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IN SOME PANICUM SUBGENUS DICHANTHELIUM.

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STUDIES OF REPRODUCTION AND VARIATION IN SOME
PANICUM SUBGENUS DICHANTHELIUM

by

Michel Georges Lelong

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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

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INTRODUCTION

Approximately 500 species have been described in the genus Panicum of the Gramineae. They are found in the Tropics and in warm temperate regions of both hemispheres. In the New World, the genus is well represented throughout South and Central America, the West Indies, Mexico, and the United States as well as the southern part of Canada.

In the latest extensive revision of the North American species of Panicum, Hitchcock and Chase (1910) subdivide this large genus of grasses into three subgenera. The first of these is the small subgenus Paurochaetium which includes five species in Texas, Mexico, Florida, and the Caribbean Islands. In these plants, the axis of the inflorescence branchlet extends beyond the base of the uppermost spikelet as a bristle. Possibly, they represent intermediate between the rest of the genus Panicum and the genus Setaria. Rominger (1962) includes them in the genus Setaria.

The second group is the subgenus Panicum, called the true Panicum by Hitchcock and Chase. It includes about 75 species of rather robust annual and perennial grasses which are widely distributed in our hemisphere from Argentina and Chile to southern Canada.

Lastly, the subgenus Dichanthelium with 110 species of small perennial plants of North America occurs as far south as Columbia and Venezuela, and exhibits its greatest diversity on the Atlantic and Gulf Coastal Plain of the United States. A few species appear to be restricted to Texas or to Florida. In general, the subgenus Dichanthelium is poorly represented in the mountainous regions of the United States.

Members of this subgenus are characterized by the production of a winter "rosette" of short broad basal leaves as well as by a somewhat unusual blooming habit described by Hitchcock and Chase (1910, p. 142) in the following manner:

In spring producing simple culms with mostly narrowly lanceolate blades and terminal panicles with numerous spikelets, these rarely perfecting seeds; the early culms branching at some or all of the nodes (in a few species from the base only) after the maturity of the primary panicles or sometimes before; the branches often repeatedly branching, the short branchlets more or less fascicled and bearing usually much reduced leaves; the terminal one or two joints of the primary culms often finally falling, the whole producing an autumnal form usually strikingly different from the vernal form; the secondary panicles reduced, the latest more or less included in the sheaths, cleistogamous and perfecting their grains. The type species is P. dichotomum L.

In this group there is an intermediate stage of branching, in which the plants do not show the characteristic vernal nor autumnal habit. Vernal culms are sometimes produced on plants during the branched condition, because of renewal of activity, due to increased moisture, excess of nutriment, injury, or other causes.

The rosette forming species of Panicum occupy a variety of habitats ranging from dry sand to bogs, with a majority of species occurring in open and disturbed dry woods and along roadsides.

As should be suspected, no clear cut demarcation exists between the two large subgenera of the genus Panicum. Such species of true Panicum as Panicum chiriquiense Hitchcock and Chase, P. latiglume Doell., P. zizanioides H.B.K., P. brachyanthum Steud. closely resemble certain rosette forming species, while P. pedicellatum Vasey, P. nodatum Hitchcock and Chase, P. scabriusculum Ell. and related forms belonging to the subgenus Dichantherium should perhaps be placed in the subgenus Panicum.

The subgenus Dichantherium of the genus Panicum, which will be referred to as "the dichantheria" in the text, is further subdivided by

Hitchcock and Chase into 17 "groups" of no definite taxonomic status, mostly on the basis of spikelet length and pubescence characteristics. The name of each of these groups is the plural form of the epithet of the species which characterizes it. While such assemblages as the Depauperata or the Latifolia are fairly clearly delimited and the species included in them present little difficulty in identification, other parts of the subgenus have long been a source of exasperation to plant taxonomists. Few dichantheria compare in difficulty with the 28 species recognized by Hitchcock and Chase in the Lanuginosa and Columbiana grouping. The present author was made aware of the need for a taxonomic reevaluation of these grasses in a previous study (Lelong 1960).

Conventional taxonomic methods have apparently not proved adequate to satisfactorily delimit the species in the subgenus Dichantherium, or to elucidate their interrelationships. Consequently, the basic objective of this investigation has been to determine whether the complexity of the dichantheria is only apparent and of a nomenclatural nature, or whether it is real and caused primarily by genetical or by environmental factors.

To accomplish this, the biology of certain species in the subgenus was studied with emphasis on reproductive behavior. An effort was made to assess the influence of certain environmental factors on the morphology of individual plants. Morphological variations of progeny and of populations in the field were observed. Finally an attempt was made to evaluate the present day taxonomy of the Lanuginosa and Columbiana groups in the light of these findings.

REVIEW OF LITERATURE
CONCERNING TAXONOMY AND CYTOLOGY OF THE DICHANTHELIA

Taxonomy of *Panicum* Subgenus *Dichanthelium*

Linnaeus (1753) described 20 species in the genus *Panicum*. Half of those entities were included in his "Spicata" group, the rest belonging to his "Paniculata" grouping. The 10 "spicata" species were later distributed by various authors into new genera such as *Setaria*, *Pennisetum*, *Echinochloa*, *Paspalum*, *Digitaria*, *Stenotaphrum*, and *Oplismenus*. Most of the species in the "Paniculata" group have been retained in the genus *Panicum*, including three species in the present day subgenus *Dichanthelium*, namely *Panicum dichotomum*, *P. clandestinum*, and *P. latifolium*. These three taxa are still considered among the most distinct species in the subgenus.

Lamarck (1798) furthered our knowledge of the dichanthelia with his description of *P. scoparium* and *P. laxiflorum*. However, he also introduced slight taxonomic confusion with his publication of *P. nitidum* and *P. nodiflorum*, difficult to separate from *P. dichotomum*. His *P. pubescens* was based on a mixture of plant material containing, according to Hitchcock and Chase (1910) "some species of *Brachiaria*" and two freely branching autumnal culms of *P. scoparium* given to him by Michaux.

Subsequently the name *P. pubescens* Lam. and *P. pubescens* Michx. were often erroneously utilized by early American botanists to refer to plants in the large polymorphic complex later placed by Fernald (1934) under *P. lanuginosum* and its varieties.

Poiret (1816) in a supplement of the *Encyclopedie Methodique* noted

that the "Panicum pubescens of Michaux is stouter in all its parts than that of Lamarck" (my translation). In addition he described a plant sent to him by Bosc from Carolina as a variety minor of P. pubescens, "folio angustioribus, floribus minoribus". The description of this plant agrees with that of a "typical" member of the present day Lanuginosa complex. However, no mention of it was made in Hitchcock and Chase's later revision. Poiret also added P. boscii to the future subgenus Dichanthelium. Michaux (1820) described P. barbulatum, considered by many botanists to be inseparable from P. dichotomum or P. nitidum.

Elliott (1816 - 1821), collecting primarily in South Carolina and Georgia, described some of our best species of dichanthelia such as P. sphaerocarpon, P. angustifolium, and P. scabriusculum. His description of P. pubescens Lam. as a plant 6-18 inches high with stem erect and decumbent, very glabrous, does not correspond with the description of either P. scoparium or any present day member of the Lanuginosa. Since P. lanuginosum was later chosen by Hitchcock and Chase (1910) as the species characteristic of their Lanuginosa grouping, it seems appropriate to include Elliott's description in the following paragraphs:

Stem 1-2 feet high, pubescent, hoary. Leaves linear or narrow-lanceolate, acute, clothed with short down; sheaths shorter than the joints, very hairy or woolly at and near the throat. Panicle expanding. Flowers small, obovate, nearly round.

This is an intermediate species between P. viscidum (= P. scoparium) and P. strigosum, smaller than the former, and every way larger than the latter. The peduncles, which are hairy in P. strigosum, are smooth in this species. Its flowers are scarcely half as large as those of P. villosum (= P. consanguineum Kunth) to which it has in habit some resemblance, and smaller than those of P. multiflorum (= P. polyanthes Schult).

Between 1816 and 1885, some 20 additional species now placed in

Panicum subgenus Dichanthelium were described by various authors. Among them we can list P. aciculare Desv. ex Poir., P. depauperatum Muhl., P. lancearium Trin., P. spretum Schult., P. xanthophysum A. Gray., P. chamaelonche Trin.

In 1885, Vasey listed 12 species and 5 varieties of rosette forming species of Panicum in his "Descriptive Catalogue of the Grasses of the United States". No species of the present day Lanuginosa group was enumerated by him. Apparently he regarded members of this complex as varieties of P. dichotomum, "a widespread species of many forms". No mention is made of P. lanuginosum and P. ovale described by Elliott in 1816 nor of P. thermale named in 1862 by Bolander.

Three years later in the first monograph of the genus Panicum in the United States, Vasey (1889) recognized 20 species and 18 varieties in the subgenus Dichanthelium. The same disposition was adopted in his monograph of the grasses of the United States and British America (1892). It is probable that the less pubescent members of the polymorphic Lanuginosa complex were regarded by him as P. nitidum var. major for which no type specimen has ever been found. Describing this variety, Vasey noted: "Here could be placed several variable forms, mostly smooth. . . .". The more hairy Lanuginosa were considered by him as P. dichotomum var. villosum later reduced by Hitchcock and Chase to a synonym of P. villosissimum Nash.

Describing P. laxiflorum var. pubescens, Vasey remarks that this entity approaches closely P. nitidum being "perhaps the P. nitidum var. ciliatum Torr". This last named variety was later included by Hitchcock and Chase in the synonymy under P. huachucae var. fasciculatum in the

midst of their Lanuginosa grouping. The circle of confusion regarding the elusive nature of Lanuginosa species was widening. Were these entities more closely related to P. dichotomum, P. nitidum and their allies or did they exhibit greater affinity with the Laxiflora of Hitchcock and Chase? This question will be reconsidered later in the discussion of the Lanuginosa and Columbiana complex.

Beal (1896) recognized only 13 species and 6 varieties of dichantheria. His description of the species P. dichotomum follows:

Plants of various forms and perhaps varieties or even species from widely separated localities too numerous to mention have reached protracted study, so far with results quite unsatisfactory. It is a pity that some of these forms ever received distinct names. For example, plants in which the nodes are clothed with dense, straight hair have been called P. barbulatum Michx. often without much regard for other peculiarities. In a similar manner if shaggy hairy or villous the plants have been known as P. pubescens Mx. or P. villosum Ell. (= P. consanguineum Kunth) or if the leaves were smooth except straight hairs on the margins, P. ciliatum Ell. or if the culms and sheaths were softly hairy P. lanuginosum Ell. Plants with smooth leaves varying considerably in other respects have received the name of P. nitidum Lam. If the leaves be smooth, flat, short, tapering much like a wedge, the plant is P. ensifolium Baldw. In a large collection there will be many specimens, each answering to one and often two or more of these names; and there will be others showing various combinations of peculiarities expressed in the names above given.

With his usual sagacity, Beal had fully recognized the complexity of this group and he wisely abstained from adding to the difficulty by naming entities before the causes for this difficulty were uncovered.

Unfortunately his warning was not heeded. Between 1895 and 1900 two overzealous botanists, Ashe and Nash, collected extensively throughout the Carolinas and indiscriminately named 92 new rosette forming species of Panicum, including 18 in the present day Lanuginosa complex.

In 1901, Scribner and Merrill prepared an annotated list of the New England species of the genus Panicum. Many of the species named a

few years earlier by Ashe and Nash were either included in their synonymy or merely regarded as varieties or forms. Two species were recognized by them within the Lanuginosa complex namely P. unciphyllum Trin., and P. lanuginosum Ell.

Describing P. unciphyllum, the authors stated that "this species is exceedingly variable and many varieties or forms might be characterized on the basis of size and habit." They then proceeded to describe two varieties and two forms under this entity, including our present day P. implicatum Scribn. and P. meridionale Ashe. They admitted that many additional variants could be given a varietal or formal ranking but "in so doing it would only add more confusion to this difficult group, as we believe that no one would be able to recognize the forms described, no matter how minutely and carefully they might be characterized."

P. lanuginosum is regarded by Scribner and Merrill as being very closely related to P. unciphyllum but characterized by a lax habit of growth, thin leaves "which generally have a peculiar lustre or sheen, pale green, a generally somewhat implicate panicles, at least in herbarium specimens, and long pubescent spikelets." They concluded by stating that "P. lanuginosum is extremely variable and often can only be separated arbitrarily from the related species. It is possible that it should be considered only as a variety of the preceding species."

Later the same year, in a comprehensive treatment of American grasses, F. Lamson-Scribner (1901) recognized 43 species of rosette forming Panicum including 5 in the present day Lanuginosa grouping namely P. implicatum Scribn., P. villosissimum Nash, P. ovale Ell.,

P. ciliiferum Nash (P. ovale) and P. atlanticum (P. villosissimum).

The most exhaustive study of the genus Panicum in North America was published in 1910 by Hitchcock and Chase. With minor modifications, their treatment of the subgenus Dichanthelium has been utilized to the present. Their classification of the group was based upon critical examination of a considerable number of specimens collected throughout the United States, Mexico, and Central America. This work is truly monumental. Spikelet length and pubescence characteristics were the principal morphological criteria used in their taxonomic treatment.

A total of 115 species further combined into 17 more or less well defined groups was recognized by Hitchcock and Chase. Two hundred and thirty-three previous names were absorbed in the synonymy. Their Lanuginosa grouping includes 21 species and 1 variety, and their Columbiana complex comprises 7 species and 1 variety. Forty-seven of the 92 species described earlier by Ashe and Nash were rejected by them.

Minor objections to Hitchcock and Chase's work were voiced by Stone (1910), Wiegand and Eames (1926), Deam (1929), Weatherby, Knowlton and Bean (1927) and Weatherby and Griscom (1934). M. L. Fernald (1921, 1929, 1934) raised more vehement criticisms against the proposed classification of the subgenus Dichanthelium. Although he recognized the difficulties inherent in this group of plants and the magnitude of the endeavor undertaken by Hitchcock and Chase, he expressed his dissatisfaction with their treatment, blaming primarily the "ultra democratic or radical reaction against orthodoxy and good usages of younger men with little or no background of general scholarship and with a minimum

of experience in exact and judicious considerations of other groups."

"For several years Ashe and Nash held the field", he added.

On the basis of his numerous years of field experience and of his exceptional "sense for affinity," Fernald recognized clearly the artificiality of many species in the subgenus Dichanthelium and the need for eliminating some of the taxa. Apparently he was of the opinion that the lack of clear interspecific delimitation in this group of plants was caused primarily by environmental influences. Criticizing the pubescence criteria used extensively by Hitchcock and Chase, he concluded (1934) that "it is safe, judging from common experience of many good field observers, to look to differences of habitats, of shade and sunshine, of chemical reactions of the soil or of moisture and aridity as largely controlling these simple responses."

In conclusion, Fernald reduced 13 species of the subgenus Dichanthelium to the rank of variety. However, he also described four new species in the complex, namely P. recognitum, P. mundum, P. benneri, and P. glutinoscabrum. In the Lanuginosa, he recognized eight species and reduced seven species recognized by Hitchcock and Chase to the rank of varieties. This taxonomic disposition is followed in the eighth edition of Gray's Manual of Botany (1950).

Gleason (1952) presents essentially the same treatment of this group of plants with slight variations.

Since Fernald's revision, the subgenus Dichanthelium has only been the object of brief and sporadic attention, mainly in connection with the preparation of state floras. Noteworthy among such efforts are the contributions of Deam (1929, 1940), Silveus (1942), and particularly

those of Shinnars (1944), Pohl (1947), Blomquist (1948), and Steyermark (1963).

The most recent comprehensive work on the subgenus Dichanthelium was undertaken by Silveus (1942). The classification of Hitchcock and Chase as well as their brief description of vegetative appearance and reproductive mechanism are adopted by the author in their entirety. The main interest of this work lies in its beautiful illustrations and photographs of practically all "species" described. Silveus also recognized the extreme variation in pubescence found even upon individual plants.

Treating of the grasses in Wisconsin, Shinnars (1944) gave valuable advice for the eventual elucidation of this group. He pointed out the difficulty encountered in attempting to work with the autumnal forms of these plants. Shinnars also initiated fresh avenues of research by examining four mass collections of Dichanthelium, carefully noting all of the rosette forming species of Panicum growing together in a given area. He summarized his findings in the following manner:

It is clear from the above that recognizable species exist, separated by pronounced gaps in diagnostic characters; and that they remain uniform and distinct when growing alone, or growing together without disturbance, but that when growing together and subject to abnormal disturbance, some commingling of characters through hybridization may take place. Study of ordinary herbarium specimens confirms these conclusions, and indicates further that apparent hybrids are not extremely common.

The brief original description of reproduction pattern proposed in 1910 by Hitchcock and Chase and cited in the introduction (page 2) was questioned by Shinnars. He observed that if the vernal flowers are indeed pollen-sterile and the autumnal ones cleistogamous, the

formation of hybrids would be very unlikely. Yet he presented fairly convincing evidence that hybridization does take place although he did not feel that many of the present day species of Panicum are the products of hybridization. Shinnars concluded that an investigation of the biology of these plants was imperatively needed.

The taxonomic treatment proposed by Shinnars for the Lanuginosa of Wisconsin included three species: Panicum albemarlense, P. praecocius, and P. implicatum. Under this last species, he included: P. lanuginosum, P. lindheimeri, P. huachucae, P. subvillosum, and P. tennesseense, noting in addition numerous possible hybrids between them and other apparently distantly related species such as P. scribnerianum.

In his treatment of the grasses of Pennsylvania (1947), Pohl reiterated previous complaints of many eminent taxonomists against the apparently impractical treatment of the Lanuginosa by Hitchcock and Chase in these words:

While P. implicatum is exceedingly variable in appearance, I am quite unable to find any clearly separable groups within it. It is possible to select various forms with more or less pubescent foliage, glabrous or pubescent panicle, lax or firm leaves, but the majority of specimens cannot be distinguished by any stable combination of characters. Minute differences in spikelet length have often been used to differentiate "species" or varieties in this group.

Pohl further stated that he frequently observed well developed caryopses in primary panicles, in contradiction to the earlier assertion of Hitchcock and Chase. P. huachucae, P. tennesseense, and P. implicatum were regarded as indistinguishable by Pohl while P. lanuginosum was considered by him to be a coastal species of rather restricted ecological tolerance. P. lindheimeri and P. meridionale were recognized as species in other groups.

Fassett (1951) agreed "in principle" with Shinnors and Pohl in his treatment of the subgenus Dichanthelium of Wisconsin. However he noted that "although a vast majority of the material from Wisconsin can be satisfactorily identified, a few sheets combine the characters of two or more species. At least some of these are probably F_1 hybrids or back crosses."

A complete swing of the pendulum from "splitting" to "lumping" is achieved in Radford's keys to the rosette forming species of Panicum of the Carolinas (1964), presumably the region of greatest diversity for this group. Altogether 39 species are recognized, including only 6 in the Lanuginosa and Columbiana groups of Hitchcock and Chase.

Table 1 summarizes the view of some authors regarding the taxonomic treatment of the Lanuginosa and Columbiana groupings.

Cytology of Panicum Subgenus Dichanthelium

Church (1929) examined meiotic phenomena in five species and four varieties of dichanthelia. He recorded a very high percentage of pollen sterility as well as loose pairing or non-pairing of bivalents, lagging, chromatin extrusion, cytomyxis, polycary, and even polyspory in the spring florets of all species investigated. He also reported irregularities in the chromosome count (7, 8, 9, 10) of microspores in Panicum lindheimeri Nash and P. sphaerocarpon Ell. These cytological abnormalities were considered by him to be evidences of the hybrid origin of these species.

Nielsen (1939) reported a somatic chromosome number of 18 for a specimen of P. lindheimeri collected in Arkansas, although the camera

Table 1. Selected taxonomic dispositions of the Lanuginosa and Columbiana groups

Hitchcock and Chase 1950 (United States)	Fernald 1950 (N.E. United States)	Pohl (Pennsylvania)	Radford 1964 (Carolinas)
<i>P. thurowii</i>	O.R. ^a	O.R.	O.R.
<i>P. occidentale</i>	O.R.	O.R.	O.R.
<i>P. pacificum</i>	O.R.	O.R.	O.R.
<i>P. thermale</i>	O.R.	O.R.	O.R.
<i>P. shastense</i>	O.R.	O.R.	O.R.
<i>P. lanuginosum</i>	<i>P. lanuginosum</i>	<i>P. lanuginosum</i>	<i>P. lanuginosum</i>
<i>P. lindheimeri</i> ^b	<i>P. lanuginosum</i> var. <i>lindheimeri</i>	<i>P. lindheimeri</i> ^b	"
<i>P. huachucae</i>	<i>P. lanuginosum</i> var. <i>fasciculatum</i>	= <i>P. implicatum</i>	"
<i>P. huachucae</i> var. <i>fasciculatum</i>	"	"	"
<i>P. tennesseense</i>	"	"	"
<i>P. languidum</i>	"	O.R.	O.R.
= <i>P. tennesseense</i>	<i>P. lanuginosum</i> var. <i>septentrionale</i>	O.R.	O.R.
<i>P. implicatum</i>	<i>P. lanuginosum</i> var. <i>implicatum</i>	<i>P. implicatum</i>	O.R.
= <i>P. huachucae</i> var. <i>fasciculatum</i>	<i>P. glutinoscabrum</i>	O.R.	O.R.
<i>P. meridionale</i>	<i>P. meridionale</i>	<i>P. meridionale</i>	= <i>P. lanuginosum</i>
<i>P. albermarlense</i>	<i>P. meridionale</i> var. <i>albermarlense</i>	"	"
<i>P. auburne</i>	<i>P. auburne</i>	O.R.	"

^aO.R. - outside of geographical range considered by author.

^bNot placed by author in the Lanuginosa group.

Table 1. (Continued)

Hitchcock and Chase 1950 (United States)	Fernald 1950 (N.E. United States)	Pohl (Pennsylvania)	Radford 1964 (Carolinas)
<i>P. praecocius</i>	<i>P. praecocius</i>	O.R.	O.R.
<i>P. subvillosum</i>	<i>P. subvillosum</i>	O.R.	O.R.
<i>P. villosissimum</i>	<i>P. villosissimum</i>	<i>P. villosissimum</i>	<i>P. villosissimum</i>
<i>P. pseudopubescens</i>	<i>P. villosissimum</i> var. <i>pseudopubescens</i>	= <i>P. commonsianum</i> (in part)	"
<i>P. scoparioides</i>	<i>P. villosissimum</i> var. <i>scoparioides</i>	O.R.	"
<i>P. benneri</i>	<i>P. benneri</i>	O.R.	O.R.
<i>P. ovale</i>	O.R.	O.R.	<i>P. ovale</i>
<i>P. malacon</i>	O.R.	O.R.	<i>P. malacon</i>
<i>P. deamii</i>	= <i>P. wilcoxianum</i>	O.R.	O.R.
<i>P. commonsianum</i>	<i>P. commonsianum</i>	<i>P. commonsianum</i> var. <i>Euchlamydeum</i>	<i>P. commonsianum</i>
<i>P. addisonii</i>	<i>P. commonsianum</i> var. <i>addisonii</i>	<i>P. commonsianum</i> var. <i>addisonii</i>	"
<i>P. wilmingtontense</i>	O.R.	O.R.	"
<i>P. columbianum</i>	<i>P. columbianum</i>	<i>P. columbianum</i>	<i>P. columbianum</i>
<i>P. tsugetorum</i>	"	"	"
<i>P. columbianum</i> var. <i>thinium</i>	= <i>P. meridionale</i>	= <i>P. meridionale</i> (in part)	O.R.
<i>P. oricola</i>	<i>P. columbianum</i> var. <i>oricola</i>	O.R.	O.R.

lucida drawing substantiating this count has only 17 visible chromosomes. The nuclear diameter is said to be $7.2\ \mu$, the diameter of a chromosome $0.5\ \mu$, and the length of a chromosome $1.5 - 2.5\ \mu$.

In a cytological study of some dichanthelia from Florida, Burton (1942) obtained chromosome counts of 18 from root tips of P. arenicoloides Ashe and P. commutatum Schult.

Hoping that a cytological study of many rosette forming Panicum species might bring about a clearer understanding of this group, Brown (1948) counted the number of somatic chromosomes in 44 additional species and 3 varieties. He obtained counts of 18 chromosomes for all material examined except for the robust P. clandestinum L. and P. boscii Poir. which had 36 chromosomes. Brown noted that the apparent morphological uniformity of these species was also reflected by their chromosomal similarity, all chromosomes being uniformly short. He expressed surprise that polyploidy and aneuploidy, which play such an important role in the speciation of the subgenus Panicum as well as in other grass genera do not appear to be operative in this complex.

Gould (1958) investigated meiosis in 13 species of dichanthelia from Texas, and his findings essentially confirm those of Brown. All plants exhibited 9 gametic chromosomes except for P. boscii var. boscii which had 18. His camera lucida drawings record essentially normal diakinesis and no mention of irregularities is made in the text.

Bowden (1960) added P. xanthophysum A. Gray from Quebec Province to the two previously recorded tetraploids among the rosette forming species of Panicum. Table 2 presents a summary of chromosome numbers reported in the subgenus Dichanthelium.

Table 2. Summary of chromosome numbers reported in Panicum subgenus Dichanthelium

Species	2n	n	Reference (author, voucher, date)
<i>P. aciculare</i> Desv.	18		Brown 2489 (1948)
<i>P. albomarginatum</i> Nash	18		Brown 2658
<i>P. angustifolium</i> Ell.	18	9	Brown 2469; Gould 7517 (1958)
<i>P. annulum</i> Ashe	18		Brown 2759
<i>P. arenicoloides</i> Ashe	18		Burton (1942)
<i>P. ashei</i> Pearson	18		Brown 2467
<i>P. barbulatum</i> Michx.	18		Brown 2474
<i>P. bennettense</i> W.V.Br.	18		Brown 2494
<i>P. bicknellii</i> Nash	18		Brown 2468
<i>P. boscii</i> Poir.	18	18	Brown 2676; Gould 7501
<i>P. boscii</i> var. <i>Molle</i> (Vasey) Hitchcock and Chase	36		Brown 2656
<i>P. caerulescens</i> Hack.	18		Brown 2622
<i>P. chamaelonche</i> Trin.	18		Brown 2524
<i>P. ciliatum</i> Ell.	18		Brown 2544
<i>P. clandestinum</i> L.	36		Brown 2561
<i>P. commutatum</i> Schult.	18		Burton (1942), Brown 2530
<i>P. consanguineum</i> Kunth	18		Brown 2481
<i>P. depauperatum</i> Muhl.	18		Brown 2510
<i>P. dichotomum</i> L.	18		Brown 2559
<i>P. ensifolium</i> Baldw.	18		Brown 2660
<i>P. huachucae</i> Ashe	18		Brown 2499
<i>P. huachucae</i> var. <i>fasciculatum</i> (Torrey) F.T. Hubb.	18		Brown 2761
<i>P. joori</i> Vasey		9	Gould 7460
<i>P. lancearium</i> Trin.	18		Brown 2522
<i>P. lanuginosum</i> Ell.	18		Brown 2502
<i>P. lanuginosum</i> Ell. var. <i>lindheimeri</i> (Nash) Fern.		9	Gould 7430
<i>P. laxiflorum</i> Lam.		9	Gould 7507
<i>P. lindheimeri</i> Nash	18	9	Brown 2582; Church (1929)
<i>P. longiligulatum</i> Nash	18	9	Brown 2595; Gould 7509
<i>P. mattamuskeetense</i> Ashe	18		Brown 2532
<i>P. microcarpon</i> Muhl.	18		Brown 2507
<i>P. mundum</i> Fern.	18		Brown 2494
<i>P. mutabile</i> Scribn. and Smith ex. Nash	18		Brown 2632
<i>P. oligosanthos</i> Schult.	18		Brown 2521

Table 2. (Continued)

Species	2n	n	Reference (author, voucher, date)
<i>P. oligosanthos</i>			
var. <i>Helleri</i> (Nash)		9	Gould 7457
Fern.			
<i>P. pedicellatum</i> Vasey		9	Gould 7675
<i>P. polyanthes</i> Schult.	18	9	Brown 2688; Gould 7506
<i>P. portoricense</i> Sess.	18		Brown 2596
<i>P. pseudopubescens</i> Nash	18		Brown 2541
<i>P. ravenelii</i> Scribn.	18	9	Brown 2536; Gould 7504
and Merr.			
<i>P. scabriusculum</i> Ell.	18		Brown 2529
<i>P. scoparium</i> Lam.	18		Brown 2486
<i>P. scribnerianum</i> Nash	18	9	Church (1929)
<i>P. sphaerocarpon</i> Ell.	18	9	Brown 2663; Gould 7482
<i>P. sphaerocarpon</i>			
var. <i>inflatum</i> (Scribn.	18		Brown 2542
and Smith) Hitchcock			
and Chase			
<i>P. spretum</i> Schult	18		Brown 2680; Gould 7502
<i>P. strigosum</i> Muhl.	18		Brown 2552
<i>P. subvillosum</i> Ashe	18	9	Church (1929)
<i>P. tennesseense</i> Ashe	18		Brown 2498
<i>P. trifolium</i> Nash	18		Brown 2533
<i>P. tsugetorum</i> Nash	18	9	Church (1929)
<i>P. villosissimum</i> Nash	18		Brown 2476
<i>P. wrightianum</i> Scribn.	18		Brown 2681
<i>P. xalapense</i> H.B.K.	18		Brown 2504
<i>P. xanthophysum</i> A. Gray	36		Bowden (1960)
<i>P. yadkinense</i> Ashe	18		Brown 2505

In brief, although the findings regarding meiosis in some dichan-
 thelia by Church, Brown and Gould appear somewhat conflicting, there
 is little doubt that the majority of the species in this group are
 diploid and that their basic chromosome number is 9. The virtual
 absence of aneuploids and the rarity of polyploids strongly limits
 the use of somatic chromosome numbers as an aid in the understanding

of interrelationship within this group of grasses. Future investigation of meiotic phenomena in the subgenus will certainly be needed to obtain a clearer picture of evolutionary patterns of speciation among these plants.

METHODS AND MATERIALS

General Outline

The broad outline of a research program which might lead to a clearer understanding of interrelationships within the subgenus Dichanthelium has been suggested by some of the botanists whose work has just been reviewed. The particular objectives of this study may be summarized as follows:

1. To investigate the biology of these grasses and particularly to ascertain whether in fact the "vernal" spikelets are chasmogamous and rarely perfect seeds, and whether the "autumnal" spikelets are cleistogamous, forming viable seeds;
2. To examine population samples of some dichanthelia taken throughout their range, carefully noting all associated species of the subgenus as well as their relative abundance at a given location;
3. To grow plants under uniform garden conditions, comparing them with wild clones, and otherwise to determine the effects of environmental changes on the morphology of these grasses, especially on those criteria used by Hitchcock and Chase in their taxonomic treatment;
4. To note uniformity or diversity of mature progeny derived from caryopses in terminal as well as in axillary panicles;
5. To examine types and other selected specimens of species in the Lanuginosa and Columbiana groups and in the light of the above findings, to attempt a taxonomic evaluation of this complex.

Source of Plant Materials and Collecting Methods

Most of the specimens and cultures used in this study were collected by the writer in the summers of 1962 and 1963 in the course of extensive field trips throughout the Central and Southeastern United States. Insofar as possible, specimens of all "species" of rosette forming Panicum growing at a given location were collected. Some of the plants were pressed and dried for future examination. Others were kept alive in plastic bags temporarily stored in ice chests. These grasses were later transplanted into six or eight inch pots and grown in the greenhouse. In addition, occasional population samples of plants in the Lanuginosa-Columbiana complex were taken during the summer trips for study of intra-population variation.

Approximately 150 additional live dichanthelia collected primarily throughout Iowa were transplanted to a uniform garden plot at Ames and their morphological variations were recorded after one year. A few of the culms were bagged prior to flowering in order to prevent cross pollination and along with open pollinated panicles they served as the principal seed source for progeny study.

Studies of Biology and Progeny Structure

Widespread and easily recognizable species representing diverse groups such as Panicum xalapense, P. dichotomum, P. commutatum, P. linearifolium, P. sphaerocarpon, and P. aciculare as well as members of the Lanuginosa complex were utilized for study of floral biology and of progeny structure.

During germination trials, full and presumably mature spikelets

were placed on moist blotters in petri dishes. Stratification was conducted in a dark refrigerator maintained at 10°C. Germinating chambers were maintained at alternating temperatures of 30°C in the daytime and 20°C at night and under a twelve hour photoperiod. The mercurial fungicide "Ceresan" used in a first series of germination attempts caused death of the seedlings soon after emergence of the coleoptile from the caryopses. In most of the later trials, no fungicide was utilized.

After germination, the weak seedlings were transferred with the help of tweezers to flats or pots with a standard greenhouse soil mixture; they were regularly watered, using at first an ultra fine spray. The progeny were collected after completion of anthesis in the terminal panicles.

Throughout the period of research and particularly in the spring and summer of 1964, frequent observations of early growth, flowering, and reproduction were made on plants growing in the greenhouse and in the garden. Anthesis was followed in the field with a 10x magnifier. In the laboratory, this process was further studied with a binocular microscope and drawings were made with the aid of a camera lucida. Pollen grains were studied and measured under a compound microscope provided with an ocular micrometer. Pollen fertility was determined by using a lacto-phenol-aniline blue solution (Sass 1951).

Examination of Herbarium Specimens

Observations of pressed specimens were made with a stereo binocular microscope fitted with an ocular micrometer measuring to one tenth of a

millimeter.

The second leaf below the inflorescence was measured and maximum width of the blade noted. Pubescence characteristics of the middle part of the same blade and of its sheath were recorded. Whenever possible, full and mature spikelets were measured.

Plants collected by the writer were utilized primarily in connection with the study of the biology and population structure of the *dichanthelia*. Specimens identified or annotated by Hitchcock and Chase served as the basis for the evaluation of their taxonomic treatment of the *Lanuginosa* and *Columbiana* groups presented in the last chapter. These specimens were kindly provided by the United States National Herbarium (US), the Missouri Botanical Garden (MO), and the Iowa State University Herbarium (ISC). Abbreviations used for these herbaria are those proposed by Lanjouw and Stafleu (1959). Mention of my own specimens in the text are followed only by voucher numbers while citation of other specimens are accompanied by the collector's name in addition. A list of selected herbarium material examined in the course of this study is presented in the appendix.

BIOLOGY OF PANICUM SUBGENUS DICHANTHELIUM

Previous Studies of Germination in the Genus Panicum

Germination of seeds in the subgenus Dichanthelium has not been investigated up to now, possibly because of the lack of known economic importance of grasses in this group. However, germination of some species in the subgenus Panicum has been studied. In all cases, some difficulty was experienced, suggesting that either the embryos underwent "physiological" dormancy or that the coverings of the seed (lemma, palea, and pericarp) were impermeable. The pericarp and seed coat of most species of Panicum constitute a thin layer over the seed and the caryopsis is in turn tightly enclosed within the thick fertile lemma and palea, sometimes incorrectly identified as the "glumes" in the literature on seed germination.

Edwards (1933) obtained an increase in germination from 0 to 40 percent by rubbing spikelets of Panicum coloratum Walt. (P. virgatum L.) in a mortar with a pestle covered with sandpaper. Toole (1940) reported maximum germination of Panicum obtusum H.B.K. seeds after 28 days of chilling at 3°C. Treating the seeds of this grass with acid also resulted in increased germination. Cullinan (1941) germinated seeds of P. maximum Jacq. by subjecting them to alternating temperatures of 15°C in light and of 35°C in dark after "degluming". Akamine (1944) working with Hawaiian range grasses obtained increased germination by treating seeds of P. prolutum F. Muell. with concentrated sulfuric acid for 6 to 12 minutes, or by moist pretreatment at 4°C. Garman and Barton (1946) found that maximum germination of well developed caryopses of P. anceps

Michx. occurred after eight weeks of moist storage at 5°C. Removal of the fertile lemma and palea, treatment with concentrated sulfuric acid, or vigorous shaking contributed in the increase of germination for one crop of seeds tested by them.

Andersen (1961) suggested two methods to germinate seeds of Browntop millet (P. ramosum L.):

1. dry treatment of the seeds for 7 days at 35°C followed by incubation on moist blotters at alternating temperatures at 5 and 35°C for a period of 7 to 28 days depending on the degree of dormancy of the seeds;
2. predrying the seeds as above, removing the "glumes" and incubating the seeds at alternating temperatures of 5 and 35°C for 7 or 14 days in light.

Similar procedures consisting of mechanical, chemical, or thermal treatment of caryopses have been successfully utilized by other workers to induce germination in related species such as Setaria italica (L.) Beauv., (Wright and Kinch 1962), Echinochloa crusgallii (L.) Beauv. (Piacco 1940), and Digitaria sanguinalis (L.) Scop. (Gainfagna and Pridham 1951).

Germination and Early Growth in the Dichanthelia

Caryopses of dichanthelia are tightly enclosed within the chartaceous lemma and palea of the fertile floret. The fruit which is white and "milky" in early development becomes light brown and hard at maturity. The glumes as well as the sterile lemma and membraneous sterile palea are usually associated with the mature caryopsis. In preliminary trials, full

spikelets of *dichanthelia* exhibited dormancy as reported in the subgenus Panicum. However, occasionally a small percentage of fertile florets germinated if placed on moist blotters at room temperature without pre-treatment. Subsequently a series of germination attempts were conducted after subjecting spikelets to various periods of prechilling at 10°C on moist blotters. Most of the spikelets tested were derived from terminal panicles of plants dried on field heaters during the preceding year. The other spikelets were taken from terminal or axillary inflorescences of grasses in the garden plots, which had been dried at room temperature about 6 months. Percentages of germination were determined three weeks after the spikelets had been placed in the germinator. The results of this germination trial, presented in Table 3, demonstrate that pre-chilling at 10°C is not generally an effective method of breaking the dormancy of *dichanthelia* spikelets.

It is probable that the artificial heat source used in drying some of the spikelets was too intense and caused death of the embryos. Generally higher percentages of germination were obtained with spikelets previously dried at room temperature. In addition some of the plump spikelets tested may not have been yet fully mature and heavy fungal infection of a few samples may have further contributed to the low percentages of germination obtained.

No consistent difference was noted between germination percentages obtained with spikelets from terminal panicles and those attained with spikelets of axillary inflorescences, whether bagged during anthesis or open pollinated.

Some of the ungerminated caryopses which had undergone pre-germination

Table 3. Germination of some dichanthelia

Florets prechilled on moist blotters for period specified, then placed in germinator for 21 days with alternating temperature: 20°C, dark, 16 hours; 30°C, light, 8 hours.

Species, voucher, source	No. of days at 10°C	<u>No. seed germinated</u> No. seed planted	% Germination
P. aciculare (2388) T.P. ^a La., Natchitoches Par.	57	27/45	60
P. aciculare (2453) T.P. Ga., Upson Co.	144	0/25	0
P. aciculare (2470) T.P. Ga., Washington Co.	125	17/50	34
P. commonsianum (2350) T.P. Ark., Newton Co.	132	1/36	3
P. commonsianum (2457) T.P. Ga., Upson Co.	44	1/20	5
" " "	91	0/36	0
P. commonsianum (2458) T.P. Ga., Washington Co.	28	16/23	70
P. commutatum (2360) T.P. Ark., Pope Co.	35	11/30	37
" " "	91	2/23	9
P. commutatum (2555) T.P. Va., Prince George Co.	132	14/54	26
P. commutatum (2597) T.P. Va., Patrick Co.	125	3/56	5

^aT.P. identifies florets obtained from terminal panicles.

A.P. identifies florets obtained from axillary panicles.

A.P.B. identifies florets obtained from axillary panicles bagged during anthesis.

Table 3. (Continued)

Species, voucher, source	No. of days at 10°C	No. seed germinated No. seed planted	% Germination
<i>P. depauperatum</i> (2549) T.P. Va., Prince George Co.	100	0/48	0
<i>P. dichotomum</i> (2625) T.P. S.C., Spartanburg Co.	132	0/56	0
<i>P. lanuginosum</i> (L-67) A.P. ^{a,b} Ia., Lee Co.	96	13/38	34
" " A.P.B. ^a	96	64/95	67
<i>P. lanuginosum</i> (2080) T.P. ^b Ia., Clarke Co.	68	4/50	8
" " A.P.B.	68	2/30	7
" " A.P.	53	3/38	8
<i>P. lanuginosum</i> (2095) A.P. ^b Ia., Marion Co.	78	3/45	7
<i>P. lanuginosum</i> (2103) T.P. ^b Ia., Marion Co.	96	24/30	80
" " A.P.	96	17/60	28
" " A.P.B.	96	35/60	58
<i>P. lanuginosum</i> (2228) A.P. ^b Ia., Delaware Co.	125	21/38	55
<i>P. lanuginosum</i> (2347) T.P. Ark., Newton Co.	28	2/30	7
" " "	100	7/60	12
<i>P. lanuginosum</i> (2357) T.P. Ark., Pope Co.	100	2/72	3
" " "	53	16/30	53

^bSpecimens grown in the experimental garden. Spikelets were dried at room temperature in open paper bags.

Table 3. (Continued)

Species, voucher, source	No. of days at 10°C	<u>No. seed germinated</u> No. seed planted	% Germination
P. lanuginosum (2359) T.P. Ark., Pope Co.	65	8/50	16
P. lanuginosum (2361) T.P. Ark., Lake Ouachita	91	31/47	66
P. lanuginosum (2441) T.P. Ala., Bullock Co.	7		7
" " "	85	42/65	65
P. lanuginosum (2442) T.P. Ala., Bullock Co.	144	22/45	49
P. lanuginosum (2444) T.P. Ala., Russel Co.	14		8
" " "	144	14/54	26
P. lanuginosum (2506) T.P. S.C., Florence Co.	91	0/58	0
P. lanuginosum (2649) T.P. Ky., Barren Co.	130	0/60	0
P. lindheimeri (2274) A.P. ^b Ill., Henry Co.	78	11/39	28
P. lindeimeri (2378) T.P. Tex., Harrison Co.	22	3/17	18
P. lindheimeri (2439) T.P. Ala., Bullock Co.	85	21/45	47
P. lindheimeri (2440) T.P. Ala., Bullock Co.	28	4/43	9
P. lindheimeri (2443) T.P. Ala., Russel Co.	144	24/60	40

Table 3. (Continued)

Species, voucher, source	No. of days at 10°C	No. seed germinated No. seed planted	% Germination
P. praecocius (2136.1) A.P. ^b Ia., Webster Co.	153	10/17	59
" " " "	153	24/74	32
P. praecocius (2136.2) A.P.B. ^b Ia., Webster Co.	176	14/33	42
P. scribnerianum (2081) T.P. ^b Ia., Clarke Co.	81	1/30	3
" " A.P.	81	5/35	14
" " A.P.B.	81	0/13	0
P. scribnerianum (2362) T.P. Ark., Lake Ouachita Co.	14	6/25	24
" " "	92	8/19	42
P. sphaerocarpon (2371) T.P. Ark., Lake Ouachita Co.	65	10/50	20
" " "	44	11/38	29
P. sphaerocarpon (2445) T.P. Ala., Russel Co.	53	3/28	11
P. sphaerocarpon (2454) T.P. Ga., Upson Co.	153	2/80	3
P. sphaerocarpon (2459) T.P. Ga., Washington Co.	125	19/53	36
P. trifolium (2390) T.P. La., Natchitoches Par.	153	6/50	12
P. villosissimum (2353) T.P. Ark., Pope Co.	84	0/39	0
" " "	35	3/26	12

Table 3. (Continued)

Species, voucher, source	No. of days at 10°C	<u>No. seed germinated</u> <u>No. seed planted</u>	% Germination
P. xalapense (2344) T.P. Ark., Newton Co.	91	0	0
P. xalapense (2611) T.P. S.C., York Co.	125	15/50	30
P. xalapense (2647) T.P. Ky., Barren Co.	64	21/46	46
P. wilcoxianum (2077) T.P. ^b Ia., Story Co.	81	5/6	83
" " A.P.	81	5/16	31

treatment unsuccessfully were tested with a dilute solution of triphenyl-tetrazolium chloride. Most of them proved to be still viable according to this test. Occasionally a few dormant spikelets left in the germinator longer than three weeks germinated. Also spikelets subjected repeatedly to alternating temperatures of 10°C and 30°C exhibited slightly higher percentages of germination than spikelets chilled only once.

Despite the inefficiency of the pre-chilling method in breaking dormancy of *dichanthelia* seeds, a sufficient number of seedlings were obtained in this manner to study progeny variability reported in a later chapter.

Spikelets obtained from mature panicles of three species of *dichanthelia* were tested in another series of germination trials reported in Table 4. All samples were treated with the fungicide Captan and various types of pretreatment were employed. Again prolonged pre-chilling contributed to an increase in the germination of some species tested. Best results were obtained after removal of the tough fertile lemma and palea tightly surrounding the mature caryopsis. Because of the small size of the fertile floret, this operation was seldom accomplished without scratching or puncturing the thin pericarp.

It is possible that the delayed germination observed in most of the *dichanthelia* tested is caused by the impermeable nature of the fertile lemma and palea or of the thin pericarp.

At the start of germination, the fertile lemma cracks along predetermined lines of weakness and the wide coleorhiza emerges first from the floret. The coleoptile soon elongates dislodging the fertile lemma

Table 4. Germination of some dichanthelia

Florets Captan-treated, germinated in petri dishes on moist blotters; alternating temperature: 20°C, dark, 16 hours; 30°C, light, 8 hours.

Species, voucher, source	Duration of test ^a days	Pre-treatment	<u>No. of seed germinated</u> <u>No. of seed planted</u>	% Germination
P. aciculare (2470) Ga., Washington Co.	50	no pre-treatment	35/62	56
"	26	14 days moist pre- chill at 10°C	7/30	23
"	20	28 days moist pre- chill at 10°C	13/30	43
"	7	removal of lemma and palea	10/20	50
P. lanuginosum (2442) Ala., Bullock Co.	44	no pre-treatment	2/100	2
"	30	14 days moist pre- chill at 10°C	6/40	15
"	20	28 days moist pre- chill at 10°C	34/40	85
"	7	removal of lemma and palea	37/40	92
P. lanuginosum (2681) Ark., Izard Co.	20	no pre-treatment	6/150	4
"	3	removal of lemma and palea	50/50	100
P. lindheimeri (2443) Ala., Russel Co.	40	no pre-treatment	0/80	0
"	5	removal of lemma and palea	29/35	83

^aSubsequent to pre-treatment, if any.

in the process. The primary root protrudes through the coleorhiza one day after germination, and the first leaf emerges usually four or five days after germination (Figure 1, A--D).

One month later three to six tillers (many more in such species as P. xalapense) have appeared from the crowded basal nodes; some of them elongate and sometimes even surpass the "primary" culm in height. Approximately 40 to 60 days after germination, ordinarily in mid June at Ames, terminal inflorescences emerge from the uppermost sheath of the elongated culm (Table 5).

The generalized description of early growth briefly outlined in the preceding paragraphs applies to most of the species examined. However, some individuals exhibit slightly different patterns of development. For example the amount of tillering, and of early branching as well as the degree of elongation of the main culms varies widely within the subgenus Dichanthelium.

Growth Habit and Ecology of Some Dichanthelia

The brief description of a "typical" dichanthelia presented by Hitchcock and Chase and cited in the introduction could not apply equally well to all members of the subgenus, as examination of such dissimilar species as P. pedicellatum Vasey, P. viscidellum Scribn., P. sphaerocarpon Ell., P. xalapense H.B.K., P. dichotomum L., and P. depauperatum Muhl. reveals.

In general, it can be said that the species of Panicum belonging to the subgenus Dichanthelium differ primarily from most species included in the subgenus Panicum by their more or less marked tendency to produce

Table 5. Number of days between germination and flowering in some *Dichanthelia*^a

Species, voucher, source	Date of germination	Date of panicle emergence	Days elapsed
<i>P. aciculare</i> (2388) T.P. ^b La., Natchitoches Par.	March 27	June 28	93
<i>P. aciculare</i> (2470) T.P. Ga., Washington Co.	June 3	July 16	43
<i>P. commutatum</i> (2555) T.P. Va., Prince George Co.	June 10	July 27	47
<i>P. lanuginosum</i> (L-67) A.P. ^b Ia., Lee Co.	May 8	June 22	45
<i>P. lanuginosum</i> (2080) T.P. Ia., Clarke Co.	April 20	June 20	61
<i>P. lanuginosum</i> (2103) A.P. Ia., Marion Co.	May 8	June 22	45
" " A.P.B. ^b	May 8	June 22	45
<i>P. lanuginosum</i> (2228) A.P. Ia., Delaware Co.	June 3	July 8	35
<i>P. lanuginosum</i> (2347) T.P. Ark., Newton Co.	May 8	June 22	45
<i>P. lanuginosum</i> (2359) T.P. Ark., Pope Co.	April 10	June 1	52
<i>P. lanuginosum</i> (2361) T.P. Ark., Lake Ouachita Co.	April 30	June 15	46
<i>P. lanuginosum</i> (2441) T.P. Ala., Bullock Co.	April 24	June 22	59
<i>P. lanuginosum</i> (2442) T.P. Ala., Bullock Co.	June 22	August 1	49
<i>P. lanuginosum</i> (2444) T.P. Ala., Russel Co.	June 22	August 5	44
<i>P. lindheimeri</i> (2274) A.P. Ill., Henry Co.	April 17	June 4	48
<i>P. lindheimeri</i> (2439) T.P. Ala., Bullock Co.	April 24	June 20	57

^aThese tests were conducted in the greenhouse under natural daylength.

^bT.P. identifies florets obtained from terminal panicles. A.P. identifies florets obtained from axillary panicles. A.P.B. identifies florets obtained from axillary panicles bagged during anthesis.

Table 5. (Continued)

Species, voucher, source	Date of germination	Date of panicle emergence	Days elapsed
<i>P. lindheimeri</i> (2443) T.P. Ala., Russel Co.	June 22	July 29	37
<i>P. praecocius</i> (2136) A.P. Ia., Webster Co.	June 31	August 5	35
" " A.P.B.	April 17	June 1	45
<i>P. scribnerianum</i> (2081) A.P. Ia., Clarke Co.	April 23	July 2	70
<i>P. scribnerianum</i> (2362) T.P. Ark., Lake Ouachita Co.	May 1	June 22	52
<i>P. sphaerocarpon</i> (2371) T.P. Ark., Lake Ouachita Co.	April 10	June 22	73
<i>P. sphaerocarpon</i> (2459) T.P. Ga., Washington Co.	June 3	July 25	52
<i>P. xalapense</i> (2611) T.P. S.C., York Co.	June 3	July 17	44
<i>P. xalapense</i> (2647) T.P. Ky., Barren Co.	April 3	June 20	78
<i>P. wilcoxianum</i> (2077) T.P. Ia., Story Co.	April 23	June 1	39

axillary branches. The winter rosettes of most *dichanthelia* constitute a conspicuous demonstration of this branching trend. They represent unexpanded culms generally with a full complement of short and broad leaves, which have developed in the axil of crowded nodes near the soil surface before the end of the preceding growing season. This branching tendency is also exhibited during the period of active growth to a more or less marked degree by different species of the subgenus. Axillary branches of the first order usually possess slightly reduced

blades and panicles, but a gradual reduction in the size of leaves and inflorescences is often apparent with each successive order of branching.

However, in the southern group *Pedicellata*, the crown is thickened into a corm-like structure and no distinct winter rosette is formed. Other species such as *P. viscidellum* Scribn., which is included by Hitchcock and Chase in their "catch all" group of tall dichanthelia called *Scoparia*, do not develop a winter rosette but are primarily stoloniferous, creeping and rooting at the nodes. The same habit of growth is also characteristic of certain dichanthelia-like species of the subgenus *Panicum* such as *P. chiriquiense* Hitchc. and Chase, *P. hirtum* Lam., *P. zizanioides* H.B.K. and others. It is conceivable that these plants represent intermediate forms between the bulk of the genus *Panicum* and the subgenus *Dichanthelium*. Grasses in closely related genera such as species of *Lasiacis* also resemble the dichanthelia.

More typical rosette forming species of *Panicum* differ also widely in their growth habit. The rosette of *P. xalapense* is very large, consisting of lax, yellowish-green leaves, often ciliate along their margins; that of *P. dichotomum* is often much reduced and made up of narrow, glabrous blades, commonly purplish underneath. The branching pattern of these two species is dissimilar. At maturity, the internodes of *P. xalapense* are telescoped at the base of the culms to such an extent that it is virtually impossible to distinguish terminal from early axillary inflorescences. Blades of axillary branches are scarcely reduced in this species. By contrast the axillary branches of *P. dichotomum* arise in the axils of well separated nodes. Axillary branching is quite extensive, and a gradual reduction in blade size

is apparent with each order of branching. Consequently late in the season this grass takes on an entirely different aspect. The proliferating ability of P. dichotomum is so great that occasionally this plant produces numerous diminutive rosettes at the aerial nodes along the primary culms.

The "rosette" of P. depauperatum is made up of a dense tuft of narrow linear blades difficult to distinguish in the summer from a number of small prairie bunchgrasses. Here the axillary branches are extremely reduced and spikelets often mature within the sheath.

P. sphaerocarpon possesses a rosette of broad, stiff cordate blades, cartilaginous along their margins; the primary culms are conspicuously elongated and the uppermost internodes bearing the large terminal panicles are usually more than half as long as the rest of the culm. Correspondingly the axillary branches appear basal and are at first scarcely reduced. The amount of axillary branching is limited. The appearance of P. sphaerocarpon and of P. depauperatum late in the growing season is quite similar to that in the early stage of their growth. Limited branching is also characteristic of some of the more robust species of *dichanthelia* placed by Hitchcock and Chase in the groups *Commutata* and *Latifolia*.

The general description of Hitchcock and Chase best applies to some species of the *Spreta* and of the *Lanuginosa* complex. P. lindheimeri and its allies produce rosettes and primary culms somewhat similar to those of P. dichotomum. The internodes are well expanded, but axillary branching is not as extensive, and in late summer the long culms often bear small fascicles of branches and branchlets at each node. Members

of the Lanuginosa-Columbiana complex exhibit the most diverse habits of growth in the subgenus Dichanthelium. Some forms seem to be pubescent versions of P. lindheimeri. Others are small, bushy, and possess very reduced blades similar to those found in the Dichotoma. Still others have rather wide and lax foliage and remain low, suggesting P. xalapense. If a glabrous, narrow-leaved, tall and rather weak plant such as P. lindheimeri were to represent one morphological extreme, and a low, pubescent, wide-leaved grass similar to P. xalapense another extreme, many possible intergrades of these forms would be represented in the Lanuginosa complex.

It should be noted that the most distinct species in the subgenus Dichanthelium often occur in relatively stable habitats while many ill-defined entities occupy greatly disturbed areas of the same region. For example, P. commutatum Schult. and P. latifolium L. are ordinarily found in mesic woods along with P. dichotomum. P. xalapense occurs commonly in drier woods, and P. aciculare and P. depauperatum appear restricted to xeric sands and clay. On the other hand, the majority of "species" included by Hitchcock and Chase in their troublesome Lanuginosa and Columbiana groupings are found most abundantly along roadsides, or in otherwise disturbed peripheral areas of dry open woods, common on the Atlantic and Gulf Coastal Plain.

Anthesis, Pollination, and Cleistogamy in the Gramineae

Baker (1953) states that a complete understanding of the biology and particularly of the reproductive method in flowering plants is a necessary prelude to taxonomic works. Such an approach becomes even

more imperative when one is dealing with "difficult" groups such as the dichanthelia in which cytogenetic data provide few clues as to inter-relationship.

Detailed accounts of anthesis and pollination in the non-cereal grasses are scarce in recent literature. The work of Harlan (1945a) demonstrating the presence of both chasmogamy and cleistogamy in the Bromus carinatus complex constitutes a notable exception. These observations were later utilized by the same author along with studies in population structures (1945b) to formulate a satisfactory hypothesis on the origin of this complex and the relations among its races. More recently, similar biosystematic approaches were adopted by Borrell (1958) in his studies of Glyceria and by Barling (1959) in his work on Poa angustifolia L.

The latest comprehensive survey of grass flowering dates back to Beddows (1931). His observations of this process were compared with the earlier reports of Godron (1873), Hackel (1906), Knuth (1909), and a few others. Emphasis was placed on genera of economic importance such as Festuca, Bromus, Hordeum, Agropyron, Lolium, and Phalaris. Of the 62 species investigated by Beddows, 33 species were usually cross pollinated, 21 were cleistogamous, and 8 were apparently fertilized by pollen from other florets of the same plant. Beddows also concluded that annual species are generally highly self fertile. Earlier, Godron had recognized three principal methods of flowering in the grasses. In most species, just before anthesis, the anthers on short filaments hide the erect stigmas. Subsequently the filaments elongate so rapidly that one can actually follow the process, and the liberated stigmas either

spread inside the floret or outside, far from the tip of the floret. The anthers then topple on their thread-like filaments, hang far below the stigmas and shed their abundant pollen. After pollination the stigmas shrink and often reenter the floret before it closes. Grasses exhibiting this type of anthesis appear best suited for cross pollination or for pollination between different florets of the same plants (geitonogamy). Their stigmas are usually naked or feather-shaped. This kind of flowering occurs in Arrhenatherum elatius (L.) Presl. and numerous species of Agrostis.

The second type of anthesis described by Godron differs mostly in regard to the exit of anthers and stigmas. Flowers usually open slightly to allow egress of stigmas and anthers simultaneously or separately. In the latter case the stigmas emerge first. They remain parallel to one another for a time, then spread above the palea and lemma or slightly below their tip. The anthers either remain close to the stigmas or tilt over slightly. This kind of flowering would allow both self or cross pollination. It is found in some species of Phalaris, Phleum, and Alopecurus with plumose stigmas as well as in Sorghum and Andropogon with brush-like stigmas.

Finally Godron described cleistogamous flowering in which anthers dehisce and shed their pollen directly onto adjacent stigmas within the enclosed floret. He observed it in species of Stipa and Leersia. Most of the 135 species belonging to 91 genera examined by him were cross pollinated; many were either autogamous and geitonogamous and a few only cleistogamous.

The subject of cleistogamy in the Gramineae was treated at some

length by Hackel (1906). He described 67 grass species in which cleistogamy occurred regularly. Unfortunately the majority of his observations were based on herbarium specimens.

Hackel recognized four types of cleistogamic grasses:

1. the facultative cleistogams in which flowers are either chasmogamous or cleistogamous, and exhibit no particular adaptations for cleistogamy. In these grasses the anthers and lodicules of chasmogamous florets are essentially of the same size and shape as those found in cleistogamous florets. Hackel suggested that environmental factors are probably responsible for this kind of cleistogamy which occurs in species such as Dactyloctenium aegyptium (L.) Beauv., Pappophorum mucronulatum Nees and Scleropoa rigida (L.) Griseb. as well as in some races of barley and wheat.

2. the dimorphic cleistogams in which open and cleistogamous florets are borne on different individuals. Cleistogamous florets bear much reduced anthers and lodicules while these organs are well developed in chasmogamous florets of the same species. Sometimes the number of anthers is reduced to one and the lodicules are lacking in the cleistogamous florets. According to Hackel, this type of cleistogamy is probably genetically controlled. It is found in such grasses as Sporobolus cryptandrus (Torr.) A. Gray, Uniola latifolia Michx., Bromus unioloids H.B.K. and in numerous species of Danthonia.

3. the strict cleistogams for which no chasmogamous form has been reported. Hackel realized that many of the species which he placed in this group would later be transferred to his second group. Numerous species of Aristida, Stipa and other genera are listed as examples of

obligate cleistogams.

4. amphigamous species which produce chasmogamous florets in terminal inflorescences and cleistogamous florets in axillary panicles partly or entirely hidden in the sheath of the subtending leaf. The term double cleistogamy has been used to describe the latter phenomenon and florets enclosed in this manner are sometimes referred to as cleistogenes. Leersia oryzoides (L.) Swartz., Stipa amphicarpa Phil., Chloris chloridea (Presl.) Hitchcock, Panicum clandestinum L. and species of Leptochloa are listed as examples of amphigamous grasses. Occasionally, the axillary cleistogamous spikelets are borne on leafless subterranean branches from the lower nodes of the culm as in Amphicarpum.

As early as 1753, Linnaeus had recognized that axillary spikelets of Panicum clandestinum remain enclosed within leaf sheaths. Hackel reported that Hitchcock, to whom he turned for an explanation of this phenomenon, informed him that "the axillary spikelets of P. clandestinum as those of most species of the group *Dichotomum* (sic) to which it belongs develop fully only two months after anthesis in the terminal panicles, which in turn produce completely chasmogamous spikelets, seldom fertile." Hitchcock also sent Hackel axillary panicles of P. lanuginosum, P. scribnerianum and P. latifolium in which cleistogamous spikelets could be found. Axillary spikelets of other species of *dichantheria* were then examined by Hackel and found to be mostly chasmogamous and borne on panicles protruding from the sheaths of subtending leaves. Only in P. neuranthum Griseb., P. consanguineum Kunth and P. perlongum Nash did Hackel find more or less enclosed small panicles with apparently

cleistogamous spikelets. These remarks come in sharp disagreement with the general description of anthesis in most dichanthelia proposed by Hitchcock and Chase.

Chase (1908, 1918) added three species of Triplasis, twelve species of Danthonia, as well as Muhlenbergia microsperma (DC.) Kunth., Cottea pappophoroides Kunth. and Enneapogon desvauxii Beauv. to the list of known cleistogamous grasses. In these plants, the cleistogenes found in the axils of the lower leaves are very dissimilar to the spikelets borne on the terminal panicles of the same culms. Chase asserted that "often, if their source were unknown, they would not be placed in the same tribe" and that "the characters common to all are simplified structure and enlarged grains".

Uphoff (1938) reviewed the subject of cleistogamic flowers. He asserted that differences between chasmogamous and cleistogamous flowers may be few or many, but that "in all cases cleistogamy is the result of an arrested development of the flower bud."

There is little agreement among botanists regarding the causes of cleistogamy. Submergence, drought, humidity, low temperature, high temperature, poor nutrition, and shade have all been suggested as factors inducing cleistogamy. In his study of the Bromus carinatus complex, Harlan (1945a) found that optimum conditions for flowering usually favored chasmogamy, while adverse conditions tended to force the plant into cleistogamy. During the flowering season, several races which he studied "produced first cleistogamous panicles, then open-flowered ones and finally cleistogamous ones again". Also "in passing from the cleistogamous flowering habit to the chasmogamous habit or from chasmogamy

back to cleistogamy" the plant sometimes produced panicles containing both types of florets. The difference in size between floral organs of open and of closed florets at anthesis were considerable. For instance, anthers of chasmogamous flowers were 6.5 mm long while those of cleistogamous florets were only 0.5 mm in length.

Brown (1952) observed a similar phenomenon in Stipa leucotricha Trin. and Rupr. Chasmogamous florets had large anthers 3.0 to 4.0 mm long while cleistogamous florets had very small anthers up to 0.6 mm long. In a series of experiments conducted by him, cleistogamy was found to be inversely related to availability of soil water during floral initiation of this grass. Ragonese and Marco (1943) noted that in Bromus unioloides H.B.K., long photoperiods induced cleistogamy while chasmogamy occurred under short photoperiods.

Anthesis and Pollination in Some Dichanthelia

No attempt was made in the present study to determine the time and sequence of floral initiation in the dichanthelia. To my knowledge, in all temperate perennial grasses investigated up to the present, the shoot apex is vegetative during winter dormancy and transition to the flowering phase occurs in the spring or early summer, approximately a month before actual emergence and anthesis of the inflorescences. For example, in Phalaris arundinacea L. and in Dactylis glomerata L. (Holt 1954), floral initiation can be detected in mid-April in Ames and inflorescences appear in May. A similar sequence of floral development is exhibited by Bromus inermis Leyss (Sass and Skogman 1951), while in the late blooming big blue stem, Andropogon gerardi Vitman, first

evidence of inflorescence initiation is not observed until late June (Holt 1958). In northwestern Louisiana (Lelong 1960), panicles of most species of *dichantheria* emerge from the sheath of the uppermost leaf in mid-March. At Ames this event does not occur until early June.

Three to five days after exertion and before complete expansion of the panicle, a few spikelets in the upper peripheral regions of the inflorescence undergo anthesis. Flowering proceeds downward and centripetally over a period of three to seven days along with spreading of the panicle branches. Ordinarily at the beginning of anthesis in terminal panicles, branches have appeared at all the nodes along the main culms and inflorescences are visible at the apex of the lowest and most mature axillary branches. They will begin anthesis before termination of this process in the terminal panicles.

Immature spikelets enclose a small ovary 0.4 to 0.5 mm long terminated by two erect styles, the tips of which bear white "bottle-brush" like stigmas. The purplish anthers, varying in length from 0.2 to 0.5 mm stand on short stout filaments. As the style elongates, the stigmas enlarge considerably, turn purple, and usually arch over the anthers covering them entirely. The large "panicoid" lodicules clasping the base of the indurate fertile palea swell greatly, forcing the floret open. Only the purple stigmatic branches are visible at first. Spikelets have been observed at this stage of anthesis for over three hours in some instances. Soon afterward, the stigmas emerge directly above the spikelet and the filaments of the stamens elongate very rapidly and almost synchronously. The anthers then dehisce and are found between the stigmas or slightly above them (Figure 2, C and D;

Figure 3, B and C). Following pollination, the spikelets close. Dry tangled remnants of the stigmas and of the anther walls are often subsequently visible outside the tips of the spikelets (Figure 2, G and H).

Pollen grains vary in size from 25 to 35 μ . They are typically spherical, smooth, monoporate, and filled with starch grains. They germinate in great numbers in contact with fresh stigmatic branches (Figure 4). While I observed the growth of pollen tubes in the stigmatic papillae of many species (Figures 5 and 6), I was never able to observe them actually penetrating the body of the ovary.

The type of flowering and pollination just described can be said to be typical of the dichanthelia. Not only was it observed on most "terminal" panicles but also on the majority of axillary inflorescences of the species studied. It is illustrated in Figure 2, C--H and in Figure 3, B--F. This kind of anthesis would appear to result in self pollination in most cases.

However, occasionally large inflorescences, usually terminal on the culms, bear spikelets which undergo a slightly different type of anthesis. They possess larger anthers approximately 1.0 mm long which hold more pollen grains than the usual stamen. In these spikelets, anthers are exerted slightly before stigmas of the same florets. Furthermore, the filaments elongate considerably and the dehiscent anthers are ultimately found dangling far below the stigmas which often spread laterally outside rather than directly above the spikelet. Clouds of pollen are readily shed by slight movement of the panicle and the general behavior is typical of that of cross pollinating grasses. Often however, one or more of the anthers dehisce prior to egress and pollen grains can be

Figure 1. Germination and spikelet structure of some dichanthelia

- A--D. Panicum lindheimeri (2442 progeny); stages of germination:
- A. coleorhiza breaking through lemma of fertile floret
 - B. view of young embryo; fertile bracts removed
 - C. side view of same; radicle breaking through coleorhiza
 - D. one week old seedling; first leaf has emerged through coleoptile
- E--H. P. commutatum (2555 progeny); spikelet and florets
- E. view of entire spikelet
 - F. short-anther floret enclosed in fertile palea; lodicules bent down and one anther removed
 - G. large anther floret within its palea; front anther removed
 - H. same as G.; fertile lemma and lodicule removed
- I--O. P. aciculare (2470 progeny); spikelets and florets
- I., J. entire spikelets
 - K. fertile floret
 - L. small-anther cleistogamous floret with fertile palea and one anther removed; lodicules bent down
 - M. large-anther chasmogamous floret within its fertile palea
 - N. same as M., after beginning of anthesis; lodicules removed
 - O. same as M.; fertile bracts and two anthers removed
- P--T. P. xalapense (2611 progeny)
- P. entire spikelet
 - Q. small-anther floret within fertile lemma
 - R. same as Q.; fertile lemma removed
 - S. large-anther floret within fertile lemma
 - T. same as S.; fertile lemma and one anther removed

Scale line is 1 mm long

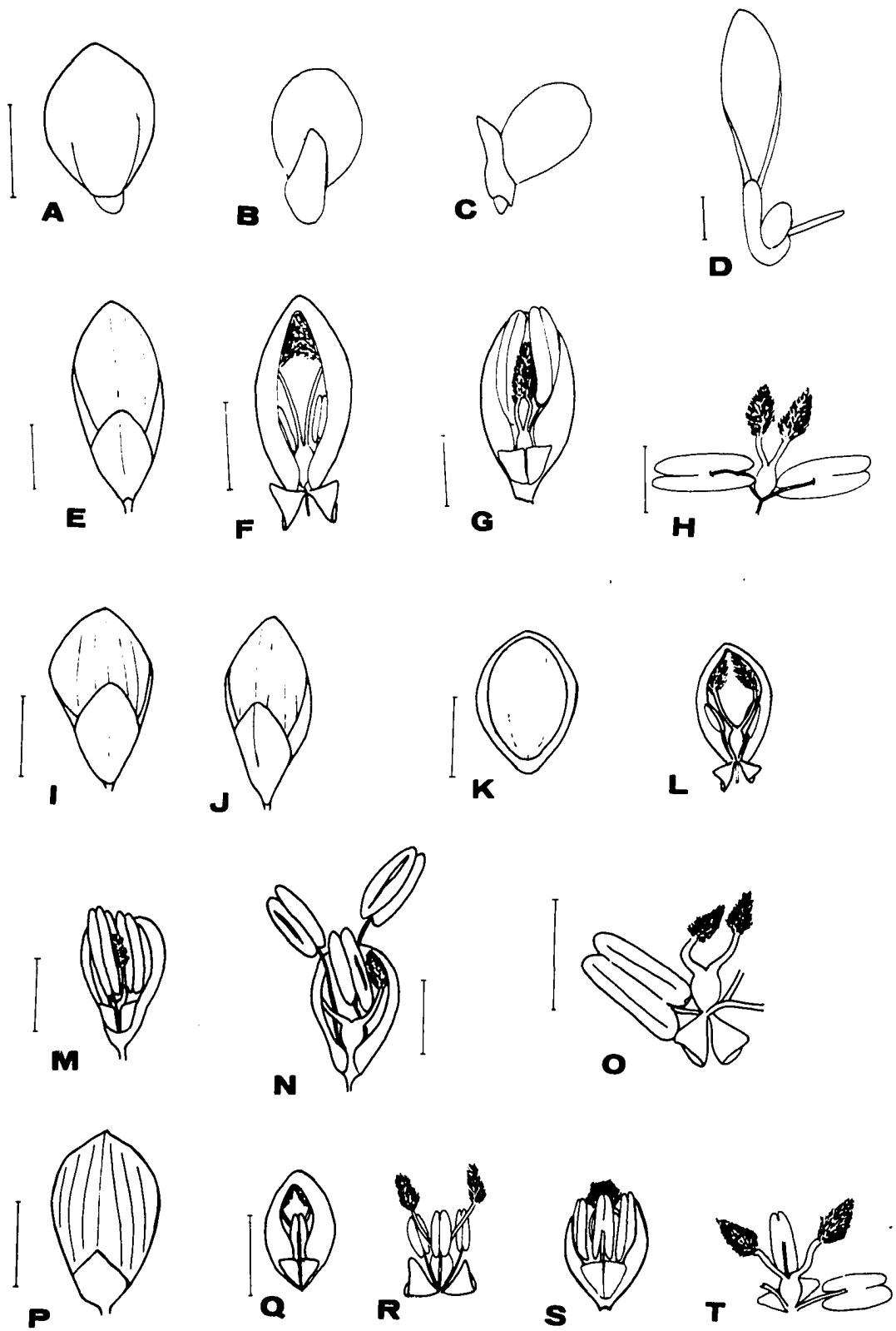


Figure 2. Types of anthesis occurring in the dichanthelia

- A--B. Panicum commutatum (2555 progeny); chasmogamous spikelets with large and well exserted anthers from terminal panicle
- C--H. Chasmogamous spikelets with small and poorly exserted anthers
 - C--E. P. lindheimeri (2274); anthesis in spikelets of terminal panicle
 - F--H. P. lanuginosum (2442 progeny); anthesis in spikelets of terminal panicle
- I--J. P. aciculare (2470 progeny); cleistogamous spikelets from terminal panicle
 - I. Entire spikelet
 - J. Fertile floret; remnants of withered stigmas and anther walls visible through semi-transparent, indurate fertile lemma

Scale line is 1 mm long

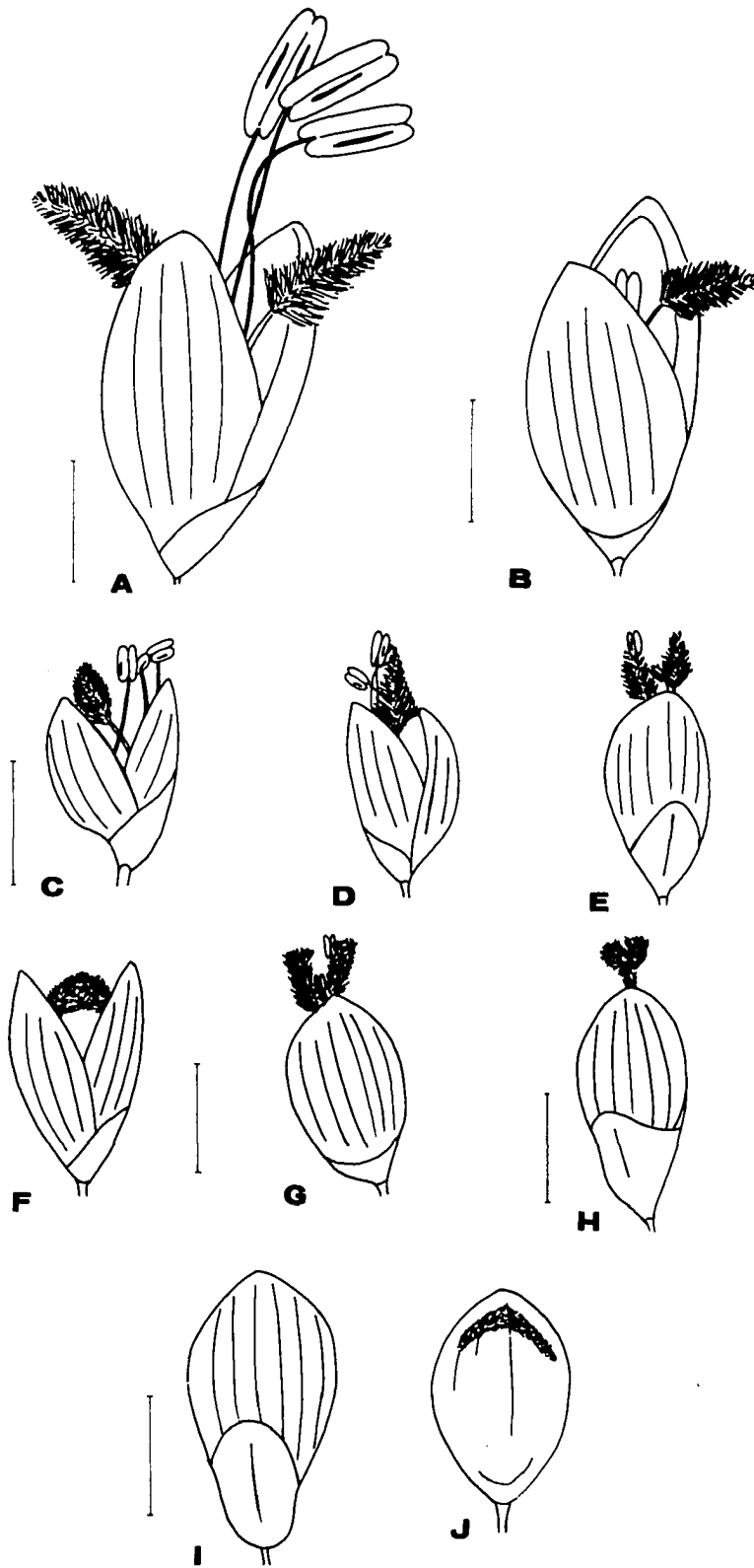


Figure 3. Anthesis in some species of Panicum subgenus Dichanthelium

- A. P. commutatum (2555 progeny); spikelets on branches of terminal panicle illustrating maximum size and exsertion of anthers observed
- B. and C. Same plant as above; two views of usual anthesis in spikelets taken from small axillary panicle
- D. P. lanuginosum var. fasciculatum (2442 progeny); branches of terminal panicle (left) and axillary panicle (right)
- E. P. lindheimeri (2441 progeny); branches of terminal panicle (left) and axillary panicle (right); note difference in size of anthers illustrated in upper right and left corners
- F. P. praecocius (2136 progeny); branches of terminal panicles (four on the left) and axillary panicles (three on the right); note whitish stigmas and yellowish anthers observed only in this species

A, D, E, F, 1.5X; B and C, 10X

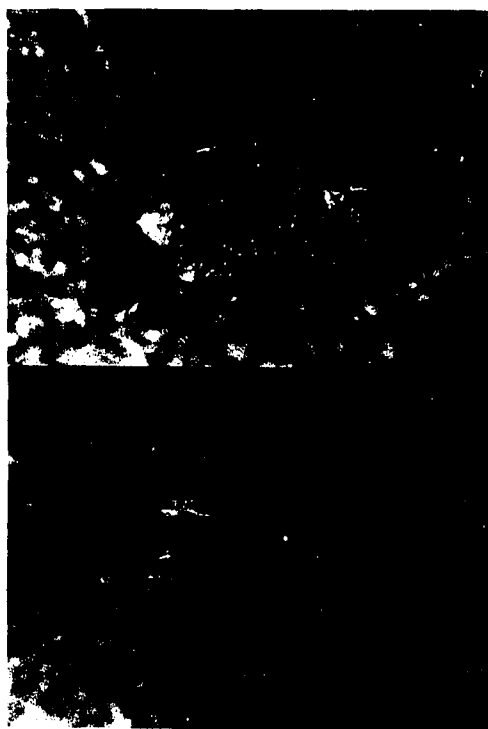


Figure 4. Pollen structure in Panicum commutatum (2555 progeny)

- A. immature anther a few days before anthesis
sectioned to show poorly filled pollen grains
- B. mature anther from adjacent spikelet sectioned
to show well stained pollen grains
- C. pollen grains from same plant illustrating some
of the variations in size encountered
- D. pollen grains with numerous starch grains visible
inside

Scale = 85 μ in A, B and C; Scale = 20 μ in D

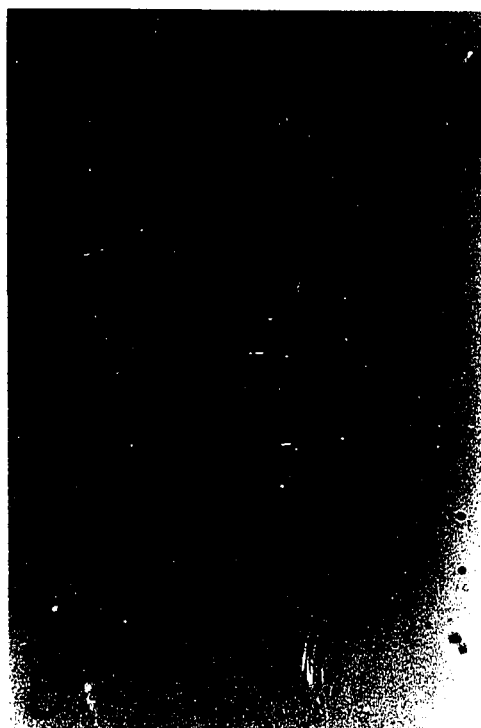
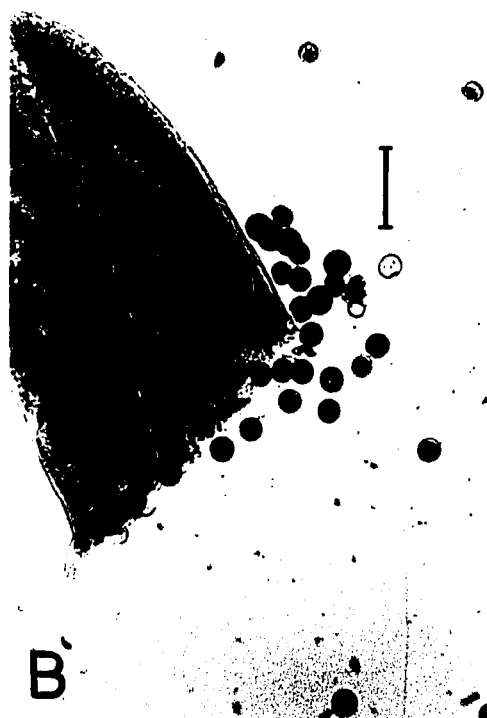


Figure 5. Stigmas and germinating pollen grains in Panicum dichotomum and P. sphaerocarpon .

- A--B. P. dichotomum (2668);
A. entire stigma
B. close up showing germinating pollen grains
- C--D. P. sphaerocarpon (2459);
C. entire stigma
D. close up showing germinating pollen grain

Scale = 85 μ in A and C; Scale = 20 μ in B and D

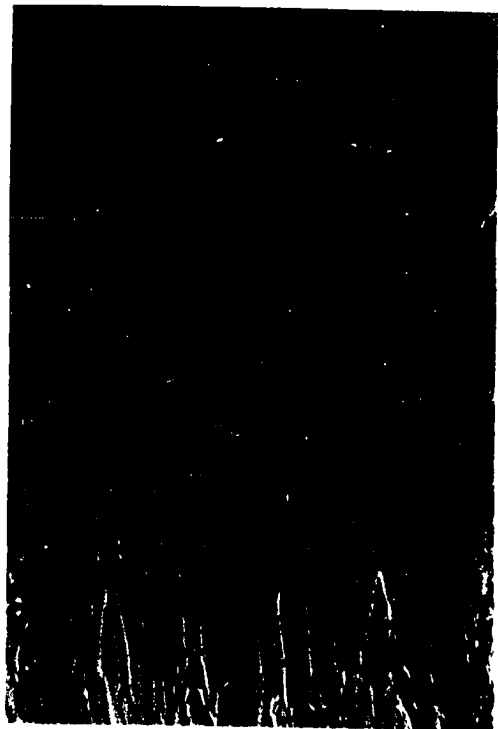
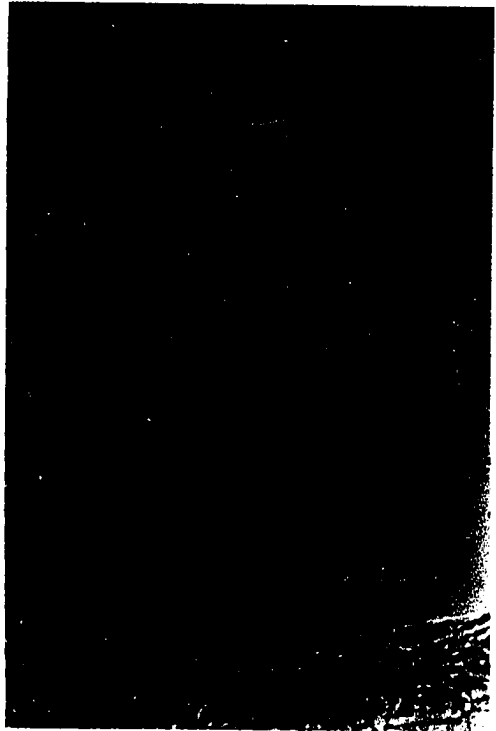
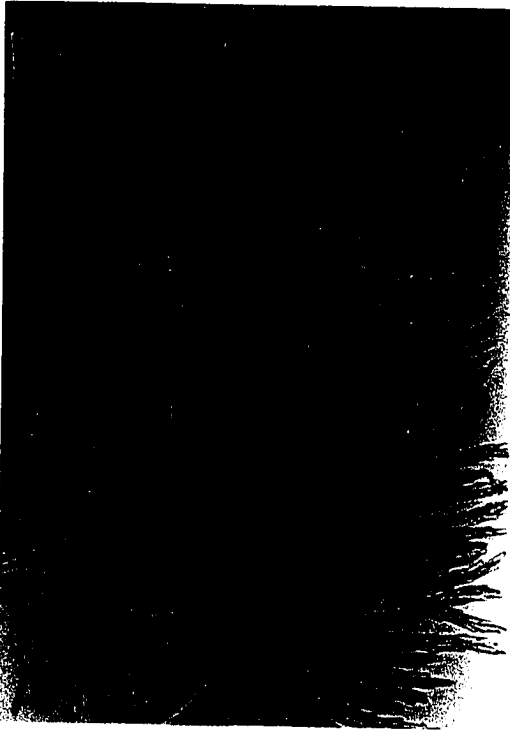


Figure 6. Pollen grains germinating on stigmatic papillae in some species of *Panicum*

- A. *Panicum xalapense* (2684); in cleistogamous floret of terminal panicle
- B. *P. praecocius* (2136); in autogamous floret of axillary panicle
- C. *P. virgatum* L. (in subgenus *Panicum*); in chasmogamous floret
- D. *P. sphaerocarpon* (2695); mass of germinating pollen grains and pollen tubes in proximity of stigmatic papillae

Scale = 20 μ



found on adjacent stigmas. Nevertheless, the chances for cross pollination in these chasmogamous florets appear greatly enhanced. In the course of this study, spikelets of this type were occasionally observed in large terminal panicles of Panicum dichotomum, P. linearifolium, P. lindheimeri, P. lanuginosum, P. aciculare, (Figure 1, M--O) and P. commutatum (Figure 1, G and H; Figure 2, A and B; Figure 3, A). They were also found infrequently in large axillary inflorescences of the first order in such stout grasses as P. commutatum. On the other hand, terminal panicles of such species of dichanthelia as P. aciculare (Figure 2, I and J) and P. scribnerianum often produce only cleistogamous spikelets.

In most dichanthelia examined, a tendency toward reduction of anther size and shortening of the filament becomes apparent in the smaller panicles terminating branches of the second, third, and subsequent orders. This trend appears to culminate in the retention of dehiscent anthers and stigmas within closed axillary florets. While generally only a few axillary spikelets are totally cleistogamous in the dichanthelia examined, practically all of the axillary florets produced by such species as P. aciculare or P. scribnerianum are cleistogamous. In addition, occasional cleistogamous spikelets are not uncommonly found at the base of some branches of the terminal panicles in most dichanthelia studied.

Maturation of cleistogamous spikelets within the sheath of the leaf subtending the panicle was detected only in grasses of the Depauperata group and in P. wilcoxianum and P. clandestinum.

Table 6 presents a summary of observations on anthesis, pollen

Table 6. Anthesis and seed set in terminal and axillary panicles of some *Dichanthelia*

Species, voucher, location	Inclusion or exertion of stigmas and anthers; anther size (mm)		% Good pollen		Caryopses Spikelets		Pollen size (μ)
	Term. panicle	Axil. panicle	Term.	Axil.	Term.	Axil.	
<i>P. aciculare</i> (2388) La.	I ^a ; 0.3-0.4	I; 0.3			29/31	40/43	
<i>P. aciculare</i> (2470) Ga.	I; 0.4-0.6 E+ ^a ; 0.9-1.1	I; 0.35	85 87	26	37/40 20/76	69/70	28-35
<i>P. arenicoloides</i> (2299) La.	I; 0.5 I; 0.3-0.5	I; 0.3-0.5	61		16/21 10/14	15/15	28-38
<i>P. commutatum</i> (2654) Ark.	E ^a ; 0.8	E; 0.5-0.8			6/16	5/14	
<i>P. commutatum</i> (2360) Ark.	E; 0.6-0.8				4/16		
<i>P. commutatum</i> (2555) Va.	E+; 0.6-1.5	E; 0.5-1.3	83	64		46/72	28-42
<i>P. dichotomum</i> (2668) Ark.	E+; 0.5-0.8	E; 0.3-0.4	90	88			23-38
<i>P. dichotomum</i> (2295) La.	I; 0.5-0.7	I; 0.3			0/18	1/5	
<i>P. dichotomum</i> (2665) Ark.		E; 0.5		66		10/35	28-35
<i>P. dichotomum</i> (2691) La.	E; 0.5-1.0		52		7/35		30-32

^aI = included (cleistogamous floret).

E = slightly exerted (presumably autogamous florets).

E+ = well exerted (autogamous or cross pollinated floret).

Table 6. (Continued)

Species, voucher, location	Inclusion or exsertion of stigmas and anthers; anther size (mm)				% Good pollen		Caryopses Spikelets		Pollen size (μ)
	Term.	panicle	Axil.	panicle	Term.	Axil.	Term.	Axil.	
P. lanuginosum (2347) Ark.	E;	0.4	E;	0.2-0.3			29/32		
P. lanuginosum (2678) Ark.	E;	0.5	E;	0.3-0.4			2/41	3/12	
P. lanuginosum (L 67)	E;	0.5	E;	0.5				30/31	
P. lanuginosum ^b . (2129) Ia.			E;	0.3-0.4				20/27	
P. lanuginosum (2444) Ala.	E;	0.5	E;	0.4		84	71/91 79/86	33/35	25-32
P. lanuginosum (2294) La.	E;	0.6-0.9	E or I;	0.3-0.4			21/30	6/8	
P. lanuginosum (L 70) Ia.	E;	0.4-0.7				80	79/100		
P. lanuginosum (2201) Ia.	E or I;	0.3-0.6	E or I;	0.3-0.4			0/36	30/143	
P. lanuginosum (L 62) Ia.	E;	0.3-0.5	E or I;	0.3-0.4			1/50	48/50	
P. lanuginosum (L 53)	E;	0.4-0.6	E;	0.3-0.5	32	40	2/50	31/51	
P. lanuginosum ^b (2230) Ia.			E or I;	0.3				43/55	
P. lanuginosum ^b (2100) Ia.	E+;	.7	E or I;	0.3			50/60	53/60	
P. lanuginosum ^b (2129) Ia.			E or I;	0.3-0.4					

^bIndicates individuals grown in experimental garden plot; other plants grown in greenhouse.

Table 6. (Continued)

Species, voucher, location	Inclusion or exsertion of stigmas and anthers; anther size (mm)		% Good pollen		Caryopses Spikelets		Pollen size (μ)
	Term. panicle	Axil. panicle	Term.	Axil.	Term.	Axil.	
<i>P. lanuginosum</i> ^b (2228) Ia.		E; 0.4-0.5		85		31/33	25-32
<i>P. lindheimeri</i> (2439) Ala.	E+; 8	E; 0.2-0.3		92	56/98	32/62	28-32
<i>P. lindheimeri</i> (2443) Ala.	E; 0.3	E or I; 0.3		69	12/20	73/110	26-32
<i>P. lindheimeri</i> (2292)	E or I; 0.6-0.7	I; 0.4-0.6	75		0/43	97/181	
<i>P. lindheimeri</i> ^b (2274)		E or I; 0.3				91/102	
<i>P. lindheimeri</i> (2274)	E; 0.4	E; 0.3			29/29	49/50	
<i>P. linearifolium</i> (2667) Ark.	E+; 1.3	I; 0.4-0.7		19	38/50	33/33	28
<i>P. linearifolium</i> (2658) Ark.		I; 0.4		84		8/8	28-30
<i>P. malacophyllum</i> (2656) Ark.	E; 0.4-0.7	E; 0.3-0.4			0/9	7/8	
<i>P. perlongum</i> (2059) Ia.	E+ or E; 0.6-1.5	I; 0.5			10/13	6/18	
<i>P. praecocius</i> (2136)	E or I; 0.5	E or I; 0.4			37/55	11/18	21-30

Table 6. (Continued)

Species, voucher, location	Inclusion or exsertion of stigmas and anthers; anther size (mm)		% Good pollen		Caryopses Spikelets		Pollen size (μ)
	Term. panicle	Axil. panicle	Term.	Axil.	Term.	Axil.	
<i>P. praecocius</i> (L 37)		E; 0.4-0.5		82		26/32	35-42
<i>P. scribnerianum</i> (2362) Ark.	I; 0.5	I; 0.5			4/8		
<i>P. scribnerianum</i> (2081) Ia.	E or I; 0.5				3/11		
<i>P. scribnerianum</i> ^b (2078) Ia.		I; 0.4				17/19	
<i>P. scribnerianum</i> ^b (L 51) Ia.		I; 0.4				8/8	
<i>P. scribnerianum</i> ^b (2094)	E or I; 0.4-0.6	I; 0.5		30	50/50	42/43	28-30
<i>P. scribnerianum</i> (L 59)	I or E; 0.5	I; 0.5		59	40/40	36/36	28-35
<i>P. sphaerocarpon</i> (2695) La.	E; 0.5	E; 0.5	2		0/46	0/41	20-25
<i>P. sphaerocarpon</i> (2696) La.	E; 0.4-0.7		78		36/41		24-30
<i>P. sphaerocarpon</i> (2459) Va.	E; 0.5 E+; 0.9-1.1	E; 0.5	55	57	57/113 17/60	65/100	28-35
<i>P. sphaerocarpon</i> (2651) Mo.	E; 0.6				20/27		
<i>P. wilcoxianum</i> (2077) Ia.	I; 0.5-0.6	I; 0.4-0.5		63	9/9	15/15	28-35

Table 6. (Continued)

Species, voucher, location	Inclusion or exsertion of stigmas and anthers; anther size (mm)		% Good pollen		Caryopses Spikelets		Pollen size (μ)
	Term. panicle	Axil. panicle	Term.	Axil.	Term.	Axil.	
P. xalapense (2660) Ark.	E; 0.4-0.5 E+; 0.8-1		50		27/30 38/45		
P. xalapense (2684) Ark.	E; 0.4-0.6 E+; 0.8-1		47		45/56 25/44		30-35
P. xalapense (2682) Ark.		E; 0.3		91		19/21	25-33
P. leibergii X P. praecocius (2107) Ia.		I; 0.5-1.0				0/19	
P. virgatum (in subgenus Panicum) Ia.	E+; 2.5-3	E+; 2.5-3					38-42

fertility, and seed set in some of the grasses examined, while Figures 1 through 6 illustrate stages of flowering and pollination in a few species of *dichanthelia*. In general there appears to be a positive correlation between pollen fertility and seed set in autogamous florets. A few exceptions can be noted in some "terminal" spikelets with well exerted stamens as well as in many cleistogamous florets.

One should be careful in determining the percentage of good pollen in these plants. A few days prior to anthesis, pollen grains in undehisced anthers are often immature and poorly filled, and could be regarded as bad (Figure 4, A and B). Similarly after exertion and dehiscence of anthers in close proximity to stigmatic branches, numerous pollen grains germinate; after extrusion of their cytoplasmic content, these grains collapse and appear unviable (Figure 6, D).

The most paradoxical situation is found in cleistogamous spikelets abundantly produced by such rosette-forming panicums as *P. aciculare* and *P. depauperatum* and their allies. Slides made of squashed and withered stigmas and anthers found on top of mature caryopses of these grasses reveal only few collapsed pollen grains even within remnants of anther walls. One could assume that these fruits develop parthenogenetically. However, small freshly dehisced anthers in less mature spikelets of the same panicles contain generally a high percentage of well filled pollen grains.

In order to ascertain whether the majority of caryopses resulted from self pollination, a number of inflorescences were bagged before the beginning of anthesis. In all cases, the seed set in enclosed inflorescences equalled or surpassed that obtained in free panicles of the

same plants.

The inclusion of individual spikelets within small foil receptacles prior to anthesis was attempted without much success. In all cases, after completion of anthesis in nearby florets, anthers and stigmas of the bagged spikelets were found still enclosed with the floret, and the ovary was either arrested in its development or clearly aborted. Slides made of the enclosed anthers revealed almost totally immature or "bad" grains while anthers of adjacent spikelets undergoing "normal" anthesis contained a high percentage of mature and well formed pollen. It appears, therefore, that foil interfered with normal maturation and liberation of pollen grains. The same process was repeated using transparent cellophane in the place of foil; two of the fifteen spikelets enclosed in this manner yielded mature caryopses cleistogamously while nearby spikelets produced fruits in the usual autogamous manner.

In Bromus carinatus Hook. and Arn. (Harlan 1945a) and in Stipa leucotricha Trin. and Rupr. (Brown 1952), it was found that optimum moisture conditions usually favored chasmogamy while cleistogamy occurred primarily under dry conditions. I tried to determine whether the same factor influences the production of cleistogamous and chasmogamous spikelets in the dichanthelia. As previously mentioned, the majority of species investigated usually produce chasmogamous spikelets with short and poorly exerted anthers about 0.5 mm long. However, occasionally these plants produce a few cleistogamous spikelets, generally on reduced axillary inflorescences. Unlike some of the cleistogenes described by Chase, these cleistogamous spikelets are hardly distinguishable from the usual autogamous spikelets abundantly produced by

the same grasses, although their floral parts tend to be slightly smaller. This type of cleistogamy, exhibited by such species as Panicum lanuginosum (sensu lato), P. xalapense, and P. sphaerocarpon seems to represent the ultimate stage in the gradual reduction in size of inflorescences and of floral parts accompanying the more or less profuse axillary branching of these plants. The number of cleistogamous florets produced by these grasses appear to be only slightly increased by reducing the amount of soil moisture available to them from the start of their growth.

In P. aciculare, P. depauperatum, and their allies, as well as in P. wilcoxianum and P. scribnerianum, the majority of the spikelets are cleistogamous. However, occasionally large terminal inflorescences emerging at the start of the growing season produce only chasmogamous florets with relatively long (1.0 mm) and well exerted anthers. Open spikelets with small, scarcely exerted anthers described at the start of this chapter as typical of the dichanthelia studied, were rarely observed in these plants. The nature of the factors promoting preponderant cleistogamy in these grasses has not been determined conclusively. Ample watering of P. aciculare from the beginning of its growth until anthesis did not prevent this plant from producing only cleistogamous spikelets. One example might serve to illustrate the elusive nature of anthesis in these plants. Progeny plants of P. aciculare (2470) started from seed in early June developed relatively small "terminal" panicles in mid-July and a great number of axillary inflorescences throughout the fall and winter. All of the spikelets produced during this period were cleistogamous although the plants were regularly watered and other dichanthelia on the same greenhouse bench exhibited "typical" autogamous

flowering. At the beginning of February a few basal culms elongated and produced very large panicles. All of the spikelets borne on these inflorescences underwent anthesis with exerted anthers about 1.0 mm long. Up to that time, I had considered this species to be obligately cleistogamous. Temperatures in the greenhouses occasionally rose to 95°F in the summer, while in the fall and winter it remained about 75°F. The most obvious difference between the external conditions during these two blooming periods was in the day length. It is possible that long photoperiod induces development of cleistogamous florets while chasmogamy occurs under short photoperiod in certain dichanthelia. Ragonese and Marco (1943) reported a similar phenomenon in Bromus unioloides H.B.K.

In all cases inflorescences of Panicum aciculare bearing chasmogamous spikelets were larger than those with cleistogamous spikelets; furthermore the culms on which large terminal inflorescences occurred were more robust and less branched than culms bearing small inflorescences. It is possible that in this species long photoperiod stimulates axillary branching which in turn limits the growth and the eventual size of the terminal panicle and of the floral parts of its component spikelets, while short photoperiods have the opposite effect.

Previous authors have attempted to separate "ecological cleistogamy" from "genetic cleistogamy". It is impossible to place the dichanthelia in either of these categories. Instead it appears that all of the dichanthelia examined are facultatively cleistogamous and that regardless of the environmental factors which limit or promote cleistogamy in these plants, some species such as P. aciculare, P. depauperatum and P. scribnerianum exhibit a much greater tendency for this condition than the other species of dichanthelia examined.

MORPHOLOGICAL VARIATIONS IN PANICUM SUBGENUS DICHANTHELIIUM

Influence of Certain Environmental

Factors Upon the Morphology of Some Dichanthelia

At the onset of this study, an attempt was made to determine the influence of the environment on the morphology of the dichanthelia. About 125 rosettes representing 10 species primarily in the Lanuginosa and Columbiana groups were collected throughout the eastern part of their range and transplanted to a uniform garden plot near Ames. Unfortunately, plants derived from the southern portion of the range did not survive the rigorous Iowa winters even after mulching. No marked differences were recorded in the pubescence pattern or the spikelet length of the surviving plants after a year in the garden. However, the general appearance of the transplants were often noticeably modified; this was especially true of grasses originally growing under conditions most unlike those in the experimental field. For example, Panicum praecocius is frequently weak and depauperate on the dense prairie sod where it often occurs. When grown under less crowded conditions, the same plant possesses more vigorous and erect culms as well as wider blades (Figure 8, B). Similarly individuals of the weedy P. lanuginosum var. fasciculatum develop stouter culms, larger blades, and denser panicles under the more fertile and open condition of the transplant garden (Figure 7, C, D, F). Lax and broad-leaved plants initially collected in shaded woods grew more erect in the uniform plot (Figure 8, F). Other illustrations of gross morphological variations between wild plants and uniform garden specimens of some dichanthelia

Figure 7. Wild and uniform garden specimens of Panicum lanuginosum
var. fasciculatum

Portions of wild plants are represented on the left of each photograph. Culms of plants from the same population or from same clone (C and D) after a year in the transplant garden are pictured on the right. Original collecting sites and voucher numbers follow:

- A. Worth County, Iowa (2175); wet prairie relic along roadside
- B. Webster County, Iowa (2129); Dolliver Memorial State Park, along shaded trail
- C. Marion County, Iowa (2103); along creek traversing pasture
- D. Marion County, Iowa (2093); eroded clay hillside along road
- E. Boone County, Iowa (2111); Holz State Forest, sandy denuded roadside
- F. Monroe County, Iowa (2095); dry weedy roadside

Scale unit = 1 dm

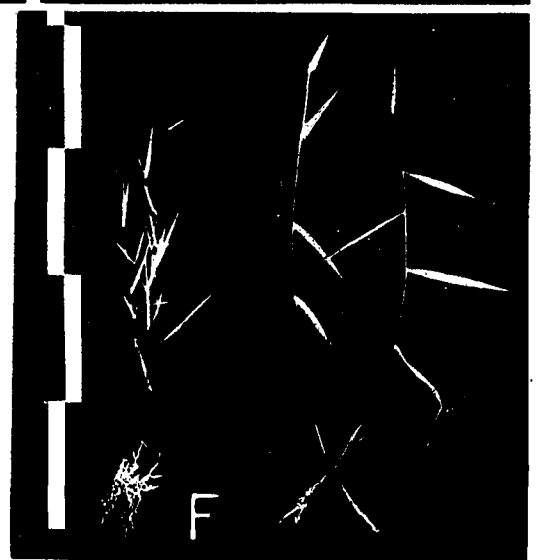
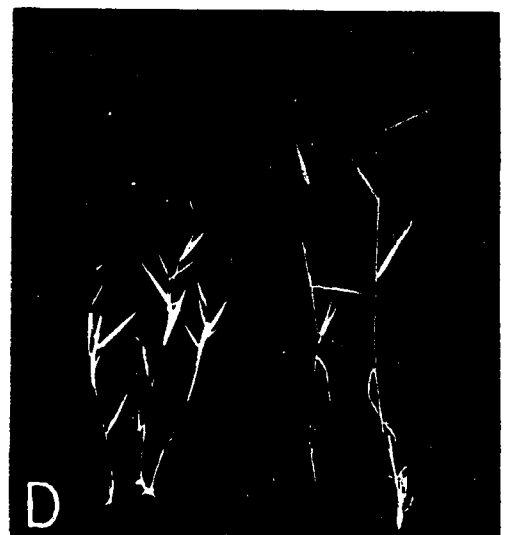
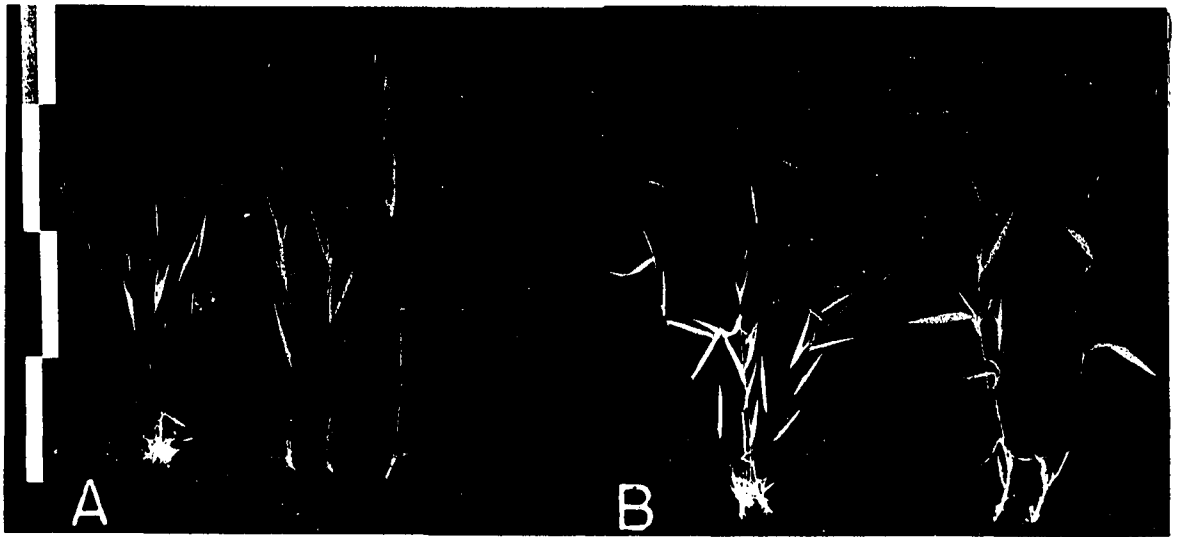
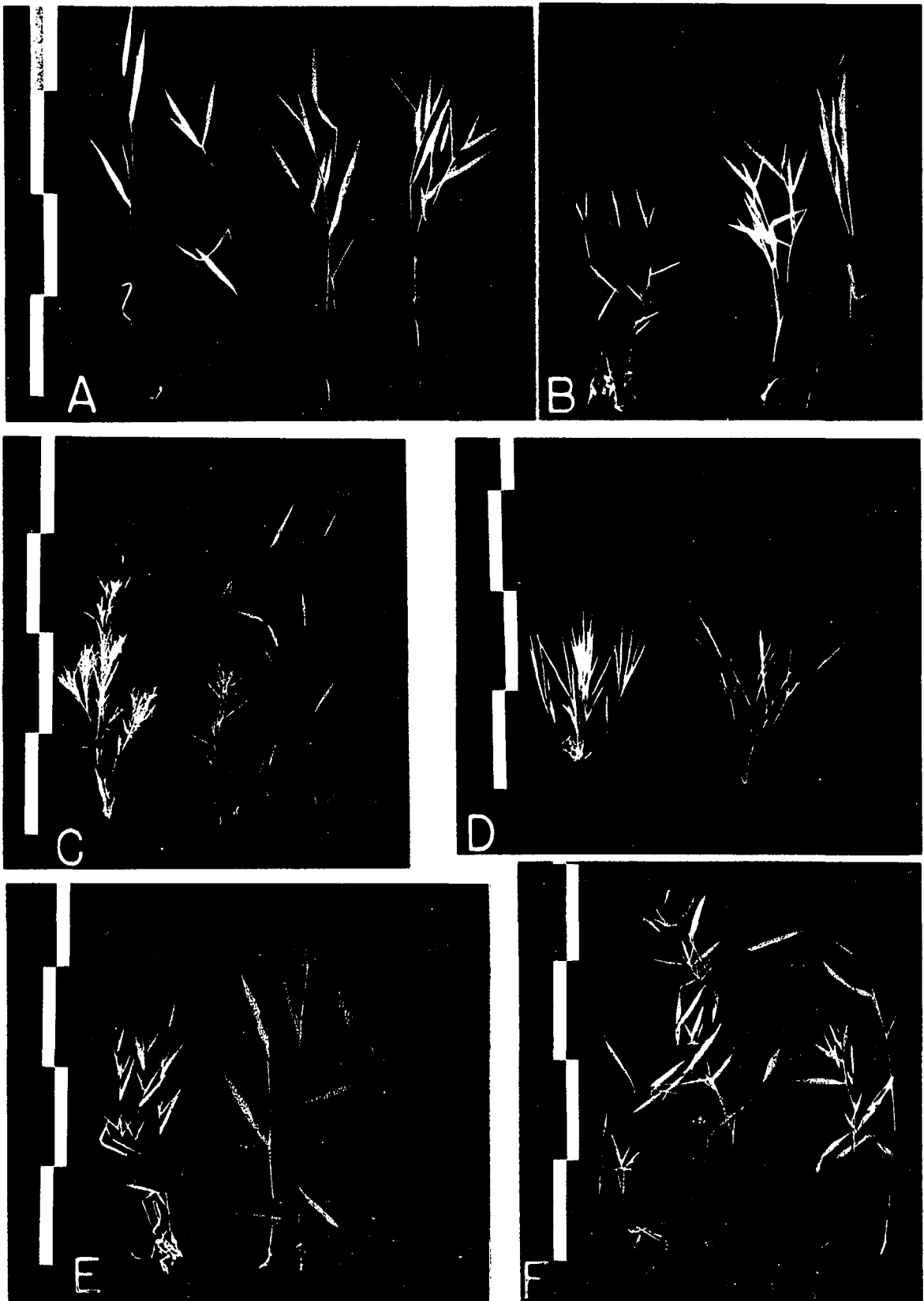


Figure 8. Wild and uniform garden specimens of various dichanthelia

Part of wild plant is on the left of each photograph. Culms of plants from same clone or from same population (C and D) after a year in the transplant garden are on the right.

- A. Panicum leibergii x P. praecocius (putative hybrid 2107); Pocahontas Co., Iowa; Kalsow Prairie Reserve
- B. P. praecocius (2136); Webster Co., Iowa; Woodman's Hollow State Park
- C. P. lindheimeri (2274); Henry Co., Illinois; abandoned coal mine yard
- D. P. wilcoxianum (2077); Story Co., Iowa; disturbed prairie relic
- E. P. lanuginosum var. fasciculatum (2158); Warren Co., Iowa; dry weedy roadside
- F. P. lanuginosum var. fasciculatum (2230); Iowa Co., Iowa; shady lane, upland woods

Scale unit = 1 dm



are shown in Figures 7 and 8.

Various controlled soil-water conditions in the greenhouse induced considerable variation in growth habit and branching pattern of plants derived from the same clone. Regularly watered plants branched extensively and developed a yellowish coloration while grasses of the same clone watered weekly appeared dark green and remained small and little branched. Probably due to the lack of expansion of the culms, the depauperate plants appeared somewhat more densely pubescent than the grasses growing under more adequate moisture conditions, but the same type of pubescence occurred in both and the spikelet length was similar.

Similar observations were made in the course of progeny testing, specifically treated in the following section. Offspring were provided with ample soil water and developed larger blades and more extensive axillary branches than wild plants of the same species (Figures 20 and 21).

Long photoperiods appear to further stimulate axillary branching in the dichanthelia. Plants started from seeds in summer by-passed the initial "unbranched" stage with large terminal panicles ordinarily exhibited by these plants. Instead they began to branch profusely from all aerial nodes even before expansion of the small terminal inflorescence (Figure 21 B, center: summer form; right: typical "spring" form).

In summary, the species of dichanthelia tested exhibited a wide but not unexpected "plasticity" in response to varying external conditions. The principal taxonomic criteria of spikelet length and of pubescence features seemed to be little affected by environmental

changes while modifications in blade size and in branching pattern were noticeable.

Morphological Variations Observed
in Progeny of Dichanthelia

Seedlings from 25 individuals belonging to 10 species of dichanthelia were grown under uniform greenhouse conditions with ample and frequent watering.

Figures 9 through 18 present a summary of observations recorded on samples of some of the progeny studied, and Figures 19 through 21 illustrate gross morphological features of parental plants and of a few offspring. Each progeny was remarkably uniform although frequently they differed from the parental plants in growth habit and in certain morphological features. The offspring were usually laxer and more profusely branched; their blades were often sensibly larger. Part if not all of these variations can probably be attributed to differences in the conditions under which they grew. Except for Panicum commutatum, which ordinarily grows in shaded mesic woods, the species tested are usually found on dry clay, on sandy roadsides, or in dry open woods.

Second generation progeny of Panicum aciculare (2470) and P. lanuginosum (2442) were also grown and found to be uniform.

The study of floral biology reported in a previous chapter revealed that the dichanthelia studied were primarily autogamous or cleistogamous. This examination also revealed that occasionally large panicles bore spikelets with relatively long and well exerted anthers which probably allow occasional cross pollination. In the light of these findings,

it can be reasonably assumed that the uniformity noted in the majority of the progeny examined resulted from preponderant self-pollination and consequent homozygosity.

However, the type of population structure derived through repeated self-pollination would resemble closely that found in groups reproducing primarily by apomixis, and it is possible that the latter method of reproduction is operative in the subgenus Dichanthelium. Apomixis has been reported in several species of Panicum subgenus Panicum, such as P. maximum Jacq. (Warmke 1952, Brown and Emery 1958), P. deustum Thunb., P. obtusum H.B.K., and P. virgatum L. (Brown and Emery 1957). Strong circumstantial evidence has been obtained that it occurs in P. coloratum L. and related species (Hutchinson and Bashaw 1964).

Morphological Variations Observed

in Population Samples of Dichanthelia

Population samples of 25 or more culms of individual species in the Lanuginosa and Columbiana groups were taken throughout the Midwest and in the southeastern part of the United States. The collection of such samples was somewhat complicated by the fact that several species of dichanthelia often grow together, at times forming elements of a single "population". Some a priori decisions were therefore necessary. For example, in sampling a population of Panicum lanuginosum or "lanuginosum-like" plants, a random assay of variability throughout the population was attempted, except that plants of such well marked species as P. commutatum, P. sphaerocarpon, P. dichotomum, P. xalapense, P. depauperatum were not included. On the other hand, the putative species delimitations employed

Figure 9. Analysis of morphological variations in progeny of Panicum lanuginosum var. fasciculatum

Seeds were obtained from terminal panicle of plant collected in Marion County, Iowa (2103) and transplanted into uniform garden; individual no. 1 represents parental plant; others represent progeny.

Portions of parental plant and of progeny are illustrated in Figure 19 A.

SPIKELET LENGTH ■ = .2 MM
 PUBESCENCE LENGTH ■ = .3 MM

BLADE WIDTH ■ = 2 MM
 PANICLE LENGTH ■ = 1 CM

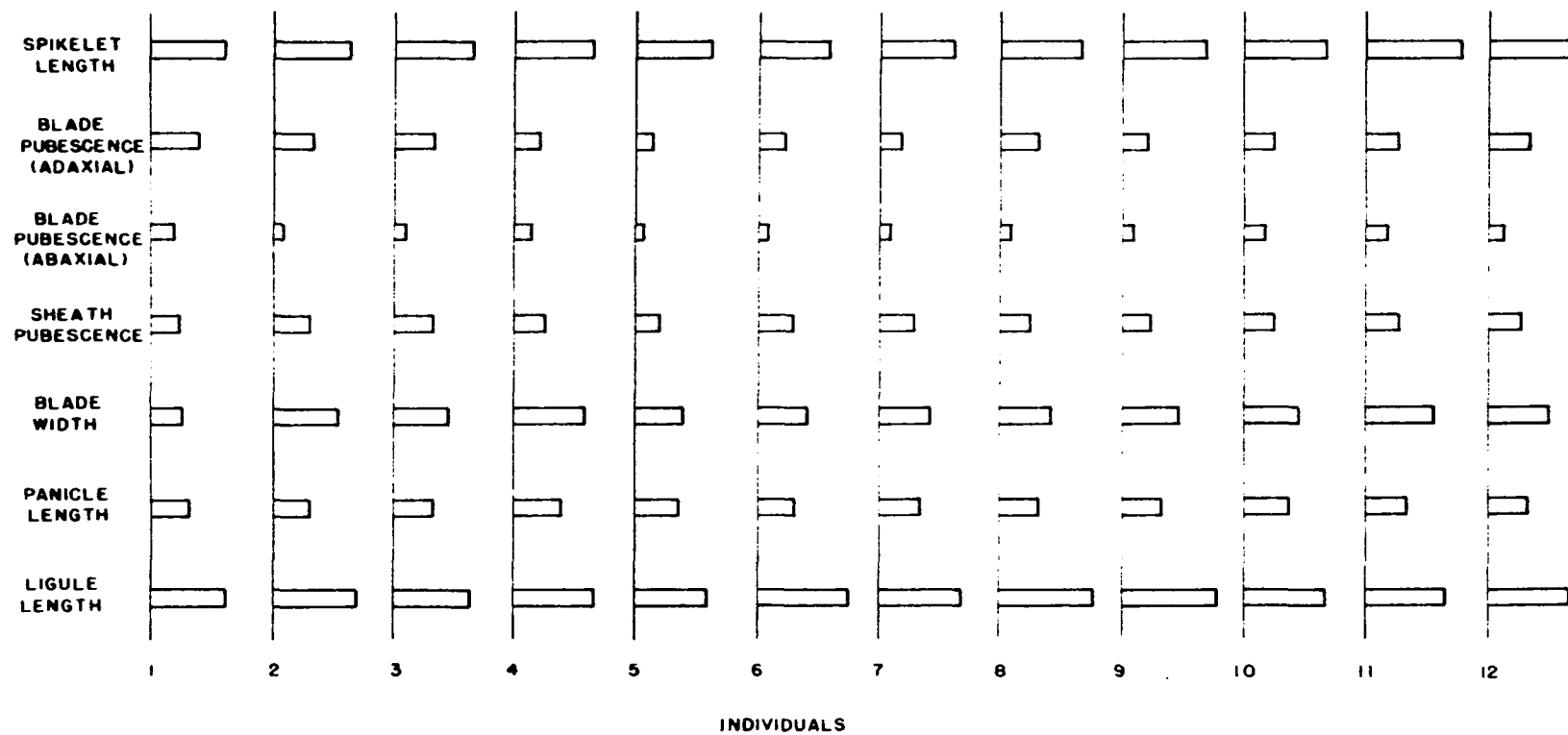


Figure 10. Analysis of morphological variations in progeny of Panicum lanuginosum var. fasciculatum

Seeds obtained from axillary panicle (bagged before anthesis) of plant collected in Marion Co., Iowa (2103) and transplanted into uniform garden; individual no. 1 represents parental plant, others represent progeny.
Portion of parental plant and of progeny are shown in Figure 19 B.

SPIKELET LENGTH ■ • .2 MM
PUBESCENCE LENGTH ■ • .3 MM

BLADE WIDTH ■ • 2 MM
PANICLE LENGTH ■ • 1 CM

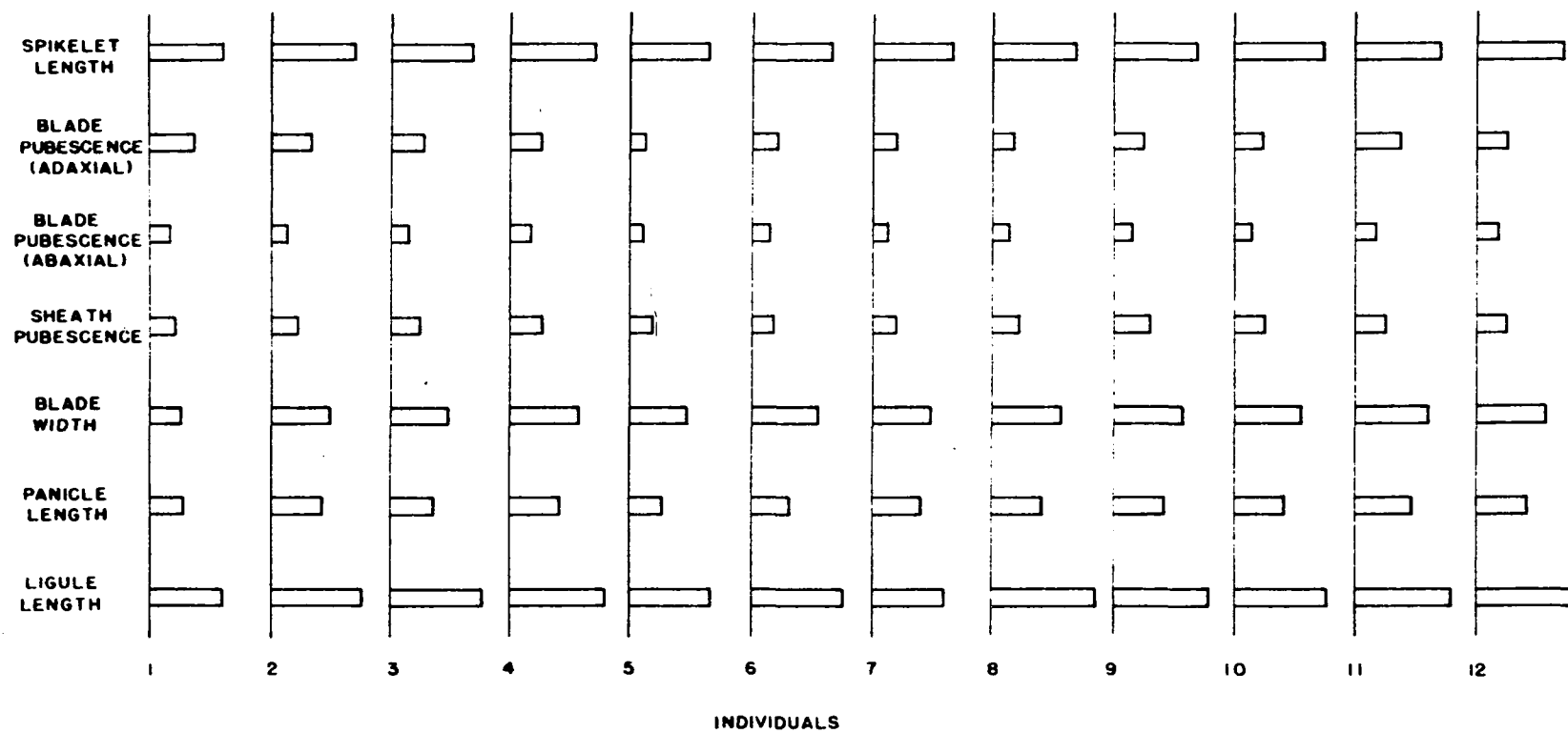


Figure 11. Analysis of morphological variations in progeny of Panicum lanuginosum var. fasciculatum

Seeds obtained from terminal panicle of plant collected in Russel Co., Alabama (2444); individual no. 1 represents parental plant, others represent progeny. Portions of parental plant and of progeny are shown in Figure 19 C.

SPIKELET LENGTH ■ = .2 MM
 PUBESCENCE LENGTH ■ = .3 MM

BLADE WIDTH ■ = 2 MM
 PANICLE LENGTH ■ = 1 CM

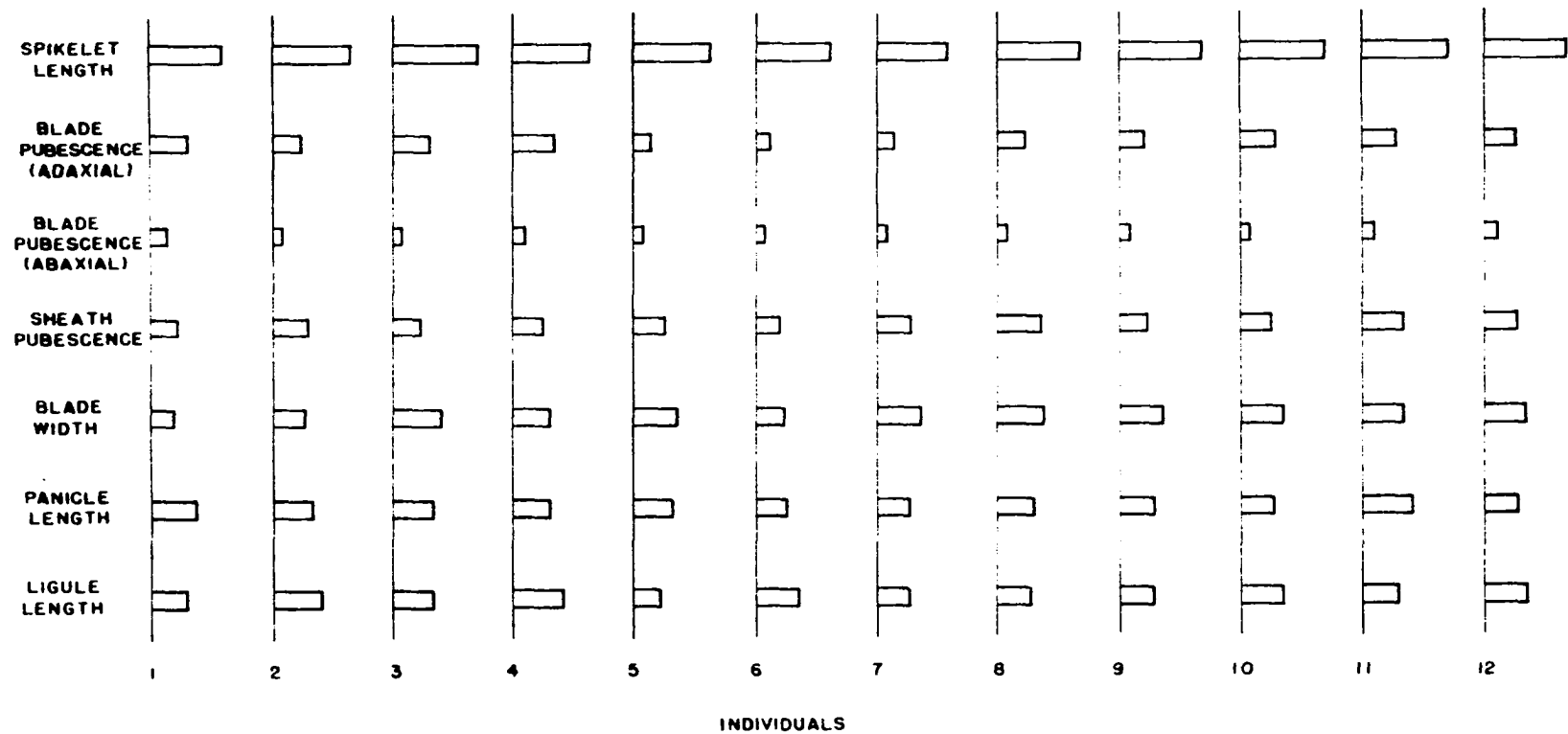


Figure 12. Analysis of morphological variations in progeny of Panicum lanuginosum var. fasciculatum

Seeds obtained from terminal panicle of plant collected in Bullock Co., Alabama (2442); individual no. 1 represents parental plant, others represent progeny.
Portions of parental plant and of progeny are shown in Figure 19 D.

SPIKELET LENGTH ■ = .2 MM
 PUBESCENCE LENGTH ■ = .3 MM

BLADE WIDTH ■ = 2 MM
 PANICLE LENGTH ■ = 1 CM

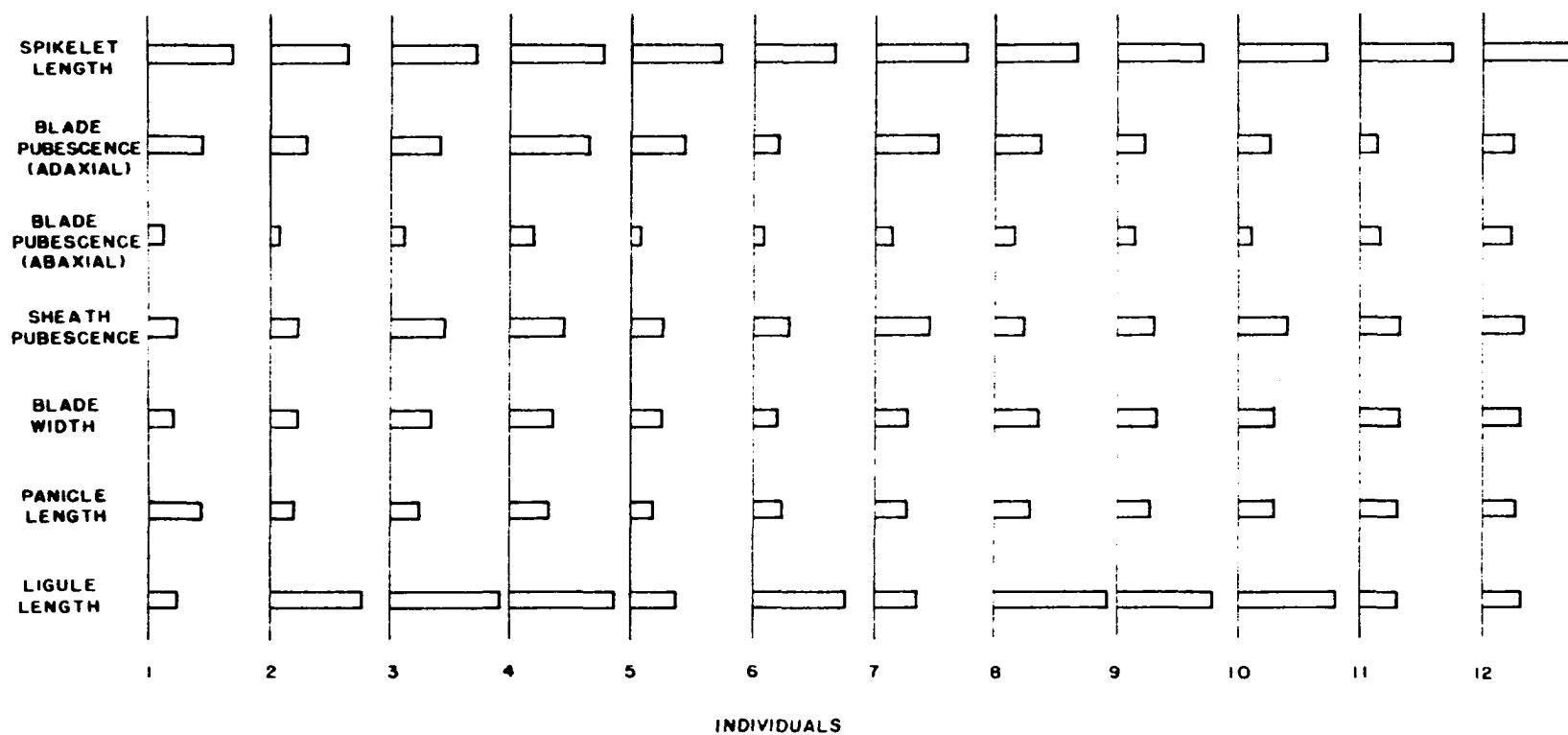


Figure 13. Analysis of morphological variations in progeny of Panicum praecocius

Seeds obtained from axillary panicles of plant collected in Webster Co., Iowa (2136) and transplanted into uniform garden; individual no. 1 represents parental plant, others represent progeny.
Portions of parental plant and of progeny are shown in Figure 20 A.

SPIKELET LENGTH ■ = .2 MM
 PUBESCENCE LENGTH ■ = .3 MM

BLADE WIDTH ■ = 2 MM
 PANICLE LENGTH ■ = 1 CM

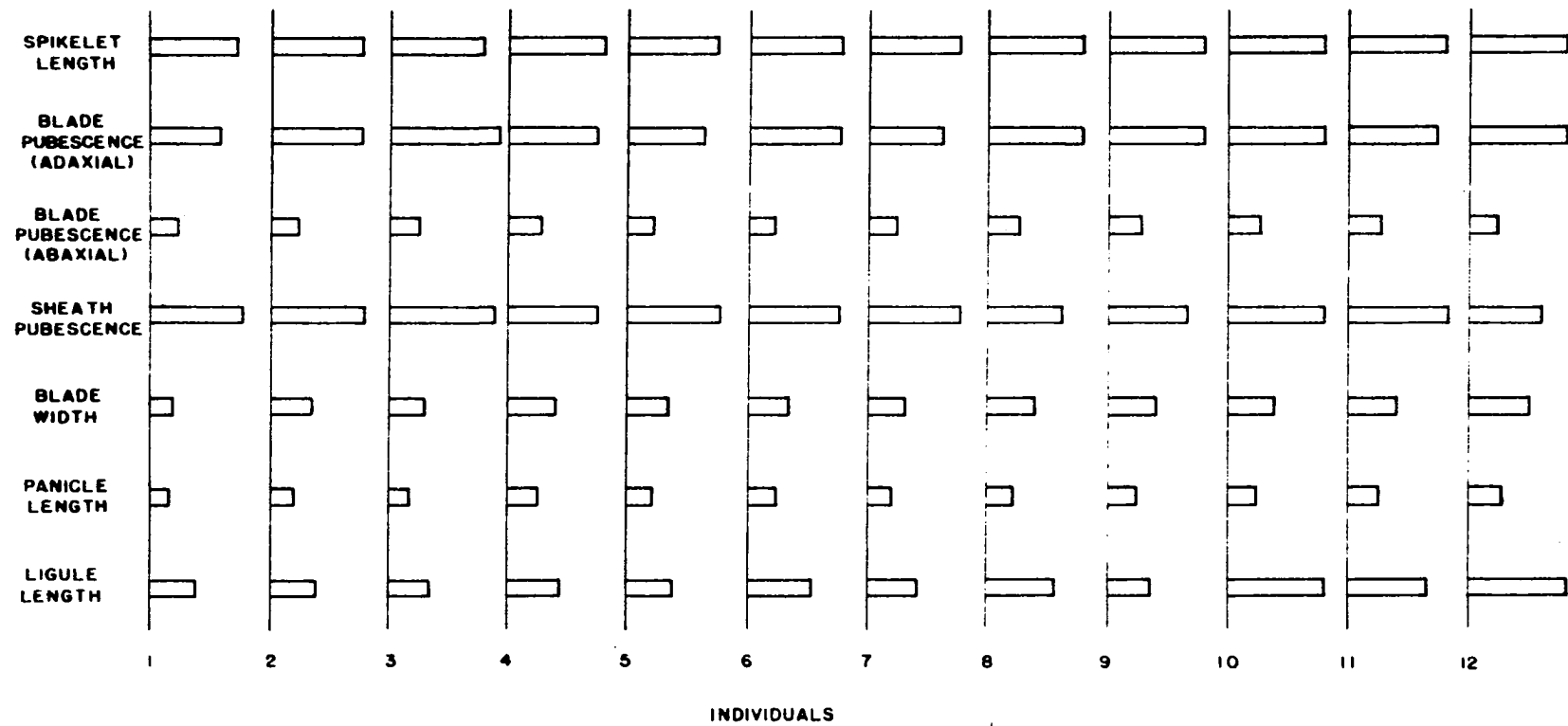


Figure 14. Analysis of morphological variations in progeny of Panicum lindheimeri

Seeds obtained from terminal panicle of plant collected in Bullock Co., Alabama (2439); individual no. 1 represents parental plant, others represent progeny.
Portions of parental plant and of progeny are shown in Figure 20 B.

SPIKELET LENGTH ■ = .2 MM

BLADE WIDTH ■ = 2 MM

PUBESCENCE LENGTH ■ = .3 MM

PANICLE LENGTH ■ = 1 CM

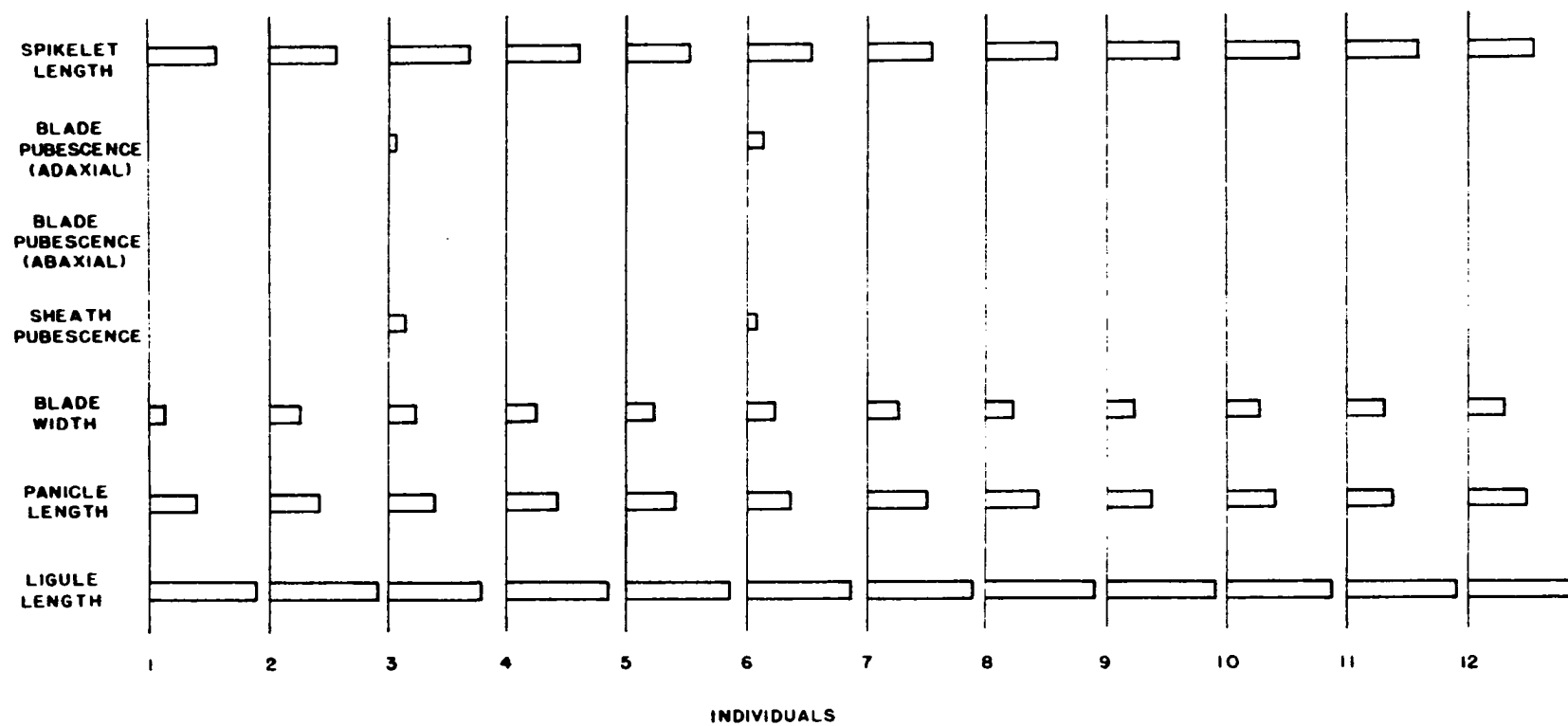


Figure 15. Analysis of morphological variations in progeny of Panicum xalapense

Seeds obtained from terminal panicles of plant collected in York Co., South Carolina (2611); individual no. 1 represents parental plant, others represent progeny. Portions of parental plant and of progeny are shown in Figure 20 C.

SPIKELET LENGTH ■ • .2 MM
 PUBESCENCE LENGTH ■ • .3 MM

BLADE WIDTH ■ • 2 MM
 PANICLE LENGTH ■ • 1 CM

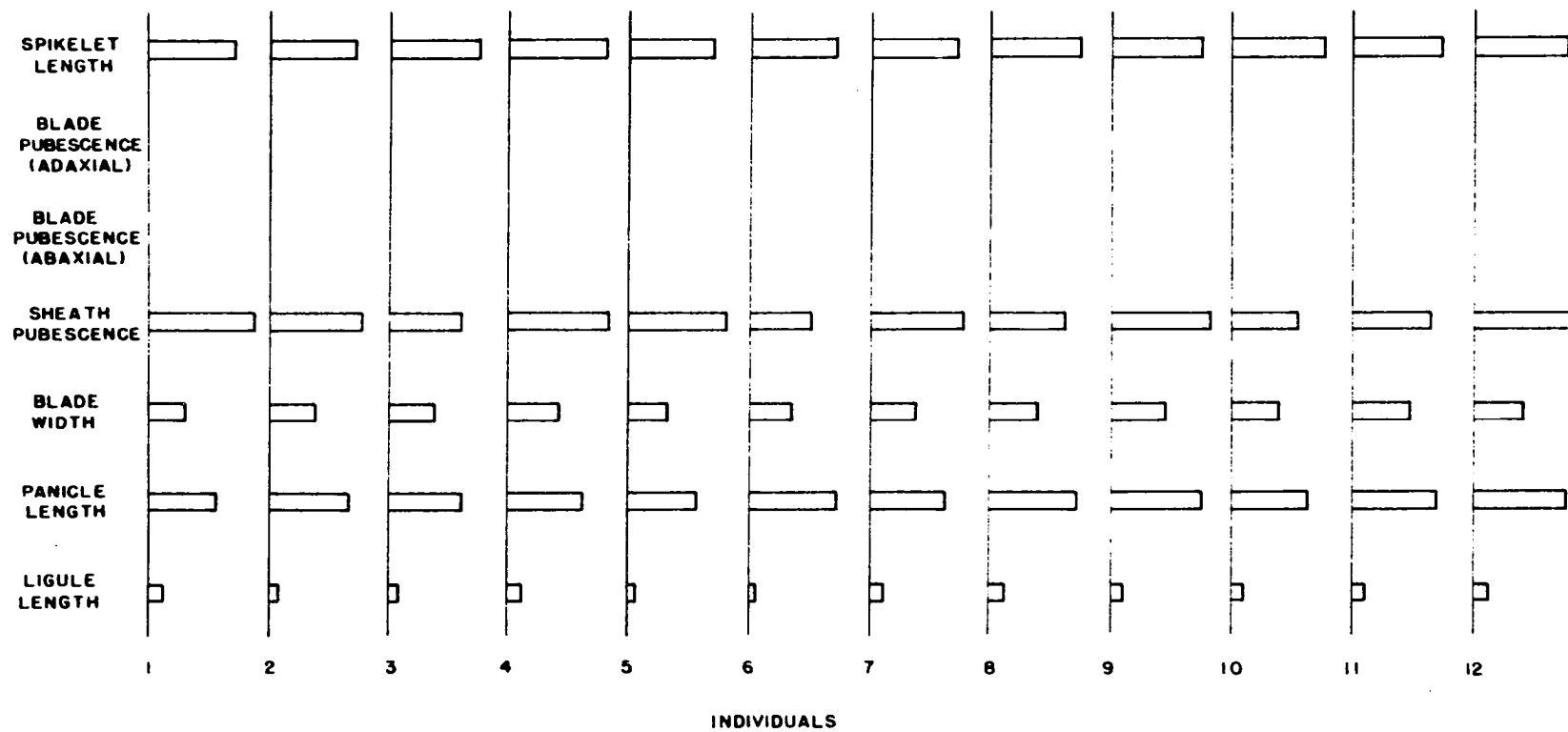


Figure 16. Analysis of morphological variations in progeny of Panicum sphaerocarpon

Seeds obtained from terminal panicles of plant collected in Washington Co., Georgia (2459); individual no. 1 represents parental plant, others represent progeny. Portions of parental plant and of progeny are shown in Figure 20 D.

SPIKELET LENGTH ■ = .2 MM
 PUBESCENCE LENGTH ■ = .3 MM

BLADE WIDTH ■ = 2 MM
 PANICLE LENGTH ■ = 1 CM

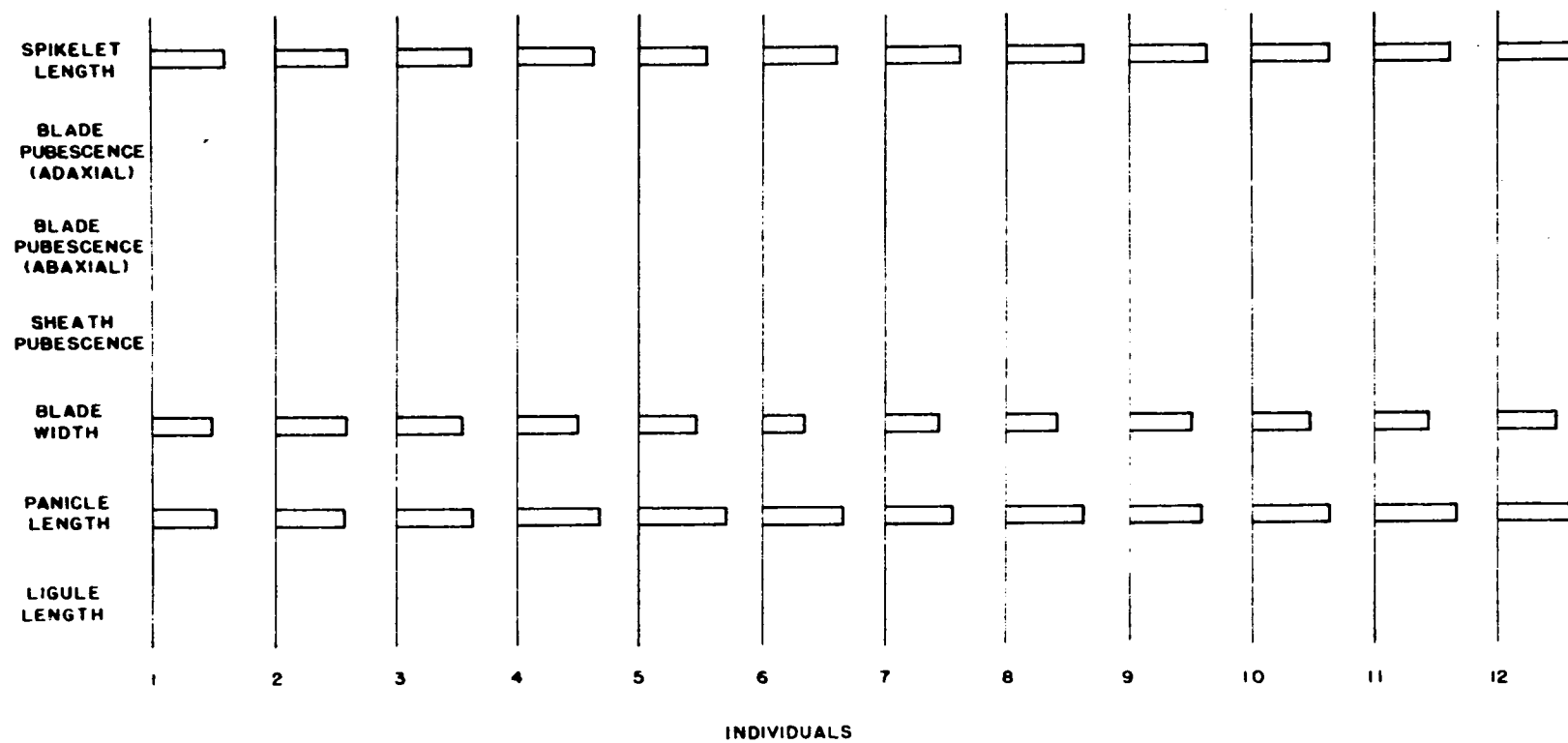


Figure 17. Analysis of morphological variations in progeny of Panicum commutatum

Seeds obtained from terminal panicles of plant collected in Prince George Co., Virginia (2555); individual no. 1 represent parental plant, others represent progeny. Portions of parental plant and of progeny are shown in Figure 21 A.

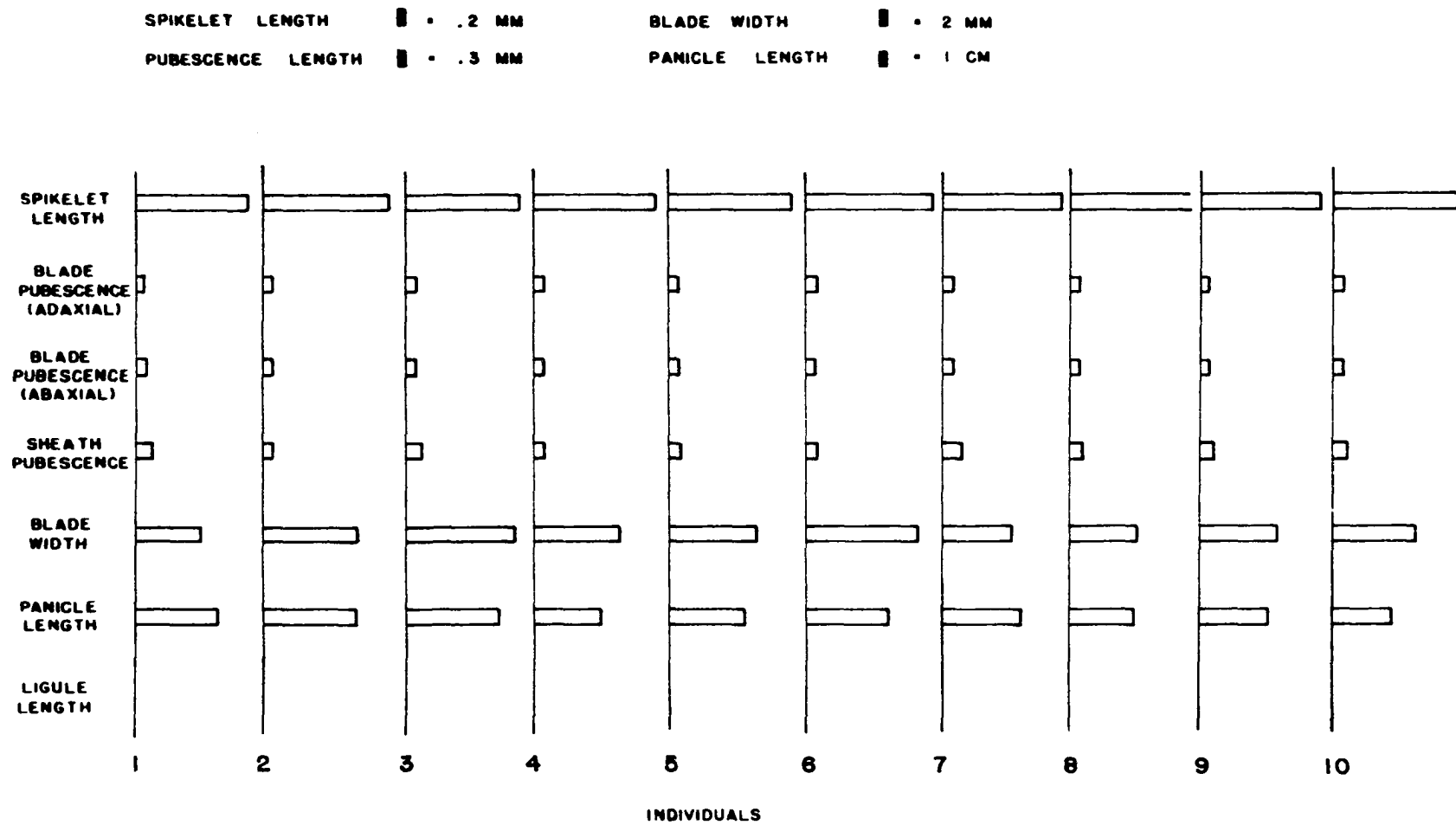


Figure 18. Analysis of morphological variations in progeny of Panicum aciculare

Seeds obtained from terminal panicle of plant collected in Washington Co., Georgia (2470); individual no. 1 represents parental plant, others represent progeny. Portions of parental plant and of progeny are shown in Figure 21 B.

SPIKELET LENGTH ■ = .2 MM
 PUBESCENCE LENGTH ■ = .3 MM

BLADE WIDTH ■ = 2 MM
 PANICLE LENGTH ■ = 1 CM

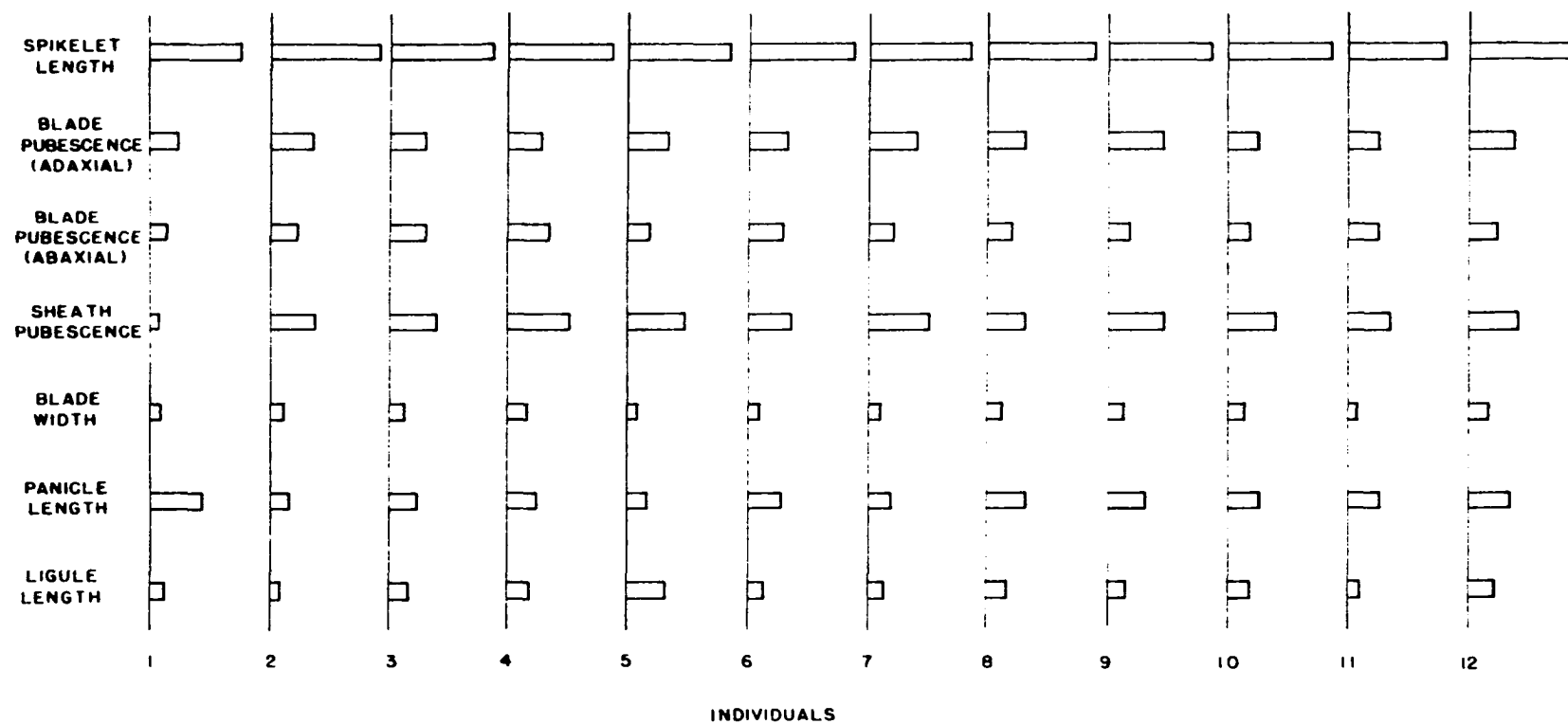


Figure 19. Parental plant and representative progeny of Panicum lanuginosum var. fasciculatum

In each photograph, part of the parental plant is shown on the left and culms of two or three progeny are shown on the right.

- A. Parental plant collected in Marion Co., Iowa (2103) and transplanted into uniform garden; seed obtained from terminal panicle. See Figure 9.
- B. Same parental plant as in A; seeds obtained from axillary panicles bagged before anthesis. See Figure 10.
- C. Parental plant collected in Russel Co., Alabama (2444); seeds obtained from terminal panicle. See Figure 11.
- D. Parental plant collected in Bullock Co., Alabama (2442); seeds obtained from terminal panicle. See Figure 12.

Scale unit = 1 dm

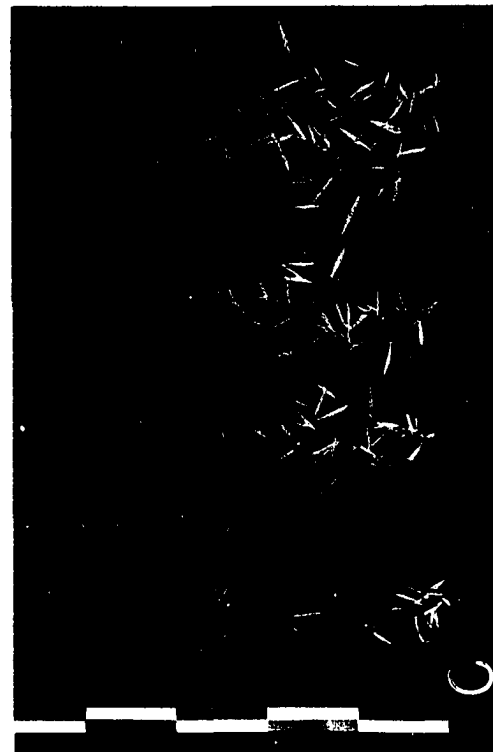
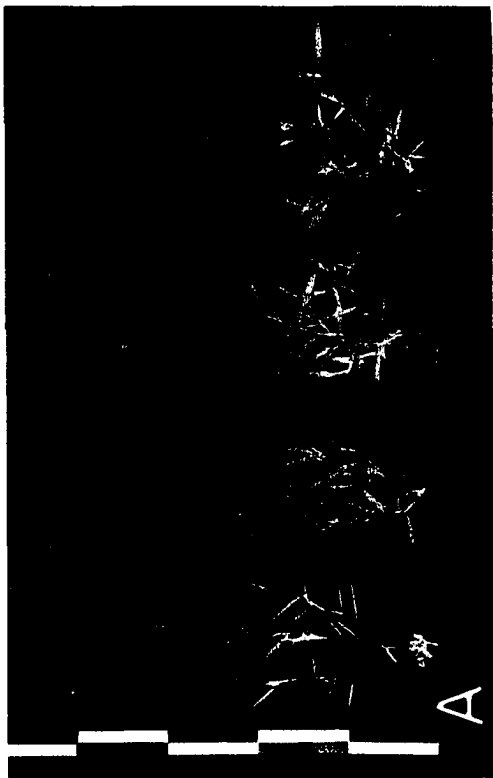
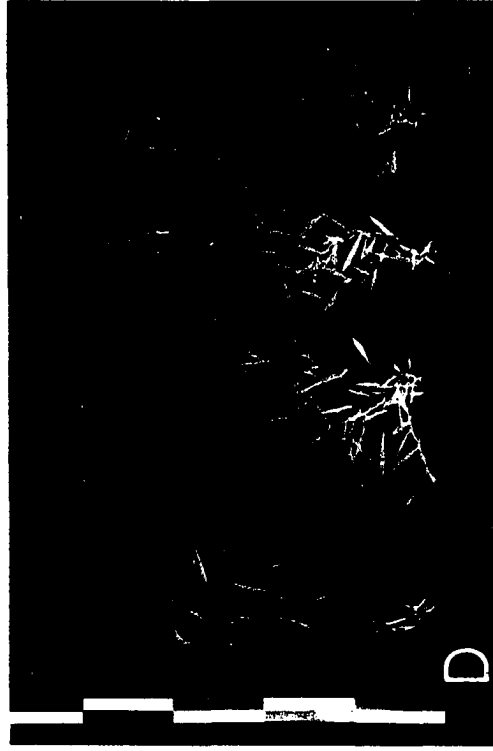


Figure 20. Parental plant and representative progeny of some dichanthelia

In each photograph, part of the parental plant is shown on the left and culms of a few progeny are shown on the right.

- A. Panicum praecocius collected in Webster Co., Iowa (2136) and transplanted into uniform garden; seeds obtained from axillary panicles. See Figure 13.
- B. P. lindheimeri collected in Bullock Co., Alabama (2439); seeds obtained from terminal panicle. See Figure 14.
- C. P. xalapense collected in York Co., South Carolina (2611); seeds obtained from terminal panicles. See Figure 15.
- D. P. sphaerocarpon collected in Washington Co., Georgia (2459) seeds obtained from terminal panicles. See Figure 16.

Scale unit = 1 dm

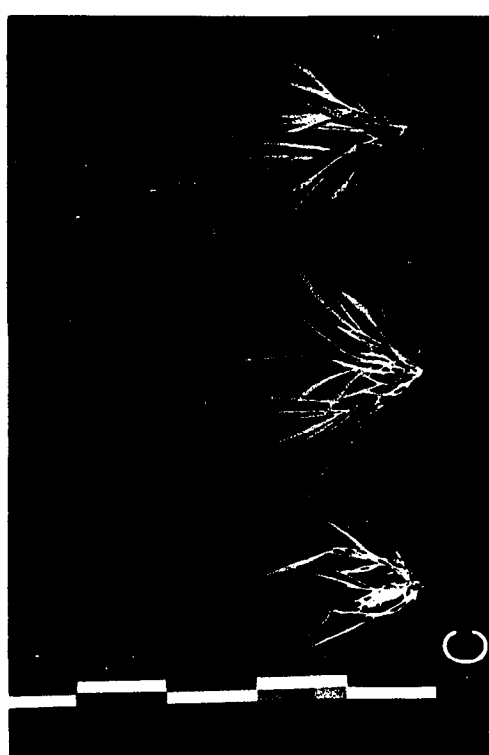
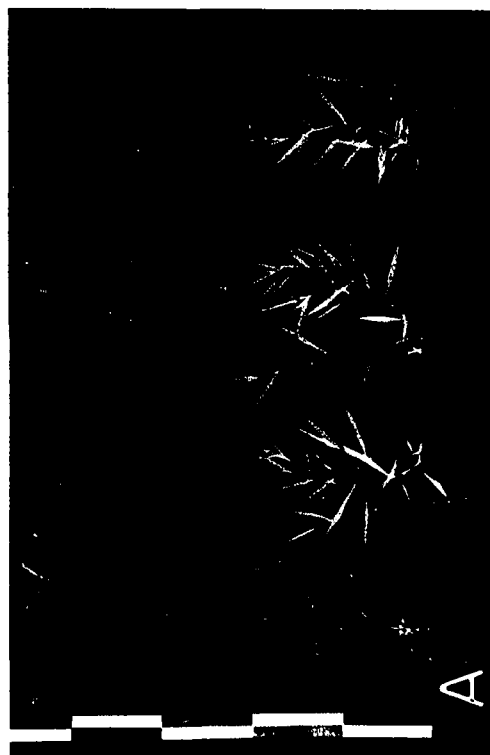
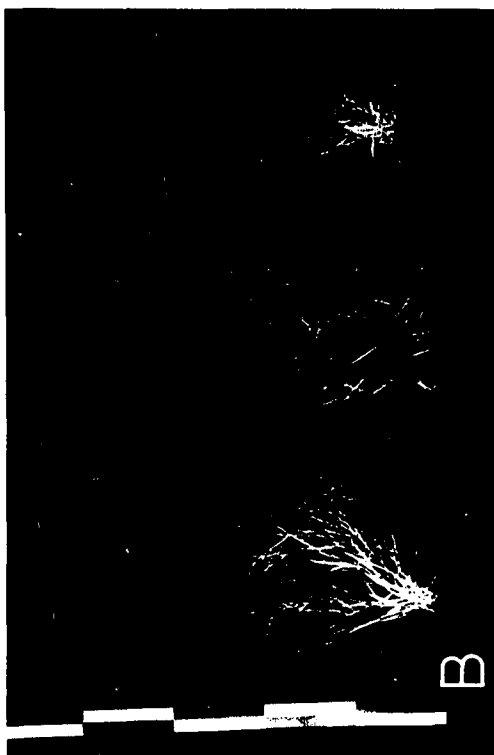


Figure 21. Parental plant and representative progeny of some dichanthelia

In each photograph, part of the parental plant is shown on the left, culms of a few progeny on the right.

- A. Panicum commutatum collected in Prince George Co., Virginia (2555); seeds obtained from terminal panicles. See Figure 17.
- B. P. aciculare collected in Washington Co., Georgia; seeds obtained from terminal panicle. See Figure 18.
- C. P. lindheimeri collected in Henry Co., Illinois; seeds obtained from axillary panicles.
- D. P. wilcoxianum collected in Story Co., Iowa; seeds obtained from terminal panicles.

Scale unit = 1 dm



for collection purposes were rendered sufficiently broad to include any variance which might be significant within a given species complex.

Variations in certain morphological characters observed in some of the samples studied are illustrated in Figures 22 through 29. In general, the individuals of a species population were essentially uniform for the seven characters examined. Only samples of Panicum lanuginosum (2361 and 2519) represented in Figures 24 and 26 respectively and of P. commonsianum (2520) shown in Figure 29 exhibited a small amount of variance in blade and sheath pubescence.

In the light of our observations on floral biology and progeny structure in the dichanthelia, these "populations" probably represent pure lines resulting from repeated selfing.

Species Association in the Dichanthelia

It is often mentioned in previous literature that several species of dichanthelia occur on the Atlantic and Gulf Coastal Plain. However, no precise indication is made of the number of species, of their morphological resemblance or dissimilarity, and of their relative abundance in a given restricted area. Certainly such information is of great importance in the eventual formulation of a working hypothesis concerning speciation in the subgenus Dichanthelium.

Analysis of morphological variations found within races of dichanthelia such as those presented in the preceding section does not reflect fully the usual structure of a population of dichanthelia. In the mid-western United States, two to five species of dichanthelia are not uncommonly found growing together in a given locality. On the Gulf and

Figure 22. Analysis of morphological variations in a population sample of Panicum lanuginosum
var. fasciculatum

Plants collected in Monroe Co., Iowa (2095)

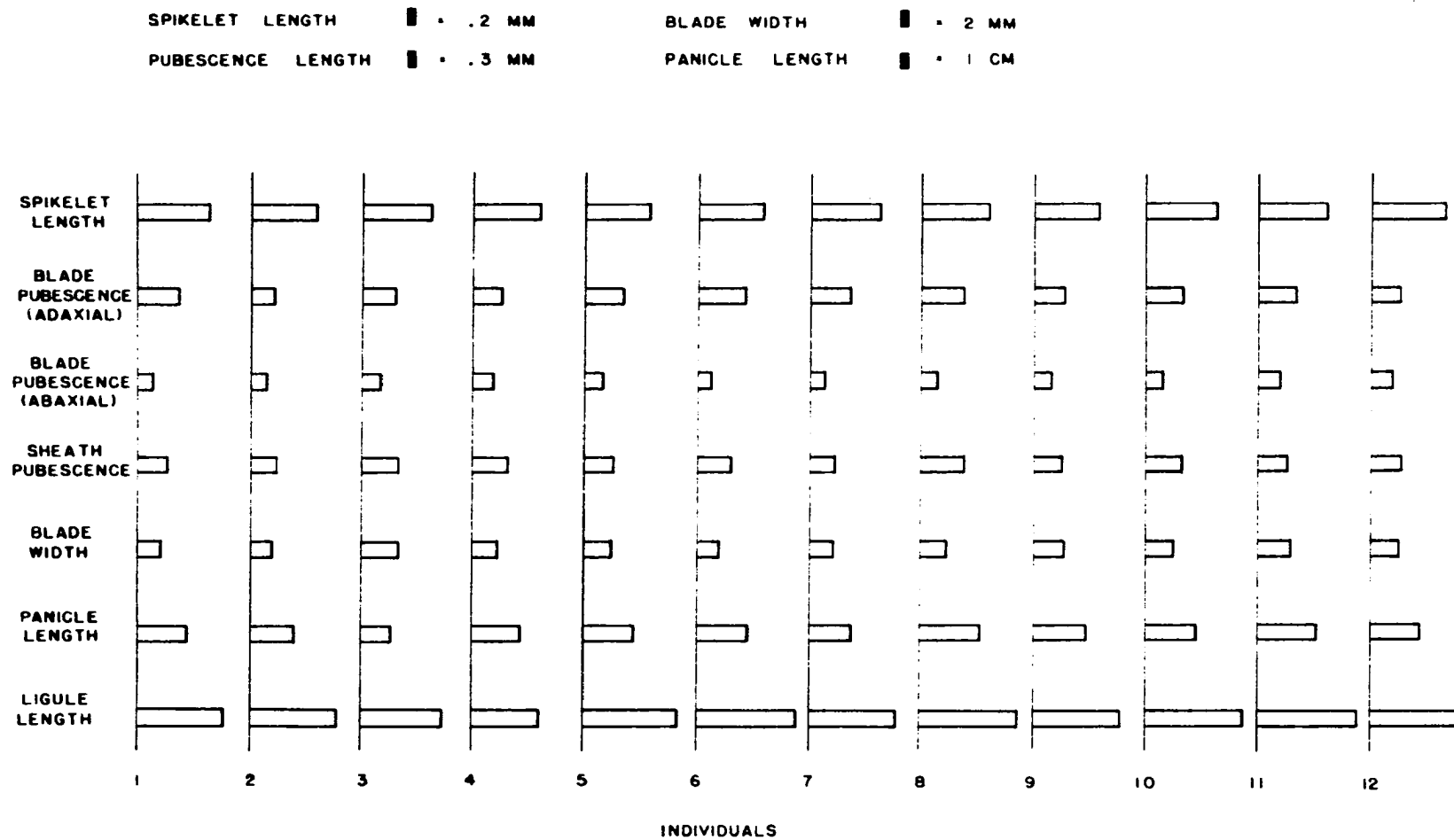


Figure 23. Analysis of morphological variations in a population sample of Panicum lanuginosum
var. fasciculatum

Plants collected in Benton Co., Missouri (2326)

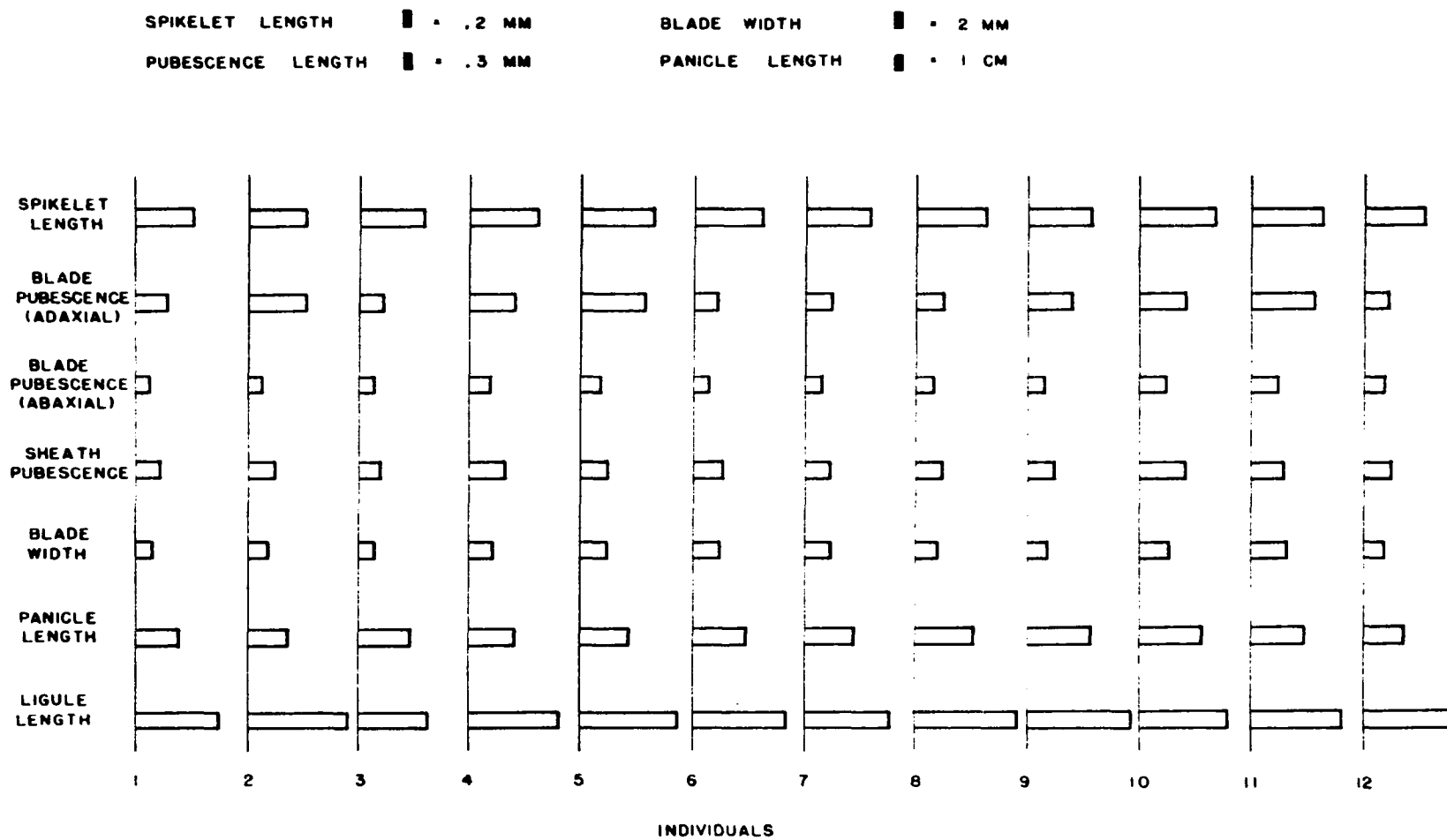


Figure 24. Analysis of morphological variations in a population sample of Panicum lanuginosum
var. fasciculatum

Plants collected in Yell Co., Arkansas (2361)

SPIKELET LENGTH ■ = .2 MM
 PUBESCENCE LENGTH ■ = .3 MM

BLADE WIDTH ■ = 2 MM
 PANICLE LENGTH ■ = 1 CM

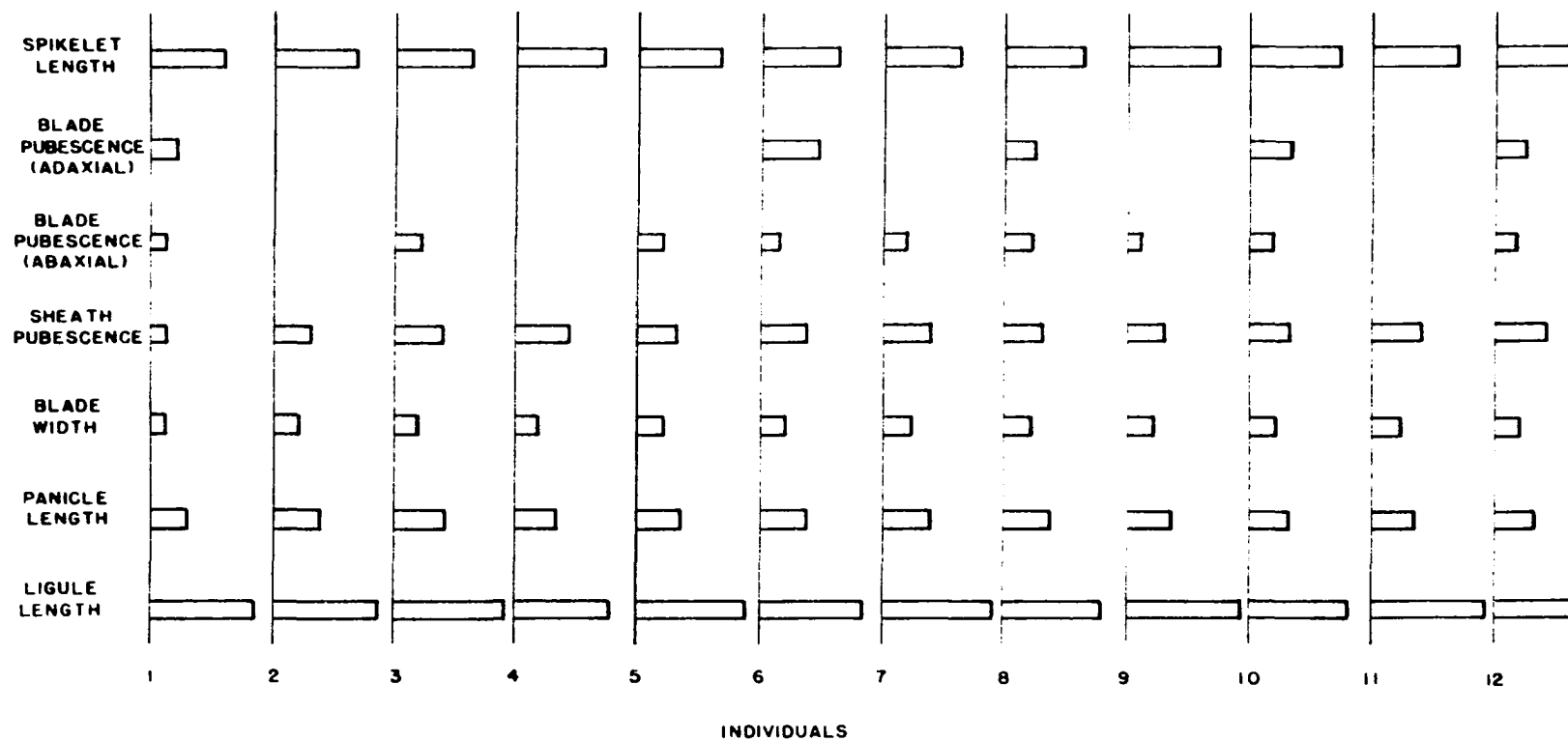


Figure 25. Analysis of morphological variations in a population sample of Panicum lanuginosum
var. fasciculatum

Plants collected in Rapides Parish, Louisiana (2399)

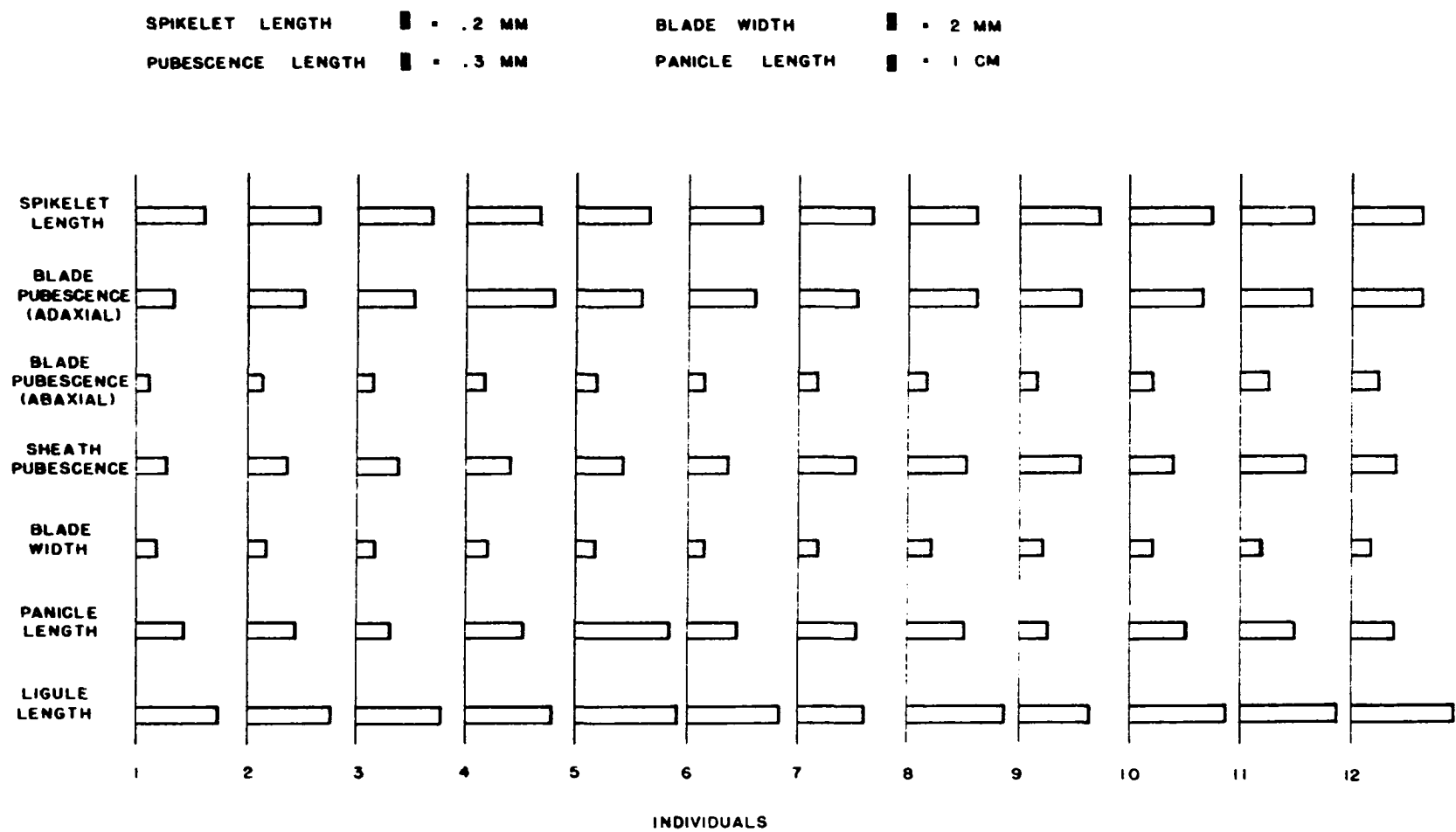


Figure 26. Analysis of morphological variations in a population sample of Panicum lanuginosum
var. fasciculatum

Plants collected in Robeson Co., North Carolina (2519)

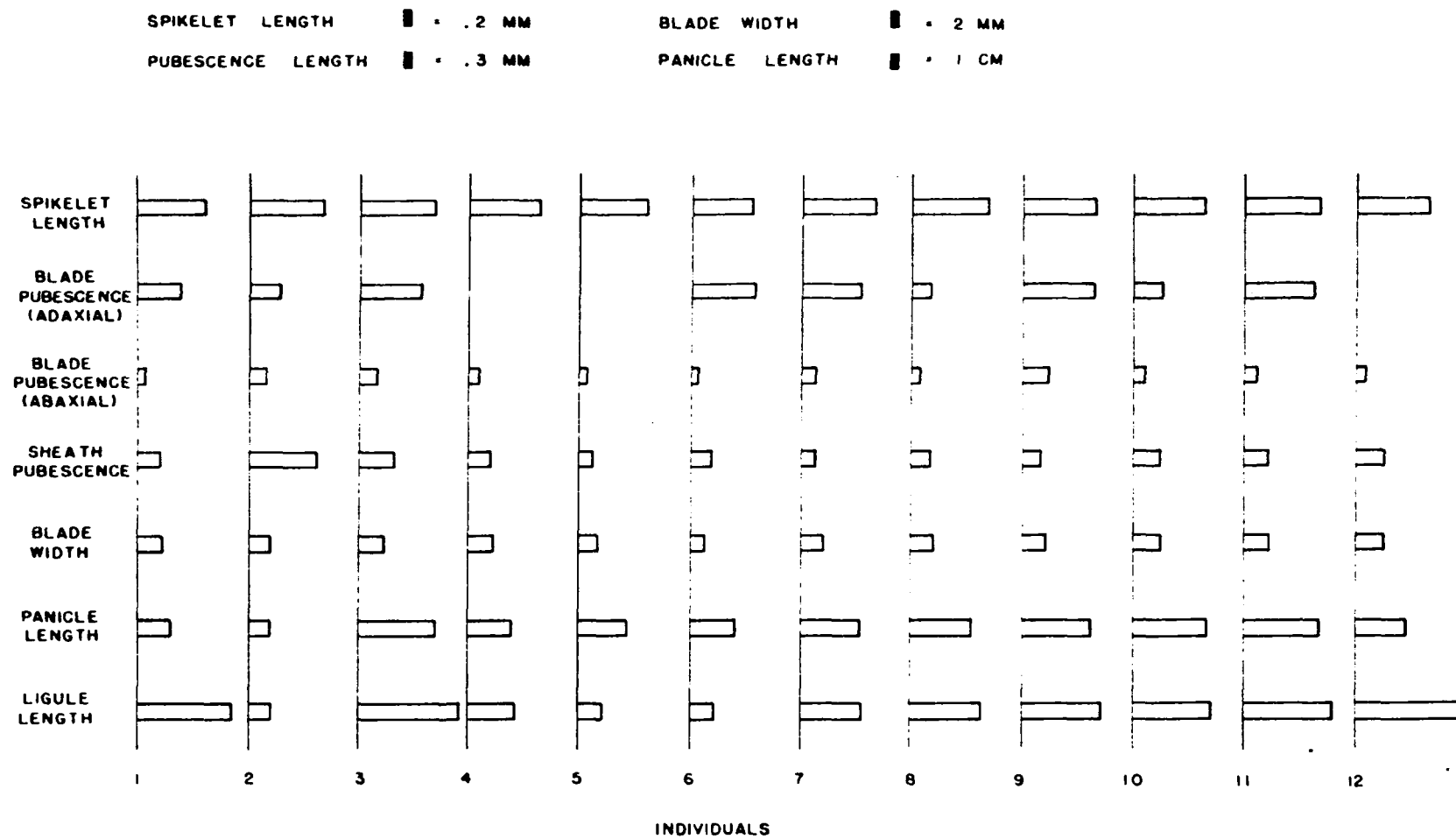


Figure 27. Analysis of morphological variations in a population sample of Panicum praecocius
Plants collected in Boone Co., Iowa (2072)

SPIKELET LENGTH ■ • .2 MM

BLADE WIDTH ■ • 2 MM

PUBESCENCE LENGTH ■ • .3 MM

PANICLE LENGTH ■ • 1 CM

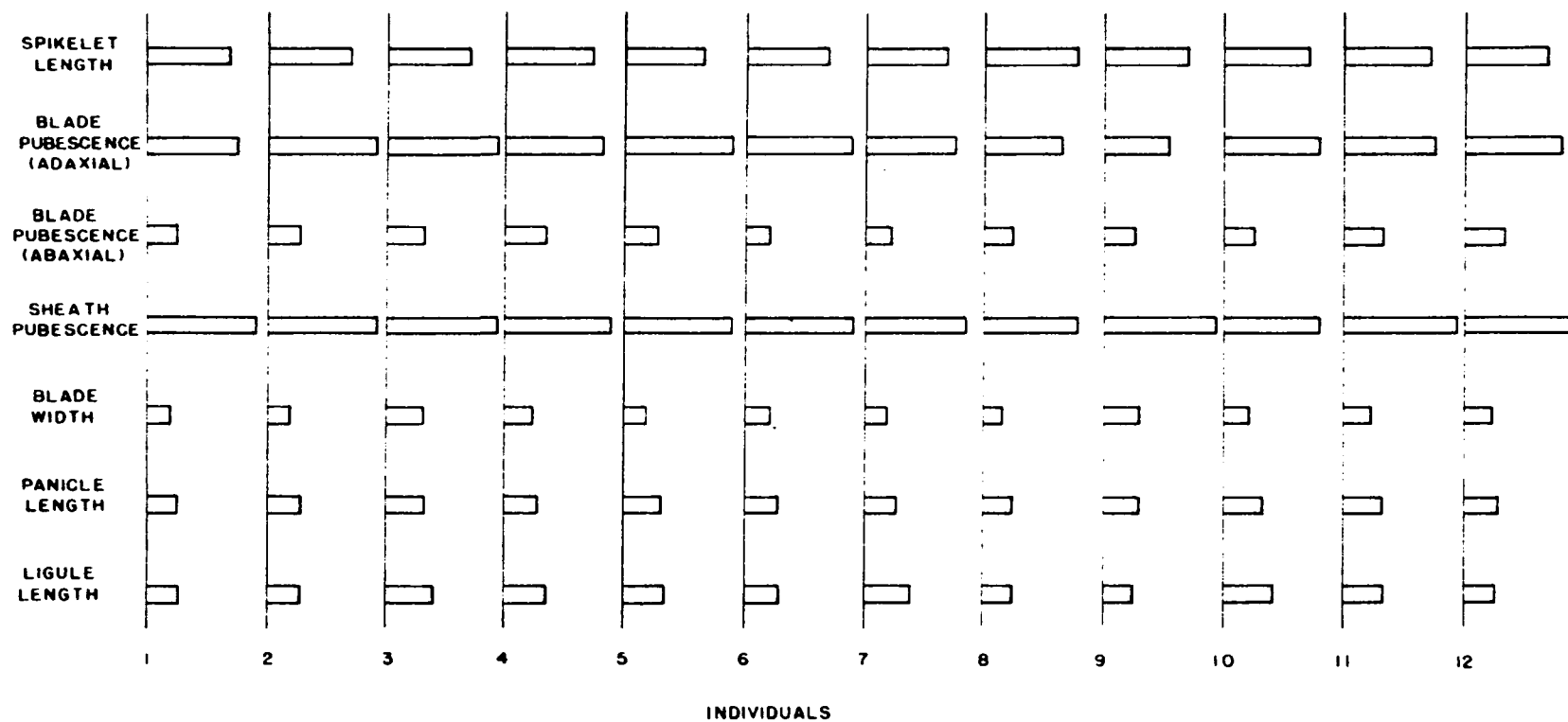


Figure 28. Analysis of morphological variations in a population sample of Panicum praecocius
Plants collected in Dickinson Co., Iowa (2184)

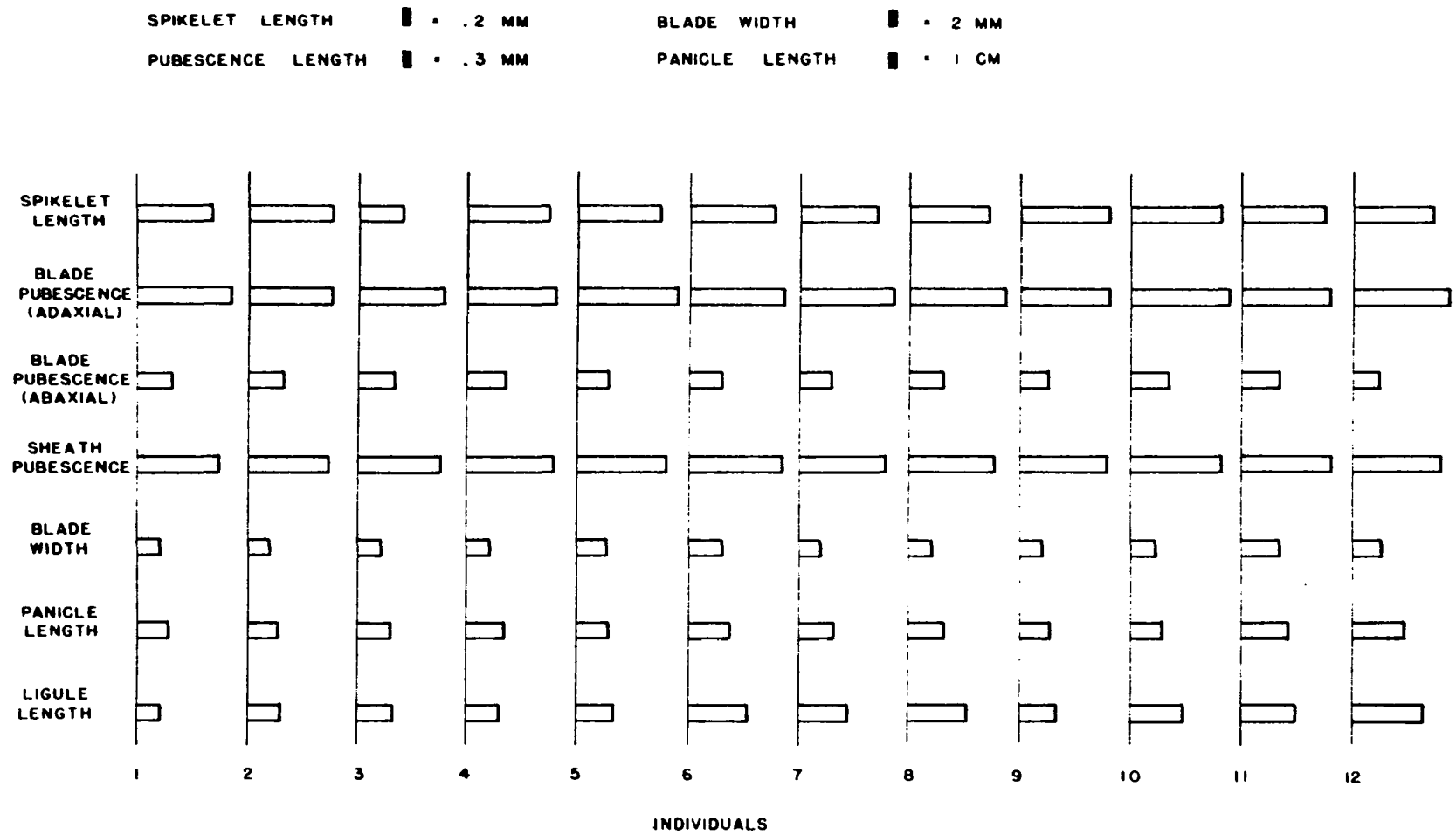
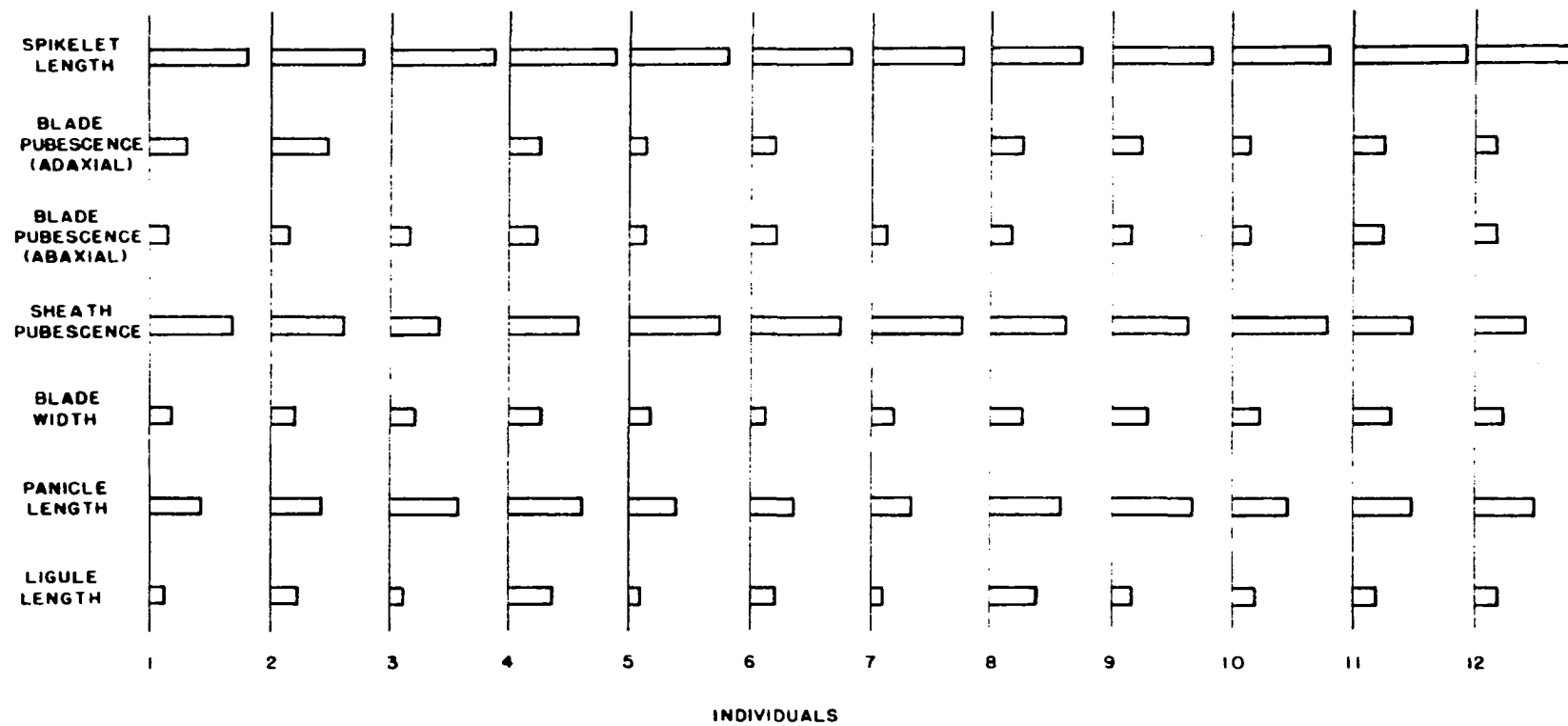


Figure 29. Analysis of morphological variations in a population sample of Panicum commonsianum
Plants collected in Robeson Co., North Carolina (2520)

SPIKELET LENGTH ■ = .2 MM
PUBESCENCE LENGTH ■ = .3 MM

BLADE WIDTH ■ = 2 MM
PANICLE LENGTH ■ = 1 CM



Atlantic Coastal Plains, 8 to 12 or more species of dichanthelia are usually found in the immediate vicinity of one another along roadsides and on the fringes of more or less disturbed woods. Well defined species such as Panicum commutatum and P. dichotomum are commonly growing along with P. boscii or P. latifolium in the shadiest part of the woods; P. xalapense and P. angustifolium generally occur in more open woods, while P. depauperatum, P. sphaerocarpon, and P. aciculare often occur on drier sand and clay. Members of the polymorphic Lanuginosa and Columbiana groups appear to exhibit the greatest ubiquity and the "weediest" tendency among the dichanthelia. Some of the forms in these assemblages succeed in establishing the largest "micropopulations" encountered in terms of number of individuals and the morphological uniformity of many such lines has been demonstrated earlier. Other atypical forms are represented only by rare individuals ordinarily overlooked in the course of population sampling.

In order to provide a more complete picture of populations of dichanthelia in the region of their greatest diversification, samples of typical species associations found on the Atlantic and Gulf Coastal Plain are illustrated in Figures 33 and 34. Some of the morphological variations exhibited by species in three of those populations are further analyzed in Figures 30, 31, and 32.

While some of the "species" such as Panicum xalapense, P. commutatum, P. dichotomum, P. aciculare, and P. depauperatum appear fairly well defined and exhibit only slight morphological variations in separate parts of their range, the majority of forms in the Lanuginosa and Columbiana groups cannot be referred consistently and with assurance to one or

another species. Instead they seem to exhibit a combination of features possessed by other more clearly defined species in the same area, or to be intermediate in many respects between them. For example, the plant identified as Panicum villosissimum in Figure 33 C can hardly be distinguished from P. commonsianum also illustrated; in turn both of these grasses appear intermediate in most respects between P. angustifolium and P. xalapense growing in the same area. However, P. villosissimum is slightly more pubescent than P. commonsianum and resembles more closely P. xalapense, while P. commonsianum is more similar to the narrow-leaved semi-glabrous P. angustifolium. At another location a similar assemblage of "species" will be encountered with slight modification (Figure 33). A less hairy form of P. xalapense, sometimes referred to as P. laxiflorum might be found. Similarly, specimens of P. angustifolium might be more robust. Consequently intermediate forms identifiable as P. villosissimum and P. commonsianum will also differ noticeably from members of the same two "species" in another part of their range. The picture is usually much more complex than in the two examples just discussed.

After close morphological examination of population samples such as those illustrated in Figures 33 and 34 and partially analyzed in Figures 31 and 32, one cannot fail to be impressed by the similarities among certain "species." Furthermore when similar species of dichanthelia are recurrently encountered throughout their geographical range along with intermediate forms, it is difficult to convince oneself that many of these "species" are not closely related.

Figure 30. Analysis of morphological variations in a mixed population of dichantheria

Plants collected in Rapides Parish, Louisiana; see illustration in Figure 33 A

- | | |
|---|------------------------------------|
| 1. <u>Panicum xalapense</u> (Freckmann 429) | 7. <u>P. villosissimum</u> (2395) |
| 2. <u>P. lanuginosum</u> (2398) | 8. <u>P. villosissimum</u> (2400) |
| 3. <u>P. lanuginosum</u> (2399) | 9. <u>P. lindheimeri</u> (2396) |
| 4. <u>P. lanuginosum</u> (2394) | 10. <u>P. angustifolium</u> (2401) |
| 5. <u>P. commonsianum</u> (2392) | 11. <u>P. oligosanthos</u> (2393) |
| 6. <u>P. commonsianum</u> (2399) | |

Also collected at this location but not represented: P. sphaerocarpon,
P. polyanthes

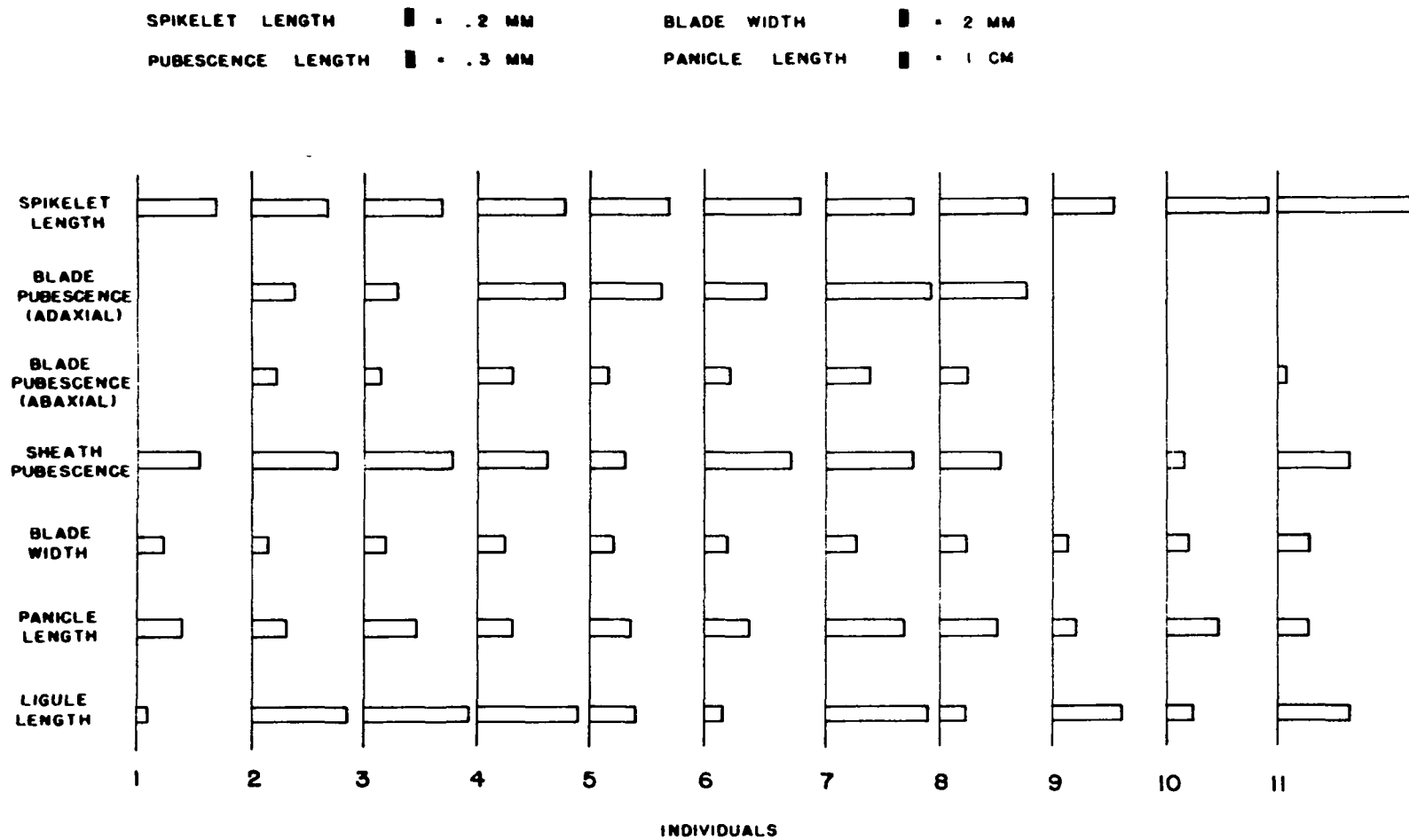


Figure 31. Analysis of morphological variations in a mixed population of *dichanthelia*

Plants collected in Jenkins Co., Georgia; see illustrations in Figure 34 A

- | | |
|--|---|
| 1. <u>Panicum angustifolium</u> (2484) | 6. <u>P. commonsianum</u> (2476) |
| 2. <u>P. consanguineum</u> (2475) | 7. <u>P. lanuginosum</u> (2483) |
| 3. <u>P. arenicoloides</u> (2482) | 8. <u>P. auburne</u> (2473) |
| 4. <u>P. aciculare</u> (2479) | 9. <u>P. dichotomum</u> (Freckmann 516) |
| 5. <u>P. commonsianum</u> (2478) | 10. <u>P. trifolium</u> (2488) |

Other species collected at this location but not represented:

P. sphaerocarpon, P. scoparium, P. microcarpon, P. ravenelii

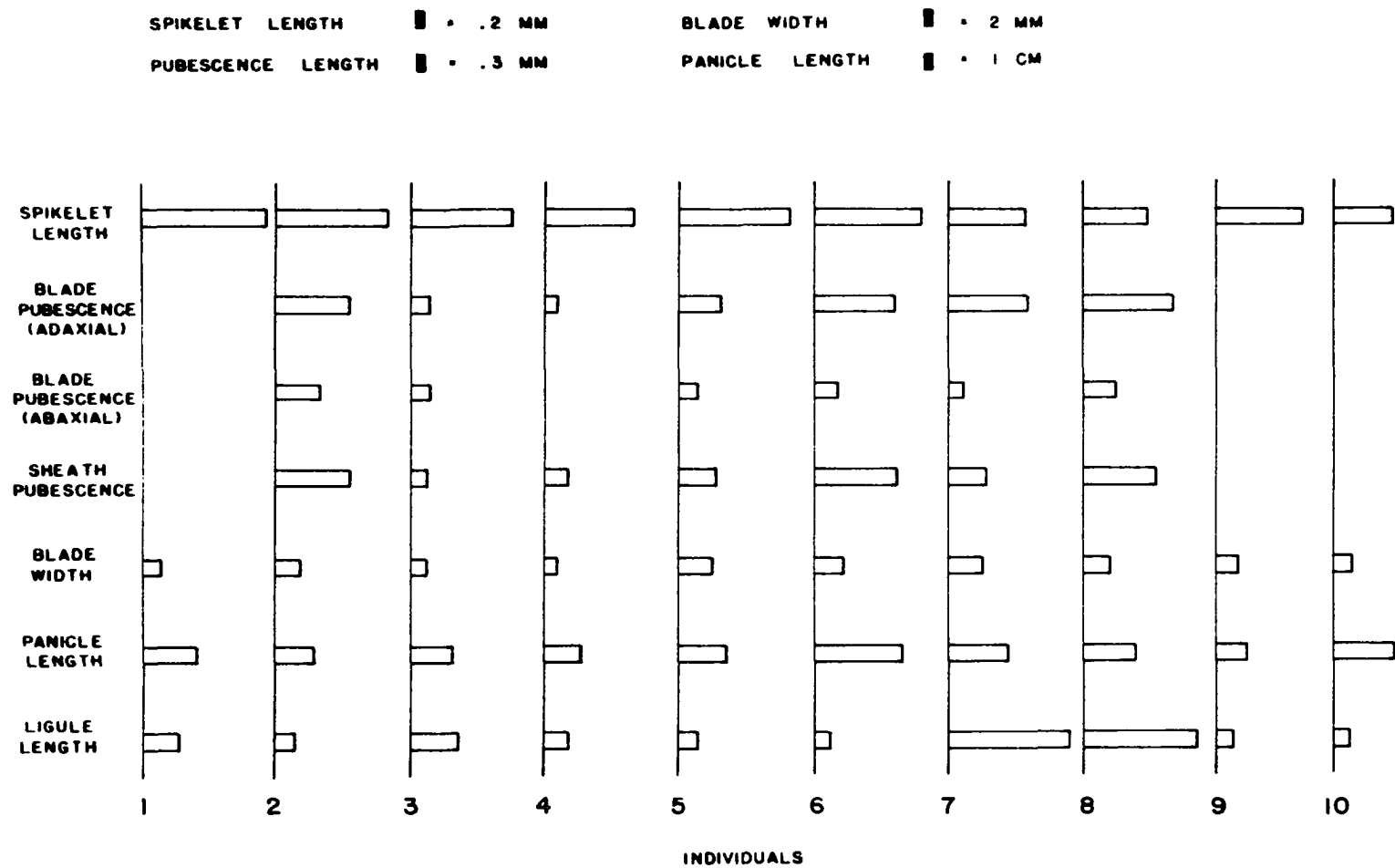


Figure 32. Analysis of morphological variations in a mixed population of *dichanthelia*

Plants collected in Robeson Co., North Carolina; see illustrations in Figure 34 B

- | | |
|------------------------------------|-----------------------------------|
| 1. <u>Panicum xalapense</u> (2512) | 6. <u>P. dichotomum</u> (2514) |
| 2. <u>P. commonsianum</u> (2508) | 7. <u>P. microcarpon</u> (2511) |
| 3. <u>P. commonsianum</u> (2509) | 8. <u>P. sphaerocarpon</u> (2507) |
| 4. <u>P. lanuginosum</u> (2513) | 9. <u>P. aciculare</u> (2510) |
| 5. <u>P. lindheimeri</u> (2516) | 10. <u>P. commutatum</u> (2512) |

Also collected here but not represented: P. ravenelii

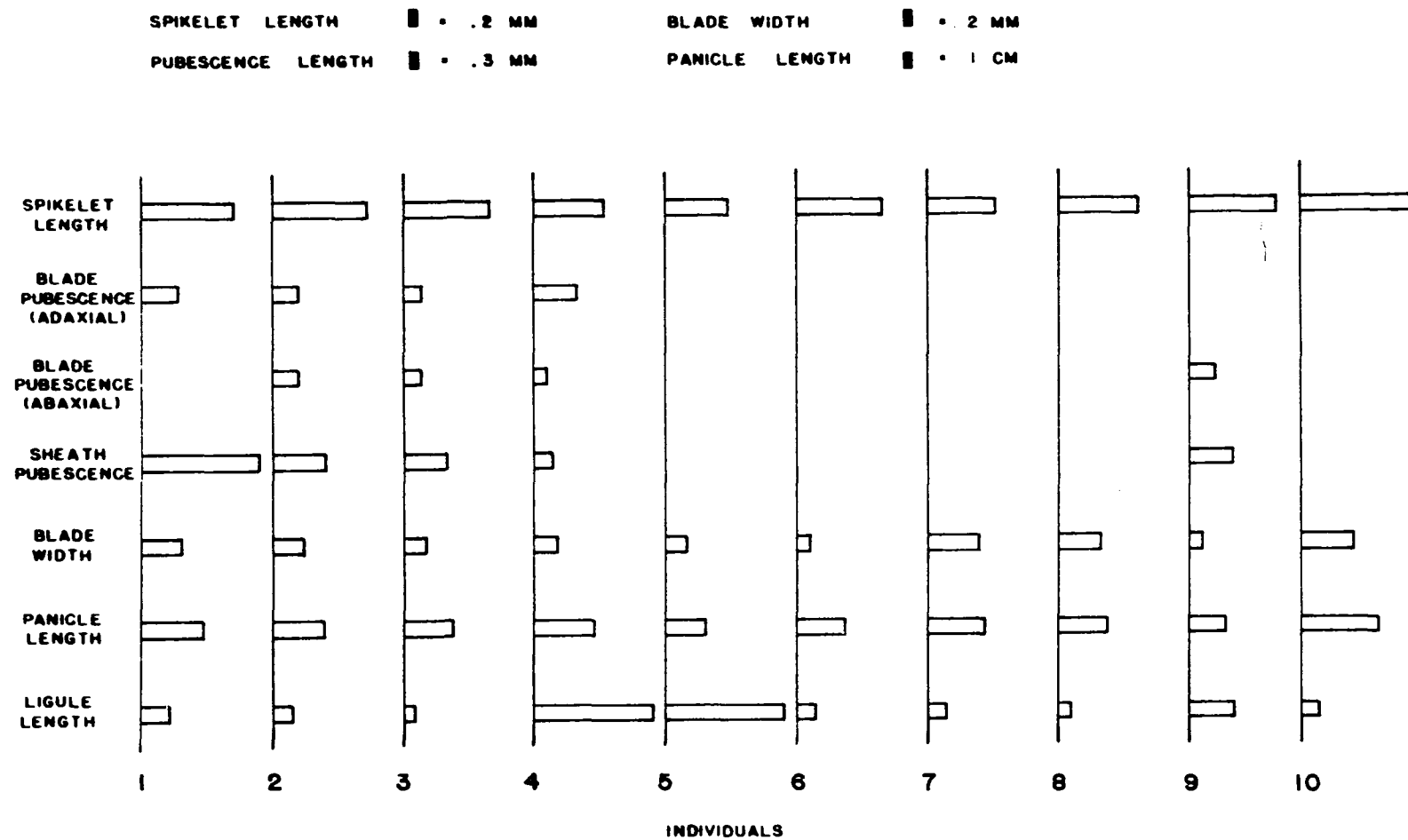


Figure 33. Species association in populations of dichanthelia

- A. Plants collected in Rapides Parish, Louisiana; see Figure 30. From left to right:
Panicum lanuginosum (2398), P. angustifolium (2401), P. villosissimum (2400),
P. lanuginosum (2394), P. commonsianum var. Addisonii (2392)
Collected at same location but not illustrated here: P. oligosanthos,
P. commonsianum, P. xalapense, P. polyanthes, P. sphaerocarpon, P. lindheimeri
- B. Plants collected in York Co., South Carolina. From left to right:
P. commonsianum (2608), P. angustifolium (2612), P. villosissimum (2614),
P. lanuginosum var. fasciculatum (2616)
Collected at same location but not illustrated here: P. laxiflorum,
P. sphaerocarpon, P. ravenelii
- C. Plants collected in Prince George Co., Virginia. From left to right:
P. commonsianum (2547), P. villosissimum (2550), P. angustifolium (2552),
P. xalapense (2548), P. lanuginosum var. fasciculatum (2553)
Collected at same location but not illustrated here: P. depauperatum,
P. microcarpon, P. ravenelii, P. sphaerocarpon
- D. Plants collected in Story Co., Iowa (dry and disturbed prairie relic); see
Figure 35. From left to right: P. perlongum (2706), P. wilcoxianum (2704),
P. praecocius (2705)
Collected at same location but not illustrated here: P. scribnerianum,
P. leibergii

Scale unit = 1 dm

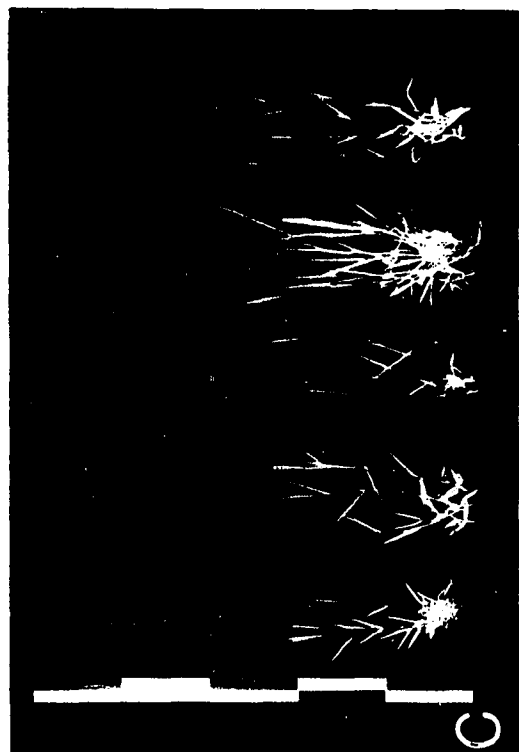
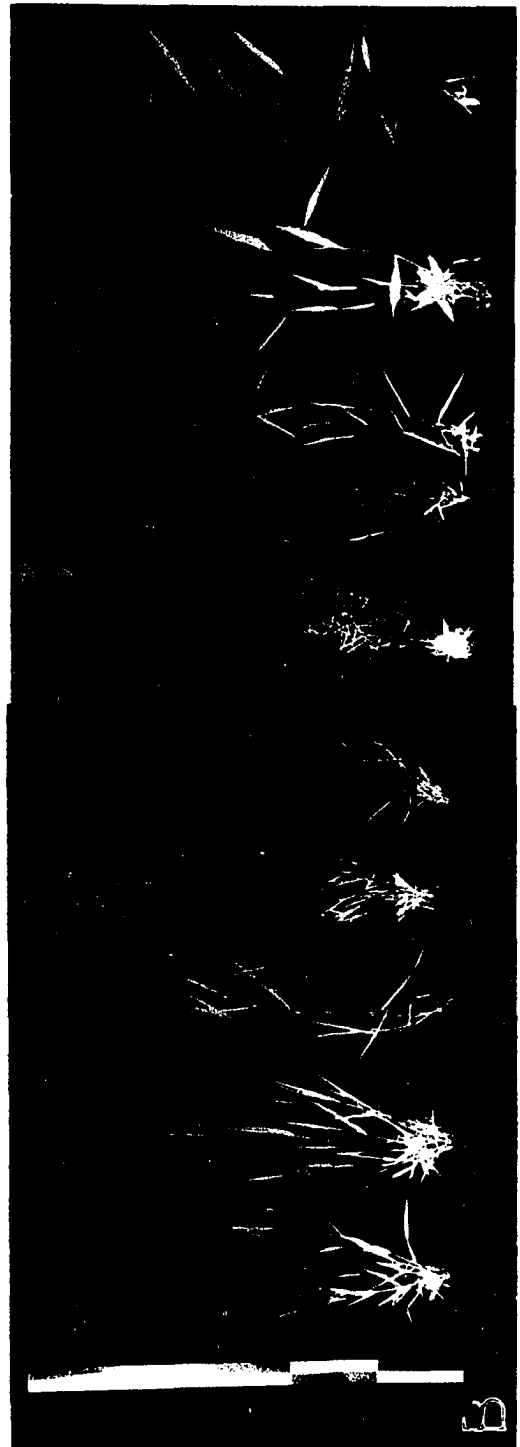


Figure 34. Species association in populations of dichanthelia

- A. Plants collected in Jenkins Co., Georgia; see Figure 31. From left to right:
Panicum aciculare (2479), P. consanguineum (2475), P. trifolium (2488),
P. sphaerocarpon (2474), P. microcarpon (2485), P. angustifolium (2484),
P. commonsianum (2476), P. commonsianum (2478), P. lanuginosum var. fasciculatum
(2483), P. auburne (2473)
Collected at same location but not illustrated here: P. arenicoloides,
P. scoparium, P. dichotomum, P. ravenelii
- B. Plants collected in Robeson Co., North Carolina; for analysis of morphological
variations, see Figure 32. From left to right: P. lanuginosum var. fasciculatum
(2513), P. xalapense (2512), P. commonsianum (2508), P. commonsianum var. addisoni
(2509), P. aciculare (2510), P. dichotomum (2514), small form of P. lindheimeri
(2521), large form of P. lindheimeri (2516), P. sphaerocarpon (2507),
P. microcarpon (2511)
Collected at same location but not illustrated here: P. angustifolium,
P. commutatum, P. ravenelii

Scale unit = 1 dm



Hybridity in the Dichanthelia

On the Atlantic and Gulf Coastal Plains where 10 or more species of dichanthelia commonly grow in close proximity, clearly intermediate plants between two given entities are not evident. Instead a complex reticulation of forms seems to exist. Towards the periphery of the range of the dichanthelia, more than four species of these plants are rarely found together. In such areas, occasional intermediate plants may be conspicuous. In Wisconsin, Shinnars (1944) reported possible hybrids between such dissimilar dichanthelia as Panicum praecocius and P. scribnerianum as well as P. linearifolium and P. praecocius. He also mentioned hybrids between P. implicatum and P. meridionale, P. implicatum and P. praecocius, as well as P. implicatum and P. tsugetorum.

In the course of the present study, I have repeatedly encountered occasional plants intermediate in their morphological characters between two wide-ranging and well defined species occupying the same general area. For example, in a prairie remnant located in Pocahontas County, Iowa, P. leibergii and P. praecocius occurred in abundance. In the summer of 1962, I collected in this area a single individual (2107) intermediate in most respects between these two distinct species. This putative hybrid is totally sterile but the transplant (Figure 8 A) is still vigorously growing after three years in the experimental garden.

Perhaps this plant is as deserving of specific rank as "species" such as P. deamii, P. wilmingtontense, P. shastense, P. benneri, P. bennettense W. V. Brown, and P. pinetorum Swallen which are also based on single more or less sterile specimens. It is possible that the

latter represent only occasional non-perpetuating hybrids.

Panicum wilcoxianum is placed by Hitchcock and Chase in their group Oligosanthia along with P. scribnerianum primarily because of its large and strongly nerved spikelets. Actually its affinity with the Depauperata, characterized by uniquely narrow and elongate blades as well as prominently nerved spikelets, appears more likely. Inferential evidence indicating that midwestern plants of P. wilcoxianum are possibly of hybrid origin is presented below.

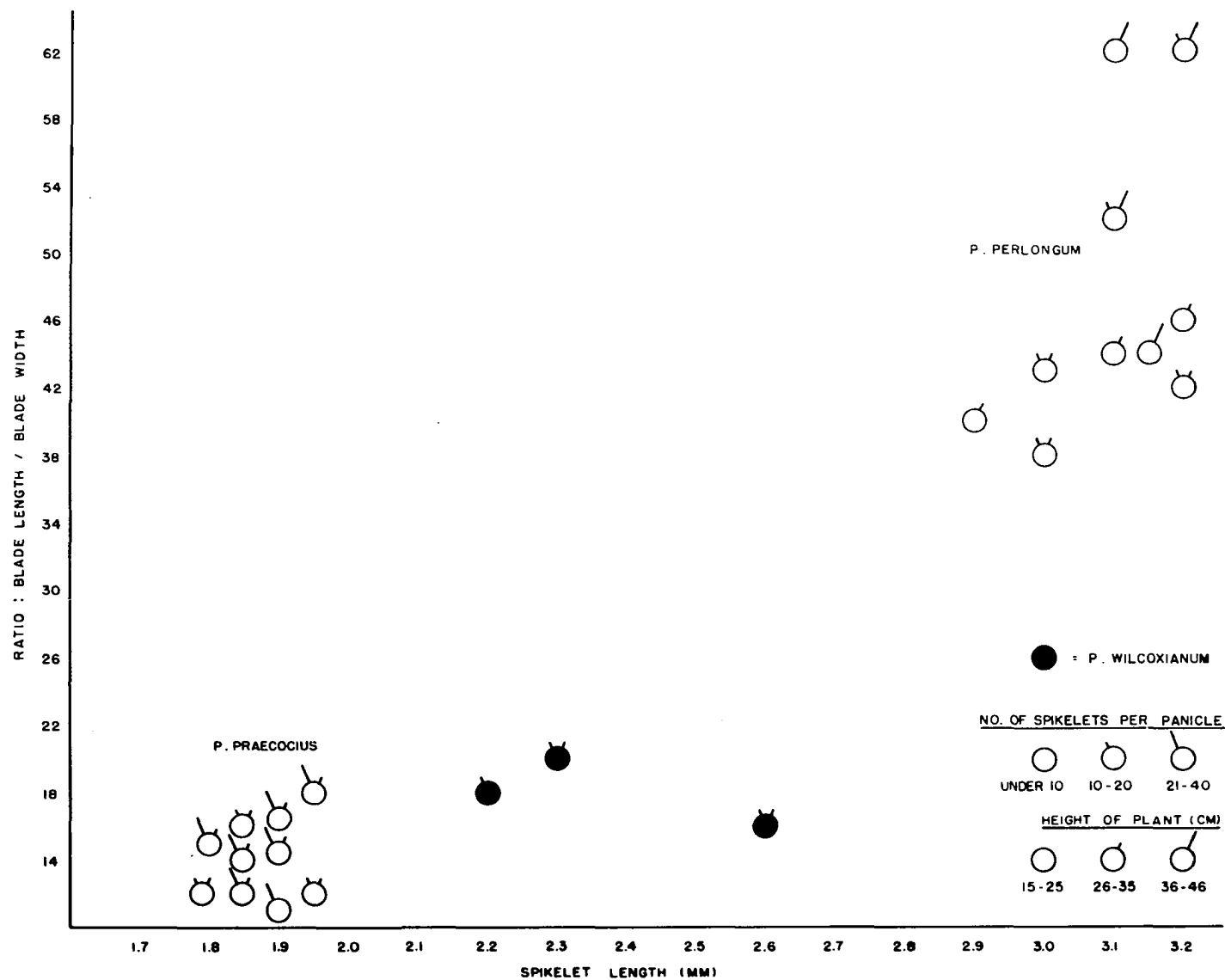
On a hilly prairie remnant north of Ames, Iowa, P. praecocius was found in abundance along with P. perlongum, P. scribnerianum, and P. leibergii. In a disturbed area partially denuded of vegetation, on the fringe of this prairie, three rosettes of P. wilcoxianum were found after much searching. Small population samples of P. perlongum and P. praecocius were taken and compared with the specimens of P. wilcoxianum. Results of this analysis are presented in Figure 35 and the plants are illustrated in Figure 33 D. The analysis shows that the P. wilcoxianum plants are intermediate between P. perlongum and P. praecocius. The following year a dense growth of weeds covered the disturbed area and while P. praecocius and P. perlongum were still abundantly represented in the adjacent prairie relic, P. wilcoxianum was apparently no longer present.

In a similar habitat near the Ames High School, in Iowa, a comparable situation was observed. During the summers of 1960 and 1961, frequent and intensive collecting was conducted and no individuals of P. wilcoxianum were found. Part of this area was subsequently greatly disturbed in connection with a building project and wide strips of ground were totally denuded of vegetation by bulldozers. In the summer of 1963, P. wilcoxianum

was found growing in abundance along with common weeds invading the bare ground. These plants were partially fertile, and robust uniform progeny were obtained from one individual (Figure 21 D). In this location Panicum perlongum is rapidly disappearing while P. praecocius and P. wilcoxianum are still found in abundance on the fringe of the prairie relic.

Despite the admission by some workers that occasional hybrids are produced in the subgenus Dichanthelium, only Church (1929) has seriously considered the hypothesis that many rosette forming species of Panicum are relatively recent products of hybridization. His views were based primarily on observations of meiotic irregularities in some of these grasses. His findings have been reviewed in an earlier chapter.

Figure 35. Analysis of population sample including Panicum praecocius, P. wilcoxianum, and P. perlongum from Story Co., Iowa (see Figure 33 D)



GENERAL DISCUSSION

Breeding Structure in the Dichanthelia

Anthesis and pollination

On the basis of my observations concerning anthesis and pollination in the dichanthelia, there appears to be little doubt that the account of this process communicated by Hitchcock to Hackel in 1906, and repeated by Hitchcock and Chase (1910, 1950) inadequately describes anthesis in most dichanthelia. It is only descriptive of anthesis in a few atypical species of the subgenus such as Panicum clandestinum, and P. depauperatum under certain conditions. In most of the species studied, the flowers are primarily autogamous with small anthers about 0.5 mm long; in a few plants such as P. aciculare most of the spikelets produced are cleistogamous. However, occasionally spikelets of the larger panicles possess relatively long anthers (1 mm), well exerted at anthesis. It is therefore conceivable that occasional cross pollination occurs among spikelets of the same panicle or among various inflorescences of the same plant.

The view that selfing is preponderant among dichanthelia is supported by bagging experiments. Panicles enclosed before anthesis consistently yielded at least as many full caryopses as free panicles of the same plant.

It is also possible that cross pollination between neighboring plants occurs in the wild. This type of pollination would probably take place between individuals of the same species or race growing in dense populations. However, rosettes of different species are often growing very close to one another and in such situations, pollination between

plants of different species could occur.

Stebbins (1950) states that self pollination, whether it be autogamy or cleistogamy, is probably a degenerate condition derived from cross pollination in response to selection pressure for immediate fitness. He convincingly demonstrates that this type of selection occurs primarily in annuals and short-lived plants growing in extreme environments, such as deserts or arctic regions. However, Stebbins recognizes also that some short-lived annuals are cross fertilized while long-lived plants such as species of Stipa and Danthonia exhibit a high degree of self pollination. To explain this apparent paradox, Stebbins postulates that the latter types of plants occur in areas with great climatic fluctuations or in pioneer associations which must be able occasionally to build up rapidly similar populations from seed in the ground. This explanation appears to account for the establishment of a high degree of selfing among dichanthelia. Indeed while species confined to relatively stable and mesic conditions such as Panicum commutatum and P. dichotomum seem to exhibit the greatest tendency for cross-pollination, plants growing in pioneer habitats such as P. lanuginosum (sensu lato) are primarily autogamous, and grasses of the subgenus occurring under the more extreme xeric conditions, such as the Depauperata and Angustifolia, show a high degree of cleistogamy.

It is possible that the caespitose and autogamous dichanthelia which generally possess the ability of forming very large numbers of seeds have been derived from more aggressively spreading rhizomatous forms with relatively few chasmogamous spikelets such as occur widely in the subgenus Panicum as well as in some related genera. Stebbins

demonstrates such a relationship between types of fertilization and growth habit in certain grass genera. Thus the dichanthelia by depending primarily on self fertilization and large seed production would have sacrificed much of their genetic flexibility for immediate adaptiveness.

Progeny and population structure

Seed for progeny tests were obtained primarily from large terminal panicles in which cross fertilization is more likely to occur. Nevertheless, with rare exception, the progeny studied were extremely homogeneous. Two progeny of the second generation were grown and found to be similarly uniform.

Samples of "races" were taken throughout the eastern part of the United States where these plants exhibit the maximum abundance and diversity. They also usually exhibited remarkable morphological uniformity.

A feature of population structure in the dichanthelia which has received little attention was emphasized in this study, namely the fact that a relatively large number of similar "species" repeatedly occur in close association with each other throughout their geographical range. These extensive "mixed populations" are usually composed of a variable number of very homogeneous "races". Some races are represented by scattered plants occupying more or less definite ecological niches. Panicum commutatum and P. dichotomum form such associations. Other races such as those formed by P. lanuginosum and P. wilcoxianum are often represented by a very large number of similar individuals occupying

disturbed habitats. In addition scattered and atypical individuals are also found in most populations which cannot be referred with certainty to any of the "species" represented in the same area.

While the occurrence of numerous uniform lines can probably be explained in a group of plants which is primarily self-fertilized, the presence of individuals exhibiting all types of morphological intergradations suggest that many of these lines or species are not totally separated by barriers of reproductive isolation.

A similar population structure has been described by Harlan (1945b) in the Bromus carinatus. In these grasses, chasmogamy and cleistogamy also occur and the expression of these pollinating mechanisms is influenced by environmental conditions. However, unlike the dichanthelia, most of these plants are hexaploids and have possibly reached a more advanced stage of relative stabilization. Also the number of "species" involved in the complex described by Harlan is not as high as that found in the subgenus Dichanthelium.

Certain species of Stipa also exhibit facultative cleistogamy but cross pollination seems to play a more important role in the reproduction of these plants.

Hybridity

Since Lotsy (1916) first suggested on the basis of little evidence that hybridization might play a major role in evolution, the importance of this process in the speciation of certain groups of plants has been amply demonstrated. Stabilization of the hybrid derivatives has frequently resulted from subsequent introgression or polyploidy. The subject has

been clearly and thoroughly reviewed by workers such as Anderson (1949) and Stebbins (1950, 1952, 1959).

Ullmann (1936) listed 74 known natural hybrids and 64 reported artificial hybrids in the Gramineae. The majority of these crosses were interspecific, and the F_1 generation exhibited all stages from complete sterility to normal fertility. In recent years the number of reported grass hybrids has been considerably augmented. Knobloch (1963) states that there are approximately 2000 reported hybrids in the gramineae.

The extent and role of hybridization in the subgenus Dichanthelium has not yet been clearly determined. On the basis of his observations of meiotic activities in a few species of the subgenus, Church (1929) expressed the view that hybridization played an important part in the evolution of this group. However, Gould (1958) studied meiosis in a far greater number of species growing in Texas where these grasses are well represented and he reported no evidence of recent hybridization among dichanthelia.

On the basis of morphological evidence, Shinnars (1944) has reported occasional putative hybrids among dichanthelia. I have earlier presented inferential evidence of the same nature.

The peculiar population structure of the dichanthelia, characterized by numerous more or less intermediate races exhibiting various degrees of sterility and ordinarily growing in disturbed habitats, suggests strongly that hybridization plays more than a minor role in speciation of these plants, at least in the heart of their present geographical range. If this were true, some of the partly fertile forms resulting from hybridization, whether they represented F_2 segregates or more

likely backcross types, would rapidly establish new homogeneous lines, while others because of inviability, weakness, or sterility would either disappear from the population or be represented by isolated individuals. This type of hypothetical population resembles closely many of the "mixed" populations of *dichantheria* encountered throughout the range of these plants and particularly on the Atlantic and Gulf Coastal Plain. The few polyploid species reported to date might represent a subsequent stage in the evolution of the subgenus.

Evidence that a similar phenomenon occurs in wild populations of violets has been produced by Brainerd (1924) and others. The occurrence of cleistogamy in these plants is well known. Natural interspecific hybrids between eastern North American species such as *Viola pedatifida* G. Don. and *V. sagittata* Ait. yield a variety of types in the F_2 and F_3 . As expected, many of these segregating forms resemble one or the other parental species but dissimilar types are also produced which eventually breed true. The strong likelihood that the unwary taxonomist will create many species out of such forms "according to the hasty methods of ordinary practice" is not ignored by Brainerd. Considering this same example, Stebbins (1950) suggested the possibility that some of the stable species with unusual leaf forms such as found in *V. palmata* L., *V. triloba* Schw., and *V. viarum* Pollard might have been derived by the stabilization of hybrid derivatives.

More definite proof of the importance of hybridization in the evolution of the subgenus *Dichantherium* will probably have to be obtained from breeding experiments and additional studies of meiotic behavior. The small size of spikelets and anthers would cause great difficulty in

emasculatation of dichanthelia but it should be possible to enclose together large panicles of different species which bear spikelets with long and well exserted anthers. Caryopses resulting from cross pollination might be obtained in this manner. Earlier phenological studies (Lelong 1960) have revealed that most species of dichanthelia undergo anthesis in their terminal panicles almost synchronously.

In any event, the possibility that many of the present day ill defined "species" of dichanthelia are relatively recent derivatives of hybridization deserves to be seriously considered. It is probable that man-made disturbances such as those accompanying logging and road construction have greatly aided this process. Additional possible morphological indications of this phenomenon should be obtained. Until now, the rare hints of species associations in the subgenus are provided by the unusually large number of accidentally "mixed" herbarium sheets which include even type material (Figure 20 D).

In the future, the collecting method advocated earlier should be followed if an eventual elucidation of interrelationships among dichanthelia is to be even partially attained. Specimens of all "species" occurring in a given population should be collected and the relative abundance and ecological preference of these entities should be indicated whenever possible.

Apomixis

Among grasses, apomixis seems to be particularly widespread in the subfamilies Panicoideae and Eragrostoideae; it has been reported in many genera of the tribes Paniceae, Andropogoneae, Chlorideae, Eragrosteae,

and Pappophoreae (Brown 1958, Brown and Emery 1958). At least four species of the subgenus Panicum are known to be apomictic. Brown and Emery (1958) have hypothesized that although most of the known apomictic grasses are polyploid and perennial, many of the sexual species of the Panicoideae whether they be diploid, polyploid, perennial, or annual probably contain "one or a few of the many genes necessary for an effective, balanced apomictic system" which can be brought together by hybridization and polyploidy.

The pattern of variation exhibited in the population of dichanthelia examined shows much similarity to that reported in certain apomictic groups, such as some species of Poa in which apomixis and sexual reproduction occur (Muntzing 1940). Facultative apomixis may occur in the subgenus Dichanthelium and be one source of taxonomic difficulties. However the evidence which we now possess rather supports the view that self-fertilization and occasional hybridization have given rise to the unusual population structure of the dichanthelia. Furthermore, the apparent occurrence of occasional hybrids in these predominantly self pollinated grasses, although it is no indication of a total lack of apomixis, would tend to suggest that sexual reproduction plays a dominant role in the propagation of the species. If our contention that hybridization plays an even greater part than suspected in the evolution of these plants is correct, the case for apomixis will be further weakened.

It is Stebbins' (1950) opinion that on the basis of the evidence at hand, "apomixis and self fertilization appear as mutually exclusive genetic systems" and that "apomixis has not developed in self fertilizing plants". It is true however that the majority of dichanthelia appear

not to be exclusively self pollinated.

Assessment of Taxonomic Characters

Hitchcock and Chase arbitrarily divided the subgenus Dichanthelium into 17 groups on the basis of growth habit, spikelet and blade size as well as pubescence features including ligule length. While such associations as the Depauperata, Laxiflora, Angustifolia, Sphaerocarpa, and the Latifolia appear quite distinct, others such as the Scoparia, Columbiana, Spreta, and Ensifolia appear to include forms which vaguely resemble each other.

On the basis of observations reported earlier, spikelet size and general blade conformation appear to be fairly reliable taxonomic traits which are easily observable, but ligule and other pubescence characteristics should be used with caution. For example, not uncommonly plants in the Lanuginosa complex possess glabrous sheaths and blades on the upper part of the primary culm, while lower leaves of the same plant are densely hairy. Differences of this type are accentuated if one compares upper cauline leaves with younger blades on axillary branches of the same grasses. The presence of double pubescence, mentioned by Silveus (1942), Shinnars (1944), Pohl (1947), and others is even more widespread than once suspected, and constitutes an additional confusing factor in the use of pubescence as a taxonomic trait. It is naturally more easily discernible in those "species" which possess few long hairs among a dense puberulence. However, a number of entities in the subgenus Dichanthelium and particularly in the Lanuginosa and the Columbiana groups possess a dense and heterogeneous mixture of hairs approximately

equal in size, but differing in nature, some being stout, ascending and papillose, others being thinner and either appressed, spreading or reflexed.

In some of the specimens examined, the upper part of one sheath was glabrous, while the middle section was sparsely covered with medium sized hairs, and the lowermost part was clothed with rather long reflexed hairs eventually forming a dense ring of retrorse hairs slightly above the node. Similarly the pubescence pattern of the adaxial blade surface often varies greatly, even on leaves of the same culm. The majority of forms in the *Lanuginosa* complex possess at least a few long hairs at the base of the upper surface of the blade and it is generally very difficult if not impossible to distinguish clearly between these long trichomes and the ligule proper. In somewhat pubescent leaves, hairs are found scattered in the marginal area only, while in densely hairy blades, the entire adaxial surface is covered with long hairs, the longest hairs usually being found along the margins and at the base. Occasionally the gradient is reversed and the distal part of the sheath and of the blade only are clothed with vestiture.

It seems, therefore, advisable not to utilize pubescence criteria too rigidly in the classification of the *dichanthelia*. Yet many of the species recognized by Hitchcock and Chase are separated on this basis. For example, the coastal *Panicum villosissimum* and *P. commonsianum* appear to be very closely related species. I have often collected them in the immediate vicinity of one another on the Atlantic Coastal Plain. While extreme forms of one or of the other can be distinguished, a number of individuals cannot be referred with certainty to one or to the other

species on the basis of their pubescence pattern. Ligule length in both species is identical although the usually denser long pubescence present on the adaxial blade surface of Panicum villosissimum, which is particularly well developed at the base of the blade, might easily be mistaken for the ligule. It appears that this oversight was made by Hitchcock and Chase. Consequently P. villosissimum was placed by them in their Lanuginosa grouping which includes all species possessing a ligule while P. commonsianum, in which the obsolete ligule is not concealed by dense long hairs, belongs to their "liguleless" Columbiana group.

Differences in pubescence characteristics are often accentuated if plants are compared at different stages of their development. Immature individuals possess shorter pubescence than mature grasses and plants collected late in the summer often appear to have more nearly glabrous primary culms as certain types of trichomes easily break or are worn off. This is particularly evident in grasses such as some Oligosanthia possessing stiff papillose pubescence. Long thin hairs similar to those found in P. villosissimum and P. praecocius are more flexible and not as readily broken off, but they tend to become greatly tangled late in the growing season.

Spikelet length appears to provide the most stable and reliable criterion for species separation in the subgenus Dichanthelium although differences of 0.2 mm among spikelets of the same panicle are not uncommonly found. Immature spikelets are somewhat more elongated than plump spikelets containing mature caryopses, especially in species like P. sphaerocarpon in which the mature spikelets are often semi-spherical.

Many individuals produce few or no caryopses in their inflorescences and this phenomenon should be taken into account when describing their spikelets.

It is surprising that many species of *dichantheria* are separated by Hitchcock and Chase on the basis of slight and inconsistent differences in spikelet length and in pubescence pattern, while much greater latitude in the same characters is allowed by these authors in the description of other species of the genus Panicum. For example in the fairly well defined *Laxiflora* grouping of the subgenus Dichantherium, Panicum laxiflorum presumably possesses spikelets 2.2 to 2.3 mm long and "leaves glabrous on both surfaces, sparsely ciliate" or occasionally pilose, while P. xalapense is described as having spikelets 1.9 to 2.0 mm long and blades "pilose on one or both surfaces or nearly glabrous, usually short ciliate". The majority of the 115 species recognized by Hitchcock and Chase in the subgenus Dichantherium are quite as poorly defined as the above entities. Yet P. dichotomiflorum Michx. placed in the subgenus Panicum is said to bear spikelets 2.0 to 3.2 mm long, and it is admitted that the "upper surface of some or all of the blades is either glabrous or sparsely pubescent or even densely pilose". This grass is somewhat atypical of most true Panicum, and resembles many *dichantheria* in its ability to produce numerous axillary branches and inflorescences. Many similar examples of inconsistency in the taxonomic treatment of the genus Panicum could be presented.

General growth habit and branching pattern can be used satisfactorily in conjunction with other criteria to identify such distinct species as P. laxiflorum, P. depauperatum, and P. dichotomum. However,

members of the *Lanuginosa* and *Columbiana* groups often exhibit a wide assortment of growth forms, briefly described in a preceding chapter. Some of this polymorphism is not uncommonly displayed on culms of the same plant. It is therefore necessary to collect generous specimens representing as fully as possible the range of variations in a given mature individual. The types of *Panicum auburne* (Figure 40 D), *P. lanuginosum* (Figure 44 A), and *P. ovale* (Figure 49 C) as well as a great number of other specimens examined by me fail distinctly in this respect.

As suggested by Shinnars (1944), individuals of the subgenus *Dichanthelium* should be collected and identified after expansion of the terminal panicles and prior to excessive axillary branching.

Taxonomic Views Concerning the Subgenus *Dichanthelium*

In the preceding pages I advanced a hypothesis concerning speciation in the subgenus *Dichanthelium* based on observations of floral biology, progeny variation, and population structure in these grasses. It has been recognized by numerous workers that plant groups in which predominant self fertilization and occasional hybridization occur do not lend themselves readily to standard taxonomic treatments. The difficulties presented by such complexes are similar in many respects to those exhibited by apomictic plants. There is no doubt that the same problems have been faced by the numerous botanists which have attempted to classify the dichanthelia. Their work has been partially reviewed in a previous chapter.

Many "kinds" of species have been described in the subgenus.

Panicum sphaerocarpon, P. xalapense, P. commutatum, P. dichotomum, P. depauperatum, P. aciculare, P. boscii, P. scribnerianum, and P. lancearium are generally "good", moderately variable and widespread species, many of which occur in the southernmost part of the range of the subgenus. Along with possibly a few other entities, they could be said to exhibit the fundamental morphological characteristics encountered throughout the entire subgenus Dichanthelium and to represent possibly the "nuclei" from which all other forms of dichanthelia have been derived.

Other "species" of dichanthelia show an obvious affinity to the ones just mentioned. For example, the northern P. latifolium appears closely related to the southern P. boscii. Similarly P. cryptanthum Ashe is morphologically inseparable from P. scabriusculum Ell.; P. ashei Pearson, P. mutabile Scribn. and Smith ex Nash, and P. joorii Vasey revolve around P. commutatum; P. perlongum Nash, P. linearifolium Scribn., and P. wernerii Scribn. share much in common with P. depauperatum. Hitchcock and Chase recognized the great similarity within each of these clusters of species and included them in their better defined groups. Fernald went a step further by including many of them in the synonymy.

Still other "species" appear clearly defined morphologically and geographically but they show a more obscure affinity with other species, for example the northern P. leibergii and the southern P. pedicellatum, P. scoparium and P. lanuginosum, P. thurowii and P. lanuginosum, P. ovinum and P. aciculare. However the bulk of the 115 species recognized by Hitchcock and Chase exhibit all types of more or less perceptible

intergradations between some of the species just mentioned; their specific boundaries have been so strictly circumscribed that few of their presumed representatives in the wild possess the same combination of characteristics arbitrarily selected to define each of these "species". When attempting to identify such entities one is led to several choices, none of which are satisfactory.

Finally, some "species" labelled as rare by Hitchcock and Chase appear to be merely sterile derivatives of sporadic hybridization. Among such forms we could include Panicum calliphyllum Ashe, some of the forms described as P. bicknelli Nash, as well as P. shastense and P. wilmingttonense.

In brief, two major alternatives are offered in the classification of such an assemblage of plants. The first choice consists in describing all minor local variants encountered in the field as new species. In this case the number of taxa recognized by Hitchcock and Chase would be multiplied several fold. Ashe and Nash obviously subscribed to this view, and the impracticability of this method has been clearly demonstrated.

The other choice consist in establishing wider specific boundaries while recognizing the more obvious variants as taxonomic varieties. This view was largely adopted by Fernald and Gleason with some measure of success.

Hitchcock and Chase (1910, 1950) adopted a course somewhat between these alternatives. They recognized clearly the weakness of indiscriminate "species naming" but they appear not to have gone quite far enough in the elimination of doubtful or indistinguishable taxa within the

subgenus. Such species as Panicum tennesseense, P. lanuginosum, P. huachucae, P. pacificum, P. occidentale are clearly inseparable even on the basis of criteria proposed by them. In all fairness to them, it should be noted that the confusion existing in the taxonomy of Panicum subgenus Dichanthelium at the turn of the century was extreme and that their classification of these grasses constituted a great improvement.

Fernald recognized early that many of the species proposed by men such as Ashe and Nash and later retained by Hitchcock and Chase were too narrowly delimited to be of any practical value. The realignments suggested by Fernald (1934) led to a notable improvement in the taxonomy of the subgenus Dichanthelium. One of the main virtues of his treatment lies in recognizing two large polymorphic complexes within the Lanuginosa and Columbiana groups, centering around P. lanuginosum and P. villosissimum respectively, and consequently in eliminating several inseparable "species". However, certain species which he described such as P. glutinoscabrum and P. benneri appear as elusive as the ones he eliminated. Fernald's retention of such species as P. subvillosum and P. auburne is also questionable. In addition, many troublesome species of dichanthelia are outside of the geographical range covered by Fernald in Gray's Manual.

LANUGINOSA AND COLUMBIANA: MORPHOLOGICAL
VARIATION AND TAXONOMIC INTERPRETATION

Hitchcock and Chase (1950) recognized 28 species and 2 varieties in their groups Lanuginosa and Columbiana in the United States. In the same groups, Fernald included 10 species and 9 varieties in the Northeastern United States, while Gleason modified Fernald's treatment slightly and recognized 9 species and 11 varieties in the same region. Seven of Hitchcock's species not treated by these two authors are outside of the geographical range covered in their manuals. A summary of these taxonomic dispositions has been presented in Table 1.

Panicum lindheimeri, regarded as a variety of P. lanuginosum by Fernald and by Gleason, differs from plants of the Lanuginosa and Columbiana groups in its completely glabrous character as well as in its elongated internodes and dense, strict fascicles of secondary branches. It was placed by Hitchcock and Chase in the Spreta grouping, which in turn appears related to the Ensifolia and Dichotoma groups. I have not included discussion of P. lindheimeri and of related species in the current work.

Following, I shall attempt to determine whether in fact specific delimitations among taxa proposed by Hitchcock and Chase are demonstrable, whether the alternative views proposed by Fernald and modified by Gleason are more satisfactory in this respect, or whether further modifications in the classification of the Lanuginosa-Columbiana complex appear warranted.

All specimens examined in the interpretation of the treatment of

Hitchcock and Chase were either identified or annotated by them. Of the 28 species recognized in these groups by Hitchcock and Chase, I was able to examine the types of 22, as well as photographs and original descriptions of the remainder. Other types, representing species reduced to synonymy by Hitchcock and Chase, were also examined. A list of herbarium specimens studied is presented in the appendix to this paper.

An effort was made to represent diagrammatically only adequate specimens collected prior to excessive axillary branching. Unfortunately some species of *Lanuginosa* are based on fragmentary or deficient specimens. The types of *Panicum lanuginosum* and *P. ovale*, described by Elliott, consists merely of the upper part of very immature culms with the panicles still mostly included in the uppermost sheath. Similarly the type material of *P. thermale* is an immature plant. The type specimens of *P. columbianum* var. *thinium* and *P. oricola* are profusely branching and spikelets of terminal panicles have fallen.

Geographical Range of Species

in the *Lanuginosa* and *Columbiana* Groups

The majority of the 28 species recognized by Hitchcock and Chase in their *Lanuginosa* and *Columbiana* groups are said to occur throughout the eastern part of the United States. A few entities such as *P. huachucae* and *P. tennesseense* presumably extend as far west as Utah and California respectively, while *P. columbianum*, *P. subvillosum*, *P. tsugetorum*, *P. implicatum*, and *P. albemarlense* are reportedly found in the Northeastern United States and adjacent Canada. Other species such as *P. commonsianum*, *P. addisonii*, *P. oricola*, *P. ovale*, and *P. malacon* are largely restricted

Table 7. Geographic distribution of species in the Lanuginosa and Columbiana groups (Continental United States)

Species	Atlantic Coastal Plain	Gulf Coastal Plain	Appalachian, Great Lakes Regions	Eastern Deciduous Forest	Prairie	Great Plains	Western United States
<i>P. huachucae</i>	x	x	x	x	x	x	x
<i>P. tennesseense</i>	x	x	x	x	x	x	x
<i>P. scoparioides</i>	x		x		x	x	
<i>P. villosissimum</i>	x	x	x	x	x	x	
<i>P. pseudopubescens</i>	x	x	x	x	x		
<i>P. tsugetorum</i>	x		x	x	x		
<i>P. implicatum</i>	x		x	x	x		
<i>P. columbianum</i>	x		x	x			
<i>P. meridionale</i>	x		x	x			
<i>P. albemarlense</i>	x		x	x			
<i>P. praecocius</i>			x		x	x	
<i>P. subvillosum</i>	x		x		x		
<i>P. auburne</i>	x	x	x				
<i>P. languidum</i>	x		x				
<i>P. lanuginosum</i>	x	x					
<i>P. commonsianum</i>	x	x					
<i>P. malacon</i>	x	x					
<i>P. ovale</i>	x	x					
<i>P. deamii</i>			x				
<i>P. oricola</i>	x						
<i>P. benneri</i>	x						
<i>P. addisonii</i>	x						
<i>P. wilmingttonense</i>	x						
<i>P. thurowii</i>		x					
<i>P. thermale</i>						x	x
<i>P. occidentale</i>							x
<i>P. pacificum</i>							x
<i>P. shastense</i>							x

to the Atlantic and Gulf Coastal Plain. In addition, Hitchcock and Chase recognized four species of *Lanuginosa* restricted to the Western United States: *Panicum occidentale*, *P. pacificum*, *P. thermale*, and *P. shastense*. This last species occurs only in Shasta County, California. Four eastern species are similarly confined to one or a few locations, namely *P. benneri*, *P. wilmingttonense*, *P. deamii*, and *P. languidum*. A summary of geographic distribution of species in the *Lanuginosa* and *Columbiana* groups is presented in Table 7. It should be noted that most of the species are sympatric over at least a part of their presumed range.

Examination of Representative Specimens

A number of specimens representing the species in the *Lanuginosa* and *Columbiana* groups are plotted in Figures 36, 37, and 38. The difficulties experienced in detecting sharp interspecific delimitations among species of this complex are clearly reflected in these illustrations. On the basis of morphological traits studied, there appears to be no consistent difference among most of the species represented. Instead one can barely discern a few overlapping "clusters" of species. We can arbitrarily separate members of the *Lanuginosa*-*Columbiana* complex into four large groups primarily on the basis of spikelet length and subdivide these groups into smaller assemblages on the basis of length of sheath pubescence in the following manner:

1. Spikelets less than 1.5 mm long, often spheroidal; blades usually less than 4.5 mm wide:
 - a. sheath with hairs 0.5 - 3.0 mm long:

P. implicatum Scribn. (IMP)¹

P. auburne Ashe (in part) (AUB)

- b. sheath puberulent often with few interspersed longer trichomes:

P. meridionale Ashe (MER)

P. albemarlense Ashe (in part) (ALB)

P. columbianum var. thinium Hitchc. and Chase (COL T)

2. Spikelets 1.5 - 1.9 mm long; blades usually over 5.0 mm wide:

- a. sheath hairs mostly 0.5 - 2.5 mm; blades predominantly lax; ligule apparently or actually to 3.0 mm long:

P. lanuginosum Ell. (LAN)

P. huachucae Ashe (HUA)

P. huachucae var. fasciculatum (Torr.) Hubb. (HUA F)

P. tennesseense Ashe (TEN)

P. pacificum Hitchc. and Chase (PAC)

P. occidentale Scribn. (OCC)

P. thermale Boland (THE)

P. subvillosum Ashe (SUB)

P. oricola Hitchc. and Chase (ORI)

P. languidum Hitchc. and Chase (LA)

P. thurowii Scribn. and Smith (THU)

¹These abbreviations are used in the illustrations presented in this chapter in lieu of specific names.

- b. sheath puberulent; blades thick with cartilaginous margins; ligule clearly obsolete:

P. columbianum Scribn. (COL)

P. tsugetorum Nash (TSU)

P. albemarlense Ashe (in part) (ALB)

3. Spikelets 2.0 - 2.7 mm:

- a. sheath with dense hairs 2.5 - 4.0 mm long; upper blade surface covered with erect hairs 2.0 - 3.0 mm long or over:

P. villosissimum Nash (VIL)

P. praecocius Hitchc. and Chase (PRA)

- b. sheath hairs 1.0 - 2.5 mm (mostly 1.0 - 1.5 mm); upper blade surface often glabrous or with scattered hairs; double pubescence often conspicuous:

P. pseudopubescens Nash (PSE)

P. commonsianum Ashe (COM)

P. addisonii Nash (ADD)

P. wilmingttonense Ashe (WIL)

P. scoparioides Ashe (SCO)

P. benneri Fernald (BEN)

P. shastense Scribn. and Merr. (SHA)

4. Spikelets over 2.7 mm:

- a. sheath hairs approximately 2.5 mm:

P. ovale Ell. (OVA)

P. deamii Hitchc. and Chase (DEA)

- b. sheath puberulent:

P. malacon Nash (MAL)

Figure 36. Morphological variation exhibited by types and other representative specimens in the Lanuginosa and the Columbiana groups

Abbreviations are explained in the list presented on pages 158 and 159.

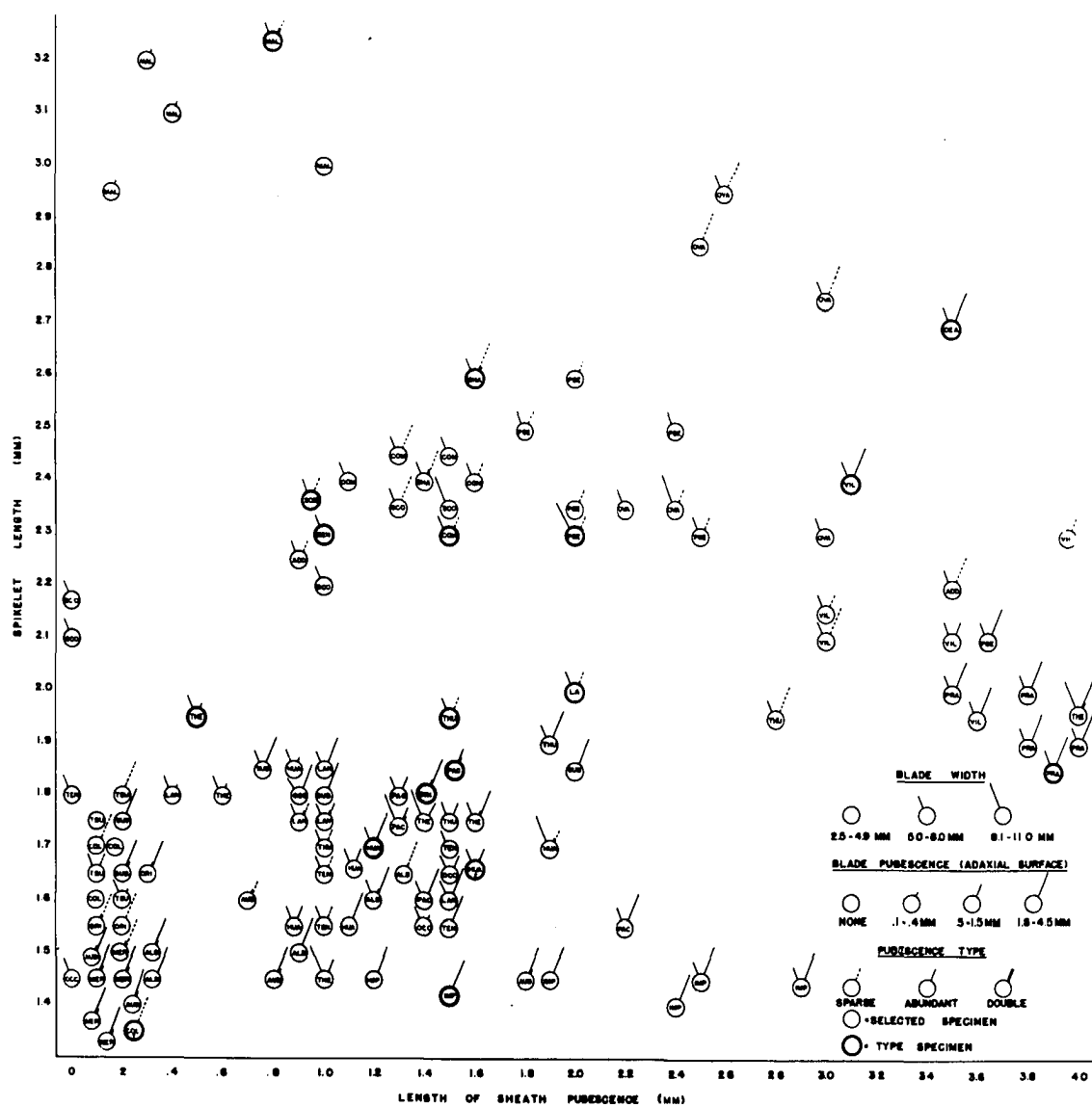


Figure 37. Morphological variation exhibited by type specimens in the Lanuginosa and the Columbiana groups

Abbreviations are explained in the list presented on pages 158 and 159.

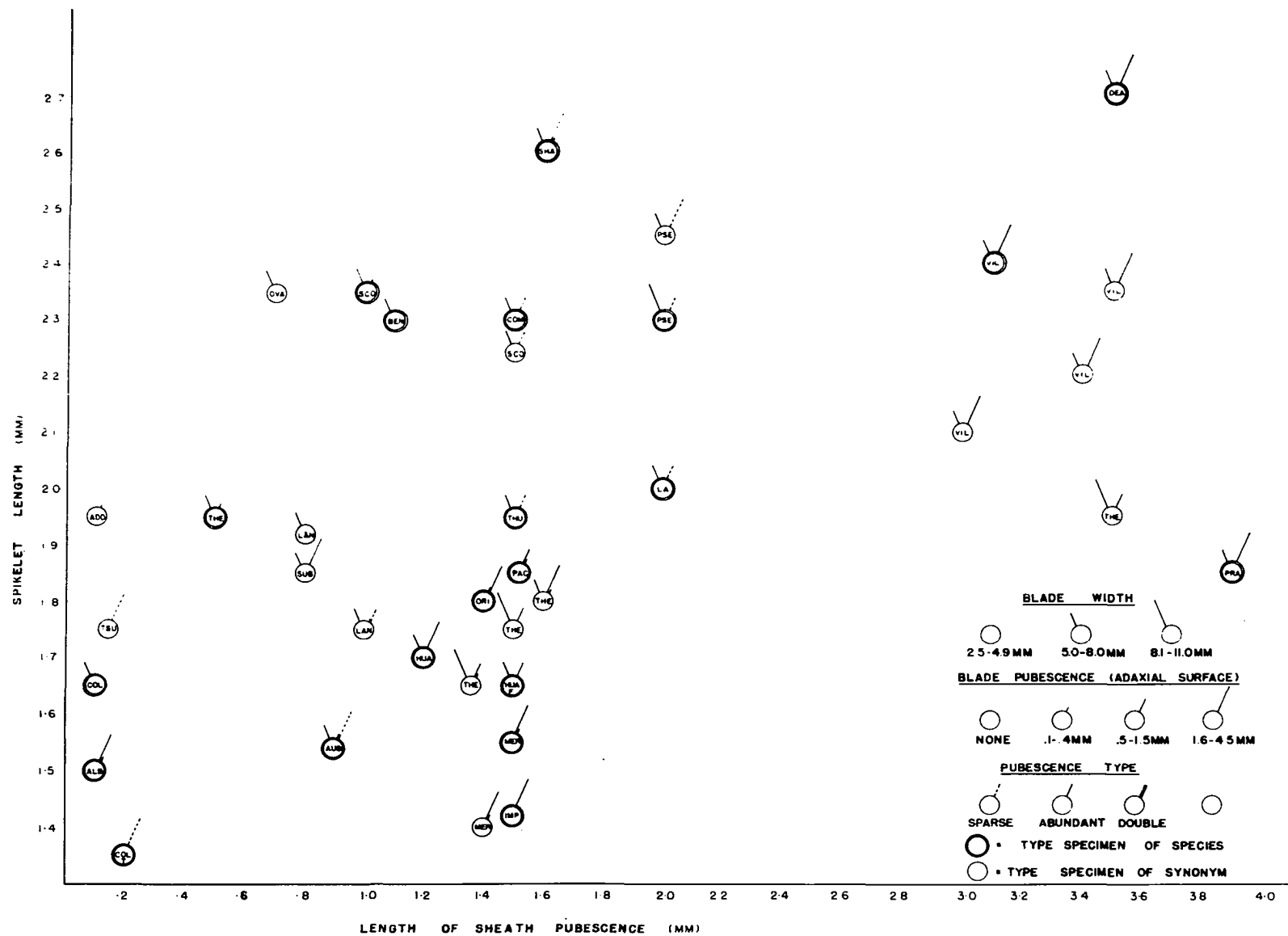
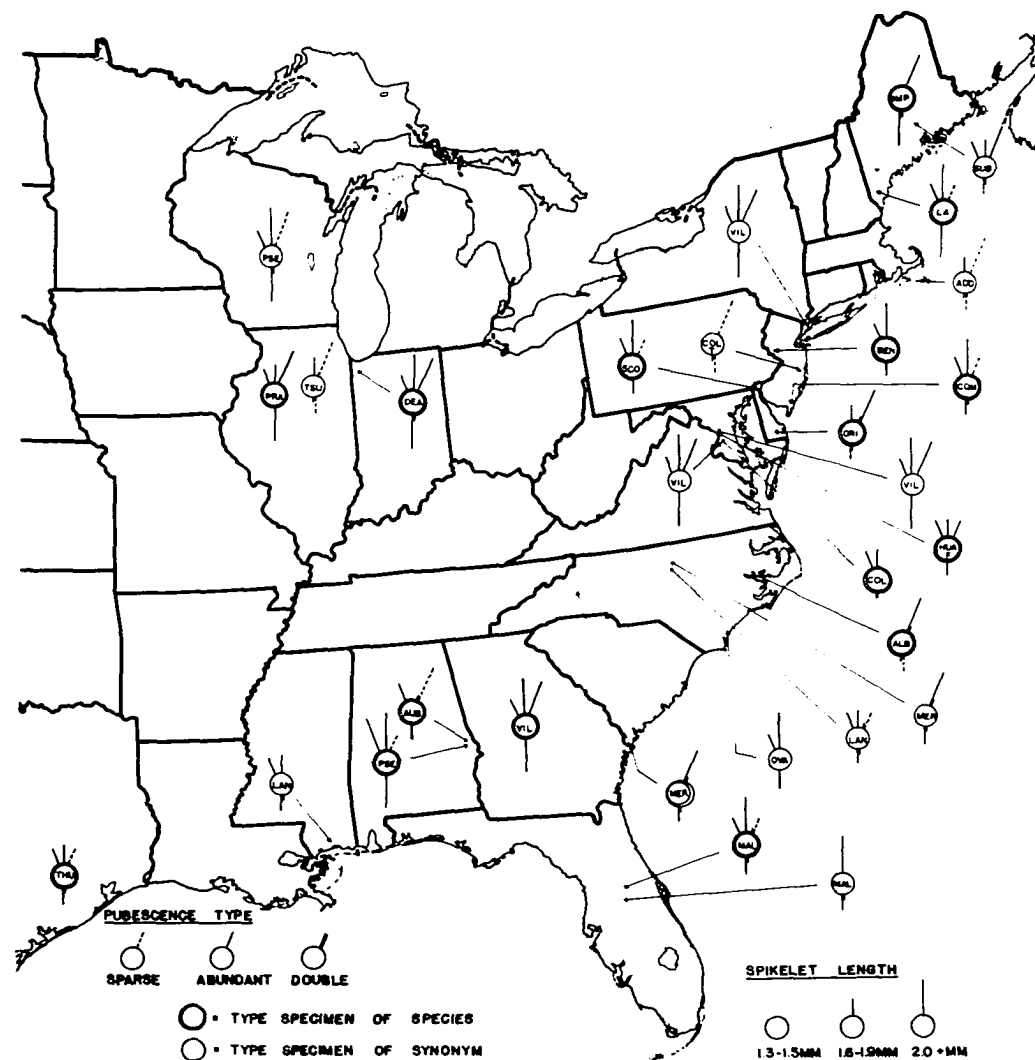
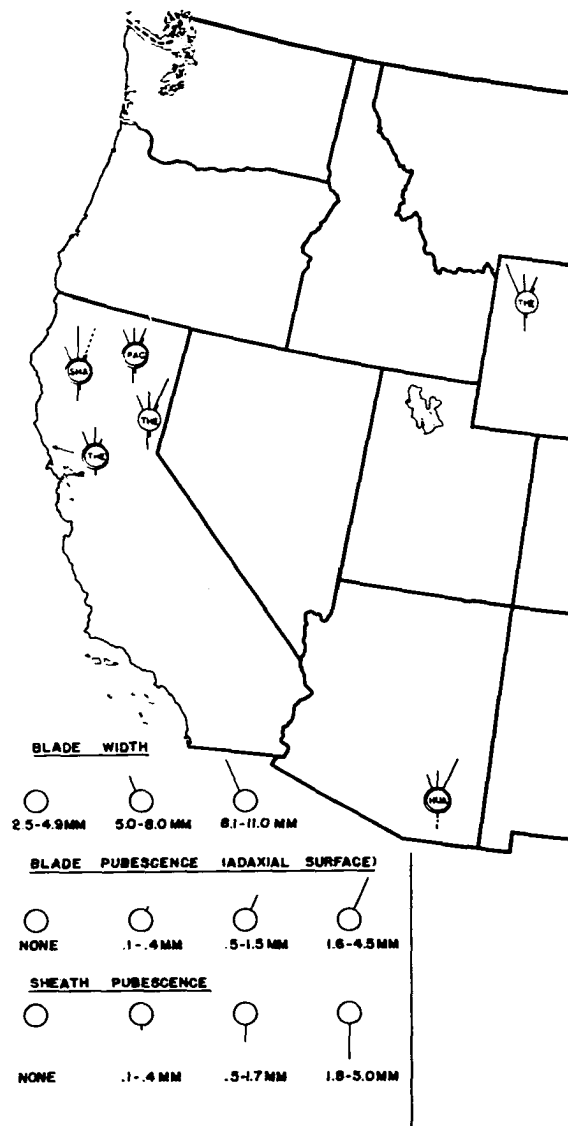


Figure 38. Geographic location and morphological variation exhibited by type specimens of species in the Lanuginosa and Columbiana groups

Type material of some taxa reduced to the rank of synonyms of these species are also represented. Abbreviations are explained in the list presented on pages 158 and 159.



In the subsequent discussion, group 1 will be designated as the Panicum implicatum - P. meridionale assemblage, group 2 as the P. lanuginosum - P. columbianum assemblage, group 3 as the P. villosissimum - P. pseudopubescens assemblage, and group 4 as the P. ovale - P. malacon assemblage.

Morphological Trends in the Lanuginosa-Columbiana Groups

The Lanuginosa-Columbiana complex appears to represent overlapping combinations of morphological traits. At one extreme we find tall, weak, and essentially glabrous plants with narrow blades forming dense fascicles of branchlets in the axils of well separated nodes late in the season. They possess small pubescent spikelets generally under 1.6 mm long. Such grasses have been assigned by various authors to P. leucothrix, P. lucidum, P. sphagnicolum, or P. longiligulatum; they were placed by Hitchcock and Chase in their Spreta and Ensifolia groups. These plants approach closely weak forms of P. lindheimeri recognized by Fernald as a variety of P. lanuginosum. Puberulent forms of the same plants have been referred to P. albemarlense, P. meridionale, P. columbianum var. thinium, while more pubescent plants come under P. implicatum.

At the other extreme are pubescent plants with wider and laxer blades often ciliate along the margins and tending to branch from the unexpanded basal nodes. These plants often possess thin hairs 3.0 mm long along the sheath or only at its base in the form of a retrorse ring of hairs. Their spikelets are pubescent and approximately 2.0 mm long. Such grasses approach P. xalapense or P. laxiflorum which form the core

of the Hitchcock and Chase "Laxiflora" grouping. Panicum villosissimum and P. praecocius possess many characters of grasses in the Laxiflora group. However the largest and most confusing assemblage of plants within the Lanuginosa-Columbiana complex consist of forms possessing a combination of traits exhibited by these two extremes. They have been included by Fernald under P. lanuginosum var. fasciculatum and by Gleason under this same variety and P. lanuginosum var. tennesseense.

Plants with pubescent sheaths and blade, and spikelets 1.6 to 1.8 mm were recognized by Hitchcock and Chase as P. huachucae, P. huachucae var. fasciculatum, and P. pacificum, while forms with more nearly glabrous blades were included by them under P. occidentale and P. tennesseense.

Pubescent plants with slightly larger spikelets up to 2.0 mm long were regarded by Hitchcock and Chase as P. languidum, P. thermale, P. lanuginosum, and P. subvillosum.

Unfortunately much intergrading of pubescence pattern either on leaves or on sheaths and of spikelet length is found within the complex, and in most cases, plants examined will not fit within the rather narrow specific limits prescribed by Hitchcock and Chase.

In addition there appears to be characters of other dichanthelia interspersed among species of the Lanuginosa-Columbiana complex. Forms of P. meridionale exhibit much the same spreading habit as well as the narrow involute blades as P. aciculare and P. wrightianum which also occur on sandy areas within the same range. Their spherical spikelets also resemble those of P. sphaerocarpon Ell. whose narrow-leaved form P. sphaerocarpon var. inflatum (Scribn. and Smith) Hitch. and Chase

in turn resembles closely Panicum columbianum. Not only are the spikelets much the same in both, but also their blades are similarly white-margined and stiff. Numerous other examples of apparent reticulation within the subgenus Dichanthelium could be presented.

Discussion

The Panicum implicatum - P. meridionale assemblage

Plants included in this assemblage are characterized by ovoidal spikelets 1.3 to 1.6 mm long and narrow leaves generally between 3.0 and 5.0 mm wide with more or less abundant long hairs on the upper blade surface. Forms with sheath pubescence between 1.5 and 2.5 mm long and dense pubescence on the adaxial leaf surface have been referred to as P. implicatum (Figures 39 and 40 A), while similar grasses possessing puberulent sheaths often with long interspersed hairs were placed by Hitchcock and Chase in P. meridionale, P. albemarlense, and P. columbianum var. thinium. While clearly puberulent forms can be assigned to P. meridionale and plants with longer hairs come under P. implicatum, the majority of specimens are intermediate between these two extremes.

The adoption of P. albemarlense for the forms with "softer, denser pubescence" and P. columbianum var. thinium for the variants with "less dense pubescence" contributes little in rendering the taxonomy of this group more natural or more practical. The type specimen of P. meridionale resembles closely that of P. implicatum (Figures 37 and 39). The type of P. albemarlense (Figure 40 B) is somewhat intermediate between these two specimens but its sheaths are predominantly puberulent; the holotype of

Panicum columbianum var. thinium approaches the latter but possesses even smaller spikelets (Figure 37). However the bulk of specimens later identified by Hitchcock and Chase as P. meridionale and P. albemarlense possess puberulent sheaths with few scattered long hairs and are totally inseparable from one another, while the majority of plants placed by them under P. implicatum possess spikelets similar to those of P. meridionale but have longer sheath pubescence (Figure 36).

Fernald regarded P. columbianum var. thinium as a synonym of P. meridionale and included P. albemarlense as a variety of this last species. I agree essentially with this view although I feel that probably P. albemarlense is not consistently distinct enough from P. meridionale (see Figure 39) to warrant a varietal ranking. Furthermore they are presumably sympatric. A tendency for conspicuous double pubescence (Figure 39) and the formation late in the growing season of depressed mats with up-curving bushy branches is noticeable in P. meridionale (sensu lato). The latter trait is also characteristic of P. aciculare and P. wrightianum, abundantly represented on the sandy Atlantic Coastal Plain (Figure 21 b).

The same prostrate autumnal form with upturned branch tips and double pubescence is often found in P. auburne (Figure 34 A, extreme right) and P. oricola. The type specimen of P. auburne (Figure 40 D) consist of two immature culms with spikelets 1.5 to 1.6 mm long and it is hardly distinguishable from P. meridionale (Figures 39 and 40 C).

P. oricola was described by Hitchcock and Chase as having double pubescence and spikelets 1.5 mm long. I have examined the type of this species and although it resembles in most respects P. auburne and

Panicum meridionale, its spikelets measure from 1.7 to 1.9 mm in length. This grass might have resulted from sporadic hybridization between the widespread P. lanuginosum var. fasciculatum and P. aciculare. However most other specimens identified by Hitchcock and Chase as P. oricola including an isotype from Cape Henry, Va. (Amer. Grass Nat. Herb. no. 152) had smaller obovate spikelets about 1.5 mm long, clear double pubescence, and narrow blades approximately 3 mm wide. They could not be separated from P. meridionale, P. columbianum var. thinium, P. albemarlense, or P. auburne (Figures 36 and 39). The type specimen might be regarded as descriptive of this elusive species, and on the basis of its spikelet length, P. oricola could be considered as a variant of P. columbianum or of P. auburne if the latter "species" is not included under P. meridionale. Fernald regarded P. oricola as a variety of P. columbianum.

Figures 36 and 37 reflect the difficulties experienced in separating even type specimens of the species just considered. The same predicament is amplified in Figure 39. P. columbianum (Figure 43 C) and its presumed variety thinium differ from the other species represented in possessing almost glabrous adaxial blade surface. However, P. columbianum (Figure 43 C) has much stiffer blades and longer spikelets than P. columbianum var. thinium (Figure 37). P. columbianum, P. oricola, P. auburne, and P. tsugetorum are distinguished from other types represented in Figure 39 by their relatively longer spikelets (see also Figure 37).

Photographs of some types of species in the P. implicatum - meridionale complex shown in Figure 40 further illustrate the similarities among species recognized by Hitchcock and Chase in this assemblage.

Figure 39. Morphological characteristics of type specimens of species in the Panicum implicatum - P. meridionale assemblage

Conspicuous double pubescence is indicated by crossbars in the graph.

- Column 1. Type of P. albemarlense Ashe (see Figure 40 B)
- Column 2. Type of P. auburne Ashe (see Figure 40 D)
- Column 3. Type of P. columbianum Scribn. (see Figure 43 C)
- Column 4. Type of P. columbianum var. thinium Hitchc. and Chase
- Column 5. Type of P. oricola Hitchc. and Chase
- Column 6. Co-type of P. meridionale Ashe (see Figure 40 C)
- Column 7. Type of P. filiculme Ashe (= P. meridionale)
- Column 8. Type of P. implicatum Scribn. (see Figure 40 A)
- Column 9. Type of P. lanuginosum var. siccanum Hitchc. and Chase (= P. tsugetorum)
(see Figure 43 D)

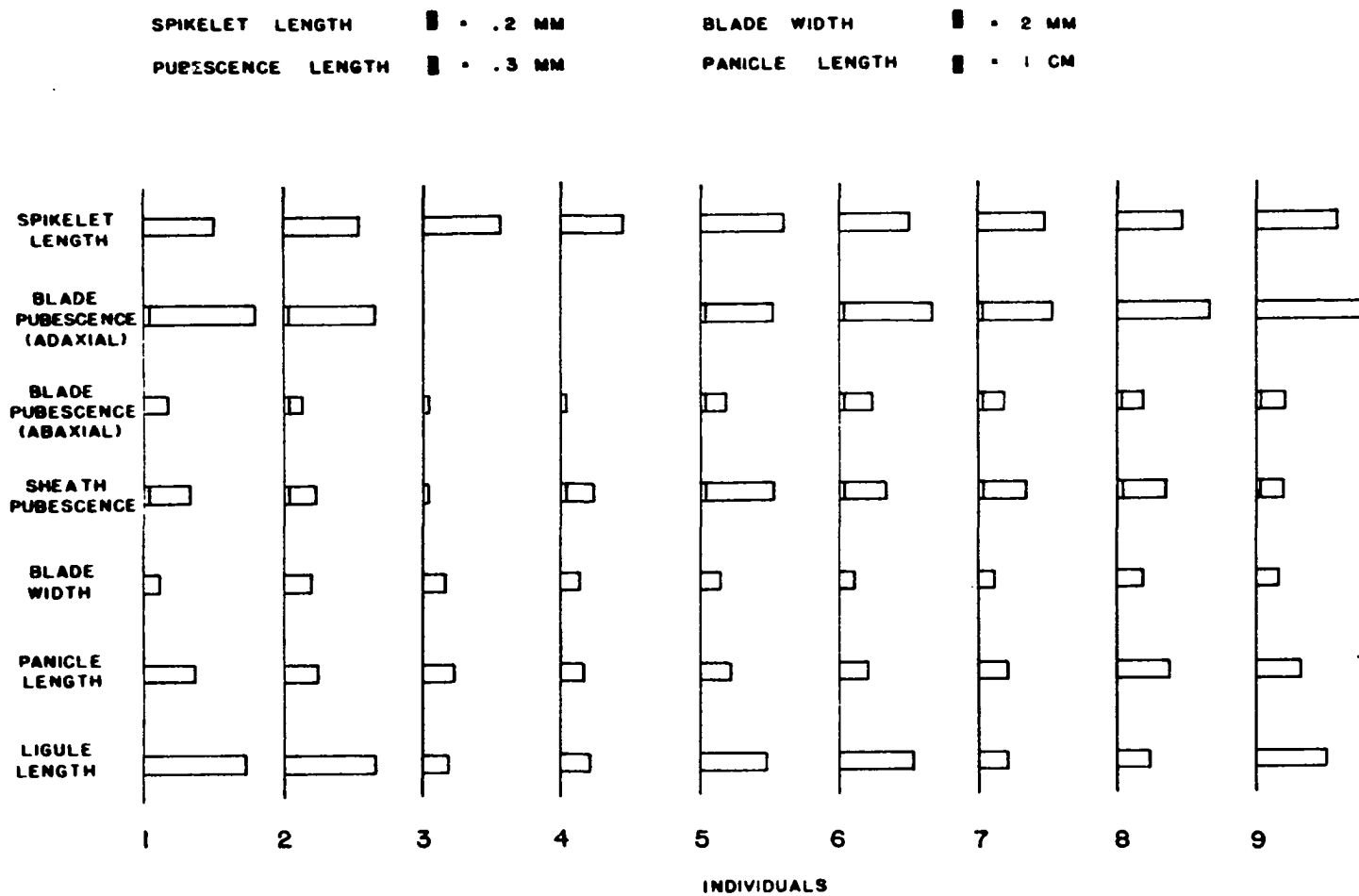
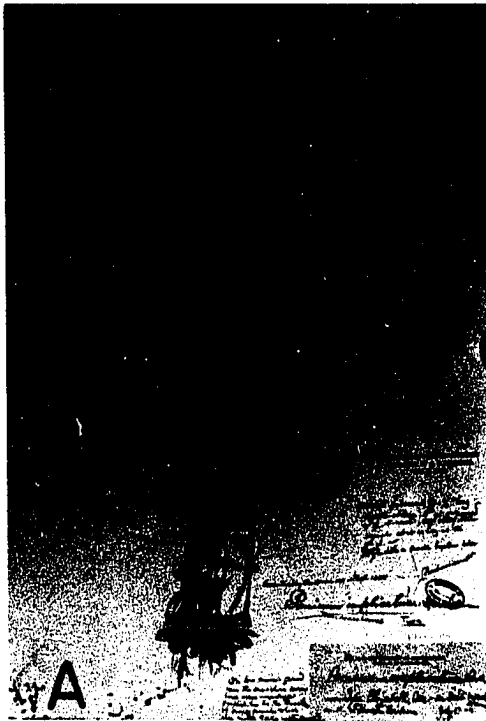


Figure 40. Type specimens of species in the *Panicum implicatum* -
P. meridionale assemblage

- A. Type of *P. implicatum* Scribn.
- B. Type of *P. albermarlense* Ashe
- C. Type of *P. meridionale* Ashe
- D. Type of *P. auburne* Ashe



The *Panicum lanuginosum* - *P. columbianum* assemblage

This assemblage of species with spikelets 1.6 to 1.9 mm long can also be arbitrarily divided into a group possessing puberulent sheaths and relatively thick blades about 5 mm wide and another with sheath hairs about 1.5 mm long and laxer blades sometimes above 5.0 mm wide. As previously mentioned, this last collection of species offers the most perplexing problem in the taxonomy of the subgenus *Dichanthelium*.

Hitchcock and Chase recognized two species with puberulent sheaths under their Columbiana grouping: *P. columbianum* and *P. tsugetorum*. Fernald considered *P. tsugetorum* as inseparable from *P. columbianum*. While puberulent forms of *P. columbianum* such as the type of this species present little difficulty in identification, occasional specimens are hardly distinguishable from less pubescent forms of the large *P. lanuginosum* complex. Evidence of the difficulty sometimes experienced in separating *P. columbianum* from *P. lanuginosum* (sensu lato) is afforded by the examination of the type of *P. lanuginosum* var. *siccanum* (Figure 43 D) originally described by Hitchcock and Chase and later regarded by the same authors as an "extremely hairy form of *P. tsugetorum*". Its resemblance to such species of *Lanuginosa* as *P. huachucae* or *P. pacificum* is further evidenced in Figure 43.

Fernald regarded *P. lindheimeri* as a small-spikelet, glabrous variety of *P. lanuginosum*, and he placed *P. huachucae*, *P. huachucae* var. *silvicola*, *P. tennesseense*, and *P. languidum* under *P. lanuginosum* var. *fasciculatum*. This last combination has been adopted throughout the present work. Unfortunately Fernald included northern glabrous forms with presumably larger spikelets under *P. lanuginosum* var. *septentrionale*.

Chase fittingly reduced this variety to a synonymy under Panicum tennesseense.

There is little doubt that P. huachucae, P. huachucae var. fasciculatum, P. tennesseense are inseparable from P. lanuginosum (Figures 36 and 37). P. languidum (Figure 44 C) could be regarded as an occasional intermediate form between P. lanuginosum (sensu Fernald) and P. villosissimum (Figure 47 D). Its spikelet measures 2.0 mm in length; its papillose sheath pubescence also reaches 2.0 mm. Fernald's decision to include P. languidum as a synonym of P. lanuginosum var. fasciculatum does not appear unwarranted for it is hardly distinguishable from the broad-leaved, large-spikelet form of this entity.

Certain specimens of P. subvillosum are hardly separable from the types of P. huachucae or P. pacificum (Figures 42, 43 A and B, 44 B), while others possess the puberulence, double pubescence, and narrow blade characteristic of P. meridionale and its allies (Figure 36). The majority of plants identified by Hitchcock and Chase as P. subvillosum have spikelets between 1.7 and 1.9 mm in length, well within the range of P. lanuginosum var. fasciculatum from which they can be distinguished only with difficulty. However they possess narrow blades with long hairs on the upper surface such as found in P. implicatum. The length of the first glume and other spikelet characteristics of P. subvillosum are also suggestive of P. praecocius.

The type specimen of P. thurowii (Figure 44 D) from Waller County, Texas, as well as other selected specimens from Texas and Louisiana appear distinct from P. lanuginosum var. fasciculatum. They are robust plants with spikelets 1.9 to 2.0 mm long and very large panicles often

10 cm in length. However, some cited specimens of Panicum thurowii from Alabama (Mohr in 1895 and 1897) as well as other collections from Texas and Louisiana (Figure 36) fall within the morphological range of P. lanuginosum var. fasciculatum. It would seem appropriate to maintain this species or to regard it as a robust variety of P. lanuginosum with which it appears to merge.

Hitchcock and Chase recognized four species of Lanuginosa endemic to the western United States: P. pacificum, P. occidentale, P. thermale and P. shastense. In addition, P. huachucae and P. tennesseense extend as far as California and Utah respectively. Morphologically P. pacificum and P. occidentale cannot be separated from P. lanuginosum var. fasciculatum (sensu Fernald) as shown in Figures 36, 37, 42, 43 A and B. The type specimen of P. pacificum (Figure 43 B) from northern California resembles in all respects that of P. huachucae (Figure 43 A). Its spikelet is pointed and measures 1.8 to 1.9 mm while those of P. huachucae are 1.6 to 1.8 mm in length. Hitchcock and Chase admit that P. huachucae, P. tennesseense, and P. pacificum intergrade "more or less". However according to them "the spreading habit and larger spikelets, together with a distinct range, make it impossible to include this western form under P. huachucae".

The holotype of P. huachucae (Figure 43 A) was collected in southern Arizona and this grass is regarded by Hitchcock and Chase as occurring throughout most of the United States except for the extreme northwestern States. Similarly P. scribnerianum occurs from the east coast to the west coast of the United States with surprising uniformity. In addition such species as P. sphaerocarpon, P. xalapense, P. aciculare, and

Panicum angustifolium are found throughout the eastern part of the United States and as far south as the northern part of South America. Therefore it appears improbable that P. pacificum, P. occidentale, and P. thermale should be excluded from the rest of the Lanuginosa complex on the basis of their presumably separate geographical range.

Some of the polymorphism exhibited in the eastern United States by members of the Lanuginosa complex is also apparent in the western part of their range and again no consistent morphological discontinuities are discernible. However Schmoll (1939) detected some of the minor variations found in the western Lanuginosa and described two new species and two varieties. St. John (1937) also described one species similar to P. occidentale. Later Hitchcock and Chase (1950) added these taxa to the large synonymy, although such forms as P. ferventicola (Figure 45 D) appear as deserving of a varietal ranking as P. tsugetorum, P. oricola, P. auburne, P. tennesseense, and many other "species" recognized by them.

The type specimen of P. occidentale (Figure 45A) appears identical in all respects to the holotype of P. thermale (Figure 45 B). It is based on a mixture of material originally identified by J.S. Presl as P. pubescens Michx (= P. lanuginosum). Scribner (1899) re-examining this mixed sheet presents this inadequate description of one of the specimens: "The other specimen does not fully agree with any of our eastern species and may well be named P. occidentale Scribn. nov. nom. (P. pubescens Presl. not. Lam. nor Michx.)" Not only should this "species" be eliminated on morphological grounds but possibly also for nomenclatural reasons.

The impossibility of separating the type specimens of Panicum thermale, P. pacificum, and P. occidentale from P. lanuginosum (sensu lato) is reflected in Figures 37 and 41. The spikelet length of these western plants varies from 1.6 to 1.9 mm and the habit of growth ranges from the weak, tall, and narrow-leaved P. pacificum to the low, bushy form described by Schmoll as P. lassenianum (Figure 45 C), which resembles in many respects P. xalapense with its uniquely extensive rosette.

Other selected specimens of P. occidentale, P. thermale, and P. pacificum represented in Figure 36 exhibit similar combinations of morphological traits as that found in the eastern and southern Lanuginosa. Puberulent, small-spikelet forms similar to P. meridionale but with slightly wider blades have been identified by Hitchcock as P. occidentale (Amer. Gr. Nat. Herb. 527; Humboldt County, Calif.) while broad-leaved plants with spikelets up to 2.0 mm and long pubescence similar to that found in P. praecocius and P. villosissimum have been referred by the same author to P. thermale (Hitchcock in 1914, Alberta). This specimen is in turn similar to the duplicate type of P. ferventicola var. papillosum (Figure 45 D) collected at the same location, as well as to the type of P. ferventicola Schmoll, from Wyoming, which however bears smaller spikelets. All these plants possess unusually broad subcordate blades as well as papillose pubescence such as found in the widespread P. scribnerianum.

Figure 41. Morphological characteristics of type specimens of some species and varieties in the Panicum lanuginosum complex

Conspicuous double pubescence is indicated by crossbars in the graph.

- Column 1. Type of P. thermale Boland (see Figure 45 B)
- Column 2. Type of P. ferventicola Schmoll (= P. thermale)
- Column 3. Type of P. ferventicola var. papillosum Schmoll (= P. thermale) (see Figure 45 D)
- Column 4. Type of P. lassenianum Schmoll (= P. thermale) (see Figure 45 C)
- Column 5. Type of P. ferventicola var. sericeum Schmoll (= P. thermale)
- Column 6. Type of P. pacificum Hitchc. and Chase (see Figure 43 B)
- Column 7. Duplicate type of P. huachucae Ashe (see Figure 43 A)
- Column 8. Type of P. huachucae var. silvicola Hitchc. and Chase (= P. huachucae var. fasciculatum)
- Column 9. Type of P. implicatum Scribn. (see Figure 40 A)

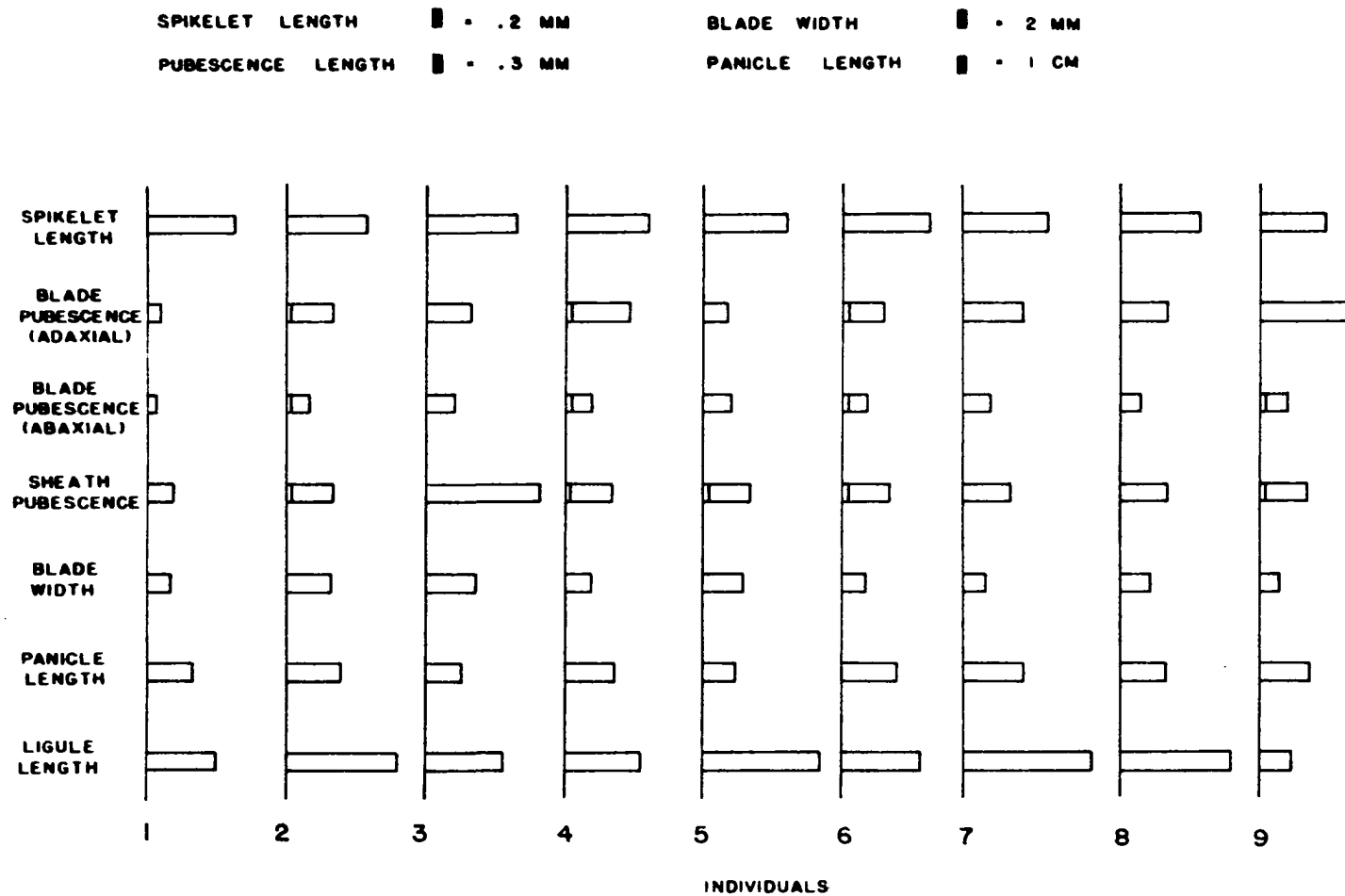


Figure 42. Morphological characteristics of type specimens of species in the Panicum lanuginosum complex compared with those of species in the P. villosissimum - P. commonsianum assemblage

Conspicuous double pubescence is indicated by crossbars in the graph.

- Column 1. Type of P. huachucae Ashe (see Figure 43 A)
- Column 2. Type of P. huachucae var. silvicola Hitchc. and Chase (= P. huachucae var. fasciculatum)
- Column 3. Type of P. pacificum Hitchc. and Chase (see Figure 43 B)
- Column 4. Type of P. subvillosum Ashe (see Figure 44 B)
- Column 5. Type of P. thermale Boland (see Figure 45 B)
- Column 6. Type of P. thurowii Scribn. and Smith (see Figure 44 D)
- Column 7. Co-type of P. villosissimum Nash (see Figure 47 A)
- Column 8. Type of P. praecocius Hitchc. and Chase (see Figure 48 B)
- Column 9. Type of P. commonsianum Ashe (see Figure 49 A)
- Column 10. Duplicate type of P. pseudopubescens Nash (see Figure 49 B)

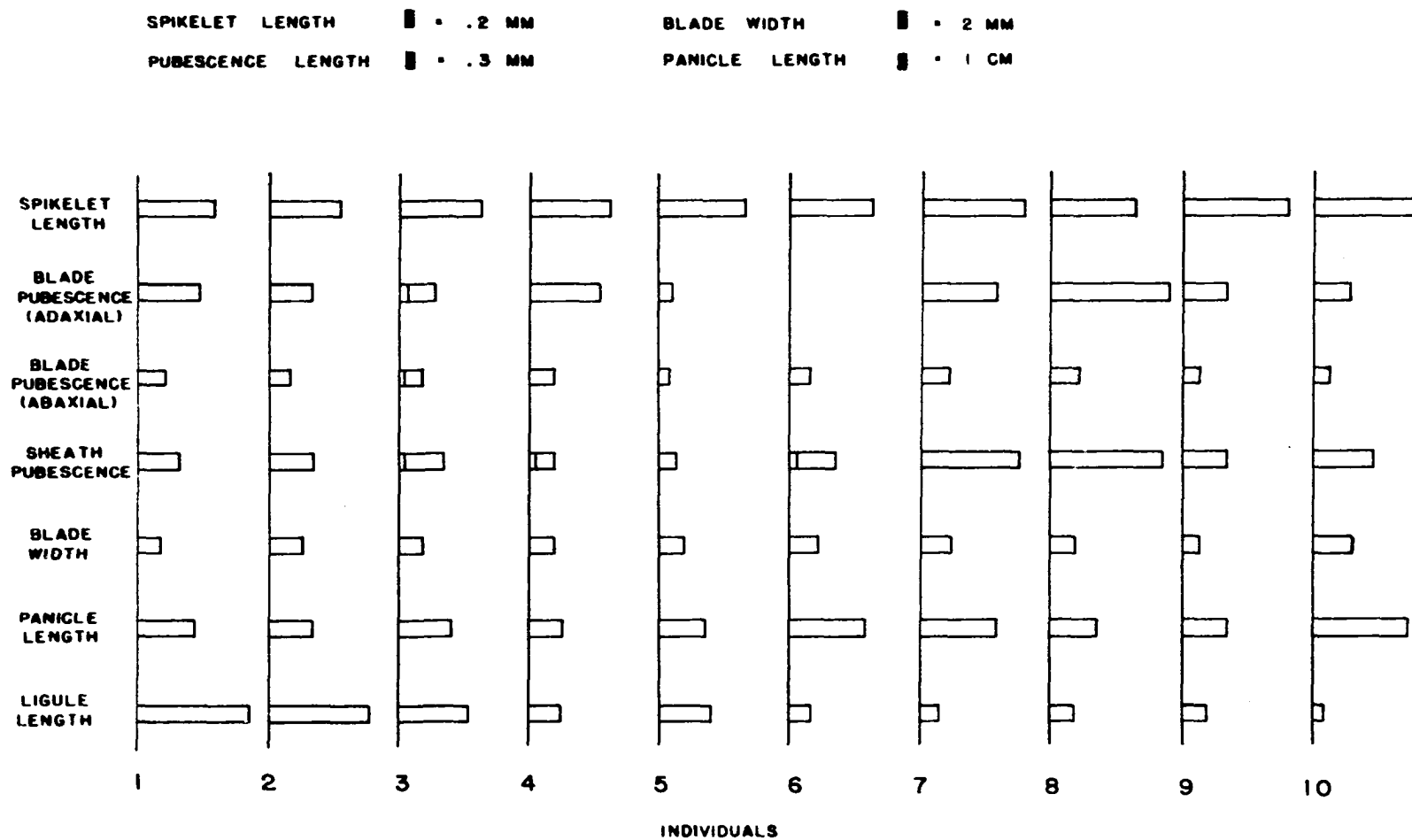


Figure 43. Type material of species in the Panicum lanuginosum - P. columbianum assemblage

- A. Duplicate type of P. huachuchae Ashe
- B. Type of P. pacificum Hitchc. and Chase
- C. Type of P. columbianum Scribn.
- D. Type of P. lanuginosum var. siccanum Hitchc. and Chase (later regarded by authors as a synonym of P. tsugetorum)

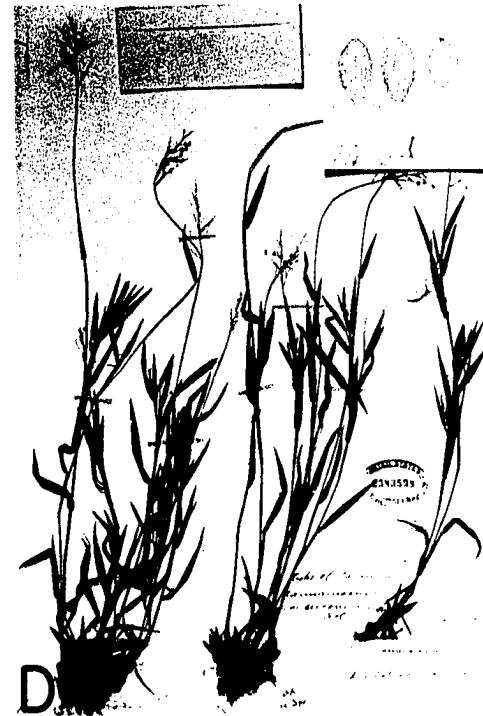


Figure 44. Type specimens of species in the Panicum lanuginosum complex

- A. Type specimen of P. lanuginosum Ell.
- B. Type specimen of P. subvillosum Ashe
- C. Type specimen of P. languidum Hitchc. and Chase
- D. Type specimen of P. thurowii Scribn. and Smith

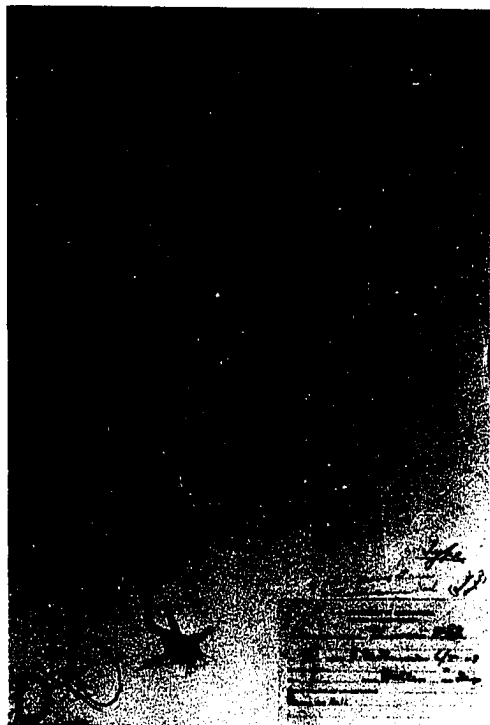
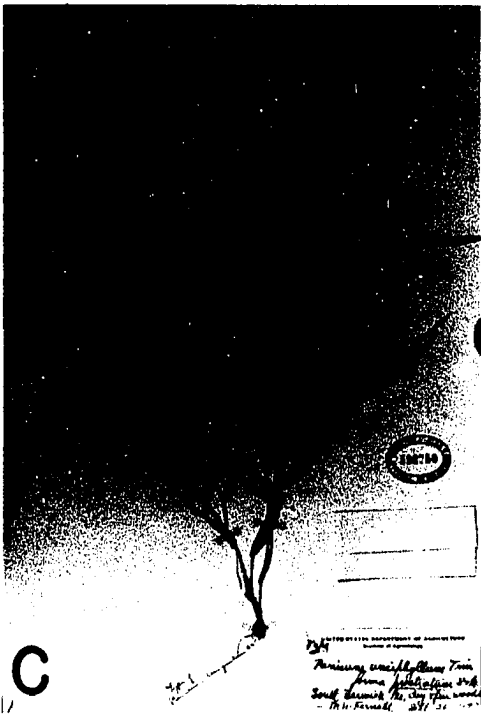
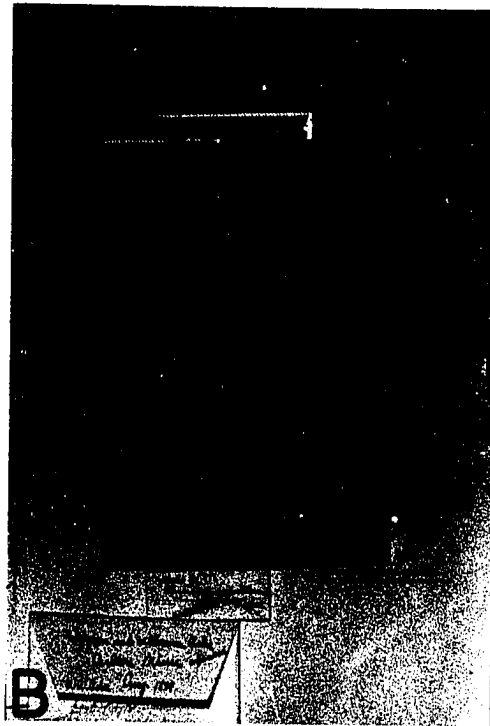
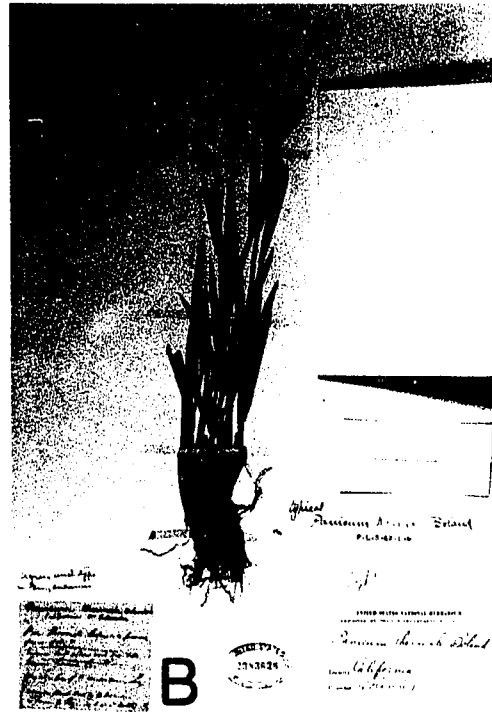


Figure 45. Proposed species and varieties for western representatives of the Panicum lanuginosum complex

- A. Type specimens of P. occidentale Scribn. (upper left), and of P. brodiei St. John (upper right), the latter regarded by Hitchcock and Chase as a synonym of the former.
- B. Type of P. thermale Boland
- C. Type of P. lassenianum Schmoll (= P. thermale)
- D. Duplicate type of P. ferventicola var. papillosum Schmoll (= P. thermale)



The *Panicum villosissimum* - *P. commonsianum* assemblage and the *P. ovale* - *P. malacon* assemblage

The morphological discontinuity between this aggregation of species and the Columbiana-Lanuginosa assemblage considered in the preceding section is fairly well defined although occasional forms such as *P. languidum* and *P. thurowii* or specimens of *P. praecocius* with shorter pubescence partly bridge the gap. Typical *P. praecocius* with spikelets 1.8 to 2.0 mm long, illustrated by the type, (Figure 48 B), can ordinarily be separated from the more southern *P. villosissimum* (Figure 47 A) with spikelets 2.3 to 2.5 mm long, but certain individuals of these two species present problems in identification. For example, the type specimen of *P. atlanticum* Nash (Figure 47 B) collected near the New York Botanical garden and reduced by Hitchcock and Chase to a synonym of *P. villosissimum* cannot be separated from forms of *P. praecocius* occurring commonly in the Midwest. Similarly the small erect type specimen of *P. xanthospermum* Scribn. (Figure 47 C) from Alabama also placed in the synonymy under *P. villosissimum* does not resemble closely the tall, geniculate type specimen of *P. villosissimum* from Georgia (see Figure 47 A). However the types of *P. atlanticum* and of *P. xanthospermum* bear large spikelets 2.2 to 2.4 mm, well within the range of *P. villosissimum*.

On the other hand the type specimen of *P. praecocius* (Figure 48 B) from Illinois can be separated only with difficulty from the type of *P. dichotomum villosum* Vasey (Figure 47 D), another synonym of *P. villosissimum*. It also resembles the type specimen of *P. villosissimum* (Figure 47 A) in its habit of growth. However, the spikelet of

Panicum praecocius is only 1.8 to 2.0 mm long, while that of P. dichotomum villosum measures 2.1 to 2.3 mm long. The type specimen of P. villosissimum possesses longer spikelets, 2.3 to 2.5 mm long.

We mentioned in a preceding chapter the difficulties sometimes experienced in separating the Coastal Plain P. villosissimum from less pubescent but similar plants referred to as P. pseudopubescens. Type specimens can be used to further illustrate this puzzling situation. The type of P. haemocarpon (Figure 48 A), accepted by Hitchcock and Chase as a synonym of P. villosissimum, resembles more closely the duplicate type specimen of P. pseudopubescens (Figure 49 B) from Alabama which possesses according to Chase unusually broad basal blades. It is also similar to the type of P. commonsianum (Figure 49 A) from New Jersey. All of these specimens bear spikelets between 2.2 and 2.4 mm long.

The type specimen of P. euchlamydeum collected in Wisconsin possesses most characteristics of P. pseudopubescens and its inclusion by Hitchcock and Chase to the synonymy of this latter species appears justified. P. commonsianum resembles also closely P. pseudopubescens. It bears the double vestiture often conspicuous on many species of this group. However its stiffly ascending narrow blades resemble those of the more robust P. malacon also found along the Atlantic coast, which is easily distinguished by its longer spikelets (3.2 to 3.5 mm). The great similarity between type specimens of P. villosissimum, P. praecocius, and P. pseudopubescens is illustrated in Figures 36 and 46.

The type specimen of P. ovale (Figure 48 C) is similar in appearance to P. pseudopubescens or to P. villosissimum, but its spikelets are distinctly larger (2.8 mm). The type of P. erythrocarpon

(Figure 49 D) from Wilmington, North Carolina reduced by Hitchcock and Chase to Panicum ovale has spikelets measuring 2.3 to 2.4 mm in length. Other specimens of P. ovale identified by Hitchcock and Chase and represented in Figure 36 fall within the range of P. commonsianum - P. pseudopubescens. This species should probably be maintained for occasional specimens with spikelets between 2.7 and 2.9 mm in length. Although its affinity with P. commonsianum (sensu Fernald) and P. villosissimum appears close, the spikelet and habit of growth of P. ovale is suggestive of the widespread P. commutatum occurring throughout the same range.

P. wilmingtonense affords a typical example of the taxonomic and nomenclatural confusion presented by many "species" in Panicum subgenus Dichanthelium. The type specimen (Figure 48 C) collected by Ashe from the type locality of P. erythrocarpon (= P. ovale) consists of five depauperate culms: the tallest and most mature culm bears spikelets 2.1 to 2.2 mm long; the least mature culm possesses spikelets 1.7 to 1.9 mm long, while the other flowering culm has spikelets 1.8 to 2.0 mm long. Hitchcock and Chase describe this species as possessing pubescent spikelets 2.0 mm long and Ashe states in the original description that its spikelets are "quite 2.0 mm long, nearly glabrous". He added that "P. wilmingtonense is closely related to P. atlanticum" (now a synonym of P. villosissimum) "but has smaller, more acute spikelets, a more slender culm, scantier pubescence and smaller leaves". Although its blades are indeed narrow, this plant is hardly separable from some forms of the more glabrous members in the P. villosissimum complex, variously ascribed to P. addisonii or P. commonsianum. The sheath

pubescence is fairly dense and measures up to 2.0 mm. Hoping to elucidate the status of this "rare species", I examined the type of Panicum alabamense (Figure 48 D) reduced by Hitchcock and Chase to synonymy under P. wilmingttonense. This specimen consists of one extremely immature culm with panicle still mostly included in the uppermost sheath and with spikelets 1.8 to 2.0 mm long. The upper part of the sheath is glabrous except for occasional hairs 0.1 mm long; the lower part of the same sheath is clothed with long hairs up to 3.0 mm long spreading to ascending. The sheaths of lower cauline leaves possess two types of pubescence: small hairs approximately 0.2 mm, as well as longer hairs about 1.0 mm throughout. It appears to be a form of P. lanuginosum var. fasciculatum. In addition two of the six specimens cited by Hitchcock and Chase under P. wilmingttonense in their monograph (1910) were closely examined. Two sheets collected by Hitchcock (316) in August, 1905 and identified by him as P. wilmingttonense are in ISC. They both consist of tall, weak, and glabrous culms in the advanced branched state, bearing narrow, stiff, white-margined blades and spikelets only 1.5 mm long. These specimens resemble in many details the forms described as P. trifolium and belong either in the Ensifolia or in the Spreta groupings of Hitchcock and Chase briefly alluded to in the beginning of this chapter. They bear no resemblance whatsoever to any other members of the P. villosissimum - P. commonsianum complex.

The other cited specimen of P. wilmingttonense (Tracy 8429), collected in 1903 near Gateswood, Alabama, is very similar to those of Hitchcock just described. It also belongs with the weak forms of P. lindheimeri,

bearing spikelets 1.4 to 1.5 mm long and could be identified as Panicum trifolium, P. albomarginatum, or P. flavovirens.

There appears to be little justification in retaining P. wilmingtonense. It should be included in the synonymy under P. commonsianum or P. commonsianum var. addisonii (Nash) Fern.

Fernald regarded P. scoparioides (Figure 50 A) as a variety of P. villosissimum distinct from P. villosissimum var. pseudopubescens. Despite the apparent similarity between P. pseudopubescens, P. commonsianum, and P. scoparioides, I feel that P. scoparioides should perhaps be regarded as a separate species including P. benneri Fern. as a synonym (Figure 46). These two species are intermediate in most aspects between P. scribnerianum and P. lanuginosum which are both widespread northwest of the Atlantic Coastal Plain. P. scoparioides possesses the stiff ascending papillose hairs and the strongly nerved spikelet of P. scribnerianum as well as the softer spreading pubescence, the smaller spikelet, and the narrower blade of P. lanuginosum. It is possible that P. scoparioides and P. benneri represent more or less stabilized derivatives of hybridization between P. lanuginosum and P. scribnerianum. Fernald (1950) stated the same hypothesis and included it in a note following his description of P. villosissimum var. scoparioides.

Only two specimens are listed by Hitchcock and Chase for P. shastense, described by them as a "rare species occurring only at Castle Crag, Shasta County, California". I examined both of these specimens. The type specimen (Figure 50 C) resembles closely P. scoparioides but the spikelet measure 2.5 to 2.7 mm while spikelets of the type of

Panicum scoparioides (Figure 50 A) are 2.3 to 2.4 mm long. The other herbarium sheet of P. shastense (Hitchcock 3072) consists of a much branched plant with spikelets 2.3 to 2.5 mm long, and long arched purplish internodes similar to those found in P. scribnerianum and P. leibergii on dense prairie sod. Double pubescence is obvious on both of these specimens.

I believe that this "rare species" is merely another resulting variant from sporadic hybridization between P. scribnerianum and western forms of P. lanuginosum (such as Heller 12452 identified as P. pacificum). Until it can be ascertained that P. shastense is indeed a rare hybrid, it should probably be regarded as a synonym of P. scoparioides. The surprisingly great similarity between western and eastern *Lanuginosa* has already been noted.

Only the type of P. deamii (Figure 50 B) was available for study. This grass was originally identified as P. perlongum by its collector, C.C. Deam, while Hitchcock and Chase regarded it as another exceptional P. pseudopubescens. Later Hitchcock and Chase described this plant as a new species under the name of P. deamii. Its affinity with P. pseudopubescens seems close although spikelets of P. deamii measure 2.7 to 2.8 mm, while spikelets of P. pseudopubescens seldom exceeds 2.5 mm in length. However, occasional specimens (Wheeler in 1900) cited by Hitchcock and Chase under this last species have spikelets 2.5 to 2.7 mm long. The general habit of growth of P. deamii as well as its erect and elongate blades are suggestive of the *Depauperata* grouping well represented in this part of the range. P. deamii could be restored to the position originally ascribed to by Hitchcock and Chase, that of an

Figure 46. Morphological characteristics observed in type specimens of accepted and reduced species in the Panicum villosissimum - P. pseudopubescens assemblage

Conspicuous double pubescence is indicated by crossbars in the graph.

- Column 1. Co-type of P. villosissimum (see Figure 47 A)
- Column 2. Type of P. dichotomum var. villosum Vasey (= P. villosissimum) (see Figure 47 D)
- Column 3. Type of P. atlanticum Nash (= P. villosissimum) (see Figure 47 B)
- Column 4. Duplicate type of P. haemacarbon Ashe (= P. villosissimum) (see Figure 48 A)
- Column 5. Type of P. praecocius Hitchc. and Chase (see Figure 48 B)
- Column 6. Duplicate type of P. pseudopubescens Nash (see Figure 49 B)
- Column 7. Type of P. euchlamydeum Shinnery (= P. pseudopubescens)
- Column 8. Type of P. scoparioides Ashe
- Column 9. Duplicate type of P. scoparioides Ashe (see Figure 50 A)
- Column 10. Type of P. benneri Fern.

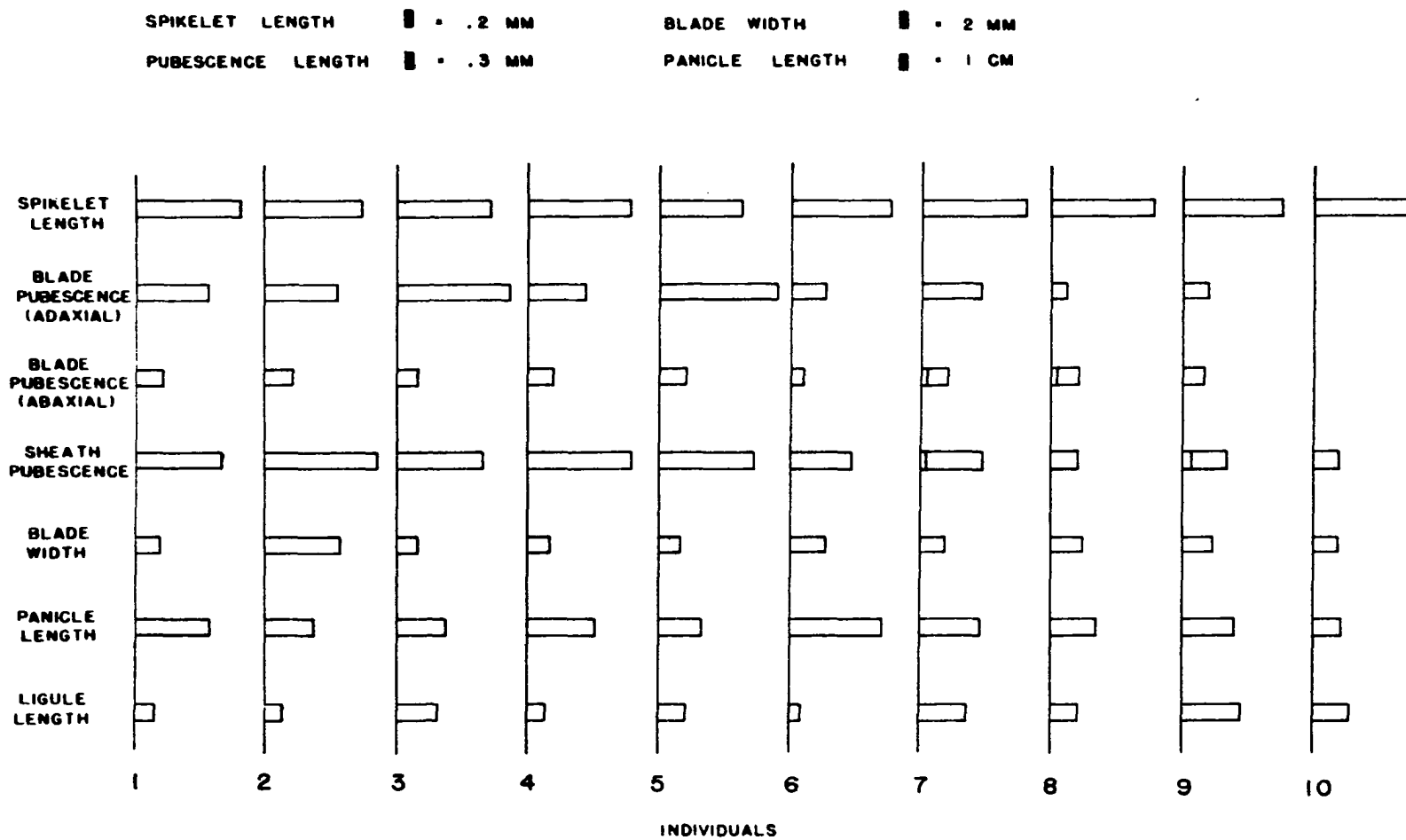


Figure 47. Type specimens of Panicum villosissimum and of some of its synonyms

- A. Co-type of P. villosissimum Nash
- B. Type of P. atlanticum Nash
- C. Type of P. xanthospermum Scribn. and Mohr
- D. Type of P. dichotomum var. villosum Vasey

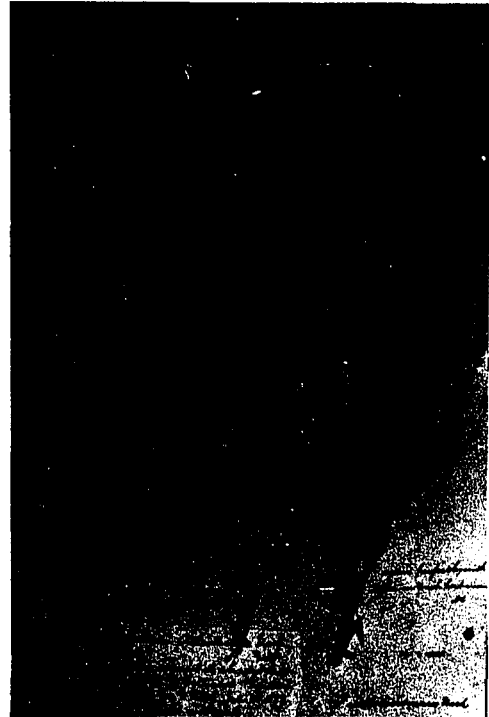


Figure 48. Type specimens of species in the Panicum villosissimum -
P. pseudopubescens assemblage

- A. Duplicate type of P. haemacarpon Ashe
(= P. villosissimum)
- B. Type of P. praecocius Hitchc. and Chase
- C. Type of P. wilmingtonense Ashe
- D. Part of type of P. alabamense Ashe
(= P. wilmingtonense)

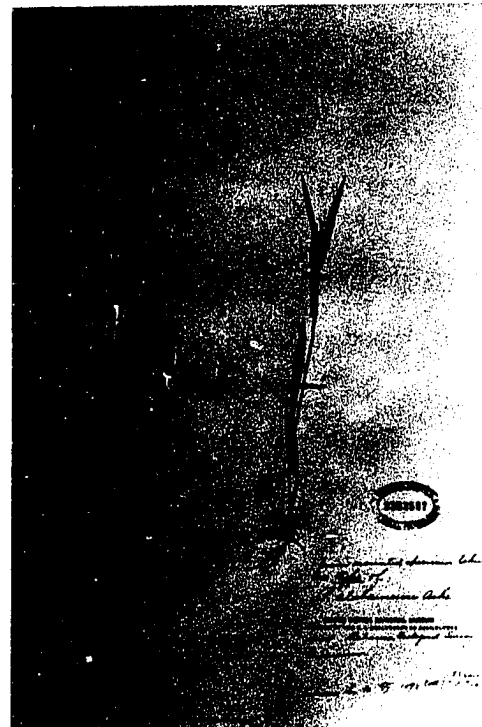


Figure 49. Type specimens of species in the Panicum villosissimum - P. pseudopubescens assemblage

- A. Type of P. commonsianum Ashe
- B. Type of P. pseudopubescens Nash
- C. Photograph of type of P. ovale Ell.
- D. Type of P. erythrocarpon Ashe (= P. ovale)

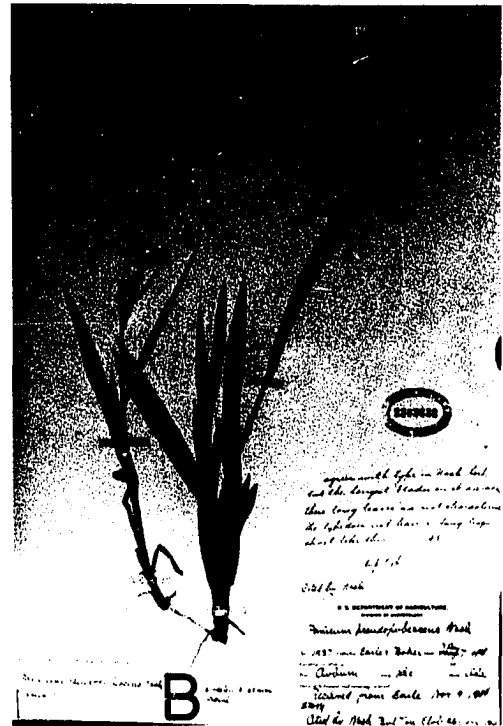
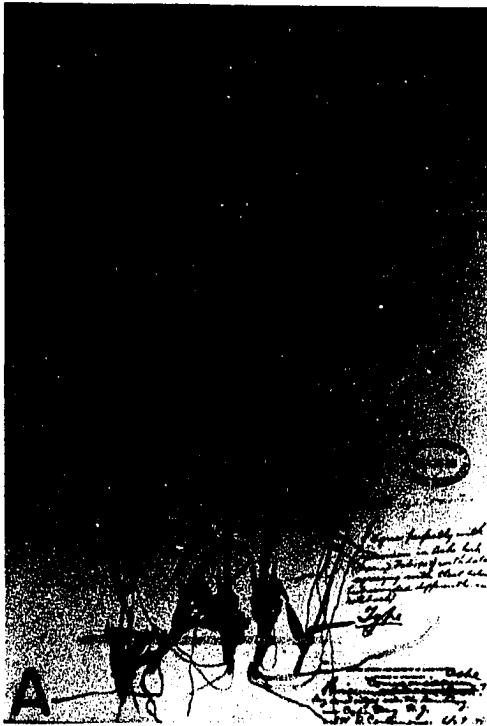
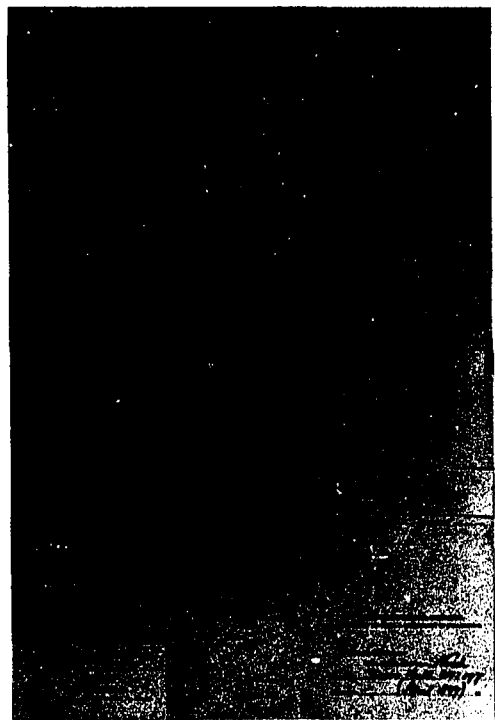


Figure 50. Type specimens of large-spikelet species in the Lanuginosa and Columbiana groups

- A. Duplicate type of *P. scoparioides* Ashe
- B. Type of *P. deamii* Hitchc. and Chase
- C. Type of *P. shastense* Scribn. and Merr.
- D. Type of *P. malacon* Nash



unusual specimen of Panicum pseudopubescens. More appropriately, this species might be placed in the Depauperata group under P. wilcoxianum (Fernald 1950).

The type specimen of P. malacon (Figure 50 D) bears spikelets 3.2 to 3.4 mm long. Other specimens of this species from Florida had spikelets ranging from 2.9 to 3.2 mm (Figure 36). The stiff, erect blades of this plant are conspicuously narrow. In growth habit, this grass is strongly suggestive of members of the Patentifolia group of Hitchcock and Chase also found primarily in Florida as well as species such as P. angustifolium or P. fusiforme in the closely related Angustifolia grouping. The same stiff habit of growth and narrow blades also characterize individuals of P. commonsianum (Figure 49 A) in the southern Atlantic Coastal Plain. P. malacon appears to stand in approximately the same relationship with P. commonsianum as P. ovale does with P. pseudopubescens. While occasional glabrous individuals of P. ovale might be mistaken for P. malacon, this last species is exceptionally well defined if compared with other dichanthelia (Figure 36).

Conclusions and Taxonomic Synopsis

Possible weaknesses of the classification system proposed by Hitchcock and Chase for the Lanuginosa and Columbiana groups have been exposed in the preceding pages. Many of the modifications suggested have already been advocated by Fernald (1934, 1950) and by Gleason (1952). Their taxonomic treatment of these plants in the northeastern United States appears far more satisfactory than that of their predecessors. However, it appears that improvement in the taxonomic

dispositions of the Lanuginosa and Columbiana groups might result from a further "widening" of specific delimitations. A more satisfactory treatment of these plants should probably follow a much more exhaustive study of the entire subgenus. Although this paper is not intended as a revisionary treatment, a provisional key to the Lanuginosa and Columbiana groups in the United States as well as a partial list of proposed synonyms follow.

1. Spikelets less than 1.6 mm long, often spheroidal; blades usually less than 4.5 mm wide
 2. Sheaths with hairs 0.5 - 3.0 mm long; adaxial blade surface covered with long erect hairs up to 4.0 mm long 1. P. implicatum
 2. Sheaths densely puberulent, hairs not over 0.3 mm long, often with few longer trichomes interspersed; adaxial blade surface similarly puberulent 2. P. meridionale
1. Spikelets 1.6 mm or more long; blades usually over 5.0 mm wide
 3. Spikelets 1.6 - 1.9 mm long
 4. Sheaths puberulent, hairs not over 0.3 mm long; ligule clearly obsolete 3. P. columbianum
 4. Sheath hairs 0.5 - 2.5 mm long, mostly 1.5 mm in length; ligule apparently 3.0 mm in length
 5. Culms leafy at base, weak; blades seldom over 5.0 mm wide; hairs on upper blade surface usually over 2.5 mm long 4. P. subvillosum
 5. Culms bearing leaves along well spaced nodes; blades 5.0 - 9.0 mm long; hairs of upper blade surface seldom over 1.0 mm in length often confined to basal part of the blade
 6. Culms robust, usually over 70 cm tall; panicle large, generally over 9 cm long; plants occasionally found in Tex., La., Ala. . . 5. P. thurowii
 6. Culms not as robust, generally below 70 cm tall; panicle smaller, rarely over 8 cm long; plants widespread throughout U.S. 6. P. lanuginosum

3. Spikelets over 1.9 mm long

7. Spikelets 1.9 - 2.6 mm long

8. Sheaths covered with dense spreading hairs 2.5 - 4.0 mm long; upper blade surface clothed with erect hairs 1.0 - 4.0 mm long
9. Spikelets seldom over 2.0 mm long; plants confined to the Great Lakes and prairie regions 7. P. praecocius
9. Spikelets generally 2.1 - 2.4 mm long; occurring primarily on the Atlantic and Gulf Coastal Plains and in the eastern deciduous forest 8. P. villosissimum
8. Sheaths and upper blade surface glabrous to puberulent or with stout ascending papillose hairs seldom over 1.5 mm long; double pubescence conspicuous
10. Sheaths puberulent, often with additional scattered ascending hairs 1.0 - 1.5 mm long; blades stiff, ascending, seldom over 6.0 mm wide; lowermost cauline blades much larger than uppermost one 9. P. commonsianum
10. Sheaths glabrous or with ascending papillose hairs up to 1.5 mm long; blades thin, lax, spreading, generally over 7.0 mm wide; lowermost cauline blades not much larger than uppermost ones; intermediate in many respects between P. scribnerianum and P. lanuginosum; possibly rare hybrids 10. P. scoparioides

7. Spikelets over 2.6 mm long

11. Spikelets 2.6 - 2.9 mm long; sheaths clothed with dense thin hairs 2.0 - 3.0 mm long; upper blade surface glabrous or with few long hairs up to 3.0 mm along the margins; Fla., Tex., and the Carolinas 11. P. ovale
11. Spikelets 2.9 - 3.2 mm long; sheaths densely puberulent, hairs 0.1 - 0.3 mm long; upper blade surface similarly puberulent; confined to Florida 12. P. malacon

List of proposed synonyms

1. P. implicatum Scribn. includes:
P. lanuginosum var. implicatum (Scribn.) Fern.
2. P. meridionale Ashe includes:
P. albemarlense Ashe
P. meridionale var. albemarlense (Ashe) Fern.
P. oricola Hitchc. and Chase in part
P. columbianum var. thinium Hitchc. and Chase
P. auburne Ashe in part
3. P. columbianum Scribn. includes:
P. tsugetorum Nash
P. oricola Hitchc. and Chase in part
P. columbianum var. oricola (Hitchc. and Chase) Fern.
4. P. subvillosum Ashe
5. P. thurowii Scribn. and Smith
6. P. lanuginosum Ell. includes:
P. huachucae Ashe
P. huachucae var. fasciculatum (Torr.) Hubb.
P. tennesseense Ashe
P. lanuginosum var. tennesseense (Ashe) Gl.
P. glutinoscabrum Fern.
P. lanuginosum var. septentrionale Fern.
P. languidum Hitchc. and Chase
P. oricola Hitchc. and Chase in part
P. auburne Ashe in part
P. lanuginosum var. fasciculatum
P. pacificum Hitchc. and Chase
P. occidentale Scribn.
P. thermale Boland
7. P. praecocius Hitchc. and Chase
8. P. villosissimum Nash includes:
P. pseudopubescens Nash in part
P. villosissimum var. pseudopubescens (Nash) Fern. in part
9. P. commonsianum Ashe includes:
P. addisonii Nash
P. commonsianum var. addisonii (Nash) Fern.
P. pseudopubescens Nash in part
P. villosissimum var. pseudopubescens (Nash) Fern. in part
P. wilmingtense Ashe

10. P. scoparioides Ashe includes:
 - P. villosissimum var. scoparioides (Ashe) Fern.
 - P. benneri Fern.
 - P. shastense Scribn. and Merr.
11. P. ovale Ell.
12. P. malacon Nash

SUMMARY

The present study was undertaken primarily to determine the causes for taxonomic difficulties presented by certain assemblages of "species" within the large subgenus Dichanthelium of the genus Panicum. These problems are best evidenced in the polymorphic Lanuginosa and Columbiana groups.

Available data concerning the cytology of the dichanthelia indicates that the majority of species are diploid ($2n = 18$). The only three known polyploids in the subgenus are Panicum boscii var. molle, P. clandestinum and P. xanthophysum. Church (1929) reported considerable meiotic irregularities in the five species of dichanthelia which he investigated while Gould (1958) recorded essentially normal meiosis in thirteen species of the subgenus.

The dichanthelia are primarily autogamous and self fertile. Certain species in the Depauperata and the Angustifolia groups exhibit a high degree of cleistogamy. Occasionally large panicles produce florets with longer anthers, exserted far beyond the stigmatic branches at anthesis, and it is probable that cross pollination results from this type of flowering.

A certain amount of morphological plasticity in the dichanthelia was revealed by transplanting representatives of several species into a uniform garden as well as by subjecting clones of the same species to various environmental conditions. However, morphological traits utilized in the separation of species appear relatively unaffected by such changes.

Progeny representing 10 species of dichanthelia were grown under

uniform greenhouse conditions and found to be essentially uniform. Population samples of "races" taken throughout the Midwest and in the southeastern part of the United States also displayed morphological uniformity.

Commonly populations of dichanthelia consist of a relatively large number of species occurring in a small area. Furthermore these "species" reveal varying degrees of morphological similarities.

Morphological evidence suggesting that certain "species" of dichanthelia are not separated by barriers of intrinsic reproductive isolation was advanced.

On the basis of the observations just reviewed, the following hypothesis concerning speciation among dichanthelia is proposed: A combination of preponderant selfing and of frequent cross pollination between races and "species" might have given rise to the complex population structure characteristically formed by the dichanthelia. Stabilization of some hybrid derivatives might have resulted from subsequent selfing, introgression, or polyploidy. The taxonomic difficulties presented by complexes derived in this manner are similar to those afforded by predominantly apomictic groups. The possibility that facultative apomixis also contributes to the multiplicity of homogeneous forms found in the subgenus Dichanthelium must be considered.

A brief evaluation of certain taxonomic dispositions proposed for the Lanuginosa and Columbiana groups was presented and it was concluded that the system proposed by Fernald and modified by Gleason was clearly more satisfactory than that advanced earlier by Hitchcock and Chase. Although this paper is not intended as a revisionary treatment,

suggestions for possible further improvement in the taxonomic treatment of the Lanuginosa and Columbiana species were made. These proposals were summarized in a provisional key presented at the end of the last chapter. Only 12 of the 28 species recognized by Hitchcock and Chase were retained.

Special consideration was given those southern and western "species" of dichanthelia occurring beyond the geographical range considered by Fernald. It is suggested that Panicum pacificum, P. occidentale, and P. thermale be regarded as synonyms of the widespread and polymorphic P. lanuginosum. P. shastense may be regarded as a result of sporadic hybridization between a western form of P. lanuginosum and the widespread P. scribnerianum. While many specimens of southern P. lanuginosum have been identified as P. thurowii, it is suggested that this species be maintained for unusually robust forms such as found throughout Texas or be regarded as a southern variety of P. lanuginosum.

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APPENDIX

Types and Some Selected Specimens of

Lanuginosa-Columbiana Species

- Type: Panicum addisonii Nash, Bull. Torrey Club 25: 83. 1898.
New Jersey, Wildwood, Bicknell in 1897. Photo of type and fragments in US.
- Synonym: Panicum owenae Bicknell, Bull. Torrey Club 35: 185.
1898. Massachusetts, Nantucket Island, Bicknell in 1907.
Type in US.
- Selected specimens: Maryland, Chesapeake Beach, Hitchcock
1617 in 1906 (ISC); Hyattsville, Chase in 1907, Amer. Gr.
Nat. Herb. no. 146 (MO). Massachusetts, Nantucket Island,
Bicknell in 1908 (ISC). New Jersey, South Lakewood, Mackenzie
3098 in 1908 (MO), Point Pleasant, Churchill 112 in 1929 (MO);
Atsion, Fogg Jr. 5674 in 1933 (MO).
- Type: Panicum albemarlense Ashe, Jour. Elisha Mitchell Soc. 16:
84. 1900. North Carolina, Scranton, Ashe in 1899. Type
in US.
- Selected specimens: Connecticut, Waterford, Graves in 1898 (US).
Delaware, Ellendale, Chase 522 in 1916 (MO). District of
Columbia, Kearney 27 in 1897 (US); Hitchcock 126 in 1906 (US).
Maryland, Pindell, Hitchcock 1628 in 1906 (US); Chesapeake
Beach, Hitchcock 1612 in 1906 (US); Beltsville, Chase 3757 in
1907 (US); Chase 3825 in 1907 (US). Massachusetts, Nantucket
Island, Bicknell in 1906 (US); Yarmouth, Fogg 3241 in 1927
(MO); Brewster, Fernald in 1913 (MO).
- Type: Panicum auburne Ashe, N.C. Agr. Exp. Sta. Bull. 175: 115.
1900. Alabama, Auburn, Earle and Baker, Ala. Biological
Survey 1527 in 1898. Type in US.
- Selected specimens: Georgia, Bainbridge, Curtiss 6811 in 1901
(US); Thompson, Bartlett 1172 in 1907 (US). North Carolina,
Wilmington, Chase 3132 in 1906 (US); Wilmington, Chase in
1916, Amer. Gr. Nat. Herb. no. 525 (MO). New York, Long
Island, Woodmere, Bicknell in 1902 (US); Long Island,
Amagansett, Chase in 1916, Amer. Gr. Nat. Herb. no. 526
(MO). North Carolina, east of Wilmington, Chase in 1916,
Amer. Gr. Nat. Herb. no. 525 (MO). South Carolina,
Orangeburg, Hitchcock 10 in 1905 (US). Virginia, Cape
Henry, Chase 2349 in 1904 (US); Gilmerton, Chase 3680 in
1906 (US); Virginia Beach, Mackenzie 1733 in 1905 (US).
- Type: Panicum benneri Fern. Rhodora 46:2. pl. 807. 1944.
New Jersey, along Delaware River, Hunterdon Co., Benner
9635 in 1941. Type in US.

Type: Panicum columbianum Scribn., U.S. Dept Agr. Div. Agrost. Bull. 7: 78. 1897. District of Columbia, Brookland, Lamson-Scribner in 1894. Type in US.

Synonyms: Panicum heterophyllum Bosc, Nees. Agrost. Bras. 227. 1829. Photograph and fragments of type in US. Type in Willdenow Herbarium.

Panicum psammophilum Nash, Bull. Torrey Club 26: 576. 1899. New Jersey, Toms River, Clute 175 in 1898. Duplicate type in US.

Selected specimens: District of Columbia, West Chevy Chase, Chase in 1905, Amer. Gr. Nat. Herb. no. 149 (MO); Deanwood, Chase in 1905, Amer. Gr. Nat. Herb. no. 148 (MO). Maryland, Chesapeake Junction, Hitchcock 2413 in 1907 (ISC). Massachusetts, Granville, Seymour 294 in 1914 (MO). Michigan, southwest of Cheboygan, Shinnars 13, 379 in 1952 (ISC). New York, Rockville Center, Bicknell 10534 in 1906 (ISC).

Type: Panicum columbianum var. thinium Hitchc. and Chase in Robinson, Rhodora 10: 64. 1908. Based on P. unciphyllum thinium Hitchc. and Chase Panicum unciphyllum var. thinium Hitchc. and Chase, Rhodora 8: 209. 1906. New Jersey, Tom's River, Chase 3577 in 1906. Type in US.

Selected specimens: Delaware, between Lewes and Cape Henlopen, Chase in 1916, Amer. Gr. Nat. Herb. no. 529 (MO). Massachusetts, Sandwich, Woodward in 1916 (ISC). New Jersey, Egg Harbor, Chase in 1916, Amer. Gr. Nat. Herb. no. 530 (MO).

Type: Panicum commonsianum Ashe, Jour. Elisha Mitchell Soc. 15: 1898. New Jersey, Cape May, Commons 341 in 1898. Type in US.

Selected specimens: Delaware, Rehoboth Beach, Fogg 1728 in 1926 (MO); Lewes, Hitchcock in 1905, Amer. Gr. Nat. Herb. no. 143 (MO). Massachusetts, Brewster, Fernald 16119 in 1918 (MO). New Jersey, Chatsworth, Hermann 4364 in 1933 (MO); Egg Harbor, Chase 7314 in 1916 (MO); Atsion, Chase 3541 in 1906 (ISC). Virginia, Cape Henry, Chase in 1905, Amer. Gr. Nat. Herb. no. 144 (MO); Franklin, Fernald and Long 7268 in 1937 (MO).

Type: Panicum deamii Hitchc. and Chase in Deam, Ind. Dept. Conserv. Pub. 82: 284. 1929. Indiana, Pine, Deam 43237 in 1929. Type in US.

Type: Panicum huachucae Ashe, Jour. Elisha Mitchell Soc. 15: 51. 1898. Arizona, Huachuca Mountains, Lemmon in 1882. Type in US.

Synonym: P. nitidum pilosum Torr. Fl. North. and Mid. U.S. 146. 1824. New York. Photograph of type in US.

Selected specimens: Arizona, Grand Canyon, Hitchcock 523 in 1915 (MO). Arkansas, Pine Bluff, Demaree 19094 in 1939 (ISC). California, near Snelling, Mason and Smith 8372 in 1949 (ISC). Illinois, Macon Co., Clokey 2435 in 1915 (MO). Iowa, Ames, Hitchcock in 1914, Amer. Gr. Nat. Herb. no. 218 (MO). Kansas, Saint George, Hitchcock 2528 in 1908 (ISC). Kentucky, Lancaster, Anderson in 1933 (MO). Minnesota, Minneapolis, Sandberg 316 in 1891 (ISC). New York, Ithaca, Eames and Wiegand in 1913 (MO). Texas, Larissa, Bush 5597 in 1909 (MO). Wisconsin, Albion, Fassett 3068 in 1926 (ISC).

Type: Panicum huachucae var. fasciculatum (Torr) Hubb., Rhodora 14: 171. 1912. Based on P. dichotomum var. fasciculatum Torr., Fl. North and Mid. U.S. 146. 1824. New Jersey. Photograph of type in U.S.

Synonyms: P. nitidum var. ciliatum Torr., Fl. North and Mid. U.S. 146. 1824. New Jersey. Photograph of type in U.S. P. huachucae var. silvicola Hitchc. and Chase in Robinson, Rhodora 10: 64. 1908. District of Columbia, Chase 2400 in 1904. Type in U.S. P. glutinoscabrum Fernald, Rhodora 49: 122. 1947. Virginia, Nansemond Co., Fernald, Long, and Clement 15186. Type in U.S.

Selected specimens: Louisiana, Lake Charles, Hitchcock 1147 in 1906 (ISC).

Type: Panicum implicatum Scribn. U.S. Dept. Agr. Div. Agrost. Bull. 11: 43. 1898. Maine, Cape Elizabeth, Lamson-Scribner in 1895. Type in U.S.

Selected specimens: Connecticut, Franklin, Woodward in 1920 (ISC). District of Columbia, Brookland, Kearney 27 in 1897. (ISC). Maine, Fayette, Chase 3392 in 1906 (ISC). Massachusetts, Cambridge, Bartlett 469 in 1906 (ISC). Michigan, Burt Lake Shore, Gleason in 1933. New York, Stockholm, Phelps 1443 in 1916 (ISC). Pennsylvania, Bradford, Hennings in 1921 (ISC). Wisconsin, The Dells Valley, Fassett and Hotchkiss in 1934 (ISC).

Type: Panicum languidum Hitchc. and Chase, U.S. Natl. Herb. Contr. 15: 232. 1910. Based on P. unciphyllum forma prostratum Scribn. and Merr. Rhodora 3: 124. 1901. Maine, South Berwick, Fernald in 1897. Type in US.

Selected specimens: Vermont, Hartland, Ruggles 49 in 1894 (US). Massachusetts, Sherborn, Loomis 1675 in 1915 (US).

Type: Panicum lanuginosum Ell. Bot. S.C. and Ga. 1: 123. 1816. Georgia, Baldwin, Photograph of type in US.

Synonyms: P. orangensis Ashe, Jour. Elisha Mitchell Soc. 15: 113. 1899. North Carolina, Chapel Hill, Ashe in 1898. Type in US.

P. ciliosum Nash, Bull. Torrey Club 26: 568. 1899.

- Mississippi, Biloxi, Tracy 4580 in 1898. Type in US.
 Selected specimens: Delaware, Lewes, Hitchcock in 1905, Amer. Gr. Nat. Herb. no. 130 (MO). Florida, Eustis, Nash in 1894 (MO). Illinois, Wady Petra, V. H. Chase in 1906 (MO). Louisiana, Lake Charles, Hitchcock 1147 in 1906 (MO); Alexandria, Ball 544 in 1899 (US). Maryland, Chesapeake Beach, Hitchcock 1613 in 1906 (US). Mississippi, Saratoga, Tracy 8416 in 1903 (US). Missouri, Pickering, Steyermark 5898 in 1938 (MO). North Carolina, Raleigh, Chase 3086 in 1906 (US). New Jersey, Wildwood, Heritage 6 in 1897 (US). South Carolina, Orangeburg, Hitchcock 1395, 1906 (US). Texas, Troup, Reverchon 2865 in 1902 (MO). Virginia, Alexandria Co., Chase in 1905 (MO); Cape Henry, Hitchcock in 1905 (US).
- Type: Panicum malacon Nash, Bull. Torrey Club 24: 197. 1897. Florida, Eustis, Nash 628 in 1894. Type in US.
 Synonym: P. strictifolium Nash, Bull. Torrey Club 26: 579. 1899. Florida, Eustis, Nash 603 in 1894. Type in US.
 Selected specimens: Florida, Dunedin, Tracy in 1900 (MO); Tarpon Springs, Churchill in 1923 (MO); Lakeland, Hitchcock 845 in 1906 (ISC).
- Type: Panicum meridionale Ashe, Jour. Elisha Mitchell Soc. 15: 59. 1898. North Carolina, Jonas Ridge, Ashe in 1893. Type in US.
 Synonym: P. filiculme Ashe, Jour. Elisha Mitchell Soc. 15: 59. 1898. Georgia, Stone Mountain, Ashe. Type in US.
 Selected specimens: Connecticut, Waterford, Graves 171 in 1898 (US). Indiana, Gibson, Bebb 2947 in 1906 (US); Dune Parks; Hill 98 in 1905 (US). Maryland, Beltsville, Chase in 1907 (MO). Massachusetts, Hyanis, Churchill in 1931 (MO). New Jersey, Atsion, Chase 3534 in 1906 (US); Forked River, Chase 3578 in 1906 (US). New York, Woodmere, Long Island, Bicknell in 1902 (US).
- Type: Panicum occidentale Scribn., Rep. Mo. Bot. Gard. 10: 48. 1899. Vancouver Island, Nootka Sound, Haenke. 1830. Photograph of type and fragments in US.
 Synonym: P. brodiei St. John, Fl. Southeast. Wash. and Adj. Idaho 51. 1937. Washington, Wawawai, Brodie in 1898. Photograph of type and fragments in US.
 Selected specimens: Canada, British Columbia, Nelson, Thompson 14, 433 in 1939 (MO). Vancouver Island, Rosendahl 1931 in 1907 (MO). United States, California, Eureka, Hitchcock in 1915, Amer. Gr. Nat. Herb. no. 527 (MO); Hume Lake, Rose 48, 217 in 1948 (MO). Oregon, Brookings, Peck 8795 in 1919 (MO). Washington, Lake Chelan, Lake and Hull 118 (MO); near Olympia, Meyer 961 (MO).
- Type: Panicum oricola Hitchc. and Chase, Rhodora 8: 208. 1906.

Delaware, Lewes, Hitchcock 47 in 1905. Type in US.
 Selected specimens: Delaware, near Cape Henlopen, Chase 7279 (MO). Massachusetts, Harwich, Fernald 315 in 1919 (MO); Yarmouth, Churchill in 1931 (MO). New Jersey, Cookstown, Hermann 4419 in 1933 (MO). Virginia, Cape Henry, Chase in 1905, Amer. Gr. Nat. Herb. no. 152 (MO).

Type: Panicum ovale Ell. Bot. S.C. and Ga. 1: 123. 1816.
 Georgia, St. Mary's, Baldwin. Photograph of type in US.

Synonym: P. ciliiferum Nash, Bull. Torrey Club 24: 195.
 1897. Florida, Eustis, Nash 147 in 1894. Photograph of type in US.

P. erythrocarpon Ashe, Jour. Elisha Mitchell Soc. 16: 90. 1900. North Carolina, north of Wilmington, Ashe in 1899. Type in US.

Selected specimens: Florida, Eustis, Hitchcock in 1894 (US); Lakeland, Hitchcock 846 in 1906 (US); Jacksonville, Curtiss 5866 in 1897 (US); Miami, Hitchcock 719 in 1906 (US); Miami, Chase 3866 in 1907 (US). South Carolina, Isle of Palms, Hitchcock 107 in 1905 (US); Aiken, Ravenel (US). Texas, Waller Co., Thurow 17 in 1906 (US).

Type: Panicum pacificum Hitchc. and Chase, U.S. Nat. Herb. Contr. 15: 229. 1910. California, Castle Crag, Hitchcock 3070, 1908. Type in US.

Selected specimens: California, near Redding, Heller 7856 in 1905 (MO); Mather, Keck 1131 in 1931 (MO). Oregon, Cottage Grove, Peck 5979 in 1916 (MO); without locality, Hall 671 in 1871 (MO). Vancouver Island, Macoun 82344 in 1909 (MO). Washington, near Chelan, Thompson 6928 in 1931 (MO).

Type: Panicum praecocius Hitchc. and Chase, Rhodora 8: 206. 1906. Illinois, Wady Petra, V. H. Chase 649 in 1900. Type in US.

Selected specimens: Illinois, Wady Petra, V. H. Chase in 1905, Amer. Gr. Nat. Herb. no. 135 (MO). Indiana, Lake Co., Umbach 3667 in 1909 (ISC). Kansas, Manhattan, Hitchcock 2500 in 1908 (ISC). Michigan, Pinckney, Hiltunen 3451 in 1961 (ISC). Missouri, Duroc, Steyermark 10, 744 in 1936 (MO). Nebraska, Lincoln, Hedgecock in 1900 (MO). Wisconsin, Dane Co., Shinnars 3731 in 1941 (ISC). Texas, Mineola, Reverchon 2847 in 1902 (MO).

Type: Panicum pseudopubescens Nash, Bull. Torrey Club 26: 577. 1899. Alabama, Auburn, Earle and Baker 1537 in 1898. Type in US.

Synonym: P. euchlamydeum Shinnars, Amer. Midl. Nat. 32: 170. 1944. Wisconsin, Adams Co., Shinnars and Shaw 4415 in 1942. Type in US.

Selected specimens: Alabama, Auburn, Earle and Baker 1522 in 1898 (US); Flomaton, Hitchcock 1048 in 1906 (US). Florida,

Lake City, Hitchcock 1013 in 1906 (US). Georgia, Stone Mountain, Hitchcock 1356 in 1906 (US). Illinois, Hanover, Gleason and Gates 2539 in 1908 (US). Michigan, Twin Lakes, Wheeler in 1900 (IS). North Carolina, Wilmington, Chase 3109 in 1906 (US). Virginia, Great Dismal Swamp, Fernald and Long 10922 in 1939 (US).

Type: Panicum scoparioides Ashe, Jour. Elisha Mitchell Soc. 15: 53. 1898. Delaware, Centreville, Commons 283 in 1873.
Type in US; duplicate type in ISC.

Selected specimens: Connecticut, Southington, Bissell 385, 5581 and 8084 in 1900, 1901, and 1902 respectively (US); East Lyme, Graves in 1903 (US). Delaware, Centreville, Commons 359 in 1873 (US). Minnesota, Ramsey Co., Oestlund in 1884 (US); Hennepin Co., Sandberg in 1890 (US).

Type: Panicum shastense Scribn. and Merr. U.S. Dept. Agr. Div. Agrost. Circ. 35: 3. 1901. California, Castle Crag, Greata in 1899. Type in US.

Selected specimens: California, Shasta Co., Hitchcock 3072 in 1908 (ISC).

Type: Panicum subvillosum Ashe. Jour. Elisha Mitchell Soc. 16: 86. 1900. Minnesota, Carlton, Ashe in 1900. Photograph of type in US.

Synonym: P. unciphyllum forma pilosum Scribn. and Merr. Rhodora 3: 124. 1901. Maine, Orono, Fernald 501 in 1891. Type in US.

Selected specimens: Canada, New Brunswick, Kent Co., Hubbard in 1914, Amer. Gr. Nat. Herb. no. 219 (MO). Nova Scotia, Bedford, Macoun 29, 368 in 1883 (US); Nova Scotia, Yarmouth Co., Fernald, Bean and White 19835 in part, 1920 (MO). Ontario, Galt, Herriot in 1898 (US). United States, Indiana, Clark Junction, Bebb 2832 in 1905 (US). Maine, Cumberland, Chamberlain 787 (US); Fayette, Chase 3391 in 1906 (US); Chesterville, Chase 3278 in 1906 (ISC). Missouri, Noel, Bush 5741 in 1909 (MO). Wisconsin, Conover, Cheney 678 in 1893 (US).

Type: Panicum tennesseense Ashe, Jour. Elisha Mitchell Soc. 15: 52. 1898. Tennessee, La Vergne Co., Biltmore 7087 in 1897. Photograph of type in US.

Selected specimens: Connecticut, Preston, Graves 11 in 1899 (US). Georgia, Stone Mountain, Hitchcock 1358 in 1906 (US). Maryland, West Chevy Chase, Chase in 1905, Amer. Gr. Nat. Herb. no. 127 (MO). Michigan, Portage Lake, Hermann 6839 in 1935 (MO). New Hampshire, Shelburne, Deane in 1915, Amer. Gr. Nat. Herb. no. 524 (MO). New York, Valley Stream, Bicknell in 1905 (US). Pennsylvania, Lancaster Co., Heller 4774 in 1901 (US). Tennessee, Knox Co., Kearney in 1893 (US). Utah, Springdale,

Jones 6069 in 1894 (US).

Type: Panicum thermale Boland. Proc. Calif. Acad. 2: 181. 1862. California, Sonoma Co., Geysers, Bolander. Type in US.

Synonyms: P. ferventicola Schmoll, Madrono 5: 92. 1939. Wyoming, Yellowstone National Park, Chase 5252 in 1908. Type in US.

P. ferventicola var. sericeum Schmoll, Madrono 5: 93. 1939. Wyoming, Yellowstone National Park, Nelson and Nelson 6037 in 1899. Type in US.

P. ferventicola var. papillosum Schmoll, Madrono 5: 94. 1939. Alberta, Banff, Hitchcock 11511 in 1914. Amer. Gr. Nat. Herb. no. 220. Type in US.

P. lassenianum Schmoll, Madrono 5: 95. 1939. California, Plumas Co., Jepson 4082 in 1910. Type in US.

Selected specimens: Alberta, Banff, Hitchcock in 1914 (MO). California, Sonoma Co., Bolander 1805 (MO). Oregon, Agness, Peck 5854 in 1917 (MO). Utah, Utah Co., Harrison 8600 in 1938 (ISC). Wyoming, Yellowstone National Park, Chase in 1908, Amer. Gr. Nat. Herb. no. 137 (MO); Yellowstone National Park, Merrill 165 in 1900 (ISC).

Type: Panicum thurowii Scribn. and Smith, U.S. Dept. Agr. Div. Agrost. Circ. 16: 5. 1899. Texas, Waller Co., Thurow 9 in 1898. Type in US.

Selected specimens: Alabama, near Mobile, Mohr in 1895 and in 1897 (US). Louisiana, Jennings, Palmer 7610 in 1915 (MO). Texas, no locality, Nealley in 1884 and in 1887 (US); Montgomery Co., Thurow in 1905 (US); Hockley, Thurow in 1893; Del Rio, Plank 41 in 1895 (US); Waller Co., Hitchcock 1171 in 1906 (ISC); Swan, Reverchon 4163 in 1903 (US); Big Sandy, Reverchon 2355 in 1901 (MO).

Type: Panicum tsugetorum Nash, Bull. Torrey Club 25: 86. 1898. New York, N.Y. Botanical Garden, Nash 287 in 1896. Photograph and fragments in US.

Synonym: P. lanuginosum var. siccanum Hitchc. and Chase, Rhodora 8: 207. 1906. Illinois, Starved Rock, Chase 1602 in 1901. Type in US.

Selected specimens: Indiana, Steuben Co., Deam in 1904 (MO); Millers (Gary), Umbach 3663 in 1909 (ISC). Maryland, near Beltsville, Chase in 1907, Amer. Gr. Nat. Herb. no. 147 (MO). Massachusetts, Framingham, Smith 740 in 1898 (MO). Michigan, Cheboygan Co., Gleason and Gleason in 1933 (ISC); Pinckney, Hiltunen 3642 in 1961 (ISC). New Jersey, Tuckerton, Chase 3612 in 1906 (ISC); Palermo, Brown in 1936 (ISC).

Type: Panicum villosissimum Nash, Bull. Torrey Club 23: 149.

1896. Georgia, Ocmulgee River Swamp, near Macon, Small in 1895. Type in US

Synonyms: P. dichotomum var. villosum Vasey, U.S. Dept. Agr. Div. Bot. Bull. 8: 31. 1889. District of Columbia, near Pierce's Mill, Rock Creek, Vasey in 1883. Type in US.

P. atlanticum Nash, Bull. Torrey Club 24: 346. 1897. New York, N.Y. Botanical Garden, Nash in 1897. Type in US.

P. haemacarpum Ashe, Jour. Elisha Mitchell Soc. 15: 55. 1898. District of Columbia, Washington, Kearney Jr. in 1897. Type in US.

P. xanthospermum Scribn. and Mohr, Contr. Nat. Herb. 6: 348. 1901. Alabama, Greenville, Mohr in 1898. Type in US.

Selected specimens: Connecticut, Franklin, Woodward in 1917 (ISC). Delaware, Lewes, Hitchcock 161 in 1905 (US). Maryland, east of Riverdale, Chase 2378 in 1904 (US). Mississippi, Taylorville, Tracy 8415 in 1903 (US). New Jersey, Wildwood Junction, Chase 3522 in 1906 (US); South Ambroy, Mackensie 1381 in 1905 (US). New York, Long Island, Bicknell in 1904 (US). Texas, Fort Worth, Bebb 2488 in 1905 (US); Denison, Bebb 2661 in 1905.

Type: Panicum wilmingtense Ashe, Jour. Elisha Mitchell Soc. 16: 86. 1900. North Carolina, near Wilmington, Ashe in 1899. Type in US.

Synonym: P. alabamense Ashe, N.C. Agr. Expt. Sta. Bull. 175: 116. 1900. Alabama, Auburn, Earle and Baker 1530 in 1898. Type in US.

Selected specimens: Alabama, Gateswood, Tracy 8429 in 1903 (MO). North Carolina, Wilmington, Hitchcock 316 in 1905 (ISC)