peduncle are referable to the first section, e.g. Little Bluestem; in the second are species with racemes digitately clustered and joints of the rachis slender, e.g. Big Bluestem. The other taxon contains no species considered in this study.

Variation shown by the two species here considered has not gone unnoticed by the taxonomist. Biotypes with one extreme character, others applying well to the species, have been given names ranging in taxonomic status from
species to form.

Big Bluestem, for example, has had at least five specific names other than the present one. In addition six varieties have been described, some of which are reductions from specific to varietal rank.

Little Bluestem has been placed in three genera other than Andropogon, has had seven specific epithets and eleven subspecific, varietal, or subvarietal descriptions. Some of these are reductions of species to lower rank. In addition two forms have been described.

While such synonymy appears, at the onset chaotic, it forceably points up the variation in morphology exhibited.

There seems to be agreement that the genus Andropogon is of southern origin. Larson (1947), on the basis of morphological and physiological evidence, suggests a "low latitude" origin of Little Bluestem. Gleason (1908) in discussing some Illinois prairie problems places the origin of the prairie in the southwest; while Harvey (1920) places the post Pleistocene center of dispersal in northeastern Texas, eastern Oklahoma and southern Kansas. Gleason (1923) places the origin of Big and Little Bluestem in the east and considers that they migrated west during the Xerothermic Period. Hubbard, Gleason and Fernald agree that the typical (oldest?) form of Little Bluestem is a Coastal Plain plant. The basis for this conclusion is not clear.
2. Ecology of Big Bluestem

The distribution of Big Bluestem given by Hitchcock and Chase (1950) is Quebec and Maine to Saskatchewan and Montana, south to Florida, Wyoming, Utah, Arizona and Mexico. In the central part of its range it "is the most important dominant of the grasslands which occupy the broad lowland valleys of the larger streams..." (Weaver and Fitzpatrick, 1934).

The Big Bluestem prairie type is described in Kansas by Schaffner, (1926); Oklahoma by Bruner, (1931); and in Texas by Tharp, (1926). Its importance is well recognized in eastern Iowa by Shimek (1925a). Northward it extends into Manitoba (Bird, 1927; Shimek, 1925b). Sampson (1921) describes Big Bluestem in Illinois as "the dominant grass of the upland prairies". Transeau (1935) recognizes that the eastern prairie peninsula is not transitional in nature and Jones (1944) states that in Ohio, at the time of settlement, the Big Bluestem grassland type was well represented.

Weaver and Fitzpatrick in 1932 and 1934 state that the Big and Little Bluestem types constitute 80% of the cover in the areas sampled. Characteristics of Big Bluestem resulting in dominance are the dense, rapid developing, sod forming type of growth, great stature resulting in dense shade, and early and pronounced tillering. As many as 200 flower stalks per square meter may be formed.
Roots below the sod or bunch fill the soil, the longer to a depth of 5-7 feet (see Weaver 1919, 1920). The relationship between soil type and root development of the Bluestems and other grasses has been described by Weaver and Darland (1949). As pointed out by Davidson and Romberg (1952) the correlation described between root distribution and soil type does not take into account possible genetic variations within the species.

Although percentage of embryo germination is low and winter killing of seedlings is severe the first year, 14 to 40 inch roots develop within two months after germination. In seven to eight weeks a bunch is formed (Weaver and Fitzpatrick, 1934).

Studies on Big Bluestem have been made regards of injury to latitudinal strains by low temperatures (Rogler, 1943); dormancy (Shepard, 1938); drought resistance of seedlings (Muehler and Weaver, 1942); the relationship between litter removal and stem density and height (Curtis and Partch, 1950); loss of vigor following inbreeding (Law and Anderson, 1940); growth following soil deposition upon rhizomes (Mueller, 1941); and growth and photoperiodicity (Rice, 1950).

3. Ecology of Little Bluestem

Hitchcock and Chase indicate the range of Little Bluestem to be from Quebec and Maine to Alberta and Idaho,
and south to Florida and Arizona. In the prairie center it is the "principal dominant of the most important upland (vegetation) type". Its areal extent is described as many times that of Big Bluestem. To the north it intermingles with *Stipa spartea* (Weaver and Fitzpatrick, 1934). To the southeast it competes mainly with Big Bluestem, westward extending into the mixed prairie (Shimek, 1915; Shantz, 1911) with relics as far west as Colorado (Livingston, 1952). In Illinois Little Bluestem originally occurred on "the more xerophytic uplands and exposed clay soils" (Sampson, 1921). In Ohio the type occurs on ridges and moraines; within the plateau it is the dominant grass of the small prairie openings frequently associated with *Sorghastrum nutans* and side-oats grama. There Big Bluestem occurs on low seepage slopes and well watered alluvial deposits.

In the prairie center, Little Bluestem ordinarily forms an uninterrupted sod with a 50-90 percent cover on steep slopes or when underlain by loess. Where sod is formed a dense, compact grass cover results with 50-300 stems per square dm. Roots fill the soil between and beneath the clumps to a depth of five feet. First year seedlings may be five inches tall with three to four tillers and eight 12-18 inch well branched roots each by late July (Weaver and Fitzpatrick, 1934).

A general loss of vigor has been shown in Little
Bluestem following inbreeding (through selfing) although to a degree not as great as that in the proceeding species (Anderson, 1940; Anderson and Aldous, 1938). Seedling drought resistance (Mueller and Weaver, 1942) and photoperiod by Larson (1947) and Rice (1950) have been studied. Cornelius (1947) has shown that latitudinal strains, when planted in Kansas, vary in time of flowering, number of grains formed, dry weight and height of the plant, and degree of winter injury.

4. The Ecotype and Related Concepts

Since its inception with Turesson (1922a), the concept of the ecotype has been applied to many plant species. Originally defined as "the product arising as a result of the genotypical response of an ecospecies or species to a particular habitat," Turesson applied the concept to such as meadow and shade forms of Lysimachia nummularia. Strains of this species when transplanted from the environments in which they were growing to a common one retained the phenotype previously thought by botanists to have been environmentally induced. Since that time the ecogenetic concept of plant variation has been expanded to include, among others, the ecospecies "a group of plants within

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3Clausen, Keck and Heisey (1940) amplify further, "It is characterized by its fitness for a particular environment within the range occupied by the ecospecies as a whole".
the cenospecies whose members are able to exchange their genes without detriment to the offspring. Ecospecies are separated from one another by internal barriers that prevent such free interchange" (Clausen, Keck and Heisey, 1940). Another is the cenospecies, a group of plants "of common evolutionary origin, so far as morphological, cytological, and experimental facts indicate" (Turesson, 1922b).

Among the many ecotypes described by Turesson (1922b and 1925) are dwarf salt meadow forms of Aster tripolium, a calcareous rock ecotype of Artemesia campestris L., and an alpine ecotype of Myosotis silvatica. In a paper in 1927 he comments upon the wide, high latitude distribution of Poa alpina and suggests that the lowland ecotype is poorly developed due to Pleistocene biotype depletion.

Although the modern foundation of the understanding of infraspecific variation in plants is based upon the works of Turesson, Faegri (1937) suggests that much of the ecotypic distinctness described has resulted from inadequate sampling.

Another Continental worker interpreting variations is J. W. Gregor (1938, 1939; Gregor, Davey, and Lang, 1936). Working with Plantago maritima he reports that transplants of this species retain the phenotype which characterized them under natural conditions. In 1938,
using coastal forms from cliffs, salt marshes and grasslands he reports that "differences between populations are largely dependent on the frequency with which certain quantitative characters, belonging to a continuously graded series, are represented".

Gregor (1939) has also been instrumental in developing the concept of the cline. This term was first introduced by Huxley in 1938 to refer to characters showing geographic regularities of distribution. Clines have been described in side-oats grama for reaction to photoperiod by Olmstead (1944) and in such characters as frequency of glandular hairs on the calyx of *Teucrium canadense*, grading from 100 percent in the Rocky Mountains to none in southern Florida (McClintock and Epling, 1946).

Clines have been described not only on the regional but also on the local level. Transitions between ecotypes are usually clinal in nature, Terrell (1952) has described forest-prairie ecoclines in *Galium boreale*.

In reality the clinal and ecotypic approaches are two different ways of attacking the same problems. Generally, however, the latter has more frequently led to causal interpretations of infraspecific variations.

Hall (1929) was the first to initiate large scale experimental garden studies in North America. With this impetus, they were carried on by two groups of investigators, one headed by F. E. Clements and the other by Jens Clausen.
The former's work has recently been summarized (Clements, Martin, and Long, 1950) but the views expressed "are at variance with practically all reliable scientific evidence" (Ownbey, 1952).

The work of Clausen, Keck, and Heisey (1940, 1943, 1948) on the other hand, has been widely cited. The results with Achillea, 1948, are particularly enlightening in view of the eleven climatic races found in a 200 mile transect across California. The ecotypes differ from one another in their physiological reactions to varying temperature and moisture regimes. Other characteristics, of a morphological nature, which "must be assumed to have survival value", while being fairly well correlated habitat to habitat are less convincingly shown to have the same causal selective value in that habitat. Lawrence (1945) has stated that, in Deschampsia caespitosa (L.) Beauv., correlation between morphology and ecotypic physiology depends upon gene linkage. In this species ecotypes are poorly defined morphologically, that is, "physiological differentiation has been independent of morphological differentiation".

While use of the "transplant method" has resulted in much new knowledge about "microevolution", one other method, that of local population sampling, has also been of value. First introduced by Anderson (1941) as "mass collection", two other workers have used it to particular
advantage. Fassett (1941) was able to relate Great Lakes populations of *Rubus parviflorus* to those of the Sierras and suggest a continuous population "during a post glacial cool humid period and subsequent bisection of the range by the aridity of the Great Plains" (the Xerothermic Period?). Woodson (1947) from studies of samples of *Asclepias tuberosa* suggests a center of origin for each of its three subspecies. Of particular interest also is the outward "diffusion" from an Ozark center of a special type of leaf shape associated with characters of supposed selective advantage.

Literature surveys pertinent to the methods and results of the ecotype and related concepts are in the works of Heisey (1940); Gregor (1944, 1946); Turrill (1946); Stebbins (1950); and Baker (1952).
METHODS AND RESULTS

1. Chromosome Number

Among the techniques which may be used in determining the degree of relationship between species and among strains of the same species is that of chromosome number and behavior. The only example of such work in the North American Andropogoneae is that of Gould (1953) in section Amphilophis. The sections Schizachyrium, containing Little Bluestem and Arthrolophis, containing Big Bluestem, have never received such intensive treatment. The value of long term exhaustive studies has been made apparent by Babcock (1947) in the genus Crepis.

During August, September and October, 1952, sod blocks of Big and Little Bluestem were collected from several prairie remnants in each of the two prairie areas in Ohio. Soil was washed from the roots and rhizomes and they were planted in the Botanic Gardens of the Ohio State University in a modified Genessee silt loam. During November and December the plants were subjected to the fluctuating temperatures of a mild winter. January 3 through 8 soil blocks, containing the roots and rhizomes were removed to the greenhouse (figure 5). There supplementary light from four banks of fluourescent 120 cm. white tubes, operating on a 14 hour day was supplied. The light suppliied an irradiance of 13-120 foot candles depending upon
the distance of the sod blocks from the source.

From these sod transplants, growing stems were removed three to four weeks before anthesis, one each from each station from which the two species had been originally collected. Anthers two mm. long were first killed in Carnoy's solution, later transferred to 70 percent alcohol, and then smeared in aceto-carmine according to Sear's technique recently reviewed by Smith (1947).

Chromosome counts in microsporocytes of Big Bluestem revealed a 2n number of 60 (figure 4). The chromosome pairs all appeared to behave as diploids. The same 2n number has been reported by Church (1940) for plants from Manhattan, Kansas; and from Fayetteville, Arkansas by Nielson in 1939. Church (1940) also reports a tetraploid strain from Anderson County, Kansas.

The chromosomes of Little Bluestem, sampled as above revealed a 2n number of 40. As in the other species, the pairs all appeared to behave as diploids. The same number is reported from Texas and Kansas by Church (1940). In plants from the vicinity of Rosebud and Damascus, Arkansas, Nielson (1939) reports two morphologically separable tetraploid strains. Church (1929, 1936) found, in variety frequent from the vicinity of Boston a 2n number of 50 with 20 bivalents and 10 univalents, and in variety villosissimus Kearney from Falmouth, Massachusetts a 2n number of 40.
Figure 4. Camera lucida drawings showing chromosomes during meiosis of the species used. Upper pair of figures is of Big Bluestem, left from the north, accession 27-4; right from the south, accession 31-4. Lower pair is of Little Bluestem, left from the north, accession 47-4; right from the south, accession 17-30. Scale equals 10 microns.
2. Germination

One of the most critical stages in the life history of a seed plant is that of germination of the embryo. The need for such studies, recently emphasized by Pelton (1953), has not been overlooked by students of prairie ecology. Studies of this type on species including the Bluestems have been made by Blake (1935), Greene and Curtis (1950), Coukos (1944), and Anderson and Aldous (1938).

Spikelets were collected in the field in each prairie remnant on three successive weekly two day periods e.g. the Marion prairie area on 18 and 25 October and 1 November; on the Adams County prairies: 19 and 26 October and 2 November.

Equal weights of spikelets from each prairie remnant of a prairie area were thoroughly mixed, selected to exclude "runts", bagged in lots of 50 each, and stored at about room temperature for 82 to 95 days. More than 20,000 spikelets were thus treated.

They were planted in lots of 50 or 100 in 50 grams of course white sand contained in petri plates, or in soil in flats. Planting in plates was at the rate of 50 per plate at about 3 mm. depth in the sand. Sufficient alkaline tap water (13 cc.) was added to saturate it to a level of within 2 to 3 mm. of the spikelets. These were then subjected to five temperature treatments. One set was
left at room temperature; the second set was subjected to 
-10°C. for 30 days; groups 3, 4, and 5 were subjected to 
temperatures of 10°C. for 30, 50, and 70 days respectively. 
The number of spikelets per treatment is indicated in 
table 1. All spikelets remained in darkness and if cold 
treated were retained in darkness during their return to 
room temperature at the end of the indicated period. Only 
during the periods of examination which followed were the 
spikelets exposed to light: this of a few minutes duration 
at two day intervals.

Beds for planting of spikelets in soil (mentioned 
above) were prepared in flats 51 x 38 x 7.7 cm., each di­
vided into two parts widthwise. The flats were lined with 
brown wrapping paper and filled to a depth of 3 cm. with 
medium-grained sand. Soil from around the roots of sod 
transplants from each prairie area was sifted to remove 
organic and mineral particles larger than 6 mm. in diamet­
er, and placed to a depth of 2 cm. in the flats. Spike­
lets, 50 or 100 to a row were planted and covered with ad­
ditional soil to a depth of 1 cm., half of each flat con­
taining soil from each prairie area. Each half flat con­
tained 15 rows of spikelets: six of Big Bluestem, three 
from each prairie area; and nine of Little Bluestem, six 
from the southern and three from the northern source.
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<th>Big Bluestem source</th>
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<tr>
<td><strong>Sand</strong></td>
<td>600</td>
<td>500</td>
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<tr>
<td><em>30 days at -10°C</em></td>
<td>300</td>
<td>300</td>
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<tr>
<td><em>°C</em></td>
<td>100</td>
<td>300</td>
</tr>
<tr>
<td><em>50 °C</em></td>
<td>100</td>
<td>300</td>
</tr>
<tr>
<td><em>70 °C</em></td>
<td>100</td>
<td>300</td>
</tr>
<tr>
<td><strong>Soil (source)</strong></td>
<td>600</td>
<td>300</td>
</tr>
<tr>
<td><strong>Gl.</strong></td>
<td>300</td>
<td>300</td>
</tr>
<tr>
<td><em>30 °C</em></td>
<td>Outside</td>
<td>300</td>
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<tr>
<td><em>50 °C</em></td>
<td>Outside</td>
<td>300</td>
</tr>
<tr>
<td><em>70 °C</em></td>
<td>Outside</td>
<td>150</td>
</tr>
<tr>
<td><strong>Ungl.</strong></td>
<td>300</td>
<td>300</td>
</tr>
<tr>
<td><em>30 °C</em></td>
<td>Outside</td>
<td>300</td>
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<tr>
<td><em>50 °C</em></td>
<td>Outside</td>
<td>300</td>
</tr>
<tr>
<td><em>70 °C</em></td>
<td>Outside</td>
<td>150</td>
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The flats were disposed of as follows: One remained at room temperature; one received 70 days of mild winter and spring temperatures (22 January through 2 April); and three, one each, were exposed to 30, 50, and 70 days at 10°C.

Upon removal of cold treated flats to room temperatures they were examined twice weekly and emergent seedlings marked with toothpicks (see figure 6).

The resultant data are plotted in figures 7 through 11. On the abscissa are the number of days following planting or removal to room temperature. On the ordinate is the real germination percentage (Lawrence, et al, 1947), that is, number of embryos germinating those able to germinate. The latter is calculated from samples of a source identical to those in the tests. Spikelets were dissected and the percentage of undeveloped ovularies of the sample was calculated. It was presumed that the embryos of fully developed grains were capable of germination under favorable conditions.

The data in figure 7 indicate the very marked effect of treatment upon the rate of germination in Little Blue-stem in coarse sand. Regardless of grain source, those receiving no cold treatment, as well as those receiving 30 days freezing, germinated at a slow rate and the final germination percentage is low. This is in contrast to those grains chilled for 30 to 70 days. A similar series
Figure 5. The grasses growing under greenhouse conditions. Photograph taken about seven weeks after removal of dormant rhizomes and roots from the botanic garden.

Figure 6. Flat of seedlings. Each toothpick marks a young plant. This flat received no cold treatment.
Figure 7. Germination of embryos of Little Bluestem in sand. Gl. = grain source the northern one, Ungl. = the southern.
Figure 7
of "germination rate curves" could be drawn for Big Blue-stem, as well as for grains of both species germinating in flats.

The results of germination of grains of Big and Little Bluestem in sand is summarized in figure 8. In the former, grains from the southern source have a somewhat higher germination percentage while in Little Bluestem the opposite is true.

Averages of real germination percentages in the two soil types, discussed above, are shown in figure 9. The same general relation between germination and treatment is shown here as in the preceding figure except that grains of Big Bluestem from both areas germinate about equally well. The effect of soil type is indicated in figures 10 and 11. In Little Bluestem the higher germination percentage is again evident with longer cold treatment, as well as the generally higher percentage in soil from the prairie area from which the grains came. The number of germinating grains of Big Bluestem from one or the other prairie area, on the other hand, appears to bear no relation to the soil from that same area.

3. Stem Elongation

Stem elongation is a function of the interaction of many internal and external complexes. Thus measurement of
Figure 3. Germination of both species in sand. In the abscissa D.F. = days at $-10^\circ$C.

Figure 9. Germination of both species in soil. Points are averages of germination percentage in two soil types. In the abscissa, Out = 70 days of mild winter and spring temperature.
Figure 10. Germination of Big Bluestem in two kinds of soil. G1, G = northern grains in glacial soil; Ungl., R. = southern grains in residual soil; Ungl., G = southern grains in northern soil; and Gl., R. = northern grains in residual soil.

Figure 11. Germination of Little Bluestem in two kinds of soil.
Figure 10

A. Gerardi

Figure 11

A. scoparius
stems of plants from different sources growing together in a fairly uniform environment may give some measure of the differential genetic constitutions of the plants under observation.

Stem length of 600 plants was measured weekly, 150 of each species from each prairie area. Measurements were begun 39 days after the buds of Big Bluestem were first seen to enlarge, and the leaves of Little Bluestem first were observed to begin elongation. Height here is considered the distance between the soil level and the highest visible ligule.

Figure 12 shows that inflorescences of Big Bluestem from the southern prairies emerge at a somewhat greater height than those from the northern prairie area, although the average dates of flowering are almost identical. The height of Little Bluestem was the same at flowering in both areas, but those transplanted from the south flowered 26 days later than those from the north. Field observations bear out all these facts but the last. The time of flowering of Little Bluestem on the Adams county prairies is about the same, or at the most a week later, than Little Bluestem to the north.

Presuming that floral initiation took place two months before the average flowering date in each strain, then that time of initiation was one during which the two strains were subjected to almost the same photoperiod. The
Figure 12. Stem elongation and flowering in Big and Little Bluestem.
Figure 12
artificial photoperiod had been exceeded by the natural only by a few minutes. However, examination of the greenhouse temperature record reveals quite different temperature regimes preceding flowering. The Adams county strain was subjected to an average 13 hour daily temperature period 21°C. or above, while the northern strain was subjected to an average 8 hour daily temperature period 21°C. or above. If the southern strain is one in which flowering is favored by relatively higher temperatures than the strain to the north the temperature-flowering observations above may be correlated.

4. Morphological Variation

Three to four weeks after flowering, twenty plants were collected from greenhouse sods representing each prairie remnant. The number taken was divided as evenly as possible among the blocks per remnant. The specimens were pressed and certain characters noted or measured, many with a 10 X binocular dissecting microscope equipped with an ocular micrometer marked in tenths of a millimeter. The characters measured are listed below. Those preceded by the letter "g" were measured on Big Bluestem only, those measured on Little Bluestem only are preceded by the letter "s". Those unmarked were measured in both species. Reference to figures 13 and 14 will aid in interpreting the characters.
1. Stem length to uppermost inflorescence.
2. Number of nodes on stem.
3. Number of racemes.
4. Length of the longest branch of the terminal raceme.
5. Number of sessile spikelets per terminal raceme.
6. Longest trichome of the bearding at the base of the rachis. This and measurements below refer to a spikelet pair (sessile and pedicellled) taken, in Big Bluestem, from the estimated middle of the longest branch of the terminal raceme; in Little Bluestem, from the actual middle pair taken from the terminal raceme.
7. Longest trichome of the bearding at the base of the second glume.
8. Length of the rachis.
9. Length of the glabrous base of the rachis, i.e. with trichomes one-half mm. or less in length.
10. Ratio: length of the glabrous base of the rachis/length of the rachis.
11. Density of rachis bearding. Number of trichomes along 1\frac{1}{2} mm. of the rachis beginning 1\frac{1}{2} mm. from its base.
12. Longest trichome of the rachis.
13. Length of the pedicellled spikelet.
14. Length of the pedicel.
15. Length of the glabrous base of the pedicel, i.e. with trichomes one-half mm. or less in length.
16. Ratio: length of the glabrous base of the pedicel/length of the pedicel.
17. Density of pedicel bearding. Number of trichomes along 1\frac{1}{2} mm. of the rachis beginning 1\frac{1}{2} mm. from its base.
18. Longest trichome of the pedicel.

Many of the above measurements were also made on population samples of 20 plants from the same prairie remnant on which the sod transplants were made. Those, in turn, are compared with measurements taken from herbarium specimens from the following states: Kansas, Missouri, Illinois, and Indiana. It should be pointed out that comparisons between population samples collected over a short period, and herbarium material collected over many years, give biased results (Lewis, 1947). Comparisons here therefore
Figure 13. A pair of spikelets of Big Bluestem. The letter "a" is at the second glume. Behind it is the first glume. "b" is at the rachis, "c" at the pedicel and "d" at the pedicled spikelet. Accession 31-4. Approximately 7X.

Figure 14. A pair of spikelets of Little Bluestem. The letters refer to the parts as above. Accession 17-2. Approximately 7X.
are made with caution.

Table 2 shows the number of specimens of each type examined. The glacial map of Flint (1945) was used as an aid in determining the origin of out-of-state specimens with reference to glacial boundary.

Table 2.
Number of specimens examined according to their source.

<table>
<thead>
<tr>
<th></th>
<th>Ohio greenhouse</th>
<th>Ohio field samp.</th>
<th>Prairie center herb. spec.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Big Bluestem</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>glaciated</td>
<td>133</td>
<td>140</td>
<td>73</td>
</tr>
<tr>
<td>unglaciated</td>
<td>132</td>
<td>120</td>
<td>40</td>
</tr>
<tr>
<td>Little Bluestem</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>glaciated</td>
<td>98</td>
<td>67</td>
<td>109</td>
</tr>
<tr>
<td>unglaciated</td>
<td>143</td>
<td>140</td>
<td>61</td>
</tr>
</tbody>
</table>

Two methods of presenting the data are used. Measurements for a particular character are grouped into size classes, the number per size class being given as the percentage of the sample. In figure 24, for example is plotted distribution of data from measurements of the longest trichome of the rachis (of a spikelet) of Big Bluestem. Plotted only are data from Ohio greenhouse sod transplants. The origin is indicated: Gl. = glaciated, i.e. plants from north of the glacial boundary, Ungl. = unglaciated, i.e. plants from the Adams County prairie area. On a work sheet measurements from plants from one prairie area were listed in increasing order of magnitude. The number of
plants per sets of sizes (size classes), for example 1.1 to 1.6 mm., was calculated. Since the number of specimens from each prairie area is not the same, 133 and 132 (see table 2), raw data from each size class is not comparable. Therefore the percent of the total per size class was calculated. Points from the same prairie area are connected by a line. It is to be noted in figure 24, that similar curves are produced by handling the data as above. Only in the larger size classes are the populations differentiated. Here the sample from the southern Ohio prairies are "offset" toward the larger size classes.

The other method employed is that of scatter diagrams. Averages of 20 samples from each prairie remnant are plotted, one character against another.

A. Big Bluestem

1. Size classes - Ohio material. Figures showing the size class distribution of data derived from measurements on Big Bluestem are divided into three groups. The first group contains those with two curves for Ohio glaciated and unglaciated prairie area samples. One sample was collected from greenhouse sod transplants, one was collected in the field. These are figures 15 through 23.

On each of the second group are plotted data from Ohio greenhouse samples, figures 24 through 29.
The third set shows the same characters as the second but were based on measurements of Ohio field population samples and from herbarium material of plants from the prairie center (figures 30 through 35).

The distribution of size classes of the longest trichome of the pedicel (figure 15) is shown to be very uniform both to the north and to the south of the glacial border in Ohio. This character and the one to follow are distinctive in this group in that they show less variability in the greenhouse than when sampled under field conditions. The field-greenhouse relationship, indicated in figure 16 is the same but in this instance the Marion prairie area sample has slightly longer pedicelled spikelets than the sample to the south.

Figures 17 through 20 show measurements of characters in which the difference between samples from glaciated and unglaciated areas are about as great in the greenhouse as in the field. In either, differentiation with reference to the sampling area, is apparent.

Figures 21, 22, and 23 show certain measurements of characters which showed greater differences between greenhouse samples than between field samples. In each there is a slight, though unmistakable trend of variation.

The data presented in figures 24 through 29 are from greenhouse population samples only. A consistent variation in most size classes between the two samples is shown by
figures 23, 24 and 25. The larger size classes, in figures 27, 28 and 29, do not show the strict offset of the previous diagrams. In all, however, a distinction may easily be made between the two population samples.

The figures mentioned above (15 through 29) reveal the following differences between the Ohio Big Bluestem populations on unglaciated Adams County, Ohio and those populations of the same species north of the border. The statements below apply to the Adams county Big Bluestem population:

1. The pedicelled spikelet is slightly shorter (figure 16).
2. There are a few more racemes per plant (figure 17).
3. The pedicel usually is somewhat shorter (figure 19).
4. The glabrous base of the pedicel is deficient in the middle size classes (figure 20).
5. The stems are somewhat longer (figure 21).
6. Nodes are more numerous per plant (figure 22).
7. The longest trichome of the rachis is usually longer (figure 24).
8. The bearding at the base of the second glume is somewhat longer (figure 25).
9. Rachises are usually shorter (figure 26).

Pedicel and rachis ratios (figures 23 and 29, respectively), while having curves differing in some respects
according to source of the material, are not consistently differentiated.

Other characters measured (figures 15, 18, 27, and 28), especially the last, are less clearly differentiated.

2. Size classes - Ohio vs. Prairie center material. Prairie center material is compared with Ohio samples in figures 30 through 35. Figure 30 shows that, in the Ohio samples, bearding at the base of the second glume is somewhat longer than that from the prairie center. Moreover it would appear that in Ohio the samples from north of the glacial border have a higher percentage of larger size classes than in the sample from the south. In the prairie states the same is true.

Figure 31 shows that the length of the rachis is shorter in the prairie center than in the Ohio sample. The curves also indicate that the Ohio sample from north of the glacial border has longer rachises than to the south. In the prairie center the opposite is true.

Figure 32 shows that the length of the glabrous base of the rachis is somewhat shorter in the prairie center than in Ohio, and that the peaks exhibited by the curves for glaciated-unglaciated Ohio and the glaciated-unglaciated prairie center are inverted with reference to one another.

From figure 33 it may be inferred that the length of
the longest trichome of the rachis is somewhat greater in the prairie states than in Ohio.

Little difference between Ohio and western samples can be interpreted from the curves exhibited by the length of the bearding at the base of the rachis (figure 34).

From size class curves for the rachis ratio, figure 35, it may be seen that the ratio is somewhat smaller in the prairie states than in Ohio. Moreover, in the samples from south of the glacial border to the west, the ratio is somewhat smaller than to the north. In Ohio the opposite is generally true.

3. Ohio material - scatter diagrams. In plotting the average measurements of a particular character from plants of the Ohio prairie remnants (figures 36-43), one set of points is represented for each area, namely the results from plants which grew in the greenhouse. In all instances, populations from north and south of the glacial border, but which grew together in a common environment, overlap. Field samples plotted, but not shown here, overlapped in some characters but did not in others.

In no instance is it possible to predict the two population positions. Nor is it possible to predict the position in either population of any particular prairie remnant. The two variables involved in each of these figures are, to a large degree, repetition of previous data. They are presented to emphasize the degree of variability within
and the differences between populations.

The results of plotting height against number of nodes are shown by figure 31. Here the distinction between the two populations is well differentiated and is even more apparent than indicated previously (figure 12).

A considerable degree of differentiation is shown by figures 37, 38, and 39: number of inflorescences vs. length of the longest branch of the terminal inflorescence, the former vs. number of nodes, and length of the pedicel vs. length of its glabrous base. Again overlapping is apparent.

Figures 40 and 41 characterize populations in which an increase in length of one character is generally accompanied by a similar increase in length of the character against which it is plotted. In these the above is true of one population but not of the other. In the former it is the Marion prairie sample, in the latter the Adams county sample exhibiting this feature.

Figures 42 and 43 are diagrams of "sympatric" populations in which overlapping is, or almost is, 100 percent. When plotted, no other character combinations exhibited such little differentiation as is indicated by these.
B. Little Bluestem

1. Size classes - Ohio material. Results of the analysis of data derived from measurements upon Little Bluestem are presented below in the same fashion as previously. In general, differentiation is more concise than in Big Bluestem, a fact not surprising in view of the known variability of the species.

The figures may be grouped artificially as follows: figures 44 through 54 show data from four sets of Ohio plants; two from each side of the glacial boundary, one each collected in the field and in the greenhouse. Another group of figures (62 through 68) show differences in Ohio and prairie center field samples from glaciated and unglaciated areas. Accompanying each of these is a figure showing the same character measured on Ohio greenhouse samples (figures 55 through 61).

Figures 44 through 49 are plotted variations in Little Bluestem in which the samples north and south of the glacial border vary more from each other in the field than they do in a common greenhouse environment. In each a slight but unmistakable difference may be seen in the two latitudinal populations. In figures 47 and 48 variation in the field is particularly evident but when greenhouse samples are taken they largely disappear.

Figures 50, 51 and 52 show variations that are as
evident in the field as in the common environment. In the latter environment however, the distinction between the Adams and Marion prairie area samples are none-the-less evident.

Figures 53 and 54 are measurements of characters (the latter figure is a ratio) which differ more widely in the common environment than in the field. In each, however, distinction may easily be made between the two populations.

The results of plotting data for certain other characters shown by figures 55 through 61. In the first virtually no differentiation is apparent. The others however show the offset curves characteristic of the species when data from it are plotted in this fashion.

From these data it is concluded that the differences listed below are evident between populations of Little Bluestem in the unglaciated Adams County area and those sampled from glaciated Ohio. Statements apply to the former.

1. The proportion of tall plants is greater (figure 44, cf. also figure 12).
2. The number of fertile spikelets per terminal raceme is greater (figure 45).
3. The pedicel is generally shorter (figure 46).
4. The pedicel bearding generally is less dense (figure 47).
5. The rachis is slightly shorter (figure 48).
6. The number of nodes per stem is greater (figure
50).

7. Generally there are fewer racemes per plant (figure 51).

8. The sterile spikelet is usually shorter (figure 53).

9. Glumes are shorter (figure 56).

10. The longest trichome at the base of the rachis is usually shorter (figure 57).

11. The longest trichome at the base of the second glume is usually shorter (figure 58).

12. The longest trichome of the rachis is usually shorter (figure 59).

13. The glabrous base of the pedicel usually is longer (figure 60).

14. The longest trichome of the pedicel is somewhat shorter (figure 61).

It is of interest also that the rachis ratio is somewhat greater in Adams county populations than in those to the north (figure 52), as is true of the pedicel ratio (figure 54).

It is apparent also that no differentiation is extant between the populations for the characters: degree of rachis bearding (figure 49) and length of the glabrous base of the rachis (figure 55).
2. Size classes - Ohio vs. Prairie center material.
By comparison of measurements of certain characters plotted for plants from the prairie center with Ohio samples it may be concluded:

1. Glume length is somewhat greater to the west. In Ohio, plants from glaciated areas have glumes somewhat longer than those growing in the unglaciated southern areas. This relationship is not evident in the prairie center (figure 62).

2. The longest trichome at the base of the rachis is generally somewhat longer in grasses of the prairie states than in those in Ohio; moreover, the length of the trichome in the sample from the unglaciated region to the west is somewhat shorter than that in the sample from glaciated areas. In Ohio this is also true (figure 63).

3. The length of the longest trichome at the base of the second glume is similar in all populations (figure 64) with the exception of populations from the unglaciated prairie center, which is truncate in the middle size classes.

4. The length of the longest trichome of the rachis (figure 65) of the prairie center sample is slightly longer than in the Ohio sample. Moreover the curves representing origin are disposed with reference to one another dissimilarly.
5. In general the Ohio material shows much wider variation in the length of the glabrous base of the pedicel than does the prairie center material. Also, a larger proportion of the samples to the west have shorter glabrous bases than Ohio plants, (figure 66).

6. The length of the longest trichome of the pedicel (figure 67) is greater in the prairie center than in Ohio. The Ohio sample curve, based on material from glaciated areas, is offset toward the larger size classes over a great range of size classes. The prairie center sample from glaciated areas is offset only in the largest size classes.

7. Generally, the length of the glabrous base of the rachis (figure 68) is greater in populations in the west than in Ohio. The Ohio-prairie center populations in unglaciated areas, are greatly dissimilar, however.

3. Ohio material - scatter diagrams. Characters measured and plotted as population averages in scatter diagrams are shown in figures 69 through 77.

The populations are quite distinct when certain characters are plotted, figure 69 through 72; others only share one common point, figures 73 and 74; some overlap but little, figures 75 and 76; and in others the degree
of overlapping is considerable, (figure 77).

The greater degree of differentiation in this species is evident when compared to that in Big Bluestem (figures 36 through 43).
DISCUSSION AND CONCLUSIONS

The late Tertiary evolution and sorting of the grassland flora east of the Rocky Mountains is suggested by the findings of Elias (1935). He reports 18 species of grasses (Agrostideae and Paniceae) from deposits formed during the establishment of grassland communities following the rise of the Rocky Mountains. This grassland expansion and the last (post glacial) one are the best substantiated.

The post glacial eastward migration of prairie communities as far as northeastern Pennsylvania has been discussed many times. An earlier eastward extension is suggested by Braun (1928a) on the basis of her interpretation of floristic components of the Adams county prairie area. More recently (1950) she interprets the presence of southeastern species in the Kentucky barrens as indicating a long period of occupancy, although the presence of barrens on non-prairie soils and the rapid reinvansion of forest following man's occupation is suggestive of a shorter period.

The most convincing evidence yet offered (Braun, 1928a) that points to early occupancy of the Adams county prairie area is floristic. Certain species, southern and western, are confined to the region, in Ohio, south of the glacial border: Ophioglossum Engelmanni, Agave virginica, Leavenworthia uniflora, Hexactris spicata, Galacta volubilis,
and Draba cuneifolia. Other typical species are known in but one station north of the boundary in Ohio, and sometimes more in Indiana: Salvia lyrata, Lobelia leptostachys A. Dc., and Muhlenbergia cuspidata.

The geologic placement of any early Pleistocene westward movement of the prairie is pure conjecture. The Toronto beds, according to Flint (1947), are of Sangamon age. Shimel (1948) after a thorough examination of the published evidence states that the beds show a "period of moderate climate similar to that of the present [in Iowa] ...". Lane's study (1941) of Aftonian pollen in an Iowa deposit indicates a climate about as warm and dry as at present. Deevey (1949) has pointed out the need for stratigraphic study of known deposits, which themselves are too few. The post glacial chronology developed from peat sampling now has an extensive literature mostly concerned with post-Pleistocene vegetation movement, these primarily within the area of glaciation. The use of the Carolina bays (see Frey, 1953) may do much toward completing knowledge of forest sequence on the Coastal Plain. In the central deciduous forest, however, with its local relict communities, a concrete method of attacking problems of climatic shifts and their consequences are lacking.

The evidence presented in the preceding sections is suggestive of a slight although rather consistent differentiation physiologically and morphologically between popu-
lations of Big and Little Bluestem from Adams county and Marion prairie areas. This variation might have arisen as a result of ecotypic differentiation or drift of an isolated population.

Ecotypic differentiation could have arisen, especially to the south, on the thin soil prairies of Adams county; either in comparatively recent times or during occupation of the land surface throughout parts of the Pleistocene.

Genetic drift, the random variation of gene frequencies especially prominent in small populations (Wright from Dobzhansky, 1951), may have occurred since the Xerothermic Period, in as much as there are but few prairies on the Illinoian till (emphasized by Braun, 1935) between the main prairie areas of Ohio and those of Adams county. If these prairies have existed during much of the Pleistocene their isolation was indeed extreme during the period that proglacial Lake Tights covered much of the landscape. That the interval was great is evidenced by the 80 feet of silts deposited on the old lake floor (see Wolfe, 1942).

It is more likely that these two types of variation have occurred simultaneously in parts of the areas studied.

That the two samples figured might be part of a latitudinal pattern of a clinal nature is not suggested here. Examination of materials from glaciated and unglaciated Ohio and from the prairie center, as indicated in figures 30 through 35, and 62 through 68, reveals that the populations bear no consistent relation to one another. For
example, in figure 65, the sample from glaciated Ohio is offset toward the larger size classes compared to the sample from south of the glacial boundary. The prairie center samples are nearly superposed.

The results of the germination tests on Big Bluestem does not suggest correlation of grain sources and percent germination with 1) cold treatment, or 2) soil type in which germination and initial growth took place. Little Bluestem however shows a higher percentage germination of northern source grains when subjected to cold treatment. Also, percentage of germination is usually higher in the soil types taken from the same prairie area in which the grains are collected.

Height of Big Bluestem is greater south than north of the glacial border. A hypothesis based on elimination of tall, late-flowering individuals to the north and their persistence south cannot be used in lieu of the data presented for Little Bluestem. In the latter species, the average height of the two populations at flowering are nearly identical.

No differentiation has taken place in the time of flowering in Big Bluestem. The differential flowering dates of Little Bluestem are not born out by field observations, and the cause cannot be explained without use of more precise experimental techniques.

The evidence from the examination of chromosomes in meiosis reveals no difference in chromosome number or
behavior in two populations of either species. Too few counts in Big Bluestem are available to ascertain its chromosome number over its entire range. All of the published records are of 30 pairs excepting Church's tetraploid strain reported for Anderson county, Kansas. Its distribution is not known.

The "splitting" perpetrated upon Little Bluestem is, as has been stated, ample evidence of its variability and was at an early date overdone. It was Hubbard (1917) who reduced the varieties to three but in so doing suggested variety villosissimus as the typical. This view has been followed by Fernald (1935), and Gleason (1952). In 1923 Gleason stated that, among others, both Big and Little Bluestem are of eastern origin. Neither, the cytological work of Church (1936, 1940), and Nielson (1939), nor morphological studies point conclusively to an eastern origin of the species. Larsen (1947) suggests "low latitude" origin for Little Bluestem and two routes of migration north, "through the central grassland region and up the Atlantic Coastal Plain".

The slight morphological differences between the two samples of Ohio material of Big and Little Bluestem suggest simple random variations in gene frequency. This variation is particularly evident in the former in such characters as: pedicel length (figure 19), stem length (figure 21), length of the rachis (figure 31), length of the glabrous base of the rachis (figure 32), and bearding at the base
of the rachis (figure 34). Pedicel bearding (figure 15), on the other hand, shows virtually no differentiation.

Well differentiated characters in Little Bluestem, shown by figures 45, 46, 50, 53, 54, and 56 through 61, contrast sharply with the virtual lack of difference in degree of pedicel bearding (figure 47), length of the rachis (figure 48), and length of the glabrous base of the rachis (figure 55).

A comparison of figures 30 through 35 reveals, in Big Bluestem, that in half of the sets of measurements (figures 31, 33, and 35) the Ohio-Prairie center samples from north of the glacial border are more nearly alike than south of the boundary from both areas. In the rest, figures 30, 32, and 34, the two populations from south of the glacial border are more closely related than those to the north. This phenomenon suggests a closer relationship between glaciated Ohio-prairie center plants and unglaciated Ohio-prairie center plants than Ohio glaciated-prairie center unglaciated and visa versa.

Examination of figures 62, 63, 65, 66, and 68 of Little Bluestem reveals that, in all instances the Ohio-prairie center populations from north of the glacial border are more alike than the Ohio-prairie center populations to the south. This fact, when coupled with seeming ecotypic development of the Ohio Little Bluestem previously discussed, is suggestive of a greater "opportunity" for
evolutionary divergence on the Ohio prairie area south of the glacial border. Whether the opportunity was in the form of "isolation", or due to influx of new genetic material during a climatic shift is not in evidence. Such problems, related to the ones mentioned on page 57, await further investigation.
SUMMARY

The interpretation of relict vegetation in time and space is one of the most difficult problems in ecological plant geography. In Ohio, one of the most prominent and well known communities is the prairie. This study is concerned with infraspecific variation in two dominant species of grasses, Big and Little Bluestem, from contrasting Ohio prairie areas. One sampling area is the Marion prairies on deep soils of glaciated north-central Ohio; the other is the Adams county prairie area characterized by shallow soils in southern Ohio south of the Illinoian glacial border.

Four methods have been used in this study. They are 1) determination of chromosome number and behavior, 2) comparison of results of grain germination in the two species from both areas, 3) measurement of stem elongation after growth was resumed by plants removed from the botanic garden to the greenhouse, and 4) morphological comparisons. In the last, population samples from both areas are compared with each other and with herbarium specimens collected on both sides of the glacial boundary in the prairie center. Comparisons are also made between sod transplants from both Ohio prairie areas which grew together in a common greenhouse environment.

Chromosomes numbers (found) are those commonly reported
for the species. They are: $2n = 60$ in Big Bluestem, and $2n = 40$ in Little Bluestem. All chromosome pairs appeared to behave as diploids.

Results from the planting of over 20,000 spikelets reveal, generally, that in both species the real germination percentage is higher when grains are subjected to 30 to 50 days at $10^\circ C$ than with either more or less cold treatment. In Big Bluestem virtually no difference, according to source, in real germination percentage exists. Embryos of Little Bluestem from south of the glacial border germinate less well with cold treatment than those to the north. Also in contrast to Big Bluestem, the other species exhibits a higher percentage germination when planted in soil from the same prairie area from which the grain was collected.

Data from the measurement of stem elongation, which continued until flowering occurred, reveal that Big Bluestem from the south flowers at a slightly greater height than the same species from the north. Flowering occurred at about the same time. The two strains of Little Bluestem flowered at the same height but those from the south flowered 28 days later than their northern counterpart. A differential temperature regime at the time of floral initiation may be responsible for the wide variance in flowering date in this species.

Results from the measurement of many morphological
characters in Big Bluestem reveal that in the Adams county populations:

1. Stems are somewhat longer.
2. There are more nodes per plant.
3. There are a few more racemes per plant.
4. The rachis is usually shorter.
5. The longest trichome of the rachis is usually longer.
6. The pedicelled spikelet is slightly shorter.
7. The pedicel is somewhat shorter.
8. The longest trichome at the base of the second glume is somewhat longer.

In the Adams County Little Bluestem population:
1. The number of nodes per stem is greater.
2. There are generally fewer racemes per plant.
3. The number of fertile spikelets per terminal raceme is greater.
4. The longest trichomes at the base of the rachis and second glume are shorter.
5. The rachis and its longest trichome are usually shorter.
6. The sterile spikelet is usually shorter.
7. The pedicel is shorter although its glabrous base is longer.
8. The pedicel bearding is generally less dense.
9. The longest trichome of the pedicel is somewhat shorter.
10. The glumes are generally shorter.

These slight morphological differences between the two samples of Ohio Big and Little Bluestem suggest random variation in gene frequency.

Where comparisons are available between Big Bluestem from Ohio and material from the prairie center it is noted that in almost half the sets of measurements the Ohio-prairie center glaciated populations are more nearly alike than the unglaciated from both areas. In the rest, the two populations from south of the glacial boundary are more closely related than those to the north. This phenomenon suggests a closer relationship between the northern Ohio-prairie center plants and southern Ohio-prairie center plants than between the plants from north of the glacial boundary in Ohio and south on the prairie center and visa versa.

Data derived from measurements on Little Bluestem suggest a closer relationship between the Ohio-prairie center plants from north of the glacial boundary than between those from the same regions south of the boundary. This fact, when coupled with seeming ecotypic development of the Ohio Little Bluestem, previously discussed, is suggestive of a greater "opportunity" for evolutionary divergence on the Ohio prairie area south of the glacial border. Whether the opportunity was in the form of "isolation", or due to influx of new genetic material during a climatic
shift is not in evidence. Such problems await further investigation.
Figure 15. In this and other figures the first letter of a pair refers to source of the specimen: from a northern glaciated area, G; or an unglaciated region, U. Of the second letters, G = greenhouse collected; F = collected in the field (Ohio); and P = prairie center e.g. in figure 30. Here size class percentages are plotted for the longest trichome of the pedicel (in mm.). Field and greenhouse samples appear together in figures 15 through 23.

Figure 16. Size class percentages are plotted for the length of the pedicelled spikelet (in mm.).

Figure 17. Size class percentages are plotted for number of racemes.
Figure 18. Size class percentages are plotted for the length of longest branch of the terminal raceme (in cm.).

Figure 19. Size class percentages are plotted for the length of the pedicel (in mm.).
Figure 20. Size class percentages are plotted for the length of the glabrous base of the pedicel (in mm.).

Figure 21. Size class percentages are plotted for stem length to the uppermost inflorescence (in cm.).
Figure 22. Size class percentages are plotted for number of nodes on the stem.

Figure 23. Size class percentages are plotted for the pedicel ratio.
Figure 22

Number of nodes

Figure 23

Ratio: length glabrous base/length pedicel
Figure 24. Shown in figures 24 through 29 are populations from greenhouse samples only. Size class percentages of the length of the longest trichome of the rachis (in mm.) are shown here.

Figure 25. Size class percentages are plotted for the length of the longest trichome of the bearding at the base of the second glume (in mm.).
Figure 26. Size class percentages are plotted for length of the rachis (in mm.).

Figure 27. Size class percentages are plotted for length of the longest trichome at the base of the rachis (in mm.).
Figure 26

% of sample

10
20
30
40

Length of rachis

1.9-26 27-34 35-42 43-50 51-58 59-66 67-74 75-82

A. Gerardi

Figure 27

Bearding at base of rachis

% of sample

6.8 9.1 12.1 15-17 18-20 21-23 24-26 27-29 30-32

A. Gerardi
Figure 28. Size class percentages for the length of the glabrous base of the rachis (in mm.) are plotted.

Figure 29. Size class percentages are plotted for the rachis ratio
Figure 28

Rachis, length of glabrous base

Figure 29

Ratio: length glabrous base / length rachis
Figure 30. In this and those through number 35 Ohio field samples are plotted with those collected in the prairie center. Size class percentages are plotted for the length (in mm.) of the longest trichome at the base of the second glume.

Figure 31. Size class percentages are plotted for the length of the rachis (in mm.).
Figure 32. Size class percentages are plotted for the length of the glabrous base of the rachis (in mm.).

Figure 33. Size class percentages are plotted for the length of the longest trichome of the rachis (in mm.).
Figure 32

A. Gerardi

% of sample

Rachis, length of glabrous base

Figure 33

A. Gerardi

% of sample

Rachis, longest trichome
Figure 34. Size class percentages are plotted for the length of the longest trichome at the base of the rachis (in mm.).

Figure 35. Size class percentages are plotted for the rachis ratio.
Figure 34

Bearding at base of rachis

Figure 35

Ratio: length glabrous base / length rachis
Figure 36. This figure and those through number 43 are scatter diagrams. X's are population averages from samples collected from greenhouse plants originally collected south of the glacial border. O's are originally from the Marion prairie area. Here number of nodes is plotted against length to uppermost inflorescence (in cm.).

Figure 37. Number of inflorescences is plotted against length of the longest branch of the terminal raceme (in cm.).
Figure 36 Length to upper inflorescence

Figure 37 Length of terminal raceme branch
Figure 38. Number of inflorescences is plotted against number of nodes.

Figure 39. The length of the glabrous base of the pedicel is plotted against the length of the pedicel (both in mm.).
Figure 39

Pedicel, length of glabrous base

Number of inflorescences

Number of nodes

A. Geraldii

GL

Ug/l
Figure 40. The length of the longest trichome at the base of the second glume is plotted against that at the base of the rachis (both in mm.).

Figure 41. The length of the rachis is plotted against the length of the glabrous base of the rachis (both in mm.).
Figure 42. The length of the glabrous base of the pedicel is plotted against the length of the glabrous base of the rachis (both in mm.).

Figure 43. The longest trichome of the bearding at the base of the rachis is plotted against the longest trichome of the rachis (both in mm.).
Figure 44. Field and greenhouse samples are plotted together in figure 44 through 54. Here size class percentages for stem length (in cm.) are plotted.

Figure 45. Size class percentages are plotted for number of fertile spikelets of the terminal raceme.
Figure 46. Size class percentages are plotted for pedicel length (in mm.).

Figure 47. Size class percentages are plotted for density of pedicel bearding.
A. scoparius

Figure 46  Pedicel length

Figure 47  Degree of pedicel bearding
Figure 48. Size class percentages are plotted for length of the rachis (in mm.).

Figure 49. Size class percentages are plotted for density of rachis bearding.
Figure 50. Size class percentages are plotted for number of nodes on the stem.

Figure 51. Size class percentages are plotted for number of racemes per plant.
Figure 50  Number of nodes

Figure 51  Number of racemes
Figure 52. Size class percentages are plotted for the rachis ratio.

Figure 53. Size class percentages are plotted for the length of the sterile spikelet (in mm.).
Figure 52

Ratio: length glabrous base / length rachis

Figure 53

Sterile spikelet, length
Figure 54. Size class percentages are plotted for the pedicel ratio.

Figure 55. Figure 55 through 61 are plotted for greenhouse samples only. Here size class percentages are plotted for length (in mm.) of the glabrous base of the rachis.
Figure 54

A. scoparius

Ratio: length glabrous base / length pedicel

Figure 55

A. scoparius

Rachis, length of glabrous base
Figure 56. Size class percentages are plotted for first glume length (in mm.).

Figure 57. Size class percentages are plotted for the length (in mm.) of the longest trichome at the base of the rachis.
Figure 56  Length of glume

Figure 67  Base of rachis, longest trichome
Figure 58. Size class percentages are plotted for the length (in mm.) of the longest trichome at the base of the second glume.

Figure 59. Size class percentages are plotted for the length of the longest trichome of the rachis (in mm.).
Figure 68 Bearding, base of second glume

Figure 69 Longest trichome of rachis
Figure 60. Size class percentages for the length (in mm.) of the glabrous base of the pedicel.

Figure 61. Size class percentages for the length (in mm.) of the longest trichome of the pedicel.
Figure 60 Pedicel, length of glabrous base

Figure 61 Pedicel bearding, longest trichome
Figure 62. Figure 62 through 68 are of Ohio field population samples and prairie-center samples. Here glume length (in mm.) is given as size class percentages.

Figure 63. Size class percentages are plotted for the length of the longest trichome at the base of the rachis (in mm.).
Figure 62  Length of glume

Figure 63  Base of rachis, longest trichome
Figure 64. Size class percentages are plotted for length of the longest trichome at the base of the second glume (in mm.).

Figure 65. Size class percentages are plotted for the length (in mm.) of the longest trichome of the rachis.
A. scoparius

Figure 64  Bearding, base of second glume

Figure 65  Longest trichome of rachis
Figure 66. Size class percentages are plotted for length (in mm.) of the glabrous base of the pedicel.

Figure 67. Size class percentages are plotted for the length (in mm.) of the longest trichome of the pedicel.
Figure 66  Pedicel, length of glabrous base

Figure 67  Pedicel bearding, longest trichome
Figure 68. Size class percentages are plotted for length (in mm.) of the glabrous base of the rachis.

Figure 69. The remainder of the figures are scatter diagrams plotted as were numbers 36 through 43. Here length of the rachis is plotted against length of the longest trichome of the rachis (both in mm.).
Figure 68: Rachis, length of glabrous base

Figure 69: Longest trichome of rachis
Figure 70. Stem length (in cm.) is plotted against glume length, (in mm.).

Figure 71. Length of the longest trichome of the pedicel is plotted against that of the rachis (both in mm.).
Figure 70

A. scoparius

Length of stem

Ungl.

Gl.

Length of glume

Figure 71

Pedicel, longest trichome

Rachis, longest trichome

A. scoparius

Ungl.

Gl.
Figure 72. The length of the longest trichome at the base of the rachis is plotted against glume length (both in mm.).

Figure 73. The density of rachis bearding is plotted against the length of the longest trichome of the rachis (in mm.).
Figure 74. The length of the glabrous base of the rachis is plotted against the length of the longest trichome of the rachis (both in mm.).

Figure 75. The number of racemes is plotted against number of nodes.
**Figure 74** Longest trichome of rachis

**Figure 75** Number of nodes
Figure 76. Stem length (in cm.) is plotted against number of nodes.

Figure 77. Number of racemes is plotted against number of spikelets per raceme.
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