Taxonomic studies in Panicum subgenus Dichanthelium

Robert Walter Freckmann

Iowa State University

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TAXONOMIC STUDIES IN PANICUM SUBGENUS DICHANTHELIUM.

Iowa State University, Ph.D., 1967
Botany

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TAXONOMIC STUDIES IN PANICUM SUBGENUS DICHANTHELIUM

by

Robert Walter Freckmann

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:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

Signature was redacted for privacy.

Dean of Graduate College

Iowa State University
Of Science and Technology
Ames, Iowa

1967
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INTRODUCTION

The genus *Panicum* is composed of three subgenera and about 500 species. Nearly 400 of the species belong to the subgenus *Panicum* which is widespread in tropical and temperate regions of both hemispheres. The other two subgenera, *Paurochaetium*, and *Dichanthelium*, are native exclusively to the New World.

The subgenus *Dichanthelium* ranges from Canada to northern South America, with the greatest concentration of species occurring on the Coastal Plain in the southeastern United States. Most of the species are plants of early stages in secondary succession of disturbed woodlands. They occur in greatest numbers at the edge of oak and pine woods, along woodland trails, in cut-over woods, in old fields with scattered shrubs and trees, and on disturbed areas between woodlands and highways. Some species grow in fairly deep shade of mature forests and some amid dense grass of prairies. But in general the plants of this subgenus do not tolerate deep shade and intense competition.

The only extensive taxonomic treatment of the entire subgenus is that of Hitchcock and Chase (1910) in which 110 species and five additional subspecies were recognized. At least six species have been added to the subgenus since that time, bringing the total to about 116 species. Most of the species for which chromosome numbers are known are diploids.
with nine pairs of chromosomes. The majority of the species are at least partially sympatric, and several of them often occur together in the same habitat. All species begin flowering in the spring within about two months of the start of the growing season and continue flowering until the end of the growing season in the autumn.

In view of the lack of barriers of geographic distribution, habitat preference, chromosome number, or flowering time among the species, the number of species in the subgenus is remarkably large. The separation of many of the species is difficult and the identification of specimens has often been left to specialists in the group. Some of the workers who have given special attention to the dichanthelia include Fernald (1934), Pohl (1947), Shinners (1944), and Silveus (1942).

The most recent work on *Panicum* subgenus *Dichanthelium* is that of Lelong (1965). He investigated various aspects of the reproductive biology of the subgenus. His findings seemed to indicate that members of the subgenus are primarily autogamous and that the strong tendency for self-pollination results in the production of local species populations which are highly uniform. He suggested that the plants occasionally out-cross and that many of the ill-defined and "rare" species are recent derivatives of hybridization between normally autogamous lines.

Lelong presented a new taxonomic disposition of the
lanuginosum and columbia num groups in which Hitchcock and Chase had recognized 28 species. Although Lelong's treatment is of a preliminary nature, it reduces the number of species to 12 and provides a basis for further, more intensive studies in the complex.

Lelong's treatment of the lanuginosum and columbia num groups left 88 species of the subgenus without recent treatment. One objective of the present study is to extend this type of preliminary taxonomic treatment through the depauperatum, laxiflorum, angustifolium, and oligosanthes groups, including another 28 species of the Hitchcock and Chase system. The four groups were selected for inclusion in this study because they included some of the species complexes which seemed to be in need of revision and because the groups which they represented are fairly discrete.

The treatment of the four groups included in this paper is based primarily on a study of the patterns of variation in morphological characters as represented in herbarium collections and population samples. Other techniques may have to be employed before an extensive taxonomic revision of the groups is possible. The present study is intended to provide a framework for future investigations.
METHODS AND MATERIALS

Field Collections

Nearly all of the living materials and the population samples as well as many of the herbarium specimens used in this study were obtained on trips taken in 1963 through 1966. The field work was concentrated in the southeastern United States, extending from Delaware to the Everglades of Florida west to southern Texas and the Ozarks of Missouri and Oklahoma. Approximately 250 collection sites were visited and 835 numbers of dichanthelia were obtained.

Since several species or entities of dichanthelia often occur together at one location and since some of these entities were suspected of hybridizing under these conditions, an effort was made to obtain specimens of all entities of dichanthelia at each location. Thus the collecting program was not restricted to the groups treated in this paper. Efforts were also made to include adequate ecological information with the collections. The information recorded included a description of the collection site, the principal trees, the degree of disturbance, and the abundance and particular microhabitat of each entity.

Insofar as possible, enough material for about four herbarium specimens was obtained for each collection number. Thus, depending on the size of the plants, the number of individuals collected usually ranged from four to about 12.
In addition, some mass collections were made, usually including 20-30 individuals.

Many live plants were also obtained. These plants were placed in polyethylene bags in the field, transported in an ice chest, and planted in the greenhouse at Iowa State University. The soil used for greenhouse cultures usually consisted of a mixture of potting soil, sand, and either gravel or crushed brick. Although the proportions were sometimes varied according to the soil type of the plant under natural conditions, it was found that a high proportion of sand and gravel with the accompanying good drainage generally gave the best results.

Some greenhouse cultures were grown from seed collected in the field. The seed was germinated on moist blotters in a petri dish at normal room temperatures following partial removal of the fertile lemma. The seedlings were transferred to greenhouse pots filled with a mixture of potting soil and a high proportion of sand. The pots were placed in trays of water to assure a constant supply of moisture to the seedling. After a few weeks the seedlings were transplanted to larger pots with the type of soil mixture described above.

Neither of the greenhouse culture methods was notably successful. Less than half of the live plants survived for more than one year. Some of the species which proved to be especially difficult to grow under these conditions were *P. latifolium*, *P. leibergii*, *P. perlongum*, *P. xanthophyllum*. 
and members of the ensifolium group.

Studies of the Reproductive Biology

Live plants, inflorescences fixed in the field in Newcomer's fixative, and herbarium specimens were used as sources of material for observations on pollination and fertility of spikelets. Spikelets were examined to determine the size of mature anthers and whether the anthers and stigmas were exerted at the time of anther dehiscence. Pollen fertility was determined for mature anthers using a lacto-phenol and aniline-blue solution (Sass, 1951). Spikelets and anthers of herbarium specimens were softened in a solution of distilled water, methyl alcohol and dioctyl sodium sulfosuccinate (Pohl, 1965).

Selection and Examination of Herbarium Specimens

Specimens in the Iowa State University herbarium (ISC) were the primary source of material for this study. All specimens of Panicum subgenus Dichanthelium in this collection were examined and all specimens of the depauperatum, laxiflorum, angustifolium, and oligosanthes groups were included in the study. In addition, the United States National Herbarium (US), and the Missouri Botanical Garden (MO) were visited for the purpose of the examination of type specimens and the selection of additional material. The specimens loaned by the latter two herbaria included nearly the entire collections of some of the rare taxa, plus certain specimens of the more com-
mon species which were selected on the basis of completeness of the specimen.

Observations of herbarium specimens were made with a stereo binocular microscope fitted with an ocular micrometer. The traits observed varied according to the taxonomic group under consideration and are enumerated in the chapters dealing with those groups.

A partial synonomy has been included for each species or infraspecific taxon treated in the four groups. The procedure of Isely (1962) has been followed to indicate the basis for inclusion of each name, as follows:

(1) Type specimen or illustration of same examined.
(2) Original description examined.
(3) Name included following the usage of another author who has examined a type specimen.
(4) Name utilization follows currently accepted usage; typification not verified.

A list of herbarium specimens examined as a part of the study of the depauperatum, laxiflorum, angustifolium, and oligosanthes groups is presented in the appendix. The abbreviations used for herbaria are those proposed by Lanjouw and Stafleu (1964).
THE DEAUPERATUM GROUP

General Observations

The deauperatum group is one of the most distinctive groups in the subgenus *Dichanthelium*. Members of this complex usually differ from other species of the subgenus in characters of leaf shape, culm branching, and patterns of internode elongation. They possess long, narrow leaves, with a length-to-width ratio of the upper culm blades often exceeding 30:1. The lower culm leaves tend to be shorter, with a length-to-width ratio of between 10:1 to 20:1, but without a distinct differentiation into the type of basal rosette found in most of the other groups. The uppermost internode is the longest, and each of the internodes downward is shorter than the one above it. A short, compact, axillary inflorescence usually arises from one of the several nodes which are telescoped together at the base of the plant.

All of the above characters are correlated and serve to define the group. Hitchcock and Chase (1910, 1951) emphasized the elongate shape of the blade in separating out the "Depauperata." Since there is some overlap in the length-to-width ratio of the lower leaves of some members of this group with exceptionally narrow-leaf individuals of some other groups, equal consideration must be given to all of the diagnostic characters in assigning a specimen to this group. Certain "Rare species" belonging to other groups including *P. bick-
nellii Nash, *P. nudicaule* Vasey, *P. wilcoxianum* Vasey, and *P. deamii* Hitchc. and Chase possess long, narrow leaves and often tend to have shortened lower internodes. These species may be related to the depauperata, possibly through hybridization. However, they are not usually included in the depauperatum complex.

In some respects the depauperata resemble certain members of the subgenus *Panicum*. For example, *P. filipes* Scribn., a member of the subgenus *Panicum*, has many of the key characters of *P. werneri* Scribn. The similarities between these two species are particularly striking in a mixed collection from Gillespie Co., Texas (Jermy, s.n., Mo). Both *P. filipes* and *P. werneri* have the same pattern of leaf and internode elongation. Both lack the distinct winter rosette which is usually a diagnostic character of the dichanthelia. Furthermore, both plants are tufted perennials with open, terminal panicles. However, the second glume and sterile lemma of *P. filipes* are extended well beyond the fertile floret, forming a more prominent beak than that which can be found in the depauperatum group. The first glume of *P. filipes* is sharply acute in contrast to the blunt first glumes of the depauperata, and the basal branches bearing inflorescences elongate in mid-summer into culms of about the same height as the main culms.

Previous Taxonomic Treatments

The depauperatum complex has been divided into three
species plus two additional varieties (e.g. Fernald, 1950, Gleason, 1952), or into four species (Hitchcock and Chase, 1910, 1951). The three species accepted in both treatments have been distinguished on the basis of two or more traits. The separation of the other two taxa depends primarily on leaf pubescence. The following key to species (Fernald, 1950) differs from the keys of Hitchcock and Chase only in employing additional characters:

Spikelets acutely beaked, 3-4.5 mm long, distinctly exceeding the fruit..................P. depauperatum
Spikelets rounded or subacute at tip, not beaked, 2-3.6 mm long, nearly conforming to the fruit.

Expanded terminal panicle one-sixth to one-half as broad as long; spikelets 2.7-3.6 mm long; fruit rounded-ellipsoid, or -obovoid, 1.6-2 mm wide..............P. perlongum
Expanded terminal panicle one-third to three-fourths as broad as long; spikelets 2-2.7 mm long; fruit narrowly ellipsoid, 1-1.3 mm wide...............P. linearifolium

One of the principal differences in the two treatments concerns the recognition of infra-specific taxa for P. depauperatum. Fernald (1921) published the var. psilophyllum for plants with "leaves wholly glabrous or sheaths sparsely setulose." He stated that it is more common in the northern part of the range of that species and that the var. depauperatum (called "typical P. depauperatum" by Fernald) possesses pilose leaves and is more common in the southern part of the range. He also described a new form of the var. psilophyllum characterized by the absence of exserted terminal panicles. He gave this the name "f. cryptostachys." Hitchcock and Chase did not
recognize these taxa.

The other principal difference in the two treatments concerns the status of _P. werneri_. Hitchcock and Chase consistently maintained this entity as a species distinct from _P. linearifolium_, separating the two species with the following dichotomy:

Sheaths pilose; spikelets 2.2 to 2.7 mm long, pilose

............................ _P. linearifolium_

Sheaths glabrous; spikelets 2.2 to 2.3 mm long, glabrous

............................ _P. werneri_

Fernald (1921) reduced _P. werneri_ to a variety of _P. linearifolium_. He stated that this glabrous variety is more common in the northern part of the species range, and that in this respect it closely parallels the relationship between _P. depauperatum_ and the var. _psilophyllum_.

Methods of Analysis

The principal source of material for the study of the depauperatum group was 212 herbarium specimens. Certain features (e.g. habit, leaf shape and pubescence, inflorescence proportions, size and pubescence of spikelet) of each specimen together with pertinent label information were recorded on data sheets. These sheets were subsequently sorted into sets according to single characters or bits of label information. Each set was then examined for apparent correlations with any other characteristic. Multiple character correlations were demonstrated by means of scatter-diagrams.
The characters selected for notation included those employed in the various keys to the taxa of the depauperata, plus those which seemed to be of potential taxonomic value. Some of the characters proved to be too variable within a single plant or too difficult to assess objectively and were dropped.

The leaf characters recorded included the pubescence of the sheath and blade, and the width of the blade. Sheath pubescence was rated arbitrarily as glabrous, setulose (with sparse, stiff, ascending trichomes), sparsely pilose (with scattered, long, slender trichomes), or pilose. The uppermost culm blades were classed as either tapered to the base or rounded at the base, and as exceptionally narrow (less than 3 mm wide), normal (3-5 mm wide), or exceptionally broad (more than 5 mm wide). In addition, the pubescence of the adaxial blade surface was described according to the type and density of trichomes.

All observations related to the inflorescence were made on a predetermined terminal panicle (in most cases, the fifth panicle from the left-hand edge of the herbarium sheet). The length and width of the inflorescence was measured as well as the length of one pedicel. The pedicel selected was that of the spikelet immediately below the spikelet terminating the main axis of the inflorescence. The total number of spikelets of the inflorescence was also recorded.

Whenever possible a spikelet containing a maturing
caryopsis was selected for notation of spikelet characters. The length and width of a spikelet and its fertile floret were measured. The presence of a small beak or a large beak was noted. This last character has received considerable emphasis in previous treatments, and it is unfortunate that the stage of development of the caryopsis affects this trait, making the application of the terms, "large beak," "small beak," and "beakless" arbitrary.

Patterns of Variation

Table 1 lists the division of the 212 herbarium specimens into taxa primarily according to the criteria of Fernald. Specimens conforming to the stated criteria of a particular species or variety, except for seemingly minor differences, have been included under that species or variety. Those specimens which contained mixtures of the critical characters of two taxa have been classed as intermediates between those taxa.

The intermediate specimens were excluded at first in order to simplify finding the characteristics which would be most effective in separating "typical" specimens of the three species. A comparison of the three species on the basis of some of the quantitative characters is presented in Table 2. The results indicate that whereas the species differ in the frequencies of these various traits, there is considerable overlap in the range of variation in these traits.

All of the 212 specimens, including intermediates, have
Table 1  Division into taxa of the specimens examined in the depauperatum group according to the criteria of Fernald (1950)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Number of specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>P. depauperatum</strong></td>
<td></td>
</tr>
<tr>
<td>var. depauperatum</td>
<td>46</td>
</tr>
<tr>
<td>var. psilophyllum</td>
<td>31</td>
</tr>
<tr>
<td>mixture of both varieties</td>
<td>2</td>
</tr>
<tr>
<td><strong>P. linearifolium</strong></td>
<td></td>
</tr>
<tr>
<td>var. linearifolium</td>
<td>35</td>
</tr>
<tr>
<td>var. werneri</td>
<td>36</td>
</tr>
<tr>
<td>mixture of both varieties</td>
<td>2</td>
</tr>
<tr>
<td><strong>P. perlongum</strong></td>
<td>43</td>
</tr>
<tr>
<td><strong>P. depauperatum-P. perlongum</strong></td>
<td>8</td>
</tr>
<tr>
<td><strong>intermediates</strong></td>
<td></td>
</tr>
<tr>
<td><strong>P. depauperatum-P. linearifolium</strong></td>
<td>8</td>
</tr>
<tr>
<td><strong>intermediates</strong></td>
<td></td>
</tr>
<tr>
<td><strong>P. perlongum-P. linearifolium</strong></td>
<td>1</td>
</tr>
<tr>
<td><strong>intermediates</strong></td>
<td></td>
</tr>
</tbody>
</table>

been plotted on a scatter-diagram. (Figure 1) designed to show correlations among some of the diagnostic characters of the three species. The width of the fertile floret and the length of the pedicel provide the best quantitative separation of the taxa. Specimens of *P. linearifolium* should be confined to the lower half of the scatter-diagram on the basis of the smaller fertile florets. Specimens of *P. perlongum* should
Table 2 A comparison of *Panicum depauperatum*, *P. perlongum*, and *P. linearifolium* (sensu lato) on the basis of three quantitative characters

<table>
<thead>
<tr>
<th>Character</th>
<th><em>P. depauperatum</em></th>
<th><em>P. perlongum</em></th>
<th><em>P. linearifolium</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Per cent of total specimens of species in each size range</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Fertile floret length in mm</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>less than 1.8</td>
<td>1</td>
<td>12</td>
<td>15</td>
</tr>
<tr>
<td>1.8</td>
<td>1</td>
<td>12</td>
<td>15</td>
</tr>
<tr>
<td>1.9</td>
<td>10</td>
<td>41</td>
<td>19</td>
</tr>
<tr>
<td>2.0</td>
<td>19</td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>2.1</td>
<td>42</td>
<td>36</td>
<td>0</td>
</tr>
<tr>
<td>2.2</td>
<td>13</td>
<td>26</td>
<td>3</td>
</tr>
<tr>
<td>2.3</td>
<td>8</td>
<td>17</td>
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<tr>
<td>2.4</td>
<td>3</td>
<td>10</td>
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</tr>
<tr>
<td>2.5</td>
<td>3</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>2.6</td>
<td>2</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>2.7</td>
<td>1</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td><strong>Fertile floret width in mm</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.8</td>
<td>1</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>0.9</td>
<td>12</td>
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<td>1.0</td>
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<td>1.6</td>
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<td></td>
</tr>
<tr>
<td>1.7</td>
<td>5</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td><strong>Number of spikelets per panicle</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5-9</td>
<td>7</td>
<td>3</td>
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</tr>
<tr>
<td>10-14</td>
<td>36</td>
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<td>15-19</td>
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Table 2 (Continued)

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<thead>
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<th>Character</th>
<th>P. depauperatum</th>
<th>P. perlongum</th>
<th>P. linearifolium</th>
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<tr>
<td>Number of spikelets per panicle</td>
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<td>25-29</td>
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<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>
Figure 1  Scatter diagram showing the relationship among four diagnostic characters of the depauperatum group of *Panicum*
occupy the upper left-hand portion of the diagram because of its combination of wider florets and short pedicels, and *P. depauperatum* should occupy the upper right-hand area on the basis of wider florets and longer pedicels.

It is apparent from Figure 1 that specimens of the depauperatum group do not segregate into three distinct taxa on the basis of these characters. There is no gap between the three species on the basis of either quantitative character. Furthermore, the other characters portrayed show imperfect correlations with the quantitative characters. Thus, it is necessary to assign a priority to one or two of these characters or to find other traits if three taxa are to be recognized. A more detailed analysis of the depauperatum complex considering one pair of entities at a time is presented below.

**Panicum depauperatum and P. perlongum**

The two characters used by both Fernald (1950) and Hitchcock and Chase (1910) to separate these two species were the larger spikelets and the prominent beak of *P. depauperatum*. However, since the presence of the beak also accounts for the increased size of the spikelet of *P. depauperatum*, only one character is actually involved. If the beak is ignored, the spikelets are essentially identical. The dimensions of the fertile florets of the two species show almost complete coincidence (Table 2). Specimens with spikelets bearing large beaks can be easily assigned to *P. depauperatum* with agreement
between both traits. But, when a specimen possesses a small beak and is therefore intermediate between the two species in this respect, it is also intermediate in spikelet length. This places considerable importance on the evaluation of the prominence of the beak. Unfortunately, the beak becomes less prominent in all specimens as the caryopsis swells with maturity and causes the tips of the second glume and sterile lemma to be drawn in around the end of the fertile floret.

Other characters have been sought to aid in assigning a specimen to one entity or the other. The traits which have proved to be of some value reflect differences in the growth forms of the two taxa. For example, individuals of *P. perlongum* are usually slender and elongate. The main culms and lower leaves tend to be erect, forming compact tufts at the base of the plant. The terminal inflorescences are usually narrow, with ascending lateral branches, shorter pedicels, and more numerous spikelets. In contrast, most individuals of *P. depauperatum* have a spreading habit. The main culms and leaf blades fan out from the base. The branches of the terminal inflorescence tend to spread at about a 45-degree angle from the main axis, making the inflorescence more than half as wide as long.

Since *P. perlongum* usually grows in dense prairie vegetation and *P. depauperatum* in more open habitats with less crowding from other grasses, it is possible that these habit characters are influenced by environmental conditions. Individuals of *P. depauperatum* grown in pots in a greenhouse developed
the usual spreading habit found in most circumstances in its natural habitats. An individual of *P. perlongum* grown under the same greenhouse conditions as the *P. depauperatum* developed a less slender and elongate general growth form than usual. However, it was still distinguishable from *P. depauperatum* in these characters.

At least eight specimens examined could not be assigned to either species because they combined traits of both or were intermediate in most characters. Some of the specimens combined the habit of *P. perlongum* with the prominently beaked spikelets of *P. depauperatum*. Thorne, 16099, ISC and Cratty _s. n._, ISC, illustrate this situation. The combination of spikelets of *P. perlongum* with the vegetative characters of *P. depauperatum* can be seen in Carver, _s. n._, ISC, Deam, 27652, US and Somes, 800, ISC. Freckmann, 921-B, ISC, Lelong, 2354, ISC, and McDill, 111, ISC, present perplexing intermixtures of the characters of both taxa in all parts of the plants.

The eight intermediate specimens were examined to determine pollen fertility and seed set. As indicated in Table 4 all eight specimens show signs of fertility either by the presence of developing caryopses or of pollen grains well-filled with cytoplasm and staining deeply in lacto-phenol and aniline-blue.

*Panicum depauperatum* and *P. linearifolium*

The basic differences between *P. depauperatum* and *P. lin-
earifolium (including _P. werneri_) are spikelet size and the presence or absence of a prominent beak. The fertile florets of _P. depauperatum_ are usually longer and wider than those of _P. linearifolium_. Spikelets of _P. depauperatum_ usually have a prominent beak which adds 0.3 to 0.7 mm to the length of the spikelets. Thus, the larger florets and prominent beak may combine to give specimens of _P. depauperatum_ a spikelet as much as 1.2 mm longer than that of some specimens of _P. linearifolium_.

The only secondary difference between these two taxa is the tendency for _P. linearifolium_ to have more spikelets per terminal inflorescence. The tendency for the members of a species-complex with smaller spikelets to have more numerous spikelets is fairly widespread in the dichanthelia. This trend can be observed in the _P. strigosum-P. polycaulon-P. ciliatum_ complex, in the _P. polyanthes-P. sphaerocarpon_ complex, in the _P. microcarpon-P. dichotomum_ complex, and others. Therefore, it is possible that the spikelet number may be partially dependent on spikelet size.

It is apparent from the scatter diagram (Figure 2) that _P. depauperatum_ and _P. linearifolium_ intergrade. A number of specimens possess small beaks, and some of these are intermediate in the length and width of the fertile florets. Most of the fertile florets have approximately the same shape as indicated by the orientation of the entries on the scatter diagram in a band from the lower left-hand portion of the
Figure 2: Intergradation between *Panicum depauperatum* and *P. linearifolium* (including *P. wernerii*)
graph to the upper right-hand portion.

**Panicum perlongum** and **P. linearifolium**

These two species differ in several characters, including spikelet size, and several features of habit. *Panicum perlongum* has larger spikelets and larger florets than *P. linearifolium*. The latter species has the same habit as *P. depauperatum* which means that the same secondary traits can be used to separate *P. perlongum* from *P. linearifolium* as were used to separate it from *P. depauperatum*.

Only one specimen encountered is intermediate between the two species in most characters. This specimen (Moore and Phinney, 10761, ISC) has spikelets 2.5-2.7 mm long, and fertile florets 2.1 mm long and 1.3 mm wide. The inflorescence is about as narrow as most *P. perlongum*, but the habit of the plant is that of *P. linearifolium*. The specimen is somewhat immature, with only a few of the spikelets at anthesis so that it is difficult to determine seed set. But over 80% of the pollen observed in nearly mature anthers was filled with cytoplasm and deeply-stained in lacto-phenol and aniline blue.

**Panicum linearifolium** and **P. wernerii**

Both Fernald and Hitchcock and Chase agreed that two taxa are included in *P. linearifolium* (*sensu lato*). However, Hitchcock and Chase regarded them as separate species, distinguished by sheath pilosity, spikelet pubescence, and spikelet length. Lamson-Scribner and Merrill (1901a) felt that *P. wernerii* could
be further distinguished by the rounded bases of the blades and the relatively elongate lower internodes.

Table 3 and Figure 3 present the results of attempts to correlate these various traits with the difference in leaf sheath pubescence. The results failed to show the expected correlations. The patterns of variation of the various characters are essentially the same for glabrous-sheath specimens as for pilose-sheath specimens.

Fernald apparently recognized the fact that no character other than sheath pubescence could be used to separate the two taxa when he reduced them to varieties. But he maintained that there is a strong correlation between sheath pubescence and geographic range, reporting that 74% of the specimens from New England and Canada had glabrous sheaths in contrast to 7% of the specimens from Missouri. I have obtained similar results with the specimens available to me. I found that 76% of the specimens from the northern part of the range of _P. linearifolium_ (sensu lato) including Canada, New England, New York, Michigan, Wisconsin, and Minnesota had glabrous sheaths. Thirty-two per cent of the specimens from the remainder of the range had glabrous sheaths. But the total range of both types is approximately the same, and both forms can be found at the northern and the southern extremes of the range. Furthermore, some single populations include both forms.
Table 3: A comparison of glabrous-sheath specimens with pilose-sheath specimens of Panicum linearifolium (including P. werneri)

<table>
<thead>
<tr>
<th>Trait</th>
<th>Per cent of specimens having trait</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>35 pilose specimens</td>
</tr>
<tr>
<td>Blades less than 3 mm wide</td>
<td>3</td>
</tr>
<tr>
<td>Blades 3-5 mm wide</td>
<td>53</td>
</tr>
<tr>
<td>Blades more than 5 mm wide</td>
<td>44</td>
</tr>
<tr>
<td>Spikelets glabrous</td>
<td>13</td>
</tr>
<tr>
<td>Spikelets sparsely pubescent</td>
<td>81</td>
</tr>
<tr>
<td>Spikelets densely pubescent</td>
<td>6</td>
</tr>
<tr>
<td>Lower internodes elongated</td>
<td>6</td>
</tr>
<tr>
<td>Spikelets with small beaks</td>
<td>36</td>
</tr>
</tbody>
</table>

The varieties of *P. depauperatum*

The two varieties of *P. depauperatum* present a pattern of variation very similar to that discussed above for *P. linearifolium*. Fernald (1921) examined 173 specimens of *P. depauperatum* from Nova Scotia, Quebec, and New England and found that 88% had glabrous sheaths. Conversely, he found that all of the material which he examined from North Carolina, Georgia, to Arkansas, Missouri, and Illinois had pilose sheaths. I found that 83% of the specimens available to me from Canada,
Figure 3. A comparison of glabrous-sheath specimens of *Panicum* depauperatum with pilose-sheath specimens of *P. depauperatum* and of glabrous-sheath specimens of *P. linearifolium* (sensu lato) with pilose-sheath specimens of *P. linearifolium*.

The length of open bars represents the percent of the total glabrous-sheath specimens possessing the indicated trait; the length of the closed bars represents the percent of the total pilose-sheath specimens possessing indicated trait.

Graphs A, B, and C include all available specimens of *P. depauperatum*; Graphs D, E, and F include all available specimens of *P. linearifolium* (including *P. werneri*).
New England, New York, Michigan, Wisconsin, and Minnesota had glabrous sheaths, in contrast to 23% of the specimens from the rest of the range.

Attempts were made to obtain a correlation of other traits with sheath pubescence. No trait investigated other than geographic range is correlated with this pubescence character. Figure 3 presents the results of three of these attempts to establish a correlation.

Thus it appears that the question of the recognition of one or two varieties in _P. depauperatum_ is almost identical with the question concerning the varieties of _P. linearifolium_. The total geographic range of the glabrous-sheath plants and the pilose-sheath plants of _P. depauperatum_ is the same. A single population from any part of the range of the species can include both pilose and glabrous individuals.

Reproductive Biology

Lelong (1965) studied various aspects of the reproductive biology of a wide variety of species of dichanthelia. He observed that many of these species produced both chasmogamous and cleistogamous spikelets. He noted that strongly chasmogamous spikelets generally produced relatively large anthers 1.0 mm or more in length. These anthers were well-exserted on long filaments just prior to the full exsertion of the stigma. The strongly cleistogamous spikelets contain small anthers, about 0.5 mm long, which are retained within the
fertile floret. As a generalization, the spikelets of the terminal inflorescences produced early in the growing season tend to be chasmogamous, with a trend toward the reduction in anther size and a retention of the anthers in spikelets of later inflorescences.

Lelong observed that the majority of the spikelets of *P. depauperatum* and *P. perlongum* are cleistogamous. He also noted that these cleistogamous spikelets presented problems in the interpretation of pollen fertility as determined through the use of lacto-phenol and aniline blue. The problem is apparently caused by the fact that the pollen grains fill with cytoplasm rapidly immediately before dehiscence of the anthers. Soon after dehiscence the grains germinate on the stigma, discharging their cytoplasm and leaving the collapsed, empty walls of the pollen grains. Since only a few spikelets of an inflorescence may have pollen at the proper stage of maturity to stain well, most of the pollen from the majority of spikelets will appear empty and collapsed.

My studies of the reproductive biology of the *depauperatum* group were carried out on two live plants of *P. depauperatum* grown in a greenhouse, on one collection of inflorescences fixed in the field in Newcomber's fixative, and on many herbarium specimens. The observations are summarized in Table 4.

My observations are in general agreement with those of
Table 4  Pollen fertility and seed set in terminal and axillary panicles of specimens of the depauperatum group of Panicum

<table>
<thead>
<tr>
<th>Taxon, collector, number, herbarium</th>
<th>Terminal inflorescence</th>
<th>Axillary inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anther size in mm</td>
<td>% Good pollen</td>
</tr>
<tr>
<td>Commons, 29, US</td>
<td>1.0</td>
<td>93</td>
</tr>
<tr>
<td>DeLisle, 1122, ISC</td>
<td>1.1</td>
<td>(90)</td>
</tr>
<tr>
<td>Freckmann, 2091, d</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freckmann, 2259, ISC</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>Lelong, 2454B, ISC</td>
<td></td>
<td>x</td>
</tr>
</tbody>
</table>

a"Good pollen" means grains spherical and filled with granular, deeply-staining cytoplasm

b"x" indicates presence of developing or mature seed

cParenthesis indicate pollen somewhat immature; count is approximate

dInflorescences fixed in the field in Newcomber's fixative
<table>
<thead>
<tr>
<th>Taxon, collector, number, herbarium</th>
<th>Terminal inflorescence</th>
<th>Axillary inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anther size in mm</td>
<td>% Good pollen</td>
</tr>
<tr>
<td><strong>P. depauperatum</strong>&lt;br/&gt;var. psilophyllum:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bartley and Pontius, s. n., US</td>
<td>1.3-1.5</td>
<td>77</td>
</tr>
<tr>
<td>Berkheimer, 19259, ISC</td>
<td>1.1</td>
<td>83</td>
</tr>
<tr>
<td>Shinners and Catenhausen, 1837, ISC</td>
<td>1.0</td>
<td>85</td>
</tr>
<tr>
<td>Smith and Smith, 915, ISC</td>
<td>1.3</td>
<td>95</td>
</tr>
<tr>
<td><strong>P. perlongum:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fraser, 768, ISC</td>
<td>x</td>
<td>0.6</td>
</tr>
<tr>
<td>Freckmann, I918, ISC</td>
<td>0.6-0.8</td>
<td>(85)</td>
</tr>
<tr>
<td>Hartley, 3656, ISC</td>
<td>1.2</td>
<td>89</td>
</tr>
<tr>
<td>Hayden, 8195, ISC</td>
<td>1.0</td>
<td>x</td>
</tr>
<tr>
<td>Hiltunen, 3464, ISC</td>
<td>x</td>
<td>0.4</td>
</tr>
<tr>
<td>Taxon, collector, number, herbarium</td>
<td>Terminal inflorescence</td>
<td>Axillary inflorescence</td>
</tr>
<tr>
<td>-----------------------------------</td>
<td>------------------------</td>
<td>------------------------</td>
</tr>
<tr>
<td></td>
<td>Anther size in mm</td>
<td>% Good pollen</td>
</tr>
<tr>
<td>Iltis, 5712, ISC</td>
<td>1.5</td>
<td>(80)</td>
</tr>
<tr>
<td>Lelong, 2131, ISC</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td>Lelong, 2147, ISC</td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Umbach, 3555, ISC</td>
<td>1.2</td>
<td>94</td>
</tr>
<tr>
<td>Wadmond and Fassett, s. n., ISC</td>
<td>1.5</td>
<td>74</td>
</tr>
<tr>
<td><strong>P. linearifolium</strong> var. linearifolium</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Berkheimer, 19256, ISC</td>
<td>0.9</td>
<td>(80)</td>
</tr>
<tr>
<td>Freckmann, 1801, ISC</td>
<td>0.5</td>
<td>(75)</td>
</tr>
<tr>
<td>Lelong, 2331, ISC</td>
<td>1.2</td>
<td></td>
</tr>
<tr>
<td>Lelong, 2346, ISC</td>
<td>1.3</td>
<td>84</td>
</tr>
<tr>
<td>Pohl, 7296, ISC</td>
<td>1.4</td>
<td>(80)</td>
</tr>
<tr>
<td>Taxon, collector, number, herbarium</td>
<td>Terminal inflorescence</td>
<td>Axillary inflorescence</td>
</tr>
<tr>
<td>----------------------------------</td>
<td>------------------------</td>
<td>------------------------</td>
</tr>
<tr>
<td></td>
<td>Anther size</td>
<td>% Good pollen</td>
</tr>
<tr>
<td>P. linearifolium var. werneri</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Allison, 510, ISC</td>
<td>1.0</td>
<td>x</td>
</tr>
<tr>
<td>Churchill, s. n., ISC</td>
<td>1.2</td>
<td>(85)</td>
</tr>
<tr>
<td>Ehlers, 1967, ISC</td>
<td>1.3</td>
<td>76</td>
</tr>
<tr>
<td>Hartley, 4239, ISC</td>
<td>1.2</td>
<td>78</td>
</tr>
<tr>
<td>P. perlongum-P. depauperatum</td>
<td></td>
<td></td>
</tr>
<tr>
<td>intermediate</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carver, s. n., ISC</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Cratty, s. n., ISC</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Deam, 27652, US</td>
<td>1.5</td>
<td>53</td>
</tr>
<tr>
<td>Freckmann, 921A, ISC</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Lelong, 2354, ISC</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>McDill, 111, ISC</td>
<td>0.6-0.8</td>
<td>x</td>
</tr>
<tr>
<td>Taxon, collector, number, herbarium</td>
<td>Terminal inflorescence</td>
<td>Axillary inflorescence</td>
</tr>
<tr>
<td>-----------------------------------</td>
<td>------------------------</td>
<td>------------------------</td>
</tr>
<tr>
<td></td>
<td>Anther size in mm</td>
<td>% Good pollen</td>
</tr>
<tr>
<td>Some, 800, ISC</td>
<td>1.2-1.5</td>
<td>(50)</td>
</tr>
<tr>
<td>Thorne, 16099, ISC</td>
<td>1.2</td>
<td>x&lt;sup&gt;e&lt;/sup&gt;</td>
</tr>
<tr>
<td>P. perlongum-P. lineari-Folium intermediate</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Moore and Phinney, 10761, ISC</td>
<td>1.4</td>
<td>(85)</td>
</tr>
</tbody>
</table>

<sup>e</sup>Heavily infested with thrips
Lelong, except that I do not believe that the terminal inflorescences are as strongly cleistogamous as he seemed to imply. The spikelets of many of the well-exserted terminal inflorescences are more than 1.0 mm long. Some spikelets were found in which both the stigmas and the anthers were well-exserted. In a few cases, the anthers were partially dehisced and the stigma contained some pollen grains which had begun to germinate, suggesting that the stigma was receptive at about the same time the anthers dehisced. This implies that many of the spikelets of the terminal inflorescences may be self-pollinated, but there is at least a chance for cross-pollination to occur.

Spikelets of the terminal inflorescence usually mature seed. It is not necessary to assume that innate sterility factors were involved in those cases in which the spikelets of the terminal panicle were found to be abortive. In some of these cases the upper portions of the culms and blades were somewhat withered or brown, suggesting that drought, a late spring frost, or some other adverse environmental factor had affected the plant. In other cases the spikelets of the terminal panicles were found to be heavily infested with thrips.

The axillary inflorescences are highly cleistogamous. The anthers are often 0.2-0.6 mm long and entangled with the stigmas within the florets. The stigmas are rarely exserted, and even then there seems to be little chance for cross-
pollination since the inflorescences are borne only three or four cm above ground level. Some of the spikelets at the base of the axillary inflorescences produce seed while partially enclosed in the sheath of the subtending leaf.

A condition transitional between these two patterns can be found in terminal panicles produced in late spring or early summer. These later terminal panicles have anthers 0.5-1.0 mm long, and although the spikelets usually open, the anthers are not well-exserted and often have dehisced before exsertion.

Considering the patterns of seed production described above, the great majority of seed must result from self-pollination. This fact may account for the apparent uniformity of most local populations of these taxa.

Conclusions

The depauperatum group is composed of three basic taxa which have been treated as separate species. An examination of herbarium specimens has shown that most specimens can be sorted into these three taxa on the basis of two or three characters. But approximately 10\% of the specimens encountered bridge the gap between the entities. I consider this percentage of intermediate specimens to be high enough to question the acceptance of the three entities as species.

The studies of fertility of typical members of the three taxa and of the intermediates suggest that there are few, if any, cytological or genetic barriers between the taxa. The
intermediate specimens are both fertile and fairly common. These facts argue against maintaining the three taxa as species.

The reproductive biology of this group must influence the decision on whether to recognize three species or less in this group. Since these plants are apparently autogamous to a great extent, there is apt to be little gene exchange between populations. There may be few barriers between _P. perlongum_, _P. depauperatum_, and _P. linearifolium_ other than habitat preferences. But since most individuals of each entity are strongly autogamous, there is little opportunity for hybridization, and even less opportunity when the prairie habitat of _P. perlongum_ is a considerable distance from the dry, open woodland habitats of _P. depauperatum_ or _P. linearifolium_. When two of these entities are found in adjacent areas there may be no niche for an F₁ hybrid, except when the habitats are somewhat disturbed. In this event a new homozygous line combining some of the traits of both parents may arise. The fact that some of the intermediate specimens were collected on disturbed edges of prairies or woodlands tends to support this hypothesis.

If the three taxa of the depauperatum group are treated as one species, the question of treating them as subspecies or varieties arises. I prefer to regard infraspecific taxa of a species as subspecies when the great majority (perhaps 90-95%) of the specimens are separable into the respective
taxa on the basis of a few traits, and to regard the taxa as varieties when the separation is more tenuous, involving many intermediate specimens. The three taxa of the depauperatum group seems to fit these criteria of subspecies.

The existence of glabrous-sheath and pilose-sheath individuals of _P. linearifolium_ and _P. depauperatum_ in all parts of the range of both entities without a correlation of this trait with any other trait suggests that these variations represent geographic clines in the frequency of this single trait. I have decided therefore, not to recognize these variants as varieties.

**Taxonomy of the Depauperatum Group**

The depauperatum group includes one species, _P. depauperatum_ Muhl. This species ranges from Newfoundland and southern Quebec west to southern Manitoba and eastern Colorado, south to east Texas, southern Mississippi, Alabama, and South Carolina. It is found in semi-open pine and oak woodlands, dry to mesic prairies, roadsides and disturbed ground, sand dunes, and occasionally in acid bogs.

The following key should separate the majority of the specimens into subspecies:

1. Mature fertile florets 1.4-1.8 mm wide; spikelets more than 2.8 mm long; panicle branches ascending, or if spreading, then spikelets with prominent beak.

2. Second glume and sterile lemma extending beyond fertile floret to form prominent beak; panicles usually more than half as wide as long, with spreading lateral branches; most pedicels more than 3.0 mm long; lower
leaves spreading; sheaths pilose or glabrous............
............................................................ ssp. depauperatum

2. Second glume and sterile lemma not forming a prominent beak; panicles usually less than half as wide as long, with strongly ascending lateral branches; pedicels, except those terminating principal branches; less than 3.0 mm long; lower leaves erect, forming compact tufts around main culms; sheaths pilose......... ssp. perlongum

1. Mature fertile florets 1.0-1.4 mm wide; spikelets less than 2.8 mm long; panicle branches spreading; spikelets lacking a prominent beak.............. ssp. linearifolium

PANICUM DEPAUPERATUM Muhl. Ssp. DEPAUPERATUM

Panicum depauperatum Muhl. Descr. Gram. 112. (1817) (2)
Panicum depauperatum var. psilophyllum f. cryptostachys Fern. Rhodora 23:194. (1921) (1,2).

Additional Synonomy

The synonomy appearing under P. depauperatum in Hitchcock and Chase (1951, p. 915) is tentatively accepted. A discussion of some aspects of the nomenclature of this taxon appears in Voss (1966).

Distribution

This subspecies ranges throughout the eastern United States and southern Canada, from Newfoundland to Minnesota south to northeast Texas and central Georgia. It appears to be more common in the eastern half of its range. It occurs predominantly on dry, often acidic soils, in open or semi-open habitats, especially in pine or oak woodlands which have been disturbed within the past few years by logging or fire. Other common habitats include sandy old fields; dry, sandy or gravelly
stream banks; sand dunes; and disturbed roadsides on sterile clay or gravel. It seems to be excluded from moist, organic soils, dense grassy vegetation, and areas of deep shade.

**PANICUM DEPAUPERATUM SSP. PERLONGUM (Nash) Comb. nov.**


**Observations on Synonomy**

The isotype of *P. pammelii* (Cratty, s. n., ISC) is a specimen intermediate between this subspecies and the ssp. *depauperatum*. It combines the habit of ssp. *perlongum* with beaked spikelets characteristic of ssp. *depauperatum*. The placement of this binomial in synonomy under either subspecies is somewhat questionable.

**Distribution**

The range of ssp. *perlongum* coincides roughly with the distribution of the tall-grass and mixed-grass prairies. The range extends from northern Indiana northwestward across central Wisconsin and Minnesota to southern Manitoba, then south to eastern Colorado and east Texas, and northeast through Arkansas to central Illinois. This subspecies usually grows in dense prairie turf on dry to mesic prairies. It occurs less commonly on dry roadcuts, in oak woodlands, and on sand dunes.
PANICUM DEPAUPERATUM SSP. LINEARIFOLIUM (Scribn.) Comb. nov.

Panicum linearifolium Scribn. in Britt. and Brown. Illustr. Flora. 3:500 (1898) (1,2). See discussion below.

Panicum werneri Scribn. in Britt. and Brown. Illustr. Flora. 3:501. (1898) (1,2).

Nomenclature and Additional Synonomy

The synonomy included in Hitchcock and Chase (1951) under P. linearifolium and P. werneri is tentatively accepted here as part of the synonomy of this subspecies.

Voss (1965) has challenged the citation of Lamson-Scribner as the author for P. linearifolium. The binomial was published in Britton and Brown's Illustrated Flora (1898) with Scribner as the cited author. The name is followed by the species description given in the same manner as that of all other species treated in the Flora, and without citation of a type or original material. Voss contends that since the description of P. linearifolium is in the same style as the other descriptions of grasses in the Flora which were written by Britton, that Britton also wrote this description. Since the person who provided the description is considered to be the more important author when the shortened form of the author citation is used, Britton should be cited as the author.

I reject Voss' contention that Britton should be credited with having described this taxon since there is no way of being certain that Britton actually wrote the description.
Distribution

The ssp. *linearifolium* ranges from Newfoundland to Minnesota, south to northeast Texas and southern Alabama and Georgia. The habitats include semi-open areas in dry oak or pine woodlands; dry, sandy fields; chert, quartzite, or limestone ridges; recently-disturbed roadcuts; and raised mounds in tamarack bogs. The soils of these habitats are usually acidic and commonly dry and well-drained. These plants do not appear to tolerate dense shade or heavy competition.
THE LAXIFLORUM GROUP

General Observations

The laxiflorum group is one of the more difficult groups of the dichanthelium to characterize. Most of the distinguishing traits, such as the lax nature of the blades and inflorescence branches, are influenced by environmental conditions. Some of the individuals of this group growing under extremely dry or sterile conditions resemble species in other groups.

"Typical" plants of the laxiflorum group have soft, lax, yellow-green foliage. The leaves tend to aggregate at the base of the plant. The basal leaves are at least as large as the lower cauline leaves and there are no distinct winter rosettes. The upper culm blades are never longer than the lower blades, and in many cases they are greatly reduced. The leaf blades are usually ciliate. Vernal culms tend to be slender and elongate with upper internodes longer than the lower and exceeding the sheaths. The inflorescence of the vernal culms is often very open and lax at maturity. Autumnal branches arise from basal nodes and bear somewhat reduced panicles. In the southern part of the range of the laxiflorum group these autumnal branches may be produced throughout the winter with a gradual transition to the vernal culms evident in March and April.

One of the more difficult groups to separate from the laxiflorum group is the ensifolium group. The striking similarity of the growth form and the close association on the
same habitat of such members of the laxiflorum group as *P. polycaulon* Nash with ensifolia species such as *P. trifolium* Nash and *P. albomarginatum* Nash probably account for the fairly high percentage of mixed herbarium sheets including specimens from both groups. These species tend to grow together in very sandy, open pinelands in the Southeast and to develop long, slender vernal culms with one to four very small bract-like cauline leaf blades.

The chief differences between the two groups are found in the leaves. Most of the ensifolium species occurring in these habitats have glabrous leaves with prominent, white, cartilaginous margins. The laxiflora species have soft leaves without the prominent cartilaginous margins, but with prominent cilia. Additional traits can be employed to separate particular species in one group from particular species in the other. It is only when the small, glabrous extremes of the laxiflorum group are encountered that the separation from the ensifolium group becomes difficult.

At the other extreme, large pilose forms of *P. laxiflorum* Lam. (including *P. xalapense* H.B.K.) can be difficult to separate from *P. villosissimum* of the lanuginosum group. Under most circumstances, these two species differ in many characters as indicated in Table 5. But exceptionally firm and densely pilose specimens of *P. laxiflorum* closely resemble lax forms of *P. villosissimum* Nash. In such cases *P. villosissimum* can be recognized by the very dense nature of the blade
Table 5  A comparison of *Panicum villosissimum* and *P. laxiflorum*

<table>
<thead>
<tr>
<th>Character</th>
<th><em>P. villosissimum</em></th>
<th><em>P. laxiflorum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Firmness of blade</td>
<td>Firm</td>
<td>Lax</td>
</tr>
<tr>
<td>Vestiture of blade</td>
<td>Densely pilose</td>
<td>Pilose, pubescent, or glabrous</td>
</tr>
<tr>
<td>Pseudoligule</td>
<td>Composed of long trichomes</td>
<td>Absent</td>
</tr>
<tr>
<td>Winter rosette</td>
<td>Late in season or absent</td>
<td>Absent</td>
</tr>
<tr>
<td>Autumnal branches</td>
<td>From mid-culm nodes, forming dense fascicles</td>
<td>From basal nodes, resembling vernal culms, forming large tufts</td>
</tr>
<tr>
<td>Spikelet length</td>
<td>2.1-2.5 mm</td>
<td>1.6-2.3 mm</td>
</tr>
<tr>
<td>Spikelet shape</td>
<td>Oblong-elliptic</td>
<td>Broadly elliptic</td>
</tr>
</tbody>
</table>

pilosity, the "pseudoligule" of long trichomes borne immediately above the true ligule, and the tendency for the autumnal branches to arise from mid-culm modes.

I have encountered at least one specimen (Cocks, 2510, US) which appears to be transitional between the laxiflorum group and possibly the dichotomum group. Hitchcock and Chase (1910) cited this specimen as *P. xalapense* ssp. *strictirameum* Hitchc. and Chase. It is discussed below.

Previous Taxonomic Treatments

Hitchcock and Chase erected the "Laxiflora" group in 1910
to include five species and one additional subspecies. The synonomy included eight more binomials. The first dichotomy of their key divided the six accepted taxa into one group of three with retrorsely-pilose sheaths and a second group of three which lacked retrorsely-pilose sheaths. The first group included _P. laxiflorum, P. xalapense, and P. xalapense ssp. strictirameum; the second group included _P. ciliatum Ell., P. polycaulon, and P. strigosum Michl. Later authors condensed the number of species within these subgroupings, but the primary distinction between the two complexes based on sheath pilosity has been maintained.

Hitchcock and Chase employed the following couplet in their key to separate _P. laxiflorum and P. xalapense:

Blades ciliate and more or less pilose on the surface; spikelets 2 mm long.............._P. xalapense

Blades glabrous or nearly so on the surface and margin; spikelets 2.2 mm long............._P. laxiflorum

In the description of _P. xalapense they noted that the vernal form was very similar to _P. laxiflorum, but that the culms and blades tended to be shorter and that the panicles tended to have more spikelets. The range of _P. laxiflorum (Hitchcock and Chase, 1951) extends from Virginia to Florida and Alabama, in contrast to _P. xalapense which extends much beyond the range of _P. laxiflorum northward to Maryland and Illinois, west to Texas and south into Mexico.

Fernald (1934) reduced _P. xalapense to synonomy under _P. laxiflorum_. He noted that some of the specimens cited as
P. laxiflorum by Hitchcock and Chase in their 1910 paper have pilose blades and spikelets 2.2-2.3 mm long. Other specimens with sparsely pilose blades and spikelets 2.2 mm long were cited as P. xalapense. He also claimed that some specimens which were "treated authoritatively as P. laxiflorum" have spikelets as small as the smallest P. xalapense. He concluded by pointing out that although the type specimen of P. xalapense (from Jalapa, Mexico, and therefore out of the range of P. laxiflorum according to Hitchcock and Chase) has spikelets 2.0 mm long, other collections of P. xalapense from the type locality have spikelets up to 2.3 mm in length.

Fernald, and Hitchcock and Chase did agree on the recognition of two infraspecific taxa within P. xalapense (P. laxiflorum, sensu lato). Hitchcock and Chase published P. xalapense ssp. strictirameum to include individuals "differing from P. xalapense (ssp. xalapense) in having ovoid, more compact panicles with ascending branches, somewhat smaller spikelets, 1.7 mm long, shorter, narrower blades than common in the species, and shorter culms." Fernald changed the status of this taxon to P. laxiflorum var. strictirameum in 1934.

Hitchcock and Chase conceded that the remaining material of the laxiflorum group was difficult to separate into species. Nevertheless, they recognized three species. Panicum ciliatum was characterized by having pubescent spikelets 1.8-2.0 mm long and essentially glabrous foliage; P. polycaulon by glabrous foliage and glabrous spikelets 1.5-1.6 mm long; and
The one separation of the three which seems to have been the most troublesome for Hitchcock and Chase (1910) was the separation of *P. polycaulon* from *P. ciliatum*. They described some of the difficulties which they encountered as follows:

The type specimens of *P. ciliatum* and *P. polycaulon* differ in the spikelet characters, the former having pubescent spikelets 2 mm long and the latter having glabrous, more obovate, turgid spikelets 1.6 mm long. Our numerous specimens, however, do not show these constant differences. Occasional specimens have glabrous spikelets as much as 2 mm long. A comparatively few specimens have pubescent spikelets that are of smaller size. We have not found any distinct differences in habit that can be coordinated with the spikelet characters. The range of the two forms is somewhat different, *P. ciliatum* extending from North Carolina to northern Florida, and *P. polycaulon* throughout Florida and southward into Cuba. It will be observed that the ranges of the two overlap in northern Florida and it is here that the intermediate specimens are found.

Certain authors have since treated these two entities as one species, *P. ciliatum* in the broad sense. Radford, Ahles, and Bell (1964) placed *P. polycaulon* in synonymy under *P. strigosum* and maintained *P. ciliatum* in the narrow sense as distinct from the other two. In fact, they employed an entirely different character to separate the two species as they delimited them. According to their key *P. strigosum* has a ligule more than 2 mm long and *P. ciliatum* a ligule less than 0.5 mm. Fernald (1950) placed *P. strigosum* under the couplet, "ligules obsolete or up to 0.5 mm long" in his key to the species of dichanthelia included in Grey's *Manual*. However, since the other two entities did not occur in the
range of the Manual, there is no indication of his views on the delimitation of the other two taxa.

Methods of Analysis

My study of the *laxiflorum* group was based primarily on the examination of 213 herbarium specimens, including 112 sheets representing the *P. laxiflorum*-*P. xalapense* complex and 101 sheets for the *P. ciliatum*-*P. polycaulon*-*P. strigosum* complex. In addition, 20 small mass collections were analyzed to obtain an indication of variation within local populations.

A data sheet was filled-out for each specimen. These data sheets were used for subsequent correlation studies and for the tables and scatter-diagrams included in this paper. The procedures for handling the data sheets were the same as those described in the chapter dealing with the depauperatum group.

The characters recorded on the data sheets included the following:

1. the width of the terminal panicle
2. the angle formed by the lowermost prominent panicle branch and the axis of the inflorescence
3. the number of spikelets per inflorescence
4. the length of a spikelet with a maturing caryopsis
5. the density of spikelet pubescence
6. the length of the second glume and sterile lemma in relation to the length of the fertile floret
7. the type and density of the vestiture of sheaths and adaxial blade surfaces
8. the presence or absence of cilia
9. the length and width of the uppermost cauline leaf blade
10. the relative length of the upper and lower leaf blade
11. the height of the tallest culm.

Patterns of Variation

The primary subdivision of the laxiflorum group into two complexes seems to be satisfactory. With few exceptions, specimens can be placed in one complex or the other on the basis of two primary characters and a few secondary characters. Members of the *P. laxiflorum-P. xalapense* complex have retrorsely-pilose sheaths and cauline leaf blades of nearly uniform size. Members of the *P. ciliatum-P. polycaulon-P. strigosum* complex have sheaths either glabrous or ascending-pilose and show a marked reduction in the size of the upper cauline leaf blades.

Plants of the *P. laxiflorum-P. xalapense* complex also tend to differ from the other complex in having longer spikelets (1.7-2.3 mm in contrast to 1.2-2.0 mm) which are always pubescent. They also have more open, lax inflorescences, and weaker cilia on the blades. Members of this complex are more widespread than the members of the *P. ciliatum-P. polycaulon-P. strigosum* complex, ranging over most of the southeastern quarter of the United States on a wider variety of habitats.
The two primary characters are well-correlated. Only about ten of the 213 specimens show the unexpected combination of either retrorsely-pilose sheaths and short blades or long blades without retrorse pilosity. One of these ten specimens (Eggert, s. n., ISC) seems to belong to the _P. laxiflorum-P. xalapense_ complex, but it is completely glabrous. A second specimen (Curtiss, 6635, ISC) is glabrous except for a few spreading hairs on the sheath. It seems to fit _P. laxiflorum_ in other traits. Seven specimens have cauline blades 4-6 cm long, but lack the retrorse pilosity and other traits of the _P. laxiflorum-P. xalapense_ complex. Another specimen (Curtiss, 4031, US) combines a retrorsely-pilose sheath with the other characters of _P. strigosum_. These last eight specimens can be treated as slightly aberrant members of the _P. ciliatum-P. polycaulon-P. strigosum_ complex.

Several characters have been proposed to separate _P. laxiflorum_ from _P. xalapense_. These characters have been compiled from Hitchcock and Chase (1910 and 1951) and Silveus (1942) and are summarized in Table 6.

The results of the attempts to correlate the three chief diagnostic characters - spikelet length, blade pilosity, and cilia - are presented in Figure 4. Because of the difficulty involved in interpreting such descriptions of leaf vestiture as "blades glabrous or nearly so" or "blades more or less pilose" in the manner in which Hitchcock and Chase meant them
Table 6  A compilation of characters used by various authors to separate Panicum laxiflorum and P. xalapense

<table>
<thead>
<tr>
<th>Character</th>
<th>P. Laxiflorum</th>
<th>P. xalapense</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of spikelets</td>
<td>more</td>
<td>fewer</td>
</tr>
<tr>
<td>Spikelet length</td>
<td>2.2 mm</td>
<td>2.0 mm</td>
</tr>
<tr>
<td>Fertile floret</td>
<td>covered at maturity</td>
<td>exposed at maturity</td>
</tr>
<tr>
<td>Blade length</td>
<td>longer</td>
<td>shorter</td>
</tr>
<tr>
<td>Blade surface</td>
<td>glabrous</td>
<td>pilose</td>
</tr>
<tr>
<td>Blade margin</td>
<td>glabrous</td>
<td>ciliate</td>
</tr>
<tr>
<td>Range</td>
<td>restricted to coastal plain, Va. to Ala.</td>
<td>southeastern U.S. and Mexico</td>
</tr>
</tbody>
</table>

It is apparent from Figure 4 that there is little correlation between any of the blade vestiture characters and
Figure 4  Correlation of spikelet length and leaf vestiture in *Panicum laxiflorum* (sensu lato)

Graph A. Open bar indicates the per cent of specimens with glabrous leaf margins having spikelet length indicated; solid bar indicates per cent of specimens with ciliate margins having spikelet length indicated.

Graph B. Open bar represents specimens with completely glabrous margins or sparsely ciliate margins; solid bar represents specimens with densely ciliate margins.

Graph C. Open bar represents specimens with glabrous adaxial blade surfaces; solid bar represents specimens with sparsely to densely pilose adaxial blade surfaces.

Graph D. Open bar represents specimens with glabrous to sparsely pilose adaxial blade surfaces; solid bar represents specimens with densely pilose adaxial blade surfaces.
Figure 5  Geographic origin and variation in critical characters of specimens of the *Panicum laxiflorum* - *P. xalapense* complex
spikelet size. Regardless of the criterion by which the specimens were divided into contrasting sets, there is only a slight tendency for the glabrous plants to have larger spikelets.

According to Hitchcock and Chase (1910), P. laxiflorum occurs primarily in Florida and along the coast to Virginia. Plants with glabrous blades and larger spikelets should, therefore, be concentrated in this region. All of the specimens of the P. laxiflorum-P. xalapense complex have been located on a map of the southeastern United States (Figure 5) with spikelet size and blade vestiture characters indicated. The map indicates that there is a concentration of specimens with larger spikelets from northern Florida with one additional large-spikelet plant from the vicinity of Washington, D. C. There is no indication that glabrous plants are confined to the range given by Hitchcock and Chase for P. laxiflorum. Thus the only trait which shows some of the expected geographic correlation is spikelet size.

The effectiveness of the remaining characters listed in Table 5 for separating P. laxiflorum from P. xalapense was tested using only those specimens which conformed exactly to the three key characters. Specimens with spikelets 2.1-2.3 mm long and glabrous blades were selected to represent P. laxiflorum and specimens with spikelets 1.7-2.0 mm long and blades both pilose and ciliate were selected to represent P. xalapense. Nine specimens of "typical" P. laxiflorum and
43 specimens of "typical" *P. xalapense* were obtained. The 60 remaining specimens with a combination of two traits of one species with one trait of the other were set aside.

The range of variation in the length of the upper culm blades was 5-13 cm for the *P. laxiflorum* specimens and 4-17 cm for *P. xalapense*. The range in the number of spikelets per vernal inflorescence of *P. laxiflorum* was 16-84, and 14 to over 100 for *P. xalapense*. All fertile florets with mature caryopses of both *P. laxiflorum* and *P. xalapense* were exposed beyond the edges of the second glume and sterile lemma. Thus, the remaining traits listed on Table 5 prove to be of no value even in separating selected specimens.

*Panicum xalapense* ssp. *strictirameum* has been characterized by the combination of small spikelets (1.6-1.8 mm long) and compact inflorescences with ascending panicle branches. Specimens meeting these criteria are rare. Some of the plants identified as ssp. (or var.) *strictirameum* represent ordinary *P. xalapense* or *P. laxiflorum* in every respect except for spikelets 1.6-1.8 mm long (e.g., Demaree, 14942, ISC; House, 2551, US). Another group of specimens have shorter, firmer blades and superficially resemble *P. ciliatum* and *P. polycaulon* except for the presence of retrorsely-pilose sheaths. One specimen (Hitchcock, 1290, ISC) includes one typical plant of *P. xalapense* plus another plant with a smaller, more compact habit. Individuals of this latter type might be the result of hybridization with one of
the members of the *P. ciliatum*-*P. polycaulon*-*P. strigosum* complex, or the result of having grown under unusually dry, sterile soil conditions.

One specimen (Cocks, 2510, US) has a combination of soft, lax foliage with narrow, compact inflorescences and small spikelets about 1.7 mm long. It is the only specimen of the laxiflorum group encountered in which the autumnal branches arise from the mid and upper culm nodes. The presence of this last trait suggests that this plant may have resulted from hybridization between *P. laxiflorum* or *P. xalapense* and a member of another group, possibly the dichotomum group. It is difficult to place this specimen in any existing taxon of the dichanthelia. It does not agree well with the holotype or the original description of *P. xalapense* ssp. *strictirameum*, although Hitchcock and Chase cited this specimen following the original description and the holotype.

The only characters which have been proposed in the literature for the separation of *P. ciliatum*, *P. polycaulon*, and *P. strigosum* are spikelet length, spikelet pubescence, and leaf pubescence. The specimens representing this complex are compared on the basis of these traits on a scatter-diagram (Figure 6). One additional trait, the height of the main culm, has been used primarily as a means of achieving a vertical separation of the specimens on the scatter diagram.

The scatter diagram summarizes the problems in the taxonomy of this complex. With the small number of charac-
Figure 6  Scatter diagram comparing *Panicum ciliatum*, *P. polycaulon*, and *P. strigosum* on the basis of the diagnostic characters
ters involved, only a few combinations are possible and most of these combinations exist. The most common combinations represent the typical forms of the species and are as follows: spikelets pubescent, 1.8-2.0 mm long, glabrous blade surfaces - *P. ciliatum*; spikelets glabrous, 1.5-1.7 mm long, blade surfaces glabrous - *P. polycaulon*; spikelets glabrous, 1.2-1.4 mm long, blade surfaces pilose - *P. strigosum*. The following "recombinations" also occur: glabrous spikelets 1.9-2.0 mm long (Chapman, 7210, MO; Ravenel, s. n., MO; Silveus, 5815, US; Tracy, 6698, MO; and MO 812904); pubescent spikelets 1.5-1.7 mm long (Tracy, 7208, ISC); spikelets 1.2 mm long and glabrous blades (Chase, 4365, US; Hitchcock, 1162, US); and spikelets 1.6 mm long with pilose blades (Curtiss, 3597, US). These "recombination" forms have been treated as atypical specimens of any of the three species depending on whether the primary emphasis was placed on blade or spikelet characters.

Reproductive Biology

Herbarium specimens and inflorescences fixed in the field in Newcomer's fixative were studied to determine if the spikelets of terminal and axillary panicles were fertile and whether they were chasmogamous or cleistogamous. The observations are summarized in Table 7. Additional observations were made on one plant of *P. laxiflorum* (sensu lato) grown in the Iowa State greenhouse.
Table 7  Pollen fertility and seed set in terminal and axillary inflorescences of plants in the laxiflorum group of Panicum

<table>
<thead>
<tr>
<th>Taxon, collector, number, herbarium</th>
<th>Terminal inflorescence</th>
<th>Axillary inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anther size in mm</td>
<td>% Good developing pollen seed</td>
</tr>
<tr>
<td>P. laxiflorum (sensu lato):</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ahles, 12848, ISC</td>
<td>0.8</td>
<td>62</td>
</tr>
<tr>
<td>Curtiss, 5537, ISC</td>
<td>0.6</td>
<td>93</td>
</tr>
<tr>
<td>Freckmann, 2077e</td>
<td>0.6</td>
<td>93</td>
</tr>
<tr>
<td>Freckmann, 2090e</td>
<td>0.8</td>
<td>(90)</td>
</tr>
<tr>
<td>Freckmann, 2099e</td>
<td>0.8</td>
<td>83</td>
</tr>
<tr>
<td>Freckmann, 2113, ISC</td>
<td>0.8</td>
<td>88</td>
</tr>
</tbody>
</table>

a "Good pollen" is defined as pollen which is spherical and well-filled with deeply-staining granular cytoplasm

b Parentheses indicate an approximation due to immaturity of pollen

c Heavily infested with thrips

d "x" indicates presence of developing seed

E Inflorescences fixed in the field in Newcomer's fixative
<table>
<thead>
<tr>
<th>Taxon, collector, number, herbarium</th>
<th>Terminal inflorescence</th>
<th>Axillary inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anther size in mm</td>
<td>% Good pollen</td>
</tr>
<tr>
<td>Freckmann, 2458, ISC</td>
<td>0.4</td>
<td>(80)</td>
</tr>
<tr>
<td>Godfrey and Radford, 52222, ISC</td>
<td>0.9</td>
<td>91</td>
</tr>
<tr>
<td>Heller and Heller, 4209, ISC</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kearney, 1179, ISC</td>
<td>0.7</td>
<td>(50)</td>
</tr>
<tr>
<td>Lelong, 2660^f</td>
<td>0.8-1.0</td>
<td>50</td>
</tr>
<tr>
<td>Lelong, 2684^f</td>
<td>0.8-1.0</td>
<td>47</td>
</tr>
<tr>
<td>Lelong, 2682^f</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F. ciliatum:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Combs, 288, US</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freckmann, 2143, ISC</td>
<td>0.4</td>
<td>80</td>
</tr>
<tr>
<td>Hitchcock, 1019, US</td>
<td>1.0</td>
<td>70</td>
</tr>
</tbody>
</table>

^Reported in lit. (Lelong, 1965)
<table>
<thead>
<tr>
<th>Taxon, collector, number, herbarium</th>
<th>Terminal inflorescence</th>
<th>Axillary inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anther size</td>
<td>% Good pollen</td>
</tr>
<tr>
<td>P. polycaulon:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chase, 4150, US</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eaton, 1402, US</td>
<td>0.8</td>
<td>87</td>
</tr>
<tr>
<td>P. strigosum:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Curtiss, 3597, ISC</td>
<td>0.7</td>
<td>(85)</td>
</tr>
<tr>
<td>Hume, s. n., US</td>
<td>0.6</td>
<td>(80)</td>
</tr>
<tr>
<td>P. ciliatum-P. polycaulon-P. strigosum intermediates:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chapman, s. n., MO 812904</td>
<td>0.6</td>
<td></td>
</tr>
<tr>
<td>Chapman, 7210, MO</td>
<td>0.4</td>
<td></td>
</tr>
<tr>
<td>Chase, 4365, US</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hitchcock, 1162, US</td>
<td>0.5</td>
<td>82</td>
</tr>
<tr>
<td>McDaniel, 3106, MO</td>
<td>0.6</td>
<td>96</td>
</tr>
<tr>
<td>Silveus, 5815, US</td>
<td>0.7</td>
<td>91</td>
</tr>
</tbody>
</table>
Spikelets of the terminal panicles of *P. laxiflorum* (sensu lato) are usually chasmogamous. This is reflected in the fact that the anthers are about 0.8 mm long. The pollen fertility according to the lacto-phenol and aniline blue test ranges from 47% to 93%, with most spikelets around 90%. Caryopses were found to be developing in most spikelets of nearly all terminal inflorescences at the proper stage of maturity. A few inflorescences were found to be heavily infested with thrips.

Although all spikelets of terminal inflorescences appear to open prior to anther dehiscence, the degree of exsertion of the anthers varies. Lelong (1965) noted this variation in the live plants of *P. xalapense* (*P. laxiflorum*, sensu lato) which he studied. He indicated that the size of the anther was related to the extent to which it was exserted. Those anthers of terminal panicles measuring 0.4-0.6 mm long were generally little exserted and tended to release pollen in close proximity to the stigmas.

The spikelets of axillary panicles (the term, axillary, is not very appropriate in this case since the culms bearing these panicles arise from the basal nodes and caudex in the same manner as the vernal culms) are generally cleistogamous. Occasionally stigmas are exserted. Anthers may be seen at the opening of the fertile floret in these cases. But in most instances the anthers are small, about 0.3 mm long, and dehisce within the closed floret. The pollen of these cleis-
together spikelets seems to be highly fertile and maturing caryopses can usually be found in older axillary panicles.

Members of the *P. ciliatum*-*P. polycaulon*-*P. strigosum* complex exhibit a similar pattern of chasmogamy and cleistogamy. Many of the spikelets of terminal panicles have anthers 0.7-1.0 mm long. These anthers tend to be exserted. Other spikelets of terminal inflorescences possess small anthers 0.4-0.6 mm long and are probably self-pollinated. The anthers of the axillary panicles are about 0.3 mm long, with only about 70-90 pollen grains per anther. The stigmas of these spikelets are rarely exserted and the spikelets normally are cleistogamous. Both terminal and axillary spikelets show a fairly high degree of pollen fertility and developing caryopses can be found in mature panicles. Thrip infestations of terminal panicles are fairly common.

Six of the specimens of the *P. ciliatum*-*P. polycaulon*-*P. strigosum* complex which possessed unusual combinations of the diagnostic traits (see discussion under "Patterns of Variation") were examined carefully to determine if there were any indications of reduced fertility in these forms as compared with the more common members of this complex. No sign of reduced fertility could be found in these plants.

The above data suggest that the great majority of the seed produced by members of the laxiflorum group results from self pollination. Since most plants produce axillary panicles through a much longer part of the growing season than that in
which they bear terminal panicles, the majority of the seed is produced in cleistogamous axillary inflorescences. In addition, some of the spikelets of the terminal inflorescences contain small anthers and appear to self-pollinate. This leaves a minority of the spikelets which are chasmo-gamous, and many of these spikelets probably receive pollen from other spikelets of the same terminal panicle or from other terminal panicles of the same plant.

Population samples of members of the laxiflorum group are generally as uniform as might be expected in view of the autogamous nature of the plants. Small mass collections of _P. ciliatum, P. polycaulon, and P. strigosum_ are quite uniform. When two of these entities occur together, the diagnostic characters remain constant. Population samples of _P. laxiflorum (sensu lato)_ exhibit a small range of variation in certain traits such as culm height and blade length, but this variation seems to depend on sunlight, soil, or on some other environmental factor.

Conclusions

The investigation of the _P. laxiflorum-P. xalapense_ complex has failed to provide a basis for the recognition of two species. Although a moderately large range of variation occurs in a few of the traits, the traits are not sufficiently correlated to be of taxonomic value. The concentration of individuals with larger spikelets in northern Florida may
indicate the presence of a local race or variety in this region. Mass collections and greenhouse transplants from this area are needed. However, with the information presently available, it seems best to unite _P. laxiflorum_ and _P. xalapense_.

The subspecies or variety _strictirameum_ should be placed in synonomy under _P. laxiflorum_. The few specimens which fit the narrow definition of this taxon occur sporadically throughout the range of the species. They seem to be aberrant forms of _P. laxiflorum_. They do not appear to constitute a natural taxon.

_Panicum ciliatum_, _P. polycaulon_, and _P. strigosum_ should be united as one species. All three entities are sympatric to a considerable extent, and they are commonly found in the same habitat. The strong tendency toward autogamy may be the chief factor involved in keeping the three entities separate. However, intermediates which combine two of the diagnostic traits of one entity with one trait of a second entity exist, and these intermediates are fertile.

It seems best to maintain the three entities as varieties of one species. This treatment reflects the apparent close relationship between the entities as well as the need for caution in completely merging these taxa.

**Taxonomy of the Laxiflorum Group**

The _laxiflorum_ group as treated here includes two
species, one of which includes three varieties. The two species can be separated by the following key:

1. Sheaths retrorsely-pilose; uppermost blade of vernal culm 4-17 cm long, at least 3/4 as long as basal leaves; blade margins glabrous or finely ciliate...........P. laxiflorum

1. Sheaths glabrous or ascending-pilose; uppermost blade of vernal culm 1.5-6.0 cm long, less than 3/4 as long as basal leaves; blade margins prominently papillose-ciliate........................................P. ciliatum

PANICUM LAXIFLORUM Lam


Nomenclature and Additional Synonomy

The additional synonomy appearing under P. laxiflorum and P. xalapense in Hitchcock and Chase (1951, pp. 919 and 926) is accepted here.

The author citation and date of publication traditionally given for P. xalapense var. strictirameum as "Hitchcock and Chase, 1910" is not correct. Hitchcock and Chase published this entity as a new subspecies in 1910 and not as a
variety. This entity was given the status of a variety in 1935 (Hitchcock, 1935) without a formal statement of the change in status of this name, but with a bibliographic reference to *P. xalapense* ssp. *strictirameum*. Therefore, the reference to *P. xalapense* var. *strictirameum* should be Hitchcock, 1935, and not Hitchcock and Chase, 1910.

**Distribution**

*Panicum laxiflorum* is found throughout the southeastern United States from Florida and the Gulf of Mexico northward to Maryland, southern Indiana, southern Illinois, and eastern and southern Missouri; and from the Atlantic coast west to eastern Oklahoma and eastern Texas. It also occurs in eastern Mexico, Guatemala, and the West Indies. It is most common on open, disturbed sites including roadsides, ditches, mowed areas between highways and woods, woodland trails, burned-over woods, open river bottomlands, and roadcuts. It also occurs in partially open areas in a variety of forest and woodland types including both wet and dry pine woods, oak-pine woods, rich mixed mesophytic forests, swamp woods of either hardwoods or bald cypress, and pine-palmetto woodlands. The soils are often sandy or clayey. Soil moisture conditions range from dry, well-drained sandy soils to wet, organic soils at the edge of marshes and swamps. The principal habitat limitation on this species seems to be its intolerance of deep forest shade and of heavy competition from dense grassy vegetation.
PANICUM CILIATUM Ell.

Distribution

This species ranges from southeastern Virginia along the Atlantic and Gulf Coastal Plain west to eastern Texas and south through Florida to the West Indies, Central America, and Colombia. It includes three varieties, with some individuals intermediate between the varieties.

1. Blades glabrous or very sparsely pilose; spikelets 1.4-2.0 mm long

2. Spikelets pubescent, 1.7-2.0 mm long...var. ciliatum

2. Spikelets glabrous, 1.4-1.7 mm long...var. glabrescens

1. Blades pilose; spikelets 1.2-1.5 mm long...var. pubescens

PANICUM CILIATUM Ell. var. CILIATUM


Additional Synonomy

The synonomy included under _P. ciliatum_ Ell. in Hitchcock and Chase (1951, p. 914) is accepted here.

Distribution

The var. _ciliatum_ ranges from North Carolina southward along the Atlantic Coastal Plain to central Florida and west along the Gulf Coastal Plain to eastern Texas and Mexico. It occurs principally in semi-open sandy flatwoods of longleaf and slash pines, often with _Vaccinium_ and _Serenoa_ in the understory. It also occurs in partly open areas in pine-sweet gum, or pine-mixed hardwood woods, and on sandy beaches. The
soils are almost always sandy and acidic, but vary in moisture conditions from wet depressions to dry sandy ridges.

**PANICUM CILIATUM VAR. GLABRESCENS** (Griseb.) Comb. nov.


**Nomenclature**

Grisebach (1864) did not use the term "variety" in designating the infraspecific taxa in the text of his *Flora*, using instead the Greek letter, $\alpha, \beta, \gamma$, etc. to enumerate the infraspecific taxa under each species. But in the preface to the text Grisebach referred to all infraspecific taxa as varieties. His description of this variety (as "*P. dichotomum L. glabrescens*"") is brief, but it fits this entity well. The type specimen in the Kew herbarium has been examined by Hitchcock.

**Distribution**

The var. *glabrescens* ranges from southern Georgia west along the Gulf coast to Mississippi and south through Florida to the West Indies. It is found in semi-open or open woodlands of longleaf and slash pines, in pocosin, in hummocks, and also on disturbed ground along trails, railroad tracks, and in gardens and fields. The soil is almost always sandy and acidic, and varies from dry and well-drained to wet and poorly-
drained.

PANICUM CILIATUM VAR. PUBESCENS (Vasey) Comb. nov.


Distribution

This variety extends from southeastern Virginia along the Coastal Plain to eastern Texas and southward through Florida and the West Indies to Central America and Colombia. The habitats include semi-open longleaf and slash pine woods, often with Vaccinium and Serenoa in the understory, poosin, hummocks, open areas in mixed pine-hardwood woods, bogs, and disturbed sandy areas along trails, roads, and railroads. The soil is usually sandy and acidic with a wide range of moisture conditions.
THE ANGUSTIFOLIUM GROUP

General Observations

The angustifolium group is characterized by the following combination of traits: erect, stiff vernal culms; narrow, firm, ascending leaf blades with prominent veins; prominently-nerved spikelets with attenuate bases; extensive autumnal branching from middle and upper nodes of the main culms; and distinct basal rosettes present in late autumn and through winter.

The leaf blade characters provide some of the best traits for distinguishing members of this group from other groups. The veins of angustifolia species are especially prominent and raised well above the level of the inter-vein leaf tissue. The blades are exceptionally narrow with a length-width ratio intermediate between the ratio for the depauperatum group and the ratios for members of other groups. Blades from the middle nodes of vernal culms had a ratio of 16:1 to 25:1 in nearly all specimens sampled. However, since exceptional specimens were found to have length-width ratios as low as 13:1 or as high as 49:1, there is an overlap in both directions with members of other groups.

Partially because of the overlap in length-width ratios of the blades with species in other groups there are cases in which the separation of angustifolia entities from entities in other groups is difficult. In most of these cases other traits can be employed to delimit the groups. The
areas of difficulty are summarized in Table 8.

* Panicum ovinum * Scribn. and Smith and * P. roanokense * 
Ashe present a very difficult problem for the separation of the angustifolium group from the dichotomum group. Much of the material of * P. ovinum * from dry, sandy habitats resembles * P. aciculare * Desv. ex Poir. and is readily distinguishable from * P. roanokense * by its pubescent blunt, turgid spikelets and shorter culms with lower sheaths overlapping. But * P. ovinum * also occurs on wet habitats with * P. roanokense *. Specimens from such habitats may possess all of the traits of * P. roanokense * except the completely glabrous spikelets.

* Panicum neuranthum * Griseb. is also quite similar to * P. roanokense *. The two entities have been found occasionally at the same location. In these cases the plants identified as * P. neuranthum * grew on nearly pure sand under dry, sterile conditions and the individuals of * P. roanokense * grew along a moist ditch or small stream under more mesic conditions. The differences between the two populations were slight, but constant.

* Panicum hirstii * Swallen is another entity which resembles * P. neuranthum * and * P. roanokense *. Swallen described * P. hirstii * in 1961, placing it in the dichotomum group and stressing the characters by which it differed from * P. roanokense *. It can be separated from * P. roanokense * by the longer blades and the slightly pointed spikelets with fertile florets not exposed.
Table 8  Comparisons between species of the angustifolium group and similar species of other groups

<table>
<thead>
<tr>
<th>Angustifolium species</th>
<th>Similar species</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Shared traits</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Contrasting traits</strong></td>
<td><strong>Contrasting traits</strong></td>
</tr>
</tbody>
</table>

**P. chrysopsidifolium:**
- Stiffly erect culms
- Stiff, villous blades
- Bearded nodes
- Spikelets 2.0 mm long, turgid
- Blades less than 5 mm wide
- Fertile florets more than 1.0 mm wide
- No glabrous ring below nodes

**P. thurowii:**
- Blades more than 5 mm wide
- Fertile florets less than 1.0 mm wide
- Glabrous ring below nodes

**P. consanguineum:**
- Stiff, ascending blades with similar dimensions
- Bearded nodes
- Villous sheaths and culms
- Spreading to decumbent, profusely-branched autumnal form
- Fertile florets 1.3-1.7 mm wide

**P. villosissimum:** (sensu lato)
- Fertile florets 1.1-1.3 mm wide
<table>
<thead>
<tr>
<th>Angustifolium species</th>
<th>Similar species</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Shared traits</strong></td>
<td><strong>Contrasting traits</strong></td>
</tr>
<tr>
<td><strong>Contrasting traits</strong></td>
<td><strong>Contrasting traits</strong></td>
</tr>
<tr>
<td>Spikelets 2.4-2.9 mm long, blunt</td>
<td>Spikelets 2.1-2.5 mm long, slightly pointed</td>
</tr>
</tbody>
</table>

**P. fusiforme:**
- Stiffly erect culms
- Stiffly ascending blades
- Crisp-puberulent culms
- Spikelets ca. 3.2 mm long, with attenuate bases
- Fertile florets 2.5 mm long, 1.4 mm wide

**P. malacon:**
- Second glume and sterile lemma extended beyond fertile floret and pointed
- Blade length-width ratio 15:1 to 25:1

**P. neuranthum:**
- Stiffly erect, glabrous culms
- Stiffly ascending, glabrous blades
- Narrow panicles with ascending branches
- Spikelets 2.0 mm long

**P. roanokense:**
- Second glume and sterile lemma shorter than fertile floret
- Blade length-width ratio 10:1 to 17:1
<table>
<thead>
<tr>
<th>Angustifolium species</th>
<th>Similar species</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Shared traits</strong></td>
<td><strong>Contrasting traits</strong></td>
</tr>
<tr>
<td><strong>Contrasting traits</strong></td>
<td></td>
</tr>
<tr>
<td>Second glume and sterile lemma usually extended</td>
<td>Second glume and sterile lemma shorter than fertile floret, and glabrous</td>
</tr>
<tr>
<td>extended beyond fertile floret, pointed, and sparsely pubescent</td>
<td></td>
</tr>
<tr>
<td>Blades generally more than 10 cm long</td>
<td>Blades generally less than 10 cm long</td>
</tr>
</tbody>
</table>

**P. ovinum:**
- Stiffly erect culms
- Stiffly ascending, glabrous blades of similar dimensions
- Spikelets 2.0 mm long
- Similar patterns of autumnal branching

**P. roanokense:**
- Spikelets pubescent
- Fertile florets rounded
- Second glume with yellow-green through-out

- Spikelets glabrous
- Fertile florets pointed
- Second glume with purple spot at base
But the separation of *P. hirsutii* from *P. neuranthum* is tenuous, depending on the glabrous spikelets and slightly more lax habit of the former.

*Panicum bennettense* W. V. Brown is an entity described by Brown in 1942 from the Bennett War Memorial grounds near Durham, N. C. Hitchcock and Chase (1951) added it to the angustifolium group apparently on the basis of its stiff leaf blades. However, the stiff nature of the blade is the only diagnostic character of the angustifolium group found in this plant, and in most other respects it resembles members of the *P. scabriusculum* complex (including *P. cryptanthum*, *P. recognitum*, and *P. mundum*). It is known only from the type collection and it is difficult to place it properly from the material available. I have not included it in the present treatment of the angustifolium group.

Some specimens of *P. villosissimum* and *P. angustifolium* Ell. are very similar to each other. These two species occur in open, sandy pine woods on the Coastal Plain. *Panicum villosissimum* normally has elliptical-ovate spikelets 2.1 to 2.5 mm long and densely villous, moderately stiff blades in contrast to the larger spikelets (2.4-2.9 mm) and nearly glabrous very stiff blades of *P. angustifolium*. But there is sufficient variation in the leaf pubescence traits and in the stiffness of the plants to make the determinations of some specimens difficult.
Table 9. Diagnostic traits of species of the angustifolium group of *Panicum* according to Hitchcock and Chase (1951)

<table>
<thead>
<tr>
<th>species</th>
<th>Spikelet length in mm</th>
<th>Spikelets pointed</th>
<th>Autumnal blades involute</th>
<th>Panicle branches ascending</th>
<th>Culms glabrous</th>
<th>Nodes bearded</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. aciculare</em></td>
<td>1.9-2.0</td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. angustifolium</em></td>
<td>2.5-2.8</td>
<td></td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. arenicolooides</em></td>
<td>2.1-2.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. bennettense</em></td>
<td>2.0</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. chrysopsidifolium</em></td>
<td>2.0</td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. consanguineum</em></td>
<td>2.6-2.8</td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. fusiforme</em></td>
<td>3.3-3.5</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. neuranthum</em></td>
<td>2.0</td>
<td>X</td>
<td>X</td>
<td>strongly</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. ovinum</em></td>
<td>2.1-2.2</td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. pinetorum</em></td>
<td>2.3-2.5</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Previous Taxonomic Treatments

Hitchcock and Chase (1910, 1951) provided the only extensive treatment of the angustifolium group. The 1951 treatment recognized ten species as listed in Table 9. The traits employed in their keys included only spikelet length, spikelets blunt vs. spikelets pointed (fusiform), blades of autumnal branches flat vs. involute, panicle branches ascending vs. spreading, culms glabrous vs. culms pubescent, and nodes bearded vs. nodes beardless.

Some earlier workers had suggested that certain species should be united. Beal (1896) reduced *P. consanguineum* Kunth. to a variety of *P. commutatum* Schult. (commutatum group). Ashe (1898) suggested that *P. consanguineum* should be united with *P. oligosanthes* Schult. (oligosanthes group). Grisebach (1866) had originally described *P. fusiforme* Hitchc. as a variety (var. *ramosum*) of *P. neuranthum*.

*Panicum chrysopsidifolium* Nash has been merged with two different species of the angustifolium group. Radford, Ahles, and Bell (1964) included it under *P. consanguineum*. Fernald (1950) placed it in synonymy under *P. aciculare*, regarding it as "the taller and looser extreme (of *P. aciculare*) with autumnal leaves less involute."

*Panicum arenicoloides* Ashe has not been united with other taxa of the angustifolium group, but the similarities between it and other angustifolium species have been discussed. Hitchcock and Chase (1910) stated that the vernal form was "inter-
mediate in appearance between that of P. angustifolium and P. aciculare." Ashe (1895) noted in the original description that it was intermediate between P. arenicolum and P. neuran-thum. Panicum arenicolum was described (Ashe, 1898) as being intermediate between P. califerae Nash (P. ovale Ell. of the lanuginosum group) and "P. demissum" (this name was mistakenly applied by Ashe to P. lancearium Trin.).

Methods of Analysis

The analysis of the angustifolium group was based primarily on the examination of 293 herbarium specimens and 22 mass collections. The more common species such as P. aciculare and P. angustifolium were represented in this study by the specimens in the Iowa State University herbarium. Additional material was obtained from MO and US herbaria for other species including the entire collection of P. bennettense, and P. pinetorum.

The characters employed in the study included those appearing in Table 9, plus fertile floret dimensions, the length and pubescence of the blade second from the top of the vernal culm, and the relative change in leaf shape and culm pubes-cence between the lower part of the vernal culms and the upper part.

Most of the diagnostic traits of angustifolia species are subjective with considerable intergradation between character states. The time of the year at which a specimen was collected
affects such traits as the ascendency of panicle branches and the spikelet length. Other traits are probably influenced in part by environmental conditions. For example, autuminal blades may appear more or less involute depending on the dryness of the soil in which the plant was growing, and also on the promptness of the collector in placing the specimen under pressure in a plant press.

Spikelet shape and length present some special problems of interpretation. Most spikelets approximately 2.0 mm long at the time of caryopsis maturity are blunt and turgid with the fertile floret about 1.7 mm long. Less mature spikelets tend to be longer, narrower, and more pointed. Mature spikelets of some larger spikelet forms also tend to be narrower and more pointed at the apex. The tendency for longer spikelets to be more attenuate at the base and more pointed at the apex results in a gradual intergradation between the blunt, obovate spikelets of "typical" *P. aciculare* at 1.9 and 2.0 mm long and the very attenuate and pointed "fusiform" spikelets of "typical" *P. fusiforme*. In most cases the same correlation between the spikelet length and spikelet shape is round in the relationship between the length and the shape of the fertile floret. However, some specimens of the *P. neuranthum* complex have small, fairly blunt fertile florets with exceptionally long, narrow, involute or "beaked" second glumes and sterile lemmas which may add 0.3 to 0.6 mm to the length of the spikelet. Because of these variables spikelet characters must be
used cautiously in a study of this group.

The different types and degrees of pubescence also intergrade and present problems of interpretation. The pubescence is always most dense on the lower internodes and at the lower and mid-culm nodes. In many cases the lower internodes are covered with fairly stiff, ascending hairs about 0.5 to 1.0 mm long. The sheaths on this part of the vernal culms are more sparsely pubescent with ascending to spreading trichomes 1.0 to 1.5 mm long. This latter type of pubescence is concentrated at the nodes and produces the "bearded" nodes in heavily pubescent plants. The upper portions of the vernal culm and the peduncle of the inflorescence are usually puberulent with very short, ascending, curved hairs. The two types of pubescence may be intermixed at some point near the middle of the vernal culm, or they may change gradually through the length of one internode.

The nearly glabrous individuals have the longer, ascending pubescence confined to the lowest internode or absent entirely, with the puberulence found on the lower and middle internodes and the culms glabrous above. The densely pubescent individuals may have only a trace of puberulence on the panicle axis and the peduncle. The nodes in this case are heavily bearded and the trichomes on the sheaths and lower internodes are dense, spreading, and close to 1.5 mm long. The only pubescence character which varies somewhat independently from this pattern is pubescence of the adaxial surface of the
blades. Although densely pubescent plants almost always have villous blades, the sparsely pubescent individuals may have blades nearly glabrous or villous. Therefore, blade pubescence has been considered independently of culm pubescence in this analysis.

Patterns of Variation

Previous studies of the angustifolium group have failed to subdivide the group into smaller complexes. The present study has also failed to define discrete complexes. Figure 7 shows the continuous nature of the variation in spikelet length in the group and also the lack of correlation between degrees of pubescence and spikelet length. It also shows that certain combinations of spikelet length and pubescence type are more common than others. These more common combinations of traits represent specimens identified as _P. aciculare_ (spikelets 2.0 mm long and moderately dense pubescence), _P. angustifolium_ (spikelets 2.5 mm long and moderately dense pubescence), and _P. consanguineum_ (spikelets 2.5 mm long and dense pubescence).

Two or more entities of the angustifolium group often occur together in the same habitat. Fifteen of the 44 sites at which I collected specimens of the angustifolium group had two or more angustifolia taxa present. The most common combination was _P. aciculare_ and _P. consanguineum_ which occurred together eight times. _Panicum aciculare_ and _P. angustifolium_
**Figure 7** Distribution of angustifolia specimens according to spikelet length

Solid bars represent specimens with bearded nodes and culms villous throughout; cross-hatched bars represent specimens with lower nodes bearded or beardless, lower internodes puberulent to ascending-villous, and upper culm internodes puberulent to glabrous; open bars represent specimens with culms glabrous throughout.
were found together four times, and *P. consanguineum* occurred with *P. angustifolium* and with *P. arenicolaoides* three times each. *Panicum angustifolium* was collected with *P. arenicolaoides* only once as was *P. neuranthum* with *P. acicularare*, and *P. neuranthum* with *P. consanguineum*.

It may be significant that two of the more distinct and readily separable entities were found together most often. *Panicum consanguineum* differs from *P. acicularare* in having larger spikelets (2.3-2.7 mm vs. 1.8-2.1 mm), denser pubescence, and consistently flat autumnal blades. All specimens in all eight of these collections could be assigned easily to one of the two taxa. No intermediates were found.

In general, most of the specimens of the other collections involving two or more entities were also assignable to one entity or the other. Few, if any specimens appear to be $F_1$ hybrids between the two taxa involved. But the range of variation in the diagnostic traits was great enough in some cases to nearly obscure the morphological gaps between the "species". Figures 8 and 9 show the patterns of variation found in two of these collections. In both instances every seemingly valid morphological trait has been employed. Except for the traits indicated, there are no consistent differences among the entities and the resemblances in general habit among the entities is striking.

The fact that certain combinations of very similar entities were not found may be due to the fairly small num-
ber of sites visited at which angustifolium group specimens were collected. It is also possible that some of these entities may exhibit subtle differences in habitat preference, or that they may represent the same taxon modified by different environmental conditions. More collections of two or more entities from one habitat are needed as well as a series of growth chamber studies to determine the amount of influence environmental factors can have on the diagnostic traits. In the absence of further data of this type the analysis of the angustifolium group must rest primarily on a study of the variation found in a series of herbarium specimens, considering each proposed taxon individually and in comparison to others.

Four of the species recognized by Hitchcock and Chase have spikelets approximately 2.0 mm long. They are distinguished from each other primarily by culm pubescence and panicle branch ascendancy. The most common of these is *P. aciculare*, defined by the involute and falcate nature of the autumnal blades, the spreading panicle branches, the moderate density of the culm pubescence ranging from ascending villous pubescence at the base to puberulent on the upper internodes, and the relatively short vernal culm blades approximately 3-6 cm long. *Panicum chrysopsidifolium* differs from *P. aciculare* by subjective traits, having denser pubescence with bearded lower and middle nodes, generally longer blades, taller culms, and flat autumnal blades overtopping vernal
Figure 8 Scatter diagram of the plants of the angustifolium group of Panicum collected at one location (Clarendon Co., S. C.)

Plants with villous blades and bearded nodes represent *P. consanguineum* (Freckmann, 2127).

Plants with nearly glabrous blades and flat autumnal blades represent *P. angustifolium* (Freckmann, 2128A).

Plants with nearly glabrous blades and involute autumnal blades represent *P. arenicoloides* (Freckmann, 2128B).
Figure 9 Scatter diagram of the plants of one collection (Freckmann, 1175, Effingham Co., Georgia) including Panicum aciculare and P. angustifolium

Open circles indicate individuals with adaxial surface of uppermost leaf blades nearly glabrous; solid circles indicate adaxial surface pubescent.
culms. The remaining two taxa, *P. ovinum* and *P. neuranthum*, are more sharply differentiated in having glabrous culms and more slender habits.

All of the specimens with pubescent culms and spikelets 1.8-2.2 mm long have been included in the analysis of *P. aciculare* and *P. chrysopsidifolium* group presented in Table 10. Two specimens with spikelets 2.2 mm long were included as a result of this arbitrary delimitation of the complex even though Hitchcock and Chase had annotated these two specimens as *P. arenicoloides*.

According to the criteria stated above for the separation of these two species, the 20 specimens with blades less than 6 cm long and beardless nodes qualify as *P. aciculare*. Eleven of these have autumnal blades present, but two of these have flat autumnal blades. These latter two specimens fail to meet this criterion of *P. aciculare*. Thus, no more than 18 specimens can be regarded as "typical" *P. aciculare*. Only ten specimens have bearded nodes and long blades. These ten can be treated as "typical" *P. chrysopsidifolium*. All of the remaining specimens (27 of 54) combine traits of the two taxa.

The specimens of the *P. aciculare* - *P. chrysopsidifolium* complex with autumnal blades present have been plotted on a scatter diagram (Figure 10) with the other pubescent specimens of the angustifolium group. The specimens of the *P. aciculare* - *P. chrysopsidifolium* complex form a fairly well-
<table>
<thead>
<tr>
<th>Criteria for set</th>
<th>No. of specimens</th>
<th>Autumnal involute</th>
<th>Blades flat</th>
<th>Autumnal branching overtopping vernal culms</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Blades less than 6 cm long:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a.) Nodes beardless, upper portion of culm sparsely puberulent</td>
<td>20</td>
<td>2</td>
<td>9</td>
<td>2</td>
</tr>
<tr>
<td>b.) Lower nodes bearded, upper portion of culm puberulent</td>
<td>16</td>
<td>1</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td>c.) Nodes bearded, upper portion of culms villous</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Blades more than 6 cm long:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a.) Nodes beardless, upper portion of culm sparsely puberulent</td>
<td>6</td>
<td>2</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>b.) Lower nodes bearded, upper portion of culm puberulent</td>
<td>6</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>c.) Nodes bearded, upper portion of culms villous</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>
Figure 10  Scatter diagram including all specimens of the angustifolium group of Panicum with lower internodes pubescent, spikelets 1.7-3.5 mm long, and having autumnal blades present.
delimited cluster on the scatter diagram, suggesting that they represent a single entity, at least on the basis of the traits employed. The variation in pubescence characters and the involute nature of the autumnal blades seems to be of little taxonomic value.

The remaining specimens on the scatter diagram all have spikelets more than 2.2 mm long. Nearly all of the specimens identified as _P. angustifolium_, _P. arenicolaoides_, _P. consanguineum_, and _P. fusiforme_ are included in this group. Only one of these four taxa seems to be separable from the rest on the basis of a multiple character correlation. This correlation involves those specimens which usually combine villous blades and bearded nodes. These specimens have all of the diagnostic features of _P. consanguineum_. A few specimens with such combinations of traits as villous blades and either bearded nodes or involute autumnal blades serve to tie _P. consanguineum_ to the other entities.

With _P. consanguineum_ removed from consideration the remaining specimens include only _P. angustifolium_, _P. arenicolaoides_, and _P. fusiforme_. According to Hitchcock and Chase (1910) _P. angustifolium_ has flat autumnal blades, spikelets 2.5-2.8 mm long, and widely spreading panicle branches. _Panicum arenicolaoides_ has spikelets 2.1-2.5 mm long, involute blades, and ascending branches. _Panicum fusiforme_ differs from _P. arenicolaoides_ in having pointed-elliptical
spikelets 3.3-3.5 mm long. The involute-leaf individuals should, therefore, show a gap between 2.6 and 3.2 mm long corresponding to the separation of _P. arenicolooides_ and _P. fusiforme_. No such gap appears on the scatter diagram between 2.6 and 3.3 mm. Specimens with involute autumnal blades occur in all spikelet-length classes and exhibit a gradual transition from the shorter, more rounded spikelets to the longer, more pointed spikelets.

It is also apparent from Figure 10 that neither of the quantitative characters separate _P. angustifolium_ from _P. arenicolooides_ or _P. fusiforme_, although there is an evident tendency for the _P. angustifolium_ specimens (those with flat autumnal blades and glabrous vernal blades with beardless nodes) to have longer vernal blades. There is also a tendency for these specimens to have widely spreading panicles with about 50% of the specimens showing this trait in contrast to about 30% of the others. However, the difference between ascending and spreading panicle branches is slight in these cases and depends in part on the maturity of the panicle.

The specimens with glabrous culms were not plotted on Figure 13 since they are fairly easily separated from those with pubescent culms. Most of these specimens represent _P. ovinum_, _P. neuranthum_, and _P. pinetorum_. _Panicum ovinum_ is distinguished from other two by the broader panicles, 3.5-6.0 cm wide with branches spreading from the main axis at an
angle of 60 to over 90 degrees. *Panicum neuranthum* and *P. pinetorum* usually have very narrow panicles, less than 2.0 cm wide, with branches erect to spreading at 30 to 40 degrees from the main axis. *Panicum ovatum*, according to Hitchcock and Chase (1951) occurs primarily in Louisiana and eastern Texas, whereas the other two taxa are found chiefly in Florida.

Twenty-one of the 29 glabrous culm specimens from Texas and Louisiana have spreading panicle branches and panicles more than 3.0 cm broad. Twenty-five of the 30 specimens from Florida have very narrow panicles, less than 3.0 cm wide and strongly-ascending panicle branches.

*Panicum pinetorum* is distinguished from *P. neuranthum* by the pointed or fusiform spikelets 2.3-2.5 mm long. Hitchcock and Chase (1951) stated that it was known only from the type locality at Bonita Springs, Florida as of 1950. Two specimens identified as *P. pinetorum* by Swallen, the author of the species, have since been reported from two other locations. However, other specimens exist which fit the criteria of this taxon. Some of these have been annotated by Hitchcock and Chase as *P. neuranthum* and as *P. fusiforme*. These specimens as well as the *P. pinetorum* specimens of Swallen, have fertile florets 1.7-1.9 mm long - approximately the same length as those of "typical" *P. neuranthum" - but have the second glumes and sterile lemmas elongated into beaks. The beaks vary in size from extremely slight projections adding only 0.1 mm to
the spikelet length to others which may add 0.6 mm. The specimens are alike in all other characters.

Reproductive Biology

Lelong (1955) included *P. aciculare* and *P. arenicolaoides* in his study of reproductive biology of the dichanthelia. He observed live plants of *P. aciculare* under different conditions in a greenhouse through at least two growing seasons, concluding that they were primarily, but facultatively, cleistogamous. He suggested that photoperiod influenced the development of cleistogamous spikelets since plants grown from seed in June produced small, cleistogamous terminal panicles in July, whereas culms which began elongation in February produced large, chasmogamous terminal panicles.

My observations were made on inflorescences fixed in Newcomer's fixative in the field and on herbarium specimens. The data concerning anther size, pollen fertility, and seed set are summarized in Table 11.

Terminal panicles of most angustifolia plants undergo anthesis in April or May. In the majority of specimens examined, the anthers are relatively large, about 0.9-1.4 mm long, and were often found to be exserted. Anthers which were beginning to release mature pollen were generally either well-exserted or slightly-exserted from florets in which the lodicules were swollen and the palea and lemma were spread apart. These spikelets appear to be protandrous with mostly
Table 11  Pollen fertility and seed set in terminal and axillary inflorescences of plants in the Angustifolium group

<table>
<thead>
<tr>
<th>Taxon, collector, number, herbarium</th>
<th>Terminal inflorescence</th>
<th>Axillary inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anther size in mm</td>
<td>% Good pollen</td>
</tr>
<tr>
<td>Curtiss, 6639, ISC</td>
<td>0.2-0.3</td>
<td>86</td>
</tr>
<tr>
<td>Freckmann, 1694, ISC</td>
<td>0.9</td>
<td>91</td>
</tr>
<tr>
<td>Freckmann, 2146, ISC</td>
<td>0.8</td>
<td>88</td>
</tr>
<tr>
<td>Henderson, 64-403, ISC</td>
<td>0.3</td>
<td>91</td>
</tr>
<tr>
<td>Lelong, 2546c, ISC</td>
<td>0.7</td>
<td>(75)&lt;sup&gt;e&lt;/sup&gt;</td>
</tr>
<tr>
<td>Lelong, 2388&lt;sup&gt;d&lt;/sup&gt;</td>
<td>0.3-0.4</td>
<td>x</td>
</tr>
</tbody>
</table>

<sup>a</sup>"Good pollen" is defined as pollen which is spherical and well-filled with deeply-stained granular cytoplasm.

<sup>b</sup>Identifications are in accordance with the key to species in Hitchcock and Chase, 1951.

<sup>c</sup>"x" indicates presence of developing seed.

<sup>d</sup>As reported in Lelong, 1965.

<sup>e</sup>Parentheses indicate pollen somewhat immature; count is approximate.
<table>
<thead>
<tr>
<th>Taxon, collector number, herbarium</th>
<th>Terminal inflorescence</th>
<th>Axillary inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anther size in mm</td>
<td>% Good pollen</td>
</tr>
<tr>
<td>Lelong, 2470^d</td>
<td>0.4-0.6</td>
<td>85</td>
</tr>
<tr>
<td></td>
<td>0.9-1.1</td>
<td>87</td>
</tr>
<tr>
<td>Pohl, 9241, ISC</td>
<td>1.1</td>
<td>55,59</td>
</tr>
<tr>
<td>F. angustifolium:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freckmann, 1561, ISC</td>
<td>0.9-1.0</td>
<td>85,79</td>
</tr>
<tr>
<td>Freckmann, 2128A, ISC</td>
<td>1.0</td>
<td>71</td>
</tr>
<tr>
<td>Freckmann, 2135, ISC</td>
<td>1.2</td>
<td>85</td>
</tr>
<tr>
<td>Freckmann, 2135^f</td>
<td>1.1</td>
<td>67</td>
</tr>
</tbody>
</table>

^fPanicles fixed in Newcomer's fixative in the field.
<table>
<thead>
<tr>
<th>Taxon, collector, number, herbarium</th>
<th>Terminal inflorescence</th>
<th>Axillary inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anther size in mm</td>
<td>% Good pollen</td>
</tr>
<tr>
<td><em>P. arenicoloides:</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Churchill, s. n., MO</td>
<td>1.1</td>
<td>95</td>
</tr>
<tr>
<td>Freckmann, 2154</td>
<td>1.2</td>
<td>75</td>
</tr>
<tr>
<td>House, 3433, MO</td>
<td>0.5</td>
<td>61</td>
</tr>
<tr>
<td>Tracy, 3635, US</td>
<td>1.0</td>
<td>92</td>
</tr>
<tr>
<td><em>P. chrysopsidifolium:</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freckmann, 2149, ISC</td>
<td>0.9</td>
<td>97</td>
</tr>
</tbody>
</table>
Table 11 (Continued)

<table>
<thead>
<tr>
<th>Taxon, collector, number, herbarium</th>
<th>Terminal inflorescence</th>
<th>Axillary inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anther size in mm</td>
<td>% Developing pollen seed</td>
</tr>
<tr>
<td><strong>P. consanguineum:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freckmann, 1095, ISC</td>
<td></td>
<td>0.3-0.6 (80)&lt;sup&gt;e&lt;/sup&gt;</td>
</tr>
<tr>
<td>Freckmann,</td>
<td>1.3</td>
<td>90</td>
</tr>
<tr>
<td>Hitchcock, 1139, US</td>
<td>1.2-1.3</td>
<td>80</td>
</tr>
<tr>
<td>Langolis, s. n., US 954555</td>
<td>1.0-1.2</td>
<td>82</td>
</tr>
<tr>
<td><strong>P. fusiforme:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hitchcock, 964, US</td>
<td>1.1</td>
<td>82, 88</td>
</tr>
<tr>
<td>Hitchcock, 980, ISC</td>
<td>1.3</td>
<td>71, 75</td>
</tr>
<tr>
<td>Small and Hosier, 5587, US</td>
<td>1.4</td>
<td>86</td>
</tr>
</tbody>
</table>

<sup>e</sup> Parentheses indicate pollen somewhat immature; count is approximate.
Table 11 (Continued)

<table>
<thead>
<tr>
<th>Taxon, collector, number, herbarium</th>
<th>Terminal inflorescence</th>
<th>Axillary inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anther size in mm</td>
<td>% Good pollen</td>
</tr>
<tr>
<td><strong>P. neuranthum:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deam, 66028, US</td>
<td>0.3-0.4</td>
<td>83</td>
</tr>
<tr>
<td>Hitchcock, 705, ISC</td>
<td>0.9</td>
<td>88</td>
</tr>
<tr>
<td>Small, Mosier, and Simpson, 6058, US</td>
<td>0.9-1.0</td>
<td>85</td>
</tr>
<tr>
<td>Standley, 12851, US</td>
<td>1.1</td>
<td>86</td>
</tr>
<tr>
<td>Swallen, 10123, US</td>
<td>0.9</td>
<td>89</td>
</tr>
<tr>
<td><strong>P. pinetorum:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LaRoche, 145, US</td>
<td>0.9</td>
<td>69</td>
</tr>
</tbody>
</table>
fertile pollen.

At about the time of anthesis in the terminal panicles branches appear from lower and middle nodes of the vernal culm. The internodes of these primary axillary branches elongate to about the same length as the internodes of the vernal culm. The panicles which terminate these branches are smaller than the terminal panicles of the vernal culms. The base of the panicle may be included in the leaf sheath at the time of anther dehiscence in the uppermost spikelets. The anthers of these spikelets are small, about 0.4-0.6 mm long, and generally included, or partially short-exserted. These panicles are transitional between the chasmogamous condition of the terminal panicles of vernal culms and later axillary panicles.

Secondary branches arise from nodes of the primary branches soon after they begin elongation. The secondary branches give rise to branches from the nodes and the process of compound branching continues through the summer into the early autumn. The internodes of the successive orders of branches undergo less elongation as the season progresses. The result is the production of a top-heavy cluster of leaves, branches, and reduced inflorescences which has been described as resembling a "miniature tree."

The panicles of these axillary branches are greatly reduced in size from the terminal panicles of the main vernal culms. They may bear only two to four spikelets in many
jases, and the lowest spikelet or pair of spikelets may mature seed while enclosed in the leaf sheath. All of the spikelets examined from these panicles have small anthers, about 0.3-0.4 mm long, which were never found to be exserted. In many cases the dry, empty anthers were still present in fertile florets with nearly mature caryopses.

The pattern of chasmogamous terminal inflorescences and cleistogamous axillary inflorescences in the angustifolium group is similar to that described for the depauperatum group and the laxiflorum group. It suggests that much of the seed produced results from self-pollination and that local populations are composed of one to a few nearly homozygous races. Many of the populations collected in the field exhibit this pattern of variability. Figure 8 is typical of some of these populations.

Conclusions

Many of the taxonomic problems of the angustifolium group seem to be due to the fact that two or three entities are discrete when found together in a local population, but nearly impossible to separate when specimens from the entire geographic range are considered. Quantitative traits such as spikelet length and blade length vary continuously and without breaks through the whole angustifolium group. Two "species" in a local population may differ by 0.2 mm in spikelet length, but the difference disappears when speci-
mens from other populations are added to it.

The qualitative differences between entities are few, consisting of such traits as glabrous culms vs. pubescent culms and involute autumnal blades vs. flat autumnal blades. In most cases these traits do not correlate well with each other or with quantitative traits. Neither quantitative nor qualitative traits correlate with geographic range or habitat, except in the case of *P. neuranthus* and *P. ovinum*.

In view of such lack of correlation between traits, the separation of species according to the Hitchcock and Chase treatments depends on single-character differences. A more satisfactory treatment requires uniting several taxa. I have chosen to recognize four species and one additional variety in the group. The plants with completely glabrous culms differ from the rest of the group by a fairly objective trait, and there is at least a tendency for these plants to have a more slender form than the other taxa. I have treated these glabrous plants as one species, *P. neuranthus*, including two weakly-delimited varieties. The variety *ovinum* is more common in the western part of the range and is characterized by the presence of open terminal panicles. The variety *neuranthus* is more common in Florida and is characterized by narrow panicles and often erect blades. The latter variety includes *P. pinetorum* which represents a form with more pointed, beaked spikelets and which is connected morphologically with more "typical" var. *neuranthus* by many
The pubescent plants with spikelets 1.6-2.2 mm long repre-
sent the very common *P. aciculare*. *Panicum chrysopsidifo-
lium* has been united with it since the differences between the
two consist of poorly correlated traits which completely in-
tergrade. *Panicum consanguineum* has been maintained in the
traditional sense. It resembles *P. angustifolium*, but differs
by traits which are as well-correlated as any in the angusti-
folium group. The remaining taxa are treated as one species,
*P. angustifolium*. *Panicum arenicoloides* and *P. fusiforme* sup-
posedly differ from it by spikelet length, ascendency of pani-
cle branches, and involute nature of autumnal blades. However,
there is a complete intergradation in spikelet length between
these forms, and no usable correlation between involute blades
and ascendency of the panicle branches.

**Taxonomy of the Angustifolium Group**

The angustifolium group includes four species with a
small percentage of individuals intermediate between these
species.

1. Culms glabrous..........................*P. neuranthum*
1. Culms pubescent, at least on the lower internodes.

2. Spikelets 1.7-2.2 mm long, blunt at the apex at
maturity..............................*P. aciculare*
2. Spikelets 2.3-3.5 mm long, rounded to pointed at the
apex.

3. Nodes beardless or only the lowermost sparsely
bearded; culms puberulent to sparsely pubescent
above; blade surfaces usually glabrous or sparsely pubescent; autumnal blades flat or involute; panicles usually open at maturity....P. argustifolium

3. Nodes bearded; culms densely ascending-villous; adaxial blade surfaces villous; autumnal blades flat; panicles compact............P. consanguineum

PANICUM NEURANTHUM Griseb.

Distribution

This species ranges from southern Arkansas south and west through east Texas southward along the Gulf coast to Veracruz, Mexico, and from the Gulf coast of Louisiana and Mississippi through southern Florida to the West Indies. It includes two varieties separated by the following key:

1. Branches of terminal panicle strongly erect to ascending; panicle usually less than 2 cm wide; spikelets blunt or with second glume and sterile lemma elongated into a beak

.................................var. neuranthum

1. Branches of terminal panicle spreading at 45 to 90 degree angle from axis; panicle 3-6 cm wide; spikelets blunt, with second glume and sterile lemma not elongated beyond fertile floret............................var. ovinum

PANICUM NEURANTHUM Griseb. VAR. NEURANTHUM


Distribution

This variety is found chiefly in southern Florida and the West Indies. Specimens from Louisiana, Arkansas, and Texas are rare and may be more closely related to plants of the var. ovinum. The var. neuranthum occurs in open pinelands
on very dry, sandy ground with *Serenos repens*, *Vacinium spp.*, and on wet ground in glades of the Everglades.

**PANICUM NEURANTHUM VAR. OVINUM** (Scribn. and Smith) Comb. nov.


**Distribution**

The var. *ovinum* ranges from southern Arkansas and Louisiana west to eastern Texas and south along the Gulf coast into Mexico to about Veracruz. A few specimens with the diagnostic features of this variety have been collected in Florida. These plants may represent unusual forms of the var. *neuranthum*.

The habitats of this variety include wet prairies and also open sandy areas, sandy savannas, and sand dunes.

**PANICUM ACICULARE** Desv. ex Poir. in Lam.


**PANICUM ARENICOLUM** Ashe. Journ. Elisha Mitchell Soc. 15:56. (1890) (1,2). See discussion below.

**PANICUM CHRYSOPTIDIFOLIUM** Nash. in Small. Fl. Southeastern U. S. 106. (1903) (1,2).

**Nomenclature and Additional Synonymy**

The additional synonymy appearing in Hitchcock and Chase, 1951 (p. 911) is tentatively accepted.

The holotype of *P. arenicolum* was not found by Hitchcock and Chase (1910) and was presumed to have been lost or destroyed. A specimen in Hitchcock's herbarium (now in US) with
the same collection data as that given by Ashe (1830) in the original description was chosen as the lectotype. That specimen fits _P. aciculare_ well in all critical characters. However, other material distributed by Ashe to ISC and MO with the same collection data represents two different entities. One sheet (MO 1837595) is _P. aciculare_, the other ISC 07445 is _P. angustifolium, sensu lato_, or _P. arenicolooides, sensu_ Hitchcock and Chase. Ashe’s description is not sufficiently detailed to indicate which of the "isotypes" was closer to the holotype.

**Distribution**

This species is almost entirely confined to the Coastal Plain, ranging from New Jersey to eastern Texas and south through Florida and the West Indies. It occurs on very sandy soils in semi-open areas of pine and oak woods, savannas, sandy roadsides, and sandy river bottomlands. It apparently requires well-aerated, acidic soils, at least partial sunlight, and freedom from intense competition of grasses and other dense herbaceous vegetation.

**PANICUM ANGUSTIFOLIUM Ell.**


Nomenclature and Additional Synonomy

The additional synonomy included in Hitchcock and Chase, (1951) under each of the three names given above is tentatively accepted.

Hitchcock and Chase (1910) examined the type of *P. angustifolium* in the Elliott Herbarium and accepted the application of the name to this entity. However, Elliott's original description raises some doubt. He recognized the similarities between many of the dichanthelia, grouping them into units in his text. But *P. angustifolium* was set apart in a group of species without obvious affinities to the other groups, with the following comment: "I insert this with some hesitation, yet I know not where to refer it." His description mentions such unusual traits for this entity as a "straggly habit."

Distribution

*Panicum angustifolium* occurs primarily on the Coastal Plain from New Jersey to eastern Texas and south through Florida and the West Indies and in Central America. It extends inland from the Coastal Plain to Tennessee and Arkansas. Common habitats include very sandy, semi-open pine woods, cutover sandy woodlands, trails, sandy railroad right-of-ways, sand dunes, and occasionally along sloughs and ditches.

**PANICUM CONSANGUINEUM** Kunth

*Panicum consanguineum* Kunth, Rev. Gram. 1:36. (1826) (3).
Additional Synonym

The additional synonomy appearing in Hitchcock and Chase (1951, p. 915) is tentatively accepted.

Distribution

This species ranges from Virginia southward along the Coastal Plain to central Florida and west to Arkansas and eastern Texas. It is usually found in dry, sandy, semi-open pine woods, in cut-over woods, along trails, and elsewhere on dry sandy soils. It also occurs occasionally in bogs and on sandy margins of streams. Apparently it can not tolerate dense shade or heavy competition in dense grassy vegetation.
THE OLIGOSANTHES GROUP

General Observations

The oligosanthes group as delimited here is characterized by the combination of relatively large spikelets (2.6-4.3 mm long) with blunt or rounded apices; moderately broad leaf blades (8-25 mm wide) with a length-to-width ratio of between 5:1 and 10:1; extensive autumnal branching beginning with long, erect lateral branches arising from lower and middle nodes of the vernal culms and ultimately producing fascicles at the summit of the main culms and branches; distinct basal rosettes produced in the autumn and persisting through winter.

The above characterization of the oligosanthes group excludes _P. wilcoxianum_ which seems to be a discordant element in an otherwise fairly homogeneous assemblage of species. Hitchcock and Chase (1910) placed _P. wilcoxianum_ in their "Oligosanthis" group probably on the basis of its blunt spikelets. However, it differs from the other oligosanthis in having very narrow blades (3-6 mm wide) with a length-to-width ratio of about 14:1 to 20:1, and in having copious, erect, slender trichomes on the adaxial blade surfaces. It also has a more slender habit than the other members of the oligosanthes group and tends to have smaller spikelets (2.3-2.8 mm long) and to produce fascicled autumnal branches at lower and middle nodes of the vernal culms.

Lelong (1965) suggested that _P. wilcoxianum_ was a result of hybridization between _P. praecocius_ (lanuginosum group)
and _P. perlongum_ (or _P. depauperatum_ ssp. _perlongum_ of the _depauperatum_ group). He noted that _P. wilcoxiannum_ possessed the same type and pattern of pubescence as _P. praecocius_ and that it was intermediate between the putative parent species in certain quantitative traits. However, regardless of the possible hybrid origin of _P. wilcoxiannum_, it does not seem to belong in the _oligosanthes_ group. Perhaps it should be transferred to the _lanuginosum_ group on the basis of its pubescence type and the pattern of autumnal branching.

_Panicum calliphyllum_ is an entity which has been associated with the _oligosanthes_ group through its proposed union with _P. xanthophysum_. Ashe (1898) noted the close resemblance in habit and leaf characters between the two when he described _P. calliphyllum_ as a new species. Lamson-Scribner and Merrill (1901a) merged the two taxa in their treatment of the New England species of _Panicum_. Blake (1913) also noted the similarities between the two in a brief discussion of the occurrence of _P. calliphyllum_ in New England and Canada. Hitchcock and Chase (1910) placed _P. calliphyllum_ in their "Bicknelliana" group which they suggested was intermediate between the _depauperatum_ and the _dichotomum_ groups.

It is difficult to place _P. calliphyllum_ in an appropriate group. It is apparently very rare, with herbarium specimens available from less than ten locations. None of the material which I have examined has any developing seed or stainable pollen. The spikelets are only about two-thirds as long
as the spikelets of *P. xanthophysum* and not blunt or turgid as is characteristic of *P. xanthophysum*. Well-developed autumnal stages of *P. callipyllum* have not been collected, although autumnal specimens (Steyermark, 20507, MO. US) assignable to *P. bicknellii* have been misidentified as *P. callipyllum*. Thus, in the absence of *P. callipyllum* specimens with the diagnostic characters of the oligosanthes group, it is necessary to exclude it from the treatment of the oligosanthes species.

Previous Taxonomic Treatments

Four species - *P. leibergii, P. malacophyllum, P. ravenelii*, and *P. xanthophysum* - have been accepted without dispute since the treatment of Hitchcock and Chase (1910). The treatment of the remaining three species recognized by Hitchcock and Chase - *P. helleri, P. oligosanthes*, and *P. scribnerianum* - has varied considerably. Hitchcock and Chase employed the following key couplets to separate these taxa:

Spikelets narrowly obovate, subacute; plants olivaceous, appressed-pubescent............................*P. oligosanthes*

Spikelets broadly obovate, turgid, blunt; plants green, pubescence, if present, not appressed.

Spikelets 3.2 to 3.3 mm long; blades firm; sheaths or some of them more or less hispid........*P. scribnerianum*

Spikelets not over 3 mm long; blades rather thin; sheaths or some of them glabrous or sparsely hispid.....

...............................................*P. helleri*

Fernald (1934) reduced the entities to varieties of *P.*
olisosanthes. He noted that Hitchcock and Chase had cited numerous specimens which failed to conform to one or more of the key characters. He later (1950) used the following key to separate the varieties:

Longer branches of vernal panicles with 1-6 remote spikelets 3.5-4 mm long, the lateral spikelets (along the branches) often on pedicels 0.5-1.5 cm long; primary blades 5-10 mm broad, their sheaths appressed-pubescent........P. oligosanthes

(typical)

Longer branches of vernal panicles with 3-12 spikelets 2.9-3.6 mm long, the lateral spikelets mostly on pedicels less than 5 mm long; larger primary leaves 6-15 mm broad, their sheaths glabrous or spreading-hirsute

Spikelets 3.2-3.6 mm long.................var. scribnerianum

Spikelets 2.9-3 (rarely -3.2) mm long.........var. helleri.

Gleason (1952) completely merged the three taxa. He noted that the members of the P. oligosanthes complex were highly variable in pubescence, but that "the well-marked extremes are completely connected by intergrading forms."

Methods of Analysis

The analysis of the oligosanthes group was based primarily on the examination of 348 herbarium specimens. Most of the effort was devoted to the analysis of the P. oligosanthes complex as represented by 191 specimens. In addition, several mass collections were consulted as well as voucher specimens obtained at intervals over three years from greenhouse plants.

The characters recorded for the analysis of the P. oligosanthes complex included the following:
1. the maximum width of the terminal inflorescence
2. the number of spikelets borne on the longest panicle branch
3. the number of spikelets in the terminal inflorescence
4. the length of the longest pedicel in the terminal inflorescence
5. the length in units of 0.05 mm of a spikelet at or past anthesis
6. the width in units of 0.05 mm of the same spikelet
7. the vestiture of the second glume and sterile lemma of the spikelet, scored as glabrous, sparsely pubescent, or densely pubescent
8. a descriptive summary of the vestiture of adaxial blade surfaces
9. a descriptive summary of types and density of sheath pubescence
10. a descriptive summary of type and density of culm pubescence.

Two calculations were made from the above data. One calculation, intended to indicate the spikelet density of the terminal panicle, was termed the inflorescence-density index and was computed by dividing the number of spikelets in the inflorescence by the maximum width of the panicle in cm. A low index value of approximately 3-8 indicated an open, diffuse inflorescence supposedly typical of _P. oligosanthes, sensu stricto_, whereas an index value of 12-20 indicated a dense, compact inflorescence more typical of _P. scribnerianum_ or _P. helleri_. The other calculation involved expressing the width of the spikelet as a per cent of the length. Specimens
of "typical" *P. oligosanthes* were expected to have values of about 45-52% and "typical" *P. scribnerianum* values of 55-66%.

Correlations among the characters recorded were sought by sorting the data sheets into various categories based on one type of measurement, followed by an inspection of each category for correlated traits, and by means of scatter diagrams. The scatter diagrams based on characters of the terminal inflorescence included only those specimens with terminal inflorescences present and well-exserted, and with spikelets at or past anthesis.

Patterns of Variation

Figure 11 presents the results of the best correlation of the critical traits of the *P. oligosanthes* complex which could be obtained using only the specimens with well-developed terminal panicles. According to the keys and descriptions of the taxa given by Hitchcock and Chase (1910) and by Fernald (1950), the specimens of *P. oligosanthes* should occupy the lower, left-hand portion of the scatter diagram on the basis of its narrow spikelets and relatively diffuse inflorescences. These specimens should have large spikelets (3.4-3.8 mm long) with long pedicels. The specimens of the other two taxa should occupy the upper, right-hand portion of the diagram. These specimens are expected to have short pedicels and spikelets less than 3.4 mm long. The *P. helleri* specimens should have spikelets less than 3.0 mm long and glabrous or sparsely
Figure 11  Relationship among the diagnostic characters of the *Panicum oligosanthes* complex (including *P. helleri* and *P. scribnerianum*)
short-pubescent culms. *Panicum scribnerianum* specimens should combine the intermediate size spikelets (3.0–3.3 mm long) with fairly densely-pubescent culms.

It is apparent from the scatter diagram that the correlations among the various traits are less pronounced than would be expected from the keys and species descriptions. Only a few specimens can be regarded as "typical" examples of any of the three entities. The traditionally-used traits which appear to be of the least taxonomic value are the characters of culm and sheath vestiture. The lack of reliable pubescence traits in this complex seems to be due to the fact that the relative density of the two basic types of trichomes (short, weak hairs, about 0.1–0.3 mm long, and long, stout hairs about 1.5–2.0 mm long) is influenced by environmental conditions and by the age of the plant. Most members of the *P. oligosanthes* complex apparently have the ability to produce both types of trichomes, although a careful examination of vernal specimens is often needed to find both types. A comparison of specimens collected in the field with those collected as vouchers from greenhouse transplants reveals that culms from the same plant can vary in the expression of these pubescence traits from very sparsely pubescent with only one type of trichome evident to densely pubescent with both types of trichomes abundant.

The three taxa of the complex have been attributed to different geographic areas with only partial overlap of
range. *Panicum oligosanthes* is supposedly confined to the southeastern United States, *P. helleri* is supposedly centered in the Ozark area, and *P. scribnerianum* is widely distributed throughout most of the United States with the exception of the Southeast. In order to demonstrate a correlation between geographic areas and various taxonomic traits, the specimens of the complex were divided into sets representing the three basic regions. Thirty-one specimens were obtained to represent the southeastern United States and came from an area in which only *P. oligosanthes*, sensu stricto, is reputed to occur. The parts of the northern and western United States which are supposedly beyond the range of *P. helleri* and *P. oligosanthes* (except for rare specimens) yielded 89 specimens. Forty-two specimens were obtained from the general region of the Ozarks and eastern Texas. Unfortunately, all three taxa have been reported from this last area, but the proportion of specimens of *P. helleri* in a sample of specimens from this area is expected to be high.

Table 12 compares the frequencies of certain traits in the three geographic regions. The limits of the quantitative traits were chosen carefully to show the greatest possible differences between the geographic areas. It is apparent from these results that certain traits tend to be concentrated in particular geographic areas, perhaps to a sufficient extent to justify the recognition of geographic varieties. But it is also apparent that at least some of the specimens encoun-
Table 12  A comparison of the specimens of Panicum oligosanthes complex from three principal geographic areas

The Ozark region includes southern Missouri, eastern Oklahoma and Texas, all of Arkansas, and northern Arkansas.

The southeastern United States includes Virginia, North Carolina, South Carolina, Georgia, Florida, Alabama, and Mississippi.

The northern and western United States includes all states north of Missouri, Kentucky, and West Virginia, and all states west of Missouri, Oklahoma, and Texas.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Percentage of specimens with indicated trait</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ozark Area</td>
</tr>
<tr>
<td>Inflorescence-density index less than 6.5</td>
<td>48</td>
</tr>
<tr>
<td>Spikelet width less than 53% of spikelet length</td>
<td>29</td>
</tr>
<tr>
<td>Spikelets glabrous</td>
<td>57</td>
</tr>
<tr>
<td>Spikelets less than 3.1 mm long</td>
<td>24</td>
</tr>
<tr>
<td>Spikelets 3.1-3.3 mm long</td>
<td>41</td>
</tr>
<tr>
<td>Spikelets more than 3.3 mm long</td>
<td>35</td>
</tr>
<tr>
<td>Culms glabrous at least on upper internodes</td>
<td>50</td>
</tr>
<tr>
<td>Sheaths glabrous</td>
<td>57</td>
</tr>
</tbody>
</table>

*Inflorescence-density index is equal to the number of spikelets in a terminal panicle divided by the maximum width in cm of the panicle.*
tered within the geographic area supposedly occupied by only one of the taxa have some traits of another taxon.

The specimens of the other four taxa of the oligosanthes group were not subjected to an analysis of the type described above for the _P. oligosanthes_ complex since no specimens were found which could be considered as an intermediate between any pair of the species.

Reproductive Biology

The details of the reproductive biology of members of the oligosanthes group are similar to those described for _angustifolium_ group. The spikelets of the terminal panicles undergo anthesis in April in the southern states to June in the northern states and southern Canada. The anthers are usually about 0.9-1.8 mm in length. They are often partially or completely exserted prior to the emergence of the stigmas. However, the exsertion of the stigmas occurs soon after the beginning of anther dehiscence and self-pollination may occur in many of these chasmogamous spikelets.

Some plants of _P. scribnerianum_ and _P. leibergii_ have terminal panicles with cleistogamous spikelets. The cleistogamous behavior of these spikelets is often indicated by the presence of anthers 0.3-0.8 mm long. Some terminal inflorescences may possess both types of spikelets. Lelong (1965) reported the occurrence of cleistogamy in at least some of the spikelets of the terminal panicles of _P. scribnerianum_. 
As indicated in Table 13, the spikelets of the terminal panicles of all members of the oligosanthes group show a fairly high degree of fertility. The amount of well-filled and deeply-stained pollen may reach 96% of the total pollen. Seed was found to be developing in at least some of the spikelets of nearly all panicles of sufficient maturity. These findings are contrary to the conclusions of Church (1929) who examined meiosis and pollen formation in terminal panicles of P. scribnerianum and reported numerous meiotic irregularities and pollen fertility of about 20-30%.

Panicum leibergii is exceptional among the members of the entire subgenus in having well-developed anthers in the so-called "sterile" florets. At least some of the spikelets of all but one of the specimens with terminal panicles possessed anthers in these lower florets. The anthers are about 1.5-1.8 mm long and appear to shed pollen at about the same time as the dehiscence of the anthers in the accompanying fertile floret. The percentage of "good" well-filled, stainable pollen is approximately the same for all anthers. But the "sterile" floret lacks a gynoecium and well-developed lodicules. The anthers are not exserted and the pollen is retained in the sterile floret after anther dehiscence.

The primary lateral branches arise shortly after the beginning of anthesis in the terminal inflorescence. The first lateral branches are nearly erect and have two to four nodes with internodes of about the same length as those of
Table 13  Pollen fertility and seed set in terminal and axillary inflorescences of plants of the ologisanthes group

<table>
<thead>
<tr>
<th>Taxon, collector, number, herbarium</th>
<th>Terminal inflorescence</th>
<th>Axillary inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anther size in mm</td>
<td>% Good&lt;sup&gt;a&lt;/sup&gt; pollen</td>
</tr>
<tr>
<td>P. helleri:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Isely, 7494, ISC</td>
<td>1.1</td>
<td>89</td>
</tr>
<tr>
<td>P. leibergii:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freckmann, 1925, ISC</td>
<td>1.4-1.6</td>
<td>66</td>
</tr>
<tr>
<td></td>
<td>1.5-1.7&lt;sup&gt;c&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>Hayden, 3137, ISC</td>
<td>1.7</td>
<td>78</td>
</tr>
<tr>
<td></td>
<td>1.7</td>
<td></td>
</tr>
<tr>
<td>Lelong, 2150, ISC</td>
<td>1.3</td>
<td>87</td>
</tr>
<tr>
<td>Monson, 2001, ISC</td>
<td>1.8-2.0</td>
<td>88</td>
</tr>
</tbody>
</table>

<sup>a</sup>Good pollen is defined as pollen which is spherical and well-filled with deeply-stained granular cytoplasm

<sup>b</sup>"x" indicates the presence of developing seed

<sup>c</sup>Lower set of figures for P. leibergii apply to anthers of "sterile" floret
Table 13  (Continued)

<table>
<thead>
<tr>
<th>Taxon, collector, number, herbarium</th>
<th>Terminal inflorescence</th>
<th>Axillary inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anther size in mm</td>
<td>% Good pollen</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paddock, 3206, ISC</td>
<td>1.4-1.6</td>
<td>72</td>
</tr>
<tr>
<td></td>
<td>1.6-1.7</td>
<td>84</td>
</tr>
<tr>
<td>Umbach, 3351, ISC</td>
<td>1.6-1.7</td>
<td>81</td>
</tr>
<tr>
<td></td>
<td>1.6-1.7</td>
<td>70</td>
</tr>
<tr>
<td><em>P. malacophyllum:</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freckmann, 2664&lt;sup&gt;d&lt;/sup&gt;</td>
<td>1.3</td>
<td>83</td>
</tr>
<tr>
<td><em>P. oligosanthes:</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Curtiss, 5864, MO</td>
<td></td>
<td>1.0</td>
</tr>
<tr>
<td>Henderson, 63-673, ISC</td>
<td>1.0-1.1</td>
<td>95</td>
</tr>
<tr>
<td>Steyermark, 10473, MO</td>
<td>1.3-1.5</td>
<td>95</td>
</tr>
<tr>
<td>Tharp, 43114, MO</td>
<td>1.5</td>
<td>86</td>
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</tbody>
</table>

<sup>d</sup>Panicles fixed in Newcomer's fixative in the field.
Table 13  (Continued)

<table>
<thead>
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<th>Taxon, collector, number, herbarium</th>
<th>Terminal inflorescence</th>
<th>Axillary inflorescence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Anther size</td>
<td>% Good pollen</td>
</tr>
<tr>
<td>P. ravenelii:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Churchill, s.n., MO 156842</td>
<td>1.4</td>
<td>82</td>
</tr>
<tr>
<td>Churchill, s. n., MO 1056844</td>
<td>1.7-1.8</td>
<td>80</td>
</tr>
<tr>
<td>Freckmann, 379, ISC</td>
<td>0.7</td>
<td>96</td>
</tr>
<tr>
<td>Freckmann, 2230, ISC</td>
<td>0.3</td>
<td>71</td>
</tr>
<tr>
<td>House, 2200, MO</td>
<td>1.7</td>
<td>94</td>
</tr>
<tr>
<td>P. scribnerianum:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freckmann, 334, ISC</td>
<td>0.9</td>
<td>42</td>
</tr>
<tr>
<td>Freckmann, 1414.1&lt;sup&gt;e&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freckmann, 1414.2A&lt;sup&gt;e&lt;/sup&gt;</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>e</sup>Live plants grown in Iowa State University greenhouse
<table>
<thead>
<tr>
<th>Taxon, collector, number, herbarium</th>
<th>Terminal inflorescence</th>
<th>Axillary inflorescences</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Anther size in mm</td>
<td>% Good pollen</td>
</tr>
<tr>
<td>Freckmann, L1414.2B°</td>
<td>1.0-1.3</td>
<td>61</td>
</tr>
<tr>
<td>Freckmann, 2450, ISC</td>
<td>1.2</td>
<td>93</td>
</tr>
<tr>
<td>Lelong, L59f</td>
<td>0.5</td>
<td>59</td>
</tr>
<tr>
<td>Lelong, 2094f</td>
<td>0.4-0.6</td>
<td>30</td>
</tr>
<tr>
<td>P. xanthophyllum:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freckmann, 1841, ISC</td>
<td>1.0-1.1</td>
<td>80</td>
</tr>
<tr>
<td>Shinners, 13378, ISC</td>
<td>1.2</td>
<td>89</td>
</tr>
</tbody>
</table>

fReported in Lelong, 1965.
the main vernal culm. These lateral branches may extend above the top of the main terminal inflorescence in some cases. The panicles which terminate these primary branches often have 20 or more spikelets. The lowermost spikelets may be included in the sheath, but the upper two or three spikelets are borne on long pedicels, as much as 20 or 30 mm in length. The spikelets of this inflorescence are cleistogamous.

Secondary branching begins shortly after the elongation of the primary branches. The secondary branches are terminated by much reduced panicles. Some of the members of the oligosanthes group may produce only two or three sets of these secondary branches. Others, including *P. malacophyllum* and the members of the *P. oligosanthes* complex, undergo repeated axillary branching into the autumn and produce dense fascicles of branches.

Conclusions

*Panicum leibergii*, *P. malacophyllum*, *P. ravenelii*, and *P. xanthophysum* seem to be among the most clearly delimited taxa in the subgenus *Dichanthelium*. There are no reported cases of apparent hybridization between any pair of these species and only one case of suspected hybridization between one of these (*P. leibergii*) and a species (*P. praecocius*) in the lanuginosum group reported in Lelong (1965). Each of the four taxa has a distinct range with very little overlap with any of the other three.
The three species recognized by Hitchcock and Chase in the *P. oligosanthes* complex are much less clearly delimited than the preceding four. The several characters used to separate these entities show only a tendency to be correlated. Fernald appears to have been justified in reducing these entities to a single species. His recognition of three geographic varieties is strengthened by the differences in the frequencies of several traits found between different geographic areas. However, the problem involved in recognizing these varieties is that whereas populations from different geographic areas can be separated easily on the basis of the frequencies of several traits, individual specimens often cannot be separated unless the place of origin of the specimen is taken as a major taxonomic criterion. I have chosen to recognize three geographic varieties with approximately the same criteria as those employed by Fernald with the knowledge that many plants are more or less intermediate between the "typical" members of the varieties.

**Taxonomy of the Oligosanthes Group**

The oligosanthes group as treated here includes five species separable by the following key:

1. Nodes densely-bearded with long spreading to reflexed hairs; culms and sheaths densely pubescent with uniform spreading hairs 1.5-3.0 mm long.

2. Spikelets 2.8-3.2 mm long; blades lax, densely velvety-pubescent on both surfaces... *P. malacophyllum*
2. Spikelets 3.8-4.3 mm long; blades firm, nearly glabrous on adaxial surface...............P. ravenelli

1. Nodes beardless and glabrous or with sparse pubescence; culms and sheaths never densely pubescent with only spreading hairs 1.5-3.0 mm long.

3. Spikelets 3.7-4.2 mm long, with narrow, pointed first glume 1.7-2.2 mm long; second glume green throughout; panicle branches ascending.

4. Blades glabrous; spikelets short-pubescent; sterile floret without anthers...............P. xanthophysum

4. Blades papillose-hispid; spikelets papillose-hispid; sterile florets usually containing anthers........

.................................P. leibergii

3. Spikelets 2.6-3.8 mm long, with broad, blunt first glume 1.0-1.6 mm long; second glume commonly orange-brown at base; panicle branches spreading ........

.................................P. oligosanthes

PANICUM MALACOPHYLLUM Nash


Nomenclature

One of the isotypes (MO 1838901) of P. malacophyllum is a mixed sheet including also P. oligosanthes var. scribnerianum. However, the original description leaves no doubt that Nash intended the name to apply to the velvety-pubescent plants and not to the specimens of P. oligosanthes var. scribnerianum.

Distribution

Panicum malacophyllum extends from the Ozark region of southern and eastern Missouri east to central Tennessee and
south throughout Arkansas and northeastern Texas and west to about central Oklahoma. It occurs in dry, open areas commonly on sandy soil. It may be abundant in the grass and early shrub-stages of secondary succession in old fields. This species also occurs at the edge of oak woods, along trails, on dry, disturbed roadsides, and on burned-over woodland. It seems to withstand crowding and intense competition from dense grassy vegetation better than most dichanthelia.

**PANICUM RAVENELII** Scribn. and Merr.


**Description**

This species ranges from Delaware south to northern Florida and west to eastern Texas. It extends northward to central Tennessee and southern Missouri. It is usually found at the edge of woods or in semi-open areas of woods on dry sandy, cherty, or clayey soils. It is not an aggressive species which invades weedy areas, and although it is of common occurrence throughout its range, it is rarely abundant in any local area.
PANICUM XANTHOPHYSUM Gray

Panicum xanthophysum Gray. Gram. et Cyp. 1: n. 28. (1834) (1,2). See discussion below.

Panicum xanthophysum f. amplifolium Scribn. in Brainerd, Jones and Eggleston. Fl. Vt. 104 (1900) (3).

Nomenclature

Gray's first use in print of the name, P. xanthophysum, was in a set of exsiccatae distributed in 1834 to several botanical institutions accompanied by sheets of printed labels entitled "Gramineae et Cyperaceae". Label no. 28 bears the name "Panicum xanthophysum, sp. nov." and includes a latin diagnosis of this taxon. Gray (1835) later described this taxon in a short paper on some new or noteworthy plants of New York. Various authors have cited the latter date for the publication of this binomial. Hitchcock and Chase (1910), however, have chosen to recognize the 1834 date for this binomial. Their decision appears to be correct since the rule (Lanjouw, 1964, Article 31) which excludes the distribution of exsiccatae as a means for effective publication applies after Jan. 1, 1953. The same rule also exempts those names appearing in exsiccatae "if the printed matter (presumably including printed labels) is also distributed independently of the exsiccatum." Since (according to Rickett and Gilly, 1942) certain institutions bound a separate set of these exsiccatum labels as a single unit filed in the library such bound sets of printed labels may be considered to constitute an effective publication of the name.
Distribution

Panicum xanthophysum is one of the few species of the subgenus Dichanthelium not found in the southeastern United States. Its range extends from southern Quebec and Ontario west to southern Manitoba, south to New England; along the Appalachian mountains to West Virginia, and south to central Michigan, central Wisconsin, and central Minnesota. It occurs primarily in semi-open areas in pine or oak woods, in recently cut-over woods, and occasionally on cliffs, ledges, and in old fields. The soils are generally sandy or thin, rocky, and acidic in nature. This species is the only known tetraploid included in this study (Bowden, 1960).

PANICUM LEIBERGII (Vasey) Scribn. in Britt. and Brown.


Distribution

Panicum leibergii is primarily a species of mesic tall grass prairies, with specimens found only occasionally on other habitats as sandy, grassy fields, semi-open areas in dry woodland, and on sandy or rocky knolls. The range includes the prairie areas from southern Manitoba south through the center of the Dakotas, Nebraska, and Kansas, and east through southern Minnesota, central Wisconsin, northern and western Indiana, nearly all of Illinois and Iowa, and the northern half of Missouri. Occasional plants have been found
in southeastern Michigan, northern Ohio, western New York, and central Pennsylvania. It has also been reported in eastern Texas.

PANICUM OLIGOSANTHES Schult.

This species includes three geographic varieties. The following key to the varieties is intended to separate the more distinct specimens of each variety.

1. Spikelets 3.3-3.8 mm long and less than 53% as wide as long; terminal inflorescences sparsely-flowered; longest pedicels often 18-25 mm long; plants of the southeastern United States..................var. oligosanthes

1. Spikelets usually 2.6-3.3 mm long and more than 53% as wide as long; terminal inflorescences densely-flowered; longest pedicels usually less than 18 mm long.

2. Spikelets 2.6-3.1 mm long, usually glabrous; culms and sheaths sparsely-pubescent to nearly glabrous; plants mostly of the Ozark area............var. helleri

2. Spikelets 3.1-3.3 mm long, usually sparsely pubescent; culms puberulent and often with scattered long hairs; sheaths usually papillose-hispid, at least at first; plants widespread, in most parts of U.S. except the Southeast..................var. scribnerianum

PANICUM OLIGOSANTHES Schult. VAR. OLIGOSANTHES

Panicum oligosanthes Schult. Mant. 2:256 (1824) (3). Based on P. pauciflorum Ell., not R. Br.


Distribution

This variety extends from Delaware south to northern Florida, west to eastern Texas and north to Tennessee and
southern Missouri. It intergrades into the other two varieties, making it difficult to delimit its range. It occurs on a variety of somewhat disturbed habitats, including semi-open areas in oak and pine woods, along trails, roadsides, at the edge of woodlands, in grass and shrub-stages of secondary succession in old fields, in cut-over woodlands, and on coastal sand dunes. The soils are generally very sandy or clayey and often dry.

**PANICUM OLIGOSANTHES** Schult. VAR. **HELLERI** (Nash) Fern.


**Distribution**

The _var. helleri_ occurs in southern Missouri, western Tennessee, Arkansas, northern Louisiana, eastern Oklahoma and northeastern Texas. It also occurs in the mountains of New Mexico and Arizona. The common habitats include prairies, grassy fields and pastures, roadsides, ditches, stream banks, borders of woods, along trails, and in semi-open areas in woods. The soil is often dry and sandy, although it can be found on a wide range of soils. This variety withstands crowding from dense grassy vegetation well.

**PANICUM OLIGOSANTHES** Schult. VAR. **SCRIBNERIANUM** (Nash) Fern.

Additional synonymy and nomenclature

The additional synonymy appearing in Hitchcock and Chase (1951, p. 923) is tentatively accepted. The proper application of the binomial, *P. scribnerianum*, is in doubt, since Nash published this name as a new name followed by two basionyms, one of S. Watson, the other of Lamson-Scribner. The two basionyms apparently apply to different entities. Hitchcock and Chase (1910) chose the first name, *P. scoparium* S. Wats., as the basionym.

Distribution

This variety is widely distributed, probably occurring in every state of the United States except in the Southeast. It also occurs in the southern parts of British Columbia, Alberta, and Saskatchewan, and in northern Mexico. It is one of the more abundant and aggressive of the dichanthelia, occurring on a broad range of habitats. It may be found on prairies, pastures, grassy fields, roadsides, sand dunes, recently exposed subsoil, in open areas around woodlands, on dry, exposed knolls and ridges, stream banks, etc. It probably occurs more often on dry, sandy or rocky soils, but it can be found on a wide range of soil types.
BIBLIOGRAPHY


Blake, S. F. 1913. Two records for Panicum calliophyllum Ashe. Rhodora 15: 99-100.


I wish to express my appreciation to Dr. Richard W. Pohl for his advice and guidance throughout this work. I also wish to thank Dr. Duane Isely for his critical reading of portions of the text and for many valuable suggestions, Mr. Aalt Boon for his assistance and advice on maintaining greenhouse cultures of Panicum, and Dr. Thomas Soderstrom, U. S. National Herbarium, and Dr. Walter Lewis, Missouri Botanical Gardens, for the loan of specimens from their herbaria.
APPENDIX

Specimens Examined

**Panicum depauperatum ssp. depauperatum**


ALABAMA: Colbert Co.: D. Isely, 3426, May 28, 1944 (ISC).


DELAWARE: New Castle Co.: A. Commons, 29, July 5, 1897 (ISC).

DISTRICT OF COLUMBIA: Kearney, s. n., May 28, 1897 (ISC); Vasey, s. n., 1884 (ISC).


ILLINOIS: Jackson Co.: H. A. Gleason, 1023, June 23, 1902 (US); H. A. Gleason, s. n., June 16, 1903 (US).

INDIANA: Lake Co.: L. M. Umbach, 1657, June 15, 1907 (ISC).


LOUISIANA: Natchitoches Par.: M. G. Lelong, s. n., Apr 22, 1959 (ISC).


NEW JERSEY: Bergen Co.: P. W. Pennell, 9435, June 16, 1918 (ISC); Cape May Co.: O. H. Brown, s. n., June 20, 1937 (ISC); Cumberland Co.: O. H. Brown, s. n., June 6, 1939 (ISC).

NEW YORK: Oneida Co.: J. V. Haberer, 3304, July 30, 1904 (US). Schenectady Co.: J. H. Wibo, s. n., no date (ISC 9847).


OHIO: Jackson Co.: Bartley and Pontius, s. n., June 2, 1934 (US).

PENNSYLVANIA: Berks Co.: D. Benkheimer, 19259, June 8, 1959 (ISC); Montgomery Co.: J. Bright, 19841, May 30, 1945 (ISC); Westmoreland Co.: P. E. Pierron, s. n., Sept. 15, 1876 (ISC).


VIRGINIA: Goochland Co.: R. W. Freckmann, 581, June 4, 1963 (ISC); Prince George Co.: R. W. Freckmann, 566, June 4, 1963 (ISC); M. G. Lelong, 2549, June 4, 1963 (ISC); G. L. Pyrah, 262, May 30, 1965 (ISC); Southampton Co.: M. L. Fernal


Panico depauperatum ssp. perlongum

COLORADO: Boulder Co.: I. W. Clokey, 4006, June 18, 1921 (ISC).

ILLINOIS: County unknown: Mead, June 7, 1848 (MO). Peoria Co.: J. R. Churchill, s.n., June 5, 1912 (MO).

INDIANA: Lake Co.: L. M. Umbach, 3555, June 21, 1909 (ISC); L. M. Umbach, 3670, June 29, 1909 (ISC).


LOUISIANA: Natchitoches Par.: E. J. Palmer, 7450, May 1, 1915 (MO).

MICHIGAN: Livingston Co.: J. K. Hiltunen, 3464, July 14, 1961 (ISC).
MINNESOTA: Goodhue Co.: W. L. Tolstead, s. n., June 15, 1937 (ISC).


NEBRASKA: Richardson Co.: H. C. Reynolds, 1268, June 12, 1940 (MO).


Panicum depauperatum ssp. linearifolium


ILLINOIS: Peoria Co.: V. H. Chase, 13409, June 18, 1953 (ISC).


OHIO: Lake Co.: H. C. Beardslee, s. n., 1871 (ISC).


York Co.: J. N. Rose and J. H. Painter, 8153, July 5, 1904 (US).


VERMONT: Windsor Co.: D. S. Carpenter, 4, June 14, 1919 (MO). County unknown: D. S. Carpenter, s. n., no date (ISC 86303).

VIRGINIA: County unknown: W. H. Camp, 1466, June 12, 1936 (US).

WEST VIRGINIA: Mineral Co.: E. E. Berkley, s. n., June 11, 1934 (US).


Intermediates between Panicum depauperatum ssp. depauperatum and ssp. perlongum


INDIANA: Harrison Co.: C. C. Deam, 27652, May 26, 1919 (US).


Intermediates between Panicum depauperatum ssp. depauperatum and ssp. linearilobum

INDIANA: Crawford Co.: R. C. Friesner, 14429, June 16, 1940 (ISC).

MINNESOTA: St. Louis Co.: O. Lakela, 14703, July 8, 1952 (ISC).


Intermediate between Panicum deseptatum
ssp. perlongum and ssp. linearifolium

MINNESOTA: Hennepin Co.: J. W. Moore and E. Phinney, 10761, June 6, 1939 (ISC).

Panicum laxiflorum (sensu lato)


DISTRICT OF COLUMBIA: L. F. Ward, s. n., 1883 (ISC).

FLORIDA: County unknown: Chapman, s. n., no date (US 954311). Brevard Co.: A. Chase, 4023, Sept. 17, 1907 (US).
Columbia Co.: Collector unknown, Aug. 1892 (ISC 65201); A. W. Bitting, 1012, Apr. 22, 1892 (US); A. S. Hitchcock, 1009, Apr. 16, 1906 (ISC). Duval Co.: Curtiss, s. n., no date (ISC 9900); A. H. Curtiss, 6602, Apr. 27, 1906 (ISC).


MARYLAND: Montgomery Co.: A. Chase, 2316, June 11, 1904 (ISC).


Panico laxiflorum X P. sp. (?)

LOUISIANA: West Feliciana Par.: R. S. Cocks, 3510, June, 1907 (US).

Panico ciliatum var. ciliatum


TEXAS: Jasper Co.: E. R. H., s. n., Nov. 27, 1902 (ISC).

Panico ciliatum var. glabrescens

ALABAMA: Baldwin Co.: S. M. Tracy, 7208, Apr. 26, 1901 (MO).


MISSISSIPPI: Jackson Co.: S. M. Tracy, 6470, July 14, 1899 (MO).

Panicum ciliatum var. pubescens

BRITISH HONDURAS: Toledo district; P. H. Gentle, 3748, Nov. 2, 1941 (MO).

COLOMBIA: Santa Maria; K. H. Smith, 163, 1898-1901 (MO).


LOUISIANA: Parish unknown: J. F. Joor, s. n., no date (MO 1838849). St. Tammany Par.: G. Arsene, 12109, May 1, 1920 (MO).


TEXAS: Robertson Co.: F. A. Barkley, 13528, Aug. 6, 1943 (MO).


*Panicum ciliatum*; specimens intermediate between two varieties:

STATE UNKNOWN: Collector unknown (Herb. Chapman), no date (MO 812904).


LOUISIANA: Calcasieu Par.: A. S. Hitchcock, 1162, Apr. 21, 1906 (US).


*Panicum neuranthum* var. *neuranthum*

ARKANSAS: Jefferson Co.: H. Eggert, s. n., June 8, 1898 (MO).

FLORIDA: County unknown: Chapman, s. n., no date (MO 1833825); S. M. Tracy, 7176, May 4, 1901 (US, MO). Charlotte Co.: G. E. LaRoche, 145, Apr. 28, 1960 (ISC); R. W. Pohl, 9155, Apr. 12, 1962 (ISC); W. A. Silveus, 5714, Apr. 26, 1940 (US).

LOUISIANA: St. Bernard Par.: Tracy and Loyd, 459, Aug. 18, 1900 (MO).

MISSISSIPPI: Jackson Co.: S. M. Tracy, 4567, May 8, 1898 (US).


_Panicum neuranthum var. ovinum_


MISSISSIPPI: Jackson Co.: S. M. Tracy, 4616, May 6, 1898 (US).

Panicum aciculare


Panicum angustifolium


Panicum consanguineum


Intermediate between Panicum aciculare and P. ovinum

TEXAS: Aransas Co.: E. C. Tharp, 50-6, Apr. 6, 1950 (ISC).

Intermediate between Panicum aciculare and P. angustifolium


Panicum malacophyllum Nash


TEXAS: Dallas Co.: H. Eggert, s. n., June 26, 1899 (MO); J. Reverchon, 1331, May 7, 1900 (MO); J. Reverchon, 1350, Aug. 26, 1900 (MO); J. Reverchon, 2562, May 21, 1901 (MO). Hood Co.: H. Eggert, s. n., May 5, 1900 (MO). Palo Pinto Co.: S. M. Tracy, 7943, June 4, 1902 (MO). Navarro Co.: J. Reverchon, 3534, Sept. 27, 1902 (MO).

**Panicum ravenelii** Scribn. and Merr.


DISTRICT OF COLUMBIA: E. S. Steele, s. n., June 12, 1900 (MO).


LOUISIANA: Natchitoches Par.: M. G. Lelong, s. n., Apr. 22, 1959 (ISC); M. G. Lelong, s. n., May 18, 1959 (ISC); M. G. Lelong, s. n., June 15, 1959 (ISC). Ouachita Par.: R. W. Freckmann, 1765, June 5, 1965 (ISC); A. S. Hitchcock, 1288, Apr. 27, 1906 (ISC).


TEXAS: County unknown: J. Reverchon, 1882, May 21, 1900 (MO).

VIRGINIA: Henrico Co.: J. R. Churchill, s. n., May 13, 1894 (MO).

Panicum xanthophyllum Gray


MASSACHUSETTS: Berkshire Co.: J. R. Churchill, s. n., Aug. 1, 1920 (ISC, ...
MICHIGAN: Cheboygan Co.: J. H. Ehlers, 2000, July 8, 1922 (ISC); F. C. Gates and M. T. Gates, 10612 July 2, 1917 (MO); H. A. Gleason and H. A. Gleason, Jr., 43, June 29, 1933 (ISC); L. H. Shinniers, 13378, June 30, 1952 (ISC).


NEW HAMPSHIRE: County unknown, J. Blake, s. n., July 12, 1864 (MO 773171). Coos Co.: W. Deane, s. n., July 25, 1864 (ISC); W. Deane, Amer. Gr. Nat. Herb. 222, July 19, 1914 (MO); A. H. Moore, 4107, June 25, 1908 (ISC); A. S. Pease, 27701, Sept. 21, 1939 (ISC).


**Panicum leibergii**


Chickasaw Co.: W. D. Spiker, s. n., June 28, 1926 (ISC).
Clay Co.: A. Hayden, 706, June 27, 1936 (ISC). Clayton Co.: 
E. Shimak, s. n., June 15, 1923 (ISC). Clinton Co.: L. H. 
Pammel, 1443, Sept. 9, 1898 (ISC). Davis Co.: A. Hayden, 
10974, June 28, 1938 (ISC). Delaware Co.: B. Shimak, s. n., 
May 31, 1923 (ISC). Dickinson Co.: A. Hayden, 3157, July 7, 
1942 (ISC). Dubuque Co.: R. W. Freckmann, 1863, July 6, 
Grundy Co.: A. E. Paddock, 3206, June 22, 1901 (ISC). Guth­ 
rie Co.: M. G. LeLong, 2164, July 2, 1962 (ISC). Hamilton 
Co.: F. H. Monson, 1928, June 21, 1956 (ISC). Hardin Co.: 
M. G. LeLong, 2150, June 25, 1962 (ISC). Howard Co.: M. G. 
LeLong, 2268, July 10, 1962 (ISC). Johnson Co.: M. P. Some, 
761, June 20, 1907 (ISC). Kossuth Co.: R. W. Pohl, 7141, 
July 21, 1951 (ISC). Lyon Co.: R. L. McDill, 159, June 21, 
1952 (ISC). Muscatine Co.: B. Shimak, s. n., May 26, 1923 
(ISC). O'Brien Co.: B. Shimak, s. n., June 22, 1930 (ISC). 
Osceola Co.: P. K. Monson, 2305, June 26, 1956 (ISC). Palo 
Alto Co.: A. Hayden, 627, June 22, 1936 (ISC). Pocahontas 
Co.: R. L. McDill, 124, June 20, 1952 (ISC). Sac Co.: F. H. 
Monson, 1822, June 13, 1956 (ISC). Story Co.: C. E. Bessey, 
4, June 8, 1875 (ISC); R. W. Freckmann, 1877, June 20, 1965 
(ISC); R. W. Freckmann, 1925, June 18, 1965 (ISC). Union 
Co.: M. G. LeLong, 2057, June 15, 1962 (ISC). Webster Co.: 
M. G. LeLong, 2137, June 22, 1962 (ISC). Winneshiek Co.: 

KANSAS: Riley Co.: A. S. Hitchcock, 2504, May 30, 1908 
(ISC).

MINNESOTA: County unknown: L. M. Humphrey, s. n., June 4, 
1929 (ISC 138413 and 138337). Kanabec Co.: J. W. Moore and 
R. M. Tryon, 17464, June 28, 1945 (ISC). Rock Co.: P. John­ 
son, 299, June 14, 1941 (ISC). Winona Co.: J. H. Holzinger, 
1896, (ISC).

PENNSYLVANIA: Centre Co.: H. A. Wahl, 1035A, July 10, 
1941 (ISC).

NORTH DAKOTA: County unknown: J. Lunell, s. n., July 9, 
1915 (ISC 144583).

WISCONSIN: Barron Co.: H. H. Iltis, 7984, Aug. 24, 1956 
(ISC). La Crosse Co.: L. H. Pammel, 10, July 23, 1897 (ISC). 
Racine Co.: S. C. Wadmond, 3426X, June 23, 1900 (ISC).

Panicum oligosanthes var. oligosanthes

ARKANSAS: Boone Co.: J. F. Brenckle, 40-230, May 27, 1940 


\textit{Panicum oligosanthes} var. \textit{helleri}


ARIZONA: County unknown: H. H. Rusby, s. n., June, 1883 (MO 1838311).

LOUISIANA: Red River Par.: R. W. Freckmann, 948, May 29, 1964 (ISC); M. G. Leelong, s. n., May 8, 1959 (ISC).


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<td>Cass Co.: Bock and Chase, 199</td>
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OREGON: Clastrop Co.: L. H. Pammel, s. n., Aug. 1, 1905 (ISC).


