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VARIATION AND RELATIONSHIPS IN SOME RHIZOMATOUS SPECIES OF MUHLENBERGIA.

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VARIATION AND RELATIONSHIPS IN SOME RHIZOMATOUS SPECIES OF MUHLENBERGIA

by

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

Major Subject: Plant Taxonomy

Approved:

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In Charge of Major Work

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Head of Major Department

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Dean of Graduate College

Iowa State University Of Science and Technology Ames, Iowa

1962
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INTRODUCTION

General Statement of Problem

The broad-leaved rhizomatous members of the genus Muhlenbergia form a fairly well delineated group which is associated, principally, with the forested regions of eastern North America. The group also is represented across central North America and in the Rocky Mountains. Two of its members, M. glomerata (Willd.) Trin. and M. racemosa (Michx.) B. S. P., have been considered as a single species by a number of authors (e.g., Deam, 1940; Davis, 1952; Gleason, 1952). But Fernald (1943) recommended maintaining them as separate species, a disposition followed by Hitchcock (1950).

The present investigation was undertaken to clarify the taxonomic status of the two above-mentioned species and, secondarily, certain other representatives of the group. An extensive study of variation in the subject taxa was proposed with emphasis on experimental methods employing a transplant garden.

Experimental Background

Investigations in variation have enriched our knowledge of the nature of species since the work of Turesson (1922a, 1922b) promoted interest in biosystematic studies utilizing the uniform garden. The present study owes a great deal to
the classical studies of Clausen, Keck, and Hiesey (1940, 1945, 1948) with transplant gardens maintained at Stanford and in the Sierra Nevada Mountains of California. Lawrence (1945) utilized the same gardens for work on ecotypic relations in *Deschampsia caespitosa* (L.) Beauv.

The uniform garden was employed in this study primarily for plants growing across the Great Plains and central prairies. Investigations have been conducted on a number of grass species of the Great Plains to determine their adjustments to its wide range of environmental conditions. Most of these studies have been from a physiological or ecological-range management point of view for plants collected on a north-to-south gradient.

Flowering time as correlated with forage production was studied by Riegel (1940) for *Bouteloua gracilis* (H. B. K.) Lag. ex Steud. and by Cornelius (1947) for *Andropogon scoparius* Michx. Responses of different geographic strains to photoperiod was studied by Olmsted (1943, 1945) for *Bouteloua* and by Larsen (1947) for *Andropogon scoparius*. Rogler (1943) investigated responses to low temperatures in *Bouteloua*, *Andropogon*, and *Panicum*. McMillan (1956a, 1956b, 1957, 1959, 1961) employed the uniform garden to study the effect of ecotypic variation on the nature of grassland communities in the Great Plains. The present author has not found that any study employing the uniform garden has been conducted on a Great
Plains species from a taxonomic point of view.

Other studies on variation that relied wholly on field and herbarium collections were those of Woodson (1947) for *Asclepias tuberosa* L., Desmarais (1952) for *Acer saccharum* Marsh. and related taxa, and Fassett (1941) for *Rubus odoratus* L. and *R. parviflorus* Nutt.

The only experimental work found for any of the species considered in this study was that of Allard and Evans (1941) on photoperiod responses of *M. frondosa* (Poir.) Fern.
METHODS AND MATERIALS

All microscopic measurements of specimens were conducted with a stereoscopic binocular microscope fitted with an ocular micrometer measuring to 0.1 millimeter. Measurements of stomates and pollen grains were made with a compound microscope fitted with an ocular micrometer. All microscopic drawings were performed with the aid of a camera lucida.

Measurements for length of palea were taken from the base of the floret to the tip of the palea. Palea length was used instead of lemma length because it was less variable and offered no problem with respect to awn tips. Measurements were taken on a number of different florets throughout the inflorescence and a median length derived. Inflorescence length was taken from the attachment of the lowest panicle branch to the tip of the inflorescence. Length of culms was taken only for that portion of the plant judged to be above ground level. The widest of the basal internodes above ground level was used for the measurement of culm width. The measurement was made in the central region of the internode.

Measurements of stomates were made on an upper leaf of the plant after first removing the chlorophyll and clearing in a solution of sodium hypochlorite. Leaf scrapes were found to be unsatisfactory for these species. Pollen stainability was tested by means of a lactophenol-aniline blue solution (Sass, 1951).
Chromosome counts were made from propio-carmine squashes and the slides made permanent by carbon dioxide freezing. The living material was killed and fixed in 3:1, absolute alcohol-glacial acetic acid. Voucher specimens were deposited in the Iowa State University Herbarium for all recorded chromosome counts.

Study of herbarium material was supplemented by that of a large number of population samples collected from the field. Where possible, random type mass collections were taken, but often the populations or colonies were so small as to warrant taking only a few specimens. Presses of double length with specially cut blotters and print paper were used for the collecting and drying of specimens. In this way most specimens could be collected without bending.

Collections for transplanting were made on a rough transect extending approximately 1,150 miles from northern Minnesota to northeastern New Mexico. Other field trips were taken through Wisconsin, Michigan, Illinois, Indiana, Ohio, Pennsylvania, New York, Vermont, New Hampshire, Maine, and through portions of Ontario, Quebec, and New Brunswick.

Rhizomes were successfully transported for about two weeks by placing them in plastic bags with damp sphagnum and storing the bags in a container with ice. All collections for the experimental garden were made in the summer of 1961. The rhizomes were planted in six-inch pots with a standard
greenhouse soil mixture. The bottoms were left open on those pots that were buried in the experimental garden. The transplant garden was fully exposed on a relatively level plot of ground consisting of a heavy loam soil.

All specimens of *M. racemosa* collected from the uniform garden in the summer of 1962 grew from rhizomes that had lain dormant in the experimental garden through the winter of 1961-1962. Although the specimens came from as far south as New Mexico, no loss was noted due to winter-kill.
TAXONOMIC CONSIDERATIONS

Generic Considerations

Although this paper is not intended as a monographic or revisionary treatment, some taxonomic considerations are in order. Hitchcock (1950, p. 369) describes the genus *Muhlenbergia* Schreb. as follows:

Spikelets 1-flowered (occasionally 2-flowered), the rachilla disarticulating above the glumes; glumes usually shorter than the lemma, sometimes as long, obtuse to acuminate or awned, keeled or convex on the back, the first sometimes small, rarely obsolete; lemma firm-membranaceous, 3-nerved (the nerves sometimes obscure or rarely an obscure additional pair), with a very short callus, rarely long-pilose, usually minutely pilose, the apex acute, awned from the tip or just below it, or from between very short lobes, sometimes only moderately tall or rarely robust grasses, tufted or rhizomatous, the culms simple or much-branched, the inflorescence a narrow (sometimes spikelike) or open panicle. Type species, *Muhlenbergia schreberi*. Named for G. H. E. Muhlenberg.

Hitchcock lists 70 species in the genus *Muhlenbergia*, the majority of them being perennials. Twenty-four species are described as rhizomatous perennials, a group that can be further divided into narrow-leaved and broad-leaved plants. The present study is concerned with six of the eleven members included in the broad-leaved rhizomatous group.

Distribution of the genus

Bews (1929) places the main center of development for the genus in southwestern United States and Mexico. Kearney, *et. al.* (1960) credit *Muhlenbergia* with being the largest
genus of grasses in Arizona. The tufted perennials, annuals, and narrow-leaved rhizomatous members are represented, principally, in the southwestern region with some extensions in the northern Rocky Mountain and midwestern regions. But the broad-leaved rhizomatous members demonstrate, as a group, a significant divergence, not only in their growth habit but also in their adaptation to the more cool and moist regions of North America. Their association with the hardwood and evergreen forests of the East and North and their occurrence in eastern Asia suggest a development concurring with that of the Arcto-Tertiary Flora of North America (Li, 1952).

The genus is restricted almost entirely to the Western Hemisphere with only a few species, mostly broad-leaved rhizomatous members, reported as being native in Japan and parts of southeastern Asia. As far as is known the species included in this study are restricted to North America.

Phylogenetic considerations

Since the genus Muhlenbergia is comprised of plants with laterally compressed spikelets having two glumes and a single fertile floret, it has been placed in the highly artificial tribe Agrostideae. Bews (1929) thought that it demonstrated affinities, in its ecological attributes and the texture of its lemmas, with Stipa and Aristida. More recent phylogenetic studies indicate much closer affinities with other genera.

Reeder (1957) found that the Muhlenbergia embryo has two
features characteristic of the Panicoid embryo and two of the Festucoid embryo. The Panicoid characteristics are the presence of an internodal region between the scutellar node and the coleoptile node in the embryo axis and the presence of a cleft between the lower scutellum and the coleorhiza. The Festucoid features are the presence of an epiblast and the nature of the first leaf (with only a few vascular bundles and the edges not overlapping). This particular combination of features, in correlation with other characters, is diagnostic of a group of grasses that has come to be known as the Chloridoid-Eragrostoid group.

Prat (1936) found leaf epidermal characteristics of Muhlenbergia to be Chloridoid in nature. Epidermises of M. glomerata and M. racemosa studied by the author demonstrated the Chloridoid relationship in having short siliceous cells shaped like double-bitted axe heads, bicellular inflated hairs, and characteristically shaped prickles (Plate 1, a and b). The two lodicules also are Chloridoid in shape (Plate 1, f).

Brown (1958) placed Muhlenbergia in the Chloridoid group on the basis of his work in leaf anatomy. The most extensive work on internal leaf anatomy of Muhlenbergia was conducted by Schwabe (1948), primarily on species occurring in Argentina. She placed the genus in Type I of Avdulov (1931) characteristic of the subfamily Sacchariferae. She stated
that it had features in common with *Eragrostis* and different from the Agrostideae in general. Anatomical studies conducted by the author on *M. racemosa* (Plate 1, d) showed that the larger vascular bundles have a complete inner sheath of sclerenchymatous cells and a partial outer sheath of thick-walled parenchyma cells, these containing specialized chloroplasts for starch storage. The chlorophyllous parenchyma outside of the starch sheath shows a tendency for radial arrangement of the cells, which is not nearly so pronounced as in the diagrammatic figures of Schwabe. Stomates are present on both surfaces of the leaf but are much more abundant on the abaxial surface. Bulliform cells are located in the furrows of the adaxial side. No colorless parenchyma cells were observed beneath the bulliform cells, as reported by Schwabe for other members of the genus. A summary of anatomical work performed on the genus to date can be found in Metcalfe (1960).

The seedling (Plate 1, c) is of the Festucoid type with a long, linear, first leaf that is almost fully developed before the appearance of the second leaf. Root hair development conforms to the characteristics of the Panicoid and Chloridoid-Eragrostoid groups, as defined by Reeder and von Maltzahn (1953) and Row and Reeder (1957). The epidermal cells in the root hair zone are all alike in size, and the root hair diverges more or less at a right angle to the axis.
of the root. The point of origin of the root hair is intermediate between the Panicoid and Festucoid types in that it is between the middle and apical portions of the cell (Plate 1, e).

Cytological evidence points to an affinity with the Panicoid and Chloridooid lines of development. The chromosomes are small and, according to extensive cytological work performed in this laboratory, with a base number of 10. Base numbers of 21 (Ono and Tateoka, 1953; Nielson and Humphrey, 1937; Bowden, 1960) and nine (Stebbins, 1947) also have been reported for Muhlenbergia.

The genus has been variously placed by workers who have attempted to reclassify the Gramineae. Prat (1936) designated a subgroup Chloridoideae within the subfamily Panicoideae to include Muhlenbergia and Sporobolus along with the tribes Chlorideae, Eragrosteae, and Zoysieae. Pilger (1954) placed Muhlenbergia in the subtribe Muhlenbergiinae of the tribe Eragrosteae within the subfamily Eragrostoideae.

Hubbard (1959) maintained Muhlenbergia in the Agrosteae, which he stated to be still a heterogeneous tribe after segregating some subtribes. Stebbins and Crampton (1960) have suggested a new system of classification for the Gramineae wherein Muhlenbergia has been placed in the tribe Eragrosteae of the subfamily Eragrostoideae. In a recent manual of grasses of India and neighboring countries, Bor (1960)
Plate 1. Leaf epidermis, seedling, leaf anatomy, root hairs, and lodicules of *Muhlenbergia*

a. Abaxial leaf surface of *M. glomerata*
   
   pa. -- papilla  
   s.c. -- siliceous cell  
   pr. -- prickle  
   b.h. -- bicellular hair

b. Abaxial leaf surface of *M. racemosa*

c. Seedling of *M. racemosa*

d. Leaf anatomy of *M. racemosa*
   
   e. sh. -- endodermal sheath  
   s. sh. -- starch sheath  
   b. c. -- bulliform cells

e. Root hairs and epidermal cells of *M. racemosa*

f. Lodicles of *M. racemosa*
Species Considerations

Differentiation of M. glomerata and M. racemosa

The most intensive work of this study was performed on M. glomerata and M. racemosa. Authors have differed in their interpretation of these taxa. A preliminary investigation was conducted into the validity of their separation into distinct species, as advocated by Fernald (1943, 1950) and Hitchcock (1950).

Morphological evidence Table 1 presents the principal differentiae that Fernald used to delimit the two:

Table 1. Morphological characteristics by which Fernald (1950) delimited M. glomerata and M. racemosa

<table>
<thead>
<tr>
<th>Structure</th>
<th>M. glomerata</th>
<th>M. racemosa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Culms:</td>
<td>generally simple with internodes and nodes puberulent</td>
<td>mostly branching from the middle nodes with internodes glabrous</td>
</tr>
<tr>
<td>Leaves:</td>
<td>sheath scarcely keeled</td>
<td>sheath keeled</td>
</tr>
<tr>
<td>Ligules:</td>
<td>minute</td>
<td>prolonged, 3-5 mm long</td>
</tr>
<tr>
<td>Anthers:</td>
<td>1.0-1.5 mm long</td>
<td>0.5-0.8 mm long</td>
</tr>
<tr>
<td>Grain:</td>
<td>oblong-cylindric, 1.2-1.5 mm long</td>
<td>linear-cylindric, 1.8-2.2 mm long</td>
</tr>
</tbody>
</table>

Observations by the author on about 1,800 specimens showed that they could be separated into two groups on the
basis of the characteristics named in Table 1. However, the author would modify some of the measurements, as detailed in the descriptions to be presented below. An additional character found to be excellent for differentiating between the two was that of hairiness on the floret. In *M. glomerata* short hairs originate from the base of the floret and also along the two edges of the lemma. In *M. racemosa* hairs originate from the base of the floret, and sometimes from the palea, but not along the edges of the lemma (Plate 2).

**Ecological evidence** *M. glomerata* generally occurs in boggy habitats in the North. *M. racemosa* extends across the Great Plains and into the Rocky Mountains in a variety of moist and upland habitats.

**Cytological evidence** Avdulov (1931) reported a chromosome number of 2n=40 for *M. racemosa*. Extensive cytological studies performed in this laboratory have confirmed Avdulov with respect to individuals of *M. racemosa*. However, individuals of *M. glomerata* provided counts of 2n=20, plus other counts ranging, approximately, from 22-28 (Plate 4).

**Anatomical evidence** Epidermal studies showed that individuals of *M. glomerata* have a greater density of prickles and much more pronounced papillae than individuals of *M. racemosa* (Plate 1, a and b). Also, cell sizes were smaller in individuals of *M. glomerata*. Stomate lengths averaged 17.6 microns vs. 19.2 microns, and pollen grains averaged
Conclusions and descriptions

The conclusion appears obvious that the two are validly considered separate species. Combinations of morphological characters can be used with consistency to differentiate between the two. Cytologically *M. racemosa* is a tetraploid and *M. glomerata* a diploid, a condition further substantiated by a comparison of cell sizes. (The aneuploid counts will be considered in some detail in a later section.) Following are descriptions of the two species incorporating measurements and observations made by the author. The measurements do not include some of the extremes found to occur in the uniform garden.

*M. glomerata* (Willd.) Trin. Perennial from creeping rhizomes with prominent leaf scales crowded to overlapping; culms stiffly erect, 0.6-1.8 mm thick, 30-120 cm tall, generally simple, occasionally branching, with internodes more or less densely and finely puberulent; nodes 5-12 (-17), scattered to crowded; blades flat, the longer ones 2-6 mm broad, 6-15 cm long; ligule generally 0.5 mm or less long, occasionally up to 0.6 mm, ciliate; panicle narrow, lobed, branches densely flowered and crowded except at the base, green to purple, 0.3-1.5 cm thick, 2.0-11.0 cm long; spikelets 3.2-8.0 mm long; glumes subequal, awned, generally at least once-and-one-third to over twice as long as the lemma;
body of lemma 2.3-3.9 mm long, only occasionally awn-tipped; hairs no longer than half the length of the lemma originating from the base of the floret and along the edges of the lemma throughout most of its length; anthers 0.8-1.5 mm long; caryopses oval to cylindrical, 1.0-1.6 mm long. (See Plate 2.)

*M. racemosa* (Michx.) B. S. P. Perennial from creeping rhizomes with prominent, overlapping scales; culms ascending to erect, 0.8-3.0 mm thick, 25-135 cm tall, branching, with internodes glabrous to generally moderately puberulent toward the summit; nodes 5-32, scattered to crowded; blades flat, the longer ones 2-6.5 mm wide, 6-18 cm long; ligule 0.7-1.5 mm long, lacerate; panicle narrow, branches densely flowered and crowded except at the base, green to purplish, 0.3-1.8 cm thick, 4.0-17.5 cm long; spikelets 3.6-7.0 mm long; glumes subequal, awned, at least once-and-one-third to over twice as long as the lemma; body of lemma 2.2-4.5 mm long, occasionally awn-tipped, rarely long awned; hairs no longer than half the length of the lemma originating from the base of the floret and sometimes from the middle of the palea; anthers 0.5-0.9 mm long; caryopses cylindrical, 1.4-2.3 mm long. (See Plate 2.)

Other species involved in study

Other species of the broad-leaved rhizomatous group involved in this study were *M. mexicana* (L.) Trin., *M. frondosa*
Plate 2. Spikelets of *M. racemosa* and *M. glomerata*

a. *M. racemosa*
b. *M. racemosa*
c. *M. glomerata*
(Poir.) Fern., M. brachyphylla Bush, and M. andina (Nutt.) Hitchc. The author accepts, essentially, the delimitation of these species as set forth in Hitchcock (1950) and Fernald (1950). The following descriptive key, incorporating some observations not mentioned in the above references, will serve to distinguish between the species included here. It is hoped that the future discussions of variation will further clarify relationships between these species.

1. Pubescence of floret silky, the hairs equalling or exceeding the floret; glumes awnless, 2.4-4.5 mm long; lemma long awned; anthers generally 0.6-1.0 mm long; leaf sheath and culm finely and densely puberulent at the nodes ................. M. andina (Plate 3)

1. Pubescence of floret usually of hairs less than half the length of the floret ................. 2

2. Glumes awned, both at least one-third longer than the body of the floret; anthers longer than 0.5 mm ................. 3

2. Glumes awnless or awn-tipped, generally shorter than the body of the floret, occasionally longer; anthers generally not over 0.5 mm long ................. 4

3. Ligule 0.5 mm or shorter; culm finely and densely puberulent, at least throughout upper half of internode; lemma with hairs from base and along edges throughout most of its length; anthers 0.8-1.5 mm long ................. M. glomerata

3. Ligule over 0.5 mm long; culm slightly to moderately puberulent toward summit of internode, or rarely glabrous; lemma with hairs from basal portion only; anthers 0.5-1.0 mm long ................. M. racemosa

4. Internodes of culm moderately to densely puberulent, at least in upper part; panicle generally well exserted and nodding; ligules, or at least some of them, well over 0.5 mm long (-1.4 mm),
lacerate; glumes awnless to awn-tipped, from slightly shorter to longer than the body of the lemma; lemma from 2.0-3.2 mm long, awnless to long-awned ....... M. mexicana (Plate 3)

4. Internodes of culms glabrous or occasionally very finely puberulent at summit of internode; panicles of lateral inflorescences partly included in sheath, or if exserted, ligules mostly less than 0.6 mm long ............... 5

5. Ligules mostly less than 0.6 mm long; terminal panicle generally well exserted; lateral panicles included to exserted; leaves borne at right angle to stem with leaves of culm generally much broader and longer than leaves of the branches; glumes abruptly narrowed to a point and shorter than the body of the lemma; lemma 2.8-3.4 mm long, long-awned to awn-tipped ................. M. brachyphylla (Plate 3)

5. Ligules mostly more than 0.6 mm long, lacerate; terminal panicle included to exserted; lateral panicles generally partly included; leaves not borne so conspicuously at right angle to stem and without sharp distinction between leaves of main culm and those of branches; glumes tapering to awn tip to somewhat abruptly narrowed, from shorter than to longer than the body of the lemma; lemma 2.5-3.8 mm long, awnless to long-awned ................. M. frondosa (Plate 3)

Chromosomal numbers

Two of the above species, M. glomerata and M. andina, are diploids with 20 somatic chromosomes, while the other four species, M. racemosa, M. mexicana, M. frondosa, and M. brachyphylla, are tetraploids with 40 somatic chromosomes. A summary of chromosomal counts as reported in the literature for these species is presented in Table 2. Meiotic figures are illustrated in Plate 4.
Plate 3. Spikelets of *M. mexicana*, *M. frondosa*, *M. brachyphylla*, and *M. andina*

a. *M. mexicana*

b. *M. frondosa*

c. *M. brachyphylla*

d. *M. andina*
Table 2. Summary of chromosomal numbers reported for species included in present study

<table>
<thead>
<tr>
<th>Species</th>
<th>2n</th>
<th>Reference</th>
</tr>
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<tbody>
<tr>
<td>M. andina</td>
<td>20</td>
<td>Stebbins (1947); Pohl (1962)</td>
</tr>
<tr>
<td>M. brachyphylla</td>
<td>40</td>
<td>Brown (1950); Pohl (1962)</td>
</tr>
<tr>
<td>M. frondosa</td>
<td>40</td>
<td>present author</td>
</tr>
<tr>
<td>M. glomerata</td>
<td>20</td>
<td>present author</td>
</tr>
<tr>
<td></td>
<td>ca. 22-28</td>
<td></td>
</tr>
<tr>
<td>M. mexicana</td>
<td>40</td>
<td>Avdulov (1931)&lt;sup&gt;a&lt;/sup&gt;; present author</td>
</tr>
<tr>
<td>M. racemosa</td>
<td>40</td>
<td>Avdulov (1931); present author</td>
</tr>
</tbody>
</table>

<sup>a</sup>Considering the confusion over the nomenclature of M. mexicana and M. frondosa at the time of Avdulov's count, quite possibly his represents a count on M. frondosa. (See Fernald, 1943.)
Plate 4. Meiotic figures in *Muhlenbergia*

a. *M. racemosa*  
   \[2n=40\]

b. *M. racemosa*  
   \[2n=40\]

c. *M. frondosa*  
   \[2n=40\]

d. *M. mexicana*  
   \[2n=40\]

e. *M. glomerata*  
   \[2n=20\]

f. *M. glomerata*  
   \[2n=20\]

g. *M. glomerata*  
   \[2n=ca. 26-28\]

h. *M. glomerata*  
   \[2n=ca. 23-24\]

i. *M. glomerata*  
   \[2n=ca. 24\]
VARIATION IN M. GLOMERATA

Biology and Ecology

M. glomerata characteristically is one of the later maturing grasses in its native habitats. Flowering and seed set generally occur in late August or September. It seldom occurs in lush, dense stands, the scaly, sparingly branched rhizomes usually producing a more scattered growth. Bagging experiments conducted by the author showed that the species is self fertile.

M. glomerata is distributed mainly in glaciated areas of the continent. In eastern North America it ranges from southern Canada to northern Iowa, Illinois, Indiana, Ohio, and to North Carolina in the Appalachian Mountains. It has been collected in north central Nebraska in the Great Plains and in the Black Hills of southwestern South Dakota. These, in all likelihood, represent relic stands of a more southern distribution of the species during the glacial and early postglacial times. It occurs in scattered locations in the Rocky Mountain regions, having been collected as far south as Utah and Colorado, and in the Cascade regions of Washington and Oregon. (See Plate 12.)

The northern limits of the species are poorly known. It has been collected at Great Slave Lake in the Northwest Territory of Canada, about 400 miles north of the northernmost location on the distributional map, and may extend much
farther north throughout the rest of its range.

The species typically occupies bogs, peaty meadows and shorelines, and similar habitats. It is adapted to acid sphagnous bogs as well as to alkaline fens and marl bogs. A number of collectors have reported its occurrence in crevices and declivities of granite outcrops that benefit from seepage. The author also had occasion to observe it in habitats of this nature. On a field trip through Maine the author found *M. glomerata* only in a very specialized habitat—in the fissures of slate outcrops along rivers. It has been reported from other habitats in that region.

Some collections of *M. glomerata* have been made in habitats that seemingly are much drier than those previously described. A number have been reported from jack pine forests on sandy soil. A few collections were made by the author on upland sites in woods and along roadways.¹

¹Curtis (1959, p. 267) used *M. racemosa* as a moisture indicator species in a graphic illustration of the behavior of some major prairie grasses in Wisconsin. He represented its percentage occurrence, on the basis of presence or absence, as gradually decreasing from forty per cent in the lowland, wet-prairie types to zero per cent in the upland, dry-prairie types. However, since the author used the nomenclature of Gleason (1952), *M. glomerata* was not recognized as an entity distinct from *M. racemosa*. In all likelihood *M. glomerata* accounted for the high percentage of occurrence in the wet-prairie habitats while *M. racemosa* possibly accounted for some of the occurrence registered in the drier prairie habitats.
Ecology of *M. mexicana*

Since *M. mexicana* necessarily will be given some consideration in this treatment of *M. glomerata*, observations on its ecology will be reviewed briefly. *M. mexicana* is sympatric with *M. glomerata* throughout much of its range but extends farther south, both in the eastern half of the United States and in the Rocky Mountains. The two grasses often frequent the same peaty habitats. But *M. mexicana* clearly demonstrates a greater tolerance for drier sites, occurring in abundance along roadways, railways, and the edges of woods, as well as along shorelines of rivers and lakes. In its southern extensions it becomes confined to the more moist habitats.

A sharp distinction was noted in the habitats of the two grasses in their occurrence at Silver Lake fen in northern Iowa. *M. glomerata* occurs in the alkaline bog whereas *M. mexicana* occurs in the marsh around the bog without any overlap being manifest.

Another species receiving some attention in this treatment of *M. glomerata* is *M. andina*. It has been reported in the middle to high elevations of all the western mountain states (Plate 13). Apparently it occurs along water courses and in the cooler canyons.
Variation According to Internodal Pattern

Internodal patterns of the type described by Prat (1934) and Anderson (1944) will be employed for describing variation in *M. glomerata*. Anderson considered the internodal-pattern graph a useful and significant tool in analyzing interspecific and infraspecific differences. He noted that plants "may differ from each other not only in the number of internodes and their absolute dimensions but in the relative sizes of successive internodes and in the pattern of change of relative size."

To represent these differences Anderson recommended the construction of graphs with the internode lengths registered on the ordinate and the ordinal number of nodes on the abscissa. Points representing the respective nodes are placed at heights above the abscissa in accordance with the lengths of the internodes. The points are then connected with a line so as to form an "internodal growth-habit curve" (present author's terminology) which describes the internodal pattern.

Over 300 specimens of *M. glomerata* were graphed according to this procedure. A variety of patterns was obtained, but two tendencies appeared to occur with the greatest consistency. For many the internode lengths tended to increase from the culm base toward the peduncle, or uppermost internode. For a number of others the internodes at the base were relatively long, those through the middle region of the culm.
decreased in length, and the final internodes elongated. (See Plates 5 and 6.)

In the first case the pattern is that of a generally ascending line, and hereafter, this pattern will be referred to as the ascending pattern. In the second case the line descends from the high point of the basal internodes through the middle nodal region until ascending abruptly for the final internodes. This pattern will be referred to as the descending pattern.

Tables 3 and 4 present some statistics on 20 individuals conforming to each internodal pattern. The tables indicate that individuals with the descending pattern, besides having more nodes, generally have a longer inflorescence, greater height, and a wider culm. Some specimens included in each list illustrate the fact that individuals of either pattern may deviate considerably from the means of these measurements.

Interpretation of the Internodal-Pattern Graphs

Figures a-j (Plate 5) represent examples of individuals of _M. glomerata_ demonstrating the ascending internodal pattern. All of these individuals have fewer than nine leaf-bearing nodes and come from the western mountain regions or from the more northern portions of the reported range of the species in eastern North America. Individuals collected from a population growing in a peat meadow in northern Minnesota
Table 3. Morphology of individuals of *M. glomerata* with ascending internodal pattern

<table>
<thead>
<tr>
<th>Approximate Location of Collection</th>
<th>length of infl.</th>
<th>width of culm</th>
<th>no. of nodes*</th>
<th>height</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper Red Lake, Minn.</td>
<td>6.7 mm</td>
<td>1.0 mm</td>
<td>8</td>
<td>51 cm</td>
</tr>
<tr>
<td>Nary, Minn.</td>
<td>3.5</td>
<td>1.0</td>
<td>6</td>
<td>53</td>
</tr>
<tr>
<td>Baudette, Minn.</td>
<td>7.0</td>
<td>0.9</td>
<td>8</td>
<td>57</td>
</tr>
<tr>
<td>Isle Royale, Mich.</td>
<td>5.0</td>
<td>0.8</td>
<td>7</td>
<td>60</td>
</tr>
<tr>
<td>White Mts., N. H.</td>
<td>7.0</td>
<td>1.3</td>
<td>7</td>
<td>45</td>
</tr>
<tr>
<td>Quebec</td>
<td>5.0</td>
<td>1.0</td>
<td>7</td>
<td>51</td>
</tr>
<tr>
<td>Gaspé Peninsula, Que.</td>
<td>5.0</td>
<td>1.0</td>
<td>7</td>
<td>51</td>
</tr>
<tr>
<td>Newfoundland</td>
<td>2.7</td>
<td>0.7</td>
<td>8</td>
<td>37</td>
</tr>
<tr>
<td>Thunder Bay, Ont.</td>
<td>3.5</td>
<td>0.9</td>
<td>6</td>
<td>46</td>
</tr>
<tr>
<td>Murray, Ont.</td>
<td>4.5</td>
<td>1.2</td>
<td>5</td>
<td>55</td>
</tr>
<tr>
<td>Kingston, Ont.</td>
<td>6.0</td>
<td>1.0</td>
<td>6</td>
<td>43</td>
</tr>
<tr>
<td>Bear Hills, Ont.</td>
<td>6.3</td>
<td>1.2</td>
<td>6</td>
<td>63</td>
</tr>
<tr>
<td>Regina Bay, Ont.</td>
<td>7.7</td>
<td>0.8</td>
<td>7</td>
<td>54</td>
</tr>
<tr>
<td>Banff, Alta.</td>
<td>7.5</td>
<td>1.2</td>
<td>6</td>
<td>42</td>
</tr>
<tr>
<td>Cardston, Alta.</td>
<td>6.3</td>
<td>1.0</td>
<td>7</td>
<td>57</td>
</tr>
<tr>
<td>Glacier Park, Mont.</td>
<td>5.5</td>
<td>1.1</td>
<td>7</td>
<td>61</td>
</tr>
<tr>
<td>Kalispell, Mont.</td>
<td>6.7</td>
<td>1.8</td>
<td>7</td>
<td>99</td>
</tr>
<tr>
<td>Holt, Mont.</td>
<td>6.8</td>
<td>0.7</td>
<td>5</td>
<td>62</td>
</tr>
<tr>
<td>Beaverhead Co., Mont.</td>
<td>3.5</td>
<td>0.7</td>
<td>7</td>
<td>37</td>
</tr>
<tr>
<td>Uintah Mts., Utah</td>
<td>3.0</td>
<td>0.8</td>
<td>7</td>
<td>60</td>
</tr>
<tr>
<td>Means</td>
<td>5.5</td>
<td>1.0</td>
<td>6.7</td>
<td>53</td>
</tr>
</tbody>
</table>

*number of leaf-bearing nodes above ground level
Table 4. Morphology of individuals of *M. glomerata* with descending internodal pattern

<table>
<thead>
<tr>
<th>Approximate Location of Collection</th>
<th>length of infl.</th>
<th>width of culm</th>
<th>no. of nodes(^a)</th>
<th>height</th>
</tr>
</thead>
<tbody>
<tr>
<td>Idington, Minn.</td>
<td>7.7 cm</td>
<td>1.1 mm</td>
<td>9</td>
<td>57 cm</td>
</tr>
<tr>
<td>Nary, Minn.</td>
<td>6.0</td>
<td>1.1</td>
<td>10</td>
<td>60</td>
</tr>
<tr>
<td>Lincoln, Minn.</td>
<td>7.5</td>
<td>0.9</td>
<td>9</td>
<td>71</td>
</tr>
<tr>
<td>Indian River, Mich.</td>
<td>8.0</td>
<td>1.1</td>
<td>10</td>
<td>80</td>
</tr>
<tr>
<td>Battlecreek, Mich.</td>
<td>9.0</td>
<td>1.2</td>
<td>14</td>
<td>103</td>
</tr>
<tr>
<td>Riverdale, Mich.</td>
<td>6.0</td>
<td>1.4</td>
<td>12</td>
<td>86</td>
</tr>
<tr>
<td>Wells Co., Ind.</td>
<td>8.2</td>
<td>1.3</td>
<td>17</td>
<td>106</td>
</tr>
<tr>
<td>Pokagon Park, Ind.</td>
<td>8.8</td>
<td>1.2</td>
<td>12</td>
<td>107</td>
</tr>
<tr>
<td>Clay Co., N. C.</td>
<td>6.0</td>
<td>0.7</td>
<td>13</td>
<td>63</td>
</tr>
<tr>
<td>Granby Co., Conn.</td>
<td>10.7</td>
<td>1.6</td>
<td>13</td>
<td>96</td>
</tr>
<tr>
<td>Brandon, Vt.</td>
<td>4.5</td>
<td>0.9</td>
<td>11</td>
<td>66</td>
</tr>
<tr>
<td>Charlotte Co., N. B.</td>
<td>5.5</td>
<td>0.7</td>
<td>7</td>
<td>46</td>
</tr>
<tr>
<td>Gloucester Co., N. B.</td>
<td>6.5</td>
<td>0.8</td>
<td>7</td>
<td>53</td>
</tr>
<tr>
<td>Madoc, Ont.</td>
<td>6.7</td>
<td>1.3</td>
<td>11</td>
<td>72</td>
</tr>
<tr>
<td>Maberley, Ont.</td>
<td>7.0</td>
<td>1.0</td>
<td>10</td>
<td>67</td>
</tr>
<tr>
<td>Ottawa, Ont.</td>
<td>7.5</td>
<td>1.1</td>
<td>10</td>
<td>64</td>
</tr>
<tr>
<td>Southwestern Ontario</td>
<td>6.2</td>
<td>1.2</td>
<td>12</td>
<td>68</td>
</tr>
<tr>
<td>Galt, Ont.</td>
<td>8.5</td>
<td>1.3</td>
<td>11</td>
<td>79</td>
</tr>
<tr>
<td>Algona District, Ont.</td>
<td>8.2</td>
<td>1.1</td>
<td>7</td>
<td>65</td>
</tr>
<tr>
<td>Glenboro, Man.</td>
<td>8.0</td>
<td>1.1</td>
<td>10</td>
<td>87</td>
</tr>
<tr>
<td>Means</td>
<td>7.3</td>
<td>1.1</td>
<td>10.7</td>
<td>75</td>
</tr>
</tbody>
</table>

\(^a\) number of leaf-bearing nodes above ground level
demonstrated a somewhat intermediate internodal pattern (Plate 5, k and l).

Individuals clearly demonstrating both internodal patterns were sometimes found in the same populations, as in the case of a population occurring in a sphagnous bog in central Minnesota (Plate 6, a).

Most of the figures on Plate 6 demonstrate the descending internodal pattern. Some individuals collected in non-boggy habitats along roadsides and in rock outcrops in Ontario and New Brunswick demonstrated this habit of growth (Plate 6, e, f, g, and i). Specimens from New England generally conformed to the descending pattern (Plate 6, j), but an individual from a higher altitude in the White Mountains of New Hampshire (Plate 6, k) demonstrated the ascending internodal pattern.

Some collections in Iowa (Plate 6, o) indicate the possible influence of some sharp habitat differences within the same climatic regime. An individual with eight leaf-bearing nodes, demonstrating the ascending pattern, was collected from a sphagnous mat at the edge of a sheltered lake in Pilot Knob Park. Another individual with 15 leaf-bearing nodes, demonstrating the descending internodal pattern, was collected from an exposed alkaline bog near Silver Lake Park.

The above descriptions of internodal patterns portray
Plate 5. Internodal-pattern graphs of field specimens of *M. glomerata*

The nodes are arranged in an ordinal fashion beginning with the basal node. The final internode is the peduncle. Localities are approximate. Chromosome numbers are from same population, but not from the identical plant.
Plate 6. Internodal-pattern graphs of field specimens of *M. glomerata*
from different locations

Nary, Minn.  
\(2n = 20\)

Nary, Minn.  
\(2n = \text{ca.} 26-28\)

Clare, Mich.  
\(2n = \text{ca.} 24-26\)

Grayling, Mich.  
\(2n = \text{ca.} 24-26\)

Kaladar, Ontario  
\(2n = \text{ca.} 24\)

Maberly, Ontario  
\(2n = 20\)

Clair, New Brunswick  
\(2n = 20\)

Idington, Minn.  
\(2n = 20\)

Madoc, Ontario  
\(2n = 20\)

Brandon, Vt.

White Mts. N.H Wash. Co. N.Y.

Buck Creek, N.C.

Angola, Ind.

Pilot Knob Park, Iowa

Silver Lake fen, Ia.
what the author believes are the principal tendencies of variation in this characteristic. Many other individuals produced internodal patterns that were highly irregular (e.g., Plate 6, c). These could not be categorized.

The ascending internodal pattern showed some geographic orientation. Practically all the plants analyzed from the western mountain regions of the United States and Canada demonstrated this internodal pattern. Both internodal patterns occurred throughout much of the reported range of the species in eastern North America, but the ascending pattern was more characteristic of plants of the northern regions. It was also found in some of the bogs in the southern regions. Plants with the descending and more irregular internodal patterns were most common throughout the southern portion of the range. In the northern portions plants with these patterns generally were collected outside of bogs.

Aneuploidy and Hybridization in *M. glomerata*

Out of 14 different collections of *M. glomerata* for which meiotic chromosome counts were obtained, six produced counts of approximately 22-28 chromosomes (Plate 4, g, h, and i). Although in most cases it was obvious that at least ten pairs of chromosomes plus some additional ones were present, the author was not confident of his ability to determine whether certain figures were bivalents, univalents, or fragments, so the abnormal counts are approximations.
The chromosome counts represented on Plates 5 and 6 of the internodal pattern graphs designate the collections upon which counts were obtained (with two additional counts being obtained after the plates were completed). The specimens are not the individuals upon which the counts were made. They are, nevertheless, from the same sites as the individuals that produced the chromosome counts. These individuals characteristically demonstrated a descending or irregular internodal pattern.

Evidence for hybridization with M. mexicana

Since M. glomerata is a diploid with 20 chromosomes, the abnormal counts of 22-28 chromosomes indicate hybridization with a tetraploid species. Field evidence strongly favors the hypothesis that M. mexicana is the other parent. The hybrids have been collected in some areas in which contact with any other of the rhizomatous species of Muhlenbergia is most unlikely, while M. mexicana is sympatric with M. glomerata throughout most of its range.

One case history is particularly revealing. A small colony of M. glomerata was found growing along a road, on an "atypical" upland site, in a beech--maple woods near Clare, Michigan. The colony was accidentally discovered while the author was making a mass collection of M. mexicana from a population growing along the same road. Probably no more than ten individuals of M. glomerata were present, mixed
with the population of *M. mexicana*. No other *M. glomerata* was found in the immediate area.

Chromosome counts of about 24-26 have been obtained on representatives of this colony. The plants resemble *M. mexicana* in having lax, narrow, greatly interrupted inflorescences and in being branched (Plate 7). They resemble *M. glomerata* in having long-awned glumes, short ligules (about 0.5 mm), long anthers (about 1.0 mm), and hairs along the edges of the lemma for most of its length. Because of the key characteristics just named, such specimens would usually be identified as *M. glomerata*.

Stomatal size and frequency also were aberrant for one of these individuals. Measurements of stomatal size and spacing on a number of individuals of *M. glomerata* and *M. racemosa* showed that as the stomates increased in length the distance between the linearly arranged stomates also increased (due to a general increase in cell size).\(^1\) Stated otherwise, the distance between the stomates is proportional to the length of the stomates. However, as the graph (Plate

\(^1\)The results obtained here bear out the conclusions of Salisbury (1927), namely, that the relative frequency of stomates is a function of cell size. Salisbury found that as cell size decreases the frequency of stomates per unit area increases. Thus, since the cells of diploids are generally smaller than the cells of tetraploids, stomates tend to be more frequent in diploids. Also, plants grown under drier conditions produced shorter stomates and, therefore, in greater frequency than did those grown under more moist conditions.
Plate 7. Inflorescences and plants of *M. glomerata*, *M. mexicana* and putative hybrid

a. left, *M. glomerata*; center, putative hybrid; right, *M. mexicana* (Mitchell Nos. 498; 502; 501)

b. left, *M. glomerata*; center, putative hybrid; right, *M. mexicana*
8) illustrates, the distance between the stomates for one of the above hybrid individuals was much greater than would be expected. On the other hand, hybrid specimens of other collections did not demonstrate this deviation.

The other aneuploid counts were obtained from individuals found growing (1) around a boggy area along a railroad near Grayling, Michigan, (2) along the edge of a hemlock--balsam fir forest near Nary, Minnesota, (3) in a peat meadow at Savage, Minnesota, (4) on a slate outcrop along a highway near Kaladar, Ontario, and (5) in a marsh near Pokagon State Park in northeastern Indiana. *M. mexicana* was found growing along with *M. glomerata* at all these locations.

Infertility does not appear to be a factor militating against these hybrids since they have been found, on occasion, to produce large numbers of good seed in the greenhouse. Tests for pollen stainability have varied a great deal, with some samples showing 80 per cent or more stainable pollen. Apparently viable pollen may be produced on a large scale.

**Evidence for hybridization with *M. andina***

Both *M. glomerata* and *M. mexicana* occur in the western mountain regions, but appear to be relatively rare. The author did not find any evidence for hybridization between the two in the West. But evidence was found for hybridization between *M. glomerata* and *M. andina*, another 20 chromosome species that occurs in the western mountains. A
collection by Marcus E. Jones in the Flathead Lake region of Montana (Sheet No. 855481, U. S. National Herbarium) was classified as a putative hybrid of this nature. Table 5 presents comparative data on the two species and the putative hybrid.

Table 5. Comparative data on a putative hybrid between M. glomerata and M. andina

<table>
<thead>
<tr>
<th></th>
<th>M. glomerata</th>
<th>Putative Hybrid</th>
<th>M. andina</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glumes long-awned</td>
<td>Glumes long-awned</td>
<td>Glumes awnless</td>
<td></td>
</tr>
<tr>
<td>Lemma awnless</td>
<td>Lemma long-awned</td>
<td>Lemma long-awned</td>
<td></td>
</tr>
<tr>
<td>Hairs on floret</td>
<td>Hairs on floret long and silky</td>
<td>Hairs on floret long and silky</td>
<td></td>
</tr>
<tr>
<td>short</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anthers generally long</td>
<td>Anthers 0.8 mm long</td>
<td>Anthers generally 0.5-0.7 mm long</td>
<td></td>
</tr>
<tr>
<td>1.0-1.2 mm long</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Tests with lactophenol-cotton blue solution showed that less than ten per cent of the pollen was plump and fully stained. One other specimen viewed by the author (Sheet No. 12888, Dept. of Agriculture, Ottawa) that was collected near Lacombe, Alberta had these same characteristics. No other evidence of hybridization was found in material from the western regions.
Plate 8. Stomatal measurements and spikelets of Muhlenbergia

a. Stomatal lengths and distance between stomates in *M. glomerata* and *M. racemosa*

Each symbol represents an average of measurements on stomates in the abaxial epidermis of an upper leaf of a plant. The symbol of *M. glomerata* farthest to the right represents an aneuploid individual.

b. Spikelet of *M. glomerata*

c. Spikelet of putative hybrid

d. Spikelet of *M. andina*
distance between stomates (in microns)

- M. glomerata
- M. racemosa

---

length of stomates (in microns)

b. 1 mm

---

c.

d.
Discussion

**Cytological implications of hybridization**

Cytological studies of pollen mother cells of the hybrid-segregates suggest possible ancestral relationships involving *M. glomerata*. The meiotic figures show that ten and more bivalents are formed, indicating that the *M. glomerata* genome is closely homologous with some members of the foreign genome. Most likely a 10-chromosome complement of the *M. mexicana* genome, granting it to be the other parent, has had a common or very close ancestry with the genome of *M. glomerata*. If such is the case, *M. mexicana* could be an amphidiploid offspring of *M. glomerata*.

The apparent homologies of these complements might also account for the fertility of the hybrids. Further, with two homologous 10-chromosome complements being present, the process of chromosomal loss could very well progress until the diploid state of 20 chromosomes is restored or an aneuploid race is formed. Thus, introgression (Anderson, 1949) would be taking place from the tetraploid level to the diploid or aneuploid level. Individuals yielding normal 20-chromosome counts actually could be introgressants.

With the plants being self-fertile, a single hybrid individual could initiate future generations of hybrid-segregates. The rhizomatous habit would enable the hybrid to propagate itself and further the chance of reproduction
by seed. The small colony along the road in the beech—maple woods probably obtained its start from the seed of a plant of *M. mexicana*. The chromosome counts show that at least some of the members of the colony are segregates, since they no longer have their full complement of 30 chromosomes.

The coupling of the rhizomatous habit with self-compatibility may be unusual for a grass species. According to Stebbins (1950, p. 167), "... among the perennial species (of grasses) those with rhizomes are almost exclusively self-incompatible and cross-fertilized." Grant (1956) observed that polyploid series are often based on self-pollinated species, whereas out-crossing favors introgression. In this case the rhizomatous habit coupled with self-compatibility appears to favor a form of introgression without back-crossing being necessary. The result is the restoration of the diploid or the establishment of an aneuploid condition.

**Population structure—role of isolated populations**

Available distributional data and information gained from personal visits to the herbaria of Montana State University, Brigham Young University, Colorado University, and Wyoming University indicate that *M. glomerata* is quite scattered in its occurrence in the mountainous regions of the West. Only rare collections of the species have been made as far south as Utah and Colorado, and it also occurs in an
isolated position in the Black Hills of South Dakota. It appears to be more frequent farther north in the Canadian Rockies. The species is much more abundantly represented in the East than it is in the West. Further, internodal-pattern studies showed that these western forms demonstrated much less variation than did those from its eastern range.

Gleason (1922) has commented that "isolated areas of a species or of vegetation are to be interpreted as results of retreating migration." The evidence indicates that *M. glomerata* is in the process of a major retreat in the West. Its more firmly established position in the eastern and more northern regions suggests that these have been the centers of migration. Its representation in the western Rockies is probably due to migration into the region during the glacial periods. This is somewhat the reverse of the direction of migration postulated by Fassett (1941) for *Rubus parviflorus*.

The future of the species in western United States will depend on what develops in some scattered, isolated populations. There are areas in the East, also, where the species is in retreat with populations evolving under isolated circumstances. Populations in northern Iowa, for instance, essentially are in positions of isolation, partly due to man's alteration of a number of the bogs and partly due to the relic nature of these stands. In other parts of its more southern range in the East, where suitable habitats are
somewhat more frequent, populations appear to be developing under conditions of partial isolation.

The population structure of *M. glomerata* may well reflect the model of Wright (1931) and Dobzhansky (1951) wherein a species population subdivided into large numbers of local populations was described as the one most favoring progressive evolution. In such a model variability within a local population is low, and some populations are sacrificed, but the variability of the species as a whole is increased. However, some poorly adapted populations (occupying the "adaptive valleys" rather than the "adaptive peaks") could become the favored ones under an environmental change. The survival of *M. glomerata* in the southern parts of its range may depend upon a development of this nature, since many of the preferred, boggy habitats are undergoing serious change.

**Role of hybrids in population structure**

*M. glomerata* may actually be accomplishing a difficult transition from one adaptive peak to another, without being obliged to traverse a nonadaptive valley, by hybridizing with *M. mexicana*. Large scale disturbance may be the factor permitting the leap. Practically all the aneuploid individuals were collected on sites that had been subject to disturbance: e.g., along a road cut through a beech--maple woods, along a railroad built through a boggy area, along a highway at the edge of a hemlock--fir forest, on a slate outcrop that was
part of a road-cut for a highway, and in a weedy peat meadow.

As a sphagnous bog, marsh, or peat bog inhabitant, *M. glomerata* is a component of some well established communities. *M. mexicana* occurs in some of these same habitats, but also occupies railroad right-of-ways and highway cuts and frequents the edge, or ecotone position between marsh and grassland and forest and grassland. The success of the introgressant may depend on a complex of conditions inherent in the nature of some of these habitats, with disturbance providing the opportunity necessary for the maintenance of the hybrid forms. Otherwise, one must question the ability of these hybrids to prevail in the face of competition with *M. mexicana*. Hybridization of any frequency with *M. mexicana* would amplify the local ecological range of *M. glomerata* and broaden its geographic range.

Hybridization might have been taking place over a much longer term than implied in the above discussion. It may be that glacial disruption and the raw habitats open to ecesis following the glaciers constituted the kinds of conditions that permitted hybridization on a large scale. Subsequently, the invasion of man might have led to a resurgence of the process in our time.

It appears, then, that the species population of *M. glomerata* is of a complex structure consisting of (1) pure *M. glomerata* populations in some of the bogs and related
habitats, (2) *M. glomerata* populations possibly adulterated by pollen from hybrids and hybrid-segregates, and (3) hybrid and hybrid-segregate populations that, apparently, can be highly successful.

The author believes that the individuals with the fewest nodes and ascending internodal pattern correspond to the "prototype" of *M. glomerata*. This, probably, is the type that prevailed along the glacial front and migrated northward following the retreating glaciers. But postglacial climatic changes involving the more southern locations would place a premium on individuals better adjusted to longer and warmer growing seasons and the more rank growth that these conditions produce. Adjustments to these conditions apparently are being accomplished by hybridization as well as by the more gradual process of mutational change. These adjustments appear to be reflected, morphologically, in an increase in nodal number with an alteration in internodal pattern. The descending internodal pattern may represent the type of variant that ultimately will prevail under these conditions.

**Disposition of *M. glomerata* var. cinnoides**

Fernald (1943) recognized that *Dactylogramma cinnoides* Link (1833), the type of the genus *Dactylogramma*, was a species of *Muhlenbergia*. He accorded the plant varietal status under the new combination, *M. setosa* (Spreng.) Trin. var. *cinnoides* (Link) Fern. The name *M. setosa* applied to
M. glomerata by Fernald at that time had to be abandoned as a later homonym of M. setosa (H. B. K.) Kunth, which is now treated as a synonym of M. microsperma (DC.) Kunth (Hermann, 1946). The correct species and varietal name then became M. glomerata (Willd.) Trin. var. cinnoides (Link) F. J. Herm.

Fernald credited the variety with being more northern in its distribution than the "typical" M. glomerata and as extending into the Rocky and Cascade Mountain regions. He did not extend the range of typical M. glomerata into the West. He described similar types of habitats for both.

Fernald distinguished the two varieties as follows:

<table>
<thead>
<tr>
<th>M. glomerata var. glomerata</th>
<th>M. glomerata var. cinnoides</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves 7-15 and tending to be crowded at the middle nodes</td>
<td>Leaves 5-8 (-10) and usually more scattered</td>
</tr>
<tr>
<td>Panicle usually purple, all but lowest branches crowded</td>
<td>Panicle usually green, more interrupted</td>
</tr>
<tr>
<td>Branches of panicle ellipsoid to rounded-obovoid</td>
<td>Branches of panicle cylindric to oblong-ovoid, often subacute</td>
</tr>
<tr>
<td>Keels and awns of glumes copiously hispid, thus giving inflorescence a &quot;misty&quot; appearance</td>
<td>Keels and awns of glumes merely scabrous</td>
</tr>
</tbody>
</table>

Fernald's variety with few nodes would correspond to the more northern and western oriented form characterized in this study by the ascending internodal pattern. But some of his other characteristics were not found to occur in combination with each other, as described, with any consistency. The
purple inflorescence, for instance, is more characteristic of the northern form than it is of the southern form. The southern form often has an interrupted inflorescence and glumes that are scabrous rather than hispid. Finally, leaves on plants with few nodes may appear more crowded than on many of the plants with more nodes because the internodes of the latter may be relatively long.

However, since Fernald's concept of a variety with few nodes can be associated with a form having a certain degree of geographic and habitat orientation, the author recommends that the nomenclature be retained but that it be applied to plants of the following description:

*M. glomerata* (Willd.) Trin. var. *cinnoides* (Link) F. J. Herm. emend. Wm. Mitch. Culms generally less than 65 cm tall and 1 mm thick, with from 5-8 leaf-bearing nodes and the internode lengths tending to increase from the culm base toward the peduncle; panicle usually less than 7.0 cm long, often purple. Typical of plants found in western portions of range in U. S. and Canada, also of many plants found primarily in bogs in eastern North America, particularly in northern portions of range.

Unfortunately, the type specimen, placed in the Botanisches Museum of Berlin, Germany, was grown from seed (collected from northwestern Canada) and may not reflect, in the truest sense, some of the characteristics employed above.
VARIATION IN M. FRONDOSA

Biology and Ecology

*M. frondosa* matures late in August and into September in its native occurrences. It often forms dense stands from stout much-branched rhizomes and may grow upright with few branches or in a sprawling fashion with many branches. The species is self-fertile and, in a sense, partially cleistogamous. This is due to the fact that the inflorescences, particularly the lateral ones, may be partially enclosed in the sheath. The enclosed florets can be found with good seed and still containing the anthers and stigma. Allard and Evans (1941) found that *M. frondosa* flowers under short-day conditions as well as long-day conditions.

The species occurs throughout eastern North America north of the gulf states into the southernmost portions of Canada. It extends far out into the Great Plains along the river systems in Oklahoma, Kansas, Nebraska, and the Dakotas (Plate 13).

The range of *M. frondosa* is centered, roughly, north of the Ohio River in central to northern Indiana, but it appears to occur in its greatest abundance throughout the southern half of Iowa and neighboring Missouri, east into Illinois, and west to Kansas and Nebraska. In this region it is very aggressive in frequenting waste places, railways, the edges of woods and shrubbery, and river banks. It often is found
in fairly deep shade. The species occurs in habitats of this nature throughout most of its range to the east coast. It becomes confined to moist sites along water courses in the central Great Plains.

The westernmost location found for *M. frondosa* in the Great Plains was along the Arkansas River in the short-grass plains at La Junta, Colorado. An isolated colony was found in 1948 along an irrigation ditch on the campus of Brigham Young University at Provo, Utah by Prof. B. F. Harrison. Quite possibly this occurrence was the result of a relatively recent introduction. Personal observation in the summer of 1961 verified the fact that the colony is maintaining itself.

**Ecology of *M. brachyphylla***

Observations on the ecology of *M. brachyphylla* also will be presented here, since it will be involved in the treatment of *M. frondosa*. It is a species of the hardwood forest stands of southeastern Nebraska, eastern Kansas, Oklahoma, and Texas and eastward at least to Illinois. Its eastern and southeastern extensions are poorly defined. (See Plate 13.)

*M. brachyphylla* is more restricted to a warmer climate than the other species considered so far. It is found characteristically in moderate to deep shade. Wherever *M. brachyphylla* was seen to occur with *M. frondosa* or *M. racemos* in Kansas and Iowa, the latter two species generally
occupied the outer edges of woods, with *M. brachyphylla* forming, at times, a considerable portion of the herbaceous understory of the woods.

**Analysis of Geographic Variation**

No attempt was made to work out patterns of variation for *M. frondosa* throughout its extensive range of distribution, but rhizomes were collected in ten different locations on a north-to-south transect and grown in the experimental garden. Also, some analyses of possible ecotypic variation on a local level were performed on populations occurring in contrasting environments.

The transplants were collected on a transect that sampled the western portion of the range of *M. frondosa*. The northernmost locality was Breckenridge, Minnesota along the west central border of the state. Other collections were made southward through Iowa and southwestward through Kansas. The southernmost collection was at Meade Co. Park, Kansas. Data obtained from specimens grown in the experimental garden are presented in Table 6.

**Interpretation of uniform garden results**

**Phenology** The date of first appearance of the inflorescence from the leaf sheath was taken as the emergence time. Generally speaking there was a gradual, unidirectional change in emergence times. The specimens from Breckenridge,
Minnesota commenced to emerge on July 8, those from central Iowa appeared in the latter part of July and early August, and those from northeastern and central Kansas emerged in late August and early September. Some specimens from southwestern Kansas reversed the trend and emerged through the middle part of August.

**Number of nodes**  Nodal number was fairly well correlated with emergence times so that a north-to-south gradient was expressed for this characteristic also. The number of nodes increased from as few as 12 for an individual from Breckenridge, Minnesota to as many as 33 for an individual from Hoisington in central Kansas.

**Height and growth habit** The correlation between height and nodal number was poor except for plants with the fewest nodes and some with the most nodes. Those with the fewest number of nodes were the shortest and some with the most nodes were the tallest. Otherwise there was much variation in this measurement when related to number of nodes.

The difference in stature and overall growth habit between individuals from the opposite ends of the transect presented the most striking demonstration of variation. Those from Breckenridge and Taylor Falls, Minnesota measured up to 49 and 66 cm in length, had an upright growth habit, and bore only a few short branches with about 10-12 inflorescences. Some individuals from Meade Co. Park, Kansas
Table 6. Morphology and phenology of collections of *M. frondosa* grown in experimental garden at Ames

<table>
<thead>
<tr>
<th>Approximate Origin of Collection(^a)</th>
<th>nodes(^b)</th>
<th>phenology(^c)</th>
<th>maximum height</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breckenridge, Minn. (3)</td>
<td>12-17</td>
<td>July 8-12</td>
<td>49 cm</td>
</tr>
<tr>
<td>Taylor Falls, Minn. (1)</td>
<td>13</td>
<td>July 22</td>
<td>66</td>
</tr>
<tr>
<td>Belmond, Iowa (5)</td>
<td>16-22</td>
<td>July 12-19</td>
<td>98</td>
</tr>
<tr>
<td>Jewell, Iowa (2)</td>
<td>13-17</td>
<td>July 19</td>
<td>92</td>
</tr>
<tr>
<td>Ames, Iowa (5)</td>
<td>20-24</td>
<td>Jul. 28-Aug. 8</td>
<td>85</td>
</tr>
<tr>
<td>Westmoreland, Kans. (1)</td>
<td>25</td>
<td>August 28</td>
<td>69</td>
</tr>
<tr>
<td>Claflin, Kans. (3)</td>
<td>26-32</td>
<td>Aug. 22-Sept. 6</td>
<td>75</td>
</tr>
<tr>
<td>Hoisington, Kans. (3)</td>
<td>28-33</td>
<td>Aug. 22-Sept. 2</td>
<td>107</td>
</tr>
<tr>
<td>Fowler, Kans. (2)</td>
<td>31</td>
<td>Aug. 28-Sept. 6</td>
<td>102</td>
</tr>
<tr>
<td>Meade, Kans. (3)</td>
<td>22-31</td>
<td>Aug. 8-25</td>
<td>108</td>
</tr>
</tbody>
</table>

\(^a\)numbers in parentheses apply to number of individuals upon which the statistics are based

\(^b\)range in numbers of leaf-bearing nodes

\(^c\)range in dates of first appearance of emerging inflorescence
measured up to 108 cm in length, had a sprawling, somewhat procumbent growth habit, and produced many strong branch-systems with literally hundreds of inflorescences. (See Plate 10.)

Analyses of Local Populations

Convergence in variation between species

Information on local variation was obtained from the analyses of some populations in central and northern Iowa. Mass collections were taken of mixed populations of *M. frondosa* and *M. racemosa* along a railroad right-of-way north of Belmond, Iowa and of *M. frondosa* and *M. brachyphylla* in a park at Ames, Iowa. The first habitat was an open grassland and the latter a shaded woodland.

If the ratio of the first glume/palea is plotted against the length of peduncle for the above species, they form three differently placed groups on a graph, as indicated by the data in Table 7.

Table 7. Separation of *M. frondosa*, *M. racemosa*, and *M. brachyphylla* on basis of ratio of first glume/palea and length of peduncle bearing terminal panicle

<table>
<thead>
<tr>
<th>Characteristic</th>
<th><em>M. frondosa</em></th>
<th><em>M. racemosa</em></th>
<th><em>M. brachyphylla</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Ratio of 1st glume/palea</td>
<td>ca. 1.0</td>
<td>ca. 1.5</td>
<td>ca. 0.7</td>
</tr>
<tr>
<td>Length of peduncle (cm)</td>
<td>ca. 4.0</td>
<td>ca. 10.5</td>
<td>ca. 8.5</td>
</tr>
</tbody>
</table>
Those specimens of *M. frondosa* with the longer glumes and longer peduncles vary in the direction of *M. racemosa*, while those with the shorter glumes and longer peduncles vary in the direction of *M. brachyphylla*.

The population of *M. frondosa* in the open grassland with *M. racemosa* demonstrated a directional trend of variation tending to converge with that of *M. racemosa*. The separation was still good, however, with the exception of one individual having an extraordinarily long peduncle and long glumes. The glume/palea ratio, however, was still below that of any of the individuals of *M. racemosa*.

Members of the population of *M. frondosa* growing in the shade with *M. brachyphylla* had relatively short glumes and long peduncles. A directional trend of variation resulted that converged and overlapped with that of *M. brachyphylla*. (See Plate 9.)

The same graphic analysis was performed on individuals collected from a number of different locations and grown in the experimental garden. The suggestion of two trends of variation in *M. frondosa* is present but not so definite as in the case of the two populations previously analyzed. (See Plate 9.)

**Ecotypic differentiation in *M. frondosa***

An attempt was made in the uniform garden to compare two small populations of *M. frondosa* growing under contrast-
Plate 9. Analyses of populations and uniform-garden specimens of *M. frondosa*, *M. racemosa*, and *M. brachyphylla* on basis of ratio of first glume/palea plotted against length of peduncle

a. Analysis of population samples from mixed populations of *M. frondosa* and *M. racemosa* and of *M. frondosa* and *M. brachyphylla*

The mixed population of *M. frondosa* and *M. racemosa* occurred in an open grassland while that of *M. frondosa* and *M. brachyphylla* occurred in a shaded woodland

b. Analysis of specimens of *M. frondosa*, *M. racemosa*, and *M. brachyphylla* grown in the uniform garden at Ames

The individuals grew from rhizomes collected from a number of different locations, including two local populations of *M. frondosa* occurring under shaded and unshaded conditions. Individuals of these two populations were grown out in the uniform garden to test the possible effects of contrasting environments on the species
a. M. frondosa: mass collection from unshaded railroad right-of-way north of Belmond, Iowa

b. M. frondosa: mass collection from shaded bottomland in Brookside Park

M. brachyphylla: at Ames, Iowa
ing conditions near Ames. One population was found in very deep shade in a bottomland woods and the other in an open grassland along a railroad above the woods.

The individuals growing in the shade had long, lax, dark green leaves, were much branched, and expressed a somewhat extended and decumbent growth habit. Those growing in the sun were very strict and had short, appressed, light green leaves and few branches. The individuals grown in the experimental garden from these habitats were somewhat intermediate, manifesting no clear distinctions by these criteria. (See Plate 10.)

On the other hand, differences in spikelet measurements obtained in the analysis of the field populations were also reflected in the uniform-garden results. The ratio of the first glume/palea describes the difference, as presented in Table 8 and on Plate 9.

Table 8. Spikelet differences in populations of *M. frondosa* occurring in contrasting environments, as denoted by ratio of first glume/palea

<table>
<thead>
<tr>
<th>Origin of Collection</th>
<th>Analysis of Field Collections</th>
<th>Analysis of Garden Specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>range in ratio:</td>
<td>range in ratio:</td>
</tr>
<tr>
<td>Shaded habitat:</td>
<td>0.63-0.75</td>
<td>0.50-0.79</td>
</tr>
<tr>
<td>Unshaded habitat:</td>
<td>1.00-1.03</td>
<td>0.68-1.04</td>
</tr>
</tbody>
</table>

Those individuals from the shaded habitat had relatively
Plate 10. Field and uniform-garden specimens of *M. frondosa*

a. left, plant grown in uniform garden from rhizome collected in Meade Co. Park, southwest Kansas (Mitchell No. 392)  
right, plant grown in uniform garden from rhizome collected at Breckenridge, west central Minnesota (Mitchell No. 571)

b. left, plant collected from deep shade habitat near Ames (Mitchell No. 557)  
right, plant collected from open grassland habitat near Ames (Mitchell No. 556)

c. left, plant grown in uniform garden from rhizome collected in above-mentioned deep shade habitat  
right, plant grown in uniform garden from rhizome collected in above-mentioned open grassland

The meter stick has been marked off in 10-centimeter divisions
shorter glumes, even when grown in the unshaded experimental garden. These findings are in keeping with the results obtained in the analysis of the two populations previously discussed.

Evidence for introgression with M. racemosa

Some individuals of M. frondosa from the Belmond, Iowa location, when grown in the uniform garden, corresponded to the most divergent individuals of the mass collection from the same location. These individuals stood out in the garden as being particularly aberrant for M. frondosa and bearing a close resemblance to M. racemosa. (See Plate 11.)

Whereas the taller individuals of M. frondosa tend to become decumbent and sprawling, these were tall and stiffly upright. Their inflorescences were much more dense than is normally true of M. frondosa, and they had relatively long peduncles and glumes (Plate 9, b).

These individuals of M. frondosa were growing in the uniform garden very close to some individuals of M. racemosa collected from the same site. Although the resemblance to M. racemosa was striking, the difference between the two was still obvious. The individuals of M. racemosa, because of the long-awned glumes, had the characteristic bushier panicle. They also showed considerable difference in height, seven individuals of M. racemosa measuring from 55-72 cm as compared to 81-98 cm for five individuals of M. frondosa.
Plate 11. Plants and inflorescences of *M. frondosa* and *M. racemosa* grown in uniform garden

a. left, plant of *M. racemosa* grown from rhizome collected along railroad north of Belmond, Iowa (Mitchell No. 574)
right, plant of *M. frondosa* grown from rhizome collected from same site as above (Mitchell No. 574A)

b. left, inflorescence of *M. frondosa* (Mitchell No. 557)
center, inflorescence of aberrant *M. frondosa* (Mitchell No. 574A above)
right, Inflorescence of *M. racemosa* (Mitchell 574 above)
Cytological studies did not indicate any abnormalities in this collection of *M. frondosa*. The typical chromosomal number of $2n=40$ was obtained with no suggestion of abnormal meiotic behavior. Also, the anther size at the time of meiosis was characteristic of *M. frondosa*, being between 0.1-0.2 mm, while that for *M. racemosa* is about 0.4 mm or a little less.

Discussion

**Ecotypic variation**

It was shown that *M. frondosa* demonstrates considerable variability in glume length. For the populations analyzed, the individuals occurring in shaded habitats had relatively short glumes compared to those occurring in unshaded habitats. It is of interest that among the other species of the broad-leaved rhizomatous group those with relatively short glumes typically are shade inhabitants. These include *M. brachyphylla*, *M. tenuiflora* (Willd.) B. S. P., *M. sylvatica* (Torr.) and *M. sobolifera* (Muhl.) Trin. The longer glumed species, such as *M. glomerata*, *M. racemosa*, and *M. mexicana* generally occur in moderate shade to full sunlight. *M. andina* also has relatively long glumes, but its particular habitat preferences are not known to the author.

Correlations of ecological and morphological data often are suggestive of genecological responses, as discussed by
Clausen and Hiesey (1958). The data, in this instance, suggest that relative glume length might reflect an adjustment to light conditions in the broad-leaved rhizomatous species of *Muhlenbergia*.

**Introgression**

The more aberrant individuals of the open grassland habitats suggest the possibility of introgression with *M. racemosa*. Particularly noteworthy is the fact that the long peduncle of these individuals is associated with an unshaded habitat.

Long peduncles on individuals collected in deep shade can be attributed, at least in part, to an environmental effect. For instance, the longer peduncles on individuals collected from the deep shade habitat measured from 6-8 cm long. Individuals collected from the same colony and grown in the unshaded experimental garden produced peduncles measuring, at the most, from 3-4.5 cm.¹ Five uniform-garden specimens of the aberrant *M. frondosa* had peduncles measuring from 10.2-17.5 cm, while the other garden specimens of *M.*

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¹The longer peduncles produced by individuals grown in the shade environment is typical of the effect, in general, of reduced light on growth in length. Under the circumstances, one would expect that individuals growing in shaded habitats would have longer glumes than those growing in unshaded habitats. The fact that the reverse was found to be true for the populations previously discussed would appear to constitute further support for the ecotypic variation hypothesis.
frondosa from 11 different collection sites had peduncles measuring from 0.3-6.5 cm. A sample of 25 individuals of M. racemosa grown in the uniform garden had peduncles measuring from 5.5-19.5 cm.

Thus, the production of extraordinarily long peduncles in full sunlight would appear to reflect a genetic difference of some consequence. With the other aberrant characteristics—the relatively long glumes, dense panicle, upright growth habit—also varying in the direction of M. racemosa, one cannot overlook the suggestion that introgression has taken place between M. frondosa and M. racemosa. Such introgressants would be expected to occur in the drier grassland sites in keeping with the ecology of M. racemosa in this region.

Stebbins (1950, 1959) and, to a greater extent, Anderson (1949, 1953) credit introgression with a very large role in accounting for detectable variation in plants. Anderson (1953), after reviewing with other associates the variation pattern in 30 genera of flowering plants in central and eastern United States, concluded that "all the readily detectable variation can be ascribed to introgression." On this basis one might suggest that the convergence of M. frondosa with M. brachyphylla in the shaded habitat also is the result of introgression.
Plate 12. Geographic distribution of *M. glomerata* and *M. racemosa*

a. *M. glomerata*

Some recent collections have been made in the region of the Great Slave Lake in the Northwest Territory of Canada, about 400 miles north of the northernmost location represented on the map in Alberta.

b. *M. racemosa*

Fernald (1950) reports the species as being adventive along railroads into the New England states.
a. Muhlenbergia glomerata

b. Muhlenbergia racemosa
Plate 13. Generalized distributional ranges of *M. frondosa* and *M. mexicana* and locations for collections of *M. brachyphylla* and *M. andina*

a. Generalized distributional range of *M. frondosa* (an isolated colony of *M. frondosa* also has been located on the campus of Brigham Young University at Provo, Utah

Locations for collections of *M. brachyphylla*

b. Generalized distributional range of *M. mexicana* with locations for collections of the species in the western mountains

Locations for collections of *M. andina*
Muhlenbergia frondosa
M. brachyphylla

a.

Muhlenbergia mexicana
M. andina

b.
VARIATION IN M. RACEMOSA

Biology and Ecology

M. racemosa is a highly variable species maturing from late July to middle September in its native habitats. It generally is found in small colonies or populations, the individuals being produced singly or in clumps from sparingly branched rhizomes. Bagging experiments conducted by the author showed that the species is self-fertile. Seeds were found to germinate without the necessity of scarification or vernalization. Grain produced in July and August in the experimental garden germinated in October from inflorescences that had fallen to the ground.

The species occurs from Oklahoma, New Mexico, and Arizona northward into Utah, Idaho, and eastern Washington, and eastward across the Great Plains into Wisconsin, Illinois, and Missouri. Fernald (1950) reports it as being adventive along railroads as far east as the New England states. It occurs as far north as the southern plains regions of Alberta, Saskatchewan, and Manitoba. (See Plate 12.)

Since the major work of the study was performed on this species, observations on its ecology will be reviewed in some detail. The range of M. racemosa is centered, roughly, in central to northwestern Nebraska. It is very similar in its ecology to M. frondosa in the Middle West, occurring in waste places, along roads and railways, and in disturbed prairies,
as well as in moister lowland sites. In eastern Kansas and Nebraska and western Iowa it may occur as a minor component of disturbed or some well developed *Andropogon* prairies (Weaver and Fitzpatrick, 1934; Aikman and Thorne, 1956). It tends to be restricted to moist sites in the drier plains regions, but exceeds *M. frondosa* in its tolerance for the drier sites.

*M. racemosa* demonstrates a wide range of adaptibility, occurring in an altitudinal range from about 8,000 feet in the Rockies of Colorado and New Mexico to about 500 feet in the Mississippi River valley of Missouri and Illinois. It was observed occurring in mesic ravines and on xeric rock outcrops in the Raton Mountains of Colorado. In the short-grass plains of southeastern Colorado it was found on moist soil along water courses and in a juniper stand on an upland sandstone bluff. It occurs on heavy clay soils as well as on sandy soils. It often is found on sites that are subject to inundation during the early part of the growing season. It may occur in deep shade, but generally is found in moderate shade to full sunlight.

From notations on herbarium sheets and comments of other authors it appears that *M. racemosa* was more abundantly represented in the past than it is today. It has been referred to as a valuable native pasture and hay plant (Beal, 1896; Sampson, 1924). Pound and Clements (1900) listed *M.*
racemosa as one of the most common grasses frequenting woods and thickets in open woodlands and along borders of streams throughout Nebraska. They described the wooded islands of the Missouri as being "covered for the most part with a loose, grassy covering of Elymus virginicus, Muhlenbergia racemosa, and Poa pratensis ... "

It was found by the author to occur as a herbaceous associate in some well developed tree and shrub communities of the western plains and mountains. It was observed as a grassy associate of communities of Pinus ponderosa—Quercus—Juniperus in Colorado and northwestern Nebraska, in P. ponderosa stands in Nebraska and the Black Hills of South Dakota, and in a Prunus—Juniperus community in northwestern Nebraska.

Comments

It was previously noted that M. racemosa may have been more abundant in the past than it is at present. In the author's viewpoint this can be attributed to three factors: (1) physical destruction of suitable sites by cultivation, etc; (2) grazing pressure; and (3) biotic competition. Only the second and third require any comment. Observations demonstrated consistently that M. racemosa could not be found on otherwise suitable sites that showed the effects of heavy grazing. It appears that the grass is quite sensitive to continual cropping. It does not seem likely that an effort would be made to maintain it as a hay plant, despite comments
of other authors, because its culm becomes woody and brittle as it matures.

As for the third factor, recent introductions into this country, such as *Agropyron repens* (L.) Beauv., *Bromus inermis* Leyss., and *Phleum pratense* L., were found to be remarkably successful in occupying and dominating many of the kinds of sites in which one would expect to find *M. racemosa*. These grasses might very well be limiting the occurrences of *M. racemosa*.

**Sampling for Uniform-Garden Studies**

A major objective of this study was to describe regional patterns of variation in *M. racemosa* and to determine whether or not they could be confirmed in the experimental garden. Since it was impossible to sample the total range of the species, a broad northeast-to-southwest transect was decided upon. Rhizomes were collected to be grown in the transplant garden from northern Minnesota (near Ray just south of International Falls), southward through eastern South Dakota, Iowa, Nebraska, Kansas, the northeastern region of New Mexico, and along the eastern front of the Rocky Mountains in Colorado. This transect sampled regions of significantly different floristic qualities and tested the effect of climatic changes on both a north-to-south gradient and an east-to-west gradient. Rhizomes from 59 different locations were successfully grown in the garden, and over 300 specimens were har-
vested and analyzed.

Herbarium Studies

The analysis of the specimens from the uniform garden was preceded by an analysis of over 1,000 specimens from field collections of the author and herbarium collections of the U. S. National Museum, Missouri Botanical Garden, University of Minnesota, and Iowa State University. The analysis of herbarium collections served to delineate regional variation from samples obtained by a host of collectors over a number of years. Therefore, the results were not subject to the prejudices of a single collector or the growing conditions of a single season. Woodson (1947) discussed in some detail the merits of herbarium collections for this kind of a study. The population samples made by the author served to supplement the herbarium specimens and to portray intrapopulation variation.

Selection of Characters

Characters selected

The characters found to be best adapted to this study were those that could be measured definitely on a continuous scale, such as number and length. Leaf shape has been used to advantage by other workers (Woodson, 1947; Desmarais, 1952). Unfortunately the organs of grasses generally are linear and therefore do not lend themselves to critical
delimitation of shape differences, particularly when some of the organs are no more than 3-4 mm long. Shape differences were noted in glumes and lemmas of *M. racemosa*, but were not easily definable.

The characters chosen for study were:

1) number of leaf-bearing nodes on the main culm above the ground level
2) length of inflorescence
3) length of palea
4) culm width
5) plant height (used for material grown in the uniform garden, but not for the field and herbarium collections)
6) length of lemma relative to palea

**Evaluation of characters**

While some characters quite obviously appear to reflect important adjustments to environmental differences, without elaborate crossing experiments and reciprocal transplants the value of most characters can be assessed only by inference. The works of Clausen, Keck, and Hiesey, as summarized by Clausen and Hiesey (1958), have shown that insignificant morphological differences may reflect fundamental adjustments of a species to varying environments.

Some principles have been formulated by previous workers for evaluating characters used to show variation. Gregor (1946, p. 254) stated that three principles dictated by Raun-
Kiaer (1934) for the study of adaptational attributes on the species level could very well "serve as working bases for the study of the ecogeographical pattern of hereditary variation at the infra-specific level." The three principles of Raunkiaer are:

The character must in the first place be essential; it must represent something fundamental in the plant's relationship to climate.

It must be fairly easy to use, so that we may easily see in nature to which life-form a plant belongs.

It must represent a single aspect of the plant, thus enabling a comparative statistical treatment of the vegetation of different regions.

Woodson (1947, p. 371) affirmed, "A good measure should be duplicable, sensitive to organic variation and should provide an unwarped scale." He argued for the use of "standard scales, such as the linear and the angular," wherever possible, as providing the advantage of a statistical treatment of a fixed, continuous scale and avoiding the arbitrariness inherent in scoring discontinuous scales.

Of the characteristics used to depict, as Gregor states it, the "eco-geographical pattern of hereditary variation" in *M. racemosa*, the author believes that number of nodes best fits the criteria discussed above. It constitutes a measurement of a continuous scale without the necessity of arbitrary scoring and, as shown by uniform-garden results, is genetically based. Further, the relationship of leaf production to the photosynthetic function and its duration would appear to
be fundamental in the relationship of a plant to its environment.

However, certain restrictions must be placed on its complete acceptance. While observing the growth of the plants in the uniform garden, the author noted that the number of nodes on the main culm produced from the dormant rhizome generally was different from the number of nodes on other shoots produced by young rhizomes during the growing season. These shoots grew quite rapidly and often with fewer nodes. The plants in the uniform garden produced these shoots in abundance. Field observations indicated that in the more competitive conditions of the native habitats their number is reduced. Herbarium specimens could be prejudiced to the extent that smaller plants produced by the younger rhizomes might be preferred for pressing and mounting. This bias can be averted in the uniform garden by careful observations and harvesting.

Another restriction is that nodal number alone may be insufficient to denote, in all cases, the significance of this measurement. In many cases the relative lengths of consecutive internodes also must be taken into consideration.

The characters of culm width and plant height, particularly the latter, are of value when correlated with number of nodes and phenology. Certain exceptions serve to emphasize the significance of the correlation.
The characters of length of inflorescence and length of palea show independent patterns of variation which, by inference, appear to have some value. That of length of lemma/palea ratio also demonstrates a pattern of variation, but no attempt at evaluation was made.

Methods for Interpreting Data

**Equal-area quadrats and metroglyphs**

The method employed by Woodson (1947), Desmarais (1952), and others in arbitrarily dividing the distributional area of a species into equal-area quadrats was used to gather the statistics into means for representation on maps. The quadrats were made approximately 125 miles on a side, and each quadrat was numbered (Plate 14). The author estimates that about 80 quadrats would cover the principal area of distribution of *M. racemosa*. Herbarium and field material from 46 of these quadrats was analyzed for projection on the map. The information was projected on the map by means of "metroglyphs" (Anderson, 1946, 1957).

Analysis of Herbarium Material

**Criteria for construction of metroglyphs**

Plate 15 depicts the variation determined from the analysis of the herbarium material and field collections. Each glyph represents information obtained from at least
Plate 14. Division of distributional area of *M. racemosa* into equal-area quadrats

Each quadrat is about 125 miles on a side

Measurements of morphological characteristics for all individuals originating in a quadrat were gathered into "quadrat-means" for translation into metroglyph form.
four individuals or population samples collected within the quadrat area (with the exception of the glyph for Quadrat 40 in New Mexico, based on the analysis of three individuals). In a few cases, where too few specimens were available from a single quadrat, the analysis of material from two neighboring quadrats was used for the construction of glyphs. These glyphs were placed on the map so as to represent both quadrats.

The measurements of each characteristic were reduced to means for each quadrat or quadrat-pair. The quadrat means were then arbitrarily divided into classes for translation into glyph form. Five classes were allotted to number of nodes and four to the other characteristics, as detailed in Table 9.

Table 9. Designations of classes for measurements of herbarium material and field collections. Statistics represent quadrat-means

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
</tr>
</thead>
<tbody>
<tr>
<td>no. of nodes</td>
<td>&lt;10</td>
<td>10-11</td>
<td>12-14</td>
<td>15-16</td>
<td>&gt;16</td>
</tr>
<tr>
<td>w. of culm (mm)</td>
<td>&lt;1.5</td>
<td>1.5-1.6</td>
<td>1.7-1.8</td>
<td>&gt;1.8</td>
<td></td>
</tr>
<tr>
<td>l. of infl. (cm)</td>
<td>&lt;7.6</td>
<td>7.6-8.7</td>
<td>8.8-9.9</td>
<td>&gt;9.9</td>
<td></td>
</tr>
<tr>
<td>l. of palea (mm)</td>
<td>&lt;3.1</td>
<td>3.1-3.2</td>
<td>3.3-3.4</td>
<td>&gt;3.4</td>
<td></td>
</tr>
</tbody>
</table>
Interpretation of Map

Number of nodes

The analysis of herbarium material showed that plants with the highest number of leaf-bearing nodes were collected in an area covering most of Kansas and southern Nebraska. A slight reduction occurred in plants collected through northern Missouri and southern Iowa into Illinois. A considerable reduction in nodal number was found in plants occurring northward into Minnesota and Wisconsin. The mean nodal numbers for quadrats in the above regions ranged from 17-20 nodes in Kansas and southern Nebraska to 11-12 nodes in northern Minnesota.

A sharp drop in nodal number occurred between the quadrats which include the southern portion of Nebraska south of the Platte River and those including much of the sandhills region in central and northwestern Nebraska. The quadrat means varied from 17-20 nodes in southern Nebraska to 11-12 nodes in northwestern Nebraska. The means were further reduced northward in North Dakota, Montana, and Wyoming.

A rapid reduction in number of nodes also occurred westward from central Kansas into New Mexico and Colorado. Nodal numbers generally varied between 9 and 11 in this Rocky Mountain region, dropping to as low as 7 in a pair of quadrats including parts of Colorado and Utah, and up to 12 in a quadrat along the Arkansas River system in Colorado.
Only a few incomplete specimens were viewed from regions of Oklahoma south of eastern Kansas. Indications were that they had about as many nodes as those in Kansas. To summarize, plants with the highest number of leaf-bearing nodes originated in a broad Kansas-southern Nebraska to southwestern Iowa-northern Missouri region. Some reduction in nodes occurred eastward and considerable reduction occurred northeastward, northward, and westward.

**Culm width**

The pattern of variability in culm width was poorly delineated in the analysis of the herbarium specimens (in contrast to the results obtained for this characteristic in the uniform garden). There was some indication of a correlation with nodal number. The means in the Kansas-southern Nebraska region mostly registered in the top two classes of measurements, but a number of quadrats in other regions, particularly to the northeast and southwest, also had plants with wide culms registering in these two classes. Plants from the northernmost tier of quadrats and some of the other more northern quadrats had narrow culms registering in the two lowest classes.

The indicated pattern was that of wide culms in the Kansas-southern Nebraska region, the culms tending to be narrower to the west and north, and considerable variability obtaining to the northeast and southwest.
Length of inflorescence

Variation in length of inflorescence reflected a pattern different from either of the above. Most of the plants with long inflorescences were collected in the Southwest—in Arizona, New Mexico, and Colorado. Some extraordinarily long inflorescences occurred on plants from this region. But plants with short inflorescences also occurred in this region, and these characteristically originated in the higher altitudes of the Rockies in Colorado and Utah and northward. Some variability obtained in the means for this measurement through the Middle West and northeastward, but in most cases the inflorescences were short. Two quadrats including parts of northern Iowa and southern to central Minnesota registered long inflorescences.

The indicated pattern, then, is one of long inflorescences in the southwestern region, a reduction in length at the higher altitudes in the Rockies of this same region and northward, and generally a reduction in length in all other regions, with some variability obtaining.

Length of palea

The pattern of variation in length of palea was similar to that for inflorescence length, but with some modifications. The longest paleas occurred in the Southwest and were only slightly shorter northward throughout the Rocky
Mountain chain and in the sandhills of Nebraska (whereas inflorescence length was considerably shorter in these regions). The means for this measurement were short in all other regions.

**Length of lemma relative to palea**

The pattern of variation recorded for lemma/palea ratio was fairly well defined. The lemma characteristically was longer than the palea for plants from the Rocky Mountain region. The lemma generally was equal to or shorter than the palea throughout the remainder of the range of distribution.

**Summary of regional variation patterns**

**Southwest** The analysis of field and herbarium specimens indicated that the plants of the Southwest usually have few nodes, from wide to narrow culms, a long inflorescence, and long paleas with the lemma exceeding the palea in length.

**Higher altitudes and northern Rockies** Plants of the higher altitudes of the Colorado Rockies and of the northern Rocky Mountain regions resemble those of the Southwest but have a narrower culm and a shorter inflorescence.

**Kansas-southern Iowa** Plants in a region through Kansas, southern Nebraska, southern Iowa, neighboring Missouri, and into Illinois usually have many nodes, a wide culm, most often a short inflorescence, short paleas, and the lemma
Plate 15. Variation in number of nodes, length of inflorescence, length of palea, width of culm, and length of lemma relative to that of the palea in herbarium and field collections of *M. racemosa*.

<table>
<thead>
<tr>
<th>NUMBER OF NODES:</th>
<th>LENGTH OF PALEA:</th>
<th>LENGTH OF LEMMA RELATIVE TO THAT OF THE PALEA:</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 10</td>
<td>&lt; 3.1 mm</td>
<td>o lemma is longer than the palea</td>
</tr>
<tr>
<td>10-11</td>
<td>3.1-3.2 mm</td>
<td>o lemma is equal to the palea</td>
</tr>
<tr>
<td>12-14</td>
<td>3.3-3.4 mm</td>
<td>o lemma is shorter than the palea</td>
</tr>
<tr>
<td>15-16</td>
<td>&gt; 3.4 mm</td>
<td></td>
</tr>
<tr>
<td>&gt; 16</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>LENGTH OF INFLORESCENCE:</th>
<th>WIDTH OF CULM:</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 7.6 cm</td>
<td>&lt; 1.5 mm</td>
</tr>
<tr>
<td>7.6-8.7 cm</td>
<td>1.5-1.6 mm</td>
</tr>
<tr>
<td>8.8-9.9 cm</td>
<td>1.7-1.8 mm</td>
</tr>
<tr>
<td>&gt; 9.9 cm</td>
<td>&gt; 1.8 mm</td>
</tr>
</tbody>
</table>
equal to or shorter than the palea.

**Northern Iowa-Minnesota and Wisconsin** Plants of the northeastern region have few to an intermediate number of nodes, a wide to narrow culm, often a short inflorescence but with some variability obtaining, short paleas, and the lemma equal to or shorter than the palea.

**Northern plains** Plants of the northern plains regions have few nodes, a narrow culm, a short inflorescence, short paleas, and the lemma about equal to the palea.

**Analysis of Uniform-Garden Results**

The interpretation of the uniform-garden results was based on the behavior of material collected from 24 quadrats in a broad northeast-southwest transect. The same characteristics were analyzed as for the herbarium material, with that of plant height added. The values of the classes designated for translation into glyph form had to be increased, except for those of length of palea, commensurate with the results obtained under the conditions of the uniform garden. Data on class designations are presented in Table 10.

There was some concern as to certain procedures prejudicing the results in the uniform garden. The plants were placed in the experimental garden as they were brought in from the field during the summer of 1961. Some were collected early in the season and had time to become established
Table 10. Designations of classes for measurements on specimens grown in the uniform garden at Ames. Statistics represent quadrat-means.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
</tr>
</thead>
<tbody>
<tr>
<td>no. of nodes</td>
<td>&lt; 12</td>
<td>12-14</td>
<td>15-17</td>
<td>18-21</td>
<td>&gt;21</td>
</tr>
<tr>
<td>w. of culm (mm)</td>
<td>&lt; 2.1</td>
<td>2.2-2.4</td>
<td>2.5-2.7</td>
<td>&gt; 2.7</td>
<td></td>
</tr>
<tr>
<td>plant height (cm)</td>
<td>&lt; 69</td>
<td>70-79</td>
<td>80-89</td>
<td>&gt; 89</td>
<td></td>
</tr>
<tr>
<td>l. of infl. (cm)</td>
<td>&lt; 8.7</td>
<td>8.8-9.9</td>
<td>10.0-11.1</td>
<td>&gt; 11.1</td>
<td></td>
</tr>
<tr>
<td>l. of palea (mm)</td>
<td>&lt; 3.0</td>
<td>3.1-3.2</td>
<td>3.3-3.4</td>
<td>&gt; 3.4</td>
<td></td>
</tr>
</tbody>
</table>
before going into winter dormancy. Others collected late in the season went into the winter simply as dormant rhizomes brought in from the field. A check was obtained on the possibility of this making a difference by some collections that were made both early and late in the growing season from the same site. This was done at two different locations. In both cases the individuals collected at different times from the same site demonstrated no essential difference in their behavior under the experimental garden conditions. Further, while individuals from the same site that were thought to be biotypically similar behaved very much alike, individuals from different locations often reacted quite differently.

Interpretation of Map

The patterns of variation produced by individuals grown in the transplant garden are depicted on Plate 16. The construction of the glyphs was based on the quadrat-means presented in Table 11.

The relatively uniform conditions of the experimental garden often sharpened distinctions between individuals, thereby making possible more critical interpretations. A discussion of the generalized regional variation patterns revealed in the uniform garden will precede a more detailed analysis of individual differences.
Table 11. Morphology of *M. racemosa* collections grown in the uniform garden at Ames. Data are means of all collections from each quadrat

<table>
<thead>
<tr>
<th>Quadrat No.</th>
<th>nodes^a^</th>
<th>ht. (cm)</th>
<th>width (mm)</th>
<th>infl. (cm)</th>
<th>palea (mm)</th>
<th>loc.^b^</th>
<th>spec.(^c)</th>
</tr>
</thead>
<tbody>
<tr>
<td>36</td>
<td>10</td>
<td>62</td>
<td>2.0</td>
<td>9.6</td>
<td>3.3</td>
<td>3</td>
<td>20</td>
</tr>
<tr>
<td>38</td>
<td>12</td>
<td>76</td>
<td>2.3</td>
<td>12.8</td>
<td>3.1</td>
<td>3</td>
<td>20</td>
</tr>
<tr>
<td>39</td>
<td>13</td>
<td>77</td>
<td>2.3</td>
<td>12.0</td>
<td>3.3</td>
<td>3</td>
<td>18</td>
</tr>
<tr>
<td>47</td>
<td>12</td>
<td>78</td>
<td>2.3</td>
<td>10.4</td>
<td>3.1</td>
<td>3</td>
<td>19</td>
</tr>
<tr>
<td>48</td>
<td>13</td>
<td>74</td>
<td>2.2</td>
<td>12.5</td>
<td>3.3</td>
<td>3</td>
<td>27</td>
</tr>
<tr>
<td>55</td>
<td>14</td>
<td>75</td>
<td>2.5</td>
<td>8.8</td>
<td>3.3</td>
<td>3</td>
<td>21</td>
</tr>
<tr>
<td>57</td>
<td>21</td>
<td>90</td>
<td>2.4</td>
<td>8.6</td>
<td>3.4</td>
<td>2</td>
<td>9</td>
</tr>
<tr>
<td>58</td>
<td>17</td>
<td>100</td>
<td>3.2</td>
<td>12.3</td>
<td>3.6</td>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>65</td>
<td>13</td>
<td>74</td>
<td>2.4</td>
<td>9.7</td>
<td>3.3</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>66</td>
<td>20</td>
<td>87</td>
<td>2.5</td>
<td>8.8</td>
<td>3.2</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>67</td>
<td>26</td>
<td>116</td>
<td>2.7</td>
<td>9.0</td>
<td>3.2</td>
<td>2</td>
<td>12</td>
</tr>
<tr>
<td>68</td>
<td>26</td>
<td>107</td>
<td>2.5</td>
<td>8.9</td>
<td>3.2</td>
<td>2</td>
<td>12</td>
</tr>
<tr>
<td>73</td>
<td>12</td>
<td>62</td>
<td>2.0</td>
<td>8.3</td>
<td>3.1</td>
<td>3</td>
<td>14</td>
</tr>
<tr>
<td>74</td>
<td>12</td>
<td>60</td>
<td>1.9</td>
<td>8.5</td>
<td>3.2</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>75</td>
<td>23</td>
<td>90</td>
<td>2.9</td>
<td>9.5</td>
<td>3.1</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>76</td>
<td>22</td>
<td>86</td>
<td>2.5</td>
<td>9.0</td>
<td>3.1</td>
<td>5</td>
<td>17</td>
</tr>
<tr>
<td>77</td>
<td>29</td>
<td>102</td>
<td>3.0</td>
<td>7.4</td>
<td>3.1</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>82-92</td>
<td>10</td>
<td>61</td>
<td>2.2</td>
<td>8.2</td>
<td>3.4</td>
<td>3</td>
<td>12</td>
</tr>
<tr>
<td>83</td>
<td>11</td>
<td>65</td>
<td>2.2</td>
<td>10.9</td>
<td>3.3</td>
<td>2</td>
<td>14</td>
</tr>
<tr>
<td>84</td>
<td>15</td>
<td>73</td>
<td>2.0</td>
<td>11.0</td>
<td>3.0</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>85</td>
<td>16</td>
<td>74</td>
<td>2.5</td>
<td>9.2</td>
<td>3.0</td>
<td>5</td>
<td>19</td>
</tr>
<tr>
<td>86</td>
<td>24</td>
<td>101</td>
<td>2.9</td>
<td>9.9</td>
<td>3.2</td>
<td>4</td>
<td>10</td>
</tr>
<tr>
<td>105</td>
<td>18</td>
<td>73</td>
<td>2.6</td>
<td>9.4</td>
<td>2.9</td>
<td>2</td>
<td>8</td>
</tr>
</tbody>
</table>

^a^number of leaf-bearing nodes

^b^number of collection localities

^c^number of specimens examined
Generalized regional variation patterns

**Southwest**  A number of the plants from northeastern New Mexico and southern Colorado repeated the characteristics of the herbarium material from the Southwest in having a small number of nodes, narrow culms, relatively short height, very long inflorescences, and long paleas. Others from this same region that did not conform to this pattern will be considered in a later discussion.

**Northern Colorado**  Collections from north of Boulder agreed with the pattern indicated by the herbarium specimens for the higher altitudes and more northern regions of the Rockies. They were very similar to the southwestern forms described above but with shorter inflorescences, narrower culms, and less height.

**Sandhills of Nebraska**  Plants of the sandhills region of Nebraska also were of this type, having few nodes, short inflorescences, and long paleas, but with culm width and stature varying to some degree.

**Kansas—southwestern Iowa**  Plants in the Kansas—southern Nebraska to southwestern Iowa—northwestern Missouri region also reflected the pattern indicated by the herbarium material in having many nodes, generally short inflorescences and short paleas, thick culms, and considerable height.

**Northern Iowa—Minnesota**  Plants from northern Iowa, Minnesota, and South Dakota as a rule had fewer nodes,
Plate 16. Variation in number of nodes, length of inflorescence, length of palea, width of culm, plant height, and length of lemma relative to that of the palea in specimens of *M. racemosa* grown in the uniform garden at Ames, Iowa.

<table>
<thead>
<tr>
<th>Number of Nodes:</th>
<th>LENGTH OF PALEA:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>● ○ &lt; 12</td>
<td>○ ○ ○ &lt; 3.1 mm</td>
</tr>
<tr>
<td>○ ○ 12-14</td>
<td>○ ○ ○ 3.1-3.2 mm</td>
</tr>
<tr>
<td>○ ○ ○ 15-17</td>
<td>○ ○ ○ 3.3-3.4 mm</td>
</tr>
<tr>
<td>○ ○ ○ ○ 18-21</td>
<td>○ ○ ○ ○ &gt; 3.4 mm</td>
</tr>
<tr>
<td>○ ○ ○ ○ ○ 2&gt;21</td>
<td>number of different locations from which rhizomes were collected</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Length of Inflorescence:</th>
</tr>
</thead>
<tbody>
<tr>
<td>● ○ &lt; 8.8 cm</td>
</tr>
<tr>
<td>○ ○ 8.8-9.9 cm</td>
</tr>
<tr>
<td>○ ○ ○ 10.0-11.1 cm</td>
</tr>
<tr>
<td>○ ○ ○ ○ &gt; 11.1 cm</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Length of Lemma Relative to That of the Palea:</th>
</tr>
</thead>
<tbody>
<tr>
<td>○ ○ lemma is longer than the palea</td>
</tr>
<tr>
<td>○ ○ lemma is equal to the palea</td>
</tr>
<tr>
<td>○ ○ lemma is shorter than the palea</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Width of Culm:</th>
</tr>
</thead>
<tbody>
<tr>
<td>● ○ &lt; 2.2 mm</td>
</tr>
<tr>
<td>○ ○ 2.3-2.4 mm</td>
</tr>
<tr>
<td>○ ○ ○ 2.5-2.7 mm</td>
</tr>
<tr>
<td>○ ○ ○ ○ &gt; 2.7 mm</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Plant Height:</th>
</tr>
</thead>
<tbody>
<tr>
<td>● ○ &lt; 70 cm</td>
</tr>
<tr>
<td>○ ○ 70-79 cm</td>
</tr>
<tr>
<td>○ ○ ○ 80-89 cm</td>
</tr>
<tr>
<td>○ ○ ○ ○ &gt; 89 cm</td>
</tr>
</tbody>
</table>
narrower culms, and shorter heights than those in the Kansan region. Collections from the two quadrats in northern Iowa and Minnesota that registered long inflorescences in the analysis of the herbarium specimens also produced long inflorescences in the transplant garden. A deviation from expected results occurred when plants from two of the northernmost quadrats produced long paleas.

**Length of lemma relative to palea**

The same trend in the length of lemma/palea ratio was demonstrated in the uniform garden as in the herbarium material. The lemma was longer than the palea for plants from the Southwest to central Kansas and was equal to or shorter than the palea for plants to the north and northeast.

**Phenological Data**

**Extremes in emergence times**

Phenology was measured by dating the first appearance of the emerging inflorescence, thus providing an emergence time. Anthesis generally occurred from 12-16 days later.

Most of the plants from all regions produced young shoots within the first week of May. Inflorescences were first exerted June 10 on individuals collected from northern Minnesota, followed on June 13 by some individuals from northern Colorado and a high altitude station in northern
New Mexico. Thus, plants from the opposite ends of the transect started coming into flower together. These individuals probably flowered a month to six weeks ahead of the time that they would have flowered in their native habitats.

Some plants from northwestern Missouri and central Kansas were the latest to come into flower. Their inflorescences first appeared on September 6. Others from northeastern and southwestern Kansas emerged as late as September 2. Therefore, almost a three months span in emergence times was demonstrated in the uniform garden. (See Plate 17.)

**Regional changes in emergence times**

**Northeastern region**  The change in emergence times was more or less gradual from northern Minnesota to south central Iowa. Generally the range in emergence times of individuals for a single quadrat was sufficient so that there was overlapping in the times of emergence between neighboring quadrats. Emergence times ranged from June 10 for some individuals from northern Minnesota to July 28 for an individual from south central Iowa. Within Iowa itself emergence times ranged from July 5 for an individual from Belmond in northern Iowa to August 22 for one from Clarinda in southwestern Iowa.

**Southern midwest region**  A seemingly significant shift took place in the total range of emergence times demonstrated by collections from central Iowa to northwestern
Missouri. Most of the plants in the central Iowa-Nebraska region emerged in late July, with a few emerging on August 1 and August 4. Some collections from about 65 to 75 miles farther south in northwestern Missouri and northeastern Kansas emerged a whole month later, as late as September 2 and September 6. Others within this same Missouri-Kansas region emerged as early as July 25 and August 1. Thus, almost a six weeks latitude in times of emergence was demonstrated for collections from this region.

All of the plants collected from northeastern-southwestern Kansas emerged in August or early September. The variability was such that no gradient was demonstrated through this Kansas region, with about a month's range in emergence times being expressed for collections from southwestern as well as northeastern Kansas.

Southwestern region A break in emergence times occurred between collections from the western-southwestern Kansas region and those from the Oklahoma Panhandle, northeastern New Mexico, and Colorado. From four to six weeks difference in initial emergence times was registered between neighboring quadrats of these two regions, and there was practically no overlap in spans of emergence times. A wide range in times of emergence was demonstrated for the southwestern region with inflorescences being exserted from June 13-August 6.
Plate 17. Emergence times of collections of M. racemosa grown in the uniform garden at Ames

Emergence time was taken as the time of first appearance of the inflorescence as it emerged from the enclosing leaf sheath.
Three collections from north of Boulder, Colorado emerged from June 13-July 8. This corresponded very closely to the June 10-July 5 span in emergence times for three collections from northern Minnesota.

**Sandhills region** Another break in emergence times, without any overlap being demonstrated, occurred between collections from the sandhills region of north central and western Nebraska and those from regions directly to the east and south. Plants from the sandhills emerged from June 28-July 19. Those from southern Nebraska emerged from July 22-August 8, while those from northeastern Nebraska and neighboring southeastern South Dakota emerged from July 28-August 4.

The results obtained for the plants from Nebraska corresponded with those obtained by McMillan (1956a, 1956b, 1957, 1959) in transplant studies of a number of grass species in the same state. He found that plants from the northwestern regions of Nebraska flowered about two weeks earlier than did those from around Lincoln in southeastern Nebraska. In the present study a four-weeks difference in emergence times was found for plants of *M. racemosa* from the same regions. (Not all of the grasses studied by McMillan demonstrated this progression in flowering times. Flowering times of *Stipa spartea* Trin., *S. comata* Trin. and Rupr., and *Oryzopsis hymenoides* (Roem. and Schult.) Ricker. were simul-
Summary of emergence times

In summary, emergence times generally showed a good correlation with nodal number, so that plants from the Kansas to southeastern Iowa region emerged the latest, and those from the southwestern, western, and northern regions emerged progressively earlier. Some notable exceptions to the correlation between nodal number and emergence times will be discussed in the following section.

Internodal Patterns

The previous considerations have served to outline the broad features of variation as demonstrated by means and ranges in measurements. The following discussion will deal more particularly with individuals, employing internodal-pattern graphs as was done for *M. glomerata*, and correlating these patterns with the other characteristics.

Plates 18-21 present a series of internodal patterns for uniform-garden specimens from 21 of the 24 quadrats represented in the experimental garden. A few field specimens are also graphed. The graphs are arranged in geographic order so that individuals from northern Minnesota will be viewed first, followed by individuals from more southern regions in Minnesota, through Iowa, northwestern Missouri,
southwestward through Kansas, the Oklahoma Panhandle, north­eastern New Mexico, northward into Colorado, and returning northeastward through Nebraska, eastern South Dakota, and finally into west central Minnesota.

**Ascending internodal pattern**

Some individuals from Ray and Park Rapids, Minnesota demonstrated the ascending internodal pattern that is characteristic of the more northern and western occurring specimens of *M. glomerata* (Plate 18, a and b). This type of pattern is produced by individuals having basal internodes that are shorter than most of the middle and upper internodes, these tending to be progressively longer. These individuals generally have fewer than 12 leaf-bearing nodes. Occasionally an individual will be found with a very short, "abortive" internode that often occurs just prior to the peduncle (Plate 18, b and g), and which therefore disrupts the pattern.

**Concave configuration**

Plants collected southward into the midwest region demonstrated an entirely different internodal pattern. These plants generally produced middle to upper internodes that were short relative to the basal internodes, or which at least did not elongate relative to the basal internodes. As a rule some of the basal internodes were longer than four centimeters, while the internodes through the middle to upper
Plate 18. Internodal-pattern graphs with morphological data of specimens of *M. racemosa* grown in the uniform garden at Ames.

The location is the approximate origin of the rhizome transplanted in the experimental garden.

Abbreviations for morphological data:

- **ht.** -- height
- **c. w.** -- culm width
- **l. of infl.** -- length of inflorescence
- **phenol.** -- emergence time
Ray, Minn.
ht: 73
c.w. 2.2
l. of infl: 8.5
phenol: Jun. 10

Park Rapids, Minn.
ht: 49
c.w. 2.1
l. of infl: 7.5
phenol: Jun. 10

Duluth, Minn
ht: 71
c.w. 2.5
l. of infl: 8.5
phenol: Jun. 28

Sartell, Minn.
ht: 69
c.w. 2.5
l. of infl: 8.8
phenol: Jun. 26

Taylor Falls, Minn.
ht: 60
c.w. 2.1
l. of infl: 12.0
phenol: Jul. 5

Silver Lake Park, Iowa
ht: 71
c.w. 2.2
l. of infl: 9.0
phenol: Jul. 12

Belmond, Ia.
ht: 71
c.w. 2.7
l. of infl: 9.7
phenol: Jul. 5

Jewell, Ia.
ht: 81
c.w. 2.8
l. of infl: 8.0
phenol: Jul. 22

Casey, Ia.
ht: 90
c.w. 2.7
l. of infl: 145
phenol: Jul. 28

Clarinda, Ia.
ht: 96
c.w. 2.6
l. of infl: 9.7
phenol: Aug. 22
portion of the culm were shorter than four centimeters. The final internodes were elongated with the peduncle being the longest.

If the internodes in the middle to upper region did not vary to any extent, the growth-habit curve just described formed a somewhat concave or depressed configuration. If the internodal measurements varied a great deal, the curve was much more irregular. Generally, once the curve dipped below the 4-cm line it tended to remain below the line until the abrupt upsweep for the final internodes. In some cases the basal internodes also failed to grow longer than four centimeters.

**Variation in southern midwest region**

The concave or depressed configuration, with most of the internodes measuring less than four centimeters, was found to be characteristic of the individuals collected through Iowa, northwestern Missouri, southern Nebraska, and all of Kansas. But some variants from this pattern were encountered in this region. For example, an individual collected near Home, Kansas (Plate 19, b) demonstrated the concave configuration but with most of the internodes measuring four centimeters or more, while another individual collected from the same location was more "typical" with most of its internodes measuring less than four centimeters. The deviate also differed from the more typical one in having fewer leaf-bearing nodes
Plate 19. Internodal-pattern graphs with morphological data of specimens of *M. racemosa* grown in the uniform garden at Ames.

Abbreviations for morphological data:

- ht. -- height
- c.w. -- culm width
- l. of infl. -- length of inflorescence
- phenol. -- emergence time
Mound City, Mo.
ht: 123  l. of infl: 8.3
c.w. 3.3  phenol: Sept. 6

Home, Kans.
ht: 101  l. of infl: 8.0
c.w. 2.4  phenol: Aug 1

Home, Kans.
ht: 103  l. of infl: 8.2
c.w. 3.0  phenol: Aug 18

Riley, Kans.
ht: 114  l. of infl: 8.3
c.w. 2.8  phenol: Aug 22

Timken, Kans.
ht: 135  l. of infl: 9.0
c.w. 3.1  phenol: Aug 15

Claflin, Kans
ht: 116  l. of infl: 9.0
c.w. 2.8  phenol: Aug 11

Scott City, Kans.
ht: 90  l. of infl: 9.0
c.w. 2.5  phenol: Aug 1
and exserting its inflorescence much earlier (Aug. 1 vs. Aug. 18). Individuals from the northwestern Missouri-southwestern Kansas region varied in number of nodes from 21-34, and in times of emergence from July 25-September 6. Thus, the large latitude in number of nodes and emergence times found in populations through this region is generally correlated with the same type of internodal pattern.

The variation that might occur in a single locality was well demonstrated for two different collections in Meade County Park, Kansas. The two collections behaved in the uniform garden as follows:

<table>
<thead>
<tr>
<th>Collection No.</th>
<th>Range in number of nodes</th>
<th>Range in emergence times</th>
<th>Average length of palea</th>
<th>Average length of inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>29-34</td>
<td>Aug. 25-Sept. 2</td>
<td>3.1</td>
<td>7.7</td>
</tr>
<tr>
<td>393</td>
<td>26-31</td>
<td>Aug. 5-25</td>
<td>3.5</td>
<td>9.0</td>
</tr>
</tbody>
</table>

The two collections definitely represented different biotypes or ranges of biotypes. The differences in emergence times are noteworthy. An individual of collection 392 with 31 nodes emerged on August 8 compared to September 2 for an individual with 30 nodes of collection 393. The internodal patterns conformed to that for the Kansan region, although on one individual a number of the basal internodes were over four centimeters long (Plate 20, a and b).

Hereafter, for purposes of discussion individuals of
the Kansan region, with most of their internodes measuring less than four centimeters, will be referred to as the "midwest form."

Variation in the southwestern region

The uniform-garden results for individuals from the Southwest were such that they could be placed, roughly, into three groups according to number of nodes, time of emergence, and height measurements as correlated with internodal pattern.

Western mountain form One group was arbitrarily termed the "western mountain form" and included individuals demonstrating an ascending to irregular internodal pattern with most of the internodes measuring more than four centimeters. These individuals had fewer than 14 leaf-bearing nodes, grew up to 80 cm in height but generally measured 60-75 cm, and emerged from June 13 to about July 8. (See Plate 20, e, g, h, and j, and Plate 21, a, c, and d.)

Robust form Another group was termed the "robust form" and featured an irregular to somewhat concave internodal pattern with most of the internodes measuring more than four centimeters. These individuals had from 14-23 nodes, measured from 85-115 cm tall, and emerged from July 1-28. (See Plate 20, c, f, and k, and Plate 21, b.)

Midwest variant A third group was termed the "midwest variant" and included individuals demonstrating the
midwest form of internodal pattern with internodes that were mostly shorter than four centimeters. These individuals had from 15-23 nodes, measured from 65-90 cm tall, and emerged from July 19-August 1. As a rule they had long inflorescences whereas the Kansan forms generally have short inflorescences.

Table 12 presents information on some representatives of these three groups with individuals from the Kansan region included for comparative purposes.

Interpretation of table

The table shows the effect of the shorter internodes on the midwest variant. Although it averaged about twice as many nodes and matured about a month later than the western mountain form, the midwest variant often grew only 10-15 per cent taller. A comparison with the robust form is even more striking. Some of the robust individuals produced as many nodes as the midwest variant but emerged about two weeks earlier and still grew considerably taller with thicker culms. Some even grew as tall as many of the Kansan representatives and in much less time. For example, an individual from Cañon City, Colorado with 14 nodes grew as tall as one from Meade County Park, Kansas with 34 nodes and matured about two months sooner.

As the table indicates the robust type individuals characteristically had long to very long inflorescences. A considerable amount of variability is demonstrated between
Table 12. Morphology and phenology of individuals of *M. racemosa* representing different behavior patterns in the uniform garden at Ames

<table>
<thead>
<tr>
<th>Approximate Origin of Collection</th>
<th>nodes(^a) (cm)</th>
<th>ht.</th>
<th>culm width</th>
<th>l. of infl.</th>
<th>l. of palea</th>
<th>phenol.(^b)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Western mountain form:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Boulder, Colo.</td>
<td>8</td>
<td>61</td>
<td>2.0</td>
<td>9.8</td>
<td>3.2</td>
<td>June 13</td>
</tr>
<tr>
<td>Ute Park, N. Mex.</td>
<td>9</td>
<td>67</td>
<td>1.7</td>
<td>10.7</td>
<td>3.2</td>
<td>June 21</td>
</tr>
<tr>
<td>Las Vegas, N. Mes.</td>
<td>10</td>
<td>73</td>
<td>2.3</td>
<td>9.5</td>
<td>3.7</td>
<td>June 24</td>
</tr>
<tr>
<td>Cañon City, Colo.</td>
<td>10</td>
<td>80</td>
<td>2.5</td>
<td>8.8</td>
<td>3.1</td>
<td>June 28</td>
</tr>
<tr>
<td>Trinchera, Colo.</td>
<td>11</td>
<td>75</td>
<td>2.0</td>
<td>16.5</td>
<td>3.4</td>
<td>July 5</td>
</tr>
<tr>
<td>Raton Pass, Colo.</td>
<td>11</td>
<td>70</td>
<td>2.1</td>
<td>9.2</td>
<td>3.4</td>
<td>June 28</td>
</tr>
<tr>
<td>Midwest variant:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kim, Colo.</td>
<td>17</td>
<td>81</td>
<td>2.4</td>
<td>11.0</td>
<td>3.2</td>
<td>July 22</td>
</tr>
<tr>
<td>Kim, Colo.</td>
<td>19</td>
<td>84</td>
<td>2.6</td>
<td>9.7</td>
<td>3.3</td>
<td>July 19</td>
</tr>
<tr>
<td>Las Vegas, N. Mex.</td>
<td>19</td>
<td>84</td>
<td>2.9</td>
<td>12.3</td>
<td>3.3</td>
<td>July 22</td>
</tr>
<tr>
<td>Las Vegas, N. Mex.</td>
<td>21</td>
<td>84</td>
<td>2.5</td>
<td>11.3</td>
<td>2.9</td>
<td>July 28</td>
</tr>
<tr>
<td>Robust form:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cañon City, Colo.</td>
<td>14</td>
<td>107</td>
<td>2.7</td>
<td>13.0</td>
<td>3.1</td>
<td>July 1</td>
</tr>
<tr>
<td>Guymon, Okla.</td>
<td>15</td>
<td>113</td>
<td>3.5</td>
<td>12.0</td>
<td>3.4</td>
<td>July 5</td>
</tr>
<tr>
<td>Española, N. Mex.</td>
<td>16</td>
<td>95</td>
<td>3.0</td>
<td>13.5</td>
<td>3.1</td>
<td>July 5</td>
</tr>
<tr>
<td>Guymon, Okla.</td>
<td>18</td>
<td>106</td>
<td>3.0</td>
<td>11.8</td>
<td>3.4</td>
<td>July 10</td>
</tr>
<tr>
<td>Guymon, Okla.</td>
<td>23</td>
<td>110</td>
<td>3.3</td>
<td>13.8</td>
<td>3.7</td>
<td>July 28</td>
</tr>
<tr>
<td>Midwest form:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sutton, Neb.</td>
<td>21</td>
<td>87</td>
<td>2.7</td>
<td>8.6</td>
<td>2.9</td>
<td>Aug. 1</td>
</tr>
<tr>
<td>Baileyville, Kans.</td>
<td>23</td>
<td>95</td>
<td>2.5</td>
<td>10.3</td>
<td>3.0</td>
<td>Aug. 15</td>
</tr>
<tr>
<td>Home, Kans.</td>
<td>27</td>
<td>103</td>
<td>3.0</td>
<td>8.2</td>
<td>2.8</td>
<td>Aug. 18</td>
</tr>
<tr>
<td>Riley, Kans.</td>
<td>30</td>
<td>114</td>
<td>2.8</td>
<td>8.3</td>
<td>2.8</td>
<td>Aug. 22</td>
</tr>
<tr>
<td>Timken, Kans.</td>
<td>31</td>
<td>135</td>
<td>3.1</td>
<td>9.0</td>
<td>3.4</td>
<td>Aug. 15</td>
</tr>
<tr>
<td>Mound City, Mo.</td>
<td>31</td>
<td>123</td>
<td>3.3</td>
<td>8.3</td>
<td>3.1</td>
<td>Sept. 6</td>
</tr>
<tr>
<td>Meade Co., Kans.</td>
<td>34</td>
<td>107</td>
<td>3.1</td>
<td>6.7</td>
<td>3.1</td>
<td>Sept. 2</td>
</tr>
</tbody>
</table>

\(^{a}\)number of leaf-bearing nodes

\(^{b}\)date of emergence of inflorescence from leaf sheath
Plate 20. Internodal pattern graphs with morphological data of specimens of *M. racemosa* grown in the uniform garden at Ames

Abbreviations for morphological data:

- ht. --- height
- c.w. --- culm width
- l. of infl. --- length of inflorescence
- l./p. --- length of lemma/palea
- phenol. --- emergence time
the other individuals of the table for this characteristic. The midwest variant of the Southwest generally had long inflorescences. The western mountain forms occasionally had long inflorescences, but usually their inflorescences were shorter than for the other southwestern forms. The midwest forms mostly had short inflorescences.

The table shows considerable variability in length of palea, but the western mountain forms and other southwestern forms generally had long paleas. Palea measurements most often were shorter on the midwest forms.

Ecology and distribution of Southwest forms

The three forms described for the Southwest are not necessarily ecologically separated. An individual of the midwest type and one of the western mountain type were collected from the same location near Las Vegas, New Mexico (Plate 20, d and e). Two individuals of entirely different types were collected from the same site on bottomland along the Arkansas River near Pueblo, Colorado (Plate 21, c—the individuals represented in the graph are specimens from the field, not from the uniform garden). A mature individual was of the western mountain type with nine leaf-bearing nodes. At the same date another had 15 leaf-bearing nodes and was prior to anthesis. This probably represented at least a month's difference in phenology. Collections made in the Arkansas River canyon west of Cañon City, although at
different locations, also were of different types (Plate 21, a and b—depicting specimens from the field). Thirteen individuals in the one collection were of the western mountain form having from 7-12 nodes and measuring 35-80 cm tall. Two individuals taken from a small colony in the other collection were of the robust type with 19 and 20 nodes, the culms measuring 118 cm and 128 cm in height.

At least four different sites were located along the Arkansas River, from the plains region at La Junta to the mountainous region in the canyon, in which the robust form was found to occur. Two of the sites were on Arkansas River bottomland and two were along irrigation ditches. The western mountain form also was found to occur through this same region, and some plants that were too young for a definite determination had the appearance of the midwest form.

**Sandhills region of Nebraska**

The individuals of the sandhills region resembled those of the western mountains and the Southwest in characteristics of height, nodal number, length of palea, and times of emergence. They had from 12-16 nodes and long paleas, grew from 60-90 cm tall and exserted their inflorescences from June 28-July 19. But their internodal patterns were either intermediate between the western mountain form and the midwest form or were quite definitely an abbreviated midwest form (Plate 21, f-j). An individual from Long Pine, Nebraska
Plate 21. Internodal-pattern graphs with morphological data of specimens of *M. racemosa* collected from the field and grown in the uniform garden at Ames

a.-c. Specimens collected from the field

d.-m. Specimens grown in the uniform garden

Abbreviations for morphological data:

- ht. — height
- c.w. — culm width
- l. of infl. — length of inflorescence
- phenol. — emergence time
Arkansas River canyon, Colo.
ht: 59
c.w. 1.8
I. of infl: 9.7
phenol: near maturity

Arkansas River canyon, Colo.
ht: 118
c.w. 2.7
I. of infl: 10.5
phenol: immature

Pueblo, Colo.
ht: 70, 81
c.w. 1.6, 1.9
I. of infl: 10.5, 7.5
phenol: mature, immature

Boulder, Colo.
ht: 61
I. of infl: 9.8
c.w. 2.0
phenol: Jun 13

Boulder, Colo.
ht: 65
I. of infl: 8.3
c.w. 2.0
phenol: Jul 3

Bingham, Neb.
ht: 62
I. of infl: 7.3
c.w. 2.1
phenol: Jul 12

Lakeside, Neb.
ht: 75
I. of infl: 8.4
c.w. 3.0
phenol: Jun 28

Mullen, Neb.
ht: 77
c.w. 2.6
I. of infl: 9.0
phenol: Jul 5

Mullen, Neb
ht: 73
c.w. 2.4
I. of infl: 10.5
phenol: Jul 7

Long Pine, Neb.
ht: 96
c.w. 3.0
I. of infl: 10.3
phenol: Jul 7

Summit, S. Dak.
ht: 42
c.w. 1.9
I. of infl: 7.0
phenol: Jun 28

Yankton, S. Dak.
ht: 89
c.w. 3.5
I. of infl: 8.8
phenol: Aug 4

Breckenridge, Minn.
ht: 84
c.w. 2.1
I. of infl: 10.5
phenol: Jul 11
(Plate 21, j) demonstrated some of the characteristics of the robust form of the Southwest in having a long inflorescence and more height than the other individuals of that region.

South Dakota-west central Minnesota

Some collections from the southeastern corner of South Dakota near the Missouri River (near Yankton) and from the west central border of Minnesota along the Red River (near Breckenridge) had considerably more nodes and later emergence times than did other collections from comparable or even more southern latitudes. They both demonstrated unmistakable midwest internodal patterns.

The South Dakota collection produced from 23-24 nodes and emerged from August 1-4 (Plate 21, k). Other collections from comparable latitudes east of there produced from 12-19 nodes and emerged from July 12-22. The Minnesota collection produced from 13-16 nodes and emerged from July 5-15 (Plate 21, m). Collections from farther south toward the eastern border of Minnesota (near Sartell and Taylor Falls) only produced from 9-12 nodes and emerged from June 28-July 8.

A collection from northeastern South Dakota drew particular attention in the uniform garden because of its stunted habit of growth. Four individuals of this collection had the distinction of producing the fewest nodes, from 5-7, and the shortest heights, from 28-42 cm, of all the individ-
uals of *M. racemosa* in the uniform garden (Plate 21, 1). The caryopses, too, were below normal in size.

Other individuals from farther north grew much taller. Those from Breckenridge about 70 miles due north grew from 67-84 cm tall. Individuals of the northernmost collection from Ray, Minnesota produced from 7-11 nodes and grew from 60-73 cm tall.

A series of photographs are presented on Plates 22 and 23 illustrating the various forms of *M. racemosa* that have been discussed in this section.

Discussion

The author proposes that variation demonstrated for *M. racemosa* was of the following general types: variation of a regional type, variation within regional types, and variation due to hybridization between regional types. Within this framework variation occurred both in gradients, or clines, and in discontinuities. Further, it is believed that a random type of variation, superimposed upon regional variation, was also shown to occur.

The characteristics used to denote variation showed some patterns of variation that were correlated and some that were independent of each other. In comparing individuals grown in the uniform garden, the characteristic of number of nodes in correlation with internodal pattern, emergence time, and height is thought to be the most fundamental for differen-
Plate 22. Field specimens and plants of *M. racemosa* grown in uniform garden at Ames

a. left, field specimen collected in Arkansas River canyon west of Cañon City, Colorado. Plant illustrates robust form with 20 leaf-bearing nodes (Mitchell No. 629)

right, specimen collected in same canyon on same day. Plant illustrates western mountain form with 10 nodes (Mitchell No. 627)

b. left, uniform-garden specimen originating from Meade Co. Park, Kansas. Plant illustrates midwest form with 34 nodes (Mitchell No. 393)

right, uniform-garden specimen originating near Guymon, Oklahoma (in panhandle). Plant illustrates robust form with 18 nodes (Mitchell No. 397)

c. left, uniform-garden specimen originating near Las Vegas, New Mexico. Plant illustrates midwest variant with 22 nodes (Mitchell No. 406)

right, uniform-garden specimen originating north of Boulder, Colorado. Plant illustrates western mountain form with 8 nodes (Mitchell No. 430)
Plate 23. Uniform-garden specimens of *M. racemosa*

a. left, midwest form with 26 nodes originating from Riley, Kansas (Mitchell No. 537)
right, plant with 14 nodes originating from sandhills near Mullen, Nebraska (Mitchell No. 445)

b. left, plant with 7 nodes from northeastern South Dakota showing stunted growth habit (Mitchell No. 568)
right, plant with 10 nodes originating from northern Minnesota (Mitchell No. 489)
tiating between the variants and in reflecting geneecological variation.

**Variation in the midwest type**

Eoclinal variation within a regional type, of the nature propounded by Gregor (1939, 1944) from his work on *Plantago maritima* L., was demonstrated for individuals of the midwest type originating from southern Iowa northward to central Minnesota. The tolerance of *M. racemosa* to the changing conditions of this north-to-south gradient appears to be expressed, at least in part, in a gradual change in number of nodes as correlated with emergence times and height. The characters of length of inflorescence, length of palea, and length of lemma/palea ratio appear to vary independently of number of nodes on this same transect.

Some unexpected variation between populations on this transect may possibly be explained on the basis of the environment of major river systems supporting individuals of a more southern type (e.g., the Yankton, South Dakota and Breckenridge, Minnesota collections) or on the basis of chance variations occurring in small, isolated populations (e.g., the stunted individuals from northeastern South Dakota).

The latter collection was made in an isolated shelter belt of an upland plains region. Much of the area around it was farmed, and there appeared to be no other suitable
habitat for *M. racemosa* in the vicinity. The phenotypic response of this collection appears to be an example of the Sewall Wright effect (1931) and therefore to reflect a biotype that has become fixed by chance in a small isolated population.

Variation cannot be described on an ecolinal basis for the region from southern Iowa to southwestern Kansas. This region supports individuals of the midwest type but permits a wide latitude in the number of nodes that individuals of a population may have. The correlation between the character of nodal number and those of emergence time and height appears to break down to some extent so that considerable variability may obtain for this combination of characteristics. However, considering the region as a whole, it supports individuals with the most nodes, latest emergence times, and, except for the robust forms in the Southwest, the greatest height.

**Variation in the southwestern regions**

The differences displayed by individuals from the Southwest appeared to be of such a nature as to warrant separating them into groups. Some individuals of the midwest type were found there, but with fewer nodes, less height, earlier emergence times, and generally longer inflorescences than was true for the Kansan forms. Individuals demonstrating an entirely different internodal pattern, much earlier emergence
times, fewer nodes, and less height also were collected in this region and found to prevail through much of the Rocky Mountain area. The differences between the midwest form and the latter individuals, termed the western mountain form, were so distinct as to suggest differentiated gene systems for the two forms.

A third type of individual found to occur in Colorado and New Mexico had from relatively few nodes to as many nodes as the midwest variant, but grew much taller than the latter and matured earlier. This type demonstrated a somewhat variable internodal pattern. The difference in maturation times between the midwest variants and the robust forms, when related to internodal growth, appears to be contrary to what one might expect. Representatives of the two types may have the same number of nodes, but those with the shortest internodes generally mature the latest.

The difference between the midwest form and the western mountain form was most striking in the uniform garden. Whereas the western mountain individuals had exerted their inflorescences and matured by late July, the midwest forms were still producing leaves that were very congested on the culm. Internodal pattern as correlated with number of nodes appears to be the best morphological means for delineating these different maturation types. Quinby and Karper (1945) studied different maturation types in *Sorghum vulgare* Pers.
They showed by extensive crossing experiments that length of internodes is influenced by maturation types and described three different internodal patterns that could be correlated with maturation types.

Thus, it appears that two differentiated gene systems with large regional occurrences have a sympatric distribution in the Southwest, occasionally frequenting the same habitats. If such is the case, one might expect that hybridization between the two would produce detectable variants.

It is likely that the robust form represents a hybrid or hybrid-segregate, since it occurs in this region of contact between the two forms where there is an abrupt shift from plains environment to mountain environment. The fact that it displays some unique characteristics in the way of heterosis would appear to constitute substantial evidence for its hybridity. Its occurrence, in turn, lends support to the hypothesis that the midwest and western mountain forms are differentiated gene systems. Chromosome counts have not provided any evidence that ploidy can account for the differences. Counts obtained on individuals of all three forms have been normal (2n=40).

The considerable height obtained by many of the robust individuals appears to be of particular significance. McMillan (1959) found that for those grasses which showed a correlation between height and times of flowering the
earlier maturing individuals were of the shorter stature. Since the same correlation was demonstrated for *M. racemosa*, any large deviation occurring in the uniform garden, which also could be shown to occur in the field, must be considered a matter of consequence. A number of these individuals located in early August 1961 along the Arkansas River in Colorado, not yet mature but well advanced beyond those to be found in Kansas a few days later, measured from 118-135 cm. The western mountain form commonly is no more than 80 cm and the midwest form no more than 100 cm in their native habitats. Some of the robust type individuals were the tallest collected in the field.

If the robust type is a hybrid form, one would expect that a population containing these individuals might also contain a number of recombinant variants. The densest stand of *M. racemosa* found by the author occurred on the western edge of Cañon City, Colorado along an irrigation ditch. It consisted of a highly variable population that included a number of individuals of the robust type. In a population sample of 35 specimens the following ranges in characteristics were obtained:

- number of nodes: 10-19
- tentative heights (most not yet fully grown): 45-135 cm
- inflorescence lengths: 6.7-12.3 cm
- palea lengths: 2.6-3.6 mm

A great deal of variation also occurred in phenology. A plant with 18 nodes was found past anthesis and producing
immature grain while a number of plants with from 11-13 nodes were found in the pre-anthesis stage. Most of the plants were in the pre- to early-anthesis stage. But allowances must be made for the fact that these characteristics were expressed under the variable conditions of a disturbed native habitat.

Coherence as a factor in discontinuous variation

Turesson (1922a, 1922b) coined the term "ecotype" to define adjoining but distinct populations of Hieracium umbellatum L. and a number of other species that he investigated. His sampling methods and descriptions suggest that he viewed ecotypic variation as applying to local populations (Turrill, 1946). The discontinuity demonstrated in this study is between regional types, conforming rather to the ecotypes described by Clausen, Keck, and Hiesey (1940) for Potentilla glandulosa Lindl. The author, however, agrees with Gregor (1944, 1946) that the term ecotype should not be applied to distinguishable variants of a large regional order.

The maintenance of the midwest and western mountain forms in the same region appears to demonstrate the principle of coherence (Clausen and Hiesey, 1958; Nobs, 1961). Clausen and Hiesey (p. 155) have summed up the principles believed to be operating here as follows:

Two principles appear to have operated in the evolution of natural races for contrasting environments. One is that such races have a mechanism enabling them to attain
a certain degree of genetic coherence in racial characteristics. The coherence tends to preserve the germ plasm in fairly well defined biological entities that are capable of surviving in their respective environmental zones. The other principle is that the genetic coherence is flexible, because the characters are not so tightly bound as to impede extensive recombination of the germ plasm. If major changes in the environment occur causing changes in selective pressures, opportunities for intercrossing between distinct ecological races are likely to increase, leading to greatly enhanced genetic diversity.

Such a genetic structure makes it possible for plants of neighboring races to occur in adjacent but ecologically distinct habitats and yet remain recognizable entities, as described in chapter I. Crossing may be fairly infrequent between distinct races in adjacent habitats because they may differ in their time of flowering as well as in their ecology.

The present races are the products of long-time selection, and have attained an equilibrium with their environments. Natural selection will therefore tend to favor the original racial combination as long as the over-all genetic structure and the habitats remain the same, although a certain amount of introgression may take place. Over long periods genes may gradually migrate across long distances from the original point of contact and may finally appear in combination where they have selective value.

The results obtained in this study, however, do not indicate that ecologically distinct habitats are necessary to support different ecological races of *M. racemosa* within the same region. The occurrence of the two forms together in habitats of the Southwest suggests a wide ecological amplitude for single genotypes.

The robust form has been mentioned as reflecting heterosis, but the possibility of transgressive segregation, demonstrated and discussed by Clausen and Hiesey (1958) and
also discussed by Stebbins (1959), suggests itself. Transgressive segregation appears mostly to be the result of hybridization on the subspecific level and occurs when new gene combinations arise that permit the introgressants to exceed either parent in one or more characteristics. Thus, it represents a means by which new adaptive norms may be formed.

Coincidence of flowering times

Because of the difference in flowering times of the two forms postulated to be involved in hybridization, the problem of successful pollination must be reviewed. Since the individuals at the higher altitudes commence their growth relatively late in the season, their flowering times could coincide with those at the lower altitudes. A mountain form that was collected along the Arkansas River in the plains region east of Pueblo, Colorado was fully mature at the time of collection. A number of individuals collected a day or two earlier at higher altitudes just 15-40 miles to the west were prior to anthesis. With the prevailing winds being from the west, or with drafts occurring from the higher to the lower altitudes, pollen of the mountain form could be borne to the midwest form occurring along the river bottoms.

Further, individuals of the western mountain form were found along the Arkansas River for over 75 miles east of the front range of the Rockies. If some of these individuals
were to be located on a site that was inundated for the early part of the growing season, their maturation might be delayed sufficiently so that the flowering time would coincide with that of any midwest forms that might be present.

Historical Considerations

The above findings and postulates reflect on the past history of the species. From the evidence obtained on flowering times, day-length requirements, and, in a few cases, chromosome numbers, McMillan (1959) has postulated three primary points for the postglacial distribution of grassland vegetation. One was in the Southeast, another was in a region including southern Oklahoma and northern Texas, and the third in a "western semi-montane area such as that now found near Colorado Springs, Colo." This evidence for a southern Great Plains station constitutes support for the theses of earlier workers, such as Harvey (1908), who postulated a center for the prairie formation during glacial times in the region of northeastern Texas, eastern Oklahoma and southern Kansas.

With glaciation forcing the tall-grass prairie formation into a much narrower zone than it occupies today, one would expect that competition and selection for the forms best adapted to these conditions would be most intense. The evolution of a gene system representing a physiological balance attuned to these intense conditions and different from the
gene system of the western populations might have taken place at this time.

Results of a previous analysis also have suggested the possibility of introgression having taken place between *M. racemosa* and *M. frondosa*, but the evidence was too limited to permit critical judgement or to infer that it was a process of importance over a large region.

If the differentiation of the midwest form occurred during a glacial period, it is most unlikely that it occurred with the advantage of a disjunct distribution. But one must also take into account the postglacial climatic changes, particularly as they have been determined for the present postglacial period. Antevs (1948), in a synthesis of evidence from various sources, estimated that the middle postglacial period, characterized by high summer temperatures, prevailed from about 5,000 to 2,500 B.C. During this time, Antevs stated, "(that) the modern lakes were reborn 4,000 years ago and that their basins were dry for long ages before 2,000 B.C." He also stated that almost all the glaciers and permanent ice in the mountain systems of the West disappeared during this time.

Conceivably, populations of *M. racemosa*, dependent on the wetter sites for survival east of the Rocky Mountains, would be substantially reduced in number, if not eliminated, under these conditions. Thus, at least a partial gap in the
distribution of the species would be effected. Even partial isolation would facilitate any differentiation already initiated under the impact of the glacier.

Contact between the midwest form and the western mountain form could have occurred, originally, thousands of years ago so that many of the individuals found in the Southwest today might represent introgressants. The robust individuals occurring along the major river systems today could be the result of more recent contact between the hybridizing forms, possibly because of a relatively recent influx of the midwest gene system during the present, more pluvial period following the xeric period.

The contact of differing gene systems would not have taken place only in the Southwest. As the midwest form migrated northward following the retreating glaciers, it would come in contact with the western form migrating eastward and northeastward. Introgression between the two forms, then, might have played an important role in the development of modern representatives throughout much of the range of the species. It might account for some of the large variability found in and between populations occurring in the Kansas-Iowa region, and also for the variability in inflorescence and palea measurements in other regions. But conditions in the eastern and southeastern portions of the range have favored the maintenance of the midwest gene system.
It appears that the western mountain form has prevailed, with modifications, through all of northwestern Nebraska, into western South Dakota, and northward. Since these portions of Nebraska and South Dakota were unglaciated, the species probably has had a long history there and might well have spread from there to other regions.

Possible Origin of *M. racemosa*

A final consideration will be that of the possible origin of the tetraploid *M. racemosa*. Its close similarity with the diploid *M. glomerata* suggests that it is an amphidiploid offspring of the latter. Attempts to determine another likely diploid parent have been unsuccessful. The author is of the opinion that *M. racemosa* arose in the western regions, possibly when *M. glomerata* was pushed southward during one of the glacial periods. Hybridization with a more arid climate species of the Southwest would lend *M. racemosa* some of the ecological qualities it now displays.

The internodal pattern of many of the individuals of the western mountain regions resembles that of the northern and western form of *M. glomerata*. The same is true for a number of individuals of *M. racemosa* collected in the Black Hills of South Dakota and Wyoming, a region in which *M. glomerata* also occurs.

Some individuals of *M. racemosa* from northern Minnesota demonstrated this same internodal pattern, but here the
species appears to be on a much more adventive footing than it is in the western regions. M. racemosa is a component of some well developed, possibly climax communities in the southern Rockies and in northwestern Nebraska and the Black Hills. Thus, ecologically it appears much more firmly established in the West than in its eastern occurrences.

If the species originally moved eastward from a western base, then contact and introgression with another species, such as M. frondosa, quite possibly could have taken place. This, coupled with intense selection pressure for a different adaptive norm in the tall-grass prairie region, could readily account for the differentiation of a midwest gene system. The succeeding events would represent a reverse migration of new gene combinations and the expansion of the range of the species.
SUMMARY

This study concerns certain members of the broad-leaved rhizomatous group in the genus *Muhlenbergia*. Observations were made on the ranges and ecological occurrences of *M. glomerata*, *M. racemosa*, *M. frondosa*, *M. mexicana*, and *M. brachyphylla*. The major objectives were to study variation and its implications in *M. glomerata* and *M. racemosa*, utilizing a transplant garden for the latter. Bagging experiments conducted on these two species showed that both are self-fertile.

The separation of *M. glomerata* and *M. racemosa* into two species by other authors was confirmed, both on morphological and chromosomal grounds. *M. racemosa* was shown to be a tetraploid and *M. glomerata* a diploid with 20 somatic chromosomes.

Variation in *M. glomerata* was described on the basis of internodal pattern which showed some correlation with number of nodes, height, length of inflorescence, and culm width. The more northerly and westerly occurring members generally had fewer nodes, less height, shorter inflorescences, and narrower culms than did those occurring in the more southerly Great Lakes regions.

A number of collections of *M. glomerata* demonstrated abnormal chromosomal counts. The evidence indicates that the tetraploid *M. mexicana* is hybridizing with *M. glomerata*. 
The hybrid-segregates show at least ten good bivalents and some loss of chromosomes from the triploid level. Thus, aneuploid races are being established with the further possibility of the diploid condition being restored. The hybrid-segregates taxonomically resemble M. glomerata. The process may be of considerable importance in expanding the ecological and geographic range of the species.

Some possible ecotypic variation was shown to occur in M. frondosa with a difference in spikelet measurements being manifest between populations occurring in the shade and others occurring in the open. The differences were maintained under experimental garden conditions. The possibility of introgression was suggested in the analysis of a mixed population of M. frondosa and M. racemosa. The same type of variation was demonstrated for individuals of the population grown in the uniform garden.

Regional patterns of variation were described for M. racemosa from the analysis of herbarium specimens and of field collections of the author. These patterns were confirmed and a genetic basis established for them by individuals grown in the experimental garden at Ames. The individuals were shown to vary in the number of nodes, height, and time of emergence of the inflorescence, these characteristics generally being correlated with internodal pattern. They also varied according to length of inflorescence, length
of palea, culm width, and lemma/palea ratio, these showing more independent patterns of variation.

A midwest form was postulated as being differentiated from a western montane form, with the two meeting along the major river systems where they approach and enter the Rocky Mountains in the Southwest. Hybridization between the two was suggested as being responsible for a third, robust form, that occurs in this region of contact.

The evidence for the differentiation of two gene systems on the order of subspecies was viewed as reflecting on the past history of the species. A western origin was proposed for *M. racemosa* with the midwest form being differentiated in the prairie formation of Oklahoma and Texas during the glacial periods.
LITERATURE CITED


Turesson, G. 1922a. The species and the variety as ecological units. Hereditas 3:100-113.


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