To the Graduate Council:

I am submitting herewith a dissertation written by Allen C. Risk entitled "Morphometric Studies of the *Sphagnum cuspidatum* Complex in the Coastal Plain of the Southeastern United States." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Botany.

David K. Smith

David K. Smith, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor and
Dean of the Graduate School

MORPHOMETRIC STUDIES OF THE *SPHAGNUM CUSPIDATUM* COMPLEX IN THE COASTAL PLAIN OF THE SOUTHEASTERN UNITED STATES

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Allen C. Risk
August 1996

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ACKNOWLEDGMENTS

My parents have been continually supportive of all of my efforts to further my education. I am grateful for all of their encouragement and love.

A special thanks must go to Joyce, my wife. She has supported the family financially and in countless other ways while I pursued this research. Additional thanks must go to Debbie Pigman for staying with my daughter while I measured specimens and analyzed data.

Dr. David K. Smith served as my major professor and provided a laboratory climate conducive to my research. His advice and assistance have been invaluable throughout this project. I also thank the other members of my committee, Drs. Dewey Bunting, Karen Hughes, and Patricia Walne, for their support.

Dr. Howard L. Setser of Morehead State University fostered my interest in plants when I was an undergraduate and gave me "free rein" in the herbarium. I learned much about botany and about life from classes and in conversations with him.

Dr. Lewis E. Anderson of Duke University gave me my first real introduction to peat mosses during the fall of 1985. I guess he is somewhat to blame for my fascination with *Sphagnum*. I have thoroughly enjoyed all of our interactions over the years, including occasional disagreements about specimen determinations.

Several friends assisted me in the field. Barry Ratliff accompanied me on many long collecting trips and both endured and enjoyed the challenges of navigating through pocosins and various other wetlands of the Coastal Plain. Homer Lynn Pigman and James Kiser also provided friendship and assistance in the field. Their patience in putting up with a slow-moving bryologist is appreciated.

Generous financial support was provided by The Department of Botany, The University of Tennessee - Knoxville, through a Graduate Teaching Assistantship and Science Alliance Funds. The Aaron J. Sharp Fund and De Selm Fund are gratefully acknowledged for support of all aspects of the research.

ABSTRACT

The *Sphagnum cuspidatum* complex, as expressed in the Coastal Plain of the southeastern United States, comprises six named entities: *S. cuspidatum* Ehrh. *ex* Hoffm., *S. fitzgeraldii* Renauld & Cardot *in* Lesq. & James, *S. mississippiense* R.E.Andrus, *S. torreyanum* Sull., *S. trinitense* Müll.Hal., and *S. viridum* Flatberg. *Sphagnum torreyanum* and *S. fitzgeraldii* are generally regarded as distinct, but the number of taxa represented by the other names is less certain.

All named taxa assignable to the complex were evaluated using 374 collections from five areas in the Coastal Plain; of these, 135 specimens were randomly selected for intensive morphometric analysis. Five morphological groups were initially recognized based on examination under a dissecting microscope: group 1, a *S. cuspidatum/S. viridum* species pair; group 2, a *S. trinitense/S. mississippiense* species pair; group 3, *S. fitzgeraldii*; group 4, *S. torreyanum*; and group 5, a single specimen interpreted as representing a hybrid between groups 1 and 3 or an undescribed taxon.

Multivariate analyses, based on measurements of twenty-two morphological characters, supported the distinctiveness of all groups. *Sphagnum cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* were separated most effectively by three characters: proportion of margin not entire of the proximal branch leaves, proximal branch leaf

length to width ratio, and outer stem cell layer differentiation. Intensive morphometric analyses within the *S. trinitense/S. mississippiense* and *S. cuspidatum/S. viridum* species pairs failed to find support for the recognition of either *S. mississippiense* or *S. viridum* as morphologically distinct within the study area.

A second component of the study was a quantitative analysis of morphological variation along temporal and moisture gradients in *S. cuspidatum*. This assessment of character variability indicated that marginal features of median and distal branch leaves and number of septa in stem leaves are too variable over seasonal and moisture gradients within individual populations to serve as reliable taxonomic characters for separating *S. cuspidatum* from *S. trinitense*. Proximal branch leaf margin features, length to width ratio of proximal branch leaves, and outer stem cell layer differentiation proved to be the most reliable characters to use in discriminating among specimens of this problematic species pair.

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INTRODUCTION

Objectives

The present research focused on taxonomic problems presented by the *Sphagnum cuspidatum* complex in the Coastal Plain of the southeastern United States (the study area). The research had two primary objectives: (1) to determine and delimit distinct morphological groups in the complex as expressed in the study area and (2) to quantify natural seasonally correlated variation in the morphology of *S. cuspidatum*.

The first objective was addressed by extensively collecting specimens assignable to the complex from five specific areas within the southeastern United States Coastal Plain (Figures 1 and 2) and measuring twenty-two morphological characters on a randomly selected subset of these specimens. The five areas sampled were the Croatan National Forest (CNF) in North Carolina, Francis Marion National Forest (FMNF) in South Carolina, Sandhills (SH) in North Carolina and South Carolina, Apalachicola National Forest and vicinity (ANF) in Florida, and De Soto National Forest and vicinity (DNF) in Mississippi (Figure 2). The morphological characters chosen were those emphasized previously by various authorities to delineate the problematic species of the complex and other features considered potentially useful in resolving groups. Multivariate and univariate methods were utilized in examining these data in a search for morphological groups.

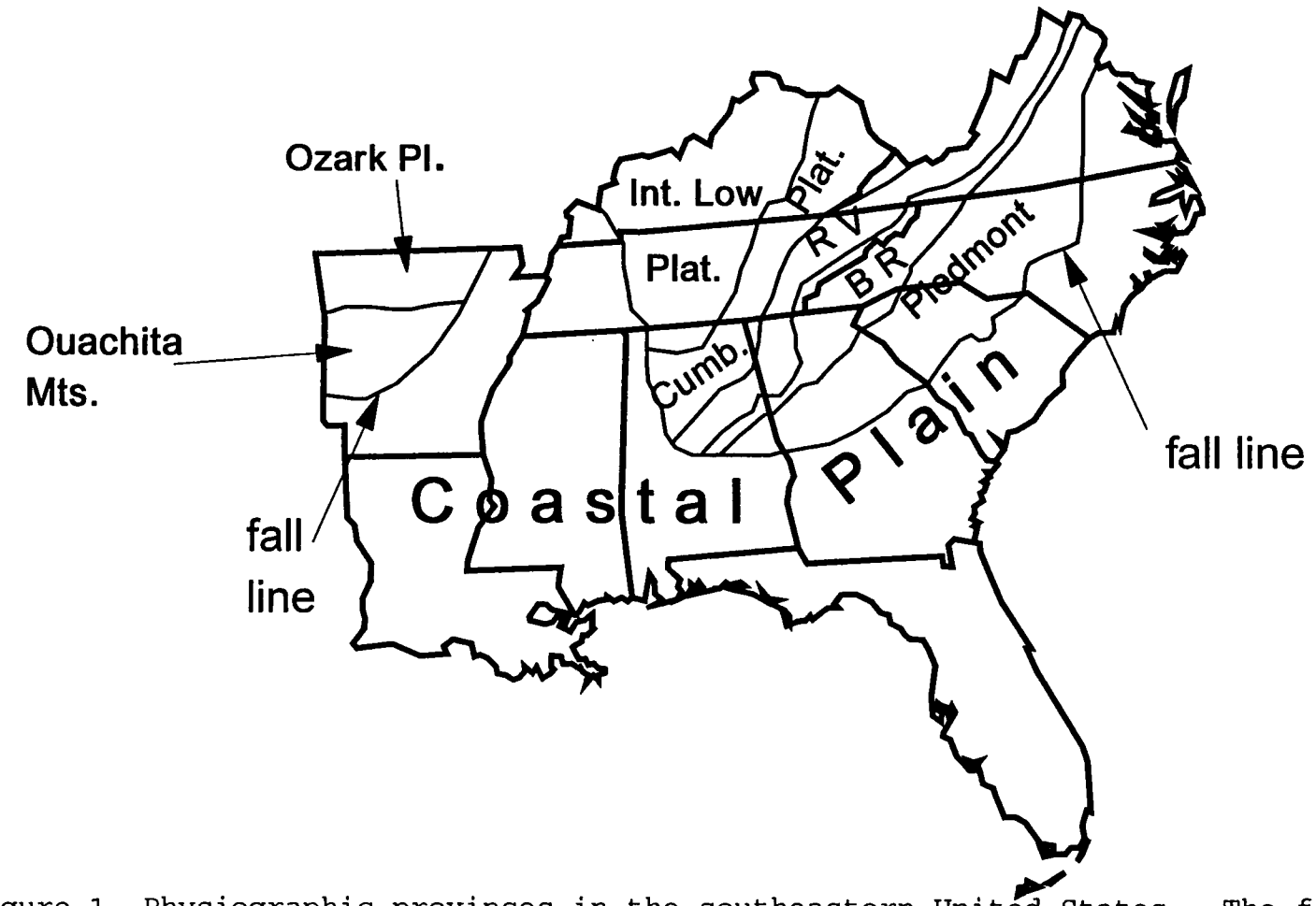


Figure 1. Physiographic provinces in the southeastern United States. The fall line is the inland boundary of the Coastal Plain. BR - Blue Ridge, RV - Ridge and Valley, Cumb. Plat. - Cumberland Plateau, Int. Low. Plat. - Interior Low Plateau.

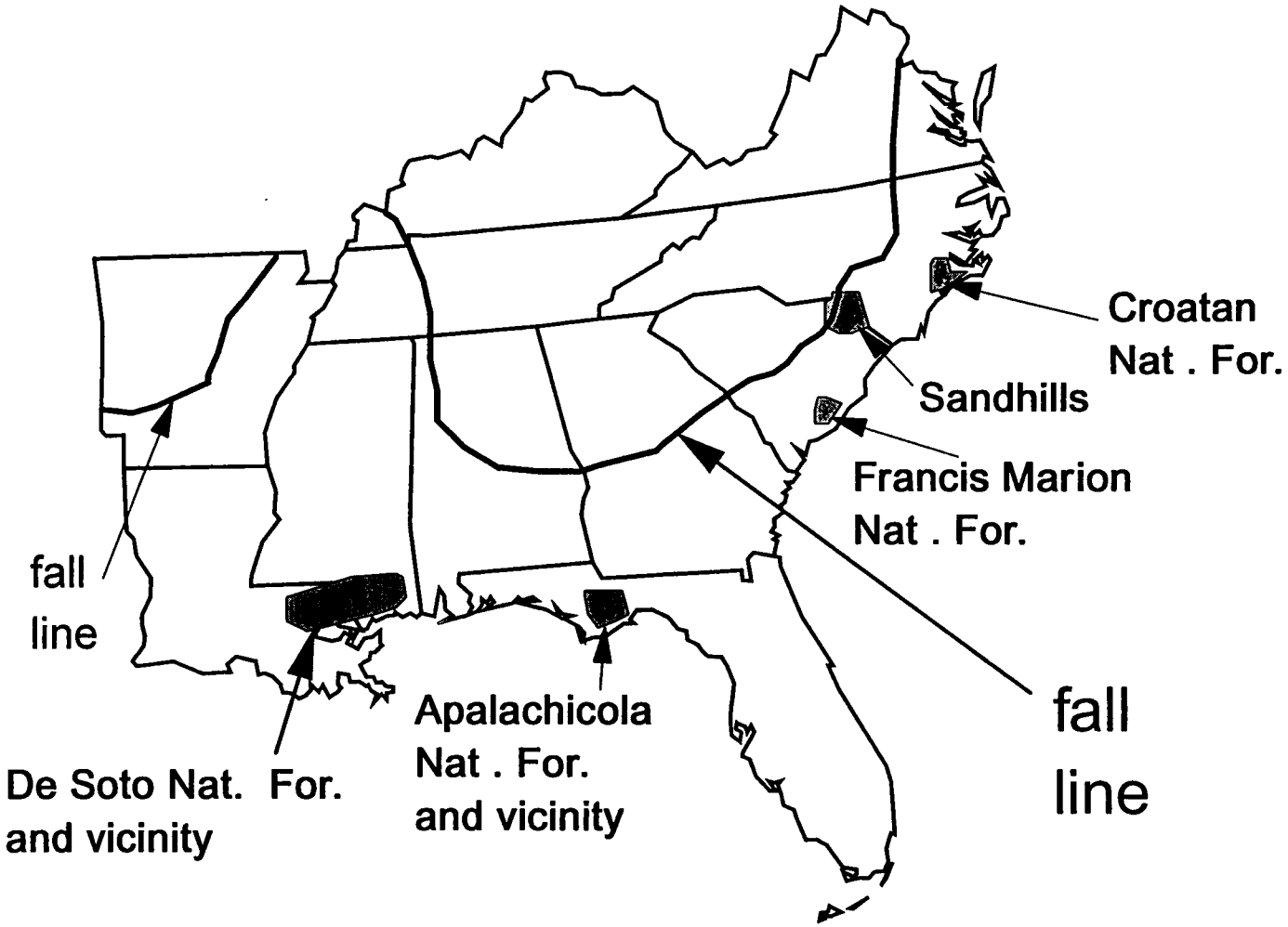


Figure 2. Locations of the five areas from which specimens were obtained for morphometric studies.

The second objective was studied to investigate the extremes of morphological variation exhibited by *S. cuspidatum* attributed to site moisture conditions. In order to quantify natural seasonally correlated variation in the morphology of *S. cuspidatum*, permanent quadrats were established at five sites in the Francis Marion National Forest. All sites were nonalluvial wetlands expected to have standing water from middle to late fall into or through the spring and the water table generally below the surface during the summer and into the fall. The quadrats comprised defined plots for repetitive sampling from which randomly selected plants were collected for measurement of nineteen morphological features. Plants within and surrounding the quadrats closely matched modern-day concepts (Andrus 1974, 1980; Crum 1984) of *S. cuspidatum*. The null hypothesis tested was that neither month nor quadrat nor their interaction had a significant effect on the morphological features of *S. cuspidatum*.

Peatlands, Peat Mosses, and the *Sphagnum cuspidatum* Complex

Peatlands cover one to two percent of the earth's land surface, with most peatlands occurring in northern temperate and boreal zones. *Sphagnum* (peat moss) is a major component of most of these peatlands (Clymo and Hayward 1982). The ecological importance of this genus in boreal wetlands is well-documented (e.g. Horton et al. 1979). In these

habitats much of the biomass of *Sphagnum* does not decay, but builds up and forms peat. The peat thus formed, as well as the living *Sphagnum*, can absorb large quantities of water. The living *Sphagnum* also actively exchanges H^+ for cations such as Ca^{2+}, Mg^{2+}, Na^+, and K^+. As peat builds up and the forming bog becomes progressively more isolated from the mineral soil, nutrient inputs may become limited to atmospheric deposition. As a result of these processes, *Sphagnum*-dominated ecosystems tend to be very wet, acidic, and nutrient poor.

Peat mosses, in addition to being ecologically important organisms, are also an anatomically isolated group. Schimper (1858), in his classic study of peat moss anatomy and taxonomy, suggested that peat mosses, on the basis of their unique morphology, should be recognized as a separate group equal in taxonomic rank to the other mosses and to the liverworts. Distinctive features of peat mosses include branches in fascicles with both divergent and pendent branches, leaves comprised of a network of chlorophyllose cells surrounding larger nonliving hyaline cells that possess fibrillose bands and pores, thallose protonematal phase, explosive dehiscence of the sporangium, and, due to the hyaline cells, a remarkable absorptive capacity (Schofield 1985).

Modern-day efforts lend credence to Schimper's opinion. Phylogenetic studies by Mishler and Churchill (1984),

Mishler et al. (1992), and Garbarry et al. (1993) placed *Sphagnum* in the moss clade, but consistently as a sister group to the other mosses. Garbarry et al. (1993) stated that, within the mosses, *Sphagnum* possesses five apomorphies related to male gametogenesis. Peat mosses do, however, share similarities with other bryophyte groups including archegoniate reproduction, certain ultrastructural features of the spermatozooid, mode of growth, and the dominance of the gametophyte generation in the life cycle (Eddy 1979).

Sphagnum is often quite common in a variety of wetland communities in the southeastern United States Coastal Plain (defined here as the Coastal Plain from North Carolina to eastern Texas - Figure 1) including cypress domes, cypress swamps, titi swamps, pocosins, Carolina bays, natural and man-made ponds and lakes, pitcher plant bogs, longleaf pine savannas (at least in the mesic to wet examples), Atlantic white cedar swamps, red maple swamps, and bays. Frequently, members of the Section *Cuspidata* are the most abundant group of *Sphagnum* in these habitats. The Section *Cuspidata* is also the most taxonomically diverse section in the southeastern Coastal Plain, with seven species listed by Anderson (1990) attributed to the region by various authorities. Andrus (1987) suggested the abundance of the *Cuspidata* species in the southeastern Coastal Plain was due to their ability to tolerate and cope with desiccation and other disturbances such as frequent fires and violent

storms. In contrast, the Section *Acutifolia* is poorly represented in the region in both diversity and biomass.

Six of the seven species of the Section *Cuspidata* present in the southeastern Coastal Plain comprise a taxonomically troublesome group that will be referred to as the *Sphagnum cuspidatum* complex. The members of the complex with their year of publication, following the nomenclature presented by Anderson (1990), are:

Sphagnum cuspidatum Ehrh. *ex* Hoffm. (1796)
S. fitzgeraldii Renauld & Cardot *in* Lesq. & James (1884)
S. mississippiense R.E.Andrus (1987)
S. torreyanum Sull. (1849)
S. trinitense Müll.Hal. (1848)
S. viridum Flatberg (1988)

[Authority abbreviations follow Brummitt and Powell (1992). The authorship for *S. fitzgeraldii* follows that suggested by Anderson (1993).].

Sphagnum recurvum P.Beauv. is the only member of the Section *Cuspidata* that occurs within the southeastern United States Coastal Plain that is not being included in the *Sphagnum cuspidatum* complex. *Sphagnum recurvum* is distinguished from the above species by characteristics of the stem as viewed in cross section, stem leaf shape, and

its tendency to grow at a higher position relative to the water table.

As will be presented in more detail in the Historical Perspective section (pp. 18 - 34), a variety of different opinions have been expressed concerning the distinctiveness of *S. cuspidatum* and *S. trinitense* (Warnstorf 1890a, 1911; Andrews 1913; Paul 1931, 1932; Blomquist 1938; Andrus 1974, 1980; Crum and Anderson 1981; Lane 1981; Crum 1984; Flatberg 1988; Anderson et al. 1992). Most of these authorities agree in recognizing two taxa here, but differ as to their degree of distinctness, how they should be ranked (as species or varieties), and as to their synonymies [contrast Andrus (1974) with Crum (1984)].

Sphagnum mississippiense was described by Andrus (1987) as a species quite similar morphologically to *S. trinitense* and endemic to southern Mississippi and eastern Louisiana. It is apparent that some present-day North American workers believe that *S. mississippiense* represents variation within *S. trinitense* (L. E. Anderson *in litt.*) whereas H. Crum (specimen annotations) assigns type specimens of *S. mississippiense* to *S. cuspidatum* var. *cuspidatum* [listed as *S. cuspidatum* Ehrh. *ex* Hoffm. by Anderson (1990)].

Flatberg (1988) described *S. viridum* as a species quite similar to *S. cuspidatum* and indicated its predominant range as European with a spotty distribution in eastern North America from Nova Scotia to Michigan and south to North

Carolina. Flatberg provided a detailed description of *S. viridum* and a detailed, amended description of *S. cuspidatum* in order to clarify the relationship between the two species. Anderson (*in litt.*) is of the opinion that *S. viridum* simply represents variation within *S. cuspidatum* whereas Andrus believes it is a good species (Andrus et al. 1994).

Thus two additional species pairs problems (*S. trinitense-S. mississippiense* and *S. cuspidatum-S. viridum*) have been superimposed on a pre-existing problematic species pair (*S. cuspidatum* and *S. trinitense*). Forms assignable to *S. cuspidatum*, *S. trinitense*, *S. mississippiense*, and *S. viridum* comprise the taxonomically troublesome core of the complex.

Sphagnum fitzgeraldii and *S. torreyanum* are included in the complex on the basis of morphological, ecological, and biogeographic similarities to the other four species. They are not considered taxonomically troublesome, however, since specimens of these two species are generally readily separable both in the field (macroscopically) and in the laboratory (microscopically) from the remainder of the complex.

Description and Delineation of the *Sphagnum cuspidatum* Complex

General Features of the *Sphagnum cuspidatum* Complex

Weak-stemmed floating aquatics or stems "stranded" on wet-moist substrates. Outer stem cells without pores or fibrils, inner stem region generally designated as the wood cylinder yellow-green (sometimes brownish). Stem leaves oblong to ovate to triangular (to elliptic in *S. fitzgeraldii*), apex acute to rounded obtuse (rounded to nearly truncate in *S. fitzgeraldii*); hyaline cells narrow, shorter above, 0-1-2 divided, often more frequently divided in the lower leaf half, fibrillose throughout to efibrillose, mostly aporose on the outer surface with occasional end pores, the inner surface frequently with membrane gaps. Branches typically four per fascicle with two spreading and two pendent, retort cells with inconspicuous necks and often in longitudinal rows. Median and distal branch leaves lanceolate to narrowly lanceolate [in *S. mississippiense* ovate-lanceolate to lanceolate to narrowly lanceolate (Andrus 1987)]; hyaline cells 5-6:1 above, 5-6 to 10-14:1 below, convex surface of hyaline cells with 2-5 small, rounded more or less elliptic pores, concave surface of hyaline cells with a few larger unringed pores or pores none (pores may be difficult to demonstrate on either surface) (Andrus 1980, Crum 1984, Warnstorf 1903, and pers. obs.).

Features That Discriminate Members of the *Sphagnum cuspidatum* Complex from Other Taxa in the Section *Cuspidata*

There are 23 species in the Section Cuspidata in North America listed by Anderson (1990). On the basis of morphology, two of these species, *S. jensenii* and *S. majus*, could perhaps be added to the *S. cuspidatum* complex. However, neither of these two boreal taxa are known from the southeast Coastal Plain (the study area). The relationships of these two species to those that occur in the Coastal Plain deserve further study.

Morphology. In combination, the following features effectively distinguish the members of the complex from other *Cuspidata* species: branch leaves noticeably elongated toward the branch tips (not always the case in forms assignable to *S. mississippiense* or terrestrial *S. cuspidatum*), weak-stemmed floating aquatics (although *S. torreyanum* can be quite stout), stem leaves deltoid to ovate-deltoid with acute to obtuse apices (oblong with broadly rounded apices in *S. fitzgeraldii*), the branch leaf hyalocysts on the outer surface with pores small, few, and limited to cell ends, on the inner surface with pores somewhat larger and in the cell corners (as emphasized earlier, these pores may be sparing or absent), and young pendent branches not paired between the rays of the capitulum. Lack of this last feature and stem leaf apex characteristics effectively distinguish members of the

complex from *S. recurvum*, a species that often co-occurs with the complex in the study area.

Ecology. Although nearly all species in the Section *Cuspidata* occur in very wet habitats, the *S. cuspidatum* complex is the most aquatic. In the southeastern United States, the members of this complex occur in habitats such as pocosin pools, vernal pools of pine-ericaceous forests, pond margins, gum-maple-cypress swamps, and cypress domes. These sites generally experience wide, seasonal water table fluctuations and, depending on pool depth and precipitation patterns, frequently dry out during part of the summer.

In the southeastern Coastal Plain, the members of the complex behave somewhat like fugitive species in that they consistently produce sporophytes in abundance, grow rapidly, and occur in disturbed (by fire, violent weather, and drought) habitats (Andrus 1987, Christensen 1988). Fire is a frequent and important ecological factor in the Coastal Plain (Christensen 1988). Pocosins and swamps, during periods of low water or drought, periodically experience fires that burn into the peaty substrates to varying depths. Such fires result in a heterogeneous microtopography where water may stand in the deeper peat burns much of or throughout the year. Abundant spore production, and perhaps dispersal of vegetative diaspores, enables the members of the complex to rapidly colonize these randomly created and periodically surface-sterilized sites. Fire also thins and

opens up the dense shrub layers that characterize many Coastal Plain plant communities, thereby renewing habitats favorable for the growth of the *Sphagnum cuspidatum* complex.

Titus et al. (1983) and Titus and Wagner (1984) found that *S. recurvum* (Section *Cuspidata*) was able to photosynthesize at a higher rate than *S. nemoreum* (=*S. capillifolium*, Section *Acutifolia*) when the two species were at equivalent, relatively low, percent dry weight moisture levels. The former species could also survive several days of desiccation whereas the latter species could not. The above studies, and the prolific sporophyte production of the *S. cuspidatum* complex, suggest that the abundance of these peat mosses in the Coastal Plain may be due to tolerance of desiccation and an ability to colonize suitable habitats as they are opened up by fire or violent weather.

The above description of habitat disturbance and dispersal abilities does not apply as well to *S. torreyanum* or the natural communities it occurs in, since the species rarely produces sporophytes in the southeast and it occurs in more permanently wet areas with a closed canopy (pers. obs.).

Distribution of the Members of the Complex

All six members of the complex are present in the southeastern Coastal Plain. *Sphagnum mississippiense* is endemic to southern Mississippi and eastern Louisiana

(Andrus 1987). *Sphagnum fitzgeraldii* is less restricted, but is confined to the region and ranges from southern Mississippi to North Carolina in the outer Coastal Plain (Andrus 1987, Anderson 1992). *Sphagnum torreyanum* reaches its southern distributional limit in the study area and extends northward through New England to southeastern Canada (Crum 1984, Andrus 1987).

The remaining three species are more widely distributed. The full range of *Sphagnum trinitense*, due to its confusing nomenclature and taxonomic history (e.g. see Warnstorf 1903, Isoviita 1966, Andrus 1974, Crum 1984, and the Historical Treatment section herein), is unclear. According to Crum (1984), material resembling this taxon occurs from Nova Scotia along the coast south to Florida and westward to Louisiana, and is also present in South America. Crum (1994) cites the species from Costa Rica as well. According to Flatberg (1988), *S. viridum* is known from coastal areas of both Europe and eastern North America, and occurs inland in North America in the Great Lakes region in both Michigan and Indiana. Material referred to *S. cuspidatum* is known from coastal regions and the Great Lakes region of eastern North America, Costa Rica, Panama, northern South America, southeast Asia, and south-central Africa (Crum 1984, 1994; Eddy 1993). South of New Jersey in the Coastal Plain, except for *S. recurvum*, members of the complex are the only Section *Cuspidata* species present.

Differentiation of the Members of the Complex

Table 1 lists characters presented by various authors as useful in distinguishing the species of the complex.

Sphagnum fitzgeraldii. This species appears to be distinct and well-defined. The plants are smaller than other members of the complex and are uniformly hemi-isophyllous (Anderson 1992) with oblong to elliptic to ovate stem leaves. Diagnostic morphological features are stem leaves serrulate in the distal one-fourth, branch leaves with broadly rounded to nearly truncate apices and serrulate nearly to the base, and capitular branches with blunt tips. Anderson et al. (1992) found that this species maintained its essential features when regenerated from capitular branch bases in axenic culture. *Sphagnum fitzgeraldii* is also ecologically distinct, occurring in pools and depressions that are dry for more of the year than is characteristic of the habitats of the other taxa of the complex (Risk 1988).

Sphagnum torreyanum. Plants are larger than those of any other species in the complex. Usually easily recognized in the field due to its bristly erect branch leaves and prominent terminal bud. Microscopically it can be separated on the basis of branch leaf chlorophyllose cells in the lower leaf half being exposed only on the convex surface. *Sphagnum torreyanum* is apparently a polyploid, with a chromosome number of n=38 (Maass and Harvey 1974). Other

Table 1. Characters emphasized by various authorities as useful in differentiating members of the *Sphagnum cuspidatum* complex.

Character	*S. cuspidatum*	*S. viridum*	*S. mississippiense*	*S. trinitense*
Relative Plant Size	medium	medium	small to medium	medium to large
Terminal Bud Prominence	none	none	slight	slight to prominent
Differentiation of Outer Stem Layers	well-differentiated	well-differentiated	usually not differentiated, but variable	usually not differentiated, but variable
Stem Leaf Shape	narrowly to broadly triangular	narrowly to broadly triangular-lingulate	elongate triangular	elongate trinagular
Stem Leaf Apex	acute to bluntly pointed	acute to bluntly pointed	slightly rounded to acute	acute to bluntly pointed
Stem Leaf Hyalocyst Septations	mostly non-septate throughout	nonseptate to sometimes septate	usually one divided	mostly one-septate, particularly in lower 1/2
Branch Leaf Stance (wet)	slightly erect and often slightly falcate	slightly erect and often slightly falcate	slightly erect to imbricate	loosely erect to imbricate
Branch Leaf Surface (dry)	slightly to strongly undulate	undulate	slightly undulate	smooth to slightly undulate
Branch Leaf Shape	long lanceolate	lanceolate	ovate to lanceolate	long lanceolate
Branch Leaf Margin	entire to slightly denticulate at apex	entire or with scattered teeth	denticulate/serrulate often to near base	serrate to serrulate
Chlorophyllose Cell Exposure on Concave Surface	well-exposed	well-exposed	well-exposed	well-exposed
Ecology/Habitats	savanna-pocosin ecotones, ponds, swamps, ditches, borrow pits	same as *S. cuspidatum* but more minerotrophic	shrubby thickets with shallow pools	same as *S. cuspidatum*
Range (world; Coastal Plain)	cosmopolitan; Louisiana to Long Island	Europe and North America; North Carolina to New Jersey	endemic to N. Am.; Mississippi and Louisiana	North America, Europe, eastern Asia; Louisiana to New York

Table 1 continued.

Character	*S. torreyanum*	*S. fitzgeraldii*
Relative Plant Size	robust	small
Terminal Bud Prominence	well-defined	usually visible
Differentiation of-Outer Stem Layers	not well-differentiated	well-differentiated
Stem Leaf Shape	ovate-deltoid	oblong-ovate to elliptic
Stem Leaf Apex	bluntly acute	rounded
Stem Leaf Hyalo-cyst Septations	undivided or sometimes septate	usually one divided
Branch Leaf Stance (wet)	bristly erect	slightly erect to almost imbricate
Branch Leaf Surface (dry)	slightly to strongly undulate	smooth
Branch Leaf Shape	slenderly long lanceolate	ovate or oblong-elliptic, sometimes nearly quadrate
Branch Leaf Margin	entire	serrate to serrulate from apex to near base
Chlorophyllose Cell Exposure on Concave Surface	enclosed to slightly exposed	well-exposed
Ecology/Habitats	blackwater lakes, cypress and white cedar swamps,	savanna-pocosin ecotones, seasonal pools
Range (world; Coastal Plain)	endemic to N. Am.; Louisiana to Long Island	endemic to N. Am.; Mississippi to North Carolina

taxa in the complex for which the chromosome number is known (*S. cuspidatum*, *S. trinitense*, *S. fitzgeraldii*) have n=19 (Bryan 1955, Anderson 1992).

Sphagnum trinitense. According to various authorities (Andrews 1913, Blomquist 1938, Andrus 1974, 1980, Crum 1984, 1994), this species differs primarily from *S. cuspidatum* in its serrulate branch leaf margins. This feature is particularly well-developed on distal branch leaves. Other characters emphasized by Andrus (1974, 1980) in recognizing *S. trinitense* include outer stem cell layers not conspicuously differentiated in size and cell wall thickness from adjacent inner stem cell layers, stem leaf hyalocysts mostly one-septate in the lower leaf half, and capitula lacking a crisped appearance.

Sphagnum mississippiense. According to Andrus (1987), this species is closely allied to *S. trinitense*. The two species are primarily distinguished by branch leaf shape. The proximal branch leaves of *S. mississippiense* being broadly ovate to ovate whereas in *S. trinitense* they are ovate-lanceolate to narrowly lanceolate (Andrus 1987).

Sphagnum cuspidatum. According to Andrus (1974, 1980) and Crum (1984), this species is distinguished by its entire-margined branch leaves that are strongly erect when dry. This is in contrast to both *S. trinitense* and *S. mississippiense* which have denticulate- to serrulate-margined branch leaves that are appressed when dry. Andrus

(1974) also indicated that *S. cuspidatum* may be separated from the above two species by its outer stem cell layers which are strongly differentiated in size and cell wall thickness from adjacent inner layers, and stem leaves with none to few hyalocysts divided.

Sphagnum viridum. This recently described species is very similar in appearance to *S. cuspidatum*. According to Flatberg (1988), *S. viridum* has a brighter green appearance in the field, less curved divergent branches, broader branch leaves that are less involute above with shorter and broader chlorocysts, stem leaves with narrower and less rhombic hyalocysts, and more coarsely papillose spores. According to Andrus et al. (1994), the best character to separate the two taxa is the length of the branch leaf hyaline cells in the middle of the lower leaf half. In wet-grown material, the length to width ratio of these hyaline cells for *S. viridum* is 6:1 and for *S. cuspidatum* is 10:1.

An Historical Perspective on the *Sphagnum cuspidatum* Complex

The historical taxonomic and nomenclatural treatment of the group is intimately tied to the work of various European and North American sphagnologists. This examination of the taxonomic evolution of the complex has two goals: (1) to present the historical treatments of the complex by European and North American authorities and (2) to evaluate how these workers dealt with the taxonomic and nomenclatural problems

posed by the complex. Most of the discussion is devoted to the *S. cuspidatum/S. trinitense* species pair, after which the other members of the complex are placed into context.

Sphagnum cuspidatum and *S. trinitense*

The period from the middle 1700's to the middle 1800's was when bryologists first began to deal seriously with the great diversity of morphologies presented by peat mosses. About a dozen species had been named in Europe by 1844 (Isoviita 1966), mostly by German and Swiss bryologists. Hooker and Taylor (1827), however, felt that few of the species described by Bridel (1826) or attributed to Germany by Nees, Hornschuch, and Sturm (1823) "will prove constant to their characters." Hooker and Taylor (1827) thought that the morphological intergradation shown by the species of *Sphagnum* seemed to "strengthen the opinion held by the older Muscologists that they are but different forms of one and the same kind." These statements seem remarkable today since, based on the descriptions and illustrations provided by Hooker and Taylor, the four species they listed for Great Britain and Ireland would be placed in different sections of the genus by modern interpretation. These statements by Hooker and Taylor also illustrate the difficulty early workers had in discriminating taxa and in recognizing morphological groups currently accepted by modern sphagnologists.

Sphagnum cuspidatum was described in 1796. A similar species, *S. recurvum* P.Beauv., was described about a decade later (*fide* Wijk et al. 1967). The latter species was often listed as a synonym of *S. cuspidatum* until at least 1869 (Sullivant 1856, Schimper 1858, Milde 1869). The differences between the above two species were sorted out during the late 1800's (Andrews 1919). In fact, present-day sphagnologists include *S. recurvum* in another taxonomically difficult group of peat mosses (the *Sphagnum recurvum* complex) (Flatberg 1992, 1994).

The variability of *S. cuspidatum* is illustrated by the numerous varieties that were described between 1800 and 1860. Four of these vars., *falcatum* Russow, *submersum* Schimper, *plumosum* Nees, Hornschuch, & Sturm, and *plumulosum* Russow, were recognized by Schimper (1858) in his beautifully illustrated monograph of the European members of the genus. Various combinations of these four varieties, as well as others, continued to be listed by both European and North American authors for the next 50 years (Milde 1869, Lesquereux and James 1884, Cardot 1887, Kindberg 1890, Warnstorf 1890a, 1890b, 1903, 1911).

Müller (1849) described *S. laxifolium* as a species that included both *S. cuspidatum* var. *plumosum* and *S. hypnoides* (A. Br. ex Bruch) Brid. Schimper (1858) treated *S. laxifolium* as synonymous with *S. cuspidatum* var. *plumosum*. Milde (1869), in contrast, recognized *S. cuspidatum* and *S.*

laxifolium as separate species and stated that he could always tell them apart. Interestingly, he also indicated it was useful to differentiate them at the species level in order not to have many variable forms placed within one species. Milde placed *S. recurvum* in the synonymy of *S. cuspidatum*, however, and thus it is difficult to determine what part of *S. cuspidatum* he was comparing with *S. laxifolium*. Eventually, through the latter half of the 1800's, European sphagnologists sorted out the *S. cuspidatum-S. recurvum* and *S. cuspidatum-S. laxifolium* problems. *Sphagnum recurvum* and *S. cuspidatum* became regarded as distinct and *S. laxifolium* was determined to be equivalent to an aquatic variety (*plumosum*) of *S. cuspidatum* (Schliephacke 1882, Kindberg 1890, Warnstorf 1903, Andrews 1919).

Müller (1849) introduced another name, *S. trinitense*, and placed this new taxon in a group of species of uncertain position, although he indicated the species was similar to *S. laxifolium*. Later workers such as Warnstorf and Andrews, who had the opportunity to examine original material of *S. trinitense*, obviously observed teeth along the branch leaf margins (Warnstorf 1890, 1903, 1911; Andrews 1913, 1936). Curiously, Müller (1849) makes no mention of this distinctive feature in the description.

Karl Schliephacke (1865) described *S. laxifolium* var. *serrulatum* from floating material collected from a deep pool

in a European bog. He stated that this variety was the only peat moss with teeth along the branch leaf margins. Thus, though Schliephacke may have made use of Müller's Synopsis (1849), this statement indicated he had not examined specimens of *S. trinitense*. In 1882, Schliephacke transferred the variety *serrulatum* to *S. cuspidatum* since he agreed by that time that *S. laxifolium* was a synonym of *S. cuspidatum*.

Austin (1877) described *S. serratum* based on material collected from Florida by J. Dounell Smith. The species was notable for its serrulate branch leaf margins and was indicated as being not dissimilar to *S. cuspidatum*.

Thus by 1882, three names were being applied to plants similar to, or taxonomically part of, *S. cuspidatum* that possessed serrulate branch leaf margins and that had been collected from three different continents: *S. trinitense*, *S. serratum*, and *S. cuspidatum* var. *serrulatum*. Several questions remained to be addressed regarding serrulate-leaved material: (1) How many taxonomic groups did these names represent?, (2) What was the appropriate rank at which to recognize these groups?, and (3) What was their distribution?

Lesquereux and James (1884), in their treatment of the mosses of North America, listed *S. serratum* as *S. cuspidatum* var. *serratum*; they made no mention of *S. trinitense*. Three years later, Cardot (1887) took the first of three critical

steps in tying together North American and European serrulate material. He listed *S. serratum* as *S. cuspidatum* var. *serratum* **and** also stated that it appeared to be identical to *S. cuspidatum* var. *serrulatum* Schliephacke. He also did not mention *S. trinitense*.

Warnstorf (1890a), in his treatment of the North American *Cuspidata*, took the second critical step when he listed *S. trinitense* as a component of the North American flora, included *S. serratum* as a synonym of *S. trinitense*, and stated that *S. trinitense* was close to *S. cuspidatum* var. *plumosum* fo. *serrulatum* Schliephacke (=*S. cuspidatum* var. *serrulatum* Schliephacke). Warnstorf (1903) then attributed *S. trinitense* to Europe's flora and included *S. cuspidatum* var. *serrulatum* and *S. serratum* as synonyms of this species. Whether or not one agrees with Warnstorf's taxonomy, his classification scheme and synonymy completed the circle and tied all three of these names together.

Warnstorf (1911) presented the only worldwide treatment of *Sphagnum*. He listed and described 342 species, and within many of them he also recognized many varieties and forms. Apparently he had altered his interpretation of serrulate-leaved material sometime after 1903. Warnstorf (1911) indicated that *S. trinitense* occurred in coastal regions of eastern North America and tropical America; Europe was not included in its range. He stated that *S. trinitense* was synonymous with *S. serratum* in part, and he

recognized 4 varieties of *S. trinitense*. He also listed *S. serratum* as a full species and listed *S. cuspidatum* var. *serratum* (Aust.) Lesq. & James and *S. trinitense* C. Müll. *apud* Warnstorf (1903) as synonyms of *S. serratum*. Warnstorf (1911) attributed *S. serratum* to central Europe, Atlantic North America, and tropical America. Four varieties were also recognized. *Sphagnum cuspidatum* var. *serrulatum* Schliephacke was listed as a synonym of *S. serratum* var. *serrulatum*. He included central Europe, Atlantic North America, Japan, and Australia in the range of *S. serratum* var. *serrulatum*. Warnstorf commented that this variety could be added to the circle of forms around *S. cuspidatum*.

Julius Röll was a contemporary of Warnstorf who had a very different outlook on the direction sphagnological research should take. In the opinion of Röll (1888), the so-called constant features of peat mosses are completely variable and thus, in his view, many of the named species and varieties of *Sphagnum* could transform from one into another under certain environmental conditions. He thus organized the numerous morphotypes of peat mosses into "Formenreihen" or series of forms and indicated that the members of a "Formenreihe" could change from one expression into another. For Röll, constant "species" corresponded to his individual "Formenreihen". The Formenreihen appear to be more or less equivalent to the taxonomically broad "Collectivspecies" presented by Warnstorf (1881).

Röll considered the study of these transformations to be of greater value than attempts to establish constant species and varieties. He interpreted what other workers were calling species and varieties as only representing one particular manifestation from a wide range of possible forms that could be obtained by that particular entity. Secondly, for Röll, the intermediate forms were just as important to study as the "typical" forms. From the standpoint of *S. cuspidatum*, Röll's viewpoint had a certain amount of validity considering the number of morphologically similar species and named varieties recognized up through the early 1900's, particularly by Warnstorf. Although Röll's ideas have been discounted, his emphasis on the phenotypic plasticity of *Sphagnum* should be kept in mind. As Paul (1932) reminded us, however, transformations between actual species do not occur.

Warnstorf was a prolific author of plant names and decidedly a taxonomic splitter. According to Andrews (1936), one cannot escape the impression that Warnstorf tried to make a new species out of nearly every exotic specimen he examined. Andrews is regarded as the North American *Sphagnum* expert from the early 1900's until about 1950. He presented a perspective rather different from that of Warnstorf. Of the 342 species listed and described for the world by Warnstorf (1911), Andrews said he would, at most, recognize 100 of them.

For North America, Andrews (1913, 1919) recognized *S. cuspidatum* (the typical variety) and *S. cuspidatum* var. *serrulatum*. He included *S. laxifolium* var. *serrulatum*, *S. trinitense*, and *S. serratum* as synonyms of the latter variety. This again connected North American serrulate-leaved material to the variety established by Schliephacke. Blomquist (1938), who followed Andrews' taxonomy, in the only treatment of the peat mosses of the southeastern United States, stated that *S. cuspidatum* var. *serrulatum* was only locally common, occurred near the coast throughout the area, always grew in water, and was easily recognized by its serrulate linear branch leaves. Paul (1931, 1932), a German bryologist, in contrast, stated that *S. cuspidatum* var. *serrulatum* and other varieties of *S. cuspidatum* based on European material only represented environmental modifications of *S. cuspidatum* and that the var. *serrulatum* had nothing to do with the American species *S. serratum* and *S. trinitense*. Thus two very different interpretations regarding the equivalence of serrulate material in Europe and North America were espoused by North American and European authorities.

Isoviita (1966), in a nomenclatural revision of European *Sphagnum*, indicated that the taxonomy and nomenclature of *S. serratum* was quite confused. He stated that it was not impossible that *S. serratum* is based on modified material of *S. cuspidatum*. Isoviita, in agreement

with Paul (1931, 1932), also indicated that the name *S. cuspidatum* var. *serrulatum* is based on European material and does not apply to North American material. The assertion that the various European varieties of *S. cuspidatum* are simply environmental modifications was also more recently echoed by Daniels and Eddy (1985).

In two North American checklists and a Flora of North America treatment, Crum et al. (1965, 1973) and Crum (1984) recognized serrulate-leaved material as *S. cuspidatum* var. *serrulatum* and equated this variety with *S. trinitense* and *S. serratum*. Anderson (1990), in the most recent checklist of North American *Sphagnum*, recognized serrulate-leaved material as *Sphagnum trinitense* and listed *S. cuspidatum* var. *serrulatum* and *S. serratum* as synonyms. Thus these more recent workers followed the nomenclatural relationships espoused earlier by Andrews.

Andrus (1974), in a monographic study of the *Sphagnum* of New York state, resurrected *S. trinitense* as a full species. He asserted that overemphasis on branch leaf margin features by Andrews led to a "neglect of this perfectly good species." According to Andrus, *S. trinitense* has a less well-differentiated stem cortex, more numerous septate cells in the stem leaves, and capitula lacking a crisped appearance as compared with *S. cuspidatum*. He also listed *S. cuspidatum* var. *serrulatum* and *S. laxifolium* var. *serrulatum* as synonyms of *S. cuspidatum*, not of *S.*

trinitense, in accordance with post-Warnstorf European authorities and in contrast with other North American authorities. Flatberg (1988) supported Andrus' taxonomic opinion and stated that *S. trinitense* "...deviates in so many essential features from *S. cuspidatum* and *S. viridum*, that its specific distinctness seems well justified."

Growth studies by Paul (1932) and Agnew (1958) showed that entire-leaved plants of *S. cuspidatum*, when grown in standing water, can produce new branches with serrulate leaves. These findings have been recently supported by axenic culture studies in which plants of *S. cuspidatum* were regenerated from excised capitular spreading branches taken from entire-leaved material (Anderson et al. 1992). The regenerants had serrulate branch leaf margins. Thus Anderson et al. (1992) stated that "the retention of *S. trinitense* as a species is counterindicated by our findings."

Lane (1981) conducted a series of morphometric analyses on the *S. cuspidatum/S. trinitense* species pair using material from the southeastern United States. He concluded, on the basis of examining branch leaf margin features, number of septa per stem leaf, and branch leaf stance when dry, that *S. cuspidatum* and *S. trinitense* were not distinct enough to be recognized as separate species. He recommended that *S. trinitense* be synonymized with *S. cuspidatum* or only recognized at the varietal level as *S. cuspidatum* var.

serrulatum. Some of Lane's comparisons, unfortunately, suffer from small sample size and biased specimen selection (the exemplar method - choosing exemplary specimens of two "species" to determine their degree of distinctness).

Sphagnum mississippiense

This species was recently described by Andrus (1987). It is quite similar to *S. trinitense*. Only four localities for *S. mississippiense* were presented, all of them in southern Mississippi and eastern Louisiana. The distinctiveness of *S. mississippiense* has not be re-evaluated since its initial publication.

Sphagnum viridum

Flatberg (1988) described *S. viridum* as a species quite similar to *S. cuspidatum*. The range for *S. viridum* given by Flatberg included Europe and North America, with a few collections cited for the southeastern United States Coastal Plain. Andrus et al. (1994) stated that North American material of *S. viridum* and *S. cuspidatum* are separable on the basis of length to width ratios of branch leaf hyaline cells.

Sphagnum torreyanum

This species was described by Sullivant (1848) as a robust peat moss with bristly erect branch leaves and

chlorophyllose cells well enclosed on the concave leaf surface. For the next 125 years this taxon was treated as a variety of *S. cuspidatum* by most authors (Braithwaite 1880; Cardot 1887; Warnstorf 1890; Andrews 1913, 1919, Andrews in Grout 1940; Crum et al. 1965). According to Andrews (1919), the var. *Torreyi* (=*S. torreyanum*) was connected by intermediate forms with the typical variety of *S. cuspidatum*. The validity of this statement was disputed by Andrus (1974), who considered *S. torreyanum* to be a distinct species. Also Crum et al. (1973), Crum (1984), and Anderson (1990) recognized it at the specific level as well.

Sphagnum torreyanum is presently considered to be endemic to coastal regions of eastern North America (Crum 1984, Andrus 1987). Warnstorf (1903), however, did attribute the species to Europe. Later European workers (Isoviita 1966, Daniels and Eddy 1985) decided that the name had been misapplied to European material.

Sphagnum fitzgeraldii

Sphagnum fitzgeraldii was described in Lesquereux and James (1884), who placed it in the *Cyclophylla*, a group comprised of noncapitulate species. Cardot (1887) correctly ascertained its affinities since he placed it in the "Sphagna Undulata," a group that corresponded to the Section *Cuspidata*.

Sphagnum fitzgeraldii has several distinctive morphological features; thus, it has consistently been recognized as a full species, with one exception. Amazingly, Warnstorf (1911) listed *S. fitzgeraldii* as *S. trinitense* var. *fitzgeraldii* and listed *S. mohrianum* Warnst. (today considered a synonym of *S. fitzgeraldii*) as *S. trinitense* var. *mohrianum*. Morphometric studies by Lane (1981) and culture studies by Anderson et al. (1992) also supported the recognition of *S. fitzgeraldii* as a full species.

Additional Comments

As indicated by this review, the taxonomic and nomenclatural problems presented by the complex are much larger, geographically speaking, than the southeastern United States Coastal Plain. Studies of types and original material will be necessary to clarify the nomenclature of the group. Future studies may address these broad nomenclatural issues.

As previously stated, European authorities accord serrulate-leaved forms of *S. cuspidatum* no taxonomic standing. By equating *S. cuspidatum* var. *serrulatum* with the names *S. trinitense* and *S. serratum*, North American authorities such as Andrews (1913, 1919), Crum (1984), Crum and Anderson (1981), and Anderson (1990) have made it unclear exactly what is to be included in their concept of

S. cuspidatum var. *serrulatum*, or in the case of Anderson (1990), his concept of *S. trinitense*.

There are at least three possible interpretations for the makeup of this taxonomic entity as used by the above authors: (1) it is a position **only** for serrulate, aquatic modifications of *S. cuspidatum*, (2) it is a position **only** for an entity that is quite similar to aquatic forms of *S. cuspidatum*, but that has serrulate branch leaf margins regardless of habitat conditions, or (3) it is a position for serrulate aquatic modifications of *S. cuspidatum* **and** another similar entity that is serrulate regardless of habitat conditions.

If (1) is true, then no taxonomic recognition is warranted since there would be no genetic basis for the variety. If (2) is true, we then have a nomenclatural problem to deal with, a question of rank to be addressed, and we must also discover how to distinguish this entity from *S. cuspidatum* under a wide range of habitat conditions. If (3) is true, then the taxon is heterogeneous and it is important that characters be discovered that can consistently separate the two entities being "lumped." The intent and interpretation of the above North American authorities is probably aligned with choice (2). Unfortunately, because of their emphasis on one variable morphological character to separate the taxa and the employment of the varietal epithet *serrulatum* as a label for

one of these taxa, the actual result obtained in many herbaria may be choice (3). This confusion results from the structure of keys presented by Blomquist (1938) and Crum (1984) and others which place all conspicuously serrulate material, regardless of its actual affinities, in the same variety. Keys in Andrus (1974, 1980) also use the branch leaf margin feature to distinguish *S. cuspidatum* and *S. trinitense*, but the feature is presented in conjunction with the stem leaf and stem characters discussed previously.

The descriptions of *S. mississippiense* and *S. viridum* have further complicated the above situation by superimposing two new species pairs problems on a significant pre-existing problem. Though *S. torreyanum* and *S. fitzgeraldii* are included as members of the complex, they are generally regarded as well-demarcated and well-defined. Thus forms presently associated with the names *S. cuspidatum*, *S. trinitense*, *S. mississippiense*, and *S. viridum* comprise the problematic core of the complex.

The complex, as a whole, is rather abundant in many areas of the Coastal Plain of the southeastern United States and a variety of morphological expressions are present. It is critical that the number of distinct morphological entities within the complex be determined. Thus an intensive study of the patterns of morphological variation exhibited by the complex in the study area can provide

important data with which to reinterpret the group and lay a solid foundation for broader study of the *Cuspidata*.

Description of the Southeastern United States Coastal Plain

The Coastal Plain is the subaerial portion of the Atlantic and Gulf Coastal Province (Walker and Coleman 1987). This includes Cape Cod, Long Island and other islands, and coastal areas extending from New Jersey to Texas. Figure 1 (p. 3) shows the boundary of the Coastal Plain in the southeastern United States. Specimens for the present study were obtained from five areas in the southeastern Coastal Plain; thus, the following discussion focuses on that portion of the Coastal Plain from North Carolina to Louisiana.

Geology, Physiography, and Topography

The outer boundary of the Coastal Plain is the sea-land interface. The sea has been at its present elevational position for the last 5000-6000 years (Stout and Marion 1993). The inner boundary is called the "fall line"; it is where crystalline rocks of the various bordering provinces meet the unconsolidated sediments of the Coastal Plain. The name "fall line" was given to this border by the early pioneers and explorers. Settlers could move easily inland through the Coastal Plain by boating upriver. Upon reaching the inland border of the Coastal Plain they met cascades and

swift water where rivers flowed over rock outcrops before descending to the Coastal Plain.

The Coastal Plain consists mostly of unconsolidated marine and alluvial sediments that dip seaward. The predominant sediments: sands, clays, gravels, limestone with some marl, eolian loess, and volcanic ash, accumulated on a basement of Paleozoic and Precambrian rocks along the trailing edge of the North American plate during the Mesozoic and the Cenozoic (Walker and Coleman 1987). These sediments range in age from lower Cretaceous to Quaternary. Generally, these deposits decrease in age as one descends from the fall line toward the coast.

The Coastal Plain has little relief relative to other physiographic provinces in the southeastern United States. Relief generally decreases toward the coast and in the outer Coastal Plain local relief is typically only a few meters. The fall line sandhills in the Carolinas and Georgia are the most "rugged" region in the Coastal Plain. In this region local relief can be 60 - 80 m.

Eustatic changes and shifts in sea level and fluvial and aeolian processes during the past 2 - 3 million years have shaped the surface of the Coastal Plain (Walker and Coleman 1987, Christensen 1988). Cooke (1931) named seven exposed terraces and scarps in the Coastal Plain and interpreted them as having been formed when sea level periodically stabilized at successively lower and lower

elevations during the Pleistocene. Due to warping of sediments, these terraces were deformed and can not be correlated across long distances by elevation (Winker and Howard 1977, Stout and Marion 1993), as suggested by Cooke (1931) and others. Relict coastal features such as dune fields, swales, and remains of mud flats are obvious on the lower terraces. These features greatly influence present-day vegetation patterns on these lower terraces (Colquhoun 1969, Christensen 1988).

Carolina Bays are a prominent landscape feature from southern Virginia to Florida. These bays are elliptical depressions with the long axis oriented in a northwest to southeast direction. A number of theories ranging from meteor showers, enclosed soundlets (Glenn 1895), and currents have been proposed to account for their origin (Christensen (1988). Typically, they exhibit a conspicuous sand rim on the south and southeast sides where very xeric conditions prevail. In contrast, the middle of the bay is usually a wetland (pocosin, savanna, and/or a cypress-gum swamp) or a lake. Thousands of these curious landforms occur in the Coastal Plain.

Climate

Trewartha and Horn (1980), following Köppen's climate classification, included the southeastern Coastal Plain in a region characterized by humid temperate climate with hot

summers and no distinct dry season. According to data published by the National Oceanic and Atmospheric Administration (1974), average annual precipitation at the five areas chosen for intensive sampling ranges from 46" (Cheraw, South Carolina, near the SH) to 60" (Hattiesburg, Mississippi, near the DNF). Average annual temperature for these five areas ranges from 62.3°F at Cheraw, SC, to 68°F at Tallahassee, Florida (near the ANF).

The outer Coastal Plain, in particular, experiences frequent violent storms, including hurricanes and the tornados they spawn. Maps presented by Chen and Gerber (1990) showed that the ANF area has one of the highest hurricane frequencies in Florida, with fourteen hurricanes having impacted the region between 1885 and 1980. In 1989, Hurricane Hugo slashed the coastline between Charleston and Georgetown, South Carolina, and essentially removed the canopy over extensive areas of the FMNF (field obs.). During 1995, several hurricanes and tropical storms lashed the Coastal Plain.

Electrical storms are frequent during the warmer months of the year in the Coastal Plain. Chen and Gerber (1990) stated that more lightning occurs in Florida than anywhere else in the United States. As a result of these storms, fires are frequent in many habitats in the Coastal Plain (Komarek 1974, Clewell 1977, Christensen 1988) and they have a great influence on community composition (Christensen

1988). Plant communities such as pocosins appear well-adapted to wildfire and some communities such as savannas are fire dependent. Komarek (1974) included the southeastern Coastal Plain in a "southern pine forest lightning fire bioclimatic region."

Vegetation

Christensen's (1988) classification of plant communities in the southeast Coastal Plain is adopted in the following account except for pocosins. Weakley and Schafale (1991), who presented a more inclusive pocosin category than Christensen (1988), are followed for that community. Only those plant communities where the *Sphagnum cuspidatum* complex can be expected to occur are discussed.

The vegetation of the southeastern Coastal Plain, as it is known today, has developed over the last 5000 - 10,000 years (Stout and Marion 1993). Largely because water is near the surface, community composition changes sharply with elevation changes of only a few meters.

Xeric Sand Communities. These communities are characterized by an overstory of *Pinus palustris* P.Mill. and an understory of *Quercus laevis* Walt. with other *Quercus* spp., *Nyssa sylvatica* Marsh., and *Diospyros virginiana* L. These communities typically occur on the upper and middle slopes and ridges in the Sandhills, on aeolian and alluvial sand deposits in the middle and lower Coastal Plain, and on

relict dune fields in the lower Coastal Plain. The soils generally have poor water retention and poor nutrient adsorptive capacity (Christensen 1980). Where clay horizons come to the surface, seeps occur with pocosin-like vegetation. Such areas often have much *Sphagnum*. The transition from a xeric *Pinus palustris* community to a pocosin is usually very abrupt.

Mesic Pine Communities. Xeric sand communities often grade into pine flatwoods or savannas as soil moisture increases. Compared to xeric sand communities, pine flatwoods have a more dense canopy and a more dense understory shrub layer. The term "flatwoods" is used for nearly any Coastal Plain forest with a prominent woody understory (Christensen 1988). *Pinus taeda* L. is often the dominant tree. The *Sphagnum cuspidatum* complex occasionally occurs in moist depressions in this community.

Savannas have an open canopy of *Pinus* with a diverse herb layer. Intermediates between flatwoods and savannas are common and relate to fire frequency. Savannas are often transitional between more xeric pine communities and pocosins or bayheads. Walker and Peet (1984) recognized three savanna groupings based on moisture: xeric, mesic, and wet. Xeric savannas have scattered *Pinus palustris* with a ground layer dominated by *Aristida stricta* Michx. and a variety of legumes. Mesic savannas have a high herb diversity with numerous graminoid species and a diverse

insectivorous flora. Seasonal pools in mesic savannas are often filled with the *Sphagnum cuspidatum* complex. Wet savannas are ecotonal; they are between mesic savannas and pocosins. They are found where fire on a mesic savanna has spread into a pocosin and eliminated the above ground portions of the shrubs. Dominant species include *Pinus serotina* Michx., *Taxodium ascendens* Brongn., *Nyssa biflora* Walt., and sprouting pocosin shrubs. Pools filled with *Sphagnum cuspidatum sensu lato* are common in these communities. The savanna community depends on frequent fires to persist. In the absence of fire, wet savannas succeed to pocosin and mesic savannas succeed to flatwoods.

Wetlands. Wetlands cover 15% of the Coastal Plain (Christensen 1988). Subdued topography and poor drainage has led to the development of a diverse array of Coastal Plain wetlands.

Coastal Plain rivers can be placed into three categories: those with their headwaters in another physiographic province, spring-fed streams that originate in the Coastal Plain, and blackwater rivers that originate in the Coastal Plain. *Sphagnum cuspidatum sensu lato* is not usually present in alluvial wetlands associated with the first two categories. Blackwater rivers, the third category, typically drain shrub bogs or bay swamps. The *Sphagnum cuspidatum* complex is often present in the backwater swamps associated with these systems. These

swamps are dominated by *Taxodium* L.C.Rich., *Nyssa biflora*, *Acer rubrum* L., *Pinus* L., and *Magnolia virginiana* L. with *Chamaecyparis thyoides* (L.) B.S.P. occasionally dominant, but less widespread.

Nonalluvial wetlands include marshes, pocosins, and ponds. Marshes are graminoid (primarily *Panicum* L., *Carex* L., *Rhynchospora* Vahl, and *Juncus* L.) dominated communities. According to Christensen (1988), they may represent an early seral stage following a disturbance in a bay, wet slash pine flatwoods, or pocosin. The *Sphagnum cuspidatum* complex may be present in such sites.

The term "pocosin" is derived from an Algonquin term for "swamp on a hill" (Christensen 1988). The pocosin classification of Weakley and Schafale (1991) included communities typically classified as pocosins as well as Atlantic white cedar forests and bays (bayheads, bay forests); the last two communities are usually discussed separately by most authors. Weakley and Schafale recognized eight categories of pocosins: low pocosin, high pocosin, pond pine woodland, peatland Atlantic white cedar forest, bay forest, streamhead pocosin, streamhead Atlantic white cedar forest, and small depression pocosin. These palustrine wetlands are characterized by nonalluvial hydrology, strongly acidic soils, and a dense shrub layer of mostly heaths (Ericaceae) and hollies (Aquifoliaceae) with evergreen sclerophyllous leaves (Weakley and Schafale 1991).

Pocosins began forming 6000 - 8000 years ago when sea level attained its present elevation (Christensen 1988). In some sections of the Carolinas, particularly the outer Coastal Plain of North Carolina, individual pocosins occupy extensive areas (1000's of hectares) on flat uplands where streamheads converge. In addition to interstream uplands, pocosins also occur in Carolina Bays (Buell 1946), swales of relict dune fields on lower terraces, seeps, stream margins, and springs in sandy areas (Christensen 1988). A brief characterization of each pocosin category follows. The descriptive information is based on Weakley and Schafale (1991) and my own field observations.

1. low pocosin - These communities are underlain by deep peat and are very ombrotrophic. The shrubs are less than 1.5 m tall. Dominant species usually are *Ilex glabra* (L.) Gray, *Lyonia lucida* (Lam.) K.Koch, *Cyrilla racemiflora* L., *Zenobia pulverulenta* (Bartr. *ex* Willd.) Pollard, and *Smilax laurifolia* L. with scattered *Pinus serotina*, *Persea palustris* (Raf.) Sarg., *Magnolia virginiana*, and *Gordonia lasianthus* (L.) Ellis. During drought, fire may burn deeply into the peat. The resulting pools often fill with peat moss. *Sphagnum* may cover 50% of the ground in these communities (Christensen 1988). The *Sphagnum cuspidatum* complex is common in this community type (field obs.).

2. high pocosin - This pocosin community is underlain by moderately thick peat and is quite ombrotrophic. It is

floristically very similar to low pocosin, and may grade into low pocosin in one direction and pond pine woodland in another. *Sphagnum* may be common, particularly in openings.

3. pond pine woodland - Pond pine woodlands are characterized by an open to nearly closed canopy of *Pinus serotina* with an understory of *Gordonia*, *Persea*, *Magnolia virginiana*, *Acer rubrum*, *Pinus taeda*, and *Chamaecyparis*. A tall (> 5 m), dense shrub layer is usually present. This community is particularly susceptible to intense fires. The *Sphagnum cuspidatum* complex is variably common in this habitat.

4. peatland Atlantic white cedar forest - This pocosin community is very similar to pond pine woodland, but is dominated by *Chamaecyparis*. Even-aged stands of *Chamaecyparis* may succeed to pond pine woodland, bay forest, or a maple-gum swamp forest. *Sphagnum cuspidatum sensu lato* is variably common.

5. bay forest - This community is dominated by *Gordonia* (loblolly bay) or *Magnolia virginiana* (sweet bay). It tends to be associated with drainages at the edges of peatlands. Early pioneers would travel around the margins of large pocosin complexes and, observing the dominance of the bay trees around the margins, would assume that the bay trees dominated the entire wetland. Thus such sites were referred to as "bays" (Wells and Boyce 1953). The *Sphagnum cuspidatum* complex is variably common in this community.

6. streamhead pocosin - This community occurs in the headwaters of small streams in the Sandhills where it receives oligotrophic runoff and seepage from upslope. Dominant species include *Lyonia lucida*, *Ilex glabra*, *Acer rubrum*, *Nyssa biflora*, and *Chamaecyparis*. Fires from adjacent uplands may burn into these pocosins; if such fires are frequent, a savanna-like community results. *Sphagnum cuspidatum sensu lato* is only rarely present.

7. streamhead Atlantic white cedar forests - This community is similar to #6, but differs in the dominance of *Chamaecyparis*. *Sphagnum* is common.

8. small depression pocosin - Small depression pocosins are dominated by a variety of shrubs including *Lyonia lucida*, *Ilex glabra*, *Cyrilla racemiflora*, *Ilex coriacea* (Pursh) Chapman, *Ilex myrtifolia* Walt., *Clethra alnifolia* L., *Vaccinium corymbosum* L., and *Kalmia carolina* Small. The *Sphagnum cuspidatum* complex is variably common in this community.

Clusters of natural ponds occur sporadically in the outer Coastal Plain. Shallow seasonal ponds and associated depressions often have an abundance of the *Sphagnum cuspidatum* complex. Concentric zones of vegetation are conspicuous at such sites, with a central aquatic zone (*Nymphaea* L., *Nuphar* Sm., *Utricularia* L.), surrounded by a herbaceous zone (*Lachnanthes caroliniana* (Lam.) Dandy, *Rhynchospora*, *Panicum*, *Drosera* L., *Sarracenia* L.,

Utricularia, *Polygala* L., *Rhexia* L.), surrounded by a pocosin shrub zone (*Lyonia lucida*, *Cyrilla racemiflora*, *Ilex glabra*), within a pine-oak-heath forest.

Descriptions of the Five Collection Areas

Descriptions of the five areas selected for intensive sampling are below. Four of the areas are in the outer Coastal Plain and one area is in the inner Coastal Plain. Their locations are shown in Figure 2 on p. 3.

Croatan National Forest (CNF). The CNF is located in Carteret, Jones, and Craven Counties, North Carolina, and extends from New Bern to Morehead City between the Neuse River estuary and Bogue Sound. Most of the collections from the CNF were made from the Patsy Pond area, the extensive pocosin complex between Great Lake and Catfish Lake, and the vicinity of Millis Swamp. Elevation ranges mostly from 9 - 15 m in these areas.

According to Mixon and Pilkey (1976), the CNF is underlain by Quaternary sands, silts, clays, and shelly sediments. The southern two-thirds of the CNF are dominated by a relict beach system near the coast called the Newport Barrier and, just to the northwest, by an extensive flat interfluvial region (Mixon and Pilkey 1976). The Newport Barrier is several miles wide and extends from Newport to Bogue. It is comprised of numerous northeast-trending ridges and swales with local relief of 5 feet or less.

These relict beach ridges are interrupted by several Carolina Bays (Mixon and Pilkey 1976). These low ridges have a *Pinus palustris* - *Quercus laevis* overstory with an ericaceous understory and the swales have pocosin-like communities.

The Patsy Pond complex is at the southwest end of the Newport Barrier and consists of numerous ponds of variable sizes and shapes surrounded by xeric-mesic forests of *Pinus palustris* and *Quercus* spp. with a diverse shrubby understory. Most of these ponds are shallow and lack standing water during much of the summer. According to Schafale (1994), these ponds are dolines (limestone sinks) and he cites this cluster of ponds as an outstanding example of small depression pond communities of national significance. The *Sphagnum cuspidatum* complex was abundant around many of these ponds and depressions in both the herbaceous and shrub zones.

An immense pocosin complex occupies the central portion of the CNF. It consists of low pocosin, high pocosin, bays, and pond pine flatwoods that grade into drier *Pinus palustris* dominated communities around the margins and where sand ridges intrude into the pocosin (Snyder 1980, Schafale and Weakley 1990). This pocosin complex contains outstanding examples of low pocosin. The *Sphagnum cuspidatum* complex was frequent in the low pocosins.

Francis Marion National Forest (FMNF). The FMNF is located in Berkeley and Charleston Counties, South Carolina, about 50 km northeast of Charleston. Most of the collections made from this forest were from an an area bounded by the communities of Honey Hill, Buck Hall, Awendaw, and Huger. Elevation ranges mostly from 6 - 15 m in this region.

Sediments in the area are primarily Pleistocene sands and silts (Colquhoun 1969). As in the CNF, the surface of the FMNF is one of primary topography as former river deltas, barrier islands, and marshes are obvious (Colquhoun 1969). Large swamps have developed in former deltas and marshes. A number of pocosins that intertongue with drier sand ridges have developed in association with a former barrier island complex and scarp that parallels the present coastline. Halfway Creek Road is presently located on part of this sand ridge. Pools and openings in these pocosins were often filled with the *Sphagnum cuspidatum* complex. Additionally, there are a number of mesic to wet savannas present in the FMNF and the transition zones from the savannas into adjacent pocosins typically had the *Sphagnum cuspidatum* complex in abundance. Hillside seeps also generally supported populations of *S. cuspidatum sensu lato* as well.

A number of Carolina Bays punctuate the landscape, with the *S. cuspidatum* complex present in several of them (pers.

obs.). Porcher (1966) documented the vascular flora of a number of these bays.

Areas in the FMNF observed with an impressive abundance of *S. cuspidatum sensu lato* include the pocosin complex south of Thompson Corner, pocosins both to the north and south of Steed Creek Road west of Halfway Creek Road, and Halfway Creek Road Carolina Bay.

Sandhills (SH). The name Sandhills refers to a belt of rolling hills capped by deep coarse sands in the inner Coastal Plain that extend from southern North Carolina, through South Carolina, and across Georgia. Specimens for the study were mostly obtained from the Carolina Sandhills National Wildlife Refuge in Chesterfield County, South Carolina, and the Sandhills Game Lands in Richmond, Moore, Scotland, and Hoke Counties, North Carolina. Elevations in these areas range from about 70 - 152 m.

Sediments in the region are Cretaceous sands (Stout and Marion 1993) that were once believed to have been part of a large inland dune system. The region is now interpreted as having been carved from an ancient delta plain where wind erosion developed dune fields on the surface (Schafale 1994). Relief here is much greater than in the four outer Coastal Plain areas as local relief is often 60 m.

The broad uplands present a stark landscape with much *Pinus palustris* above an understory of *Quercus laevis*, *Diospyros virginiana*, and *Nyssa sylvatica*. These same

species, as well as *Quercus marilandica* Muenchh. and *Liquidambar styriciflua* L., also appear in slightly more mesic areas; but where clays and less permeable organic layers are interbedded with the dry, highly permeable sands, dramatic shifts in vegetation occur (Christensen 1980). In a distance of only a few meters one can go from a xeric *Pinus palustris-Quercus laevis* community to a pocosin. *Sphagnum* is often abundant at these seeps, although the *S. cuspidatum* complex is rare here.

Pocosins in the region are mostly streamhead pocosin or streamhead Atlantic white cedar swamps (Weakley and Schafale 1991). Dominant species include *Lyonia lucida*, *Ilex glabra*, and *Cyrilla racemiflora* with admixtures of *Myrica heterophylla* Raf., *Magnolia virginiana*, *Persea palustris*, *Acer rubrum*, and *Liriodendron tulipifera* L. Fire is rather frequent in the *Pinus palustris* dominated communities and occasionally will burn into the pocosins. Pocosins that burn frequently have shrubs widely spaced and a diverse herb layer that includes many rare species (Schafale 1994). In the absence of fire, the pocosins become amazingly dense and nearly impenetrable. *Sphagnum cuspidatum sensu lato* appeared to be rare in this community. Streamhead Atlantic white cedar swamps are relatively uncommon in the region, but generally have an abundance of *Sphagnum*.

Most bottomland swamps in the Sandhills would be classified as Coastal Plain small stream swamp (blackwater

subtype) in the classification of Schafale and Weakley (1990). Such backwater swamps along the larger streams in the SH may have shallow water present from late fall through the spring. Typically, *Nyssa biflora* and *Acer rubrum* are dominant with *Taxodium* abundant in the wetter areas. The shrub layer usually includes *Lyonia lucida*, *Persea*, *Cyrilla*, and *Smilax laurifolia*. Some swamps also have much *Chamaecyparis thyoides* and *Magnolia virginiana*. The *Sphagnum cuspidatum* complex is sometimes common in such swamps, particularly toward the upland margin of the swamp. Upstream a blackwater swamp will grade into streamhead pocosin or streamhead Atlantic white cedar swamp and downstream will grade into bottomland hardwood swamp, cypress-gum swamp, or Coastal Plain levee forest (Schafale and Weakley 1990).

There are numerous impoundments in the Sandhills. Typically these ponds and lakes are surrounded by pocosin vegetation with *Taxodium* and *Nyssa* in the shallower water. Old mill ponds that have partially filled in often have impressive amounts of the *Sphagnum cuspidatum* complex.

Apalachicola National Forest (ANF) and Vicinity. The ANF is located in Liberty, Franklin, Leon, and Wakulla Counties, Florida. For the present study, collections were mostly made from Liberty County. Elevations in the region range from 9 - 24 m.

The ANF is within the Apalachicola Delta District. This is a clastic terrain formed by sediments from the Apalachicola River. Quaternary alluvium, marl, and peat are the dominant deposits. Prominent landscape features include relict deltas, ridges, and lagoons, river terraces, delta plains, and barrier islands (Brown et al. 1990).

As in the FMNF and CNF, these relict coastal features greatly influence present-day vegetation patterns. *Pinus* flatwoods with *Serenoa repens* (Bartr.) Small, *Aristida* L., and *Ilex* spp. dominate relict barrier islands and spits. These flatwoods may intertongue with and grade into herb bogs or savannas which grade down to *Cliftonia monophylla* (Lam.) Britt. *ex* Sarg. and *Cyrilla* thickets and swamp forests and eventually to a cypress swamp (Ewel 1990). Extensive swamps have developed on mud flats and delta plains and areas with deeper, more permanent water typically have much *Taxodium* and *Nyssa biflora*. *Chamaecyparis thyoides* occasionally dominates shallow peat swamps in the ANF.

Sphagnum cuspidatum sensu lato was encountered in titi thickets, cypress swamps, natural pond margins, mesic-wet savannas, roadside ditches, and in borrow pits.

De Soto National Forest and Vicinity (DNF). The DNF is located in southern Mississippi between Biloxi and Hattiesburg. Most collections from this area were made from the southern portion of the forest in Stone and Harrison

Counties. Some collections were also made in Greene, George, and Jackson Counties, Mississippi, and in St. Tammany Parish, Louisiana. Elevation ranges from 5 - 30 m in the region.

Lowe (1921) recognized ten topographic/floristic regions in Mississippi. The *Sphagnum* collections obtained during the present study are from the Coastal Pine Meadows Region and Longleaf Pine Region. The Coastal Pine Meadows region is underlain by Holocene Coastal Deposits (loam, sand, gravel, and clay) (Geologic Map of Mississippi 1985). Groundwater lies near the surface in this region, thus marshes and swamps with black, peaty, and acid soils are quite common (Lowe 1921). These meadows are sometimes called "pitcher plant bogs." Floristically they are very similar to the savannas of the CNF and FMNF and the herb bogs/savannas of the ANF. The *Sphagnum cuspidatum* complex is often present around the margins of these bogs and in adjacent shrub thickets.

The Longleaf Pine Region is underlain by the Pleistocene (or Pliocene?) Citronelle Formation and the Miocene Pascagoula and Hattiesburg Formation. Both of these formations consist primarily of sands, gravels, and clays (Geologic Map of Mississippi 1985). In the southern part of this region, low swales and flats are poorly drained and thus wetlands such as pitcher plant bogs, titi swamps, shrub bogs/thickets, and nonalluvial cypress swamps are frequent.

The *Sphagnum cuspidatum* complex was particularly abundant at a wetland 1.5. miles southeast of the Chickasawhay River in Greene County, the titi swamp between Hester Creek and Rt. 419 in Harrison County, and at a cypress swamp near the junction of Rt. 397 and U.S.F.S. 397C in Stone County.

Morphometric Studies

Analysis of All Collections from the Five Areas

Methods

Specimens were collected in each of five areas in the southeastern Coastal Plain between 1991 and 1995: De Soto National Forest and vicinity (DNF) (18 - 22 June 1993 and 21 - 23 October 1993), Apalachicola National Forest and vicinity (ANF) (20 - 22 March 1991 and 21 - 24 1995), Francis Marion National Forest (FMNF) (23 - 25 March 1994, 20 - 21 October 1994, 3 January 1995, and 7 - 8 April 1995), Croatan National Forest (CNF) (23 - 24 March 1993 and 14 - 17 July 1995), and the Sandhills (SH) (19 - 22 March 1994, 4 - 5 January 1995, and 19 - 21 May 1995).

These five large areas were chosen because they were known to have numerous localities where members of the complex occurred (sometimes in great abundance), supported some of the best remaining natural communities in the southeastern Coastal Plain, and all members of the complex had been reported from one or more of the areas. Additionally, since large-acreage landowners were involved, once permission was obtained to collect specimens, this allowed access to extensive land areas.

Potential sites within each area were identified by inspection of topographic maps, discussions with knowledgeable individuals, and field reconnaissance. Depending on the quantity of material and the range of morphologies encountered, one to ten collections were made

at each site. A consistent effort was made to check each site carefully and to collect all morphological expressions of the complex present at each site. Natural habitats were strongly emphasized in the choice of sites visited. Roadside ditches were only sparingly examined. Some impoundments, particularly in the SH, were explored for material, however. Specimens were catalogued and lightly to moderately pressed on the day of collection.

A total of 374 collections of members of the complex was made from the five areas. The number of specimens collected at each area was DNF (74), ANF (62), FMNF (80), CNF (73), and SH (85).

On a per site basis, for each of the five areas, specimens were sorted into morphological groups based on their appearance under a dissecting microscope. (A site, herein, is broadly defined to be a particular habitat/community type in a local area.)

One specimen was randomly selected for morphometric analysis from each designated morphological group from each site for each of the five areas. The number of specimens selected in this manner from each area was CNF (25), FMNF (34), SH (25), ANF (21), and DNF (30), for a total of 135 specimens.

Two stems were randomly selected from each specimen for morphometric analysis. The selected stems were rehydrated in hot water. Branches and stems were stained with crystal

violet prior to examination. Twenty-two morphological characters were measured on each of the two stems. Over 48,000 measurements were made for this study.

Characters Studied. The sample size for each character per stem is indicated parenthetically after the character name. This is followed by a description of procedures used in making the measurements, the measurement units, and the abbreviation used for the character in the principal components analysis tables.

1. **proximal branch leaf length** (6) - The proximal position on a branch is defined as one-tenth of the distance from the branch base to the branch apex. The branch leaf nearest this position was identified and removed for measurement. Then the leaf immediately distal and the leaf immediately proximal to this leaf were also removed for measurement. This was done on two branches per stem by selecting the longest erect branch from the branch fascicle nearest to 1 cm below the stem apex and the longest erect branch from the branch fascicle nearest to 2 cm below the stem apex. Thus 6 proximal branch leaves were measured per stem. This and the other branch leaf length and width measurements were made with the leaves in a small drop of water without a cover slip. For the purpose of clarity, it should be stated that the measurement of branch length included only the branch itself and did

not include leaves that extended beyond the branch apex. Millimeters. PRLFLMM.

2. proximal branch width (6) - The greatest width of each leaf was measured. The same leaves were used as for character 1. Millimeters. PRLFWMM.

3. median branch leaf length (6) - The median position on a branch is defined as one half of the distance from the branch base to the branch apex. The same branches and procedures were used as for character 1. Millimeters. MEDLFLMM.

4. median branch leaf width (6) - The same leaves and procedures were used as for character 3. Millimeters. MEDLFWMM.

5. distal branch leaf length (6) - The distal position on a branch is defined as three-fourths of the distance from the branch base to the branch apex. The same branches and procedures were used as for character 1. Millimeters. DISLFLMM.

6. distal branch leaf width (6) - The same leaves and procedures were used as for character 5. Millimeters. DISLFWMM.

7. proportion of proximal branch leaf margin not entire (6) - The same leaves were used as for character 1. This character includes both denticulations and serrulations along the margin. A denticulation is defined as a projection from the leaf margin that lacks

a gap between the projection and the body of the leaf. A serrulation is defined as a projection along the leaf margin in which a gap exists between the "tooth" and the body of the leaf (Figure 3). Each leaf received a score from 0 to 10: 0 - entire, 1 - margin projections confined to distal 0.1 of leaf, 2 - margin projections extending below the distal 0.1 of the leaf but not extending below the distal 0.2 of the leaf, 3 - ..., 4 - ..., 5 - ..., 6 - ..., 7 - ..., 8 - ..., 9 - ..., 10 - margin projections present down to the proximal 0.1 of the leaf. PROXD.

8. proximal branch leaf serrulation (6) - The same leaves were used as for character 1. This character was scored as described above for character 7. PROXS.

Figure 3 shows an example of scoring a leaf for characters 7 and 8.

9. proportion of median branch leaf margin not entire (6) - The same leaves were used as for character 3. This character was scored as described above for character 7. MEDD.

10 . median branch leaf serrulation (6) - The same leaves were used as for character 3. This character was scored as described above for character 7. MEDS.

11. proportion of distal branch leaf margin not entire (6) - The same leaves were used as for character 5.

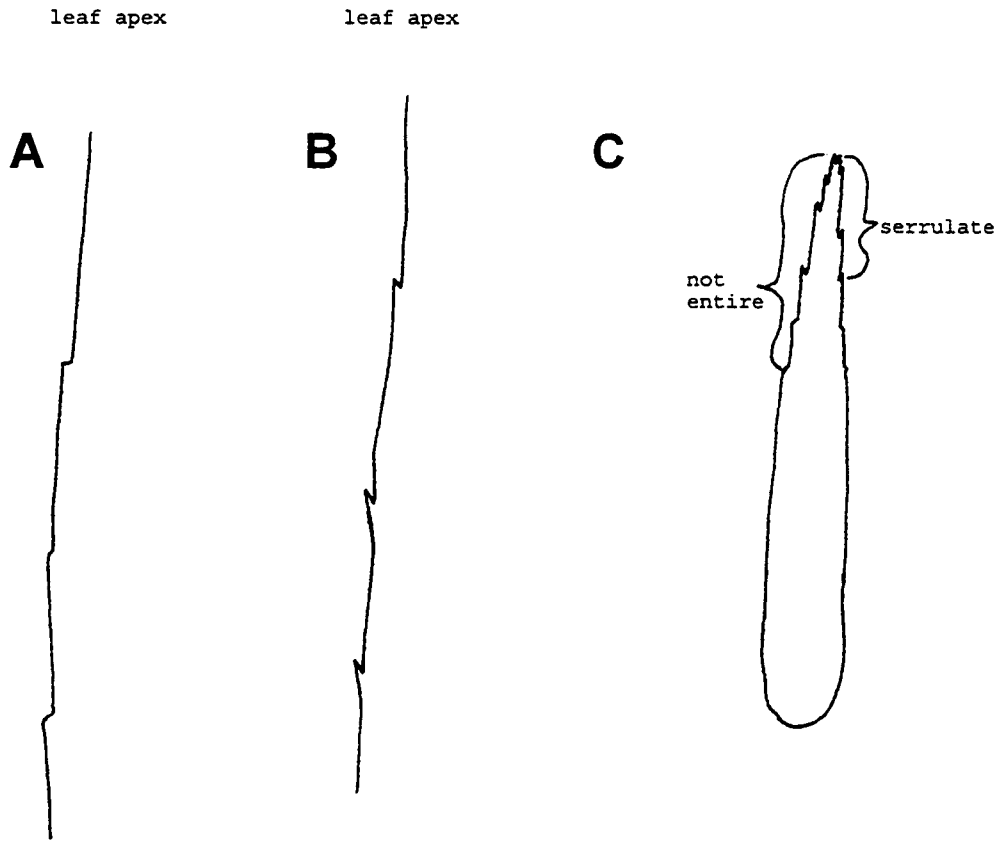


Figure 3. Illustrations of branch leaf margin features and methods of scoring these characters. A. Branch leaf margin denticulations. B. Branch leaf margin serrulations. Both A and B show the left leaf margin. Note that a line, that is perpendicular to the long axis of the leaf, drawn from the tip of a serrulation to the leaf midline, will enclose a gap between the serrulation and the leaf body. Such a gap will not be enclosed by a line connecting the tip of a denticulation with the leaf midline. C. Branch leaf outline with method for scoring proportion of margin not entire and serrulation indicated.

This character was scored as described above for character 7. DISTD.

12. distal branch leaf serrulation (6) - The same leaves were used as for character 5. This character was scored as described above for character 7. DISTS.

13. median branch leaf hyaline cell length (20) - Two of the median branch leaves from each branch used above were randomly selected. Five laterally adjacent, centrally located cells were measured in each leaf. This character was measured with the convex leaf surface up. Micrometers. HYALLUM.

14. median branch leaf hyaline cell width (20) - The same leaves were used as for character 13. This character was measured with the convex leaf surface up. Micrometers. HYALWUM.

15. branch leaf chlorophyllose cell length (40) - The same leaves were used as for character 13. Ten cells near the leaf apex were measured by following them, one after another, around apical hyaline cells. This character was measured with the convex leaf surface up. Micrometers. CHLLUM.

16. stem leaf length (5) - Five stem leaves were removed from each stem between 1 cm and 3 cm below the stem apex. Both this character and character 17 were measured with the stem leaves in a small drop of water covered by a cover slip. Millimeters. STLFLMM.

17. stem leaf width (5) - The same leaves were used as for character 16. The measurement was made at the leaf base. Millimeters. STLFWMM. (The "Blattohr", which come off of the stem to varying degrees during the dissection process, were not included in the width measurement. The Blattohr or "leaf ears/lobes" are groups of tunicate-shaped cells which radiate laterally from the outside bases of stem leaves. See Kindberg (1890), p. 90, for an illustration of the Blattohr.)

18. number of septate cells in viewing field - The same leaves were used as for character 16. The number of septate cells in the viewing field (500X) of the Wild M12 Compound Microscope was counted with the objective centered in the lower half of each leaf. The area of the viewing field was 0.07 mm^2. The proportion of a typical stem leaf this accounted for is depicted in Figure 4. SEPTA.

19. diameter of a row of five adjacent cells in the outermost layer of the stem (3) - Stem cross sections were made in the same stem region that the stem leaves were taken from. The diameter of a row of five adjacent cells was measured on three cross sections. Micrometers. HYDM1UM.

20. diameter of a row of five adjacent cells in the second layer of the stem (3) - The same procedure was followed as for character 19. Micrometers. HYDM2UM.

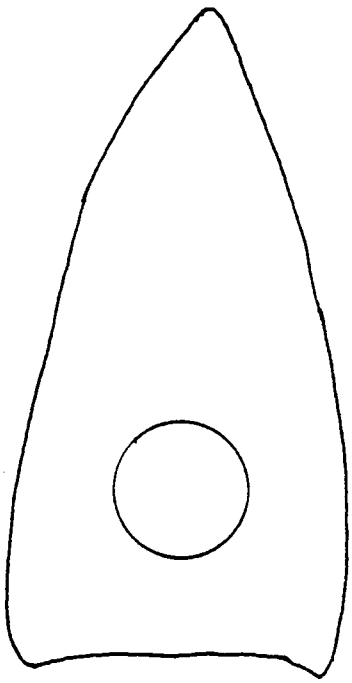


Figure 4. Location of viewing field (the circle) in lower half of stem leaf for obtaining the number of septate hyaline cells. The size of the circle indicates the size of the viewing field relative to the size of an average stem leaf. The diameter of the viewing field is 0.30 mm.

21. diameter of a row of five adjacent cells in the third layer of the stem (3) - The same procedure was followed as for character 19. Micrometers. HYDM3UM.

22. diameter of row of five adjacent cells in the fourth layer of the stem (3) - The same procedure was followed as for character 19. Micrometers. HYDM4UM.

Note: Sphagnologists (e.g. Warnstorf 1881, 1890a, 1903, 1911; Andrus 1974, 1980; Crum 1984; Daniels and Eddy 1985; Flatberg 1988) generally refer to the outer cells of the stem of all members of the genus as a cortex. The degree of cortex differentiation is, in fact, emphasized by Andrus (1974, 1980) as one of several characters useful in separating *S. cuspidatum* from *S. trinitense*. Illustrations in Kindberg (1890) first drew my attention to the fact that, in members of the Section *Sphagnum*, stem leaves do not attach to the cortex, but rather attach to the wood cylinder. In contrast, stem leaves in species in the other sections of the genus attach directly to the outermost stem cells, that is to the "cortex." The site of attachment of an organ such as a stem leaf can reasonably be viewed as an evolutionarily conservative feature. These differences with respect to stem leaf insertion would suggest that the cortex of Section *Sphagnum* and the "cortex" of the other sections are not equivalent or homologous tissues, but rather that the wood cylinder of the Section *Sphagnum* is equivalent to the "cortex" **and** the wood cylinder of the other sections of

the genus. For the reason discussed above I refer to characters 19 - 22 as stem cell layer diameters rather than "cortex."

The sampling of the region 1 - 3 cm below the stem apex for branches and stems was utilized in order to establish a consistent method for repetitious treatment of specimens. This region of the plant represents the most recent growth below the capitulum and has fully developed branches, branch leaves, stems, and stem leaves in prime condition. Stems not eligible for the morphometric study were male plants with antheridia-bearing branches in the region to be sampled (perigonial leaves are greatly reduced in size), diminutive stems (juvenile), and obviously damaged stems.

Characters 1 - 6, 16, and 17 were measured with a Wild M5 Stereomicroscope equipped with an ocular micrometer and characters 7 - 15 and 18 - 22 with a Wild M12 Compound Microscope equipped with an ocular micrometer.

The measurements were averaged for each character on a per stem basis prior to statistical analysis.

Statistical Treatment. Two multivariate methods, principal components analysis (on the correlation matrices) and canonical discriminant analysis, were used to explore the data, to search for groups, and to compare the groups thus identified.

Principal Components Analysis. Often in multivariate data sets, most of the overall variation in the data can be

summarized by a relatively small number of axes, each of which is related to the original variable axes to varying degrees. Principal components analysis takes the variables and finds linear combinations of them to produce uncorrelated indices. These indices are axes referred to as principal components (Manly 1994). There can be up to as many principal components as original variables. The principal components are ordered such that the variation accounted for by principal component one is greater than the variation accounted for by principal component two and so forth. Since the principal components are uncorrelated with one another, variation accounted for by each axis is then independent of that accounted for by other principal components. If most of the variation in the original data is accounted for by the first few principal components, then the researcher has "reduced" the data to a manageable number of dimensions. The latter situation is more likely to be the case when the original variables are highly correlated (Manly 1994). The first few principal components can then be plotted with the individual sample locations indicated by symbols. Specimens or samples from different taxonomic groups would be expected to cluster in different regions of these plots if the groups differ with respect to the characters measured.

In order that one variable does not have an inordinate effect on the outcome, the procedure normally codes the

original variables such that each variable has a mean of zero and a variance of one. Thus the total variance of this new data set now simply equals the number of original variables multiplied by one. The sum of the variances of the principal components will also equal this product. The variances of the principal components are the eigenvalues of the sample covariance matrix (Manly 1994). The eigenvalue for principal component one will be larger than the eigenvalue for principal component two and so forth. The magnitude of an eigenvalue is an index of the amount of variation the associated principal component accounts for. For example, an eigenvalue of 5.0 for principal component one, would indicate that this axis accounts for five variables "worth" of variation.

Principal components analysis also generates an eigenvector for each component. Each eigenvector consists of coefficients for each variable. From an interpretive standpoint, these can be thought of as axis weightings with respect to the individual variables. Variables with coefficients of relatively large magnitude on a particular principal component are thus important in accounting for the separation of samples/specimens along that axis.

Thus the above features of principal components analysis make it a very useful statistical tool with which to examine multivariate data sets for patterns. The method

is also useful in the evaluation of previously established groups.

Plots of principal components discussed as results of this research only present the first three components. These three components accomplished group separation while the remaining components (4 - 22) were related primarily to within group variation.

Canonical Discriminant Analysis. Once preliminary taxonomic groups have been identified, it is useful to evaluate the consistency with which specimens can be assigned to these groups. A category of methodologies called discriminant functions analysis was developed for such a purpose. Canonical discriminant analysis, which works very much like principal components analysis, erects axes which maximize the separation of designated groups and minimize within group variation. The axes are called canonical discriminant functions or canonical variates. There will be as many canonical variates as the number of variables **or** one less than the number of groups. The first canonical variate is oriented such that it yields the maximum possible F-ratio (variation between groups divided by variation within groups). The second canonical variate yields the next highest possible F-ratio given the constraint that it is not correlated with the first canonical variate, and so forth. Dissimilarities among the groups can be represented by Mahalanobis distance. This

multivariate distance measure takes into account correlations between variables (Manly 1994).

Taxonomic groups identified by the initial sorting procedure (dissecting microscope) and further supported by the above multivariate methods were then compared on a character by character basis with a one-way analysis of variance.

SAS for Windows 6.11 was used for data analysis. Plots and graphs were generated by importing output from SAS into Freelance for Windows 2.1.

Results

Overall, five, distinct morphological groups based on appearance under a dissecting microscope were recognizable: (1) specimens with recurved capitular branch leaves that were generally undulate below and tubular above, plants small relative to those in group 4, (2) specimens with capitular branch leaves smooth, appressed, and not tubular above, capitulum with sharply pointed branches, and with branch leaf apices narrowly rounded or sharply pointed, (3) specimens with capitular branch leaves smooth, appressed and not tubular above, capitulum with blunt-tipped branches, and with branch leaf apices truncate to broadly rounded, (4) specimens with recurved capitular branch leaves that were generally undulate below and tubular above, plants large relative to those in group 1, and (5) one specimen with

plants similar in size to those in group 1, with long linear branch leaves possessing more or less parallel margins, truncate apices, and slightly undulate surfaces; brownish green in color; capitular branches conspicuously upright.

Group 1 corresponded to the *S. cuspidatum/S. viridum* species pair, group 2 to the *S. trinitense/S. mississippiense* species pair, group 3 to S. *fitzgeraldii*, and group 4 to *S. torreyanum* (based on present-day concepts of these species). Group 5, which included only one specimen from the FMNF, is morphologically intermediate between Group 1 and Group 3. The specimen may represent a hybrid between the latter two groups or an undescribed taxon. Group 1 is indicated by S. cusp/vir, group 2 is indicated by S. trin/miss, and group 5 is indicated by Hybrid? on the legends in the various plots presented in this and other results sections.

All specimens collected from the CNF, FMNF, and ANF were initially assigned to the *S. cuspidatum/S. viridum*, *S. trinitense/S. mississippiense*, or *S. fitzgeraldii* groups after inspection under a dissecting microscope. All specimens collected from the DNF were initially assigned to either the *S. cuspidatum/S. viridum* or *S. trinitense/S. mississippiense* groups. All specimens collected from the SH were initially assigned to the *S. cuspidatum/S. viridum*, *S. trinitense/S. mississippiense*, or *S. torreyanum* groups. Thus results from separate analyses of the CNF, FMNF, and

the ANF specimens will be presented together, followed by the DNF results, and the SH results.

The overall patterns shown by the principal components analysis plots from the CNF, FMNF, and ANF in Figures 5, 6, and 7 indicate the initial sorting of specimens yielded cohesive, but not necessarily highly distinctive, groups. *Sphagnum fitzgeraldii* is generally distinct from *S. cuspidatum/S. viridum* on these plots and forms a unit more or less attached to one end of the *S. trinitense/S. mississippiense* point scatter on the CNF and FMNF plots. On the ANF plots, the *S. fitzgeraldii* specimens form a very distinct group. *Sphagnum fitzgeraldii* specimens consistently had low principal component two scores for each of these three areas.

The *S. trinitense/S. mississippiense* and the *S. cuspidatum/S. viridum* specimens form adjacent, generally distinct units that exhibit slight overlap on a given plot. This overlap basically disappears when both plots from each area are considered.

Principal component 1 had high weightings in all three areas for median branch leaf width; proximal, median, and distal branch leaves proportion of margin not entire; median and distal branch leaf serrulation; and chlorophyllose cell length. Principal component 2 had high weightings for hyaline cell width, stem leaf width, and diameter of the outermost stem cell layer (Tables 2, 3, and 4). For each of

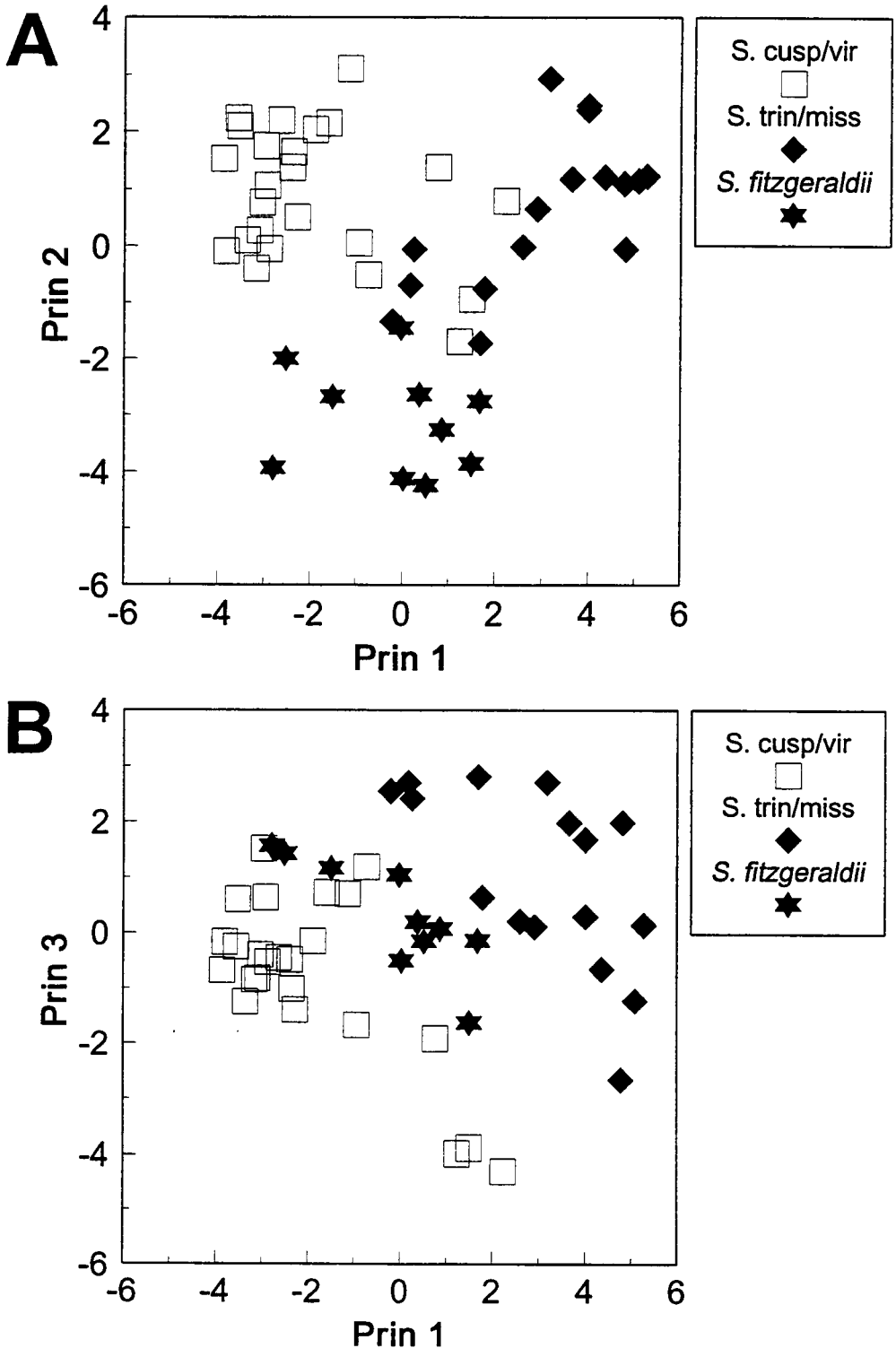


Figure 5. Principal components analysis plots of specimens collected from the Croatan National Forest. A. Prin 2 plotted on prin 1. B. Prin 3 plotted on prin1.

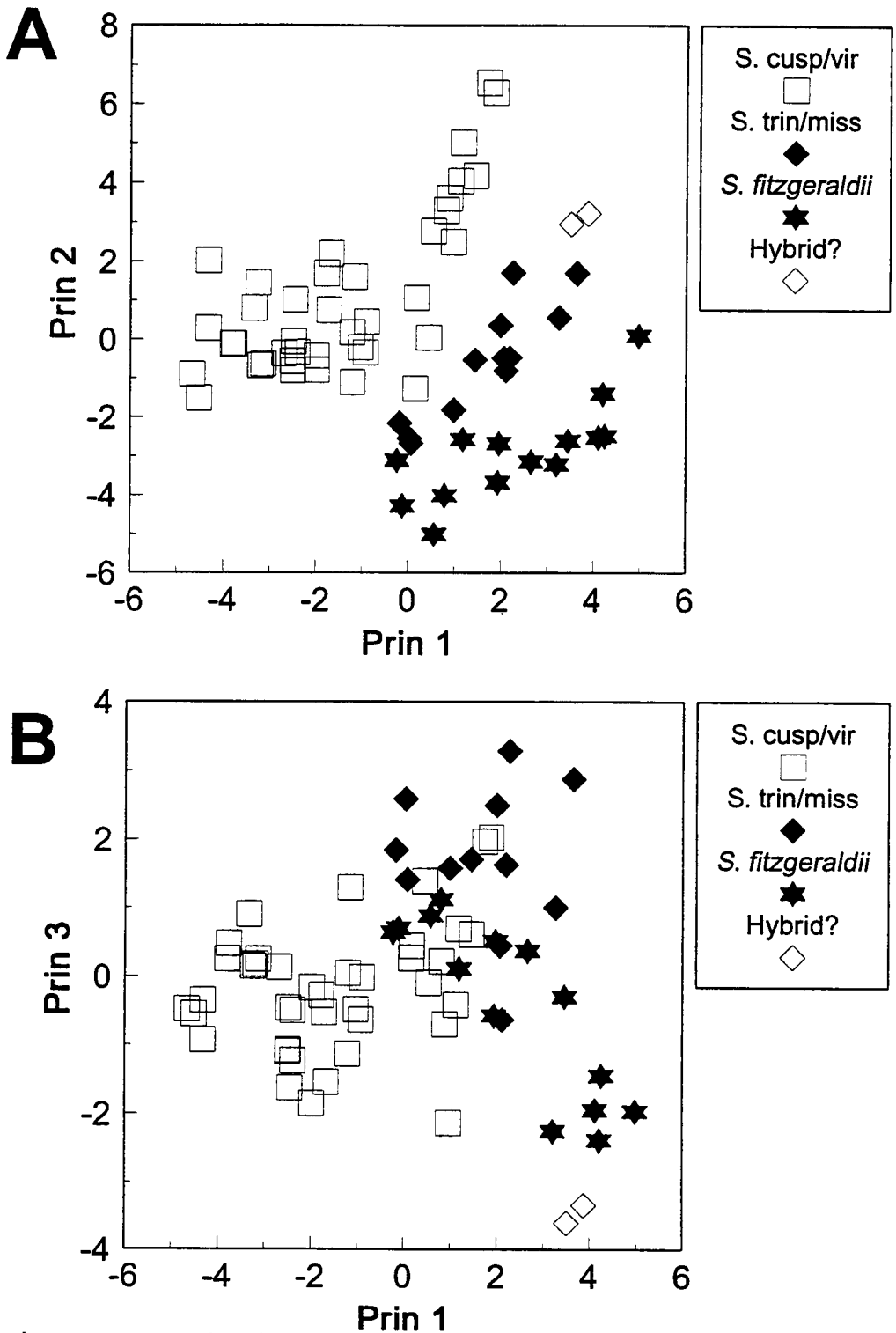


Figure 6. Principal components analysis plots of specimens collected from the Francis Marion National Forest. A. Prin 2 plotted on prin 1. B. Prin 3 plotted on prin 1.

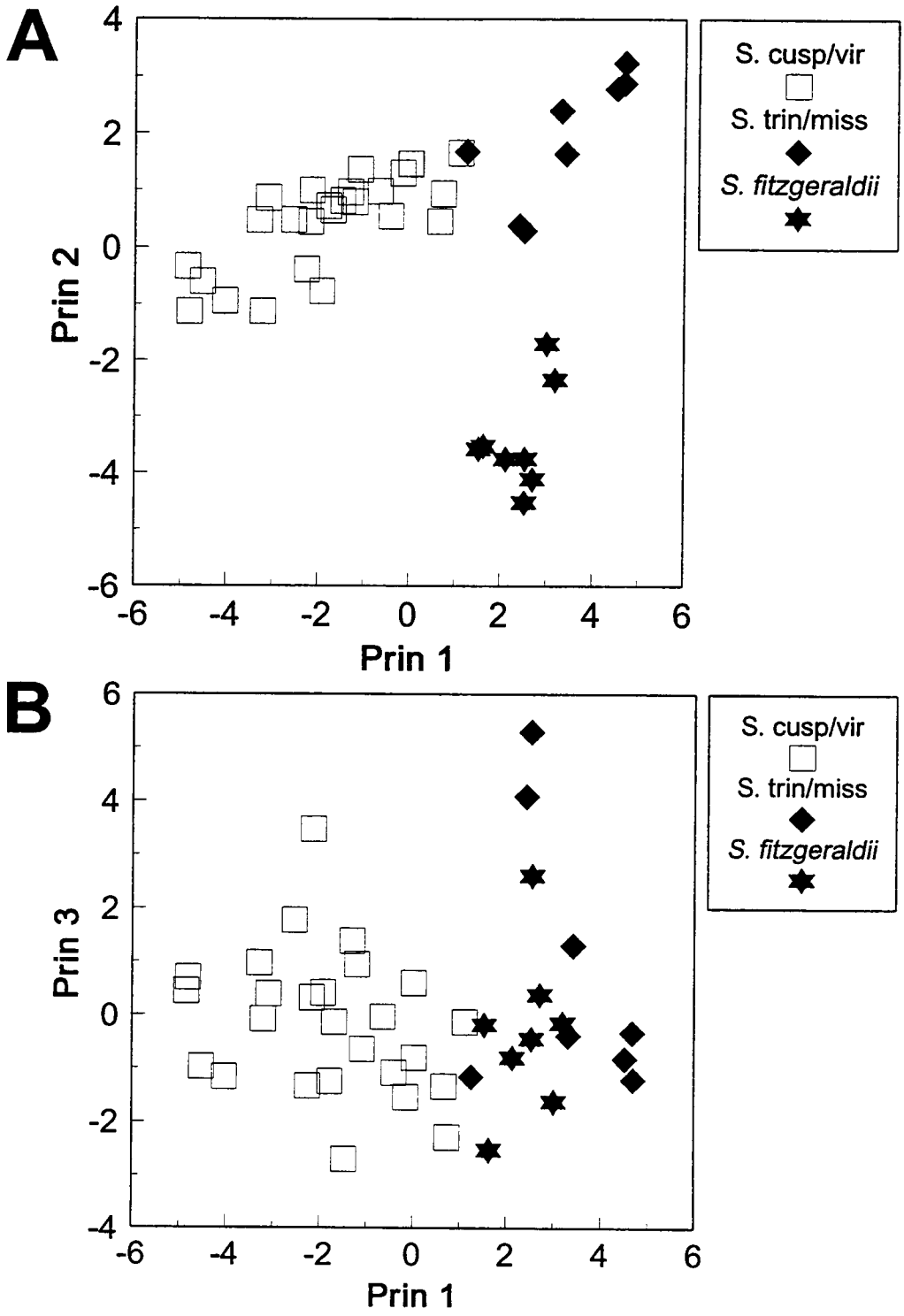


Figure 7. Principal components analysis plots of specimens collected from the Apalachicola National Forest and vicinity. A. Prin 2 plotted on prin 1. B. Prin 3 plotted on prin 1.

Table 2. Eigenvectors for the first three principal components from a principal components analysis of specimens collected from the Croatan National Forest.

Character	PRIN1	PRIN2	PRIN3
PRLFLMM	0.126874	0.097303	-.100380
PRLFWMM	0.192849	0.074886	0.387408
MEDLFLMM	0.290581	0.149065	-.258604
MEDLFWMM	0.259383	0.116250	0.102517
DISLFLMM	0.245963	0.173001	-.308887
DISLFWMM	0.192813	0.120751	0.042297
PROXD	0.213374	-.270402	0.277697
PROXS	0.188407	-.147363	0.159794
MEDD	0.279605	-.240848	0.103954
MEDS	0.324854	-.096580	-.034257
DISTD	0.257565	-.222601	0.069929
DISTS	0.310251	-.107433	-.089816
HYALLUM	0.212130	-.065456	-.403940
HYALWUM	-.033222	-.264905	0.194364
CHLLUM	0.265932	-.000617	-.361405
STLFLMM	0.201658	-.089469	-.011427
STLFWMM	0.059568	0.417574	0.163692
HYDM1UM	-.043964	0.237340	-.101250
HYDM2UM	0.026482	0.402845	0.050648
HYDM3UM	0.182280	0.304640	0.268085
HYDM4UM	0.168724	0.335499	0.194540
SEPTA	0.211248	-.024620	0.238013

Table 3. Eigenvectors for the first three principal components from a principal components analysis of specimens collected from the Francis Marion National Forest.

Character	PRIN1	PRIN2	PRIN3
PRLFLMM	0.062528	0.229395	-.513832
PRLFWMM	0.174653	0.060716	-.199165
MEDLFLMM	0.208523	0.308826	-.135165
MEDLFWMM	0.226157	0.247349	0.087005
DISLFLMM	0.185985	0.294884	-.017722
DISLFWMM	0.127980	0.255041	0.261400
PROXD	0.244906	-.275519	0.033547
PROXS	0.218995	-.131425	-.269983
MEDD	0.335627	-.121514	0.170578
MEDS	0.326955	-.110163	0.044903
DISTD	0.318260	-.109979	0.160112
DISTS	0.351439	-.095228	0.093418
HYALLUM	0.300158	0.180189	-.066821
HYALWUM	0.026469	-.221765	0.215338
CHLLUM	0.302187	0.194957	-.007232
STLFLMM	0.137309	0.002678	-.352885
STLFWMM	-.206848	0.300940	-.048121
HYDM1UM	0.005433	0.235225	-.045158
HYDM2UM	-.120963	0.302871	0.043427
HYDM3UM	0.013070	0.303813	0.348807
HYDM4UM	-.018576	0.210069	0.396687
SEPTA	-.093692	0.012798	-.040618

Table 4. Eigenvectors for the first three principal components from a principal components analysis of specimens collected from the Apalachicola National Forest and vicinity.

Character	PRIN1	PRIN2	PRIN3
PRLFLMM	-.130645	0.073680	0.150030
PRLFWMM	0.103816	-.202195	0.254499
MEDLFLMM	0.197855	0.394173	0.037448
MEDLFWMM	0.307911	-.007729	0.090484
DISLFLMM	0.153565	0.383975	0.059636
DISLFWMM	0.274460	-.067228	0.066090
PROXD	0.305453	-.175458	0.126552
PROXS	0.160592	-.331235	0.205933
MEDD	0.338929	-.049278	0.043639
MEDS	0.333730	-.060304	0.118349
DISTD	0.286641	-.011107	0.021161
DISTS	0.335947	-.062979	0.102982
HYALLUM	0.158956	0.225632	-.098628
HYALWUM	0.017987	-.438636	-.068922
CHLLUM	0.214998	0.328759	-.036713
STLFLMM	-.104483	-.087747	0.108546
STLFWMM	-.217632	0.228020	0.247066
HYDM1UM	-.166711	-.220642	0.290872
HYDM2UM	-.190075	0.042519	0.345323
HYDM3UM	-.039209	0.142316	0.493000
HYDM4UM	-.005679	0.113453	0.495048
SEPTA	-.057783	-.030658	0.170861

these three areas the first three components accounted for about 64% of the total variation (Table 5, 6, and 7). *Sphagnum cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* separate primarily along principal component 1 in the ANF and the CNF, whereas they are separated by principal components 1 and 2 in combination in the FMNF. *Sphagnum fitzgeraldii* is primarily separated by its low principal component 2 scores (Figures 5, 6, and 7).

The hybrid? specimen indicated in Figure 6 is positioned at one end of the array of *S. trinitense/S. mississippiense* specimens in the principal component 2 on principal component 1 plot. The hybrid? is located in an intermediate position with respect to one end of the point spread shown by *S. cuspidatum/S. viridum* and *S. fitzgeraldii* on the plot as well. This hybrid? specimen also separates from the other groups along principal component 3 (Figure 6). Obviously a larger number of hybrid? specimens are needed in order to reasonably evaluate its hypothesized morphological intermediacy between *S. cuspidatum/S. viridum* and *S. fitzgeraldii*.

The *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* groups from the DNF are mostly well separated by principal components 1 and 2 in combination (Figure 8). These two axes, respectively, accounted for 37% and 16% of the total variation (Table 8). As Table 9 shows, branch leaf shape and margin features as well as

Table 5. Eigenvalues, proportion of variance accounted for by each component, and cumulative variance explained from a principal components analysis of specimens collected from the Croatan National Forest.

Principal Component	Eigenvalue	Proportion	Cumulative
PRIN1	7.76133	0.352788	0.35279
PRIN2	3.84901	0.174955	0.52774
PRIN3	2.72871	0.124032	0.65178
PRIN4	1.70507	0.077503	0.72928
PRIN5	1.25354	0.056979	0.78626
PRIN6	1.18969	0.054077	0.84033
PRIN7	0.73097	0.033226	0.87356
PRIN8	0.61558	0.027981	0.90154
PRIN9	0.47827	0.021739	0.92328
PRIN10	0.40197	0.018271	0.94155
PRIN11	0.32293	0.014679	0.95623
PRIN12	0.20650	0.009386	0.96562
PRIN13	0.17165	0.007802	0.97342
PRIN14	0.13545	0.006157	0.97958
PRIN15	0.10126	0.004603	0.98418
PRIN16	0.08268	0.003758	0.98794
PRIN17	0.07276	0.003307	0.99124
PRIN18	0.05912	0.002687	0.99393
PRIN19	0.05539	0.002518	0.99645
PRIN20	0.03563	0.001619	0.99807
PRIN21	0.03076	0.001398	0.99947
PRIN22	0.01173	0.000533	1.00000

Table 6. Eigenvalues, proportion of variance accounted for by each component, and cumulative variance explained from a principal components analysis of specimens collected from the Francis Marion National Forest.

Principal Component	Eigenvalue	Proportion	Cumulative
PRIN1	6.35452	0.288842	0.28884
PRIN2	5.90365	0.268348	0.55719
PRIN3	1.95974	0.089079	0.64627
PRIN4	1.63473	0.074306	0.72057
PRIN5	1.46821	0.066737	0.78731
PRIN6	1.04137	0.047335	0.83465
PRIN7	0.72576	0.032989	0.86764
PRIN8	0.62099	0.028227	0.89586
PRIN9	0.56299	0.025590	0.92145
PRIN10	0.36551	0.016614	0.93807
PRIN11	0.26425	0.012012	0.95008
PRIN12	0.21672	0.009851	0.95993
PRIN13	0.18774	0.008534	0.96846
PRIN14	0.14762	0.006710	0.97517
PRIN15	0.13059	0.005936	0.98111
PRIN16	0.11768	0.005349	0.98646
PRIN17	0.08695	0.003952	0.99041
PRIN18	0.07975	0.003625	0.99403
PRIN19	0.04592	0.002087	0.99612
PRIN20	0.03651	0.001659	0.99778
PRIN21	0.03233	0.001470	0.99925
PRIN22	0.01647	0.000749	1.00000

Table 7. Eigenvalues, proportion of variance accounted for by each component, and cumulative variance explained from a principal components analysis of specimens collected from the Apalachicola National Forest and vicinity.

Principal Component	Eigenvalue	Proportion	Cumulative
PRIN1	7.41802	0.337183	0.33718
PRIN2	3.90930	0.177695	0.51488
PRIN3	2.73151	0.124160	0.63904
PRIN4	1.99901	0.090864	0.72990
PRIN5	1.32556	0.060253	0.79015
PRIN6	0.86539	0.039336	0.82949
PRIN7	0.77838	0.035381	0.86487
PRIN8	0.69643	0.031656	0.89653
PRIN9	0.50144	0.022793	0.91932
PRIN10	0.41532	0.018878	0.93820
PRIN11	0.30066	0.013666	0.95187
PRIN12	0.23100	0.010500	0.96237
PRIN13	0.19170	0.008713	0.97108
PRIN14	0.14568	0.006622	0.97770
PRIN15	0.13531	0.006150	0.98385
PRIN16	0.10276	0.004671	0.98852
PRIN17	0.09614	0.004370	0.99289
PRIN18	0.06230	0.002832	0.99572
PRIN19	0.04126	0.001875	0.99760
PRIN20	0.02295	0.001043	0.99864
PRIN21	0.01669	0.000759	0.99940
PRIN22	0.01317	0.000599	1.00000

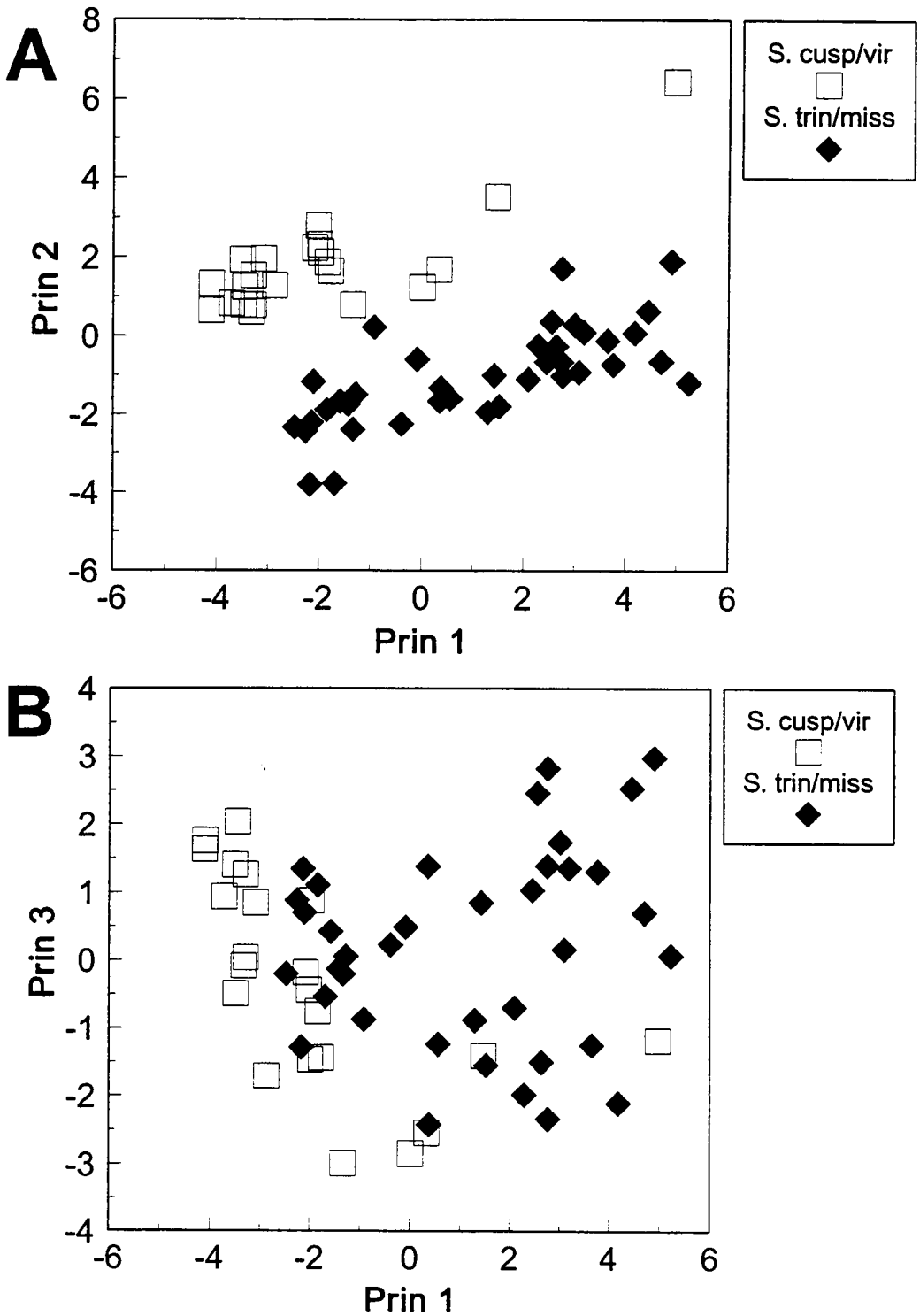


Figure 8. Principal components analysis plots of specimens collected from the De Soto National Forest and vicinity. A. Prin 2 plotted on prin 1. B. Prin 3 plotted on prin 1.

Table 8. Eigenvalues, proportion of variance accounted for by each component, and cumulative variance explained from a principal components analysis of specimens collected from the De Soto National Forest and vicinity.

Principal Component	Eigenvalue	Proportion	Cumulative
PRIN1	7.66858	0.365171	0.36517
PRIN2	3.45097	0.164332	0.52950
PRIN3	2.19044	0.104307	0.63381
PRIN4	1.62567	0.077413	0.71122
PRIN5	1.22791	0.058472	0.76969
PRIN6	0.85252	0.040596	0.81029
PRIN7	0.78493	0.037378	0.84767
PRIN8	0.56613	0.026958	0.87463
PRIN9	0.46424	0.022106	0.89673
PRIN10	0.41425	0.019726	0.91646
PRIN11	0.30929	0.014728	0.93119
PRIN12	0.29862	0.014220	0.94541
PRIN13	0.24559	0.011695	0.95710
PRIN14	0.23133	0.011016	0.96812
PRIN15	0.17185	0.008183	0.97630
PRIN16	0.14852	0.007073	0.98337
PRIN17	0.13117	0.006246	0.98962
PRIN18	0.08454	0.004026	0.99365
PRIN19	0.07295	0.003474	0.99712
PRIN20	0.03185	0.001517	0.99864
PRIN21	0.02865	0.001364	1.00000
PRIN22	0.00000	0.000000	1.00000

Table 9. Eigenvectors for the first three principal components from a principal components analysis of specimens collected from the De Soto National Forest and vicinity.

Character	PRIN1	PRIN2	PRIN3
PRLFLMM	0.082515	0.469015	-.080962
PRLFWMM	0.236132	0.129877	0.200318
MEDLFLMM	0.270613	0.245567	-.228260
MEDLFWMM	0.266525	-.027274	0.248005
DISLFLMM	0.247033	0.144951	-.302457
DISLFWMM	0.244333	-.131535	0.139012
PROXD	0.269021	-.097986	0.237512
PROXS	0.000000	0.000000	0.000000
MEDD	0.299357	-.215506	0.058713
MEDS	0.275494	0.139164	-.003128
DISTD	0.282096	-.232169	-.083718
DISTS	0.287478	-.035531	-.091607
HYALLUM	0.294965	0.039701	-.160280
HYALWUM	0.041031	0.039991	0.366965
CHLLUM	0.273100	0.050619	-.107424
STLFLMM	0.211760	0.302038	-.046696
STLFWMM	-.068906	0.339380	0.082690
HYDM1UM	-.116340	0.361850	0.189144
HYDM2UM	-.059025	0.369919	0.349300
HYDM3UM	0.142301	0.077859	0.365162
HYDM4UM	0.144030	-.167746	0.307141
SEPTA	-.038227	-.138214	0.295396

chlorophyllose cell length and stem leaf length weight heavily on principal component 1 and proximal branch leaf length, stem leaf length, stem leaf width, and the cell diameter of stem layers one and two weight heavily on principal component 2. Principal component 3 is mostly related to variation within each of these groups and does not separate them (Figure 8).

Specimens from the SH designated as *S. torreyanum* and as *S. cuspidatum/S. viridum* are mostly well separated along principal component 1; thus, they appear as relatively distinct groups on both plots in Figure 9. Specimens designated as *S. trinitense/S. mississippiense* are not distinct on the plots from those designated as *S. cuspidatum/S. viridum* nor do the former specimens form a cohesive entity on the plot of principal component 2 on principal component 1. Characters with heavier weightings on principal component 1 are proximal, median, and distal branch leaf width, all of the branch leaf margin characters, stem leaf width, and number of septa per stem leaf. Principal component 2 has heavier weightings for all six branch leaf length and width characters, median branch leaf serrulation, hyaline and chlorophyllose cell length, and the diameter of cells in stem layer four (Table 10). This axis does not separate groups. It mainly accounts for variation among the *S. cuspidatum/S. viridum* specimens and among the *S. torreyanum* specimens (Figure 9). These two groups of

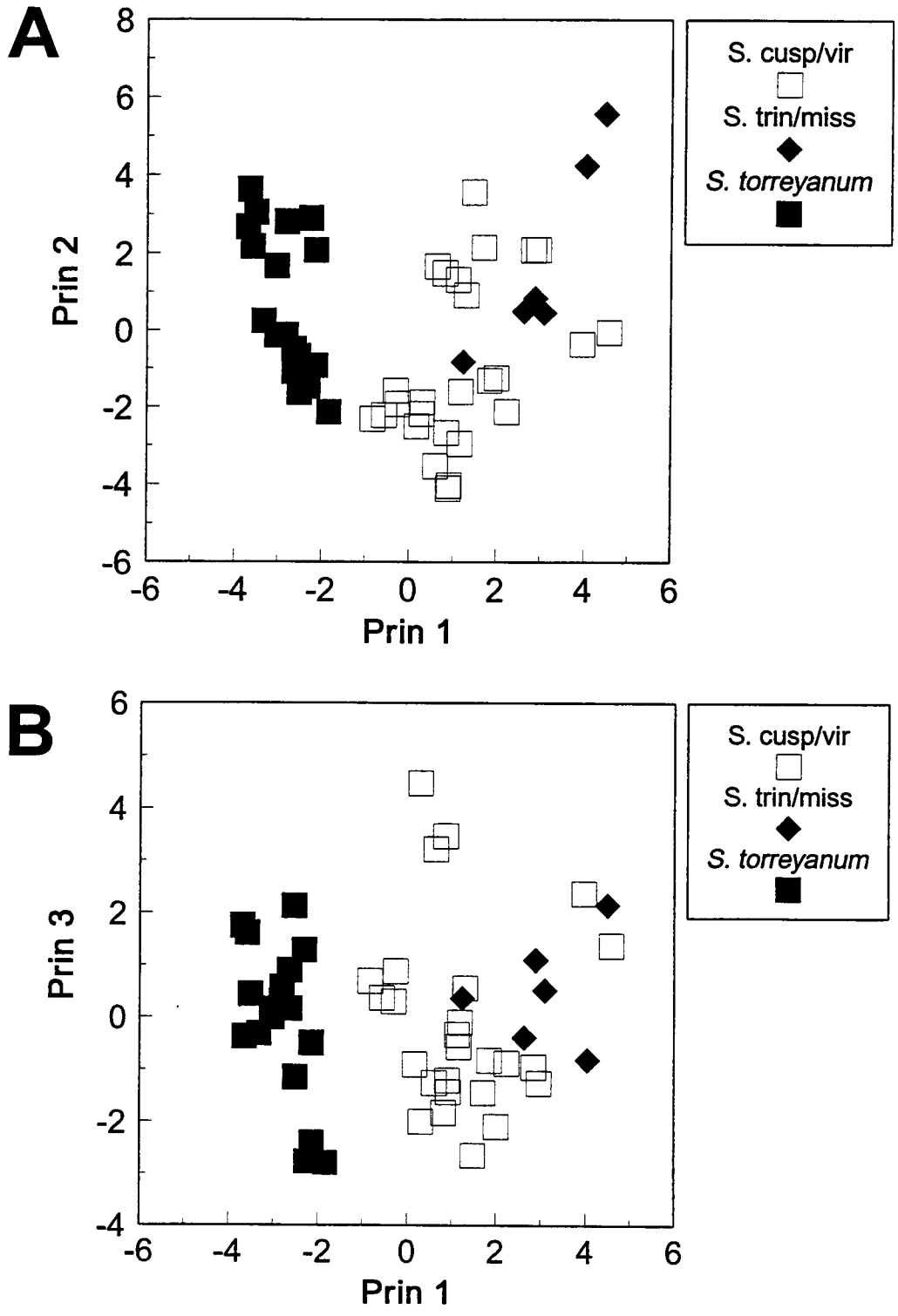


Figure 9. Principal components analysis plots of specimens collected from the Sandhills. A. Prin 2 plotted on prin 1. B. Prin 3 plotted on prin 1.

Table 10. Eigenvectors for the first three principal components from a principal components analysis of specimens collected from the Sandhills.

Character	PRIN1	PRIN2	PRIN3
PRLFLMM	-.080672	0.161508	0.201331
PRLFWMM	-.184470	0.225504	0.180802
MEDLFLMM	0.015329	0.364123	-.191410
MEDLFWMM	-.211131	0.313041	-.089558
DISLFLMM	0.044204	0.292535	-.269966
DISLFWMM	-.203721	0.281700	-.141396
PROXD	0.316739	0.092552	0.084636
PROXS	0.172333	0.166606	0.132207
MEDD	0.385228	0.062545	0.010222
MEDS	0.282516	0.221245	0.022816
DISTD	0.384282	0.019666	-.027994
DISTS	0.331265	0.170661	-.042529
HYALLUM	0.011856	0.382278	-.164171
HYALWUM	-.099603	0.139175	0.015533
CHLLUM	0.135534	0.341476	-.081841
STLFLMM	0.066631	0.160782	0.327710
STLFWMM	-.332201	0.161161	0.041629
HYDM1UM	0.103541	-.044282	0.306364
HYDM2UM	-.060879	0.123729	0.409534
HYDM3UM	-.068851	0.064040	0.456602
HYDM4UM	-.072254	0.228841	0.361948
SEPTA	0.296532	-.034353	0.131519

specimens also show extensive variation along principal component 3. Principal component 1, principal component 2, and principal component 3 accounted for 27%, 24%, and 12% of the total variation, respectively (Table 11).

Figure 10 is a plot of principal component 2 on principal component 1 that includes specimens collected from all five areas together. Specimens designated by dissecting microscope examination as *S. torreyanum* and as *S. fitzgeraldii* stand out as mostly distinct groups from an intervening mixed cloud of specimens designated as *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense*. Characters with the heaviest weightings on principal component 1 were median and distal branch leaf length, all six branch leaf margin characters, hyaline cell length, and chlorophyllose cell length. Principal component 2 had heavier weightings for median and distal branch leaf length and width, proximal branch leaf proportion of margin not entire, stem leaf width, and the diameters of cells in stem layers 2 - 4 (Table 12).

The plot of principal component 3 on principal component 1 (Figure 11) shows a different pattern from the previous figure. Specimens designated as *S. trinitense/S. mississippiense* and as *S. cuspidatum/S. viridum* are clustered into adjacent, but different regions on the plot. Some of the *S. torreyanum* specimens are mixed with some of the *S. cuspidatum/S. viridum* specimens and the *S.*

Table 11. Eigenvalues, proportion of variance accounted for by each component, and cumulative variance explained from a principal components analysis of specimens collected from the Sandhills.

Principal Component	Eigenvalue	Proportion	Cumulative
PRIN1	5.95713	0.270779	0.27078
PRIN2	5.25923	0.239056	0.50983
PRIN3	2.57407	0.117003	0.62684
PRIN4	2.09328	0.095149	0.72199
PRIN5	1.30316	0.059235	0.78122
PRIN6	1.05835	0.048107	0.82933
PRIN7	0.82886	0.037675	0.86700
PRIN8	0.56247	0.025567	0.89257
PRIN9	0.51692	0.023496	0.91607
PRIN10	0.46662	0.021210	0.93728
PRIN11	0.35189	0.015995	0.95327
PRIN12	0.29020	0.013191	0.96646
PRIN13	0.18108	0.008231	0.97469
PRIN14	0.13907	0.006321	0.98101
PRIN15	0.11385	0.005175	0.98619
PRIN16	0.07917	0.003599	0.98979
PRIN17	0.07626	0.003466	0.99326
PRIN18	0.05858	0.002663	0.99592
PRIN19	0.03566	0.001621	0.99754
PRIN20	0.02106	0.000957	0.99850
PRIN21	0.01803	0.000819	0.99932
PRIN22	0.01505	0.000684	1.00000

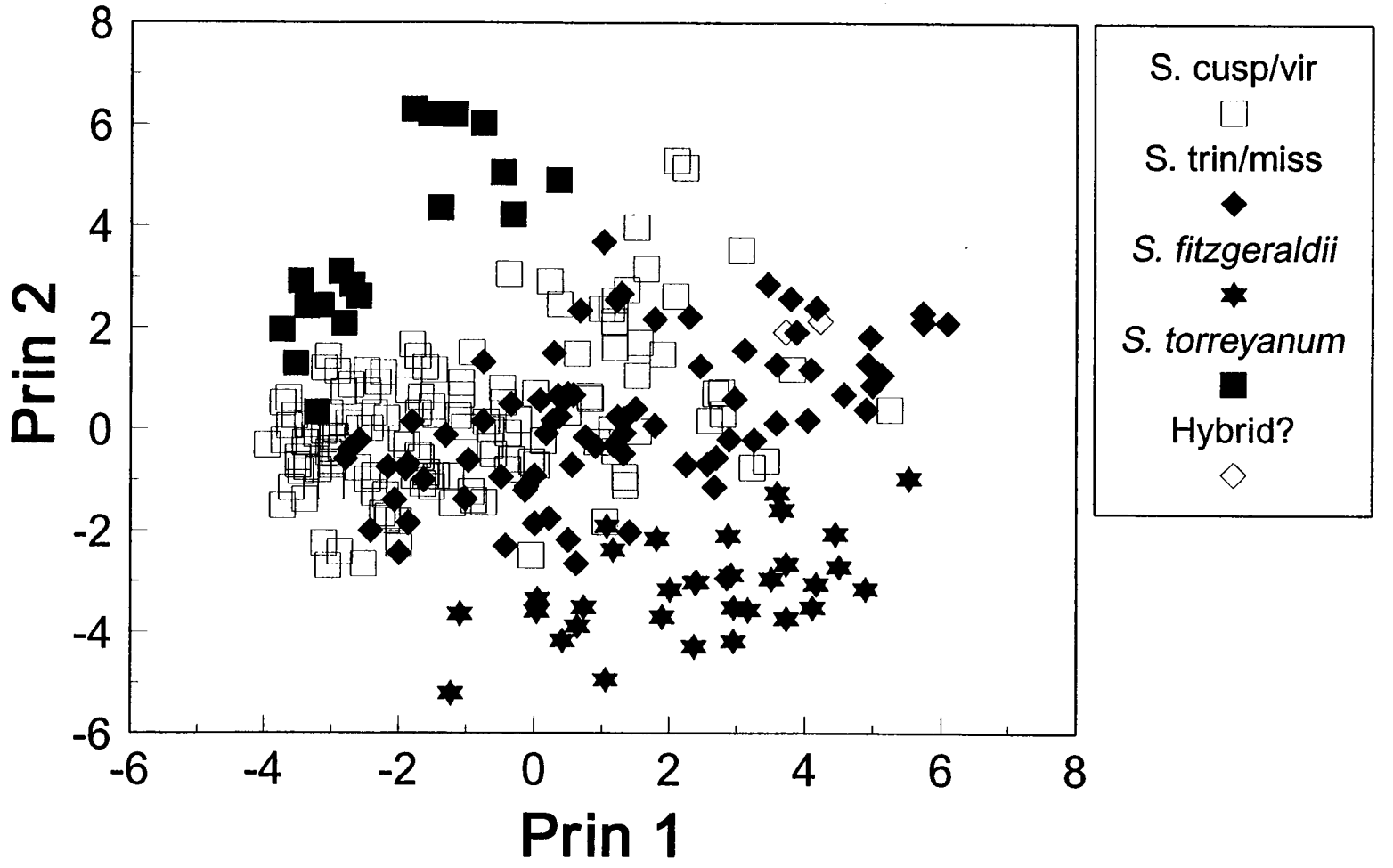


Figure 10. Plot of principal component 2 on principal component 1 from a principal components analysis of specimens collected from all five areas.

Table 12. Eigenvectors for the first three principal components from a principal components analysis of specimens collected from all five areas.

Character	PRIN1	PRIN2	PRIN3
PRLFLMM	0.072856	0.177957	-.173887
PRLFWMM	0.083273	0.178935	0.406490
MEDLFLMM	0.269401	0.279153	-.222584
MEDLFWMM	0.169105	0.279767	0.349679
DISLFLMM	0.226698	0.263790	-.232412
DISLFWMM	0.111007	0.283715	0.307395
PROXD	0.279771	-.200910	0.248864
PROXS	0.216720	-.128035	0.109360
MEDD	0.339008	-.152939	0.103194
MEDS	0.348394	-.081520	0.010542
DISTD	0.304256	-.170091	-.007565
DISTS	0.358000	-.084571	-.035551
HYALLUM	0.283418	0.162253	-.178793
HYALWUM	-.048389	-.101771	0.403829
CHLLUM	0.304410	0.163348	-.204443
STLFLMM	0.152752	0.013708	0.010464
STLFWMM	-.169902	0.380135	0.073934
HYDM1UM	-.029522	0.080959	-.269365
HYDM2UM	-.098046	0.301165	-.109262
HYDM3UM	-.008473	0.322267	0.163189
HYDM4UM	0.018833	0.297330	0.195656
SEPTA	0.046324	-.097921	0.080029

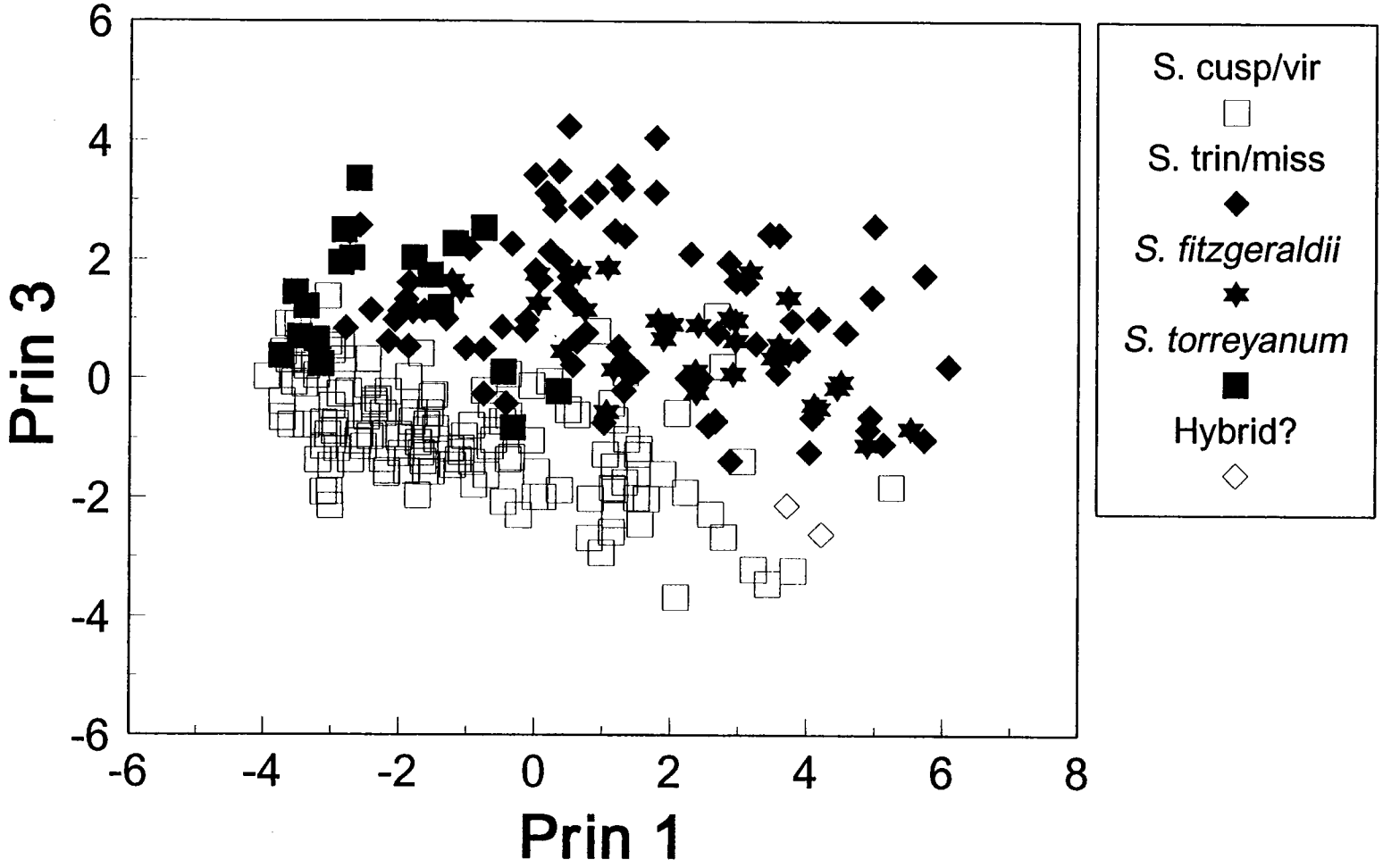


Figure 11. Plot of principal component 3 on principal component 1 from a principal components analysis of specimens collected from all five areas.

fitzgeraldii specimens are mixed with the *S. trinitense/S. mississippiense* specimens. Another feature of this plot is that the *S. cuspidatum/S. viridum* specimens form a conspicuously tighter unit than do the *S. trinitense/S. mississippiense* specimens. Characters weighting most heavily on principal component 3 were proximal branch leaf width, median and distal branch leaf length and width, proximal branch leaf proportion of margin not entire, hyaline cell width, chlorophyllose cell length, and the diameters of cells in stem layers 1 and 4 (Table 12). These two groups, *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense*, are separated by principal components 1 and 3 in combination; thus, branch leaf shape, branch leaf margin characters, and the diameter of cells in stem layers one and four together appear to distinguish these two groups.

The first three components accounted for 28%, 19%, and 10% of the variation, respectively (Table 13).

The canonical discriminant analysis strongly supported the four larger groups initially established by examination under a dissecting microscope. Figure 12, a plot of the first two canonical variates, shows four discrete groups. The hybrid? specimen clusters with the *S. cuspidatum/S. viridum* group in Figure 12, but separates from the latter group along canonical variate 4 (not plotted herein). According to the discriminant functions analysis, the

Table 13. Eigenvalues, proportion of variance accounted for by each component, and cumulative variance explained from a principal components analysis of specimens collected from all five areas.

Principal Component	Eigenvalue	Proportion	Cumulative
PRIN1	6.15276	0.279671	0.27967
PRIN2	4.07315	0.185143	0.46481
PRIN3	2.26289	0.102859	0.56767
PRIN4	2.00332	0.091060	0.65873
PRIN5	1.55527	0.070694	0.72943
PRIN6	0.97390	0.044268	0.77370
PRIN7	0.89941	0.040882	0.81458
PRIN8	0.84136	0.038243	0.85282
PRIN9	0.66123	0.030056	0.88288
PRIN10	0.47791	0.021723	0.90460
PRIN11	0.34947	0.015885	0.92049
PRIN12	0.28656	0.013025	0.93351
PRIN13	0.27301	0.012409	0.94592
PRIN14	0.23433	0.010651	0.95657
PRIN15	0.20253	0.009206	0.96578
PRIN16	0.16855	0.007661	0.97344
PRIN17	0.15643	0.007111	0.98055
PRIN18	0.13306	0.006048	0.98660
PRIN19	0.13016	0.005916	0.99251
PRIN20	0.06471	0.002941	0.99546
PRIN21	0.06206	0.002821	0.99828
PRIN22	0.03793	0.001724	1.00000

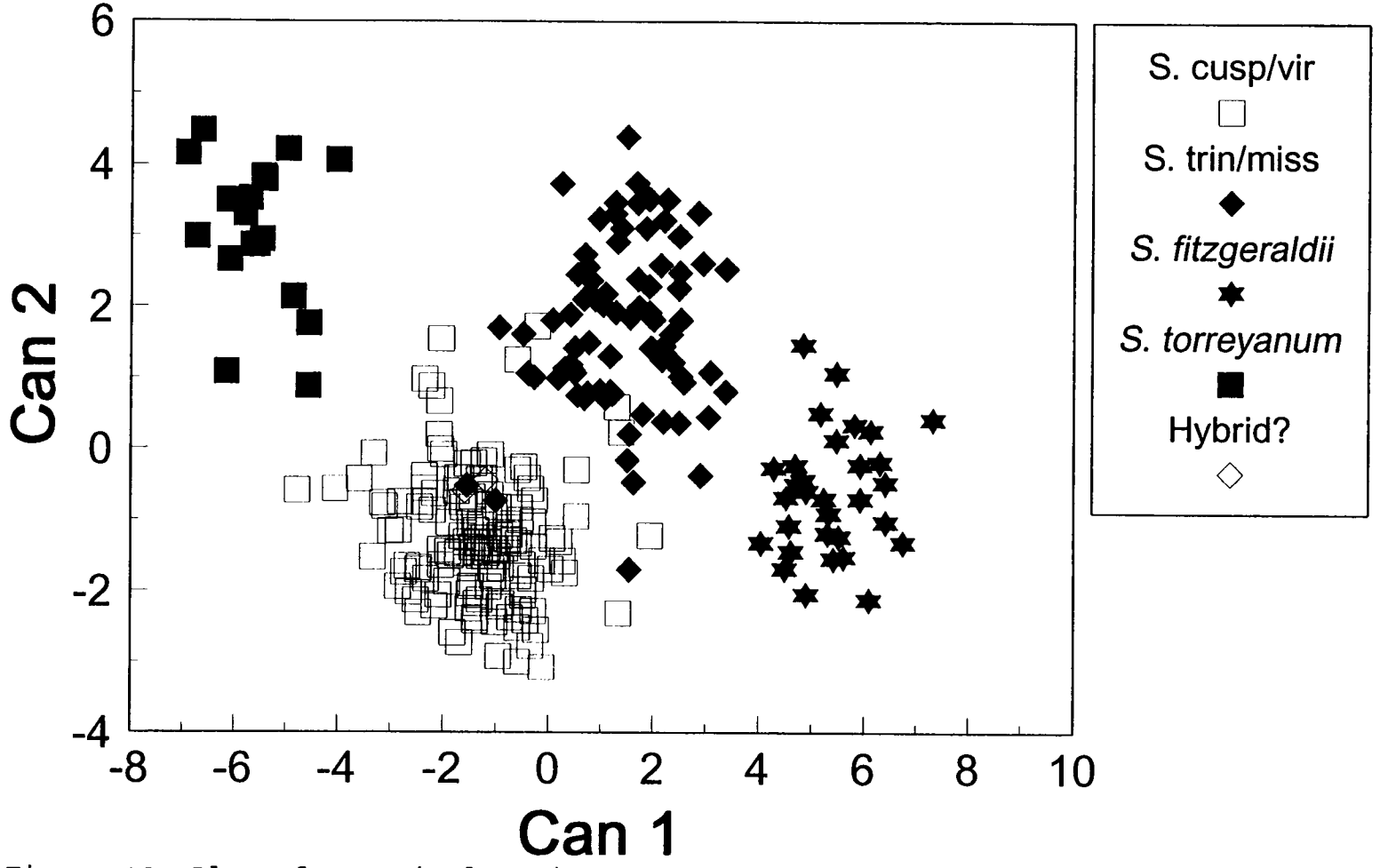


Figure 12. Plot of canonical variate 2 on canonical variate 1 from a canonical discriminant analysis of specimens collected from all five areas.

proportion of specimens correctly classified was very high (Table 14) with the only misclassifications being between the *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* groups and the *S cuspidatum/S. viridum* and Hybrid? groups.

The arrangement of the groups shown in Figure 12 is quite similar to that presented earlier on the principal components analysis plot (Figure 10) in that *S. torreyanum* and *S. fitzgeraldii* are the most widely separated groups. The latter two groups of specimens also had the greatest separation as indicated by a Mahalanobis distance criterion (Table 15). The groups *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* are intermediate on the plot between the *S. torreyanum* and *S. fitzgeraldii* specimens and separate from each other along a combination of canonical variates one and two. The small (16.80) Mahalanobis distance between the *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* groups indicates their overall similarity (Table 15).

The *Sphagnum cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* Pair

Methods

In order to more clearly evaluate the distinctiveness of the *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* groups, the *S. fitzgeraldii* and *S.*

Table 14. Classification of specimens collected from all five areas by a discriminant functions analysis. Values on the diagonal (in bold) are the proportion of specimens correctly classified according to the discriminant function. The accompanying values in each row indicate the percentage of specimens misclassified by the grouping criteria according to the discriminant function. 1 - *S. cuspidatum/S. viridum*, 2 - *S. trinitense/S. mississippiense*, 3 - *S. fitzgeraldii*, 4 - *S. torreyanum*, 5 - Hybrid?.

Taxon	1	2	3	4	5
1	**95.65**	3.62	0.00	0.00	0.72
2	3.75	**96.25**	0.00	0.00	0.00
3	0.00	0.00	**100.00**	0.00	0.00
4	0.00	0.00	0.00	**100.00**	0.00
5	0.00	0.00	0.00	0.00	**100.00**

Table 15. Mahalanobis distances between groups from a canonical discriminant analysis of specimens collected from all five areas. 1 - *S. cuspidatum/S. viridum*, 2 - *S. trinitense/S. mississippiense*, 3 - *S. fitzgeraldii*, 4 - *S. torreyanum*, 5 - Hybrid?.

Taxon	1	2	3	4
2	16.80			
3	50.33	31.01		
4	45.38	65.14	134.55	
5	26.22	38.54	77.10	65.67

torreyanum specimens were removed and a principal components analysis was conducted on the remaining specimens.

Results

As in the more inclusive analysis, the *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* groups are fairly well-mixed when principal component 2 is plotted on principal component 1 (Figure 13). The plot of principal component 3 on principal component 1, however, effects a nice separation between these two groups, despite a small number of specimens from each group that appear to have been misclassified (Figure 14).

Characters with heavier weightings on principal component 1 were median and distal branch leaf length and width, all six branch leaf margin characters, hyaline cell length, and chlorophyllose cell length. Characters with higher weightings on principal component 3 were branch leaf shape features, proximal branch leaf proportion of margin not entire and serrulation, hyaline cell length and width, chlorophyllose cell length, the diameters of cells in stem layers 1 and 2, and number of septa per stem leaf (Table 16). Interestingly, the three branch leaf length characters each had negative weightings on principal component 3 and the three branch leaf width characters each had positive weightings on this same axis (Table 16). Since the two groups are separated principally along this axis, the

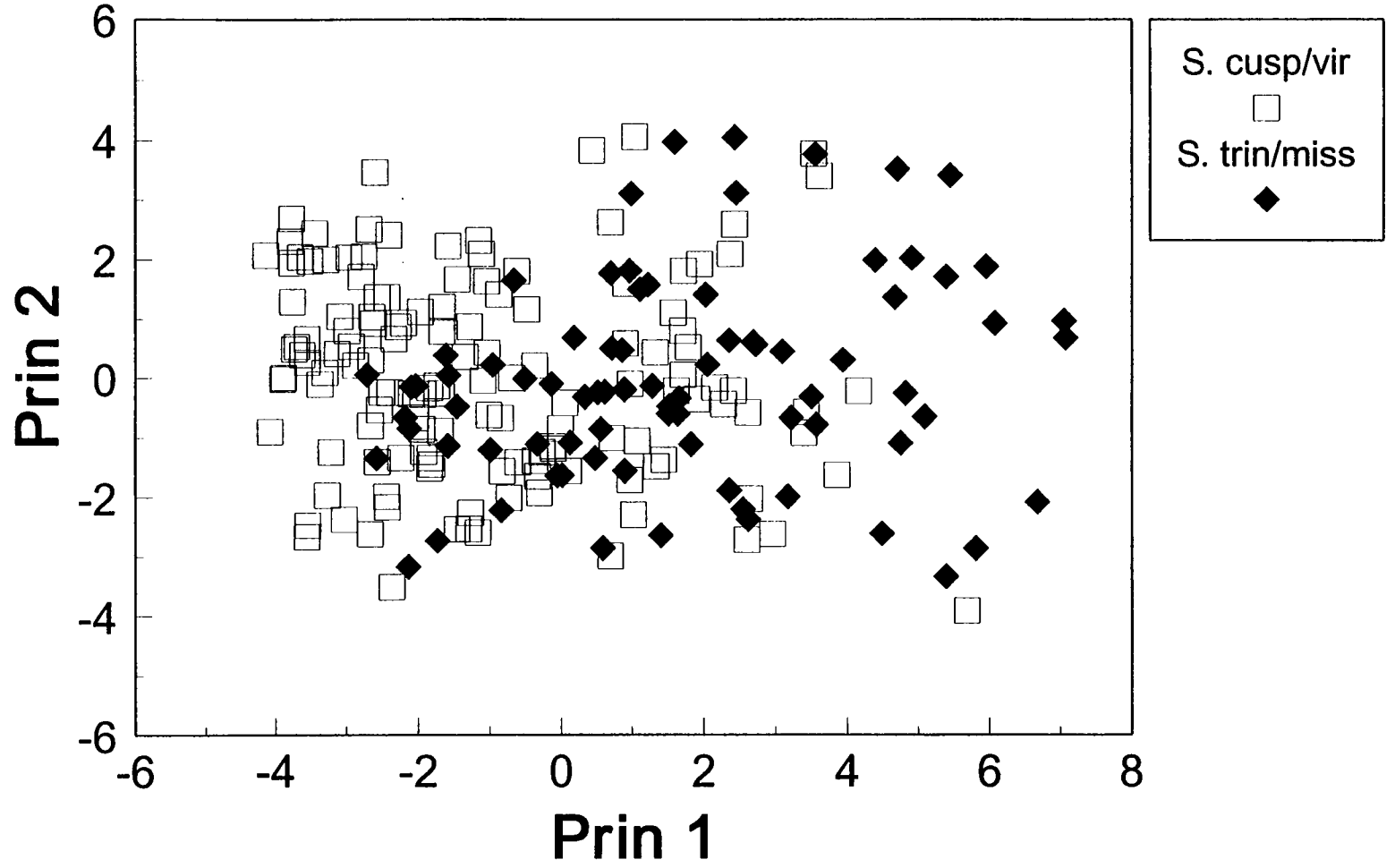


Figure 13. Plot of principal component 2 on principal component 1 from a principal components analysis of *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* specimens collected from all five areas.

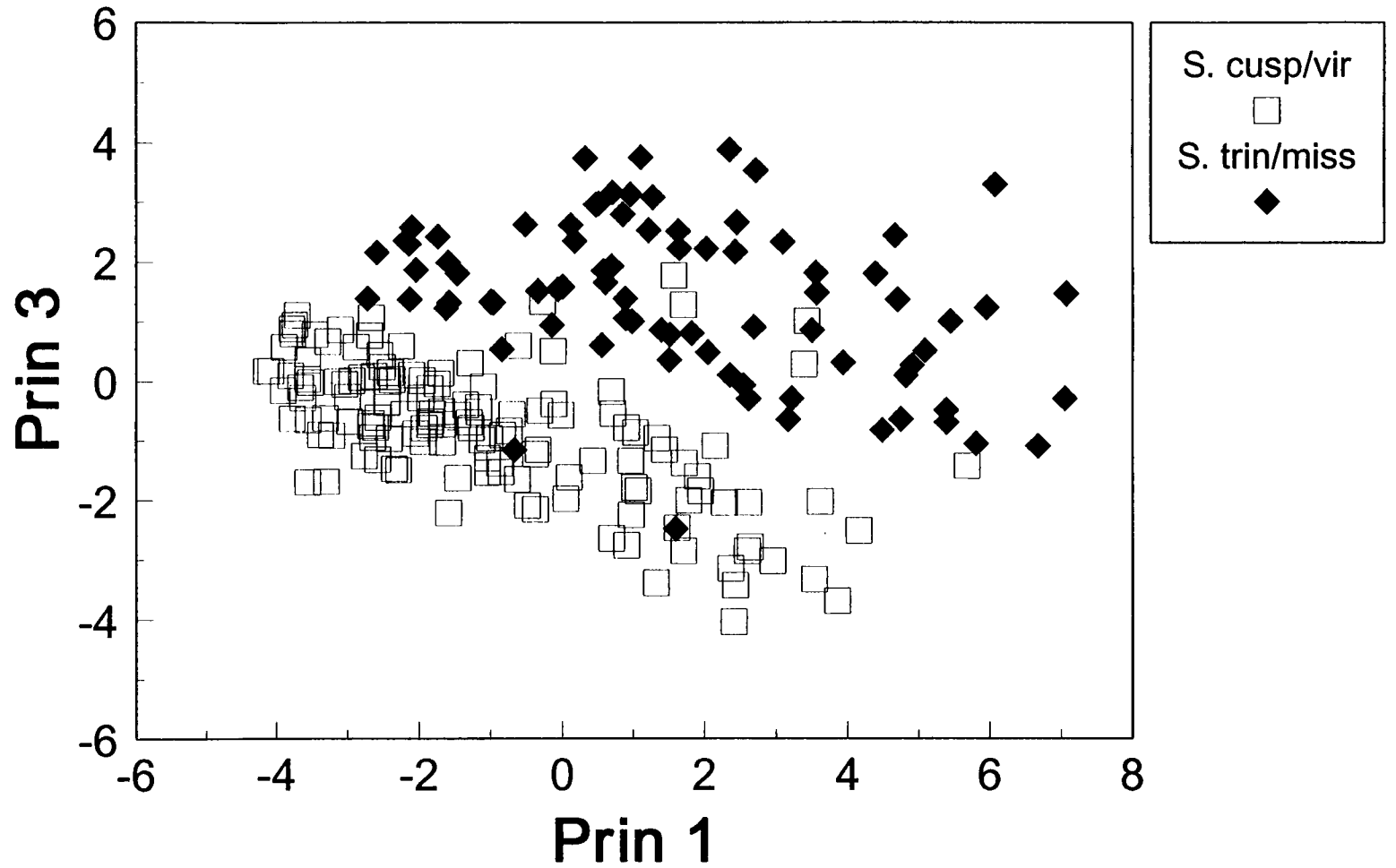


Figure 14. Plot of principal component 3 on principal component 1 from a principal components analysis of *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* specimens collected from all five areas.

Table 16. Eigenvectors for the first three principal components from a principal components analysis of *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* specimens collected from all five areas.

Character	PRIN1	PRIN2	PRIN3
PRLFLMM	0.068932	0.251204	-.242514
PRLFWMM	0.121838	0.287749	0.307703
MEDLFLMM	0.308267	-.014142	-.277438
MEDLFWMM	0.262363	0.134815	0.179387
DISLFLMM	0.273913	-.067809	-.276553
DISLFWMM	0.221214	0.095354	0.131000
PROXD	0.246379	-.011960	0.300237
PROXS	0.163594	0.089414	0.157496
MEDD	0.316142	-.096801	0.144116
MEDS	0.311620	-.054077	-.001571
DISTD	0.288470	-.144470	0.063095
DISTS	0.324593	-.096061	-.039836
HYALLUM	0.261170	-.028635	-.250470
HYALWUM	-.069569	0.105393	0.352492
CHLLUM	0.294725	-.045527	-.229573
STLFLMM	0.106293	0.226701	-.039705
STLFWMM	-.053486	0.385136	-.012508
HYDM1UM	-.075108	0.355996	-.349946
HYDM2UM	-.035161	0.449464	-.233225
HYDM3UM	0.122087	0.366517	0.103728
HYDM4UM	0.151943	0.277379	0.152462
SEPTA	0.023299	0.133233	0.223924

weightings suggest leaf shape may be useful in separating these two groups. The plot of principal component 3 on principal component 1 also suggests that these two groups differ with respect to morphological variability. The *S. cuspidatum/S. viridum* group is a mostly compact elongate cluster whereas the *S. trinitense/S. mississippiense* group is conspicuously more widespread on the plot (Figure 14).

The first three principal components accounted for 32%, 13%, and 12% of the variance, respectively (Table 17).

The *Sphagnum trinitense/S. mississippiense* Species Pair

The analyses presented above indicated that specimens from the DNF initially designated by inspection under a dissecting microscope as part of a *S. trinitense/S. mississipiense* species pair were morphologically distinct from those in the *S. cuspidatum/S. viridum* species pair. The objective of this section of analysis is to determine if more than one consistently recognizable morphological group exists within what I have heretofore referred to as the *S. trinitense/S. mississippiense* species pair.

Methods

Nineteen of the thirty specimens included in the previous morphometric analyses from the De Soto National Forest and vicinity had been assigned to the *S. trinitense/S. mississippiense* species pair based on

Table 17. Eigenvalues, proportion of variance accounted for by each component, and cumulative variance explained from a principal components analysis of *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* specimens collected from all five areas.

Principal Component	Eigenvalue	Proportion	Cumulative
PRIN1	7.10916	0.323144	0.32314
PRIN2	2.86447	0.130203	0.45335
PRIN3	2.57530	0.117059	0.57041
PRIN4	1.64689	0.074859	0.64526
PRIN5	1.61692	0.073496	0.71876
PRIN6	1.10270	0.050123	0.76888
PRIN7	0.90739	0.041245	0.81013
PRIN8	0.73059	0.033208	0.84334
PRIN9	0.56945	0.025884	0.86922
PRIN10	0.52465	0.023848	0.89307
PRIN11	0.40155	0.018252	0.91132
PRIN12	0.35963	0.016347	0.92767
PRIN13	0.30104	0.013684	0.94135
PRIN14	0.26206	0.011912	0.95326
PRIN15	0.21380	0.009718	0.96298
PRIN16	0.19711	0.008960	0.97194
PRIN17	0.16526	0.007512	0.97945
PRIN18	0.14967	0.006803	0.98626
PRIN19	0.12066	0.005485	0.99174
PRIN20	0.08354	0.003797	0.99554
PRIN21	0.06563	0.002983	0.99852
PRIN22	0.03254	0.001479	1.00000

appearance under a dissecting microscope. In order to enlarge the sample size, herbarium loans obtained from BING, DUKE, LAF, and FLAS, as well as those in TENN, were examined for specimens that met three criteria: (1) collected from the southern Mississippi/eastern Louisiana region, (2) assignable to the *S. trinitense/S. mississippiense* species pair based on appearance under a dissecting microscope, and (3) ample material in the packet for dissection and measurement. (Nearly all such specimens at DUKE, BING, TENN, and FLAS were duplicates of material at LAF collected by William D. Reese or Jacob Valentine.) Thirteen specimens variously identified by other bryologists as *S. trinitense*, *S. mississippiense*, or *S. cuspidatum*, and three paratypes of *S. mississippiense*, that fit these three criteria were found. The following six characters were measured on two stems from each of these sixteen specimens (see Appendix B for a list of specimens examined): proximal branch leaf length, proximal branch leaf width, median branch leaf length, median branch leaf width, distal branch leaf length, and distal branch leaf width. Sample sizes and sampling procdures for these six characters were identical to those employed in the larger morphometric study. Thus thirty-five specimens were included in the present analysis of the *S. trinitense/S. mississippiense* species pair (19 - my collections from the DNF + 13 + 3 paratypes).

Results

Andrus (1987) stated that *S. mississippiense* and *S. trinitense* are best separated by the former's ovate to broadly ovate proximal branch leaves as compared to the ovate-lanceolate to lanceolate proximal branch leaves of the latter species. Thus, the proximal branch leaf variables will be examined first.

Figure 15 contains bar charts for proximal branch leaf length, width, and length to width ratio. These distributions are somewhat suggestive of normal distributions, but are skewed to the right. The distributions do not suggest the presence of two morphological groups that can be distinguished by proximal branch leaf shape - i.e. they are not bimodal.

In order to further evaluate this set of specimens, all six variables were included in a principal components analysis. The principal components plots shown in Figures 16 and 17 suggest the specimens are from one variable entity. The first three components accounted for 57%, 20%, and 14% of the total variation, respectively (Table 18). The weightings of each character on the components shown in Table 19 are very informative. All six variables have more or less equivalent positive weightings on principal component 1. Thus this axis is a leaf size axis. All three length variables had more or less equivalent negative weightings on principal component 2 and all three width

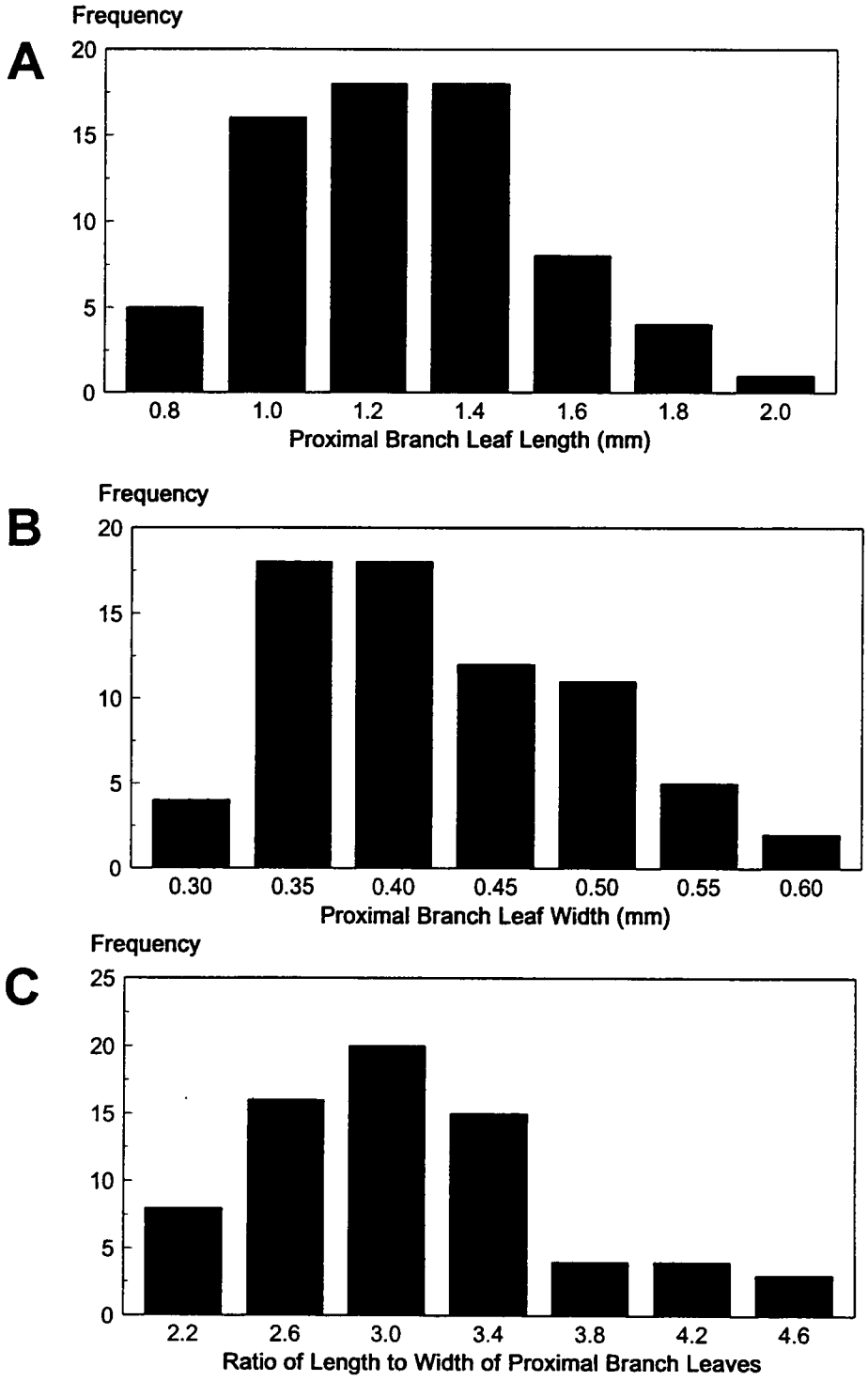


Figure 15. Bar charts of *S. trinitense/S. mississippiense* specimens collected from southern Mississippi and eastern Louisiana. A. proximal branch leaf length. B. proximal branch leaf width. C. ratio of length to width of proximal branch leaves.

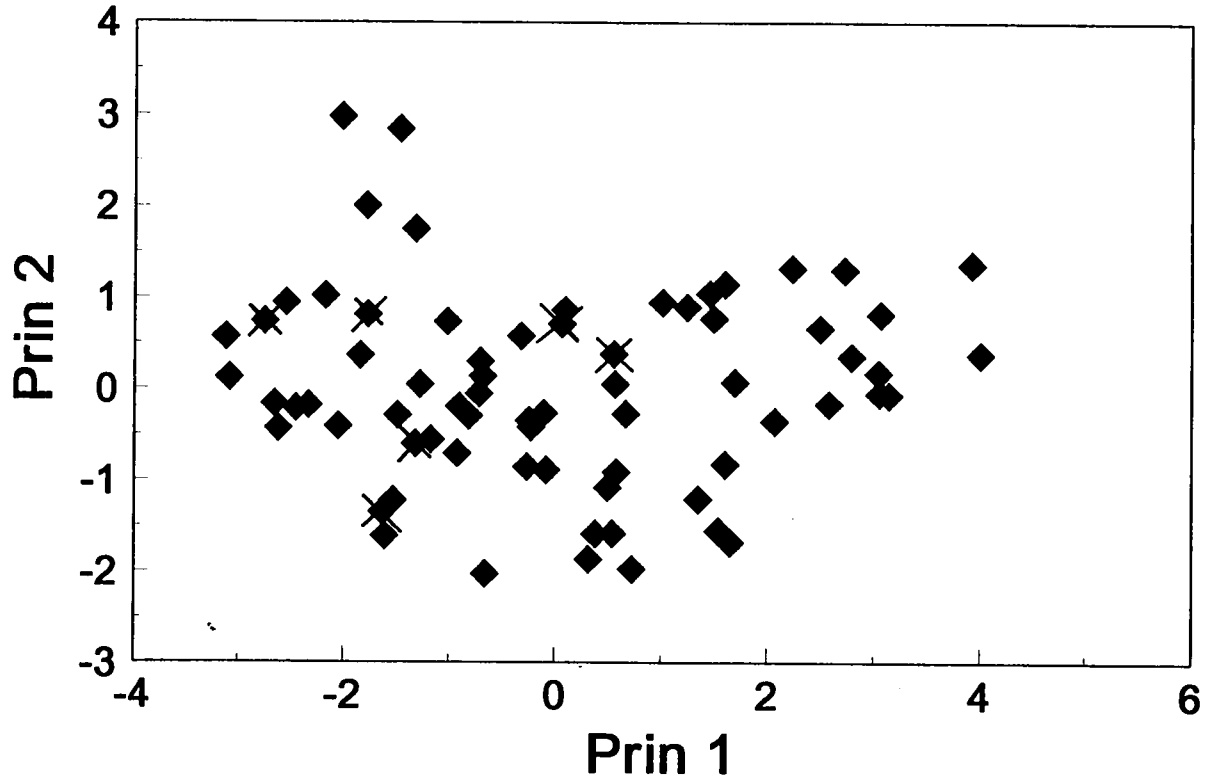


Figure 16. Plot of principal component 2 on principal component 1 from a principal components analysis of thirty-five specimens assignable to *S. trinitense/S. mississippiense* from southern Mississippi and eastern Louisiana. X - indicates paratype stems.

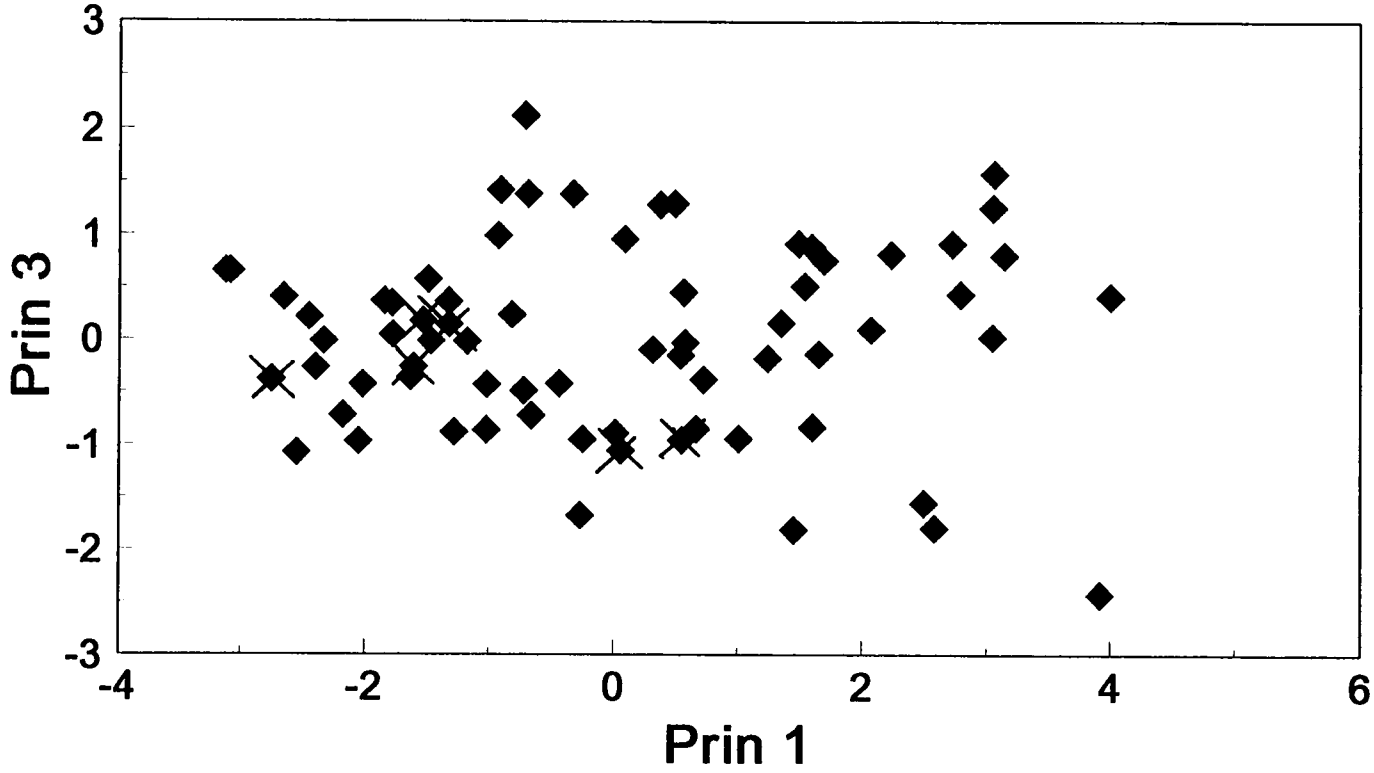


Figure 17. Plot of principal component 3 on principal component 1 from a principal components analysis of thirty-five specimens assignable to *S. trinitense/S. mississippiense* from southern Mississippi and eastern Louisiana. X - indicates paratype stems.

Table 18. Eigenvalues, proportion of variance accounted for by each component, and cumulative variance explained from a principal components analysis of thirty-five specimens assignable to *S. trinitense/S. mississippiense* collected from southern Mississippi and eastern Louisiana.

Principal Component	Eigenvalue	Proportion	Cumulative
PRIN1	3.43227	0.572046	0.57205
PRIN2	1.20202	0.200337	0.77238
PRIN3	0.81849	0.136415	0.90880
PRIN4	0.27354	0.045590	0.95439
PRIN5	0.17374	0.028957	0.98335
PRIN6	0.09993	0.016655	1.00000

Table 19. Eigenvectors for the first three principal components from a principal components analysis of thirty-five specimens assignable to *S. trinitense/S. mississippiense* collected from southern Mississippi and eastern Louisiana.

Character	PRIN1	PRIN2	PRIN3
PRLFLMM	0.374431	-.376894	0.546591
PRLFWMM	0.389308	0.223573	0.612254
MLFLMM	0.451875	-.380801	-.266620
MLFWMM	0.429037	0.463801	-.104857
DLFLMM	0.408533	-.426989	-.395599
DLFWMM	0.391251	0.515292	-.296316

variables had positive weightings on this same axis (Table 19). Thus principal component 2 is a leaf shape axis where specimens with high principal component 2 scores have shorter, broader leaves and specimens with lower principal component 2 scores have longer, narrower leaves. If two leaf shape groups were present among the specimens, then one would expect a gap between groups of points along principal component 2. No such gap is evident along this axis. The plot of principal component 3 on principal component 1 also fails to distinguish two groups. Nor are the six paratype stems clustered in such a way in either Figure 16 or Figure 17 that would indicate the presence of two taxa. Both plots suggest one variable group is present.

Figure 18 again shows the plot of principal component 2 on principal component 1, but in this plot the symbols have been replaced by the proximal branch leaf length to width ratio for each stem. As the eigenvectors in Table 19 indicated, principal component 2 is a leaf shape axis. Specimens with large positive and large negative scores along principal component 2 are obviously quite different for the proximal branch leaf length to width ratio, but they are well-connected by intermediates. In fact, the "intermediates" are not the exception, they are the norm. The plot suggests a continuum of variation for this character.

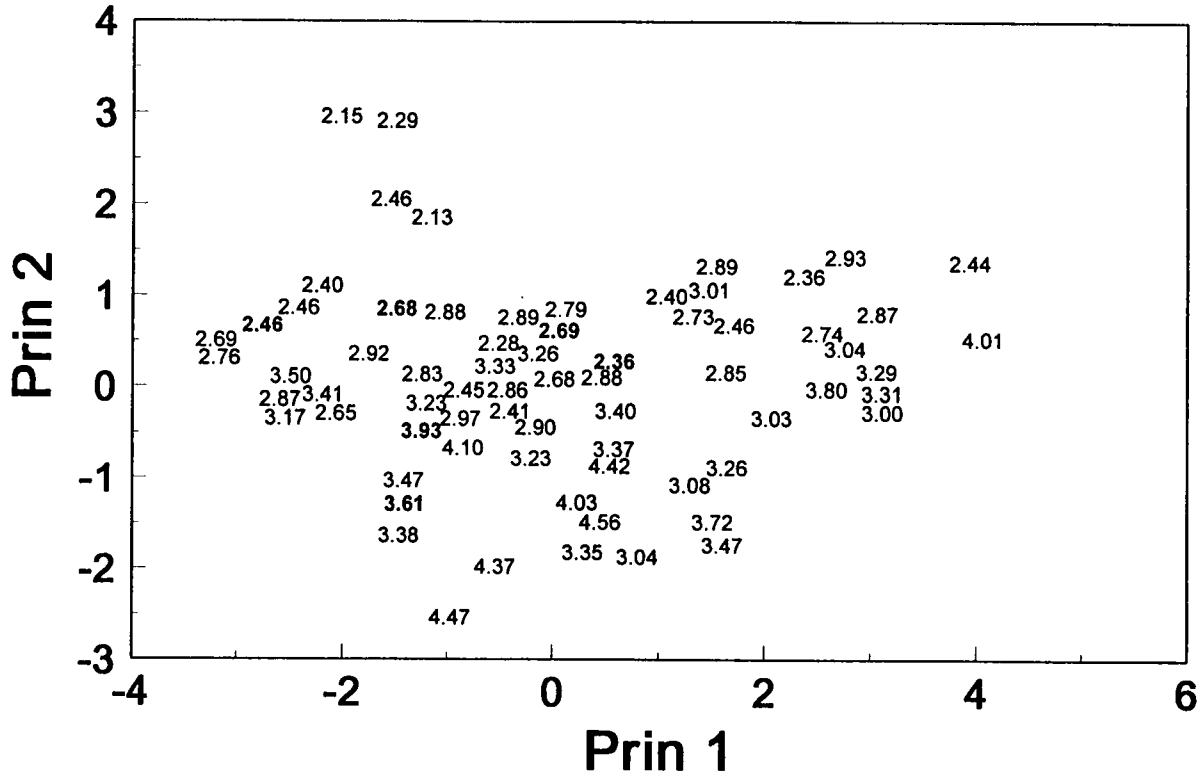


Figure 18. Plot of principal component two on principal component one from a principal components analysis of *S. trinitense/S. mississippiense* from southern Mississippi and eastern Louisiana with the proximal branch leaf length to width ratio values plotted in place of a symbol. The six paratype stems are in bold.

The six paratype stems are restricted to the left two-thirds of the plot, but as the values on Figure 18 indicate, specimens with low ratios are not restricted to this part of the plot. The paratype proximal branch leaf length to width ratios fit well within the continuum of variation exhibited by the specimens.

One additional, more inclusive analysis was conducted to evaluate the number of morphological groups in the *S. trinitense/S. mississippiense* species pair. Bar charts of proximal branch leaf length, width, and length to width ratio were constructed using the *S. trinitense/S. mississippiense* specimens collected from all five of the study areas in the southeastern Coastal Plain. This analysis included 40 specimens. As Figure 19 shows, the distribution patterns are similar to those seen earlier in Figure 15. The proximal branch leaf length distribution is skewed to the right with most leaves ranging from 1.1 to 1.7 mm long. The leaf width distribution has a fairly normal appearance, but is skewed to the right. The length to width ratio distribution is also slightly skewed to the right with most ratios between 2.8 and 4.4 inclusive. None of these distributions are bimodal and none of them suggest the presence of two morphological groups on the basis of proximal branch leaf shape. These bar charts suggest a continuum of variation.

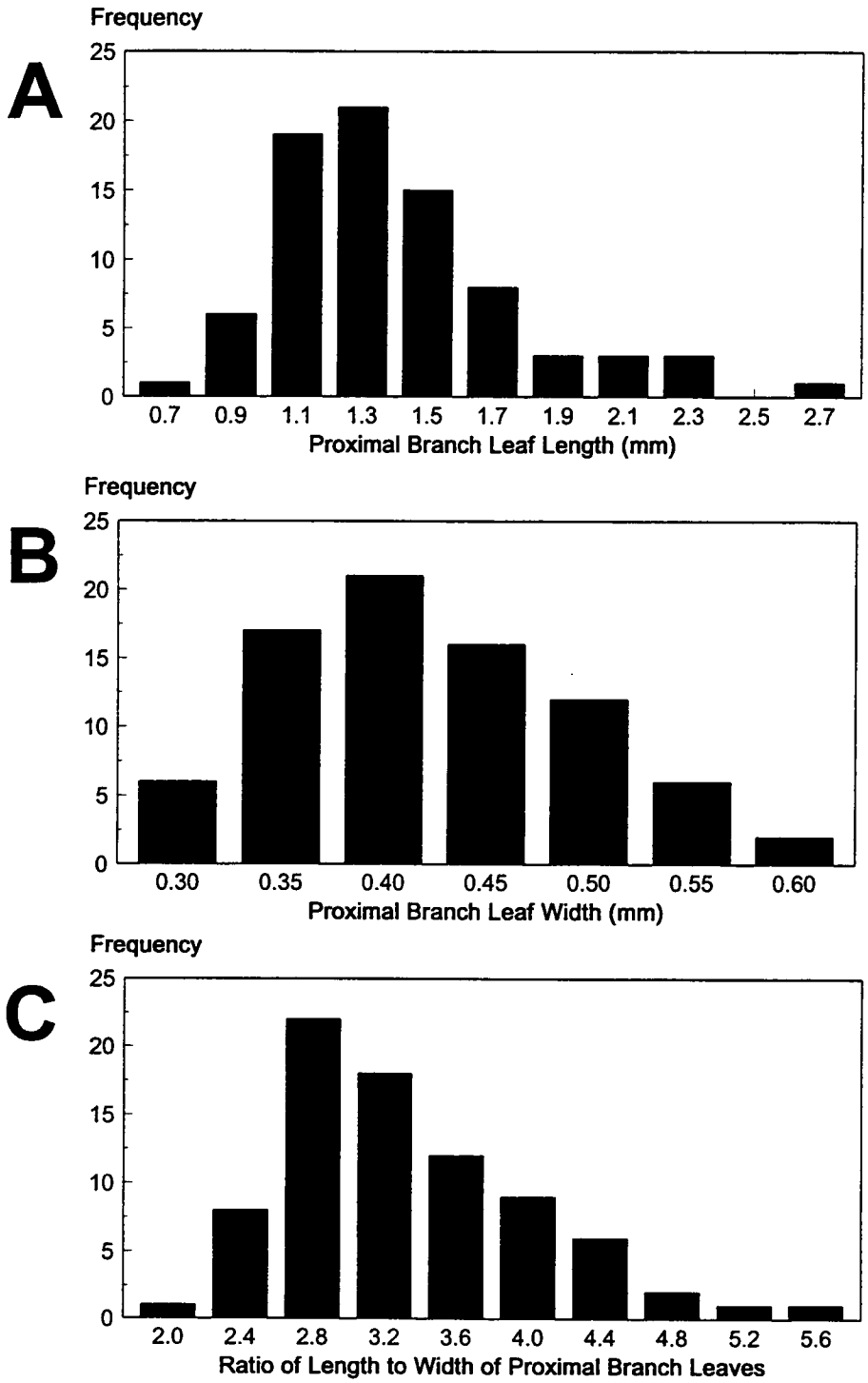


Figure 19. Bar charts of specimens from all five areas designated as belonging to the *S. trinitense/ S. mississippiense* species pair. A. proximal branch leaf length (mm). B. proximal branch leaf width (mm). C. proximal branch leaf length to width ratio.

The *Sphagnum cuspidatum/S. viridum* Species Pair

Methods

Specimens that had been identified as *S. viridum* by either R. E. Andrus or K. I. Flatberg and collected from the southeastern United States Coastal Plain were assembled from specimens on loan from BING, DUKE, FLAS, and LAF. Ten specimens were randomly selected from this pool of collections for morphometric analysis. The same 22 characters were measured on these ten specimens and the same procedures followed as in the larger morphometric study. Patterns of variation exhibited by these ten specimens in relation to patterns exhibited by specimens collected from the five areas were evaluated by principal components analysis and by inspection of frequency distributions of selected characters.

Results

Figures 20 and 21 are principal components analysis plots of all specimens from the five areas plus the ten *S. viridum* specimens. The *S. viridum* specimens are grouped in the most dense portion of the *S. cuspidatum/S. viridum* point scatter on both plots. Thus these specimens indeed appear to be most similar morphologically to those designated earlier as *S. cuspidatum/S. viridum*.

Figure 22 is a principal components analysis plot from an analysis of only the ten *S. viridum* specimens and those

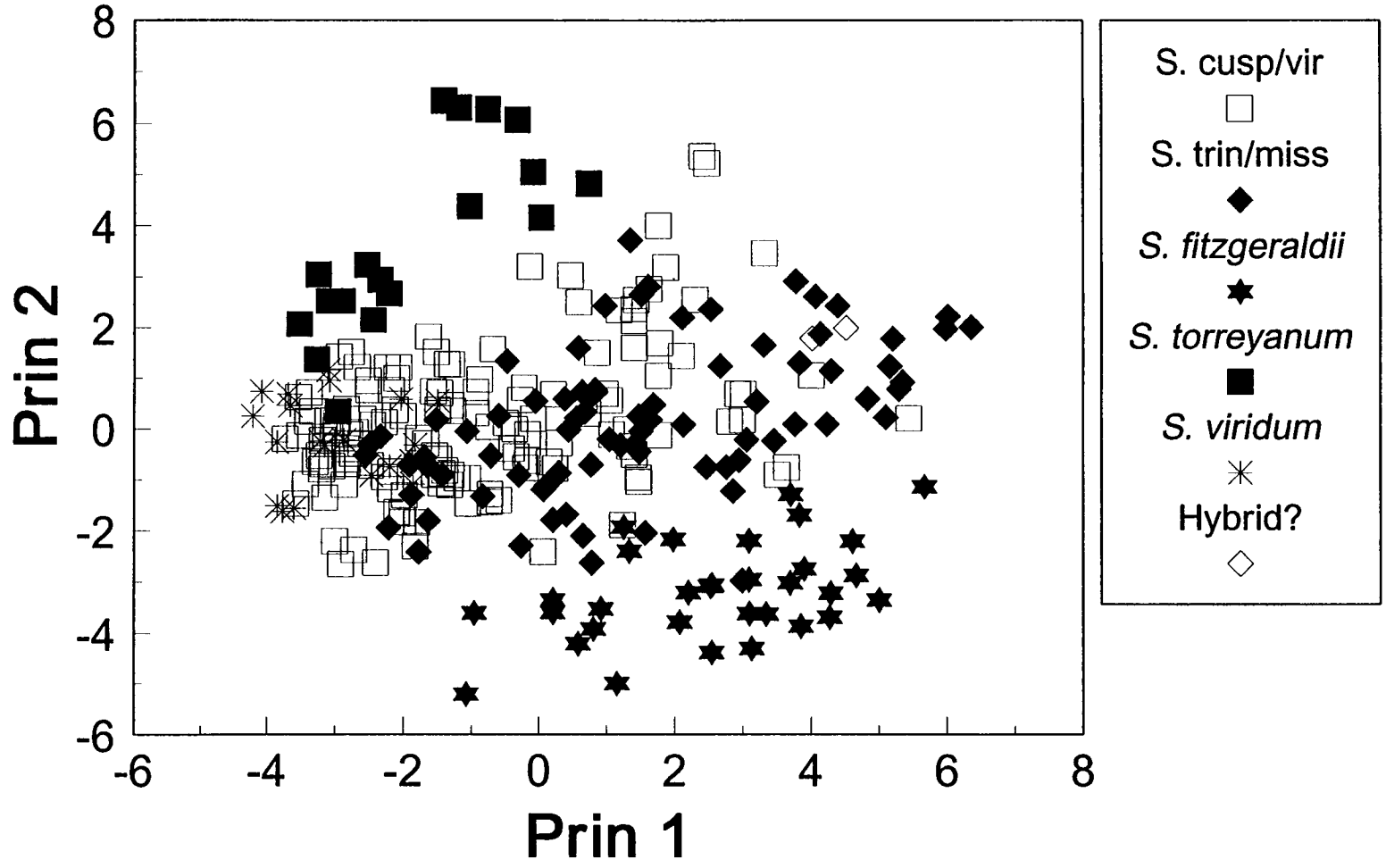


Figure 20. Plot of principal component 2 on principal component 1 from a principal components analysis of specimens collected from all five areas plus the ten *S. viridum* specimens.

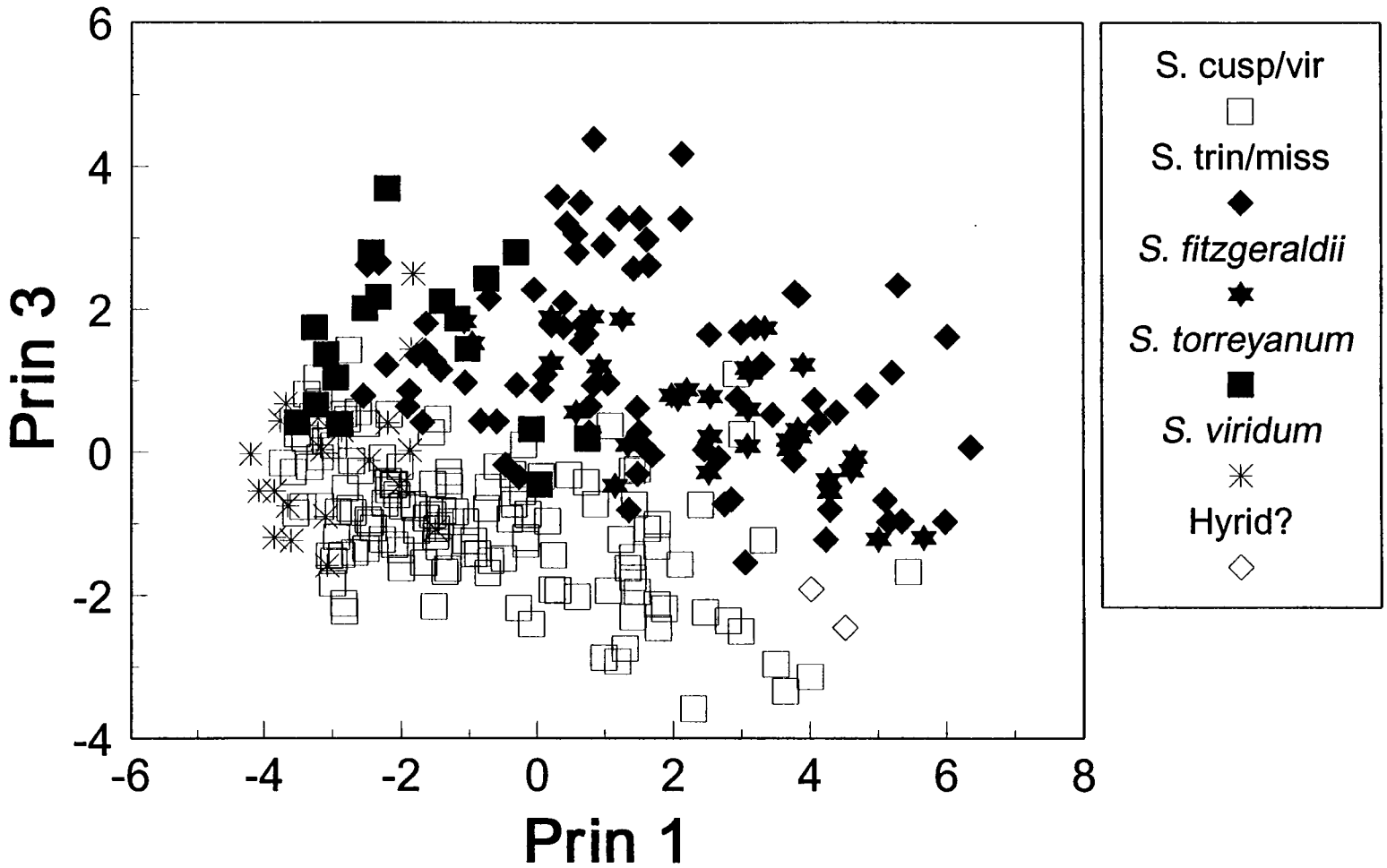


Figure 21. Plot of principal component 3 on principal component 1 from a principal components analysis of specimens collected from all five areas plus the ten *S. viridum* specimens.

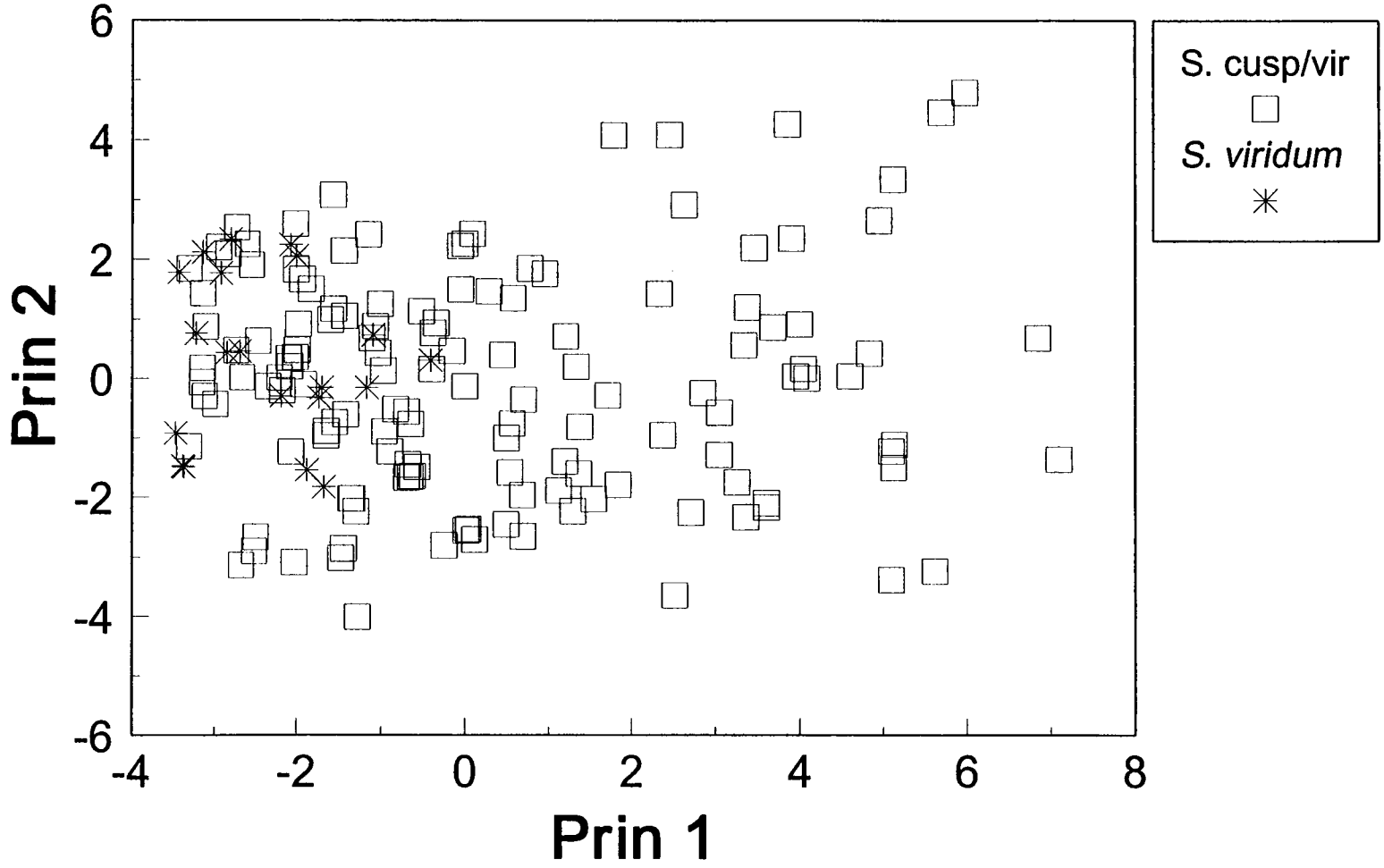


Figure 22. Plot of principal component 2 on principal component 1 from a principal components analysis of *S. cuspidatum/S. viridum* specimens collected from all five areas plus the ten *S. viridum* specimens.

belonging to the *S. cuspidatum/S. viridum* group. As in Figures 20 and 21, the *S. viridum* specimens are conspicuously clustered toward the left end of the plot. Toward the right, from the dense cluster consisting of a mix of *S. viridum* and *S. cuspidatum/S. viridum* specimens, the density of points continually decreases.

Principal component 1 accounted for 31% of the total variation (Table 20). Inspection of Table 21 shows this axis to be most heavily weighted by median and distal branch leaf length and width, median and distal branch leaf proportion of margin not entire and serrulation, hyaline cell length, and chlorophyllose cell length. Thus, principal component 1 is primarily a branch leaf size, branch leaf cell length, and branch leaf margin axis. The low scores of *S. viridum* specimens on principal component 1 suggests that specimens identified as *S. viridum* have relatively shorter leaves with entire or mostly entire margins and shorter leaf cells.

Figure 23 presents four bar charts showing frequency distributions based on measurements of 79 specimens (69 *S. cuspidatum/S. viridum* and 10 *S. viridum*). Except for proximal branch leaf length to width ratio, the characters presented were emphasized by Flatberg (1988) in discriminating *S. viridum* from *S. cuspidatum*. Although the distributions shown in all four of the bar charts are skewed to the right, none of them suggest that two taxa are

Table 20. Eigenvalues, proportion of variance accounted by each component, and cumulative variance explained from a principal components analysis of the *S. cuspidatum/S. viridum* specimens collected from all five areas plus the ten *S. viridum* specimens.

Principal Component	Eigenvalue	Proportion	Cumulative
PRIN1	6.82776	0.310353	0.31035
PRIN2	3.34447	0.152022	0.46237
PRIN3	2.18104	0.099138	0.56151
PRIN4	1.83473	0.083397	0.64491
PRIN5	1.34459	0.061118	0.70603
PRIN6	1.04433	0.047469	0.75350
PRIN7	0.89764	0.040802	0.79430
PRIN8	0.79202	0.036001	0.83030
PRIN9	0.59764	0.027166	0.85746
PRIN10	0.56395	0.025634	0.88310
PRIN11	0.47226	0.021466	0.90456
PRIN12	0.39549	0.017977	0.92254
PRIN13	0.36926	0.016785	0.93933
PRIN14	0.32077	0.014581	0.95391
PRIN15	0.23985	0.010902	0.96481
PRIN16	0.21708	0.009867	0.97468
PRIN17	0.17826	0.008103	0.98278
PRIN18	0.12135	0.005516	0.98830
PRIN19	0.09085	0.004130	0.99242
PRIN20	0.07432	0.003378	0.99580
PRIN21	0.06819	0.003100	0.99890
PRIN22	0.02413	0.001097	1.00000

Table 21. Eigenvectors for the first three principal components from a principal components analysis of *S. cuspidatum/S. viridum* specimens collected from all five areas plus the ten *S. viridum* specimens.

Character	PRIN1	PRIN2	PRIN3
PRLFLMM	0.145736	0.144077	-.183448
PRLFWMM	-.021143	0.259423	-.218486
MEDLFLMM	0.351433	0.045727	-.159051
MEDLFWMM	0.211635	0.179211	-.251353
DISLFLMM	0.333505	-.016396	-.097490
DISLFWMM	0.220246	0.105397	-.152242
PROXD	0.099226	-.167029	0.372418
PROXS	0.062428	-.057356	0.373184
MEDD	0.309250	-.147561	0.179782
MEDS	0.296247	-.070349	0.139577
DISTD	0.293944	-.179515	0.086297
DISTS	0.328802	-.107251	0.114071
HYALLUM	0.327283	0.028761	-.210480
HYALWUM	-.112720	0.076728	-.304125
CHLLUM	0.325594	0.053792	-.129049
STLFLMM	0.121666	0.176586	-.020133
STLFWMM	-.062112	0.341485	-.091902
HYDM1UM	0.027821	0.399338	0.176737
HYDM2UM	0.006393	0.447017	0.165725
HYDM3UM	0.068004	0.342521	0.311578
HYDM4UM	0.089434	0.360653	0.313450
SEPTA	-.026475	0.025031	0.175778

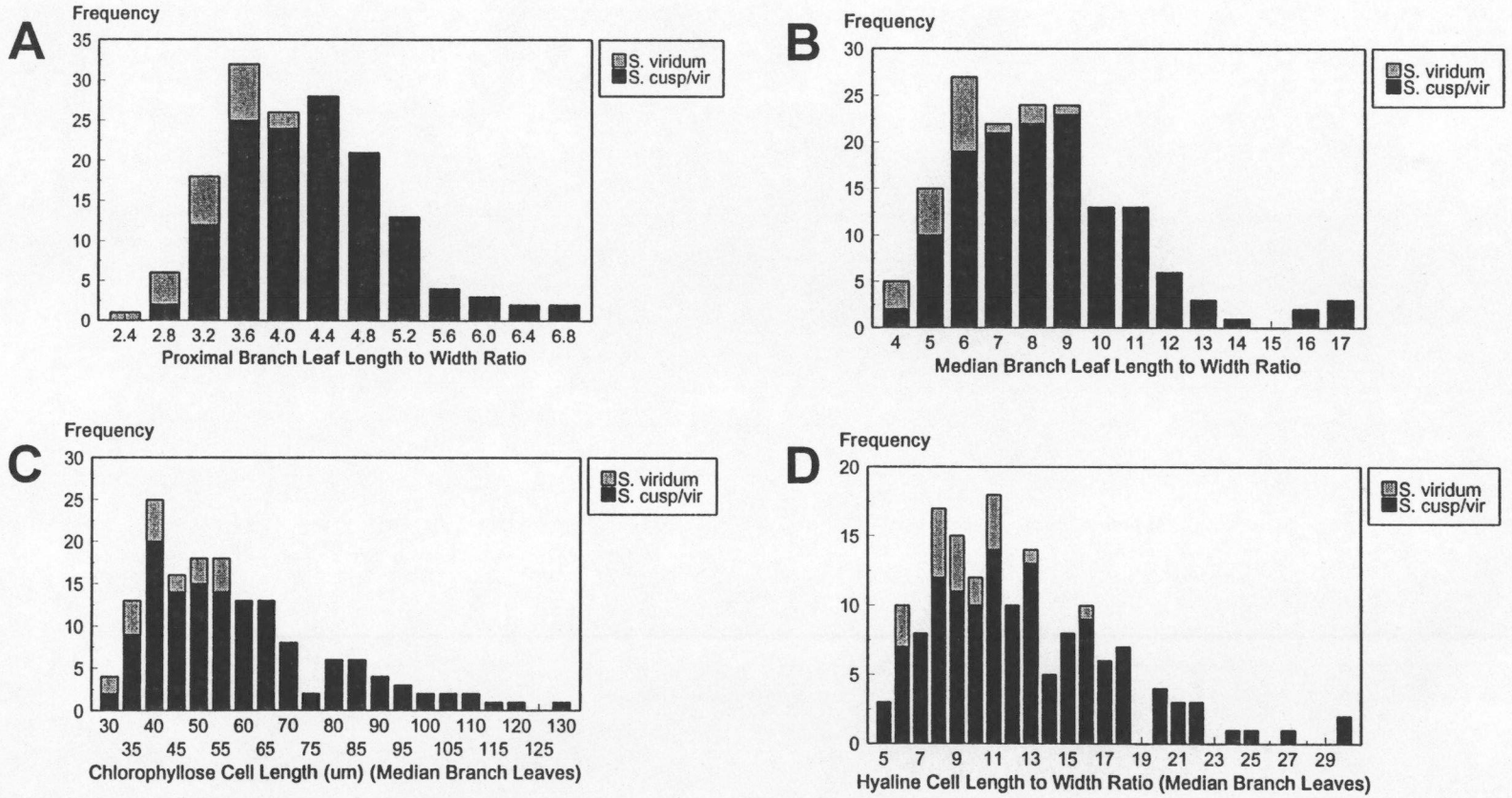


Figure 23. Bar charts of specimens designated as *S. cuspidatum/S. viridum* collected from all five areas plus the ten *S. viridum* specimens. A. proximal branch leaf length to width ratio. B. Median branch leaf length to width ratio. C. Chlorophyllose cell length (median branch leaves). D. Hyaline cell length to width ratio (median branch leaves).

present. The distributions show that the specimens designated as *S. viridum* are, however, confined to the lower half of the range of variation for each of the four characters. These bar charts, interpreted in conjunction with the principal components analysis plots of Figures 20, 21, and 22 suggest the *S. cuspidatum/S. viridum* and *S. viridum* specimens belong to one variable taxon.

Univariate Comparisons of Groups

Methods

Since the multivariate analyses supported the recognition of the morphological groups designated by inspection under a dissecting microscope, the four larger groups were then compared on a character by character basis. Group 5, consisting solely of the Hybrid? specimen, was not included in these comparisons.

Both parametric and nonparametric statistical methods for comparing group means assume homogeneity of variances. Parametric methods also assume the data are normally distributed for each variable within groups. Homogeneity of variances was evaluated by the F_{max}-test (Sokal and Rohlf 1969a). This test compares the ratio of the largest group variance to the smallest group variance with the maximum F-ratio distribution. The variance ratio was compared with the 0.05 critical value for four groups and fifteen degrees of freedom (Table T in Sokal and Rohlf 1969b). Nine

characters failed this test: all six branch leaf margin characters, stem leaf width, number of septate cells in viewing field, and diameter of 5 cells in stem layer three.

The other thirteen characters were evaluated for normality using the NORMAL option of PROC UNIVARIATE in SAS. This procedure indicated that none of these remaining characters were normally distributed for all groups. Even though normal-based tests for equality of means are considered robust with respect to the assumption of normality, it was decided to employ a nonparametric approach. The data for each of the remaining thirteen variables were ranked and then the groups compared by a one-way analysis of variance. Tukey's studentized range test was used to compare the group means. The test criterion was $P \leq 0.05$.

Results

The analyses indicated that there were statistically significant differences between groups for all thirteen characters compared except for hyaline cell leaf length. Statistically significant differences were found among all groups only for median branch leaf width (Table 22).

The *Sphagnum cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* groups were significantly different for proximal branch leaf length, all three branch leaf width variables, hyaline cell width, chlorophyllose cell length,

Table 22. Means and standard deviations for each character by group. The groups are (1) *S. cuspidatum/S. viridum*, (2) *S. trinitense/S. mississippiense*, (3) *S. fitzgeraldii*, and (4) *S. torreyanum*. Statistically significant differences between group means from a one-way analysis of variance on on each character are indicated by letter superscripts ($P \leq 0.05$). Tukey's studentized range test was used to compare the means. An analysis of variance was not carried out on the six branch leaf margin characters, stem leaf width, number of septate cells in viewing field, and diameter of 5 cells in stem layer three due to unequal variances across groups for these variables.

	Group			
Character	1 (n=138)	2 (n=80)	3 (n=32)	4 (n=18)
proximal branch leaf length (mm)	1.54 (0.30)[a]	1.40 (0.38)[b]	1.34 (0.27)[b]	1.56 (0.49)[a]
proxmial branch leaf width (mm)	0.36 (0.05)[a]	0.42 (0.07)[b,c]	0.38 (0.04)[c]	0.44 (0.08)[b]
median branch leaf length (mm)	2.94 (1.15)[a]	3.18 (1.40)[a]	2.29 (0.69)[b]	3.25 (1.15)[a]
median branch leaf width (mm)	0.34 (0.07)[a]	0.44 (0.10)[b]	0.38 (0.07)[c]	0.53 (0.11)[d]
distal branch leaf length (mm)	3.47 (1.35)[a]	3.47 (1.26)[a]	2.55 (0.82)[b]	3.64 (1.62)[a,b]
distal branch leaf width (mm)	0.29 (0.08)[a]	0.36 (0.08)[b]	0.31 (0.06)[a]	0.48 (0.13)[c]
prop. of margin not entire (pr. br. lvs.)	1.35 (2.14)	5.01 (2.95)	8.66 (1.21)	0.01 (0.04)
proximal branch leaf serrulation	0.02 (0.14)	0.44 (1.07)	1.77 (1.65)	0
prop. of margin not entire (med. br. lvs.)	3.99 (2.79)	7.90 (2.36)	9.52 (0.61)	0.12 (0.40)
median branch leaf serrulation	0.85 (1.62)	3.27 (3.46)	5.86 (2.70)	0
prop.of margin not entire (dist. br. lvs.)	6.07 (2.83)	8.57 (1.71)	9.69 (0.37)	0.18 (0.24)
distal branch leaf serrulation	2.06 (2.43)	4.09 (3.20)	6.71 (2.45)	0
hyaline cell length (μm)	156.79 (48.46)[a]	168.68 (38.36)[a]	176.79 (49.31)[a]	161.76 (50.23)[a]
hyaline cell width (μm)	12.76 (2.85)[a]	15.43 (3.88)[b]	15.72 (2.41)[b]	13.03 (3.00)[a]
chlorophyllose cell length (μm)	60.68 (21.64)[a]	72.01 (22.66)[b]	64.18 (17.03)[a,b]	57.11 (20.54)[a]
stem leaf length (mm)	1.30 (0.21)[a,c]	1.38 (0.24)[a,b]	1.44 (0.23)[b]	1.16 (0.17)[c]
stem leaf width (mm)	0.75 (0.10)	0.70 (0.10)	0.40 (0.05)	1.08 (0.13)
number of septate cells in viewing field	10.40 (5.45)	12.54 (4.05)	10.35 (4.90)	1.57 (1.43)
diameter of 5 cells in stem layer one (μm)	152.40 (20.70)[a]	130.30 (18.29)[b]	146.85 (23.00)[a]	124.89 (14.99)[b]
diameter of 5 cells in stem layer two (μm)	151.45 (21.79)[a]	136.31 (21.35)[b]	120.03 (25.24)[c]	154.00 (24.99)[a]
diameter of 5 cells in stem layer three (μm)	86.38 (20.52)	97.52 (17.23)	65.35 (8.40)	108.71 (21.83)
diameter of 5 cells in stem layer four (μm)	77.33 (12.60)[a]	90.92 (13.74)[b]	63.28 (11.31)[c]	93.42 (10.28)[b]

and three of the four diameter of stem cell layer characters (Table 22).

The means and standard deviations for the branch leaf margin characters suggest that the leaf margin features of proximal and median leaves more effectively separate *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* than do those of the distal leaves. It is quite apparent also that the branch leaves of *S. cuspidatum/S. viridum* are not consistently entire, as indicated by various authorities (Table 22).

The data presented in Table 23 indicate that the *S. trinitense/S. mississippiense* group has slightly lower length to width ratios for branch leaves from all three positions and more narrowly shaped stem leaves as compared with the *S. cuspidatum/S. viridum* group. The ratio of the sum of the diameters of the outer two stem cell layers to the sum of stem cell layers three and four is substantially different between these two groups as well.

As Figures 24 and 25 indicate, plots of proportion of margin not entire of proximal branch leaves on proximal branch leaf length to width ratio and the former character on ratio of stem cell layer diameter can yield effective separations of the *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* groups. Though there is some scatter, the great majority of *S. cuspidatum/S. viridum* stems plot separately from the body of the *S. trinitense/S.*

Table 23. Means and standard deviations for six character ratios for groups 1 - 4. The groups are (1) *S. cuspidatum/S. viridum*, (2) *S. trinitense/S. mississippiense*, (3) *S. fitzgeraldii*, and (4) *S. torreyanum*.

	Group			
Character	**1 (n=138)**	**2 (n=80)**	**3 (n=32)**	**4 (n=18)**
proximal branch leaf length to width ratio	4.35 (0.84)	3.31 (0.70)	3.49 (0.53)	3.52 (0.80)
median branch leaf length to width ratio	8.66 (2.69)	7.14 (2.36)	6.18 (2.03)	6.15 (1.87)
distal branch leaf length to width ratio	11.89 (3.41)	9.85 (3.23)	8.60 (3.62)	7.60 (2.61)
hyaline cell length to width ratio	12.98 (5.21)	11.77 (4.54)	11.69 (4.51)	12.93 (4.88)
stem leaf length to width ratio	1.77 (0.41)	1.99 (0.34)	3.64 (0.79)	1.08 (0.12)
(stem cell layer 1 + stem cell layer 2)/(stem cell layer 3 + stem cell layer 4)	1.89 (0.25)	1.43 (0.21)	2.09 (0.31)	1.39 (0.19)

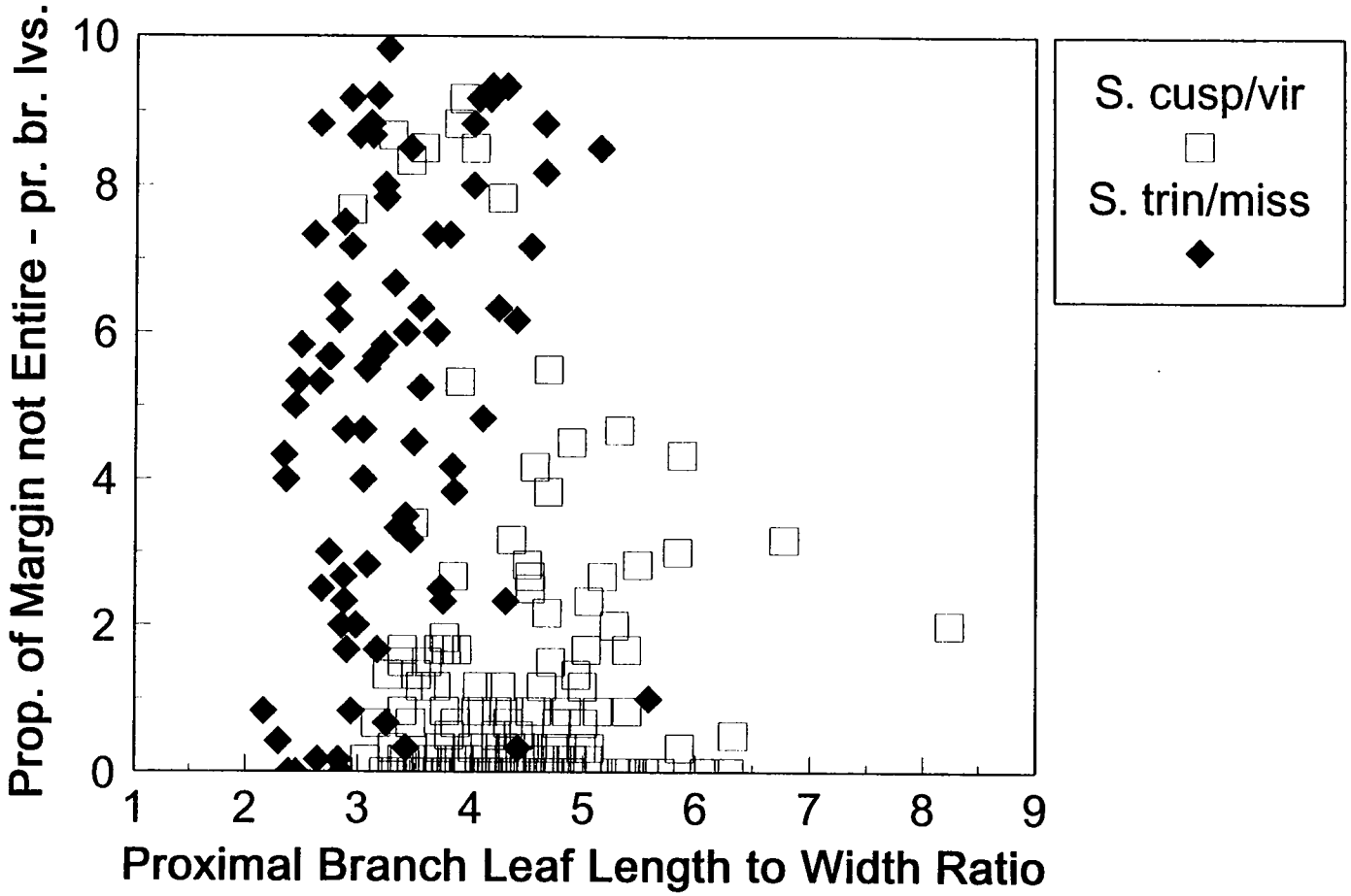


Figure 24. Plot of proportion of margin not entire - proximal branch leaves on proximal branch leaf length to width ratio for *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense*. There are approximately 100 stems of *S. cuspidatum/S.viridum* plotted in the sample dense region between 3 and 6 on the horizontal axis with a score of less than 2 on the y-axis.

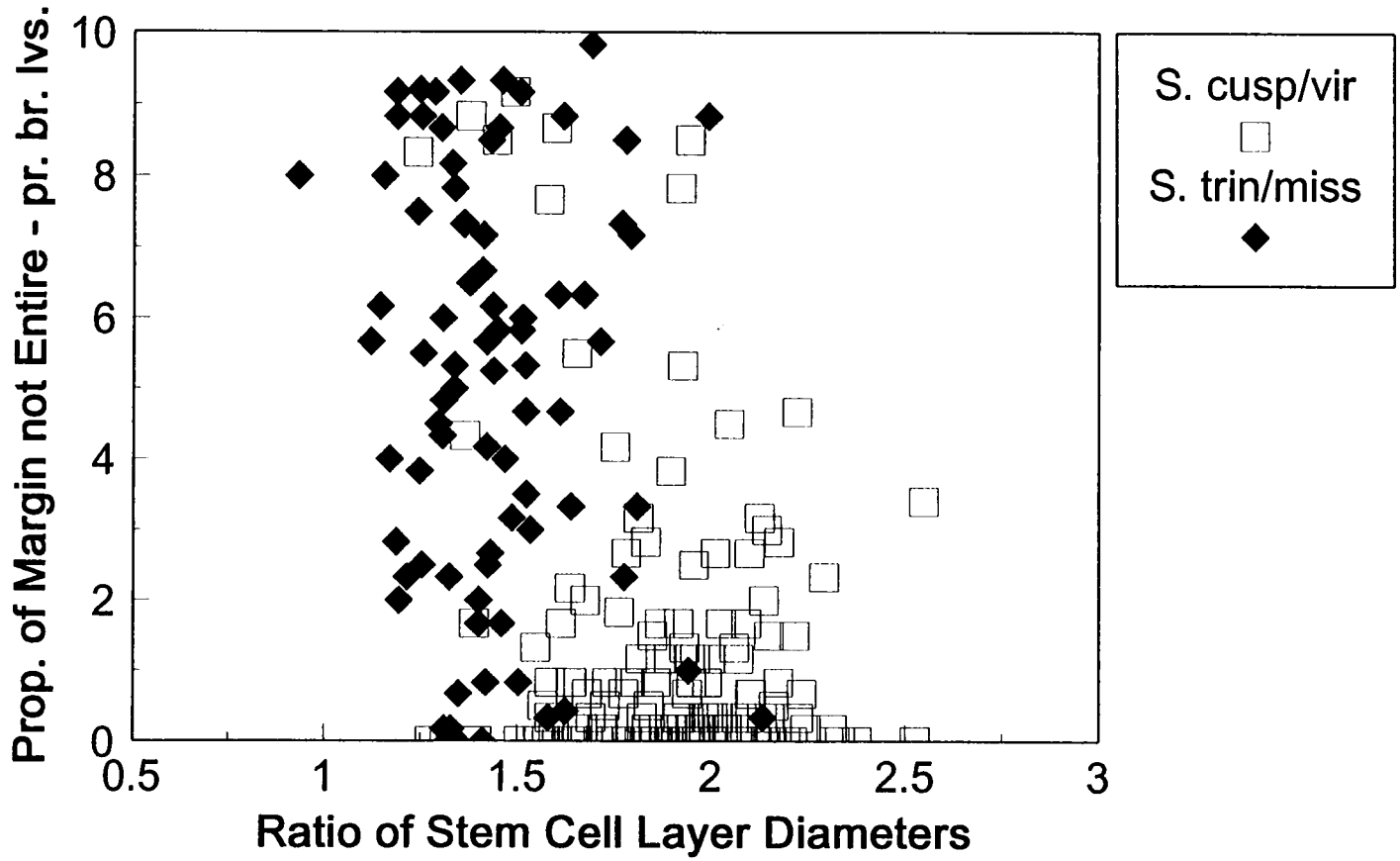


Figure 25. Plot of proportion of margin not entire - proximal branch leaves on ratio of stem cell layer diameters for *S. cuspidatum/S. viridum* and *S. trinitense/ S. mississippiense*. There are approximately 100 stems of *S. cuspidatum/S. viridum* plotted in the sample dense region between 1.5 and 2.5 on the horizontal axis with a score of less than 2 on the vertical axis.

mississippiense point spread. The variation patterns exhibited on the plots by the two groups are quite different as well. *Sphagnum cuspidatum/S. viridum* is highly concentrated in a small region on or near the horizontal axis in both plots with a small proportion of samples scattered upward. In contrast, *S. trinitense/S. mississippiense* is fairly evenly distributed along the vertical axis in both plots. The plots also indicate, as did the multivariate analyses, that a small number of specimens may have been initially misclassified.

The *Sphagnum torreyanum* specimens were significantly different from the three other groups for median and distal branch leaf width (Table 22). Though not statistically compared, the *S. torreyanum* specimen group also had the broadest stem leaves and the lowest number of septate cells in the viewing field. The margins of branch leaves from all three positions were consistently entire in this group, in contrast to the other groups, including *S. cuspidatum/S. viridum*. The *S. torreyanum* specimens were also distinctive in that the diameter of cells in the outer stem layer is conspicuously less than the diameter of cells in stem layer two (Table 22). The latter feature was observed to be quite consistent. Table 23 indicates that the stem leaf length to width ratio may be diagnostic for the *S. torreyanum* group as well.

Table 22 indicates that the *S. fitzgeraldii* specimens were significantly different from each of the other groups for the diameters of cells in stem layers two and four. Proportion of margin not entire and serrulation scores for branch leaves from all three positions were higher for *S. fitzgeraldii* than any other group. The stem leaves in the *S. fitzgeraldii* specimen group were also much narrower than in any other group.

Two ratios, stem leaf length to width and the diameter of the stem cell layers, appear to be useful in distinguishing *S. fitzgeraldii* as well (Table 23).

Discussion and Conclusions

The recognition of the four morphological groups corresponding to *S. cuspidatum/S. viridum*, *S. trinitense/S. mississippiense*, *S. fitzgeraldii*, and *S. torreyanum* that were sorted by inspection under a dissecting microscope was supported by the multivariate and univariate analyses. The specimens included in the analyses were collected from a variety of habitat conditions from a broad geographical range in the Coastal Plain. Thus, considering the morphological plasticity exhibited by *Sphagnum*, these groups appear to be quite distinct.

Sphagnum torreyanum and *S. fitzgeraldii*

Two of the four groups corresponded to *S. torreyanum* and *S. fitzgeraldii*. Even though the morphological characters that were measured were not biased to achieve a separation of these two groups, specimens assigned to groups 3 and 4 (corresponding to *S. fitzgeraldii* and *S. torreyanum*, respectively) formed coherent and discrete groups in the various analyses. The designation of these two taxa as full species seems well-justified.

Sphagnum cuspidatum/S. viridum and *S. trinitense/S. mississippiense*

Lane (1981) and Anderson et al. (1992) expressed doubts concerning the specific distinctness of *S. cuspidatum* and *S. trinitense*. The results presented herein, however, clearly support the recognition of two groups that correspond to *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense*.

The univariate analysis indicated there were significant differences between these two groups for nine of the thirteen characters compared. Inspection of Table 22 reveals that for most of these nine characters the differences between the means are too small to be taxonomically useful. The standard deviations for these characters also indicate that their distributions overlap somewhat as well. Thus no single character was found that can cleanly separate these two groups of specimens.

Although the means for the six branch leaf length and width variables were only slightly different for *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense*, these variables were important in discriminating these two groups in a principal components analysis (see the eigenvector for principal component 3 in Table 16). Also, the data in Table 23 indicate that branch leaf length to width ratios may be more useful in diagnosing these groups than single leaf dimension characters.

Leaf margin features should be de-emphasized as a character for separating these two groups or combined with other characters as mentioned by Andrus (1974, 1980). Data shown in Table 22 suggest that the margins of proximal branch leaves should be inspected if one desires to use entire versus denticulate/serrulate branch leaves in a key to separate these two groups. The proximal branch leaves of *S. cuspidatum/S. viridum* are usually entire or have denticulations restricted to the distal one-fifth, whereas in *S. trinitense/S. mississippiense* denticulations are generally present and extend down to the lower half of the leaf margin. Thus the proximal branch leaves should be examined for proportion of margin not entire when attempting to assign specimens to one or the other of these two groups. The results of this study suggest that this character, used in conjunction with proximal branch leaf shape and the ratio

of stem cell layer diameters, provides for an effective separation.

Sphagnum cuspidatum and *S. viridum*

Only one variable taxon was indicated by the results for the specimens examined from this group. The frequency distributions for the four characters presented in Table 23 demonstrate continuous variation as one would expect from a single taxon when specimens are sampled across a large number of natural populations.

Plots presented by Flatberg (1988) and comments in Andrus et al. (1994) indicate that unless one compares specimens of *S. cuspidatum* and *S. viridum* from equivalent habitats, they can not be morphometrically distinguished. If this is correct, it is unlikely that such morphologically similar species would be sorted by the methods employed in this study. Furthermore, it becomes an arbitrary exercise to sort and name herbarium specimens as either *S. cuspidatum* or *S. viridum* if one does not know the exact habitat conditions under which the plants grew and developed.

Daniels (1993) criticized the recognition of species when taxonomic characters are measured and plotted for a number of populations of each "species," groups are not separated or there is extensive overlap among the constituent populations. I find myself in agreement with Daniels.

Several characters mentioned by Flatberg (1988) as useful in discriminating *S. viridum* from *S. cuspidatum* were not evaluated in this study. These are color, orientation of branches relative to the stem, proportion of branch leaf length that is involute, branch leaf chlorophyllose cell size in cross section, and hyalocyst shape in stem leaves. Future studies could include an examination of these features in regard to this species pair.

Flatberg (1988) also indicated that both *S. viridum* and *S. cuspidatum* are sexually dimorphic. Thus in attempting to separate them one should compare males with males and females with females. This is an important consideration to the present study because the sex of many of the stems were not determinable and thus the analyses were not partitioned by sex of the plant.

Study of *S. viridum* using specimens identified as this taxon from the southeastern United States Coastal Plain, does not support recognizing this species as morphologically distinct from *S. cuspidatum* in the study area. *Sphagnum viridum* and *S. cuspidatum* are both wide ranging species. Further study is certainly needed to resolve this taxonomic issue in a broader geographic context.

Sphagnum trinitense and *S. mississippiense*

No morphological basis was found in this study for recognizing two taxa within this specimen group. A

continuum of variation, typical of a single species, was observed in the frequency distributions for all characters examined.

Several attempts to sort this specimen group by appearance under a dissecting microscope into smaller groups on the basis of branch and branch leaf characteristics proved unsatisfactory. Owing to the continuous variation, it was impossible to distinguish two subsets of specimens that might correspond to *S. trinitense* and *S. mississippiense*. Furthermore, within a given site, all specimens tended to be relatively uniform in appearance.

Seasonal Morphology Study

The objective of this study was to obtain quantitative data on variation along both seasonal and wetness gradients for nineteen morphological characters of *S. cuspidatum*. *Sphagnum cuspidatum* was chosen for the study because (1) the species frequently grows in extensive stands in pool complexes associated with pocosins and swamps and (2) it has a notoriously variable morphology depending on site conditions (Schliephacke 1865, Röll 1888, Paul 1932, Agnew 1958, Rice and Schuepp 1995). Paul (1932) even suggested that the highly variable morphology of *S. cuspidatum* could be used as a "character" to distinguish it from other, less variable, aquatic taxa.

The impetus for the study was to test the stability of characters traditionally used by various authorities to distinguish *S. cuspidatum* from *S. trinitense*. Plants of *S. cuspidatum* that have developed on wet-moist peat typically produce branch leaves with entire to mostly entire margins whereas plants that have developed in standing water frequently exhibit denticulate to serrulate margins (field observations). Since branch leaf margin features have been emphasized in separating *S. cuspidatum* (entire) and *S. trinitense* (serrulate), it has been one goal of this study to understand natural variation in these and other features of presumed and potential taxonomic utility. Thus, my primary interest in the study was not to determine the cause or causes of the observed phenotypic variation or even to

correlate the variation with various environmental parameters. Rather, it was to demonstrate that substantial morphological variation may indeed occur within a given population of *S. cuspidatum* along temporal and spatial gradients.

Methods

Five sites in the Francis Marion National Forest with an abundance of material assignable to *S. cuspidatum* on the basis of characters emphasized by Andrus (1974, 1980) and Crum (1984) were selected. These sites were: (1) Awendaw Quad, large opening in a pocosin about 2.0 km (air distance) southeast of Thompson Corner at 33°6'40"N-79°34'10"W, (2) Ocean Bay Quad, savanna-pocosin ecotone 100 m west of the junction of Forest Service Roads 174 and 176 at 33°4'45"N-79°42'12"W, (3) Ocean Bay Quad, *Acer rubrum - Magnolia virginiana* swamp near the Wambaw Swamp Wilderness boundary, about 30 m east of Forest Service Road 5099 at 33°4'40"N-79°38'10"W, (4) Ocean Bay Quad, pocosin about 300 m west of Forest Service Road 224 at 33°3'45"N-79°39'13"W, and (5) Ocean Bay Quad, pocosin/bay in the northwest end of Halfway Creek Road Carolina Bay at 33°2'11"N-79°43'0"W.

At each site, a pool area supporting extensive stands of *S. cuspidatum* was selected and three quadrat (0.25 m^2) locations were permanently marked with wooden stakes. Quadrat 1 was located at the pool/depression margin, quadrat

2 was located in an area of intermediate pool/depression depth, and quadrat 3 was located in the deepest nearby part of the pool/depression area. *Sphagnum cuspidatum* covered all or nearly all of each quadrat at each site. The seasonal pools in these habitats were generally extensive and shallow, with an average elevation difference of 11.4 cm (min.=5.0 cm, max.=25.0 cm) for the pool bottoms of quadrats 1 and 3 for the five sites.

Since stems were being sampled along a spatial gradient at each site, the possibility of plant movement was an important consideration to the study. The high density of *S. cuspidatum* at each site, however, precluded plants from randomly floating around.

Five stems were randomly selected from each quadrat at each site four times from October 1994 to July 1995 at roughly three month intervals. The sampling dates were 20 - 21 October 1994, 3 January 1995, 7 - 8 April 1995, and 27 July 1995.

The following nineteen characters were measured on each stem: proximal branch leaf length, proximal branch leaf width, median branch leaf length, median branch leaf width, distal branch leaf length, distal branch leaf width, proportion of proximal branch leaf margin not entire, proximal branch leaf serrulation, proportion of median branch leaf margin not entire, median branch leaf serrulation, proportion of distal branch leaf margin not

entire, distal branch leaf serrulation, stem leaf length, stem leaf width, number of septate cells in viewing field (stem leaves), and diameter of five cells in a row in each of stem layers one through four.

Sample sizes for each character and sampling procedures were identical for each of these characters as described earlier in the morphometric study of specimens from the CNF, SH, FMNF, ANF, and DNF. Juvenile stems, male plants with perigonial leaves in the region to be sampled, and obviously damaged stems were not eligible for measurement and analysis.

In order to estimate plant growth between site visits, small plastic clasps were placed 2 cm below the stem apex on each of twenty stems in a marked (wooden stake) area **adjacent** to the quadrats at each site. The clasps were tightened to the point such that the plants held the plastic markers securely between branch fascicles, but were not so tight that the stems were pinched. After marking, depending on site conditions, the stems were refloated in the pool or laid on the moist substrate followed by substantial rewetting in order to re-establish capillary contact. During the January, April, and July site visits these marked stems were collected, the portion of each stem above the plastic clasp cut, and a new set of stems marked with clasps. Stem elongation was measured in the laboratory to the nearest 0.1 cm.

Inspection of standard deviations indicated the six branch leaf margin characters had unequal variances from both a month and quadrat standpoint within each site. Variation in the means of these characters and that of several character ratios are presented in a series of three dimensional plots. The variances for the other 13 characters appeared to be more or less equivalent. The sample size of five stems on a month by quadrat basis was too small to conduct a normality test, but results from the larger morphometric study indicated that the data for each of these characters were probably not normally distributed. Thus, for each site, the data were ranked for each variable and a two-way analysis of variance, including the interaction term, was performed on the ranks with month and quadrat specified as the main effects in the model. The null hypothesis tested was that neither month nor quadrat nor their interaction had a significant effect on the morphological characters measured at any of the sites.

Results

Averaged over all sites, the mean increases in stem length shown by the marked stems adjacent to the quadrats from October to January, January to April, and April to July, respectively, were 6.1 cm, 3.5 cm, and 1.8 cm, for a total of 11.4 cm of stem elongation over a nine month period. Thus, it is very likely that different cohorts of

branches and stem portions on plants taken from the quadrats were being used for measurements at each sampling period.

A total of 83 (out of 195 possible) main effects and interactions were significant (Tables 24 and 25). Most of these were due to main effects (month and quadrat). Only seven interactions (month by quadrat) were significant. Seven significant interactions (out of 65) is only slightly more than would be expected by chance alone.

There was a significant month effect for distal branch leaf length at all five sites. Both median branch leaf length and width showed a significant month effect at four of the sites. Proximal branch leaf length, distal branch leaf length and width, stem leaf width, and the diameter of cells in stem layer three showed a significant quadrat effect at four of the five sites (Tables 24 and 25). Thus five of the six branch leaf size characters showed significant spatial (quadrat - wetness gradient) or temporal (month) variation at most of the sites.

A high degree of variability was also indicated for branch leaf margin features (Figures 26 - 35). These figures illustrate that the populations of *S. cuspidatum* vary among sites with regard to degree of entire to serrulate branch leaf margins and also that *S. cuspidatum* does not have consistently entire branch leaves. However, the proportion of margin not entire and serrulation scores for proximal branch leaves were considerably lower and less

Table 24. Analysis of variance table for thirteen morphological characters on stems from the Thompson Corner Pocosin, 174, and 5099 sites. The model tested significance of variation among both months and quadrats and the interaction between these two main effects. SS=sum of squares, F=variance ratio used to assess significance of parameters in the model. df for mth=3, df for Qd=2, df for MthXQd=6, df for Error=48. *=P≤0.05, **=P≤0.01, ***=P≤0.001.

	Thompson Corner Pocosin		174		5099	
Character	SS	F	SS	F	SS	F
proximal branch leaf length (mm)						
Mth	3981.97	5.97**	4397.40	8.68***	968.83	1.25
Qd	1634.48	3.68*	4226.70	12.52***	2644.28	5.12**
MthXQd	1699.56	1.27	1248.60	1.23	1957.99	1.26
Error	10665.50		8103.80		12405.40	
Proximal branch leaf width (mm)						
Mth	1384.23	2.09	1904.63	4.44**	2139.10	2.48
Qd	4153.90	9.42***	7257.10	25.36***	1084.90	1.89
MthXQd	1818.97	1.37	1897.07	2.21	906.10	0.53
Error	10583.40		6868.20		13791.40	
median branch leaf length (mm)						
Mth	9224.70	34.71***	5549.90	27.48***	228.57	0.54
Qd	3387.10	19.12***	7147.68	53.08***	8724.90	30.89***
MthXQd	1130.10	2.13	2062.03	5.10***	2260.63	2.67*
Error	4252.10		3231.90		6777.90	
median branch leaf width (mm)						
Mth	10073.57	33.60***	314.70	0.89	3180.43	6.29**
Qd	2496.48	12.49***	10199.73	43.32***	5763.68	17.11***
MthXQd	608.96	1.02	1809.38	2.56*	926.09	0.92
Error	4797.50		5650.70		8086.30	

Table 24 continued.

	Thompson Corner Pocosin		174		5099	
Character	SS	F	SS	F	SS	F
distal branch leaf length (mm)						
Mth	11453.77	59.51***	1463.23	12.00***	2167.53	3.73*
Qd	2351.70	18.33***	14044.23	172.79***	6049.42	15.63***
MthXQd	1108.23	2.88*	533.84	2.19	488.64	0.42
Error	3079.30		1950.70		9288.40	
distal branch leaf width (mm)						
Mth	9244.43	34.44***	184.40	0.62	963.30	1.44
Qd	3734.80	20.87***	12406.80	62.76***	4824.93	10.81***
MthXQd	688.87	1.28	631.80	1.07	1386.48	1.04
Error	4294.90		4744.50		10712.30	
stem leaf length (mm)						
Mth	3235.33	4.17*	2791.23	10.75***	5700.93	9.23***
Qd	1012.23	1.96	7363.53	42.55***	1748.77	4.25*
MthXQd	1320.14	0.85	3675.84	7.08***	654.89	0.53
Error	12409.80		4153.40		9877.90	
stem leaf width (mm)						
Mth	175.27	0.36	1333.37	3.10*	9.77	0.01
Qd	9579.33	29.26***	8367.78	29.16***	2866.83	5.54**
MthXQd	360.11	0.37	1362.26	1.58	2687.61	1.73
Error	7856.30		6887.10		12413.30	

Table 24 continued.

	Thompson Corner Pocosin		174		5099	
Character	SS	F	SS	F	SS	F
septa						
Mth	2470.10	4.64**	187.23	0.37	5123.93	9.10***
Qd	113.70	0.32	8834.58	26.39***	1627.90	4.34*
MthXQd	6884.70	6.47***	897.29	0.89	2222.77	1.97
Error	8512.50		8035.90		9004.90	
diameter of 5 cells in stem layer 1 (μm)						
Mth	686.70	0.95	323.10	0.90	414.93	0.46
Qd	5145.53	10.63***	11334.93	47.17***	1329.77	2.21
MthXQd	532.18	0.37	554.48	0.77	1797.49	1.00
Error	11616.10		5767.50		14433.30	
diameter of 5 cells in stem layer 2 (μm)						
Mth	1043.37	1.88	134.23	0.35	336.10	0.44
Qd	6640.73	17.93***	10423.53	40.27***	4307.48	8.50***
MthXQd	1412.01	1.27	1213.24	1.56	1167.03	0.77
Error	8887.40		6211.50		12165.40	
diameter of 5 cells in stem layer 3 (μm)						
Mth	1231.10	1.77	829.33	2.18	174.90	0.18
Qd	4687.23	10.14***	9889.90	39.01***	1377.98	2.15
MthXQd	958.68	0.69	1168.27	1.54	1036.93	0.54
Error	11098.50		6084.00		15378.20	

Table 24 continued.

	Thompson Corner Pocosin		174		5099	
Character	SS	F	SS	F	SS	F
diameter of 5 cells in stem layer 4 (μm)						
Mth	1630.23	3.58*	1721.83	2.99*	1077.83	1.32
Qd	6801.60	22.41***	6661.90	17.36***	2566.43	4.73*
MthXQd	2249.07	2.47*	377.17	0.33	1296.04	0.80
Error	7284.60		9209.60		13022.70	

Table 25. Analysis of variance table for thirteen morphological characters on stems from the 224 and Halfway Creek Road Carolina Bay sites. The model tested significance of variation among both months and quadrats and the interaction between these two main effects. SS=sum of squares, F=variance ratio used to assess significance of parameters in the model. df for mth=3, df for Qd=2, df for MthXQd=6, df for Error=48. *=P≤0.05, **=P≤0.01, ***=P≤0.001.

	224		Halfway Cr. Rd. Carol. Bay	
Character	SS	F	SS	F
proximal branch leaf length (mm)				
Mth	3517.50	5.58**	1386.93	1.44
Qd	1449.61	3.45*	321.53	0.50
MthXQd	2257.88	1.79	911.94	0.47
Error	9869.50		15359.10	
proximal branch leaf width (mm)				
Mth	522.74	0.54	3868.63	5.44**
Qd	498.11	0.77	755.73	1.59
MthXQd	724.54	0.37	1959.04	1.38
Error	15278.60		11379.10	
median branch leaf length (mm)				
Mth	6950.04	13.11***	10130.97	25.93***
Qd	1046.38	2.96	125.10	0.48
MthXQd	801.93	0.76	1486.03	1.90
Error	8307.15		6252.40	
median branch leaf width (mm)				
Mth	2277.53	3.27*	9674.10	23.60***
Qd	1453.65	3.13	813.93	2.98
MthXQd	2425.07	1.74	927.37	1.13
Error	10896.75		6559.60	

Table 25 continued.

	224		Halfway Cr. Rd. Carol. Bay	
Character	SS	F	SS	F
distal branch leaf length (mm)				
Mth	3100.97	5.26**	11710.83	38.08***
Qd	2976.79	7.57**	0.07	0.00
MthXQd	1784.55	1.51	1362.69	2.22
Error	9243.19		4919.90	
distal branch leaf width (mm)				
Mth	4124.82	7.71***	9657.43	21.23***
Qd	2552.67	7.15**	386.58	1.27
MthXQd	1995.46	1.86	588.59	0.65
Error	8384.55		7279.40	
stem leaf length (mm)				
Mth	563.74	0.63	190.80	0.18
Qd	276.75	0.46	156.17	0.23
MthXQd	2197.62	1.22	1042.53	0.50
Error	14052.89		16592.00	
stem leaf width (mm)				
Mth	706.04	0.89	4921.83	7.67***
Qd	2861.28	5.40**	541.30	1.27
MthXQd	1053.29	0.66	2243.37	1.75
Error	12461.39		10265.50	

Table 25 continued.

	224		Halfway Cr. Rd. Carol. Bay	
Character	SS	F	SS	F
septa				
Mth	1985.01	2.59	1742.50	2.31
Qd	1551.14	3.04	2651.93	5.27**
MthXQd	1564.70	1.02	1509.08	1.00
Error	12001.65		12078.50	
diameter of 5 cells in stem layer 1 (μm)				
Mth	1644.23	2.01	8278.77	14.98***
Qd	2098.65	3.85*	511.67	1.39
MthXQd	531.32	0.32	349.06	0.32
Error	12822.79		8845.00	
diameter of 5 cells in stem layer 2 (μm)				
Mth	2949.99	3.77*	7341.43	11.93***
Qd	845.15	1.62	1.22	0.00
MthXQd	1045.06	0.67	790.24	0.64
Error	12248.80		9844.60	
diameter of 5 cells in stem layer 3 (μm)				
Mth	802.20	0.94	4978.73	6.67***
Qd	1820.29	3.19*	453.70	0.91
MthXQd	1068.06	0.62	598.17	0.40
Error	13392.95		11949.90	

Table 25 continued.

	224		Halfway Cr. Rd. Carol. Bay	
Character	SS	F	SS	F
diameter of 5 cells in stem layer 4 (μm)				
Mth	1319.20	1.38	5169.23	6.71***
Qd	325.73	0.51	177.17	0.34
MthXQd	512.79	0.27	289.99	0.19
Error	14931.29		12331.10	

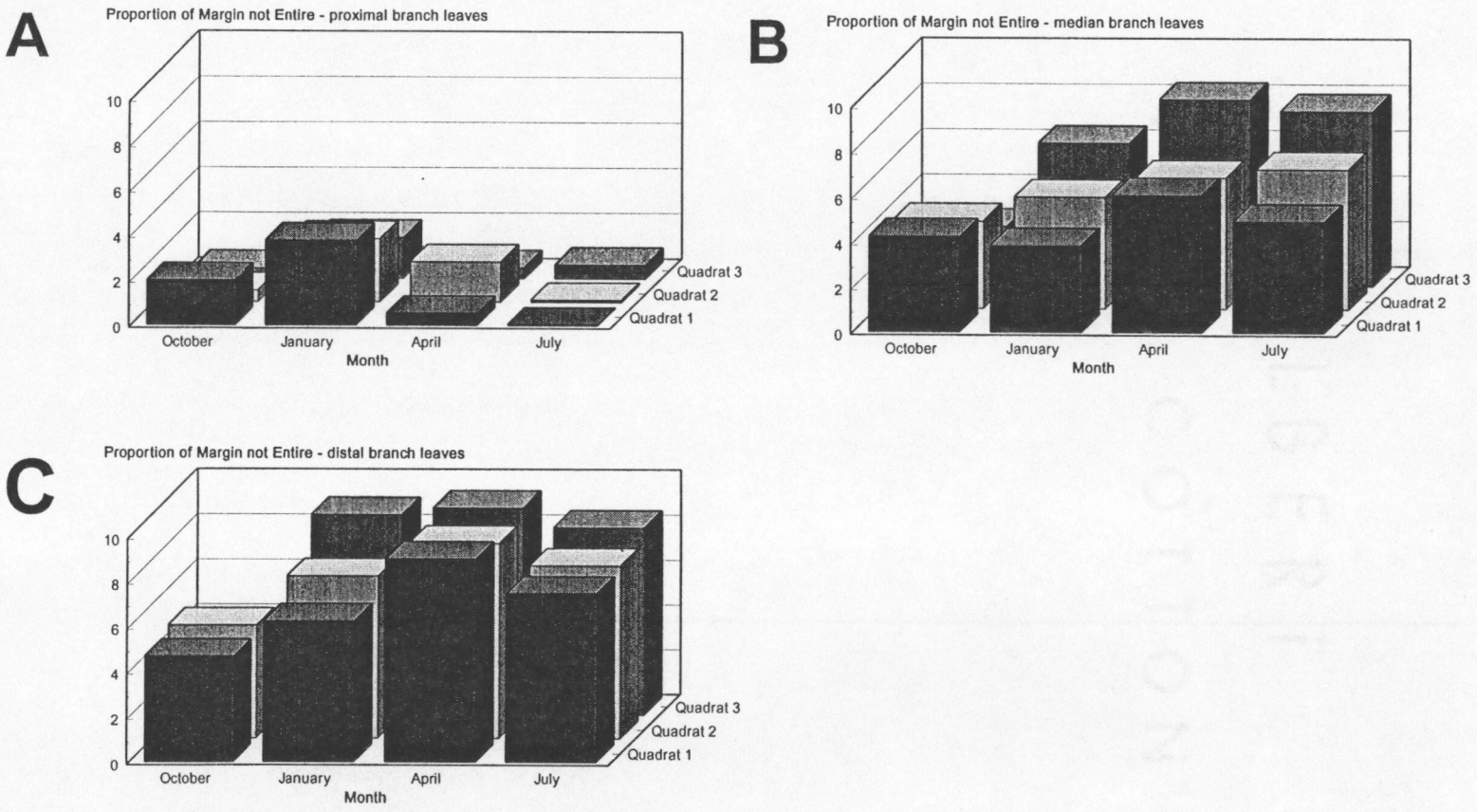


Figure 26. Variation in the means of the character "proportion of margin not entire" over a one year period along a moisture gradient in plants at the Thompson Corner Pocosin site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

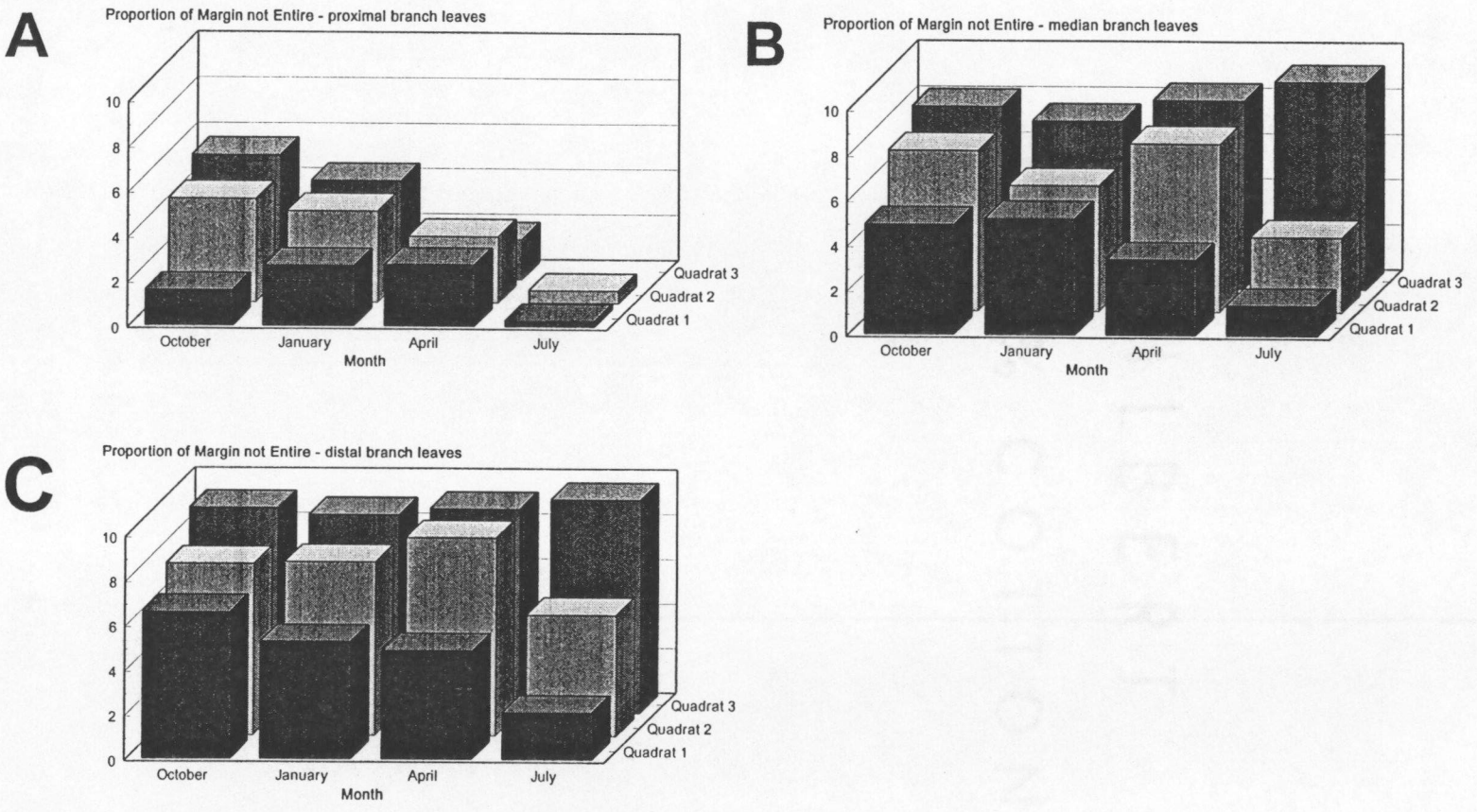


Figure 27. Variation in the means of the character "proportion of margin not entire" over a one year period along a moisture gradient in plants at the 174 site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

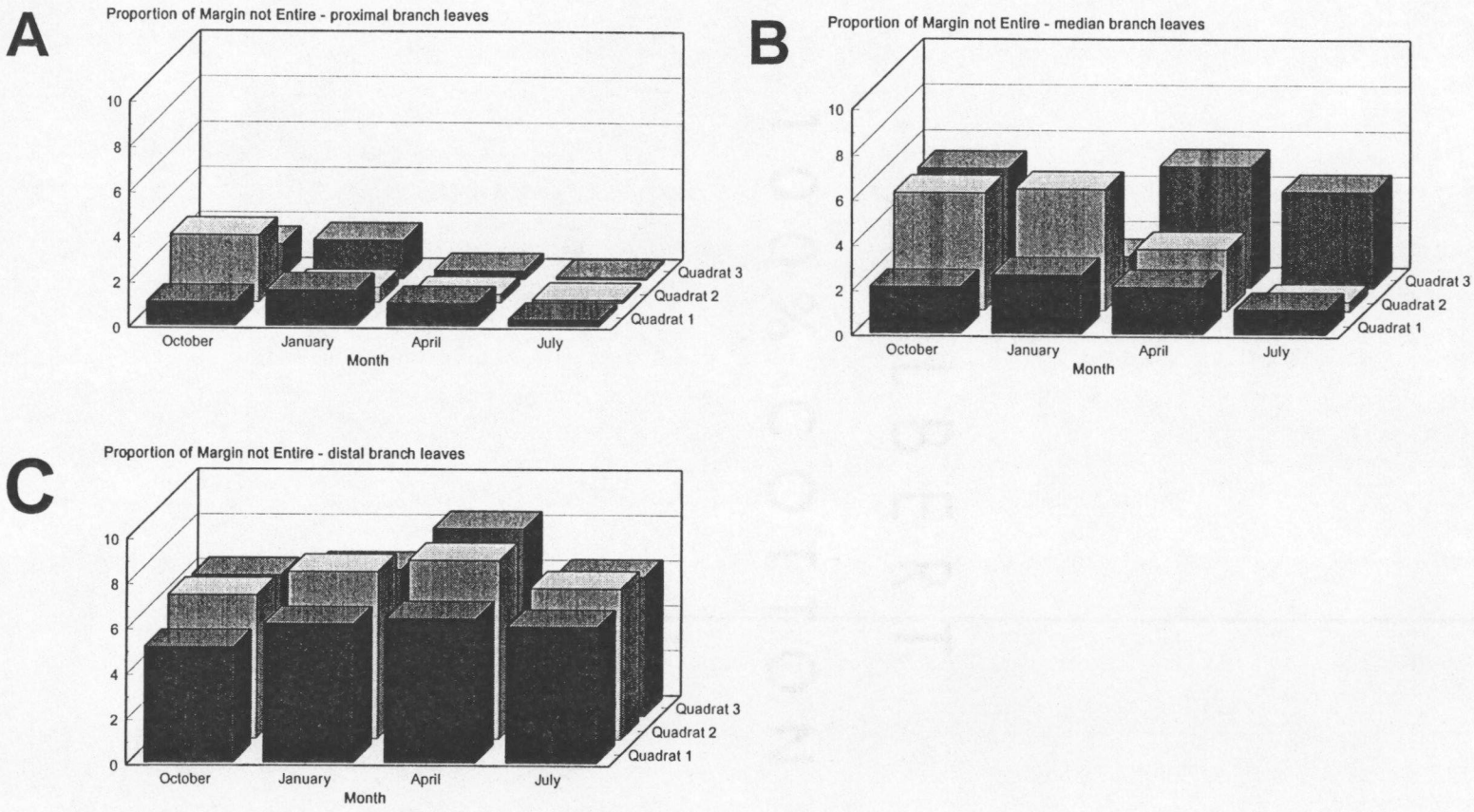


Figure 28. Variation in the means of the character "proportion of margin not entire" over a one year period along a moisture gradient in plants at the 5099 site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

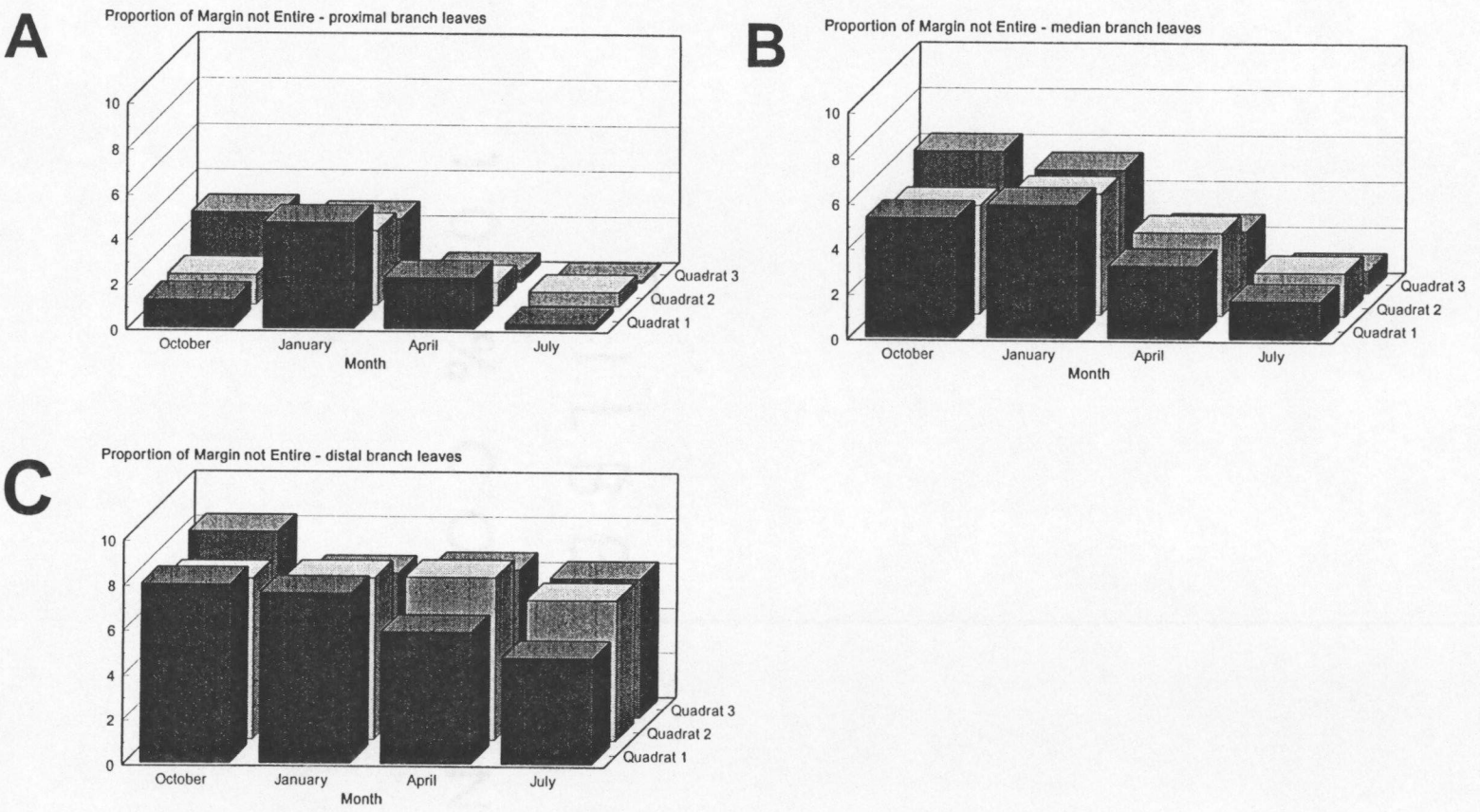


Figure 29. Variation in the means of the character "proportion of margin not entire" over a one year period along a moisture gradient in plants at the 224 site. site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

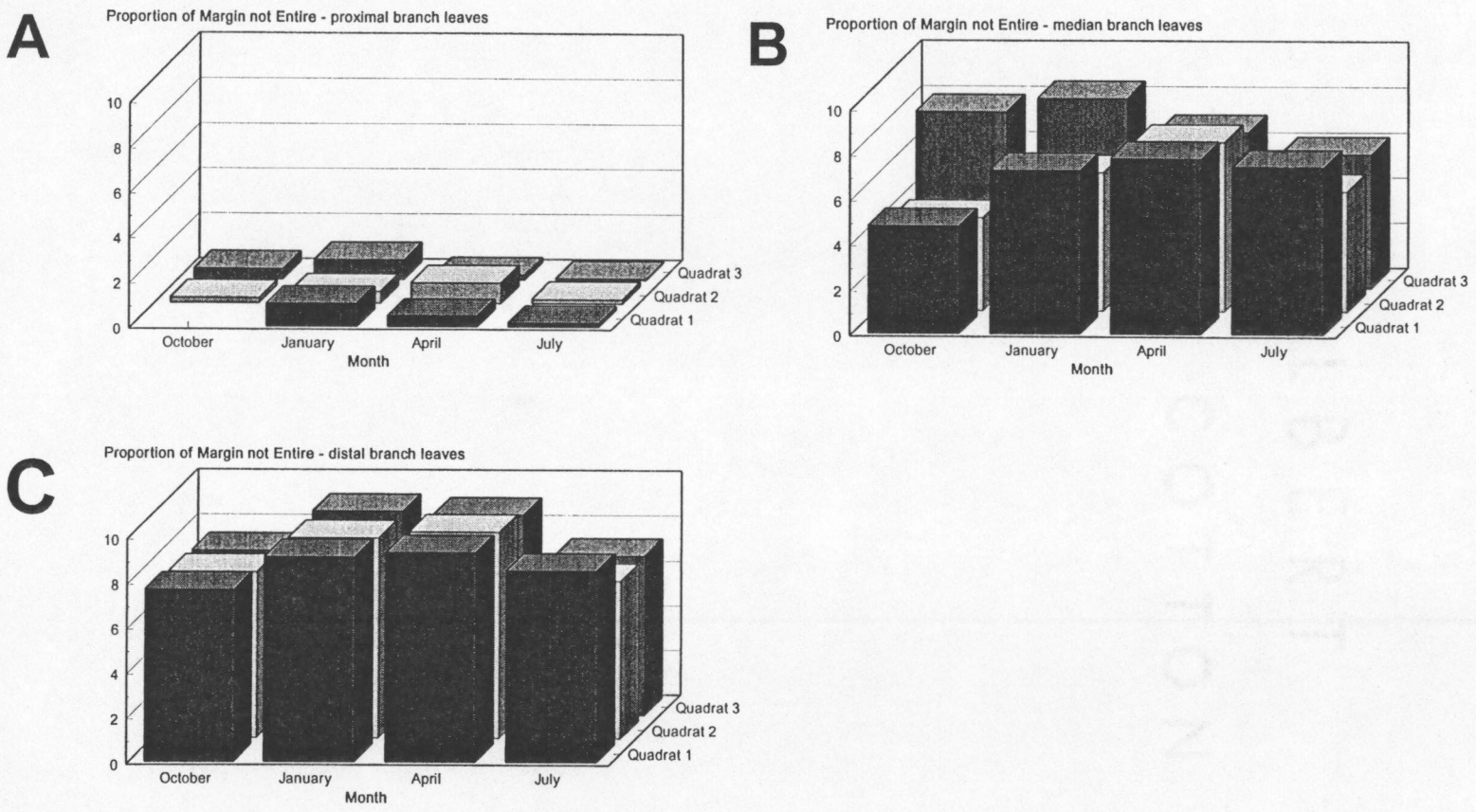


Figure 30. Variation in the means of the character "proportion of margin not entire" over a one year period along a moisture gradient in plants at the Halfway Creek Road Carolina Bay site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

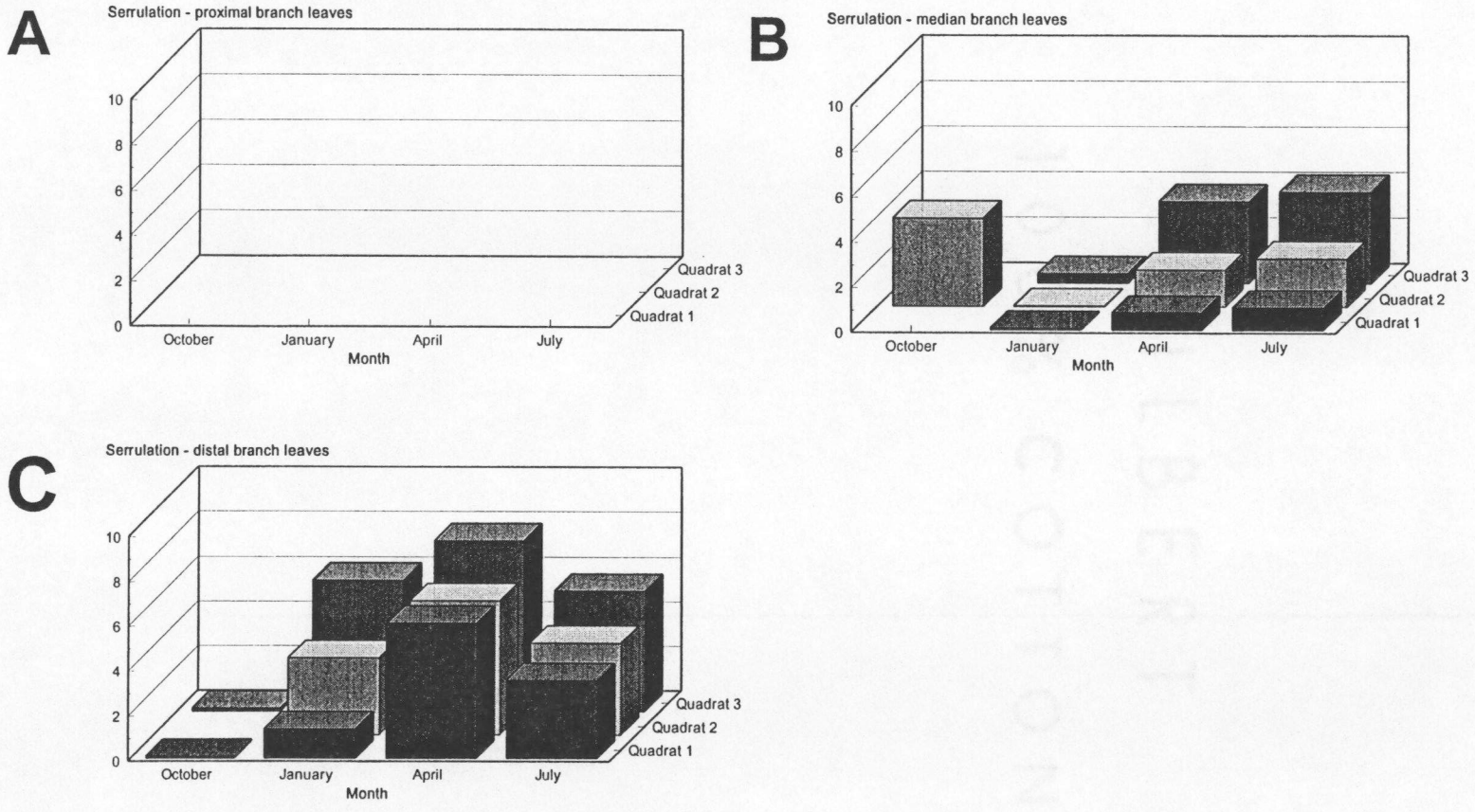


Figure 31. Variation in the means of the character "serrulation" over a one year period along a moisture gradient in plants at the Thompson Corner Pocosin site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

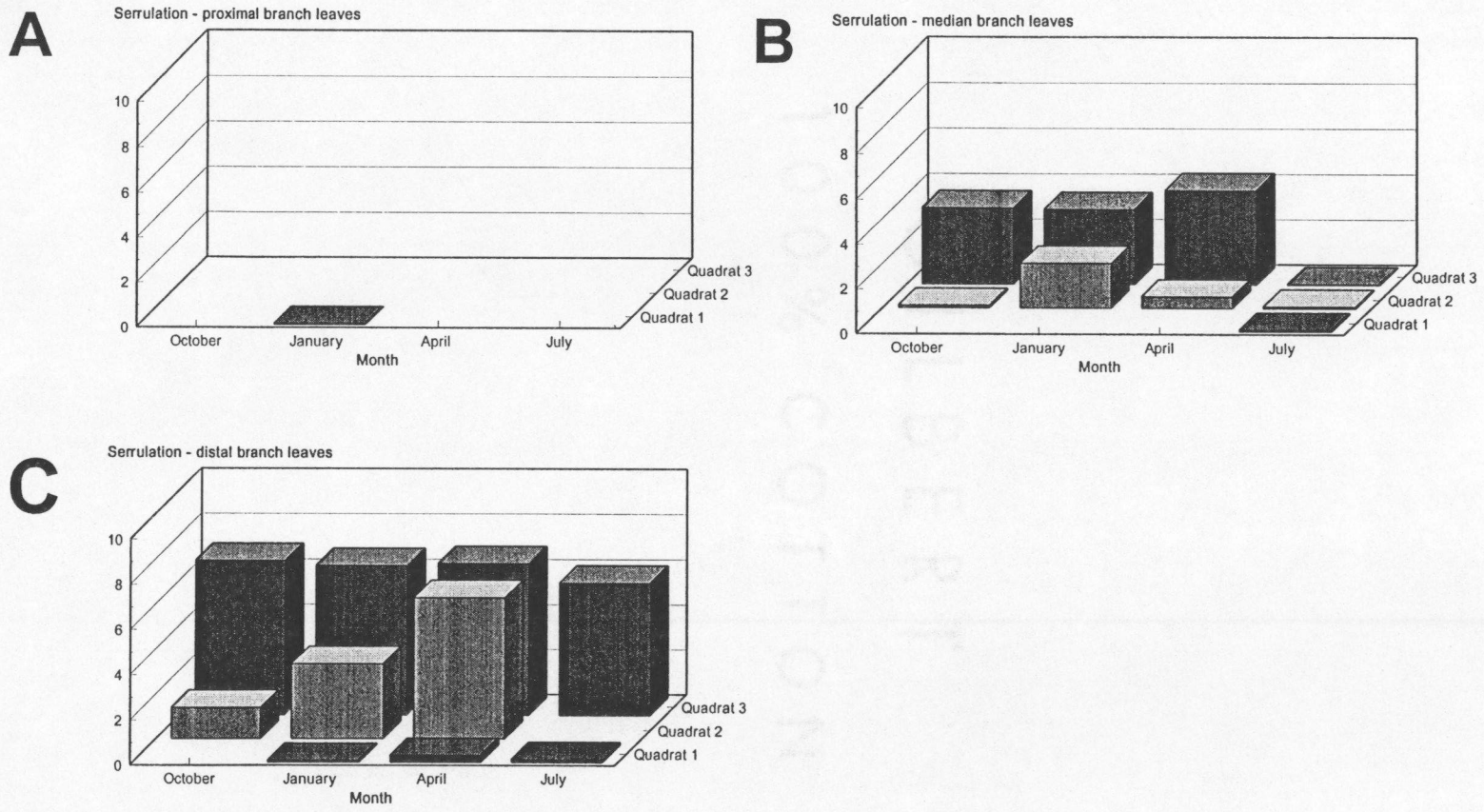


Figure 32. Variation in the means of the character "serrulation" over a one year period along a moisture gradient in plants at the 174 site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

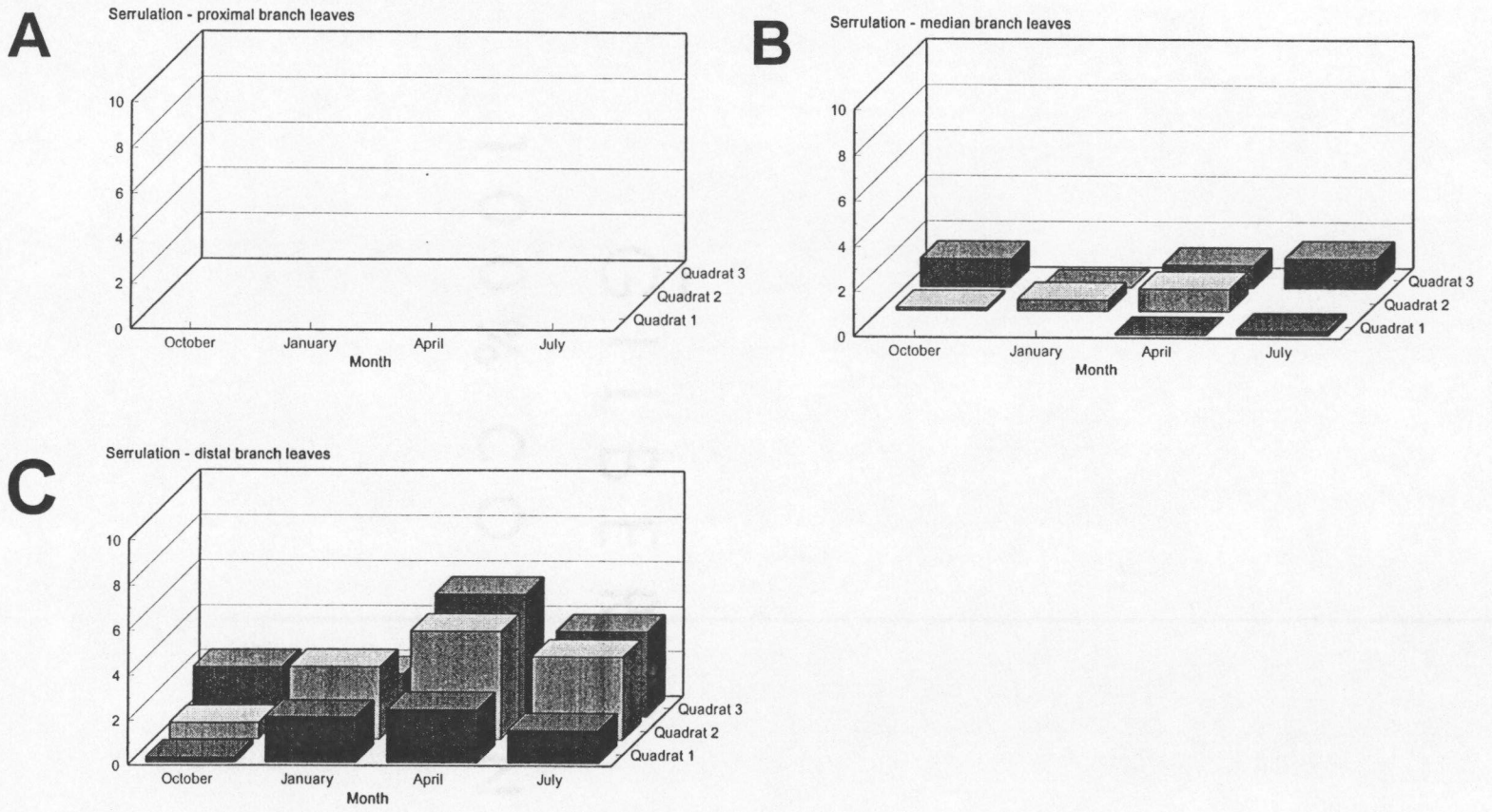


Figure 33. Variation in the means of the character "serrulation" over a one year period along a moisture gradient in plants at the 5099 site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

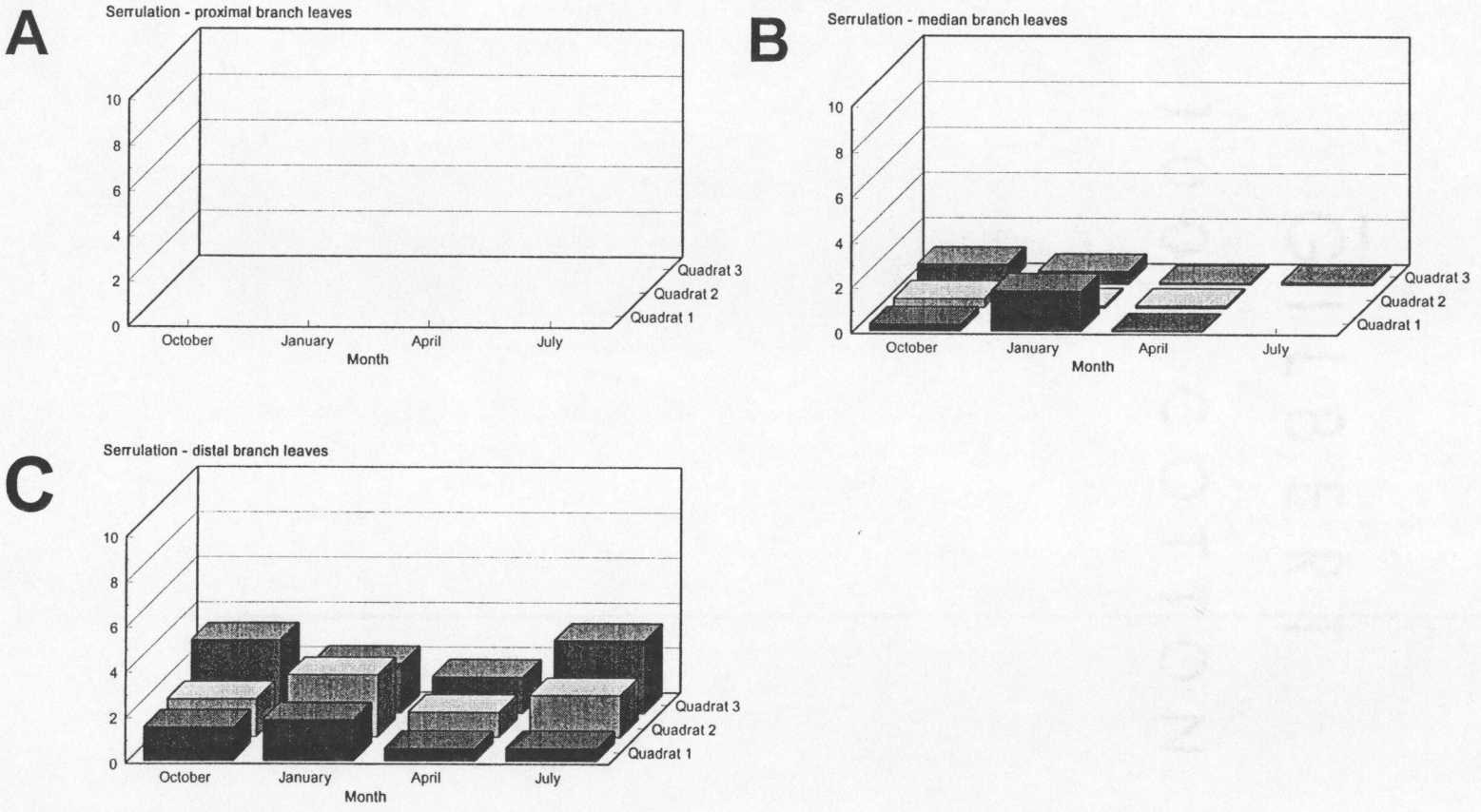


Figure 34. Variation in the means of the character "serrulation" over a one year period along a moisture gradient in plants at the 224 site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

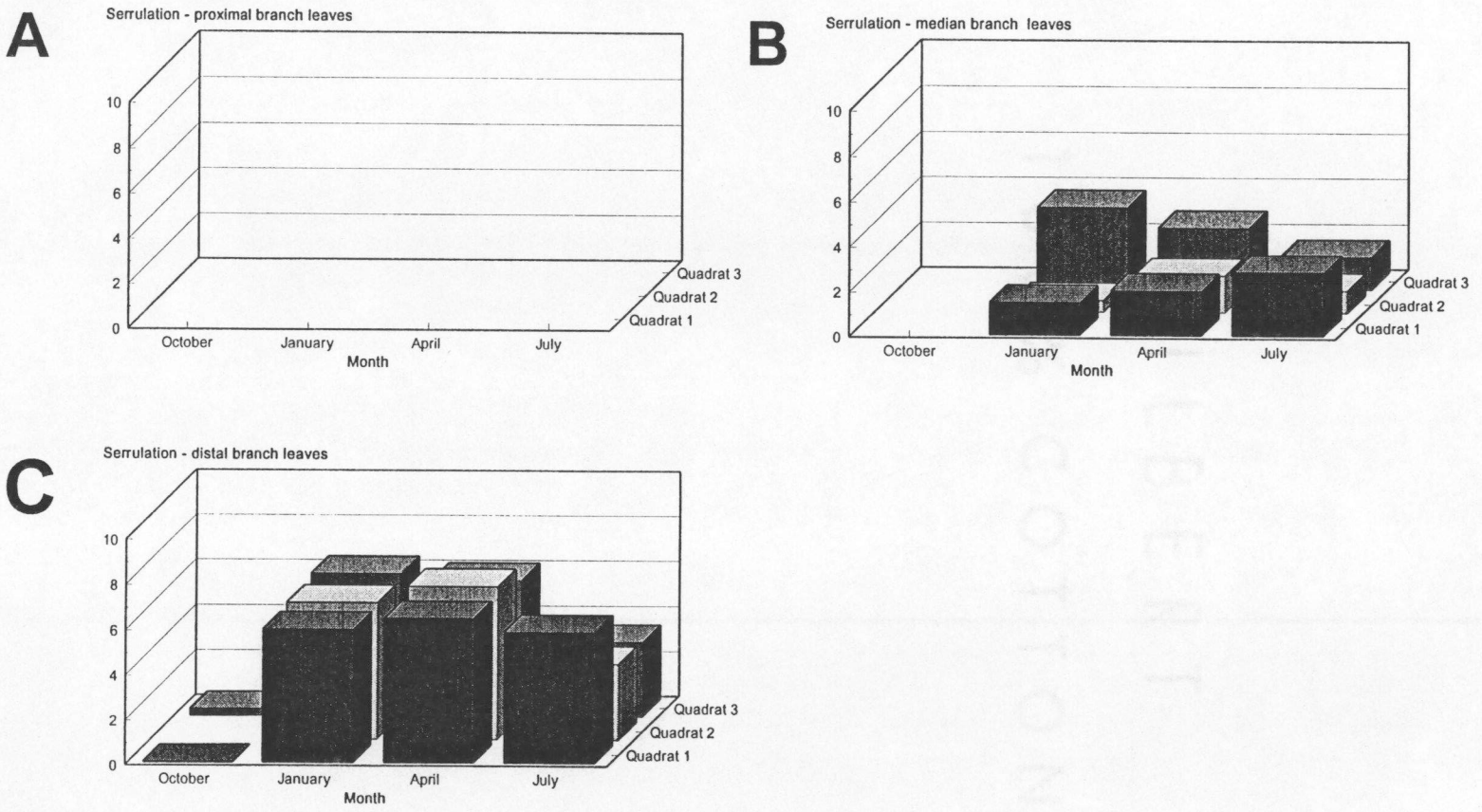


Figure 35. Variation in the means of the character "serrulation" over a one year period along a moisture gradient in plants at the Halfway Creek Road Carolina Bay site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

spatiotemporally variable than were these features on median and distal branch leaves. Proximal branch leaves from the 174 site, however, did exhibit a considerable degree of variation by month and by quadrat for proportion of margin not entire (Figure 27). With the exception of one leaf (Figure 32), serrulations were not observed on proximal branch leaves during the study.

The overall patterns of variation in proportion of margin not entire for median branch leaves more or less mimic the patterns of variation for this character exhibited by distal branch leaves (Figures 26 - 30). The variation patterns are also similar, but to a lesser degree, for the character "serrulation" for leaves from these two positions (Figures 31 - 35).

Plots from the Thompson Corner Pocosin and 174 sites suggest strong month and quadrat effects for both median and distal branch leaf serrulation (Figures 31 and 32). There also appears to be a month effect for distal branch leaf serrulation at the 5099 and Halfway Creek Road Carolina Bay sites (Figures 33 and 35).

Length to width ratios for branch leaves from the three branch positions exhibited rather different levels of variability at four of the five sites (Figures 36 - 39). Proximal branch leaf length to width ratio is rather constant at all sites. Median and distal branch leaf length to width ratios varied considerably at all sites except the

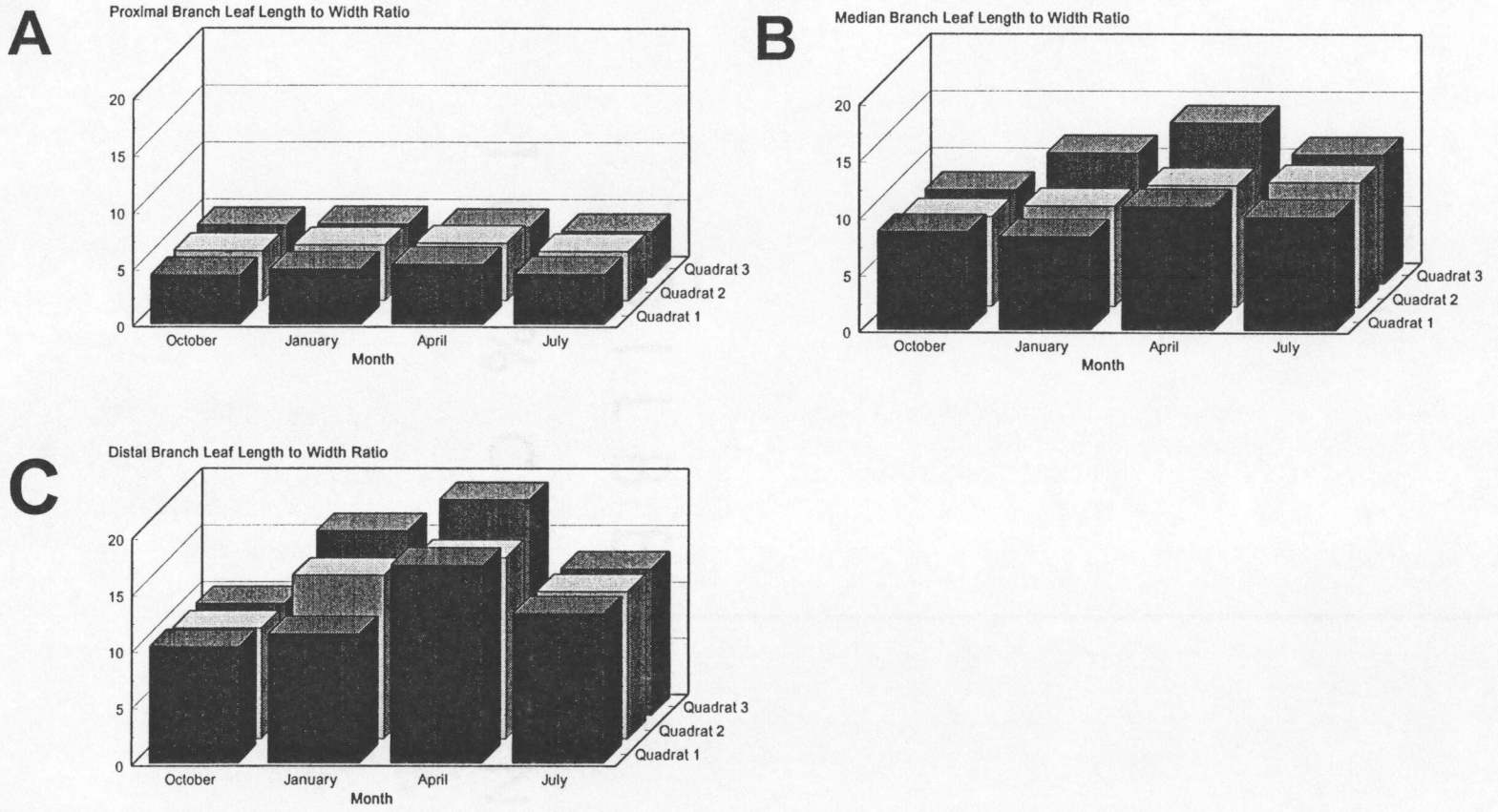


Figure 36. Variation in the means of branch leaf length to width ratios over a one year period along a moisture gradient in plants at the Thompson Corner Pocosin site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

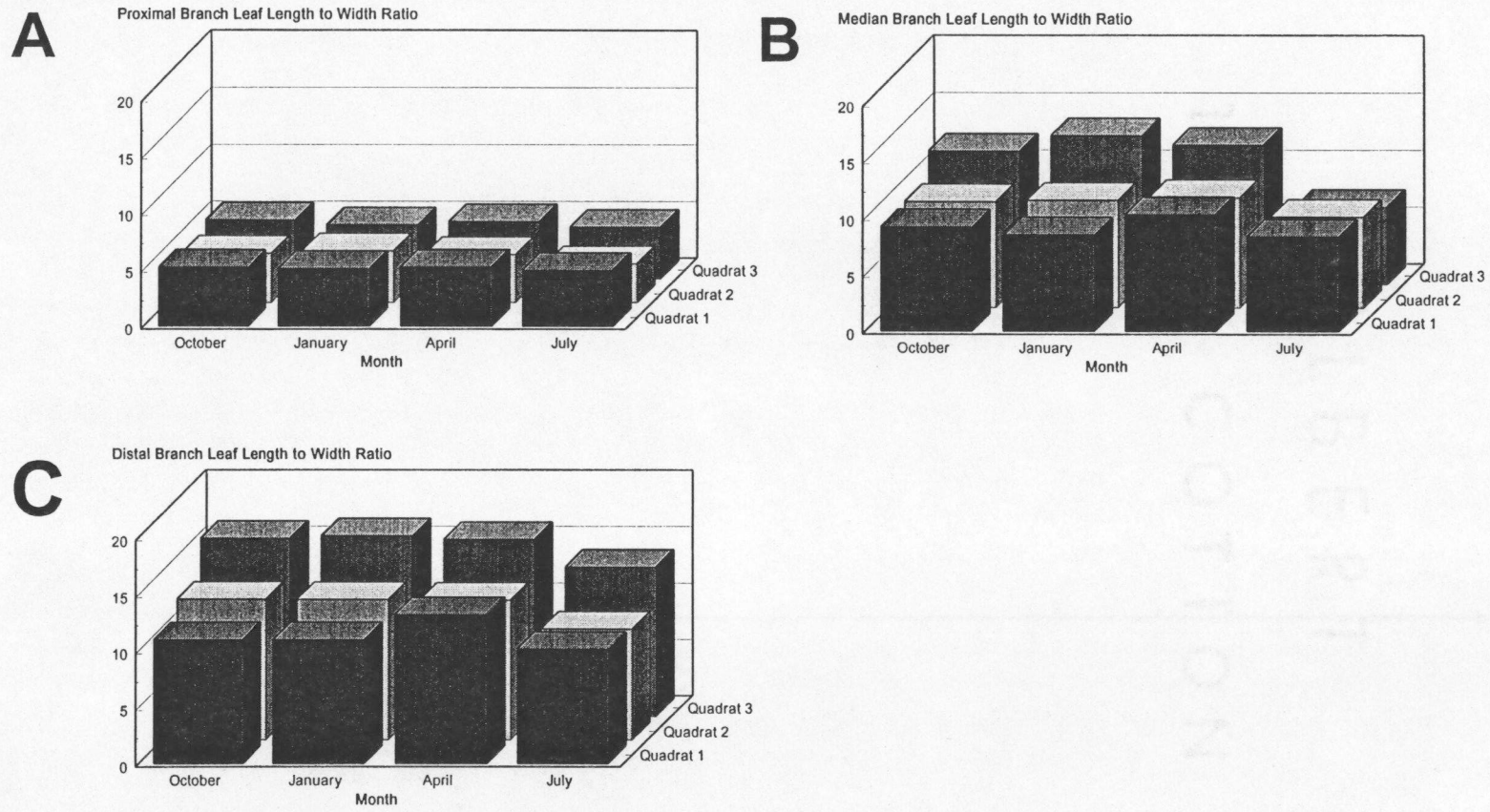


Figure 37. Variation in the means of branch leaf length to width ratios over a one year period along a moisture gradient in plants at the 174 site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

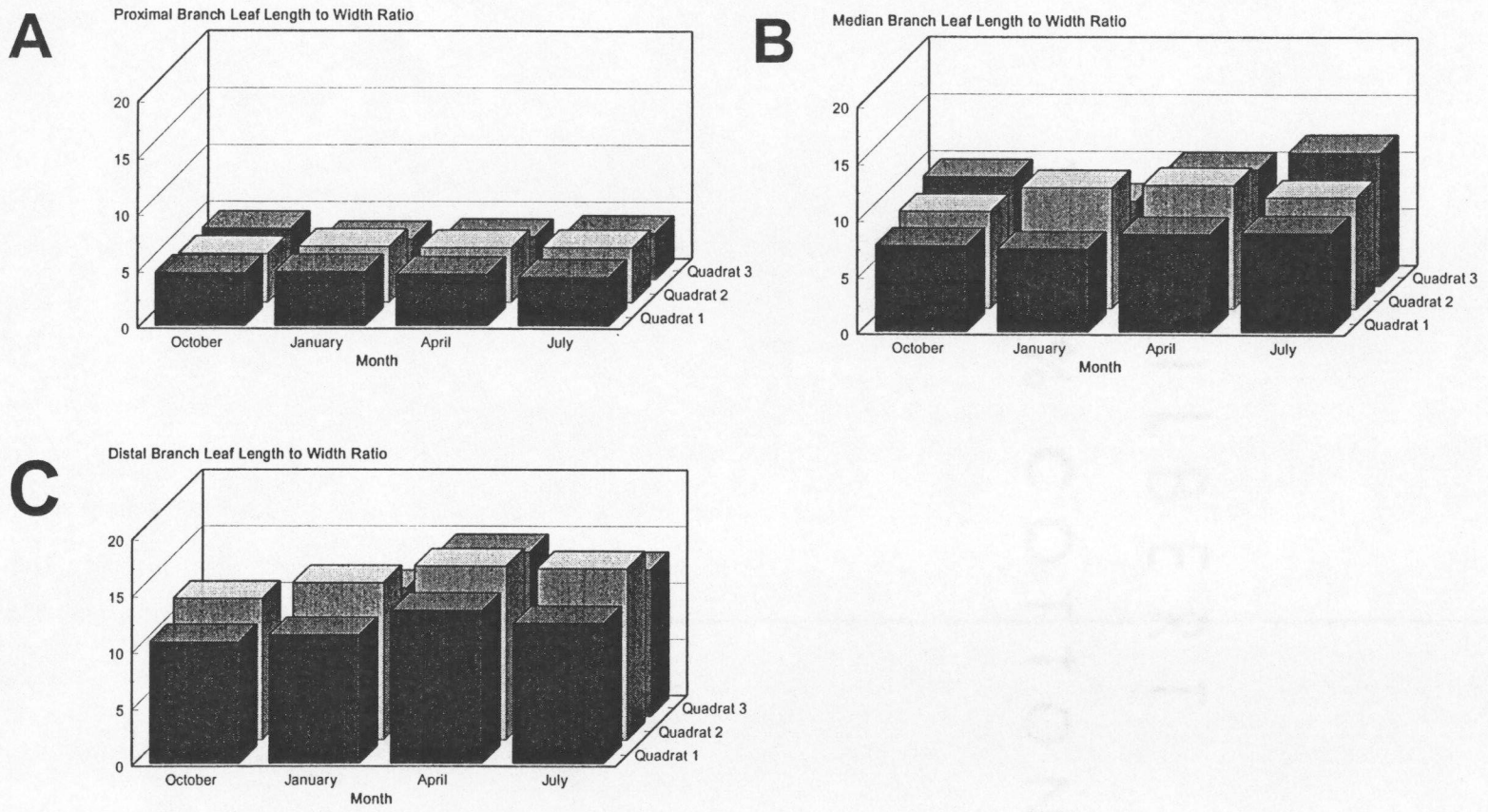


Figure 38. Variation in the means of branch leaf length to width ratios over a one year period along a moisture gradient in plants at the 5099 site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

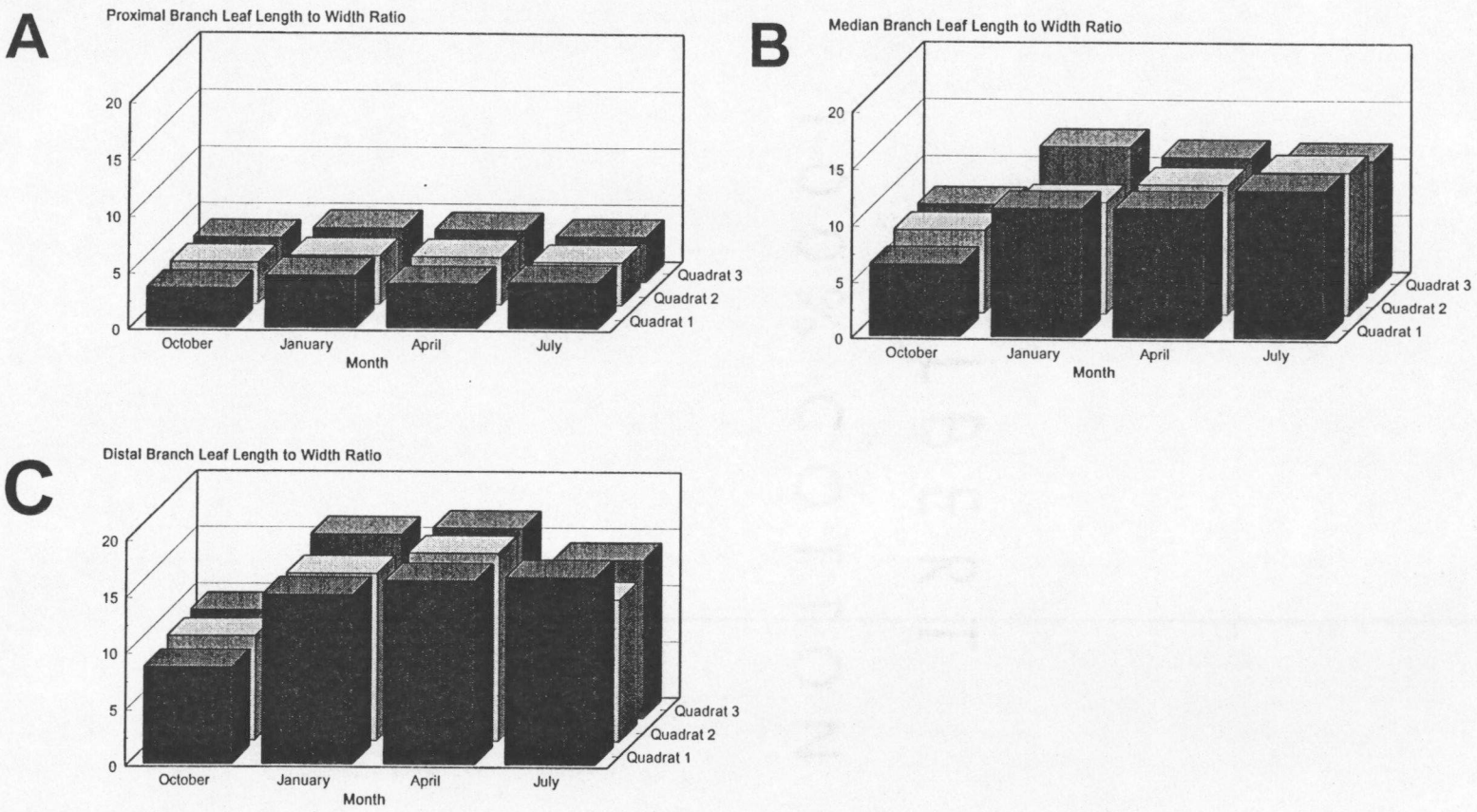


Figure 39. Variation in the means of branch leaf length to width ratios over a one year period along a moisture gradient in plants at the Halfway Creek Road Carolina Bay site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

224 site (Figure 40).

The number of septa per stem leaf appeared to be both spatially and temporally variable (Tables 24 and 25 and Figures 41 - 45).

Figures 41 - 45 suggest that the ratio of the sum of the diameters of stem cell layers one and two to that of stem cell layers three and four was reasonably constant at all sites.

Discussion

The results have several implications regarding the choice of taxonomic characters to use in discriminating *S. cuspidatum* and *S. trinitense*. Median and distal branch leaf margins ranged from entire to strongly serrulate in the same populations over a one year period. Thus, leaves from these two positions do not appear to be morphologically stable enough to reliably distinguish the two taxa. Proximal branch leaf margins, however, were much more consistent in appearance. Proximal branch leaves lacked serrulations and generally had denticulations restricted to the distal one-fourth. Thus, the results indicate that proximal branch leaves are much more appropriate to use than are median and distal branch leaves when making specimen determinations involving *S. cuspidatum* and *S. trinitense*.

The value of "number of septate cells per stem leaf" as a taxonomic character separating *S. cuspidatum* and *S.*

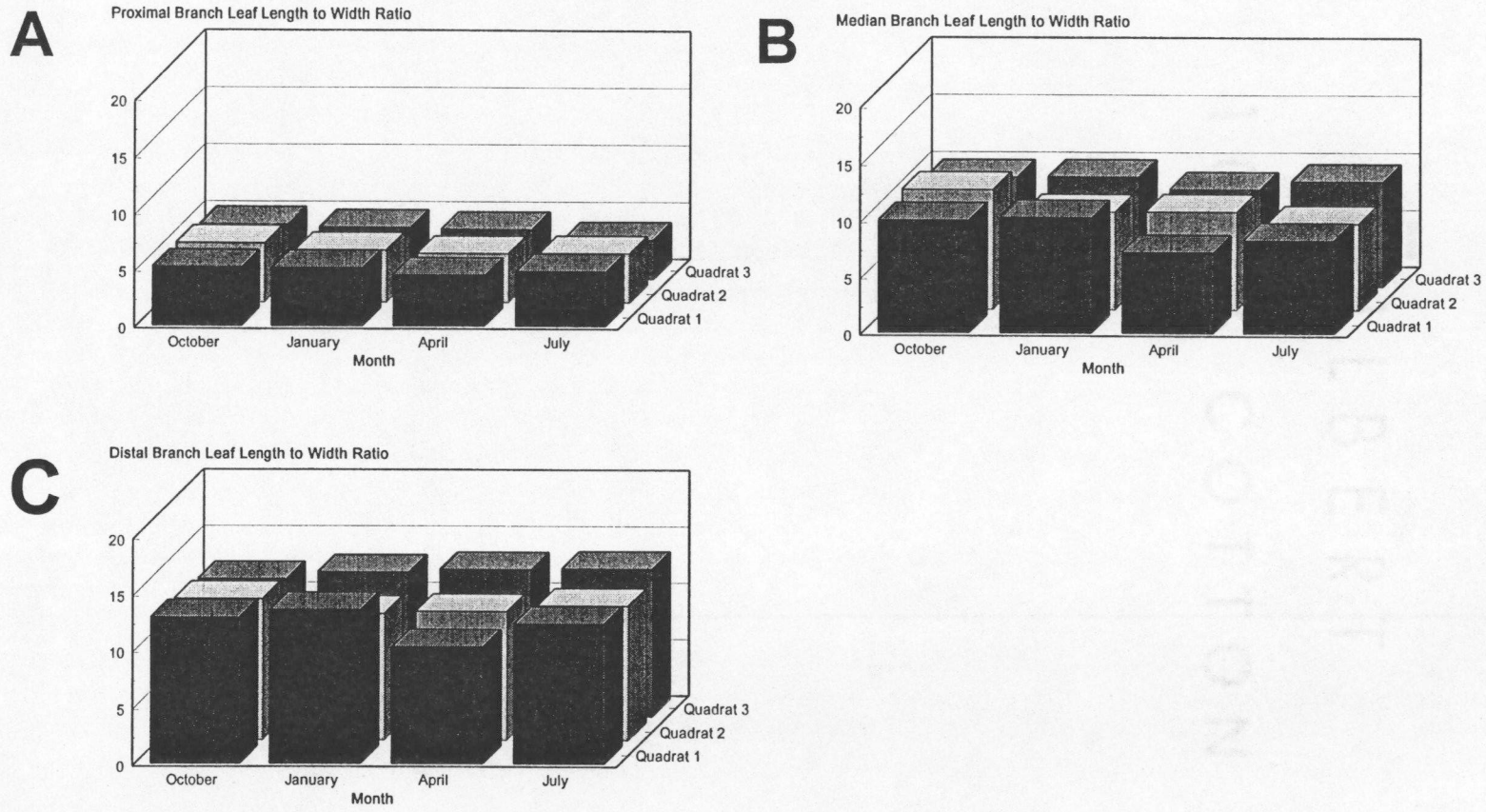


Figure 40. Variation in the means of branch leaf length to width ratios over a one year period along a moisture gradient in plants at the 224 site. A. proximal branch leaves. B. median branch leaves. C. distal branch leaves.

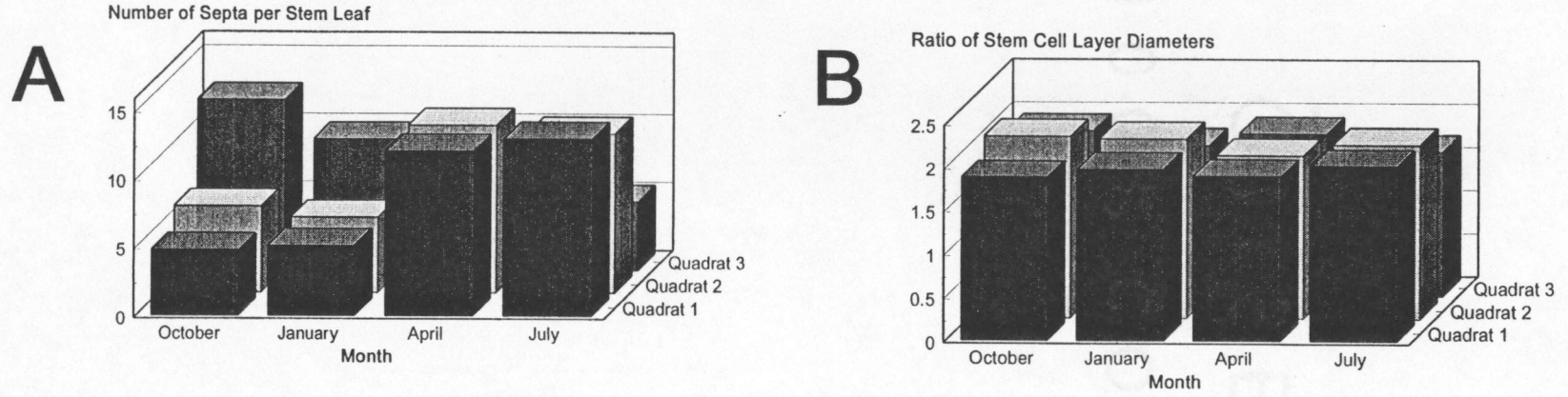


Figure 41. Variation in the means of stem leaf and stem characters over a one year period along a moisture gradient in plants at the Thompson Corner Pocosin site. A. number of septa per stem leaf. B. ratio of stem cell layer diameters.

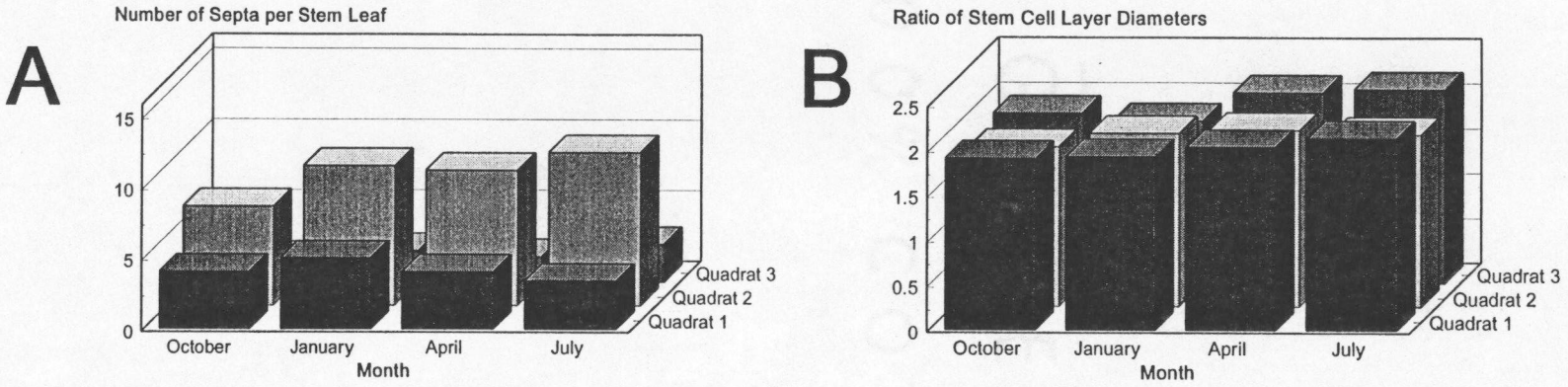


Figure 42. Variation in the means of stem leaf and stem characters over a one year period along a moisture gradient in plants at the 174 site. A. number of septa per stem leaf. B. ratio of stem cell layer diameters.

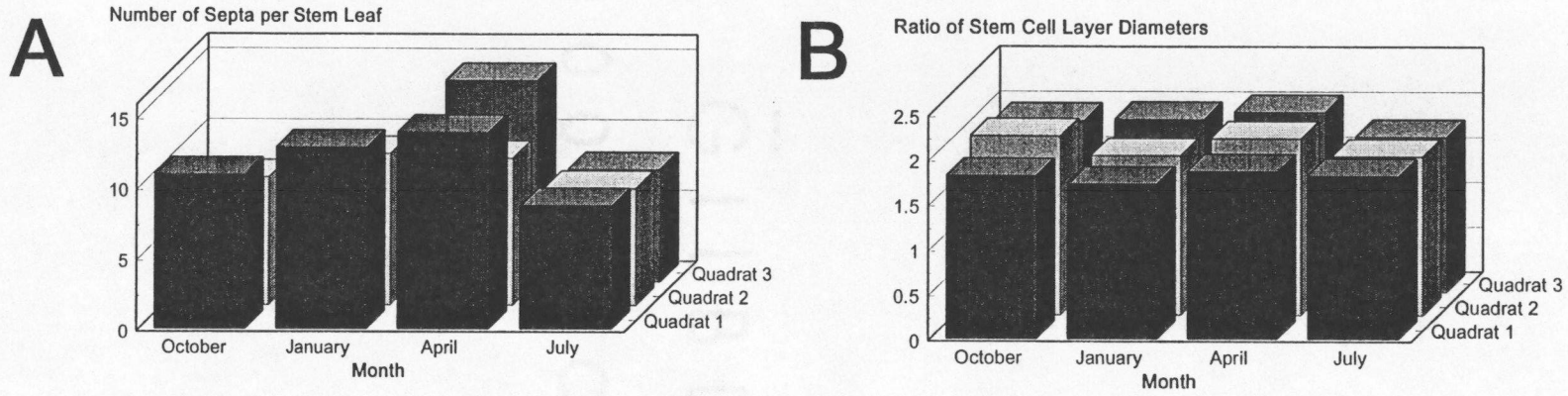


Figure 43. Variation in the means of stem leaf and stem characters over a one year period along a moisture gradient in plants at the 5099 site. A. number of septa per stem leaf. B. ratio of stem cell layer diameters.

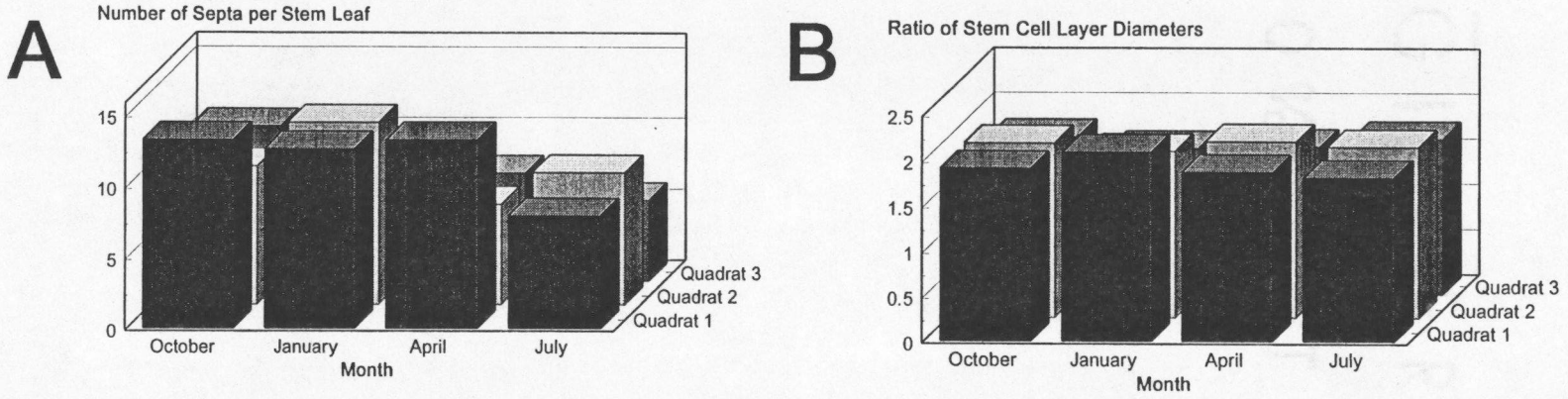


Figure 44. Variation in the means of stem leaf and stem characters over a one year period along a moisture gradient in plants at the 224 site. A. number of septa per stem leaf. B. ratio of stem cell layer diameters.

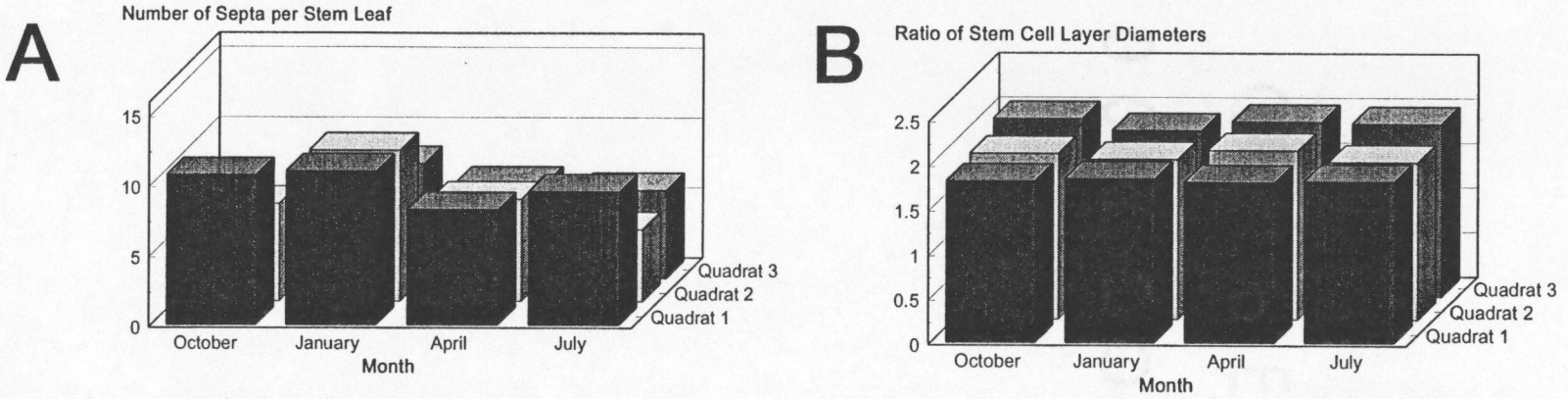


Figure 45. Variation in the means of stem leaf and stem characters over a one year period along a moisture gradient in plants at the Halfway Creek Road Carolina Bay site. A. number of septa per stem leaf. B. ratio of stem cell layer diameters.

trinitense is not supported by the results. This character is simply too variable to effectively sort specimens, given the proximity of the means for *S. cuspidatum* (mean of 10.40) and *S. trinitense* (mean of 12.54) from the specimens collected from the five areas (Table 22).

Andrus (1974) was the first worker to emphasize comparing the degree of differentiation in size of the outer stem cell layers versus adjacent inner stem cell layers as a means of separating *S. cuspidatum* and *S. trinitense*. This character, expressed as a ratio, [(layer one diameter + layer two diameter)/(layer 3 diameter + layer 4 diameter)], was found to be relatively stable across months and across quadrats. Thus this character is highly constant and reliable for distinguishing specimens of *S. cuspidatum* and *S. trinitense* collected from a wide range of conditions.

Although the large morphometric study indicated that the *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* groups had somewhat different branch leaf length to width ratios at all three positions, only the proximal branch leaf length to width ratio is probably suitable as a taxonomic character. Median and distal branch leaf length to width ratios were found to be highly variable both spatially and temporally.

No attempt was made to ascertain the genetic variability of the plants within and between quadrats at a site or between sites. It is quite likely that genetic

variation made an important contribution to the observed phenotypic variation and may have been an important determinant in the different character response patterns observed at different sites. On the other hand, the ability of *Sphagnum* to form extensive clonal mats leaves open the possibility that one or more of the quadrats at each site could have been covered by one genetic entity.

Flatberg (1988, 1994) has recently drawn attention to slight sexual dimorphism in the *Cuspidata*, including *S. cuspidatum*. Thus some of the observed morphological variation could be due to differing proportions of male to female stems being randomly sampled across months, across quadrats, and across sites. Potentially compounding this is the possibility that male and female plants did not have parallel responses to the month and quadrat gradients.

Additionally, between site variation in the patterns of significant effects indicated by the analysis of variance may also be due to hydrologic, chemical, floristic, insolation, and other differences between sites.

Characters that are highly variable along the wetness and temporal gradients examined in this study are clearly not suitable or recommended as taxonomic characters. Proximal branch leaf margin, stem cell layer diameter ratio, and proximal branch leaf length to width ratio are the most stable potential taxonomic characters. Because of their highly variable nature, median and distal branch leaf

margins appear to have limited taxonomic utility.

Field Observations

A diligent effort was made to explore a wide range of natural wetland communities in the five areas selected for specimen collection. It is the intent of this section to relate the morphological groups delineated by the morphometric analyses to the habitats from which they were collected. It is hoped that these field observations enrich and increase the value of the taxonomic information presented previously herein.

Croatan National Forest

Sphagnum cuspidatum/S. viridum, *S. trinitense/S. mississippiense*, and *S. fitzgeraldii* were collected from the CNF.

Sphagnum cuspidatum/S. viridum was fairly common in pools and depressions of low pocosins. Specimens of this group were usually not present in high pocosins except in openings created by disturbance. The taxon was common in shallow pools at savanna-pocosin ecotones around Millis Savanna and Millis Swamp. This group was scarce in the numerous ponds between Broad Creek and the town of Ocean (the Patsy Pond complex), where approximately ten of these ponds were carefully examined and *S. cuspidatum/S. viridum* was only observed in three of them. Elsewhere, water-filled depressions or wet areas in recently or chronically disturbed sites such as abandoned logging roads, trails, and powerline right-of-ways would occasionally support this

group. *Sphagnum trinitense/S. mississippiense* was not observed in such sites and *S. fitzgeraldii* was present only if these sites were associated with pocosins.

Sphagnum trinitense/S. mississippiense was only observed in association with seasonal ponds. The group was present in nearly every pond visited in the Patsy Pond Complex, often in considerable abundance. As mentioned above, three of these ponds also supported *S. cuspidatum/S. viridum*, and at these sites the latter group occurred in mixture with *S. trinitense/S. mississippiense*. Individuals of the two groups had conspicuously different appearances in the field (Figure 46). At a mostly filled-in, seasonal pond in another area (Carteret Co., Masontown Quad, north F. S. 177A, near jct. of F. S. 177 and 177A), *S. trinitense/S. mississippiense* covered much of the ground beneath dense stands of *Woodwardia virginica* (L.) Sm. and a variety of shrubs, particularly *Zenobia pulverulenta* (Bartr. *ex* Willd.) Pollard. *Sphagnum cuspidatum/S. viridum* was not observed at this site.

Sphagnum fitzgeraldii appeared to be limited to shallow, seasonal pools associated with mesic savannas, savanna-pocosin ecotones, low pocosins, or near ponds. The species was noted as particularly abundant in shallow pools in and around Millis Savanna.



Figure 46. Field mixture of *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense*. The plants with the larger, stellate, flat-topped capitula and bristly erect branch leaves are *S. cuspidatum/S. viridum* and the plants with the smaller, rounded capitula with appressed branch leaves (thus each branch is shaped like a straightened cow's horn) are *S. trinitense/S. mississippiense*. (Risk 8140. Pond margin at west end of Patsy Pond, Carteret Co., NC.)

Francis Marion National Forest

Sphagnum cuspidatum/S. viridum, *S. trinitense/S. mississippiense*, and *S. fitzgeraldii* were collected in the FMNF.

Several pocosin areas in this forest had impressive amounts of *S. cuspidatum/S. viridum*. Large openings in the pocosins south of Thompson Corner were filled with this taxon. This group also covered many acres in the large openings in the pocosins south of Steed Creek Road (ca. 0.8 km west of Halfway Creek Road). Both of the above sites are associated with a relict barrier island system (based on inspection of maps in Colquhoun 1969). *Sphagnum cuspidatum/S. viridum* was also generally present in mesic to wet savannas, savanna-pocosin ecotones, and in pond cypress swamps. *Sphagnum cuspidatum/S. viridum* was particularly abundant nearly throughout the interior of Halfway Creek Road Carolina Bay (long axis about 1.4 km). The bay is a pan mostly occupied by a *Taxodium ascendens-Nyssa biflora* swamp with shallow standing water throughout much of the year.

Sphagnum trinitense/S. mississippiense was only rarely to infrequently encountered. This group was observed in an *Acer rubrum-Magnolia virginiana* swamp, a mesic savanna, a roadside ditch, a borrow pit, and a hillside seep. *Sphagnum trinitense/S. mississippiense* was only observed in abundance at the mesic savanna 1 km west of Cropnel Dam Creek on the

north side of Steed Creek Road. Here it often filled the numerous shallow pools in association with a diverse insectivorous flora. On the north side of this savanna, *S. trinitense/S. mississippiense* co-occurred with *S. cuspidatum/S. viridum* in a *Pinus serotina-Acer rubrum* flatwoods. *Sphagnum trinitense/S. mississippiense* was not observed in the pocosin complexes of the FMNF.

Sphagnum fitzgeraldii was infrequent and was encountered primarily in savanna-pocosin ecotones and in depressions of mesic-wet savannas. The species frequently co-occurred in mixture with *S. cuspidatum/S. viridum*.

Sandhills

Sphagnum cuspidatum/S. viridum, *S. trinitense/S. mississippiense*, and *S. torreyanum* were collected in the SH.

Extensive exploration along Black Creek in the Carolina Sandhills National Wildlife Refuge (CSNWR) and Sandhills State Forest in South Carolina and along Drowning Creek-Lumber River in the Sandhills Gamelands in North Carolina resulted in the discovery of numerous populations of *S. torreyanum*. Many of these populations were quite large. The discovery of these populations is significant since the species is generally considered to be rare in the southeastern United States (e.g. Amoroso and Weakley 1995). *Sphagnum torreyanum* appeared to favor seasonal pools at the upper edge of these backwater swamps, where it grew in

monospecific stands or with *S. portoricense* and/or *S. carolinianum*. In the CSNWR and vicinity, the species appeared to be most vigorous in areas with extensive shallow pools, thin shrub layers, and a well-developed, relatively mature canopy of *Nyssa biflora*, *Acer rubrum*, and occasional *Taxodium*. As illustrated in Figure 47, these conditions typically occurred just downslope of a hillside pocosin and upslope of a silt-laden, frequently flooded zone.

Sphagnum torreyanum was collected from a number of impoundments as well. My observations suggest the species is more likely to be found in older impoundments that have partially filled-in than in young ponds/lakes.

Sphagnum cuspidatum/S. viridum appeared to be very rare in natural wetlands of the region. It was observed, despite intensive searching, in only three such sites, a streamhead savanna/pocosin and two bottomland swamps. The group, in contrast, was frequently observed in unnatural wetlands such as old mill ponds, other man-made ponds, borrow pits, and streamheads with deep pools where drainage was impeded by road berms.

Sphagnum trinitense/S. mississippiense also appeared to be quite scarce in the SH as it was found only in a couple of impoundments and in one streamhead where deep pools had formed due to the damming effect of a road crossing. My field observations suggest that *S. trinitense/S. mississippiense* is rare in natural wetlands in the SH. This

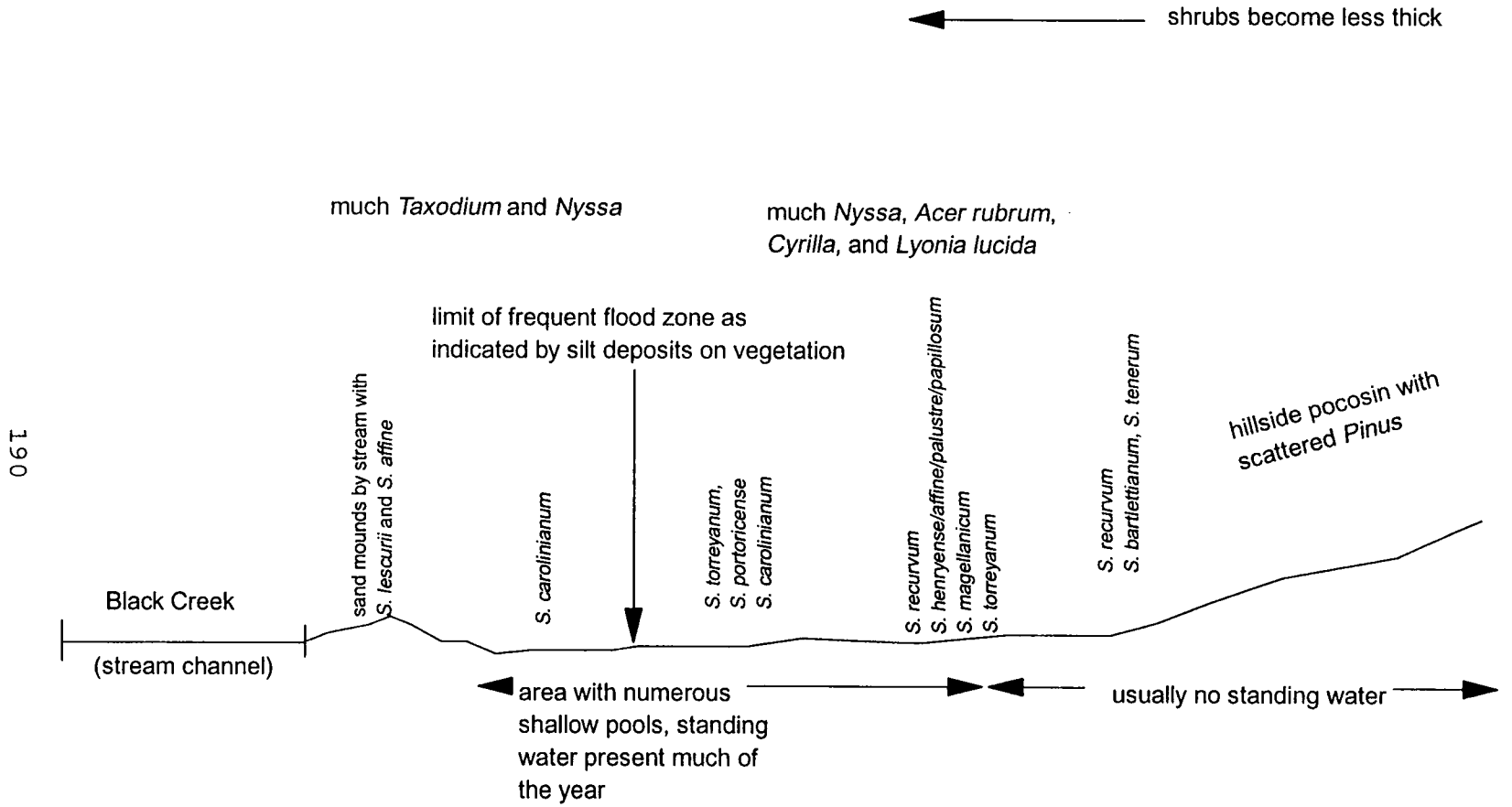


Figure 47. Typical arrangement of *Sphagnum* species along a transect from Black Creek, through a backwater swamp, and up to an adjoining hillside pocosin in the Carolina Sandhills National Wildlife Refuge.

supposition is further supported by an examination of numerous herbarium specimens (DUKE) collected from the SH. With the exception of two collections, all specimens of *S. trinitense/S. mississippiense* from the SH were collected from impoundments. Nearly all specimens (DUKE) of *S. cuspidatum/S. viridum* from the SH were from altered or artificial wetlands as well.

Thus my field observations suggest that *S. torreyanum* is the most common member of the complex in natural wetlands of the Sandhills. *Sphagnum cuspidatum/S. viridum* and *S. trinitense/S. mississippiense* may be rare in such habitats.

Apalachicola National Forest and Vicinity

Sphagnum cuspidatum/S. viridum, *S. trinitense/S. mississippiense*, and *S. fitzgeraldii* were collected from this area.

Sphagnum cuspidatum/S. viridum appeared to be much more common than the other two groups. *Sphagnum cuspidatum/S. viridum* was collected from shrubby thickets with shallow pools, *Cliftonia* swamp forests, pond margins, and at savanna-cypress swamp ecotones. The group was not observed in the numerous savannas and savanna-swamp ecotones in the Post Office Bay area, though *S. portoricense* was often impressively abundant here.

Sphagnum trinitense/S. mississippiense appeared to be scarce in the western half of the ANF as it was collected

only from along the margins of two ponds and one roadside ditch.

Sphagnum fitzgeraldii was infrequently observed. It was collected from hillside seeps, savanna pools, and roadside ditches.

Members of the complex were not easily found in natural wetlands in the western half of the ANF except in the vicinity of Sumatra and along Rt. 65 in the vicinity of Wilma.

De Soto National Forest and Vicinity

Sphagnum cuspidatum/S. viridum and *S. trinitense/S. mississippiense* were collected from this area. Although *S. fitzgeraldii* is attributed to southern Mississippi by Andrus (1987), it was not collected during this study. The species may be rare or at least very local in its distribution in this region.

Sphagnum trinitense/S. mississippiense was collected from shrubby thickets with shallow pools, pitcher plant bogs, cypress-gum swamps, titi swamps, and pond margins. This group clearly occurred in greater abundance and in a greater variety of habitats in the DNF and vicinity than in any one of the other four areas from which collections were made.

Sphagnum cuspidatum/S. viridum was generally found in the same habitats as *S. trinitense/S. mississippiense*, but

was clearly less abundant and more ecologically restricted within all habitat types than the latter group. For example, in cypress-gum swamps and titi swamps, where they often co-occurred, *S. trinitense/S. mississippiense* would typically range from floating in pools to well above the water table, whereas *S. cuspidatum/S. viridum* would typically occur only in a few scattered patches along pool margins or around tree bases above the water table.

Sphagnum cuspidatum/S. viridum and *S. trinitense/mississippiense* were both incredibly abundant over a multi-acre area in a wetland 1.5 miles southeast of the Chickasawhay River in Greene County, Mississippi. Other areas where one or both of these species pairs were in abundance were the titi swamp between Hester Creek and Rt. 419, the cypress swamp near the junction of Rt. 397 and U.S.F.S. 397C, and the cypress swamp just north of LA 36 near the Illinois Central Railroad crossing in St. Tammany Parish, Louisiana.

Overall

The two species pairs, *S. cuspidatum/S. viridum* and *S. trinitense/S. mississippiense*, appear to have different habitat preferences and abundance patterns in all five areas. In the CNF, FMNF, SH, and ANF, specimens assignable to *S. trinitense/S. mississippiense* were infrequently encountered. With the exception of a few sites in the FMNF,

S. trinitense/S. mississippiense was collected only from ponds or borrow pits in these four areas. In contrast, *S. cuspidatum/S. viridum* was relatively more abundant and much more widespread in these same areas.

The above pattern was reversed in the DNF with *S. cuspidatum/S. viridum* being the more ecologically restricted and less widespread of the two groups. The ecological breadth exhibited by *S. trinitense/S. mississippiense* in the DNF may be reflect a release from competition due to the near absence of *S. fitzgeraldii* and the lower abundance of *S. cuspidatum/S. viridum* in the area.

On the basis of macroscopic appearance, the *S. trinitense/S. mississippiense* group also appeared to be more morphologically variable in the DNF than in the other four areas. Studies directed toward relating the degree of morphological variability to ecological amplitude in *S. trinitense/S. mississippiense* might provide additional valuable insights into the biology of peat mosses.

The discovery of numerous populations of *S. torreyanum* in the swamp forests of the Sandhills Game Land and the Carolina Sandhills National Wildlife Refuge suggests that additional sites for the species might be found in other portions of the Sandhills region in the Carolinas and Georgia. Most, if not all, of the previously known sites for the species in the Sandhills were from man-made impoundments.

Summation and Conclusions

Morphometric studies of the *Sphagnum cuspidatum* complex in the Coastal Plain of the southeastern United States support the recognition of four species: *S. cuspidatum*, *S. fitzgeraldii*, *S. torreyanum*, and *S. trinitense*. *Sphagnum mississippiense* (Andrus 1987) is interpreted as representing variation within *S. trinitense*. *Sphagnum viridum* (Flatberg 1988) that has been attributed to the southeastern Coastal Plain represents one end of a continuum of variation consistent with that of *S. cuspidatum*.

The specific status of *S. torreyanum* and *S. fitzgeraldii* is supported by morphometric analyses and field observations. Both species are ecologically defined, easily recognized in the field, and taxonomically distinct from other members of the complex on the basis of several microscopic characters.

I agree with the opinion of Andrus (1974) that overemphasis on branch leaf margin features (median and distal branch leaves) has contributed to the neglect of *S. trinitense*. Furthermore, it is my opinion, that statements by various authorities on *S. cuspidatum* having entire (or very nearly so) branch leaf margins is taxonomically misleading. Such a characterization of *S. cuspidatum* is highly inaccurate as the species is expressed in the study area. My own experience suggests that most specimens of *S. cuspidatum* in the southeastern Coastal Plain, floating in pools, will produce denticulate to serrulate margins on the

median and distal leaves. Thus, plants with strongly serrulate median and distal branch leaves should not be assumed to be *S. trinitense*. The occasional identification of such aquatic forms of *S. cuspidatum* as *S. trinitense* has added to the confusion regarding the distinctiveness of these two species.

The results of the morphometric and the seasonal morphology studies presented herein point to the proximal branch leaves as a source of taxonomic characters for the separation of *S. cuspidatum* and *S. trinitense*. The seasonal morphology study demonstrated that proximal branch leaves are much more constant in their characters than median and distal branch leaves. Proximal branch leaf margin and shape, in combination with the appearance of the outer stem cell layers in cross section, provide the most reliable means for separating specimens of these two species.

Additionally, *S. cuspidatum* and *S. trinitense* appear to differ ecologically. In the SH, CNF, FMNF, and ANF, *S. cuspidatum* occurred in a greater variety of habitats and in greater abundance than *S. trinitense*. Except for a few sites in the FMNF, *S. trinitense* was observed in these four areas only in ponds/lakes or pond-like habitats such as borrow pits. Exactly the opposite pattern was observed in the DNF with *S. trinitense* present in shallow depressions in shrub thickets, swamps, ponds, and savannas. In the DNF, *S. cuspidatum* was present in the same habitats, but was less

widespread and less abundant. The underlying basis for the shift in abundance patterns is unknown. These differences in abundance patterns and ecologies lend further support to the recognition of *S. cuspidatum* and *S. trinitense* as separate species.

Sphagnum cuspidatum and *S. trinitense* are often easily distinguished in the field when growing under nonaquatic conditions. In such situations, the capitular branch leaves of *S. cuspidatum* are erect (wet) or recurved (dry), and tubular above, whereas capitular branch leaves of *S. trinitense* are appressed (wet or dry) and not tubular above. Microscopic features of proximal branch leaves and outer stem layers also effectively distinguish between these taxa under such conditions as well.

In situations where the plants are floating, however, the branch leaves of *S. cuspidatum* become much more elongate, lose their tendency to become recurved and tubular above when dry, and tend to be appressed. Additionally, the margins of median and distal leaves become denticulate/serrulate. Thus aquatic specimens of *S. cuspidatum* can be quite difficult to distinguish from aquatic specimens of *S. trinitense*.

Comparative studies are needed to evaluate the reaction norms of *S. cuspidatum* and *S. trinitense* over moisture gradients ranging from strongly emergent to submersed. Such studies could clarify our understanding of the morphological

expressions exhibited by both species over the wide range of moisture conditions in which they occur in the Coastal Plain.

Data from enzyme electrophoresis could be used to estimate the genetic similarity of the four species recognized herein and to further evaluate forms associated with the names *S. mississippiense* and *S. viridum*. The technique may also provide insight into the origin of *S. torreyanum*. The reported chromosome number for *S. torreyanum* (purported polyploid) is twice that reported for *S. cuspidatum*, *S. trinitense*, and *S. fitzgeraldii*. *Sphagnum torreyanum* may have been derived through polyploidy from species within or closely related to the complex.

Although time consuming, intensive morphometric studies can provide a solid basis for making taxonomic decisions. The examination of a large number of specimens allows one to assess the nature of variation patterns exhibited by a group for one or more characters. As a result of this work I find no basis to recognize the species names *S. mississippiense* and *S. viridum* as distinct taxa of the *S. cuspidatum* complex in the southeastern Coastal Plain. The analysis of characters indicates they are better regarded as extremes of continuous morphological variation.

Key to the *Sphagnum cuspidatum* Complex in the Coastal Plain of the Southeastern United States

1. Plants robust, coarse, and stout-stemmed; branch leaves bristly erect when wet; cells of the outermost layer of the stem smaller than those of the second cell layer of the stem; stem leaves as broad as long .....*S. torreyanum*

1. Plants usually smaller, softer, and weak-stemmed; branch leaves imbricate to slightly appressed or only weakly erect when wet; cells of the outermost layer of the stem as large as or larger than those of the second cell layer of the stem; stem leaves 1.3 or more times as long as wide 2

2. Capitular branches truncate and ascending; branch leaves with truncate to broadly rounded apices and with nearly parallel sides; stem leaves typically narrower at the base than at the middle.....*S. fitzgeraldii*

2. Capitular branches not truncate and not noticeably ascending; branch leaves with narrow or sharply pointed apices, sides not parallel; stem leaves broader at the base than at the middle.....3

3. Plants with capitular branch leaves recurved and tubular in the distal half (highly aquatic forms will often lack these two features); capitula with a crisped appearance, usually flat-topped in side view; proximal branch leaves entire or only denticulate near the apices; outer stem cell layers strongly differentiated in size from inner stem cell layers.....*S. cuspidatum*

3. Plants with capitular branch leaves imbricate to appressed and not tubular in the distal half; capitula without a crisped appearance, capitula usually hemispheric in side view, capitular branches with the appearance of straightened horns; proximal branch leaves usually denticulate to halfway down the margin or more; outer stem cell layers poorly differentiated in size from inner stem cell layers.....*S. trinitense*

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Appendices

Appendix A

Locality Data for Specimens from the Five Areas

To facilitate use of this listing, the collections are ordered by collection number within each area. The number in parentheses after the collection number indicates the group designation based on appearance under a dissecting microscope. The designations correspond to: (1) *Sphagnum cuspidatum/S. viridum*, (2) *S. trinitense/S. mississippiense*, (3) *S. fitzgeraldii*, (4) *S. torreyanum*, and (5) Hybrid?. A complete set of these specimens is in TENN and in the herbarium of Morehead State University. A nearly complete set is at DUKE.

Apalachicola National Forest

20 March 1991

5042 (2) - Walton Co., 11.0 miles north of Bruce via Rt. 81.

22 March 1991

5089 (1) - Liberty Co., 6.6 miles northwest of Sumatra via Rt. 379, slightly south of F.S. 123-2.

17 March 1992

6097 (3) - Liberty Co., Sumatra Quad, 1 mile east of Sumatra on Rt. 22, 150 yds. north of road. 30°1'20"N-84°57'52"W.

6098 (1) - ".

21 March 1995

7964 (1) - Liberty Co., Hosford Quad, "Hosford Bog", 1.7 miles west of Hosford on Hwy. 20, north side of road.

7965 (1) - Liberty Co., Telogia Quad, 5.6 miles south of Hosford on Rt. 65, near Western Br., ca. 100 yds. west of road. 30°19'5"N-84°49'39"W.

7969 (1) - Liberty Co., Telogia Quad, 5.6 miles south of Hosford on Rt. 65, near Western Br., slightly east of road. 30°19'5"N-84°49'35"W.

7974 (1) - Liberty Co., Telogia Quad, 5.9 miles south of Hosford on Rt. 65, 100 yds. north of F. S. 132, west side of road. 30°18'47"N-84°49'42"W.

7979 (1) - Liberty Co., Telogia Quad, 6.5 miles south of Hosford on Rt. 65, 70 yds. west of road. 30°18'17"N-84°49'53"W.

7986 (3) - Liberty Co., Telogia Quad, 9.9 miles south of Hosford on Rt. 65, 90 yds. south of F.S. 117, west side of Rt. 65. 30°15'45"N-84°51'10"W.

7987 (1) - ".

22 March 1995

7998 (2) - Liberty Co., Woods Quad, Camel Pond, north shore, near west end of swimming area. 30°16'30"N-84°59'21"W.

8000 (2) - ".

23 March 1995

8005 (1) - Franklin Co., Forbes Island Quad, south side of F. S. 100, across from turnoff to Wright Lake. 29°59'30"N-85°0'5"W.

8012 (1) - Franklin Co., Sumatra Quad, 0.9 mile east of Sumatra on Rt. 22, ca. 150 yds. north of Rt. 22. 30°1'20"N-84°57'53"W.

8014 (1) - Franklin Co., Sumatra Quad, 1.4 miles east of Sumatra, 0.4 mile from Rt. 22 on F.S. 135, 75 yds. south of road. 30°1'8"N-84°57'25"W.

8019 (3) - Franklin Co., Sumatra Quad, 1.0 mile east of Rt. 65 on F. S. 165, south side of road. 30°0'8"N-84°57'10"W.

8021 (1) - ".

24 March 1995

8031 (1) - Liberty Co., Telogia Quad, 1.0 mile east of F.S. 103 on F.S. 105, south of F.S. 105. 30°16'52"N-84°51'20"W.

8037 (3) - Liberty Co., Woods Quad, 0.3 mile west of F.S. 103 on F.S. 105, ca. 100 yds. south of road. 30°16'37"N-84°52'32"W.

8046 (2) - Liberty Co., Woods Quad, ca. 2 air miles east of Camel Pond, pond just west of Sheep Island, along edge of pond north of boat ramp. 30°16'10"N-84°57'30"W.

Croatan National Forest

23 March 1993

6660 (1) - Craven Co., Catfish Lake Quad, north side of Rt. 1100, 0.3 mile southwest of West Prong Brice Cr. 34°56'7"N-77°4'11W.

6666 (1) - Craven Co., Catfish Lake Quad, 1.1 miles northwest of northwest corner of Great Lake, slightly south of Sheep Ridge Wilderness boundary. 34°8'23"N-77°4'50"W.

6671 (3) - ".

6675 (1) - Catfish Lake Quad, north side of Rt. 1100, 100 yds. west of West Prong Brice Cr. 34°56'16"N-77°3'58"W.

6685 (1) - Carteret Co., Masontown Quad, south side of Rt. 1112, west side of Millis Swamp. 34°46'5"N-76°58'25"W.

6686 (3) - ".

6703 (3) - Carteret Co., Masontown Quad, savanna on east side of Millis Swamp. 34°45'57"N-76°58'14"W.

6707 (1) - Carteret Co., Masontown Quad, savanna on east side of Millis Swamp. 34°45'57"N-76°58'14"W.

14 July 1995

8126 (2) - Carteret Co., Salter Path Quad, 0.7 mile west of Broad Cr., 150 yds. north of Hwy. 24. 34°43'17"N-76°57'32"W.

8127 (2) - Carteret Co., Salter Path Quad, 0.7 mile west of Broad Cr., 0.2 mile north of Hwy. 24. 34°43'23"N-76°57'33"W.

8130 (2) - Carteret Co., Salter Path Quad, 0.8 mile west of Broad Cr., 0.2 mile north of Hwy. 24. 34°43'20"N-76°57'39"W.

8135 (3) - Carteret Co., Salter Path Quad, 0.7 mile west of Broad Cr., 0.2 mile north of Hwy. 24. 34°43'25"N-76°57'36"W.

8137 (2) - Carteret Co., Salter Path Quad, Patsy Pond, 1 mile west of Broad Cr., 0.5 mile north of Hwy. 24. 34°43'32"N-76°57'22"W.

8140 (1) - Carteret Co., Salter Path Quad, Patsy Pond, 1 mile west of Broad Cr., 0.5 mile north of Hwy. 24. 34°43'32"N-76°57'22"W.

8143 (2) - Carteret Co., Masontown Quad, pond near jct. of F.S. 177 and 177A (pond is north of 177A). 34°47'5"N-

76°57'14"W.

15 July 1995

8147a (1) - Jones Co., Maysville Quad, 300 yds. north of F.S. 766. 34°59'26"N-77°10'57"W.

8150 (1) - ".

16 July 1995

8154 (3) - Carteret Co., Hadnot Creek Quad, western edge of Pocosin Wilderness, along F.S. 1105. 34°46'58"N-77°3'0"W.

8157 (1) - Carteret Co., Hadnot Creek Quad, Pocosin Wilderness, ca. 0.4 mile east of end of F.S. 1105. 34°46'49"N-77°2'18"W.

8160 (1) - Carteret Co., Masontown Quad, south of Rt. 1140 and west of Meadows Br., ca. 50 yds. east of house at south end of subdivision. 34°46'50"N-76°54'9"W.

17 July 1995

8161 (2) - Carteret Co., Salter Path Quad, pond 1.4 miles west of Broad Cr., 0.2 miles north of Hwy. 24. 34°43'13"N-76°43'13"W.

8166 (2) - Carteret Co., Salter Path Quad, sinkhole 1.4 miles west of Broad Cr., 0.25 miles north of Hwy. 24. 34°43'16"N-76°43'17"W.

8170 (1) - Carteret Co., Salter Path Quad, pond 1.4 miles west of Broad Cr., 0.35 mile north of Hwy. 24. 34°43'20"N-76°43'15"W.

8173 (1) - Carteret Co., Salter Path Quad, pond 1.4 miles west of Broad Cr., 0.4 mile north of Hwy. 24. 34°43'22"N-76°43'19"W.

8174 (2) - ".

<u>De Soto National Forest and Vicinity</u>

18 June 1993

6807 (2) - Louisiana, St. Tammany Parish, Hickory Quad, 2.9 miles west of Hickory on LA 36, just west of Illinois Central Railroad, north side of road. 30°25'0"N-89°50'0"W.

6814 (1) - Hancock Co., Bay St. Louis Quad, Waveland, wooded

area surrounded by McLaurin St., Old Spanish Trail, and Nicholson Avenue. 30°18'2"N-89°22'27"W.

19 June 1993

6823 (2) - Jackson Co., Gautier North Quad, Sandhill Crane National Wildlife Refuge, along Gautier-Vancleave Rd., 2.4 miles southest of Rt. 57, south side of road. 30°27'44"N-88°40'50"W.

6828 (2) - George Co., Benndale Quad, 6 miles west of Pascagoula R., on MS 26, ca. 50-60 yds. north of road. 30°51'12"N-88°52'0"W.

20 June 1993

6834 (1) - Harrison Co., Airey Quad, 0.1 mile east of West Cr. along Tuxachanie Trail, south side of trail. 30°40'4"N-89°6'55"W.

6835 (2) - ".

6840 (1) - Airey Quad, 0.1 mile east of West Cr. on Tuxachanie Trail, north side of trail. 30°40'8"N-89°6'55"W.

6846 (2) - Ramsey Springs Quad, 0.65 mile west of MS65 on Rt. 397, at jct. of Rt. 397 and F.S. 397C. 30°37'30"N-88°55'45"W.

6848 (2) - ".

6851 (1) - ".

21 June 1993

6858 (2) - Harrison Co., White Plains Quad, 1.5 air miles southwest of White Plains, 0.2 mile south of Tuxachanie Cr. on Rt. 439. 30°32'32"N-88°57'11"W.

6866 (2) - Harrison Co., White Plains Quad, 0.4 mile southwest of Tuxachanie Cr. on Rt. 439. 30°32'28"N-88°57'14"W.

6868 (1) - ".

22 June 1993

6869a (2) - Harrison Co., Airey Quad, near Tuxachanie Trail, northwest side of Duck Pond (impoundment on tributary of Spike Buck Cr.). 30°40'30"N-89°1'30"W.

21 October 1993

6960 (2) - Harrison Co., White Plains Quad, Long Br., slightly east of F.S. 413. 30°34'44"N-88°58'37"W.

6963 (2) - Harrison Co., White Plains Quad, Long Br., slightly west of F.S. 413. 30°34'45"N-88°58'39"W.

6972 (2) - Harrison Co., White Plains Quad, 1.25 miles northwest of White Plains, east of end of F.S. 413-A. 30°34'7"N-88°56'54"W.

6973 (2) - ".

6975 (1) - ".

6977 (2) - ".

22 October 1993

6981 (1) - Harrison Co., Beatrice Quad, along north side of Rt. 402, between Tuxachanie Cr. and Bridge Br. 30°37'59"N-88°59'20"W.

6982 (1) - ".

6997 (2) - Harrison Co., White Plains Quad, swamp area .25 mile north of Tuxachanie Cr. and east of Rt. 413. 30°36'10"N-88°58'10"W.

7005 (2) - Harrison Co., White Plains Quad, 1.4 miles northwest of White Plains Church, between Hester Cr. and Rt. 419. 30°33'36"N-88°57'55"W.

7010 (1) - ".

7011 (2) - ".

7016 (1) - ".

7018 (2) - ".

23 October 1993

7028 (2) - Greene Co., Leakesville Quad, 1.3 miles southwest of Chickasawhay R. on Rt. 63, south side of road. 31°8'24"N-88°31'51"W.

7031 (1) - ".

Francis Marion National Forest

23 March 1994

7235 (1) - Charleston Co., Ocean Bay Quad, 4.7 air miles west-northwest of Awendaw, 0.4 miles southeast of Hwy. 98 and Hwy. 133 jct. 33°3'34"N-79°41'2"W.

7240 (2) - Berkeley Co., Ocean Bay Quad, 5.5 air miles northwest of Awendaw, 0.1 mile southeast of F.S. 174-176 jct. 33°4'41"N-79°42'10"W.

7247 (1) - Berkeley Co., Ocean Bay Quad, 5.5 air miles northwest of Awendaw, 0.2 mile southeast of F.S. 174-176 jct. 33°4'38"N-79°42'9"W.

7250 (2) - Berkeley Co., Ocean Bay Quad, 0.6 mile west of Cropnel Dam Cr., north side of Steed Creek Rd. (Hwy 133). 33°4'32"N-79°43'50"W.

7252 (2) - Berkeley Co., Ocean Bay Quad, 0.6 mile west of Cropnel Dam Cr., north side of Steed Creek Rd. (Hwy 133). 33°4'32"N-79°43'50"W.

7254 (1) - ".

24 March 1994

7260 (1) - Charleston Co., Awendaw Quad, ca. 6 air miles northeast of Awendaw, 0.1 mile southwest of jct. of F.S. 220 & 221. 33°6'24"N-79°34'6"W.

7264 (3) - Charleston Co., Awendaw Quad, ca. 6 air miles northeast of Awendaw, 0.1 mile southwest of jct. of F.S. 220 & 221. 33°6'24"N-79°34'6"W.

7267 (1) - Charleston Co., Awendaw Quad, ca. 7 air miles northeast of Awendaw, along F.S. 221 south of Thompson Corner. 33°6'40"N-79°34'10"W.

7271 (1) - ".

7275 (1) - Charleston Co., ca. 7 air miles northeast of Awendaw, along F.S. 221 south of Thompson Corner. 33°6'52"N-79°34'15"W.

7284 (1) - Charleston Co., ca. 7 air miles northeast of Awendaw, along F.S. 221 south of Thompson Corner. 33°6'58"N-79°34'17"W.

7286 (3) - Berkeley Co., Honey Hill Quad, head of Big Morgan Br., slightly east of F.S. 212. 33°12'3"N-79°30'8"W.

7293 (1) - ".

7296 (2) - ".

25 March 1994

7302 (1) - Charleston Co., Ocean Bay Quad, Halfway Creek Road Carolina Bay, southeast end of bay. 33°2'7"N-79°43'3"W.

7306 (1) - Charleston Co., Ocean Bay Quad, Halfway Creek Road Carolina Bay, interior of bay. 33°2'7"N-79°43'3"W.

7311 (1) - Charleston Co., Ocean Bay Quad, ca. 3 air miles northwest of Awendaw, Wambaw Swamp area, ca. 0.2 mile southwest of sharp curve in F.S. 224. 33°3'45"N-79°39'13"W. (in pocosin-like area).

7316 (3) - ".

7319 (1) - same data as for 7311. (in transition area between pocosin and cypress swamp).

7324 (1) - Charleston Co., Ocean bay Quad, ca. 3.1 air miles north-northwest of Awendaw, near Wambaw Swamp Wilderness, east of F.S. 5099. 33°4'40"N-79°38'10"W.

7329 (2) - ".

7330 (1) - ".

20 October 1994

7723 (1) - Charleston Co., Awendaw Quad, along F.S. 217-A, 0.2 mile east of F.S. 217. 33°5'19"N-79°36'46"W.

7724 (2) - ".

21 October 1994

7727 (3) - Berkeley Co., Ocean Bay Quad, 100 yds. west of F.S. 174-176 jct. 33°4'45"N-79°42'12"W.

7730 (1) - Berkeley Co., Ocean Bay Quad, 0.6 mile west of Halfway Creek Rd.-Steed Creek Rd. jct. on Steed Creek Rd., south side of road. 33°3'51"N-79°42'3"W.

3 January 1995

7809 (1) - Charleston Co., Awendaw Quad, 0.3 mile southwest of Thompson Corner (jct. of F.S. 221 & 215). 33°7'27"N-79°35'24"W.

7812 (3) - Berkeley Co., Ocean Bay Quad, 150 yds. west of F.S. 174-176 jct. 33°4'45"N-79°42'12"W.

7 April 1995

8051 (3) - Charleston Co., Awendaw Quad, ca. 7 air miles northeast of Awendaw, along F.S. 221 south of Thompson Corner. 33°6'40"N-79°34'10"W.

8057 (3) - Berkeley Co., Ocean Bay Quad, 0.4 mile east of F.S. 174 on F.S. 176, ca. 150 yds. south of road. 33°4'42"N-79°41'45"W.

8058 (5) - ".

8 April 1995

8069 (1) - Berkeley Co., Bethera Quad, Ocean Bay Natural Area, south end of Little Ocean Bay, 200 yds. north of road (F.S. 110). 33°13'49"N-79°46'25"W.

8071 (1) - Berkeley Co., Bethera Quad, south of F.S. 110, across from Little Ocean Bay. 33°13'40"N-79°46'25"W.

Sandhills

19 March 1994

7098 (1) - North Carolina, Richmond Co., Sandhills Game Land, Marston Quad, Gum Swamp Lake, 0.2 mile southwest of outlet. 34°54'32"N-79°33'55"W.

7101 (4) - same as 7098 except at 34°54'35"N-79°33'47"W.

7107 (1) - North Carolina, Richmond Co., Sandhills Game Land, near Gum Swamp Lake, across road from outlet of lake. 34°54'35"N-79°33'46"W. Shallow open pool (borrow pit).

7109 (1) - ", but in moist depression of forested area.

20 March 1994

7119 (4) - North Carolina, Richmond Co., Hamlet Quad, 3.4 miles north of Hamlet, Falling Cr., ca. 0.2 mile east of road. 34°56'27"N-79°42'5"W.

7126 (2) - North Carolina, Richmond Co., Hamlet Quad, ca. 6.5 miles east of Rockingham on U.S. 1, Gibson Pond (impounded Chock Cr.). 34°58'19"N-79°39'26"W.

7131 (4) - ".

7148 (1) - North Carolina, Scotland Co., Silver Hill Quad, Sandhills Game Land, Drowning Cr., 0.5 mile southwest of Rt. 1412 bridge, 40 yds. west of road. 34°58'10"N-79°23'5"W.

7154 (4) - same data as for 7148, except for 0.6 mile west of Rt. 1412 bridge. 34°58'32"N-79°23'7"W.

21 March 1994

7183 (1) - South Carolina, Chesterfield Co., Carolina Sandhills National Wildlife Refuge, Middendorf Quad, Lightwood Log Br., Beaver Pond. 34°35'13"N-80°12'52"W.

22 March 1994

7211 (4) - South Carolina, Chesterfield Co., Sandhills State Forest, Black Cr., ca. 0.5 mile south of U.S. 1, east of stream. 34°30'32"N-80°10'50"W.

7215 (1) - ".

7228 (1) - South Carolina, Chesterfield Co., Jefferson NE Quad, 3 air miles south-southeast of Evans Mill, head of tributary of Gum Branch. 34°41'5"N-80°20'13"W.

22 October 1994

7748 (4) - South Carolina, Chesterfield Co., Carolina Sandhills National Wildlife Refuge, Middendorf Quad, Black Cr., ca. 0.2 mile south of Old Wire Rd., west side of creek. 34°32'41"N-80°10'25"W.

4 January 1995

7837 (1) - South Carolina, Chesterfield Co., Carolina Sandhills National Wildlife Refuge, Angelus Quad, head of Big Sandy Cr. 34°36'14"N-80°15'50"W.

7856 (1) - same as 7837, except Middendorf Quad, 0.7 mile north of High Rock, ca. 0.2 mile west of Black Cr. 34°34'53"N-80°9'52"W.

5 January 1995

7874 (4) - South Carolina, Chesterfield Co., Carolina Sandhills National Wildlife Refuge, Middendorf Quad, ca. 0.7 air mile northwest of Middendorf, Black Cr. 34°31'31"N-80°10'25"W.

19 May 1995

8077 (2) - North Carolina, Richmond Co., Sandhills Game

Land, Hoffman Quad, unnamed trib. of Drowning Cr. 35°3'43"N-79°35'26"W.

8084 (1) - North Carolina, Richmond Co., Sandhills Game Land, Hoffman Quad, Lake Bagget (impoundment of Bones Fk.), east shoreline. 35°2'45"N-79°37'18"W.

20 May 1995

8085 (1) - North Carolina, Scotland Co., Silver Hill Quad, 0.5 mile southwest of Silver Hill, Monroe Mill Pond, north side of pond. 34°53'8"N-79°29'28"W.

8088 (4) - ", but at 34°53'8"N-79°29'33"W.

8092 (1) - North Carolina, Scotland Co., Sandhills Game Land, Silver Hill Quad, 0.9 mile west of U.S. 15-501 on Rt. 1332. 34°57'34"N-79°27'38"W.

8096 (4) - North Carolina, Hoke Co., Pinebluff Quad, Drowning Cr., east of U.S. 15-501. 35°1'25"N-79°26'23"W.

8099 (2) - North Carolina, Scotland Co., Sandhills Game Land, Pinebluff Quad, at end of dirt road near game land boundary. 35°0'10"N-79°25'52"W.

8102 (1) - ".

Appendix B

Additional Collections Examined in the Analysis of the *Sphagnum trinitense/S. mississippiense* Species Pair

The information for each listed collection was taken directly from the label on each specimen. Scientific names not italicized on the labels are not italicized herein.

Louisiana, Livingston Parish.

W. D. Reese 11258. *Sphagnum cuspidatum* var. *serrulatum* (det. W. D. Reese). Annotated as *S. cuspidatum* var. *serrulatum* by H. Crum, as *S. trinitense* by R. E. Andrus. Rest area, S side of I-12, 1 mi. W of Holden Exit. Level, wet, open, cut-over Pinus taeda-oak forest. Mostly pine. Some sphagnum in wet depressions. Abundant in small, boggy depression. 8 March 1971. (LAF).

M. G. Manuel 932. *Sphagnum subsecundum* Nees (det. M. G. Manuel). Annotated *S. trinitense* by R. E. Andrus. Rest area one mile west of Holden exit on I-12. Area had been cut over. Alt. ca. 40 ft., Slope flat, assoc. Plants: Pinus taeda L., Myrica sp., and Quercus sp. Long 90°47'W and Lat. 30°30' ca 10"N. 8 March 1971. (BING).

Louisiana, St. Tammany Parish.

W. D. Reese 13757. *Sphagnum cuspidatum* var. *serrulatum* (det. W. D. Reese). Annotated as *S. trinitense* R. E. Andrus. Grassy slash pine forest with wet depressions, 1 - 1.5 mi E of railroad overpass at Florenville on La 36. Magnolia virginiana in low places. Abundant; stranded and dry in low area. 4 Nov. 1978. (LAF).

W. D. Reese 13791. *Sphagnum cuspidatum* var. *serrulatum* (det. W. D. Reese). Annotated as *S. mississippiensis* by R. E. Andrus, as *S. cuspidatum* var. *cuspidatum* by H. Crum. Gravel road ca 8-9 mi E of Abita Springs, Sect. 33-34; shrubby Sphagnum bog right along road, N side. Abundant in bog, now dry. 4 Nov. 1978. (LAF). (**Paratype** of *S. mississippiense* R.E.Andrus).

W. D. Reese 18186. *Sphagnum mississippiensis* Andrus (dup. ver. by R. E. Andrus 1993). 3.2 mi. W of Hickory on LA 36, just W of the Illinois Central RR overpass, N side of road; low, wet pinus-Taxodium forest. Locally abundant in the forest but not common. Growing side by side with WDR 18185 (*S. cuspidatum* Ehrh. cf. *S. viridum* Flatberg) but the two apparently not mingling. 18 June 1993. (LAF).

Mississippi, George County.

W. D. Reese 3030. *Sphagnum subsecundum* Nees. Annotated as *S. cuspidatum* var. *serrulatum* by H. Crum, as *S. trinitense* by R. E. Andrus, as *S. mississippiensis* by R. E. Andrus, as *S. cuspidatum* var. *cuspidatum* by H. Crum. 6.5 miles w of the Pascagoula River on Miss. 26. Abundant in boggy thickets in an open flatwoods. 10 July 1960. (LAF). (**Paratype** of *S. mississippiense* R.E.Andrus.)

Mississippi, Hancock County.

W. D. Reese 3139. *Sphagnum subsecundum* Nees ? (det. W. D. Reese). Annotated as *S. cuspidatum* var. *serrulatum* by H. Crum, as *S. trinitense* by R. E. Andrus. 1.8 miles sse of Santa Rosa along Miss. 43. On soil and litter in wet pine woods along dry slough. 11 July 1960. (LAF).

H. L. Clark 6004. *Sphagnum cuspidatum* var. *serrulatum* (det. W. D. Reese). Annotated as *S. trinitense* by R. E. Andrus. Site of National Aeronautics and Space Administration. National Space Technology Laboratories (formerly Mississippi Test Facility): adjoining east Pearl River. 13 km SE of Picayune. ca. 60 km NE of New Orleans. (long. 89°35', lat. 30°25'). Among sedges in open savanna. Between Drainage Ditch A and Bldg. 1000. 12 March 1976. (LAF).

H. L. Clark 6005. *Sphagnum cuspidatum* var. *serrulatum* (det. W. D. Reese). Annotated as *S. trinitense* by R. E. Andrus. Same locality, habitat, and date as H. L. Clark 6004 above. (LAF).

Mississippi, Jackson County.

W. D. Reese 13928. *Sphagnum cuspidatum* (det. W. D. Reese). Annotated as *S. mississippiensis* by R. E. Andrus, as *S. cuspidatum* var. *cuspidatum* by H. Crum. Sandhill Crane National Wildlife Refuge. Savannas and flatwoods, depression. 21-22 June 1979. (LAF). (**Paratype** of *S. mississippiense* R.E.Andrus.)

J. M. Valentine 9A. *Sphagnum fitzgeraldii* Ren. *ex* Lesq. & James (dup. det. R. E. Andrus 1984). Annotated as *S. trinitense* C. Mull. mixed with *S. lescurii* Sull. by L. E. Anderson. Mississippi Sandhill Crane National Wildlife Refuge. Pine savannah near the dump; ca 3/4 mi due N of I-10 and W of the Vancleave Road. 28-29 June 1982. (DUKE).

J. M. Valentine s.n. *Sphagnum cuspidatum* Ehrh (det. W. D. Reese). Mississippi Sandhill Crane National Wildlife Refuge. Pine savannah. 22 Oct. 1982. (LAF).

L. E. Anderson 24470A. *Sphagnum cuspidatum* Hoffm. (det. by L. E. Anderson). 3 miles west of Hurley. Wet sandy soil, edge of roadside ditch. 11 Nov. 1983. (DUKE).

J. M. Valentine, Jr. s.n. "H". *Sphagnum cuspidatum* Ehrh. *ex.* Hoffm. (det. W. D. Reese). Mississippi Sandhill Crane National Wildlife Refuge. Pine flatwoods; in rain pools and depressions. 9 Dec. 1983. (LAF).

J. M. Valentine, Jr. s.n. "B". *Sphagnum cuspidatum* Ehrh. *ex* Hoffm. (det. W. D. Reese). Mississippi Sandhill Crane National Wildlife Refuge. Wet depressions in pine-Taxodium swamp. 14 Dec. 1983. (LAF).

W. D. Reese 18187. *Sphagnum mississippiensis* Andrus (det. W. D. Reese). Mississippi Sandhill Crane National Wildlife Refuge, Ocean Springs Unit, vic. of nesting territory 7, ca. 100 m W of East Perigal Road, just S of Perigal Bayou; wet open savanna with scattered pine and Taxodium. A single small population ca. 4 m diam., in shallow water with S. perichaetiale and abundant S. cyclophyllum. With Jacob M. Valentine and Scott Hereford. 7 July 1993. (LAF).

Appendix C

The Ten Additional Collections Examined in the Analysis of the *Sphagnum cuspidatum/S. viridum* Species Pair

The information for each listed collection was taken directly from the label on each specimen. Scientific names not italicized on the labels are not italicized herein.

Florida, Franklin County.

B. H. Allen 7585. *Sphagnum viridum fide* R. E. Andrus. Cypress swamp, ca 0.9 mi from Hickory Landing Campground along FS 101B, ca 2 mi SW of Sumatra. T.6S.; R.8W; sec 2. In boggy depression at margins of Cypress swamp. 1 Dec. 1988. (BING).

Louisiana, St. Tammany Parish.

W. D. Reese 18185. *Sphagnum viridum fide* R. E. Andrus. 3.2 miles W of Hickory on LA 36, just W of the Illinois Central RR overpass, N side of road; low, wet pinus-Taxodium forest. Very abundant in the forest. Growing side by side with WDR 18186, but the two not mingling. 18 June 1993. (BING).

Mississippi, Jackson County.

J. M. Valentine 1. *Sphagnum viridum fide* R. E. Andrus. Pine savannah near the dump; ca 3/4 mi due N of I-10 and W of the Vancleave Road; Mississippi Sandhill Crane National Wildlife Refuge. 28-29 June 1982. (BING).

North Carolina, Bladen County.

L. E. Anderson and H. Crum 21982. *Sphagnum viridum fide* R. E. Andrus. Bethel Trail Savannah, Bladen Lakes State Park, east of Elizabethtown. 6 May 1975. (DUKE).

L. E. Anderson 22988. *Sphagnum viridum fide* K. I. Flatberg. White Lake. Hummocks, edge of pocosin. 27 July 1978. (DUKE).

North Carolina, Brunswick County.

R. E. Andrus & L. E. Anderson 3337. *Sphagnum viridum fide* R. E. Andrus. 1.3 mi. W of Orton. Pretty Pond. 12 June 1975. (BING).

L. E. Anderson 21555. *Sphagnum viridum fide* R. E. Andrus. Green Swamp, 5 miles northwest of Supply. Edge of standing water, roadside ditch, savannah. 6 June 1973. (DUKE).

L. E. Anderson 21675. *Sphagnum viridum fide* R. E. Andrus. 9.7 miles southeast of SUPPLY. Pools among low shrubs, cut-over pocosin. 22 May 1974. (DUKE).

North Carolina, Richmond County.

L. E. Anderson 23267. *Sphagnum viridum fide* R. E. Andrus. Gum Swamp Lake, 8.6 miles northeast of HAMLET. Shaded boggy area, lake margin. 6 Oct. 1979. (BING).

North Carolina, Robeson County.

A. C. Risk 1078. *Sphagnum viridum fide* R. E. Andrus. Dunahoe Bay, 3 miles west of St. Pauls, east of Rt. 1743, near junction of Hwy. 20 and Rt. 1743. In small, moist ditch in north side of bay. 30 May 1986. (DUKE).

VITA

Allen C. Risk was born on 14 May 1962 in Lexington, Kentucky, the son of Jerry A. and Betty T. Risk of Versailles, Kentucky. He attended public schools in Versailles and Carrollton, Kentucky, and graduated from Carroll County High School in 1980. In 1985, he graduated from Morehead State University in Morehead, Kentucky, with a Bachelor of Science degree in Biology. In 1988, he received a Master of Science degree in Botany from Duke University in Durham, North Carolina. After teaching high school for a year at West Montgomery High School in Montgomery County, North Carolina, he spent four years as an instructor at Morehead State University.

Allen married Joyce Ann Pigman of Mallie, Kentucky, on 18 August 1984. He has one daughter, Tabitha, born on 31 January 1986.