1991

Multivariate analysis of the Carex brevior group in Iowa

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MULTIVARIATE ANALYSIS OF THE CAREX BREVIOR GROUP IN IOWA

An Abstract of a Thesis

Submitted

In Partial Fulfillment

of the Requirements for the Degree

Master of Arts

Scott C. Zager

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December 1991

ABSTRACT

In Iowa, the most troublesome sedges to identify are Carex brevior, C. festucacea, C. molesta, C. normalis, C. tenera, and C. tenera var. echinodes. These taxa form the C. brevior group--part of an even larger aggregate of species associated with C. straminea. Their morphological features are indistinct and intergrade into one another. Botanists have had difficulty classifying members of this aggregate for nearly 200 years. Some authors have viewed the taxa as separate species, others as polymorphic forms of a single species. Much of the contention has centered upon the variation of taxonomic characters used to delimit and distinguish species.

The objectives of my study were: 1) to randomly sample up to 30 specimens from each population, at several populations of each taxa, to obtain statistical parameters for morphological characters and ascertain if variation occurs within populations, between populations, and between taxa; 2) to evaluate 44 characters and 12 character ratios for each taxa by Univariate Analysis and Stepwise Discriminant Analysis (SDA) and obtain reliable taxonomic characters or character combinations; and 3) to test the validity of taxonomic classifications within the C. brevior group by determining if the morphological forms are significantly different using Canonical Discriminant Analysis (CDA).

There were 450 samples collected at 15 sites (21 populations). The taxa were mostly found in different micro-habitats. Most character means were significantly different ($p < 0.0001$), e.g., means of C. molesta and C. brevior were significantly different for 52 of the 56 characters tested. However, single

characters could not reliably separate taxa because of overlapping ranges of variation. CDA revealed taxa to be significantly different ($F = 24.08$; $p < 0.0001$) along 4 canonical axes. SDA identified character combinations or suites which could reliably delimit and distinguish taxa. There were no subgroups observed within the taxa. Most of the variation expressed by each taxon was found within populations and there were few differences between populations. The characters varied in predictable patterns and this variation is mostly attributed to phenotypic plasticity. However, specimens were found at sympatric sites with unusual character states or mixed character suites, suggesting they are putative hybrids.

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Entitled: MULTIVARIATE ANALYSIS OF THE CAREX BREVIOR GROUP IN IOWA

has been approved as meeting the thesis requirement for the Degree of Master of Arts.

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Date Dr. Daryl D. Smith, Member, Thesis Committee

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ACKNOWLEDGEMENTS

I have the privilege of being Dr. Lawrence J. Eilers' last graduate student; an honor he bestowed upon me for two years after his retirement. Mere words cannot express the magnitude of my gratitude nor my appreciation for his allowing me to perform this study under his direction. While primarily a floristic botanist, he has supervised my study with great insight, always focusing my thoughts toward the principles of good scientific research. He has been a true mentor in every sense. If this study has any significance, it is because he has disciplined my thoughts. If it has any error, it is because he would not restrain my enthusiasm. He has been a leader in preserving Iowa's diminishing natural areas, but he has expressed that his most cherished legacy is the students he has encouraged to become botanists, ecologists and conservationists. I was also fortunate to have assistance from Dr. Kay Klier, a plant taxonomist, whose career I predict will be equally as rewarding to the students she instructs.

I wish to express my gratitude to my committee members Dr. Jane Kotenko and Dr. Paul Christiansen. I especially wish to thank Dr. Daryl Smith who gave me the opportunity to study at the University of Northern Iowa. All are individuals which I greatly admire.

I wish to thank other University of Northern Iowa faculty: Dr. P. Whitson, Dr. O. Schwartz, Dr. A. Orr and Dr. J. Trainer.

I wish to acknowledge The Iowa Academy of Science for funding travel expenses during this study. I also wish to thank Donna Ware and the Delzie Demaree Travel Award Committee for the opportunity to visit the Missouri

Botanical Gardens. I wish to thank the College of Natural Sciences, University of Northern Iowa, for the Lantz Fellowship Award which enabled me to initiate this study.

I wish to thank all the curators for loans, especially Dr. P. Holmgren (NY) and A. E. Schuyler (PH) for their hospitality. Also, I wish to thank Dr. C. Reimers for his assistance in Philadelphia. I gratefully acknowledge Dr. P. Rothrock for his correspondence and assistance in identifying important taxa. I deeply appreciate Dr. A. A. Reznicek for his clarification of Carex straminea. Other individuals I wish to thank include Mark Leoschke, Barbara Wilson and John Nehnevaj for field assistance. I wish to thank Al Ehley, and the Roadside Assistance Office for a place to write.

I wish to thank the Iowa Department of Natural Resources for permission to collect in State Parks and the Iowa State Preserves Advisory Board for permission to collect on Iowa preserves. More thanks to The Iowa Nature Conservancy for reviewing my study and permission to visit their preserves, and the Iowa-Illinois Gas and Electric Company for permission to visit Big Sand Mound Preserve.

Finally, I would like to express my special appreciation to my wife Patty Vander Waal, without whose patience, love, and sacrifice this study would not have been possible. I wish also to thank my parents for their encouragement and support, especially my father who recognized that the world needs good biologists.

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CHAPTER 1

INTRODUCTION

> The same person who has made up his mind that the grasses are very difficult to identify is pretty apt to consider the sedges almost impossible. (Harrington 1977)

Carex is the largest genus within the Cyperaceae, with an estimated 2,000 species. They have a worldwide distribution, but are predominately found in temperate and boreal climates. Mackenzie (1931-1935) listed over 500 species for North America alone. Eilers and Roosa (1991) list 108 species of Carex in Iowa, making it the largest genus in the state. Members of the genus Carex (carices) are found thoughout Iowa in nearly every habitat including residential yards, but are more prevalent in wetlands meadows, river sloughs, marsh borders and fens.

The most troublesome Iowa sedges are Carex brevior, C. festucacea, C. molesta, C. normalis, C. tenera and C. tenera var. echinodes (Gilly 1946). These form a species complex which I informally call the C. brevior group (Table 1). These six taxa are part of an even larger aggregate of species associated with C. straminea, whose morphological features intergrade into one another. Botanists have had difficulty classifying members of this aggregate for nearly two centuries.

The objectives of my study were: 1) to randomly sample up to 30 specimens from each population, at several populations of each taxa, to obtain statistical parameters for morphological characters and ascertain if variation occurs within populations, between populations, and between taxa; 2) to evaluate 44 characters and 12 character ratios for each taxa by Univariate Analysis and Stepwise Discriminant Analysis (SDA) and obtain reliable taxonomic characters

or character combinations; and 3) to test the validity of taxonomic classifications within the C. brevior group by determining if the morphological forms are significantly different using Canonical Discriminant Analysis (CDA).

Table 1. The Iowa taxa of the Carex brevior group (Cyperaceae).

Code	Taxon
B	Carex brevior (Dewey) Mackenzie
F	Carex festucacea Schkuhr ex Willdenow
M	Carex molesta Mackenzie ex Bright
N	Carex normalis (Dewey) Mackenzie
T	Carex tenera Dewey
E	Carex tenera var. echinodes (Fernald) Wiegand

Statement of Problem

Carices are often difficult to classify because of their unique morphology and confusing taxonomic history. Recognition of taxa requires fruits which are mature but not overripe. The perigynia are frequently small, sometimes 2 mm or less in length, and features of the perigynium such as nerves and serrations are important. Accurate measurements of the perigynia are crucial (Voss 1972). Individual taxonomic characters overlap among the taxa and cannot be relied upon with certainty. This, combined with a large number of similar taxa, makes accurate taxonomic keys arduous to construct and use. Many carices were

described before typification of taxa was common practice. In many cases, early authors of taxonomic names did not fully comprehend the boundaries of their classifications. They either included morphological forms of what later became separate species or described only one of the many forms of a particular taxon. Some caricologists placed too much emphasis on a single character for identification. Since Willdenow (in Schkuhr 1801) first described C. straminea there have been no less than 22 treatments involving this species and its allies, including the C. brevior group. During their careers, noted Carex monographers L. H. Bailey, M. L. Fernald and K. K. Mackenzie interchanged names and taxa, e.g., nearly all the currently accepted taxa of the C. brevior group carried the name C. straminea at one time, either as the perceived "type" form or as one of its varieties. Past and present difficulties associated with Carex taxonomy, especially the C. brevior group, can be attributed to nearly two centuries of confusion while botanists struggled to separate taxa through studies of morphology, genetics and ecology in an effort to formulate modern species concepts.

Tuckerman (1843) and many other 19th century botanists classified microspecies of the C. straminea aggregate as varieties of C. straminea. L. H. Bailey (1883) called C. straminea and its allies one of the six most troublesome groups of carices in North America. Bailey (1885) wrote, "C. straminea is remarkable from the fact that all its varieties are connected with the type by a complete series of gradations. The individuals of these intermediate forms are also common." Boott (1862) wrote, "I believe that any one patiently studying the

group from ample material will be obliged to admit that it is impossible to discover exclusive characters on which any satisfactory specific distinctions can be found."

K. K. Mackenzie (1931-1935) described 533 species of Carex in North America alone with very few varieties. He restored the taxa of the C. straminea group to species status, often using highly variable morphological features of the inflorescence, leaf sheath and perigynia. Modern morphological studies of other groups have shown that the characters used by Mackenzie for species distinctions were among the most variable (Reznicek and Ball 1974; Waterway 1990). Fernald (1942) was so exasperated with Mackenzie's choice of taxonomic characters that he wrote, "Suffering for many years from abnormal vision, [Mackenzie] thought he saw. . . what some others could not detect." Gilly (1946) wrote in his monograph:

> . . .the section Ovales comprises one of the most difficult species-groups of the genus Carex. I believe that Mackenzie, and most other modern workers as well, have recognized entirely too many species in this section of the genus. Because of variation among individuals of single colonies, the value of certain characters for the identification of and recognition of species may well be questioned.

M. L. Fernald, who began his long botanical career as a Carex monographer, recognized many of the species in question (Fernald 1950), but challenged the taxonomic characters used to separate them (Fernald 1942). Specimens of the C. brevior group can be categorized into characteristic morphological forms which reoccur throughout regions of North America. These forms have been described under various names in several historical publications. The question becomes: are these forms separate species or polymorphic forms of

a single species?. If they are distinct species then reliable characters are necessary to deliminate and distinguish them. To ascertain the reliablity of taxonomic characters, it is necessary to delimit their ranges of variation. The classification of the C. brevior group, and other similar groups of sedges, hinges on whether taxonomic characters vary because of genetic differences or enviromental influences.

Genetic studies of species groups have indicated that there are low levels of genetic variation within populations and that most of the genetic variation within species occurs between populations (Whitkus 1988; Bruederle and Fairbrothers 1986; Waterway 1990; Bruederle and Jensen 1991). Therefore, it is likely that variation within populations can be attributed to environmental influences (Smith 1967 1969; Smith and Faulkner 1976).

The morphological forms which Mackenzie and others describe are discernable if not entirely distinct for the C. brevior group. These forms consistently reoccur in discrete habitats throughout their geographic distribution. Herbarium studies alone can not determine if variation can be attributed to overlapping taxa or a single polymorphic species (Gilly 1946). Extensive morphological study of each taxon is required at the population level, at multiple sites, to determine if variation occurs within populations or between them (Sokal and Rohlf 1969; Sneath and Sokal 1973). Univariate statistics of randomly collected samples can determine character parameters and multivariate analysis can evaluate taxonomic classifications using several characters in combination even though individual characters overlap among taxa (Sneath and Sokal 1973;

SAS Institute Inc. 1988). Random sampling techniques are required to remove research bias in the selection of morphological forms for statistical analysis and allow statistical inferences to be made about populations of Iowa taxa (Sokal and Rohlf 1969).

Taxonomic Classifications

The Genus Carex

Members of the genus Carex (Cyperaceae) are usually not appreciated for their spectacular floral displays, because Carex is comprised of perennial grass-like species with highly reduced, wind pollinated flowers. Nonetheless, a few species such as C. grayii Carey have inflorescences large enough to be noticed and admired. Peattie (1939) commented that among his colleagues at the U. S. Department of Economic Botany, sedges were most noted for their uselessness. In reality, they are a significant forage for livestock in alpine meadows, steppes, and tundra regions of western North America, northern Europe, USSR and Iceland (Catling et al. 1990). While some species are serious weeds, others have potential applications for controlling erosion and trapping nutrients.

Morphology. Members of the genus Carex (carices) have unisexual flowers subtended by a scale-like bract. The flowers are adapted for wind-pollination and lack vestiges of the perianth found in other sedges, such as bristles or scales. Carices are recognized by a unique structure called the perigynium, a sack-like leaf which completely encloses the pistillate flower and resulting achene. The ovary of the pistillate flower is either lenticular or trigonous with 2 or 3 styles. The perigynium and subtending scale is commonly refered to as the female floret.

However it is more accurately termed a spikelet, because inside the perigynium, and ventral to the pistillate flower, is an aborted axis refered to as the rachilla. Anatomical evidence suggests that the pistillate flower, perigynia and rachilla are derived from an ancestral, multifloral spike (Smith 1966; Smith and Faulkner 1976). The male floret has 3 stamens subtended by a scale-like bract. The vascular arrangement of the staminate floret suggests that it was derived from three, uni-staminate flowers (Smith 1966). Staminate and pistillate structures and their subtending scales will be termed "florets" in the vernacular sense for purposes of this discussion. The florets are arranged in spikes which are either unisexual or bisexual.

Subgeneric classifications. The various arrangements of florets and spikes in the inflorescence provides much of the basis for sub-generic classification within Carex. Gilly (1950 1952) described 111 inflorescence types in 988 species of Carex. There are 3 subgenera of Carex from which 71 sections are described for North America (Mackenzie 1931-1935). Within the sections are subsections, which are further divided into aggregates of morphologically similar species. Species have often been sub-classified into varieties and forms.

Kukenthal (1909) described four subgenera within Carex, of which, Rezincek (1990) recognizes Carex (Eucarex), Indocarex and Vignea. A fourth subgenus, Primocarex Kukenthal, is not recognized because it is thought to be an artificial conglomeration of taxa with only a single spike in the inflorescence.

The genus Carex has been further subdivided into sections and subsections. Tuckerman (1843) was the first to devise a natural classifications system for Carex

apart from the Linnaean system of subgenera (Gray 1843; Robertson 1979). Tuckerman (1843) proposed five sections which he further divided into subsections. Species were grouped into analytical categories and aggregations of morphologically similar species which were treated as varieties of a base species, such as C. straminea. Bailey's (1886) classification system included subgenera, Tuckerman's sections, and subsections (which included the section Ovales). Kukenthal (1909) wrote the most recent worldwide treatment of the genus Carex. His system of subgenera and sections are still in use today (Mackenzie 1931-1935; Fernald 1950; Gleason and Cronquist 1963; Voss 1972, etc.). Mackenzie (1931-1935) created sub-sectional divisions, but never specified their rank. He gave each subdivision a name based on a representative species (e.g., C. festucacea for his subdivision Festucaceae). Hermann (1974) ranked Mackenzie's subdivisions as subsections. I have accepted Mackenzie's Festucaceae and Tribuloideae as subsections, mainly for convenience, but I do not know if these are accepted as nomenclaturally valid. Whitkus (1981) claims they are not.

Recent studies have attempted to define taxa within aggregates or complexes of morphologically similar species (Reznicek and Ball 1974; Whitkus and Packer 1984; Standley 1985 1987; Rettig 1986; Crins and Ball 1989; Bruederle et al. 1989). I have used the term, "species aggregate" as defined by Davis and Heywood (1973) to describe C. straminea and its allies. These form a group of component species, which are taxonomically distinct and presumably closely related but difficult to distinguish. Microspecies within species aggregates tend to have fewer distinguishing characters than other species of the genus. But

it remains to be determined if taxonomic characters of the Carex brevior group are constant and whether the species are effectively isolated from one another.

The Subgenera of Carex

Subgenus Carex generally has unisexual terminal spikes. The lateral spikes are either unisexual or androgynous (monoecious spikes with superior staminate florets). The spikes are mostly peduncled, but occasionally sessile. The ovaries are mostly tri-stigmatic, but sometimes bistigmatic. These result in trigonous or lenticular achenes, respectfully. The perigynia are usually terete or trigonous but a variety of shapes are known. Carex is the largest subgenus with 1,400 species distributed throughout the world (Reznicek 1990).

Subgenus Indocarex has bisexual, androgynous spikes (superior staminate florets) and tristigmatic achenes. The perigynia are trigonous or somewhat terete. There are about 100 species found primarily in the tropics and subtropics of southeast asia, but also in the Paleotropics and Neotropics (Rezinecek 1990).

Subgenus Vignea, which includes the C. brevior group, has bisexual spikes which are usually sessile on the rachis of the inflorescence. The lenticular achenes are usually bistigmatic. Most spikes are androgynous but at least 5 sections, including the Ovales, are gynaecandrous with superior female florets on the bisexual spike. Vignea carices are found mainly in North and South America and in the temperate and boreal regions of Eurasia with some representatives in the Paleotropics (Rezinicek 1990).

The Section Ovales Kunth.

The section Ovales has the largest number of species and is considered the most difficult among North America carices (Mackenzie 1931). Gilly (1946) listed 15 species of the section Ovales in Iowa (Table 2). These are recognized by gynaecandrous spikes with female florets located above the male florets. The perigynia are flat and winged at their margins. The achene is plano-convex or lenticular (biconvex). The following is taken from Mackenzie (1931-1935):

> [Rhizomes] densely caespitose, or with more or less prolonged rootstocks; culms triangular, hollow; leaf-sheaths not red-dotted nor cross-rugulose ventrally, [hyaline] but sometimes green-striated; spikes from 2 or 3 up to 20, with several to many perigynia, the terminal gynaecandrous, the lateral pistillate or gynaecandrous, simple, the inflorescence varying from capitate to moniliform; lower bracts from inconspicuous to very conspicuous; perigynia varying from scale-like or flat (except where distended by achene) to thick and strongly plano-convex, the body subulate to reniform, narrowly to broadly wing-margined, appressed or ascending or spreading, little corky-thickened at base, promimently beaked, the beak sutured dorsally, bidentate, or obliquely cut, usually becoming bidentulate or bidentate, usually serrulate on the margins, rarely smooth; achenes lenticular, apiculate, jointed with the straight, slender style; stigmas 2.

Table 2. Taxa of the Carex, section Ovales in Iowa (Gilly 1946).

Carex bebbii Olney,
Carex bicknellii Britton
Carex brevior (Dewey) Mackenzie
Carex cristatella (Dewey) Britton
Carex festucacea Schkuhr ex Willdenow
Carex molesta Mackenzie ex Bright
Carex muskingumensis Schweinitz
Carex normalis (Dewey) Mackenzie
Carex scoparia Schkuhr
Carex projecta Mackenzie
Carex suberecta (Olney) Britton
Carex sychnocephala Carey
Carex tenera Dewey
Carex tribuloides Wahlenberg

The Subsection Festucaceae Mackenzie (nomina nuda).

Mackenzie's subdivisions were treated as subsections by Hermann (1974), but it is not certain if they were ever validly published. Mackenzie (1931-1935) provided a description to the Festucaceae Mackenzie in a dichotimous key to his Ovales subdivisions which are repeated here in text form:

> Bracts not leaf-like nor conspicuously exceeding [the inflorescence]; perigynia with beak flattened and margined at tip, serrulate to the apex, often bidentate as well as obliquely cut dorsally; scales shorter than the perigynia and noticebly narrower above, largely exposing perigynia above; sterile culms [often poorly developed, leaf-blades erect or ascending, usually clustered at apex]; perigynium-body not obovate, widest near the middle or base.

The Carex brevior Group

The following synopsis of common characteristics of the C. brevior group was adapted from Mackenzie's (1931) descriptions of C. brevior, C. festucacea, C. molesta, C. normalis, and C. tenera:

Vegetative characters: roots densely cespetose; rhizomes short, black and fibrillose; fertile culms 3-10 (15) dm long, slender to base, stiffly erect, ascending or nodding, usually exceeding the leaves, sharply triangular and roughened on the angles beneigth inflorescence, culm base brownish to black and clothed with scenescent leaves, lower nodes not exposed; leaves well developed, either 3-6 or 4-7 regularly distributed on the lower 1/3 to 1/2 of the fertile culm; leaf blades light-green or yellow-green, flat, V-shaped or flanged V-shaped (inversely W-shaped) (terms follow Metcalfe 1971), thin or thick, erect, ascending or spreading, 0.75 to 4 dm long, 1.5-2.5 mm, either 2-4 mm or 4-6 mm wide, rough to very rough on margins; sheaths tight (loose on C. normalis), dorsal side sometimes

septate-nodulose with green or green and white mottled coloration, ventral surface conspicuously white-hyaline, prolonged beyond base of blade and continuous with ligule; vegetative culms conspicuous, with ascending or spreading leaves bunched at apex.

Inflorescence characters: spikes (inflorescence units), gynaecandrous, 3-10, varying from aggregate, aggregate to spreading at base, moniliform (spike tips approximate to spike bases), or strongly moniliform arrangements, rachis flexuous to stiffly erect, 2.5-10 in length, 7-15 mm in width; varying from subglobose to obovoid, 6-16 mm long, 4-8 mm wide, apex varing from blunt to tapering, spike-base varying from truncate, rounded, tapering to long-clavate (lateral spike bases sometimes differing from terminal bases); staminate florets few to numerous, ranging from inconspicuous to nearly half the spike; inflorescence bracts either short and scale-like or with a setaceous bristle of varying length; scales ovate, apex obtuse, acute or short accuminate, green-hyaline with 3-nerved center (golden yellow at maturity), scale width narrower than or equal to perigynium width, scale length shorter than or exceeds perigynium beak.

Perigynium characters: perigynia 10-30 per spike, appressed, ascending or widely spreading, plano-convex or slightly concavo-convex, subcircular, broadly ovate or narrowly ovate, rounded at base, tapering, constricted to abruptly narrowed to beak tip, 2.5-6 mm long, 1-4 mm wide, narrowly or broadly winged to base, serrulate above middle, membraneous or coriaceous, faintly to strongly 5-7 nerved on dorsal surface over achene, faintly to strongly (0-7) nerved on ventral surface over achene (sometimes strongly nerved at perigynium base), some

species with nerves in the wings, usually green-white becoming brown or straw-colored at maturity; beak length 1/4 to 1/2 perigynium length, beaks are obliquely cut at apex, bidentate, with dorsal (abaxial) suture.

Achene characters: achenes ovate, elliptical to oblong, 1.25-2 mm long, 1-1.75 mm wide, apiculate, sub-stipitate to stipitate at base, yellow to brown; styles straight (sometimes bent at base), jointed with achene, deciduous, 2 stigmas.

The Taxonomic History of the Carex brevior Group.

The C. brevior group is an informal name for 5 species and one variety which resemble one another and presumably are closely related. The morphological forms intergrade into one another and are part of an even larger aggregate of North American carices which Boott (1862) called "C. straminea and its allies." Specimens of the C. brevior group have been closely associated with the name C. straminea. There have been at least 22 different taxonomic treatments which included the Carex straminea aggregate. These treatments either classified taxa within the aggregate as varieties of C. straminea or as distinct species. L. H. Bailey (1885) combined seven currently recognized taxa under the name C. straminea without describing any varieties, while Olney (1870) created numerous varieties and forms in an effort to descriptively document variation within the aggregate. In addition, there has been ambiguity about which form or taxon was represented by the type of Carex straminea. There were periods of time when specimens of either Carex brevior or Carex tenera were thought to be the "typical" form of Carex straminea. Treatments of these periods describe and illustrate Carex brevior or Carex tenera as Carex straminea. What

follows is a brief description of the taxonomic history for each taxa of the Carex brevior group and Carex straminea. A referenced nomenclator of the C. brevior group and C. straminea is provided in Appendix A.

Taxonomy of Carex straminea

The taxonomic problems associated with C. straminea began with the original description by Willdenow in Schkuhr's (1801) monograph. According to A. A. Reznicek (pers. comm.), Willdenow received the Reverend Klaproth's specimen from North America probably before 1800. Willdenow named it C. straminea and sent it with a short description to Schkuhr. Willdenow's original description of the perigynium was "capsulis obovatis acuminatus" and Schkuhr's illustration (1801: Tab. G No. 34) shows an obovate perigynium with a short acuminate beak. No specimen filed under C. straminea in Willdenow's Herbarium in Berlin nor in Schkuhr's Herbarium in Halle fits this description or illustration. Willdenow (1805) changed his description of C. straminea in the fourth revision of Linneaus' Species Plantarum. The perigynium was then described as "fructibus subrotundo-ovatis rostratis bidentatis", i.e., the perigynium subcircular to ovate, provided with a long, bidentate beak. Schkuhr (1806) repeated Willdenow's second description in his revision and illustrated (Fig. 174) the perigynium of Klaproth's specimen No.17177 to show a round body and a long narrow beak. Schkuhr annotated the herbarium sheet of C. straminea at Halle with "the neck of the capsule in No.34 is drawn somewhat too short" (Reznicek pers. comm.). The confusion over the true identity of C. straminea lasted until Svensen (1938) fixed the type to Klaproth's specimen in Willdenow's

Herbarium. In the interim, several specimens of other taxa were erroneously identified as C. straminea, and the name was attached by various botanists to specimens of C. brevior (Dewey) Mackenzie, C. tenera Dewey and C. albolutescens Schweinitz (Boott 1862; Bailey 1889; Mackenzie 1922).

Besides the type specimen of C. straminea collected by Klaproth, there are specimens of other taxa attached to the herbarium sheets of Schkuhr and Willdenow. Most are too immature and fragmented for positive identification by Dr. A. A. Reznicek (pers. comm). Schkuhr's specimens were received from Reverend Muhlenberg: one is C. cristatella (Dewey) Britton; the other resembles C. bebbii (Bailey) Fernald or C. normalis (Dewey) Mackenzie. Attached with Willdenow's type of C. straminea is another specimen, possibly C. tribuloides Wahlenberg. Also, Schkuhr's herbarium sheet of C. straminea has a fragment packet containing perigynia of Willdenow's type (Reznicek pers. comm.). I have examined Muhlenberg's herbarium at PH and found specimens of C. cristatella and C. normalis filed under the name of C. straminea.

Mackenzie (1915) finally sorted out the true identity of C. brevior, C. tenera, and C. festucacea, but he misinterpreted specimens of C. albolutescens as C. straminea. Mackenzie (1922 1931 1940) viewed the two Schkuhr illustrations of C. straminea as variants of C. albolutescens. Initially, Mackenzie (1915) wrote that Schkuhr's (1801) illustration was the true form of C. straminea and that Schkuhr's (1806) illustration depicts C. straminea var. brevior Dewey. Later, Mackenzie (1922) declared C. albolutescens a synonym for C. straminea sensu Mackenzie (1915). Mackenzie's (1940) figure 184 of C. straminea depicts a

perigynium taken from a specimen of C. albolutescens. The body of this perigynium is nearly oval and closely resembles Schkuhr's (1806) figure 174. Svenson (1938) discovered that the name C. straminea should be applied to specimens known by C. richii Mackenzie. This in turn required the name C. albolutescens Schweinitz be revived for the taxon treated as C. straminea by Mackenzie (Rothrock 1991).

The Taxonomy of Carex brevior

Many specimens of C. brevior were annotated, described, and/or illustrated as the "typical form" of C. straminea by Torrey (1836), Carey (1856), Boott (1862), and Bailey (1886). I attribute the erroneous association of C. brevior and C. albolutescens with the name C. straminea to Chester Dewey, who serially published his monograph on the genus Carex from 1818 until his death in 1867. In Dewey's (1826a) original description of C. straminea var. brevior, he wrote, "It was this variety which was described by Willdenow and to which the name was given." Dewey also suggested that C. albolutescens is a variety of C. straminea. Late in his life, Dewey (1867) annotated Schweinitz's isotype (GH) of C. albolutescens as a synonym for his variety brevior.

C. albolutescens was initially described by Schweinitz (1824) in a leg of a key, but it never appeared in Schweinitz's (1826) monograph edited by John Torrey. Bailey (1893) restored the name C. albolutescens to specimens annotated by Torrey as C. straminea var. foenea (= C. longii) (In Muhlengerg's herbarium (PH), I found specimens labeled Carex foenea Muhlenberg to be a synonym for C. longii Mackenzie).

Dewey (1826a) cites Wahlenberg (1803) as the source of the primary description for C. straminea Willdenow. Wahlenberg (1803) described the perigynium of C. straminea as being subcircular to obovate. Many forms of the perigynia of C. brevior are subcircular (Boott 1862). Typically, the perigynia of C. albolutescens is obovate (Rothrock 1991), but it also has orbicular forms (Mackenzie 1931).

The Taxonomy of Carex tenera

Bailey (1889; 1890) mistakenly associated Willdenow's type of C. straminea with specimens known by Carey, Sartwell and Olney as C. tenera Dewey (= C. hormathodes). Following this, specimens of the typical form of C. tenera Dewey were named C. straminea by Mackenzie (1896 1913), Fernald (1902 1908) and Kukenthal (1909). Specimens of C. hormathodes Fernald were mistaken for C. tenera Dewey by Sartwell, Olney, Bailey (1883; 1885), Mackenzie (1896; 1913) and Fernald (1902). In fact, Chester Dewey facetiously annotated specimens of C. hormathodes as C. tenera Olney not Dewey, essentially accusing S. T. Olney for the origin of the error. Much chagrined by this, Olney wrote a long annotation claiming he was "surprised on receiving Boott's (1862) illustration to find myself quoted under these plants as C. tenera Olney" (GH). Kukenthal (1909) cited illustrations of C. hormathodes as depicting C. tenera Dewey. Fernald (1906) distinguished Dewey's "original" specimens of C. tenera Dewey (GH) from specimens of C. hormathodes (Boott) Fernald; meanwhile, Dewey's type specimens of C. tenera were classified as C. straminea until Mackenzie (1915). Mackenzie (1931-1935) designated Dewey's original specimens of C.

tenera as lectotypes. The best illustration of Dewey's original C. tenera is Boott's (1862) figure 384.

The Taxonomy of Carex tenera var. echinodes

Fernald (1902 1950) described C. tenera var. echinodes Fernald as having "tips of the slightly longer perigynia divergent and conspicuous." Kukenthal (1909) reduced its classification to forma echinodes. Neither classification is recognized by Mackenzie or later authors. Mackenzie's (1940) illustration of the perigynium of C. tenera appears similar to variety echinodes with a relatively narrower perigynium and slightly longer beak than Dewey's type. The illustrations of Gleason (1952) and Voss (1972) were taken from Mackenzie (1940). Many other authors have used these illustrations.

The Taxonomy of Carex festucacea

The taxonomy of C. festucacea Schkuhr ex Willdenow is equally as confusing. The original description of C. festucacea by Schkuhr appeared in Willdenow (1805). Later, Schkuhr (1806) illustrated C. festucacea in figure 173. The type specimens of C. festucacea are missing, however, Schkuhr's illustration fixes the application of the name (Rothrock 1991). Dewey (1824 1836) placed too much emphasis on clavate spike bases for the recognition of C. festucacea. Despite Torrey's (1836) warning that this character was unreliable, many later botanists used the clubbed-shaped spike base as the only criteria for recognizing C. festucacea. Consequently, specimens of several taxa were identified as C. festucacea (see Boott 1862).

Somehow the name C. festucacea became associated with specimens currently named C. merritt-fernaldii (Bailey 1889, Mackenzie 1896 1913 and Fernald 1902 1908). Fernald (1902) wrote: "Schkuhr's C. straminea of figure 174 which we now know to be different from Willdenow's plant of that name, was an extreme form of C. festucacea (= C. merritt-fernaldii)." Both Fernald (1902 1908) and Mackenzie (1896 1913), described and illustrated specimens of C. merritt-fernaldii Mackenzie under the name C. festucacea (Mackenzie 1922). Fernald (1902 1908) classified specimens of C. brevior as C. festucacea var. brevior (Dewey) Fernald.

The Taxonomy of Carex normalis

Specimens now known as C. normalis (Dewey) Mackenzie have been well defined and easily recognized since Dewey's (1836) original description as C. mirabilis. However, there have been several different varietal synonyms assigned to the taxon reflecting the various interpretations of its relationship to other species: Tuckerman (1843) classified it as a variety of C. straminea; Boott (1862) saw it as a variety of C. cristatella; and Olney (1870) treated it as a variety of C. tribuloides. The morphology of C. normalis is intermediate between C. tenera and C. tribuloides. These species represent two distinctive morphological aggregates of species recognized by Mackenzie (1931-1935) as subsections Festucaceae and Tribuloideae.

Fernald (1902) described "C. normalis" var. perlonga which he later reduced to a forma perlonga (Fernald 1950).

The Taxonomy of Carex molesta

Mackenzie (1931-1935) described C. molesta and distributed isotypes from Quindaro, Wyandotte County, Kansas. However, Bright (1930) previously published the name C. molesta Mackenzie with a description of a specimen from Pennsylvania. Rothrock (1978) has cited this specimen as the type and declared the proper name to be C. molesta Mackenzie ex Bright. Bright's isotype (PH) is the same species as Mackenzie's isotypes (KSU). Gates (1940) classified the taxon as C. brevior var. molesta. Gleason (1952) and later Cronquist (Gleason and Cronquist 1963) considered the taxon as part of C. brevior or a putative hybrid created by C. brevior x C. normalis. Both Fernald (1950) and Voss (1972) recognized C. molesta as a distinct species.

Carex Evolution, Morphology and Genetics

Phylogenetic Development of the Inflorescence

Evolutionary relationships among and within the genera of the tribe Cariceae (Carex, Kobresia, Unicinia, and Schoenoxiphium) are poorly understood and probably remain so until generic and subgeneric relationships are well defined (Reznicek 1990; Crins 1990). Evolutionary hypotheses for the Cariceae are based primarily on developmental patterns of the perigynium and inflorescence among the genera (Gilly 1950 1952; Nelmes 1952; Smith and Faulkner 1976; Rezincek 1990). It is generally assumed that Carex species with monospicate inflorescences are derived from precursors with multiple spikes on highly branched inflorescences through a series of reductions in a manner similar to Zimmerman's (1930) theory of organogenesis. The opposing hypotheses best

espoused by Smith and Faulkner (1976) and Rezinicek (1990) differ on which subgenera of Carex have the primitive or the advanced form of the inflorescence. While the interpretations differ, both hypotheses agree that the diverse forms of the inflorescence, caused by developmental differences in inflorescence meristems, reflect the evolution (or phylogeny) of the tribe. Morphological development explains the great diversity of inflorescence types among the subgenera, but it also provides insight to the origin of morphological variation expressed by species.

The phylogenetic interpretation of the perigynium is widely disputed, as witnessed by the 18 names recorded for it by Holm (1896). In contrast to its interpretation as a prophyll, it has been considered as a reduced bract, a pericarp, a nectary or disk, a perianth and a utricle. At one time the perigynium was held to be homologous with the palea of the Poaceae and defined as a single bract with its margins fused into a suture on the abaxial or dorsal side (Townsend 1885). Snell (1936) considered it to be a prophyll, or the first leaf of a lateral axis in monocots. In Carex, the prophyll is reduced to a bladeless sheath. Smith and Faulkner (1976) hypothesized that the perigynium was derived from another type of prophyll once called an ochrea (Townsend 1885) but now called a cladoprophyll (Holm 1896). The cladoprophyll is a bladeless leaf sheath surounding bases of inflorescence branches (i.e., peduncles of lateral spikes) of subgenera Indocarex and Carex (Holm 1896; Snell 1936; Holttum 1948; Blaser 1944; Smith and Faulkner 1976). Cladoprophylls are often hidden inside the sheath of a subtending leaf or bract and are either sterile or fertile. Holm (1896)

distinguished the fertile cladoprophylls as "anthroprophylls". There is a third type of prophyll sessile to spike bases of carices within the subgenus Indocarex. Reznicek (1990) describes these as "perigynium-like prophylls" and used the term "inflorescence prophyll" to distinquish them from cladoprophylls.

Anatomical studies of the vascular bundles of the cladoprophyll and the perigynium support the conclusion that they are reduced leaves. Both their vascular morphology and relative position are that of a leaf sheath of Carex (Snell 1936). In addition, morphological studies have shown there is an aborted rachilla or spikelet axis at the ovary base within the perigynium (Snell 1936; Smith 1966). In some species of the tribe Cariceae the rachilla is prolonged and exerted beyond the apical orifice of the perigynium. Therefore, the combined structures of the pistillate flower, rachilla, perigynium and subtending scale, are not actually a single "floret" but a reduced multiforal spikelet in the base of a reduced bract (Snell 1936; Svensen 1972; Rezinecek 1990). The ovary is axillary to an aborted spikelet axis and the scale is analogous to the lower glume of grasses. In addition, the vascular system of carices indicates that the so called "male florets" of the inflorescence are actually derived from at least three male flowers of a former spikelet (Smith 1966).

Smith and Faulkner (1976) believe that Carex prophylls were derived entirely by a process of reduction: 1) the cladoprophyll was created when the lamina was lost, leaving a tubular sheath enclosing the bases of spike peduncles; 2) the development of the rachilla ceased leaving a spike with a solitary ovary (floret); 3) the peduncle supporting the derived "floret" diminished, leaving the ovary and the aborted rachilla inside a tubular "perigynium".

In contrast, Reznicek (1990) hypothesizes independent evolution of the cladoprophyll and perigynium. Reznicek believes the two prophylls were derived by a combination of reduction and proliferation of the rachilla: 1) an ancestral species developed a perigynium precursor which later diversified into what became the tribe Cariceae; 2) cladoprophylls in the subgenus Carex originated from empty pistillate scales at the bases of spikes; 3) the inflorescence prophylls of Indocarex were derived from a perigynium whose rachilla proliferated into the characteristic multifloral spike of Indocarex. Reznicek states his theory is more inclusive of tropical species of Carex, while other theories were based mainly on temperate species.

It is not within the scope of this paper to fully discuss the different hypotheses: Reznicek (1990) does that quite adequately. However, a discussion of the morphological development of the inflorescence is necessary to understand taxonomic relationships within species aggregates. On the basis of morphological development of the apical meristem in Carex and related genera (tribe Cariceae), it is generally accepted that: 1) any inflorescence of Carex can be interpreted as a repeatedly branching system in which each ultimate branch either develops into a flower or aborts; 2) apart from abortion, Cariceae meristems have three possible outcomes: they may become i) male flowers, ii) female flowers, or iii) develop into compound structures, namely spikes; 3) the growth of a male flower primordium is determinate, but growth of a spike primordium is indeterminate and it may develop into anything from a one-flowered female spikelet to a branched bisexual spike; 4) the differences in inflorescence morphology which

characterize the subgenera of Carex are explicable in terms of the relative degree in development of the meristem at female flower nodes (Smith 1966; Smith and Faulkner 1976).

Phenotypic Plasticity and Meristematic Development

The morphology of the inflorescence varies considerably within the genus Carex. Gilly (1950 1952) described 111 inflorescence types in the 988 species he examined. As described above, each of these inflorescence types are derived from three possible outcomes of the meristem, indicating that genetic mutations alter the morphological arrangement of the inflorescence. Large morphological differences between suprasectional taxa may have resulted from an accumulation of gene mutations responsible for inflorescence development. Minute differences of the inflorescences observed within species aggregates may be attributed to a smaller number of developmental alterations. However, morphological development due to genetic differences may be moderated by the environment. Meristems of Carex are affected by hormonal imbalances created by environmental stress which affect the regulation of genes (Smith 1967; Smith 1969; Smith and Faulkner 1976).

Phenotypic variation within species may be attributed to the substitution of any of the possible meristematic outcomes which can occur in the development of the inflorescence. Inflorescence development is controlled by plant hormones. Smith (1967) applied various auxins and cytokinins during and after the transition to the flowering stage. He found that auxins: 1) reduced the number of inflorescences produced while maintaining the number of florets per

inflorescence; 2) increased the number of lateral spikes; 3) induced the production of female florets in potential male sites; and 4) increased the ratio of female florets to male florets in the inflorescence. Kinetins applied continuously throughout the growing season completely suppressed the development of the inflorescence. Specimens treated with 3 weekly treatments exhibited: 1) increased branching in vegetative shoots; 2) reduced numbers of inflorescences and reduced numbers of florets per inflorescence; 3) reduced the height and internode length of the inflorescence, and 4) suppressed branching of the inflorescence. Smith (1969) observed similar morphological responses in specimens where leaves and roots were removed. Removal of leaves upsets initiation and growth of the inflorescence and Smith (1969) concluded that the continued stimuli from leaves is essential for normal development. Removal of roots or root apices disrupts inflorescence initiation and branching, and Smith (1969) concluded that actively growing roots is essential for normal branching to occur. He suggested that normal branching of the inflorescence may depend on an adequate supply of cytokinin from the roots. Smith and Faulkner (1976) discuss an example of inflorescence abnormalities produced in C. flacca which had been trampled by cattle (while dormant) during a wet winter. The abnormalities discribed were similar to those observed by the application of hormones (Smith 1967). Smith and Faulkner (1976) suggested that sex expression within Carex inflorescence can be explained by physiological gradients controled by environmental conditions.

Genetics

Cytogenetics. The unique cytogenetic structure of Carex accounts for both the large morphological diversity between subgenera as well as the morphological similarity of microspecies within species aggregates. The centromere is diffused and not localized on any one portion of the chromosome (Davies 1956). Carex chromosomes have a sticky matrix causing the ends to agglutinate together to form a conglomerate chromosome network with an irregular outline. Chromosomes readily fragment with a portion of the centromere. These pieces can be included in future meiotic divisions, either as separate entities (chromosomes) or by reattachment (Davies 1956).

Wahl (1940) observed a reversal of meiotic divisions. The centromere splits, separating the chromatids during the first meiotic division; the second meiotic division is reductional. Wahl (1940) wrote, "The same number of chromosomes were always found at both metaphase I and II while different and quite irregular numbers were frequently found in the microspore nucleus of a hybrid plant, or an individual with multivalents." Davies (1956) concluded that the reversal of these two divisions preserves chromosomal aberrations.

Agmatoploidy. Aneuploidy is common throughout Carex. Aneuploid chromosome series have been documented in subgenera, sections, species-complexes, and within species (Hielborn 1928 1939; Tanaka 1940; Wahl 1940; Davies 1956; Faulkner 1972; Whitkus 1981 1988; Whitkus and Packer 1984; Hoshino 1981; Nishikawa et al. 1984; Standley 1985; Crins and Ball 1988). In the Carex species examined, there exists a series of chromosome numbers with

haploid numbers ranging from n = 6 to n = 56 (Heilborn 1939; Wahl 1940; Davies 1956; Hoshino 1981). It was speculated that Carex exhibited a high degree of polyploidy, octoploid or higher (Wahl 1940). Heilborn (1939) considered the basic chromosome number was 7, because n = 28, 42, 56 occur in the literature most frequently. Chromosome counts not divisable by 7 were probably produced by aneuploidy. After tabulating chromosome counts of 305 species and 16 varieties, Tanaka (1949) proposed that base ploidy numbers 6, 8, 9, 10 and 12 were secondarily balanced from initial ploidy numbers 3, 4, and 5. These researchers hypothesized that Carex evolution occurred initially by multiple increases in chromosome sets (polyploidy) followed by singular additions and deletions of chromosomes (aneuploidy) (Hielborn 1939; Wahl 1940; Tanaka 1940 1949).

However, Tanaka (1949) reported that no polyploid species had been found in the genus. Davies (1956) stated that autopolyploidy is exceedingly rare in the genus and plays a very small part in the evolution of Carex and she concluded:

> The series [in Carex chromosomes] have almost certainly arisen in the first instance by chromosome breakage, agmatoploidy, and hence the species evolved through small and gradual changes in the course of time. It would therefore seem likely that the lower-numbered species have given arise to the higher numbered, and consequently the series is ascending. However, the fact that the aneuploid series of numbers have arisen by fragmentation, explains why the species with the higher numbers of chromosomes have increasingly smaller chromosomes.

Davies (1956) hypothesis is supported by a more recent study of 50 taxa (46 species and 4 varieties) in 21 sections of Carex (Hoshino 1981). Crins and

Ball concluded that agmatoploidy has been the dominate process of chromosomal evolution in the Carex, section Ceratocystis. Grant (1981) wrote that "fusion and fission of chromosomes (agamatoploidy) in Carex is the accepted hypothesis for chromosome number evolution in the genus, although strict aneuploidy cannot be ruled out."

Davies (1956) found chromosome morphology is a useful taxonomic character which is correlated with morphological arrangements of species within sections. Hoshino (1981) found chromosome races in different habitats and regions of geographic distribution of a species. Speciation is probably initiated by chromosome aberrations forming chromosome races which became geographically isolated. Whitkus (1981) hypothesized that the section Ovales diversified during the pleistocene as glacial ice retreated. He speculated that precursor species colonized the exposed glacial till. Through geologic time, the homogenous glacial landscape differentiated into discrete habitats or microhabitats, ecologically isolating chromosome races which later evolved into species.

Hybridization. Hybridization also played a role in the evolution of Carex (Tanaka 1949; Whitkus 1988). Cytogenetic research in Carex involves using natural and artificial hybrids among closely related species. Heilborn (1928) counted chromosomes at meiotic stages of natural hybrids--specifically heterotypic metaphases in pollen mother-cells. Following meiosis, Heilborn observed variation in the number and size of chromosomes. Meiotic divisions of hybrids results in the formation of functional gametes with additional chromosomes. New chromosome numbers arise in hybrids through the formation of univalents in

meiosis. Tanaka (1940) made crosses in 13 species to yield 19 hybrid combinations. The artificial crosses were successful 37.3% of the time, and Tanaka suggested that natural hybidization occurred frequently and contributed to the origin of aneuploidy.

Intraspecific hybrids are a common occurrance in the genus and Tanaka (1949) reported that 90 out of 149 species examined had several karyotype numbers. Some species were found with as much as 6 different chromosome numbers in an aneuploid series. Hybrid karyotypes are found in the C. brevior group. Wahl (1940) reported that C. festucacea has a trivalent karyotype (2n = 71) which is frequently heteromorphic (Tanaka 1949). Also, C. tenera has races with different chromosome numbers. The C. brevior group forms an aneuploid series (Wahl 1940).

Tanaka (1949) reported that intraspecific hybrids [n = 9 x n = 10 and n = 17 x n = 18] proved fertile with karyotypes composed of herteromorphic bivalent or trivalent chromosomes. Frequently, karyotypes were found with univalents derived from the duplication of chromosomes. Hybrid crosses with larger chromosome numbers [n = 19 x n = 22] varied from cell to cell resulting in differing counts of quadrivalent, trivalent, bivalent and univalent chromosomes (Tanaka 1949). Many of the bivalent chromosomes where non-homologous or heteromorphic pairings. Such structural hybrids account for the production of the aneuploidy in the genus Carex. They result from the duplication or the loss of a few chromosomes through meiotic irregularity. Chromosome hybrids have minimal reductions in fertility (Tanaka 1949; Davies 1955; Faulkner 1973).

Artificial hybridization studies in Carex have concluded that closely related species are easily crossed. Reproductive isolation is maintained in nature through differences in geographical distribution and habitat (Davies 1955; Faulkner 1973; Hoshino 1981; Standley 1985; Whitkus 1988).

Tanaka (1949) documented morphological differences in seed shape which he attributed to extra chromosomes. Davies (1956) noted that chromosome races with differing karyotype numbers can be larger and more robust than most forms of the species. Wahl noted that C. tenera (n = 27) was the larger more robust form of the species.

Population genetics of species aggregates. Carex populations are genetically uniform exibiting little if any heterozygosity and reproductive isolation occurs mainly by selfing or in-breeding (Whitkus 1988; Bruederle & Jensen 1986).

Whitkus (1988) conducted artificial selfing and hybridization among species and races within the C. macloviana D'Urv aggregate (C. macloviana D'Urv. [n = 43]; C. preslii Steudel [n = 40,41]; and C. pachystachya Cham. ex. Steudel [n = 37,38,39,41]. The races exhibited no morphological differences except for the C. pachystachya n = 41 race which represents one extreme of the range of variation within the species (Whitkus and Packer 1984). Isozyme studies showed that members of this group exhibited little genetic diversity with very low levels of heterozygosity and species and races are distinct in nature as no populations are known where two races or species interbreed (Whitkus 1988). Whitkus found that: 1) these plants are self compatible; 2) interracial and interspecific crosses were significant; 3) crosses within races or species were more successful than

interracial or interspecific crosses; 4) there was equal to greater degree of success in selfing than in outcrossing; and 5) apomixis was not a significant occurrance. Whitkus (1988) concluded that an autogamous mating system, one which favors selfing over out-crossing, would maintain reproductive isolation in mixed populations.

Similar conclusions were reached in isozyme studies of the C. crinita Lam. complex (Bruederle and Fairbrothers 1986). The majority of genetic variation was distributed among taxa indicating species are highly differentiated, while allozymes revealed low levels of intrapopulational genetic variation. Within populations of a species, Bruederle and Fairbrothers (1986) found significant deviations from the Hardy-Weinberg expected heterozygosity and high positive values for Wright's fixation index suggesting high levels of inbreeding. The genetic structure of C. flava and C. viridula is also similar to that reported for the C. crinita Lam. complex (Bruederle and Jensen 1991). Genetic diversity was highest among populations within a taxon with relatively little variation found within populations. Low values for the number of alleles per polymorphic locus, proportion of polymorphic loci, and Hardy-Weinberg expected heterozygosity indicate that C. flava and C. viridula are effecting a selfing or in-breeding behavior (Bruederle and Jensen 1991). Genetic diversity was very low within populations of C. mendocenensis and C. gynodynama; and chromosome numbers varied in both species but not within populations (Waterway 1990).

Genetics of the Carex brevior group. Wahl (1940) collected chromosome data from members of the C. brevior group: C. tenera n = 26, 27, and 28; C.

normalis n = 34; C. molesta n = 34; and C. festucacea n = 34 + 3 trivalents. The chromosomal races of C. tenera exhibit some variation in form, with race n = 27 representing the larger, more robust extreme of the species. The trivalent in C. festucacea usually consists of two medium and one small univalents (in three out of 24 plates counted there were 35 bivalents and 1 univalents, the smallest univalent separate from the other pair).

Summary of Literature

Based on the literature, it is clear that members of the C. brevior group form an aneuploid series of morphologically similar, yet probably distinct taxa. These species occur naturally in Iowa and are a subset of the C. straminea aggregate. A review of their taxonomic history clearly indicates a need to study these species at the population level, at multiple sites, to determine which characters (if any) can be used to reliably separate these taxa. If taxa exhibit low genetic variability, as the literature suggests, then morphlogical variation occurring within populations may be attributed to phenotypic plasticity. The significance of taxonomic classifications can be determined using modern statistical techniques. However, due to the nature of the group, any morphological differences will be minute, requiring accurate measurement of morphological characters from a large number of specimens in order to reduce sampling error.

CHAPTER 2

METHODS

Herbarium Study

A preliminary survey of herbaria was undertaken to determine which carices of the section Ovales had previously been collected in Iowa. Specimens of the the Carex straminea aggregate were examined at the following herbaria: University of Northern Iowa, Cedar Falls (ISTC), University of Iowa, Iowa City (SUI), Iowa State University, Ames (ISC), and the Missouri Botanical Gardens, St. Louis (Mo) (abbreviations taken from Holmgren et al. 1981). In order to compare taxonomic literature with historical collections and annotations, loans were obtained from the Gray Herbarium (GH), Bailey Hortorium (BH), Kansas State University (KSU), Missouri Botanical Garden (MO), Philadelphia Academy of Natural Science (PH), and the New York Botanical Gardens (NY).

I visited PH and NY to view their extensive Carex collection and examine specimens of the Carex straminea aggregate collected throughout their geographic range. PH houses the exherbaria of Rev. G. H. E. Muhlenberg, who sent numerous specimens to Willdenow (1805) for description, and that of Rev. Lewis D. De Schweinitz, who with John Torrey, published one of the first critical treatments of Carex in North America (Schweinitz 1824 1826). Most of the specimens illustrated by H. C. Creutzburg for Mackenzie (1940) are found at PH. Creutzburg's illustrations serve to fix Mackenzie's concepts of species to carefully chosen specimens. In addition the Carex collection of Bayard Long, long time co-worker of M. L. Fernald is housed at PH. Both institutions contain several Carex

type specimens, especially PH. The Carex collection of K. K. Mackenzie, some 40,000 specimens, are housed at NY. Representative specimens were borrowed and compared directly to Iowa collections. No morphological data from these specimens were statistically analyzed.

Field Collections

During the growing seasons of 1989 and 1990, a comprehensive field survey of mature fruiting plants was conducted in Iowa for the Carex brevior group. Populations of these taxa were studied from the end of May through August 1989. Two additional populations were visited in June 1990.

Potential study sites were obtained from labels of herbarium specimens and from Iowa floristic studies (Eilers 1975; Roosa, Leoschke, and Eilers 1989). Many former collection sites were revisited. However, most known habitats previously occupied by the group had disappeared, e.g., ephemeral marsh borders, savannas, woodland edges, disturbed grasslands, river raceways, sand dunes and roadsides. Therefore, supplemental sites, with similar habitats, were obtained from documents of the State of Iowa Preserves Advisory Board, Iowa Department of Natural Resources, The Iowa Chapter of the Nature Conservancy and from local county conservation boards. Over 100 sites were investigated throughout Iowa, from which 22 populations were sampled from 15 sites, resulting in over 500 specimen collections.

At each study site, population boundaries for each taxon present were delimited during a preliminary inspection of the area. Ecological attributes within population boundaries were noted, including soil type, topography, and

associated species. The number of plants with fertile culms was estimated for each population. The plants to be sampled were selected according to predetermined numbers randomly generated by a Hewlett-Packard HP-11C calculator. The calculator would generate a decimal value to the hundredths position which was then multiplied by the population size estimate to obtain a whole number. Plants were counted as I walked through the population along a prescribed route, always beginning at the point where I first discovered the population. Along the route, plants were counted from left to right then right to left in about a 5 meter strip. As the count proceeded specimens assigned a predetermined number were collected as a random sample. For statistical analysis, up to 30 plants with mature fruit were sampled from each population. A sample was defined as those portions of a plant collected for character analysis later in the laboratory. A plant (genet) was defined as all the culms (ramets) generated from a common rootstock or short rhizome (Bernard 1990). Within the plant, there can be morphological variation among individual ramets. This variation appears mainly among characters correlated with culm size and developmental stage. In an effort to standardize the selection of vegetatative and fertile culms from which characters were measured, I selected the tallest, most robust culm of each plant, provided it had all the necessary structures. Occasionally there were other ramets with unusual features. These were measured separately as form B of the same sample. Unidentified specimens were classified as unknowns and treated separately until their taxonomic status could be ascertained. Separate groupings of plants within a larger site were considered together as one population.

Laboratory Evaluation

I measured 44 morphological characters (31 quantitative and 13 qualitative) from each dried specimen (Table 3). There were 32 characters measured of the infructescence, perigynium, and achene. The remaining 12 characters were obtained from vegetative and fertile culms. An additional 12 ratios of characters were calculated by the computer for each specimen. Features of the culm and infructescence were measured to the nearest cm or mm as appropriate. Smaller reproductive structures were measured with an optical reticule (12 lines per mm) in a dissecting scope. When evaluating qualitative characters, separate states were assigned a numerical value for statistical analyses.

Statistical Analyses

Morphological data were analyzed using univariate and multivariate statistical procedures (SAS Institute Inc. 1988). These tested the hypothesis that taxa within the Carex brevior group are morphologically distinct and identified useful taxonomic characters. All samples were treated as preclassified Operational Taxonomic Units (OTUs).

Univariate Analyses

The variables of each taxon were analyzed by the SAS Univariate Procedure to obtain means, standard deviations, variances and frequency distributions. Frequency distributions can indicate if further segregations within taxa are needed. Deviations from a normal frequency distribution, such as a bi-modal histogram, may indicate significant differences between populations within a taxon. For each histogram, the SAS Univariate Procedure lists specimens with

the 5 smallest and 5 largest character values of the distribution. This is useful for recognizing specimens which may be misclassified or express character values intermediate with other taxa. The SAS t-test Procedure was performed on paired combinations of taxa in order to identify significant differences ($p < 0.0001$) between variable means.

Table 3. Suite of characters used in scoring specimens for analysis. Vegetative characters were excluded from multivariate analysis. Ratios were derived from measured attributes of characters for each specimen (see Figures 1, 2, and 3).

Fertile Culm Characters:

1 Number of leaves
2 Culm width at widest point (mm).
3 Extended leaf height (cm).
4 Culm height (cm).
5 Height to upper leaf base (cm).
6 Culm height to upper leaf base/ culm height (ratio 5/4).
7 Upper leaf length (cm).
8 Upper leaf width (mm).

Vegetative Culm Characters:

9 Number of leaves.
10 Culm width (mm).
11 Leaves extended height (cm).
12 Culm height to upper sheath apex (cm).

Inflorescence Characters:

13 Inflorescence shape:
(1) linear
(2) oblong
(3) ovoid
(4) globose

14 Inflorescence length (mm).
15 Inflorescence width at widest point (mm).
16 Inflorescence width/length (ratio 15/14).

(table 3 continues)

Spike Characters (Inflorescent Units)(Reznicek 1990):

17 Number of spikes.
18 Spike arrangement:
(1) closely aggregated
(2) loosely aggregated to spreading
(3) moniliform (spikes approximate)
(4) strongly moniliform.

19 Spike length (mm).
20 Spike width at widest point (mm).
21 Spike width/length (ratio 20/19).
22 Spike shape:
(1) subglobose (4) obovoid
(2) globose (5) oblong
(3) ovoid (6) turbinate-obconical.

23 Spike apex shape:
(1) truncate (4) rounded
(2) blunt (5) pointed.
(3) tapering

24 Terminal spike base shape:
(1) truncate (4) short clavate
(2) rounded (5) clavate.
(3) tapering

25 Lateral spike base shape (See 24).
26 Cycles of male florets on terminal spike (Number of revolutions around spike).
27 Cycles of female florets on terminal spike (Number of revolutions around spike including apical floret).
28 Cycles of male florets on lateral spike (Number of revolutions around spike).
29 Cycles of female florets on lateral spike (Number of revolutions around spike including apical floret).
30 Terminal male cycles/terminal female cycles (ratio 26/27).
31 Lateral male cycles/lateral female cycles (ratio 28/29).

Perigynium Scale Characters:

32 Scale length (mm).
33 Scale width (mm).
34 Scale length/perigynia length (ratio 32/36).
35 Scale width/perigynia width (ratio 33/37).

(table 3 continues)

Perigynium Characters:

36 Perigynia length (mm).
37 Perigynia width (mm).
38 Perigynia length from base to widest point (mm).
39 Perigynia width/length (ratio 37/36).
40 Perigynia body shape width/length (Figure 1):
(1) narrowly elliptic (1:3)
(2) elliptic (1:2)
(3) elliptic (2:3)
(4) widely elliptic (5:6)
(5) circular (1:1)
(6) subrotund (6:5)

41 Perigynia length to widest point/perigynia length (ratio 38/36).
42 Position of widest point on perigynium:
(1) mid-point
(2) various intermediate positions
(3) lower third

43 Beak length (apex of achene to tip) (mm).
44 Beak length/perigynia length (ratio 43/36).
45 Beak shape (from perigynium mid-point to beak apex):
(1) tapered
(2) slightly constricted
(3) abruptly constricted

46 Number of ventral nerves on perigynium over achene.
47 Appearance of ventral nerves:
(1) strongly elevated above periynium tissue
(2) finely imbeded in perigynium tissue
(3) barely visible
(4) absent

48 Number of dorsal nerves over achene on perigynia.
49 Perigynia dorsal nerve quality (See No. 47).

Achene Characters:

50 Achene length (mm).
51 Achene width (mm).
52 Achene width/length (ratio 51/50).
53 Achene shape width/length (see 40).
54 Achene position of widest point (see 42).
55 Achene length/perigynia length (ratio 50/36).
56 Achene width/perigynia width (ratio 51/37).

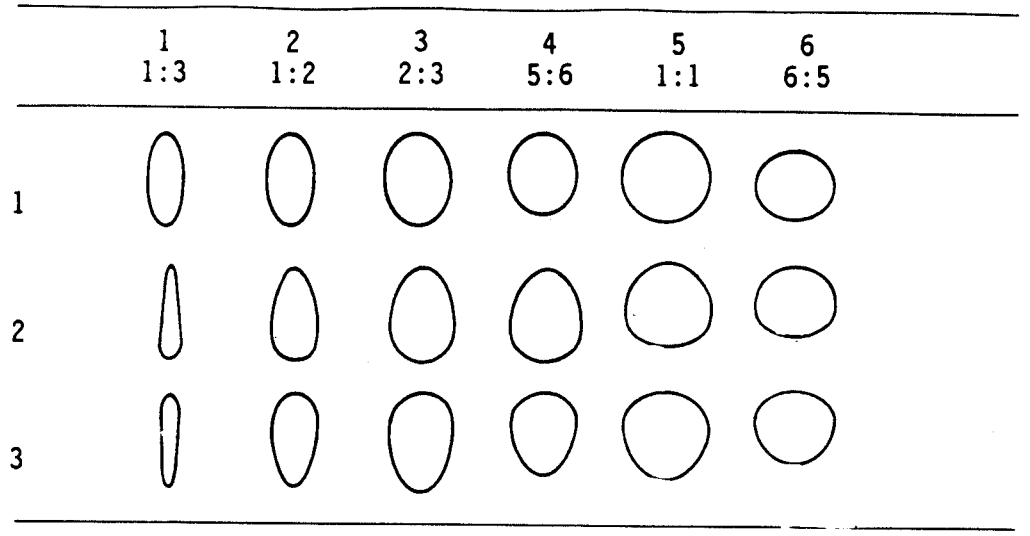


Figure 1. Symmetric plane diagrams adapted from Radford et al. (1974). Horizontal numbers correspond to character states given in Table 3: numbers 40 and 53. Columnar numbers correspond to character states given in Table 3: numbers 42 and 54.

Multivariate Analysis

The validity of taxonomic classifications within the Carex brevior group can be tested using linear discriminant functions. These are F-statistics based on the generalized squared distances between taxon means or (cluster centroids when specimens are plotted in n-dimensional space). In general, multivariate analysis enumerates the various states of a character along a vector. Specimens are plotted at a specific point along this vector depending on the magnitude of the character state they express. The vector's length is a measure of the magnitude of the total variation expressed by all the specimens displaying that character. The set of character vectors which separates the most specimens becomes the first canonical axis. A canonical axis is a suite of correlated character vectors

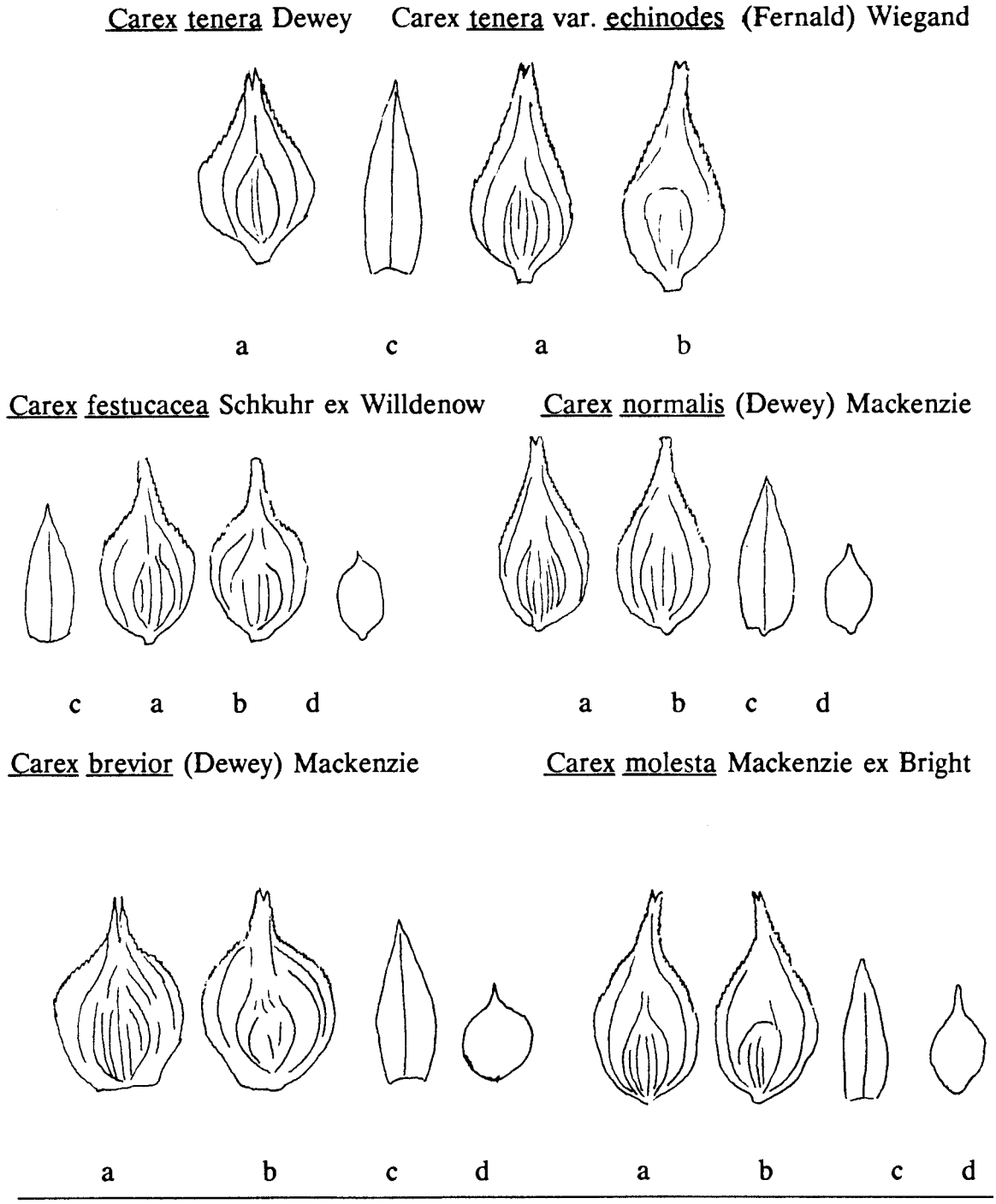


Figure 2. Perigynia of the Carex brevior group (redrawn from Mackenzie (1940) except for C. tenera which is redrawn from Boott (1862). (a) Dorsal surface of perigynium, (b) ventral surface of perigynium, (c) subtending perigynium scale, and (d) achene.

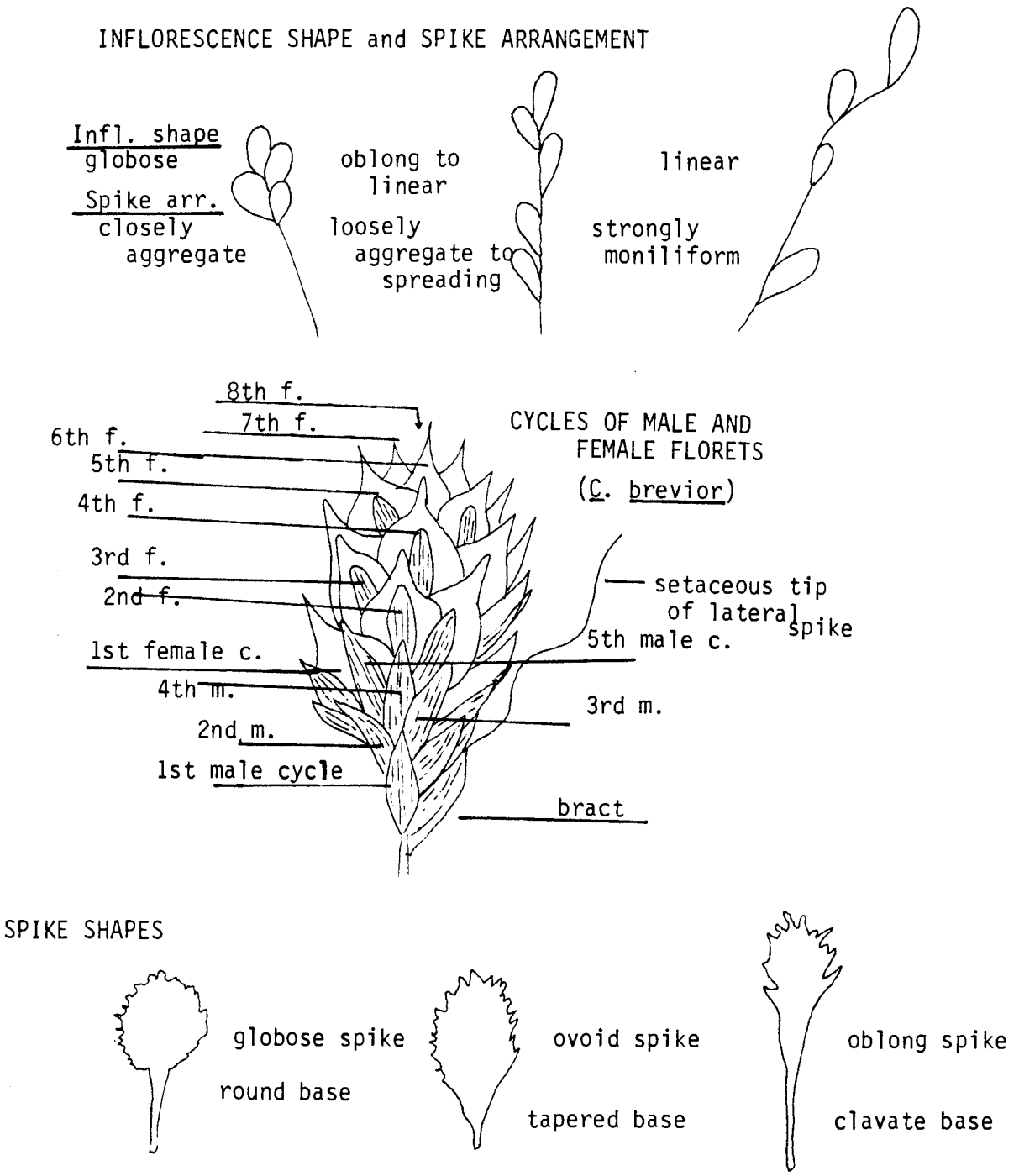


Figure 3. Features of the inflorescence and spike (adapted from Mackenzie (1940).

with a parallel direction. Characters correlated to the first canonical axis explain the largest proportion of the total variation of all the characters expressed by the dataset. Eigenvalues represent the proportion of the total variation explained by a particular canonical axis.

Each character is assigned a canonical coefficient which is the proportion of the character's variation correlated to a canonical axis. A canonical value for each character is determined by multiplying a character's canonical coeficient by the magnitude of the character state expressed by a specimen. A specimen is plotted along a canonical axis by summation of all its canonical values. When specimens exhibit several discriminating characters, they can be plotted along several canonical axes--each with it's own combination of correlated characters. Canonical axes were orthogonally arranged. This results in a multidimensional ordination by which relationships between specimens are illustrated in n-dimensional space. In canonical plots, close proximity among a set of specimens suggests a relationship, such as members of the same taxon. This is illustrated in canonical plots as a cluster of specimens. The relative distance between cluster centroids compared to the average distance from the centroid to each of the plotted specimens within the cluster, can be used as a measure of significance to test whether the total variation between taxa is greater than the total variation within each taxon.

Discriminant Function Analysis (DFA) is a multivariate procedure used primarily to classify OTUs into two or more known classes on the basis of one or more variables. This contrasts with Principle Component Analysis which assumes

no prior class membership because its purpose is to construct a classification scheme. DFA is able to distinguish taxa which closely resemble one another by analyzing variables together even though individual variables overlap considerably between taxa. DFA has two important uses: 1) it can determine if taxonomic classifications are significantly different, and 2) it can evaluate the contribution each character makes in distinguishing taxa (Sneath and Sokal 1973). Stepwise DFA lists characters with the most discriminating power according to the amount of overall variance explained by each character. DFA and Stepwise DFA was performed by SAS DISCRIM procedure. SAS DISCRIM Posterior Error-rate Estimates evaluates the probability that a particular OTU was misclassified.

SAS Canonical Analysis is a DFA procedure which summarizes between-class variation and is capable of plotting specimens on canonical axes. Each canonical plot was illustrated twice in order to depict relationships among specimens according to taxonomic classification and collection site. Specimens occupying intermediate positions between group clusters on cannonical plots were re-examined. Posterior classification of unknown specimens were made when such OTUs fell within a taxon cluster.

CHAPTER 3

RESULTS

Most of the field study was accomplished during the summer of 1989 and completed in June 1990 when populations of Carex festucacea and C. molesta were sampled. Populations of the C. brevior group (Table 1) were sampled at 15 sites throughout Iowa (Table 4). Eight of these were sympatric sites with more than one taxon present (Table 5). The taxa were found in discrete habitats, albeit some were microsites with small environmental differences. There were 450 randomly collected specimens measured for univariate analysis. However, 82 specimens were excluded from multivaritate analysis because of missing values for one or more variables. Sample sites, population sample size, total sample size for each taxon (N), and sampling dates are provided in Table 5. Field observations coupled with herbarium study justify listing C. tenera var. echinodes as a new taxon for Iowa.

Field Observations

Growth Habit of Iowa Ovales

Iowa carices of the section Ovales, (Table 2) exhibit a phalanx growth form (Bernard 1990). Individual plants (genets) reproduce vegetatively from short rhizomes becoming caespitose with numerous vegetative and fertile culms (ramets). At anthesis, genets usually have well developed vegetative culms with nodes and vascular tissue. Within populations, vegetative culms of all developmental stages were present, ranging from those in the protective prophyll (a coleoptile-like sheath which protects the meristem and leaves while

Table 4. Identification codes, site names and county location.

CODE	SITE NAME	COUNTY LOCATION
BSM	Big Sand Mound Nature Preserve	Lousia
CHSP	Cedar Hills Sand Prairie	Black Hawk
FA	Falls Access Wildlife Area	Black Hawk
GWSP	Geo. Wythe State Park	Black Hawk
HP	Hayden Prairie State Preserve	Howard
TFSP	Lake of Three Fires State Park	Taylor
MCP	Martin County Park	Cherokee
OTC	Orono Township Cemetary	Muscatine
PKSP	Palisades-Kepler State Park	Linn
PMP	Private Mesic Prairie	Black Hawk
RTP	Rolling Thunder Prairie	Warren
SRCP	Split Rock County Park	Chickasaw
SCP	Starr's Cave Preserve	Des Moines
VLSP	Viking Lake State Park	Montogomery
WP	Williams Prairie TNC Preserve	Johnson

they develop from the bud of the rhizome) to fully developed ramets with internodes. Some appeared to be pseudoculms or false stems made up of a series of overlapping leaf sheaths. Pseudoculms are recognized by "leaf bases borne very close together, as a rosette, on a tightly compacted stem without discernable internodes (Reznicek and Catling 1986)." These "pseudoculms" appear to be a developmental stage and had no taxonomic value within the C. brevior group. The meristems of late-growing vegetative shoots are capable of overwintering above ground, developing into fertile culms the following spring.

Iowa Ovales carices exhibit sympodial growth where culms develop from apical meristems of rhizomes. The rhizome forms lateral buds which may develop on any side of the developing culm. These lateral buds may produce culms and may eventually form into rhizome branches (Figure 4). The number of

Table 5. Taxon, site code, canonoical plot site code[1], sample size[2], other species presence (mixed or sympatric populations)[3], and date collected.

TAXON	SITE CODE	CANON. SITE	SAMPLE SIZE	MIXED POP.	DATE COLLECTED
Carex brevior	BSM	o	32	*	06-13/89
	SCP	m	2		06-15/89
	CHSP	l	29		06-17/89
	GWSP	i	20		06-22/89
	PKSP	h	10	*	06-26/89
	TFSP	g	19	*	06-27/89
	RTP	d	11		07-03/89
	WP	b	3	*	07-09-89
Total N			126		
Carex festucacea	BSM	a	26	*	06-15/90
Carex molesta	OTC	n	25	*	06-14/89
	SCP	m	31		06-15/89
	FA	j	1		06-22/89
	PKSP	h	16	*	06-26/89
	TFSP	g	4	*	06-27/89
	WP	b	13	*	07-09/89
	BSM	o	2	*	06-15/89
	BSM	a	28	*	06-15/90
Total N			120		
Carex normalis	SRCP	p	2	*	06-09/89
	SCP	m	2	*	06-15/89
	HP	k	2	*	06-20/89
	VLSP	f	1		06-29/89
	PMP	c	22		07-07/89
Total N			29		
Carex tenera	SRCP	p	25	*	06-09/89
	HP	k	26	*	06-20/89
Total N			51		
Carex tenera var. echinodes	MCP	e	16		06-30/89

[1]See Figures 4-6: canonical plots of specimens by site.
[2]A total of 450 specimens were collected of which 368 were statistically analyzed.
[3](*) indicates sympatric site.

ramets per genet were observed to vary from 1 to 160 culms. The circumferences of genets measured at the base ranged from 3.5 cm for a solitary ramet, to 110 cm for 160 ramets. Diagrams of some observed growth patterns are given in Figure 4.

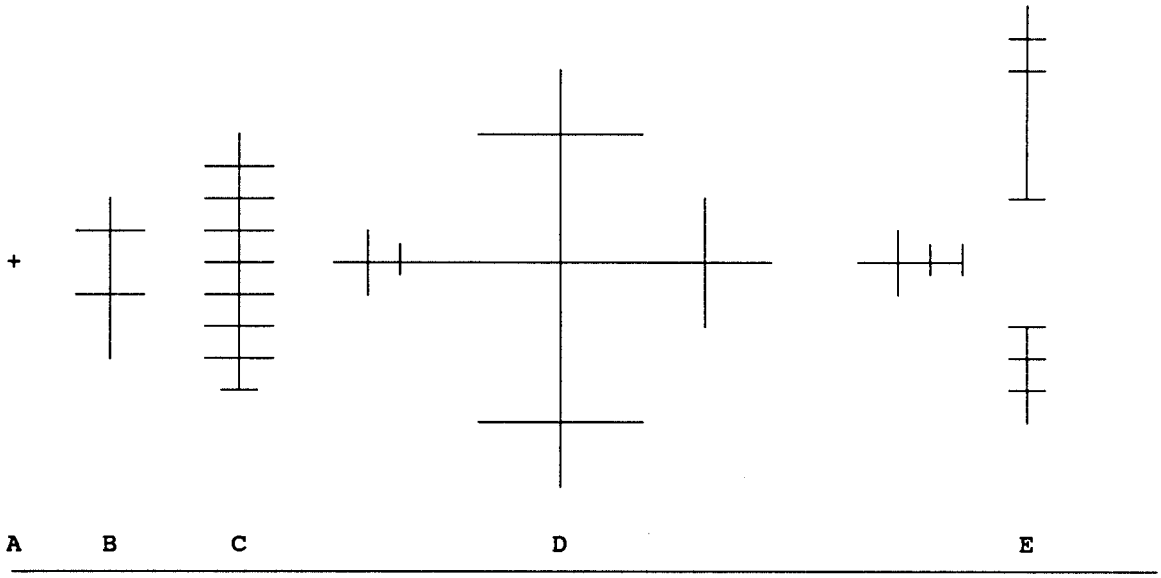


Figure 4. Aerial views of rhizome growth patterns depicting locations of meristems and ramets along rhizome axes. (A) Initial culm developed from seed. (B) Rhizome elongating in 2 directions with 2 apical meristems and 6 culms. (C) Rhizome elongating in one direction with 1 apical meristem and 15 culms. (D) Rhizome appendages elongating in several directions at ends of 4 branches (rhizome has many meristems and culms at the ends, but is barren at center). (E) Fragmented rhizome branches elongating in one to many directions away from the origin.

In grassland habitats, C. brevior and C. bicknellii exhibited directional rhizome growth. These plants appeared to move along the ground in interstitial zones between clumps of grasses, forming new shoots at the growing end and dying at the other end. Often a rhizome would be devoid of shoots for much of

its length, having culms only near the apical meristem. Clusters of culms, appearing to be individual genets separated by several centimeters, would sometimes be connected underground by rhizome branches. In other cases, decay would disintegrate the connecting rhizome leaving individual clusters of ramets scattered throughout an area of two square meters. Several clumps of C. bicknellii ramets were seen at Hayden Prairie in a fairy-ring pattern appearing to originated from a central point. A plant was observed which aborted apical growth of the rhizome when it collided with the roots of Andropogon gerardii. One of the lateral buds then resumed growth, resulting in a rhizome with a 90 degree bend. Generally, the rhizome produces a fibrous root mass (rhizosphere) which forms a thick mat below the soil surface. I found rhizosphere diameters about 3 times that of the genet base (10-20 ramets) in one population of C. brevior growing in disturbed sandy soil. The fibrous root mass of C. brevior provided sites for the establishment of other species. I observed seedlings of Poa pratense and forbs growing in the fibrous roots while none were observed in the soil composed of eolian sand alone. The rhizosperes of larger genets of C. molesta (ramets > 100) occupied sub-surface areas up to a meter in diameter on mud flats along a creek.

Ecological Characteristics

Iowa Ovales are opportunistic species that produce several fertile culms. They quickly dominate disturbed habitats such as marsh drawdowns, shifting sand, sediment deposits and old fields. Ovales carices are weak perennials, and are often replaced in many habitats by more aggresive species with stronger

rhizomatous growth. For example, without continuous disturbance, C. molesta would be crowded out of moist, organic soils by Phalaris arundinacea L. In stable habitats, such as prairie grasslands or wet sedge-meadows, Ovales were found in microsites characterized by localized environmental stress or in ecotonal zones, e.g., woodland edges or interfaces between dry uplands and low wetlands.

Field observations of Carex brevior. At Big Sand Mound (BSM), a region of drifting sand along the Mississippi River, scattered genets of C. brevior were found in swales, slope bases and slight depressions. Most individuals of the population were found along woodland edges. This distribution seems related to increased availablity of soil moisture and reduced competition. At the Cedar Hills Sand Prairie Preserve (CHSP), a few individuals of C. brevior were found persisting in an ecotonal zone between prairie grasses and tussocks of C. stricta. However, a larger number of more vigorous plants were found in an old field of eolian sand currently reverting back to prairie.

C. brevior was also found in old pastures and prairies on loamy soil and on riparian sand bars. At BSM, C. brevior was associated with Ulmus pumila, Calmovilfa longifolia, Eragrostis trichodes, Koleria macrantha, Andropogon gerardii, Carex muhlenbergia, Stipa spp., Asclepias amplexicaulis, Helianthus annuus, Plantago aristata, Tephrosia virginiana, Lithospermum canescens, Tradescantia ohioensis, Amorpha canescens, Mirabilis nyctaginea, and Chenopodium spp.

Field observations of Carex molesta. C. molesta was often found near C. brevior at many sites, but in different microhabitats. C. molesta is larger and

more robust, tending to favor moist, organic soils while C. brevior favors dryer, sandier soils. During sampling, this difference would not be immediately detected because of specimens with intermediate characteristics. The best example of this occured at Palisades-Kepler State Park (PKSP) on an old river channel transecting a meander. There were natural sand levies at both ends, creating a linear, stagnant pool which had been receding. After the initial survey, I began sampling C. brevior on the sandy soil on top of the levy. As I sampled down the 12 foot slope toward the water, I collected samples which displayed intermediate character states. These specimens were difficult to classify. Typical forms of C. molesta were found on slope bases in wet soil composed of organic silts and sand. Both species were also sympatric at William's Prairie Preserve (WP) which has a swale topography. C. brevior was found on small ridges and C. molesta was found in the occasionally flooded swales.

Carex molesta was also sympatric with C. festucacea at BSM, where large genets of both taxa were intermingled on clayey sub-soil exposed when a 6 meter high levy was constructed along the Mississippi river. They and Ambrosia artemisiifolia were the dominant herbaceous cover. Even though ramets of both taxa were intertwined together, they were easily distinguished by features of the perigynia and inflorescence.

C. molesta was also found in the partial shade of alluvial and upland woods, wet-mesic prairies, and roadside ditches. Associated species at PKSP were Phalaris arundinacea, Elymus virginicus, C. stipata, C. cristatella, C. tribuloides, C. annectens, C. brevior, Solidago gigantea, Rudbeckia laciniata, and Salix interior.

Field Observations of Carex festucacea. There was only one population of C. festucacea sampled (BSM). A solitary specimen was collected in a depauperate upland prairie at Gull Point State Park (GPSP) in Dickinson County, IA. This specimen appears to be a disjunct population because all the historical collections were made in eastern Iowa. In addition, Wheeler and Ownbey (1984) report the only Minnesota collection site of C. festucacea is north of Dickinson County, IA.

At BSM, C. festucacea was sympatric with both C. molesta and C. brevior. Specimen # F:101a was collected with C. molesta in partial shade at the base of large sand dune. Its perigynia resembles C. molesta in being slightly longer and lanceolate shaped; however, its spikes are obovate and the inflorescence is moniliform. Most of the specimens of C. festucacea at BSM were found on exposed clay subsoil. The specimens at GPSP was collected on an upland prairie at the edge of a trail which cut into a slope.

Field Observations of Carex tenera. Scattered plants of C. tenera were found in wet-meadows and grasslands. Genets were found growing among several species at Hayden Prairie Preserve (HP) and Split Rock County Park (SRCP). Genets usually had a small number of ramets ($N \leq 20$), but some were occasionally found with up to 60 ramets. The slender culms were weak and frequently nodding. C. tenera perferred open areas in moist organic soils bordering wetter soils. Disturbances to the habitat favored C. tenera, e.g., at SRCP most of the plants were found in an area drained by a deeply cut road ditch. Other forms of disturbance to the natural community were evident.

There were an estimated 350 genets of C. tenera in about 3 acres at SRCP. They were in wet-mesic meadows, bordering areas dominated by C. stricta, C. hystricina and C. suberecta. C. tenera was associated with the following forbs: Silphium perfoliatum, Geum triflorum, Zizia aurea, Saxifraga pensylvanica, Veronicatrum virginicum and Cypripedium candidum. At Hayden prairie, C. tenera was found in a narrow ecotonal strip between borders of prairie uplands and wet sedge-meadows bordering a prairie creek. Occasionally it was found at higher elevations in depressions and swales amid the upland prairie. Several ramets of C. tenera were seen in fire-breaks mowed the previous year. This form of disturbance greatly favored C. tenera over more competitive species.

Field Observations of Carex normalis. Small numbers of C. normalis plants were infrequently observed in open oak woods throughout the state. The plant closely resembles C. sparganioides which is more common in the same woodland habitats. This species has androgynous spikes with male florets at the apex, but its vegetative features are nearly indistinguishable from C. normalis. The spreading perigynia of both species are loosely held by the inferior scales and are easily shattered from the spike. The largest population of C. normalis was sampled at Viking Lake State Park (VLSP) where they occupied a transitional zone between the Bromis inermis bordering the lake, and the densely shaded understory of an oak forest. The plants were scattered among a brier patch of Ribes missouriensis and Rubus allegheniensis. Unfortunately, only one of these plants could be analyzed by multivariate methods because of missing perigynia. However, a second population was measured in the field before the perigynia

shattered. These were found at a six acre private mesic prairie (PMP) near Cedar Falls. About 30 genets of C. normalis occupied a 3 meter by 1 meter strip of prairie which received sediments from an adjacent cultivated field. Plants were also found in dirt piles and flood plains. Two plants of C. normalis were collected at SRCP in drained loamy soil beneath an aspen thicket bordering a sedge-meadow where C. tenera was found.

At Viking Lake State Park (VLSP), C. normalis was associated with Carya ovata, Quercus borealis, Q. macrocarpa, Ribes missiourense, Zanthoxylum americanum, Rubus allegheniensis, Toxicodendron rydbergii, Desmodium glutinosum, Poa pretensis, Elymus villosa, and C. sparganioides.

Field Observations of Carex tenera var. echinodes. The taxonomic status of C. tenera var. echinodes has been uncertain since its original description (Fernald 1902). The vegetative features are similar to C. tenera with narrow leaves and culms. The spikes are arranged in a bead-like pattern (moniliform) along the rachis which is thin and flexuous. This gives the inflorescence a nodding or zig-zag appearance. The characteristics of the perigynia and spikes closely resemble those of C. normalis except the perigynia are slightly larger. I found only one population of C. tenera var. echinodes in wet woods. Most of the plants were located in a roadside where water seeped into the ditch at Martin County Park (MCP). A few plants were scattered in a densely forested ravine along an intermittant stream. Such a habitat is very different from either the open meadows of C. tenera or the well-drained savanna of C. normalis. Associate species at MCP were Carya cordiformis, Ulmus rubra, Tilia americana,

Acer negundo, Prunus americana, Junglans nigra, Ostrya virginiana, Sanguinea canadensis, Polygonatum biflora, Smilicina racemosa, Viburnum rafinesqueii, Triosteum perfoliatum, Rhamnus cathardica, Osmorhiza longistylis, Hydrophillum virginianum, and C. blanda.

Statistical Analyses

Univariate Analyses

Univariate analysis was performed on the 43 measured characters and 13 computer derived character ratios (Table 3) to obtain means, standard deviation and minimum-maximum values (Tables 6). Comparative box plots depicting means, modes, interquartile range (an interquartile range is the distance betweent the 25th and the 75th sample percentiles), and minimum-maximum ranges are given for important taxonomic characters (Figure 5). Box plots represent histograms. Characters with normal distributions have means equal to the modes, equal distances to interquartile boundaries, and equal length of the tails. A character with a leptokurtic distribution has a narrow interquartile range where a disproportion of the specimens have character states near the mean. A character with a skewed distribution to the right has a mode separate and to the right of the mean; and the left tail is long, extending the lower boundary further away from the mean than the upper boundary.

Test of normality. Normal frequency distributions are necessary for multivariate analysis by parametric methods. Normal distributions were obtained for most characters of C. brevior (N = 147) and C. molesta (N = 131)

Table 6. Character description, taxon, sample size (N), mean, standard deviation (SD), mininium value and maximum value.

Taxon	N	Mean	SD	Minimum	Maximum
1. Fertile culm number of leaves.					
C. brevior	147	3.24	0.72	2.00	5.00
C. tenera var. echinodes	29	3.59	0.78	3.00	6.00
C. festucacea	31	3.03	0.55	2.00	4.00
C. molesta	131	3.54	0.83	2.00	6.00
C. normalis	52	3.98	0.70	2.00	6.00
C. tenera	58	3.50	0.57	2.00	5.00
2. Fertile culm width at widest point (mm).					
C. brevior	147	2.10	0.42	1.00	3.00
C. tenera var. echinodes	29	1.88	0.29	1.50	2.50
C. festucacea	33	2.06	0.24	1.50	3.00
C. molesta	131	2.17	0.48	1.00	3.50
C. normalis	52	3.11	0.39	2.50	4.00
C. tenera	58	1.86	0.31	1.00	2.50
3. Fertile culm extended leaf height (cm).					
C. brevior	141	35.84	8.94	18.00	65.00
C. tenera var. echinodes	27	55.22	7.61	44.00	71.00
C. festucacea	31	44.06	10.75	25.00	77.00
C. molesta	128	51.63	10.72	31.00	76.00
C. normalis	51	69.69	11.64	39.00	104.00
C. tenera	58	48.72	7.82	29.00	77.00
4. Fertile culm height (cm).					
C. brevior	147	63.26	19.01	29.00	116.00
C. tenera var. echinodes	29	80.00	11.06	56.00	99.00
C. festucacea	33	84.15	14.84	56.00	117.00
C. molesta	131	78.94	13.50	36.00	112.00
C. normalis	52	104.42	15.20	61.00	142.00
C. tenera	58	59.28	8.53	41.00	76.00

(table continues)

Taxon	N	Mean	SD	Minimum	Maximum
5. Culm height to upper leaf base (cm).					
C. brevior	141	18.49	6.08	7.00	38.00
C. tenera var. echinodes	27	24.93	5.00	17.00	37.00
C. festucacea	31	22.97	7.14	11.00	41.00
C. molesta	128	27.98	7.56	13.00	50.00
C. normalis	51	32.98	6.61	0.00	47.00
C. tenera	58	21.67	4.74	9.00	36.00
6. Ratio: Fertile culm height to upper leaf base/fertile culm height.					
C. brevior	141	0.30	0.08	0.16	0.81
C. tenera var. echinodes	27	0.31	0.05	0.23	0.42
C. festucacea	31	0.27	0.06	0.20	0.46
C. molesta	128	0.36	0.08	0.21	0.56
C. normalis	51	0.32	0.07	0.00	0.52
C. tenera	58	0.37	0.06	0.22	0.52
7. Fertile culm upper leaf length (cm).					
C. brevior	142	17.30	4.40	7.00	31.00
C. tenera var. echinodes	27	30.30	4.74	23.00	46.00
C. festucacea	31	21.10	4.44	12.00	36.00
C. molesta	128	23.65	5.05	14.00	38.00
C. normalis	51	36.71	8.51	27.00	64.00
C. tenera	58	27.05	4.77	15.00	41.00
8. Fertile culm upper leaf width (mm).					
C. brevior	146	2.46	0.48	1.50	3.50
C. tenera var. echinodes	29	2.41	0.46	1.50	3.00
C. festucacea	28	2.84	0.31	2.00	3.50
C. molesta	130	2.79	0.47	1.50	4.00
C. normalis	52	3.82	0.44	3.00	5.00
C. tenera	58	2.11	0.38	1.00	3.00

(table continues)

Taxon	N	Mean	SD	Minimum	Maximum
9. Vegetative culm number of leaves.					
C. brevior	66	7.35	1.58	3.00	12.00
C. tenera var. echinodes	29	8.24	1.15	7.00	10.00
C. festucacea	9	9.11	1.36	7.00	12.00
C. molesta	55	8.22	1.97	3.00	13.00
C. normalis	32	7.44	1.19	5.00	10.00
C. tenera	33	4.97	1.26	0.00	7.00
10. Vegetative culm width (mm).					
C. brevior	67	1.86	0.55	1.00	3.00
C. tenera var. echinodes	29	1.74	0.41	1.00	2.50
C. festucacea	9	1.61	0.49	1.00	2.50
C. molesta	55	1.87	0.42	1.00	3.00
C. normalis	32	2.78	0.52	1.50	4.00
C. tenera	33	1.44	0.46	0.00	2.00
11. Vegetative culm extended leaves height (cm).					
C. brevior	67	34.76	8.81	20.00	67.00
C. tenera var. echinodes	29	56.28	6.84	42.00	66.00
C. festucacea	9	55.22	11.29	41.00	79.00
C. molesta	55	50.31	14.48	11.00	82.00
C. normalis	32	63.38	18.68	22.00	110.00
C. tenera	33	38.88	11.25	0.00	60.00
12. Vegetative culm height to upper sheath apex (cm).					
C. brevior	67	14.54	5.21	5.00	33.00
C. tenera var. echinodes	29	23.97	4.91	14.00	33.00
C. festucacea	9	27.22	7.17	19.00	42.00
C. molesta	55	24.49	8.91	7.00	47.00
C. normalis	32	23.66	8.83	10.00	42.00
C. tenera	33	13.39	4.95	0.00	21.00

(table continues)

Taxon	N	Mean	SD	Minimum	Maximum
13. Inflorescence shape (See Table EE for quality states).					
C. brevior	147	1.61	0.81	1.00	3.00
C. tenera var. echinodes	29	1.00	0.00	1.00	1.00
C. festucacea	33	1.53	0.62	1.00	3.00
C. molesta	131	2.58	0.87	1.00	4.00
C. normalis	52	1.92	0.96	1.00	3.00
C. tenera	58	1.14	0,40	1.00	3.00
14. Inflorescence length (mm).					
C. brevior	147	29.18	7.60	13.00	52.00
C. tenera var. echinodes	29	39.21	7.33	24.00	53.00
C. festucacea	33	41.67	8.20	27.00	58.00
C. molesta	131	21.00	3.59	13.00	34.00
C. normalis	52	27.60	5.14	16.00	45.00
C. tenera	58	36.34	7.13	22.00	57.00
15. Inflorescence width (mm).					
C. brevior	145	10.30	2.31	5.00	18.00
C. tenera var. echinodes	24	9.25	1.73	5.00	12.00
C. festucacea	33	10.03	2.05	5.00	15.00
C. molesta	131	12.26	1.75	7.00	16.00
C. normalis	39	9.74	1.94	6.00	16.00
C. tenera	58	7.91	1.61	5.00	13.00
16. Ratio inflorescence width to length.					
C. brevior	145	0.37	0.11	0.15	0.77
C. tenera var. echinodes	24	0.24	0.07	0.13	0.37
C. festucacea	33	0.25	0.08	0.12	0.44
C. molesta	131	0.60	0.11	0.32	0.92
C. normalis	39	0.34	0.08	0.19	0.55
C. tenera	58	0.22	0.06	0.10	0.43

(table continues)

Taxon	N	Mean	SD	Minimum	Maximum
17. Spike number.					
C. brevior	146	4.18	0.80	3.00	6.00
C. tenera var. echinodes	29	5.79	0.86	5.00	8.00
C. festucacea	33	6.06	1.27	4.00	9.00
C. molesta	131	4.15	0.96	2.00	9.00
C. normalis	52	7.21	1.30	4.00	10.00
C. tenera	58	4.98	0.98	3.00	7.00
18. Spike arrangement (See Table EE for quality states).					
C. brevior	146	2.45	0.93	1.00	4.00
C. tenera var. echinodes	29	3.52	0.63	2.00	4.00
C. festucacea	33	2.76	0.85	1.00	4.00
C. molesta	131	1.39	0.57	1.00	3.50
C. normalis	52	1.72	0.61	1.00	4.00
C. tenera	58	3.48	0.63	2.00	4.00
19. Spike length (mm).					
C. brevior	146	12.15	2.12	7.00	17.00
C. tenera var. echinodes	19	10.26	1.33	8.00	13.00
C. festucacea	33	11.52	2.09	7.00	15.00
C. molesta	130	10.49	1.91	6.00	16.00
C. normalis	32	10.00	1.68	7.00	13.00
C. tenera	58	10.33	1.98	6.00	15.00
20. Spike width (mm).					
C. brevior	145	6.48	0.94	4.00	12.00
C. tenera var. echinodes	19	6.37	0.96	4.00	8.00
C. festucacea	33	5.82	1.04	4.00	10.00
C. molesta	130	7.50	1.02	5.00	12.00
C. normalis	32	5.72	0.92	4.00	7.00
C. tenera	58	5.43	0.75	4.00	7.00

(table continues)

Taxon	N	Mean	SD	Minimum	Maximum
21. Ratio: Terminal spike width/length.					
C. brevior	145	0.55	0.10	0.31	1.00
C. tenera var. echinodes	19	0.63	0.10	0.36	0.80
C. festucacea	33	0.52	0.11	0.38	0.77
C. molesta	130	0.73	0.14	0.50	1.20
C. normalis	32	0.58	0.13	0.42	1.00
C. tenera	58	0.54	0.11	0.36	1.00
22. Spike shape (See Table EE for quality states).					
C. brevior	142	3.87	0.65	2.00	6.00
C. tenera var. echinodes	19	4.63	0.96	4.00	6.00
C. festucacea	33	3.76	0.66	1.00	5.00
C. molesta	129	2.95	0.55	2.00	4.00
C. normalis	31	3.68	0.60	2.00	4.00
C. tenera	57	4.02	0.44	3.00	6.00
23. Spike apex shape (see Table 3 for quality states).					
C. brevior	138	3.43	0.87	1.00	5.00
C. tenera var. echinodes	19	2.63	0.76	2.00	4.00
C. festucacea	32	2.50	1.02	2.00	6.00
C. molesta	129	3.69	0.50	1.40	4.00
C. normalis	31	2.81	0.70	2.00	5.00
C. tenera	57	3.37	0.86	2.00	5.00
24. Terminal spike base shape (see Table 3 for quality states).					
C. brevior	147	4.14	0.96	1.00	5.00
C. tenera var. echinodes	29	4.72	0.59	3.00	5.00
C. festucacea	33	4.33	0.82	3.00	5.00
C. molesta	131	2.33	0.79	1.00	4.50
C. normalis	52	3.36	1.12	1.00	5.00
C. tenera	58	4.33	0.76	3.00	5.00

(table continues)

Taxon	N	Mean	SD	Minimum	Maximum
25. Lateral spike base shape (see Table 3 for quality states).					
C. brevior	146	3.25	0.98	1.00	5.00
C. tenera var. echinodes	29	3.14	0.35	3.00	4.00
C. festucacea	33	3.73	0.94	2.00	5.00
C. molesta	131	1.78	0.50	1.00	3.00
C. normalis	51	2.11	1.02	1.00	5.00
C. tenera	57	3.28	0.64	2.00	5.00
26. Terminal spike number of cycles of male florets.					
C. brevior	147	5.77	2.18	1.00	11.00
C. tenera var. echinodes	29	4.38	1.15	2.00	7.00
C. festucacea	33	9.70	4.06	0.00	17.00
C. molesta	130	4.27	1.89	0.00	9.00
C. normalis	52	5.04	2.55	0.00	15.00
C. tenera	58	5.24	1.94	2.00	11.00
27. Terminal spike number of cycles of female florets.					
C. brevior	147	11.57	2.74	6.00	24.00
C. tenera var. echinodes	29	11.10	1.93	8.00	15.00
C. festucacea	33	18.64	3.64	9.00	27.00
C. molesta	130	15.96	3.04	9.00	24.00
C. normalis	52	15.31	2.40	10.00	22.00
C. tenera	58	10.24	3.52	5.00	16.00
28. Lateral spike number of cycles of male florets.					
C. brevior	146	4.91	2.24	1.00	11.00
C. tenera var. echinodes	29	2.79	0.98	1.00	4.00
C. festucacea	33	8.15	4.42	1.00	17.00
C. molesta	130	2.87	1.22	0.00	7.00
C. normalis	51	3.33	1.62	1.00	9.00
C. tenera	57	3.75	1.73	1.00	9.00

(table continues)

Taxon	N	Mean	SD	Minimum	Maximum
29. Lateral spike number of cycles of female florets.					
C. brevior	146	11.64	2.78	6.00	22.00
C. tenera var. echinodes	28	10.07	2.07	6.00	14.00
C. festucacea	33	20.36	3.39	12.00	26.00
C. molesta	130	15.08	3.24	0.00	25.00
C. normalis	51	15.08	2.42	10.00	21.00
C. tenera	57	11.21	3.69	5.00	19.00
30. Ratio: terminal spike male cycles to female cycles.					
C. brevior	147	0.53	0.25	0.07	1.14
C. tenera var. echinodes	29	0.41	0.13	0.20	0.67
C. festucacea	33	0.56	0.31	0.00	1.42
C. molesta	130	0.27	0.12	0.00	0.56
C. normalis	52	0.34	0.23	0.00	1.50
C. tenera	58	0.55	0.23	0.15	1.00
31. Ratio: lateral spike male cycles/female cycles.					
C. brevior	146	0.45	0.23	0.06	1.11
C. tenera var. echinodes	28	0.29	0.11	0.10	0.67
C. festucacea	33	0.43	0.29	0.05	1.33
C. molesta	129	0.19	0.08	0.05	0.40
C. normalis	51	0.22	0.11	0.05	0.64
C. tenera	57	0.36	0.20	0.12	1.00
32. Scale length (mm).					
C. brevior	147	3.35	0.34	2.50	4.42
C. tenera var. echinodes	29	2.76	0.15	2.50	3.08
C. festucacea	33	2.64	0.22	2.17	3.00
C. molesta	131	3.00	0.26	2.33	3.50
C. normalis	52	2.57	0.28	1.92	3.00
C. tenera	58	2.78	0.20	2.33	3.33

(table continues)

Taxon	N	Mean	SD	Minimum	Maximum
33. Scale width (mm).					
C. brevior	147	1.29	0.17	0.92	1.83
C. tenera var. echinodes	29	1.17	0.11	0.92	1.42
C. festucacea	33	1.14	0.13	0.92	1.50
C. molesta	131	1.17	0.13	0.83	1.50
C. normalis	52	1.23	0.18	0.92	1.75
C. tenera	58	1.13	0.16	0.83	1.50
34. Ratio: scale length/perigynium length.					
C. brevior	146	0.92	0.10	0.66	1.23
C. tenera var. echinodes	29	0.66	0.05	0.57	0.80
C. festucacea	33	0.88	0.10	0.70	1.09
C. molesta	131	0.74	0.06	0.60	0.91
C. normalis	52	0.75	0.08	0.53	1.03
C. tenera	54	0.94	0.11	0.67	1.26
35. Ratio: scale width/perigynium width.					
C. brevior	146	0.51	0.08	0.37	0.78
C. tenera var. echinodes	29	0.68	0.08	0.55	0.83
C. festucacea	33	0.64	0.10	0.42	0.85
C. molesta	131	0.51	0.06	0.38	0.75
C. normalis	52	0.71	0.12	0.48	1.13
C. tenera	54	0.69	0.13	0.45	1.00
36. Perigynium length (mm).					
C. brevior	146	3.67	0.43	2.67	5.17
C. tenera var. echinodes	29	4.18	0.31	3.67	4.75
C. festucacea	33	3.04	0.33	2.50	3.92
C. molesta	131	4.06	0.32	3.08	4.75
C. normalis	52	3.42	0.37	2.75	4.08
C. tenera	54	3.02	0.34	2.17	3.83

(table continues)

Taxon	N	Mean	SD	Minimum	Maximum
37. Perigynium width (mm).					
C. brevior	146	2.56	0.31	1.50	3.25
C. tenera var. echinodes	29	1.74	0.14	1.50	2.08
C. festucacea	33	1.80	0.19	1.42	2.25
C. molesta	131	2.32	0.20	1.75	2.92
C. normalis	52	1.75	0.23	1.33	2.25
C. tenera	54	1.65	0.20	1.00	2.00
38. Perigynium length from base to widest point (mm).					
C. brevior	146	1.32	0.21	0.75	1.75
C. tenera var. echinodes	29	1.11	0.19	0.83	1.50
C. festucacea	33	1.01	0.15	0.75	1.33
C. molesta	131	1.37	0.18	1.00	1.92
C. normalis	52	0.98	0.16	0.58	1.25
C. tenera	54	0.96	0.15	0.58	1.42
39. Ratio: perigynium width/perigynium length.					
C. brevior	146	0.70	0.08	0.45	0.97
C. tenera var. echinodes	29	0.42	0.04	0.35	0.53
C. festucacea	33	0.60	0.07	0.45	0.82
C. molesta	131	0.57	0.05	0.45	0.73
C. normalis	52	0.51	0.06	0.38	0.70
C. tenera	54	0.55	0.07	0.36	0.71
40. Perigynium shape -- width/length (see Table 3 for quality states).					
C. brevior	146	6.87	0.65	6.00	8.00
C. tenera var. echinodes	29	4.00	0.00	4.00	4.00
C. festucacea	33	6.55	0.62	5.00	8.00
C. molesta	131	5.94	0.76	4.00	7.00
C. normalis	52	5.35	1.43	3.00	8.00
C. tenera	54	5.41	0.60	4.00	7.00

(table continues)

Taxon	N	Mean	SD	Minimum	Maximum
41. Ratio: perigynium length to widest point/perigynium length.					
C. brevior	146	0.36	0.04	0.24	0.49
C. tenera var. echinodes	29	0.26	0.03	0.21	0.32
C. festucacea	33	0.33	0.03	0.26	0.41
C. molesta	131	0.34	0.03	0.24	0.45
C. normalis	52	0.29	0.03	0.21	0.34
C. tenera	54	0.32	0.04	0.24	0.39
42. Perigynium shape -- position of widest point position (Table 3).					
C. brevior	146	1.45	0.86	1.00	4.00
C. tenera var. echinodes	29	3.00	0.00	3.00	3.00
C. festucacea	33	1.06	0.35	1.00	3.00
C. molesta	131	1.71	0.97	1.00	4.00
C. normalis	52	2.08	1.01	1.00	3.00
C. tenera	54	2.96	0.27	1.00	3.00
43. Beak length (mm) (as measured from apex of achene to beak apex).					
C. brevior	146	1.71	0.33	1.08	2.75
C. tenera var. echinodes	29	2.27	0.24	1.92	2.67
C. festucacea	33	1.35	0.22	1.00	1.83
C. molesta	131	2.16	0.26	1.50	3.00
C. normalis	52	1.72	0.25	1.25	2.33
C. tenera	54	1.52	0.22	0.92	1.92
44. Ratio: beak length/perigynium length.					
C. brevior	146	0.46	0.06	0.36	0.79
C. tenera var. echinodes	29	0.54	0.04	0.46	0.71
C. festucacea	33	0.44	0.04	0.36	0.50
C. molesta	131	0.53	0.04	0.36	0.65
C. normalis	52	0.50	0.04	0.43	0.58
C. tenera	54	0.50	0.06	0.39	0.71

(table continues)

Taxon	N	Mean	SD	Minimum	Maximum
45. Beak taper (see Table 3 for quality states).					
C. brevior	146	2.64	0.53	1.00	3.00
C. tenera var. echinodes	29	1.12	0.32	1.00	2.00
C. festucacea	33	2.00	0.72	1.00	3.00
C. molesta	131	1.59	0.45	1.00	3.00
C. normalis	52	1.13	0.30	1.00	2.00
C. tenera	54	1.55	0.84	1.00	4.00
46. Number of nerves on ventral face of perigynium over achene.					
C. brevior	146	0.40	0.98	0.00	6.00
C. tenera var. echinodes	29	3.45	1.15	1.00	5.00
C. festucacea	33	3.18	1.57	0.00	6.00
C. molesta	131	3.15	1.61	0.00	6.00
C. normalis	52	4.38	1.40	0.00	8.00
C. tenera	53	4.34	1.09	3.00	7.00
47. Ventral nerve appearance (see Table 3).					
C. brevior	146	3.79	0.56	1.00	4.00
C. tenera var. echinodes	29	1.26	0.54	1.00	3.00
C. festucacea	33	2.53	1.01	1.00	4.00
C. molesta	131	2.46	1.02	1.00	4.00
C. normalis	52	1.66	0.83	1.00	4.00
C. tenera	53	1.74	0.74	1.00	3.00
48. Number of nerves on dorsal face of perigynium over achene.					
C. brevior	146	2.99	1.46	0.00	7.00
C. tenera var. echinodes	29	5.66	1.26	3.00	8.00
C. festucacea	33	5.33	1.51	0.00	7.00
C. molesta	131	5.02	1.23	2.00	8.00
C. normalis	52	6.63	1.19	3.00	9.00
C. tenera	53	6.94	0.97	5.00	9.00

(table continues)

Taxon	N	Mean	SD	Minimum	Maximum
49. Dorsal nerve appearance.					
C. brevior	146	2.27	0.96	1.00	4.00
C. tenera var. echinodes	29	2.24	0.56	1.00	3.00
C. festucacea	33	2.11	0.57	1.00	4.00
C. molesta	131	2.06	0.62	1.00	3.50
C. normalis	52	2.26	0.47	1.00	3.00
C. tenera	53	2.37	0.55	1.00	3.50
50. Achene length (mm).					
C. brevior	146	1.75	0.12	1.42	2.00
C. tenera var. echinodes	29	1.67	0.10	1.50	1.83
C. festucacea	33	1.56	0.09	1.42	1.75
C. molesta	129	1.66	0.11	1.42	2.00
C. normalis	52	1.45	0.12	1.17	1.67
C. tenera	52	1.40	0.09	1.17	1.58
51. Achene width (mm).					
C. brevior	146	1.41	0.12	1.00	1.67
C. tenera var. echinodes	29	1.01	0.05	0.92	1.08
C. festucacea	33	1.05	0.09	0.92	1.33
C. molesta	129	1.16	0.08	0.92	1.42
C. normalis	52	1.04	0.10	0.83	1.33
C. tenera	52	1.03	0.07	0.92	1.17
52. Ratio: achene width/length.					
C. brevior	146	0.81	0.06	0.65	1.00
C. tenera var. echinodes	29	0.61	0.04	0.52	0.72
C. festucacea	33	0.68	0.05	0.58	0.83
C. molesta	129	0.70	0.05	0.58	0.89
C. normalis	52	0.72	0.07	0.59	0.89
C. tenera	52	0.74	0.06	0.61	0.87

(table continues)

Taxon	N	Mean	SD	Minimum	Maximum
53. Achene shape -- width/length (see Table 3 for quality states).					
C. brevior	145	6.27	0.69	4.00	8.00
C. tenera var. echinodes	29	4.76	0.44	4.00	5.00
C. festucacea	33	5.61	0.56	5.00	7.00
C. molesta	128	5.52	0.52	5.00	7.00
C. normalis	52	5.63	0.63	4.00	7.00
C. tenera	52	5.21	0.89	3.00	6.00
54. Achene shape -- position of widest point (Table 3).					
C. brevior	145	2.26	1.14	1.00	4.00
C. tenera var. echinodes	29	2.59	0.82	1.00	3.00
C. festucacea	33	1.30	0.73	1.00	3.00
C. molesta	128	1.82	1.29	1.00	4.00
C. normalis	52	2.10	1.09	1.00	4.00
C. tenera	52	2.46	0.90	1.00	3.00
55. Ratio: achene length/perigynium length.					
C. brevior	146	0.48	0.04	0.35	0.57
C. tenera var. echinodes	29	0.40	0.03	0.32	0.45
C. festucacea	33	0.52	0.05	0.44	0.67
C. molesta	129	0.41	0.03	0.34	0.50
C. normalis	52	0.43	0.03	0.36	0.50
C. tenera	52	0.47	0.05	0.38	0.62
56. Ratio: achene width/perigynium width.					
C. brevior	146	0.55	0.06	0.42	0.83
C. tenera var. echinodes	29	0.58	0.05	0.48	0.67
C. festucacea	33	0.59	0.04	0.48	0.67
C. molesta	129	0.50	0.04	0.42	0.63
C. normalis	52	0.60	0.06	0.50	0.75
C. tenera	52	0.63	0.07	0.50	0.92

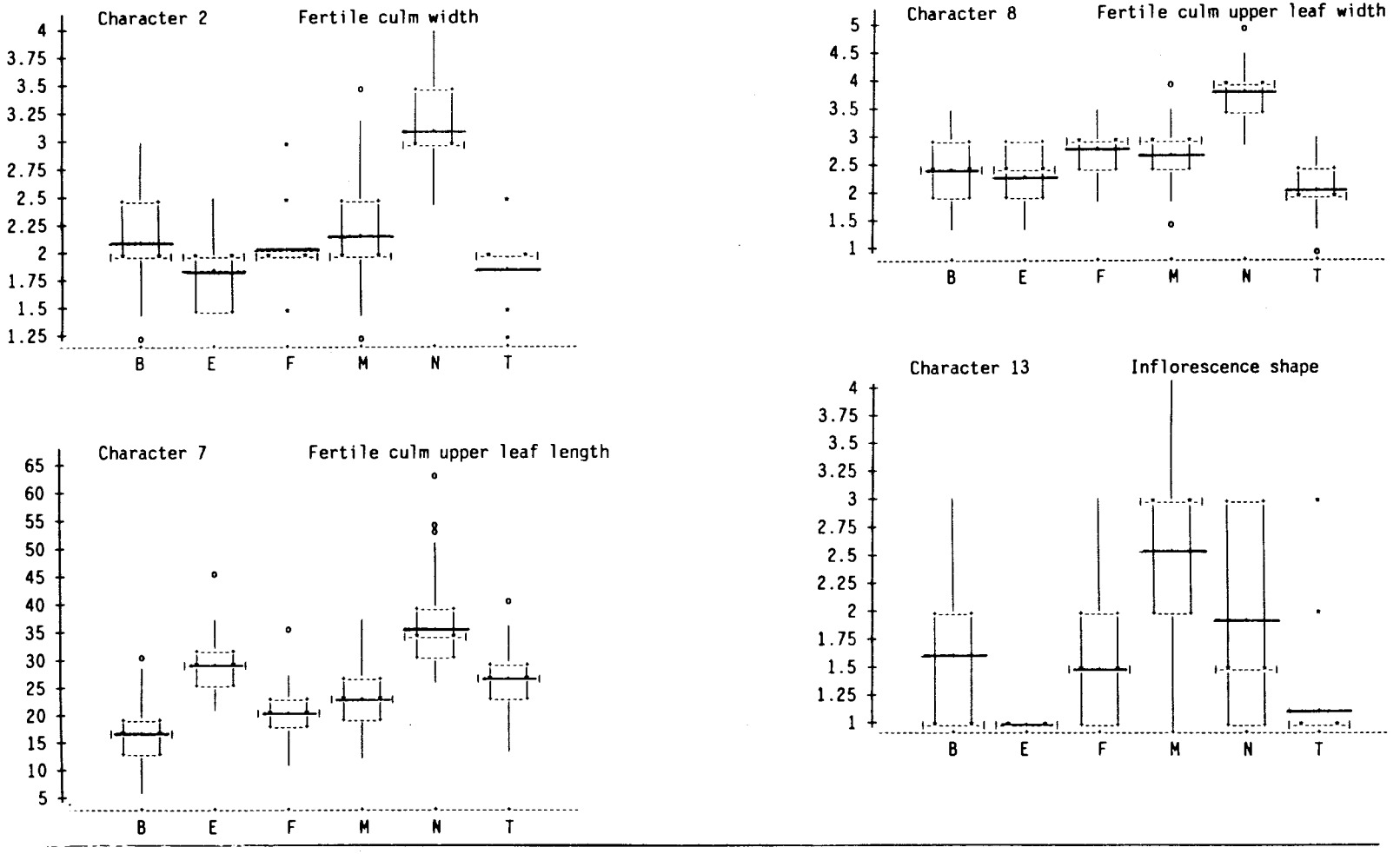
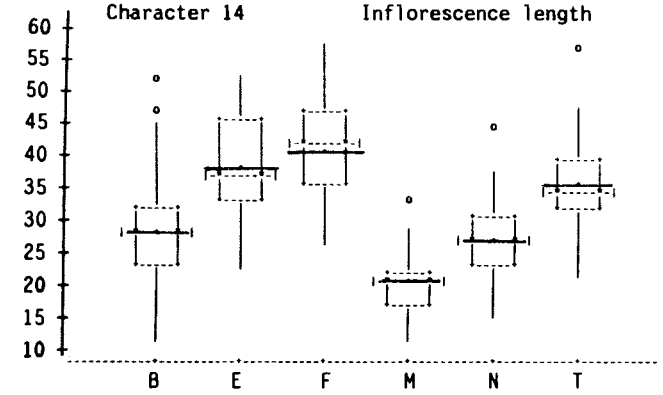
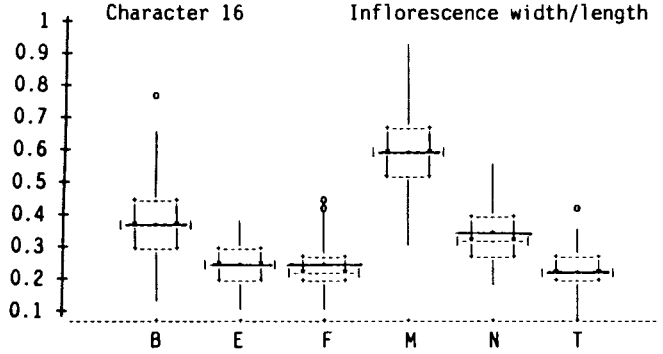
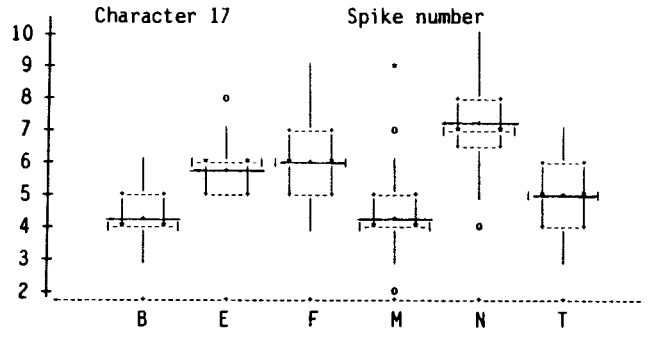
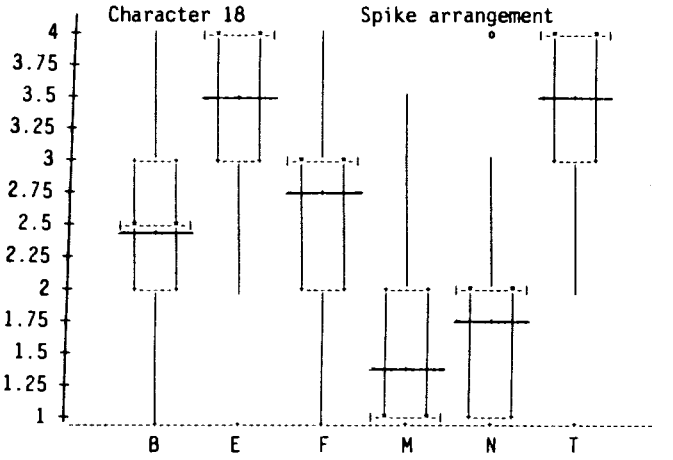


Figure 5. Box plots of selected characters of Carex brevior (B), C. tenera var. echinodes (E), C. molesta (M), C. normalis (N), and C. tenera (T). Means indicated by heavy line; mode by capped line; and box indicates interquartile (25th to 75th percentile).









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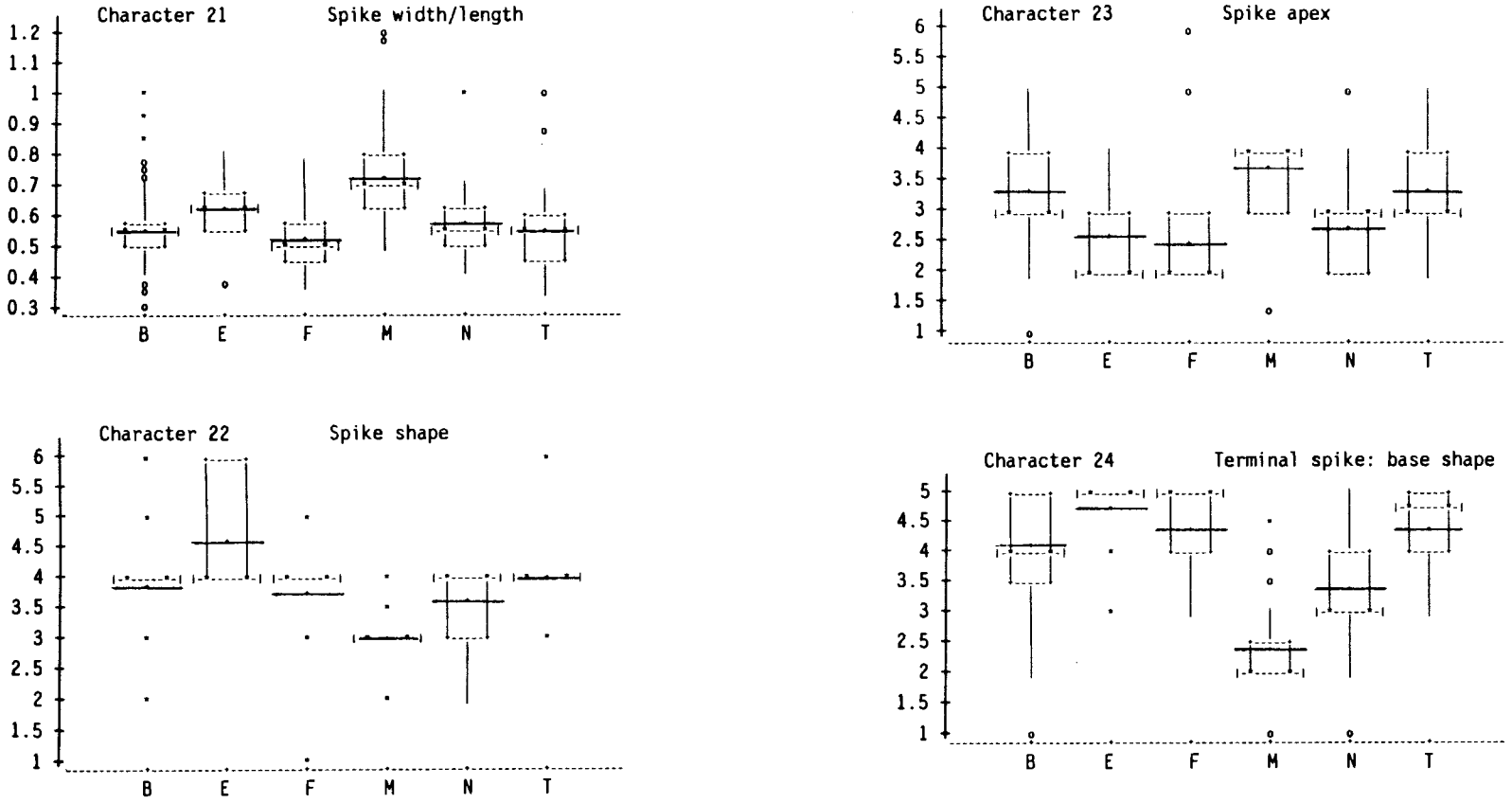
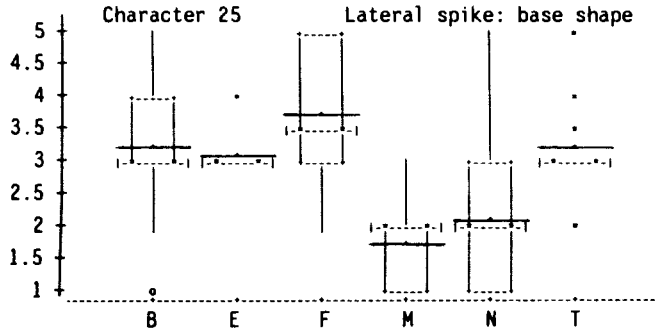
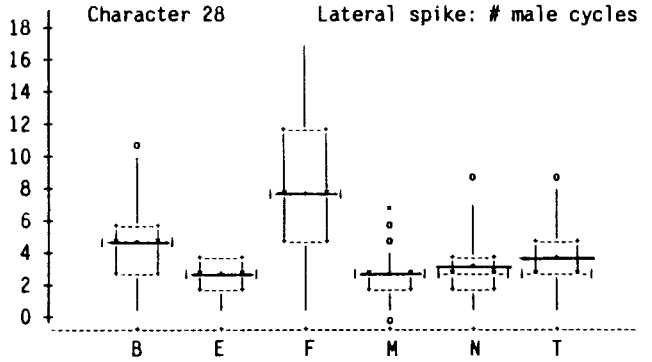
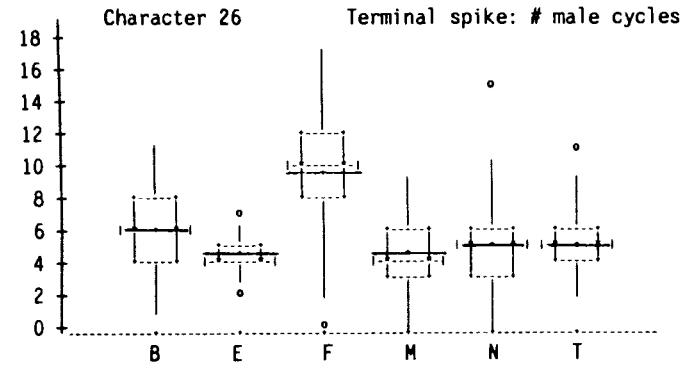
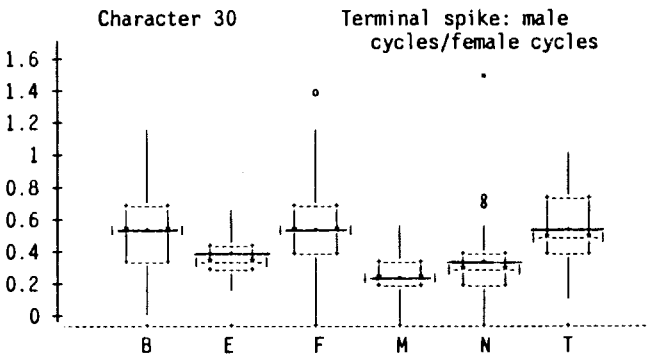


Figure 5. Box plots of selected characters of Carex brevior (B), C. tenera var. echinodes (E), C. molesta (M), C. normalis (N), and C. tenera (T). Means indicated by heavy line; mode by capped line; and box indicates interquartile (25th to 75th percentile). (table continues)









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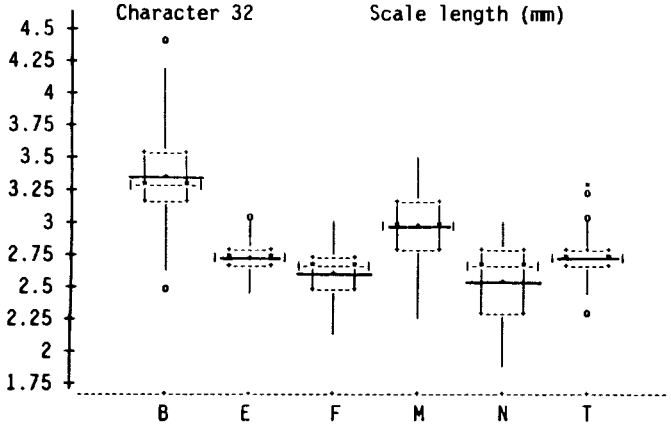

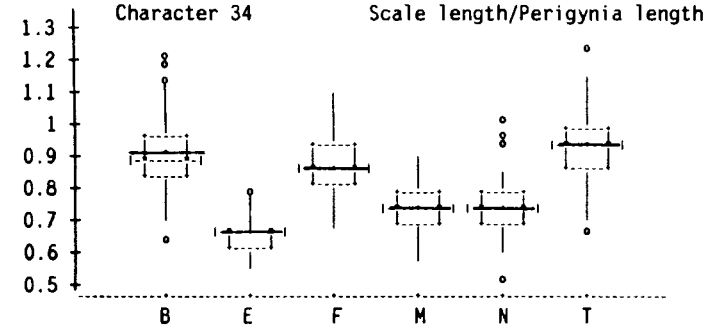

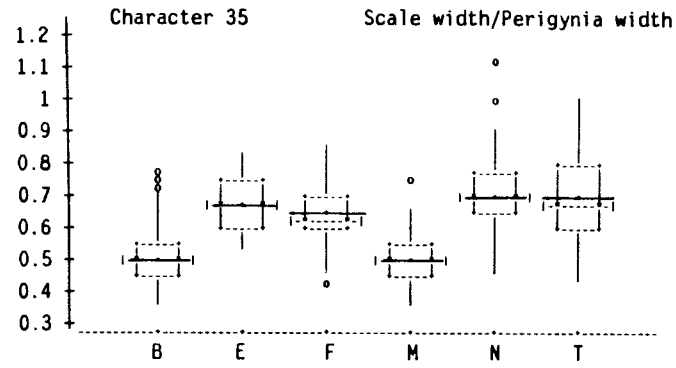

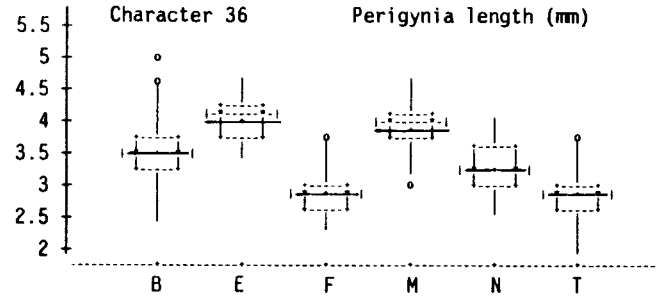

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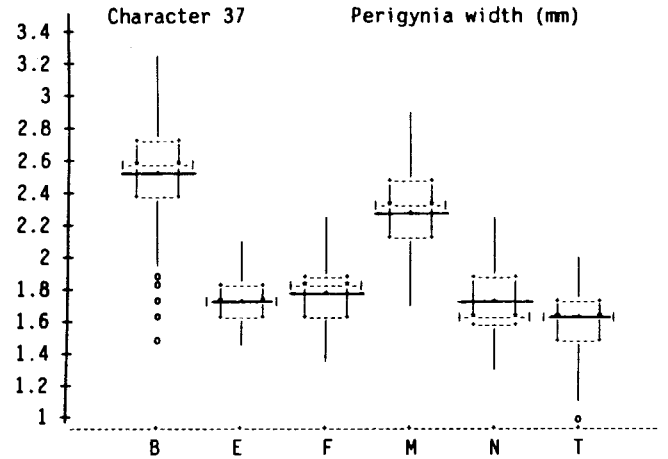

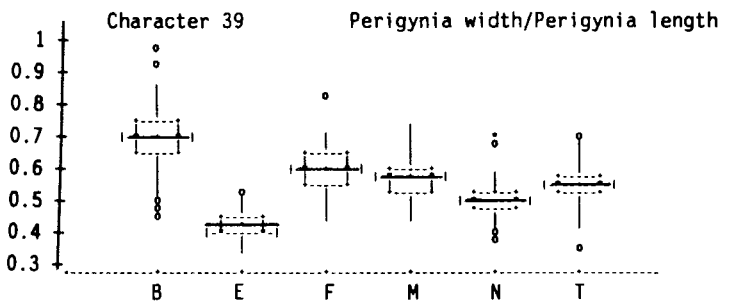

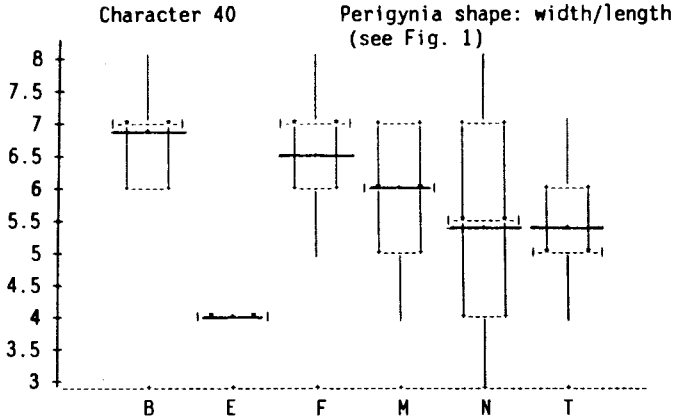

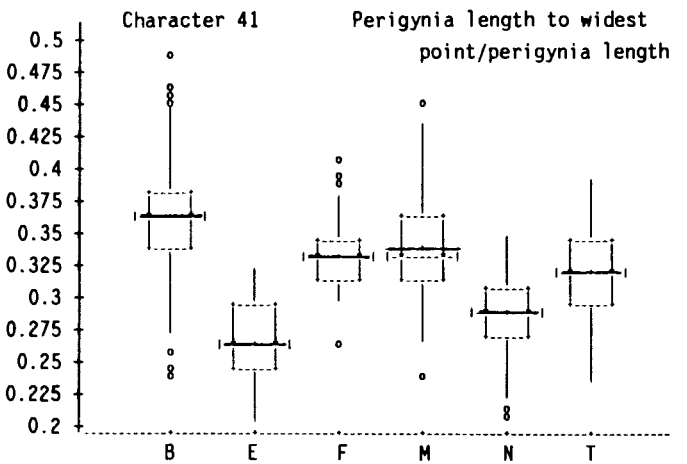

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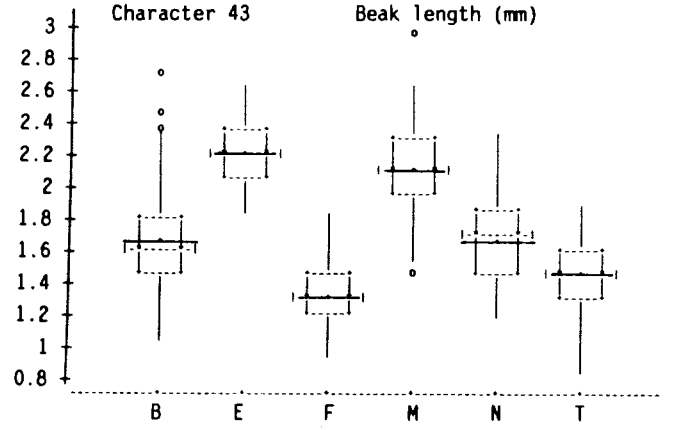
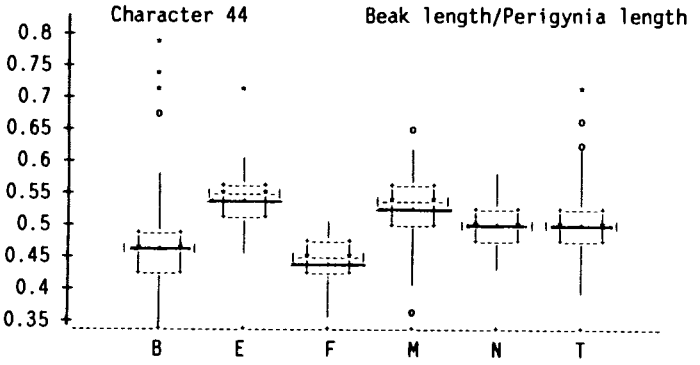
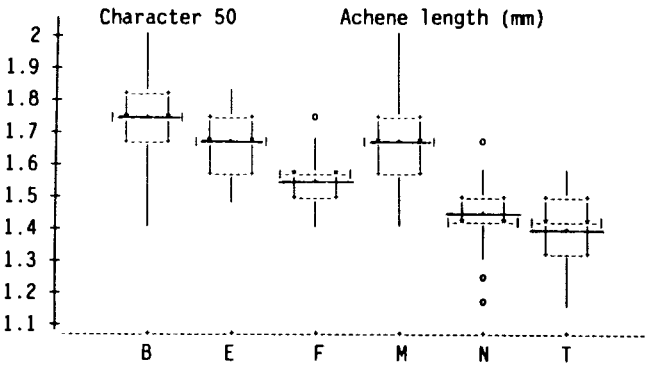






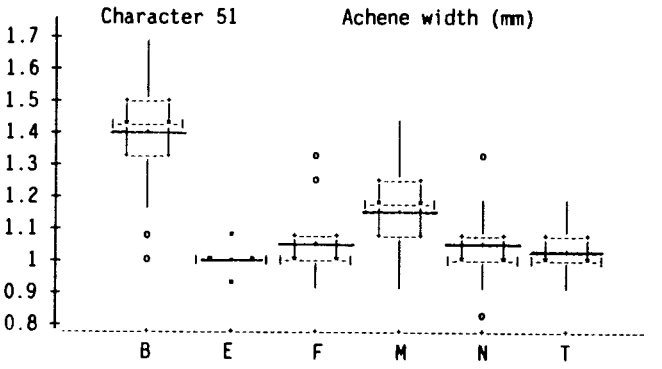
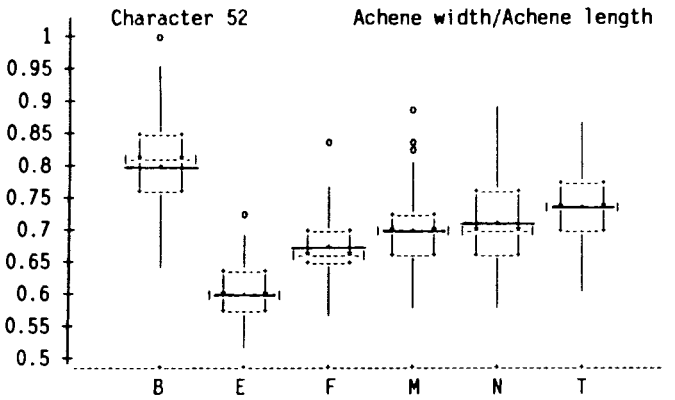
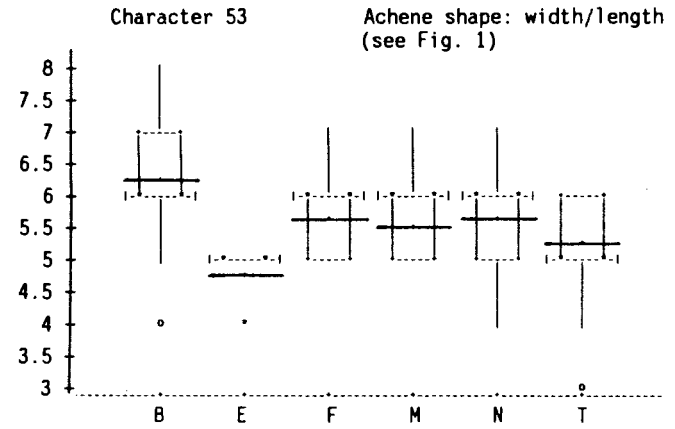
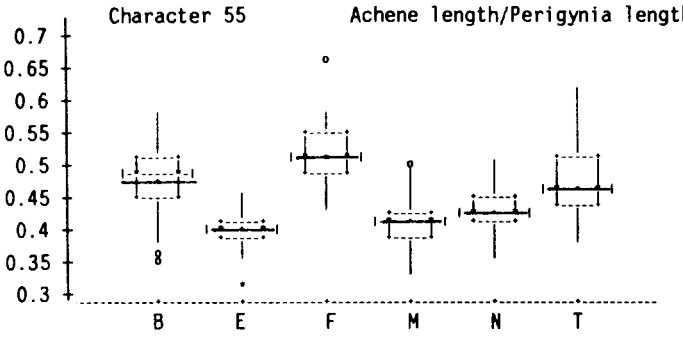


Figure 5. Box plots of selected characters of Carex brevior (B), C. tenera var. echinodes (E), C. molesta (M), C. normalis (N), and C. tenera (T). Means indicated by heavy line; mode by capped line; and box indicates interquartile (25th to 75th percentile). (table continues)







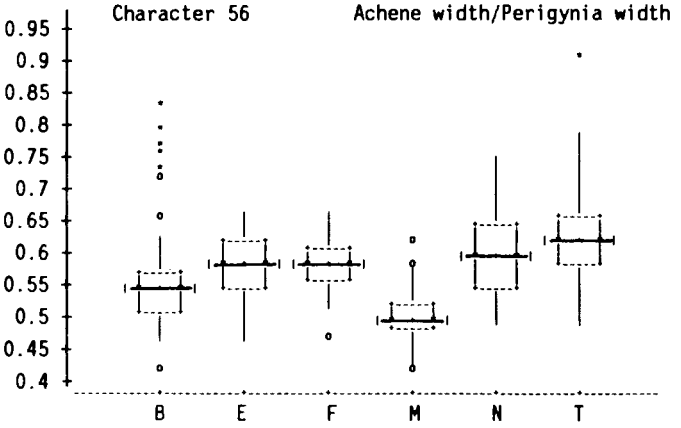


Figure 5. Box plots of selected characters of Carex brevior (B), C. tenera var. echinodes (E), C. molesta (M), C. normalis (N), and C. tenera (T). Means indicated by heavy line; mode by capped line; and box indicates interquartile (25th to 75th percentile). (table continues)

because of their large sample sizes. The remaining taxa have much smaller sample sizes (Table 5), nonetheless, their character distributions tended toward normal bell-shaped curves. High values for the Shapiro-Wilk statistic, a measure of frequency distribution shape, indicate that characters of taxa with smaller sample sizes were normally distributed; however, these estimates were not always significant ($p < 0.05$). The lack of significance inplies that while the dataset tends toward a normal distribution, it may not provide a true estimate of the mean or include the entire range of variation for some characters of C. normalis, C. festucacea, C. tenera, and C. tenera var. echinodes. Many of the qualitative characters also had normal distributions because character states were ordered along a gradual scale where intermediate values could be used. Based on these results, it was decided that multivariate analysis could be performed by parametric methods.

Infraspecific variation. Most of the frequency distributions for continuous characters were normal bell-shaped curves indicating that no further infraspecific subgroupings were necessary within the C. brevior group. Also, normal distributions for the entire dataset of each taxon indicates there are no significant differences between populations. This is compatible with the results obtained from multivariate analysis.

Univariate tests of taxonomic significance. Pairwise comparisons of taxa using the the students t-test was not useful in selecting distinguishing characters for this dataset. For example, C. molesta and C. brevior have significantly different means for 52 of the 56 characters analyzed ($p < 0.0001$). However,

frequency distributions for all the characters overlapped extensively (Table 6 and Figure 5). Consequently, no single character can reliably separate this difficult pair of taxa. Likewise, C. festucacea (N = 30) and C. tenera (N = 58) are also a troublesome pair to distinguish with only 24 characters having significantly different means ($p < 0.0001$) yet with overlapping ranges of variation. The t-test comparisons of other taxa yielded similar results: separate character means but overlapping variation. The extensive overlap of taxonomic characters made it difficult to separate taxa on the basis of univariate statistics alone. Multivariate analysis was necessary to identify character combinations capable of maximizing differences between taxa.

Multivariate Analyses

Canonical Discriminant Analysis (CFA) plots specimens according to a classification variable using canonical values in a manner similar to Principal Component Analysis. The discriminating power of a canonical axis is a proportion of the total variation of the entire dataset explained by variables correlated to that axis. Specimens are assigned a canonical value for each canonical axis. A canonical value of a specimen represents the combined character states for suites of variables correlated along a particular axis. Specimens can be plotted in n-dimensional space depending on the number of canonical axes.

Multivariate tests of taxonomic significance. The SAS CANDISC procedure plotted the randomly collected specimens of the C. brevior group into six distinct taxon clusters along four canonical axes (Figures 6-8). The Wilks'

Lambda Test determined that the six clusters are significantly different with an F-value of 24.08 ($p < 0.0001$). Multivariate analysis suggests that C. brevior, C. festucacea, C. molesta, C. normalis, C. tenera, and C. tenera var. echinodes are distinct morphological forms and justifies their recognition as separate taxa.

Character variables which are highly correlated may actually be measuring the same features of the plant. This would essentially double-weight the discriminating power of that particular morphological feature. Upon examination of DISCRIM Within-class Correlation Coefficients, I found 11 character pairs which were highly correlated with the absolute value of $r \geq 0.7500$. One character of each pair was removed and the dataset was reanalyzed by discrimant and canonical methods. The taxon classes were still significantly different with a slightly higher F-statistic of 26.75 ($P < 0.0001$), indicating that the removed characters were more variable within the taxa than between them.

While measuring vegetative characters 9-12 in the laboratory, I determined these features have limited taxonomic usefulness for the C. brevior group. This was confirmed by DFA when low F-values for vegetative characters 9-12 were obtained, thus indicating these characters had little discriminating power for separating taxa. In an effort to save time, I began evalutating vegetative culms only on every 5th specimen. However, multivariate analysis rejects samples with missing variables, and if characters 9-12 were included in multivariate analysis, then my total sample size would have been reduced to one-fifth of the original sample size. Therefore, characters 9-12 were removed from the final multivariate analysis in order to increase sample sizes.

Infraspecific variation. To determine if there were any morphological differences between populations within a taxon, the same canonical plots were re-illustrated to identify specimens by their population codes (Table 5). The distribution of population codes within taxon clusters is important. Specimens of each population were found throughout taxon clusters in all three canonical plots (Figures 9-11). No significant patterns within any of the clusters were observed, indicating that no further subgroupings are necessary within species of the C. brevior group. The distribution of population codes also indicates that most of the total morphological variation expressed by Iowa taxa occurs within populations.

Specimens of sympatric populations occupy canonical positions in between taxon clusters and are predominately found in hemispheres of the taxon clusters closest to the sympatric species (Figure 12). Removal of specimens collected at sympatric sites reduces morphological variation, eliminates overlap of taxon clusters, and results in higher F-values of significance. This is readily observed in sympatric populations of C. brevior and C. molesta. It is evident that some portion of the total morphological variation within Iowa taxa is found only among sympatric populations.

Taxonomic Characters

Suites of morphological characters are correlated to each canonical axis which are orthogonal to one another. All the canonical axes separate C. brevior and C. molesta from the rest of the taxa. Morphological characters correlated to Canonical axes 1 and 2 distinguish C. brevior from Carex molesta. Canonical axis

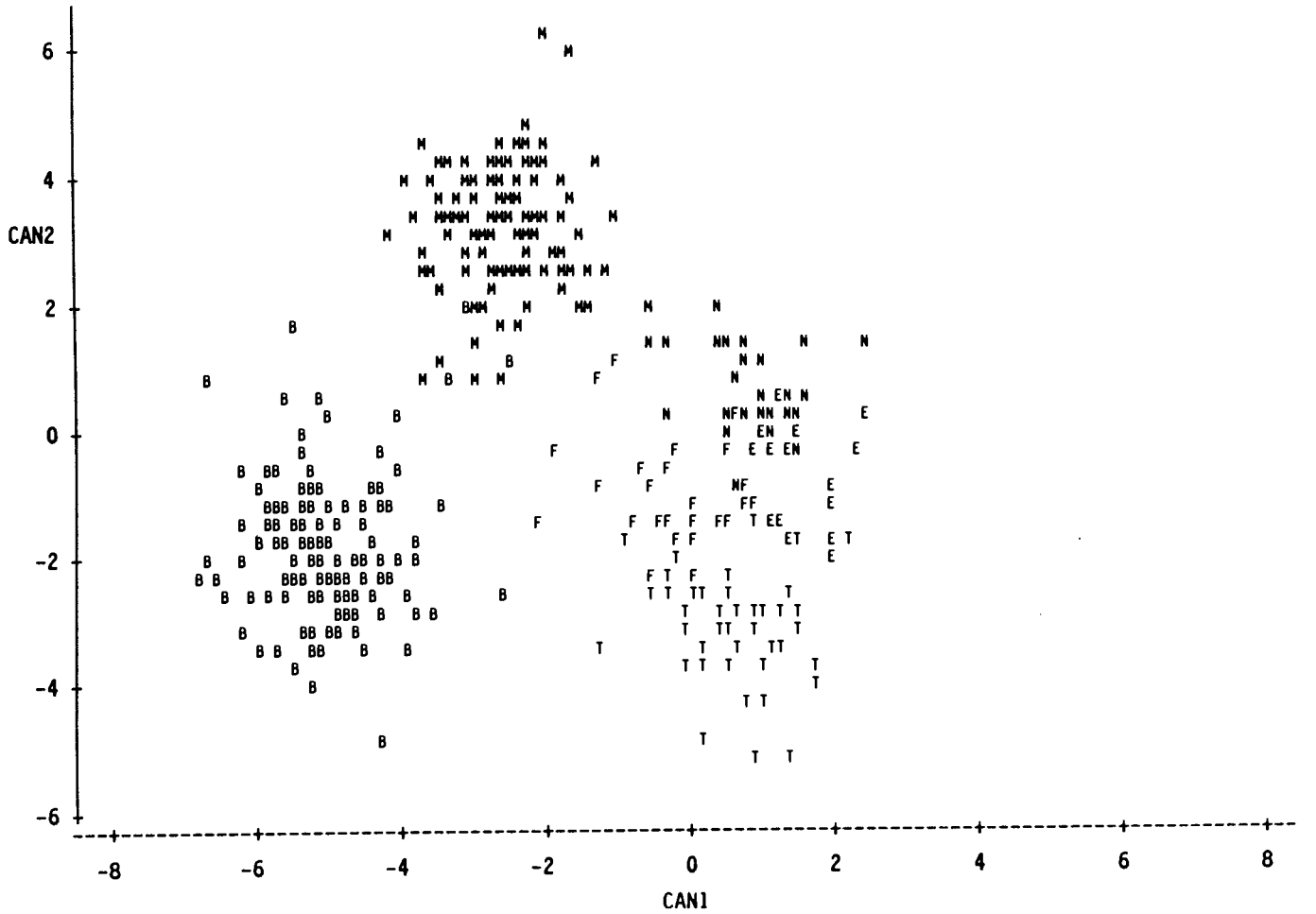


Figure 6. Plot of canonical axes 1 and 2 showing ordination of Carex brevior (B), Carex festucacea (F), Carex molesta (M), Carex normalis (N), Carex tenera (T), and Carex tenera var. echinodes (E). Taxon clusters were significantly different at F = 24.08.

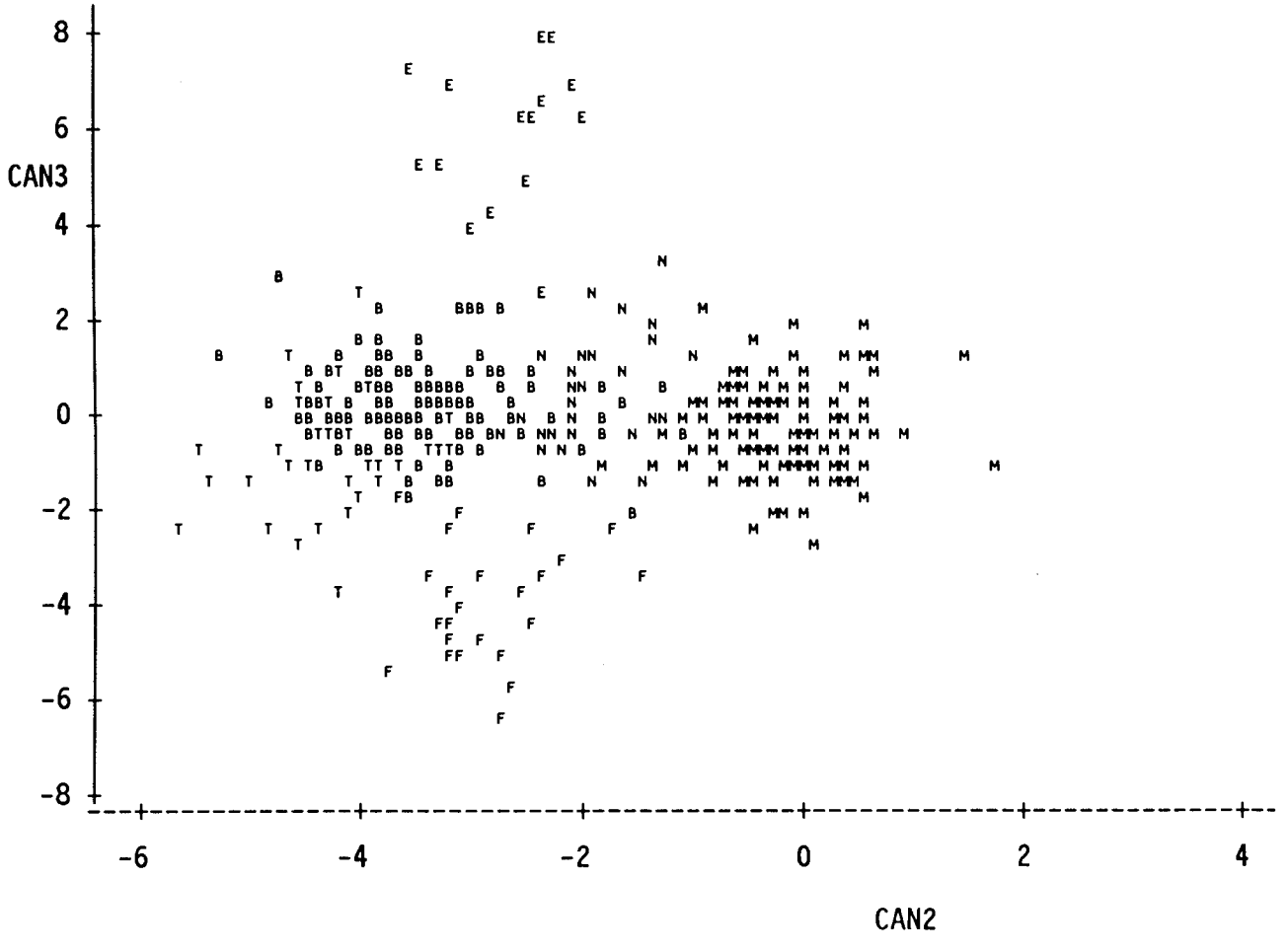


Figure 7. Plot of canonical axes 2 and 3 showing ordination of Carex brevior (B), Carex festucacea (F), Carex molesta (M), Carex normalis (N), Carex tenera (T), and Carex tenera var. echinodes (E). Taxon clusters were significantly different at F = 24.08.

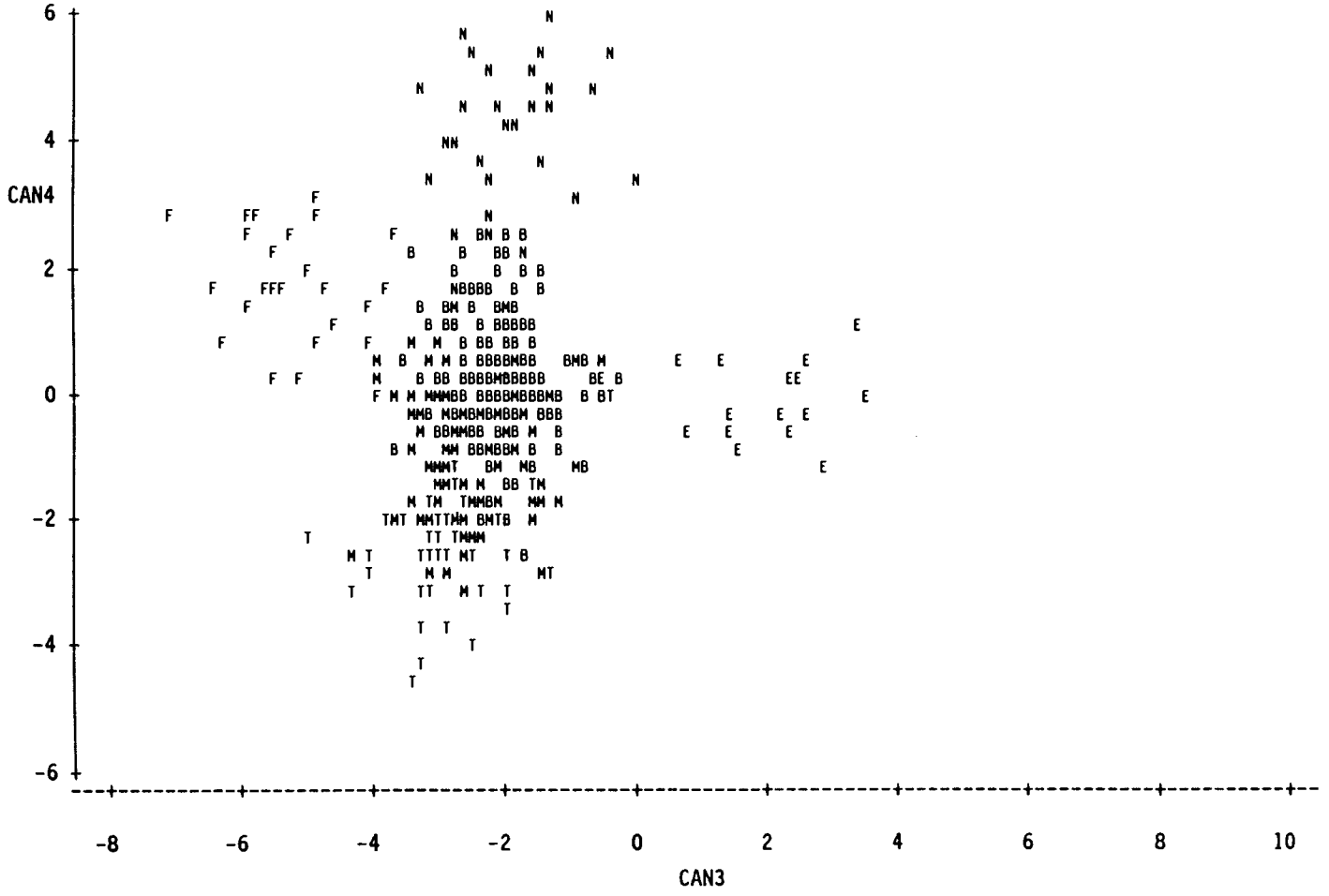


Figure 8. Plot of canonical axes 3 and 4 showing ordination of Carex brevior (B), Carex festucacea (F), Carex molesta (M), Carex normalis (N), Carex tenera (T), and Carex tenera var. echinodes (E). Taxon clusters were significantly different at F = 24.08.

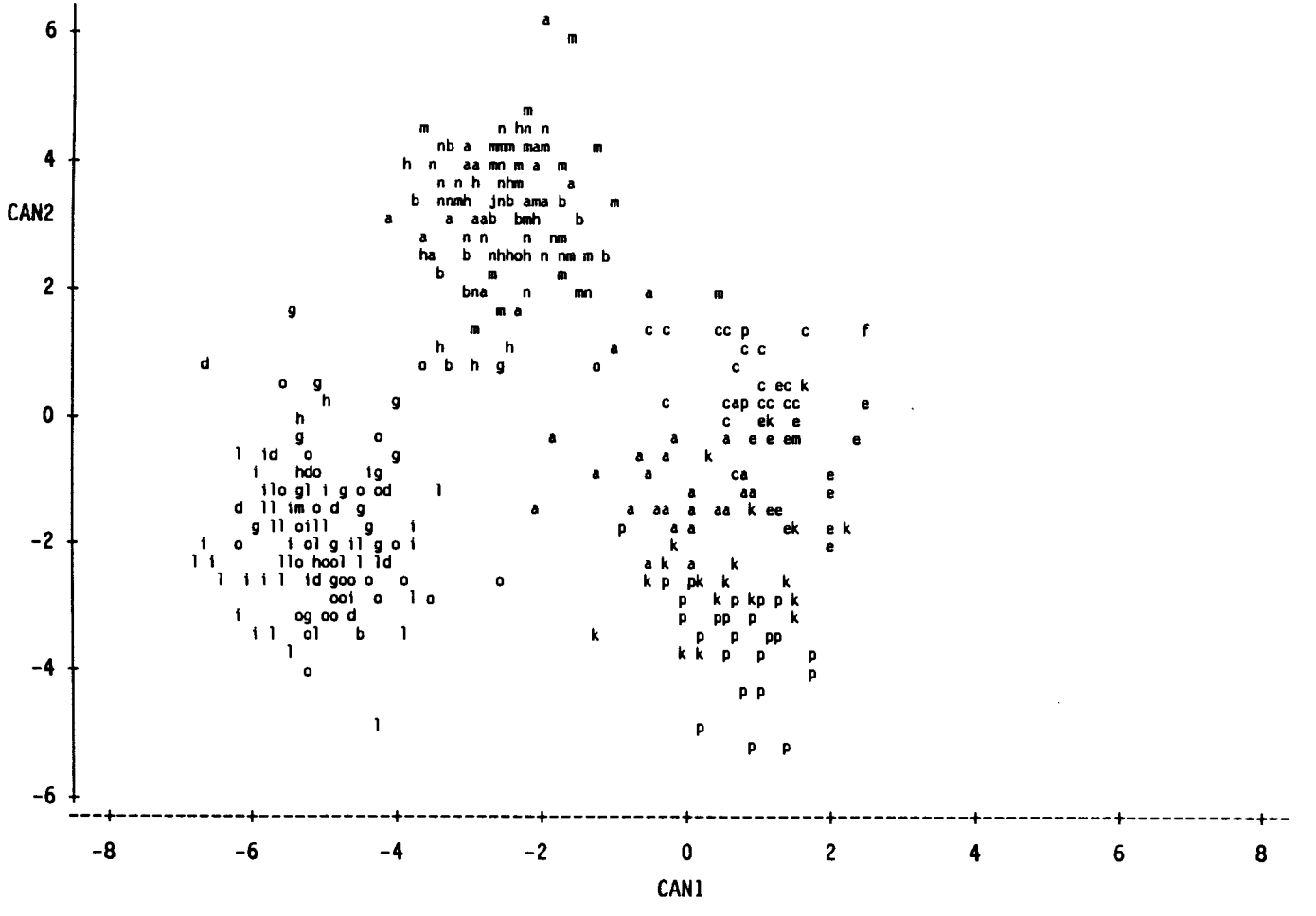


Figure 9. Plot of canonical axes 1 and 2 showing ordination of specimens according to population codes of collection sites (Table 5) (Compare with Figure 6).

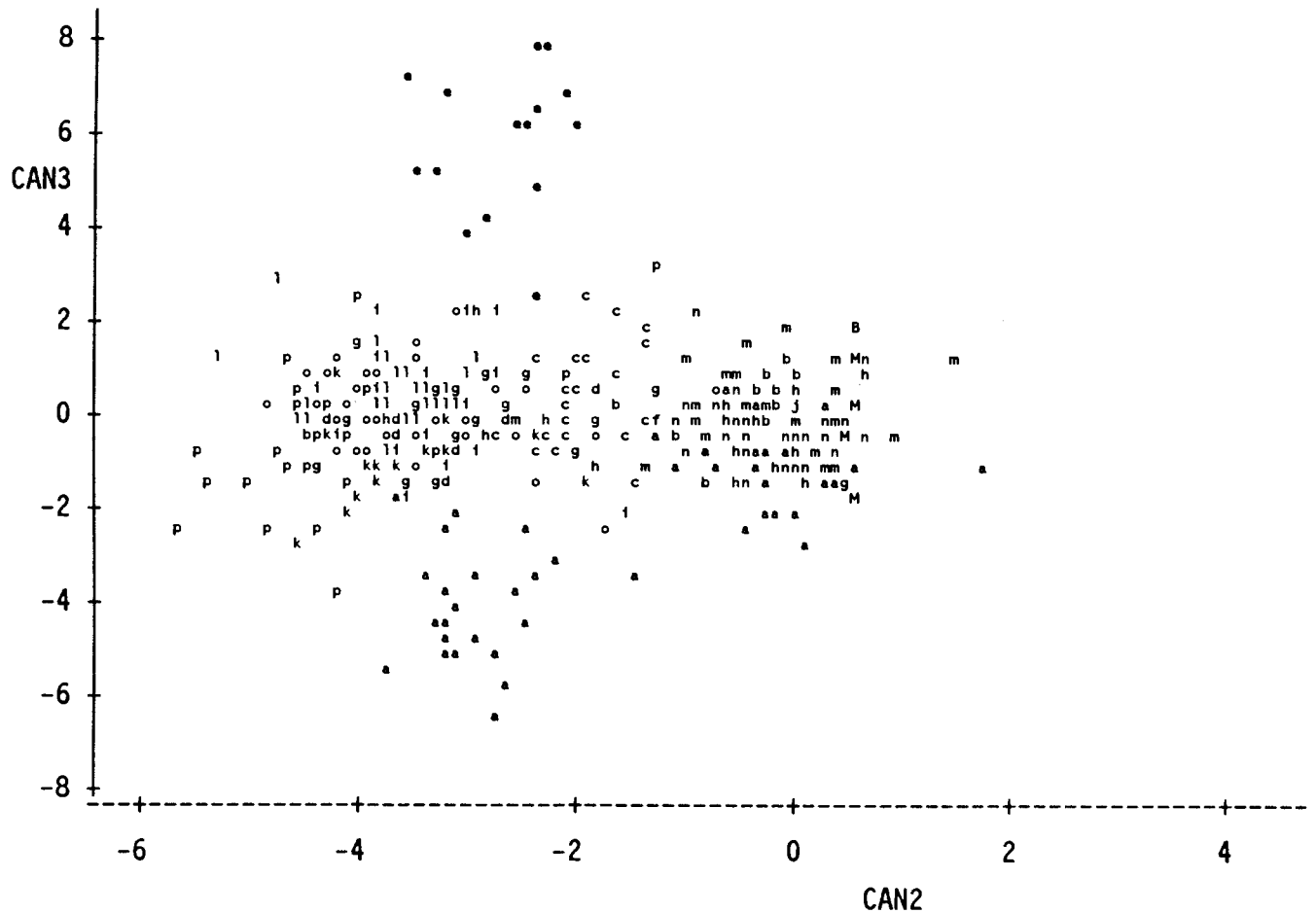


Figure 10. Plot of canonical axes 2 and 3 showing ordination of specimens according to population codes of collection sites (Table 5) (Compare with Figure 7).

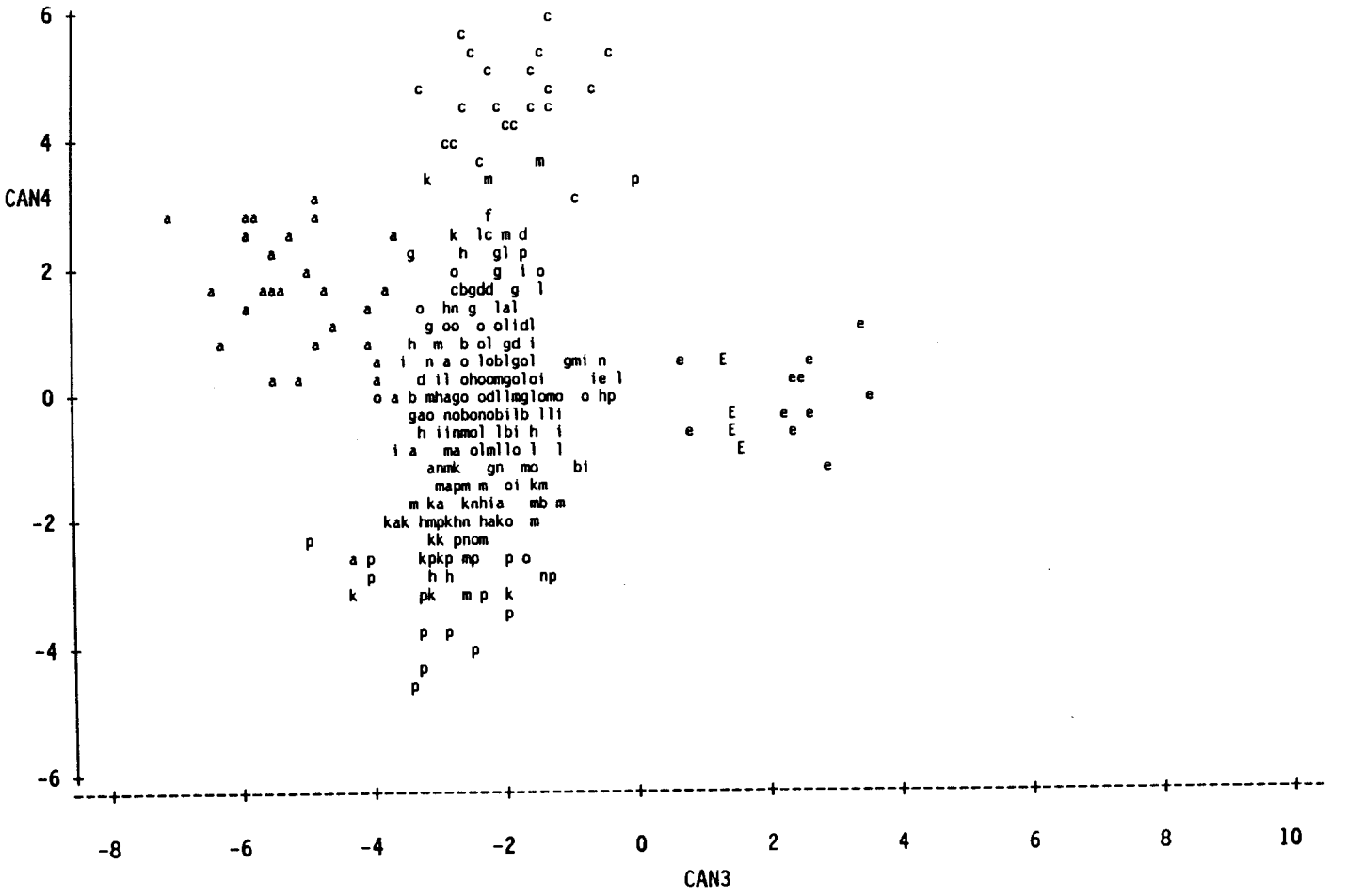


Figure 11. Plot of canonical axes 3 and 4 showing ordination of specimens according to population codes of collection sites (Table 5) (Compare with Figure 8).

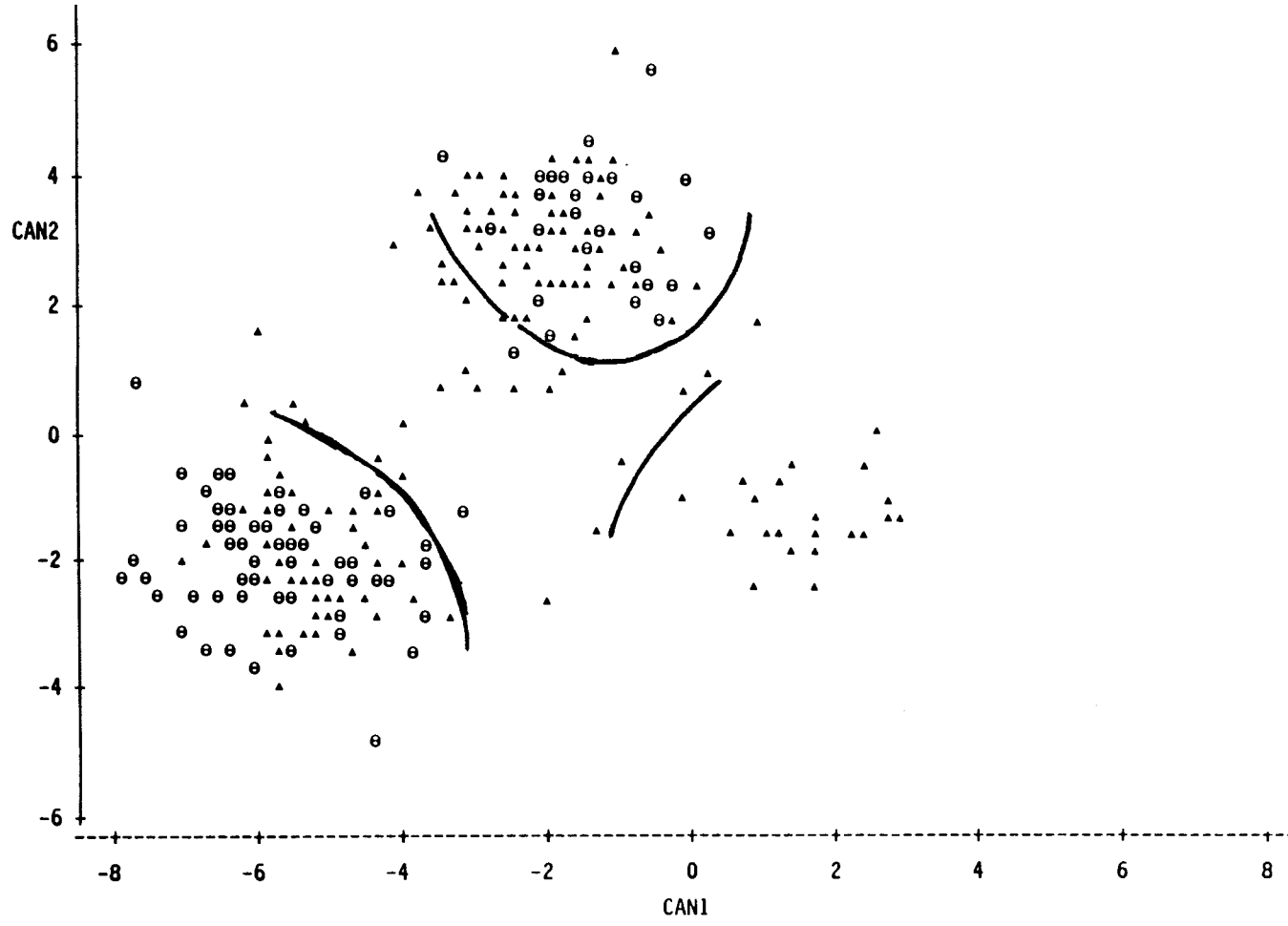


Figure 12. Plot of canonical axes 1 and 2 ordinating specimens of Carex brevior, Carex molesta andCarex festucacea by whether they were collected at allopatric sites (θ) or sympatric sites (▲) (Table 5). Lines delimit boundaries of intermediate specimens (Compare with Figure 6).

3 separates C. festucacea from C. tenera var. echinodes; and canonical axis 4 separates C. normalis from C. tenera.

The SAS CANDISC procedure provides total-sample correlations between the canonical coefficients and the character variables. Canonical characters with the highest absolute value are the most significant characters for that particular canonical axis. Eigenvalues are measures of significance for canonical axes. They represent the ratio of between-class variation to the within-class variation of the morphological characters corresponding to a particular cannonical axis. Eigenvalues for each canonical axis indicate the proportion of the total variation attributed to those characters that are correlated to a particular axis (Table 7).

Table 7. Eigenvalue and the percentage of the total variation explained by each canonical axis.

Canonical Axis	Eigenvalue	% Total Variation
Can1	10.57	45%
Can2	6.03	26%
Can3	2.82	12%
Can4	2.66	11%

Stepwise Discriminant Analysis. The Stepwise Discriminate Analysis selects taxonomic characters on the basis of their overall discriminating power as measured by the F-statistic. Morphological characters are correlated to Euclidean vectors between taxon clusters plotted in n-dimensional space. Morphological variation of a character is represented by vector length. Significance of each character is determined by the ratio of the average variation between taxa to the average variation within taxa (see Table 8).

Table 8. Stepwise discriminant characters separating Carex brevior, C. festucacea, C. molesta, C. normalis, C. tenera and C. tenera var. echinodes.

Character Label		Partial R^2	F-Statistic[1]
51	Achene width	0.7170	183.386
16	Inflorescence width/length	0.6591	139.564
8	F. culm upper leaf width	0.4834	67.380
36	Perigynia length	0.4357	55.431
29	Lateral spike female cycles	0.3938	46.523
7	F. culm upper leaf length	0.3015	30.817
48	Dorsal nerve number	0.2441	22.996
14	Inflorescence length	0.2333	21.610
17	Spike number	0.2590	24.748
24	Terminal spike base shape	0.1721	14.672
28	Lateral spike male cycles	0.1460	12.034
32	Scale length	0.1378	11.222
55	Achene l./perigynia length	0.1350	10.923
45	Beak shape	0.1136	8.944
4	Fertile culm height	0.1099	8.597
38	Perigynia l. to widest point	0.0980	7.536
41	Perigynia l. to w. pt./l.	0.1260	9.976
47	Ventral nerve appearance	0.0871	6.585
46	Ventral nerve number	0.0829	6.223
42	Perigynia shape	0.0797	5.939
2	Fertile culm width	0.0839	6.262
35	Scale w./perigynia width	0.0683	4.998
43	Beak length	0.0664	4.836
33	Scale width	0.0614	4.436
39	Perigynia width/length	0.0629	4.535
37	Perigynia width	0.1312	10.182
34	Scale l./perigynia length	0.1298	10.024
52	Achene width/length	0.0745	5.395
22	Spike shape	0.0405	2.822
26	Terminal spike male cycles	0.0398	2.761
15	Inflorescence width	0.0399	2.759
40	Perigynia shape (l./w.)	0.0429	2.970
27	Terminal spike female cycles	0.0365	2.502
20	Spike width	0.0356	2.429
44	Beak l./perigynia length	0.0288	1.947
19	Spike length	0.0272	1.834
23	Spike apex shape	0.0260	1.749

[1]Characters are arranged in descending order of significance by Wilk's Lambda (not given). The F-statistic is provided for comparison.

Table 8 lists morphlogical characters selected by SAS STEPDISC procedure for separating all six taxa of the C. brevior group. Characters are ranked in descending order of significance according to Wilk's Lambda. The F-statistic, another measure of significance, is provided because it is more commonly used. The partial R^2 is a proportion of the morphological variation explained by the character. Unknown specimens can be identified by sequentially comparing discriminate features of the plant with the box plots and minimum/maximum values of the dataset (Figure 5 and Table 6). For construction of dichotomous keys, STEPDISC identified key characters for segregating subgroups within the C. brevior group. Canonical plots show that C. brevior and C. molesta can be grouped together for comparison to the rest of the group. Table 9 lists characters which separate C. brevior and C. molesta from C. festucacea, C. normalis, C. tenera, and C. tenera var. echinodes. Table 10 lists characters separating C. festucacea, C. tenera var. echinodes, C. tenera and C. normalis into two pairs. STEPDISC also provided character suites to separate difficult pairs of taxa (Tables 11-14).

Morphological Descriptions

Discriminant characters provided by STEPDISC were combined into character suites to create species descriptions. These character combinations will separate taxa within the C. brevior group when considered together. These descriptions include means and interquartile ranges (compare with Figure 5 and Table 6).

Table 9. Stepwise discriminant characters separating the C. brevior group into two subgroups for dichotimous key construction:
Subgroup A = C. brevior and C. molesta;
Subgroup B = C. festucacea, C. normalis, C. tenera and C. tenera var. echinodes.

Character Label		Partial R^2	F-Statistic[1]
37	Perigynia width	0.6040	558.312
14	Inflorescence length	0.3039	159.329
48	Dorsal nerve number	0.1700	74.547
17	Spike number	0.1080	43.963
16	Infloresence width/length	0.1185	48.599
47	Ventral nerve number	0.0505	19.199
24	Terminal spike base shape	0.0535	20.339
32	Scale length	0.0524	19.841
50	Achene length	0.0331	12.272
35	Scale width/perigynia width	0.0321	11.845
51	Achene width	0.0295	10.818
23	Spike apex shape	0.0025	9.967
20	Spike width	0.0272	8.938
7	Fertile culm upper leaf length	0.0246	12.168
29	Lateral spike female cycles	0.0242	8.758
41	Perigynia l. to w. pt./length	0.0199	7.138
44	Beak length/perigynia length	0.0247	8.882
33	Scale width	0.0146	5.200
56	Achene width/perigynia width	0.0179	6.355

[1]Characters are arranged in descending order of significance by Wilk's Lambda (not given). The F-statistic is provided for comparison.

Carex molesta: 3-5 globose spikes with spreading beaks, spike arrangement closely aggregate to spreading at base of inflorescence, rachis stiffly erect; lateral spike base shape round with few male florets (2-3 male cycles on lateral spikes); perigynia lanceolate to ellipitic; 3-4 ventral nerves; scale length/perigynium length 0.69-(0.71)-0.79, perigynium 3.08-(4.06)-4.25 mm long, 2.17-(2.32)-2.50 mm wide; beak 2.00-(2.16)-2.33 mm long, beak length/periginium length 0.50-(0.53)-0.56, beak shape tapered; achene 1.08-(1.16)-1.25 mm wide, achene shape ovate; leaf width < 4 mm.

Table 10. Stepwise discriminant characters separating Carex festucacea, C. normalis, C. tenera and C. tenera var. echinodes into two pairs: Pair 1 = C. normalis and C. tenera var. echinodes; Pair 2 = C. festucacea and C. tenera.

Character	Label[1]
36	Perigynia length
2	Fertile culm width
38	Perigynia length to widest point
8	Upper leaf width
23	Lateral spike female cycles
31	Lateral spike male/female cycles
23	Spike apex shape
32	Scale length
4	Fertile culm height
46	Ventral nerve number
41	Perigynia length to widest point/perigynia length
15	Inflorescence width
47	Ventral nerve appearance
45	Beak shape
39	Perigynia width/length
35	Scale width/perigynia width
4	Spike number

[1]Characters are arranged in descending order of significance by Wilk's Lambda (not given).

Carex brevior: 3-5 spikes varying from globose to obovate with ascending beaks, spike arrangement loosely aggregate to strongly moniliform, rachis erect to nodding; lateral spike base shape tapered to strongly clavate with several male florets (3-6 male cycles on lateral spike); perigynia subrotund to circular, no ventral nerves or nerved at base only; scale length/perigynium length 0.86-(0.92)-0.98; perigynium 3.41-(3.67)-3.9 mm long, 2.42-(2.56)-2.75 mm wide; beak 1.50-(1.71)-1.83 mm long, beak length/perigynia length 0.42-(0.46)-0.49, beak shape abruptly constricted; achene 1.33-(1.41)-1.5 mm wide, achene shape oval to ovate; leaf width < 4 mm.

Table 11. Stepwise discriminant characters for separating Carex brevior and C. molesta.

Character Label[1]
45 Beak shape
24 Terminal spike base shape
34 Scale length/perigynia length
51 Achene width
29 Lateral spike female cycles
7 Fertile culm upper leaf length
46 Ventral nerve number
16 Inflorescence width/length
43 Beak length
35 Scale width/perigynia width
26 Terminal spike male cycles
15 Inflorescence width
20 Spike width

[1]Characters are arranged in descending order of significance by Wilk's Lambda (not given).

Table 12. Stepwise discriminant characters for separating Carex festucacea and C. tenera.

Character Label[1]
42 Perigynia shape (position of widest point)
22 Spike shape
26 Terminal spike male cycles
2 Fertile culm width
50 Achene length
8 Fertile culm upper leaf width
15 Inflorescence width
27 Terminal spike female cycles
47 Ventral nerve appearance
48 Dorsal nerve number
38 Perigynia length to widest point (mm)
51 Achene width
52 Achene width/length
4 Fertile culm height
17 Spike number
32 Scale length
33 Scale width
39 Perigynia width/length
45 Beak shape

Table 13. Stepwise disciminant characters for separating Carex brevior and C. festucacea.

Character Label[1]
29 Lateral spike female cycles
51 Achene width
26 Terminal spike male cycles
47 Ventral nerve appearance
33 Scale width
17 Spike number
38 Perigynia length to widest point
14 Inflorescence length
32 Scale length
21 Spike width/length
27 Terminal spike female cycles
48 Dorsal nerve number
19 Spike length

[1]Characters are arranged in descending order of significance by Wilk's Lambda (not given).

Table 14. Stepwise discriminate characters for separating Carex normalis and C. tenera var. echinodes.

Character Label[1]
8 Fertile culm upper leaf length
40 Perigynia shape (width/length ratio)
48 Dorsal nerve number
32 Scale length
4 Fertile culm height
2 Fertile culm width
20 Spike width
1 Fertile culm leaf number
27 Terminal spike female cycles
3 Fertile culm leaf extended length
38 Perigynia length to widest point
18 Spike arrangement

[1]Characters are arranged in descending order of significance by Wilk's Lambda (not given).

Carex normalis: 4-10 spikes varying from ovoid to obovoid with spreading beaks, spike arrangement aggregate to spreading at base, rachis stiffly erect; lateral spike base usually round to tapering with few male florets (2-4 male cycles on lateral spikes); perigynia narrowly ovate, 3-5 ventral nerves; scale length/perigynium length 0.71-(0.75)-0.79; perigynium 3.08-(3.42)-3.71 mm long, 1.58-(1.75)-1.92 mm wide; beaks 1.50-(1.72)-1.92 mm long, beak length/perigynia length 0.47-(0.50)-0.53, beak shape tapered; achene 1.0-(1.04)-1.08 mm wide, achene shape elliptic to ovate; leaf width > 4 mm.

Carex festucacea: 4-9 spikes varying from subrotund to obovate with spreading beaks, spike arrangement moniliform, rachis nodding, lateral spike base clavate with numerous male florets (5-12 male cycles on lateral spikes); perigynia round to elliptic, 3-4 ventral nerves; scale length/perigynium length 0.82-(0.88)-0.94; perigynium 2.75-(3.04)-3.17 mm long, 1.67-(1.80)-1.92 mm wide; beak 1.25-(1.35)-1.50 mm long, beak length/perigynium length 0.42-(0.44)-0.47, beak shape abruptly constricted; achene 1.0-(1.05)-1.08 mm wide, achene shape elliptic; leaf width < 4 mm.

Carex tenera: 3-7 spikes varying from ovoid to oblong with ascending beaks, spike arrangement varying from aggregate at inflorescence apex to moniliform, rachis weak nodding, flexuous, often zig-zagging; lateral spike base tapered with few male florets (3-6 male cycles on lateral spikes); perigynia broadly ovate, 4-5 ventral nerves, scale length/perigynium length 0.67-(0.94)-1.0; perigynium 2.75-(3.02)-3.12 mm long, 1.50-(1.65)-1.75 mm wide, beak 1.33-(1.52)-1.67 mm long, beak length/perigynium length 0.47-(0.5)-0.53, beak shape tapered; achene 1.0-(1.03)-1.08 mm wide, achene shape ovate; leaf width $\leq$ 3 mm.

Carex tenera var. echinodes: 5-8 spikes varying from ovoid to oblong with widely spreading beaks (echinate), spike arrangement strongly moniliform, rachis nodding, flexuous, or often zig-zagging, lateral spike base tapered with very few male florets (2-4 male cycles on lateral spikes); perigynia narrowly lanceolate to ovate, 3-4 ventral nerves; scale length/perigynium length 0.62-(0.66)-0.69; perigynium 3.91-(4.18)-4.42 mm long, 1.67-(1.74)-1.83 mm wide, beak 2.08-(2.27)-2.42 mm long, beak length/perigynium length 0.51-(0.54)-0.56, beak shape tapered; achene 1.01 mm wide, achene shape narrowly ovate; leaf width $\leq$ 3 mm.

Intermediate Specimens with Mixed Character Suites

Typically, suites of certain character states are highly correlated to a specific taxon, e.g., compare C. molesta with C. brevior. However, at sympatric sites, specimens growing between different taxa tend to have mixed character suites, i.e., they display mixed character states not usually found together on one specimen.

Collection numbers of specimens with mixed character suites are presented in Table 15. These specimens are found in canonical plots in intermediate positions between taxon clusters and are identified as "intermediate specimens". Intermediate specimens were assigned mixed classification probabilities by the SAS DISCRIM Posterior Probablility of Classification Error. I disagreed with SAS DISCRIM classifications of some specimens, because I assigned different weights to certain characters (these specimens are identified by a "**"). Specimens with primary classification probabilities less than 0.9999 were collected at sympatric sites. I could detect mixed character suites in specimens with

Table 15. Specimens displaying mixed character suites as identified by (1) mixed classifications of SAS DISCRIM[1] procedure; (2) intermediate location between taxon classes on canonical plots; and (3) observation of atypical character combinations.

Taxon Code[2]		Site Code[3]		DISCRIM-Classifications[4] Posterior Probabilities		Coordinates[5] CAN1	CAN2
B:104	*	BSM	!	B:0.9966	T:0.0034	-0.255	-2.526
B:110		BSM	!	B:0.9998	M:0.0002	-2.722	-0.170
B:120b		BSM	!	B:0.9985	M:0.0015	-2.691	-0.338
B:194		CHSP		B:0.9999	M:0.0001	-1.446	-1.268
B:292		PKSP	!	B:0.9999	M:0.0001	Not Plotted	
B:295		PKSP	!	B:0.9999	M:0.0001	-2.942	-2.340
B:319	*	PKSP	!	B:0.9954	M:0.0046	-3.756	0.646
B:327	*	PKSP	!	B:0.9554	M:0.0451	-2.414	0.419
B:318	**	PKSP	!	M:0.9966	B:0.0044	-0.247	1.166
B:520	**	WP	!	M:0.9029	B:0.0971	-1.277	0.977
B:530	**	WP	!	M:0.9996	B:0.0004	-1.027	1.857
M:101b	*	BSM	!	M:0.9494	B:0.0506	-1.914	0.763
M:137		OTC	!	M:0.9997	B:0.0003	-1.017	1.979
M:147		OTC	!	M:0.9998	B:0.0002	-0.868	2.074
M:160a				M:0.9999	B:0.0001	-0.284	1.628
M:308	*	PKSP	!	M:0.9786	B:0.0214	-0.879	0.724
M:314	*	PKSP	!	M:0.9804	B:0.0148	-1.557	1.065
M:328	*	PKSP	!	M:0.9852	B:0.0148	-0.366	0.776
M:906		BSM	!	M:0.9993	F:0.0007	2.441	1.906
F:101a	*	BSM	!	F:0.7575	M:0.2425	1.512	0.863
F:894		BSM	!	F:0.9999	B:0.0001	1.768	1.283
B:945	**	BSM	!	F:0.9998	B:0.0002	0.400	-1.316
T:055	*	SRCP	![6]	T:0.9671	E:0.0329	2.776	-2.678

[1]SAS DISCRIM Posterior Probability Error-rate Estimates.

[2]Letter represents Taxon code with collection number (Tab. 1).
(*) marks specimens with DISCRIM classification of $P \geq 0.0034$).
(**) author classified specimen differently than SAS DISCRIM.

[3]See site identification codes (Tab. 2).
(!) denotes sympatric site.

[4]First column represents DISCRIM posterior classification of the OTU by Taxon code followed by probability of certainty. Second column represents probability that the OTU should be classified into second taxon.

[5]Canonical coordinates for axes 1 and 2.

[6]Specimen collected near C. normalis and C. tenera.

secondary classification probabilities greater than 0.0034 (identified with a "*"). Specimens with mixed SAS DISCRIM probabilities less than 0.0034 tended to display character states at the extreme tails of univariate frequency distributions for that taxa. The habitats of intermediate specimens were greatly disturbed sites: sandy river raceways (PKSP); flooded prairie swales between dry knolls (WP); eolian sand dunes (BSM); or exposed subsoil (BSM).

Intermediate Specimens of Carex brevior and Carex molesta

Specimens B:318, B:520 and B:530 ("B" = C. brevior) occupied intermediate positions between taxon clusters of C. molesta and C. brevior. They are atypical with mixed characters. Their primary SAS DISCRIM classification was C. molesta, but other features of their perigynia and inflorescence are more representative of C. brevior. DISCRIM classified B:318, B:520 and B:530 as C. molesta because they had shorter scale lengths; narrowly ovate achene shapes with shorter achene lengths; short spike lengths; high spike width/length ratio (i.e. round spikes); round terminal spike bases; few male florets on lateral spikes; spikes aggregated on inflorescence; low ratio: male cycles/female cycles on lateral spikes; low ratio: achene width/perigynia width; strongly to finely nerved ventrally; high dorsal nerve count; and tapering beaks. I classified them as C. brevior because of the subrotund shape of the perigynia and ascending beaks. Many perigynia had no ventral nerves. These specimens were found in typical C. brevior habitats on elevated knolls (B:520 and B:530) or well-drained sand (B:318).

Mixed character suites for B:292 and B:295 include C. molesta features with round, approximate spikes; ellipical perigynia, tapering beaks, strongly ventral nerves; and C. brevior features with lateral spikes with tapering bases and high ratio: male cycles/female cycles; long achene length; high scale length to perigynia length ratio; and they are shorter plants with short leaves. To me they resemble C. brevior more than C. molesta.

Mixed character suites for M:308 and M:314 ("M" = C. molesta) include C. brevior features with moniliform spikes with ascending beaks and moderatly clavate or tapering bases. However, perigynia are more like those of C. molesta with lanceolate shapes and ventral nerves. Both specimens were collected in a soil type typical of C. molesta with moist organic silts mixed with sand.

Intermediate Specimens of Carex molesta and Carex festucacea

An itermediate specimen of C. molesta and C. festucacea was found at BSM. C. molesta traits for M:906 include circular to oval perigynia with tapering beaks. C. festucacea traits include high inflorescence length; low inflorescence width/length; moniliform spike arrangement (approximate spike tips); spike bases clavate; high number of male cycles (9) on terminal spike; high ratio: terminal spike male cycles/female cycle; no ventral nerves on perigynia.

The specimen labeled F:101a was collected with M:101b at the base of a sand slope (BSM). It was initially analyzed as an unknown and only classified as C. festucacea after seeing results of canonical analysis. It most resembles C. brevior in overall appearance. Character states for F:101a normally attributed to C. festucacea include narrow achene width (1.0); low ratio: achene

length/perigynia length; low perigynium length to widest point/perigynia length (= 0.44); long beak length = 1.42 mm. However, character states normally attribruted to C. molesta were globose spikes, short inflorescence, high inflorescence width/length, perigynia wider than 2mm, lowest value of female cycles on terminal spike (9, next value 12); lowest lateral female cycles; ovate perigynia bodies (all C. festucacea specimens had oval bodies); tapered beaks; low scale width/perigynia width (= 0.48); low scale length/perigynia length (= 0.79); ventral nerves at base only; and ascending beaks.

Intermediate specimens of Carex brevior and Carex festucacea

Mixed character suites for F:945 include lanceolate to narrowly ovate perigynia with no ventral nerves (perigynia extremely long for C. festucacea); moniliform spike arrangement; strongly clavate spike bases; spikes oblong, spike beaks ascending to spreading; long achene length and width yet achene is elliptically shaped; the highest lateral male cycles/ female tiers ratio of any specimen of C. brevior and C. festucacea; and the lowest scale width/perigynia width for festucacea (= 0.42 next highest 0.48).

B:104 was collected in a small depression on a large sand dune at BSM. Many of the characters were within the normal distributions for C. brevior: moniliform spike arrangement and perigynia ascending to spreading. However, features of the perigynium were more like C. festucacea: low perigynium length, strongly 3-nerved ventrally low perigynia length, perigynia width under 2 mm, narrow achene width, elliptically shaped achene, high number of dorsal nerves, 3 ventral nerves, low scale length and width, extremely low beak length, high

achene length to perigynia length ratio, and the length-to-widest-point-of-perigynia is near the mean for C. festucacea.

Intermediate specimens of Carex tenera and Carex normalis. At SRCP, I randomly collected a specimen (T:55) growing in the meadow at the edge of an aspen thicket. This specimen had perigynia very similar with those of C. normalis, collected about 2 meters away growing in gray-loam soil beneath the aspens. The vegetative features were like those of C. tenera which grew in moist peat or muck soil.

CHAPTER 4

DISCUSSION

This study demonstrates that: 1) Carex brevior, C. festucacea, C. molesta, C. normalis, C. tenera, and C. tenera var. echinodes are morphologically distinct taxa; 2) there are suites of taxonomic characters useful in classifying and recognizing taxa; and 3) while taxonomic characters vary, most of this variation occurs within populations in predictable patterns.

Taxonomic Classifications

This study was conducted under the premise that current taxonomic classifications for the C. brevior group were valid. I based this determination upon the examination of an extensive number of specimens collected throughout the eastern and central United States. I concentrated mainly on the study of historical specimens cited or annotated by authors in their treatments of the C. straminea aggregate. I was able to use multivariate statistics, specifically Discriminant Function Analysis (DFA), to test the hypothesis that morphological forms within the C. brevior group are significantly different. This procedure differs from most taxonomic studies which assume no apriori classification and use Principle Component Analysis to formulate a classification scheme. Random sampling removed any bias in the selection of specimens and enabled me to estimate frequencies of occurrance for morphological forms within populations, between populations, and among taxa. It was only by randomly collecting up to 30 samples per population, from multiple populations, that I was able to determine if morphological differences between taxa were significant. Normal

distributions for characters states indicate that the sample size was sufficient to include most of the variation expressed by the taxa. The results of this study show that: 1) Iowa representatives of the C. brevior group are significantly different from one another, 2) there are suites of correlated morphological characters capable of distinguishing taxa, and 3) taxonomic characters vary in predictable patterns according to current theories of Carex morphological development and cytogenetics.

This study has two limitations: 1) three taxa were collected from only one or two populations, and 2) only Iowa specimens of the C. brevior group were sampled. However, results from taxa with fewer sample sites were in agreement with results obtained from more extensive collections of C. brevior and C. molesta. In addition, my examination of herbarium specimens indicates that the Iowa specimens documented in this study accurately represent morphological forms found throughout the entire geographic distribution of the taxa, i.e., characters of specimens collected from other regions agree with the character distribution parameters provided in Table 6 for Iowa collections. For example, Rothrock (1991) has shown Carex festucacea to be a distinct species using Principal Component Analysis of selected herbarium specimens. Multivariate analysis of a single population of C. festucacea in Iowa (BSM) identified taxonomic characters similar to those selected by Rothrock (1991). Character means were similar in both studies (within one standard deviation) for inflorescence length, number of spikes per inflorescence, spike length, perigynium width, perigynium length from base to widest point, number of ventral nerves, achene body width/length ratio, and achene width.

Taxonomic Characters

This study documents that morphological characters of the C. brevior group vary within populations in a characteristic pattern. Much of this variation can be explained using current theories of morphological development and cytogenetic evolution. It is likely, based on genetic research of other Carex populations, that most of the variation documented in this study can be attributed to 1) genetic differences between taxa, 2) phenotypic plasticity, and 3) hybridization. These conclusions are probably applicable to the rest of the C. straminea aggregate and perhaps the section Ovales as well.

DFA selected taxonomic characters based on statistical measures of significance (Wilk's lambda and the F-values). Yet univariate analysis demonstrates that these characters overlap among taxa. Therefore, individual characters cannot distinguish the taxa alone, but must be used in combination with other characters to create character suites cabable of separating taxa. I will now discuss the taxonomic applications and limitations of these characters.

Vegetative Characteristics

Mackenzie (1931-1935) used vegetative characters to create subsectional divisions within the genus Carex. Subsections Tribuloideae and Festucaceae were distinguished by features of the culm and leaves (number, width, length, cross-section, sheaths etc.). These vegetative characters are correlated with taxonomic features of the perigynium. One exception is C. normalis which has vegetative qualities of C. tribuloides but perigynium features similar to C. festucacea (representative species of Mackenzie's subsections). Leaf

characteristics distinguish the C. brevior group and subsection Festucacea from subsection Tribuloideae, which includes C. tribuloides, C. cristatella, C. projecta, and C. muskingumensis. The Festucaceae have narrower (≤ 4 mm), v-shaped leaves, whose bases are on lower third of the fertile culm. While the Tribuloideae, usually have wide (> 5 mm), w-shaped or phlanged shaped leaves, with leaf bases mostly two-thirds the length of the fertile culm. C. normalis is unusual for the Festucaceae, because it has wide, phlanged shaped leaves, whose bases are up to one-half the culm's length. The perigynia of C. normalis are characteristic of the Festucacea with ovate perigynia (instead of obovate) which are uniformly winged to the base (instead of wings constricted at mid-point of perigynia, narrowing toward the base).

Some authors make use of color, leaf shapes, leaf ligules and sheaths, as well as the presence and absence of vegetative culms. I found these features useful in the field for comparing one specimen to another, but could not make use of them otherwise. Within a group of morphologically similar taxa such as the C. brevior group, I have observed that many vegetative characters are unreliable and nearly impossible to quantify for statistical analysis. However, Rothrock (1991) has quantified several features of the leaf sheath and culm for distinguishing C. festucacea, C. albolutescens and C. longii.

Vegetative culms express useful characteristics and should always be examined. However, they are not capable of distinguishing taxa within the C. brevior group. When characters of vegetative culms were included in stepwise discriminant analyses they had relatively low discriminating power. For example,

the number of leaves on vegetative culms for C. molesta varied from 3-13 which included the entire range of all the other taxa combined. The width of the largest vegetative culms were smaller than the width of fertile culms for all taxa. Vegetative culms varied considerably within the genet, while fertile culm widths were consistent. Vegetative features such as ventral sheath surfaces (hyaline vs. green-striated), ligules, leaf cross-sections, etc., are easier to observe on vegetative culms than on senescent fertile culms.

Variation of vegetative characters. Size, shape and color of both types of culms varied in similar manner in all taxa. Generally, genets of the same taxa were a darker green in shaded areas while those in open sun were a yellowish-green. Shaded plants and plants in dense herbaceous cover often had thinner, rounder and more elongated culms than plants in open and disturbed habitats.

Hyaline portions of ventral sheaths cannot be seen on smaller culms even from those taxa where this is a characteristic feature. C. suberecta is described as green-striated to the mouth of the ventral sheaths and this is a consistent feature. However, I have only seen specimens collected from highly competitive sedge-meadows bordering fens where the culms are less than 3mm wide. Typically, C. tenera and C. scoparia have hyaline ventral sheaths, but these are often not expressed. The absence of hyaline sheaths can be attributed to poorly developed culms often found in dense herbaceous cover or shaded areas. The dorsal sheath of several taxa, especially C. brevior and C. bicknellii, have the green-white mottled color which Mackenzie described as characteristic of C. normalis. I have found features of the sheath are not reliable enough to be primary key characters in opening leads.

Pseudoculms represent one of many morphological stages in the development of culms in the C. brevior group. Leaves of these specimens were clustered at the apex of the culm and surrounded by a sheath originating from the culm's base. The height of the extended leaves was consistently about 11 cm for all taxa of the C. brevior group. When the outside sheath was removed and the leaves were dissected away, I exposed apical meristems on a 3-4 cm culm. It appears that the leaves are clustered within the sheath because the internodes have not yet elongated. I found vegetative culms at several morphological stages of development in every population from those still in the coleoptile-like prophyll to well developed vegetative culms with vascular tissue, nodes and internodes. True vegetative culms with nodes and internodes were found on nearly every genet. These were occasionally more numerous than culms with fertile inflorescences. Vegetative culms are capable of overwintering above ground, ultimately developing into inflorescences the following spring.

Inflorescence Characteristics

Most of the evidence for the taxonomic classification of Carex is based on the features of the inflorescence, spike and perigynium. While each taxon exhibits distinctive forms of these structures, they vary considerably in shape, size and color. Inflorescence characters are most useful in segregating subgroups within the C. brevior group. Useful characters include the average length of the inflorescence, inflorescence width/length ratio, and the arrangement and number of spikes.

Variation within the inflorescence. Inflorescence morphology is determined primarily by internodal distances. The manner by which spikes are arranged along the rachis of the inflorescence varied in all populations of each taxon from aggregate to moniliform. Morphological extremes were seen and measured in ramets of the same genet. Strongly moniliform spike arrangements in C. brevior and C. festucacea were moderately correlated with longer inflorescence lengths. Inflorescence lengths in both taxa were also moderately correlated with an increased number of male floret cycles on lateral spikes. The number of male floret cycles was correlated with clavate spike bases. I observed internode distances of the axis between male florets with varying lengths. This added to the clavate appearance of spike bases. These variations suggest that inflorescence morphology is controlled by growth hormones which affect the internode lengths of inflorescences and spikes (Smith 1967 1969).

Spike Characteristics

Spike shape and size are the most useful taxonomic characteristics of the inflorescence. Spike appearance is influenced by the number of florets, the internodal distances between florets, and the ratio of male to female florets on the spike. Spreading perigynium beaks give the spike an echinate or bristly appearance with round apices and bases. Ascending beaks give the appearance of acute spike tips and elliptic spikes. Spike length and lengths of the male and female portion of the spike are useful but highly variable characters and must be used cautiously. The number of male florets and their internode length determine whether a spike base is round or clavate.

Variation of spike characters. Florets develop spirally around the rachilla. The spiral ascends from right to left as viewed laterally--clockwise if viewed from the top. The spikes are indeterminate. Empty pistillate scales are always present at the apex because the perigynia never develop. The number of female cycles varies in all taxa and spike shapes can be attributed to development. An increasing number of female florets will change the overall shape of the spike from globose to elliptic (or obovate to oblong, depending on the number of male florets). Whether perigynia beaks are appressed or spreading may depend on the number of perigynia per measured length of the rachilla. Shorter internode lengths between florets compresses perigynia on spike axes causing their beaks to spread apart as the perigynia mature. C. brevior has longer spike axes, relatively few perigynia, and ascending beaks. In contrast, C. molesta has a greater number of perigynia compressed on shorter spike axes causing the perigynia to spread widely giving the spike a bristly or echinite appearance. Long perigynium beaks, short spike lengths and proportionally low numbers of male florets accentuates the round appearance of spikes in C. normalis, C. molesta and C. tenera var. echinodes.

Meristems of the inflorescence develop into male florets, female florets or elongate into spikes (Smith 1966). I found sexual structures in many specimens where they do not normally occur. In all taxa, I frequently observed stamens in positions where perigynia or spikes normally developed. Also, isolated male florets were found in various positions between the second and seventh cycles of the female portion of the spike. At the base of each spike, there is a subtending

bract on the rachis. The bract of the lowest spike is usually setaceous and often exceeds the inflorescence. Stamens are found in nearly every spike bract except the lowest. Occasionally the spike axis aborts and no spike develops leaving an empty bract. More frequently, additional spikes form in the subtending bract of the terminal spike. These extra spikes have one to several perigynia. One such spike developed from a male floret position in the second cycle of the terminal spike (F:893). These observations support morphological evidence which indicates that Carex florets are actually reduced spikelets with an aborted rachilla. Smith (1967) experimented with the addition of plant hormones to developing meristems. He determined that various hormones could alter the outcome of the meristems and affect the numbers of male florets, female florets, or lateral spikes.

Club-shaped or clavate spike bases are a diagnostic feature for C. festucacea. However, spike bases vary considerably in all taxa and this distinctive feature is not always present in C. festucacea. The spike morphology is determined by the number of floret cycles around the axis and internode distances. The number of cycles of staminate florets varies in all taxa, especially in terminal spike bases. However, the number of male cycles in lateral spikes is more consistent. Therefore, lateral spike bases exhibit more useful characteristics.

Scale and Bract Characteristics

The size of the scale in relation to the perigynium is a distinctive quality. The ratio: scale width/perigynium width segregates C. brevior and C. molesta from the rest of the taxa, while the ratio: scale length/perigynia length separates

this pair from each other. Scale length/perigynium length also distinguishes C. tenera var. echinodes due to its longer perigynia. I cannot discern any differences in color, nervation or shape of the pistillate scales in any taxa, except C. brevior, whose pistillate scales are usually longer than other taxa. C. festucacea was reported by Dewey (1824) to have staminate scales with accuminate tips, but this is not true for Iowa specimens.

Variation of scale and bract characters. Scales vary in shape and size depending on position. Staminate scales near the spike base are shorter with truncate or obtuse tips. Scale length becomes normal with acute tips by the third cycle of male florets. Bracts subtending spikes are mostly indistinguishable from staminate scales except for the lowest bract which is usually setaceous. Often the bristled tip of the lowest spike bract equals the length of the inflorescence.

Perigynium Characteristics

Perigynium characteristics account for 39% of the total number of characters analyzed in this study. Stepwise Discriminate Analysis of the entire dataset selected a total of 37 characters with discriminant powers; about 35% of these were perigynium traits. Historically, all specific and varietal classifications in Carex are based on the perigynium. Therefore, using traditional species concepts, distinguishing characteristics of a taxon's life history, habitat, rhizome, culm, leaf or inflorescence must be correlated with recognizable features of this unique structure. Critical examination of perigynia is necessary for accurate identifications of specimens in the C. brevior group. But the perigynium can never be the only criteria for recognition because its distinguishing features vary

considerably within populations, or even within genets, or they may be absent. The most characteristic perigynia are found between one-half to two-thirds the spike length as measured from the base.

The size and shape of the perigynia account for much of the variablity between taxa. Average perigynium lengths of the C. brevior group range from 3 mm to 4.25 mm. However, perigynia lengths vary even within the same spike and their ranges of variation overlap among the taxa. Perigynium width separates the C. brevior group into two subgroups. Taxa with lanceolate or narrowly ovate perigynia seldom exceed 2 mm in width, i.e., C. brevior and C. molesta with circular or elliptic perigynium shapes characteristically have perigynia widths 2 mm or greater. Similarly, the location of the widest point on the body of the perigynium is also a good taxonomic character. The ratio of the length-to-the-widest-point divided by the perigynium length is a reliable measure of this characteristic shape. Perigynium shape separates C. tenera var. echinodes and C. normalis, which are narrowly ovate, from C. brevior, whose perigynia are consistently circular. C. molesta and C. festucacea tend to have elliptical perigynium bodies while C. tenera perigynia tend to be ovate. Perigynium shapes were also measured qualitatively using an adaptation of standard shapes provided by Radford et al. (1974). The two methods for enumerating perigynium shapes essentially double-weighted the discriminating power of this feature. However, removal of the second qualitative measure did not significantly alter the canonical distances between taxon classes, while its inclusion gives greater clarity in defining shape characteristics.

The size and shape of perigynium beaks are good taxonomic characters. In order to reduce ambiguity, I measured beak length from the apex of the achene to the tip of the perigynium teeth. Within taxa, beak length is directly proportional to perigynium length and beak lengths overlap among taxa. Therefore, it is not a distinctive trait. A more useful taxonomic character is the ratio: beak length/perigynium length. This feature separates C. brevior and C. festucacea from other taxa. Beak shape is based on the outline of the perigynium from the mid-point to the beak apex. Tapered beaks are characteristc of C. tenera, C. tenera var. echinodes, C. molesta, and C. normalis. Constricted beaks curve inwards above the achene, forming short, narrow beaks charcteristic of C. brevior and C. festucacea. Beak shape is a good secondary character.

The quality and number of perigynium nerves over the achene have taxonomic merit. However, nerves are difficult to see on immature perigynia. Strongly-nerved perigynia have relatively thick nerves elevated above the surface of the perigynium. Fine nerves are imbedded within the tissue of the perigynium or just slightly raised. Nerve quality is subjective, therefore comparisons must be made with known specimens. C. brevior typically does not express perigynium nerves on the ventral surface and is the only taxon of the group readily identified by nerve counts.

Characteristics of the Achene

Achene width and achene shape are useful for separating C. brevior and C. molesta from other taxa. Like other characters, they have separate means with overlapping ranges of variation. Ratios of achene width/perigynium width and achene length/perigynium length are good secondary characters.

Sources of Morphological Variation

Most of the morphological variation expressed by Iowa specimens of the C. brevior group is found at the population level because there are no detectable differences in population patterns within taxon clusters. This is indicated by the uniform distribution of population codes within taxon clusters in canonical plots (Figures 9-11) and normal distributions of single characters (Figure 5). Also, specimens of sympatric populations of C. brevior and C. molesta occupied somewhat intermediate positions in canonical plots between allopatric populations within the taxon clusters of these two species (Figure 12 and Table 15). I believe the variation documented in this study may be attributed to phenotypic plasticity and hybridization.

Phenotypic Plasticity

Studies of microspecies within species aggregates have shown that there is low genetic variation in Carex populations (Whitkus 1988; Bruederle and Fairbrothers 1986; Waterway 1990; Bruederle and Jensen 1991). Whikus (1988) demonstrated that microspecies reproduced primarily by selfing resulting in homozygous populations with low genetic diversity. If populations of the C. brevior group exhibit low genetic diversity as has been documented for other species aggregates, then the variation recorded within populations is probably due to phenotypic plasticity controlled by environmental gradients. These conclusions are supported by studies of developmental morphology in the genus Carex (Smith 1966 1967 1969). Based on the results of this study and past research, I have concluded the variation found within Iowa taxa is largely due to phenotypic

plasticity, while variation among the taxa is due to genetic differences probably maintained by pre-zygotic reproductive barriers and different habitat preferences.

Hybridization

An additional and substantially different type of morphological variation is observed at sympatric population sites. Specimens from sympatric populations occupy intermediate positions between taxon clusters on canonical plots. In addition, a disproportionate number of specimens from sympatric sites are found in hemispheric regions of taxon clusters which are closest to the sympatric taxon. Removal of specimens collected at sympatric sites would eliminate overlap of clusters, increase the distance between cluster centroids and result in higher F-values of significance. Canonical plots demonstrate that specimens from each population are homogeneously distributed throughout each cluster, i.e. no secondary patterns are evident within taxon clusters. However, allopatric populations (single species sites) for C. brevior and C. molesta form a tighter pattern around cluster centroids while specimens from sympatric populations (multiple species sites) tend to form looser patterns in peripheral regions intermediate between taxon clusters (Figure 12). Nearly all the specimens plotted within this intermediate zone were specimens collected in close proximity to members of another taxa (Table 15). While suites of correlated characters separate taxa, intermediate specimens from sympatric sites have mixed character suites, i.e., they express character states attributed to both taxa found at the site. These are difficult specimens to classify.

The canonical pattern of C. festucacea specimens, collected at BSM, is characteristic of a sympatric population. There is a tight grouping of specimens near the taxon centroid, and a second more diffuse grouping in a narrow peripheral segment forming an intermediate band between associate species, C. brevior and C. molesta.

The presence of mixed character suites within specimens collected at sympatric sites may be evidence of hybridization or introgression. Cytogenetic research has shown that hybridization between morphologically similar species with small differences in chromosome number is common in Carex. Tanaka (1940 1949) suggests naturally occurring hybridization may be a common form of speciation within Carex. The frequent occurance of specimens with mixed character states suggests that hybridization is occurring between taxa of the Carex brevior group.

Although inconclusive, evidence from field observations of C. tenera var. echinodes combined with morphological analysis supports the conclusion that this taxon may have originated from a naturally occurring hybrid cross between C. tenera and C. normalis. C. tenera var. echinodes displays a mixed combination of character states with perigynia very similar to C. normalis, but vegetative characters similar to C. tenera. C. tenera was found in moist high-organic soils formed under prairie vegetation, while C. normalis was found in well-drained, grayish-loam soils formed under prairie and hardwood forest. A population of C. tenera var. echinodes was collected at a shaded hill-side seep in Martin County Park. This habitat is unique to C. tenera var. echinodes. Specimens of C. tenera

var. echinodes are plotted in between C. tenera and C. normalis on the second canonical axis (Figures 6 and 7). A specimen of C. tenera (T:55) was collected 3 meters away from two specimens of C. normalis at SRCP. T:55 closely resembles C. tenera var. echinodes. It was found growing in an intermediate or transition zone between peat soil and upland loam where C. tenera and C. normalis were found.

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APPENDIX A

NOMENCLATOR OF THE CAREX BREVIOR GROUP

CAREX STRAMINEA Willdenow ex Schkuhr Willdenow (1805)

C. straminea Schkuhr ex Willdenow Schkuhr (1801) No. 49, Plate G, Fig. 34.

C. straminea Schkuhr ex Willdenow Wahlenberg (1803) No. 38, p 145 [p 119 of (1806) translation] (= C. brevior?).

C. straminea Schkuhr ex Willdenow Willdenow (1805) No. 73, p 242.

C. straminea Schkuhr ex Willdenow Schkuhr (1806) No. 62, Tab. Xxx, Fig. 174.

C. straminea Schkuhr ex Willdenow Muhlenberg (1817) p 229.

C. straminea Schkuhr ex Willdenow Schweinitz (1824) No. 35 (= C. brevior?).

C. straminea Willdenow ex Schkuhr Schweinitz (1826) No. 34 (= C. brevior?).

C. straminea Wahlenberg non Willdenow Dewey (1826a) p 157.

C. straminea Willdenow ex Schkuhr Torrey (1836) No. 37, p 395 (= C. brevior).

Vignea straminea Rafinesque (1840) [The Good Book and the Amenities of Nature p 27: See Merrill 1949].

C. straminea Willdenow ex Schkuhr Tuckerman (1843)

C. straminea Willdenow ex Schkuhr Carey (1856) No. 41, p 516 (= C. brevior).

C. straminea var. aperta F. Boott Boott (1862) p 120, Fig. 385 (p. p.).

C. straminea var. aperta [forma] major Olney Olney (1870) Exsiccatae Carices Americanae-Boreali (p. p.).

C. straminea var. aperta F. Boott Bailey (1886) p 152 (p. p.).

C. straminea var. aperta F. Boott Bailey (1889 1890) p 24. and p 622 (p. p.).

Carex tenera Dewey Mackenzie (1896) No. 200, Fig. 870, p 358.

C. tenera var. Richii Fernald Fernald (1902) No. 12, p 475, Figs. 33 and 34.

C. hormathodes var. Richii Fernald Fernald (1906 1908) pp 165-166, and No. 12, p 220, Fig. 358.

C. straminea var. tenera forma Richii Kukenthal Kukenthal (1909) No. 167, p 206.

C. hormathodes Fernald Mackenzie (1913) No. 71, p 384, Fig. 938.

C. Richii Mackenzie Mackenzie (1931 1940) No. 180, p 160, and plate 180.

C. straminea Willdenow ex Schkuhr Fernald (1950) No. 94, p 327, Fig. 597.

CAREX FESTUCACEA Schkuhr ex Willdenow (1805)

C. festucacea Schkuhr ex Willdenow Willdenow (1805) No. 72, p 242.

C. festucacea Schkuhr ex Willdenow Schkuhr (1806) No. 62, p 23, Fig. 173.

C. festucacea Schkuhr ex Willdenow Muhlenberg (1817) p 249.

C. festucacea Schkuhr ex Willdenow Schweinitz (1824) p 66.

C. festucacea Schkuhr ex Willdenow Dewey (1824) No. 15, p 96.

C. festucacea Schkuhr ex Willdenow Schweinitz (1826) No. 37, p 316.

C. festucacea Schkuhr ex Willdenow Torrey (1836) No. 36, p 394.

C. straminea var. festucacea Gay (1838) [Ann. Sci. Nat. (II) x. 363 [Bailey (1889) footnotes that description founded on C. normalis and C. adusta at Kew].

C. straminea var. festucacea Gay Tuckerman (1843)

C. festucacea Schkuhr ex Willdenow Carey (1856) No. 39, p 516.

C. straminea var. festucacea Gay Boott (1862) p 120, Fig. 386.

C. straminea var. festucacea Gay Carey (1867) No. 44, p 580.

C. straminea var. (No. 1) Bock (1875) [Linneae 39: 117].

C. straminea Willdenow ex Schkuhr Bailey (1886) [p. p.] No. 283, p 149.

C. straminea var. brevior Dewey Bailey (1889) [p. p.] No. 31, p 22.

C. straminea var. brevior Dewey Bailey (1890) [p. p.] No. 132, p 622.

Not C. festucacea Willdenow sensu Mackenzie (1896) No. 201, p 359, Fig. 871. (= C. brevior and C. merritt-fernaldii)

C. straminea Willdenow Mackenzie (1896) [p. p.] No. 198, p 358, Fig. 868.

C. straminea Willdenow Fernald (1902) [p. p.] No. 11, p 474.

Not C. festucacea Schkuhr sensu Fernald (1902) No. 16, p 477, Figs. 47, 48. (= C. merritt-fernaldii).

C. straminea Willdenow Fernald (1908) [p. p.] No. 11, p 219.

Not C. festucacea Sckuhuhr sensu Fernald (1908) No. 17, p 220-221, Fig. 363 (= C. merritt-fernaldii).

C. straminea var. festucacea (Schkuhr) Tuckerman Kukenthal (1909) p 206.

C. straminea Willdenow Mackenzie (1913) [p. p.] No. 66, p 382.

Not C. festucacea Schkuhr sensu Mackenzie (1913) No. 69, p 383, Fig. 936 (= C. brevior and C. merritt-fernaldii).

C. festucacea Schkuhr ex Willdenow Mackenzie (1915) p 608.

C. festucacea Schkuhr ex Willdenow Mackenzie (1931) No. 165, p 150.

C. festucacea Schkuhr ex Willdenow Mackenzie (1940) No. 165.

C. festucacea Sckhuhr ex Willdenow Fernald (1950) No. 81, p 325, Fig. 583.

C. festucacea Schkuhr ex Willdenow Rothrock (1991) No. 2, p 63, Figs. 2-5.

CAREX TENERA Dewey (1824 & 1825)

C. tenera (Mihi) Dewey (1824) No. 17, p 97 and Dewey (1825) Plate III, Fig. 9.

C. straminea var. minor Dewey Dewey (1826) p 318, Tab. N, Fig. 45.

C. tenera Dewey Schweinitz (1826) No. 41, p 319.

C. straminea var. minor Dewey. Torrey (1836) No. 38, p 395.

C. straminea var. minor F. Boott ex Hook (1839) [Flora Boreal America 2:

215: See Gray Herbarium Index].

C. straminea var. tenera (Dewey) Barratt (1840) [N. Amer. Caric. no. 51: see Gray Herbarium Index].

Diemisia tenera Rafinesque (1840) [The Good Book and the Amenities of Nature: see Merrill (1949)].

C. straminea var. moniliformis Tuckerman (1843) [p. p.].

C. festucacea var. tenera Carey (1856) No. 39, p 516 [Also 1st ed. Gray's Manual (1848) p 545] (= C. hormathodes?).

C. straminea var. tenera Boott (1862) p 120, Fig 384.

C. mirabilis var. tenera (Dewey) L. Provancher (1863) [Flora Canada 2: 648].

C. tenera (Dewey) forma erecta Olney (1870) Exsiccattae fasc. ii, No. 14.

C. straminea var. (No. 2) Boeckl. (1875) [Linneae 39: 117].

C. straminea Willd Bailey (1886) [p. p.] No. 283, p 149.

C. straminea Willdenow Bailey (1889) No. 31, p 21-22.

C. straminea Willdenow Bailey (1890) No. 132, p 621.

C. moniliformis (Tuckerman) Britton (1890) [Cat. plants N.J. p 278].

C. straminea Willdenow Mackenzie (1896) No. 198, p 358, Fig. 868.

C. straminea Willdenow Fernald (1902) No. 11, p 474, Fig. 28 and 29.

C. straminea Willdenow Fernald (1908) No. 11, p 219, Fig. 354.

C. straminea Willdenow Kukenthal (1909) No. 167, p 205, and p 204, Fig 34, E & F.

C. straminea Willdenow Mackenzie (1913) No. 66, p 382, Fig. 932.

C. tenera Dewey Mackenzie (1915) p 606-607.

C. tenera Dewey Mackenzie (1931) No. 162, p 148.

C. tenera Dewey Mackenzie (1940) No. 162 (perigynium illustration is of var.

echinodes not of Dewey's lectotype).

C. tenera Dewey Fernald (1950) No.80, p 325, Fig. 581.

CAREX TENERA (Dewey) VAR. ECHINODES (Fernald) Wiegand Fernald (1902).

C. straminea var. echinodes Fernald (1902) No. 11, p 474, Fig. 30.

C. straminea var. echinodes Fernald (1908) No. 11, p 219, Fig. 355

C. straminea forma echinodes Fernald Kukenthal (1909) No. 167, p 206.

C. festucacea var. echinodes (Fernald) Farwell (1923) [Papers Mich. Acad. 2: 17]

C. tenera (Dewey) var. echinodes (Fernald) Wiegand (1924) [Rhodora 26: 2.].

C. tenera Dewey Mackenzie (1931) [included in description] No. 162, p 148.

C. tenera Dewey Mackenzie (1940) No. 162 [illustration of perigynium is of var. echinodes].

C. tenera var. echinodes Fernald Wiegand Fernald (1950) No. 80, p 325, Fig. 582.

CAREX BREVIOR (Dewey) Mackenzie (1915).

C. straminea Willdenow Wahlenberg (1803) ? No. 38, p 145 [p 119 of 1806 translation].

C. straminea var. brevior Dewey (1826) p 158.

C. straminea Willdenow Torrey (1836) No. 38, p 395.

C. straminea var. Schkuhrii Gay (1838) [Ann. Sci. Nat. 10: 364].

C. straminea var. intermedia Gay (1838) [Ann. Sci. Nat. 10: 363. Bailey (1889) footnotes that Kew Herbarium has C. brevior and C. silicea. However, Gray Herbarium Index applies it to C. festucacea].

C. straminea var. Schkuhrii (Mihi) Tuckerman (1843) [This is cited as the typical form for C. straminea, but should be applied to C. brevior].

C. straminea Willdenow Carey (1856) No. 41, p 516.
C. straminea var. typica Boott (1862) p 121, Fig. 387.

C. straminea Willdenow Bailey (1886) [p. p.] No. 283, p 149.

C. straminea var. brevior Dewey Bailey (1889) No. 31, p 22.

C. straminea var. brevior Dewey Bailey (1890) No. 132, p 623.

C. festucacea Schkuhr Mackenzie (1896) [p. p.] No. 201, p 359, Fig. 871 (illustration of C. merritt-fernaldii).

C. festucacea var. brevior (Dewey) Fernald (1902) No. 16, p 477, Figs. 49-51.

C. festucacea var. brevior (Dewey) Fernald (1908) No. 17, p 221, Fig. 364.

C. straminea var. brevior Dewey Kukenthal (1909) No. 167, p 207.

C. festucacea Schkuhr sensu Mackenzie (1913) No. 69, p 383, Fig. 936.

C. brevior (Dewey) Mackenzie comb. nov. Mackenzie (1915) p 603-605.

C. brevior (Dewey) Mackenzie ex Lunell (1915) [American Midland Naturalist 4: 235 - Not listed in text!].

C. brevior (Dewey) Mackenzie (1931) No. 167, No. 151.

C. brevior (Dewey) Mackenzie (1940) No. 167.

C. brevior (Dewey) Mackenzie Fernald (1950) No. 86, p 326, Fig. 588.

C. NORMALIS (Dewey) Mackenzie Dewey (1936)

C. mirabilis Dewey (1836) p 63, Tab Bb. Fig. 92. [Not C. mirabilis Host (1809)].

C. straminea var. mirabilis (Dewey) Tuckerman (1843).

C. festucacea var. mirabilis (Dewey) Carey (1856) No. 59, p 516 [Also 1st ed Gray's Manual (1848) p 545].

C. cristata Schw. Kunze (1851) [p. p.] [Supplement to the Reidgraser] [pl. 44, Fig. a, e, f.

C. cristata Schweinitz Boott (1862) [p. p.] No. 276. p 117, Fig. 374.

C. cristata var. mirabilis (Dewey) Carey? ex Gray (1867) No. 41, p 580.
C. lagopodioides var. mirabilis Olney (1870) Exsiccattae fasc. ii no. 9.

C. tribuloides var. cristata Bailey (1883) [See Mackenzie (1931)].

C. straminea var. mirabilis (Dewey) Tuckerman Bailey (1886) ["mostly, some specimens of Dewey and others listed under C. tribuloides var. cristata"] No. 283, p 150.

C. mirabilis Dewey [and including] var. perlonga Fernald Fernald (1902) No. 10, p 473, Figs. 25-27.

C. mirabilis Dewey [including] var. perlonga Fernald Fernald (1908) No. 10, p 219, Figs. 352-353.

C. straminea var. mirabilis Tuckerman [including] forma perlonga Fernald Kukenthal (1909) No. 167, p 207.

C. normalis (Dewey) Mackenzie (1910) p 244.

C. normalis var. perlonga (Fernald) Burnham (1919) [Torreya 19: 131].

C. normalis (Dewey) Mackenzie (1931) No. 164, p 149.

C. normalis (Dewey) Mackenzie (1940) No. 164.

C. normalis forma perlonga Fernald (1942) p 285.

C. normalis (Dewey) Mackenzie [including] forma perlonga Fernald (1950) No. 79, p 324-325, Figs. 579-580.

C. molesta Mackenzie ex Bright (1930).

C. molesta Mackenzie ex Bright (1930) p 20 [See Rothrock (1978)].

C. molesta Mackenzie (1931) No. 166, p 151.

C. molesta Mackenzie (1940) No. 166.

C. brevior var. molesta (Mackenzie) F.C. Gates (1940) p 135.

C. molesta Mackenzie Fernald (1950) No. 87, p 326, Fig. 589.

C. brevior (Dewey) Mackenzie Gleason and Cronquist (1952) [p. p.] No. 80, p 325 [authors consider the taxon a possible hybrid C. brevior x C. normalis].