Species limits, phylogeny and niche evolution: a case study in *Carex* (Cyperaceae)

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2007 - 10 - 01

A thesis submitted to McGill University in partial fulfilment of the requirements for the degree of Doctor of Philosophy

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DEDICATION

This dissertation is dedicated to Jim Pringle and Tony Reznicek. Their patience and generosity in sharing their understanding of botany inspired me to follow in their footsteps.

ACKNOWLEDGEMENTS

This project would not have been possible without the assistance of a great many people. Over the course of six months of fieldwork, I benefited from the help of a team of enthusiastic botanists, and I am very grateful for their assistance in often trying field conditions: Tracy Eades, David Kaiser, Marjorie Mercure, Laura Plourde and Elly Smith. A number of local experts provided in situ assistance in locating populations: James Donaldson, Janet Ebert, Rob Naczi, Sam Norris, Dan Spaulding, Tom Wieboldt and Theo Witsell. Gary Kauffman, Bruce Sorrie and Staria Vanderpool generously provided warm, dry accommodations in addition to their botanical expertise. Charles Bryson, Phillip Hyatt and Tony Reznicek provided locality information and general collecting advice based on their own extensive experience with *Carex* in the southeastern states.

In the lab, Laurie Consaul was very helpful, providing advice, assistance, and an example of laboratory practice well worth emulating. The DNA extractions and some of the amplified fragment length polymorphism (AFLP) procedures for some of the outgroup species (ca. 30 samples) used in the phylogenetic analysis were conducted by paid work-study students in the Waterway lab over the past several years. Marjorie Mercure provided the French translation of my dissertation abstract. Pierre Legendre, Brian McGill and Jari Oksanen gave me useful suggestions for the statistical analyses. I am grateful for the assistance of the curators of all the herbaria who sent loans for this study, and especially to Ruth Newell, curator of ACAD, for processing and housing a portion of those loans on my behalf. I am very thankful to have had the assistance of Tracy Eades. In addition to helping me during fieldwork, Tracy managed the bulk of my herbarium loans, assisted with countless small yet critical tasks in the lab, gave me a place to stay, entertained me during long hours in the workroom, and improved my posture.

Chris Ulrey (Blue Ridge Parkway) and Sue Powell and Keith Langdon (Great Smoky Mountains) provided assistance in obtaining permits for sampling in U. S. National Parks. Al Cire, Fred Huber, Mark Pistrang, Robin Roecker, David Taylor and Cindy Wentworth provided assistance in obtaining permits for sampling in U. S. National Forests. Permits for collecting at Droop Mountain Battlefield State Park were obtained through the West Virginia Department of Natural Resources, and Rachel Wagoner assisted in securing permits for Ohiopyle State Park in Pennsylvania.

I received financial support from the Natural Sciences and Engineering Research Council of Canada, the Fonds Québécois de la Recherche sur la Nature et les Technologies, the Southern Appalachian Botanical Society Core Fellowship, the Botanical Society of America Karling Award, the Highlands Biological Station Olive Memorial fund, a Mountain Lake Biological Station grants-in-aid award, and the Garden Club of America and the Center for Plant Conservation Beatty Fellowship. The equipment used to develop amplified fragment length polymorphism (AFLP) markers was funded in part by the Canadian Foundation for Innovation.

I used Free Software (Stallman 2002a) almost exclusively in the production of this dissertation, including R (R Development Core Team 2006), GRASS (GRASS Development Team 2006), LATEX(Lamport 1994) and GNU Emacs (Stallman 2002b). I am thankful for the efforts of the highly skilled volunteers who develop and distribute these programs. They provide a tremendous resource to the scientific community. I would also like to thank my committee, Anne Bruneau, Sylvie DeBlois and Terry Wheeler for providing advice and encouragement throughout my work. My supervisor, Marcia Waterway, provided vital support at all stages of this project. She forced me to be both thorough and concise, and never let me get away with sloppy thinking or incomplete work. I started this project as a naturalist. Marcia taught me how to be a scientist.

Finally, I would like to thank my wife Laurel for her continuing support in this and all my various projects. She made the worst parts bearable, and the best parts even better.

Contributions of Authors

This dissertation is presented in manuscript style. Chapters 3–6 are self-contained papers, written for submission to a journal with myself as first author, and my supervisor Marcia Waterway as second author. In each case I designed and implemented the sampling program, conducted the analysis, and wrote the paper. Dr. Waterway contributed general guidance throughout this process, and extensive editorial assistance during the preparation of the manuscripts. The first manuscript (Chapter 3) has been accepted, pending minor revisions, for publication in the journal *Systematic Botany*. I have also included, in Appendix D, a paper documenting my preliminary fieldwork. This was published in the journal *Castanea* (Smith et al. 2006). I was first author, responsible for the majority of the included data and all analysis and writing. My co-authors, James T. Donaldson, Tom F. Wieboldt and Gary L. Kauffman, provided additional locality data based on their collections in Tennessee, North Carolina, Virginia and West Virginia. Marcia Waterway provided editorial assistance.

ABSTRACT

Two conflicting processes are believed to influence the relationship between taxonomic and ecological diversity: adaptive radiation and niche conservatism. No consensus has yet emerged regarding the conditions that favour conservatism of traits due to common ancestry over adaptive radiation and the resulting ecological divergence. *Carex* is an ideal group for studying these phenomena, as it is incredibly diverse taxonomically and ecologically, and includes many recently formed lineages. I chose a group of eight closely related *Carex* taxa from eastern North America as the focus of my study. Multivariate analysis of 30–33 morphological variables measured on 456 plants from 110 populations confirmed the existence of eight different entities. Analysis of 141 AFLP fragments from 435 plants from the same populations revealed the same eight groups. I recognise each of these taxa as distinct species. These include C. roanensis, a globally rare species whose taxonomic status had been questioned, and C. complanata and C. hirsutella, a pair of species that some authors had considered a single variable taxon. Six previously unknown sterile or nearly sterile hybrids are documented with a combination of morphology, restriction fragment, and AFLP data. Parsimony and distance analyses of the AFLP data failed to fully resolve the phylogeny of this group, but did establish consistent estimates of the relative evolutionary distances among species. Morphology does not reflect the phylogenetic relationships in this group. There were significant differences among species for niche measures calculated from climate variables, ecological niche models, and local habitat variables. Niche divergence was significantly correlated with phylogenetic distance, indicating niche conservatism is an important process governing ecological evolution in this group. Furthermore, the shape of the relationship suggested that phylogenetic distance limits the maximum possible ecological divergence, but within this limit other unmeasured factors also contribute to the observed pattern. Comparing my results to other recent work, I propose a framework for identifying the factors that influence the strength of niche conservatism.

ABRÉGÉ

Deux processus conflictuels influenceraient la relation entre la diversité taxonomique et écologique: la radiation adaptative et le conservatisme de niche. Aucun consensus n'a encore émergé quant aux conditions qui favorisent le conservatisme de traits par ascendance commune plutôt que la radiation adaptative et la divergence écologique qui en résulte. Le genre *Carex* est le groupe idéal pour étudier ces phénomènes, étant incrovablement diversifié aux plans taxonomique et écologique et incluant plusieurs lignées récemment formées. J'ai choisi un groupe de huit taxons étroitement reliés de *Carex* de l'Est de l'Amérique du Nord pour mon étude. Des analyses multivariées de 30–33 variables morphologiques, mesurées sur 456 plants provenant de 110 populations, ont confirmé l'existence de huit entités. L'analyse de 141 fragments AFLP de 435 plants des mêmes populations a révélé les mêmes huit groupes. Je reconnais chacun de ces taxons comme étant une espèce distincte. Ces espèces incluent C. roanensis, une espèce globalement rare dont le statut taxonomique a été questionné, ainsi que C. complanata et C. hirsutella, une paire d'espèce que certains auteurs avaient considéré comme un seul taxon variable. Six hybrides stériles ou presque auparavant inconnus sont documentés avec une combinaison de morphologie, de fragments de restriction et de données AFLP. Les analyses de parcimonie et de distance n'ont pu résoudre entièrement la phylogénie de ce groupe mais ont pu établir des estimés cohérents des distances évolutives relatives entre les espèces. La morphologie ne reflète pas les relations phylogénétiques de ce groupe. Il y avait des différences significatives entre les espèces pour les mesures de niche calculées partir de variables climatiques, de modèles de niche écologique et de variables de l'habitat local. La divergence de niche était significativement corrélée la distance phylogénétique, identifiant le conservatisme de niche comme un processus important gouvernant l'évolution écologique dans ce groupe. La forme de la relation suggérait que la distance phylogénétique limite la divergence écologique maximale possible mais que dans cette limite, d'autres facteurs non-mesurés contribuent également au patron observé. Comparant mes résultats d'autres travaux récents, je propose un cadre pour identifier les facteurs qui influencent la force du conservatisme de niche.

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CHAPTER 1 Introduction

The species is a unifying concept in biology. It is the principal product of taxonomy, and the relationships among species in space and time are central themes in ecology and evolution, respectively. The research program documented by this thesis draws on all three disciplines in an investigation of the closely related *Carex* roanensis and *C. complanata* species complexes. Specifically, I address the following objectives:

- 1. What are the species limits in this group? How many distinct species are there, and how can we distinguish among them?
- 2. *How are these species related?* What are the phylogenetic relationships among these species?
- 3. Do the phylogenetic relationships among these species reflect differences in their ecology? Is phylogenetic divergence related to ecological divergence? How is taxonomic diversity related to ecological diversity?

My aim is to evaluate two competing hypotheses regarding the processes governing niche evolution. The first hypothesis is that closely related species will occupy more similar niches than distant relatives. This prediction follows from the theory of niche conservatism, whereby closely related species share the ecological characteristics of their common ancestor. The alternate hypothesis is that close relatives are no more likely than distant relatives to occupy similar niches. This follows from the theory of adaptive radiation, whereby speciation is associated with the evolution of novel ecological strategies. The signature of adaptive radiation is a lineage of closely related species that occupy widely differing niches.

There is growing evidence supporting both of these hypotheses. Furthermore, they are not necessarily mutually exclusive. Some niche characteristics may be conserved in a lineage, while others evolve rapidly. In this dissertation I develop a framework for evaluating the influence of niche conservatism and adaptive radiation along different niche axes.

In chapter 2 I review the literature relating to species concepts and the ecological niche, the fundamental ideas at the center of this study. I also summarize the biology of *Carex*. The extraordinary ecological and taxonomic diversity of this genus makes it an ideal model system for examining evolutionary ecology. In chapters 3 and 4, I evaluate the species limits in the *C. roanensis* and *C. complanata* complexes, establishing the taxonomic context for the study (objective 1). Chapter 5 is a phylogenetic analysis of these species (objective 2), providing the necessary framework for chapter 6, which examines the relationship between phylogenetic and ecological diversity (objective 3).

Complete lists of populations sampled and herbarium specimens examined for all chapters are presented in Appendix A and C, and representative gels from my molecular analysis are presented in Appendix B. Appendix D is a summary of my preliminary fieldwork, previously published in the journal Castanea (Smith et al. 2006).

CHAPTER 2 Literature Review

2.1 The Species

The species concept is central to our understanding of natural history. Linnaeus' Species Plantarum (1753) and Darwin's The Origin of Species (1859), which are arguably the two most important publications in natural history, addressed different aspects of the species. But the idea that the variation evident in living organisms is partitioned among discrete groups of related individuals predates either of these documents. Many of the names published by Linnaeus date from antiquity (Fernald 1950; Stearn 1973). Furthermore, there is considerable evidence that the species concept is remarkably consistent across cultures, at least for macroscopic organisms (Mayr 1963; Berlin 1973; Berlin et al. 1974).

Despite the universal acceptance of the idea of the species, there is no one objective definition of this term that satisfies all biologists. Linnaeus (1753) did not address the issue at all, despite providing a comprehensive catalog of species and a systematic framework for their taxonomic organization, description and recognition. Darwin (1859) noted that his contemporaries engaged in "endless disputes" over the correct diagnosis of species, and anticipated that his theory of evolution would put an end to such debate. He suggested that the species was an artificial category, part of a continuum of divergence between varieties and higher Linnean categories. In his view, by abandoning the assumption that species are anything more than a theoretical construct, "we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species" (Darwin 1859). However, the endless disputes over the diagnosis of species have continued, despite Darwin's hopes. This is due in part to the reluctance of many biologists to reject the reality of species — including Darwin himself (see Coyne and Orr 2004, chapter one). Even for those investigators who subscribe to the view that the species is an artificial construct, the substantial challenge of assessing variation among varieties and deciding "whether the differences be sufficiently important to deserve a specific name" (Darwin 1859) remains.

This is an important issue for all biologists. Species are simultaneously one of the principal products of systematics and the necessary raw material for ecology and evolutionary research. This concept underlies all of organismal biology, so it is imperative that we establish a clear understanding of it. Such a complicated issue is unlikely to have a simple or universal solution, which makes it even more important that we clearly articulate our vision for the application of this term.

Many competing visions for the species concept have been promoted (reviewed in Coyne and Orr 2004), but none that I have seen fully meets the needs of an empirical taxonomist engaged in delineating species. Davis and Nixon's (1992)¹ Phylogenetic Species Concept (PSC) comes closest to providing a theoretically sound and operational approach. They treat species as "the minimal terminals for phylogenetic analysis," in other words, that level of the phylogeny where further division would result in groups related by reticulate rather than hierarchic relationships. As such a species is neither monophyletic nor paraphyletic, but rather is the smallest group

¹ The species concepts I discuss have been developed by numerous authors over many years. For simplicity I refer the reader to their most recent comprehensive articulations. Related references are found in each of the cited works, as well as in the review of Coyne and Orr (2004).

that can be used to develop phylogenetic analyses at higher levels (species within genera, genera within families etc.). This definition equates species with recognizable discrete aggregations of populations. Overlapping character states between two populations is taken as evidence of a reticulate relationship, acknowledged by treating both populations as belonging to a single species.

Davis and Nixon (1992) envisioned that species be defined by diagnostic qualitative characters. Luckow (1995) noted that non-overlapping quantitative characters can serve the same role. Furthermore, she suggested that several overlapping quantitative characters subjected to multivariate analysis are entirely appropriate for use in delineating species. This is an important point, because in morphological studies of closely related taxa there may not be any qualitative characters that can differentiate among otherwise quantitatively discrete species (Henderson 2004).

There are two flaws in Davis and Nixon's (1992) program that preclude me from adopting their species concept in its entirety. First, they consider any population that has a unique combination of character states distinct from all other populations as a distinct species. With the rapidly increasing resolution of molecular techniques such an approach could lead to new species being carved off existing taxa based on single nucleotide changes, which would degrade the value of the species as a concept (Olmstead 1995).

The second problem relates to the importance of populations in defining species. Davis and Nixon (1992) advocate using populations as the basic unit in delineating species, rather than individuals. Their species concept rests on identifying the units within which ancestry patterns are reticulate. The only evidence applicable to this problem is population level variation in character states. Two individuals in separate populations may display contrasting character states, but if those states are variable within each population the individuals, and populations, should be included within a single species.

The problem arises when confronted with mixed populations. Following Davis and Nixon's (1992) protocol, there is no way to distinguish between two species growing in a mixed population and a single variable species (Baum and Donaghue 1995). The decision to lump or split is left to the subjectivity or *a priori* assumptions of the observer.

Even with these deficiencies the PSC surpasses other models for systematic work. As Luckow (1995) explains, mechanistic models such as Mayr's (1995) Biological Species Concept (BSC) are founded on assumptions about the speciation process. This limits further investigation: "by making assumptions about mechanisms of speciation in order to diagnose species, we rob ourselves of the opportunity to test hypotheses about the speciation process itself" (Luckow 1995). The BSC also suffers from its limited applicability. Reproductive isolation only applies to sexually reproducing organisms, and other mechanisms could be equally or more important in maintaining distinct species. Typically, defenders of the BSC dismiss exceptional cases as insignificant (for a particularly glaring example, see Mayr 1992), but I think a truly instructive species concept should be generally applicable. Another weakness of the BSC is that reproductive isolation can rarely be directly assessed. While Mayr (1992) rejects the necessity for a species concept to be operational, those of us working on empirical problems do require a workable method.

An alternative to the BSC and other mechanistic species concepts is Baum and Donoghue's (1995) Genealogical Species Concept (GSC, also referred to as the Phylogenetic Species Concept). Their position is that systematics is fundamentally concerned with revealing phylogenetic relationships among organisms, so the process of defining species must be explicitly based on those relationships. They posit that a species can only be diagnosed by revealing its relationship to other species. In fact, they go so far as to claim that any other approach to the species is in fact anti-scientific (a "decision not to engage in the scientific enterprise"). I would argue that species need to be diagnosed in order that their relationships to other species can then be assessed in two discrete (though complex) steps.

The invective of Baum and Donaghue (1995), and especially Mayr (1995), highlights a fundamental misunderstanding of the role of phenetics in systematics. To Baum and Donaghue (1995) it is a retreat to pure description, abandoning any desire to reveal the underlying causes of empirical patterns. Mayr (1995) insists that phenetics is synonymous with typology. Davis and Nixon (1992) recognise the true role of phenetics, as a careful reader of Sneath and Sokal (1973) will recognise. The phenetic identification of discrete biological entities is the first necessary step in any phylogenetic study. By using a theory-neutral species concept taxonomists can enter into phylogenetic analysis with objectively defined species and minimal lingering assumptions. Phenetics doesn't preclude evolutionary approaches to taxonomy; it enables them.

The irony of the species concept debate is that most taxonomists, whether or not they support phenetics as a valid approach, apply it in diagnosing species (Futuyma 1998). The difference is semantic. A pheneticist will recognise two species based on their discrete morphology. An adherent to the biological species concept will recognise two species based on their reproductive isolation, as inferred from their discrete morphology. To my mind the phenetic "approach" is more straightforward.

The problem of how best to diagnose species remains. I take from Davis and Nixon (1992) the idea that species are the smallest diagnosable groups which can be used to conduct phylogenetic analyses. In the case of sexually reproducing species this assumes that overlapping variation is indicative of reticulate inheritance. Reproductive isolation is not an explicit requirement however, and overlapping variation in asexual species can serve as evidence that the lineages resemble a common ancestor strongly enough to warrant being assigned to the same species.

I also agree with Davis and Nixon (1992) in stressing the importance of population level variation. However, since there is no way to distinguish between mixed and variable populations, I used individuals as my operational taxonomic units (OTUs). I sampled within populations to assess local variation, but I did not assume that co-occurring individuals belong to the same species.

I differ from Davis and Nixon (1992) in my understanding of "diagnosable". A single character, uncorrelated with any other, should always be treated with caution in systematic research. In fact, no single data set (gene sequence, morphology, cy-tology etc.) can guarantee error-free taxonomy. The most responsible approach to diagnosing species is to find congruence between multiple data sets. I suggest that this can be treated as an iterative process: a taxonomy based on one type of data can and should be revised based on the addition of new data from other sources.

Congruence among datasets will provide strong support for the resulting taxonomic hypothesis. Interpretation of conflicting datasets is more complex. The molecular data may reveal discrete groups that cannot be distinguished morphologically, suggesting the presence of cryptic species or significant population-level divergence. Alternatively, if morphological groups are indistinguishable using molecular data, phenotypic plasticity may be responsible for the observed variation. All the available data must be considered in such situations, and firm conclusions reserved until adequate data is available to address uncertainties.

The most rigorous sampling approach to diagnosing species comes from studying sympatric populations. There are many examples of organisms with intergradation between adjacent populations while more distant populations are distinct (Futuyma 1998). Studying putative species where they co-occur is the surest way to distinguish between a single geographically variable entity and two discrete ones.

2.2 The Niche

In many ways, the niche concept serves the same role in ecology as the species concept does in systematics; that is, it encapsulates our efforts to explain the distribution of organisms in an ecological framework. Like the species concept, there is no precise definition of the niche that satisfies all ecologists. The first use of the term niche in an ecological context is generally attributed to Grinnell (1917), although it was actually introduced by R. H. Johnson in a publication from 1910 (cited by Gaffney 1975). Grinnell's niche was essentially an element of the landscape, the smallest biologically meaningful geographical division. As such, it could be occupied by a single species or subspecies (Grinnell 1924). Should that species be absent from a location, the empty niche remained. Most later authors considered the Grinnellian niche to be an autecological phenomenon, a formalization of the idea of habitat (e.g. Whittaker et al. 1973; Leibold 1995). However, James et al. (1984) argued that Grinnell (1924) had intended the niche to represent both habitat requirements and biotic interactions.

In contrast, Elton (1927) used the term niche to describe the functional role of a species in a community, emphasizing competition for limiting resources. Theoretical development of this idea lead to 'Gause's Principle', the expectation that two species that compete for the same resource cannot stably coexist in a community (Gause 1934). This proved to be a rich area for ecological research, and lead to the Eltonian niche being adopted for general use by ecologists (Odum 1953; Clarke 1954; Dice 1952). Indeed, some of the most influential papers in ecology addressed this issue (Macarthur 1958; Macarthur and Levins 1967).

However, the contrasting views of the niche proffered by Elton (1927) and Grinnell (1924) became intertwined, giving rise to confusion as to what the term actually meant. To address this problem, Hutchinson (1957) formalized the niche definition as a multi-dimensional hypervolume. The space occupied by this volume was defined by axes representing physical and biological variables. Points within the hypervolume correspond to the conditions necessary for the survival and reproduction of the species. Thus, if one were to measure all the requirements for the persistence of a species, which might include tolerable conditions in terms of temperature, moisture, predation, or competition, it would be possible to produce a niche hypervolume that completely defined the ecological properties of that species. This is of course not possible, but Hutchinson's model provided a useful abstraction to clarify "what is usually meant by an ecological niche" (Hutchinson 1957).

Unfortunately, there was a flaw in Hutchinson's 1957 presentation that resulted in his work increasing, rather than decreasing, confusion surrounding the niche concept. He stated that the niche axes were composed of both physical and biological variables, but discussed the application of his model only in terms of competition. He defined the fundamental niche as the total hypervolume, and the realized niche as the subset of that volume that a species could occupy in the face of interspecific competition. This lead many readers to conclude that he intended for biotic and abiotic factors to be treated as qualitatively different influences in defining the niche (e.g. Soberón and Peterson 2005). Some authors drew from his emphasis on competition that his model was an extension of the Eltonian niche-as-functional-role concept (Whittaker et al. 1973; James et al. 1984), while others thought that his physical niche-axes were more consistent with the Grinnellian niche-as-habitat model (Leibold 1995). A common response among Hutchinson's critics was to address the perceived weaknesses in the model by providing more detailed alternatives, with particular subsets of the Hutchinsonian niche isolated and explicitly named in hopes of improving clarity. Thus, Whittaker et al. (1973) restricted the niche to represent the functional role of a species, and recommended habitat as the preferred term for the environmental requirements of a species, and ecotope for the combination of both concepts. Vandermeer (1972) took a similar approach, providing several pages of definitions of different aspects of the niche as the basis for reformulating it in a more cohesive form. More recently, Leibold (1995) took a mechanistic approach to the niche. He noted that previous evaluations of the niche concept focussed on the difference between the Grinnellian "habitat" and Eltonian "functional" approaches. His own contribution recognized a "requirements" niche and an "impacts" niche, which appears to be more of a nomenclatural than theoretical change.

Ultimately, these criticisms fail to improve upon Hutchinson's 1957 model. They all provide much more detailed specification of the various aspects of the niche that the author's consider most important. But in doing so they undermine the real strength of the niche hypervolume concept. Hutchinson's model is effective as a consequence of its generality. It provides a level of abstraction that enables its ready application to a wide variety of investigations. This was clearly demonstrated by Maguire (1973). In an extended discussion of Hutchinson's niche model, he provided examples of its utility in examining population dynamics, competitive and predatorprey interactions, life history and niche evolution. He noted that "from the point of view of the species ... its exclusion from part of its fundamental niche by other species does not differ from its exclusion from part of its niche by physico-chemical conditions." In other words, Hutchinson's realized niche can be used to evaluate the influence of any niche axis, not just those related to competition. More generally, the hypervolume concept can be adapted to most variations of the niche by selecting appropriate coordinate axes. Of course, it will never be possible to completely quantify the niche of a species in its entirety; investigators will have to clearly identify which niche components they are examining in any study.

The multivariate nature of the Hutchinsonian niche suggests the use of multivariate statistical analysis in its evaluation. Green (1971, 1974) developed a rigorous statistical framework for such analyses. He identified three challenges to be addressed. First, there is a practical limit to the number of environmental parameters that can be measured. It is possible that two species that are identically distributed with respect to a set of measured variables nevertheless are distinct in some unmeasured dimension. As a consequence, while we can demonstrate that two species occupy different niche spaces, we cannot prove that two species occupy the same niche space. Second, a large proportion of environmental parameters are likely to be correlated, invariant, or irrelevant to the species of interest. Third, patterns in a high-dimensional dataset are likely to be difficult to interpret.

There is no solution to the first problem, other than to remain cautious when interpreting data that suggests different species are occupying the same niche. Green (1971, 1974) resolved the second and third challenges through the application of linear discriminant analysis (LDA, also called multiple discriminant analysis or canonical variates analysis) to his data. LDA is a form of canonical ordination (Legendre and Legendre 1998), with several properties that make it an ideal choice for niche analysis. The ordination procedure employed in LDA preserves the Mahalanobis distance among group centroids. This means that the relative contribution of each variable to the total distance is scaled by its variance and covariance. Consequently, invariant or redundant variables have a relatively low impact on the analysis. Furthermore, as with all ordinations, a potentially large fraction of the information in the original data can be visualized as a two-dimensional diagram. Alternatively, the Mahalanobis distance itself can be used to reduce the niche distances among species to a single set of values (see chapter 6).

Identifying and documenting niche axes relevant to plant community ecology has become an important avenue for research. Researchers have identified niche separation among plant species with respect to soil mineral use (Garten 1978), rooting depth (Parrish and Bazzaz 1976), pollination (Parrish and Bazzaz 1979), hydrology (Pickett and Bazzaz 1978; Silvertown et al. 1999; Dabros 2004), ecophysiology (Grace and Wetzel 1982; Luttge et al. 2001), climatic tolerances (Austin et al. 1990), and seasonality in resource acquisition (McKane et al. 2002). Such studies have declined in popularity, possibly as a consequence of dissatisfaction among ecologists with the definition of the niche (Chase and Leibold 2003). Silvertown (2004) found only 13 studies published since 1990 that documented niche separation within plant communities. However, it should be noted that he accepted only those studies that evaluated at least two of four proposed criteria for niche separation, so his survey does not represent the full spectrum of plant community research during this period. Nevertheless, Silvertown (2004) concludes that "it is time for the niche to be rehabilitated and for plant ecologists, in particular, to investigate its role in a more sophisticated fashion."

The niche has undergone a renewal of sorts in recent years, as a consequence of two emerging themes in ecological research. First is the development of neutral theory (Bell 2001; Hubbell 2001; Holyoak et al. 2006). Neutral theory challenges traditional niche theory not by questioning the existence of ecological differences among species, but rather by demonstrating that these differences may be irrelevant in explaining the distribution and diversity of species in a community. The success of neutral models in explaining observed patterns of community organization may ultimately lead to a major rethinking of niche theory. However, some researchers have reacted to neutral theory by providing more rigorously documented examples of communities structured by niche separation (Gilbert and Lechowicz 2004). Consequently, neutral theory may lead to a more thorough understanding of the influence of niche divergence in community structure, as well as revealing situations where comparable diversity is maintained by purely stochastic processes.

The second development in niche research involves the scope of investigation. Traditionally, niche differences have been examined in the context of co-occurring species within a community. Increasingly, investigators are exploring patterns of niche divergence among related species within a phylogenetic lineage. In this context, the niche is not a tool for examining ecological dynamics in a community; instead it is a framework for examining evolutionary dynamics in a phylogenetic lineage. Early examples include the work of Huntley et al. (1989), who demonstrated that Fagus species in North America and Europe occupied very similar climatic niches, and Bayer et al. (1991) who found evidence of niche divergence among related species of Antennaria in western North America.

Three methodological advances have enabled a rapid expansion of such studies in the last ten years. First, the ongoing development of molecular systematic techniques has lead to increasing availability of well-resolved phylogenies. This information is critical to evolutionary research, in that it provides rigorous, objective, and quantifiable measures of phylogenetic divergence among taxa. Second, museum collections data is now routinely available in digital format via the world wide web (Graham et al. 2004a). Sometimes these records are georeferenced, and if they are not on-line resources such as Topozone (www.topozone.com) and GoogleEarth (earth.google.com) enable ready access to the information necessary to acquire geographic co-ordinates for them. The result is that individual researchers can now take advantage of the vast storehouse of information available in natural history collections.

The third important methodological advance was the development of increasingly sophisticated software for developing ecological niche models (ENM, also referred to as species distribution models: Guisan and Thuiller 2005; Peterson 2006). ENMs provide a framework for combining distribution records with geospatial data (e.g. Hijmans et al. 2005) to produce predictive models of the niche of a species. This approach to niche description is much coarser than that produced by traditional fieldwork. However, it makes it possible to incorporate the full geographic distribution of a species in quantifying its ecological requirements. To effect a similar assessment using field sampling would be unfeasible for wide-ranging species, or for lineages that span different continents.

Shifting the focus from ecological communities to evolutionary lineages has lead researchers to examine a different aspect of niche theory. Traditional niche theory is associated with competitive interactions and the associated shifts in niche breadth and location that presumably enable species within a community to co-exist (Begon et al. 1990). In an evolutionary context, biologists have focussed on the pattern of niche divergence within lineages. Two contrasting patterns have been identified: adaptive radiation and niche conservatism. Adaptive radiations arise when a single ancestral species gives rise to a lineage of descendant species, each occupying a different niche (Schluter 2000). This is consistent with Darwin's (1859) original concept of evolution driven by natural selection, and has remained a strong focus in organismal research (Orr and Smith 1998; Coyne and Orr 2004). A number of dramatic examples have been documented recently (Losos et al. 2003; Gillespie 2004).

In contrast to adaptive radiation, niche conservatism is the tendency of related species to share the ecological characteristics of their shared ancestor. Theoretical research suggests that it should be common, as in most situations stabilizing selection maintaining the optimal niche of a species is expected to be stronger than divergent selection for marginal habitats (Holt 1996). A large body of empirical evidence has accumulated to support this view (Lechowicz 1984; Huntley et al. 1989; Prinzing et al. 2001; Ackerly 2003; Hoffmann 2005), increasingly from studies employing ENM analysis (Peterson et al. 1999; Wiens and Graham 2005; Kozak and Wiens 2006).

Resolving the tensions between these two ideas remains a pressing issue in evolutionary ecology, and motivates much of the work presented in subsequent chapters of this thesis. For further discussion, see chapter 6.

2.3 Carex

The taxonomic and ecological diversity of the genus *Carex* make it an ideal system for exploring the relationship between niche evolution and speciation. It is one of the largest plant genera, with ca. 2000 species worldwide (Ball and Reznicek 2002). All species are herbaceous perennials, and form tufted or spreading clones via rhizomes (Bernard 1990). Most species are monoecious, with unisexual flowers arranged in spikelets (actually reduced inflorescence branches). The flowers themselves are relatively inconspicuous, with the perianth reduced to a single subtending scale and a sac-like perigynium enclosing the achene. They are generally considered to be anemophilous, although there is some evidence that Syrphid flies may, at least occasionally, act as pollen vectors (Leerveld 1984). The perigynia of many wetland species are inflated, suggesting that they disperse by floating in water currents (Catling et al. 1990), while myrmechory has been documented in some forest species (Handel 1976, 1978). The small fruits of most species are readily dispersed by animals, and can be a prominent component of the sock flora (pers. obs.).

Carex shares several unique cytological features with all other members of the Cyperaceae (and some Juncaceae): diffuse centromeres, post-reductional meiosis

(where the first meiotic division is equational, followed by a reductional division: Davies 1956), and by pollen formation in which three of the four microspores are aborted (Ball et al. 2002). The diffuse centromeres are particularly interesting. Without a defined centromere, it appears that *Carex* chromosomes can occasionally break into smaller pieces while remaining functional. This process (agmatoploidy) is the most likely explanation for the occurrence of aneuploid series within and among species in *Carex* and may be an important component of their evolution (Wahl 1940; Davies 1956). Whitkus (1988) conducted extensive crossing experiments between closely related species and chromosome races within species. While he found that chromosome races were not reproductively isolated, he suggested that the loss or gain of chromosomes may be important in the radiation of *Carex* species.

Predominantly associated with wetlands, *Carex* is actually well represented in essentially all temperate, boreal, arctic and alpine habitats. Twenty or more species may co-occur within a few hectares in temperate forests (Ball and Reznicek 2002), and I have documented 56 species within a single 800 hectare nature sanctuary in southern Ontario (Smith 2003).

Taxonomically, *Carex* is placed in the tribe Cariceae of the family Cyperaceae. Numerous studies have shown strong support for the monophyly of the Cariceae (Muasya et al. 1998; Yen and Olmstead 2000; Waterway and Starr 2007). However, generic arrangements within the tribe remain problematic, particularly with respect to the placement of unispicate *Carex* species relative to other Cariceae genera (Roalson et al. 2001). Starr et al. (2004) examined the phylogenetic relationships of unispicate species from all the genera in the tribe. They found that the dioecious species were related to *Carex*, while the monoecious species were placed within *Kobresia* or *Schoenoxiphium*. All recent investigations of the Cariceae have demonstrated the paraphyletic nature of *Carex* (Yen and Olmstead 2000; Roalson et al. 2001; Starr et al. 2004; Waterway and Starr 2007; Waterway et al. in press).

The circumscription of *Carex* as a whole will need to be revised to account for these developments, although there is still too much remaining uncertainty to determine the appropriate realignment. The number of species involved and their broad global distribution has hampered efforts to produce a rigorous modern revision. Traditional sectional arrangements based on morphology (Kükenthal 1909; Mackenzie 1931-1935) are generally recognised as being inadequate (Reznicek 1990; Ball and Reznicek 2002). *Carex* subgenus *Vignea*, distinguished from other subgenera by the combination of sessile spikelets and bistigmatic ovaries, is strongly supported by recent molecular studies (Roalson et al. 2001; Ford et al. 2006a; Waterway and Starr 2007). However, the other subgenera, and many of the traditional sections, are not monophyletic (Ford et al. 2006a; Waterway and Starr 2007; Waterway et al. in press). The lack of well-supported infraspecific clades despite the development of substantial molecular datasets suggests that many groups in this genus may be the result of recent or rapid radiation.

In addition to ongoing phylogenetic investigations, species-level taxonomy is a very active area of research for *Carex*, especially in eastern North America. Many variable, widespread species have recently been shown to be complexes of several overlooked cryptic species. At least 20 new species have been described from this region in the last 14 years, including: *Carex brysonii*, *C. godfreyi* (Naczi 1993) *C. basiantha*, *C. superata* (Naczi et al. 1998), *C. timida* (Naczi and Ford 2001), *C. acidicola*, *C. calcifugens*, *C. paeninsulae*, *C. thornei*, *C. kraliana*, *C. gholsonii*, *C. godsonii*, *C. godsonii*, *C. godsonii*, *C. godsonii*, *C. godsonii*, *C. godsonii*, *C. calcifugens*, *C. paeninsulae*, *C. thornei*, *C. kraliana*, *C. gholsonii*, *C. godsonii*, *C. godsonii*, *C. godsonii*, *C. godsonii*, *C. godsonii*, *C. godsonii*, *C. calcifugens*, *C. paeninsulae*, *C. thornei*, *C. kraliana*, *C. gholsonii*, *C. godsonii*, *C. godsonii*,

infirminervia (Naczi et al. 2002a), C. cumberlandensis (Naczi et al. 2001), C. juniperorum (Catling et al. 1993), C. cordillerana (Saarela and Ford 2001), C. molestiformis (Reznicek and Rothrock 1997). Most of these discoveries are the product of morphological re-evaluations of existing species, although some have also been confirmed with genetic data (e.g. Ford et al. 1998; Ford and Naczi 2001). Ford et al. (2006b) observed that subtle differences in morphology frequently conceal marked genetic discontinuities among Carex species.

2.4 Molecular Markers: Amplified Fragment Length Polymorphisms

These discoveries suggest that a combination of morphology and molecular data should be applied to resolving the taxonomy of *Carex* species. Ford et al. (2006b) demonstrated the potential of amplified fragment length polymorphism data (AFLP) markers for clarifying taxon boundaries in groups characterized by limited morphological variation. AFLP data has also been applied successfully to phylogenetic problems in *Carex* (Hipp and Rothrock 2002), and are generally recognized as a useful source of information for investigations of relationships among populations and closely related species (Mueller and Wolfenbarger 1999).

AFLP assays combine restriction fragment and polymerase chain reaction techniques (Vos et al. 1995). First, purified DNA is digested with two restriction enzymes. AFLP adaptors are joined to the fragment ends as the DNA is digested. At this point each fragment is bounded by adaptors of known sequence, but there are far more fragments than can be visualized accurately. A subset of these fragments is amplified by using primer pairs based on the adaptor sequences, extended by 1 to 3 arbitrarily chosen bases. In effect, this reduces the number of fragments by a factor of 4, 16, or 64. To reduce the number of amplification artefacts, two amplifications are routinely used, the first using primers extended by a single base, and the second using primers extended by up to 3 bases. Following PCR amplification the fragments

Criterion	AFLP	RAPD	SSR	RFLP	Allozymes
Information Content	High	High	Low	Low	Low
Replicability	High	Variable	High	High	High
Resolution	High	Moderate	High	High	Moderate
Ease of use	Easy	Easy	Difficult	Difficult	Easy
Development time	Short	Short	Long	Long	Short

Table 2.1: Comparison of common molecular markers, after Mueller and Wolfenbarger (1999)

can be visualized using gel electrophoresis or an automated DNA sequencer. Each sample in an assay is then characterized by the presence or absence of fragments of a given length. Generally, fragments of a given length are assumed to be unique, independent, dominant markers.

AFLPs provide several advantages over other molecular markers: they can be used to quickly and reliably generate hundreds of characters without prior knowledge of the genome in question; they are repeatable, with error rates of only 0–2% between assays; they can be generated from very small amounts of tissue, minimizing the impact of sampling on populations of conservation concern; and samples can be stored dry before processing, and need not be frozen. These characteristics make AFLPs ideal for use in systematic studies of closely related species, particularly when prolonged fieldwork is required. A summary of the strengths and weaknesses of AFLPs relative to other commonly used molecular markers is shown in Table 2.1. Aside from the relative ease of use, meta-analysis of direct comparisons among a variety of DNA markers suggests that genetic diversity statistics revealed by AFLP show a close correlation to those produced by RAPD, ISSR, and under some conditions SSR (Nybom 2004).

AFLP assays provide a suite of presence/absence characters. These characters are often referred to as dominant markers (Mueller and Wolfenbarger 1999). This is
not correct. Detailed pedigree studies reviewed by Mueller and Wolfenbarger report between 4% and 15% of polymorphic AFLP markers are co-dominant. However, there is no way to determine which markers represent alternate alleles from a single locus without conducting extensive controlled crosses. Most published studies do not include such verification measures. As a consequence, while AFLP markers are assumed to be dominant, in most cases we do not know if this is true.

AFLP markers have another shortcoming. There is no way to determine directly from AFLP assays if markers of identical length are composed of homologous DNA fragments. This issue can be resolved by direct sequencing of markers of equal size. Parsons and Shaw (2001) sequenced a subset of their AFLP markers, and found that fragments that were indistinguishable in initial assays differed by only 0-3% of their sequence. This result supported their assumption that markers of equal length were in fact homologous characters.

Despite these shortcomings, most investigators believe that the high number of characters produced by AFLP assays more than compensate for the small proportion of those characters that are incorrectly interpreted, as shown in Table 2.2. The majority of studies using AFLPs no longer include tests of the assumptions associated with these markers, and all those that did determined that they were within acceptable tolerance levels. It is noteworthy that of the studies included in Table 2.2, Despres et al. (2002), Despres et al. (2003), and Gobert et al. (2002) all used AFLP assays after other molecular techniques had failed to reveal informative genetic variation.

AFLP data can be interpreted with a variety of analytical techniques. Because of the number of characters produced, principal co-ordinates analysis is often used to visualize variation in AFLP markers. Since the probabilities of gaining and losing AFLP restriction sites are most likely not equal (as for RFLPs and RAPDs, Swofford

Study	Issue	Assumptions Tested
Beardsley et al. (2003)	Phylogeny	None
Bruneau et al. (2005)	Species Limits	None
Cardoso et al. (2000)	Population Genetics	None
Coart et al. (2003)	Population Genetics	Repeatability
Despres et al. (2002)	Phylogeography	None
Despres et al. (2003)	Phylogeny	None
Ford et al. $(2006b)$	Species Limits	None
Gobert et al. (2002)	Hybridization	None
Kai et al. (2002)	Hybridization	None
Martínez-Ortega et al. (2004)	Species Limits	Repeatability
Palacios et al. (1999)	Population Genetics	Repeatability
Parsons and Shaw (2001)	Species Limits	Homology
Teo et al. (2002)	Hybridization	None
Wolf et al. (2004)	Population Genetics	Repeatability
Zawko et al. (2001)	Population Genetics	None
Zerega et al. (2005)	Species Limits	None

Table 2.2: Recent studies using AFLP markers

et al. 1996) the PCoA should be based on an asymmetrical coefficient that downweights or ignores double-zeros. Genetically distinct populations or taxa will appear as discrete clusters on a principle co-ordinates plot; hybrids may appear in a position intermediate to the parental taxa. Hybrids may also be revealed by a mixture of markers unique to the parental taxa, as in isozyme analysis (Kai et al. 2002; Teo et al. 2002). Dendrograms based on genetic distance are also routinely used in the interpretation of AFLP assays. Analysis of molecular variance (AMOVA Excoffier et al. 1992, 2005) and F_{st} analogs can also be calculated to assess population genetic structure and gene flow.

CHAPTER 3

Evaluating the taxonomic status of the globally rare *Carex roanensis* and allied species using morphology and amplified fragment length polymorphisms

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The following chapter addresses taxonomic issues in the *Carex roanensis* complex. The species boundaries in this group are uncertain, especially with respect to the globally rare *Carex roanensis*. Due to the rarity of this species, resolving its taxonomic status has important conservation implications: if it is a distinct species, it will warrant consideration in conservation planning by land managers. In the context of this thesis, establishing the taxonomic boundaries among these species is a critical first step in examining their phylogenetic and ecological relationships in later chapters. This chapter has been accepted, pending minor revisions, for publication in the journal Systematic Botany.

3.1 Abstract

We used a combination of amplified fragment length polymorphisms (AFLP) and morphological data from 272 individuals from 59 populations to investigate species limits in the *Carex roanensis* complex. Principal coordinate analysis of the morphological data suggested four entities corresponding to *C. aestivalis, C. roanensis, C. swanii*, and *C. virescens*, but clear discrimination was not possible. In contrast, the AFLP data showed marked discontinuities among these four species, including specimens that were morphologically ambiguous. Analysis of molecular variance revealed significant population structure within each species, but without any correlation to morphology, and limited geographical pattern. This study confirms the species-level distinction between the common and widespread taxa C. swanii and C. virescens, as well as that of the globally rare Appalachian endemic C. roanensis.

3.2 Introduction

Carex roanensis Hermann is a globally rare (G2 NatureServe 2006) taxon, endemic to unglaciated areas of the southern Appalachian Mountains from northern Georgia to southwestern Pennsylvania (Smith et al. 2006). It is characterized by its cespitose habit, sheathing bracts, linear spikes, and publication leaves and perigynia. Hermann described it as a new species in 1947. However, he noted that further investigation may reveal it to be an extreme form or variety of either of two other taxa. It differs from C. aestivalis Curtis ex Gray, which has glabrous perigynia, and from C. virescens Muhlenberg ex Willdenow, which has shorter perigynia and non-sheathing bracts. Carex aestivalis is restricted almost entirely to the Appalachians, while C. virescens is broadly distributed across the eastern U.S.A. and southern Canada. The need for further research remained when Waterway (2002) prepared the treatment of C. roanensis for the Flora of North America. Wieboldt et al. (1998) had noted significant variation in the length of bract sheaths in C. roanensis. This is particularly noteworthy, as sheathing bracts are one of the characters used to distinguish between section *Porocystis* Dumortier, which includes *C. virescens*, (Ball 2002), and section Hymenochlaenae (Drejer) L. H. Bailey, where C. roanensis and C. aestivalis are now placed (Waterway 2002). Hermann (1947) suggested that these two sections may not form natural groups, a hypothesis corroborated by recent work (Waterway 2006; Waterway and Starr 2007). A major reorganization of these sections is anticipated, pending the outcome of ongoing molecular studies (Waterway in prep.).

Carex virescens has also been implicated in another unresolved taxonomic issue, this one involving *C. swanii* (Fernald) Mackenzie. They are both common, widespread taxa of eastern North America. They occur in forest communities throughout much of their range, frequently in syntopic populations, with *C. swanii* also growing in more open habitats. Most recent authors have treated these as two distinct species (Hermann 1941; Fernald 1950; Voss 1972; Wofford 1989; Gleason and Cronquist 1991; Mohlenbrock 1999; Yatskievych 1999; Ball 2002; Jones 2005), with *C. virescens* differing from *C. swanii* mainly by having longer, narrower spikes. However, in preparing the treatment of section *Porocystis* for the Flora of North America, Ball observed that these taxa were "not always clearly distinct", and a thorough investigation is required to clarify their status (pers. comm.).

The objective of our study was to clarify the species-level taxonomy of this group. Specifically, we address the following problems:

- 1. Is *Carex roanensis* a distinct species, or does it represent variation within *C. virescens* or *C. aestivalis*?
- 2. Is *Carex swanii* distinct from *C. virescens*, and if so what characters best distinguish between them?

This work addresses taxa that remain difficult to place using currently available keys, further justifying the need for thorough morphological examination. The taxonomic status of *Carex roanensis* also has important conservation implications, due to its rarity. It is currently listed as "Imperiled" globally, and "Critically Imperiled" or "Imperiled" in all states where it is known to occur (NatureServe 2006).

For the purposes of this study we define distinct species as groups of reproductively and evolutionarily distinct organisms, as inferred from discontinuities in assayed characters. This is largely consistent with the phylogenetic species concept of Davis and Nixon (1992). However, their technique of population aggregation analysis (PAA) is not appropriate for this study. We are investigating taxa that may be co-occurring yet distinct species. PAA assumes that individuals can be reliably assigned to populations, with no possibility of mixed-species populations. We therefore modify their approach by treating all individuals as separate 'populations' in their sense (for related discussion see Henderson 2004). We also follow Luckow (1995) in equating discontinuities in multivariate space with discontinuities in any single character.

Morphology continues to be the primary approach to species-level taxonomy in *Carex* (e.g., Naczi et al. 1998; Rothrock and Reznicek 2000; Naczi and Ford 2001; Reznicek and González-Elizondo 2001; Rothrock and Reznicek 2001; Saarela and Ford 2001; Naczi et al. 2002a). Morphological data allow us to directly assess the work of previous authors whose work was based entirely on such data. Amplified fragment length polymorphisms (AFLP) are a useful complement to morphology. Their highly variable nature makes them an ideal source of information for assessing genetic variability among populations and closely related species (Mueller and Wolfenbarger 1999). They have been successful in assessing species-limits in a number of plant groups (van den Berg et al. 2002; Coart et al. 2002; Saarela et al. 2003; Martínez-Ortega et al. 2004; Bruneau et al. 2005; Zerega et al. 2005), including *Carex* (Ford et al. 2006b).

3.3 Methods

3.3.1 Sampling

We sampled 59 populations (9 to 21 per taxon) from 2003 to 2005 (listed in the Appendix A). Populations were selected to reflect the geographic range of the taxa, emphasizing the southern Appalachian mountains where all four are sympatric. This provides the strongest test of the distinction among these taxa: if they are species,

the discontinuities among them will still be apparent even when they are growing together. Our sampling included fourteen mixed populations: six with *C. swanii* and *C. virescens*, two with *C. aestivalis* and *C. roanensis*, two with *C. virescens* and *C. roanensis*, and four with *C. virescens*, *C. aestivalis* and *C. roanensis*.

Within each population we randomly selected 20 individuals using the ignorant man method (Ward 1974). Only specimens with firm, mature nutlets were considered. Fewer individuals were taken for small populations and incidental collections. All intermediate or otherwise unusual individuals encountered were also collected. For each individual, we collected a fruiting stem, and when possible, a vegetative shoot, and placed fresh leaves on silica gel. All samples and population vouchers are deposited at MTMG.

3.3.2 Morphology

We randomly selected four individuals from each full population for inclusion in the morphological survey. Additional individuals were assayed from populations that demonstrated unusual or extreme morphology, and all intermediate specimens were included. In total, 233 specimens were measured in this portion of the study.

Morphological characters were drawn from published keys (Fernald 1950; Voss 1972; Gleason and Cronquist 1991; Mohlenbrock 1999; Yatskievych 1999; Ball 2002) and pilot studies, and are listed in Table 3.1. Large characters were measured in mm with a ruler, smaller characters in 1/15 mm increments using a dissecting microscope with an ocular micrometer. We used the results of the Box-Cox function (Legendre and Legendre 1998, as implemented in the R Package of Casgrain and Legendre 2001) and visual interpretation of histograms to select normalizing functions for morphological variables, as listed in Table 3.1. Characters that were too heavily skewed to be normalized were recoded as presence-absence, also noted in the table.

Table 3.1: Morphological characters and their normalizing transformations. \pm refers to binary coding (presence/absence); γ values refer to the Box-Cox transformation: $x^{trans} = (x^{\gamma} - 1)/\gamma$

Character	Transformation	
Maximum leaf width on fruiting culm	ln	
Ligule length	ln	
Distal internode length	$\gamma = 0.16574$	
Proximal bract length	$\gamma = 0.3015$	
Inflorescence length	ln	
Bract length/inflorescence length	$\gamma = 0.15583$	
Number of spikes	ln	
Terminal spike length	\sqrt{x}	
Terminal spike: pistillate length/staminate length	$\gamma = 0.40884$	
Pistillate portion of terminal spike: width	ln	
Staminate portion of terminal spike: width	None	
Number of perigynia on the proximal cm of the terminal spike	ln	
Proximal spike length	$\gamma = 0.39294$	
Width of proximal spike	None	
Number of perigynia on the proximal cm of the proximal spike	ln	
Proximal peduncle length	$\gamma = -0.12889$	
Proximal bract sheath length $> 1 \text{ mm}$	\pm	
Staminate scale awn	\pm	
Staminate scale awn length / staminate scale body length	None	
Pistillate scale body length	None	
Pistillate scale awn length	ln	
Perigynium length	None	
Perigynium width	\sqrt{x}	
Perigynium length/width	ln	
Perigynium hair	\pm	
Nutlet length	None	
Nutlet width	None	
Nutlet length/width	$\gamma = -1.39867$	
Stipe length	None	
Anther length	None	

To assess overall morphological variation, we computed similarities from the data using the Gower coefficient (Gower 1971). We chose the Gower coefficient because it allows for the combination of quantitative and qualitative data, and can accommodate missing data. This allowed us to include anther characters in the overall analysis, despite the fact that they are frequently lost by the time an individual bears mature fruit. No standardization was required, as the Gower coefficient incorporates ranging. We took $\sqrt{1-\text{Gower coefficient}}$ as our distance measure, as recommended by Legendre and Legendre (1998), and then applied Principal Coordinate Analysis (PCoA) to this distance matrix. The Gower coefficient does not produce strictly Euclidean distances, particularly when variables with missing values are included. As a consequence, some of the PCoA analyses produced axes with negative eigenvalues. In all cases these axes accounted for a very small proportion of the total variance ($\ll 1\%$), and, as we restricted our analysis to only the two most informative axes, we elected not to apply any correction methods to eliminate the negative eigenvalues (as discussed in Legendre and Legendre 1998).

One of the disadvantages of PCoA relative to other ordination methods, such as Principal Components Analysis or Discriminant Analysis, is that PCoA provides no way to directly assess the relative contributions (loadings) of individual variables to the ordination axes (Legendre and Legendre 1998). However, it is possible to assess the contribution of individual variables with multiple regression analysis. Appropriate functions are provided in the vegan Package (Oksanen et al. 2006). This software calculates loadings for each variable, using the multivariate regression coefficients of the variable with each of the ordination axes, and scaled by the value of the multiple regression correlation coefficient. Thus, variables that contribute strongly to an ordination axis will produce a loading near one or negative one. Loadings near zero indicate variables that contribute relatively little to an axis. Variables with missing values cannot be analyzed with this technique, but it otherwise allows for calculation of values comparable to the loading values provided by other ordination techniques. We also examined characters singly and in pairs with graphs and t-tests to determine which provided the most effective discrimination among taxa.

3.3.3 Amplified fragment length polymorphisms

Initially, all specimens included in the morphological survey were included in the AFLP study. Due to amplification failures not all specimens yielded readily scored AFLP bands. In these cases other individuals from the same population were substituted. Following initial analysis, additional specimens from populations showing interesting patterns of genetic variation were added to the AFLP survey. In total, 249 specimens from 59 populations were assayed for AFLP markers, with 210 individuals included in both datasets.

For each specimen we ground 50 mg of silica-dried leaf tissue with the Autogen Autogrinder48 (AutoGen, Holliston, Massachusetts, USA). We suspended the ground tissue in a modified CTAB buffer (as described by Doyle and Doyle 1987, but without β -mercaptoethanol), and transfered it to the Autogen 850 DNA isolation system for extraction and purification. The standard plant DNA protocol supplied with the robot was used with the following modifications: the drying temperature was reduced from 50 °C to 30 °C, and the drying time was increased from 15 to 30 minutes. We replaced the Autogen reagents with the following: Reagent 1: 5M Potassium acetate with acetic acid (60 mL of 5M potassium acetate, 11.5 mL of glacial acetic acid, 28.5 mL of ddH₂0), Reagent 2: 3% SDS, Reagent 3: 100% chloroform, Reagent 4: 100% isopropanol, Reagent 5: 70% ethanol, Reagent 6: TE buffer.

AFLP protocols followed Vos et al. (1995), with modifications described by Wolf et al. (2004) for the restriction, ligation, and preselective PCR steps, except that we used a total volume of 25 μ L for the preselective PCR step. For selective amplifications we used the reagents and protocols provided by LI-COR (Lincoln, Nebraska, USA) with their IRDye®AFLP Selective Amplification Kit. We also used identical unlabeled *Mse* +3 primer from Sigma-Genosys (Oakville, Ontario, Canada). Fragments were visualized using a LI-COR Model 4300 DNA Analyzer and SagaMX scoring software following the standard protocols provided for that equipment.

We screened 24 primer pairs, selecting five that consistently produced clear, variable, and readily scored bands: $Mse + CAA \times EcoRI + AAG$; $Mse + CAC \times EcoRI + AGC$; $Mse + CTA \times EcoRI + ACT$; $Mse + CAA \times EcoRI + ACG$; and $Mse + CAG \times EcoRI + AAC$. To assess the reliability of bands we replicated 34 samples 2–5 times each. The replicated samples included 22 samples from the *Carex roanensis* complex, and 12 samples from the *Carex complanata* complex (see Chapter 4). Bands that were inconsistent among replicates were excluded from analysis.

A distance matrix was calculated from the AFLP data using a distance matrix using $\sqrt{1 - \text{Jaccard coefficient}}$. The Jaccard similarity coefficient ignores bands that are absent in both individuals, as appropriate for AFLP data. Bands of equal size are assumed to be homologous (an assumption supported by some empirical evidence, see Parsons and Shaw 2001). Therefore it is reasonable to treat shared bands as evidence of real genetic similarity between individuals. However, any number of mutations may result in the loss of a band, such that shared band absences between individuals cannot be assumed to indicate a shared mutation event in a common ancestor. The AFLP distance matrix was subjected to PCoA to visualize the overall variation in the data. As the relationships among different subsets of the four taxa are likely not easily visualized on the same two axes, we repeated the PCoA on different subsets of the total data, as appropriate for each of our research objectives. We also analyzed the partitioning of variance among appropriate hierarchical structures using analysis of molecular variance (AMOVA: Excoffier et al. 1992). Groups identified with PCoA were subjected to AMOVA to ascertain whether they had any meaningful internal structure, either at the population level, or among geographic regions. We calculated the genetic distance among taxa using Nei's coefficient (Nei 1972), as suggested by Felsenstein (2004a) for use when both drift and mutation contribute to divergence. Diagnostic bands between pairs of taxa were tabulated using two criteria. First, we identified all bands that were present in all individuals of one taxon and absent in all individuals as being 'absolutely diagnostic' for that taxon-pair. Second, the frequency of a band in each taxon was calculated, and bands with frequency differences between two taxa > 0.95 and < 1.00 were scored as 'nearly diagnostic'.

All PCoA and univariate analyses were completed using the R Statistical Computing Environment (version 2.4.0, R Development Core Team 2006), with multivariate functions provided in the **vegan** package (version 1.8-2, Oksanen et al. 2006). AMOVA analysis was conducted using Arlequin (Excoffier et al. 2005). Genetic distances were calculated using PHYLIP (Felsenstein 2004b).

3.3.4 Herbarium Records.

More than 2000 specimens from the following herbaria were examined for this project: ACAD, B, BM, BRIT, CAN, CLEMS, DUKE, EKY, ETSU, GA, GH, K, KANU, MARY, MICH, MO, MSC, MTMG, NCU, NEB, NEBC, NKY, NY, NYS, OKL, SMU, TAES, TAWES, TENN, USCH, VDB, VPI, WIS, WV (herbarium acronyms follow Holmgren and Holmgren 1990). County-level distribution maps were prepared by plotting a single point in each county where one or more voucher specimens for the species in question was examined. *Carex roanensis* is an exception, as we have plotted every known population of this globally rare taxon (Smith et al. 2006). Any discrepancies with the NatureServe (NatureServe 2006) database were reported to the appropriate Conservation Data Centers.

3.4 Results

3.4.1 Overall

After excluding inconsistent fragments, the AFLP assays produced 139 readily scored bands (41, 29, 27, 23, and 19 bands per primer pair). Nine bands were monomorphic over all individuals. In total, 246 distinct fingerprints were recorded, with three fingerprints shared by two individuals each, as discussed below. In all cases the AFLP analysis provided more definitive results than the morphological data. Several specimens that were morphologically ambiguous were unequivocally assigned to genetic groups and these assignments were used in the detailed analysis of morphological characters and in the related figures.

3.4.2 Carex roanensis, C. virescens, and C. aestivalis

PCoA was an effective tool for analyzing the morphological characters for this group, capturing 38% of the variation on the first two axes (Fig. 3.1A). The characters with the highest loadings on the first axis are the number of perigynia on the proximal cm of the proximal spike (0.80), lowest peduncle length (-0.79), perigynium length/width ratio (-0.78), and total inflorescence length (-0.74). The highest loadings on the second axis are leaf width (0.59), pistillate scale length (0.57), and nutlet width (0.56).

The ordination plot (Fig. 3.1A) shows that *Carex aestivalis* is cleanly separated from the other two taxa morphologically. This is primarily due to the influence of the perigynium hair character — the points for *C. aestivalis* overlap with those of the other taxa, particularly *C. roanensis*, when that character is excluded (data not shown). During fieldwork we located one specimen that was intermediate in this respect, with both pubescent and glabrous perigynia on the same plant. This plant



Figure 3.1: Principal coordinates analysis (PCoA) for *Carex virescens*, *C. roanensis* and *C. aestivalis*. A. morphological distance ($\sqrt{1 - \text{Gower coefficient}}$) calculated from 30 variables. B. genetic distance ($\sqrt{1 - \text{Jaccard coefficient}}$) calculated from 139 AFLP fragments. X and Y axes are plotted with equal scales, preserving the geometric distance among points.

was collected from the Carter Co., TN population where both *C. roanensis* and *C. aestivalis* co-occur. Its AFLP fingerprint was unequivocally placed with *C. roanensis*. A few additional specimens with both pubescent and glabrous fruits were found in herbarium collections. These plants were generally collected late in the season and were in poor condition, suggesting that the absence of hairs may have been the result of stress or senescence. In addition to perigynium vestiture, nutlet width and leaf width provide some discrimination between *C. aestivalis* and *C. roanensis*. Both of these characters are significantly different between taxa (t-tests, df = 85, p \ll 0.001), but as shown in Fig. 3.2 they still overlap enough to preclude using them as the sole basis for a determination. Perigynium vestiture also clearly separates *C. aestivalis* from *C. virescens*, as the latter is always pubescent. Perigynium length and density along the proximal cm of the proximal spike provide good separation of *C. virescens* from both *C. aestivalis* and *C. roanensis*, as shown in Fig. 3.3.



Figure 3.2: Key morphological characters distinguishing between *Carex roanensis* and *C. aestivalis*. Boxes enclose the interquartile range, with a bar marking the median. The whiskers extend up to 1.5 times the interquartile range, with any remaining outliers plotted individually, as described in McGill et al. 1978.



Figure 3.3: Scatter plot of two characters distinguishing *Carex virescens* from C. roanensis and C. aestivalis

Table 3.2: Summary of shared AFLP bands and genetic distances. Values in the lower triangle of the matrix are the number of diagnostic bands for the taxon in the row, distinguishing it from the taxon in the column, i.e., bands that are present in all specimens of one taxon and absent from all specimens of the other. Numbers in parentheses are the number of nearly diagnostic bands, i.e., bands with a frequency difference > 0.95 but < 1.00 between the two taxa. Values in the upper triangle are the pair-wise genetic distances (Nei 1972) between species calculated from band frequencies.

Taxa	C. aestivalis	C. roanensis	C. swanii	C. virescens
C. aestivalis		0.109	0.240	0.096
$C. \ roan ensis$	3(1)		0.286	0.118
$C. \ swanii$	3(8)	1(12)		0.256
C. virescens	1(5)	1(2)	1(14)	

The ordination of the AFLP data shows the same overall pattern as that using morphological data, but with much clearer separation among groups (Fig. 3.1B). Thirteen of 139 bands are fixed within this group, with three absent from all individuals of all three taxa. Each individual of *C. aestivalis* and *C. roanensis* had a unique genotype, as did all but two specimens of *C. virescens*, both from the Illinois population. Pairwise comparisons of diagnostic bands and genetic distances among these taxa are shown in Table 3.2.

3.4.3 Carex swanii and C. virescens

PCoA analysis of the morphological data for *Carex swanii* and *C. virescens* was effective, with 32% of the total variation represented on the first two axes. The resulting ordination shows evident morphological separation (Fig. 3.4A). However, depauperate specimens remain difficult to place, and there is no clear demarcation between the two taxa. The first coordinate axis shows the clearest separation between the two taxa. The variables with the highest loadings on this axis are the number of perigynia on the proximal cm of the proximal spike (-0.70), terminal spike length (0.69), and proximal spike length (0.67). There are statistically significant differences



Figure 3.4: Principal coordinates analysis (PCoA) for *Carex virescens* and *C. swanii*. A. morphological distance ($\sqrt{1 - \text{Gower coefficient}}$) calculated from 30 variables. B. genetic distance ($\sqrt{1 - \text{Jaccard coefficient}}$) calculated from 139 AFLP fragments. X and Y axes are plotted with equal scales, preserving the geometric distance among points.

between C. swanii and C. virescens for each of these variables (t-tests, df = 144, p $\ll 0.001$, Fig. 3.5).

The AFLP data reveals that this subtle morphological variation reflects striking genetic differences, as shown in Fig. 3.4B. Although only one band was absolutely diagnostic for these two taxa, 15 bands were nearly diagnostic (Table 3.2). Of the 139 fragments scored, 13 were present in all specimens and 7 were absent in all specimens of these two taxa. Three fingerprints were shared by multiple individuals: two individuals from the Illinois population of *C. virescens* were identical, as were two individuals in the *C. swanii* population from Fayette County, Pennsylvania. The same *C. swanii* genotype was present in two individuals in the population from Pike County, Arkansas.



Figure 3.5: Key morphological characters distinguishing between *Carex virescens* and *C. swanii*. All lengths reported in mm. Number of perigynia indicates the number of perigynia on the proximal cm of the proximal spike; two outlying specimens of *C. swanii*, with 51 and 53 perigynia are not plotted. Boxes enclose the interquartile range, with a bar marking the median. The whiskers extend up to 1.5 times the interquartile range, with any remaining outliers plotted individually.

3.4.4 Population structure

Analysis of molecular variation reveals that most of the variation is explained by taxon membership when each taxon is treated as a separate group (Table 3.3). However, within each taxon the majority of variation is explained by differences among individuals. The differences among taxa, populations, and groups were significant in all cases (p < 0.001). Despite the statistical significance of the population-level variation, clear geographic structure was only evident for *C. virescens*. PCoA of AFLP data for *C. virescens* alone revealed separation between the western-most populations sampled, those from Hardin Co., Illinois, Lawrence Co., Alabama, and Anderson Co., Tennessee, and the remaining 13 populations (Fig. 3.6). This regional divergence explains fully one-quarter of the total variation in this species (Table 3.3). However, we could find no corresponding pattern in the morphological data.

Table 3.3: Analysis of molecular variance (AMOVA). Variation was partitioned among species, among populations nested within species and among individuals within populations for the all-species analysis; and among individuals nested within populations for each single-taxon analysis. The results of an additional analysis for *C. virescens* are also reported, with variation partitioned between regions (described in the text), among populations within regions, and among individuals within populations. Abbreviations are as follows: SV, source of variation; df, degrees of freedom; SSD, sum of squares; VC, variance-component estimates and %TV, percentage of total variance. All cases: p < 0.001, based on 20000 permutations.

Taxon	SV	df	SSD	VC	%TV
All species	species	3	2122.72	11.37	63.00
	populations	55	644.86	1.58	8.76
	individuals	194	968.74	5.10	28.24
C. aestivalis	populations	12	168.96	2.21	28.62
	individuals	38	209.16	5.50	71.38
$C. \ roan ensis$	populations	8	125.58	1.86	22.55
	individuals	36	230.42	6.40	77.45
$C. \ swanii$	populations	20	175.86	1.16	20.81
	individuals	58	256.85	4.43	79.19
C. virescens	populations	15	174.45	1.51	24.32
	individuals	58	272.32	4.70	75.68
C. virescens	regions	1	51.15	1.95	25.79
	populations	14	123.30	0.90	11.98
	individuals	58	272.32	4.70	62.23

3.4.5 Geographic distribution

Carex swanii has the broadest distribution of any species in this group, and its range includes the entire geographic extent of the other three taxa (Fig. 3.7A). *Carex swanii* occurs throughout the Appalachians, along large portions of the Mid-Atlantic Coastal Plain north into the Atlantic Highlands as far as Nova Scotia, west to the Northern Lakes and Forests ecoregion in northern Michigan, and south to the Ouachita Mountains in Arkansas and Oklahoma (Ecoregion names follow the Commission for Environmental Cooperation (1997)). Additionally, it has been introduced at one location in British Columbia (not mapped).



Figure 3.6: Principal coordinates analysis (PCoA) for eastern and western populations of *Carex virescens*. Genetic distance ($\sqrt{1 - \text{Jaccard coefficient}}$) calculated from 139 AFLP fragments. X and Y axes are plotted with equal scales, preserving the geometric distance among points.

The range of C. virescens includes nearly the entire extent of the Appalachian mountains, from Alabama to Vermont and New Hampshire, and extends into the coastal counties of southern Maine (Fig. 3.7B). In the Southeast it is restricted to the Blue Ridge and Ridge and Valley ecoregions, while it crosses the Piedmont into the Mixed Wood Plains and Atlantic Highlands ecoregions in the Northeast. Its distribution becomes sparser westward, where it extends into the Central U.S., Mixed Wood, and Southeastern U.S. Plains ecoregions of Indiana, Illinois, Ohio, and southern parts Michigan and the province of Ontario. The southwestern limit of its range lies at the eastern edge of the Ozark Highlands in southeastern Missouri. While not as widespread as C. swanii, the range of C. virescens includes the full extent of both C. aestivalis and C. roanensis.



Figure 3.7: Geographic distribution, based on examined herbarium specimens. A. *Carex swanii* (a single introduced population in British Columbia not shown), B. *C. virescens*, C. *C. aestivalis*, D. *C. roanensis*.

Carex aestivalis occurs in the Appalachian Mountains, from northern Georgia to Vermont and New Hampshire (Fig. 3.7C). It is most abundant in the southern Blue Ridge and Ridge and Valley ecoregions, becoming rarer northwards into the Northeastern Highlands. Its northwestern range limit is in the Northern Appalachian Plateau and the North Central Appalachian ecoregions in New York and Pennsylvania.

Carex roanensis is found at higher elevations in the Blue Ridge, Ridge and Valley and Central Appalachian ecoregions, reaching its northern limit in the Western Allegheny Plateau region of southwestern Pennsylvania (Smith et al. 2006). Its range falls entirely within that of *C. aestivalis* (Fig. 3.7D).

3.5 Discussion

Our results strongly support the recognition of *C. roanensis* as a species, distinct from *C. virescens* and *C. aestivalis*. It is clearly separated from *C. aestivalis* by its pubescent perigynia, as indicated in existing keys (Wofford 1989; Waterway 2002; Jones 2005). Previous authors have not developed characters that explicitly separate *Carex virescens* from *C. aestivalis* and *C. roanensis* because they have not been treated within the same section. The sections are distinguished by their proximal inflorescence bracts, which are reported to be sheathing in sect. *Hymenochlaenae* and sheathless in sect. *Porocystis*. This character is not reliable, however: of 36 *C. roanensis* specimens included in this study, 15 had proximal bract sheaths less than 2 mm long, and seven had sheaths less than 1 mm. *Carex virescens* is more consistent, but five of 66 specimens had sheaths longer than 2 mm. Even a few *C. aestivalis* are problematic: four of 51 specimens had sheaths 2 mm or less, and three of these were less than one mm. Perigynium length and density along the proximal cm of the lowest spike provide more reliable discrimination (Fig. 3.3).

Phenology also helps distinguish *C. aestivalis* from its close relatives. *Carex aestivalis* flowers and fruits as much as two weeks later than both *C. virescens* and *C. roanensis*. This is of limited value in herbarium study, but is very useful in the field, particularly in mixed populations.

The congruence of the morphological and molecular datasets, particularly with the clear genetic differentiation, confirms that *C. swanii* and *C. virescens* are most appropriately recognized as distinct species. Robust specimens of both species are easily distinguished, but the characters used in most keys are misleading for depauperate individuals. Most authors have used spike and anther length to distinguish between these taxa (e.g., Fernald 1950; Gleason and Cronquist 1991; Ball 2002). However, there is considerable overlap in these characters (Figs. 3.5A and 3.5B). As suggested by the loadings, the number of perigynia on the proximal cm of the proximal spike does indeed provide the clearest separation of the taxa (Fig. 3.5C). Extreme specimens of either taxon overlap with the range of the other, but this overlap is less than in any other character. Fernald (1950) and Gleason and Cronquist (1991) both include this character in their keys, but without providing an objective measure with which to apply it. Other characters that help differentiate these species are staminate and pistillate scale length, and ligule length (Figs. 3.5D, 3.5E and 3.5F). However, the overlapping ranges of these variables make them less useful as key characters.

The taxonomic relationship between C. virescens and C. swanii was the source of much debate among prominent caricologists of the 19th century. Following Muhlenberg's original diagnosis of C. virescens (in Willdenow 1797-1810), Schweinitz (1824) recognized C. costata as a segregate species, based on perceived differences in leaf sheath coloration and perigynium texture. Britton (1895) supported the recognition of this new species, which he renamed C. costellata to distinguish it from the previously published C. costata Presl. Britton's (1895) description of C. costellata refers to "narrowly cylindric, many-flowered, rather loose" spikes, which differed from the then-current concept of C. virescens as having shorter, broader spikes. Fernald (1906) took issue with this interpretation. Muhlenberg (in Willdenow 1797-1810) had described C. virescens as having linear spikes with somewhat nerved perigynia. In Fernald's (1906) view, there were "two extreme variations" in C. virescens: one with long, narrow spikes corresponding to the original description and the other with oblong-cylindric to subglobose spikes. Britton (1895) and Schweinitz (1824) considered the latter form to be the plant of Muhlenberg's description, but Fernald (1906) reduced it to C. virescens var. swanii, citing "numerous transitional specimens" as justification for the lower rank. Bicknell (1908) argued that both taxa should be recognized as distinct species, and followed Britton's nomenclature (1895).

Mackenzie (1910) also thought the distinctions between the two taxa warranted recognition at the species level. However, he reasoned that since Muhlenberg's type specimen was part of a mixed collection and did not conform to the published description, the description alone should be used to determine the true identity of Muhlenberg's *C. virescens*. As Fernald (1906) had already stated, the description was of a plant with long, narrow spikes. Thus, Mackenzie (1910) concluded that this was the true *C. virescens*, and he elevated the other taxon to species status as *C. swanii* (Fernald) Mackenzie. The type specimen of *C. virescens* at B is in fact a depauperate individual, with short spikes intermediate between typical *C. swanii* and *C. virescens*. However, the number of perigynia on the proximal portion of the proximal spike unambiguously places it within *C. virescens*. This confirms the interpretation of Mackenzie (1910) and Fernald (1906).

AMOVA results further support the recognition of all four taxa as distinct species. Analysis of the total dataset revealed that most of the variation is explained by differences among taxa while most of the variation within taxa is explained by differences among individuals (Table 3.3). The intra-species population differences never accounted for more than half as much variation as was explained by interspecies differences, suggesting that, though statistically significant, the population differences do not warrant taxonomic recognition. The divergence between the three southwestern-most populations of C. virescens and the rest of that species could reflect meaningful phylogeographic or even taxonomic structure. However, as our sampling focused primarily on the southern Appalachians, out data does not allow for robust examination of these possibilities. Not only do both datasets confirm the morphological and genetic discontinuities among these four species, our sampling confirms that these distinctions hold even when the taxa are growing in close proximity. We found 14 locations where two or more taxa were growing intermixed, with different species frequently within a few centimetres of each other. In all cases individuals were unequivocally identified with the AFLP markers, even when they were superficially similar. These are windpollinated species with overlapping flowering times; any gene flow between them should have been detectable in these mixed populations, but none was apparent.

We could confirm 45 populations of *C. roanensis* (Fig. 3.7D), including one previously unreported collection from Oconee Co., South Carolina (Burrell's Ford, Chattooga River, 16 May 1981, *M.G. Douglass 467*, CLEMS). This record was originally determined as *C. virescens*. It is the first record for South Carolina, from a location 30 km east of the historic Rabun Co., Georgia, population and 4 km south of the North Carolina border. The recognition of *Carex roanensis* as a distinct species has important conservation implications. *Carex roanensis* meets the Nature-Serve criteria for classification as "vulnerable to extinction" based on the number of extant populations (NatureServe 2006). Conservation agencies and land managers will need to give it appropriate consideration. The AFLP data did not reveal any clear geographic pattern to the genetic diversity in this species, but the significant among-population variation does suggest that more extensive population sampling should be conducted to ensure that management strategies adequately conserve the genetic variability of this species.

Our herbarium survey suggests that C. virescens should be removed from the flora of Arkansas, as all vouchers from that state were misidentified specimens of C. swanii (Fig. 3.7B). Similarly, although it is listed for Wisconsin and Quebec

(NatureServe 2006), no vouchers could be located for either jurisdiction. After consulting the local natural heritage botanists we conclude that these reports probably stem from confusion over the application of the name C. virescens var. swanii, and should be removed from their floras.

Carex swanii has not previously been reported from Alabama, but we found a single specimen from Jackson County (SW Pleasant Grove, 8 July 1992, *R. Jones* 7149, VDB, Fig. 3.7A). This is a minor extension, as this species also occurs in adjacent counties in Tennessee. We did not see the specimen for Ross Island, New Brunswick, reported by Hinds (2000), but we do not doubt the validity of this record as it is not far from the known populations in Nova Scotia, and no other species that could easily be confused with *C. swanii* occurs in that area.

Although *C. aestivalis* is reported from Alabama (NatureServe 2006), we found no vouchers to confirm this (Fig. 3.7C). If it does indeed grow in Alabama this would represent a minor range extension beyond the closest records we have seen from Grundy County, Tennessee. We also found no vouchers for the state of New Jersey, but records from adjoining regions of Pennsylvania and New York suggest that it likely also occurs in the northern counties of New Jersey.

The AFLP data suggest a closer relationship between C. virescens, C. roanensis and C. aestivalis than between C. virescens and C. swanii. Carex swanii is distinguished from the other three taxa by 11–15 nearly fixed bands, compared to only 3–6 such bands among the other three species (Table 3.2). This is also reflected in the much larger genetic distance between C. swanii and the other three taxa, compared to the distances among those species (Table 3.2). Furthermore, AFLP-based PCoA ordinations and NJ phenograms of all four species (data not shown) plot C. swanii well removed from the other three taxa. This is consistent with the results of Waterway (2006), which show that despite their morphological similarity C. swanii and *C. virescens* actually belong to different clades. In fact, while sequence-based phylogenetic analysis reveals that *C. virescens* is part of a well supported clade with *C. roanensis* and *C. aestivalis*, *C. swanii* appears to be more closely related to other members of the traditional section *Porocystis*: *C. complanata* Torrey & Hooker, *C. hirsutella* Mackenzie, *C. bushii* Mackenzie, and *C. caroliniana* Schweinitz. These four taxa represent another unresolved taxonomic problem (Chapter 4).

Clear genetic separation among species with limited morphological divergence, as demonstrated here with *C. swanii* and *C. virescens*, has been observed in other *Carex* sections, notably *Phyllostachyae* (Naczi and Ford 2001) and *Careyanae* (Ford et al. 2006b). Naczi and Ford (2001) hypothesized that this could be an indication of symplesiomorphic morphology. This retention of ancestral morphological characteristics may in turn suggest a recent and rapid radiation of these *Carex* sections in eastern North America, a hypothesis further supported by the short branch lengths and poor resolution for these groups in sequence-based phylogenetic studies (Waterway 2006).

The low numbers of absolutely fixed genetic differences among species also suggests a recent origin for this group. The mean number of fixed differences in pair-wise comparisons between species in this study was only 1.67 (range 1–3, Table 3.2), and no species has a fragment that would distinguish it from all other taxa. Ford et al. (2006b), in their study of *Carex digitalis* s.l., did not report the number of absolutely diagnostic bands, but instead tabulated the number of bands that were absent in some taxa and present in > 50% of specimens in others. By this measure they determined that 20–65 bands distinguished among cryptic *Carex* species. Applying that criterion to our data reveals 3–9 bands distinguishing among species in our study (data not shown). Given that we scored only 130 polymorphic fragments, compared to the 248 fragments assayed by Ford et al., this represents roughly comparable levels of variation. In contrast, Vollan et al. (2006) found 10 fixed differences between *Carex lachenalii* Schkuhr and *C. cannescens* L. However, their results may not accurately reflect the distinctions between these species, as their sampling focused on quantifying variation among infraspecific northern and southern hemisphere populations, rather than between species. Broader sampling may reveal variation in some of these apparently fixed bands. Our results are comparable to those of Martínez-Ortega et al. (2004), who investigated cryptic species of *Veronica*. They scored 518 polymorphic bands and found a median number of three bands (range 0–9) distinguished among species. Coart et al. (2002) found no diagnostic bands between two species of *Quercus*, using a dataset of 170 polymorphic fragments from four primer pairs. They screened an additional 60 primer pairs for possible species-specific markers, but could not confirm any. They attributed this to hybridization events between the taxa in their study. We cannot distinguish between recurrent hybridization and recent origin with the data presented here.

These comparisons highlight two important points. First, absolutely diagnostic bands are rare among closely related species. Second, and most important in the context of these studies, individual diagnostic markers are not necessary to resolve the species-limits among closely related species. The AFLP data from each of the three studies discussed above reveal clear, taxonomically meaningful patterns, despite the paucity or total absence of diagnostic markers.

3.6 Taxonomic Treatment

Although sequence-based comparisons (Waterway 2006) suggest that only three of the four species investigated here constitute a monophyletic group, all four give field botanists some difficulty in making confident determinations. We therefore provide here a key and descriptions of all four species to facilitate their reliable identification.

3.6.1 Description

Cespitose. Culms 15–115 cm tall, dark maroon at base, with sheaths and sometimes also the leaves, culms and perigynia pubescent. Inflorescences with 2–6 spikes, the terminal one gynecandrous, the lateral pistillate and short to long pedunculate on erect or somewhat nodding peduncles. Perigynia trigonous, 1.6–4 mm long, beakless.

3.6.2 Key

Plants are frequently entirely reproductive, without vegetative pseudoculms: the reported leaf widths are for the reproductive culms only. When present, vegetative pseudoculms often have much wider leaves. Leaf hair characters should be assessed for well-developed basal leaves. Fruit characters should be measured from mature, well-formed perigynia and scales from the middle of the terminal spike. All quantitative characters overlap to some degree. The most consistent characters are listed first, but difficult specimens require careful consideration of the entire plant to ensure accurate identification.

1. Perigynia hirsute

2. Proximal spike with < 21 perigynia on the proximal cm, lateral spikes narrowly clavate to cylindrical

3.7 Species Accounts

CAREX AESTIVALIS M. A. Curtis ex A. Gray, Amer. J. Sci. Arts 42: 28. 1842. TYPE: U.S.A. North Carolina: Burke Co. Table Mountain. No date recorded. *Curtis s.n.* (Holotype: MO scanned image!; isotype GH!)

Culms: sparsely pubescent on basal sheaths, 25–75 cm. Leaves: glabrous to sparsely pubescent basally, ligules 0.8–4.7 mm; blades 1.4–3.6 mm wide. Inflorescences: 64–400 mm long; 4–6 narrowly terete spikes on slender arching peduncles; terminal spike 15–54 mm long, pistillate portion 4–31 × 1.9–3.3 mm, staminate portion 9–27 mm long; proximal spike with 2–7 perigynia along proximal cm, bract sheath 3–48 mm, peduncle 8–113 mm, 24–72 × 0.6–2.5 mm. Pistillate scales: 1.3– 2.5 mm, awnless or with a short awn up to 0.5 mm. Staminate scales: 2.6–4.9 mm long. Anthers: 1.5–2.7 mm. Perigynia: glabrous, 2.5–3.5 × 0.8–1.2 mm. Nutlets: short stipitate, 1.3–2.2 x 0.9–1.1 mm.

Plants growing in full sun tend to be shorter, densely tufted and more erect. Shade-grown plants, particularly in rich sites, develop much longer, more arching culms. In addition to the morphological traits described above, *C. aestivalis* flowers and fruits approximately two weeks later than the other species in this complex.

Mid- to high-elevation rocky forests and open balds in the southern Appalachians, and somewhat lower elevations northward into Vermont and New Hampshire. Often found on exposed rock faces. Often co-occurs with *C. virescens*, and where their ranges overlap, *C. roanensis*.

CAREX ROANENSIS F. J. Hermann, Castanea 12: 113. 1947. TYPE: U.S.A. Tennessee: Carter Co. rich, moist soil under beech, above toll road to Roan Mountain, alt. 4700 ft, 2 Aug 1936, *D. M. Brown 255* (Holotype: US; isotypes DUKE, MICH!)

Culms: Pubescent on basal sheaths, 40–90 cm. Leaves: ligules 1.3–7 mm; blades pilose 2.7–4.5 mm wide. Inflorescences: 60–209 mm long; 3–6 narrowly terete spikes on arching to ascending peduncles; terminal spike 20–50 mm long, pistillate portion $7-32 \times 2-3.8$ mm, staminate portion 6–25 mm long; proximal spike with 2–7 perigynia along proximal cm, bract sheath 1–23 mm, peduncle 8–42 mm, 20–61 x 1.3–2.6 mm. Pistillate scales: 1.6–2.4 mm, awnless or with a short awn up to 0.5 mm. Staminate scales: 3.2–5.1 mm long. Anthers: 2–3.3 mm. Perigynia: pubescent, rarely some glabrous perigynia on depauperate specimens, 2.6–3.6 × 1–1.6 mm. Nutlets: short stipitate, 1.8–2.1 × 1–1.2 mm.

See comments under C. virescens below.

Mid- to high-elevation forests in the southern Appalachians, from northern Georgia to Pennsylvania. Rich cove and northern hardwood forests, usually on more sparsely vegetated slopes. Often co-occurs with *C. aestivalis* and *C. virescens*.

CAREX VIRESCENS Muhlenberg ex Willdenow, Sp. Pl. 4(1):251. 1805. TYPE: U.S.A. no date or location, *Muhlenberg s.n.* (Holotype: B!)

Culms: sparsely pilose basally, 25–100 cm. Leaves: ligules 2–11.2 mm; blades pilose, often densely so, 2–4 mm wide. Inflorescences: 29–82 mm long; usually 3 terete to narrowly ellipsoid spikes on erect peduncles; terminal spike 16–38 mm long, pistillate portion 8–23 x 2.1–4 mm, staminate portion 6–20 mm long; proximal spike with 7–19 perigynia along proximal cm, bract sheathless, or rarely with a sheath up to 2 mm, peduncle up to 11 mm, 5–36 × 1.3–3.1 mm. Pistillate scales: 1.2–2 mm, awnless or with a short awn up to 0.5 mm. Staminate scales: 2.5–4.2 mm long. Anthers: 1.3–2.5 mm. Perigynia: pubescent, 2–2.6 × 0.9–1.5 mm. Nutlets: not stipitate, 1.5–1.9 × 0.9–1.3.

Robust specimens may be difficult to distinguish from C. roanensis. Careful measurement of perigynium length, fruit density on the lowest spike, and the length

of the proximal bract sheath are required. Depauperate specimens often resemble C. swanii. Fruit density may be determined even late in the season by counting perigynia scars on the spike rachis. On extreme individuals, with proximal spikes less than 15 mm long, the perigynia overlap only partially with the fruits above and below, giving the spike a beaded profile. In contrast, C. swanii almost always has more pronounced overlap between fruits, giving the proximal spike a fuller, more elliptic profile.

Widespread across the eastern U.S.A., ranging north into southeastern Canada. Usually in openings in rich forest habitats, but also along field edges and roadsides. Co-occurs frequently with *C. swanii*, and often with *C. roanensis* and *C. aestivalis* where their ranges overlap.

CAREX SWANII (Fernald) Mackenzie, Bull. Torrey Bot. Club 37: 246. 1910. TYPE: U.S.A. Vermont: Manchester, 24 June 1898, A. Day 202. (Holotype: GH!).

Culms: sparsely pilose, 15–90 cm. Leaves: ligules 1–4; blades densely pilose, 1.5– 3.1 mm wide. Inflorescences: 10–57 mm long; usually 3 narrowly to widely ellipsoid spikes; terminal spike 7–21 mm long, pistillate portion 4–13 × 2.6–4.5 mm, staminate portion 2–9 mm long; proximal spike with 15–53 perigynia along the proximal cm, bract sheathless, peduncle up to 11 mm, 4–19 × 1.9–4 mm. Pistillate scales: 0.9–1.5 mm, often with a short awn 0.3–0.8 mm. Staminate scales: 1.5–3 mm long. Anthers: 0.9–1.6 mm. Perigynia: pubescent, 1.7–2.3 × 1–1.5 mm. Nutlets: not stipitate, 1.3–1.8 × 0.8–1.3 mm.

In rich sites, robust individuals with exceptionally long spikes may occur. These individuals are distinguished from C. virescens by careful examination of the perigynia density on the proximal spike, and by their thicker, more ellipsoid spikes. See also comments above under C. virescens.

Widespread across the eastern USA, ranging north into southeastern Canada. Forest openings in both rich and poor, acidic habitats, open fields, and wet meadows. May co-occur with any of the species in this group.

CHAPTER 4

Evaluating species limits and hybridization in the *Carex complanata* complex using morphology, amplified fragment length polymorphisms, and restriction fragment analysis

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In the previous chapter I established the species limits in the *Carex roanen*sis complex. The following chapter addresses similar issues the *Carex complanata* complex. These two groups are closely-related, and their phylogenetic connections are the subject of Chapter 5. Before any phylogenetic analysis is possible, however, several taxonomic questions need to be clarified. The boundaries in this complex are uncertain, especially with respect to *Carex complanata* and *C. hirsutella*. These two taxa have been treated as a single variable species by some recent authors, and as two distinct species by others. Some authors have speculated that any distinctions between the taxa in this group are blurred by hybridization. All the taxa in this group are widespread, and they are often dominant members of their communities. As such, clarifying their taxonomic relationships may contribute to a better understanding of the ecology of these communities. In the context of this thesis, establishing the taxonomic boundaries among these species is a critical first step in examining their phylogenetic and ecological relationships in later chapters.

4.1 Abstract

We used a combination of morphology, amplified fragment length polymorphisms (AFLP), and restriction site data from 245 individuals from 51 populations to investigate species limits and hybridization in the *Carex complanata* complex. Principal coordinate analysis of the morphological data shows clear separation of entities corresponding to *C. bushii* and *C. caroliniana*. However, only leaf indumentum reliably distinguished between *C. hirsutella* and *C. complanata*. Despite this very subtle difference, AFLP data reveals very clear genetic separation of these two taxa. Contrary to the assertions of previous authors, we found no evidence of introgression among *C. complanata*, *C. caroliniana* and *C. bushii*. Relatively high genetic variation within *C. hirsutella* may be an indication of limited gene-flow between this species and one or more other species, but further work is necessary to clarify this issue. We document six previously undescribed sterile or nearly sterile hybrids involving the species in this complex.

4.2 Introduction

Carex complanata Torrey & Hooker is a common, widespread species of open habitats in the southeastern United States. It is characterized by a gynecandrous terminal spike, nearly sessile pistillate lateral spikes, glabrous perigynia, and sparsely pilose leaf sheaths, the lowest of which are strongly reddened. The earliest description of this taxon, as *C. triceps* Michaux, encompassed variants that are now recognized as five different taxa. *Carex hirsutella* Mackenzie was first distinguished by Willdenow in 1805 (as *C. hirsuta*), differing from *C. complanata* s. s. by having copiously pilose leaves. Whether or not this distinction warranted taxonomic recognition was the subject of debate among prominent caricologists (Bailey 1889a; Mackenzie 1910, 1923). Recent treatments vary, with some recognizing both as full species (Fernald 1950; Ball 2002; Jones 2005), and others considering them as two subspecies of *C.* *complanata* (Gleason and Cronquist 1991), or as a single variable taxon (Wofford 1989). A further complication results from disjunct populations of *C. complanata* from central America, which have been recognized as *C. complanata* ssp. *tropicalis* (Reznicek and González-Elizondo 2001), based on subtle differences in the staminate scales.

Within the C. complanata-C. hirsutella complex, plants with rounded perigynia and cuspidate pistillate scales were recognized by Dewey (as C. hirsuta var. cuspidata, in Wood 1861) and Kükenthal (as C. triceps var. longicuspis, 1909). Mackenzie (1910) elevated these plants to species status as C. bushii Mackenzie. The fifth group in this complex, with rounded perigynia and short scales, was described as C. caroliniana, by Schweinitz in 1824. Some later authors treated it as a variety of C. complanata (as C. triceps var. smithii Porter), while others subsumed C. bushii within it (as C. caroliniana var. cuspidata (Dewey) Shinners). Most recent authors have treated these two taxa as distinct species (e.g., Wofford 1989; Gleason and Cronquist 1991; Mohlenbrock 1999; Yatskievych 1999; Ball 2002; Jones 2005). However, Correll and Johnston (1970) suggested that these taxa intergrade or hybridize with each other and C. complanata, and all three species should perhaps be considered a single variable species; this hypothesis has never been rigorously examined. Many *Carex* hybrids have been reported in older floras and monographs (reviewed in Cayouette and Catling 1992), but often without supporting evidence. Recent investigators, bringing multiple lines of evidence to bear on the problem, have established that hybridization is an important aspect of the taxonomy of some *Carex* sections (Kukkonen and Toivonen 1988; Cavouette and Catling 1992; Waterway 1994).

The objective of our study was to clarify the species-level taxonomy of the *Carex* complanata complex. Specifically, we address the following problems:

1. Is Carex hirsutella distinct from C. complanata?
- 2. What is the appropriate taxonomic treatment for the *Carex complanata* morphological complex (including *C. bushii*, *C. caroliniana*, and *C. hirsutella*)?
- 3. Is there any evidence to support the contention that hybridization plays a significant role in the evolution of this group?

For the purposes of this study we define distinct species as groups of reproductively and evolutionarily distinct organisms, as inferred from discontinuities in assayed characters. We developed both morphological and molecular (amplified fragment length polymorphisms, AFLP) datasets for the same individuals (for discussion see section 3.2). In addition to the two taxonomic datasets, we examined herbarium specimens to determine the geographic distribution of the taxa in this study.

4.3 Methods

4.3.1 Sampling

To assess the species-level taxonomic issues surrounding C. complanata, C. caroliniana, C. bushii and C. hirsutella, we sampled 51 populations (8 to 19 per taxon) from 2003 to 2005 (listed in Appendix A). Populations were selected to reflect the geographic range of the taxa, emphasizing the southern coastal plain and piedmont regions where all four taxa are sympatric. This provides the strongest test of the distinction among these taxa: if they are distinct species, the discontinuities among them will still be apparent even when they are growing together. Our sampling included nine mixed populations: Carex complanata and C. hirsutella co-occurred at two locations, C. complanata and C. caroliniana at one location, C. bushii and C.hirsutella at four locations, and C. bushii, C. complanata, and C. hirsutella at two locations. In addition, many of the monotypic populations we sampled were within 1 km of at least one other taxon in this complex. Within each population we randomly selected 20 individuals using the ignorant man method (Ward 1974). Only specimens with firm, mature nutlets were considered. Fewer individuals were taken from small populations or incidental collections. All intermediate or otherwise unusual individuals encountered were also collected, including several putative hybrids, identified as such by their closed anthers, aborted fruits, and intermediate morphology relative to possible parental species (Cayouette and Catling 1992). We took a fruiting stem, and when possible a vegetative shoot, from each individual. In addition, fresh leaves from the same individuals were placed on silica gel for later DNA extraction. All samples and population vouchers are deposited at MTMG.

We were not able to collect any population samples of *Carex complanata* ssp. tropicalis. Our analysis of this subspecies is therefore limited to herbarium specimens. We did collect samples from four populations of *Carex oxylepis* Torrey & Hooker for use in evaluating a putative hybrid. We also used samples from 20 populations of *Carex swanii* (Fernald) Mackenzie, documented in Chapter 3, in evaluating two other hybrids.

4.3.2 Morphology

We randomly selected five individuals from each full population for inclusion in the morphological survey. Additional individuals were assayed from populations that demonstrated unusual or extreme morphology, and all intermediate specimens were included. For *Carex complanata* ssp. *tropicalis* we selected six mature, complete specimens for inclusion in the analysis. In total, 223 individuals were measured in this portion of the study.

Morphological characters were drawn from published keys (Ball 2002; Reznicek and González-Elizondo 2001; Mohlenbrock 1999; Yatskievych 1999; Gleason and Cronquist 1991; Voss 1972; Fernald 1950) and pilot studies, and are listed in Table 4.1. Large characters were measured in mm with a ruler, smaller characters in 1/15 mm increments using a dissecting microscope with an ocular micrometer.

We used visual interpretation of histograms and normal quantile plots (Sokal and Rohlf 1995) to select normalizing functions for morphological variables, as listed in Table 4.1. Characters that were too heavily skewed to be normalized were recoded as presence-absence, also noted in Table 4.1.

To assess overall morphological variation, we computed similarities from the data using the Gower coefficient (Gower 1971), converted to a distance measure as $\sqrt{1-\text{Gower coefficient}}$, as recommended by Legendre and Legendre (1998). We then applied Principal Co-ordinate Analysis (PCoA) to the distance matrix. We restricted our analysis to only the two most informative axes, and elected not to apply any correction methods to eliminate the negative eigenvalues (as discussed in Legendre and Legendre 1998). Axis loadings were calculated using multiple regression statistics (Oksanen et al. 2006, as described in section 3.3.2).

4.3.3 Amplified fragment length polymorphisms

Initially, all specimens included in the morphological survey of the *C. complanata* complex were included in the AFLP study. Due to amplification failures not all specimens yielded readily scored AFLP bands. In these cases other individuals from the same population were substituted. Following initial analysis, specimens from populations showing interesting patterns of genetic variation were added to the AFLP survey. A total of 186 specimens from the *C. complanata* complex were assayed for AFLP markers, with 161 individuals included in both datasets.

DNA was isolated from each sample using a modified CTAB extraction (Doyle and Doyle 1987). AFLP protocols followed Vos et al. (1995), with modifications described by Wolf et al. (2004) for the restriction, ligation, and preselective PCR

Character	Transformation
Culm height	\sqrt{x}
Maximum leaf width on fruiting culm	\sqrt{x}
Adaxial leaf surface pilose	±
Abaxial leaf surface pilose	±
Ligule length	\sqrt{x}
Distal leaf length	\sqrt{x}
Inflorescence length	ln
Spike number	None
Distal node length	\sqrt{x}
Node length between inflorescence and distal leaf	ln
Distal lateral bract length	ln
Terminal spike bract length	ln
Terminal spike bract awn	±
Length of pistillate portion of terminal spike	\sqrt{x}
Length of staminate portion of terminal spike	\sqrt{x}
Width of pistillate portion of terminal spike	ln
Length of proximal spike	\sqrt{x}
Width of proximal spike	ln
Perigynia ascending vs. spreading	±
Width of pistillate scale	None
Pistillate scale hair	±
Pistillate scale awn length	\sqrt{x}
Pistillate scale total length	\sqrt{x}
Perigynium length/scale length	ln
Perigynium length	None
Perigynium width	None
Perigynium length/perigynium width	None
Perigynium cross-section round vs. flattened	±
Perigynium apex rounded vs. beaked	±
Nutlet length	None
Nutlet width	None
Nutlet apiculus straight vs contorted	\pm
Anther length	ln

Table 4.1: Morphological characters and their normalizing transformations for the Carex complanata complex. \pm refers to binary coding (presence/absence)

steps, as described in section 3.3.3. We screened 24 primer pairs, selecting five that appeared to consistently produce clear, variable, and readily scored bands: Mse + CAA × EcoRI + AAG; Mse + CAC × EcoRI + AGC; Mse + CTA × EcoRI + ACT; Mse + CAA × EcoRI + ACG; and Mse + CAG × EcoRI + AAC. To assess the reliability of bands we replicated 34 samples 2-5 times each. The replicated samples included 12 samples from the *Carex complanata* complex, and 22 samples from the *Carex roanensis* complex (see Chapter 3). Bands that were inconsistent among replicates were excluded from analysis.

A distance matrix was calculated using $\sqrt{1 - \text{Jaccard coefficient}}$, as appropriate for AFLP data (see section 3.3.3). This matrix was subjected to PCoA to visualize the overall variation in the data. As the relationships among different subsets of taxa are not likely to be easily visualized on the same two axes, we repeated the PCoA on different subsets of the total data, as appropriate for each of our research objectives.

We analyzed the partitioning of variance among appropriate hierarchical structures using analysis of molecular variance (AMOVA: Excoffier et al. 1992). Groups identified with PCoA were subjected to AMOVA to ascertain whether they had any meaningful internal structure, either at the population level, or among geographic regions. We calculated the genetic distance among taxa using Nei's coefficient (Nei 1972), as suggested by Felsenstein (2004a) for use when both drift and mutation contribute to divergence. Diagnostic bands between pairs of taxa were tabulated using two criteria. First, we identified all bands that were present in all individuals of one taxon and absent in all individuals of the other as being 'absolutely diagnostic' for that taxon-pair. Second, the frequency of a band in each taxon was calculated, and bands with frequency differences between two taxa > 0.95 but < 1.00 were scored as 'nearly diagnostic'. All PCoA and univariate analyses were completed using the R Statistical Computing Environment (version 2.4.0, R Development Core Team 2006), with multivariate functions provided in the **vegan** package (version 1.8-2, Oksanen et al. 2006). AMOVA analysis was completed using Arlequin (Excoffier et al. 2005). Genetic distances were calculated using PHYLIP (Felsenstein 2004b).

4.3.4 Hybrids

We used three lines of evidence to investigate putative hybrid individuals. The first line of evidence, used in the field to identify possible hybrids, was morphology. Traditionally, hybrid origin has been invoked to explain the occurrence of individuals morphologically intermediate between two well defined species (Cayouette and Catling 1992), particularly when the putative hybrid is found growing with the suspected parents.

The second line of evidence was the AFLP data. AFLP fingerprints have been used in a number of plant groups to confirm the existence of hybrids (Gobert et al. 2002; Teo et al. 2002). The presence of diagnostic AFLP fragments from both suspected parents has been taken as evidence of hybrid origin, as has intermediate placement in ordination plots.

As a third line of evidence, we developed restriction fragment markers that uniquely identified the genomes of the species in this study. Using previously collected sequence data (Waterway 2006) we screened commercially available restriction enzymes for taxon-specific banding patterns for the taxa in this group. We used ITS and ETS nuclear gene regions and the rpL16 chloroplast regions, with DdeI, BstUI, and TseI enzymes from New England Biolabs. We used the supplied restriction buffers, diluted to 1x, with 3 units of enzyme and 15μ l of template DNA. Restriction reactions were incubated at the suggested temperature (37° C, 60° C or 65° C) for ca. 140 minutes before being visualized on a 2% agarose gel.

4.3.5 Herbarium Records

More than 2300 herbarium specimens from the following herbaria were examined for this project: B, BM, CAN, cb, CLEMS, EKY, GA, GH, K, KANU, MARY, MICH, MO, MSC, MTMG, NCU, NEB, NY, NYS, OKL, TAES, TAMU, TAWES, USCH, VPI, WV (herbarium acronyms follow Holmgren and Holmgren 1990, except cb, the personal herbarium of Charles Bryson, Southern Weed Science Research Unit, U.S. Department of Agriculture, Stoneville Mississippi). County-level distribution maps were prepared using only the specimens we examined. Any discrepancies with the NatureServe (NatureServe 2006) database were reported to the appropriate Conservation Data Centers.

4.4 Results

4.4.1 Overall

After excluding inconsistent fragments, the AFLP assays produced 134 scorable bands (39, 28, 26, 23, and 18 bands per primer pair). Three bands were each present in only a single individual, and four were fixed in all individuals. Every individual had a unique AFLP fingerprint. In all cases the AFLP analysis provided more definitive results than the morphological data. Several specimens that were morphologically ambiguous were unequivocally assigned to genetic groups and these assignments were used in the detailed analysis of morphological characters and in the related figures.

4.4.2 Carex complanata and C. hirsutella

The morphological PCoA for these taxa shows clear separation, although only 28% of the total variation is captured on the first two axes (Figure 4.1A). Our analysis demonstrates that the distinction between *C. complanata* and *C. hirsutella* is due almost entirely to the leaf vestiture characters: while the taxa are clearly separated in plots based on the full dataset (Figure 4.1A), removing the leaf hair characters obscures the distinction as each taxon grades into the other (Figure 4.2). *Carex*

complanata and C. hirsutella display statistically significant differences in several quantitative characters (t-tests, all p < 0.01). However, these characters overlap extensively, as shown in Figure 4.3.

We collected unusually hairy plants from the Texas and South Carolina populations of C. complanata. Two of the Texas plants were pilose on the adaxial leaf surface, as in C. hirsutella, but glabrous on the abaxial leaf surface, as in typical C. complanata. The adaxial leaf surfaces of some of the South Carolina plants were short-hirsute to almost scabrous, contrasting with the pilose leaves of C. hirsutella and the near-glabrous leaves of typical C. complanata. We scored these individuals as lacking pilose adaxial leaf surfaces for the morphological analysis. We observed these shorter, almost scabrous hairs on a number of herbarium specimens from South Carolina. However, most plants in both the Texas and South Carolina populations were the typically glabrous C. complanata, and we found no differences in the AFLP data to confirm a genetic basis for this variation (see below). All plants from these populations were coded as C. complanata in the PCoA plots, based on the results of the AFLP analysis (below).

In marked contrast to their morphological ambiguity, C. complanata and C.hirsutella are clearly separated by AFLP markers (Figure 4.1B). Of the 134 AFLP bands scored, 10 are fixed in all individuals of these two taxa, and three are universally absent, leaving 125 polymorphic fragments. There were five nearly diagnostic bands distinguishing between C. complanata and C. hirsutella, and two absolutely diagnostic bands (Table 4.2). The problematic specimens from Texas and South Carolina are placed unambiguously within the C. complanata data cloud.

4.4.3 Carex complanata, C. hirsutella, C. bushii and C. caroliniana

PCoA analysis was effective for this group, with 37% of the morphological variation presented on two axes (Figure 4.1C). *Carex bushii* is clearly separated from



Figure 4.1: Principal co-ordinates analysis (PCoA) of the *Carex complanata* complex. A. and C. Morphological distance ($\sqrt{1-\text{Gower coefficient}}$) calculated from 33 variables, including leaf vestiture characters. B. and D. Genetic distance ($\sqrt{1-\text{Jaccard coefficient}}$) calculated from 134 AFLP fragments. The axes are plotted with equal scales, preserving the geometric distances among points.



Figure 4.2: Principal co-ordinates analysis (PCoA) of the morphological distance $(\sqrt{1 - \text{Gower coefficient}})$ calculated from 31 variables, excluding leaf vestiture characters, for *Carex complanata* and *C. hirsutella*. The axes are plotted with equal scales, preserving the geometric distances among points.

Table 4.2: Summary of shared AFLP bands and genetic distances. Values in the lower triangle of the matrix are the number of diagnostic bands for the taxon in the row, distinguishing it from the taxon in the column, i.e., bands that are present in all specimens of one taxon and absent from all specimens of the other. Numbers in parentheses are the number of nearly diagnostic bands, i.e., bands with a frequency difference > 0.95 but < 1.00 between the two taxa. Values in the upper triangle are the pair-wise genetic distances (Nei 1972) between species calculated from band frequencies.

Taxa	C. bushii	C. caroliniana	C. complanata	C. hirsutella
C. bushii		0.083	0.158	0.112
$C.\ caroliniana$	2(0)		0.231	0.127
$C.\ complanata$	3(1)	6(3)		0.193
C. hirsutella	1(1)	1(2)	2(5)	



Figure 4.3: Key morphological characters distinguishing among *Carex bushii*, *C. complanata*, *C. caroliniana* and *C. hirsutella*. All measurements reported in mm. In panel B: four outlying specimens of *C. bushii* with terminal spikes 8.0, 8.0, 8.3, and 8.7 mm wide are not plotted. In panel C: three outlying specimens of *C. bushii* with ligules 8.7, 9.7, and 12.7 mm long are not plotted.

all other taxa. *C. caroliniana* also forms a discrete cluster, although some outlying specimens are placed at the edge of the *C. complanata* cloud. The highest loadings for quantitative characters on the first axis are perigynium width (-0.51) and pistillate scale length (-0.39). The highest loadings on the second axis are pistillate scale length (0.47), pistillate scale awn length (0.40) and leaf width (0.39). The quantitative characters that provide the most consistent pair-wise discrimination are shown in Figure 4.3.

Several qualitative characters contribute to the plot. All specimens of C. bushii and C. caroliniana had perigynia with a rounded, somewhat inflated cross-section. In contrast, all of the C. hirsutella and C. complanata specimens had a flattened profile, although this distinction is not always clear, even on fresh material. Leaf vestiture was also variable among taxa. Carex hirsutella was always pilose on both surfaces, while 95% of C. bushii specimens were pilose on the abaxial surface, and 34% on the adaxial surface. This contrasts markedly with *Carex caroliniana*, which was always glabrous adaxially, and only 3% of specimens were pilose on the abaxial surface. 18% of *C. complanata* specimens were pilose abaxially. The pistillate scales of 73% of *C. bushii* specimens had long hairs on the back and margins, a condition observed in less than 3% of individuals of the other taxa. A suite of characters were present in most *C. bushii* and *C. caroliniana* specimens and absent in most *C. complanata* and *C. hirsutella*: perigynia spreading (rather than ascending), nutlet apiculus strongly contorted, and perigynium apex with a short, somewhat indistinct beak (rather than rounded).

The demarcation between C. caroliniana and C. complanata in Figure 4.1C appears somewhat uncertain, due to several outlying specimens of C. caroliniana. However, the figure is dominated by the difference between C. bushii and the other three taxa. Repeating the analysis after excluding C. bushii reveals unambiguous separation of C. caroliniana and C. complanata (data not shown).

Despite the difficulty in placing some specimens morphologically, AFLP markers reveal a clear and consistent genetic distinction among all four taxa in the C. complanata complex (Figure 4.1D). In pairwise comparisons there are between two and nine nearly diagnostic bands between taxa (Table 4.2). The PCoA plot of C. complanata, C. hirsutella, C. caroliniana, and C. bushii is dominated by the variation between C. hirsutella and C. complanata, obscuring the difference between C. caroliniana and C. bushii (Figure 4.1D). Repeating the analysis after removing C. complanata reveals clear separation of the remaining three taxa (Figure 4.4). There is markedly more variation among Carex hirsutella specimens than among any of the other taxa. Most of this variation can be attributed to specimens collected at the two Pennsylvania locations, as shown in Figure 4.4. This variation also includes several putative hybrid individuals, as discussed below.



Figure 4.4: Principal co-ordinates analysis (PCoA) of the genetic distance $(\sqrt{1-\text{Jaccard coefficient}})$ calculated from 134 AFLP fragments for *Carex bushii*, *C. caroliniana*, *C. hirsutella* and putative hybrids. '*hirsutella PA*' indicates individuals from the two Pennsylvania populations of *C. hirsutella*; 'Hybrid 1' indicates putative *C. hirsutella* × *C. caroliniana* hybrids; 'Hybrid 2' indicates putative *C. bushii* hybrids. The axes are plotted with equal scales, preserving the geometric distance among points.

4.4.4 Carex complanata ssp. tropicalis

PCoA analysis of morphological variation within *Carex complanata* is shown in Figure 4.5A, and the key characters used to distinguish *C. complanata* ssp. *tropicalis* from *C. complanata* s. s. are plotted in Figure 4.5B. None of the other morphological characters provided better discrimination between the two subspecies. Both plots indicate that, while extreme, ssp. *tropicalis* lies almost entirely within the range of morphological variation exhibited by *C. complanata* s. s.

4.4.5 Population structure

The variation among populations within each taxon is shown in Table 4.3. In all cases, most of the variation is among individuals, rather than populations. However, there is significant population structure (p < 0.001) in all taxa. The source of the



Figure 4.5: Morphological differences between *Carex complanata* s. s. and *C. complanata* ssp. *tropicalis*. A. PCoA of morphological distance ($\sqrt{1 - \text{Gower coefficient}}$) calculated from 33 variables. B. Scatter-plot of key characters.

population structure is most evident for *C. hirsutella* and *C. caroliniana*. PCoA analysis of the *C. hirsutella* specimens (Figure 4.4) shows clear, but not complete, separation of the specimens from the two Pennsylvania populations from the rest of the samples. AMOVA analysis confirms this distinction: when we repeated the AMOVA for *C. hirsutella* with the Pennsylvania populations in a separate group from the rest of the samples, 34.52% of the variance was explained by this regional difference, while variance among populations within regions was reduced to 5.31% (Table 4.4). However, within *C. hirsutella* 16 bands are fixed, and 17 are absent, leaving 101 polymorphic markers, and there are no diagnostic or nearly diagnostic bands distinguishing the Pennsylvania populations from the rest of the taxon. The only morphological character that reflected this division was the length of the pistillate scale awns. The Pennsylvania specimens had awns 0–0.27 mm (mean = 0.09 mm, sd = 0.11), which placed them in the lowest third of all *C. hirsutella* specimens (total range was 0–0.93 mm, mean = 0.31 mm, sd = 0.17).

Table 4.3: Analysis of molecular variance (AMOVA). Variation was partitioned among individuals nested within populations for each taxon. Abbreviations are as follows: SV, source of variation; df, degrees of freedom; SSD, sum of squares; VC, variance-component estimates and %TV, percentage of total variance. All cases: p < 0.001, based on 20000 permutations.

Taxon	SV	df	SSD	VC	% TV
All species	species	3	1141.48	8.30	47.81
	populations	47	696.312	2.19	12.63
	individuals	135	927.58	6.87	39.57
C. bushii	populations	9	165.99	3.10	30.64
	individuals	27	189.42	7.02	69.36
C. caroliniana	populations	7	104.17	2.94	36.99
	individuals	19	95.23	5.01	63.01
C. complanata	populations	13	138.36	1.34	17.29
	individuals	31	198.00	6.39	82.71
C. hirsutella	populations	18	287.79	2.07	21.28
	individuals	58	444.93	7.67	78.72

Table 4.4: Analysis of molecular variance (AMOVA) performed with different geographic groupings. Abbreviations are as follows: SV, source of variation; df, degrees of freedom; VC, variance component estimates; %TV, percentage of total variance. All cases: p < 0.001 based on 20000 permutations. Regions are listed by state: AL: Alabama, IL: Illinois, MS: Mississippi, NC: North Carolina (two populations), TX: Texas.

Taxon	Region	SV	df	VC	%TV
C. hirsutella	Pennsylvania +	regions	1	4.40	34.52
	Non-Pennsylvania	populations	17	0.67	5.31
		individuals	58	7.67	60.17
$C.\ caroliniana$	(TX + LA + MS) +	regions	1	2.74	29.85
	(AL + SC + NC + IL)	populations	6	1.42	15.51
		individuals	19	5.01	54.65



Figure 4.6: Population structure in *Carex caroliniana*. A. Principal co-ordinates analysis (PCoA) of the genetic distance ($\sqrt{1 - \text{Jaccard coefficient}}$) calculated from 134 AFLP fragments. The axes are plotted with equal scales, preserving the geometric distance among points. B. Key morphological characters distinguishing southwestern populations. Southwest populations include Texas, Louisiana, and Mississippi; Northeast populations include Alabama, South Carolina, North Carolina, Illinois and Tennessee.

Carex caroliniana also showed geographically-oriented population structure. The three populations from the southwest extent of our sampling (Texas, Louisiana and Mississippi) form a distinct cloud in PCoA analysis (Figure 4.6A). This division is confirmed by the AMOVA analysis (Table 4.4). After isolating these three populations, the groupings explained 29.85% of the variance, and the variance among populations within groups fell to 15.51%. Within *Carex caroliniana* 42 bands are fixed, and 34 are absent, leaving only 58 polymorphic bands, and none of these bands are nearly or absolutely diagnostic. Morphologically, these two groups differ subtly in nutlet size, as shown in Figure 4.6B. The differences in the length and width of nutlets between the northeastern and southwestern populations are significant (p < 0.001%, t tests, df = 35). The difference in mean length is 0.15 mm, while the difference in mean width is 0.12 mm.

Although they have significant population structure (p < 0.001), we found no geographic basis for this variation in *C. bushii* or *C. complanata*.

4.4.6 Hybrids

We found suspected hybrids involving Carex complanata, C. hirsutella, C. caroliniana, C. bushii, C. swanii and C. oxylepis as possible parental-species. However, there was not enough sequence variation to distinguish among all possible combinations using restriction fragments. Restricting the ETS sequence with BstUI revealed a unique banding pattern for C. complanata (Figure 4.7, lanes N and S). Only C. *complanata* produced the 194 bp fragment (fragment 2), and the 133 bp fragment was present in all species except C. complanata. We anticipated this same restriction would allow for identification of the genomes of C. bushii and C. caroliniana. which produce a 23 bp fragment not present in any other species (fragment 7). However, we were unable to consistently visualize these small fragments on agarose gel (compare lanes D, L, O, and P, all of which are expected to display fragment 7) so we are less confident in the interpretation of this marker. Similarly, restricting the ITS sequence with *TseI* reveals a 548 bp fragment shared only by *C. swanii* and *C.* oxylepis. Carex oxylepis also produced some smaller fragments, but they were small and inconsistently visualized. Restricting the rpL16 intron (cpDNA) with DdeI produced a unique 354 bp fragment for C. swanii, which in all other taxa is replaced by two bands 180 bp and 200 bp long.

$Carex \ complanata \ imes \ oxylep is$

We collected a single specimen putatively identified as *Carex complanata* \times *oxylepis* in Greenwood County, SC. Morphologically, it appears intermediate to the two suspected parents. The inflorescence is 48 mm long, with lateral spikelets 14–22 mm long, within the range reported for *Carex oxylepis* but longer than *Carex complanata* (reported below). The perigynia have the distinct short beak of *C. oxylepis*,



Figure 4.7: Restriction fragments produced from a digestion of the ETS gene region with the BstUI enzyme. Lanes: A. C. complanata \times C. oxylepis hybrid; B. C. complanata \times C. caroliniana hybrid; C. C. caroliniana \times C. hirsutella hybrid; D. C. caroliniana; E. C. hirsutella; F. C. swanii; G. C. caroliniana \times C. hirsutella hybrid; H. C. bushii \times C. hirsutella hybrid; I. C. bushii \times C. hirsutella hybrid; J. C. bushii \times C. hirsutella hybrid; K. C. bushii \times C. hirsutella hybrid; J. C. oxylepis; N. C. complanata; O. C. bushii \times C. hirsutella hybrid; L. C. bushii; M. C. oxylepis; R. C. swanii \times C. complanata hybrid; S. C. complanata. Fragments: 1. 248 bp; 2. 194 bp; 3. 154 bp; 4. 133 bp; 5. 61 bp; 6. 38 bp; 7. 23 bp.

but are the length of typical *C. complanata* perigynia (3 mm) (*C. oxylepis* is reported as 3.5–5 mm, Waterway 2002). The nutlets were undeveloped, and the anthers on this specimen were apparently sterile, as they had not dehisced and remained hidden behind the staminate scales. The plant was growing in a roadside ditch surrounded by a population of *C. complanata* (SCGRCo) and within a few metres of a population of *C. oxylepis* growing in an adjacent wooded floodplain (SCGROx).

In a PCoA plot of the AFLP data for C. complanata, C. oxylepis and the single hybrid, the hybrid was placed intermediate between the two taxa (Figure 4.8A) There are nine nearly or absolutely diagnostic bands distinguishing between C. complanata and C. oxylepis. All nine of these bands are present in the putative hybrid.

The ETS restriction with *BstUI* reveals the presence of the 194 bp *C. complanata* band in this hybrid, as well as the 133 bp non-*C. complanata* band (lane A, fragments



Figure 4.8: Principal co-ordinates analysis (PCoA) of the genetic distance $(\sqrt{1 - \text{Jaccard coefficient}})$ among putative hybrids and suspected parental species, calculated from AFLP fragments. The axes are plotted with equal scales, preserving the geometric distance among points. A. Carex complanata × oxylepis, B. Carex swanii × C. complanata, C. Carex bushii × swanii, D. Carex caroliniana × complanata.

2 and 4). The *TseI* restriction of the ITS gene region produces the 548 bp fragment found only in *C. swanii* and *C. oxylepis*, but *C. swanii* does not occur within 100 km of this location.

$Carex \; swanii \; imes \; complanata$

Another putative hybrid was collected from the Greers Lake vicinity (Van Buren Co., Arkansas), where populations of *C. complanata*, *C. hirsutella*, and *C. bushii* were collected (ARVBCo, ARVBHi, ARVBBu). Additionally, *Carex swanii* is infrequent in the area. The putative hybrid had very sparsely hirsute perigynia, with sparsely pilose sheaths and abaxial leaf surfaces; the adaxial leaf surface was mostly glabrous. The nutlets were undeveloped, but the anthers were partly exserted and dehiscing at the time of collection.

In PCoA plots of AFLP data (Figure 4.8B), this hybrid was placed intermediate between *Carex swanii* and *C. complanata*. Twelve of 14 nearly or absolutely diagnostic bands distinguishing between *C. complanata* and *C. swanii* were present in the hybrid. The ITS restriction with *TseI* revealed the 548 bp fragment shared by *C. oxylepis* and *C. swanii*, while the ETS restriction with *BstUI* produced the unique 194 bp fragment from *C. complanata*. A restriction digest of the chloroplast gene region rpL16 with the *DdeI* enzyme revealed the unique two-band pattern that characterizes *C. swanii*. *Carex oxylepis* was not found in the Greers Lake vicinity, although it is within the range of that species.

$Carex \ bushii \ imes \ swanii$

We discovered another putative hybrid at the Brandywine Creek State Park location (New Castle Co., Delaware) where we collected population samples of *C. bushii* and *C. hirsutella. Carex swanii* was also present at this location, although in very low numbers. The hybrid had apparently low fertility, with closed anthers remaining behind the staminate scales, and only a single mature nutlet. The perigynia were sparsely public public the pistillate scales had awns 0.5 mm long, which projected beyond the perigynia, and both the pistillate and staminate scales were somewhat rust-coloured. The perigynia themselves had an acute apex which in some cases resembled an indistinct beak. The one mature nutlet had a contorted apiculus.

In PCoA plots of AFLP data, this hybrid was placed approximately half-way between *C. bushii* and *C. swanii* (Figure 4.8C). Four of six nearly diagnostic bands between these two species were present in the hybrid. The ITS restriction with *TseI* revealed the 548 bp fragment shared by *C. oxylepis* and *C. swanii* was present in this hybrid. The *rpL16* digestion with *DdeI* produced the non-*C. swanii* three-band pattern for this hybrid.

$Carex\ caroliniana\ imes\ complanata$

This hybrid was collected at the same location as the putative *Carex complanata* \times *oxylepis* cross described above. The actual collection was made several hundred metres away in a roadside ditch where both *C. complanata* and *C. caroliniana* were growing together. The specimen was partially sterile, with only a few mature nutlets and unexserted, closed anthers. The perigynia resembled *C. caroliniana*, with a round cross-section and an acute, almost beaked apex, and the nutlets had a contorted apiculus. The pistillate scales had awns 0.5 mm long, more typical of *C. complanata*.

PCoA analysis of AFLP data for this hybrid was limited to four primer pairs, as the fifth primer pair failed to amplify for this individual. In the ordination the hybrid is placed intermediate between *C. complanata* and *C. caroliniana* (Figure 4.8D). Of the 98 bands scored, six are nearly or absolutely diagnostic between *C. caroliniana* and *C. complanata*. Four of these bands are present in the hybrid. The ETS restriction with *BstUI* shows the presence of the *C. complanata* 194 bp fragment in the hybrid, as well as the 133 fragment that is present in all taxa except C. complanata.

$Carex\ caroliniana\ imes\ hir sutella$

We collected three possible hybrids at the location of the Glenn Road, Durham Co., NC population of *Carex caroliniana* (NCDU1Ca). *Carex hirsutella* was present in low numbers within a few hundred metres of this location. The hybrids were pilose on the leaf sheaths, but had mostly glabrous leaves. The perigynia were rounded in cross-section, with an acute apex. The nutlets had not matured, although the anthers had dehisced and many had already separated from the stamen filament. Both putative parents had mature achenes at the time these hybrids were collected.

In the PCoA plots of AFLP data, these three hybrids are placed within the range of variation observed for C. hirsutella (Figure 4.4). Of the three absolutely or nearly diagnostic bands between these two species, all three are present in one hybrid, while the other two individuals display two out of three of these bands. We found no restriction fragment pattern that reliably distinguished between the C. hirsutella and C. caroliniana genome.

$Carex \ bushii \ imes \ hir sutella$

We identified possible *Carex bushii* \times *hirsutella* hybrids at several locations: Canaan Valley, Tucker Co., WV (three individuals), Calico Rock, Izard Co., AR, and Iron Springs Recreation Area, Garland Co., AR. We sampled populations of *C. bushii* from each of these locations, *Carex hirsutella* from both Canaan Valley and Garland Co., and *C. complanata* at the Garland Co. location. *Carex hirsutella* was also present at Calico Rock, but in low numbers. These hybrids were densely hirsute on both leaf surfaces and the leaf sheaths. Perigynium shape varied from rounded to flattened in cross-section. Both the pistillate and staminate scales were strongly reddened and very sparsely pilose, as in typical *C. bushii*, but in dimension were intermediate between *C. bushii* and *C. hirsutella*, with lengths between 2.7 and 3.4 mm. Phenologically, they differed from both putative parents, retaining green perigynia at a time when the spikelets of both potential parents were mature and shattering.

We had limited success extracting and amplifying DNA from these plants. Only the three individuals from Canaan Valley produced readily scored AFLP fragments, and in the PCoA plot of these data they are placed at the periphery of the C. *hirsutella* cloud (Figure 4.4). Of the two diagnostic bands, one was present in two of the putative hybrids, while the second was absent from all three. We found no diagnostic restriction fragment patterns that could distinguish between the C. *hirsutella* and C. *bushii* genomes.

4.4.7 Geographic distribution

Carex bushii has the western-most distribution of the taxa in this complex (Figure 4.9A). It is most common in Central Plains ecoregions of eastern Kansas, Oklahoma and Texas (ecoregion names follow the Commission for Environmental Cooperation (1997)) where it is commonly a dominant component of prairie habitats. It becomes more infrequent eastward, and is often associated with disturbed habitats. The single Michigan record is almost certainly an introduction (A. A. Reznicek, Univ. of Michigan, pers. comm.; Menapace and Wujek 1987). The same is true of the single South Carolina record, which was collected from a roadside ditch in otherwise unsuitable habitat. It reaches its northeastern limit in the Great Lakes/Hudson Lowlands of New York, with one record from the Northern Coastal Zone of Massachusetts. In the Southeast it extends into the Piedmont and Southeastern Coastal Plain regions. However, it is documented by fewer than five records in each of Alabama, Georgia, South Carolina and North Carolina. We did not see any vouchers for Maine and Florida, and the natural heritage programs for those states had no



Figure 4.9: Geographic distribution, based on examined herbarium specimens. A. *Carex bushii*, B. *C. caroliniana*, C. *C. complanata*, D. *C. hirsutella*.

documented records, although it has been reported (NatureServe 2006). Among the other species of the *C. complanata* complex, *Carex bushii* most frequently co-occurs with *C. hirsutella*.

Carex caroliniana occurs across much of the same area as C. bushii, but is more evenly distributed. It is well documented in the Central and Southeastern Plains of Texas, Arkansas, Louisiana and Mississippi, with populations as far west as the Irregular Central Plains of Kansas and the Cross Timbers region of Oklahoma. It is frequent in the Piedmont, extending to the Atlantic Coastal Plain in South Carolina. In the north, it is uncommon in Pennsylvania, and is known only from historic records in the North Central Appalachian region of southwestern New York. It is generally absent from the higher elevations in the Appalachians (Figure 4.9B). *Carex caroliniana* may co-occur with any of the other species in the *C. complanata* complex, usually in wet-mesic prairies and old fields. It also grows in wetter habitats, including wet meadows and floodplain forests.

Carex complanata has the most southerly distribution of this group, with disjunct populations in Chiapas, Mexico and Alta Verapaz, Guatemala (the so-called *C. complanata* ssp. *tropicalis*, Reznicek and González-Elizondo 2001) in addition to the area shown in Figure 4.9C. It is primarily restricted to the Coastal Plains and Piedmont regions from Texas to Delaware, but occurs sporadically in the Ozark Mountains and Arkansas Valley in Oklahoma and Arkansas, and north into the Interior and Western Allegheny Plateau regions of Kentucky. All specimens labelled as *C. complanata* that we saw from Missouri and West Virginia were actually *C. hirsutella. Carex complanata* is usually found in dry to wet-mesic open prairies and meadows. However, it is rarely found in damp forests, particularly in northern Arkansas where it co-occurs with *C. swanii* in wooded sinks.

Carex hirsutella grows across the northeastern United States, from the Flint Hills and Ouachita Mountains to the Piedmont and Atlantic Coastal Plain, north to the St. Lawrence and Lake Erie Lowlands and Southern Michigan Drift Plains. It has been reported from Texas and Louisiana (NatureServe 2006), but all specimens we examined from these states were actually *C. complanata*. The only record for Nebraska is probably an introduction.

4.5 Discussion

Our results strongly support the recognition of *Carex complanata* and *C. hir-sutella* as two distinct species. The only consistent morphological character distinguishing between them is the presence and extent of leaf pubescence. In some *Carex* species this character is quite variable, an observation that lead some caricologists

to lump these taxa within a single species (Bailey 1889a; Mackenzie 1910; Wofford 1989; Gleason and Cronquist 1991). However, the AFLP data presented here (Figure 4.1B) confirm that this one morphological character reflects a real genetic distinction between the two taxa. This conclusion is further supported by the observation that this distinction holds even when both taxa are growing intermixed. In most cases the presence of hairs on the adaxial leaf surface will suffice in identifying which species is in hand. However, the nature of the hair is also an important character, as some individuals of *Carex complanata* may have stiff, almost scabrous hairs on the adaxial leaf surface, contrasting with the longer pilose hairs of typical *Carex hirsutella*, particularly in collections from South Carolina.

Carex bushii is clearly distinct morphologically from the other taxa in the Carex complanata complex (Figure 4.1C). A number of quantitative characters provide fairly reliable discrimination. The most consistent is pistillate scale length (including awn). As shown in Figure 4.3A, C. bushii is cleanly separated from C. caroliniana for this character. Only two specimens of C. hirsutella had scales 3 mm long, and no C. bushii specimens had scales less than 3 mm. Carex complanata overlaps slightly more, with four specimens having scales longer than 3.3 mm, whereas C. bushii has five specimens less than 3.3 mm. A similar pattern can be seen for perigynium length and terminal spike width (Figure 4.3 B and D), with the greatest character overlap between C. complanata and C. bushii.

Ball (2002) described *C. bushii* as having papillose or pubescent perigynia, but this was incorrect (P. W. Ball pers. comm.). The only specimens we found with hairy perigynia were sterile hybrids, as discussed below. However, there are a number of other qualitative characters that help distinguish it from the other taxa. The crosssectional shape of the perigynium is used in most keys to distinguish *C. bushii* and *C. caroliniana*, which are round, from the more flattened shape of *C. hirsutella* and *C. complanata*. While very reliable, this character can be difficult to interpret, especially on herbarium specimens. The perigynia are often somewhat distorted when pressed. Furthermore, the ventral face of the perigynium is often distended around the upper nutlet edge in *C. complanata* and *C. hirsutella*, rounding out their otherwise flat cross-section. The shape of the perigynia on immature specimens is particularly difficult to ascertain, and identification is often not possible before the fruit has ripened. *Carex bushii* is also notable in having sparse pilose hairs on the midrib and abaxial surface of the pistillate and staminate scales of most individuals, a condition that occurred only rarely in the other taxa.

While *Carex caroliniana* is less clearly marked than *C. bushii* morphologically, field identification is facilitated by its phenology. This taxon flowers and fruits as much as two weeks earlier than the other taxa in the complex. However, this characteristic is less useful in herbarium study, and immature specimens remain difficult to place. When perigynium shape is ambiguous, the shorter scales of *C. caroliniana* help distinguish it from *C. complanata* and *C. bushii* (4.3A), while its glabrous leaves differentiate it from *C. hirsutella*.

The division of *Carex complanata* into two subspecies is based on very subtle morphological differences (Figure 4.5). Applying the key characters used by Reznicek and González-Elizondo (2001) to our data, 24 of 57 *Carex complanata* specimens from the U.S.A. would be determined as ssp. *tropicalis*. This contrasts markedly with the results reported by Reznicek and González-Elizondo (2001), who found almost complete separation of the two putative subspecies based on these characters. The discrepancy may be due to differences in sampling. We used multiple randomly selected individuals from 14 populations from across the range of *C. complanata*, resulting in a more representative sample of the variation present within the species. Reznicek and González-Elizondo (2001) did not report the specimens used to represent *C. complanata* s. s. in their study, so we assume they were based on herbarium collections, which are not generally collected in a systematic way. Given the much larger morphological overlap than originally reported, we conclude that there is not yet enough evidence to recognize *Carex complanata* ssp. *tropicalis* as a distinct subspecies.

The AMOVA results show significant among-population variation for all four species in this study (Table 4.3). This is not unexpected, as the limited dispersal ability of *Carex* and the patchy distribution of suitable habitat should result in much greater inbreeding within local populations than migration among them. The inflorescences of all the taxa in this group are very compact, and the flowering time of male and female flowers overlaps. As a consequence, dehiscing anthers and receptive stigmas are often very close or even touching, suggesting that self-pollination may be common. Indeed, in other *Carex* groups selfing has been shown to produce a higher proportion of viable seeds than outcrossing (Whitkus 1988).

The absence of geographic structure in *Carex complanata* may be attributable to its relatively even distribution across the southeastern U.S.A., primarily south of the Appalachian Mountains (Figure 4.9C). This is an area of limited topographic heterogeneity, with relatively few barriers to occasional long-distance dispersal events that could effectively scramble any geographic structure that may develop. In contrast, *Carex caroliniana* has a patchier distribution across the interior plateaus and along the lower elevations on the east and west slopes of the Appalachians. The complex topography of this region provides many potential boundaries to gene flow. In particular, the paucity of collections from much of Alabama and Tennessee could reflect an absence of suitable habitat. This may in turn create a real barrier to gene flow between populations from Texas, Louisiana, and Mississippi and the rest of the range of the species, as suggested by our data (Table 4.4). More sampling, particularly from the western and northern extent of its range in Arkansas, Kentucky and West Virginia, will be necessary before drawing firm conclusions as to the phylogeographic implications of these patterns. Similarly, more information is needed before we can determine whether the genetic and morphological divergence that distinguishes between our southwestern and northeastern samples reflects taxonomically meaningful variation.

We did not detect any geographic population structure in *Carex bushii*. However, this species is most common and abundant in Kansas and Oklahoma (Figure 4.9A), areas that we did not sample. Indeed, much of our sampling is from areas where C. *bushii* is in fact infrequent or rare. As such, our data may not reflect the full range of variation in this species. Our sampling strategy was appropriate for examining the relationship between C. *bushii* and its close relatives, but is inadequate for detailed analysis of intra-specific variation.

The divergence between the Pennsylvania populations of *Carex hirsutella* and the rest of that species is quite interesting (Figure 4.4). They could reflect geographic population structuring, similar to that we found for *C. caroliniana*. As these are the northern-most populations of this species that we sampled, more data from populations in New York, Ontario, and Michigan would be helpful in confirming this hypothesis. Another possible explanation is suggested by the placement of suspected hybrids in the PCoA ordination (Figure 4.4). While identity of these possible hybrids is uncertain, we suspect points labelled as 'Hybrid 1' are *C. caroliniana* × *hirsutella*, and those labelled 'Hybrid 2' are *C. bushii* × *hirsutella*. The fact that these putative hybrids are plotted within the cloud of *C. hirsutella* points suggests that the divergence of the Pennsylvania populations may be the result of introgression involving one or more other taxa. It is important to note that morphologically, the Pennsylvania C. hirsutella populations were unremarkable, differing from typical C. hirsutella only in very slight differences in the pistillate scales. Thus, it is unlikely that they represent F1 hybrids, but rather could be the result of stabilized back-crosses between hybrids and pure C. hirsutella.

As mentioned above, *Carex hirsutella* is implicated in two possible hybrid taxa. While we could not confirm this conclusively, two lines of evidence support our hypothesis. First, the morphology of the putative hybrids was intermediate to that of their suspected parents. In the case of *C. caroliniana* \times *hirsutella*, the aberrant individuals had the rounded perigynia and glabrous leaves of *C. caroliniana*. At the same time, they were phenologically closer to *C. hirsutella*, with a few anthers remaining at a time when *C. caroliniana* flowers had all been shed and the ripe spikelets were beginning to shatter. Unlike neighbouring plants of both parents, the hybrids had not produced any mature nutlets. The second line of evidence is the AFLP data, which places them on the periphery of the *C. hirsutella* point cloud (Figure 4.4).

In the case of the suspected *C. bushii* × *hirsutella* hybrids, we again draw on a combination of morphology and AFLP data to support our hypothesis. The sparsely pilose floral scales suggest *C. bushii*, while the perigynium shape and pistillate scale length was intermediate between *C. hirsutella* and *C. bushii*. As above, the AFLP data place them on the periphery of the *C. hirsutella* point cloud. We cannot conclusively exclude the possibility that all six of these individuals are environmentally-induced aberrant forms of *C. hirsutella*; further data will be needed to confirm the identity of these individuals. However, with the data in hand the most likely explanation is that they are indeed hybrids. We have considerably stronger evidence to document the parentage of the other hybrids we discovered. For *Carex complanata*

 \times oxylepis and *C. swanii* \times complanata the combination of intermediate morphology, intermediate AFLP placement, and the presence of restriction fragment markers unique to both parent species provide solid, if not undeniable, evidence. In the case of *C. swanii* \times complanata, the presence of restriction fragments diagnostic for the *C. swanii* chloroplast genome in the putative hybrid indicate that *C. swanii* was the female parent. The data for *C. bushii* \times *swanii* is somewhat weaker, as we could not find a restriction fragment marker that would confirm the presence of the *C. bushii* presence of the *C. swanii* nuclear genome in the hybrid. However, we can confirm the presence of the *C. swanii* nuclear genome and a non-*C. swanii* chloroplast genome. This, combined with morphological and AFLP data showing intermediate position of the hybrid between *C. swanii* and *C. bushii*, suggests very strongly that this individual is a hybrid of those two species.

Cytological information, often helpful in evaluating potential hybrids (Cayouette and Catling 1992), is lacking in this group. We were unable to obtain chromosome counts from field collections transferred to the greenhouse, and published counts are available only for *C. swanii* (2n = 54), *C. hirsutella* (2n = 52) and *C. bushii* (2n =48) (Wahl 1940). The varying chromosome numbers suggest that any hybrids among these three taxa would suffer limited fertility. However, this problem may be less pronounced in *Carex* than in other taxa. Whitkus (1988) conducted experimental crosses among intra-specific chromosome races as well as among closely related *Carex* species, and concluded "that changes in chromosome number have little to no effect on compatibility among closely related species".

Carex swanii has previously been reported to hybridize with *C. arctata* Boott (Mackenzie 1913), *C. debilis* Michx. var. *rudgei* L. Bailey (Mackenzie 1913; Fernald 1950), and *C. gracillima* Schwein. (Ferguson 1924). While these reports did not include descriptions of the hybrids themselves, it is unlikely that they are references

to the hybrids newly described here. Carex swanii, C. complanata, C. bushii, and their putative hybrids all have compact and densely-flowered spikes. This contrasts sharply with the elongate, sparsely-flowered spikes of Carex arctata, C. debilis and C. gracillima. Nothing in the morphology of the hybrid individuals we document suggests that the latter three species are involved as parents. Similarly, while C. hirsutella has been reported to hybridize with C. gracillima Schwein. (Bailey 1889b), the C. hirsutella hybrids we describe have the compact inflorescence typical of the C. complanata complex and distinct from C. gracillima. We are not aware of any previous reports of hybrids involving C. oxylepis.

Correll and Johnston (1970) did suggest that *C. complanata*, *C. caroliniana* and *C. bushii* frequently hybridize, but without supporting evidence or descriptions of the hybrids. We confirm only one of these possibilities, *C. caroliniana* \times *complanata*, and the clear genetic separation among all three species (Figure 4.1D) provides strong evidence against any widespread or recurrent introgression among them.

The assertions of Correll and Johnston (1970) notwithstanding, all the hybrids we investigated here are previously undescribed. Cayouette and Catling (1991) recommend against formally naming rare or poorly documented hybrids. In our study, the better documented hybrids are all apparently very rare, with only a single individual identified in two years of extensive field work (i.e., *C. complanata* \times *oxylepis*, *C. swanii* \times *complanata*, *C. caroliniana* \times *complanata*, *C. bushii* \times *swanii*). On the other hand, while the putative *C. hirsutella* hybrids may be more common, uncertainty surrounding their hybrid status suggests formal naming may be premature.

Overall, our study supports the recognition of *C. hirsutella*, *C. complanata*, *C. bushii*, and *C. caroliniana* as distinct species. However, we found the distinctions between *C. complanata* ssp. *tropicalis* and *C. complanata* s. s. are too subtle to merit recognition as a distinct subspecies. For the most part, we refute the contention that

taxonomic boundaries among these species are marred by extensive hybridization or intergradation (Correll and Johnston 1970). In most cases we found hybrid individuals were completely sterile, with no evidence of transfer of extra-specific genes into C. complanata, C. caroliniana and C. bushii. However, introgression appears to be a possible explanation for genetic divergence of two Pennsylvania populations of C.hirsutella from the rest of that species. Further investigation of northern populations of C. hirsutella will be necessary to confirm this.

4.6 Taxonomic Treatment

It appears that this group does not form a complete monophyletic group (Waterway 2006, chapter 5). However, as the correct identification of these species provides field botanists with some difficulty, we provide here a key and descriptions to facilitate their reliable identification.

4.6.1 Description

Cespitose. Culms 15–115 cm tall with sheaths and sometimes also the leaves pubescent. Culms dark maroon at base. Plants are frequently entirely reproductive, without vegetative pseudoculms: the reported leaf widths are for the reproductive culms only. When present, vegetative pseudoculms often have much wider leaves, occasionally up to 5 mm. Inflorescences with 2–6 spikes (rarely only a single spike), the terminal one gynecandrous, the lateral pistillate and short pedunculate on erect nodding peduncles. Perigynia trigonous, 1.8–4 mm long, beakless but sometimes with an acute apex resembling an indistinct beak. Single measurements are lengths, double measurements (i.e., 7.9–14 × 4.2–6.3 mm) are length × width, unless otherwise noted.

4.6.2 Key

Fruit characters should be measured from mature, well-formed perigynia and scales from the middle of the terminal spike. Leaf hair characters should be assessed for well-developed basal leaves. All quantitative characters overlap to some degree. The most consistent characters are listed first, but difficult specimens require careful consideration of the entire plant to ensure accurate identification. Sterile hybrids occasionally form in mixed populations, and may be recognized by their undeveloped nutlets and fully formed but closed anthers. They otherwise present a variable combination of characters from their parents.

2. Adaxial leaf surface densely pilose, perigynia flattened in cross section

2. Adaxial leaf surface glabrous or glabrescent, occasionally with short, almost scabrous hairs; perigynia round or flattened in cross section

4.7 Species Accounts

CAREX COMPLANATA Torrey & Hooker, Ann. Lyceum Nat. Hist. New York 3:408. 1836. Type U.S.A. Texas. [no date], T. Drummond. 442. (Isotypes: TEX scanned image!, GH!). Culms: glabrous, 16–93 cm. Leaves: ligules 0.5–2.6 mm; sparsely pilose sheaths and abaxial surfaces, glabrous or nearly so adaxially, 1.5–3.3 mm wide. Inflorescences: 3–5 spikes, 14–43 mm; terminal spike clavate, 7.5–24.3 mm, pistillate portion 7.9–14 × 4.2–6.3 mm, staminate portion 1.5–11.3 mm; lateral spikes thick-cylindric to ellipsoid, proximal spike 5.7–14.2 × 3–5.6 mm. Pistillate scales: rarely red-tinged, 2.2–3.5 mm including an awn up to 0.7 mm. Anthers: 1.3–2.2 mm. Perigynia: ascending when ripe, apex usually rounded, 2–3.3 × 1.2–2.1 mm. Nutlets: apiculus usually short and straight, 1.7–2.2 × 1.1–1.5 mm.

When assessing the leaf surface, the lower leaves should be used. Both C. hirsutella and C. complanata may have glabrous upper leaves. As discussed above, occasional specimens have short, stiff hairs on the adaxial leaf surface.

Widespread on the southeastern coastal plain, dry to moderately wet open habitats and occasionally in open, acidic forests. Often co-occurs with *C. caroliniana* and *C. bushii*, and occasionally with *C. hirsutella* where their ranges overlap.

CAREX HIRSUTELLA Mackenzie, Bull. Torrey Bot. Club 50:349. 1923. Type U.S.A. Pennsylvania. [no date], G. H. E. Muhlenberg. 147. (Holotype: HAL).

Culms: 32–94 cm. Leaves: ligules 1–4.3 mm; densely pilose sheaths and both abaxial and adaxial blade surfaces, 1.5–3.9 mm. Inflorescences: usually 3 spikes 13–41 mm; terminal spike clavate, 6.3–26.7 mm, pistillate portion 4.3–12.7 × 3.8– 5.7 mm, staminate portion 2.7–10 mm; lateral spikes thick-cylindric to ellipsoid, proximal spike 5–18 × 3.8–5.7 mm. Pistillate scales: rarely red-tinged, 2–3 mm including an awn up to 0.7 mm. Anthers: 1.1–2.4 mm. Perigynia: ascending when ripe, flattened in cross section, apex usually round, 2.2–2.9 × 1.4–1.9 mm. Nutlets: apiculus usually short and straight, 1.6–2.1 × 1.1–1.3 mm.

See comments above under C. complanata regarding leaf pubescence.

Widespread across the northeastern USA and southeastern Canada. Dry to moderately wet open habitats, acidic forests, and occasionally richer sites. In poor sites it often co-occurs with *C. bushii*, *C. caroliniana*, and, where their ranges overlap, *C. complanata*. Occasionally found in richer sites, where it may co-occur with *C. swanii* and *C. virescens*, and very rarely with *C. roanensis*.

CAREX CAROLINIANA Schweinitz, Ann. Lyceum Nat. History New York 1:67, 1824. Type: U.S.A.? No date or locality, specimen in the Schweinitz herbarium, PH accession 1038735. (Holotype: PH scanned image!).

Culms: 30-88 cm. Leaves: ligules 1-5.3 mm; sparsely pilose sheaths, glabrous blades, 1.6-2.6 mm wide. Inflorescences: usually 3 spikes, 13-29 mm; terminal spike clavate, 7.5-21 mm, pistillate portion 5-11 \times 3.8-5.5 mm, staminate portion 1.6-9 mm; lateral spikes thick-cylindric to ellipsoid, proximal spike 5.3-12.9 \times 3.3-5.3 mm. Pistillate scales: often strongly red-tinged, 1.5-2.7 mm, usually awnless. Anthers: 1.2-1.7 mm. Perigynia: spreading when ripe, round in cross-section, often with an acute, slightly beaked apex, 1.8-2.9 \times 1.3-2.4 mm. Nutlets: often with a strongly contorted apiculus, 1.6-2.1 \times 1.1-2 mm.

Immature specimens remain extremely difficult to distinguish from C. complanata. Phenology may be helpful, as C. caroliniana flowers and fruits approximately two weeks earlier. However, in mixed populations both species may be present with mature fruit at the same time. The more prominently acute, often slightly beaked perigynia of C. caroliniana are often distinctive, even on immature specimens.

Widespread across the eastern USA. Most common in floodplain meadows and forests. In open habitats it often co-occurs with *C. complanata* and *C. hirsutella*, and occasionally with *C. swanii*.
CAREX BUSHII Mackenzie, Bull. Torrey Bot. Club 37: 241. 1910. Type U.S.A. Arkansas. Fulton. 30 April 1905. B. F. Bush 2514. (Holotype: NY scanned image!).

Culms: 22–115 cm. Leaves: ligules 0.8–6.5 mm; pilose sheaths and abaxial blade surfaces, occasionally also on the adaxial blade surfaces, 2–4 mm wide. Inflorescences: 2–3 spikes, 15–40 mm; terminal spike clavate, 8.7–30.1 mm, pistillate portion 6.6–17 \times 5–8 mm, staminate portion 3–15.7 mm; lateral spikes orbicular to thick-cylindric, proximal spike 4.7–15.3 \times 5–7.5 mm. Pistillate scales: often sparsely pilose, strongly red-tinged, 3–5.2 mm including an awn 0.5–1.7 mm. Anthers: 1.7–3.4 mm. Perigynia: spreading when ripe, round in cross-section, often with an acute, slightly beaked apex, 2.6–3.9 \times 1.7–2.7 mm. Nutlets: usually with a strongly contorted apiculus, 1.9–2.7 \times 1.4–1.9 mm.

Immature specimens are usually distinguished by the very thick staminate portion of the terminal spike, which is often as thick or slightly thicker than the pistillate portion. When mature, the long pistillate scales give the spike a bristly profile.

Habitat: Widespread across the eastern USA. Most common and abundant in open prairies in the western portion of its range. Eastward it is found in meadows and disturbed areas. Often co-occurs with *C. hirsutella* or *C. complanata*.

CHAPTER 5 Phylogenetic position of *Carex* section *Porocystis*, inferred from amplified fragment length polymorphisms

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Having firmly established the boundaries among the eight species in the *Carex* roanensis and *C. complanata* complexes, the following chapter addresses the phylogenetic relationships among them. While the species involved have traditionally been placed in two separate sections, recent investigations using DNA sequence data have demonstrated that these sections are unnatural. Some of the results of this work have been unexpected: *C. swanii* appears to be more closely related to the *C. complanata* complex than the *C. roanensis* complex, despite its morphological similarity to *C. virescens*. Similarly, despite being treated as a single species by some authors, *C. complanata* and *C. hirsutella* may not even be sister-species. Clarifying these issues, and improving overall resolution of the relationships among these eight taxa is an important step in obtaining a clearer understanding of species-level evolution in *Carex*. In the context of this thesis, establishing quantifiable estimates of phylogenetic divergence among these taxa, in the form of patristic distances, is key to testing the relationship between taxonomic and ecological divergence.

5.1 Abstract

We used amplified fragment length polymorphisms (AFLP) to reconstruct the phylogeny of species in the *Carex roanensis* and *C. complanata* complexes. While

these eight species are traditionally placed in two different sections, recent investigations have revealed that this arrangement is unnatural. DNA-based reconstructions indicate a close relationship between the two complexes. However, the resolution of species-level arrangements within this group are uncertain, as is the relationship of this group to other *Carex* species. Our study included 491 individuals, including the eight species in the C. complanata and C. roanensis complexes, as well as 17 putative outgroup taxa. The results confirm the division of the two complexes into three monophyletic clades: Carex aestivalis, C. roanensis and C. virescens (the ARV clade); C. bushii, C. caroliniana, C. hirsutella and C. swanii (the BCHS clade); and C. complanata. However, the arrangement within each clade remains uncertain, with different, weakly supported topologies produced by distance and parsimony analyses. The alternative topologies differ by relatively small differences in patrictic distances, suggesting that branch lengths may be a more accurate measure of relationship than branch order in this instance. We cannot determine whether or not this group as a whole is monophyletic, due in part to uncertainty surrounding the placement of several outgroup taxa. Variation in the AFLP data for the thoroughly sampled ingroup taxa suggests that more extensive sampling of the outgroup taxa will be necessary to clarify these relationships.

5.2 Introduction

Carex section *Porocystis* Dumortier is a group of 11 primarily New World species (Reznicek and González-Elizondo 2001). They are characterized by tri-stigmatic ovaries and beakless or very short-beaked perigynia that are pubescent in some species; spikes on short, erect peduncles, the terminal one gynecandrous or staminate, the lateral ones pistillate with sheathless bracts; and culms red-maroon at base, with sheaths and often the leaves pilose (Mackenzie 1931-1935; Reznicek and González-Elizondo 2001; Ball 2002). Eight species occur in North America north of Mexico: C. bushii Mackenzie, C. caroliniana Schweinitz, C. complanata Torrey & Hooker, C. hirsutella Mackenzie, C. pallescens Linnaeus, C. swanii (Fernald) Mackenzie, C. torreyi Tuckermann and C. virescens Muhlenberg ex Willdenow. Carex pallescens is also found in northern Eurasia, and disjunct populations of C. complanata occur in southern Mexico and Guatemala. Carex boliviensis Van Heurck & Müll. Arg. and C. angustispica Reznicek & González are known from Mexico and Central America, and C. tovarensis Reznicek & Wheeler from northern Venezuela.

All recent taxonomic treatments of this group have followed Mackenzie (1931-1935), who referred to the group as section *Virescentes* Kunth (Gleason and Cronquist 1991; Reznicek and González-Elizondo 2001; Ball 2002). However, the traditional sectional arrangement of *Carex*, based primarily on morphology, has resulted in many unnatural groupings (Crins 1990). Re-examination of section *Hymenochlaenae* with a combination of morphology and molecular data revealed that that section is polyphyletic, and a clade containing most of section *Porocystis* is nested within it (Waterway 2006; Waterway et al. in press; Waterway and Starr 2007).

This work has important ramifications for the circumscription of section *Porocystis*. One of the clearest outcomes is that *C. pallescens* is not a close relative to the rest of the section. Analyses with 3–5 gene regions, and 2453–4013 bp consistently place *C. pallescens* well removed from the rest of the section (Waterway and Starr 2007; Waterway 2006). *Carex torreyi* was not included in this analysis, but in a separate study Roalson et al. (2001) placed it in a clade with *C. pallescens*, although no other members of section *Porocystis* were included in the analysis. *Carex pallescens* and *C. torreyi* are distinct from the rest of section *Porocystis* in their staminate terminal spikes and more northern distribution: *C. pallescens* ranges into northern Ontario and Labrador, while the northern range limit of *C. torreyi* is found in

Manitoba, Saskatchewan and Alberta. All other species have gynecandrous terminal spikes, and no other species occur farther north than extreme southern Quebec.

Another outcome of these studies is the recovery of a well-supported clade with *C. virescens* and two species currently placed in section *Hymenochlaenae*, *C. aestivalis* M. A. Curtis ex A. Gray and *C. roanensis* Hermann. These three species share many similarities in morphology, including their long-cylindric spikes, perigynium shape and size, habit, and geographic and ecological distribution (Chapter 3, Smith et al. 2006). However, it is suprising that this clade does not include *C. swanii. Carex swanii* and *C. virescens* are very similar in morphology and distribution, and were treated as subspecies or varieties of the same species by some authors (Chapter 3).

Instead *Carex swanii* is placed in a clade with *C. bushii*, *C. caroliniana* and *C. hirsutella*. This group of species shares relatively short, ellipsoid or thick-cylindric spikes. *Carex complanata* is sister to this group, but without significant bootstrap support. Again, this is surprising because *C. complanata* is extremely similar in morphology to *C. hirsutella* (Chapter 3); some recent treatments lump both taxa within a single species (e.g., Gleason and Cronquist 1991).

While these results greatly improve our understanding of this group, several questions remain. The placement of C. complanata relative to the other species remains uncertain, as does the relationship between the C. bushii-C. caroliniana-C. hirsutella-C. swanii (BCHS) and the C. aestivalis-C. roanensis-C. virescens (ARV) clades. We cannot determine if these two clades form a monophyletic group, and if so, what the relationship between this group and the rest of section Hymenochlaenae is, with the existing data. The objective of our study was to examine these issues. Since a five-gene, 4013 bp dataset was not informative enough to provide a fully resolved and well-supported topology, we elected to apply amplified fragment length

polymorphism (AFLP) markers to this problem. AFLP fragments provide an extremely variable source of taxonomic information, useful for examining relationships within species and among closely related species (Mueller and Wolfenbarger 1999). They have been used successfully in addressing the phylogeny of a wide variety of closely related plant species (Badr et al. 2000; Hipp and Rothrock 2002; Beardsley et al. 2003; Despres et al. 2003; Chao et al. 2005; Koopman 2005; Zerega et al. 2005).

5.3 Methods

5.3.1 Taxon sampling

For the ingroup of our study (the BCHS and ARV clades and *C. complanata*) we collected population samples from across the range of each species, as documented in Chapters 3 and 4. We also sampled populations for the species of sections *Hy-menochlaenae* and *Hallerianae* that were identified by Waterway (2006) as close relatives to this group: *C. oxylepis* Torrey & Hooker, *C. misera* Buckley, *C. venusta* Dewey, *C. debilis* Michaux, *C. tenax* Chapman ex Dewey and *C. dasycarpa* Muhlenberg.

As possible outgroups, we included individual samples from nine additional species from the "Gracillima Group", identified in Waterway (2006) as the closest relatives to our study taxa. We did not include any of the Central or South American members of section *Porocystis*. All population and individual samples are listed in Appendix A, and vouchers are deposited at MTMG.

5.3.2 Amplified fragment length polymorphisms

We extracted DNA from silica-dried leaf tissue using a CTAB extraction and assayed five AFLP primer pairs for each sample (Vos et al. 1995). The detailed protocols are presented in Chapter 3. Appropriate evolutionary models for the analysis of AFLP markers have not been developed, so researchers using them to infer phylogenies have selected techniques designed for different kinds of data (Felsenstein 2004a). Of the available approaches, Felsenstein (2004a) recommends using distance methods, citing similarities between the expected evolution of AFLP fragments and that of restriction-sites. He also suggests parsimony analysis may be appropriate. Of the parsimony methods, Dollo is offered as preferable to Wagner, given the asymmetry in the rate of fragment losses vs fragment gains in AFLP data. In contrast, Nei and Kumar (2000) recommend treating the presence and absence of a particular fragment as two alternate alleles at a single locus, and using the frequencies of these alleles in a population to calculate the genetic distances (Nei 1972).

We used each of these methods. For the Dollo parsimony analysis, we used the dollop program in the PHYLIP suite (Felsenstein 2004b), using the standard settings. For the Wagner parsimony we used PAUP* (Swofford 2003), with a parsimony ratchet (Nixon 1999) protocol generated by PRAP (Müeller 2004). We used the recommended settings for PRAP: 10 random addition sequences with 200 ratchet iterations for each repetition, 25% of all characters given double-weighting in each iteration. The single most parsimonious tree found by the parsimony ratchet was subjected to an additional 10 hours of heuristic TBR searching, and all mostparsimonious trees were saved. Bootstrap support was calculated using PAUP*, with 10000 repetitions, initial trees formed by random sequence addition and only a single tree saved during branch-swapping (i.e., multrees = no). This bootstrap approach was first proposed by DeBry and Olmstead (2000), and Waterway and Starr (2007) found it was much faster than conventional bootstrap algorithms, while yielding very similar results. For the first distance analysis, we calculated a distance matrix among all individuals using a modified version of Nei and Li's (1979) distance, as calculated by the **restdist** program of the PHYLIP suite (for details, see the documentation distributed with Felsenstein 2004b). We generated neighbour-joining trees from this matrix, and assessed bootstrap support from 1000 repetitions generated with the PHYLIP programs neighbor and seqboot, respectively.

For the distance analyses based on fragment frequencies, we first calculated the frequency of each band within populations and within species. Outgroup species that were represented by three or fewer samples were treated as a single population. Distances among species or populations were calculated with the PHYLIP program gendist, and the resulting matrices were used to construct neighbour-joining trees. Bootstrap support was calculated from 1000 repetitions.

In all analyses, we repeated the bootstrap procedure with different taxa removed. This allowed us to assess how much of the uncertainty in the trees was attributable to those particular taxa. In particular, we excluded the Pennsylvania populations of *C. hirsutella*, which display unusually high genetic divergence from the rest of that species, possibly as a result of introgressive hybridization (Chapter 4); and a group of four outgroup species for which different analyses inferred markedly different relationships with respect to the BCHS and ARV clades: *C. misera*, *C. oxylepis*, *C. tenax* and *C. dasycarpa*. *Carex pallescens* was designated the outgroup for all analyses, as suggested by its placement in the sequence-based analyses. In all cases we used *C. pallescens* to root the trees, as suggested by its placement in the analysis of Waterway (2006).

Our sampling within ingroup species was much more exhaustive than for the outgroup species. Preliminary analysis revealed a great deal of uncertainty with respect to the relationships among outgroup species, and between the ingroup and the outgroup. Consequently, we repeated all the analyses with only the eight ingroup species, in order to evaluate their relationships with greater confidence.

5.4 Results

5.4.1 Overall

Five AFLP markers yielded 141 readily scored bands, two of which were fixed across all individuals, leaving 139 parsimony-informative characters. Dollo parsimony failed completely, as the most parsimonious tree was an almost entirely unresolved comb (not shown). Wagner parsimony was more effective, with the majority-rule consensus of the 416073 most-parsimonious trees resolving most species as mono-phyletic (Figure 5.1), but with no bootstrap support above the species level. Branch lengths within species are generally longer than those between species, as shown in Figure 5.2. The extremely low CI value (0.04) indicates a high level of homoplasy in this data. The overall topology and bootstrap support for the neighbour-joining trees based on restriction-site distances between individuals (Figures 5.3 and 5.4) and fragment frequency between populations (Figure 5.5) and between species (Figure 5.6) were similar. Notable differences are discussed below.

5.4.2 The ARV clade

The ARV clade was recovered as a monophyletic group in all analyses. However, bootstrap support for this clade was strong only in the fragment-frequency distance trees (Figures 5.5 and 5.6). In all other cases bootstrap support increased in the analyses excluding *C. misera* and *C. oxylepis*. These two taxa are placed sister to the ARV clade in the fragment-frequency-by-species (Figure 5.6) and restrictionsite distance (Figure 5.4) phylograms. Taken together, this suggests that the weak support for the ARV clade is due in part to uncertainty regarding the placement of *C. oxylepis* and *C. misera*. This uncertainty may reflect inadequate sampling of these species. The ingroup species in our study were represented by 27–79 samples each,



Figure 5.1: Majority-rule consensus cladogram of 416073 most-parsimonious trees based on 141 AFLP fragments. Numbers above branches indicate percent bootstrap support based on 10000 replicates. Bootstrap support for the branch leading to *Carex hirsutella* (indicated by *) is the value when the Pennsylvania populations are excluded. Numbers below branches indicate bootstrap support in analysis excluding *C. dasycarpa, C. tenax, C. misera* and *C. oxylepis*.



Figure 5.2: Phylogram of one of 416073 most-parsimonious trees based on 141 AFLP fragments. Analysis included basal outgroups, which are not shown.



Figure 5.3: Neighbour-joining cladogram based on Nei and Li's restriction-site distance calculated from 141 AFLP fragments. Majority-rule consensus of 1000 bootstrap replicates. Numbers above branches indicate percent bootstrap support. Numbers below branches indicate support in analysis excluding *C. dasycarpa*, *C. tenax*, *C. misera* and *C. oxylepis*. Bootstrap support for the branch leading to *C. hirsutella* (indicated by *) is the value when Pennsylvania populations are excluded.



Figure 5.4: Neighbour-Joining phylogram based on Nei and Li's restriction-site distance calculated from 141 AFLP fragments. Analysis included basal outgroups, which are not shown.



Figure 5.5: Neighbour-joining cladogram based on frequency of 141 AFLP fragments within sampled populations, using Nei's genetic distance. Majority rule consensus of 1000 bootstrap replicates. Numbers above branches indicate percent bootstrap support. Numbers below branches indicate support in analysis excluding *C. dasycarpa*, *C. tenax*, *C. misera* and *C. oxylepis*. Bootstrap support for the branch leading to *C. hirsutella* (indicated by *) is the value when Pennsylvania populations are excluded.



Figure 5.6: Neighbour-joing phylogram based on frequency of 141 AFLP fragments within species, using Nei's genetic distance. Numbers above branches indicate percent bootstrap support. Numbers below branches indicate support in analysis excluding *C. dasycarpa*, *C. tenax*, *C. misera* and *C. oxylepis*. Bootstrap calculated from 1000 replicates.

while we used 12 or fewer individuals from each outgroup species. Given the evident variation in the ingroup taxa, more extensive sampling of outgroup species may be necessary to acquire a truly representative picture of their phylogenetic relationships.

Within the ARV clade, C. aestivalis was paraphyletic in the parsimony analysis, but not in any of the distance trees, and only the fragment-frequency-by-population analysis yielded strong bootstrap support for this species as a lineage (Figure 5.5). *Carex aestivalis* was sister to the C. virescens-C. roanensis branch in all analyses except the restriction-site distance tree, which placed C. roanensis sister to a C. aestivalis-C. virescens branch (Figure 5.4). However, this arrangement was not stable; the C. virescens-C. roanensis clade appears in the bootstrap consensus tree for the restriction-site distances, as it does in all the other analyses (Figure 5.3). Despite the consistent placement of C. virescens and C. roanensis as sister species, none of the analyses produced bootstrap support greater than 54% for this clade.

5.4.3 The BCHS clade

All analyses showed the BCHS clade to be a monophyletic group. Again, bootstrap support was strong only in the fragment-frequency distance trees (Figures 5.5 and 5.6), but excluding taxa from the analysis produced only slightly higher bootstrap values for the other analyses. Within the clade, *C. bushii* was paraphyletic in the parsimony analysis, but monophyletic in all others. Excluding the Pennsylvania *C. hirsutella* populations improved the bootstrap support for this species in the parsimony and restriction-site distance analyses, but did not result in improved bootstrap support or changes in toplogy elsewhere in the tree. *Carex swanii* was sister to the other three species in every case. *Carex caroliniana* was sister to *C. bushii*, and this clade was sister to *C. hirsutella*, in all but the parsimony analysis. In the parsimony analysis *C. hirsutella* and *C. caroliniana* are positioned sister to each other, nested within the paraphyletic *C. bushii*. Despite the fairly consistent topology recovered by each analysis, there was no bootstrap support for any of the internal structure of the BCHS clade.

5.4.4 Carex complanata

Every analysis placed C. complanata sister to the BCHS clade. Bootstrap support for this combined clade was generally very weak, with the exception of the fragment-frequency-by-species analysis. When C. tenax and C. dasycarpa were excluded from this analysis the bootstrap support for the C. complanata + BCHS clade increased from 66% to 85%. Carex tenax and C. dasycarpa were sister to the C. complanata + BCHS clade in this analysis, suggesting that the generally poor bootstrap support is due in part to uncertainty in the placement of these two species. As mentioned above, the small number of samples from Carex tenax and C. dasycarpa may contribute to their uncertain placement in our analysis.

5.4.5 The combined ARV-BCHS clade

A combined clade of *C. complanata* and the ARV and BCHS clades together was recovered only in the parsimony analysis (Figure 5.1). In all other cases either *C. oxylepis* and *C. misera*, *C. tenaxa* and *C. dasycarpa*, or all four of these species, were nested within the combined clade. Excluding these four species produced strong bootstrap support for the remaining eight species (76–90%), with *C. debilis* and *C. venusta* in a clade sister to this group (Figures 5.3, 5.5 and 5.6).

5.4.6 Eight-species analysis

The ARV clade appeared in all of the eight-species analyses with 88–99% bootstrap support (Figures 5.7–5.10), but the internal structure was inconsistent. *Carex aestivalis* was recovered as a paraphyletic grade basal to the *C. virescens-C. roanensis* clade in the parsimony analysis (Figure 5.7), and as sister to *C. virescens* in the restriction-site distance analysis (Figure 5.8), but without good bootstrap support. In both fragment-frequency trees C. virescens and C. roanensis form a clade with 62-70% bootstrap support (Figures 5.9 and 5.10).

Similarly, the BCHS clade was recovered in all of the eight-species analyses, but with varying bootstrap support and internal structure. The parsimony analysis, restriction-site distance and fragment-frequency-by-species analyses produced moderate to strong bootstrap support for the clade (72%, 73% and 98%, respectively, Figures 5.7, 5.8 and 5.10). None of the analyses produced significant bootstrap support for any of the internal branches, and *C. bushii* was a paraphyletic grade in the parsimony analysis (Figure 5.7). *C. complanata* was placed between the BCHS and ARV clade in all analyses with moderate to strong bootstrap support (73% to 99%) for the intervening branches. The one exception was the fragment-frequencyby-population analysis, for which the position of *C. complanata* relative to the BCHS clade had bootstrap support < 50% (Figure 5.9).

5.5 Discussion

Overall, our results add little to the previous sequence-based analysis of this group (Waterway 2006). As in that analysis, we recovered the ARV clade, the BCHS clade, and placed C. complanata sister to the BCHS clade. However, the sister relationship between C. complanata and the BCHS clade does not have strong bootstrap support in the analysis that included all outgroup taxa. Some of the uncertainty surrounding this arrangement is related to ambiguity in the placement of C. tenax and C. dasycarpa. These two species share the thick-cylindric, erect, short-peduncled spikes and pubescent leaves characteristic of this group, suggesting they may well belong there, but the available data precludes drawing firm conclusions. The low sample size we used for these and other outgroup species may be a serious short-coming of our analysis. The well-sampled ingroup species demonstrated substantial infraspecific variation. If the outgroup species are comparably heterogeneous for



Figure 5.7: Unrooted majority-rule consensus cladogram of 100000 mostparsimonious trees based on 141 AFLP fragments, analysis limited to the eight ingroup species. Numbers on branches indicate bootstrap support, calculated from 10000 replicates.

AFLP markers, broader sampling may be required to adequately assess their phylogenetic relationships with this approach.

Similarly, we cannot discount the possibility that C. oxylepis and C. misera are associated with the ARV clade. Both of those species have linear-cylindric, gynecandrous spikes and pubescent leaf sheaths, as do the members of the ARV clade. In the sequence-based analysis C. oxylepis is sister to C. davisii (Waterway 2006), a clade with moderately strong bootstrap support. Carex oxylepis and C.davisii are similar in perigynia shape and inflorescence morphology, in addition to the characters listed above, suggesting their placement in the sequence-based analysis may be more likely than the arrangements we found here. The placement of C. misera



Figure 5.8: Unrooted neighbour-joining phylogram based on Nei and Li's restrictionsite distance calculated from 141 AFLP fragments. Analysis limited to the eight ingroup species. Numbers on branches indicate percent bootstrap support calculated from 1000 replicates.

is ambiguous in the sequence analysis. It does share several characteristics with the ARV clade members, including spike shape, pubescent perigynia, and Appalachian distribution.

The poor performance of the AFLP-based analyses for this group may be a consequence of inappropriate levels of variation. Phenetic analysis of this data provided very fine-grain resolution (Chapters 3 and 4). Each of the ingroup species was represented by 27–79 samples, and all but six individuals produced a unique fingerprint; up to 50% of the variation in the data was within, rather than between species. Despres et al. (2003) found similar levels of intraspecific variation in an AFLP dataset, and



Figure 5.9: Unrooted neighbour-joining phylogram based on frequency of 141 AFLP fragments within sampled populations, using Nei's genetic distance. Analysis limited to the eight ingroup species. Numbers on branches indicate percent bootstrap support, calculated from 1000 replicates.



Figure 5.10: Unrooted neighbour-joining phylogram based on frequency of 141 AFLP fragments within species, using Nei's genetic distance. Analysis limited to the eight ingroup species. Numbers on branches indicate percent bootstrap support, calculated from 1000 replicates.

attributed it to the retention of ancestral polymorphisms in closely related species, although homoplasy may also contribute to this pattern. Within the ingroup species of our study, there were only 23 bands that were fixed in one species and entirely absent in another. In pair-wise comparisons, no two species had more than 10 such bands distinguishing between them. The remaining 118 bands were present in varying frequencies in all ingroup species. This intra-specific variability is evident in the phylograms (Figures 5.2, 5.4, 5.6 and 5.8–5.10), where the branch lengths within species are markedly longer than the internal branches between species. Waterway (2006) also found limited interspecific divergence; ITS sequences among our ingroup differed by only 3–13 base pairs in that study. Koopman (2005) found that AFLP markers performed inconsistently in phylogenetic reconstructions among taxa with ITS divergence less than ten base pairs. The short internal branches in each clade could also be interpreted as evidence of a rapid radiation, with speciation events within each clade arising in quick succession. As a consequence, a clear genetic signature of the first split may not have developed before the next one occurred. Coalescent processes come into play in such cases, further complicating efforts to infer phylogenetic relationships (Felsenstein 2004a).

The paraphyletic arrangement of C. aestivalis and C. bushii in the parsimony analysis is interesting. Both of these species form discrete entities clearly distinct from their closest relatives in phenetic analysis of the same AFLP data (Chapters 3 and 4). This may be a consequence of the poor fit between the assumptions of parsimony analysis and the actual evolution of AFLP markers. Most of the concerns Backeljau et al. (1995) raised regarding parsimony analysis of RAPD data apply equally to AFLPs: the unequal rates of fragment gains vs fragment losses does not correspond to either Wagner or Dollo parsimony (see also Koopman 2005); the presence of individual bases with high mutation rates at priming sites may result in the repeated gain and loss of fragments within lineages or populations; and the noncodominant inheritance of AFLP fragments does not correspond to existing models of molecular evolution. Despite all these shortcomings, AFLP data has been used successfully in parsimony analysis of closely related species (Beardsley et al. 2003; Despres et al. 2003; Koopman 2005). It is possible that successful parsimony analysis of AFLP data is possible only with species that diverged long enough ago to have developed a clear genetic signal that can be resolved despite the inadequacies of the parsimony model. In other words, the poor fit between parsimony and AFLP evolution may only be apparent for very recently formed species. On the other hand, many phylogenetic studies using AFLP data did not use parsimony analysis at all (Heun et al. 1997; Badr et al. 2000; Bruneau et al. 2005; Chao et al. 2005; Ozkan et al. 2005; Wassom and Tranel 2005). Of course, we cannot determine whether these authors did not report parsimony analyses due to their failure, or they rejected parsimony *a priori* as an invalid approach. In either case, the successful application of parsimony analysis to AFLP data appears to be the exception.

Given the shortcomings of the data, there are only a handful of conclusions that can be drawn from this study with any confidence. The lack of any bootstrap support for the arrangement of the outgroup taxa precludes any interpretation of their placement in our analysis. Neither can we assess the monophyly of the combined ARV-BCHS-*C. complanata* clade, due to the inconsistent placement of *C. misera*, *C. oxylepis*, *C. tenax* and *C. dasycarpa*. Proper resolution of this problem will require more intensive sampling for AFLP markers of all the species in Figure 5.1. *Carex caroliniana* was represented by only 27 samples from six populations, and was clearly resolved as a monophyletic group in all analyses. This may provide a useful sampling target for the outgroup species.

More can be ascertained regarding the relationships among our ingroup taxa. Our analyses indicate clear separation between the ARV and BCHS clades. This confirms that *C. virescens* and *C. swanii* are not sister-species, and their morphological resemblance reflects symplesiomorphy or convergence. Similarly, *C. complanata* and *C. hirsutella* are not sister-species, despite differing in only one subtle aspect of their morphology, leaf pubescence (Chapter 4). The placement of *C. complanata* on a branch distinct from the other two clades is also well supported by our 8-species analysis.

While we cannot draw further conclusions regarding the topology of the ingroup, it is interesting to note that the remaining uncertainty centers on relatively short internal branches. Whether *C. roanensis* is sister to *C. aestivalis* or *C. virescens* will make very little difference to the patristic distances among these taxa. Similarly, changing the branching order among *C. bushii*, *C. caroliniana*, *C. swanii* and *C.* *hirsutella* would result in relatively small changes in the branch lengths in that clade. Consequently, while the topology of these clades remains uncertain, the actual patristic distances recovered in our analysis likely are relatively accurate reflections of the evolutionary relationships of this group.

CHAPTER 6

Evolutionary ecology of *Carex*: a case study in niche conservatism

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In the previous chapters I established the taxonomic boundaries among the species in this study, and developed four alternative hypotheses of their phylogenetic relationships. In the following chapter I build on this systematic information to examine the relationship between the ecological niche and phylogenetic divergence. I develop four different measures of niche distance, and contrast these with patristic distances to test the relationship between ecological and phylogenetic divergence. In the context of this thesis, this addresses my third research objective.

6.1 Abstract

The increasing availability of well-resolved phylogenies and geospatial climatic data has spurred a renewed interest in niche conservatism. Recent research has produced examples of both the presence and absence of niche conservatism, suggesting this process is context-dependent. We present a case-study using eight *Carex* species. This group is characterized by very subtle differences in morphology, and is apparently the result of rapid radiation. The species are widespread across eastern North America, with broad areas of sympatry. This provides a useful contrast to other studies, many of which have focused on allopatric vertebrates. We develop four datasets: georeferenced distribution records for each of the eight species; climatic variables associated with each distribution record; ecological niche models combining the first two datasets to produce predictions of the optimal niche of each species; and local habitat variables measured at field sites across the range of these species. Our results indicate conservatism with respect to climatic, geographic, and local niche axes. The shape of the relationship between niche and patristic distances suggests that phylogenetic divergence acts as a limiting factor on ecological divergence: both close and distant relatives were ecologically similar, but only distant relatives demonstrated high levels of ecological divergence. We discuss the implications of these results, and suggest three area for further investigation: identifying the phylogenetic scale at which niche conservatism is strongest; identifying which niche axes are most affected; and identifying biological or biogeographic conditions that enhance or diminish the influence of niche conservatism.

6.2 Introduction

Taxonomic and ecological diversity are intimately linked in evolutionary theory. Darwin (1859) postulated that the success of species in a lineage was due in part to their sharing advantageous characteristics of their common ancestor. This tendency for species to retain ancestral ecological characteristics, now referred to as niche conservatism, has become a central theme in evolutionary research (Holt 1996; Ackerly 2003; Wiens and Graham 2005). However, Darwin (1859) also associated speciation with divergent natural selection, whereby a single variable species gives rise to multiple ecologically discrete entities. In the extreme, this produces adaptive radiations (Schluter 2000), with closely related species occupying widely divergent niches. The extent to which ecological processes influence taxonomic divergence has been the subject of many recent studies (Orr and Smith 1998; Schluter 2001; Losos et al. 2003; Gillespie 2004).

Assessing the relative contributions of niche conservatism and divergent selection to speciation presents a formidable challenge. The theoretical expectation is that niche conservatism should be the dominant process (Holt 1996; Ackerly 2003; Wiens 2004). Selection is strongest in environments experienced by the majority of individuals and where reproductive output is highest; in the absence of barriers to gene flow, this leads to strong niche conservatism as the reproductive advantage enjoyed by large populations occurring in the optimal niche overwhelms any adaptive evolution in small populations in marginal environments (Holt 1996). This theory was validated in part by pioneering studies that demonstrated that the niche of a species can be used to predict that of its close relatives (Huntley et al. 1989; Peterson et al. 1999). A great deal of additional data has since accumulated to support this view, documenting niche conservatism both within species over geologic time scales (Martínez-Meyer and Peterson 2006) and between close relatives over evolutionary time scales (Prinzing et al. 2001; Hoffmann 2005). However, many counter examples demonstrating that niches are evolutionarily labile have also been documented. These examples include investigations of the taxonomic distribution of co-occurring species within communities (Vellend et al. 2000; Silvertown et al. 2001; Cavender-Bares et al. 2004) as well as the ecological distribution of closely related species (Rice et al. 2003; Losos et al. 2003; Gillespie 2004; Graham et al. 2004b; Knouft et al. 2006).

Ackerly (2003) reconciled this apparent contradiction by arguing that "local adaptation occurs within narrow bounds, in the context of deeper levels of conservatism among more distantly related lineages." Indeed, there is some evidence for the simultaneous conservation and divergence of different suites of ecological traits within a single lineage. Cavender-Bares et al. (2004) found that in *Quercus* communities, traits related to habitat specialization evolved rapidly, and closely related species often occupied very different habitats. In contrast, traits associated with reproductive ecology were conserved, such that the distantly related species that occupied the same environmental niche occupied complementary recruitment niches. Waterway et al. (in press) demonstrated niche conservatism in *Carex* at the scale of broad habitat categories (i.e., wetland vs. upland niches), which contrasted with rapid ecological divergence among related species with respect to finer-scale habitat partitioning (Vellend et al. 2000; Dabros 2004). Silvertown et al. (2006) presented a hierarchical model of niche evolution that could explain such patterns. Niche traits related to α diversity, i.e., species co-occurrence within a habitat, are expected to evolve rapidly, leaving no signal of phylogenetic conservatism. In contrast, niche traits associated with β and γ diversity (the distribution of species among habitats and among regions, respectively) should evolve at a slower rate. In other words, niche traits that govern a species' capacity to tolerate general habitat conditions should be conserved, while those traits associated with finer-scale partitioning within a habitat are expected to be evolutionarily labile. Silvertown et al. (2006) presented preliminary data to support this theory, but further investigation is necessary to confirm their hypothesis.

Wiens and Graham (2005) concluded that simple documentation of niche conservatism is no longer a productive avenue for research, as the outcome of such studies ultimately depends on the scale of the investigation: the niche of related species will always resemble that of their common ancestor, varying only in the degree of fidelity. However, if we shift our focus from the binary question "Are niches conserved?" to the multivariate question "In what ways does the niche evolve within a lineage?" we stand to gain a more nuanced understanding of the evolutionary processes involved.

Carex provides an ideal model system in which to explore these concepts. This large genus is taxonomically and ecologically diverse, with ca. 2000 species and represented in nearly all temperate, boreal, arctic and alpine habitats (Ball and Reznicek 2002). Many species are distinguished by very subtle morphological characteristics. Conflicting patterns among morphological and molecular data in phenetic analyses combined with short branch-lengths in phylogenetic analyses suggest that many groups are the result of recent or rapid radiations (Naczi and Ford 2001; Ford et al. 2006b; Waterway 2006; Waterway et al. in press, see also Chapters 3 and 4). Waterway et al. (in press) demonstrated the potential for using *Carex* to study niche evolution at a broad scale, but noted the need for further investigation at finer scales, both taxonomically and ecologically. This study extends their work by examining niche divergence at climatic, geographic, and local scales among a small group of well-studied *Carex* species.

Our study group is comprised of eight closely-related species in the 'Gracillima' group of Waterway (2006): *C. aestivalis* Curtis ex Gray, *C. bushii* Mackenzie, *C. caroliniana* Schweinitz, *C. complanata* Torrey & Hooker, *C. hirsutella* Mackenzie, *C. roanensis* Hermann, *C. swanii* (Fernald) Mackenzie and *C. virescens* Muhlenberg ex Willdenow. This suite of species was traditionally treated in two different sections (*Hymenochlaenae* and *Porocystis*), but this arrangement is unnatural (Waterway 2006; Waterway and Starr 2007). Some phylogenetic uncertainty remains, as discussed below. However, it is unquestionably a group of very closely related species, the taxonomy of which has been confirmed by rigorous examination of morphological and molecular data (Chapters 3 and 4). Additionally, all of the species in this study and all of their close relatives are North American endemics, and most are restricted to the eastern U.S.A. This suggests that the clade as a whole evolved *in situ*. If this is indeed the case then they evolved within a common biogeographic context.

The objective of our study was to quantify the relationship between phylogenetic (patristic) distance among species and measures of niche divergence at different scales (climatic, geographic, and local). We hypothesized that coarse-scale niche parameters (i.e., climatic tolerances) would be strongly conserved, while fine-scale (i.e., the α niche of Silvertown et al. 2006) parameters would evolve more rapidly. The expected pattern is therefore a relatively strong correlation between phylogenetic distance and distance in regional-scale climatic or geographic niches, but no relationship between phylogenetic distance and distance in a niche-space defined by local-scale niche parameters.

We follow the niche concept of Hutchinson (1957): a hypervolume defined by the biotic and abiotic parameters necessary for the persistence of the species in question. We do not attempt to estimate the fundamental niche in total, but rather simplified representations corresponding to that portion of the niche that can be delineated with climatic variables, geographic range, or local habitat conditions.

6.3 Methods

6.3.1 Climatic Niche

Distribution Data

We produced a dataset of distribution records for each species in this study using herbarium records. We examined more than 4300 specimens from ACAD, B, BM, BRIT, CAN, CLEMS, DUKE, EKY, ETSU, GA, GH, K, KANU, MARY, MICH, MO, MSC, MTMG, NCU, NEB, NEBC, NKY, NY, NYS, OKL, SMU, TAES, TAWES, TAMU, TENN, USCH, VDB, VPI, WIS, WV (herbarium acronyms follow Holmgren and Holmgren 1990). A recognized shortcoming of museum collections is the inclusion of misidentified specimens (Graham et al. 2004a); we confirmed the determination of each specimen using the results of our taxonomic revision of this group (Chapters 3 and 4), and excluded any specimen that could not be unequivocally identified. The counties near herbaria and universities are often over-represented in collections. To limit the potential bias this introduces, we restricted the data to include at most three records from each species for each county in which it is recorded. We excluded the single record of *C. swanii* from British Columbia as a recent introduction. We also excluded the disjunct populations of *C. complanata* from southern Mexico and Guatemala. These populations are separated from the rest of the species by at least 1500 km, with no apparent opportunity for contemporary gene flow. This strongly suggests that any niche evolution in these populations is no longer linked to that of the populations in the southeastern U.S.A. The total dataset included 2772 records (43 to 651 records per species, mean 346.5, median 352.5). We acquired geographic coordinates for specimens primarily through reference to the on-line databases Topozone (www.topozone.com) and GoogleEarth (earth.google.com).

Climatic Variables

The climatic variables we used were drawn from the WORLDCLIM dataset (Hijmans et al. 2005). This dataset provides 30 second grid resolution (ca. 0.74 km² in the region of this study) raster coverage for 19 variables describing the seasonal and annual distribution of temperature and precipitation. From the total dataset we selected a subset of seven variables: annual mean temperature, mean temperature during the driest quarter, mean temperature during the wettest quarter, temperature seasonality (standard deviation of weekly mean temperature), annual precipitation, precipitation seasonality (co-efficient of variation of weekly mean precipitation) and precipitation in the warmest quarter. This group was selected to minimize the correlation among variables: the highest correlation between any two of these variables over the study area was 0.73.

Distance measures

We extracted the values of the seven climatic variables for each of the 2772 location records, and used these values to calculate Mahalanobis distances among all species (Mahalanobis 1936; Legendre and Legendre 1998). We chose the Mahalanobis distance because this metric controls for correlations among variables, such that redundancy in the input data does not lead to unintentional weighting of related variables. The resulting values are the distances among species centroids in climate-space, and thus estimate niche divergence in the climatically-defined region of their fundamental niche. We tested the overall significance of these distances by calculating Wilkes λ (Legendre and Legendre 1998) for 999 permutations of the individual records among species, and comparing the result to the value calculated for the unpermuted data. This is equivalent to a MANOVA test, but the permutation test does not depend on the assumption that the data are from a multivariate normal distribution. We also plotted linear discriminant analysis (LDA) ordinations (which preserve the Mahalanobis distance among groups) to visualize the niche distances among species. To examine phylogenetic patterns evident in individual niche parameters, we calculated the mean of each climatic variable for each species, and used these values to produce distances among taxa for comparison with patristic distances via Mantel tests (described below). To test for the significance of differences among species for single variables we permuted individual records among species, and used the resulting ANOVA F-value as our test statistic.

6.3.2 Ecological Niche Models

The recent development of a variety of ecological niche modelling techniques (ENM, also referred to as species distribution models: Guisan and Thuiller 2005; Peterson 2006) has provided a rich source of data to apply to investigations of niche evolution. These models provide mechanisms for combining the wealth of occurrence data present in museum collections with geospatial information (Graham et al. 2004a). The result is a geographic prediction of the 'niche' of the species, as defined by the geospatial variables used. However, there is some debate as to what aspect

of the niche is actually estimated by an ENM (Soberón and Peterson 2005; Araújo and Guisan 2006).

Jackson and Overpeck (2000) noted that the fundamental niche is a theoretical construct that is unlikely to be represented in its entirety in the real world. This follows from their observation that many niche variables co-vary, such that not all theoretically possible combinations actually occur. For example, locations with mean July temperatures > 25° C and mean January temperatures < -20° C, or with serpentine soils and mid-continental climate, do not exist in North America. To address this theoretical shortcoming, they introduced the concept of the 'potential niche', defined as that subset of the fundamental niche that actually exists in the current landscape.

Ecological niche models provide a framework for estimating the potential niche. The first step of the process requires finding the optimal climatic conditions of a species, based on conditions at locations where that species is known to occur, and, for some variants, locations where the species is known to be absent. In effect, this is a description of the niche of a species in climate-space. If the distribution records of the species capture the full range of tolerable climatic conditions, these data approximate the fundamental climatic niche; otherwise these data are an estimation of the realized niche (Soberón and Peterson 2005). In practice it will be difficult to distinguish between these two situations, but if the species in question are wellcollected, and no significant dispersal-limiting geographic boundaries are present in their range, the climatic data is most likely an acceptable measure of the fundamental niche.

In the second step, the ENM is projected onto a landscape where the model parameters are known. In effect, the model prediction is constrained to the actual combinations of climatic variables that exist within that landscape: the potential niche. We further restricted the study boundary to include only those ecoregions that contained one or more records of the study species, using ecoregion boundaries defined by the Commission for Environmental Cooperation (1997). This limits the ENM to the shared geographic context of the study species (for related discussion see Peterson et al. 2001; Soberón and Peterson 2005).

We used Maxent version 2.3 (described in Phillips et al. 2006) to generate ecological niche models, using the distribution records as training data and the climatic variables as explanatory variables. Maxent uses a machine-learning approach to find the optimal predictive distribution model, based on maximum entropy criteria. Compared to most other niche modelling approaches, Maxent has the advantage of requiring only presence data for model training. This is especially important when dealing with museum collections, as absence data is rarely available. Maxent is a relatively new method for ecological niche modelling, but it outperforms many of the more established methods (Elith et al. 2006), particularly for small sample sizes (Hernandez et al. 2006; Pearson et al. 2007). It has been applied successfully to niche modelling problems at a variety of spatial and temporal scales (Kozak and Wiens 2006; Miller and Knouft 2006; Yesson and Culham 2006; Pearson et al. 2007). We used the default modeling parameters recommended by Phillips et al. (2006): convergence threshold = 10^{-5} , maximum iterations = 500, regularization multiplier = 1.

Maxent models assign a probability to each grid cell. This probability is a measure of the predicted suitability of the environment at that pixel for the species being modelled, with the sum of probabilities for all cells equal to one. As individual grid cell probabilities are very small, Maxent converts them to cumulative probabilities to facilitate interpretation. The cumulative probability of a grid cell indicates the proportion of cells that have equal or lower habitat suitability. The continuous cumulative probability map can thus be transformed to a binary presence-absence map by re-scoring all the grid cells with cumulative probabilities below an arbitrary threshold as absences, and all grid cells above the threshold as presences. The selection of appropriate thresholds is an area of ongoing research (Liu et al. 2005), and a preferred approach has not been identified for use with Maxent models. Pearson et al. (2007) reported good performance using a fixed threshold of 10%, but the particular context and objectives of every study must be weighed before a suitable choice can be made. In our study the primary objective was to provide an objective comparison of the relative differences among the niches of the study species, and absolute accuracy was of secondary importance. Furthermore, we suspect C. bushii occasionally forms transient populations in areas where ecological or climatological conditions preclude its survival beyond a few seasons (Chapter 4). The short-term persistence of a species in unsuitable habitats may well be a common phenomenon (Pulliam 2000), and presents a challenge in interpreting ENM (Guisan and Thuiller 2005). However, there is no direct way to address it. After examining several alternatives, we found that the 10% threshold did provide a reasonable balance between capturing the known distribution of each species while excluding outliers whose persistence is questionable.

Distance measures

We used the Horn index of niche-overlap (Horn 1966) to quantify the distance between the ENM models. This metric is based on information theory, and simulation studies show that it is a relatively unbiased estimator of niche overlap (Smith and Zaret 1982; Krebs 1989). We applied this measure by treating the geographic area
of the niche models as the only niche resource using the formula:

Distance_{*jk*} = 1 -
$$\frac{(p_j + p_k)\log(p_j + p_k) - p_j\log p_j - p_k\log p_j}{2\log 2}$$

where p_j and p_k are the proportions of the modelled ranges of species j and k that overlap with that of the other species. This measure provides a symmetric distance contrasting the ENMs for each species directly.

In addition, we calculated the absolute differences in geographic area of the modelled range among species. This is a measure of dispersion rather than location, allowing us to assess paterns of niche generalization and specialization with respect to the potential climatic niche.

6.3.3 Local Niche

To assess niche differences at the local scale (i.e., the environment within a few metres of the plants), we sampled habitat variables at randomly selected plants from 84 populations (7–14 per species). We selected populations from across the range of each species, emphasizing areas of sympatry. Fine-scale niche partitioning is assumed to play an important role in enabling sympatric species to co-exist, while competitive release may confound efforts to quantify such differences in populations outside the area of sympatry (Begon et al. 1990). In particular, we sampled populations from the southern Appalachians, where *Carex roanensis*, *C. aestivalis*, *C. virescens* and *C. swanii* are sympatric; and the northern coastal plain/piedmont region where *C. complanata*, *C. hirsutella*, *C. swanii*, *C. bushii* and *C. caroliniana* co-occur. All sampled populations are listed in Appendix A. We centered our sampling plots on three randomly selected plants within each population, with a minimum of 5 m between plots. Fourteen populations were not large enough to accommodate three plots, so only one or two plots were sampled at these sites, as noted in Appendix A.

Plant niches are commonly inferred from community composition data. However, the geographic scale of our study precludes the use of associated species to describe the niche of the study species in an objective way. Differences in the associated flora between species with different geographic distributions may reflect differences in the local species-pools rather than real ecological divergence (Medail et al. 2002). Accordingly, we sampled habitat features that are not linked to geography, as listed in Table 6.1. Slope was assessed for the steepest 2.5 m long gradient centred on the focal plant, using a clinometer. We determined the canopy height by calculating the height of a representative tree using a clinometer. Litter depth was measured immediately adjacent to the focal plant. Soil samples were collected from the top 10 cm of soil immediately adjacent to the focal plant. Soil acidity was assessed using a Cornell pH Test Kit (Cornell Nutrient Analysis Laboratories, Ithaca, NY). Soil texture class was assessed manually (McRae 1988). The resulting texture class was recoded into the relative composition of sand, silt and clay using a soil triangle (Soil Survey Division Staff 1993), with organic soils assigned a 0 for all three categories. The composition of exposed substrate was evaluated visually for a 1 m^2 circle around the focal plant. We used visual inspection of histograms and quantile-quantile plots to find normalizing functions for each variable; the only recoding we used was applying a square-root transformation to the slope variable. We calculated total local niche distances between species as well as distances calculated from each variable in isolation, using the same distances and significance tests as described above for climatic niche distances.

6.3.4 Phylogenetic distance

We calculated patristic distances among the eight study species from unrooted phylograms produced from parsimony and distance analyses of AFLP data (Chapter 5). We chose the analyses limited to the eight study species, as the outgroup

Variable	Scale					
Slope	%					
Size of nearest trail	faint, small, maintained, surfaced, road					
Distance from nearest trail	0 m, < 1 m, 13 m, > 3 m					
Canopy height	m					
Canopy cover	percent cover class					
Litter Depth	cm					
Soil acidity	pH					
Soil texture:						
Sand	%					
Silt	%					
Clay	%					
Substrate type:						
Rock	percent cover class					
Moss	percent cover class					
Woody debris	percent cover class					
Exposed soil	percent cover class					
Litter	percent cover class					

Table 6.1: Ecological Variables. Percent cover was measured on a seven class scale: none, 1-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-100%

relationships for this clade remain uncertain, in part due to the limited sampling of putative outgroup taxa. In addition some uncertainties remain surrounding the phylogenetic relationships among the species in this study. However, the various possible topologies generated by the AFLP analyses differ by relatively small differences in branch lengths, such that the alternate topologies all produce similar patristic distances among taxa. All phylograms show three distinct clades: the *C. aestivalis*, *C. roanensis* and *C. virescens*, or ARV clade, the *C. bushii*, *C. caroliniana*, *C. hirsutella* and *C. swanii* or BCHS clade, and *C. complanata*, which forms a polytomy with the other two clades. Consequently, while we cannot use the phylogenetic relationships among these taxa to unequivocally establish sister-species pairs, we are confident that the branch lengths among taxa are an accurate reflection of their evolutionary relationship. We used four different phylograms to generate patristic distances: neighbourjoining trees based on AFLP band-frequency within populations and within species (using the distance of Nei 1972), a neighbour-joining tree based on restriction-site distances (using the distance of Nei and Li 1979), and one of the most-parsimonious trees generated by Wagner parsimony analysis. For the phylogram based on AFLP band-frequency-by-species, we summed the branch-lengths between species to generate distances. For the other trees we calculated the median patristic distance between all populations or individuals of each pair of species to generate a single distance.

6.3.5 Statistical tests

We tested the relationships between the niche and phylogenetic distances using the Mantel test with the Spearman correlation coefficient (Legendre and Legendre 1998). The standard Mantel test is based on a linear model, and may not provide an adequate test of non-linear relationships. Using the Spearman coefficient rather than the usual Mantel correlation coefficient provides a more robust test of non-linear relationships.

We also used quantile regression to assess the relationship between niche and phylogenetic distances. Quantile regression provides a more complete analysis of the relationship between two variables than standard regression techniques (Cade and Noon 2001). Quantile regression is particularly valuable in examining limiting factors in ecological studies. In the context of this study, we were investigating the role of phylogenetic distance as a limiting factor of niche divergence, suggesting that quantile regression may provide valuable insight. However, analyzing distance matrices in a regression analysis violates the assumption of independence among sample data points. This precludes the interpretation of the quantile regression parameters as tests of statistical significance, so we restricted our use of this technique to a purely descriptive role. All statistical analyses were completed using R version 2.4.1 (R Development Core Team 2006), with multivariate functions provided in the vegan package (Oksanen et al. 2006) and quantile regression functions from the Quantreg package (Koenker 2007). Preparation of GIS data, including clipping raster data layers, extracting climatic variables for georeferenced herbarium records, and preparing Maxent prediction maps, was done with the GRASS program (GRASS Development Team 2006). We extracted patristic distances from phylograms with the PATRIS-TIC program (Fourment and Gibbs 2006).

6.4 Results

The climatic niche variables are summarized in Figure 6.1, and LDA ordinations for the total analysis, as well as for distances within the ARV and BCHS clades are presented in Figure 6.2. The permutation tests revealed statistically significant differences among species for all three analyses, as well as for each variable examined individually (p = 0.001). In each of the ordinations, most of the variation was captured on the first axis (63–86%). Examining the standardized canonical coefficient for this axis reveals that mean annual temperature was the most influential variable in distinguishing among all species and among species within each clade (Table 6.3). The distances among species are shown in Table 6.2. The ENM predictions are shown in Figure 6.3, and the Horn distances calculated from model overlap are presented in Table 6.2. Absolute differences in model area and Mahalanobis distances based on local niche variables are presented in Table 6.4.

The ENMs for the ARV clade are all centred on the Appalachian Mountains, with the *Carex roanensis* model entirely within the prediction for *C. aestivalis*, which in turn is nested within the ENM for *C. virescens*. In the BCHS clade, the models for *C. swanii* and *C. hirsutella* overlap almost completely, with the *C. swanii* projection extending further north, and including the highest elevations of the Appalachians,

Table 6.2: Climatic Niche and ENM Distances. Values in the upper triangle are the Mahalanobis distances among species for seven WORLDCLIM variables recorded for 2772 georeferenced herbarium records. Values in the lower triangle are Horn niche overlap distances calculated from ENM models.

	acsti. Cesti: Cesti:	Concentration of the second	⁰²⁷ escers	busher.	Capoliti Cap	heisened	Sugar.	Compoleneese
a estival is		1.2	4.0	15.2	14.3	9.1	5.8	15.9
roan ensis	0.41		4.9	15.7	13.3	9.6	7.0	13.6
virescens	0.41	0.56		6.2	4.4	1.4	0.3	7.1
bushii	0.78	0.81	0.55		2.6	2.4	4.9	5.5
caroliniana	0.90	0.86	0.62	0.33		1.6	4.0	1.7
hirsutella	0.64	0.72	0.33	0.32	0.36		0.8	4.7
swanii	0.50	0.64	0.19	0.47	0.55	0.21		7.6
complanata	0.92	0.89	0.84	0.69	0.40	0.70	0.79	

which are absent from the ENMs for the rest of the BCHS clade. The *C. bushii* model extends further northwest into the plains than any other species, but with a similar general distribution to that of *C. caroliniana*. The *Carex complanata* ENM differed from all the other taxa in its southeastern distribution.

Much of the variability in the local-niche variables is associated with a split between open old-field or prairie habitats on level ground, contrasted with forested slopes. The ARV species are all associated with high slopes, high canopy cover, and

Table 6.3: Comparison of the standardized canonical coefficients for climatic variables on the first canonical axis of the total analysis, and for the ARV and BCHS clades examined separately.

Discriminant variable	Total Analysis	ARV Clade	BCHS Clade
Annual precipitation	0.62	-0.27	0.14
Mean annual temperature	-1.91	1.25	-1.38
Temperature seasonality	-0.53	1.17	-0.17
Precipitation seasonality	0.05	-0.22	-0.37
Mean temp. in driest quarter	0.08	0.06	0.37
Mean precip. in warmest quarter	-0.29	-0.04	0.04
Mean temp. in wettest quarter	0.11	-0.18	0.02



Figure 6.1: Climatic Variables. Precipitation is plotted in cm, temperature in $^{\circ}$ C, and seasonality in units of standard deviation and co-efficient of variation (×100) for temperature and precipitation respectively. Boxplots show the median value and inter-quartile range, while whiskers extend to the most extreme values within 1.5 times the interquartile length from the lower and upper quartiles, and all additional outliers are plotted individually.



Figure 6.2: Linear discriminant analysis of climatic variables. Species names mark the mean values for that taxon on each axis (shifted slightly in some cases to reduce overlap), surrounded by the 90% confidence ellipse. The axis labels indicate the proportion of total variance explained. A. The full data set. B. Results for the ARV clade in isolation. C. Results for the BCHS clade in isolation. X and Y axes are plotted with equal scales, preserving the geometric distance among points.



Figure 6.3: Ecological Niche Models. Gray (light) shading indicates the extent of the study area and red (dark) shading is the Maxent climate suitability model for each species. The georeferenced herbarium records that the models were built from are indicated with an x. Maps are plotted on a 15° grid, with the intersections indicated with + symbols.

Table 6.4: Range Size Differences and Local Niche Distances. Values in the upper triangle are the absolute differences in the predicted range size, expressed in 10^5 km² units. Values in the lower triangle are the Mahalanobis distances among species for 15 local habitat variables for 231 plots at 84 field sites.

	acsti. Cesti: Cesti:	Dap Case.	⁰²⁷ escers	derse and a series	Capality.	beissurcedo	Sugnes.	Compoleneese
a estival is		1.8	4.7	12.4	9.2	10.1	8.7	5.7
roan ensis	6.2		6.5	14.2	11.0	11.9	10.5	7.5
virescens	3.7	1.0		7.7	4.5	5.4	4.0	1.0
bushii	22.7	20.6	17.5		3.2	2.3	3.7	6.8
caroliniana	16.7	13.0	11.4	5.8		0.9	0.5	3.5
hirsutella	13.2	11.6	8.8	4.0	1.8		1.4	4.5
swanii	7.2	7.7	4.9	12.1	5.2	4.2		3.0
complanata	17.6	14.4	12.0	3.6	2.1	1.1	6.1	

high proportion of exposed soil or rocky substrate (Figure 6.4). For the most part, the BCHS species and *C. complanata* are associated with relatively level ground, low canopy cover, and lower levels of exposed soil and rocky substrate. This last category is a reflection of the denser vegetation in the open field habitats: there is less exposed substrate of any kind here relative to the open understory of forest communities. *Carex swanii* is somewhat intermediate in terms of local-niche, occurring both in forest openings and old-fields. We recorded organic soils (coded as 0% sand, silt and clay) only for *Carex aestivalis*. This was unexpected, as this species is most common in high-elevation forests and exposed rock outcrops. However, within these habitats it frequently grows in rock fissures that do not contain any mineral soil. There were statistically significant differences among all species (p = 0.001), and within the ARV (p = 0.007) and BCHS clades (p = 0.001) for the overall local niche distance. Among individual variables, only litter depth and soil sand content were not significantly different among species (p > 0.15, all others p < 0.05). Within the ARV clade only canopy cover, moss cover, soil silt content, and pH were significantly different (p < 0.03), while trail distance, canopy height, canopy cover, moss cover, wood cover, litter cover, litter depth, and slope were all significantly different (p < 0.05) among the BCHS species.

The LDA of local niche variables captured most of the variation on the first axis (69-89%, Figure 6.5). For the overall analysis, the first axis separated the ARV clade from *C. bushii*, *C. caroliniana*, *C. complanata* and *C. hirsutella*, with *C. swanii* intermediate between the two groups. The most influential variable on this axis is trail distance (Table 6.5), reflecting the different disturbance regimes in the two habitat types. The ARV species are most frequently found on or adjacent to trails, and are relatively rare in undisturbed forest. The BCHS species and *C. complanata*, on the other hand, are less restricted to the localized disturbance associated with trails, and often occur more or less continuously across prairie and old-field communities.

Trail distance is also an important variable separating the species in the ARV clade (Table 6.5). This is due in part to the frequent occurrence of C. aestivalis on rock faces. These features may be a consequence of road construction or a limiting factor in the routing of footpaths, such that both kinds of "trail" are often found adjacent to the base of rocky cliffs. The lower position of C. aestivalis on the first LDA axis is also a reflection of its association with low pH organic soil, and lower canopy heights. This last pattern arises from the occurrence of C. aestivalis in high-elevation bald habitats in addition to the closed-canopy forests more typical of C. roanensis and C. virescens.

The importance of trail distance and canopy cover (Table 6.5) in explaining niche differences within the BCHS clade reflects a gradient from C. bushii, which rarely grows under forest canopy, through C. hirsutella and C. caroliniana, both of which occur in both open and wooded habitats, to C. swanii, which is more frequent

Discriminant variable	Total Analysis	ARV Clade	BCHS Clade		
Trail size	0.22	0.37	-0.35		
Trail distance	-1.31	-0.68	0.65		
Canopy height	-0.00	0.44	-0.07		
Canopy cover	-0.11	-0.00	0.53		
Litter depth	-0.04	0.06	-0.13		
pН	-0.05	0.50	-0.16		
Slope	-0.73	0.13	-0.13		
Soil textu					
Sand	0.19	0.27	-0.70		
Clay	0.03	0.25	-0.22		
Silt	0.03	0.37	-0.52		
Substrate type:					
Rock cover	-0.50	-0.06	0.15		
Moss cover	-0.33	-0.28	-0.02		
Wood cover	-0.41	0.25	0.20		
Soil cover	-0.35	0.35	0.20		
Litter cover	-0.72	0.08	0.58		

Table 6.5: Comparison of the standardized canonical coefficients for local niche variables on the first canonical axis of the total analysis, and for the ARV and BCHS clades examined separately.

in forests than in open fields. However, the single most important variable discriminating among these four species is soil sand content, indicating edaphic factors are an important niche trait among these species. It is also evident from the plots of single niche variables (Fig. 6.4) that *C. caroliniana* is associated with consistently higher soil clay content than the other species. This reflects the association of this species with floodplain habitats.

Mantel tests of the four niche distances against each of the four different patristic distance measures produced qualitatively very similar results. All of the tests using the band-frequency-by-species and band-frequency-by-population phylograms (Nei 1972) were statistically significant (p < 0.04). For the restriction-site phylogram all tests were statistically significant (p < 0.04) except for the correlation between phylogenetic distance and local niche distance, which was marginally significant (p =



Figure 6.4: Site Variables. Variables without an indicated scale are reported in classes, as described in Table 6.1. Boxplots show the median value and inter-quartile range, while whiskers extend to the most extreme values within 1.5 times the interquartile length from the lower and upper quartiles, and all additional outliers are plotted individually.



Figure 6.5: Linear discrimant analysis of local niche variables. Species names mark the mean values for that taxon on each axis (shifted slightly in some cases to reduce overlap), surrounded by the 90% confidence ellipse. The axis labels indicate the proportion of total variance explained. A. The full data set. B. Results for the ARV clade in isolation. C. Results for the BCHS clade in isolation. X and Y axes are plotted with equal scales, preserving the geometric distance among points.

0.06). None of the tests using the parsimony phylogram distances were significant (p range 0.051 to 0.105). Scatter plots contrasting niche distances against each of the different phylogenetic distances reveal the same patterns; the plots of niche distances against the band-frequency-by-species are representative (Figure 6.6).

Quantile regression for the climatic niche and ENM overlap distances reveal that the upper quantiles display a much stronger relationship with phylogenetic distance than the lower quantiles. The other two distance measures suggest the same pattern, but more subtly.

Mantel tests of individual climatic niche variables revealed significant or marginally significant correlations for precipitation in warmest quarter and annual precipitation (p < 0.07). However, annual precipitation was not significantly correlated with the parsimony-based patristic distance. Of the individual local niche variables, slope, rock cover, soil cover and wood cover were all significantly or marginally significantly correlated with all patristic distance measures (p < 0.06).

6.5 Discussion

For the most part, the ENM predictions describe contiguous areas that correspond to the input location records (Figure 6.3). This suggests that geographic barriers have not prevented the study species from dispersing to and establishing in areas of appropriate climate (Peterson 2006). We can infer from this that, within the geographic extent of our study, the ENM provides an adequate representation of the potential climatic niche. Had the ENMs predicted extensive areas beyond the known range of the species it would indicate that dispersal limitation or unmeasured nicheaxes prevent the species from occupying areas of suitable climate (see discussion in Soberón and Peterson 2005).

A notable exception is the disjunct region of suitable climate for *C. aestivalis* and *C. roanensis* in southwestern Nova Scotia. This area is separated from the known



Figure 6.6: Scatterplots contrasting niche distances with phylogenetic distance. Reported values for p and r are for Mantel tests between each pair of distances using Spearman's correlation coefficient and 10000 permutations. Quantile regression lines are plotted for the following quantiles: 10 and 90 (dotted), 25 and 75 (dashed), and 50 (median, solid). The phylogenetic distance is the patristic distance from the neighbour-joining tree based on AFLP band-frequency differences among species (Nei 1972). A. The climatic niche distance is the Mahalanobis distance calculated from seven climatic variables for each of 2772 georeferenced herbarium records. B. The geographic niche overlap distance is 1 - Horn Index (Horn 1966) calculated from the proportion of geographic overlap in ecological niche models. C. Range size difference is the Mahalanobis distance is the Mahalanobis distance at 231 plots at 84 field sites.

range of these two species by 1100 km and 1700 km (measured as the minimum overland distance), respectively, of apparently unsuitable climate. However, the small extent of this area relative to the total range of each species is unlikely to influence our overall results, although it does suggest that dispersal limitation has prevented these two species from establishing in Nova Scotia. It is also interesting to note that the ENM for *Carex roanensis* includes areas of northern and eastern Pennsylvania, New Jersey, and parts of New England, regions which are beyond the known range for this taxon. *Carex roanensis* is poorly known, and has apparently been overlooked in the field (Smith et al. 2006). Its recent discovery in collections from northern Pennsylvania (pers. comm., Steve Grund, Pennsylvania Natural Heritage Program, Pittsburgh) suggests that the apparent over-prediction of the ENM may indicate areas to search for previously over-looked populations of this globally rare species.

The Mantel tests indicate a strong signal of niche conservatism. The correlation was robust, with only minor changes in calculated significance levels for three of the four alternative phylogenies used in the tests. Even for the phylogeny based on parsimony analysis, which we suspect may be an inappropriate method for our AFLP data (Chapter 5), calculated p values never exceeded 0.105. Contrary to expectation, this correlation held for the local-niche as well as the climatic niche. This suggests that niche diversification in this group has proceeded by successively finer partitioning of available habitat, rather than a combination of conservatism along some niche axes and divergence along others. Of course, we cannot exclude the possibility that niche evolution within clades involves divergent adaptation along unmeasured niche axes. A shortcoming of our method is that it does not allow us to directly assess niche conservatism within terminal clades of three or four species, since there are not enough distance values in these groups to allow for robust permutation tests. While the overall niche distances showed niche conservatism at all scales, some individual climate and local niche variables did not. This is interesting, as we expected differences in the strength of niche conservatism to occur between, not within hierarchical niche levels. However, we need to be cautious in interpreting such results, particularly with respect to the local niche. The local niche variables are relatively coarse surrogate measures. For example, canopy height per se is unlikely to have a direct impact on the niche of understory herbs, but may be a useful measure of the age or structure of a forest stand. This, in turn, is associated with a suite of characteristics that do influence the environment experienced by understory species. Accordingly, it is difficult to assign meaning to patterns associated with one particular niche variable with no apparent direct influence on the species in question. However, while the importance of individual niche variables is uncertain, in aggregate we are confident that they do capture important components of the environment as experienced by our study species.

We also note that our local niche variables, with which we had hoped to capture variation within the α niche, were more effective at the β niche scale. Much of the apparent variation in these variables is related to broad differences between habitat types (forest vs. open), rather than finer distinctions within these habitats. Consequently, we cannot rule out the possibility that the observed pattern of niche conservatism does not extend to the α niche, which would be consistent with the theory proposed by Silvertown et al. (2006). Our local niche variables may have better reflected the α niche had we been able to include some measure of water availability. This is an important niche factor controlling plant communities (Silvertown et al. 1999; Gilbert and Lechowicz 2004), but is difficult to measure consistently across sites from a large geographic range. The presence of a phylogeny-niche correlation is a clear signal of niche conservatism. However, the shape of this relationship, as illustrated through quantile regression, indicates it is not a simple linear correlation. It is evident, particularly in the climatic niche and geographic niche overlap plots, that the relationship between phylogeny and niche distance is much stronger for the upper quantiles of the sample than for the lower quantiles. This is the pattern expected when the explanatory variable (in this case, phylogenetic distance), is one of many limiting factors (Cade and Noon 2001). Our results indicate that phylogenetic distance may impose an upper limit on niche divergence between two species, but below that limit other factors influence the actual observed distance. Another suggestive pattern in the quantile regression analysis is the group of outliers above the 75th quantile. Again, this is most evident for the climatic niche and geographic niche overlap plots. These outliers are contrasts between species with simultaneously high niche and phylogenetic divergence. As such, the pattern may indicate that the influence of niche conservatism in restraining evolutionary divergence is limited to very closely related species.

Confirming this conclusion will require extending this analysis to include more distant relatives. Based on our results, we hypothesize that the niche-phylogeny correlation will be recovered from branches restricted to only very close relatives, but not from more inclusive clades. If this is indeed the case, it will validate our methodology as a useful tool in identifying the phylogenetic scale at which niche conservatism influences evolutionary processes. While our results suggest that the local-niche and climatic niche diverge at comparable rates, it may also prove fruitful to develop additional measures to assess different aspects of each species' ecology. Assessing the α niche in lineages that include species with widely varying geographic and ecological distribution presents a special challenge. Greenhouse experiments have proven an effective way to assess the relative physiological response of *Carex* species to experimentally manipulated environmental conditions (Dabros 2004), and may be an important tool in addressing this problem.

The major obstacle in extending this work is acquiring a well-resolved, wellsupported phylogeny for the entire 'Gracillima' Group. This will be challenging, as inconsistencies remain in analyses based on five gene regions and AFLP data (Waterway 2006, Chapter 5). However, similar analyses have been conducted for different taxa, and provide informative contrasts to our study. Rice et al. (2003) were the first to assess niche conservatism in the framework of a Mantel test between ENM-derived distances and phylogenetic distances. They found no correlation in the *Aphelocoma* jays, indicating that this taxon was characterized by rapid ecological diversification. While their analysis differed from ours in specific details, the overall approach is comparable: they developed niche distances based on ENM projections in geographic space, and distances between species centroids in environmental space.

Given their similar analytical approach, the absence of any signal of niche conservatism in the *Aphelocoma* jays is likely a reflection of biological differences. The most important difference may be the extent of phylogenetic divergence. Rice et al. (2003) produced a fairly well supported phylogeny for the 10 species in their study with an order of magnitude less sequence data than now available for *Carex* (Waterway 2006). While it is impossible to quantitatively compare phylogenetic analyses at such broad taxonomic scales, this suggests that the *Aphelocoma* jays have undergone more substantial phylogenetic divergence than the *Carex* species in our study. Given their highly mobile nature, the jays are capable of much more extensive exposure to environments with divergent selection pressure, another factor which could have contributed to their high rate of niche evolution.

The landmark study of Peterson et al. (1999) provided compelling evidence of niche conservatism in 21 sister-species pairs of non-migratory birds, as well as 11 mammal pairs and five butterfly pairs, distributed north and south of the Isthmus of Tehuantepec. This study was also based on ENM data, but did not explicitly quantify the extent of phylogenetic divergence among species. The most obvious difference between this situation and the Aphelocoma data is the presence of a well-established geographic barrier dividing the distribution of the sister-species studied by Peterson et al. (1999). Thus, speciation in that group was presumably a strictly vicariant process. There are no apparent geographic barriers among the Aphelocoma species, with members of the genus ranging widely across the southern U.S.A. Reinforcement of niche divergence following secondary contact (Coyne and Orr 2004) among these species may have played a role in speeding evolution in that group relative to what occurred in the Tehuantepec scenario. This suggests another hypothesis for further investigation: is the phylogenetic context within which niche conservatism acts extended in situations where geographic barriers prevent secondary contact? In other words, does the niche conservatism described by Peterson et al. (1999) represent a special case resulting from its particular geographic context, or is the rapid evolution of the Aphelocoma jays an anomaly?

There is only one other study that we are aware of that used the Mantel test to asses relationship between ENM-generated niche-distances and phylogenetic distances: a study of the *Anolis sagrei* group on Cuba (Knouft et al. 2006). The methods in that study are comparable to those used by Rice et al. (2003) and in our work, including generating measures of niche overlap in geographic and environmental space from ENM data and contrasting them with phylogenetic distances recovered from molecular data. The results of the Mantel tests revealed no significant relationship between niche distance and phylogenetic divergence, and examples of all possible combinations of niche-phylogeny relationships among species were recovered, i.e., similar and divergent niches for both close and distant relatives, including niche divergence among allopatric sister species. However, close examination of their data indicates that a correlation may exist between niche and phylogenetic distance for the most closely related species in the study, but the variation increases dramatically as the phylogenetic distance increases. This is consistent with our hypothesis that niche conservatism is clearly expressed only for very close relatives. The phylogenetic analysis of the *Anolis sangrei* group recovered a completely resolved topology with very high support (bootstrap values > 96%) from a 1500 bp dataset, which provides weak support for our contention that these species have undergone more extensive phylogenetic distances across such large taxonomic scales must be interpreted with caution, but the pattern is coarse enough to warrant consideration.

One of the first attempts to identify niche conservatism in plants was an investigation of *Fagus* species from North America and Europe (Huntley et al. 1989). They found that projecting the climatic niche of species from one continent to the other provided a statistically significant prediction of the range of the resident taxa. This indicates strong niche conservatism between species separated since at least the mid-Tertiary. Ricklefs and Latham (1992) found a similar correlation in the Asian and North American geographic ranges of herbaceous taxa with members on both continents. However, this pattern was not present in woody taxa, which lead them to hypothesize that niche conservatism may be more pronounced in ecological specialists than in generalists. More recently, Hoffmann (2005) examined niche conservatism in *Arabidopsis*. He found patterns of overall niche conservatism in the genus, but with episodes of convergent evolution of the climatic niche in different regions of their phylogeny. He used a uniquely developed system combining published range maps with climatic data. This approach has not been evaluated critically, but is presumably comparable to conventional ENM analysis. Prinzing et al. (2001) examined niche conservatism in more than 100 European plant species along six different environmental gradients. They found considerable niche conservatism, with the general degree and taxonomic pattern of the conservatism varied widely among different gradients. This analysis was based on the quantitative convergence index (QVI) concept (Ackerly and Donoghue 1998), which quantifies convergence as a function of the tree-length for the character of interest, equivalent to 1 - Retention Index (Farris 1989). The same approach was used by Yesson and Culham (2006) in their investigation of the climatic niche of *Cyclamen* species. They determined that 8 of 14 climatic variables demonstrate phylogenetic conservatism. However, there was no evidence of niche conservatism as estimated from the ENMs calculated from these variables. Thus, while individual niche axes were conserved, the overall climatic niche was not. Martínez-Meyer and Peterson (2006), drawing on pollen records for 8 North American plant species, demonstrated climatic niche conservatism during a 20000-year period of marked climatic variation.

The growing interest in niche conservatism, generated in part by the new possibilities enabled by ENM analysis, has yielded intriguing data from a broad variety of evolutionary systems. The results of these studies suggest that niche conservatism is a context-dependent phenomena, indicating that more studies assessing patterns in different ecological, phylogenetic, and geographic contexts are necessary to expand our understanding of this topic. However, as Wiens and Graham (2005) point out, simply identifying additional examples of niche conservatism will not be enough. It is already well-established as an evolutionary process. Based on our own results, and a review of recent work in this area, we see three important questions that need to be addressed:

What is the phylogenetic scale at which niche conservatism is an important process? Our study is one of only three investigations that we are aware of to explicitly quantify the extent of phylogenetic divergence in examining niche evolution. The conflicting results of these three studies suggest that the influence of niche conservatism, at least as estimated by climatic variables, is evident only for very closely related species. We have demonstrated the potential for Mantel matrix analysis to identify not just the presence of a phylogeny-ecology correlation, but to provide a means to identify the scale at which that correlation breaks down. Advancing this practice will require extending it to include large, fully resolved phylogenies that include very recently diverged species as well as more distant relatives.

What aspects of the niche are most strongly influenced by niche conservatism? Contrasting results for different niche axes (Prinzing et al. 2001), as well as between single axes and composite niche models (Yesson and Culham 2006) suggest that the evolution of different aspects of the niche may proceed at very different rates. Cavender-Bares et al. (2004) established this with community-level studies, and Silvertown et al. (2006) developed a theoretical framework identifying the ecological scales where niche conservatism is most likely to play a strong role. These ideas should be examined in the context of phylogenetic lineages.

Can particular biological or biogeographic phenomena be identified that enhance or diminish the strength of niche conservatism? Species with overlapping ranges (Rice et al. 2003) appear to demonstrate more rapid and convergent niche evolution than is evident in species separated by geographic barriers (Huntley et al. 1989; Peterson et al. 1999). This may be a consequence of reinforcement of niche divergence following secondary contact. Drawing firm conclusions will require examining large clades that include both sympatric and allopatric lineages. It is also interesting to note that niche conservatism is more consistently recovered in analyses of plants than animals. The higher dispersal ability and increased potential for direct competitive interactions among highly motile taxa may increase their rate of niche evolution. Ricklefs and Latham (1992) posited that niche conservatism is strongest in ecological specialists; this suggests that investigations of lineages that contain both specialists and generalists may yield further insights into the influence of niche conservatism in structuring evolutionary patterns.

CHAPTER 7 Summary and Conclusions

In this final section I briefly summarize the major contributions of this dissertation, and discuss its implications for future research.

7.1 Contributions to science

7.1.1 Taxonomy

A. Confirmed the taxonomic status of *Carex roanensis*

A combination of morphology and AFLP data confirm that *Carex roanensis* is most appropriately recognized at the species level. Due to a lack of information, previous authors had expressed uncertainty regarding this issue. I developed improved keys, which will enable field botanists to better identify *Carex roanensis* in the field. This is an important point, as I documented 30 previously overlooked populations of this species, including new state records for Pennsylvania and South Carolina.

B. Confirmed the distinction between *Carex swanii* and *C. virescens*

These two taxa were the subject of much debate between prominent caricologists. Despite their very similar morphology, my AFLP analysis confirms that they are discrete entities best recognized as separate species. I developed improved keys to allow field botanists to more reliably distinguish between these taxa. I also clarified issues surrounding their ranges, removing *Carex virescens* from the flora of Arkansas, and identifying previously overlooked collections of *Carex swanii* from Alabama.

C. Confirmed the distinction between *Carex complanata* and *C. hirsutella*

These two taxa are distinguished by very subtle physical differences, and many botanists consider them a single variable species. My work demonstrates that only a single morphological trait reliably discriminates between them, but they are nevertheless very clearly distinct genetically. Consequently, I have recognized them as separate species. My work allowed me to correct distribution records for both species, removing *Carex complanata* from the floras of West Virginia and Missouri, removing *Carex hirsutella* from the flora of Louisiana.

D. Rejected the hypothesis that the *Carex complanata* complex is a single variable species

Some authors had suggested that the four taxa in the *Carex complanata* complex are in fact a single variable species, with hybridization blurring any distinctions among them. I used a combination of morphology, AFLP fragments, and restriction enzyme analysis to identify hybrids involving these species. The results show that while hybridization does occur, it is rare, and the resulting individuals appear to have limited fertility. The AFLP data show no evidence of gene-flow between taxa, and I conclude that they are indeed discrete species. I developed keys to improve the ability of field botanists to discriminate among these species, and documented six previously unknown hybrids.

7.1.2 Phylogeny

A. Confirmed the close relationship among *Carex aestivalis*, *C. roa*nensis and *C. virescens* (the ARV clade)

Previous molecular analysis recovered a well-supported branch containing these three species. My phylogenetic analysis of the AFLP data confirms this arrangement. This is noteworthy, as these three species are traditionally placed in two different sections. This indicates that this arrangement is unnatural, and will need to be revised. Furthermore, it is interesting that *Carex swanii* is not part of this clade. *Carex virescens* and *C. swanii* are so similar in morphology that some authors have considered them a single species. My analysis shows that their physical similarity is a consequence of either retained ancestral characteristics, or convergent evolution. In either case, their morphology does not reflect their evolutionary relationship.

B. Confirmed the close relationship among *Carex bushii*, *C. car*oliniana, *C. hirsutella* and *C. swanii* (the BCHS clade)

This group of species are all traditionally placed in section *Porocystis*. Recent molecular work identified them as forming a well-supported clade, and my AFLPbased analysis confirms it. This is noteworthy in that it separates *C. swanii* from *C. virescens*, as discussed above. Similarly, this arrangement separates *Carex complanata* from *C. hirsutella*, two species that are extremely similar in morphology. Again, this suggests that the physical characteristics of these species reflect retained ancestral characteristics or convergent evolution. This pattern, combined with the poor resolution of the phylogeny of this group as a whole, suggests that these eight species are the product of a recent, rapid radiation.

7.1.3 Evolutionary Ecology

A. Confirmed ecological differentiation among all eight species

My analysis shows statistically significant differences in ecological variables among all eight species and among species within the ARV and BCHS clade. This confirms niche divergence in this group along axes represented by climate variables, ecological niche models, and local habitat variables.

B. Confirmed a significant relationship between niche distance and phylogenetic distance

I compared the niche distances calculated from each of my ecological data-sets to the evolutionary distances derived from my phylogenetic analysis, and found a statistically significant correlation. This is evidence for niche conservatism: closely related species are more likely to occupy similar habitats than distant relatives. Furthermore, the shape of the pattern suggests that it is not a simple linear relationship. Phylogenetic divergence appears to act as a limiting factor on ecological divergence. The upper limit of ecological divergence is constrained by phylogenetic distance, but within this limit other factors govern niche evolution. Thus, close relatives are restricted to similar niches, while distant relatives may occupy similar or different niches.

7.2 Future Directions

My results have resolved the major outstanding issues surrounding the taxonomy of the *Carex roanensis* and *C. complanata* complexes. Further investigation may be warranted to determine the extent of geographic population structure in *C. virescens* and *C. caroliniana*. The AFLP data presented here suggests that the internal division within these species is much smaller than the differences among species, so it is unlikely to be important taxonomically. However, it may indicate interesting phylogeographic patterns. The apparent structure in the AFLP data for *C. hirsutella* is also interesting, and further research will be needed to determine if this is an indication of inter-specific gene-flow.

Clearly, more work is needed to clarify the phylogeny of this group. The differing, weakly-supported topologies produced from the AFLP data suggest that branching events within the ARV and BCHS clades occurred very rapidly. Consequently, no single data source may be informative enough to provide full resolution of this issue. Explicitly combining AFLP and DNA sequence data may be a fruitful approach. I was unable to determine the relationship of the eight species in this study to other members of the 'Gracillima' group. More extensive sampling of the outgroup is needed; the variability in the AFLP data precludes basing analyses on single representatives of a species. Among the ingroup species, *Carex caroliniana* was recovered as a well-supported monophyletic clade in all analyses, based on 27 samples from six populations. This suggests a minimum sampling effort for future work on the outgroup species.

My work has not addressed the three members of section *Porocystis* from Central and South America: *Carex angustispica*, *C. boliviensis* and *C. tovariensis*. These species have not yet been included in any molecular systematics study. The data presented here showed that morphological similarity is not a reliable predictor of phylogenetic relationship in section *Porocystis*. This is further amplified by the finding that *C. pallescens* and *C. torreyi* are clearly not close relatives of the other members of section *Porocystis* in North America. Consequently, further work is required to determine if the Central and South American species are in fact closely related to the taxa in this study.

My analysis clearly demonstrates a significant relationship between phylogenetic distance and niche divergence. I did not expect to find niche conservatism at all niche scales measured. However, careful consideration of my local niche variables suggests that they reflect differences between habitats, rather than within habitats. As such, my study did not fully address fine-scale niche divergence. Most notably, I did not measure water availability. This is likely an important niche factor, but is difficult to assess in a consistent way for sites that are widely dispersed geographically. Measurement of soil nutrients may also provide useful insight into the α niche. The difficulty of assessing these variables in widespread field locations suggests that greenhouse experiments may provide a more manageable venue for further research.

The results of my analysis of niche conservatism have important implications for further investigations of the subject. Very few studies have explicitly quantified the extent of phylogenetic divergence among the taxa they examine. Rather, they focus on the potential for species of varying levels of relationship to predict each other's niche. The results are therefore limited to binary conclusions - close relatives are or are not better predictors of each other's niche than null expectations. The approach I used allows for more nuanced interpretation: what is the shape of the relationship between niche distance and phylogenetic distance? The results of my study indicate that it is not a simple linear relationship. Closely related species are strongly constrained to occupy similar niches, but the strength of this relationship diminishes over time. Further research is necessary to determine which niche traits are most constrained by niche conservatism; if the phylogenetic scale at which niche conservatism acts varies for different niche axes; and what biological or biogeographic factors influence the strength of niche conservatism.

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Appendices

APPENDIX A Population and Individual Samples

Unless otherwise noted, population samples are comprised of 20 randomly selected specimens. Rather than assign a collection number to each individual, populations are identified by a unique code representing the state and county of collection, and each specimen is identified by number. For example, the *C. aestivalis* population from Rabun County, Georgia has the code GRA, with individual specimens GRA1 – GRA20. All vouchers, with full locality data and GPS coordinates, are deposited at MTMG. Individual samples are comprised of one or more individuals selected as representative exemplars of their species. Documenting vouchers are deposited at MTMG. All populations of *Carex aestivalis*, *C. bushii*, *C. caroliniana*, *C. complanata*, *C. hirsutella*, *C. roanensis*, *C. swanii* and *C. virescens* were included in the ecological survey, except those marked with an *. Unless otherwise noted, three ecological samples were taken at each population.

Carex aestivalis. 13 populations. U.S.A. Georgia: Rabun Co., Rabun Bald, GRA. Union Co., Brasstown Bald, GUA. Kentucky: Harlan Co., Black Mountain, SR 160, KYHA. Wayne Co., Daniel Boone National Forest, SR 154 at Tennessee border, KYWA. North Carolina: Macon Co., Wayah Bald, NCMA. Transylvania Co., Blue Ridge Parkway & US276, NCTA. Pennsylvania: Fayette Co., Ohiopyle State Park, Beech Trail, (small population, 3 samples taken) PAFA*. Potter Co., Susquehannock State Forest, East Fork Road, PAPA*. Tennessee: Carter Co., Carvers Gap Creek Road & Appalachian Trail at North Carolina border, TNCA. Sevier Co., Alum Cave trail, TNSA. Virginia: Floyd Co., Buffalo Mountain, VAFA. Smyth Co., Mt. Rogers National Recreation Area, Mt. Rogers Trail & SR603, VASA.

West Virginia: Randolph Co., Rich Mountain near Blue Rock Knob, WVRA.

Carex arctata. One individual collection. Canada. Quebec: Vallée-du-Richelieu Co., Mont St. Hilaire, 23 June 1996, A. Bond arc-msh.

Carex bushii. U.S.A. Alabama: Etowah Co., Gadsden Airport Road (small population, 5 samples taken), ALETBu^{*}. Arkansas: Garland Co., Ouachita National Forest, north of Iron Springs Recreation Area on SR7, ARGABu (two ecological samples). Izard Co., SR5 near Calico Rock Airport, ARIZBu. Pope Co., Ozark National Forest, Piney Creeks WMA, Kings Bluff Trail, ARPOBu (one ecological sample). Van Buren Co., Clinton, Greers Ferry Lake, ARVBBu (one ecological sample). Delaware: New Castle Co., Brandywine Creek State Park, DEB-WBu. Mississippi: Chickasaw Co., Tombigbee National Forest, CR 413 west of Owl Creek Mound Archaeological Site, MSCHBu. Tennessee: Monroe Co., Sweetwater, Old Kingston Road & I75, TNMOBu. Texas: Robertson Co., Old San Antonio Road/FM 1940, TXROBu. West Virginia: Tucker Co., Canaan Valley NWR, WVCABu (two ecological samples).

Carex caroliniana. U.S.A. Alabama: Marshall Co., Guntersville Dam, AL-MACa. Illinois: Pope Co. Shawnee National Forest, Lake Glendale Recreation Area, ILPOCa. Louisiana: Grant Co., Kisatchie National Forest, Catahoula District, Saddle Bayou, LAGRCa. Mississippi: Holmes Co., south of Cruger, Hwy 49E, MSHOCa. North Carolina: Durham Co., Glenn Road, Glenn Stone Subdivision, NCDU1Ca. Ellerbe Creek (small population, 3 samples taken), NCDU2Ca^{*}. South Carolina: Greenwood Co., Cuffytown Creek & SSR 44, SCGRCa. Texas: San Jacinto Co., FM 2025 south of Coldspring, TXSJCa.

Carex castanea. Three individual collection. Canada. Quebec: Pontiac Co., alvar near Bristol, 19 June 1999, M. J. Waterway 99.083. Matapedia Co., near St. Leon le Grand, 11 May 1997, *M. J. Waterway 3095.* Cultivated: Garden-grown in Ann Arbor, MI, by A. A. Reznicek, collected 13 May 1997, *M. J. Waterway s.n.*

Carex complanata. U.S.A. Alabama: Etowah Co., Gadsden Airport Road, ALETCO. Arkansas: Garland Co., Ouachita National Forest, north of Iron Springs Campground on SR7 (mixed with C. hirsutella and C. bushii), ARGACo^{*}. Stone Co., Ozark National Forest, Sylamore WMA, SR14, Bearpen Sink, ARSTCo (one ecological sample). Van Buren Co., Clinton, Greers Ferry Lake, ARVBCo*. Delaware: Kent Co., Dover, DEKECo. Georgia: Walker Co., Chattahoochee National Forest, Johns Mountain WMA, Pocket Road (small population, 5 samples taken), GAWACo^{*}. Louisiana: Natchitoches Parish, Kisatchie National Forest, Kisatchie District, FR 341 & FR 339, LANACo. Mississippi: Jasper Co., west of Barnett, under I59 overpass, MSJACo. Marshall Co., Wall Doxey State Park (a single plant growing with C. hirsutella), MSWDCo^{*}. North Carolina: Orange Co., Triangle Conservancy, Jones Ferry Road, NCORCo. South Carolina: Greenwood Co., Beaverdam Creek & SSR 44, SCGRCo. Tennessee: Cumberland Co., Rockwood, Airport Road/SR299 (small population, 5 samples taken), TNCUCo^{*}. Texas: San Jacinto Co., Sam Houston National Forest, Big Creek Scenic Area, TXSJCo. Virginia: Appomattox Co., Holiday Lake State Park, VAAPCo.

Carex dasycarpa. One population. U.S.A. Alabama: Houston Co., Chatahoochee State Park ALHODa.

Carex davisii. One individual collection. Canada. Ontario: Essex Co., NE of Amherstburg, 10 June 1990, M. J. Waterway 3731.

Carex debilis. Two populations. U.S.A. Louisiana: Grant Co, Kisatchie National Forest, LAGRDe. Virgina: Appomattox Co., Holiday Lake State Park, VAAPDe. Carex formosa. Two individual collections. Canada. Ontario: Stormont, Dundas and Glengarry United Counties, Cornwall, McConnel Blvd., 20 May 1991,

M. J. Waterway 3852. Hastings Co., 27 June 2005, M. J. Waterway 2005.036

Carex gracillima. One individual collection. Canada. Quebec: Vallée-du-Richelieu Co., Mont St. Hilaire, 6 May 1998 M. J. Waterway MSH-gra98.

Carex gynodynama. Two individual collections. U.S.A. California: Mendocino Co., near Gualala, 29 May 1999, M. J. Waterway 99.037; near Boonville 29 May 1999, M. J. Waterway 99.032.

Carex hirsutella. U.S.A. Alabama: Etowah Co., Gadsden Airport Road (two plants growing with *C. bushii* and *C. complanata*), ALETHi^{*}. Lawrence Co., Bankhead National Forest, Black Warrior WMA, FR 229, ALLAHi. Arkansas: Garland Co., Ouachita National Forest, north of Iron Springs Campground on SR7, ARGAHi. Izard Co., SR5 near Calico Rock Airport (one plant growing with *C. bushii*), ARIZHi^{*}. Pope Co., Ozark National Forest, Piney Creeks WMA, Kings Bluff Trail, ARPOHi (two ecological samples). Van Buren Co., Clinton, Greers Ferry Lake, ARVBHi^{*}. Delaware: New Castle Co., Brandywine Creek State Park, DEB-WHi. Georgia: Stephens Co., Chattahoochee National Forest, Lake Russell WMA, GASTHi. Union Co., Trackrock Gap Road (small population, one sample taken), GAUHi^{*}. Illinois: Hardin Co., Shawnee National Forest, Garden of the Gods, ILHAHi. Mississippi: Marshall Co., Wall Doxey State Park MSWDHi. North Carolina: Orange Co., Duke Forest, Whitfield Road, NCORHi. Pennsylvania: Bradford Co., State Game Lands, West Franklin, Schrader Creek Road, PABRHi^{*}. Fayette Co., Ohiopyle State Park, Kentuck Campground, PAFAHi (one ecological sample). South Carolina: Fairfield Co., Ridgeway, SSR 106 & Interstate 77, SC-FAHi. Tennessee: Loudon Co., Tellico Parkway, TNLOHi. Cumberland Co., Rockwood, Airport Road/SR299 (small population, 5 samples taken), TNCUHi*. Virginia: Appomattox Co., Appomattox Buckingham State Forest, VAAPHi. West Virginia: Tucker Co., Canaan Valley NWR, WVCAHi*.

Carex hirtifolia. Three individual collections. Canada. Quebec: Vallée-du-Richelieu Co., Mont St. Hilaire, collected from a greenhouse-cultivated sample, 5 December 1997, M. J. Waterway MSHhir2; Mont St. Hilaire, 5 May 1999, M. J. Waterway 99.003.

Carex hirtissima. Three individual collections. U.S.A. California: Butte Co.,
near Forbestown, Penny Pines Midas Plantation, 27 May 1999, M. J. Waterway
99.024 (typical form)& 99.025 (glabrous form). Yuba Co., Challenge Cut-Off Road,
27 May 1999, M. J. Waterway 99.026

Carex mendocinensis. Three individual collections. U.S.A. California: Mendocino Co., near Gualala, 29 May 1999, M. J. Waterway 99.036. Del Norte Co., near Gasquet, 2 June 1999, M. J. Waterway 99.050; Hwy 199, at Darlingtonia picnic area, 2 June 1999, M. J. Waterway 99.051.

Carex misera. Two populations. U.S.A. North Carolina: Macon Co., Whiteside Mt, NCMaM. Tennessee: Sevier Co., Mt. LeConte, TNSM.

Carex oxylepis. One individual and three populations. U.S.A. Alabama: Marshall Co., Guntersville Dam, ALMAOx. Arkansas: Greene Co., Gaynes Cemetery ARGROxMississippi: Pontotoc Co., Trace State Park, 14 May 2004 *T. W. Smith* 499.

Carex pallescens. Three individual collections. Canada. Quebec: Arundel Co., near Arundel, along road from Arundel to Harrington, 21 July 1999, Y. Bérubé YB99-025. Vaudreuil-Soulanges Co., Hudson, 21 June 2002, M. J. Waterway 2002.081. Switzerland. Bern: Berner Oberland, NW of Grindelwald, near
First on trail toward Bachalpsee, 30 June 2003, M. J. Waterway 2003.048

Carex planostachys. Two individual collections. U.S.A. Arkansas: Little River Co., SW of Foreman, 6 May 2001, M. J. Waterway 2001.069 & 2001.072.

Carex roanensis. 9 populations. U.S.A. Kentucky: Harlan Co., Black Mountain, SR 160, KYHR. North Carolina: Buncombe Co., Pisgah National Forest, Sugarhouse Cove, NCBR. Mitchell Co., Carvers Gap Creek Road & Appalachian Trail at Tennessee border, NCMR. Transylvania Co., Pisgah National Forest, Cove Creek NCTR. Pennsylvania: Fayette Co., Ohiopyle State Park, Sugar Run Trail, (small population, 7 samples taken) PAFR (one ecological sample). Tennessee: Carter Co., Cherokee National Forest, FR50, TNCR. Virginia: Floyd Co., Buffalo Mountain, VAFR. Smyth Co., Jefferson National Forest, Quebec, SR670 & Appalachian Trail, VASR. West Virginia: Pocahontas Co., Droop Mountain Battlefield State Park, WVPR.

Carex swanii. 21 populations. Canada. Ontario: Norfolk Co., Backus Woods, ONTS*. U.S.A. Arkansas: Greene Co., Gaynes Cemetery (small population, 2 samples taken), ARGRS*. Montgomery Co., Ouachita National Forest, Ragweed Valley Road, (small population, five samples taken) ARMOS (one ecological sample). Montgomery Co., just north of Pike Co., Ouachita National Forest, Little Missouri River & CR4, ARPIS. Stone Co., Ozark National Forest, Sylamore WMA, SR14, Bearpen Sink, ARSTS. Georgia: Rabun Co., SR28 & Chattooga River, GRS. Union Co., Trackrock Gap Road, GUS. Illinois: Pope Co., Glendale Lake Recreation Area, ILGLSw. Michigan: Ottawa Co., WNW of Holland, MICHSw*. North Carolina: Macon Co., Wayah Bald, NCMaS. Mitchell Co., Bean Creek Road, NCMiS. Transylvania Co., Pisgah National Forest, Pink Beds Picnic Area, NCTS. **Pennsyl**vania: Bedford Co., Cumberland Valley PABS*. Fayette Co., Ohiopyle State Park PAFAS (two ecological samples). **Tennessee:** Blount Co., Great Smokey Mountains National Park, Cades Cove, TBS. Tennessee: Cumberland Co., Rockwood, Airport Road/SR299 (a single plant growing with *C. hirsutella* and *C. complanata*), TNCUS*. Grundy Co., SR399 near South Cumberland State Park, TNGS. **Virginia:** Dickenson Co., Jefferson National Forest, SR80, VADS. Giles Co., Mountain Lake Research Station, VAGS. **West Virginia:** Tucker Co., Canaan Valley NWR, WVCAS. Pocahontas Co., Droop Mountain Battlefield State Park, WVPS.

Carex tenax. U.S.A. Louisiana: Natchitoches Parish, Kisatchie National Forest, Kisatchie District, FR 341 & FR 339, LANAT.

Carex venusta. One population and five individuals. U.S.A. New Jersey: Atlantic Co., edge of Brigantine National Wildlife Refuge, 9 June 1998, *M. J. Waterway* 98.081, 98.082 & 98.083. Florida: Santa Rosa Co., 8 May 2000, *M. J. Waterway* 2000.047. Walton Co., 8 May 2000, *M. J. Waterway* 2000.049B. North Carolina: Scotland Co., Sandhills gameland NCSCVe.

Carex virescens. 17 populations. Canada. Ontario: Norfolk Co., Backus Woods, ONTV^{*}. U.S.A. Alabama: Lawrence Co., Bankhead National Forest, Sipsey Wilderness, (small population, three samples taken) ALLAV^{*}. Georgia: Rabun Co., SR28 & Chattooga River, GRV. Union Co., Trackrock Gap Road, GUV. Illinois: Hardin Co., Garden of the Gods ILGGV (one ecological sample). North Carolina: Macon Co., Wayah Bald, NCMV. Transylvania Co., Pisgah National Forest, Pink Beds Picnic Area, NCTV. Pennsylvania: Fayette Co., Ohiopyle State Park, Sugar Run Trail, PAFAV (one ecological sample). Ohiopyle State Park, Meadow Run Trail, PAFA2V^{*}. Potter Co., Susquehannock State Park, State Highway 44, PAPV^{*}. Tennessee: Blount Co., Great Smokey Mountains National Park,

TBV (two ecological samples). Anderson Co., Laurel Grove, TNAV. Carter Co., Cherokee National Forest, FR50, TNCV. **Virginia:** Floyd Co., Buffalo Mountain, VAFV. Smyth Co., Jefferson National Forest, Quebec, SR670 & Appalachian Trail, VASV. Wise Co., VAWV. **West Virginia:** Pocahontas Co., Droop Mountain Battlefield State Park, WVPV.

APPENDIX B Gels

This appendix contains representative examples of the gels produced in the course of my research. Figures B.1–B.5 are representative examples of my AFLP data. Only one gel per primer pair is presented; a complete set of gels and the associated data will be on file in the Department of Plant Science as a digital appendix. The scored AFLP fragments are labelled with their size in base-pairs. The species of the sample in each lane is indicated with a letter as follows: A: *C. aestivalis*, B: *C. bushii*, C: *C. complanata*, D: *C. debilis*; H: *C. hirsutella*, L: *C. caroliniana*, M: *C. misera*; N: *C. venusta*; O: *C. oxylepis*; R: *C. roanensis*, S: *C. swanii*, T: *C. tenax*; V: *C. virescens*; Y: *C. dasycarpa*. Putative hybrids are identified by number as follows: 1. *C. caroliniana* \times *hirsutella*; 2. *C. complanata* \times *oxylepis*; 3. *C. caroliniana* \times *insutella*; other unlabelled lanes were treated as reaction failures and not scored. Figures B.6–B.9 document restriction digests of amplified DNA regions analyzed in Chapter 4.



Figure B.1: AFLP gel for the MseI + CAA \times EcoRI + ACG primer pair



Figure B.2: AFLP gel for the $MseI + CAG \times EcoRI + AAC$ primer pair



Figure B.3: AFLP gel for the $MseI + CTA \times EcoRI + ACT$ primer pair



Figure B.4: AFLP gel for the $MseI + CAC \times EcoRI + AGC$ primer pair



Figure B.5: AFLP gel for the MseI + CAA \times EcoRI + AAG primer pair



Figure B.6: Restriction fragments produced from a digestion of the chloroplast rpl16 gene region with the DdeI enyzme. Lanes: A. C. hirsutella; B. C. swanii; C–D. C. bushii; E. C. swanii; F. C. hirsutella; G. C. swanii \times complanata; H. C. bushii \times swanii. Fragments: 1. 500 bp; 2. 354 bp; 3. 200 bp; 4. 180 bp.



Figure B.7: Restriction fragments produced from a digestion of the chloroplast rpl16 gene region with the DdeI enyzme. Lanes: A. C. swanii × complanata hybrid; B. C. bushii × swanii hybrid; C–D. C. swanii; E–F. C. oxylepis; G–H. C. complanata. Fragments: 1. 500 bp; 2. 354 bp; 3. 200 bp; 4. 180 bp.



Figure B.8: Restriction fragments produced from a digestion of the ITS gene region with the *TseI* enyzme. Lanes: A. *C. bushii* × *swanii* hybrid; B. *C. swanii* × *complanata* hybrid; C–D. *C. caroliniana* × *hirsutella*; E. *C. complanata* × *oxylepis*; F–I. *C. bushii* × *hirsutella*; J–K. *C. bushii*. L–M. *C. complanata*; N. *C. hirsutella*; O–P. *C. oxylepis*; Q. *C. caroliniana*; R. *C. bushii*; S. *C. swanii*. Fragments: 1. 620 bp; 2. 574 bp; 3. 548 bp.



Figure B.9: Restriction fragments produced from a digestion of the ITS gene region with the *TseI* enyzme. Lanes: A. C. caroliniana × complanata hybrid; B. C. bushii × hirsutella hybrid; C. C. swanii; D. C. hirsutella; E. C. caroliniana; F. C. hirsutella; G. C. caroliniana; H. C. swanii; I. C. complanata; J. C. bushii; K. C. carolinana × hirsutella; L–M. C. bushii × hirsutella; N–O. C. oxylepis; P. C. bushii × swanii; Q. C. swanii × complanata; R. C. complanata × oxylepis; S. C. complanata. Fragments: 1. 620 bp; 2. 574 bp; 3. 548 bp.
APPENDIX C Herbarium Specimens Examined

Carex aestivalis. U. S. A. Connecticut: Litchfield Co., Sage's Ravine, Salisbury, A. E. Blewitt s.n. 1908 (GH); New Haven Co., New Haven, R. W. Woodward s.n. 21 Jun 1914 (NEBC); New London Co., Franklin, R. W. Woodward s.n. 16 Jul 1904 (NEBC); New London Co., Town of Franklin, R. W. Woodward s.n. 27 Jul 1904 (NEBC).

Georgia: Rabun Co., Rabun Bald, J. A. Churchill 86129 4 Jul 1986 (MSC, BRIT); Rabun Co., Rabun Bald, Robert Kral 60305 31 May 1977 (KANU); Rabun Co., Rabin Bald, Milsted 1032 14 Jul 1996 (GA); Towns Co., Hightower Bald, W. H. Duncan 6933 4 Aug 1946 (MARY); Towns Co., Tray Mountain, L. G. Chafin 699 12 Jul 1987 (CLEMS); Union Co., Coosa Bald, L. Chafin 632-A 7 Jun 1987 (NYS); Union Co., Coosa Bald, L. Chaffin 569B 18 May 1987 (GA).

Kentucky: Harlan Co., Big Black Mountain, L. E. McKinney 6479 27 Jun 1995 (MICH);
Harlan Co., Black Mountain, T. F. Wieboldt 10479 6 Jul 2000 (VPI); Letcher Co., Stonega Gap,
R. Hannan s.n. 4 Oct 1998 (EKY); McReary Co., Sheltowee Trace, G. W. Libby 476 30 Jun 1994 (EKY); Wayne Co., Marcum Branch Hollow, G. W. Libby 1004 12 Jul 1995 (EKY).

Maryland: Garrett Co., Big Savage River, D. D. Boone 840808-SN 8 Aug 1984 (TAWES).

Massachusetts: New Ashford, J. R. Churchill s.n. 11 Aug 1915 (WIS); Franklin Co., Ashfield,

J. R. Churchill s.n. 19 Jun 1921 (KANU); Hampshire Co., Middlefield, M. L. Fernald 9050 26
Jun 1913 (KANU); Norfolk Co., Blue Hills Reservation, N. T. Kidder s.n. 21 Jun 1921 (KANU);
Suffolk Co., Arnold Arboretum, E. J. Palmer 45966 28 May 1942 (KANU); Suffolk Co., Revere,

C. E. Faxon s.n. 16 Jul 1880 (NEBC).

New Hampshire: Cheshire Co., Surry, M. L. Fernald 242 23 Jul 1899 (NEBC).

New York: East Jewett Twp., C. L. Shear s.n. 14 Jul 1893 (MSC); Allegany Co., Alma Hill, R. T. Clausen 3917 18 Jun 1939 (NYS); Cattaraugus Co., Allegany SP, H. D. House 12766 29 Jul 1926 (NYS); Cattaraugus Co., Allegany SP, H. D. House 12319 17 Jul 1926 (NYS); Cayuga Co., Dresserville Gulf, Town of Sempronius, Charles Atwood s.n. 12 Sep 1896 (CAN); Cayuga Co., Moravia, C. Atwood s.n. 11 Jul 1882 (NYS); Cayuga Co., Sempronius, Charles Atwood s.n. 27 Sep 1914 (WIS); Cortland Co., NW of Homes, S. J. Smith 2633 27 Jun 1946 (NYS); Delaware Co., Middletown, K.L. Brooks 4890 21 Jun 1969 (NYS); Delaware Co., Town of Kortright, K. L. Brooks 1781 19 Jul 1952 (NYS); Delaware Co., West Harpersfield, K. L. Brooks 1673 11 Jul 1952 (NYS); Erie Co., Hamburg, F. W. Johnson s.n. 7 Jul 1918 (NYS); Erie Co., South Wales, F. W. Johnson s.n. 2 Jul 1927 (NYS); Greene Co., Windham High Peak, H. K. Svenson 6476 28 Aug 1934 (VDB); Greene Co., Kaaterskill Clove, S. J. Smith 33978 28 Jul 1962 (NYS); Greene Co., Spruceton, R. Naczi 7478 4 Jul 1998 (MICH); Greene Co., Windham, H. K. Svenson 7852 12 Jun 1936 (SMU); Greene Co., Windham High Peak, H. K. Stevenson 6476 28 Aug 1934 (NY); Madison Co., Erieville, S. J. Smith 19718 14 Jun 1955 (NYS); Rensselaer Co., Town of Grafton, Grafton Lakes SP, P. Weatherbee 4437 23 Jun 1997 (NYS); Sullivan Co., Claryville, W. H. Jones 50 25 Jun 1934 (NYS); Tompkins Co., Caroline, A. J. Eames 11594 13 Jul 1919 (NYS); Ulster Co., Denning, W. H. Jones 48 27 Jun 1934 (NYS); Ulster Co., Hardenburg, Mongaup Mt., W. H. Jones 47 28 Jun 1934 (NYS); Ulster Co., Mt. Pleasant/Olive townline, J. Bierhorst 7 6 Jun 1996 (NYS); Ulster Co., Oliversea, S. J. Smith 20221 15 Jun 1956 (NYS); Ulster Co., Town of Olive, K. L. Brooks 7051 15 Jul 1987 (NYS); Ulster Co., Woodland, S. J. Smith 6833 16 Jun 1950 (NYS).

North Carolina: Mts. Of North Carolina, Wm. M. Canby 30.669 1 Jun 1868 (CAN); Alleghany Co., Alligator Back, P. D. McMillan 2469 8 Jun 1997 (USCH); Alleghany Co., Sparta, J. A. Churchill s.n. 15 Jun 1957 (MSC); Ashe Co., Bluff Mountain, A. E. Radford 44058 24 Jun 1961 (WIS); Avery Co., Crevices on Hanging Rock Mt., A. E. Radford 44091 24 Jun 1961 (WV); Buncombe Co., Mount Pisgah, C. K. Dodge 5178 2 Jul 1897 (MICH); Buncombe Co., Snow Bald Mt., J. E. Benedict, Jr. 2641 28 Jul 1933 (VPI); Buncumbe Co., Asheville, J. A. Churchill 85212 19 Aug 1985 (WIS); Clay Co., W. side of Little Bald, A. Cronquist 5556 25 Jul 1948 (MICH); Clay Co., 12 miles E of Murphy, A. A. Reznicek 7462 16 May 1985 (MICH); Graham Co., Robbinsville, F. J. Hermann 19378 11 Jun 1964 (MICH); Haywood Co., Blue Ridge Parkway, Phillip E. Hyatt 8811 29 Jul 1999 (MICH); Haywood Co., Sandymush Bald, A. F. Mark s.n. 2 Jul 1956 (DUKE); Jackson Co., Pisgah National Forest, SSE of Waynesville, Charles T. Bryson 6721 26 Jul 1987 (WIS); Jackson Co., Wesner Bald, A. F. Mark s.n. 20 Jun 1956 (DUKE); Jackson Co., White Water Falls, A. E. Hodge 441 11 Sep 1983 (CLEMS); Jackson Co., Whiteside Mt., R. K. Godfrey 51739 5 Aug 1951 (MICH); Macon Co., SE of Reynolds Gap, Phillip E. Hyatt 8209 6 Jul 1998 (MICH); Macon Co., Coweeta Hydrologic Lab, Phillip E. Hyatt 6098 2 Jul 1994 (MICH); Macon Co., Coweeta Hydrologic Laboratory, J. R. Manhart 55 9 Jun 1980 (MICH); Macon Co., Cowetta Hydrological Lab, Phillip E. Hyatt 6101 2 Jul 1994 (NKY); Macon Co., Franklin vicinity, Phillip

E. Hyatt 6106 17 Jul 1994 (MICH); Macon Co., Highlands, Glenn Falls, J. A. Churchill 87527 5
Jul 1987 (WIS); Macon Co., Scaley Mounatin vicinity, Phillip E. Hyatt 7802 4 Oct 1997 (MICH);
Mitchell Co., near summit of Roan Mt., A. H. Curtis 3192 (SMU); Mitchell Co., Mt. Mitchell, Rev. John Davis s.n. 26 Jul 1917 (UC); Mitchell Co., Roan Mountain, near summit, A. H. Curtiss 17887 (WIS); Mitchell Co., Roan Mt., J. W. Chickering, Jr. s.n. 12 Jul 1880 (WIS); Swain Co., Andrew's Bald Trail, William B. Fox s.n. 24 Aug 1940 (WV); Watauga Co., W of Blowing Rock, H. E. ahles 43759 18 Jun 1958 (VDB); Watauga Co., Boone, Rich Mountain, D. E. Boufford 16344 12 Jun 1975 (WIS); Watauga Co., Long Hope Valley, 4 mi NW of Todd, T. F. Wieboldt 7014 20 Sep 1989 (VPI); Watauga Co., Rich Mountain, NW of Boone, D. E. Boufford 16344 12 Jun 1975 (VDB); Yancey Co., below summit of Mt. Mitchell, R. Kral 64311 29 Aug 1979 (VDB); Yancey Co., S slopes of Mt. Mitchell, C. T. Bryson 6788 29 Jul 1987 (MICH).

Pennsylvania: Bradford Co., ENE of Laquin, *R. Naczi 2640* 18 Jun 1990 (MICH); Bradford Co., Sylvania, *R. Naczi 4172* 15 Jun 1994 (NKY); Bradford Co., West Franklin, *R. Naczi 2636* 17 Jun 1990 (MICH); Fayette Co., Ohiopyle, *Brown 51* 3 Jul 1905 (KANU); Jefferson Co., ENE of Desire, *H. A. Wahl 2808* 24 Jun 1947 (SMU); Lackawanna Co., E of Maple Lake, *S. L. Glowenke 6497* 20 Jun 1946 (GH); Lackawanna Co., NNE of Chinchilla, *S. L. Glowenke 6931* 1 Jul 1946 (GH); Lycoming Co., S of Ralston, *H. A. Wahl 112* 4 Jun 1938 (GH); McKean Co., *John Bright s.n.* 3 Jul 1921 (WV); McKean Co., S. of Kane, *R. H. True 22* 23 Jun 1932 (MICH); Sullivan Co., E of Hillsgrove, *W. A. Wahl 18200* 16 Jun 1957 (GH); Tioga Co., N of Williamsport, *D. Castaner 8502* 6 Jun 1985 (MICH); Warren Co., Hansen Tract, Columbus Township, *J. K. Bissell JKB:1994:123* 3 Aug 1994 (MICH).

South Carolina: Greenville Co., Rainbow Falls, L. L. Gaddy 173 6 Jun 1981 (CLEMS); McCormick Co., Cuffeytown Creek, NE of McCormick, A. E. Radford 22310 11 May 1957 (NY); Oconee Co., East Fork of the Chattoga River trail, L. L. Gaddy s.n. 2 Jun 1986 (CLEMS); Oconee Co., Sumter National Forest, N of Walhalla, A. A. Reznicek 8981 23 May 1992 (VDB);

Tennessee: Blount Co., Great Smoky Mt. NP Park Headquarters, Metcalf Bottoms, K. E. Rogers s.n. 20 May 1966 (SMU); Blount Co., Metcalf Bottoms, Great Smoky Mt. NP, K. Rogers 41228 24 May 1966 (SMU); Blount Co., Great Smoky Mt. NP, Running Fork Auto Tour, S. & G. Jones 4930 22 May 1990 (WIS); Carter Co., Summit Roan Mt. R. Kral 60731 3 Aug 1977 (VDB); Carter Co., Roan Mt. SP, summit of Roan Mtn., R. Carter 3183 14 Jul 1982 (VDB); Cocke Co., Great Smoky Mt. NP, summit of 'Old Black', V. E. McNeilus s.n. 3 Aug 1980 (WIS); Cocke Co., Great Smokey Mt. National Park, Maddron Bald Trail, V. E. McNeilus s.n. 22 Jun 1980 (WIS); Grundy Co., Savage Gulf Natural Area, T. S. Patrick 379 21 Aug 1977 (BRIT); Grundy Co., Savage Gulf Natural Area, T. S. Patrick 267 8 Jun 1977 (VDB); Monroe Co., Rt. 129, V. E. McNeilus 89-349 3 Jun 1989 (WIS); Monroe Co., Tellico Plains, J. A. Churchill 93457 8 May 1993 (MICH); Morgan Co., Wartburg, Potter Falls, V. E. McNeilus s.n. 2 Jun 1985 (WIS); Putnam Co., Monterey, R. Kral 63862 16 Jun 1979 (VDB); Sevier Co., Great Smoky Mt. NP, Chimney Tops, K. E. Rogers 43641 29 Jun 1969 (SMU); Sevier Co., Alum Cave trail, Mt. LeConte, J. K. Underwood 121 24 Jun 1933 (MICH); Sevier Co., Great Smoky Mountains NP, Brushy Mountain, F. R. Fosberg 18674 13 Jun 1942 (SMU); Sevier Co., Great Smoky Mountains NP, Chimney Tops, C. T. Bryson 3686 19 Jul 1984 (MICH); Sevier Co., Mt. LeConte, Rainbow Falls, William B. Fox s.n. 21 Aug 1940 (WV); Sevier Co., Great Smoky Mt. NP, Mt. LeConte, V. E. McNeilus s.n. 11 Jul 1981 (WIS); Sevier Co., Great Smoky Mt. NP, Mt. LeConte, V. E. McNeilus s.n. 26 Jul 1980 (WIS); Sevier Co., Great Smoky Mt. NP, Clingman's Dome, V. E. McNeilus s.n. 16 Aug 1980 (WIS); Sevier Co., Great Smoky Mt. NP, Elkmont, V. E. McNeilus s.n. 22 May 1982 (WIS); Unicoi Co., Flag Pond, N of Big Bald, J. A. Churchill 85290 20 Jul 1985 (MSC); Unicoi Co., Unaka Mt., V. E. McNeilus s.n. 5 Aug 1982 (WIS);

Vermont: Bennington Co., Mt. Equinox, P. F. Zika 3867 3 Jul 1981 (GH); Bennington Co., Pownal, J. R. Churchill s.n. 13 Jun 1903 (GH);

Virginia: Bedford Co., Blue Ridge Parkway, between Apple Orchard and Thunder Ridge, J.
B. Nelson 15987 29 Jul 1994 (USCH); Botetonot Co., Apple Orchard Mt., C. E. Stevens 16721
13 Aug 1978 (VPI); Craig Co., Hanging Rock, Potts Mt., C. E. Stevens 15541 1 Jul 1978 (VPI);
Floyd Co., Buffalo Mt., C. E. Stevens 12967 18 Jun 1976 (VPI); Giles Co., Kire, H. H. Iltis 1900
25 Jul 1943 (SMU); Giles Co., Allegheny Mountains, Salt Pond Rattlesnake Mountain, H. H. Iltis
19.747 27 Jul 1958 (SMU); Giles Co., Beanfield Mt., W of Mountain Lake, John M. Fogg Jr. 17057
1 Jul 1949 (MICH); Giles Co., Salt Pond Mountain, Allegheny Mountains, Hugh H. Iltis s.n. 27
Jul 1958 (WIS); Grayson Co., Buck Mt., C. E. Stevens 2114 17 Jun 1970 (VPI); Grayson Co.,
Mt. Rogers, J. K. Small s.n. 29 Jun 1892 (MSC); Grayson Co., Point Lookout Mountain, N of
Independence. T. F. Wieboldt 7234 4 Jun 1990 (VPI); Grayson Co., Point Lookout Mountain, N of
Independence. T. F Wieboldt 7316 31 Jul 1990 (MICH); Highland Co., Allegheny Mt., NW of Blue
Grass, G. P. Fleming 9297 23 Jun 1994 (VPI); Madison Co., Stony Man Mt., S. J. Smith 4770 13
Sep 1948 (NYS); Madison Co., Stony Man, Shenandoah NP, C. E. Stevens 10951 5 Jul 1975 (VPI);

Marion Co., Mt. Rogers, J. A. Churchill 70517 16 May 1970 (MSC); Nelson Co., Three Ridges
Mountain, F. Watson 816 30 Aug 1976 (CLEMS); Page Co., Shenandoah NP, Appalachian Trail, SW SKYLAND F. J. Hermann 10752 27 Oct 1940 (MICH); Patrick Co., Twelve O'Clock Knob,
SE side of Rock Castle Gorge, T. F. Wieboldt 9264 27 Jul 1995 (VPI); Russell Co., Beartown
Mt./Clinch Mt. WMA, J. F. Townsend 3099 18 Jun 2003 (VPI); Smyth Co., Iron Mt., C. E.
Stevens 2160 19 Jun 1970 (VPI); Smyth Co., Troutdale, Mt. Rogers, J. A. Churchill s.n. 6 Jun
1970 (MSC); Tazewell Co., Morris Knob, C. E. Stevens 7399 20 Jul 1973 (VPI); Washington Co.,
Brumley Mt., W of The Butt. C. E. Stevens 7448 21 Jul 1973 (VPI);

West Virginia: Randolph Co., Monangahela National Forest, Spruce Knob Lake, *Bev Walters* 612 8 Jul 1997 (MICH); Randolph Co., Monongahela National Forest, Wymer, *A. W. Cusick* 29,609 30 May 1991 (MICH).

Carex bushii. U. S. A. Alabama: Colbert Co., Colbert Co. Rd 101, J. H. Wiersma 1725 6 May 1980 (GA); Sumter Co., S of Boyd, S. McDaniel 10545 28 Apr 1968 (GA).

Arkansas: Ashley Co., Hamburg, Larry J. Harms 2274 3 May 1965 (KANU); Baxter Co., Mountain Home, Phillip E. Hyatt 2797.03 5 May 1990 (MICH); Columbia Co., Taylor, Phillip E. Hyatt 6388 6 May 1995 (MICH); Crawford Co., Natural Dam, Phillip E. Hyatt 9311 18 May 2000 (MICH); Hot Springs Co., Brawley Cemetery, Phillip E. Hyatt 5384 17 May 1993 (MICH); Izard Co., sandstone glade, Phillip E. Hyatt 5601 4 Jun 1993 (MICH); Izard Co., Calico Rock, B. L. Lipscomb 1576 30 May 1976 (NCU); Izard Co., Calico Rock, Phillip E. Hyatt 4399.33 27 May 1992 (MICH); Johnson Co., Clarksville, R. Naczi 3895 19 May 1994 (MICH); LaFayette Co., Bradley, Phillip E. Hyatt 6261 22 Apr 1995 (MICH); Lincoln Co., Star City, Phillip E. Hyatt 7539 20 May 1997 (MICH); Lonoke Co., Carlisle, A. A. Reznicek 9263 17 May 1993 (MICH); Lonoke Co., Little Rock, S. D. Jones 2565 28 Apr 1989 (MICH); Miller Co., Foulk, Phillip E. Hyatt 6340 23 Apr 1995 (MICH); Monroe Co., Fargo, R. Naczi 2454 21 May 1990 (MICH); Perry Co., Fourche Mt., Phillip E. Hyatt 8046 3 May 1998 (MICH); Polk Co., Highway 270, D. Castaner 9668 13 May 1987 (TAES); Polk Co., Queen Wilhelmina SP, C. T. Bryson 4315 10 May 1986 (MICH); Pope Co., Atkins, Crow Mt., G. E. Tucker 4412 10 May 1967 (NCU); Prairie Co., Hazen, C. T. Bryson 12325 17 May 1993 (MICH); Scott Co., Haw Creek, Phillip E. Hyatt 7456 17 May 1997 (MICH); Scott Co., Ouchita NF, Poteau Mt., Phillip E. Hyatt 7464 18 May 1997 (MICH); Scott Co., Waldron, Phillip E. Hyatt 4043.64 2 Jun 1991 (MICH); Stone Co., Ashe's Juniper Glade, Ozark NF, Phillip E. Hyatt 5527 26 May 1993 (MICH); Van Buren Co., Hwy 9, Phillip E. Hyatt 5418 18 May 1993

(MICH); Washington Co., Fayetteville, *D. Sadler 109* 20 Jun 1990 (OKL); White Co., Steprock Community, *Phillip E. Hyatt 6015* 11 May 1994 (MICH).

Delaware: New Castle Co., Talleyville, R. Naczi 2563 12 Jun 1990 (MICH).

Georgia: Clarke Co., Athens, J. H. Pyron 1798 18 May 1937 (GA); Clarke Co., Athens, J.
R. Manhart 46 29 May 1980 (MICH); Cook Co., Rt. 37, V. E. McNeilus 92-289 22 May 1992 (TAES).

Illinois: Jackson Co., Desoto Railroad Prairie, *D. Ladd 4003* 3 Jun 1979 (MO); Perry Co., Pyramid SP, *J. Raveill 165* 21 May 1981 (MO); Randolph Co., Sparta, *W. M. Bailey 1454* 25 Jun 1951 (NCU).

Indiana: Davies Co., Washington, N. C. Henderson 67-593 22 May 1967 (NCU); Posey Co.,
SW Mt. Vernon, F. J. Hermann 6662 15 Jun 1935 (GH); Posey Co., SW of Mt. Vernon, C. C.
Deam 42929 25 May 1926 (GH); Spencer Co., Bloomfield, C. C. Deam 55020 4 Jun 1934 (MICH).

Iowa: Page Co., Tarkio Township, *B. Wilson 3884* 3 Jul 1990 (MICH); Washington Co., Washington, *T. Cady s.n.* 14 Jun 1997 (MICH); Washington Co., Washington, *T. Cady s.n.* 14 Jun 1997 (MICH).

Kansas: Allen Co., Carlyle, Caleb A. Morse 3005 1 May 1999 (KANU); Allen Co., Humboldt, Ole A. Kolstad 1336 8 Jun 1964 (KANU); Allen Co., Moran, Ole A. Kolstad 1391 9 Jun 1964 (KANU); Anderson Co., Garnett, Ole A. Kolstad 2168 2 Jun 1964 (KANU); Anderson Co., Harris, Ole A. Kolstad 1318 8 Jun 1964 (KANU); Anderson Co., Welda, Craig C. Freeman 9101 7 Jun 1997 (KANU); Anderson Co., Westphalia, Caleb A. Morse 8409 1 Jul 2002 (KANU); Anderson Co., Westphalia, Caleb A. Morse 9526 13 Jun 2003 (KANU); Anderson Co., Westphalia, Craig C Freeman 17013 16 May 2001 (KANU); Atchison Co., Lancaster, Ralph Brooks 4651 21 Jun 1973 (KANU); Bourbon Co., Crawford Co. line, Ole A. Kolstad 2181 2 Jun 1964 (KANU); Bourbon Co., Hiattville, Steve Stephens 47602 27 May 1971 (KANU); Bourbon Co., KS 7, Craig C. Freeman 2386 15 Jun 1987 (KANU); Bourbon Co., Uniontown, Ole A. Kolstad 1400 9 Jun 1964 (KANU); Brown Co., Brown Co State Lake, Ole A. Kolstad 2607 23 Jun 1964 (KANU); Brown Co., Ronald L. McGregor 38891 25 May 1988 (KANU); Butler Co., Augusta, William T. Barker 2446 16 Jun 1966 (KANU); Butler Co., Beaumont, Steve Stephens 85770 26 Jun 1975 (KANU); Butler Co., Butler Co. State Lake, Steve Stephens 4463 7 Jun 1966 (KANU); Butler Co., Keighley, Steve Stephens 3115 13 May 1966 (KANU); Butler Co., Latham, Steve Stephens 3110 13 May 1966 (KANU); Chase Co., Bazaar, Steve Stephens 4573 8 Jun 1966 (KANU); Cherokee Co., A. S. Hitchcock 1020 7 May 1897

(MICH); Cherokee Co., Baxter Springs, Ole A. Kolstad 2202 2 Jun 1964 (KANU); Cherokee Co., Baxter Springs, Ronald L. McGregor 38209 28 May 1987 (KANU); Cherokee Co., Crestline, Steve Stephens 4117 2 Jun 1966 (KANU); Cherokee Co., Galena, Ronald L. McGregor 38218 28 May 1987 (KANU); Cherokee Co., KS 7, Ole A. Kolstad 2193 2 Jun 1964 (KANU); Cherokee Co., Pittsburg, A. A. Reznicek 9828 29 May 1994 (MICH); Cherokee Co., Riverton, Ralph E. Brooks 15949 10 Jun 1982 (KANU); Cherokee Co., Scammon, Ole A. Kolstad 2243 3 Jun 1964 (KANU); Cherokee Co., Skidmore, Ole A Kolstad 2240 3 Jun 1964 (KANU); Cloud Co., Miltonvale, S. V. Fraser 28 5 Jun 1936 (NCU); Coffey Co., Burlington, Ole A. Kolstad 2504 20 Jun 1964 (KANU); Coffey Co., Halls Summit, Craig C. Freeman 14812 14 Jun 2000 (KANU); Coffey Co., Lebo, C. A. Morse 3048 19 May 1999 (MICH); Coffey Co., Waverly, Craig C Freeman 17060 16 May 2001 (KANU); Coffey Co., Woodson Co. line, William T Barker 2337 14 Jun 1966 (KANU); Crawford Co., Farlington, Steve Stephens 4015 1 Jun 1966 (KANU); Crawford Co., Farlington, Steve Stephens 3998 1 Jun 1966 (KANU); Crawford Co., Farlington, Ole A. Kolstad 2185 2 Jun 1964 (KANU); Crawford Co., Frontenac, Ronald L. McGregor 38199 27 May 1987 (KANU); Crawford Co., Girard, Ole A. Kolstad 2276 4 Jun 1964 (KANU); Crawford Co., Cherokee, Caleb A. Morse 9592 17 Jun 2003 (KANU); Crawford Co., Pittsburg, Ole A. Kolstad 2262 4 Jun 1964 (KANU); Douglas Co., Lawrence, Ole A. Kolstad 2149 25 May 1964 (KANU); Douglas Co., Baldwin City, Ole A. Kolstad 2139 22 May 1964 (KANU); Douglas Co., Baldwin City, Craig C. Freeman 3456 27 May 1991 (KANU); Douglas Co., Baldwin Creek, R. L. McGregor 40484 18 May 1992 (OKL); Douglas Co., Clinton Reservoir, C. Morse 272 4 Jun 1995 (MICH); Douglas Co., Clinton Reservoir, C. Morse 741 21 Jun 1996 (MICH); Douglas Co., Haskell Bottoms, Wayne Robuck 251 30 May 1968 (KANU); Douglas Co., Baldwin City, Caleb A. Morse 5603 6 May 2001 (KANU); Douglas Co., Lawrence, Hetzer 536 2 Jun 1950 (KANU); Douglas Co., Lawrence, Ronald L. McGregor 36213 20 May 1985 (KANU); Douglas Co., Lawrence, Ole A. Kolstad 2161 29 May 1964 (KANU); Douglas Co., Lawrence, Ronald L. McGregor 4471 15 Aug 1950 (KANU); Douglas Co., Lawrence, Hetzer 541 7 Jun 1950 (KANU); Douglas Co., Lecompton, Ronald L. McGregor 17469 18 May 1963 (KANU); Douglas Co., Stull, Caleb A. Morse 4384 3 May 2000 (KANU); Douglas Co., Stull, Caleb A. Morse 9425 26 May 2003 (KANU); Douglas Co., Baldwin Creek, Ronald L. McGregor 40484 18 May 1992 (KANU); Douglas Co., Ronald L. McGregor 39988 9 Jun 1989 (KANU); Douglas Co., Caleb A. Morse 237 18 May 1995 (KANU); Douglas Co., Dorothy Akin Memorial Prairie, Ronald L. McGregor 40181 11 Jun 1990 (KANU); Douglas Co., Dorothy Akin Memorial Prairie, Caleb A. Morse 237 18 May

1995 (KANU); Elk Co., Busby, Caleb A. Morse 5717 10 May 2001 (KANU); Elk Co., Busby, Caleb A. Morse 5740 10 May 2001 (KANU); Elk Co., Fall River, Caleb A. Morse 5634 10 May 2001 (KANU); Franklin Co., Douglas-Franklin line, Hetzer 556 8 Jun 1950 (KANU); Franklin Co., Ottawa, Ralph Brooks 4456 19 Jun 1973 (KANU); Franklin Co., Ottawa, William T. Barker 2280 6 Jun 1966 (KANU); Franklin Co., Ottawa, Hetzer 206 6 Jun 1949 (KANU); Franklin Co., Ottawa, Hetzer 550 8 Jun 1950 (KANU); Franklin Co., Ottawa, Hetzer 200 6 Jun 1949 (KANU); Franklin Co., Richmond, Ole A. Kolstad 1370 8 Jun 1964 (KANU); Franklin Co., Richmond, Craig C. Freeman 17002 16 May 2001 (KANU); Franklin Co., Richmond, Ronald L. McGregor 10099 14 May 1955 (KANU); Franklin Co., Ronald L. McGregor 38146 22 May 1987 (KANU); Franklin Co., Williamsburg, Craig C. Freeman 14817 14 Jun 2000 (KANU); Greenwood Co., Eureka, Craig C. Freeman 14795 14 Jun 2000 (KANU); Greenwood Co., Fall River SP, William T. Barker 3711 7 Jun 1967 (KANU); Greenwood Co., Fall River, Craig C. Freeman 8066 29 Jun 1996 (KANU); Greenwood Co., Madison, Craig C. Freeman 14805 14 Jun 2000 (KANU); Greenwood Co., Neal, Steve Stephens 89639 21 Jun 1978 (KANU); Greenwood Co., Severy, Craig C. Freeman 14784 14 Jun 2000 (KANU); Jefferson Co., Kansas Ecological Reserves Site #5001, Kelly Kindscher H0403 6 Jun 1989 (KANU); Jefferson Co., Williamstown, Ole A. Kolstad 2580 23 Jun 1964 (KANU); Johnson Co., Aubry, Caleb A. Morse 4697 30 May 2000 (KANU); Johnson Co., Clearview City, C. A. Morse 4568 19 May 2000 (MICH); Johnson Co., DeSoto, Craig C. Freeman 14746 1 Jun 2000 (KANU); Johnson Co., DeSoto, Craig C. Freeman 5013 25 Jun 1993 (KANU); Johnson Co., Gardner, Craig C. Freeman 4925 21 May 1993 (KANU); Johnson Co., Kill Creek Rd Caleb A. Morse 1232 20 May 1997 (KANU); Johnson Co., Sunflower Army Ammunition Plant, C. C. Freeman 5013 25 Jun 1992 (OKL); Labette Co., Oswego, Ole A. Kolstad 2297 4 Jun 1964 (KANU); Labette Co., Parsons, Craig C. Freeman 6180 21 Jun 1994 (KANU); Leavenworth Co., Eudora, Caleb A. Morse 5769 17 May 2001 (KANU); Linn Co., Blue Mound City Lake, C. A. Morse 4661 24 May 2000 (NEB); Linn Co., Boicourt, Caleb A. Morse 8090 10 Jun 2002 (KANU); Linn Co., La Cygne, Caleb A. Morse 7964 23 May 2002 (KANU); Linn Co., Pleasanton, Craig C. Freeman 14881 19 Jun 2000 (KANU); Linn Co., Trading Post, Caleb A. Morse 8142 10 Jun 2002 (KANU); Linn Co., Trading Post, Caleb A. Morse 10426 14 May 2004 (KANU); Lyon Co., Allen, Ronald L. McGregor 15622 3 Jun 1960 (KANU); Lyon Co., Reading, Ralph Brooks 3509 15 May 1972 (KANU); Lyon Co., Saffordville, Caleb A. Morse 3443 9 Jun 1999 (KANU); Miami Co., Johnson Co. line, Jennifer Milburn 1028 11 Jun 1994 (KANU); Miami Co., Johnson Co. line, Jennifer Milburn 1010 11 Jun

1994 (KANU); Miami Co., MO state line, Jennifer Milburn 921a 6 Jun 1994 (KANU); Miami Co., Beagle, Caleb A. Morse 6565 15 Jun 2001 (KANU); Miami Co., Franklin Co. line, Craig C. Freeman 2474 14 May 1988 (KANU); Miami Co., Jingo, Caleb A. Morse 10488 20 May 2004 (KANU); Miami Co., Miami Co. State Lake, Ole A. Kolstad 2050 16 May 1964 (KANU); Miami Co., Paola, Craig C. Freeman 14899 19 Jun 2000 (KANU); Miami Co., Paola, Ralph Brooks 4845 28 Jun 1973 (KANU); Miami Co., Somerset, C. A. Morse 4733 30 May 2000 (MICH); Montgomery Co., Cherryvale, William T Barker 2174 3 Jun 1966 (KANU); Montgomery Co., Montgomery Co. State Lake, Ronald L. McGregor 40401 30 May 1991 (KANU); Montgomery Co., Montgomery Co. State Lake, Ronald L. McGregor 40384 30 May 1991 (KANU); Montgomery Co., Montgomery Co. State Lake, Ronald L. McGregor 38275 4 Sep 1987 (KANU); Montgomery Co., Ronald L. McGregor 38870 12 May 1988 (KANU); Neosho Co., St. Paul, W. W. Holland 948 23 May 1965 (KANU); Neosho Co., St. Paul, W. W. Holland 895 10 May 1965 (KANU); Neosho Co., Thayer, W. W. Holland 5470 26 May 1986 (KANU); Neosho Co., Walnut Grove, W. W. Holland 455 28 May 1964 (NCU); Osage Co., U.S. 56, Ralph E. Brooks 18717 27 May 1987 (KANU); Osage Co., Osage City Cemetery, C. C. Freeman 12585 12 Jun 1999 (NEB); Osage Co., Osage City, Craig C. Freeman 18841 14 Jun 2002 (KANU); Osage Co., Osage City, Ralph E. Brooks 16636 1 Jun 1983 (KANU); Osage Co., Overbrook, Ralph E. Brooks 18704 27 May 1987 (KANU); Ottawa Co., Minneapolis, Ronald L. McGregor 37030 19 May 1986 (KANU); Republic Co., Agenda, Ralph E. Brooks 16741 12 Jul 1983 (KANU); Republic Co., Gordon E. Morley 393 28 Jun 1960 (KANU); Republic Co., Talmo, Jeff Elliott 888 1 Jul 1995 (KANU); Riley Co., Ogden, Craig C. Freeman 18780 21 May 2002 (KANU); Saline Co., Brookville, Jeff Elliott 1532 21 May 2003 (KANU); Saline Co., Brookville, Craig C. Freeman 19807 20 May 2003 (KANU); Saline Co., John C. Hancin 2268 28 May 1939 (KANU); Shawnee Co., Wakarusa, Craig C. Freeman 14865 17 Jun 2000 (KANU); Sumner Co., Gueda Springs, Craig C. Freeman 14778 13 Jun 2000 (KANU); Sumner Co., Mulvane, Dick W. Birkholz 2040a 9 Jun 1967 (KANU); Sumner Co., Slate Creek Wetland, M. D. Proctor 604 6 Jun 1993 (OKL); Wabaunsee Co., Chalk, Steve Stephens 3496 19 May 1966 (KANU); Wabaunsee Co., Maple Hill, Robert E. Russell 588 21 May 1997 (KANU); Washington Co., Washington Co. State Lake, Ronald L. McGregor 39067 6 Jun 1988 (KANU); Washington Co., Washington, Ralph Brooks 16658 15 Jun 1983 (KANU); Washington Co., Washington Co. State Lake, Steve Stephens 55384 21 Jun 1972 (KANU); Wilson Co., Buffalo, Steve Stephens 85302 19 Jun 1975 (KANU); Wilson Co., Neodesha, Ole A. Kolstad 3098 9 Jun 1965 (KANU); Wilson Co., Ronald L. McGregor 38351

27 Jun 1987 (KANU); Woodson Co., Yates Center, Caleb A. Morse 8237 18 Jun 2002 (KANU);
Woodson Co., Lake Fegan, Ole A. Kolstad 201 11 May 1963 (KANU); Woodson Co., Rose, Caleb A. Morse 8220 18 Jun 2002 (KANU); Woodson Co., Cross Timbers SP, Toronto, Gary Weisenberger s.n. 4 Jun 2004 (KANU); Woodson Co., Toronto, Caleb A. Morse 8283 19 Jun 2002 (KANU);
Woodson Co., Woodson State Fishing Lake, Toronto, Caleb A. Morse 5610 10 May 2001 (KANU);
Woodson Co., Woodson Co. State Lake, Ole A. Kolstad 230 11 May 1963 (KANU); Woodson Co., Woodson Co. State Lake, Ronald L. McGregor 40340 29 May 1991 (KANU); Woodson Co.,
Woodson Co. State Lake Ralph Brooks 12109 8 Jun 1976 (KANU); Woodson Co., Woodson Co.
State Lake, Ronald L. McGregor 40355 29 May 1991 (KANU); Woodson Co., Yates Center City
Lake, Ole A. Kolstad 2514 20 Jun 1964 (KANU); Woodson Co., Yates Center, Kermit L. Johnson 1289 17 Jun 1968 (KANU).

Kentucky: Bulitt Co., Bernheim Forest, A. Hotchkiss s.n. 27 May 1951 (NYS); Hickman Co., Jackson Purchase Area, L. E. McKinney 4187 5 May 1990 (EKY); Hickman Co., Murphy's Pond, L. E. McKinney 4187 7 May 1990 (TAES); Madison Co., Igloo 1509, G. Libby OB-348 2 Jun 1993 (MICH).

Louisiana: Morehouse Co., Bayou Bartholomew, C. T. Bryson 11456 30 Apr 1992 (MICH); Rapides Co., Kisatchie Forest, D. A. Duncan 57026 11 May 1957 (TAES); Union Co., La 143, D. C. Moore 625 14 Apr 1983 (cb); Vernon Co., Ft. Polk Army Post, C. M. Allen PLK1120 11 Apr 1992 (OKL).

Maryland: Carroll Co., Eldersburg, W. D. Longbottom 3138 16 Jun 1992 (MARY); Cecil Co., Pilot, D. D. Boone 830607-SN 7 Jun 1983 (TAWES); Cecil Co., Rising Sun, C. Lea 1878 3 Jun 2000 (MARY); Frederick Co., Flat Run, E. Baltass 306 16 Jun 1951 (MARY); Montgomery Co., Falls Island at Great Falls, C. Lea 1932 5 Jun 2000 (MARY).

Massachusetts: Hampshire Co., Northampton, *H. E. Ahles 81791* 3 Jul 1976 (NCU). Michigan: Charlevoix Co., Beaver Island, *F. Menapace 16* 11 Jul 1985 (MICH).

Mississippi: Chickasaw Co., Buena Vista, C. T. Bryson 11569 14 May 1992 (CLEMS); Chickasaw Co., Trebloc, C. T. Bryson 11556 14 May 1992 (MICH); Franklin Co., Sullivan, E J Palmer 67330 11 Jun 1958 (KANU); Grenada Co., Camp McCain, C. T. Bryson 15192 20 May 1996 (MICH); Grenada Co., Holcomb, C. T. Bryson 11538 14 May 1992 (CLEMS); Kemper Co., C. T. Bryson 8569 15 May 1989 (MICH); Lee Co., Tupelo, C. T. Bryson 3225 1 May 1982 (MICH);
Lee Co., Tupelo, C. T. Bryson 3389 29 May 1982 (MICH); Lee Co., Tupelo, C. T. Bryson 9905

18 May 1990 (TAES); Lowndes Co., Artesia, C. T. Bryson 8562 15 May 1989 (MICH); Lowndes
Co., Mayhew, C. T. Bryson 9868 17 May 1990 (MICH); Panola Co., Batesville, C. T. Bryson 12441 1 Jun 1993 (MICH); Pontotoc Co., Natchez Trace Parkway, C. T. Bryson 3782 27 Apr 1985 (MICH); Rankin Co., Richland, C. T. Bryson 15069 30 Apr 1996 (MICH); Tate Co., Senitobia, C. T. Bryson 10021 18 May 1990 (TAES);

Missouri: Barry Co., Wheaton, D. Castaner 7499 26 May 1983 (MICH); Benton Co., D. Castaner 6285 16 May 1981 (MICH); Benton Co., Lake Creek Town, D. Castaner 6286 16 May 1981 (VPI); Boone Co., Grindstone Park, P. M. McKenzie 1572 25 May 1995 (MO); Calloway Co., Dixie State Rec. Area, V. E. McNeilus 92-562 8 Jul 1992 (MICH); Calloway Co., Kingdom City, V. E. McNeilus 94-534 5 Jun 1994 (MSC); Clark Co., Little Rollins Creek, B. Summers 8724 22 Jun 1998 (MO); Dade Co., Greenfield, E. J. Palmer 52187 10 Jun 1951 (KANU); Henry Co., Clinton, W. Folsted 12812 5 Jun 1953 (NEB); Jasper Co., Joplin, E. J. Palmer 49155 8 Jun 1949 (KANU); Jasper Co., Webb City, E. J. Palmer 17411 8 May 1920 (KANU); Johnson Co., Knob Noster SP, R. Mullikin 567 8 Jun 1972 (NEB); Marion Co., Hunnewell, A. A. Reznicek 9874 31 May 1994 (MICH); Montgomery Co., High Hill, A. E. Brant 580 26 May 1985 (TAES); Montgomery Co., Montgomery City, R. E. Gereau 1129 19 May 1984 (TAES); Pettis Co., Greenridge, D. Castaner 6250 16 May 1981 (MICH); Pulaski Co., Ft. Leonard Wood Army Base, R. T. Ovrebo W0132 5 May 1989 (OKL); Pulaski Co., Happy Hollow Picnic Area, R. T. Ovrebo W0132 5 May 1989 (KANU); Randolph Co., D. Castaner 7590 3 Jun 1983 (MICH); Scott Co., Hwy H off Benton Rd, Travis Brooks 7755 18 May 1975 (KANU); Shelby Co., Clarence, P. M. McKenzie 1413 11 Jun 1994 (MICH); St. Francois Co., J. Kessler 7196 16 Jun 1983 (TAES); St. Francois Co., Knob Lick, D. Castaner 6571 14 Jun 1981 (MICH); St. Louis Co., St. Louis, H. Eggert s.n. 21 Jun 1887 (MICH); Stoddard Co., Dudley, R. Naczi 1960 22 May 1988 (MICH); Texas Co., Slabtown, B. Summers 5831 22 Jun 1993 (MO); Vernon Co., Nevada, W. D. Longbottom 3530 24 May 1993 (MARY); Webster Co., R. E. Gereau 1765 28 Apr 1985 (TAES).

Nebraska: Burt Co., Tekamah, S. B. Rolfsmeier 16227 29 May 2001 (NEB); Gage Co., Diamond Lake Wildlife Management Area, R. F. Steinauer s.n. 21 May 1999 (NEB); Gage Co., Odell, Steven B Rolfsmeier 8744 2 Jun 1991 (KANU); Jefferson Co., DeBoer Prairie, R. F. Steinhauer 299 9 Jun 1998 (NEB); Jefferson Co., Endicot, S. P. Churchill 3562 13 Jun 1974 (NEB); Jefferson Co., Fairbury, S. P. Churchill 3538A 13 Jun 1974 (NEB); Jefferson Co., Fairbury, Steven B. Rolfsmeier 6246 2 Jun 1990 (KANU); Jefferson Co., Rock Creek State Historical Park, Fairbury, S. Rolfsmeier 6246 2 Jun 1990 (NEB); Jefferson Co., Rock Glen WMA, G. Steinhauer 228 12 Jun 1997 (NEB); Pawnee Co., Elk Creek, R. F. Steinhauer 1537 24 May 2001 (NEB); Pawnee Co., Joe Gyhra Prairie, R. Steinhauer 72 7 Jul 1997 (NEB); Pawnee Co., Steinauer Catholic cemetery, Robert F. Steinauer 1541 31 May 2001 (KANU); Pawnee Co., Steinauer, Steven B. Rolfsmeier 13310 20 Jun 1997 (KANU);

New Jersey: Hunterdon Co., Delaware Township, J. D. Mitchell 641 22 Jun 1993 (MICH).

New York: Albany Co., Alcove, W. J. Crins 7641 3 Jul 1989 (NYS); Albany Co., New Scotland, H. D. House 20376 19 Jun 1933 (NYS); Albany Co., South Westerlo, G. C. Tucker 6038 4 Jun 1991 (NYS); Columbia Co., German Town, R. McVaugh 3318 17 Jul 1935 (NYS); Columbia Co., Livingston, H. D. House 22696 26 Jun 1935 (NYS); Dutchess Co., Rhinecliff, H. D. House 19282 23 Jun 1932 (NYS); Dutchess Co., Stanford, R. E. Zaremba 4260 6 Jul 1987 (NYS); Oneida Co., Yorkville, J. V. Haberer 1125 1 Jun 1902 (NYS); Onondaga Co., Tully, S. M. Young 1086 27 Jun 1991 (NYS); Orange Co., Harriman SP, J. G. Barbour 787 9 Jun 1993 (NYS); Orange Co., Lake Frederick, J. G. Barbour 862 16 Jun 1993 (NYS); Orange Co., West Point, J. G. Barbour 2165 9 Jul 1994 (NYS); Putnam Co., Town of Patterson, G. C. Tucker 4448 1 Jul 1989 (NYS); Rensselaer Co., Brainerd, H. D. House 21370 8 Jun 1934 (NYS); Rensselaer Co., Town of Schaghticoke, W. Broderick 2002:16 13 Jun 2002 (NYS); Rensselaer Co., West Sand Lake, H. D. House 20354 18 Jun 1933 (NYS); Rockland Co., Bear Mt. SP: Doodletown, G. C. Tucker 9698 8 Jun 1994 (NYS); Rockland Co., Bear Mt. SP: Iona Island, R. S. Mitchell 8364 2 Jul 1993 (NYS); Rockland Co., Harriman SP, J. G. Barbour 2112 30 Jun 1994 (NYS); Rockland Co., Orangetown, R. E. Zaremba 4221 15 Jul 1987 (NYS); Rockland Co., Stony Point, Iona Island, R. E. Zaremba 4220 15 Jul 1987 (NYS); Schenectady Co., Mariaville Lake, T. C. Baim 3375 13 Jul 1950 (NYS); St. Lawrence Co., Town of Waddington, A. M. Johnson 2850 17 Jun 2005 (NYS); Ulster Co., Township of Olive, J. Bierhorst s.n. 30 Jun 1993 (NYS); Ulster Co., Wawarsing; Shawangunk Mts., R. E. Zaremba 9800 16 Jun 1992 (NYS); Washington Co., Lake George Region, S. H. Burnham s.n. 8 Jul 1898 (NYS); Westchester Co., Bedford, Francis W. Pennell 7145 24 Jun 1916 (KANU); Westchester Co., Mount Kisco, Francis W Pennell 7181 25 Jun 1916 (KANU); Westchester Co., Mount Pleasant, *R. E. Zaremba 2603* 10 Jul 1986 (NYS).

North Carolina: Durham Co., S. W. Leonard 1522 29 May 1968 (MICH); Rowan Co., Spencer, A. E. Radford 11540 26 May 1956 (NCU).

Ohio: Jackson Co., J. S. McCormac 5559 6 Jun 1994 (MICH).

Oklahoma: R. Bebb 2756 29 Apr 1905 (OKL); Adair Co., Sequoyah Co. line, M. Huft 1178 14 May 1980 (OKL); Atoka Co., McGee Creek Wildlife Management Area, B. Hoagland AB-19 24 May 2000 (OKL); Atoka Co., Stringtown, P. Folley 2631 27 May 2001 (OKL); Bryan Co., Durant, J. Taylor 1426 18 Apr 1963 (OKL); Bryan Co., Hendrix, Phillip E. Hyatt 7970 20 Apr 1998 (MICH); Bryan Co., Mead, J. Taylor 1519 30 Apr 1963 (OKL); Cherokee Co., Ft. Gibson, C. S. Wallis 7083-1 2 Jun 1958 (OKL); Cherokee Co., Talequah, S. F. Glassman 1466 24 Apr 1948 (OKL); Choctaw Co., Hugo, B. Hoagland HUGO279 16 May 2001 (OKL); Choctaw Co., Jeter Prairie, S. Carpenter 1382 8 Jun 1997 (OKL); Cleveland Co., Lexington WMA, P. Folley 2181 1 May 1998 (OKL); Cleveland Co., Lexington WMA, M. D. Proctor 596 4 May 1993 (OKL); Cleveland Co., Lexington WMA, P. Folley 2180 1 May 1998 (OKL); Coal Co., Coalgate, A. Buthod AB-2179 1 May 2001 (OKL); Craig Co., Welch, B. Hoagland 1314 7 Jun 1999 (OKL); Craig Co., Welch, B. Hoagland 1333 7 Jun 1999 (OKL); Craig Co., White Oak Prairie, P. Folley 2482 22 May 2000 (OKL); Creek Co., Deep Fork WMA, D. Benesh DFX257 23 Jun 1998 (OKL); Creek Co., Old Mannford, B. Hoagland Key-091 15 May 2002 (OKL); Delaware Co., Dripping Springs, M. Hopkins 3211 7 May 1938 (OKL); Delaware Co., Grove, U. T. Waterfall 9963 30 May 1951 (OKL); Delaware Co., Jay, D. Castaner 7472 26 May 1983 (MICH); Delaware Co., Oklahoma Ozarks, C. S. Wallis 1597 23 May 1954 (OKL); Haskell Co., Stigler, D. Benesh e054 5 May 1998 (OKL); Johnston Co., Blue River, S. D. Jones 10228 20 May 1993 (VPI); Johnston Co., Ravia, L. K. Magrath 12678 25 Apr 1982 (OKL); Johnston Co., Troy, G. J. Goodman 7922 4 May 1969 (OKL); Latimer Co., Bengal, F. H. Means Jr. 3421 28 May 1968 (OKL); Latimer Co., Robbers Cave SP, G. J. Goodman 7113 6 May 1961 (OKL); Latimer Co., Wilburton, M. Hopkins 1695 7 May 1937 (MICH); LeFlore Co., State Line Historical Site, C. T. Bryson 4314 10 May 1986 (MICH); LeFlore Co., Walnut Mt., P Folley 2752 14 May 2003 (OKL); LeFlore Co., Cameron, A. A. Reznicek 9333 19 May 1993 (MICH); LeFlore Co., Fanshawe, G. J. Goodman 2551 5 May 1935 (OKL); LeFlore Co., Howe, M. Nee 27251 9 May 1983 (MICH); LeFlore Co., Winding Stair Mountains, S. D. Jones 10163 19 May 1993 (MICH); Mayes Co., Locust Grove, U. T. Waterfall 6946 7 Jun 1947 (OKL); Mayes Co., Pryor, J. K. Small 12225 2 May 1925 (OKL); Mayes Co., Pryor Creek, R. Bebb 2750 13 May 1905 (OKL); McIntosh Co., B. Hoagland m9.074 5 May 1999 (OKL); McIntosh Co., E of Henryetta, S. R. Hill 11172 17 May 1982 (MARY); Murray Co., Davis, Caleb A. Morse 5567 30 Apr 2001 (KANU); Murray Co., Davis, Caleb A. Morse 5567 30 Apr 2001 (KANU); Murray Co., Sulphur, U. T. Waterfall 6462 23 Apr 1946 (OKL); Murray Co., Sulphur, G. J. Goodman 7910 3 May 1969

(OKL); Murray Co., Sulphur, U. T. Waterfall 6484 24 May 1946 (OKL); Muskogee Co., R. Bebb 5119 2 May 1940 (OKL); Muskogee Co., R. Bebb 5306 24 May 1940 (OKL); Muskogee Co., Braggs Hill, R. Bebb 3748 28 Apr 1939 (OKL); Muskogee Co., Camp Gruber, M. D. Proctor GRU0374 13 May 1993 (OKL); Nowata Co., Nowata, B. Hoagland OOL089 25 Apr 2000 (OKL); Nowata Co., Oolagah Wildlife Management Area, B. Hoaqland OOL109 25 Apr 2000 (OKL); Nowata Co., Oolagah Wildlife Management Area, B. Hoagland OOL348 31 May 2000 (OKL); Okfuskee Co., D. Benesh e039 5 May 1998 (OKL); Osage Co., P. Folley 1826 1 Jun 1996 (OKL); Osage Co., Pawhuska, Steve Stephens 76912 28 May 1974 (KANU); Osage Co., Western Wall WA, P. Folley 2314 1 May 1999 (OKL); Payne Co., Cushing, L. K. Magrath 20529 22 May 1999 (OKL); Payne Co., Cushing City Park, P. Folley 2330 22 May 1999 (OKL); Payne Co., Manning Prairie, P. Folley 2331 22 May 1999 (OKL); Payne Co., Schlegel, P. Folley 1429 27 May 1995 (OKL); Payne Co., Schlegel, L. K. Magrath 20517 22 May 1999 (OKL); Payne Co., Stillwater, L. E. McKinney 2586 12 May 1987 (MICH); Payne Co., Stillwater, C A Taylor 11950 25 May 1983 (KANU); Payne Co., Stillwater, U. T. Waterfall 10803 12 Jun 1952 (OKL); Pittsburg Co., B. Hoagland m9.167 14 Jun 1999 (OKL); Pushmataha Co., Clayton, F. H. Means Jr. 3311 11 May 1968 (OKL); Wagoner Co., R. Bebb 5427 1 Jun 1940 (OKL); Wagoner Co., R. Bebb 3871 3 May 1939 (OKL); Wagoner Co., R. Bebb 3869 3 May 1939 (OKL); Wagoner Co., Wagoner, R. Bebb 3956 15 May 1939 (OKL); Washington Co., Copan, Steve Stephens 76959 28 May 1974 (KANU).

Pennsylvania: Adams Co., Gettysburg Nat. Mil. Park, D. Brunton 10266 18 May 1991 (MICH); Bedford Co., Breezewood, D. Berkheimer 8901 22 Jun 1947 (VPI); Bedford Co., Alum Bank, D. Berkheimer 3177 19 Jun 1942 (MICH); Berks Co., Morgantown, W. C. Brumbach 5457 24 Jun 1966 (MSC); Bucks Co., Upper Black Eddy, R. Hine s.n. 15 Jul 1925 (WV); Bucks Co., Beaver Creek, F. J. Hermann 4285 4 Jun 1933 (NCU); Bucks Co., Tinicum Creek, F. J. Hermann 3438 12 Jul 1932 (MICH); Butler Co., Moraine SP, J. K. Bissell 1995:049 14 Jun 1995 (MICH); Centre Co., Coburn, H. A. Wahl 2589 17 Jun 1938 (NCU); Centre Co., Potter's Mills, H. A. Wahl 1006 16 Jun 1941 (NEB); Chester Co., Nottingham Barrens, F. W. Pennell 3694 22 Jun 1912 (NEB); Chester Co., Phoenixville, H. A. Stone s.n. 5 Jun 1927 (GH); Lehigh Co., Powder Valley, H. W. Pretz 8149 11 Jun 1916 (MSC); Montgomery Co., Frederick, E. T. Wherry s.n. 21 Jun 1958 (VPI); Montgomery Co., Baederwood District, Abington Township, J. Bright 19833 30 May 1945 (WV); Northampton Co., Wydnor, R. L. Schaeffer 13866 9 Jul 1941 (GH).

South Carolina: Oconee Co., Sumter National Forest, A. A. Reznicek 8983 23 May 1992 (MICH); Oconee Co., Walhalla, A. A. Reznicek 8983 23 May 1992 (TAES).

Tennessee: Cumberland Co., Rockwood Airport, V. E. McNeilus 94-161 13 May 1994 (MSC); Cumberland Co., Rockwood Airport, V. E. McNeilus 94-154 13 May 1994 (MICH); Knox Co., Powell Station, K. Rogers 41123 28 May 1966 (NCU); Rutherford Co., La Vergne, E. Quarterman 2032 11 May 1947 (KANU).

Texas: Brazos Co., J. S. Carter 15 7 Apr 1997 (TAES); Brazos Co., H. Ness s.n. 10 Apr 1901 (TAES); Brazos Co., S. D. Jones 1106 3 Apr 1988 (TAES); Brazos Co., College Station, L. E. Brown 566 9 May 1966 (WV); Brazos Co., Bryan, S. D. Jones 4089 24 Mar 1990 (MICH); Brazos Co., Bryan, O. Brown 67 7 Apr 1967 (TAES); Brazos Co., Bryan-College station, D. McCasland 44 11 Apr 1995 (TAES); Brazos Co., College, H. Jennings s.n. 8 Apr 1890 (MICH); Brazos Co., College Station, S. D. Jones 2407 7 Apr 1989 (TAES); Brazos Co., College Station, M. Eaglesham 020 27 Mar 1986 (TAMU); Brazos Co., College Station, G. A. Engling 317 22 Apr 1950 (TAMU); Brazos Co., College Station, F. Gould 12509 13 May 1968 (TAES); Brazos Co., College Station, R. Lonard s.n. 19 Apr 1967 (TAES); Brazos Co., College Station, J. E. Smith Jr. 297 17 Apr 1993 (MICH); Brazos Co., College Station, S. D. Jones 9965 27 Apr 1993 (MICH); Brazos Co., College Station, S. L. Hatch 6220 27 Apr 1993 (TAES); Brazos Co., College Station, P. Fryxell 2613 4 Apr 1976 (MICH); Brazos Co., College Station, R. Lonard 2278 15 Apr 1969 (TAES); Brazos Co., North Oakwood, R. G. Reeves 45 17 Apr 1940 (TAES); Brazos Co., Plainsman, S. D. Jones 1075 27 Apr 1988 (TAES); Burleson Co., Clay, G. Ajilvsqi 8379 14 Apr 1983 (TAMU); Burleson Co., Snook, J. Bridgforth 67 7 Apr 2001 (TAMU); Burleson Co., Somerville, J. Bridgforth 66 7 Apr 2001 (TAMU); Colorado Co., Sealy, S. L. Orzell 13166 21 Apr 1990 (MICH); Dallas Co., Dallas, E. S. Nixon 1327 26 Apr 1969 (TAES); Dallas Co., Seagoville, C. L. Lundell 10631 16 May 1941 (MICH); Franklin Co., Mt. Vernon, S. D. Jones 2853 15 May 1989 (TAES); Grayson Co., Denison, R. Bebb 2702 12 May 1905 (OKL); Grimes Co., Carlos, S. D. Jones 2503 21 Apr 1989 (MICH); Grimes Co., Navasota, L. C. Higgins 3939 31 Mar 1971 (MICH); Jasper Co., Angelina NF, S. L. Orzell 6309 15 Apr 1988 (MICH); Madison Co., FM 247, A. K. Neill 2629 17 May 1999 (TAMU); Madison Co., Navasota River, A. K. Neill 407 29 Mar 1997 (TAMU); Madison Co., Madisonville, F. Gould 8562 10 Apr 1959 (TAES); Newton Co., J. Kessler 6275 23 Jun 1982 (TAES); Red River Co., FR 2825, S. D. Jones 2872 15 May 1989 (TAES); Red River Co., Hwy 37, S. D. Jones 2872 15 May 1989 (MICH); Robertson Co., Easterly, S. D. Jones 6335 10 Apr 1991 (MICH); Robertson

Co., Benchley, T. Hightower 115 21 Apr 1983 (TAMU); Robertson Co., Benchley, T. Hightower 120
21 Apr 1983 (TAMU); Robertson Co., Benchley, J. E. Wood 263 2 Apr 1950 (TAMU); Robertson
Co., Hearne, S. D. Jones 8275 18 Apr 1992 (MICH); Robertson Co., New Baden, T. Starbuck
1717 16 Apr 1982 (TAES); Robertson Co., Wheelock, T. Starbuck 1757 18 Apr 1982 (TAMU);
San Jacinto Co., Big Creek, J. Kessler 2872 1 Apr 1979 (TAES); San Jacinto Co., Sam Houston
NF, J. Kessler 3347 28 Apr 1979 (TAES); Trinity Co., Applesprings, E. S. Nixon 17440 17 Apr
1990 (TAES); Van Zandt Co., Ben Wheeler, D. S. Correll 16207 3 May 1957 (NCU); Walker Co.,
Huntsville, H. B. Parks 7823 11 May 1934 (TAES); Walker Co., Pontsville, S. E. Wolff 4966 12
Apr 1934 (TAES); Walker Co., Riverside, S. Orzell 6472 21 Apr 1988 (MICH); Waller Co., Waller,
S. D. Jones 2414 15 Apr 1989 (TAES); Washington Co., Peaceable Kingdom, J. Kessler 5513 13
Apr 1982 (TAES).

Virginia: Fairfax Co., Gainesville, F. R. Fosberg 54197 28 May 1972 (VPI); Fauquier Co.,
Marshall, G. P. Fleming 1715 4 Jun 1985 (VPI); Fauquier Co., The Plains, G. P. Fleming 3080
28 May 1988 (VPI); Fauquier Co., Archwood Meadow, J. B. Nelson 13188 8 Jul 1992 (MICH);
Fauquier Co., Buck Mt., H. A. Allard 3063 20 Jun 1937 (VPI); Fauquier Co., Western slope of Bull
Run Mts., H. A. Allard 4916 5 Jun 1938 (VPI); Montgomery Co., Blacksburg, T. F. Wieboldt 5075
6 Jun 1984 (VPI); Montgomery Co., Pilot, D. W. Ogle 4720 22 Jun 1981 (VPI); Prince William
Co., SW of Nokesville, G. P. Fleming 6618 10 Jun 1992 (VPI); Prince William Co., Manassas
National Battlefield Park, G. P. Fleming 13101 27 May 1997 (VPI); Washington Co., Cedarville,
D. W. Ogle 1395 18 May 1975 (VPI).

West Virginia: Doddridge Co., Morgans Run Road, W. N. Grafton s.n. 26 May 2005 (WV);
Grant Co., Cabins, H. A. Davis 4385 25 Jun 1941 (WV); Grant Co., Petersburg, J. F. Clovis 1961
30 May 1973 (WV); Hardy Co., South Branch WMA, W. N. Grafton s.n. 25 May 2005 (WV);
Lewis Co., Jacksonville, W. N. Grafton s.n. 6 Jun 1980 (WV); Monongalia Co., Crooked Run, J.
L. Dawson 21342 5 Jun 1979 (WV).

Wisconsin: Iowa Co., Barneveld, E. H. Zimmerman 307 18 Jul 1996 (MICH);

Carex caroliniana U. S. A. Alabama: Maddison Co., Ardmore, R. Kral 84668 19 May 1995 (MICH); Morgan Co., Decatur, D. Isley 3391 25 May 1944 (MSC); Morgan Co., Florette, R. Naczi 1084 9 May 1986 (MICH); Pickens Co., Pickensville, C. T. Bryson 3164 16 May 1981 (GA); Pickens Co., Reform, R. Kral 55516 19 May 1975 (MICH).

Arkansas: Stuttgart Co., Stuttgart, Phillip E. Hyatt 7301 5 Apr 1997 (MICH); Bradley Co., Warren, C. T. Bryson 4262 9 May 1986 (MICH); Chicot Co., Eudora, R. D. Thomas 128214 30 Apr 1992 (USCH); Chicot Co., Eudora, C. T. Bryson 11503 30 Apr 1992 (CLEMS); Clark Co., Whelen Springs, Phillip E. Hyatt 8498 1 May 1999 (MICH); Clay Co., Pollard, Phillip E. Hyatt 4377.11 22 May 1992 (MICH); Cleveland Co., Fordyce, S. D. Jones 8490 14 May 1992 (MICH); Columbia Co., Plainfield, Phillip E. Hyatt 8550 8 May 1999 (MICH); Dallas Co., Saline River, Phillip E. Hyatt 6514 28 May 1995 (MICH); Faulkner Co., Phillip E. Hyatt 6476 28 May 1995 (MICH); Grant Co., U. S. Hwy 167, Phillip E. Hyatt 6497 28 May 1995 (MICH); Greene Co., Halliday, Phillip E. Hyatt 5946 9 May 1994 (MICH); Hempstead Co., Fulton, S. D. Jones 2580 28 Apr 1989 (MICH); Independence Co., Newark, Phillip E. Hyatt 5563 29 May 1993 (MICH); Jefferson Co., Pine Bluff, Phillip E. Hyatt 7293 5 Apr 1997 (MICH); Lafayette Co., Ark Hwy 29, Phillip E. Hyatt 6362 6 May 1995 (MICH); Lawrence Co., Hoxie, Larry J. Harms 2231 2 May 1965 (KANU); Lonoke Co., Kerr, A. A. Reznicek 9277 17 May 1993 (MICH); Miller Co., Texarkana, B. F. Bush s.n. 28 Apr 1905 (WV); Monroe Co., Blackton, Phillip E. Hyatt 7135 24 May 1996 (MICH); Nevada Co., Reader, Phillip E. Hyatt 8484 1 May 1999 (MICH); Ouachita Co., Ouachita River, Phillip E. Hyatt 8531 1 May 1999 (MICH); Perry Co., South Fourche Recreation Area, Phillip E. Hyatt 8041 3 May 1998 (MICH); Phillips Co., Marvell, Larry J. Harms 2243 3 May 1965 (KANU); Sevier Co., DeQueen, Phillip E. Hyatt 6317 23 Apr 1995 (MICH); Union Co., El Dorado, ca 1 mi N, Andrew Grammer s.n. 30 Apr 2001 (KANU); Union Co., Louisiana Border, Phillip E. Hyatt 6404 13 May 1995 (MICH); White Co., Henry Gray WMA, Phillip E. Hyatt 5993 11 May 1994 (MICH); Woodruff Co., Gray's vicinity, Phillip E. Hyatt 7104 24 May 1996 (MICH); Woodruff Co., McCrory, Phillip E. Hyatt 7096 24 May 1996 (MICH); Yell Co., Rover, Phillip E. Hyatt 8072 3 May 1998 (MICH); Yell Co., Plainview, D. Demaree 52414 24 May 1965 (NCU).

Delaware: Wilmington, Anonymous 1897 (NCU); New Castle, Talleyville, R. Naczi 2564 12 Jun 1990 (MICH).

District of Columbia: Along Potomac River, C. Lea 1691 27 May 2000 (MARY); Along Potomac River, C. Lea 1693 27 May 2000 (TAWES).

Florida: Jackson Co., Buena Vista Landing, A. K. Gholson Jr. 11295 23 Apr 1985 (MICH). Georgia: Baker Co., Jones Ecological Research Center, Flora of Ichauway, L. K. Kirkman 3246 25 Mar 1994 (GA); Baker Co., SW of Newton, L. C. Anderson 16420 18 May 1996 (GA); Clarke Co., Athens, J. R. Manhart 31 3 May 1980 (MICH); Elbert Co., McCalla Island, W. C. Credle 2812 29 Apr 1980 (CLEMS); Elbert Co., Savannah River Project, W. C. Credle 2871 2 Jun 1980 (CLEMS); Gordon Co., New Echota State Historic Site, C. H. Gomez 2351 5 May 2000 (GA);
Greene Co., Apalachee River, J. E. Seward 1132 9 May 1992 (GA); Hart Co., Savannah River, J. R. Manhart 303 23 May 1981 (MICH); McDuffie Co., Thompson, Phillip E. Hyatt 10171 28 Apr 2001 (MICH); Montgomery Co., Mount Vernon, R. Naczi 5248 5 May 1996 (MICH); Wilcox Co., Oscewichee Spring, W. K. George s.n. 22 Apr 1989 (MICH); Wilkes Co., Tignal, C. H. Fitzgerald 269 24 May 1970 (GA).

Illinois: Alexander Co., Tamms, S. R. Hill 31849 23 Jun 1999 (MICH); Clinton Co., Eldon Hazlett SP, A. Brant 1802 3 Jun 1988 (MO); Jackson Co., Murphysboro, S. R. Hill 30252 19 May 1998 (MICH); Johnson Co., Bell Pond Natural Area, L. R. Phillippe 13956 22 May 1990 (MICH); Lawrence Co., Lawrenceville, N. C. Henderson 72-11 3 Jun 1972 (MO); Saline Co., Harrisburg, S. Hill 26426 4 May 1995 (TAES); Saline Co., Shawnee NF, Phillip E. Hyatt 4354 20 May 1992 (MICH).

Indiana: Crawford Co., Leavenworth, F. J. Hermann 6687 16 Jun 1935 (MICH); Gibson Co., Petoka, C. C. Deam 13313 9 Jun 1913 (WV); Jefferson Co., Chelsea, E. Banta 7 19 Jun 1935 (MICH); Lawrence Co., Springville, R. M. Kriebel 1792 6 Jun 1934 (MICH); Sullivan Co., Oaktown, A. A. Reznicek 10846 8 Jun 1999 (MICH).

Kansas: Cherokee Co., Baxter Springs, Ronald L. McGregor 36189 16 May 1985 (KANU);
Cherokee Co., Baxter Springs, Ronald L. McGregor 40314 1 May 1991 (KANU); Cherokee Co.,
Chetopa, Ole A. Kolstad 2233 3 Jun 1964 (KANU); Cherokee Co., Ronald L. McGregor 38796 5
May 1988 (KANU); Linn Co., Marais De Cygne Wildlife Refuge, Ole A. Kolstad 2313 10 Jun 1964 (KANU); Linn Co., Trading Post, Caleb A. Morse 10475 20 May 2004 (KANU); Linn Co., Trading
Post, Caleb A. Morse 10413 14 May 2004 (KANU); Neosho Co., St. Paul, W. W. Holland 5467
25 May 1986 (KANU); Neosho Co., St. Paul, Ralph Brooks 5582 17 May 1974 (KANU); Neosho
Co., St. Paul, W. W. Holland 418 24 May 1964 (KANU).

Kentucky: Caldwell Co., Dawson Springs, L. E. McKinney 5060 28 May 1998 (EKY); Calloway Co., Backusburg, R. Athey 5098 27 May 1985 (EKY); Campbell Co., Silver Grove, A. A. Reznicek 9988 27 May 1995 (MICH); Campbell Co., Silver Grove, G. F. Buddell II s.n. 31 May 1980 (NCU); Christian Co., Patton Road, L. E. McKinney 5457 18 May 1993 (MICH); Fleming Co., Plummers Landing, R. Hannan 6645 29 May 1981 (EKY); Franklin Co., Twilight Dr. Swamp Twilight Dr. Swamp, wet meadow. S. Rice s.n. 9 Jul 1984 (EKY); Hardin Co., Rolling Fork River, R. Cranfill 780 30 May 1978 (MICH); Hickman Co., Murphy's Pond, J. T. Grubbs 143 12 May 1987 (NYS); Jefferson Co., Louisville, M. E. Wharton 44598 20 Jun 1939 (MICH); Knox Co., Gray, L. E. McKinney 5386 10 May 1993 (MICH); Laurel Co., Charlie Cheeks Swamp, R. Jones 6357 16 Jun 1990 (EKY); Lincoln Co., Green River, B. Hoagland s.n. 13 Jun 1988 (EKY); Lyon Co., SR 274, L. E. McKinney 4972 5 May 1992 (EKY); Madison Co., Muddy Creek, G. W. Libby OB-332 31 May 1993 (EKY); Madison Co., Richmond, G. W. Libby GB-332 31 May 1993 (MICH); Menifee Co., Rt. 460, C. Hanley 14 29 Jun 1988 (EKY); Powell Co., Clay City Swamps, J. MacGregor s.n. 2 Jun 1974 (EKY); Trigg Co., Barkley Lake SP, L. E. McKinney 4985 4 May 1992 (EKY).

Louisiana: Catahoula Co., Rosefield, R. D. Thomas 2849 8 Apr 1967 (NCU); Franklin Co., , R. D. Thomas 2258 6 Apr 1967 (NCU); Grant Co., Catahoula Ranger Dist., Baghdad, Phillip E. Hyatt 7399 7 May 1997 (MICH); Grant Co., Catahoula Ranger District of Kisatchie NF, Iatt Creek, Phillip E. Hyatt 6960 18 Apr 1996 (MICH); Grant Co., Packton, Phillip E. Hyatt 10215 2 May 2001 (MICH); Natchitoches Co., Kisatchie NF, Phillip E. Hyatt 8106 6 May 1998 (MICH); Ouachita Co., Monroe, R. D. Thomas 99598 20 May 1987 (TAES); Ouachita Co., Monroe, R. Kral 8421 5 Apr 1959 (NCU); Rapides Co., Alexandria, Phillip E. Hyatt 7385 7 May 1997 (MICH); Vernon Co., Leesville, Cooley 3873 27 Apr 1955 (NCU); Webster Co., Shreveport, Larry J. Harms 2288 4 May 1965 (KANU).

Maryland: Riverdale, A. Chase 2380 22 Jun 1904 (OKL); Allegany Co., Sideling Hill Bioreserve, C. T. Frye 2012 18 May 1999 (TAWES); Allegany Co., Town creek, C. T. Frye 2017 19 May 1999 (TAWES); Charles Co., Pomonkey, C. Lea 2539 30 May 2001 (TAWES); Charles Co., Pomonkey, C. Lea 2055 16 Jun 2000 (MARY); Montgomery Co., Bear Island, C. Lea 1581 14 May 2000 (MARY); Montgomery Co., Great Falls, J. A. Churchill s.n. 2 Jun 1967 (MSC).

Mississippi: Bolivar Co., Benoit, C. T. Bryson 10050 22 May 1990 (TAES); Bolivar Co.,
Boyle, C. T. Bryson 5486 27 Apr 1987 (MICH); Carroll Co., US 82, C. T. Bryson 13418 25 Apr
1994 (MICH); Choctaw Co., French Camp, C. T. Bryson 13753 20 May 1994 (MICH); Clay Co.,
R. Webster 1527 18 May 1978 (TAES); Clay Co., West Point, C. T. Bryson 3314 18 May 1982
(MICH); Coahoma Co., Tutwiler, C. T. Bryson 7475 4 May 1988 (MICH); Grenada Co., Hunt
Lake, C. T. Bryson 15189 20 May 1996 (MICH); Holmes Co., Coxburg, C. T. Bryson 11235 14
Apr 1992 (TAES); Holmes Co., Tchula, C. T. Bryson 8945 2 May 1990 (TAES); Holmes Co.,
Tchula, C. T. Bryson 8936 2 May 1990 (MICH); Humphreys Co., Belzoni, C. T. Bryson 8956 2
May 1990 (TAES); Issaquena Co., Mayersville, C. T. Bryson 15159 15 May 1996 (MICH); Kemper

Co., Wahalak Creek, C. T. Bryson 8573 15 May 1989 (MICH); Leake Co., Thomastown, C. T. Bryson 13776 20 May 1994 (MICH); Leflore Co., Yazoo River Run, C. T. Bryson 3752 27 Apr 1985 (MICH); LeFlore Co., Grenwood, C. T. Bryson 13399 23 Apr 1994 (MICH); Leflore Co., Minter, C. T. Bryson 7258 21 Apr 1988 (MICH); LeFlore Co., Minter, C. T. Bryson 7256 21 Apr 1988 (MICH); Lowndes Co., Mayhew, C. T. Bryson 3286 10 May 1982 (MICH); Newton Co., Newton, C. T. Bryson 3257 8 May 1982 (MICH); Newton Co., Newton, C. T. Bryson 8842 13 Apr 1990 (MICH); Oktibbeha Co., Starkville, C. T. Bryson 3192 24 Apr 1982 (MICH); Panola Co., Batesville, C. T. Bryson 7549 4 May 1988 (MICH); Quitman Co., Marks, C. T. Bryson 7529 4 May 1988 (MICH); Sunflower Co., Indianola, C. T. Bryson 7391 29 Apr 1988 (MICH); Sunflower Co., Indianola, C. T. Bryson 7380 29 Apr 1988 (USCH); Sunflower Co., Ruleville, C. T. Bryson 11514 8 May 1992 (CLEMS); Tunica Co., Tunica, C. T. Bryson 11406 24 Apr 1992 (CLEMS); Washington Co., Helm, C. T. Bryson 4232 22 Apr 1986 (MICH); Washington Co., Helm, C. T. Bryson 3611 24 Apr 1984 (MICH); Washington Co., Hollandale, C. T. Bryson 3471 1 May 1983 (MICH); Washington Co., Leroy Percy SP, C. T. Bryson 19169 29 Apr 2002 (USCH); Washington Co., Stoneville, C. T. Bryson 3465 24 Apr 1983 (MICH); Webster Co., Cumberland, C. T. Bryson 3772 27 Apr 1985 (MICH).

Missouri: Barton Co., Hwy 126, D. Castaner 7411 25 May 1983 (MICH); Barton Co.,
Nashville, E. J. Palmer 53843 20 May 1952 (NCU); Bollinger Co., Castor River Conservation
Area, A. E. Brant 4233 18 May 1999 (MO); Bollinger Co., Dongola, B. Jacobs 00-30 8 Jun 2000
(MO); Jasper Co., D. Castaner 7422 25 May 1983 (MICH); Jasper Co., Jasper, J. F. Breuckle
40-103 27 May 1940 (OKL); New Madrid, East Prairie, S. D. Jones 8612 18 May 1992 (MICH);
Reynolds Co., Johnson Shut-Ins SP, P. M. McKenzie 2009 13 May 2002 (MO); St. Louis, St.
Louis, H. Eggert s.n. 10 Jun 1887 (MICH); Stoddard Co., Dudley, R. Naczi 1275 23 May 1986
(MICH); Stoddard Co., Otter Slough Conservation Area, A. E. Brant 4390 31 May 2000 (MO);
Vernon Co., Washington Township, D. Castaner 6827 19 May 1982 (TAES).

New Jersey: Burlington Co., Delaware River, F. J. Hermann 4248 1 Jun 1933 (MICH); Burlington Co., Riverton, F. J. Hermann 4248 1 Jun 1933 (OKL); Gloucester Co., Repaupo, F. J. Hermann 4435 16 Jun 1933 (OKL);

North Carolina: Anson Co., Lilesville, A. E. Radford 43629 20 May 1961 (NCU); Bladen Co., Elizabethtown, A. E. Radford 4089 20 May 1949 (NCU); Chatham Co., Old Mill site above Mason Place, Anonymous 28 Apr 1957 (NCU); Chatham Co., Mt. Carmel, A. E. Radford 4061 7 May 1949 (NCU); Chatham Co., Farrington, A. E. Radford 42709 31 May 1959 (NCU); Chatham Co., Seaforth, A. E. Radford 43794 31 May 1961 (NCU); Davidson Co., Beaverdam Creek headwaters, P. D. McMillan 2944 7 May 1998 (CLEMS); Davidson Co., Denton, A. E. Radford 12851 16 Jun 1956 (NCU); Durham Co., Bland, A. E. Radford 43113 31 May 1960 (NCU); Durham Co., Duke Forest, M. Palmer 1130 26 May 1987 (MICH); Durham Co., Durham, R. K. Godfrey 3835 4 May 1938 (NCU); Durham Co., Morrisville, R. K. Godfrey 3645 21 Apr 1938 (NCU); Durham Co., Orange County Line, S. W. Leonard 1480 23 May 1968 (NCU); Forsyth Co., Stanleyville, H. E. Ahles 40856 17 May 1958 (NCU); Granville Co., Creedmor, A. E. Radford 43920 16 Jun 1961 (NCU); Guilford Co., Rockingham-Guilford line, L. Melvin 3471 24 May 1956 (NCU); Johnston Co., Clayton, A. E. Radford 21673 29 Apr 1957 (NCU); Johnston Co., Smithfield, A. E. Radford 4035 30 Apr 1949 (NCU); Lee Co., Lockville Dam, L. S. Beard 380 25 Apr 1955 (NCU); Moore Co., Glendon, A. E. Radford 43376 11 Jun 1960 (NCU); Person Co., McGhees Mill, A. E. Radford 43164 2 Jun 1960 (NCU); Randolph Co., Farmer, A. E. Radford 43006 24 May 1960 (NCU); Richmond Co., Ellerbe, A. E. Radford 11488 19 May 1956 (NCU); Rockingham Co., Foushee, A. E. Radford 43832 8 Jun 1961 (NCU); Rowan Co., E. Spencer, A. E. Radford 11538 26 May 1956 (NCU); Stanly Co., Albermarle, A. E. Radford 10594 4 May 1956 (NCU); Wake Co., Rolesville, A. E. Radford 42944 22 May 1960 (NCU); Warren Co., Elberon, A. E. Radford 43754 29 May 1961 (NCU).

Ohio: Scioto Co., Green Township, A. Cusick 21546 12 May 1982 (MICH); Summit Co., Twinsburg, G. Wilder 9728 9 Jun 1998 (MICH); Tuscarawas Co., New Philadelphia, A. W. Cusick 10885 13 Jun 1970 (NCU).

Oklahoma: Bryan Co., Oberlin, J. Taylor 1389B 16 Apr 1963 (OKL); Creek Co., Keystone WMA, B. Hoagland KEY-074 15 May 2002 (OKL); McCurtain Co., Red Slough WMA, B. Hoagland RSGS074 12 Apr 1999 (OKL); McCurtain Co., Tom, U. T. Waterfall 11338 18 Apr 1953 (OKL); Okfuskee Co., Deep Fork WMA, D. Benesh DFX096 1 May 1998 (OKL); Okmulgee Co., Eufaula WMA, B. Hoagland DF0051 23 May 1996 (OKL).

Pennsylvania: South Philadelphis, A. MacElwee 1748 19 Jun 1900 (NCU); Bedford Co.,
Ryot, D. Berkheimer 3210 19 Jun 1942 (GH); Bedford Co., Bedford, S. P. Grund 1905 11 Jun 1997 (USCH); Berks Co., French Creek SP, L. A. Standley 1502 20 Jun 1987 (MICH); Bucks Co.,
Bristol, R. R. Dreisbach 2170 7 Jun 1924 (MICH); Fulton Co., Harrisonville, H. A. Wahl 2019 1
Jun 1947 (GH); Fulton Co., Warfordsburg, J. A. Churchill s.n. 13 Jun 1966 (MSC); Perry Co.,

Liverpool, J. M. Fogg Jr. 15839 20 Jun 1939 (GH); Philadelphia Co., Cobb's Creek, F. J. Hermann 3079 28 May 1932 (MICH); York Co., McCalls Ferry, Joseph Crawford s.n. 1 Jul 1904 (KANU).

South Carolina: Abbeville Co., Calhoun Falls, A. E. Radford 22722 13 May 1957 (NCU); Abbeville Co., Savannah River Project, M. G. Douglass 1449 7 Jun 1978 (CLEMS); Anderson Co., Fair Play, H. E. Ahles 13428 31 May 1956 (NCU); Barnwell Co., Savannah River Operations Area, W. T. Batson s.n. 4 May 1953 (NCU); Berkeley Co., Cross, W. T. Batson s.n. 30 Apr 1956 (USCH); Berkeley Co., Mulberry Plantation, P. D. McMillan 5188 2 Jun 2001 (CLEMS); Berkeley Co., Cross, W. T. Batson 1244 8 Apr 1956 (USCH); Berkeley Co., Berekeley Country Club, P. D. McMillan 5183 2 Jun 2001 (CLEMS); Berkeley Co., Lewisfield Plantation, P. D. McMillan 5041 29 Apr 2001 (CLEMS); Chesterfield Co., Cheraw, A. E. Radford 12239 5 Jun 1956 (NCU); Edgefield Co., Sumter NF, Forks Analysis Area, J. B. Nelson 17160 25 Apr 1996 (USCH); Fairfield Co., Winnsboro, C. N. Horn 8002 21 May 1994 (MICH); Fairfield Co., Winnsboro, C. N. Horn 7960 6 May 1994 (MICH); Greenwood Co., Gaines, J. B. Nelson 22543 26 Apr 2002 (USCH); Greenwood Co., Gaines, J. B. Nelson 22543 26 Apr 2002 (USCH); Hampton Co., Belmont Plantation, R. D. Porcher Jr. 289 5 Sep 1971 (USCH); Jasper Co., Tillman, A. E. Radford 44530 20 Apr 1962 (NCU); Lexington Co., Old Saluda Mill Site, J. B. Nelson 14054 7 May 1993 (USCH); Newberry Co., Maybinton, J. B. Nelson 20368 23 Apr 1999 (USCH); Oconee Co., Lake Hartwell, L. L. Gaddy s.n. 28 May 1986 (CLEMS); Orangeburg Co., Santee Cooper Widlife Management Area, A. B. Pittman 04270102 27 Apr 2001 (USCH); Pickens Co., Jocassee Gorges, P. D. McMillan 6329 5 May 2002 (CLEMS); Pickens Co., Pendleton, J. F. Townsend 1501 20 May 1997 (CLEMS); Sumter Co., Sumter, A. E. Radford 23803 4 Jun 1957 (NCU).

Tennessee: Blount Co., Great Smoky Mountain NP, Abram's Creek, V. E. McNeilus 89-339 3 Jun 1989 (MSC); Coffee Co., Arnold Center, R. Kral 55318 9 May 1975 (MICH); Coffee Co., Arnold Village, K. E. Rogers 44784 18 May 1966 (NCU); Coffee Co., Double Pond, V. E. McNeilus 92-408 1 Jun 1992 (MICH); Coffee Co., Manchester, K. E. Rogers 44752 18 May 1966 (NCU); Dickson Co., White Bluff, R. Kral 55411 13 May 1975 (MICH); Hamilton Co., Chicamauga Creek, V. E. McNeilus 91-292 23 May 1991 (MICH); Tipton Co., Hatchie River, L. E. McKinney 2493 8 May 1987 (MICH).

Texas: Mineola, J. Reverchon 2451 24 Apr 1907 (WV); Angelina Co., Angelina River, E.
S. Nixon 17479 12 Apr 1990 (TAES); Bowie Co., Texarkana Lake, Larry J. Harms 2319 4 May 1965 (KANU); Brazos Co., College Station, W. S. Jennings 259 11 Apr 1949 (TAMU); Brazos Co.,

College Station, S. D. Jones 6351 11 Apr 1991 (MICH); Brazos Co., College Station, E. L. Usrey 57 30 Mar 1950 (TAES); Burleson Co., Davidson Creek, S. D. Jones 1199 29 Apr 1988 (TAES);
Galveston Co., Dickinson, F. R. Waller 3611 5 May 1975 (TAES); Galveston Co., League City, F. R. Waller 3443 31 Mar 1975 (TAES); Gregg Co., Longview, R. R. Haynes 4779 24 Apr 1975 (NCU); Grimes Co., Hwy 105, J. Kessler 4250 28 Apr 1980 (TAES); Harris Co., Langham Creek, L. E. Brown 21914b 21 Mar 1998 (TAES); Harris Co., Nimitz High School, J. Kessler 2885 5 Apr 1979 (TAMU); Harris Co., Tomball, L. Brown 15889 29 Mar 1992 (TAES); Harris Co., Tomball, S. D. Jones 2523 15 Apr 1989 (OKL); Houston Co., Davy Crocket NF, Neches Bluff Overlook, S. L. Orzell 6420 20 Apr 1988 (MICH); Jasper Co., Angelina NF, Bouton Lake, S. L. Orzell 5078 18 Apr 1987 (MICH); Jefferson Co., Beaumont, C. L. Lundell 11238 16 Apr 1942 (MICH); Jefferson Co., Voth, S. L. Orzell 8968 4 Apr 1989 (MICH); Leon Co., Keechi Creek WMA, A.Neill 3021 21 Apr 2000 (TAMU); Liberty Co., Trinity River, E. S. Nixon 4259 28 Apr 1972 (NCU); Madison Co., Navasota River, A. K. Neill 1337 2 Apr 1998 (TAMU); Robertson Co., Ridge, T. Starbuck 1854 27 Apr 1982 (TAMU).

Virginia: Arlington Co., 4 Mile Run Area, E. H. Walker 728 1 Jun 1930 (MARY); Bath Co., Nimrod Hall, G. P. Fleming 13393 25 Jun 1997 (VPI); Culpeper Co., Culpeper, G. P. Fleming 4014 27 May 1989 (VPI); Cumberland Co., 14 mi NE of Farmville (Prince Edward Co.), T. F. Wieboldt 5509 17 May 1985 (VPI); Fairfax Co., Pleasant Valley Rd, T. Bradley 23205 14 May 1990 (CLEMS); Fairfax Co., Elklick Run, T. Bradley s.n. 23 May 1976 (VPI); Greensville Co., Jarratt, J. C. Ludwig 89039 30 Apr 1989 (VPI); Hanover Co., Vontay, J. C. Ludwig 2087 24 May 1993 (VPI); King George, Chotank Swamp, D. M. E. Ware 8259 18 Jun 1983 (CLEMS); King William, Zoar SF, Aylett, G. P. Fleming 13093 23 May 1997 (VPI); Loudoun Co., Broad Run, H. A. Allard 20315 1 Jun 1952 (WV); Loudoun Co., Elklick Run, M. T. Strong 87-097 14 Jun 1987 (USCH); Lunenburg Co., Lunenburg, T. F. Wieboldt 5991 3 Jun 1986 (VPI); Mecklenburg Co., Kerr Reservoir/Bluestone WMA, Clarksville, G. P. Fleming 13227 4 Jun 1997 (VPI); Orange Co., Palmyra Church, T. Bradley 23253 21 May 1990 (CLEMS); Orange Co., VA 20, T. Bradley 20453 21 Jun 1984 (NCU); Powhatan Co., Fine Creek Mill, C. Corcoran 695 18 Jun 1976 (NCU); Prince William, Occoquan Bay National Wildlife Refuge, Woodbridge, M. T. Strong 1602 30 May 1998 (MICH); Prince William, Camp Upshur, B. W. Hoagland QUN0366 18 Jun 1994 (OKL); Prince William County, Combat Village, M. D. Proctor QUN0255 18 May 1994 (OKL); Pulaski

Co., Pulaski, *T. F. Wieboldt 6347* 29 May 1987 (VPI); Roanoke Co., Wabun, *T. F. Wieboldt 6368* 3 Jun 1987 (VPI).

West Virginia: Berkeley Co., Sleepy Creek Lake dam, W. N. Grafton s.n. 27 Jun 2004 (WV);
Berks Co., Gibraltar, W. C. Brumbach 3515 6 Jun 1943 (WV); Mason Co., McClintic WMA, N. Grafton 21 Jun 2005 (WV); Raleigh Co., Sandstone Falls SP, T. F. Wieboldt 5540 21 May 1985 (VPI); Summers Co., Pipestem SP, T. F. Wieboldt 6380 7 Jun 1987 (WV); Tyler Co., Little, W. N. Grafton s.n. 1 Jun 1980 (WV); Upshur Co., Buckhannon, G. B. Rossbach 4620 30 May 1963 (WV); Wirt Co., Palestine, E. A. Bartholomew W-4127 25 Jun 1956 (WV).

Carex complanata. Mexico. Chiapas: Jitotol, P. H. Raven 20059 25 Jan 1965 (MICH);
Colonia el Laurel, G. Davidse 29623 13 Nov 1984 (MICH); Jitotol, W. Anderson 13243 20 Oct 1983 (MICH); Pueblo Nuevo Solistahuacan, P. H. Raven 19879 23 Jan 1965 (MICH); Tenejapa, D. E. Breedlove 12943 10 Oct 1965 (MICH); Colinia Ach'lum, S. Gonzalez 10493 11 Jul 1997 (MICH);
Paraje Matsab, A. S. Ton 943 12 May 1966 (MICH); Tenejapa, S. Gonzalez 10469 10 Jul 1997 (MICH).

Guatemala. Baja Verapaz Co., Sierra de las Minas, L. O. Williams 43413 6 Jan 1974 (MICH).

U. S. A. Alabama: Bibb Co., Centreville, C. T. Bryson 8524 3 May 1988 (MICH); Butler Co., Oaky Streak, R. Naczi 4691 17 May 1995 (MICH); Clay Co., Talladega NF, A. A. Reznicek 7449 14 May 1985 (MICH); Dallas Co., Selma, R. Kral 82493 23 May 1993 (MICH); DeKalb Co., Ft. Payne, R. Naczi 7267 25 May 1998 (VPI); Escambie Co., Little Rock, S. D. Jones 8942 28 May 1992 (MICH); Marion Co., Hamilton, C. T. Bryson 7619 8 May 1988 (TAES); Mobile Co., Mobile Municipal Park, M. G. Lelong 5698 12 May 1971 (NCU); Monroe Co., Midway, R. Naczi 4002 24 May 1994 (MICH); Montgomery Co., Montgomery, R. Kral 55858 24 May 1975 (MICH); Sumter Co., York, R. Kral 26402 7 May 1966 (GA); Tuscaloosa Co., Eight-acre Rock, Roland M Harper 3652 28 Apr 1938 (KANU); Tuscaloosa Co., Tuscaloosa, R. McVaugh 8568 30 May 1947 (MICH).

Arkansas: Calhoun Co., Harrell, R. D. Thomas 133946 19 May 1993 (MICH); Clark Co., S of Hot Springs Co., J. Kessler 4390 25 May 1981 (TAES); Clark Co., Whelen Springs, Phillip E. Hyatt 8502 1 May 1999 (MICH); Cleveland Co., Marks Mill Battleground, C. T. Bryson 4266 9 May 1986 (MICH); Columbia Co., Bussey, Phillip E. Hyatt 6378 6 May 1995 (MICH); Dallas Co., US 167, Phillip E. Hyatt 6512 28 May 1995 (MICH); Dallas Co., Fordyce, L. H. Shinners 19905 1 May 1955 (NCU); Desha Co., McGhee, Phillip E. Hyatt 6604 8 Jun 1995 (MICH); Hot Springs Co., Oak Grove, Phillip E. Hyatt 10288 20 May 2001 (MICH); Jefferson Co., Pine Bluff Arsenal, S.
A. Walker 96.20 30 May 1996 (OKL); Lafayette Co., Hwy 29, Phillip E. Hyatt 6358 6 May 1995 (MICH); Lincoln Co., Star City, Phillip E. Hyatt 7533 20 May 1997 (MICH); Miller Co., Foulk, Phillip E. Hyatt 6348 23 Apr 1995 (MICH); Miller Co., Three States, Phillip E. Hyatt 8567 23 May 1999 (MICH); Ouachita Co., Ouachita Co. Rd 67, Phillip E. Hyatt 6412 13 May 1995 (MICH);
Perry Co., Ozark Highland Trail, Phillip E. Hyatt 8032 3 May 1998 (MICH); Perry Co., Alpin, Phillip E. Hyatt 5434 18 May 1993 (MICH); Pike Co., Delight, Phillip E. Hyatt 6280 22 Apr 1995 (MICH); Polk Co., Rich Mountain, S. D. Jones 4667 14 May 1990 (MICH); Pulaski Co., US 65, C. T. Bryson 12224 16 May 1993 (MICH); Saline Co., AR 167, C. T. Bryson 12229 16 May 1993 (MICH); Saline Co., Ark 367, Phillip E. Hyatt 6487 28 May 1995 (MICH); Saline Co., Hensley, D. Sadler 254 9 Jun 1990 (OKL); Sevier Co., DeQueen, Phillip E. Hyatt 7449 17 May 1997 (MICH); Union Co., Lockhart, R. D. Thomas 110149 24 May 1989 (VPI); Yell Co., Aly, Phillip E. Hyatt 8079 3 May 1998 (MICH).

Delaware: Kent Co., Dinahs Corner, *R. Naczi 9368* 12 Jun 2002 (MICH); New Castle Co., New Castle, *F. J. Hermann 3382* 7 Jul 1932 (MICH).

Florida: Calhoun Co., Blountstown, L. C. Anderson 11929 9 May 1989 (USCH); Gadsden
Co., Tallahassee, R. K. Godfrey 59523 17 May 1960 (MSC); Gadsden Co., Tallahassee, R. K.
Godfrey 63568 28 Apr 1964 (NCU); Jefferson Co., Monticello, R. Kral 6373 19 Apr 1958 (NCU);
Jefferson Co., Monticello Agricultural Research Center, J. B. Nelson 2425 29 Apr 1983 (USCH);
Leon Co., Lake Iamonia, R. K. Godfrey 73490 4 May 1974 (NCU); Liberty Co., Telogia, L. C.
Anderson 19768 22 May 2001 (USCH); Tallahassee Co., Tallahassee, R. K. Godfrey 59523 17 May 1960 (NCU).

Georgia: Baker Co., Ivy Mill Pond, R. F. Thorne 4048 20 May 1947 (GA); Baker Co., Jones
Ecological Research Center, L. K. Kirkman 2105 6 May 1992 (GA); Baldwin Co., GA 49, D. E.
Boufford 18463 18 May 1976 (NCU); Barton Co., Allatoona, W. H. Duncan 8310 13 Jun 1948
(GA); Bartow Co., Adairsville, W. H. Duncan 12566 18 Jun 1951 (GA); Bartow Co., Adairsville,
W. H. Duncan 12319 6 May 1951 (CLEMS); Bartow Co., Adairsville, W. H. Duncan 12402 18
May 1951 (MARY); Bartow Co., Big Pelfrey Pond, Cassville Mt., P. F-C Greear 64294 1 Jul 1964
(GA); Brooks Co., Quitman, W. R. Faircloth 4252 21 Apr 1967 (NCU); Bryan Co., Fort Stewart
Military Reservation, M. O. Moore 1824 30 Apr 1993 (USCH); Bryan Co., Fort Stewart Military
Reservation, T. M. Zebryk 0358 10 Jun 1992 (GA); Butts Co., Jackson, W. J. Crins 9799 2 May

1994 (MICH); Chatham Co., Port Wentworth, W. H. Duncan 21030 15 Jun 1958 (GA); Cook Co., Rt. 37, V. E. McNeilus 92-289 22 May 1992 (MICH); Dade Co., Lookout Mt., A. Cronquist 5411 27 Jun 1948 (MICH); Decatur Co., Chattahoochee, S. J. Smith 3096 14 Apr 1947 (MICH); Decatur Co., Lake Seminole, J. R. Manhart 402 13 Mar 1982 (MICH); DeKalb Co., Stone Mt., J. M. Reade E8053 25 May 1929 (GA); Early Co., Columbia Dam, G. E. Gibbs 109 4 Jun 1970 (GA); Early Co., Gilberts Landing, G. E. Gibbs 114 4 Jun 1970 (GA); Emanuel Co., Swainsboro, G. E. Gibbs 52 7 May 1970 (GA); Emanuel Co., Oak Park, D. E. Boufford 20592 30 Apr 1979 (GA); Floyd Co., Mount Berry, H. C. Jones s.n. 2 Jun 1939 (GA); Gwinnett Co., Apalachee River, J. E. Seward 1197 23 May 1992 (GA); Harris Co., Flora of Callaway Gardens, Sweeney 425 21 Apr 1999 (GA); Harris Co., Pine Mountain, S. B. Jones 20796 18 May 1971 (NCU); Heard Co., Franklin, J. H. Pyron 2832 30 Apr 1938 (MARY); Jefferson Co., Louisville, G. E. Gibbs 95 15 May 1970 (GA); Long Co., Beards Bluff, J. R. Bozeman 10291 23 Jun 1967 (NCU); Marion Co., G. E. Gibbs 117 4 Jun 1970 (GA); Pike Co., Concord, A. Cronquist 5232 21 May 1948 (MICH); Rockdale Co., Convers, A. Cronquist 5179 14 May 1948 (MICH); Rockdale Co., Convers, Phillip E. Hyatt 11465 15 May 2003 (GA); Screven Co., Blackwater Creek, G. E. Gibbs 6 21 Apr 1970 (GA); Walker Co., Lafayette, W. H. Duncan 12634 20 Jun 1951 (GA); Wilcox Co., Abbeville, R. L. Lane Jr. 2241 21 Apr 1968 (GA); Wilcox Co., Abbeville, R. L. Lane, Jr. 2245 21 Apr 1968 (GA).

Kentucky: Adair Co., Pellyton, R. Naczi 7446 18 Jun 1998 (MICH); Laural Co., Lily SurfaceMine Experimental Area, R. L. Thompson 583 23 Jun 1981 (BRIT); Laurel Co., Charlie Creek
Swamp, S. Walker 616 13 Jun 1993 (EKY); Laurel Co., Rock Creek Gorge, R. L. Thompson 891112 23 Jun 1989 (EKY); Letcher Co., Lilley Cornett Woods Research Station, J. D. Sole 772 25
May 1979 (EKY); McCreary Co., Al Nolin Farm, R. Jones 6467 22 Jun 1990 (EKY); Montgomery
Co., Jeffersonville, M. E. Wharton 27890 23 Jun 1938 (MICH); Pulaski Co., Woodstock, J. R.
Abbott 673 21 Jun 1991 (EKY); Whitley Co., Grove Powerline, S. Walker 635 21 Jun 1993 (EKY).

Louisiana: Slidell, K. Rogers 2248 21 Apr 1969 (NCU); Acadia Co., Midland, C. M. Allen 14944 17 Apr 1987 (cb); Bienville Co., Saline, C. H. Allen s.n. 14 May 1977 (WV); Caldwell Co., Hwy 165, J. Kessler 7066 23 May 1983 (TAES); Caldwell Co., Copenhagen, S. Hill 29928 15 Apr 1998 (MICH); Claiborne Co., Kisatchie NF, Phillip E. Hyatt 8013 27 Apr 1998 (MICH); Grant Co., Georgetown, R. D. Thomas 109884 17 May 1989 (NCU); Grant Co., Packton, Phillip E. Hyatt 7987 29 Apr 1998 (MICH); Jefferson Davis Co., Elton, C. M. Allen 14924 17 Apr 1987 (cb); Jefferson Davis Co., Panchoville, J. W. Thieret 30797 26 Apr 1969 (NCU); LaSalle Co., Chickasaw Creek, P. Laird 392 27 Apr 1974 (MICH); Lasalle Co., Olla, J. Kessler 7063 23 May 1983 (TAES); Morehouse Co., Perryville, R. Kral 8653 24 Apr 1959 (VPI); Morehouse Co., Jones, R. D. Thomas 128306 30 Apr 1992 (USCH); Natchitoches Co., Creston, R. D. Thomas 110531 30 May 1989 (NCU); Natchitoches Co., Kisatchie Bayou, Phillip E. Hyatt 10930 10 May 2002 (MICH); Natchitoches Co., Kisatchie NF, R. D. Thomas 103896 19 Apr 1988 (cb); Ouachita Co., Schwartz, R. Kral 8628 24 Apr 1959 (VPI); Ouachita Co., Luna, R. D. Thomas 159189 30 Apr 1999 (KANU); Ouachita Co., West Monroe, R. D. Thomas 13708 16 May 1969 (KANU); Rapides Co., LA 167, H. H. Iltis 21656 19 Apr 1963 (NCU); Rapides Co., Alexandria, C. R. Ball 470 27 May 1899 (NEB); Rapides Co., Kisatchie, D. A. Duncan 57026 11 May 1957 (MICH); Rapides Co., Pineville, C. T. Bryson 13456 16 May 1994 (MICH); St. Martin Co., St. Martinville, J. Hunt 32 20 Apr 1976 (NCU); St. Tammany Co., Madisonville, R. D. Thomas 83507 17 May 1983 (MSC); Tangipahoa Co., Bedico, R. D. Thomas 83456 17 May 1983 (MSC); Vernon Co., Fort Polk, C. Allen 18704 24 Apr 2002 (USCH); Vernon Co., Fort Polk, C. Allen 18715 30 Apr 2002 (USCH); Washington Co., C. M. Allen 8280 13 Jun 1978 (NCU); Washington Co., Franklinton, K. Rogers 8030 13 May 1972 (NCU); Washington Co., Sheridan, K. Rogers 8046 13 May 1972 (NCU); West Caroll Co., Kilbourne, C. T. Bryson 11486 30 Apr 1992 (CLEMS); West Carroll Co., Kilbourne, R. D. Thomas 128255 30 Apr 1992 (USCH).

Maryland: Calvert Co., Cove Point, B. Steury 980513.25 13 May 1998 (MICH); Charles Co., Kerrick Swamp, M. T. Strong 2730 24 Jun 2001 (MICH); Charles Co., Zekiah Swamp, G. Marlowe 791 18 Jun 1950 (MARY); Lasalle Co., LA 124, P. Laird 554 27 May 1974 (MARY); Montgomery Co., Bear Island, C. Lea 1585 14 May 2000 (MARY); Prince Georges Co., Cheltenham Wetland Park, W. D. Longbottom 2106 3 Jun 1991 (MARY); Prince Georges Co., Beltsville, B. Swanton 1618 7 Jul 1939 (MARY); Somerset Co., Town of Princess Anne, W. D. Longbottom 2998 27 May 1992 (MARY); St. Mary's Co., Tall Timbers, J. E. Bennedict Jr. 6254 13 Jul 1958 (VPI); St. Mary's Co., Tall Timbers, J. E. Benedict Jr 2803 3 Jun 1934 (NCU); Talbot Co., Wittman, C. Lea 1970 10 Jun 2000 (MARY); Talbot Co., Easton, E. C. Earle 2513 2 Jun 1940 (WV); Wicomico Co., Green Hill, C. Lea 1655 20 May 2000 (MARY); Worcester Co., Berlin, C. Lea 1860A 31 May 2000 (MARY); Worchester Co., Snow Hill, H. O'Neill 7521 8 Jun 1931 (MICH).

Mississippi: Attala Co., Kosciusko, C. T. Bryson 8929 2 May 1990 (MICH); Chickasaw Co., Davis Lake, C. T. Bryson 15241 20 May 1996 (MICH); Choctaw Co., Jeff Busby Park, C. T. Bryson 13742 20 May 1994 (MICH); Clarke Co., Quitman, C. T. Bryson 13635 18 May 1994 (MICH); Clay Co., West Point, C. T. Bryson 3306 18 May 1982 (MICH); Forrest Co., Geiger Lake, K. E. Rogers 6248-c 15 May 1971 (NCU); Forrest Co., Paul B. Johnson SP, C. T. Bryson 5542 29 Apr 1987 (MICH); Greene Co., Hwy 8, S. B. Jones Jr 2817 23 Apr 1965 (NCU); Greene Co., Sand Hill, C. T. Bryson 13640 18 May 1994 (MICH); Hancock Co., Bay St. Louis, A. B. Langlois s.n. 28 Apr 1885 (MICH); Harrison Co., Coopolis, S. M. Tracy 4120 24 Apr 1898 (KANU); Harrison Co., Mill Creek Bog, C. T. Bryson 10670 12 Apr 1991 (TAES); Hinds Co., Jackson, C. T. Bryson 15132 9 May 1996 (MICH); Itawamba Co., Dorsey, C. T. Bryson 13804 24 May 1994 (MICH); Itawamba Co., Fulton, C. T. Bryson 12397 26 May 1993 (MICH); Jackson Co., Hurley, C. T. Bryson 4171 15 Apr 1986 (MICH); Lamar Co., Lake Serene, K. E. Rogers 1175 14 May 1969 (NCU); Lowndes Co., Mayhew, C. T. Bryson 9869 17 May 1990 (MICH); Madison Co., Jackson, R. Webster 1524 8 May 1978 (TAES); Montgomery Co., Wenard, S. D. Jones 4741 16 May 1990 (MICH); Oktibbeha Co., Sturgis, C. T. Bryson 3831 8 May 1985 (MICH); Oktibbeha Co., Sturgis, C. T. Bryson 8612 16 May 1989 (MICH); Pearl River Co., Picayune, F. H. Sargent 8128 21 Apr 1964 (NCU); Pearl River Co., Picayune, C. T. Bryson 13555 17 May 1994 (MICH); Pearl River Co., Poplarville, C. T. Bryson 10689 12 Apr 1991 (TAES); Perry Co., Beaumont, C. T. Bryson 15047 30 Apr 1996 (MICH); Perry Co., Janice, R. Naczi 5124 30 Apr 1996 (MICH); Perry Co., Runnelstown, C. T. Bryson 13598 18 May 1994 (MICH); Rankin Co., Pelahatchie, C. T. Bryson 3244 8 May 1982 (MICH); Scott Co., Bienville NF, C. T. Bryson 10803 10 May 1991 (TAES); Stone Co., Stone/Harrison Co. Line, C. T. Bryson 10671 12 Apr 1991 (TAES); Walthall Co., McGee Creek, C. T. Bryson 10702 12 Apr 1991 (TAES); Warren Co., Redwood, C. T. Bryson 11253 14 Apr 1992 (USCH); Wayne Co., Wayne/Greene Co. Line, C. T. Bryson 13643 18 May 1994 (MICH); Webster Co., Tomnolen, C. T. Bryson 7780 25 May 1988 (MICH); Winston Co., Louisville, C. T. Bryson 3340 22 May 1982 (MICH); Yalobusha Co., Gums, C. T. Bryson 15228 20 May 1996 (MICH).

North Carolina: Anson Co., Lilesville, A. E. Radford 43647 20 May 1961 (NCU); Beaufort Co., Chocowinity, A. E. Radford 33417 17 May 1958 (NCU); Bertie Co., Windsor, H. E. Ahles 41353 29 May 1958 (NCU); Brunswick Co., Wilmington, A. E. Radford 269 4 May 1940 (NCU); Caswell Co., Frogsboro, D. F. Brunton 12609 5 Jul 1996 (MICH); Catawba Co., Long Island, J. A. McNeely 1415 11 May 1960 (NCU); Chatham Co., Merry Oaks, A. E. Radford 42863 18 May 1960 (NCU); Chowan Co., Albermarle Sound, H. E. Ahles 44135 24 Jun 1958 (USCH); Chowan Co., St. Johns, H. E. Ahles 44161 24 Jun 1958 (NCU); Chowan Co., Yeopim, H. E. Ahles 39857 9 May

1957 (NCU); Craven Co., Croatan NF, J. R. Snyder 821 17 May 1976 (NCU); Cumberland Co., Linden, H. E. Ahles 24376 4 May 1957 (NCU); Davidson Co., Silver Valley, A. E. Radford 12748 16 Jun 1956 (NCU); Davie Co., Cooleemee, A. E. Radford 10943 11 May 1956 (NCU); Durham Co., Durham, H. L. Blomquist 14511 20 May 1949 (NY); Durham Co., Durham, H L Blomquist 13455 23 May 1944 (KANU); Edgecombe Co., Rocky Mount, A. E. Radford 33983 27 May 1958 (NCU); Franklin Co., Mapleville, W. B. Fox 4847 23 Jun 1951 (MICH); Gaston Co., Spencer Mt., H. E. Ahles 15020 21 Jun 1956 (NCU); Gates Co., White Oak Pocosin, J. A. Duke 831 30 May 1958 (NCU); Granville Co., Tar River, B. R. Dayton 1677 21 May 1964 (NCU); Granville Co., Creedmoor, A. E. Radford 45470 12 Jun 1968 (NCU); Guilford Co., Gibsonville, C. R. Bell 12463 3 Jun 1958 (NCU); Halifax Co., Halifax, H. E. Ahles 14851 19 Jun 1956 (NCU); Hartford Co., Winton, H. E. Ahles 41569 30 May 1958 (NCU); Hertford Co., Como, H. E. Ahles 41643 30 May 1958 (NCU); Hoke Co., Antioch, H. E. Ahles 25088 12 May 1957 (NCU); Hyde Co., Scranton, A. E. Radford 33682 18 May 1958 (NCU); Johnston Co., Smithfield, A. E. Radford 1079 22 May 1941 (NCU); Johnston Co., Wendell, A. E. Radford 25190 19 Jun 1957 (NCU); Jones Co., Hargetts Store, A. E. Radford 37144 18 Jul 1958 (NCU); Lee Co., Sanford, A. E. Radford 2013 18 May 1946 (NCU); Lenoir Co., Seven Springs, A. E. Radford 22170 6 May 1957 (NCU); Martin Co., Smithwick, A. E. Radford 35475 16 Jun 1958 (NCU); Moore Co., Eastwood, A. E. Radford 43347 11 Jun 1960 (NCU); Northampton Co., US 158, H. E. Ahles 41767 31 May 1958 (NCU); Pamlico Co., Olympia, A. E. Radford 35829 5 Jul 1958 (NCU); Pasquotank Co., Weeksville, H. E. Ahles 40038 10 May 1958 (NCU); Perquimans Co., Snug Harbor, L. J. Uttal 9774 12 Jun 1973 (VPI); Pitt Co., Bethel, A. E. Radford 34791 14 Jun 1958 (NCU); Pitt Co., Staton, A. E. Radford 34949 14 Jun 1958 (MICH); Randolph Co., Sawyer mine site, D. E. Wickland 972 19 May 1976 (NCU); Richmond Co., Hoffman, A. E. Radford 11285 19 May 1956 (NCU); Scotland Co., Silver Hill, H. E. Ahles 24784 8 May 1957 (NCU); Stanly Co., Albermarle, H. E. Ahles 11863 3 May 1956 (NCU); Stokes Co., Walnut Cove, A. E. Radford 34610 4 Jun 1958 (NCU); Stokes Co., Walnut Cove, A. E. Radford 34706 4 Jun 1958 (NCU); Tyrell Co., St. Rd. 1200 & St. Rd. 1308, C. B. McDonald 1722 17 May 1980 (WV); Tyrrell Co., Newfoundland, A. E. Radford 33862 18 May 1958 (NCU); Union Co., Monroe, H. E. Ahles 27558 7 Jun 1957 (NCU); Wake Co., Morrisville, A. E. Radford 42702 17 May 1959 (NCU); Warren Co., Oine, H. E. Ahles 12806 24 May 1956 (NCU); Washington Co., Hoke, A. E. Radford 35071 15 Jun 1958 (NCU); Wayne Co., Princeton, A. E. Radford 25613 21

Jun 1957 (NCU); Wayne Co., Princeton, A. E. Radford 21939 3 May 1957 (NCU); Wilson Co., Sims, A. E. Radford 38036 28 Jul 1958 (NCU).

Oklahoma: Choctaw Co., Sawyer, B. W. Hoagland HUGO187 15 May 2001 (OKL); Choctaw Co., Schooler Lake, S. Carpenter s.n. 18 May 1995 (OKL); Latimer Co., Robbers' Cave SP, P. Folley 2278 24 Apr 1999 (OKL); McCurtain Co., Red Slough WMA, F. Johnson RSGS344 24 Jun 1999 (OKL).

Pennsylvania: Philadelphia, J. B. Bristow 22 20 Jun 1880 (MSC).

South Carolina: Abbeville Co., Abbeville, C. N. Horn 9063 13 May 1995 (CLEMS); Abbeville Co., Calhoun Falls, A. E. Radford 22677 13 May 1957 (NCU); Abbeville Co., Lowndesville, W. C. Credle 725 21 May 1979 (NCU); Abbeville Co., Lowndesville, C. C. Douglass 1773 23 May 1984 (NCU); Abbeville Co., Richard Russell Dam and Lake Area, W. C. Creadle 2914 12 Jun 1980 (CLEMS); Aiken Co., Savannah River Plant, J. B. Nelson 3255 1 May 1984 (USCH); Aiken Co., Savannah River Project, A. E. Hodge 837 8 May 1984 (CLEMS); Aiken Co., Savannah River Site, Phillip E. Hyatt 5935 4 May 1994 (USCH); Aiken Co., Savannah River Site, T. Govus 88 18 May 1993 (USCH); Aiken Co., SRP, F. Gabrielson 232 3 Jun 1966 (NCU); Allendale Co., Barton, C. R. Bell 2644 13 May 1956 (NCU); Bamberg Co., Bamberg, C. N. Horn 4424 28 May 1991 (USCH); Bamberg Co., Denmark, J. B. Nelson 15475 27 May 1994 (USCH); Barnwell Co., Savannah River Operations Area, W. T. Batson s.n. 2 Jul 1952 (USCH); Barnwell Co., Carolina Bays, A. E. Hodge 942 23 May 1984 (CLEMS); Barnwell Co., Savannah River Operations, W. T. Batson s.n. 28 Apr 1952 (NCU); Barnwell Co., Savannah River Plant, A. E. Hodge 942 23 May 1984 (USCH); Barnwell Co., Savannah River Site, Phillip E. Hyatt 5883 22 Apr 1994 (USCH); Barnwell Co., Sister Lake, A. E. Hodge 823 8 May 1984 (CLEMS); Beaufort Co., Callawassie Island, C. A. Aulbach-Smith 2094 27 Apr 1982 (CLEMS); Beaufort Co., Combahee River, P. D. McMillan 2181 11 Apr 1997 (USCH); Beaufort Co., Yemassee, H. E. Ahles 12317 10 May 1956 (NCU); Berkeley Co., Francis Marion NF, S. R. Hill 18007 15 May 1987 (CLEMS); Berkeley Co., Huger, J. B. Nelson 14096 14 May 1993 (USCH); Berkeley Co., Moncks Corner, J. B. Nelson 7630 18 May 1989 (USCH); Berkeley Co., Moncks Corner, H. E. Ahles 26472 27 May 1957 (NCU); Berkeley Co., Oakley, H. E. Ahles 26529 27 May 1957 (NCU); Berkeley Co., Santee Experimental Forest, S. R. Hill 22987 25 Apr 1992 (CLEMS); Charleston Co., Palmetto Islands Co. Park, M. M. Smith 815 7 Aug 1985 (CLEMS); Charleston Co., Colleton-Charelston Co. Line, H. E. Ahles 25735 20 May 1957 (NCU); Cherokee Co., Blacksburg, R. Kral 60153 26 May 1977 (USCH); Chester Co., Lowrys, C.

R. Bell 7395 13 May 1957 (NCU); Chesterfield Co., Carolina Sandhills National Wildlife Refuge, J. Castrale 107 8 May 1977 (USCH); Clarendon Co., Manning, J. B. Nelson 14031 30 Apr 1993 (USCH); Clarendon Co., St. Paul, A. E. Radford 24356 11 Jun 1957 (NCU); Clarendon Co., St. Paul, A. E. Radford 24372 11 Jun 1957 (NCU); Colleton Co., Bells, C. R. Bell 2311 7 May 1956 (NCU); Colleton Co., Edisto, D. Soblo 496 15 May 1987 (USCH); Darlington Co., Hartsville, J. B. Norton s.n. 26 Apr 1921 (NCU); Dillon Co., Dillon, H. E. Ahles 27806 12 Jun 1957 (NCU); Dillon Co., Little Pee Dee SP, M. T. Strong 2327 19 May 2000 (MICH); Edgefield Co., Edgefield, J. B. Nelson 18128 24 Apr 1997 (USCH); Edgefield Co., Sumter NF, J. B. Nelson 17208 8 May 1996 (USCH); Edgefield Co., Trenton, A. E. Radford 22569 12 May 1957 (NCU); Fairfield Co., Lake Wateree, J. R. Clonts s.n. 24 Apr 1976 (MICH); Fairfield Co., Monticello, J. B. Nelson 2571 22 Jun 1983 (USCH); Fairfield Co., Winnsboro, C. N. Horn 2694 4 Jun 1988 (TAES); Florence Co., Cowards, C. R. Bell 13396 30 Jun 1958 (NCU); Florence Co., Lake City, C. R. Bell 6125 19 Apr 1957 (NCU); Georgetown Co., Rhems, A. E. Radford 21484 22 Apr 1957 (NCU); Greenwood Co., Hodges, A. E. Radford 23001 25 May 1957 (NCU); Hampton Co., Belmont Plantation, R. D. Porcher Jr. 282 20 May 1971 (USCH); Hampton Co., Yemassee, C. R. Bell 2593 12 May 1956 (WV); Horry Co., Conway, C. N. Horn 3356 25 May 1989 (USCH); Jasper Co., Hazzard's Creek, C. A. Aulbach-Smith 2133 28 Apr 1982 (USCH); Jasper Co., SC 170, C. R. Bell 2413 9 May 1956 (NCU); Jasper Co., Hardeeville, J. B. Nelson 15384 26 Apr 1994 (USCH); Jasper Co., Hardeeville, C. A. Aulbach-Smith 3098 9 May 1984 (USCH); Jasper Co., Hardeeville, J. A. Churchill s.n. 10 May 1969 (MSC); Jasper Co., Hardeeville, J. B. Nelson 15384 26 Apr 1994 (USCH); Kershaw Co., Westville, A. E. Radford 23784 4 Jun 1957 (NCU); Lancaster Co., Lancaster, H. E. Ahles 27287 6 Jun 1957 (NCU); Laurens Co., Clinton, C. N. Horn 6585 8 May 1993 (USCH); Laurens Co., Mountville, C. R. Bell 8058 3 Jun 1957 (NCU); Lee Co., Bishopville, A. E. Radford 24146 6 Jun 1957 (NCU); Lexington Co., Cayce, W. T. Batson s.n. 2 Jun 1963 (USCH); Marion Co., SC 908, J. Nelson 10566 3 May 1991 (MICH); Marlboro Co., Blenheim, A. E. Radford 12662 10 Jun 1956 (NCU); McCormick Co., Clarks Hill, A. E. Radford 22368 11 May 1957 (NCU); McCormick Co., Sumter NF, J. B. Nelson 17177 8 May 1996 (USCH); Newberry Co., Newberry, C. N. Horn 2159 11 Jul 1987 (USCH); Newberry Co., Newberry, J. B. Nelson 22649 23 May 2002 (USCH); Newberry Co., Pomaria, J. B. Nelson 22636 23 May 2002 (USCH); Oconee Co., Chauga River, J. D. Tobe 847 5 Jun 1986 (CLEMS); Orangeburg Co., Orangeburg, H. E. Ahles 25237 18 May 1957 (NCU); Orangeburg Co., Sixteen Island in Lake Marion, A. B. Pittman 04180102 18 Apr 2001 (USCH);

Pickens Co., Pendleton, J. F. Townsend 1501 20 May 1997 (CLEMS); Richland Co., Columbia Country Club, J. B. Nelson 7521 15 May 1989 (USCH); Richland Co., Eau Clair, A. B. Pittman 05109724 10 May 1997 (USCH); Richland Co., Ballentine, J. B. Nelson 15571 10 Jun 1994 (MICH); Richland Co., Columbia, C. N. Horn 5465 21 Jul 1992 (MICH); Richland Co., Congaree Swamp National Monument, L. L. Gaddy 052998 29 May 1998 (USCH); Richland Co., Fort Jackson, J. B. Nelson 10297 22 Apr 1991 (USCH); Saluda Co., Saluda River, C. A. Aulbach-Smith 2626 23 Jun 1983 (USCH); Saluda Co., Sumter NF, J. B. Nelson 5438 15 May 1987 (USCH); Saluda Co., Ridge Spring, A. E. Radford 23069 26 May 1957 (NCU); Union Co., Padgets Creek, C. N. Horn 5532 1 Aug 1992 (MICH); Union Co., Sumter NF, C. N. Horn 6802 5 Jun 1993 (MICH); Williamsburg Co., Black River, J. B. Nelson 7589 18 May 1989 (USCH); Williamsburg Co., Cades, J. B. Nelson 17304 7 Jun 1996 (USCH); Williamsburg Co., Cades Savannah, J. F. Townsend 1005 7 Jun 1996 (CLEMS); Williamsburg Co., Coopers, A. E. Radford 24784 12 Jun 1957 (NCU); York Co., Clover, D. F. Brunton 12200 27 May 1995 (MICH); York Co., Kings Mountain SP, D. E. Kennemore Jr. 436 20 May 1993 (USCH).

Tennessee: Bledsoe Co., Mt. Zion School, *R. Jones* 4767b 22 May 1987 (EKY); Coffee Co., Double Pond, *V. E. McNeilus* 92-411 1 Jun 1992 (MICH); Cumberland Co., Crossville Memorial Airport, *V. E. McNeilus* 89-410 17 Jun 1989 (MSC); Cumberland Co., Mayland, *V. E. McNeilus* 89-424 17 Jun 1989 (MICH); Fentress Co., Hwy 154, *R. Jones* 4803 31 May 1987 (EKY); Franklin Co., Tullahoma, *H. R. DeSelm* s.n. 31 May 1962 (NCU); Hardin Co., Cravan Rd., *H. R. DeSelm* s.n. 10 Jun 1993 (EKY); Loudon Co., Sweet Water, *H. DeSelm* 242 26 May 1979 (EKY); Morgan Co., Lilly Bridge, *V. E. McNeilus* 90-360 19 Jun 1990 (TAES); Putnam Co., Baxter, *V. E. McNeilus* 95-291 3 Jun 1995 (MICH); Scott Co., US 27, *R. Jones* 6449 22 Jun 1990 (EKY); Van Buren Co., Bledsoe Co. Line, *V. E. McNeilus* 92-521 27 Jun 1992 (MICH).

Texas: Jefferson, R. Bebb 2625 11 May 1905 (OKL); Jefferson, R. Bebb 2562 10 May 1905 (OKL); Anderson Co., Engeling WMA, E. Bridges 13723 21 May 1990 (MICH); Angelina Co., Angelina NF, S. L. Orzell 9075 10 Apr 1989 (MICH); Hardin Co., Kountze, S. D. Jones 2608 29 Apr 1989 (TAES); Hardin Co., Lumberton, R. Jordan 5 17 Apr 1993 (TAES); Hardin Co., Lumberton, R. Jordan 1 17 Apr 1993 (TAES); Hardin Co., Silsbee, H. B. Parks 22297? 15 May 1937 (TAES); Harris Co., Nimitz High School Outdoor Learning Center, J. Kessler 3332 17 Apr 1980 (TAES); Henderson Co., Slaughter Lakes, S. L. Orzell 6563 4 May 1988 (MICH); Houston Co., Hwy 21, S. D. Jones 1041 6 Apr 1988 (TAES); Houston Co., Houston, R. Bebb 1204 20 May

1900 (OKL); Jasper Co., FM 105, S. D. Jones 1659 22 May 1988 (TAES); Jasper Co., Angelina NF, S. Orzell 6239 13 Apr 1988 (MICH); Leon Co., Eunice, S. Orzell 6507 3 May 1988 (MICH); Madison Co., Lenz Property, A. K. Neill 1338 2 Apr 1998 (TAMU); Milam Co., Milano, S. E. Wolff 3975 22 May 1933 (TAES); Montgomery Co., Sam Houston NF, L. E. Brown 21786 8 Mar 1998 (TAES); Nacagdoches Co., Nacagdoches, J. A. Churchill s.n. 27 Apr 1955 (MSC); Nacagdoches Co., Nacogdoches, E. S. Nixon 2425 18 May 1971 (TAES); Orange Co., FM 105, S. D. Jones 1638 22 May 1988 (TAES); Panola Co., Carthage, C. L. Lundell 10493 7 May 1941 (MICH); Polk Co., Hwy 190, S. D. Jones 1459 11 May 1988 (TAES); Robertson Co., Mill Creek Bog, H. D. Wilson 3706 9 May 1981 (TAMU); Robertson Co., Mill Creek Bog, S. D. Jones 1090 30 Apr 1988 (TAES); San Jacinto Co., Big Creek, S. L. Orzell 6452 21 Apr 1988 (MICH); Shelby Co., FM 139, S. D. Jones 1331 17 May 1988 (TAES); Shelby Co., Chambers Creek Bayou, S. D. Jones 1363 17 May 1988 (TAES); Smith Co., Bier Creek, D. Wilkinson 787 14 Apr 1972 (MARY); Tyler Co., Big Thicket National Preserve, R. Jordan 6 4 May 1993 (TAES); Walker Co., Hwy 75, J. Kessler 5678 7 May 1982 (TAES); Walker Co., Hunstville, S. E. Wolff 4973 13 Apr 1934 (TAES); Walker Co., Huntsville, D. S. Correll 27360 11 May 1963 (NCU); Walker Co., Huntsville, B. L. Lipscomb 1705 2 Jun 1976 (NCU); Wood Co., Hwy 49, S. D. Jones 2835 13 May 1989 (TAES); Wood Co., Wood Co. Rd 3990, S. D. Jones 2918 16 May 1989 (TAES); Wood Co., Crow, C. L. Lundell 9472 14 Jun 1940 (MICH).

Virginia: City of Hampton, P. Baldwin 786 17 May 1993 (VPI); Accomack Co., New Church, T. Bradley 23590 17 Jun 1990 (CLEMS); Chesapeake Co., Dismal Swamp, Emery C Leonard; Ellsworth P Killip 371 2 Jun 1921 (KANU); Fairfax Co., Ft. Hunt, S. F. Blake s.n. 17 Jun 1933 (NCU); Greensville Co., Quarrell's Creek, Merritt L Fernald; J B Lewis 14581 22 Jun 1944 (KANU); James City Co., Jamestown Island, L. E. Loetterle 823 24 May 1970 (NCU); King George Co., D. M. E. Ware 8238 18 Jun 1983 (CLEMS); Madison Co., Aroda, T. Bradley 23364 10 Jun 1990 (USCH); Nansemond Co., Blackwater River, H. E. Ahles 58176 22 Jun 1963 (NCU); Norfolk Co., Portsmouth, N. L. Britton s.n. 25 May 1893 (NEB); Pittsylvania Co., Co. Rd 630, W. R. Ruska s.n. 20 Jul 1968 (NCU); Prince George Co., Petersburg, R. Kral 13202 6 Jul 1961 (VPI); Richmond Co., Ivandale, T. Bradley 22377 11 Jun 1988 (CLEMS); Suffolk Co., South Quay, R. H. Simmons s.n. 20 May 2000 (MICH); Surry Co., VEPCO Surry Nuclear Power Station, D. M. E. Ware 4849 6 Jun 1973 (NCU); Surry Co., VEPCO Surry Nuclear Power Station, D. M. E. Ware 5337 23 May 1974 (NCU). Carex hirsutella. Canada. Quebec: Brome-Missisquoi Co., Cowansville, W. G. Dore 1026 24 Jun 1934 (CAN); Brome-Missisquoi Co., Bedford, J-P. Bernard 5093 28 Jul 1955 (CAN); Brome-Missisquoi Co., Frelighsburg, M. Raymond 47 21 Jun 1952 (CAN).

Ontario: Elgin Co., West Lorne, M. J. Oldham 15913 7 Oct 1993 (MICH); Essex Co., Cedar Creek, W. Botham 1650 17 Jun 1974 (CAN); Essex Co., Essex, A. A. Reznicek 7752 9 Jul 1986 (MICH); Essex Co., Gosfield, M. J. Oldham 2901 26 Jun 1982 (MICH); Essex Co., Gosfield, M. J. Oldham 2892 26 Jun 1982 (MICH); Essex Co., Harrow, M. J. Oldham 11052 11 Jun 1990 (MICH); Essex Co., Kingsville, M. J. Oldham 2901 26 Jun 1982 (CAN); Haldimand-Norfolk Co., Cayuga, M. J. Oldham 17283 17 Jun 1995 (MICH); Haldimand-Norfolk Co., Dunville, M. J. Oldham 6391 22 Jun 1986 (MICH); Haldimand-Norfolk Co., Port Dover, D. A. Sutherland 7046 10 Jun 1986 (CAN); Kent Co., Bothwell, R. Klinkenburg 198 2 Aug 1982 (MICH); Kent Co., Clearville, V. R. Brownell 83-105 13 Jun 1983 (CAN); Middlesex Co., Parkhill, M. J. Oldham 14158 13 Aug 1992 (MICH); Niagara Co., Niagara Falls, Macoun 16545 25 Jun 1892 (CAN); Niagara Co., Niagara River Whirlpool, Macoun 33748 9 Jul 1901 (CAN); Niagara Co., Queenston Heights, Macoun 16661 7 Jun 1882 (CAN).

U. S. A. Western Reserve, G. B. Ashcroft s.n. 1 Jun 1897 (TAES).

Alabama: Lauderdale Co., Florian, D. Isely 3554 25 Jun 1944 (MSC); Lawrence Co., Bankhead NF, C. T. Bryson 7587 8 May 1988 (MSC); Madison Co., Huntsville, C. T. Bryson 3539 23 May 1983 (MICH); Madison Co., Monte Sano Mt., J. R. Manhart 263 9 May 1981 (MICH); Madison Co., Monte Sano Mt., C. T. Bryson 4394 25 May 1986 (MICH); Madison Co., Monte Sano Mt., C. T. Bryson 2889 8 May 1980 (GA); Madison Co., Monte Sano Mt., C. T. Bryson 2047 27 May 1978 (GA).

Arkansas: R. Bebb 4024 21 May 1939 (OKL); Baxter Co., Henderson, D. Castaner 8409
22 May 1985 (MICH); Baxter Co., Henderson, D. Castaner 8418 22 May 1985 (VPI); Clay Co.,
Pollard, Phillip E. Hyatt 4381.11 22 May 1992 (MICH); Crawford Co., Figure Five Community,
Phillip E. Hyatt 9301 18 May 2000 (MICH); Fulton Co., Salem Quad., S. Orzell 1947 23 May 1985 (MICH); Fulton Co., Hwy 87, D. Castaner 8428 22 May 1985 (MICH); Fulton Co., Salem, Larry
J. Harms 2219 2 May 1965 (KANU); Garland Co., Iron Springs Rec. Area, A. A. Reznicek 8496
5 Jun 1989 (MICH); Greene Co., U. S. Hwy. 412, Phillip E. Hyatt 4622.38 7 Jun 1992 (MICH);
Greene Co., Crowley's Ridge SP, Phillip E. Hyatt 4070.28 16 Jun 1991 (MICH); Jackson Co.,
Heffington, Phillip E. Hyatt 10361 26 May 2001 (MICH); Lee Co., St. Francis NF, Phillip E. Hyatt

4637.39 9 Jun 1992 (MICH); Madison Co., Combs, E. B. Smith 3835 19 Jun 1984 (WV); Marion Co., Bull Shoals Lake, Phillip E. Hyatt 4054.45 8 Jul 1991 (MICH); Marion Co., Hand Valley, Phillip E. Hyatt 4823.45 1 May 1992 (MICH); Monroe Co., Fargo, R. Naczi 2455 21 May 1990 (MICH); Montgomery Co., Albert Pike Campground, Phillip E. Hyatt 9277 18 May 2000 (MICH); Montgomery Co., Cox Springs, C. T. Bryson 4275 10 May 1986 (MICH); Montgomery Co., Little Missouri River Falls Rec. Area, C. T. Bryson 4350 10 May 1986 (MICH); Montgomery Co., Mena, D. E. Boufford 25489 8 May 1991 (MICH); Phillips Co., St. Francis NF, Phillip E. Hyatt 4657.54 11 Jun 1992 (MICH); Polk Co., Cossatot River Rec. Area, S. D. Jones 10146 18 May 1993 (MICH); Polk Co., Mena, D. E. Boufford 25511 9 May 1991 (MICH); Polk Co., Mena, C. T. Bryson 4318 10 May 1986 (MSC); Polk Co., Mena, D. E. Boufford 25604 13 May 1991 (MICH); Polk Co., Rich Mt., C. T. Bryson 4294 10 May 1986 (MICH); Pulaski Co., North Little Rock, J. Kessler 7093 23 Jun 1983 (TAES); Randolph Co., Sutton Freewill Baptist Church, Phillip E. Hyatt 5964 9 May 1994 (MICH); Saline Co., Congo Rd., L. E. McKinney 2536 9 May 1987 (MICH); Scott Co., Y City, D. E. Boufford 25571 11 May 1991 (MICH); Searcy Co., Buffalo National River, Phillip E. Hyatt 5679 17 Jun 1993 (MICH); Sebastain Co., New Hartford, Phillip E. Hyatt 7461 18 May 1997 (MICH); Sharp Co., Hwy 230, D. Castaner 9097 9 May 1986 (MICH); Sharp Co., Cherokee Village, Phillip E. Hyatt 4327.68 12 May 1992 (MICH); Sharp Co., Poughkeepsie, Phillip E. Hyatt 7167 25 May 1996 (MICH); Stone Co., Ozark NF, Phillip E. Hyatt 5543 27 May 1993 (MICH); Stone Co., Sylamore Ranger District, Phillip E. Hyatt 5324 13 May 1993 (MICH); Van Buren Co., Fairfield Bay, Phillip E. Hyatt 5293 8 May 1993 (MICH); White Co., Sunnydale, Phillip E. Hyatt 4031.73 26 May 1991 (MICH); Yell Co., Rover, Phillip E. Hyatt 8074 3 May 1998 (MICH).

Connecticut: Hartford Co., Berlin, G. B. Rossbach 992 8 Jun 1956 (NCU); Hartford Co., Cedar Mt., C. A. Weatherby 3077 24 Jun 1913 (GH); Hartford Co., Noyes Brook Region, A. W. Drigg s.n. 27 Jun 1902 (GH); Hartford Co., Short Mt., L. J. Mehrhoff 12131 17 Jun 1987 (MICH); Hartford Co., Southington, L. Andrews s.n. 19 Jun 1898 (GH); Hartford Co., Simsbury, W. H. Moorhead III 3223 22 Jul 1996 (GH); Hartford Co., Wethersfield, V. Marttala 3141 20 Jul 1973 (MICH); Litchfield Co., Salisbury, L. J. Mehrhoff 15765 10 Jul 1992 (MICH); Litchfield Co., Woodbury. Rag Land, W. H. Moorehead III 3228 25 Jul 1996 (GH); Middlesex Co., Middletown, C. A. Weatherby 4492 4 Jul 1919 (GH); New Haven Co., Hamden, A. E. Blewitt 1670 19 Jun 1913 (GH); New Haven Co., New Haven, L. Mehrhoff 16259 16 Sep 1992 (MICH); New Haven Co., Southbury, L. J. Mehrhoff 15644 15 Jun 1992 (MICH). District of Columbia: Potomac, Agnes Chase 2392 25 Jun 1904 (MICH); Potomac Valley, Mt. Rainier, A. Chase 2415 2 Jul 1904 (MICH); Washington, D. C., E. S. Stute s.n. 1896 (MICH).

Georgia: Bartow Co., Allatoona Station, G. W. McDowell 613 13 Jun 1948 (CLEMS); Elbert Co., Savannah River, W. H. Duncan 9419 25 Apr 1949 (GA); Elbert Co., Richard Russell Dam and Lake Area, W. C. Credle 731 21 May 1979 (CLEMS); Elbert Co., Richard Russell Dam and Lake Area, M. G. Douglass 1438 31 May 1978 (CLEMS); Elbert Co., Russell Dam and Lake area, C. C. Douglass 1438 31 May 1978 (USCH); Elbert Co., Savannah River Site, W. C. Credle 731 21 May 1979 (NCU); Elbert Co., Savannah River Site, C. C. Douglass 1438 31 May 1978 (USCH); Elbert Co., Savannah River Site, W. C. Credle 731 21 May 1979 (NCU); Elbert Co., Savannah River Site, C. C. Douglass 1438 31 May 1978 (NCU); Lincoln Co., Graves Mt., W. H. Duncan 11142 24 Jun 1950 (GA); Stephens Co., Lake Russell WMA, J. Cruse 752 18 May 1995 (GA).

Illinois: Alexander Co., Shawnee NF, L. R. Phillipe 24299 25 May 1994 (MICH); Champaign Co., Urbana, H. A. Gleason s.n. 26 May 1902 (GH); Champaign Co., Urbana, A. S. Pease 13079 30 May 1911 (GH); Christian Co., Taylorville, R. A. Evers 86923 1 Jun 1966 (NCU); Cook Co., Hickory Hills, S. Hill 29331 11 Jun 1997 (MICH); Cook/Lake Co., Deer Park, H. Haleuman s.n. 1 Jun 1895 (NEB); Franklin Co., Rend Lake, T. G. Lammers 9472 25 Jun 1995 (MICH); Jackson Co., Makanda, H. A. Gleason s.n. 12 Jun 1903 (GH); Jackson Co., Makanda, H. A. Gleason 1058 23 Jun 1903 (GH); Jackson Co., Murphysboro SP, D. Castaner 2298 1 Jun 1972 (MO); Johnson Co., Bell Pond Natural Area, L. R. Phillipe 14086 21 Jun 1990 (MICH); Johnson Co., Shawnee NF, A. S. Biaqi 2885 30 Jul 1994 (MSC); Macon Co., Timbered Hill, I. W. Clokey 2279 18 Jun 1915 (NEB); Marshall Co., Steuben Twp., V. H. Chase 1811 7 Jun 1908 (GH); McDonough Co., Emmet, S. Hill 29261 5 Jun 1997 (MICH); Peoria Co., Bellevue, V. H. Chase 8901 10 Jul 1947 (MICH); Peoria Co., Bellevue, near, Virginius H Chase 8722 7 Jun 1947 (KANU); Peoria Co., Glen Oak Park, V. H. Chase 3583 22 Jun 1921 (MICH); Peoria Co., Medina Tp., V. H. Chase 7839 4 Jul 1941 (MO); Peoria Co., Peoria, R. Bebb 2771 5 Jun 1905 (OKL); Peoria Co., Peoria, F. E. McDonald s.n. 1 Jul 1912 (MSC); Peoria Co., Peoria, F. E. McDonald s.n. 1 Jun 1904 (OKL); Peoria Co., Peoria, F. E. McDonald s.n. 1 Jul 1895 (MSC); Peoria Co., Peoria, R. Bebb 2771 5 Jun 1905 (OKL); Peoria Co., Peoria Heights, V. H. Chase 13735 27 Jun 1954 (USCH); Perry Co., Pyramid SP, J. Raveill 109 21 May 1981 (MO); Piatt Co., Monticello, G. N. Jones 43083 19 Jun 1966 (WV); St. Clair Co., Imbs Station, J. O. Neill 16004 14 Jul 1962 (NCU); Tazewell Co., East Peoria, Virginius H Chase 13432 23 Jun 1953 (KANU); Tazewell Co., Morton, S. Hill 29691 7 Aug 1997 (MICH); Union Co., Atwood Ridge Research Natural Area, L. R. Phillipe 19085 5 Jun 1991
(MICH); Vermilion Co., Hillery, H. A. Gleason s.n. 1 Jun 1907 (NYS); Washington Co., Posen Woods, L. R. Phillipe 14224 16 Jul 1990 (MICH); White Co., Enfield, R. A. Evers 33105 21 May 1952 (NCU); Will Co., Mokina, A. Chase 160 22 Jun 1897 (MSC); Will/Kendal Co., Joliet, C. F. Wheeler 258 15 Jun 1904 (GH).

Indiana: Chesterton, L. M. Umbach s.n. 16 Jun 1900 (OKL); Marengo, C. C. Deam 13450 21 Jun 1913 (MICH); Brown Co., Mt. Zion, C. C. Deam 48399 24 May 1930 (MICH); Clark Co., Jeffersonville, C. C. Deam 27617 25 May 1919 (GH); Clarke Co., C. C. Deam 6465 25 May 1910 (MICH); Crawford Co., Fredonia, F. J. Hermann 6682 16 Jun 1935 (MICH); Crawford Co., Leavenworth, C. C. Deam 23464 5 Jun 1917 (WV); Floyd Co., New Albany, C. C. Deam 27935 13 Jun 1919 (WV); Flovd Co., New Albany, C. C. Deam 13257 8 Jun 1913 (MICH); Fountain Co., Portland Arch, F. B. Buser 6510 2 Jun 1956 (NCU); Franklin Co., Androsonville, R. C. Friesner 4436 16 Jul 1932 (MICH); Harrison Co., Palmyra, F. J. Hermann 6711 17 Jun 1935 (GH); Harrison Co., Elisabeth, C. C. Deam 27864 11 Jun 1919 (GH); Jefferson Co., Wirt, E. Banta 6 22 Jun 1935 (MICH); Jennings Co., Muscatatuck SP, R. C. Friesner 16708 23 May 1942 (GH); Lawrence Co., Bryantsville, R. M. Kriebel 2174 10 Jun 1934 (MICH); Lawrence Co., Williams, R. M. Kriebel 1763 3 Jun 1934 (MO); Owen Co., Hubble, C. C. Deam 46882 13 Jun 1929 (GH); Perry Co., Tell City, C. C. Deam 25111 4 Jun 1918 (MICH); Ripley Co., Batesville, C. C. Deam 6824 27 Jun 1910 (WV); Scott Co., Lexington, C. C. Deam 16291 22 Jun 1915 (WV); Spencer Co., Gentryville, C. C. Deam 25163 6 Jun 1918 (MICH); St. Joseph Co., Notre Dame, P E Hebert s.n. 27 Jun 1952 (KANU); Tippecanoe Co., Soldiers Home, F. J. Hermann 6066 3 Jun 1934 (MICH); Wayne Co., Centerville, C. C. Deam 13116 3 Jun 1913 (WV).

Iowa: Lee Co., Donellson, B. Shimek s.n. 15 Jul 1928 (OKL); Lee Co., Warren, B. Shimek s.n. 31 May 1933 (NEB); Wapello Co., Cliffland, R. A. Davidson 272 9 Jul 1953 (NCU); Wapello Co., Cliftland, A. Hayden 9210 (MICH); Washington Co., Ainsworth, T. Cady s.n. 7 Jun 1998 (MICH); Washington Co., Ainsworth, T. Cady s.n. 7 Jun 1998 (MICH).

Kansas: Cherokee Co., Baxter Springs, R. L. McGregor 15686 18 Jun 1960 (NCU); Cherokee
Co., Baxter Springs, Ralph Brooks 16252 2 Aug 1982 (KANU); Cherokee Co., Baxter Springs,
Ronald L. McGregor 1656 3 Jul 1948 (KANU); Cherokee Co., Crestline, Ole A. Kolstad 2252 3
Jun 1964 (KANU); Cherokee Co., Crestline, Ronald L. McGregor 38229 28 May 1987 (KANU);
Cherokee Co., Galena, William T. Barker 2122 3 Jun 1966 (KANU); Cherokee Co., Crestline,
Caleb A. Morse 9674 17 Jun 2003 (KANU); Douglas Co., Baldwin City, Craig C. Freeman 2517

5 Jun 1988 (KANU); Douglas Co., Big Springs, Craig C. Freeman 19063 25 Jun 2002 (KANU);
Douglas Co., Lawrence, University of Kansas Campus West, Ronald L. McGregor 40489 26 May
1992 (KANU); Douglas Co., Univ. of Kansas Campus West, R. L. McGregor 40537 15 Jun 1992
(OKL); Greenwood Co., Severy, C. C. Freeman 14786 14 Jun 2000 (MSC); Jackson Co., Mayetta,
Frank J Norman 15 19 May 2001 (KANU); Jefferson Co., McClouth, Craig C. Freeman 20045A
30 Jun 2004 (KANU); Jefferson Co., Perry, Erin Questad s.n. 2 Jun 2004 (KANU); Jefferson
Co., Perry, Suneeti Jog s.n. 2 Jun 2004 (KANU); Jefferson Co., Williamstown, Caleb A. Morse
9436 27 May 2003 (KANU); Labette Co., Mound Valley, Ronald L. McGregor 37228 17 Jun 1986
(KANU); Linn Co., La Cygne, Caleb A. Morse 7958 23 May 2002 (KANU); Linn Co., La Cygne,
Caleb A. Morse 8356 24 Jun 2002 (KANU); Linn Co., La Cygne, Caleb A. Morse 8018 23 May
2002 (KANU); Linn Co., Trading Post, Caleb A. Morse 10429 14 May 2004 (KANU); Miami Co.,
Jingo, Caleb A. Morse 10489 20 May 2004 (KANU); Miami Co., Somerset, C. A. Morse 4744 30
May 2000 (NEB); Miami Co., Somerset, Caleb A. Morse 8032 29 May 2002 (KANU); Neosho Co.,
Thayer, W. Holland 5470 26 May 1986 (KANU); Wilson Co., Neodesha, Ole A. Kolstad 3099
9 Jun 1965 (KANU).

Kentucky: Barren Co., Scottsville Rd., C. Lapham 36 23 May 1993 (EKY); Bath Co., Olympian Springs, F. T. McFarland 4386 11 Jun 1938 (MICH); Bath Co., Peeled Oak, M. E. Wharton 2448a 2 Jun 1938 (MICH); Bell Co., Cumberland Gap NP, D. F. Brunton 10350 24 May 1991 (MICH); Boyle Co., Central Kentucky Wildlife Refuge, L. E. McKinney 4992 13 May 1992 (EKY); Boyle Co., Junction City, M. E. Wharton 667 3 Jul 1937 (MICH); Bullitt Co., Lake Nevin, C. R. Gunn 347 16 Jun 1955 (NCU); Bullitt Co., Phelps Knob, R. Hannan 6423 13 May 1981 (EKY); Caldwell Co., Bald Knob, R. Hannan 03709 20 May 1980 (EKY); Calloway Co., Ft. Heiman, L. E. McKinney 4167 30 May 1990 (EKY); Campbell Co., Silver Grove, R. Naczi 4768A 3 Jun 1995 (MICH); Carlisle Co., Arlington, L. G. Hickok 8 6 Jun 1969 (NCU); Carlisle Co., Arlington, D. O'Dell s.n. 18 Jul 1962 (NCU); Carter Co., Carter Caves SP, D. F. Brunton 10292 20 May 1991 (MICH); Casey Co., Liberty, M. Wharton 4334 14 Jun 1939 (MICH); Clinton Co., Seventy-Six Falls, L. E. McKinney 6457 31 May 1995 (MICH); Edmonson Co., Mammoth Cave, Davies s.n. 17 Jun 1950 (NCU); Estill Co., Red River, M. Wharton 2268 19 May 1938 (MICH); Estill Co., Burnham Woods, R. G. Guetig 637 13 Jun 1988 (EKY); Estill Co., Burnham Woods, R. G. Gueting 298 24 Jun 1987 (EKY); Estill Co., White Oak Cliff, R. G. Guetig 912 24 Aug 1988 (EKY); Fleming Co., Sprulock Gap, R. Hannan 6775 3 Jun 1981 (EKY); Franklin Co., Echo

Spring Swamp, Steve Rice s.n. 12 Jul 1984 (EKY); Franklin Co., Fault Hill, Steve Rice s.n. 24 May 1983 (EKY); Fulton Co., Cavce, D. O'Dell 1133 24 Jul 1962 (NCU); Garrard Co., Maywoods Environmental and Educational Laboratory, D. A. Godbey 132 26 May 1983 (EKY); Grant Co., Crittenden, R. Naczi 7887 17 May 1999 (MICH); Greenup Co., Jesse Stuart State Nature Preserve, L. E. McKinney 6243 8 Jun 1994 (MICH); Hardin Co., Alexander Seep, R. Cranfill 319 2 Jul 1977 (MICH); Hardin Co., Cap Hollow, R. Cranfill 664 24 May 1978 (MICH); Hardin Co., Elizabethtown, Landon E. McKinney 4640 11 May 1991 (VDB); Hardin Co., Ft. Knox Army Post, R. A. Thompson K0334 6 Aug 1990 (OKL); Hardin Co., Vernon Douglas State Nature Preserve, L. E. McKinney 4640 11 May 1991 (EKY); Knott Co., Breeding Creek area, L. E. McKinney 6197 20 May 1994 (MICH); Laurel Co., Rock Creek Gorge, R. L. Thompson 89-814 29 May 1989 (EKY); Laurel Co., Rock Creek Gorge, R. L. Thompson 86-151 31 May 1986 (EKY); Laurel Co., Rock Creek Gorge, R. L. Thompson 89-676 24 May 1989 (EKY); Lawrence Co., Fallsburg, A. W. Cusick 30913 24 May 1993 (MICH); Lawrence Co., Summit, A. W. Cusick 30972 1 Jun 1993 (VPI); Lewis Co., Hymes Knob, L. E. McKinney 6390 16 May 1995 (MICH); Lincoln Co., Crab Orchard, M. Wharton 2103 10 May 1938 (MICH); Lyon Co., Lyon/Trigg County Line, L. E. McKinney 4975 5 May 1992 (EKY); Madison Co., Berea, D. D. Taylor 1479 30 May 1982 (NCU); Madison Co., Bluegrass Army Depot, G. W. Libby OB-675 28 Jul 1993 (MICH); Madison Co., Bluegrass Army Depot, G. W. Libby OB-296 26 May 1993 (MICH); Madison Co., Kentucky River Palisades, J. S. Lassetter 2991 23 Jun 1978 (EKY); Madison Co., Pilot Knob, M. Wharton 712 6 Jul 1937 (MICH); Marion Co., Jessietown, R. Hannan 7275 22 Jun 1981 (EKY); Meade Co., Battletown, R. C.H. 109 10 Jun 1949 (NCU); Metcalfe Co., US 68, W. Meijer s.n. 24 May 1969 (NCU); Muhlenberg Co., Sector 1, L. E. McKinney 5674 1 Jun 1993 (EKY); Pike Co., Brushy Creek, F. Levy s.n. 10 Jun 1983 (NCU); Rockcastle Co., Anglin Falls Hollow, N. Denton 0426 8 Jun 1989 (EKY); Rockcastle Co., Livingstone, H. E. Ahles 54431 17 Jun 1961 (NCU); Rowan Co., Cave Run Lake, Daniel Boone NF, W. D. Longbottom 3564 25 May 1993 (MARY); Trigg Co., Fort Campbell Military Reservation, L. E. McKinney 5448 18 May 1993 (MICH); Trigg Co., Ft. Campbell Army Post, F. L. Johnson CAM0135 7 Jun 1991 (OKL); Trigg Co., Land Between The Lakes, W. H. Ellis 1084 7 Jun 1966 (NCU); Union Co., Sullivan, J. Conrad 1019 27 May 1970 (NCU); Warren Co., Woodburn, D. F. Brunton 10304 21 May 1991 (MICH); Wayne Co., Monticello, R. Naczi 7967 20 May 1999 (MICH); Whitley Co., Hwy 1277, L. E. McKinney 5428 14 May 1993 (MICH); Whitley Co., Grove Road, L. E. McKinney 5428 14 May 1993 (EKY).

Maine: Clinton Co., Maple Rapids, G. W. Parmelee 96 19 Jun 1952 (MICH).

Maryland: Beltonvale, A. Chase 876 4 Jul 1907 (MICH); Potomac Valley, Chevy Chase, A. Chase 2461 13 Jul 1904 (OKL); Allegany Co., La Valle, D. D. Boone 840605-SN 5 Jun 1984 (TAWES); Allegany Co., Martin Mt., C. T. Frye 2084 11 Aug 1999 (TAWES); Allegany Co., Selinger Marsh, Flintstone, C. Lea 2137 28 Jun 2000 (MARY); Anne Arundel Co., Broad Creek Park, W. D. Longbottom 2963 23 May 1992 (MARY); Carroll Co., Westminster, R. S. Thompson 31 1 Jul 1943 (MARY); Cecil Co., Rising Sun, C. Lea 1879 3 Jun 2000 (MARY); Frederick Co., Catoctin Mt., S. S. Tepfer 1324 8 Jun 1941 (MARY); Frederick Co., Catoctin Range, E. Baltass 271 30 May 1951 (MARY); Frederick Co., Cunningham Falls, R. Wiegand 880601-SN 1 Jun 1988 (TAWES); Montgomery Co., Along Travailan Road, W. D. Longbottom 3595 10 Jun 1993 (MARY); Montgomery Co., Bear Island, C. Lea 1584 14 May 2000 (MARY); Montgomery Co., Blockhouse Point Park, Darnestown, C. Lea 2067 17 Jun 2000 (MARY); Montgomery Co., Great Falls NP, Bear Island, C. Lea 881 16 May 1998 (TAWES); Prince Georges Co., Dillum, B. Swanton 1619 14 Jun 1989 (MARY); Prince George's Co., Beltsville, B. Swanton 1586 20 Jun 1939 (MARY); Washington Co., US 40, D. D. Boone 850704-SN 4 Jul 1985 (TAWES); Washington Co., Shupoburg, B. Swanton 1621 7 Jun 1939 (MARY); Washington Co., Elk Ridge, R. E. Riefner, Jr. 80-206 5 Jul 1980 (MICH).

Massachusetts: Hampden Co., Holyoke, H. E. Ahles 86665 1 Jun 1979 (WV).

Michigan: Grand Rapids, E. J. Cole s.n. 18 Jun 1898 (MICH); Clinton Co., Maple Rapids,
G. W. Parmelee 46 17 Jun 1952 (MICH); Clinton Co., Maple Rapids, G. W. Parmelee 133 20
Jun 1952 (MSC); Clinton Co., Maple Rapids, G. W. Parmelee 74 18 Jun 1952 (MSC); Ionia Co.,
North Plains, C. F. Wheeler s.n. 26 Jun 1889 (MICH); Ionia Co., North Plains, C. F. Wheeler
s.n. 19 Jun 1890 (MICH); Kalamazoo Co., Goose Lake, C. R. Hanes 117 25 Jun 1934 (MICH);
Kalamazoo Co., Schoolcraft Twp., C. R. Hanes s.n. 25 Jun 1934 (MICH); Lenawee Co., Madison
Twp., R. W. Smith 2548 18 Jun 1988 (MICH); Washtenaw Co., Whitmore Lake, F. J. Hermann
9470 1 Jun 1938 (MICH); Wayne Co., Detroit, E. C. Almendinger s.n. 14 Jul 1877 (MICH).

Mississippi: Attala Co., Kosciusko, C. T. Bryson 4144 12 Apr 1986 (MICH); Benton Co., US Hwy 78, C. T. Bryson 9974 18 May 1990 (MICH); Benton Co., Ashland, C. T. Bryson 14797 21 Apr 1995 (MICH); Carroll Co., Carrollton, C. T. Bryson 5426 22 Apr 1987 (MICH); Grenada Co., Camp McCain, C. T. Bryson 15214 20 May 1996 (MICH); Grenada Co., Gore Springs, C. T. Bryson 3360 25 May 1982 (MICH); Lafayette Co., Oxford, C. T. Bryson 5617 5 May 1987 (MICH); Lee Co., Tupelo, C. T. Bryson 3221 1 May 1982 (MICH); Lee Co., Tupelo, C. T. Bryson 3386 29
May 1982 (MICH); Lowndes Co., Mayhew, C. T. Bryson 9869 17 May 1990 (MSC); Lowndes Co.,
Mayhew, C. T. Bryson 3272 10 May 1982 (MICH); Marshall Co., Holly Springs, C. T. Bryson 994 18 May 1990 (MICH); Pontotoc Co., Sherman, C. T. Bryson 9935 18 May 1990 (MICH);
Tishomingo Co., Mingo, C. T. Bryson 11687 17 May 1992 (TAES); Yalobusha Co., Holly Springs
NF, C. T. Bryson 12469 2 Jul 1993 (MICH).

Missouri: Benton Co., Lake Creek, D. Castaner 6297 16 May 1981 (TAES); Boone Co., Bradford Farms, P. M. McKenzie 1448 23 Jun 1994 (MICH); Boone Co., Columbia, Norlan C Henderson 66-559 1 Jul 1966 (KANU); Butler Co., Hwy 67, J. Kessler 7234 15 Jun 1981 (TAES); Calloway Co., Dixie State Rec. Area, V. E. McNeilus 92-557 8 Jul 1992 (MICH); Calloway Co., Kingdom City, V. E. McNeilus 94-525 5 Jun 1994 (MSC); Camden Co., Lake of the Ozarks SP, T. B. Croat 17099 13 May 1972 (NCU); Cape Girardeau Co., Cape Girardeau, Travis E Brooks 6363 8 Jun 1972 (KANU); Cape Girardeau Co., Cape Girardeau, Travis Brooks 6921 24 May 1973 (KANU); Cape Girardeau Co., Cape Girardeau, Travis Brooks 6917 24 May 1973 (KANU); Cape Girardeau Co., Cape Girardeau, Travis Brooks 6942 24 May 1973 (KANU); Christian Co., Busiek State Forest, D. Castaner 9224 22 May 1986 (MICH); Christian Co., Nixa, R. W. Sanders 75005 30 Jun 1975 (MICH); Dent Co., State Hwy 19, T. G. Lammers 9437 24 Jun 1995 (MICH); Douglas Co., State Hwy 181, T. G. Lammers 9419 23 Jun 1995 (MICH); Douglas Co., Hwy 14, D. Castaner 8365 21 May 1985 (MICH); Dunklin Co., Malden, P. M. McKenzie 1856 3 Jun 1999 (MO); Greene Co., Springfield, D. Sutherland 1609 31 May 1968 (NEB); Howell Co., White Ranch Conservation Area, B. Summers 9706 9 May 2001 (MO); Iron Co., Taum Sauk Mt., P. M. McKenzie 1400 8 Jun 1994 (MICH); Jefferson Co., DeSoto, P. H. Raven 26978 11 May 1986 (NCU); Jefferson Co., Goldman, G. Davidse 3355 3 Jun 1973 (MSC); Johnson Co., Knob Noster SP, K. Campbell 105 10 Jun 1976 (MICH); Laclede Co., Bennett Springs SP, K. Campbell 177 2 Jul 1977 (MICH); Miller Co., Brumley, Steve Stephens 56368 6 Jul 1972 (KANU); Miller Co., Iberia, J. A. Stevermark 13046 4 Jul 1934 (MICH); Miller Co., Lake Ozark SP, K. Campbell 166 4 Jun 1977 (MICH); Morgan Co., Hwy CC, D. Castaner 6312 16 May 1981 (MICH); Ozark Co., Route O, D. Castaner 8432 22 May 1985 (VPI); Perry Co., State route V, R. Carter 7902 16 Jul 1989 (TAES); Perry Co., McBride, D. Castaner 7078 13 Jun 1982 (MICH); Phelps Co., Rolla, T. G. Lammers 9401 23 Jun 1995 (MICH); Pike Co., Eolia, John Davis s.n. 26 May 1918 (KANU); Pulaski Co., Ft. Leonard Wood Army Base, R. T. Ovrebo W0253 4 Jun 1989 (OKL); Pulaski Co., Ft. Leonard Wood Army Base, R.

T. Ovrebo W0306 6 Jun 1989 (OKL); Pulaski Co., Ft. Leonard Wood Army Base, R. T. Ovrebo W0344 8 Jun 1989 (OKL); Pulaski Co., Ft. Leonard Wood Army Base, R. T. Ovrebo W0189 2 Jun 1989 (OKL); Pulaski Co., St. Robert, J. A. Raveill 3056 15 Jun 1992 (EKY); Pulaski Co., R. T. Ovrebo W0253 4 Jun 1989 (KANU); Reynolds Co., Ellington, Ronald L. McGregor 17198 14 Jun 1962 (KANU); Reynolds Co., Lesterville, D. M. E. Ware 3670 8 Jun 1971 (CLEMS); Saint Genevieve Co., Hawn SP, R. Randrianaivo 420 18 May 1999 (MICH); Scott Co., Morley Quad, P. M. McKenzie 1998 13 May 2002 (MO); Scott Co., Morly, S. D. Jones 8555 16 May 1992 (MICH); Scott Co., unknown, Travis E. Brooks 6394 14 Jun 1972 (KANU); Shannon Co., Mark Twain NF, D. Castaner 9774 3 Jun 1987 (MICH); Shannon Co., Round Springs, D. M. Eggers 608 18 May 1963 (NCU); St. Clair Co., Roscoe, D. Castaner 6493 6 Jun 1981 (MICH); St. Francois Co., St. Francois SP, P. M. McKenzie 1426 18 Jun 1994 (MICH); St. Louis Co., Missouri Baptist College, J. Lang 4006 14 Jun 1969 (NCU); St. Louis Co., Allenton, Ralph E. Brooks 16724 27 Jun 1983 (KANU); St. Louis Co., Babler SP, S. P. Churchill 2929 22 May 1974 (NEB); St. Louis Co., Clayton, J. A. Steyermark 9202 13 May 1930 (MICH); Stone Co., Galena, E. J. Palmer 5742 25 May 1914 (MICH); Taney Co., Swan, B. F. Bush 4498 17 May 1907 (WV); Texas Co., Highway 17, D. Castaner 11238 3 Jun 1994 (MO); Texas Co., Mt. Grove, G. L. Pyrah s.n. 26 May 1978 (NCU); Washington Co., Hwy 57, D. Castaner 6580 14 Jun 1981 (MICH); Wayne Co., Route D, D. Castaner 9824 4 Jun 1987 (MICH); Wright Co., State Rt. 95, M. A. Vincent 7024 23 Jun 1995 (MICH).

Nebraska: Lancaster Co., Olive Creek Wildlife Management Area, G. Steinauer 296 19 Jun 1999 (NEB).

New Jersey: Hunterdon Co., Delaware Township, J. D. Mitchell 644 22 Jun 1993 (MICH); Morris Co., Morristown, R. H. True 438 6 Jul 1935 (VPI); Somerset Co., Watchung, Harold N. Moldenke 1783 21 Jun 1931 (WV).

New York: Albany Co., Alcove, W. J. Crins 7629 3 Jul 1989 (NYS); Albany Co., South Westerlo, G. C. Tucker 7270 28 Jun 1992 (NYS); Albany Co., Westerlo, G. C. Tucker 6077 17 Jun 1991 (NYS); Broome Co., Tracy Creek, R. T. Clausen 7278 1 Aug 1948 (NYS); Cayuga Co., Springport, A. J. Eames 11586 19 Jun 1919 (MICH); Chemung Co., Chemung, R. E. Zaremba 8713 2 Jun 1991 (NYS); Columbia Co., Blue Stores, R. McVaugh 3214 12 Jul 1935 (NYS); Columbia Co., Kinderhook, R. McVaugh 1836 30 Jul 1933 (NYS); Columbia Co., Green River, R. McVaugh 3530 30 Jul 1935 (NYS); Columbia Co., Elizaville, R. McVaugh 3198 11 Jul 1935 (NYS); Columbia Co.,

Germantown, R. McVaugh 3312 17 Jul 1935 (NYS); Columbia Co., Livingston, H. D. House 22663 26 Jun 1935 (NYS); Columbia Co., New Forge, R. McVauqh 3472 27 Jul 1935 (NYS); Columbia Co., Town of Cofake, R. McVaugh 3573 31 Jul 1935 (NYS); Dutchess Co., Astor Point, T. Weldy 1875 2 Jul 1997 (NYS); Dutchess Co., Clinton, R. E. Zaremba 3022 1986 (NYS); Dutchess Co., Hyde Park, H. E. Ahles 71463 18 Jun 1971 (MICH); Dutchess Co., Hyde Park, H E Ahles 71445 18 Jun 1971 (KANU); Dutchess Co., Hyde Park, H. E. Ahles 71451 18 Jun 1971 (NEB); Dutchess Co., Hyde Park, H. E. Ahles 71463 18 Jun 1971 (NCU); Dutchess Co., Rhine Cliff, H. D. House 19280 23 Jun 1932 (NYS); Dutchess Co., Stissing Mt., C. H. Peck s.n. (NYS); Dutchess Co., Town of Dover, G. C. Tucker 4518 8 Jul 1989 (NYS); Erie Co., Hamburg, G. C. Hicks s.n. 30 Jun 1928 (MSC); Greene Co., Rudowitz Farm, G. C. Tucker 5334 16 Jun 1990 (MICH); Greene Co., Catskill, H. D. House 32340 1 Jun 1949 (NYS); Greene Co., Greenville, G. C. Tucker 6067 16 Jun 1991 (NYS); Greene Co., Greenville, G. C. Tucker 7659 8 Aug 1992 (NYS); Greene Co., Palenville, S. J. Smith 20227 15 Jun 1956 (NYS); Oneida Co., Deerfield Ravine, J. V. Haberer 3893 13 Jul 1912 (NYS); Onondaga Co., Bare Mt., D. DeLaubenfels s.n. 25 Jul 1996 (NYS); Onondaga Co., Highland Forest County Park near Tully, S. M. Young s.n. 5 Jul 1992 (NYS); Onondaga Co., Township of Clay, D. J. DeLaubenfels s.n. 8 Jul 1997 (NYS); Onondaga Co., Township of Fabius, Apulia, D. Delaubenfels s.n. 2 Jul 1996 (NYS); Orange Co., U. S. military academy reservation, J. G. Barbour 38 12 Jun 1992 (MICH); Orange Co., Camp Buckner Rifle Range, J. G. Barbour 816 13 Jun 1994 (MICH); Orange Co., Harriman SP, J. G. Barbour 788 9 Jun 1993 (MICH); Orange Co., US Military Academy Reservation, J. G. Barbour 858 16 Jun 1993 (NYS); Orange Co., Vail's Gate, H. D. House 25755 14 Jun 1938 (NYS); Rensselaer Co., Grafton Lakes SP, P. Weatherbee 4369 16 Jun 1997 (NYS); Rensselaer Co., Pittstown, H. D. House 19417 2 Jul 1932 (NYS); Rensslauer Co., SE of West Sandlake, H. D. House 20354a 18 Jun 1933 (NYS); Richmond Co., New York City, R. E. Zaremba 3529 19 Jan 1986 (NYS); Richmond Co., New York City, R. E. Zaremba 2650 19 Jul 1985 (NYS); Richmond Co., Staten Island, S. H. Burnham 917a 29 May 1902 (OKL); Rockland Co., Harriman SP, J. G. Barbour 936 30 Jun 1993 (NYS); Rockland Co., Iona Island, S. Young 1954 17 Jun 1998 (NYS); Saratoga Co., Ballston Springs, H. D. House 19127 10 Jun 1932 (NYS); Saratoga Co., Clifton Park, H. D. House 22803 1 Aug 1935 (NYS); Saratoga Co., Saratoga Lake, H. D. House 24582 9 Jun 1937 (NYS); Schenectady Co., Plotterkill Preserve, S. M. Young 1691 25 Jun 1995 (NYS); Schuyler Co., Park Station, S. J. Smith 2445 1 Jun 1945 (NYS); Suffolk Co., Greenport, R. Latham 23752 1 Jun 1945 (NYS); Tompkins Co.,

Newfield Township, W. C. Wilson s.n. 11 Jun 1936 (NYS); Tompkins Co., Ithaca, A. J. Eames s.n. 28 Jun 1915 (NYS); Ulster Co., Lake Katrine, H. D. House 25651 30 Jun 1938 (NYS); Ulster Co., Marbletown, H. F. Dunbar 1146 13 Jun 1958 (NYS); Ulster Co., Saugerties, G. B. Rossbach 4048 12 Jun 1962 (WV); Ulster Co., Town of Olive, J. Bierhorst 35 20 Jun 1996 (NYS); Ulster Co., Town of Olive, Boiceville, J. Bierhorst s.n. 19 Jun 1998 (NYS); Ulster Co., Town of Olive, West Shokan, J. Bierhorst s.n. 9 Aug 1997 (NYS); Warren Co., Brayton, H. D. House 28674 20 Jun 1942 (OKL); Warren Co., Lake George, H. D. House 26761 18 Jul 1939 (NYS); Warren Co., Queensbury, H. D. House 27978 15 Jul 1941 (NYS); Washington Co., Lake George, S. H. Burnham s.n. 29 Jun 1915 (NYS); Washington Co., Lake George, R. E. Zaremba 4635 17 Jul 1987 (NYS); Westchester Co., Anthony's Nose, T. Weldy 2045 9 Jun 1998 (NYS).

North Carolina: Ashe Co., Bluff Mt., G. E. Tucker 2599 4 Jun 1965 (NCU); Ashe Co., The Peak, S. W. Leonard 3275 31 May 1970 (NCU); Buncombe Co., Biltmore, W. W. Ashe s.n. 12 Jun 1897 (NCU); Buncombe Co., Biltmore, W. W. Ashe 235c 12 Jun 1897 (NCU); Buncombe Co., Reynolds, J. A. Churchill 86044 25 May 1986 (MSC); Caswell Co., Anderson, C. R. Bell 11872 22 May 1958 (NCU); Caswell Co., Hightower, C. R. Bell 11855 22 May 1958 (NCU); Chatham Co., Mt. Carmel Church, A. E. Radford 4056 7 May 1949 (NCU); Cherokee Co., Patrick, K. E. Rogers 41623 18 Jun 1968 (NCU); Davidson Co., Beaverdam Creek headwaters, P. D. McMillan 2945 7 May 1998 (CLEMS); Davidson Co., Silver Valley, A. E. Radford 12755 16 Jun 1956 (NCU); Durham Co., Bland, A. E. Radford 43119 31 May 1960 (NCU); Durham Co., Bland, A. E. Radford 43127 31 May 1960 (NCU); Durham Co., Weaver, H. E. Ahles 57944 15 May 1963 (NCU); Forsyth Co., Kernersville, H. E. Ahles 40695 17 May 1958 (NCU); Forsyth Co., Kernersville, H. E. Ahles 40714 17 May 1958 (NCU); Granville Co., Dickerson, H. E. Ahles 12671 22 May 1956 (NCU); Harnett Co., Lillington, H. Laing 1276 15 May 1957 (NCU); Haywood Co., Crabtree, H. E. Ahles 42194 5 Jun 1958 (NCU); Iredell Co., US 21, H. E. Ahles 41059 18 May 1958 (NCU); Lee Co., Salem Church, S. Stewart 522 9 Jun 1958 (NCU); Macon Co., Ellijay, A. E. Radford s.n. 24 Jun 1946 (NCU); Macon Co., Ellijay, A. E. Radford 22646 (NCU); Macon Co., Ellijay PO, A E Radford 31547 (KANU); Madison Co., Marshall, H. E. Ahles 42428 6 Jun 1958 (NCU); Mecklenburg Co., Stephens Rd., J. F. Matthews s.n. 27 May 1993 (MICH); Montgomery Co., Mt. Gilead, A. E. Radford 13210 24 Jun 1956 (NCU); Montgomery Co., Uwharrie, E. F. Wells 3012 18 May 1970 (NCU); Montgomery Co., Uwharrie, A. E. Radford 2984 18 May 1970 (OKL); Montgomery Co., Uwharrie Wildlife Management Area, E. F. Wells 1131 15 Jun 1969 (NCU); Orange Co., Chapel

Hill, A. E. Radford 587a 10 May 1940 (NCU); Orange Co., Chapel Hill, W. C. Coker s.n. 14
May 1910 (NCU); Orange Co., Hillsboro, A. E. Radford 42905 20 May 1960 (NCU); Person Co.,
Woodsdale, C. R. Bell 12265 2 Jun 1958 (NCU); Person Co., Woodsdale, A. E. Radford 43177 2
Jun 1960 (NCU); Randolph Co., Liberty, C. R. Bell 11979 27 May 1958 (NCU); Randolph Co., New
Hope, A. E. Radford 43014 24 May 1960 (NCU); Rockingham Co., Thompsonville, A. E. Radford
13543 7 Jul 1956 (NCU); Rowan Co., Cleveland, A. E. Radford 11571 26 May 1956 (NCU); Rowan
Co., Spencer, A. E. Radford 11511 26 May 1956 (NCU); Stokes Co., Belews Creek, A. E. Radford
34494 4 Jun 1958 (NCU); Vance Co., Townsville, H. E. Ahles 12753 22 May 1956 (NCU); Wake
Co., William B. Umstead SP, G. P. Sawyer Jr. 1114 20 Jun 1964 (TAES).

Ohio: Holiday Inn, Turnpike exit 11, C. B. Stott 1789 16 Jun 1969 (MSC); Vermillion,
C. L. Mosley s.n. 3 Sep 1896 (MSC); Champaign Co., Urbana, J. Samples s.n. 5 Jun 1840 (MICH); Coshocton Co., Coshocton, H. N. Moldenke 12545 17 May 1942 (WV); Cuyahoga Co.,
Independence, S. A. Reznicek 52 10 Jun 1982 (MICH); Cuyahoga Co., Independence, S. A. Reznicek 58 10 Jun 1982 (MICH); Franklin Co., Pickerington Pond, J. S. McCormac 4710 12 Jun 1992 (MICH); Jackson Co., Jackson, J. A. Churchill s.n. 25 Jun 1956 (MSC); Jefferson Co., Annapolis,
A. W. Cusick 458 29 May 1965 (NCU); Lawrence Co., Co. Rt. 6, A. Cusick 22702 6 Jul 1983 (MICH); Lorain Co., Chance Creek, F. O. Grover s.n. 31 Jul 1912 (MICH); Lorain Co., Oak
Point, F. O. Grover s.n. 3 Jun 1922 (MICH); Mahoning Co., Berlin Twp., A. W. Cusick 10874 8 Jun 1970 (NCU); Monroe Co., St. Rt. 26, A. W. Cusick 9970 21 Aug 1969 (NCU); Monroe Co.,
Monroe Lake, A. W. Cusick 7505 14 Jun 1968 (NCU); Muskingum Co., White Eyes Creek, A. Cusick 22749 19 Jul 1983 (MICH); Ross Co., Betsch Fen, D. Minney 07-1 15 Jul 1992 (MICH);
Scioto Co., Shawnee State Forest, D. Demaree 10668 24 May 1934 (MO); Tuscarawas Co., Sandy Twp., A. W. Cusick 5021 3 Jul 1967 (NCU).

Oklahoma: Adair Co., Kansas, U. T. Waterfall 9579 7 Jul 1950 (OKL); Atoka Co., Sandhills
Nature Preserve, P. Folley 1514 4 Aug 1995 (OKL); Bryan Co., Bennington, J. Taylor 1675 17
May 1963 (OKL); Cherokee Co., White Oak Branch, M. D. Proctor GRU0329 12 May 1993 (OKL);
Cherokee Co., Quallis Rd., M. D. Proctor GRU0517 15 Jun 1993 (OKL); Cherokee Co., Tahlequah,
G. J. Goodman 4717 1 May 1948 (OKL); Cherokee Co., Eldon, P. Folley 2044 6 Jun 1997 (OKL);
Cherokee Co., Tahlequah, U. T. Waterfall 10059 25 Jun 1951 (TAES); Cherokee Co., US 62, S.
D. Jones 11132 26 May 1994 (MICH); Delaware Co., Dripping Springs, C. S. Wallis 4444 30 Jun
1957 (OKL); Delaware Co., Little Kansas, C. S. Wallis 7351 12 Jul 1958 (NCU); Delaware Co.,

Siloam Springs, U. T. Waterfall 8211 8 Jul 1948 (OKL); Haskell Co., Hancock Mt., D. Benesh e087
6 May 1998 (OKL); Latimer Co., R. Bebb 5504 30 May 1940 (OKL); LeFlore Co., US 259, L. K. Magrath 17823 10 May 1990 (OKL); LeFlore Co., Smithville, L. K. Magrath 17895 16 May 1990 (OKL); Mayes Co., Oklahoma Ozarks, C. S. Wallis 3204 27 May 1956 (OKL); McCurtain Co., Broken Bow, M. Fisher s.n. 6 Jun 1978 (OKL); McCurtain Co., Eagletown, E. L. Little, Jr. 1481
4 Jun 1930 (OKL); McCurtain Co., Weston, D. Castaner 9693 14 May 1987 (MICH); McIntosh Co., Canadian River, A. Buthod AB-4181 10 May 2002 (OKL); Muskogee Co., Braggs Mt., M. D. Procher GRU0366 13 May 1993 (OKL); Muskogee Co., Greenleaf Lake, U. T. Waterfall 9496 17
Jun 1950 (OKL); Nowata Co., Oolagah Wildlife Management Area, B. Hoagland OOL475 5 Jul 2000 (OKL); Pontotoc Co., P. Folley 1427 13 May 1995 (OKL); Sequoyah Co., Marble City, G. J. Goodman 7440 4 May 1963 (OKL).

Pennsylvania: Adams Co., Gettysburg Nat. Military Park, D. F. Brunton 10270 18 May 1991 (MICH); Alleghany Co., Pittsburgh, A. E. Jennings s.n. 17 Jun 1908 (NCU); Bedford Co., Bedford, D. Berkheimer 2679 22 Jun 1941 (GH); Bedford Co., Bedford, J. A. Churchill s.n. 15 Jun 1958 (MSC); Bedford Co., West End, H. Duppstadt s.n. 15 Jun 1969 (WV); Bedford Co., West End, Homer Duppstadt s.n. 19 Jun 1969 (KANU); Berks Co., Moselem Station, H. Wilkens 5533-x 26 Jun 1938 (GH); Berks Co., Lobachsville, D. Berkheimer 3711 10 Jun 1943 (MICH); Berks Co., Friedensburg, H. Wilkens 5844 10 Jun 1939 (GH); Bradford Co., Bentley Creek, H. A. Wahl 17384 16 Jun 1956 (NCU); Bradford Co., Franklindale, R. Naczi 2609 15 Jun 1990 (TAES); Bradford Co., Franklindale, R. Naczi 2586 15 Jun 1990 (MICH); Bucks Co., Beaver Creek, F. J. Hermann 4286 4 Jun 1933 (MICH); Bucks Co., Argus, C. D. Fretz s.n. 19 Jun 1923 (GH); Bucks Co., Ottsville, F. J. Hermann 4286 4 Jun 1933 (OKL); Bucks Co., Plumbsteadville, R. R. Dresbach 1666 29 Jul 1923 (MICH); Bucks Co., Telford, W. M. Benner 1606 5 Jun 1921 (MICH); Bucks Co., Upper Black Eddy, R. H. Time s.n. 10 Jun 1925 (WV); Bucks Co., Upper Black Eddy, R. H. Time s.n. 30 Jun 1931 (WV); Butler Co., Rt. 528, L. K. Henry s.n. 15 Jul 1946 (NCU); Butler Co., Epworth League Woods, L. K. Henry s.n. 5 Jun 1952 (NCU); Centre Co., State College, P. E. Rothrock 654 17 Jul 1975 (MICH); Centre Co., Unionville, H. A. Wahl 990 2 Jun 1941 (NEB); Chester Co., Paoli, F. W. Pennell 3908 26 Jun 1912 (NEB); Chester Co., Struct Road Station, H. E. Stone 296 30 May 1925 (GH); Clearfield Co., Ansonville, E. B. Ehrle 2348 13 Jun 1957 (NYS); Clearfield Co., Clearfield, E. B. Ehrle 1901 10 Jun 1956 (NCU); Delaware Co., Addingham, R. R. Dreisbach 1492 16 Jun 1923 (MICH); Delaware Co., Swarthmore, F. J. Hermann 3098 29 May 1932 (MICH); Delaware Co.,

Williamson School, R. R. Dresibach 2253 29 Jun 1924 (MICH); Delaware Co., Williamson School, F. J. Hermann 4340 10 Jun 1933 (GH); Elk Co., Caledonia, H. A. Wahl 18928 10 Jun 1959 (NCU);
Huntingdon Co., Barree, H. A. Wahl 1020 17 Jun 1941 (NEB); Lebanon Co., Newmanstown, C. S. Keener 237 16 Jun 1959 (WV); Lehigh Co., Hosensack, H. W. Pretz 12578 21 Jun 1925 (MSC);
Lehigh Co., Mosserville, 1 N, R. L. Schaeffer, Jr 35721 28 Jun 1951 (KANU); Mifflin Co., Bald
Eagle State Forest, A. W. Cusick 31045 17 Jun 1993 (MICH); Monroe Co., Poplar Valley, F. B.
Buser 11637 12 Jun 1978 (GH); Montgomery Co., Glasgow, David Berkheimer 4822 8 Jun 1944 (KANU); Montgomery Co., Schwenksville, E. T. Wherry s.n. 5 Jun 1960 (VPI); Northampton
Co., Chapman Quarries, R. L. Schaeffer 13012 23 Jun 1941 (GH); Northampton Co., Stouts, R.
L. Schaeffer 26324 3 Jul 1947 (GH); Northampton Co., Slate Valley, R. L. Schaeffer 7366 11 Jul
1940 (GH); Northampton Co., Portland, L. F. Randolph 72 5 Jun 1922 (GH); Northampton Co.,
Point Phillip, B. Long 43946 28 Jun 1934 (GH); Schuylkill Co., St. Clair, J. A. Churchill s.n. 14
Aug 1969 (MSC); Snyder Co., Meiserville, P. E. Rothrock 512 13 Jun 1975 (NCU); Union Co.,
Glen Iron, P. E. Rothrock 505 13 Jun 1975 (NCU).

South Carolina: Abbeville Co., Abbeville, C. N. Horn 9058 13 May 1995 (USCH); Abbeville Co., Cedar Springs, J. B. Nelson 21099 21 Apr 2000 (USCH); Abbeville Co., Richard Russell Dam and Lake Area, W. C. Credle 843 6 Jun 1979 (CLEMS); Abbeville Co., Richard Russell Dam and Lake Area, W. C. Credle 725 21 May 1979 (CLEMS); Abbeville Co., Sumter NF, J. B. Nelson 17265 31 May 1996 (MICH); Cherokee Co., Gaffney, H. E. Ahles 26970 4 Jun 1957 (NCU); Cherokee Co., Kings Mt. National Military Park, D. E. Kennemore Jr. 310 17 May 1993 (USCH); Chester Co., Big Sky Prairie, A. Darr 1713 6 Jun 2003 (USCH); Edgefield Co., Mt. Creek, A. E. Hodge 861 9 May 1984 (CLEMS); Edgefield Co., Horn Creek Analysis Area, J. B. Nelson 18045 2 Apr 1997 (USCH); Edgefield Co., Horn Creek Analysis Area, J. B. Nelson 18166 4 May 1997 (USCH); Edgefield Co., Sumter NF, J. B. Nelson 17265 31 May 1996 (USCH); Edgefield Co., Sumter NF, J. B. Nelson 17438 8 Jul 1996 (USCH); Edgefield Co., Trenton, A. E. Radford 22535 12 May 1957 (NCU); Fairfield Co., Ridgeway, J. B. Nelson 18303 24 May 1997 (USCH); Fairfield Co., Winnsboro, J. B. Nelson 19069 19 Apr 1998 (USCH); Lancaster Co., Forty Acre Rock, J. C. Coffey 23 4 Apr 1963 (USCH); Lancaster Co., Kershaw, B. F. Williamson 957 3 Jun 1961 (NCU); Newberry Co., Pomaria, J. B. Nelson 22628 23 May 2002 (USCH); Oconee Co., Earle's Ford Campground, R. W. Gettman 337 29 Jun 1973 (CLEMS); Oconee Co., Station Cove, L. L. Gaddy s.n. 22 Apr 1986 (CLEMS); Spartanburg Co., Cross Anchor, J. B. Nelson 22469 17 Apr 2002 (USCH); Union Co., Sumter Nat Forest, C. N. Horn 6643 14 May 1993 (MICH); Union Co., Tinker's Creek, O. M. Freeman 56148 14 May 1956 (NCU); York Co., Kings Mt. National Military Park, D. E. Kennemore Jr. 491 7 Jun 1993 (USCH); York Co., Kings Mt. SP, D. E. Kennemore Jr. 681 6 Jul 1993 (USCH); York Co., Kings Mt. SP, D. E. Kennemore Jr. 642 8 Jun 1993 (USCH); York Co., Kings Mt. SP, D. E. Kennemore Jr. 1379 5 Jun 1994 (USCH); York Co., Rock Hill, J. B. Nelson 4630 30 Apr 1986 (USCH).

Tennessee: Benton Co., Rt 191, Hal R. DeSelm s.n. 10 May 1993 (EKY); Bradley Co., Cleveland, L. R. Hesler 1087 26 May 1934 (NCU); Carroll Co., Thompson School Road, Hal R. DeSelm s.n. 21 Jun 1993 (EKY); Cheatham Co., Henrietta, E. W. Chester 81-289 31 May 1981 (NCU); Cheatham Co., Pegram, H. K. Svenson 10339 12 Jul 1939 (NYS); Clay Co., Celina, V. E. McNeilus 91-313 13 May 1991 (NEB); Coffee Co., A. E. D. C. Wildland Management area. K. E. Rogers 44794 19 May 1966 (NCU); Davidson Co., Bordeaux, R. Kral 42638 16 May 1971 (VPI); Davidson Co., Couchville Barrens, V. E. McNeilus 88-520 10 Jun 1988 (TAES); Davidson Co., Pearcy Priest Lake, G. Gonsoulin 3072 12 May 1973 (WV); Dickson Co., White Bluff, R. Kral 55382 13 May 1975 (VDB); Fayette Co., Amour Rd., Hal R. DeSelm s.n. 18 Aug 1993 (EKY); Humphreys Co., Cuba Landing, R. Kral 80415B 10 May 1992 (VDB); Knox Co., Northshore Drive, V. E. McNeilus 88-336 16 May 1988 (TAES); Knox Co., Knoxville, V. E. McNeilus 88336 16 May 1988 (MSC); Knox Co., Knoxville, A. Ruth s.n. 1 May 1894 (MICH); Knox Co., Knoxville, A. Ruth s.n. 1 May 1895 (MSC); Knox Co., Mascot, A. J. Sharp 734 2 Jun 1946 (NCU); Lawrence Co., Laurel Hill Lake, R Kral 55485 18 May 1975 (MICH); Loudon Co., Centerville, V. E. McNeilus 90-164 30 Apr 1990 (TAES); Marion Co., Fiery Gizzard Gorges, R. C. Clark 1814a 16 May 1965 (NCU); McNairy Co., Henderson, S. M. Bain 251 5 May 1893 (MSC); Meigs Co., Fezzell Road, H. R. DeSelm 197 3 Jun 1974 (EKY); Monroe Co., Tellico Plains, J. A. Churchill 93456 2 Jul 1993 (MICH); Montgomery Co., Clarksville, A. Clebsch s.n. 4 Jun 1950 (NCU); Roane Co., Fairview: Spiers Trailer, H. R. DeSelm 197 3 Jun 1974 (EKY); Rutherford Co., Smyrna, R. Kral 55369 9 May 1975 (MICH); Stewart Co., Land Between the Lakes, W. H. Willis s.n. 21 May 1966 (NCU); Sumner Co., Taylor Hollow, R. Carter 1806 17 May 1979 (VDB); Unicoi Co., Unicoi, J. A. Churchill 90-1512 22 May 1990 (MSC); Williamson Co., Fernvale, R. Kral 85884 19 May 1996 (MICH).

Vermont: Bennington Co., Barbera's Pond Road, D. E. Boufford 17906 12 Aug 1975 (NCU);
Rutland Co., Benson, Clarence H. Knowlton s.n. 19 Jul 1917 (KANU); Rutland Co., Brandon,
D. L. Dutton 973 3 Jul 1918 (GH); Rutland Co., Hubbardton, W. W. Eggleston s.n. 17 Jul 1898

(KANU); Rutland Co., Ira, G. L. Kirk s.n. 10 Jun 1911 (GH); Rutland Co., Sudbury, E. H. Eames 9160 5 Aug 1915 (GH); Windham Co., Brattleboro, L. A. Wheeler 84803 14 Jun 1922 (GH).

Virginia: City of Newport News, Fort Eustis, P. K. Appler 576 16 May 1973 (NCU); Albermarle Co., Bucks Elbow Mt., C. E. Stevens 7066 24 Jun 1973 (VPI); Alleghany Co., Natural Well, G. P. Fleming 13065 21 May 1997 (VPI); Arlington Co., Washington-Lee Highschool, A. Higginson 129 25 May 1946 (MARY); Augusta Co., Sherando, E. P. Killip 32570 7 Jun 1938 (MICH); Augusta Co., Elliott Knob, H. A. Allard 668 23 Jun 1935 (VPI); Bath Co., Millboro, J. F. Townsend 2866 7 Aug 2002 (VPI); Bedford Co., A. H. Curtiss s.n. (KANU); Botetourt Co., Craig Co. Line, T. F. Wieboldt 4751 18 Jul 1983 (VPI); Charles City Co., Wayside, D. M. E. Ware 4706 11 May 1973 (NCU); City of Norfolk Co., Norfolk Botanical Gardens, G. P. Frank 242 16 Jun 1980 (VPI); Clarke Co., Ashby Gap, T. Bradley 23421 12 Jun 1990 (CLEMS); Craig Co., New Castle, T. F. Wieboldt 5683 17 Jul 1985 (MICH); Culpeper Co., Buzzard Mt., H. A. Allard 20686 6 Jun 1953 (WV); Culpeper Co., Buzzard Mt., H. A. Allard 21470 6 Jun 1963 (KANU); Culpeper Co., Mt. Pony, H. A. Allard 2689 16 May 1937 (VPI); Culpeper Co., Winston, J. A. Churchill s.n. 28 Jul 1970 (MSC); Culpepper Co., Culpepper, H. A. Allard 1453 15 May 1936 (VPI); Cumberland Co., Duncan's Store, T. F. Wieboldt 7143 11 May 1990 (VPI); Dickenson Co., Cluichco, D. W. Ogle s.n. 14 Jul 1987 (VPI); Fairfax Co., Fairfax, F. H. Sargent s.n. 12 Jun 1949 (KANU); Fairfax Co., Ft. Hunt, S. F. Blake s.n. 17 Jun 1933 (MSC); Fauguier Co., Beverly Mills, J. A. Churchill s.n. 26 May 1968 (MSC); Fauquier Co., High Point, H. A. Allard 4926 5 Jun 1938 (VPI); Fauquier Co., Hopewell Gap, H. A. Allard 498 2 Jun 1935 (KANU); Fauquier Co., Pond Mt., H. A. Allard 11258 20 May 1945 (WV); Fauquier Co., Western slope of Bull Run Mts, H. A. Allard 4734 15 May 1938 (VPI); Fauquier Co., Western slope of Bull Run Mts, H. A. Allard 11239 13 May 1945 (VPI); Fauquier Co., White Rocks, H. A. Allard 8710 25 May 1941 (VPI); Fluvanna Co., Rt. 629, G. M. Diggs Jr. 264 17 Jun 1975 (NCU); Fluvanna Co., Hardware, C. E. Stevens 4872 18 May 1972 (VPI); Franklin Co., Ferrum, T. F. Wieboldt 9213 11 May 1995 (VPI); Greene Co., McMullen, T. F. Wieboldt 2511 3 Jul 1976 (NCU); Henry Co., VA 87, G. B. Straley 69103 15 May 1969 (VPI); Highland Co., Bear Mt., A. B. Davenport s.n. 25 Jun 1988 (VPI); Lee Co., Jonesville, L. J. Uttal 13184 7 Jun 1984 (VPI); Lee Co., Thomas Cemetery, J. C. Ludwig 2726 22 May 1996 (VPI); Lee Co., Jonesville, T. F. Wieboldt 5043 30 May 1984 (VPI); Lee Co., N Tyler, D. W. Ogle s.n. 21 May 1990 (VPI); Lee Co., The Cedars, D. W. Ogle 1393 20 May 1979 (VPI); Lee Co., Jonesville, L. U. Uttal 7186 5 Jun 1970 (VPI); Loudoun Co., Headwaters of Elklick Run, M. T.

Strong 87-098 14 Jun 1987 (USCH); Loudoun Co., Goose Creek, H. A. Allard 21436 24 May 1953 (WV); Loudoun Co., Centerville, E. H. Walker 5604 24 Jun 1950 (MARY); Loudoun Co., Goose Greek, H. A. Allard 20252 30 May 1952 (WV); Madison Co., Aroda, T. Bradley 23363 10 Jun 1990 (CLEMS); Montgomery Co., Ellett Creek bridge, L. J. Uttal 9723 21 May 1973 (CLEMS); Montgomery Co., Blacksburg, M. L. Smyth 4526 2 Jun 1978 (VPI); Montgomery Co., Ironto, R. Kral 10724 6 Jul 1960 (NCU); Montgomery Co., Poverty Creek, L. J. Uttal 8113 22 Jun 1971 (VPI); Montgomery Co., Roanoke Valley, W. B. McIntosh s.n. 24 Jun 1947 (VPI); Orange Co., Burr Hill, T. Bradley 23292 21 May 1990 (CLEMS); Orange Co., Burr Hill, T. Bradley 23280 21 May 1990 (CLEMS); Page Co., Jollett, T. Bradley 19084 24 May 1983 (NCU); Powhatan Co., Fine Creek, C. M. Corcoran 326 10 May 1976 (NCU); Prince Edward Co., Farmville, A. M. Harvill 21313 23 May 1969 (NCU); Prince Edward Co., Twin Lakes SP, J. F. Townsend 3241 30 Jun 2004 (VPI); Prince William Co., Bull Run Mts, H. A. Allard 7716 9 Jun 1940 (NY); Prince William Co., Eastern slope of Bull Run Mts, H. A. Allard 7715 9 Jun 1940 (VPI); Prince William Co., Quantico Marine Base, B. W. Hoagland QUN0395 19 Jun 1994 (OKL); Pulaski Co., Big Reed Island Creek Rd, L. J. Uttal 7177 4 Jun 1970 (VPI); Roanoke Co., Bennett Springs, L. J. Uttal 8715 22 May 1972 (VPI); Russell Co., Clinch Mt., D. W. Ogle 5950 25 Jun 1985 (VPI); Russell Co., N Clinch River, D. W. Ogle 5644 19 Jun 1983 (VPI); Russell Co., Russell Co. Park, D. W. Ogle 6026 26 May 1986 (VPI); Scott Co., Gate City, T. F. Wieboldt 8625 21 Jun 1993 (VPI); Shenandoah Co., Short Mt., H. A. Allard 8827 6 Jun 1941 (VPI); Shenandoah Co., Hudson Crossroads, A. W. Cusick 23542 13 Jun 1984 (NCU); Shenandoah Co., Mill Mt., H. A. Allard 4855 28 May 1938 (VPI); Smyth Co., Hungry Hollow, J. K. Small s.n. 7 Jun 1892 (MSC); Smyth Co., Marion, R. Leedy 1401 30 May 1978 (VPI); Spotsylvania Co., Massaponax, T. Bradley 19131 28 May 1983 (NCU); Westmoreland Co., Westmoreland SP, J. Dodge 1395 4 Jun 1999 (VPI); Wise Co., Powell Mt., T. F. Wieboldt 6678 2 Jun 1988 (MICH); Wythe Co., Wytheville, T. F. Wieboldt 5639 27 Jun 1985 (VPI).

West Virginia: Barbour Co., Tygart Valley River, G. B. Rossbach 9779 26 Jun 1986 (WV); Barbour Co., Pediddle Road, W. N. Grafton s.n. 3 Jul 1997 (WV); Berkeley Co., Sleepy Creek Lake Dam, W. N. Grafton s.n. 27 Jun 2004 (WV); Berkeley Co., Tomahawk, E. L. Core 5881 10 Jul 1937 (WV); Braxton Co., Gassaway, F. J. Boggs Jr. s.n. 5 Jun 1953 (WV); Cabell Co., Roland Park, F. A. Gilbert 473 21 Jun 1936 (WV); Doddridge Co., Ashley, E. L. Core 5595 8 Jul 1937 (WV); Fayette Co., Ames Heights, D. W. Suiter 1580 20 Jun 1993 (WV); Fayette Co., New River Gorge, W. N. Grafton s.n. 4 Jul 1972 (WV); Gilmer Co., Tanner Creek, E. A. Bartholomew s.n. 31 Jul 1965 (WV); Grant Co., Bayard, A. W. Cusick 24286 28 May 1985 (WV); Grant Co., Cabins, G. B. Rossbach s.n. 30 May 1953 (WV); Grant Co., Day Park at Arthur, W. N. Grafton s.n. 22 Jun 2000 (WV); Grant Co., Monongahela NF, A. Cusick 23523 12 Jun 1984 (MICH); Hancock Co., Orchard Run, Hillcrest Wildlife Management Area, W. N. Grafton s.n. 7 Jul 2005 (WV); Hardy Co., Alleghenies, H. A. Allard 6732 8 Jun 1939 (WV); Harrison Co., Dog Run Lake, W. N. Grafton s.n. 1 Jun 1997 (WV); Jackson Co., Ripley, R. Guthrie s.n. 16 May 1953 (WV); Kanawha Co., Camp Carlisle on Blue Creek., W. N. Grafton s.n. 25 May 1980 (WV); Kanawha Co., Nitro, Redinour Park, G. C. Tucker 7108 11 Jun 1992 (NYS); Lewis Co., Jackson's Mill Camp Reservoir, W. N. Grafton s.n. 9 Jun 1995 (WV); Lincoln Co., Fez School, William N. Grafton s.n. 28 May 1980 (WV); Lincoln Co., Fez, William N. Grafton s.n. 28 May 1980 (WV); Marion Co., Fairview, E. L. Core 5211 5 Jul 1937 (WV); Mason Co., Pt. Pleasant, H. C. Dahl s.n. 1 Apr 1951 (WV); Mason Co., Arbuckle Twp., M. A. Vincent 4701 22 May 1991 (WV); Mercer Co., Eads Mill, W. N. Grafton s.n. 7 Jun 1987 (WV); Mercer Co., Pipestem SP, W. N. Grafton s.n. 28 Jun 1997 (WV); Monongalia Co., Morgantown, W. N. Grafton s.n. 26 May 1997 (WV); Monongalia Co., White Park in Morgantown, W. N. Grafton s.n. 24 May 1995 (WV); Pendleton Co., Thorn Creek Rd, W. N. Grafton s.n. 2 Jun 1998 (WV); Pocahontas Co., Frost, W. N. Grafton s.n. 11 Jun 1996 (WV); Preston Co., Arthurdale, H. A. Davis 6386 16 Jun 1944 (WV); Preston Co., US Rt. 50, A. W. Cusick 23471 10 Jun 1984 (WV); Raleigh Co., Batoff Mt., J. P. Tosh 1126 31 May 1941 (WV); Randolph Co., Huttonsville, E. E. Hutton s.n. 29 May 1959 (WV); Ritchie Co., Pennsboro, E. L. Core 5657 8 Jul 1937 (WV); Roane Co., Charles Fark Lake, W. N. Grafton s.n. 26 Jun 2001 (WV); Roane Co., Hungry Beech Preserve, W. N. Grafton s.n. 21 Jun 1979 (WV); Summers Co., Bluestone SP, W. N. Grafton s.n. 14 Jul 1996 (WV); Summers Co., Pipestem SP, W. N. Grafton s.n. 27 Jun 1997 (WV); Summers Co., Stony Creek, W. N. Grafton s.n. 22 Jun 1976 (WV); Tucker Co., Canaan Valley, H. A. Allard 12295 21 Jun 1947 (WV); Upshur Co., Buckhannon, G. B. Rossbach 2640 16 Jun 1961 (WV); Upshur Co., Buckhannon, G. B. Rossbach s.n. 23 Jun 1954 (WV); Wayne Co., Buffalo Creek, L. Plymale 405 3 Jun 1938 (WV); Wayne Co., Doane Hollow, Cabwaylingo State Forest, W. N. Grafton s.n. 27 Jun 1998 (WV); Wayne Co., Nestlow, A. W. Cusick 33182 26 Jun 1996 (WV); Wayne Co., Prichard, J. B. Nelson 19535 17 Jul 1998 (WV); Wirt Co., Palestine Bass Hatchery, E. A. Bartholomew W-4123 5 Jun 1956 (NCU); Wirt Co., Elizabeth, E. A. Bartholomew W-4124 24 Jun 1956 (WV); Wirt Co., Elizabeth, E. A. Bartholomew W 4110 (WV); Wirt Co., Palestine, E. A. Bartholomew s.n. 27 May 1942 (NCU); Wirt Co., Palestine, E. A. Bartholomew W1941-1054 24 May 1941 (WV); Wirt Co., Reedy Creek, E. A. Bartholomew
 W-4123 5 Jun 1956 (WV).

Carex roanensis. U. S. A. South Carolina: Oconee Co., Burrell's Ford, Chattooga River, M. G. Douglass 467 16 May 1981 (CLEMS).

West Virginia: Preston Co., Aurora, E.S. Steele 17 Aug 1898 (NY).

All other known records of C. roanensis were published in Smith et al. (2006) (Appendix D).

Carex swanii. Canada. British Columbia: Southern Hernando Island, G. B. Stratley 8510 11 Jun 1995 (MICH).

Nova Scotia: Annapolis Co., Granville, *M. L. Fernald 23487* 18 Jul 1921 (CAN); Shelburne Co., Islands Provincial Park, *M. J. Oldham 13880* 26 Jun 1992 (MICH); Yarmouth Co., Lake George, *M. L. Fernald 23486* 16 Jul 1921 (CAN); Yarmouth Co., Yarmouth, *A. S. Pease* 4 Jul 1920 (KANU).

Ontario: Elgin Co., Bayham Township, M. J. Oldham 12778 16 Jun 1991 (WIS); Elgin Co., Port Burwell Provincial Park, M. J. Oldham 15213 23 Jul 1993 (MICH); Essex Co., Ruscom River, M. J. Oldham 3000 6 Jul 1982 (MICH); Essex Co., Anderson Tp., M. J. Oldham 2761 14 Jun 1982 (MICH); Essex Co., Arner, Macoun 33750 2 Aug 1901 (CAN); Essex Co., Cedar Creek, M. J. Oldham 6699 12 Aug 1986 (MICH); Essex Co., Essex Centre, Macoun 32085 1 Jul 1882 (CAN); Essex Co., Harrow, M. J. Oldham 2686 6 Jun 1982 (CAN); Essex Co., Hillman Creek Marsh, S. J. Darbyshire 2606 24 Jun 1985 (CAN); Essex Co., Hillman Sand Hills, M. J. Oldham 1648 13 Jul 1981 (MICH); Essex Co., Kingsville, M. J. Oldham 2916 26 Jun 1982 (CAN); Essex Co., Learnington Anonymous s.n. 30 Jun 1882 (MTMG); Essex Co., Learnington, T. J. W. Burgess s.n. 30 Jun 1882 (MICH); Essex Co., Learnington, T. Burgess s.n. 1 Jul 1882 (CAN); Essex Co., Learnington, M. J. Oldham 1648 13 Jul 1981 (CAN); Essex Co., Learnington, T. J. W. Burgess s.n. 1 Jul 1882 (MTMG); Essex Co., Harrow, A. A. Reznicek 7159 19 Jun 1983 (MICH); Essex Co., Oxley Poison Oak Swamp, M. J. Oldham 2686 6 Jun 1982 (TAES); Essex Co., Reaume Prairie, M. J. Oldham 11056 12 Jun 1990 (CAN); Essex Co., Ruscom River, M. J. Oldham 3000 6 Jul 1982 (CAN); Essex Co., Tilbury West Conservation Area, M. J. Oldham 16410 18 Jul 1994 (MICH); Essex Co., Kingsville, M. J. Oldham 2916 26 Jun 1982 (MICH); Haldimand-Norfolk Co., Deer Creek, D. A. Sutherland 7191 25 Jun 1986 (CAN); Kent Co., Wheatley Provincial Park, A. A. Reznicek s.n. 3 Sep 1979 (MICH); Kent Co., Wheatley Provincial Park, M. J. Oldham 2835 21 Jun 1982 (MICH); Lambton Co., Walpole Island, P. F. Maycock 7504 18 Jun 1985 (MICH); Middlesex Co.,

Meadowlily Woods, London, *M. J. Oldham 8565* 30 Aug 1988 (MICH); Middlesex Co., Sydenham River valley, *M. J. Oldham 15135* 13 Jul 1993 (MICH); Perth Co., Ellice Swamp, *M. J. Oldham* 15257 27 Jul 1993 (MICH).

Quebec: Brome Co., Glen Sutton, Marie-Victorin 56374 28 Jun 1941 (CAN); Brome Co., Sutton, Marie-Victorin 55268 22 Jun 1941 (CAN); Missisquoi Co., Frelighsburg, L. Cinq-Mars 67-90 29 Jun 1967 (CAN); Missisquoi Co., Frelighsburg, M. J. Oldham 7408 18 Jun 1987 (TAES); Missisquoi Co., Frelighsburg, Marcel Raymond s.n. 24 Jun 1953 (WIS).

U. S. A. D. Clark s.n. 1 Jul 1899 (MSC); H. C. Cowles s.n. 24 Jun 1892 (MICH); Flora of the Western Reserve, G. B. Ashcroft 7441 1 Jun 1897 (WIS).

Alabama: Jackson Co., Pleasant Grove, R. Jones 7149 8 Jul 1992 (VDB).

Arkansas: Garland Co., Hot Springs NP, C. T. Bryson 5763 24 May 1987 (MICH); Garland Co., Iron Springs Recreation Area, A. A. Reznicek 8494 5 Jun 1989 (MICH); Garland Co., Ouachita National Forest, R. Naczi 3930 19 May 1994 (NKY); Independence Co., McHue vicinity, Phillip E. Hyatt 5578.32 30 May 1993 (MICH); Montgomery Co., Norman, R. Kral 77536 12 May 1990 (VDB); Montgomery Co., Camp Albert Pike Rec. Area, J. Rettig 554 20 May 1982 (VDB); Montgomery Co., Caddo Gap, R. Kral 77563 12 May 1990 (VDB); Montgomery Co., Cox Springs, C. T. Bryson 4272 10 May 1986 (MICH); Montgomery Co., Little Missouri River Falls Rec. Area, C. T. Bryson 4349 10 May 1986 (MICH); Montgomery Co., Newton, R. Kral 76434 26 May 1989 (VDB); Montgomery Co., Ouchita NF: Caney Creek WMA, S. D. Jones 10102 18 May 1993 (VPI); Polk Co., Shady Lake Campground, Charles T. Bryson 4340 10 May 1986 (VDB); Polk Co., McKinley Mt., R. Kral 76412 23 May 1989 (VDB); Polk Co., Cossatat River, S. Jones 4638 13 May 1990 (VDB); Polk Co., Rich Mountain, S. Jones 4668 14 May 1990 (VDB); Polk Co., Big Fork State Natural Area, R. Kral 76335 22 May 1989 (VDB); Stone Co., Ozark National Forest, Phillip E. Hyatt 4108.69 26 Jun 1991 (BRIT); Stone Co., St. Martin's River Access point, David Castaner 9092 9 May 1986 (MICH); Stone Co., Sylamore District of the Ozark National Forest, Phillip E. Hyatt 4115.69 10 Jul 1991 (MICH); Van Buren Co., Conway Co., Phillip E. Hyatt 5429 18 May 1993 (MICH).

Connecticut: East Lyme, E. J. Alexander s.n. 19 Jun 1936 (NY); Portland, S. W. Starmer s.n. 21 Jun 1896 (SMU); Windham, C. A. Weatherby s.n. 16 Jul 1932 (WIS); Fairfield Co., Fairfield, E. H. Eames s.n 18 Jun 1901 (MSC); Fairfield Co., New Fairfield, F. C. Seymour 19,909 14 Jul 1962 (SMU); Fairfield Co., Winnipauk, F. C. Seymour 20528 21 Jun 1963 (GH); Hartford Co., Hartford, A. W. Driggs 3 15 Jun 1901 (GH); Hartford Co., Hartford, Charles Wright s.n. 16
Jun 1875 (WIS); Litchfield Co., Colebrook, L. J. Mehroff 19484 27 Jun 1997 (MICH); Litchfield
Co., Housatonic State Forest, L. J. Mehrhoff 8034 23 Jun 1983 (MICH); Middlesex Co., Durham,
C. A. Weatherby 3061 22 Jun 1913 (GH); Middlesex Co., Old Saybrook, S. R. Hill 16812 9 Jun
1986 (TAES); Middlesex Co., Portland, F. W. Starmer s.n. 21 Jun 1896 (GH); New Haven Co.,
Wallingford, L. J. Mehroff 20873 6 Jul 2000 (MICH); New Haven Co., Waterbury, A. E. Blewitt
238 28 Jul 1910 (GH); New London Co., Bishops Cove development, S. R. Hill 21744 22 Jul
1990 (MICH); New London Co., Salem, G. C. Tucker 4214 13 Sep 1988 (NYS); New London Co.,
Town of Franklin, R. W. Woodward s.n. 21 Jun 1906 (GH); New London Co., Town of Franklin,
R. W. Woodward s.n. 10 Oct 1909 (GH); Tolland Co., Mansfield, L. J. Mehrhoff 6377 25 Jun
1982 (MICH); Tolland Co., Tolland, L. J. Mehrhoff 15782 11 Jul 1992 (MICH); Windham Co.,
Thompson, C. A. Weatherby 4644 27 Jun 1920 (GH); Windham Co., Woodstock, C. Schweinfurth
s.n. 16 Jun 1934 (GH).

Delaware: New Castle Co., State Rd. Station, R. R. Dreisbach 4323 27 Jun 1926 (MICH).
District of Columbia: G. Vasey s.n. 1880 (MSC); Briar Ditch Valley, E. C. Leonard 21137 20
Jun 1960 (KANU); Washington, D. C., George Versey s.n. 1884 (WIS).

Georgia: Rabun Co., Pine Mountain, J. A. Churchill 91-267 14 Jun 1991 (MSC); Rabun Co., Warwoman Dell Creek, Phillip E. Hyatt 6064 29 May 1994 (MICH).

Illinois: Cook Co., Palos Hills, S. R. Hill 29307 11 Jun 1997 (MICH); Cook Co., Thornton, A. Chase s.n. 13 Jun 1898 (MSC); Iroquois Co., Indiana State Line, A. A. Reznicek 10838 6 Jun 1999 (MICH); McDonough Co., Macomb, S. R. Hill 31499 18 May 1999 (MICH); Perry Co., Pyramid SP, J. Reveill 1354 11 Jun 1982 (MO); Winnebago Co., Rock Cut Forest Preserve, Egbert W. Fell 55-489 18 Jun 1955 (WIS); Winnebago Co., Rock River Valley, E. W. Fell 56-243 24 Jun 1956 (GH).

Indiana: Chesterton, L. M. Umbach s.n. 16 Jun 1900 (WIS); Chesterton, L. M. Umbach 12329 16 Jun 1900 (WIS); Allen Co., Godfrey Indian Reserve, C. C. Deam 1154 24 Jun 1906 (MICH); Bartholomew Co., Columbus, C. C. Deam 23,165 27 May 1917 (MICH); Cass Co., Hoover, C. C. Deam 45,811 2 Jul 1928 (MICH); Elkhart Co., Simonton Lake, C. C. Deam 55,036 15 Jun 1934 (MICH); Laporte Co., Michigan City, D. Castaner 8521 8 Jun 1985 (MO); Lawrence Co., Heltonville, R. M. Kriebel 2176 17 Jun 1934 (MICH); Lawrence Co., Springville, R. M. Kriebel 1783 6 Jun 1934 (MICH); Lawrence Co., Springville, R. M. Kriebel 1790 6 Jun 1934 (WIS); Porter Co., Furnessville, M. W. Lyon Jr. s.n. 13 Jul 1924 (MICH); Porter Co., Tremont, M. W. Lyon Jr. s.n. 2 Aug 1925 (MICH); Porter Co., Tremont, H. R. Bennett 7032 11 Jun 1960 (SMU); Putnam Co., Greencastle, E. J. Grimes 683 8 Aug 1911 (GH); St. Joseph Co., Granger, Chas. C. Deam 55086 15 Jun 1934 (WIS).

Kansas: Douglas Co., Baldwin City, Caleb A Morse 8383 27 Jun 2002 (KANU).

Kentucky: Barren Co., Haywood, R. Naczi 6465 14 Jun 1997 (NKY); Bath Co., Black Shale Region, M. E. Wharton 2448b 2 Jun 1938 (MICH); Bell Co., Henderson Fork Road Surface-Mined Area, Ralph L. Thompson 93-161 19 Jun 1993 (NKY); Bell Co., Cumberland Gap NP, D. F. Brunton 10355 24 May 1991 (MICH); Bell Co., Pineville, R. Naczi 6714 25 Jun 1997 (NKY); Boone Co., Petersburg, R. Naczi 4104 12 Jun 1994 (NKY); Boyle Co., Black Shale Region, M. E. Wharton 952 21 Jul 1937 (MICH); Calloway Co., Ky 614, R. Athey 2826 25 Jun 1974 (VDB); Calloway Co., Croppie Hollow Shores Subdivision, R. Athey 2291 21 May 1973 (VDB); Campbell Co., Silver Grove, R. Naczi 226 12 Jun 1996 (NKY); Campbell Co., Silver Grove, R. Naczi 129 12 Jun 1996 (NKY); Clinton Co., Lakewood Estates, L. E. McKinney 6454 31 May 1995 (MICH); Edmonson Co., Mammoth Cave NP, Landon E. McKinney 2869-2 25 May 1988 (VDB); Franklin Co., Echo Springs Swamp, S. Rice s.n. 12 Jul 1984 (EKY); Graves Co., Mayfield, R. Athey 2356 19 Jun 1973 (VDB); Hardin Co., Ribbon Snake Lake, R. Cranfill 265 18 May 1977 (MICH); Hopkins Co., St. Charles, L. E. McKinney 4274 2 Jun 1990 (EKY); Larue Co., Magnolia, Landon McKinney 5083 5 Jun 1992 (NKY); Laurel Co., Chalie Cheek Swamp, R. Naczi 7385 15 Jun 1998 (MICH); Laurel Co., Lily, David D. Taylor 511 1 Jun 1981 (WV); Laurel Co., Rock Creek Gorge, R. L. Thompson 89-770 29 May 1989 (EKY); Letcher Co., Lilley Cornett Woods Research Station, J. D. Sole 161 2 Jun 1978 (EKY); Letcher Co., Whitesburg, John W. Thieret 60618 16 Jul 1999 (NKY); Lewis Co., Thackers Chapel, Cusick 25365 14 Jun 1986 (NCU); Madison Co., Dunncannon Lane, D. A. Miller 22 26 Jun 1990 (EKY); Madison Co., Moberly Quadrangle, G. W. Libby OB-329 31 May 1993 (MICH); Madison Co., Richmond, R. Peter 781 1 Jun 1834 (MICH); McCracken Co., Metropolis Lake State Nature Preserve, L. E. McKinney 6290 16 Jun 1994 (MICH); McCreary Co., Daniel Boon NF, S. Jones 4982 24 May 1990 (VDB); McCreary Co., Honeybee, R. Naczi 6555 19 Jun 1997 (NKY); McCreary Co., Whitley City, John W. Thieret 57424 16 May 1994 (NKY); McCreary Co., Whitley City, John W. Thieret 55284 24 Jun 1984 (NKY); Mulhenberg Co., Lake Malone SP, J. Conrad s.n. 25 May 1969 (NCU); Nelson Co., Howardstown, Landon McKinney 5097 3 Jun 1992 (NKY); Owlsey Co., Sturgeon Creek, L. E. McKinney 4687 18 May 1991 (EKY);

Owsley Co., Sturgeon Creek, Landon E. McKinney 4687 18 May 1991 (VDB); Pike Co., Pine Mt., F. Levy s.n. 18 Aug 1982 (NCU); Pulaski Co., Woodstock, J. R. Abbott 375 1 Jun 1991 (EKY); Rockcastle Co., Morning View Church, R. Hannan 2004 30 May 1979 (EKY); Rockcastle Co., Rigsby's Swamp, R. R. Hannan 160 10 Jun 1977 (EKY); Wolfe Co., Natural Bridge SP, K. Feeman 240 19 May 1998 (EKY).

Maine: Cumberland Co., Casco Bay, R. H. True 262 25 Aug 1923 (GH); Cumberland Co.,
Casco Bay, Great Chegeague Island, M. L. Fernald 1519 2 Jul 1909 (GH); Cumberland Co., Oxford,
E. B. Chamberlain s.n. 1 Jul 1907 (GH); Cumberland Co., York Hill, Town of North Yarmouth,
E. B. Chamberlain 839 20 Jul 1905 (GH); Kennebec Co., Litchfield, Fellows 4732 7 Aug 1912 (GH); Knox Co., Camden, G. B. Rossbach 3847 7 Aug 1956 (NCU); Knox Co., Camden, G. G.
Kennedy s.n. 12 Jul 1902 (GH); Oxford Co., Dixfield, J. C. Parlin 2135 3 Jul 1907 (GH); Waldo
Co., Lincolnville, G. B. Rossbach 4586 22 Jul 1958 (NCU).

Maryland: Allegany Co., Selinger Marsh, C. Lea 2141 28 Jun 2000 (MARY); Anne Arundel Co., Annapolis, F. R. Fosberg 43642 12 May 1963 (VDB); Anne Arundel Co., Davidsonville, F. H. Sargent 6070 8 Jun 1952 (WIS); Anne Arundel Co., Patuxent River Park, W. D. Longbottom 3040 3 Jun 1992 (MARY); Anne Arundel Co., Town of Pasadena, W. D. Longbottom 3032 2 Jun 1992 (MARY); Calvert Co., Cove Point, B. W. Steury 960615.43 15 Jun 1996 (MICH); Calvert Co., Scientist's Cliffs, F. R. Fosberg 43738 5 Jun 1963 (MICH); Caroline Co., Lentz Road, C. T. Frye 960613-578 13 Jun 1996 (TAWES); Carroll Co., Morgan Run, C. Lea 2079 17 Jun 2000 (MARY); Cecil Co., Elk Neck SP, O. H. Thompson 511 24 May 1973 (MARY); Charles Co., Nanjemov, S. R. Hill 9208 7 Jun 1980 (MARY); Dorchester Co., Chicone Woods, C. Lea 1899 4 Jun 2000 (MARY); Frederick Co., Catoctin Mt. Highway, C. Lea 1718 28 May 2000 (MARY); Frederick Co., Catoctin Mt. Park, C. J. Hickey II 398 30 Jun 1973 (NCU); Frederick Co., Catoctin Mt., S. S. Tepfer 1351 8 Jun 1941 (MARY); Frederick Co., Catoctin Mt., S. S. Tepfer 1324a 8 Jun 1941 (MARY); Garrett Co., Mineral Spring, C. Lea 2217 30 Jun 2000 (MARY); Garrett Co., New Germany, C. Lea 2152 29 Jun 2000 (MARY); Garrett Co., Mt. Nebo Wildlife Management Area, C. Lea 2186 29 Jun 2000 (MARY); Harford Co., Aberdeen Proving Grounds, B. W. Hoagland ABR0230 9 Jun 1994 (OKL); Harford Co., Rocks SP, C. Lea 1855 29 May 2000 (MARY); Kent Co., Millington Wildlife Management Area, W. D. Longbottom 3090 9 Jun 1992 (MARY); Montgomery Co., Burtonsville, J. C. Ludwig 86102 17 Jun 1986 (VPI); Montgomery Co., Great Falls, F. H. Sargent s.n. 19 Jun 1949 (KANU); Montgomery Co., Linden, J. E. Benedict Jr. 5865 19 Jun 1951 (VPI); Montgomery

Co., Marsden Tract, C. Lea 1233 19 Jun 1999 (MARY); Montgomery Co., Great Falls NP, Bear Island, C. Lea 882 16 May 1998 (TAWES); Montgomery Co., Great Falls, E. L. Morris s.n. 28 May 1899 (NEB); Prince Georges Co., Accokeek, S. R. Hill 14193 14 Jun 1984 (TAES); Prince Georges Co., Fort Washington, J. E. Benedict Jr. 5957 21 May 1953 (VPI); Prince George's Co., BARC, R. F. Whitcomb s.n. 13 Jun 1995 (MARY); Prince George's Co., Beltsville Agricultural Research Center (BARC), R. F. Whitcomb s.n. 19 Jun 1995 (MARY); Prince George's Co., College Park, Anonymous s.n. 17 Jun 1929 (MARY); Prince George's Co., Chillum, B. Swanton 1590 14 Jun 1939 (MARY); Prince George's Co., Potomac Valley, A. Chase 3766 4 Jul 1907 (MICH); Prince George's Co., Laurel, B. Swanton 1588 14 Jul 1939 (MARY); Prince George's Co., University of Maryland, College, G. Tanaka 17 24 May 1962 (MARY); Somerset Co., Venton, C. Lea 1643 20 May 2000 (MARY); St. Marys Co., Clements, L. B. Smith 5415 7 Jul 1951 (MARY); St. Mary's Co., California, C. Lea 2042 16 Jun 2000 (MARY); Talbot Co., Wittman, C. Lea 1969 10 Jun 2000 (MARY); Washington Co., Greenbrier SP, C. Lea 1767 28 May 2000 (MARY); Washington Co., Washington Monument SP, C. Lea 1757 28 May 2000 (MARY); Wicomico Co., Martins Corner, Wicomico 2994 27 May 1992 (MARY); Worcester Co., Pocomoke State Forest, C. Lea 1610 20 May 2000 (MARY); Worcester Co., Rte. 611, C. Lea 1277 2 Jul 1999 (MARY).

Massachusetts: Amherst, T. Delevoryas s.n. 10 Jun 1949 (NCU); Arlington, Clarence H. Knowlton 28338 22 Jun 1907 (WIS); Bradford Clearing, J. R. Churchill s.n 17 Jun 1914 (VDB);
Cheshire, J. R. Churchill s.n. 20 Jul 1915 (WIS); Greenwich, Flora of the Swift River Watershed, A. S. Goodale s.n. 13 Jul 1931 (OKL); Lexington Woods, F. C. Seymour s.n. 2 Aug 1913 (WIS);
Martha's Vineyard Farm Pond, A. B. Seymour s.n. 1 Jul 1911 (WIS); South Deerfield, R. B. Livingston s.n. 9 Jun 1960 (NCU); Wellesley Simpson, K. M. Wiegand s.n. 25 Jun 1909 (NY);
Winchester, H. H. Bartlett 185 4 Jul 1905 (MICH); Woods Hole, Falmouth, D. F. Brunton 8680
29 Sep 1988 (MICH); Berkshire Co., Lanesboro, J. R. Churchill 82 25 Jul 1916 (WIS); Bristol
Co., J. A. Cushman 1013 2 Jul 1907 (NCU); Bristol Co., Rehoboth, F. C. Seymour 7495 22 Jun 1947 (WIS); Essex Co., Hamilton-Essex, A. B. Seymour s.n. 27 Jun 1908 (KANU); Essex Co.,
Handover, J. Blake 3355 21 Jun 1880 (MICH); Hampden Co., Granville, F. C. Seymour 177 20
Jun 1914 (WIS); Hampshire Co., Hatfield, H. E. Ahles 75633 30 Jun 1972 (KANU); Hampshire
Co., Northampton, H. E. Ahles 86956 25 Jun 1979 (BRIT); Hampshire Co., Northampton, H. E.
Ahles 81777 3 Jul 1976 (TAES); Nantucket Co., Nantucket Island, R. F. Steinauer 807 25 Sep
1999 (NEB); Norfolk Co., Blue Hills Reservation, Nathaniel T. Kidder s.n. 15 Jul 1919 (KANU);

Norfolk Co., Dedbam, H. H. Bartlett 788 4 Jul 1907 (MICH); Norfolk Co., Milton, Nathaniel T. Kidder s.n. 28 Jun 1886 (KANU); Norfolk Co., Neponsed Reservation, H. H. Bartlett 843 14 Jul 1907 (MICH); Norfolk Co., Norfolk, R. A. Ware s.n. 18 Jun 1911 (NCU); Norfolk Co., Sharon, J. Blake s.n. (KANU); Plymouth Co., Manomet, H. E. Ahles 80259 22 Jun 1975 (WIS); Worcester Co., Douglas, B. N. Gates s.n. 14 Jun 1954 (WIS); Worcester Co., Lancaster, F. C. Seymour s.n. 7 Jul 1943 (WIS); Worcester Co., Lancaster, F. C. Seymour 24816 7 Jul 1943 (SMU); Worcester Co., Oxford, B. N. Gates 17707 9 Sep 1957 (WIS); Worcester Co., Spencer, Doris Audette s.n. 5 Jul 1948 (WIS); Worcester Co., Warren, Winnifred C. Gates 31791 18 Jun 1954 (WIS).

Michigan: Hein Lakes Woods, J. Cole 7988 1 Jul 1897 (MICH); Magician Lake Woods, L. M. Umbach 7095 19 Jul 1915 (WIS); Alcona Co., Harrisville Village, R. Garlitz 1533 4 Jul 1986 (MSC); Alger Co., Munising, M. R. Panskar 84242 24 Jul 1984 (MICH); Allegan Co., Allegan, C. W. Bazuin 4681 28 Jun 1942 (MSC); Allegan Co., Bear Creek, C. W. Bazun 7453 18 Jul 1947 (MSC); Allegan Co., Crooked Lake, C. W. Bazun 8873 21 Jun 1952 (MSC); Allegan Co., Heath Twp., G. W. Parmelee s.n. 30 Jul 1950 (MSC); Barry Co., Gun Lake, G. W. Parmelee 83 15 Jun 1954 (MSC); Berrien Co., Harbert, H. T. D. s.n. 22 Aug 1917 (MSC); Berrien Co., Love Creek Nature Center, M. Hamodie 754 7 Aug 1980 (MICH); Berrien Co., Niles, J. Ng 223 17 Jun 1981 (MTMG); Berrien Co., Niles, James Ng 326 1 Jul 1981 (MSC); Berrien Co., Paw Paw Lake, H. T. D. s.n. 15 Aug 1917 (MSC); Calhoun Co., East Fulton, C. R. Hanes 3813 20 Jun 1938 (MICH); Cass Co., Howard Twp., G. W. Parmelee 1603 24 Jul 1950 (MICH); Cass Co., Jefferson Twp, G. W. Parmelee s.n. 25 Jul 1950 (MSC); Cass Co., Magician Lake, F. C. Gates 1318 4 Aug 1906 (MICH); Cass Co., Jones, B. M. Robertson 213 15 Jun 1939 (MICH); Hillsdale Co., Wayside Memorial Roadside Park, P. Fritsch 402 14 Jun 1987 (MICH); Jackson Co., Leoni Twp., G. W. Parmelee 1346 8 Jul 1950 (MSC); Kalamazoo Co., S. R. Crispin 697 6 Aug 1980 (MSC); Kalamazoo Co., Beard, C. R. Hanes s.n. 17 Jul 1940 (MICH); Kalamazoo Co., Fulton, C. R. Hanes 569 1 Aug 1939 (MICH); Kalamazoo Co., Whitman Lake, P. J. Hiqman 611 15 Jun 1994 (MICH); Kent Co., City of Walker, Edward M Smith 3971 16 Jun 1996 (KANU); Kent Co., Courtland Twp., G. W. Parmelee 1295 27 Jun 1950 (MSC); Kent Co., Mud Lake, C. W. Bazuin 11244 17 Jun 1940 (MSC); Kent Co., Oakfield Twp., C. W. Bazuin 1522 5 Jul 1940 (MSC); Kent Co., Wabasis Lake Rd., C. W. Bazuin 1484 4 Jul 1940 (MSC); Lenawee Co., Dover Twp., R. W. Smith 3981 13 Jun 1998 (MICH); Lenawee Co., Madison Twp., R. W. Smith 2552 18 Jun 1988 (MICH); Lenawee Co., Madison Twp., R. W. Smith 2170 4 Jun 1987 (MICH); Lenawee Co., Madison Twp., R. W. Smith 2353 12 Jul 1987 (MICH); Lenawee Co., Raisin Twp., R. W. Smith 1652 26 Jun 1986 (MICH); Lenawee Co., Whaley Rd, R. W. Smith 3968 13 Jun 1998 (MSC); Monroe Co., Lulu, J. A. Churchill s.n. 16 Jun 1964 (MSC); Montcalm Co., Crystal Lake, C. F. Wheeler 291 10 Jul 1900 (MSC); Muskegon Co., Lake Harbor, C. D. McLouth s.n. 20 Jul 1899 (MSC); Oakland Co., Royal Oak, C. Billington s.n. 22 Jun 1918 (MICH); Ottawa Co., Blodgett Camp, C. W. Bazun 1343 26 Jun 1940 (MSC); Ottawa Co., Campbell Site, F. G. Goff 385 10 Jul 1979 (MSC); Ottawa Co., Campbell Site, F. G. Goff 1180 9 Aug 1979 (MSC); Ottawa Co., Grand Haven Twp., C. W. Bazuin 1343 26 Jun 1940 (MSC); Ottawa Co., Grand Haven Twp., C. W. Bazuin 1607 12 Jul 1940 (MSC); Ottawa Co., Grand Haven Twp., C. W. Bazun 511 28 Jun 1939 (MSC); Ottawa Co., Sand Creek, C. W. Bazuin 1556 10 Jul 1940 (MSC); Ottawa Co., Spring Lake, C. W. Bazuin 7812 5 Jul 1948 (MICH); Saginaw Co., Birch Run, R. Garlitz 3591 11 Jun 1992 (MICH); Saginaw Co., Frankenmuth Twp., J. A. Churchill s.n. 9 Jul 1965 (MSC); Schoolcraft Co., Hiawatha National Forest, L. B. Gerdes 963 10 Jul 1995 (MICH); St. Clair Co., Port Huron, C. K. Dodge s.n. 5 Jul 1898 (MICH); St. Joseph Co., Constantine Twp., G. W. Parmelee 1510 18 Jul 1950 (MSC); St. Joseph Co., Three Rvers, A. A. Reznicek 8692 26 Aug 1990 (MICH); St. Joseph Co., Minf School, C. R. Hanes 3921 13 Jul 1939 (MICH); St.Clair Co., Port Huron, C. K. Dodge s.n. 7 Jul 1910 (MICH); Van Buren Co., H. S. Pepoon s.n. 1 Jul 1904 (MSC); Washtenaw Co., Whitmore Lake, C. A. Davis s.n. 16 Jun 1900 (MICH); Wayne Co., Livonia Twp., Steere Schmidt s.n. 1936 (WIS); Wayne Co., Detroit, E. C. Almendinger s.n. 24 Aug 1111 (MICH); Wayne Co., Detroit L. Holzer (MICH); Wayne Co., Detroit, Sister Vincent de Paul s.n. 19 Jul 1948 (KANU); Wayne Co., Detroit, E. C. Aldmendinger s.n. 14 Jul 1877 (MICH); Wayne Co., Sumpter twp., W. W. Brodowicz 945 26 Jun 1991 (MICH).

Mississippi: Chickasaw Co., Van Vleet, C. T. Bryson 19155 27 Apr 2002 (USCH); Grenada Co., Gore Springs, C. T. Bryson 4000 5 Jun 1985 (VDB); Grenada Co., Gore Springs, M. W. Morris 2929 15 Jul 1987 (VDB); Itawamba Co., Fulton, V. E. McNeilus s.n. 4 Jul 1982 (WIS); LaFayette Co., Oxford, Phillip E. Hyatt 6641 9 Jun 1995 (MICH); Lafayette Co., Presbyterian Camp Hopewell, C. T. Bryson 12410 1 Jun 1993 (MICH); Marshall Co., Wall Doxey SP, C. T. Bryson 10006 18 May 1990 (CLEMS); Tishomingo Co., Tennesse Tombigbee Waterway and Natchez Trace Park, C. T. Bryson 13841 25 May 1994 (MICH).

Missouri: Bollinger Co., Dark Cypress Swamp Conservation Area, A. E. Brant 4757 23 Aug 2001 (MO); Butler Co., H. Eggert s.n. 11 Jun 1893 (NCU); Cape Girardeau Co., Cape Girardeau,

Travis Brooks 6923 24 May 1973 (WV); Dunklin Co., Wilhemina State Forest, A. A. Reznicek 9430
22 May 1993 (MICH); New Madrid Co., Des Cyprie Slough, P. M. McKenzie 1468 2 Aug 1994 (MICH); Schuyler Co., Pleasant Grove, B. F. Bush 339 20 May 1900 (NCU); Scott Co., Hwy H, Travis Brooks 7751 18 May 1975 (WV); Scott Co., Blodgett, S. Jones 8532 16 May 1992 (BRIT); Scott Co., General Watkins Conservation Area, P. M. McKenzie 1704 4 Jun 1996 (MICH); Scott Co., Morley Quad, P. M. McKenzie 1995 13 May 2002 (MO); Scott Co., Petite Isle sand prairie, P. M. McKenzie 1482 3 Aug 1994 (MICH); Shannon Co., Angeline Conservation Area, B. Summers 9736 29 May 2001 (MO); Stoddard Co., Holly Ridge Natural Area, J. A. Raveill 2314 10 May 1985 (MICH).

New Hampshire: B. L. Robinson 312 15 Jul 1897 (MSC); Carroll Co., Tomworth, F. L. Steele
s.n. 15 Jul 1950 (GH); Cheshire Co., Alstead, E. F. Williams s.n. 28 Jul 1901 (GH); Cheshire
Co., Hinsdale, D. E. Boufford 6465 29 Jun 1972 (VPI); Cheshire Co., Keene, C. H. Knowlton s.n.
23 Aug 1922 (GH); Cheshire Co., Rindge, C. F Batchelder s.n. 11 Aug 1925 (GH); Cheshire Co.,
Walpole, H. E. Ahles 75362 21 Jun 1972 (NCU); Grafton Co., Hanover, E. F. Williams s.n. 18 Jul
1910 (GH); Hillsboro Co., Pelham, C. A. Weatherby s.n. 6 Jul 1946 (GH); Hillsboro Co., Temple
F. C. Seymour s.n. 9 Aug 1928 (WIS); Hillsborough Co., Hancock, L. Griscom 14575 21 Jun
1931 (GH); Hillsborough Co., Hillsborough, C. F. Batchelder s.n. 28 Jul 1920 (GH); Hillsborough
Co., Mason, C. F. Batchelder s.n. 12 Jul 1916 (GH); Hillsborough Co., Peterborough, W. Deane
s.n. 3 Aug 1909 (GH); Merrimack Co., Shaker Village, V. E. McNeilus s.n. 25 Aug 1983 (WIS);
Rockingham Co., Derry, C. F. Batchelder s.n. 21 Aug 1918 (GH); Rockingham Co., Exeter, A.
S. Pease 30466 24 Jul 1943 (GH); Rockingham Co., Raymond, A. S. Pease 30447 14 Aug 1943 (GH); Rockingham Co., South Hampton, S. K. Harris 25395 20 Oct 1962 (GH); Rockingham Co.,
Windham, S. K. Harris 26873 13 Sep 1964 (GH); Strafford Co., Barrington, A. R. Hodgdon 3760
28 Jun 1941 (GH); Strafford Co., Modburn, A. R. Hodgden 14049 7 Jul 1964 (MTMG).

New Jersey: Atlantic Co., Estell Manor, *G. Moore 1518* 6 Jun 1993 (VDB); Cape May Co., Cape May, *Earl L. Core 5139* 20 Jun 1937 (WV); Cumberland Co., Maurice River Twp., *G. Moore 1512* 6 Jun 1993 (VDB); Cumberland Co., Fairton, *R. R. Dreisbach 4274* 19 Jun 1926 (MICH); Morris Co., Budd Lake, *L. Bowes 1785* 23 Jun 1935 (NYS); Morris Co., Green Village, *R. H. True 663* 4 Jul 1935 (VPI).

New York: Albany Co., Karner, W. J. Crins 8109 24 Jun 1990 (NYS); Albany Co., Westerlo, G. C. Tucker 6629 22 Aug 1991 (NYS); Cattaraugua Co., Alleghany SP, W. P. Alexander s.n. 2

Aug 1930 (NYS); Cattaraugus Co., Conewango, S. J. Smith 22651 18 Jun 1957 (NYS); Cayuga Co., New Hope, N. Hotchkiss 2927 9 Jul 1928 (NYS); Cayuga Co., Lickville, C. Atwood s.n. 26 Jun 1897 (NYS); Chautauqua Co., French Creek, D. Goldman 682 16 Jun 1993 (NYS); Chenango Co., Pharsalia, E. E. Davis 991 19 Jul 1931 (NYS); Columbia Co., Clanerack, R. McVaugh 3990 22 Sep 1935 (NYS); Delaware Co., Delhi, K. L. Brooks 391 27 Jun 1951 (NYS); Delaware Co., Kortright, K. L. Brooks 1568 15 Jun 1952 (NYS); Delaware Co., Town of Kortright, K. L. Brooks 3040 6 Jul 1954 (NYS); Dutchess Co., Stissing Mt. C. H. Peck s.n. (NYS); Franklin Co., Brayton Hollow, S. J. Smith 10337 11 Jul 1951 (NYS); Greene Co., Tannersville Pond, G. R. Proctor 1922 25 Jun 1946 (SMU); Greene Co., Hunter, R. Naczi 8584 3 Jul 2000 (NKY); Hamilton Co., West Stony Creek, S. J. Smith 4469 10 Jul 1948 (NYS); Herkimer Co., J. V. Haberer 1440 15 Jun 1911 (NYS); Herkinns Co., Frankfurt, J. V. H. 3755 21 Jul 1885 (MICH); Jefferson Co., Lorraine, N. Hotchkiss 2503 29 Jun 1927 (NYS); Jefferson Co., Pleasant Lake, N. Hotchkiss 2747 26 Jul 1927 (NYS); Lewis Co., Castorland, N. Hotchkiss 2663 24 Jul 1927 (NYS); Lewis Co., Fort Drum, C. Popolizio 799 20 Jul 1992 (NYS); Madison Co., Lenox, R. L. Crockett s.n. 5 Aug 1939 (NYS); Madison Co., North Brookfield, H. D. House 17611 24 Jun 1930 (NYS); Madison Co., North Wanluis, H. D. House 23141 30 Aug 1935 (NYS); Madison Co., Oneida, H. D. House 16298 4 Jul 1929 (NYS); Myoming Co., Hermitage-Java Center Road, W. A. Matthews 5335 19 Jul 1951 (SMU); Oneida Co., McConnellsville, H. D. House 16275 2 Jul 1929 (NYS); Oneida Co., New London, R. L. Crockett s.n. 12 Jun 1939 (NYS); Oneida Co., Seymour, J. V. Haberer 3899 (NYS); Oneida Co., Taburg, William Rhoades s.n. 18 Jul 1922 (WIS); Oneida Co., Verona, H. D. House A-6072 22 Jun 1918 (NYS); Onondaga Co., Jamesville, H. D. House 31649 7 Aug 1948 (NYS); Orange Co., Black Rock Forest, S. Clemants 3782 1 Aug 1990 (NYS); Orange Co., Harriman SP, J. G. Barbour 983 8 Jul 1993 (NYS); Orange Co., Harriman SP: N of Lake Askoti on 7 Lakes Drive, J. G. Barbour 2304 25 Aug 1994 (NYS); Orange Co., Harriman SP: Southern ridge top of Black Mountain, R. S. Mitchell 9084 21 Jun 1995 (NYS); Oswego Co., Oswego, Baim 5757 19 Jul 1963 (NYS); Oswego Co., Cleveland, H. D. House 15939 26 Jun 1928 (NYS); Oswego Co., Hastings, R. H. True 127 8 Jul 1931 (NYS); Oswego Co., Sandy Creek, N. Hotchkiss 3020 17 Jul 1928 (OKL); Otsego Co., Wharton, S. J. Smith 20478 28 Jun 1956 (NYS); Putnam Co., Town of SE Brewster, K. L. Brooks 2881 12 Jun 1954 (NYS); Rensselaer Co., Berlin, H. D. House 19331 29 Jun 1932 (NYS); Rensselaer Co., Grafton Lakes SP, P. Weatherbee 4527 2 Jul 1997 (NYS); Rensselaer Co., Hoosick, H. E. Ahles 66975 23 Jun 1967 (NCU); Rensselaer Co., Town of Schaghticoke, W. Broderick s.n. 13 Jun 2002

(NYS); Richmond Co., Staten Island, P. Dowell 5909 7 Aug 1909 (VDB); Rockland Co., Bear Mountain SP, J. G. Barbour 907 25 Jun 1994 (NYS); Rockland Co., Harriman SP, J. G. Barbour 2135 30 Jun 1994 (NYS); Rockland Co., Harriman SP, R. S. Mitchell 8806 15 Jun 1994 (NYS); Rockland Co., Nanuet, E. G. Whitney 4092 17 Jun 1935 (NYS); Schenectady Co., Mariaville Lake, T. C. Baim 3366 13 Jul 1950 (NYS); Schenectady Co., Schenectady, T. Baim s.n. 3 Sep 1947 (NYS); Schenectady Co., Schenectady, T. C. Baim s.n. 18 Jun 1941 (NYS); St. Lawrence Co., Potsdam, N. C. Eldblom 2798 5 Sep 1993 (NYS); St. Lawrence Co., Sodom State Forest/Madrid, A. M. Johnson 606 3 Jul 1988 (NYS); Suffolk Co., Brookhaven, R. E. Zaremba 2648 1985 (NYS); Suffolk Co., East Hampton, R. E. Zaremba 2207 30 May 1985 (NYS); Suffolk Co., Fishers Island, G. C. Tucker 6123 26 Jun 1991 (NYS); Suffolk Co., Greenport, Long Island, R. Latham 36289 6 Jun 1959 (NYS); Suffolk Co., Huntington, R. E. Zaremba 2651 1985 (NYS); Suffolk Co., Montauk, R. Latham 5638 2 Jul 1927 (NYS); Suffolk Co., Orient, R. Latham 28237 1 Aug 1938 (NYS); Suffolk Co., Sag Harbour, R. Latham 33255 30 Jun 1955 (NYS); Suffolk Co., West Hills County Park, A Greller s.n. 13 Jun 1992 (NYS); Sullivan Co., Eldred, S. J. Smith 21458 7 Aug 1956 (NYS); Sullivan Co., Long Eddy, S. J. Smith 20313 22 Jun 1956 (NYS); Sullivan Co., Rondout Reservoir, S. J. Smith 20425 23 Jun 1956 (NYS); Sullivan Co., Town of Callicoon, K. L. Brooks 6130 21 Jun 1975 (NYS); Tompkins Co., Townley Swamp, A. Gershoy 7723 7 Aug 1917 (MICH); Tompkins Co., Besemer, R. T. Clausen 7122 5 Aug 1947 (NYS); Tompkins Co., Dryden, K. M. Wiegand X19667 20 Jun 1937 (WIS); Ulster Co., Town of Olive, J. Bierhorst 149 21 Jun 1996 (NYS); Ulster Co., Warwarsing, H. F. Dunbar 1124 16 Jul 1958 (NYS); Ulster Co., Woodland, S. J. Smith 6835 16 Jun 1950 (NYS); Warren Co., Brayton, H. D. House 29250 23 Jun 1943 (OKL); Warren Co., Warrensburg, E. G. Whitney 4168 26 Jun 1935 (NYS); Washington Co., Lake George, H. D. House 28608 9 Jun 1942 (NYS); Westchester Co., Mount Kisco, Francis W. Pennell 7179 25 Jun 1916 (KANU); Westchester Co., North Castle, Cranberry Lake County Park, R. E. Zaremba 3020 9 Jun 1986 (NYS).

North Carolina: Alleghany Co., Little Glade Branch, P. D. McMillan 2445 8 Jun 1997 (USCH); Avery Co., Banners Elk, H. E. Ahles 43588 17 Jun 1958 (NCU); Avery Co., Hanging Rock, A. E. Radford 44088 1 Jul 1961 (USCH); Bertie Co., Windsor, H. E. Ahles 41219 29 May 1958 (NCU); Cherokee Co., Patrick, K. E. Rogers 41622 18 Jun 1968 (SMU); Chowan Co., Valhalla, H. E. Ahles 39880 9 May 1958 (NCU); Edgecombe Co., Sharpsburg, A. A. Reznicek 34009 27 May 1958 (NCU); Gates Co., White Oak Pocosin J. A. Duke 830 30 May 1958 (NCU); Graham

Co., Joyce Kilmer Memorial Forest, B. A. Ford 8929 17 May 1989 (NYS); Halifax Co., Halifax, H.
E. Ahles 17151 19 Jul 1956 (NCU); Henderson Co., Flat Rock, F. R. Fosberg 18827 17 Jun 1942 (NCU); Hertford Co., Harrelsville, H. E. Ahles 41706 30 May 1958 (NCU); Macon Co., Coweeta Hydrologic Lab, Phillip E. Hyatt 8635 28 May 1999 (MICH); Macon Co., Wayah Bald, D. E. Boufford 16576 20 Jun 1975 (NCU); Madison Co., Fairview Methodist Church, J. B. Nelson 16,618 16 Jun 1995 (MICH); Madison Co., Hot Springs, J. B. Nelson 16618 16 Jun 1995 (USCH); Mitchell Co., Spruce Pine, H. E. Ahles 43190 16 Jun 1958 (NCU); Northampton Co., US 158, H. E. Ahles 41768 31 May 1958 (NCU); Pasquotank Co., US 17-158, H. E. Ahles 44412 25 Jun 1958 (NCU); Surry Co., Low Gap, A. E. Radford 13149 23 Jun 1956 (NCU); Transylvania Co., Fork River Bridge, A. E. Radford 44592 10 Jun 1962 (WV).

Ohio: Brown Co., Sardinia, Michael A. Vincent 4683 22 May 1991 (WV); Cuyahoga Co.,
Westlake, A. W. Cusick 31060A 23 Jun 1993 (GH); Cuyahoga Co., Highland Heights, Suneeti Jog 483 18 Jun 2001 (KANU); Erie Co., Plum Brook Station, A. W. Cusick 21,723 22 Jun 1982 (MICH); Erie Co., Sandusky, A. W. Cusick 31851 14 Jul 1994 (VPI); Lake Co., Little Mountain, J. M. Greenman 147 2 Aug 1897 (GH); Lucas Co., Whitehouse Quad., A. W. Cusick 31,090 12 Jul 1993 (MICH); Portage Co., Gott Fen Preserve, A. W. Cusick 23,563 19 Jun 1984 (MICH); Portage Co., Nelson, T. S. Cooperrider 5951 27 Jun 1960 (NCU); Portage Co., Nelson-Kennedy Ledges SP, A. W. Cusick 25,567 21 Jul 1986 (MICH); Summit Co., Singer A. W. Cusick 10090 4 Jul 1969 (NCU); Wood Co., Steidtmann Sanctuary, A. W. Cusick 21,780 7 Jul 1982 (MICH).

Oklahoma: Atoka Co., Boehler Community, B. L. Lipscomb 1483 15 May 1976 (MICH); Atoka Co., Sand Hills, J. Taylor 33133 28 May 1985 (BRIT); LeFlore Co., State Line Historical Site, C. T. Bryson 4306 10 May 1986 (VDB); Leflore Co., Honobia, A. A. Reznicek 9352 19 May 1993 (MICH); McCurtain Co., Battiest site, L. K. Mcgrath 17845 11 May 1990 (OKL); McCurtain Co., Battiest, J. Taylor 26357 4 Jun 1978 (SMU); McCurtain Co., Battiest site, L. K. Magrath 17845 11 May 1990 (MICH).

Pennsylvania: West Plula, A. MacElwee s.n. 5 Jun 1892 (GH); Adams Co., Michaux SP, J.
E. Benedict 2854 4 Jul 1934 (VPI); Bedford Co., Wolf Swamp Watershed, Homer Duppstadt s.n.
12 Jun 1970 (WV); Bedford Co., Robinsonville, David Berkheimer 9787 16 Jun 1948 (KANU);
Berks Co., McKnights Gap, D. Berkheimer 2555 12 Jun 1941 (GH); Berks Co., Fleetwood, W.
C. Brumbach 433-33 13 Jul 1933 (GH); Berks Co., Olney Furnace, H. Wilkens 5843-a 10 Jun
1939 (GH); Berks Co., Reading, W. C. Brumbach 293-32 9 Jun 1932 (GH); Berks Co., Reading,

H. Wilkens 115 15 Jun 1929 (GH); Bradford Co., Albany R. Naczi 4129 14 Jun 1994 (MICH); Bradford Co., Burlington, H. A. Wahl 19083 18 Jun 1959 (NCU); Bradford Co., Le Roy, H. A. Wahl 1057 22 Jun 1941 (NEB); Bradford Co., New Albany, R. Naczi 4129 14 Jun 1994 (NKY); Bradford Co., Franklindale, R. Naczi 2605 15 Jun 1990 (MICH); Center Co., Coburn, H. A. Wahl s.n. 13 Jun 1934 (WIS); Centre Co., Ingleby, H. A. Wahl 25166 17 Jun 1936 (NCU); Centre Co., State Game Lands #176, P. E. Rothrock 564 19 Jun 1975 (MICH); Chester Co., Strafford, J. W. Adams 765 4 Jun 1927 (VPI); Chester Co., Kemblesville, George R Proctor 1840 15 Jun 1946 (KANU); Chester Co., Landenberg, E. C. Earle 5109 27 Jun 1958 (SMU); Clearfield Co., Ansonville, E. B. Erle 2347 13 Jun 1957 (NYS); Clinton Co., Rosecrans Bog Natural Area, R. Naczi 7904 4 Jul 1995 (MICH); Columbia Co., West Branch Fishing Creek, F. R. Fosberg 16004 5 Sep 1938 (GH); Delaware Co., Darby Creek, F. J. Hermann 3182 7 Jun 1932 (MICH); Delaware Co., Ringham, R. R. Dreisbach 14929 16 Jun 1923 (MICH); Delaware Co., Havenford, H. E. Stone s.n. 3 Jul 1926 (SMU); Delaware Co., Eagle Road, J. M. Fogg Jr. 2192 11 Jun 1927 (GH); Fayette Co., Ohiopyle, J. Bright 8407 26 Jun 1934 (SMU); Forest Co., Greene Township, D. E. Boufford 21102 17 Jun 1979 (NCU); Jefferson Co., Heath Twp., A. W. Cusick 31,027 14 Jun 1993 (MICH); Lackawanna Co., Old Forge, P. E. Rothrock 572 21 Jun 1975 (NCU); Lancaster Co., Blainsport, C. S. Keener 3575 26 Jun 1979 (MICH); Lancaster Co., Jenkins Corner, G. L. Miller 7-46 19 Oct 1963 (NCU); Lawrence Co., Portersville, F. J. Hermann 9518 29 Jun 1938 (GH); Lebanon Co., Twin Grove Park, Carl S. Keener 131 11 Jun 1959 (WV); Lehigh Co., Kuhn's Woods, H. W. Pretz 12873 18 Jul 1926 (MICH); Luzerne Co., Nuangola, P. E. Rothrock 597 22 Jun 1975 (NCU); Maercer Co., West Salem Twp., A. W. Cusick 23,657 11 Jul 1984 (MICH); Monroe Co., Pocono Plateau, R. R. Tatnall 4266 29 Jun 1939 (GH); Philadelphia Co., Fox Chase, F. J. Hermann 3155 4 Jun 1932 (OKL); Philadelphia Co., West Philadelphia, F. J. Hermann 3147 2 Jun 1932 (GH); Pike Co., Delaware State Forest, R. Naczi 4873 1 Jul 1995 (MICH); Pike Co., Greentown, R. Naczi 4873 1 Jul 1995 (NKY); Snyder Co., Meiserville, P. E. Rothrock 513 13 Jun 1975 (MICH); Somerset Co., Berlin. L. E. McKinney 2201 13 Jun 1986 (VDB); Sullivan Co., Eaglesmere, T. S. Githens s.n. 4 Aug 1945 (WV); Susquehanna Co., Susquehanna, J. A. Graves s.n. 1 Jul 1897 (NEB); Wayne Co., Cold Spring, H. A. Wahl 14409 24 Jul 1954 (SMU).

Rhode Island: Newport Co., Tiverton, S. N. F. Sanford s.n. 11 Jun 1912 (GH); Providence
Co., Glocester, F. C. Seymour 19,216 14 Jun 1961 (SMU); Providence Co., North Smithfield, F.
W. Hunnewell 18680 10 Jul 1947 (GH); Providence Co., Providence, J. F. Collins s.n. 19 Jun

1892 (GH); Washington Co., North of Ashaway, Hopkinton, M. L. Fernald s.n. 1 Sep 1919 (GH);Washington Co., Wyoming, H. E. Ahles 79151 19 Aug 1974 (WIS).

South Carolina: Greenville Co., Table Rock Reservoir, S. R. Hill 23492' 22 Jun 1992 (CLEMS); Oconee Co., Big Bend Road, L. L. Gaddy s.n. 30 May 1986 (CLEMS); Oconee Co., Whitewater Falls, L. L. Gaddy s.n. 13 Jun 1987 (CLEMS); Pickens Co., Cane Creek Watershed, L. Waldrop W-277 19 May 1998 (MICH); Pickens Co., NC-SC State line, H. E. Ahles 14269 6 Jun 1956 (KANU); Pickens Co., Wadakoe Mountain, P. D. McMillan 6327 30 Apr 2002 (CLEMS); Pickens Co., Wadakoe Mountain, P. D. McMillan 6315 30 Apr 2002 (CLEMS).

Tennessee: Bledsoe Co., Fall Creek Falls SP, C. T. Bryson 11826 27 Jun 1992 (VDB); Blount Co., Cades Cove, R. D. Thomas s.n. 24 Jul 1965 (NCU); Blount Co., Great Smoky Mountains NP, R. E. Shanks 2301 27 Jun 1943 (VDB); Blount Co., Great Smoky Mountains NP, D. E. Boufford 22891 28 May 1982 (BRIT); Blount Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 21 Jun 1980 (WIS); Blount Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 19 May 1984 (WIS); Blount Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 15 Jun 1982 (WIS); Blount Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 14 Jun 1981 (WIS); Blount Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 12 Jul 1981 (WIS); Blount Co., Great Smokey Mt. NP, V. E. McNeilus s.n. 2 Aug 1980 (WIS); Blount Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 21 Jun 1980 (WIS); Cannon Co., Short Mt., L. E. McKinney 322 15 Jun 1981 (VDB); Carroll Co., New Hope Church, H. R. DeSelm s.n. 22 Jun 1993 (EKY); Carter Co., Ripshin Bog, P. Somers s.n. 15 Jul 1982 (VDB); Cocke Co., Del Rio, J. A. Churchill 88037 8 Jul 1988 (MSC); Cocke Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 22 Jun 1980 (WIS); Coffee Co., Manchester, R. Kral 76194 10 May 1989 (VDB); Cumberland Co., Cressville Airport, R. Kral 42762 21 May 1971 (VDB); Cumberland Co., Fairfield Glades, R. Kral 82539 29 May 1993 (VDB); Cumberland Co., Catoosa Game Refuge, L. J. Uttal 8053 12 Jun 1971 (VPI); Cumberland Co., Cressville Airport, R. Kral 42762 21 May 1971 (EKY); Fentress/Morgan Co., Clear Fork River, D. D. Horn 336 27 May 1979 (VDB); Franklin Co., Sewanee, Anonymous s.n. 4 Jul 1942 (VDB); Grainger Co., Hwy 25E, A. A. Reznicek 9540 22 Jun 1993 (MICH); Grundy Co., Monteagle, R. Kral 46503 17 May 1972 (VDB); Grundy Co., Collins Quad, W. R. Jones 4785 22 May 1987 (EKY); Grundy Co., Savage Gulf Natural Area, T. S. Patrick 253 11 Jul 1977 (VDB); Hickman Co., Bondswitch, R. Kral 73999 6 Jun 1987 (VDB); Humphreys Co., Cuba Landing, R. Kral 80423 10 May 1992 (VDB); Jackson Co., Gainsboro, V. E. McNeilus 94-225 19 May 1994 (WIS); Marion Co., Fiery Gizzard Gorges, R. C. Clark 1873 16 May 1965 (NCU);

Monroe Co., Exit 62 along I-75, V. E. McNeilus 92-445 13 Jun 1992 (WIS); Monroe Co., Tellico, V. E. McNeilus s.n. 16 May 1982 (WIS); Monroe Co., Tellico Plains, J. A. Churchill 93321 11 May 1993 (MICH); Montgomery Co., Guthrie, R. Kral 76639 21 Jun 1989 (VDB); Montgomery Co., Guthrie, R. Kral 52696 16 May 1974 (VDB); Montgomery Co., Clarksville, E. W. Chester 81-296 2 Jun 1981 (NCU); Montgomery Co., Smith Branch Recreation Area, E. W. Chester 81-296 2 Jun 1981 (VDB); Morgan Co., Brewstertown Rd., R. Kral 84766 23 May 1995 (VDB); Morgan Co., Wartburg, R. Kral 83487 12 May 1994 (VDB); Morgan Co., Wartburg, S. Jones 4971 24 May 1990 (MICH); Morgan Co., Gatewood bridge area, V. E. McNeilus s.n. 20 Jun 1982 (WIS); Morgan Co., Rt. 27, V. E. McNeilus 89-375 10 Jun 1989 (WIS); Morgan Co., Lansing, V. E. McNeilus 90-363 19 Jun 1990 (WIS); Morgan Co., Rockwood, V. E. McNeilus 94-288 29 May 1994 (WIS); Morgan Co., Rugby, J. K. U. 843 28 May 1934 (MICH); Morgan Co., Cookeville, R. Kral 82542 29 May 1993 (MICH); Morgan Co., Vicinity of Lilly Bridge, V. E. McNeilus 90-363 19 Jun 1990 (VDB); Overton Co., East Branch of Obey River, V. E. McNeilus 93-1131 22 Jun 1993 (WIS); Overton Co., Livingston, V. E. McNeilus 94-277 31 May 1994 (WIS); Putnam Co., Monerey, V. E. McNeilus 89-370 10 Jun 1989 (WIS); Rhea Co., Whites Creek, V. E. McNeilus 88-152 9 Jun 1988 (WIS); Rhea Co., Dayton, V. E. McNeilus s.n. 23 May 1982 (WIS); Sequatchie Co., Dunlap, R. Kral 77728 29 May 1990 (VDB); Sevier Co., Chilhowee Mt., R. D. Thomas s.n. 9 Jun 1965 (SMU); Sevier Co., Elkmont Campground, GSMNP, B. A. Ford 8942 18 May 1989 (NYS); Sevier Co., Gatlinburg, Ken E Rogers 34018 22 May 1965 (KANU); Sevier Co., Great Smoky Mt. NP, V. E. McNeilus 90-270 6 Jun 1990 (VDB); Sevier Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 24 May 1981 (WIS); Sevier Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 26 Jul 1980 (WIS); Sevier Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 22 May 1983 (WIS); Sevier Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 24 May 1981 (WIS); Unicoi Co., Beauty Spot Mt., A. J. Sharp 43469 21 Jun 1969 (SMU); Unicoi Co., Ernestville, J. A. Churchill 92-189 10 Aug 1992 (MSC); Wayne Co., Natchez Trace, R. Kral 55470 18 May 1975 (VDB); White Co., Sparta, V. E. McNeilus s.n. 1 Jun 1980 (WIS).

Vermont: Bennington Co., Rupert, M. P. Marshall 1219 17 Jul 1976 (NCU); Burlington
Co., North Pownal, M. P. Marshall 1048 12 Aug 1975 (NCU); Burlington Co., Rupert, M. P.
Marshall 1205 17 Jul 1976 (NCU); Chittenden Co., Williston, C. H. Knowlton s.n. 12 Jul 1945
(GH); Rutland Co., Middleton Springs, C. H. Knowlton s.n. 13 Jun 1918 (GH); Windham Co.,
Brookline, L. A. Wheeler 84401 17 Jun 1911 (GH); Windham Co., Jamaica, L. A. Wheeler 18

11 Jul 1913 (GH); Windham Co., Marlboro, R. J. Eaton 5849 9 Sep 1965 (GH); Windham Co.,
Brookline, L. A. Wheeler s.n. 17 Jun 1911 (GH); Windham Co., Townshand, L. A. Wheeler s.n.
23 Jun 1912 (GH); Windsor Co., Woodstock, E. M. Kittredge B1056 18 Jul 1928 (GH).

Virginia: City of Newport News, P. K. Appler 552 10 May 1973 (NCU); Albermarle Co., Keene, C. E. Stevens 1132 22 Jun 1969 (NCU); Albermarle Co., Keene, C. E. Stevens 2225 25 Jun 1970 (VPI); Albermarle Co., Scottsville, C. E. Stevens 1899 23 May 1970 (VPI); Alleghany Co., McGraw's Gap., R. Kral 9329 6 Aug 1959 (VDB); Arlington Co., Washington-Lee High School, J. Higginson 125 25 May 1946 (MARY); Bath Co., Armstrong, C. E. Stevens 4018 7 Aug 1971 (VPI); Bath Co., Armstrong, C. E. Stevens 3663 3 Jul 1971 (VPI); Caroline Co., Golansville, T. Bradley 19122 28 May 1983 (NCU); Carroll Co., Mt. Airy, J. R. Manhart 311 30 Apr 1981 (MICH); Charles City Co., Ruthville, D. M. E. Ware 2340 20 Jun 1969 (VDB); Craig Co., New Castle, T. F. Wieboldt 5684 17 Jul 1985 (MICH); Dickenson Co., Breaks SP, R. Kral 12700 14 Jun 1961 (VDB); Fauquier Co., Pond Mt., H. A. Allard (WV); Fauquier Co., Western slope of Bull Run Mountains, H. A. Allard 1581 24 May 1936 (VPI); Fauquier Co., Western slope of Bull Run Mountains, H. A. Allard 5035 12 Jun 1938 (VPI); Fauquier Co., Western slope of Bull Run Mountains, H. A. Allard 744 30 Jun 1935 (VPI); Floyd Co., Check, G. P. Frank 615 17 Jul 1981 (VPI); Giles Co., Mt. Lake, R. Kral 10682 29 Jun 1960 (VDB); Giles Co., Mt. Lake, R. Kral 10657 29 Jun 1960 (VDB); Giles Co., White Pine Lodge, R. E. Shanks 15254 13 Jun 1950 (VDB); Giles Co., Big Stoney Creek and Applachian Trail, G. P. Frank 578 24 Jun 1981 (VPI); Giles Co., Fork Mountain, L. J. Uttal 10436 11 Jun 1974 (NCU); Giles Co., Mt. Lake Biological Station, L. J. Mussleman 4307 21 Jun 1971 (NCU); Giles Co., Mt. Lake, R Kral 10682 29 Jun 1960 (NCU); Giles Co., Mt. Lake, R Kral 10657 29 Jun 1960 (NCU); Grayson Co., Whitetop, T. F. Wieboldt 8925 22 Jun 1994 (VPI); James City Co., College of William and Mary, A. C. Barans 814 14 May 1969 (NCU); King and Queen Co., Helmet, T. Bradley 23645 24 Jun 1990 (CLEMS); King and Queen Co., Salvia, T. Bradley 23686 24 Jun 1990 (CLEMS); King George Co., Caledon SP, D. M. E. Ware 8175 8 Jun 1983 (CLEMS); Lancaster Co., Devil's Bottom, T. Weldy 376 17 May 1994 (BRIT); Loudoun Co., Diabase, H. A. Allard 21457 24 May 1953 (WV); Mathews Co., North, M. van Montfrans 321 24 May 1979 (BRIT); Montgomery Co., Blacksburg, T. F. Wieboldt 10283 28 Jul 1999 (VPI); Nansemond Co., Blackwater River, H. E. Ahles 58154 22 Jun 1963 (NCU); Nansemond Co., Blackwater River, H. E. Ahles 58178 22 Jun 1963 (NCU); New Kent Co., Ware Creek, M. S. Gillespie 709 29 May 1970 (NCU); Orange Co., Rhoadesville, T. Bradley 19216 4 Jun

1983 (NCU); Orange Co., Steets Shop, T. Bradley 23236 21 May 1990 (CLEMS); Powhatan Co.,
Rt. 671, C. M. Corcoran 612 4 Jun 1976 (NCU); Pulaski Co., Radford Army Munitions Plant, New
River, T. F. Wieboldt 10009 9 Jul 1998 (VPI); Roanoke Co., Haven's WMA, Ft. Lewis Mt., N. A.
Mason s.n. 28 May 1991 (VPI); Shenandoah Co., Peters Run, A. M. Harvill 21745 24 Jun 1969 (NCU); Spotsylvania Co., Fredericksburg, Hugh H. Iltis 2803 16 Jun 1947 (WIS); Spottsylvania
Co., Fredericksburg, Hugh H. Iltis 2814 16 Jun 1947 (WIS); Stafford Co., Mt. Joy, C. L. Kelloff 550 29 May 1988 (USCH); Tazewell Co., Cedar Bluff, R. Kral 12919 29 Jun 1961 (VDB); William
Co., Occoquan Bay National Wildlife Refuge, M. T. Strong 1608 30 May 1998 (MICH); Wythe
Co., Little Walker Mt., T. F. Wieboldt 6385 10 Jun 1987 (MICH).

West Virginia: Barbour Co., Nestorville, Earl L. Core 5921 14 Jul 1937 (WV); Fayette Co., Manns Creek, William N. Grafton s.n. 4 Jun 1995 (WV); Fayette Co., Stonecliff, Violet S. Phillips s.n. 6 Jul 1968 (WV); Fayette Co., Cunard, Dale W. Suiter DWS 662 18 Jun 1993 (WV); Grant Co., Gormania, William N. Grafton s.n. 16 Jun 1995 (WV); Grant Co., Mt. Storm, Earl L. Core 6036 15 Jul 1937 (WV); Kanawha Co., Camp Camelot, Emily Williams s.n. 25 May 1980 (WV); Kanawha Co., Kanawha State Forest, Margaret E. Denison 68-161 25 May 1968 (WV); Kanawha Co., Kanawha State Forest, Margaret E. Denison 67-92 19 Jul 1967 (WV); Kanawha Co., Kanawha State Forest, Margaret E. Denison 67-87 14 Jul 1967 (WV); Monongalia Co., SRC II site, Forest L. Oserow 21342 28 Jun 1979 (WV); Monongalia Co., Greer, William N. Grafton s.n. 4 Jul 1995 (WV); Monongalia Co., Cheat View, Gene M. Silberhorn 1395 29 May 1965 (WV); Morgan Co., Cacapon SP, Wm. Homer Duppstadt s.n. 1 Jun 1977 (WV); Morgan Co., Brosius, R. M. Downs 2737 1 Jul 1968 (NCU); Morgan Co., Cacapon Mt. SP, T. F. Wieboldt 6212 13 Aug 1986 (WIS); Nicholas Co., Meadow River, William N. Grafton s.n. 13 Jun 1992 (WV); Preston Co., Allbright, William N. Grafton s.n. 27 Jun 1988 (WV); Preston Co., WVU Forest, William N. Grafton s.n. 11 Jul 1997 (WV); Raleigh Co., Fairdale, William N. Grafton s.n. 30 Jun 1974 (WV); Randolph Co., Dolly Sods Mt., H. A. Davis 4383 25 Jun 1941 (WV); Randolph Co., Huttonsville, Eugene E. Hutton s.n. 1 Jun 1941 (WV); Randolph Co., Huttonville, E. E. Hutton s.n. 30 Jun 1960 (VPI); Randolph Co., Monangahela National Forest, B. Walters 611 8 Jul 1997 (MICH); Tucker Co., Clover Run, William N. Grafton s.n. 9 Jun 1995 (WV); Tucker Co., Camp Kidd near St. George, William N. Grafton s.n. 16 Jun 1997 (WV); Tucker Co., Canaan Valley, H. A. Allard 11439 30 Jul 1945 (WV); Tucker Co., Canaan Valley Earl L. Core 2875 29 Jun 1931 (WV); Upshur Co., Buckhannon, G. B. Rossbach 1374 21 Jun 1959 (WV); Upshur Co., Little Kanwha River, H. A.

Davis 6991 8 Jun 1945 (WV); Webster Co., Cowen, William N. Grafton s.n. 11 Jun 1998 (WV);
Webster Co., Curtin, A. W. Cusick 28888 31 May 1990 (WV).

Wisconsin: Kenosha Co., Berryville, S. C. Wadmond 3088 14 Jul 1900 (WIS); Waukesha Co., Upper Martins Woods, Theodore S. Cochrane 10035 19 Jun 1982 (WIS); Waushara Co., Little Silver Creek, Katherine D. Rill 6091 13 Aug 1983 (WIS).

Carex virescens. Canada. Ontario: Elgin Co., Aldborough Township, M. J. Oldham 15367
9 Aug 1993 (MICH); Elgin Co., Straffordville, M. J. Oldham 12782 16 Jun 1991 (MICH); Elgin Co., Reive Bog, M. J. Oldham 14910 14 Jun 1993 (MICH); Elgin Co., Rodney, M. J. Oldham 15300 29 Jul 1993 (MICH); Elgin Co., Eagle, M. J. Oldham 15914 7 Oct 1993 (MICH); Elgin Co., Bayham Township, M. J. Oldham 12782 16 Jun 1991 (WIS); Elgin Co., Clearville, V. R. Brownell 83-401 10 Jul 1983 (CAN); Elgin Co., Goldie's Fern Woods, I. D. Macdonald 17941 9 Sep 1986 (MICH); Elgin Co., Port Butwell Provincial Park, M. J. Oldham 10947 6 Jun 1990 (MICH); Elgin Co., West Lorne, M. J. Oldham 9480 26 Jun 1989 (MICH); Elgin Co., West Lorne, Jane M. Bowles KE861399 3 Jul 1986 (MICH); Essex Co., Learnington, M. J. Oldham 4036 2 Aug 1983 (MICH); Haldimand-Norfolk Co., Deer Creek Conservation Area, D. A. Sutherland 7123 18 Jun 1986 (CAN); Kent Co., Clearville, V. R. Brownell 83-462 11 Jul 1983 (CAN); Middlesex Co., Skunk's Misery, M. J. Oldham 14870 7 Jun 1993 (MICH).

U. S. A. F. F. Forbes 744 29 Jul 1900 (OKL).

Alabama: Lauderdale Co., Zip City, R. Kral 82304 19 May 1993 (VDB); Lawrence Co.,
Bankhead National Forest, C. T. Bryson 7589 8 May 1988 (VDB); Madison Co., Monte Sano SP,
C. T. Bryson 2050 27 May 1978 (VDB); Madison Co., Huntsville, C. T. Bryson 3538 23 May
1983 (MICH); Madison Co., Huntsville, C. T. Bryson 3528 22 May 1983 (MICH); Madison Co.,
Huntsville, C. T. Bryson 3540 23 May 1983 (MICH); Madison Co., Huntsville, Charles T. Bryson
3897 11 May 1985 (WIS); Madison Co., Huntsville, C. T. Bryson 2039 27 May 1978 (VDB);
Madison Co., Monte Sano Mt., J. R. Manhart 264 9 May 1981 (MICH); Madison Co., Monte Sano
Mt., James R. Manhart 264 9 May 1981 (WIS); Madison Co., Monte Sano Mt., C. T. Bryson 2890
8 May 1980 (GA); Madison Co., Monte Sano SP, C. T. Bryson 3897 11 May 1985 (VDB); Winston
Co., Lawrence County Rd, S. Jones 4855 18 May 1990 (WIS); Winston Co., Sipsey River Rec.
Area, C. T. Bryson 4380 23 May 1986 (VDB).

Connecticut: Fairfield Co., Danbury , L. J. Mehrhoff 12644 31 May 1989 (MICH); Fairfield Co., Easton, E. H. Eames s.n. 30 Jun 1901 (WIS); Fairfield Co., Huntington, E. H. Eames s.n. 25

Jun 1902 (GH); Fairfield Co., North Stamford, P. S. Green 138/63 23 Jun 1963 (GH); Hartford Co., Hartland, C. A. Weatherby 5326 9 Jul 1934 (GH); Hartford Co., New Britain - Plainsville, C. Wright s.n. 7 Jul 1882 (GH); Hartford Co., Southington, L. Andrews 558 27 Jun 1898 (GH); Hartford Co., Southington, A. R. Hodgdan s.n. 14 Jul 1964 (MTMG); Litchfield Co., Watertown, A. E. Blewitt 543 7 Jun 1910 (GH); Middlesex Co., East Haddaw, C. A. Weatherby 2185 23 Jun 1907 (GH); New Haven Co., Derby, C. A. Weatherby D2037 4 Jul 1920 (GH); New Haven Co., Guilford, W. R. Dudley s.n. 9 Jul 1904 (GH); New Haven Co., Oxford, E. B. Harger 6945 19 Jul 1917 (GH); New London Co., Voluntown, L. J. Mehrhoff 15620 12 Jun 1992 (MICH); Tolland Co., Bolton, C. A. Weatherby s.n. 12 Jul 1913 (GH); Windham Co., Pomfret, C. A. Weatherby 5188 24 Jun 1923 (GH); Windham Co., Windham, C. A. Weatherby 534 16 Jul 1932 (SMU); Windham Co., Windham, C. A. Weatherby s.n. 16 Jul 1932 (NCU).

Delaware: New Castle Co., Brandywine woods, W. M. Canby s.n. 18 Jun 1896 (NCU); New Castle Co., Mt Cuba, A. C. s.n. 22 Jun 1876 (MARY).

District of Columbia: Fairfax Co., Dead Run Area, E. H. Walker 538 11 May 1930 (MARY). Georgia: Dade Co., Cloudalnd Canyon SP, J. R. Manhart 363 12 Jun 1981 (MICH); Dade Co., Cloudland Canyon, A. Cronquist 5160 8 May 1948 (GA); Dawson Co., Etowah River Basin, L. Kruse 02-131 8 May 2002 (GA); Dawson Co., Etowah River Basin, L. Kruse 02-131 8 May 2002 (GA); Fannin Co., Cooper Creek Recreation Area, E. W. Wood 17326 15 Jul 1975 (NCU); Gilmer Co., Frosty Mt., Phillip E. Hyatt 11476 12 Jul 2003 (GA); Lumpkine Co., Etowah River Basin, L. Kruse 01-595 8 Aug 2001 (GA); Murray Co., Chattahoochee National Forest, D. E. Boufford 22857 17 May 1982 (VDB); Murray Co., Grassy Mt., J. A. Moore 1035 11 Aug 2001 (GA); Murray Co., Grassy Mt., J. A. Moore 685 11 May 2001 (GA); Murray Co., Grassy Mt., J. A. Moore 1148 22 Sep 2001 (GA); Rabun Co., Burton, A. Cronquist 5533 24 Jul 1948 (VDB); Rabun Co., Ellicott Rock, D. M. DuMond 1084 31 May 1968 (GA); Rabun Co., Black Rock Mt. SP, A. A. Reznicek 9002 25 May 1992 (MICH); Rabun Co., Pine Mt., J. A. Churchill 91-268 14 Jun 1991 (MSC); Rabun Co., Warwoman WMA, Milsted 744 22 May 1996 (GA); Rabun Co., Warwoman WMA, Milsted 845 12 Jun 1996 (GA); Rabun Co., Warwoman WMA, Milsted 829 12 Jun 1996 (GA); Stephens Co., Toccoa, D. E. Boufford 16846 30 Jun 1975 (NCU); Union Co., Wolfpen Gap, A. Cronquist 4519 1 Jun 1947 (SMU); Union Co., Coosa Bald, Cooper Creek WMA, L. Chaffin 569B 18 May 1987 (GA).

Illinois: Alexander Co., Gale, R. A. Evers 90439 16 May 1967 (NCU).

Indiana: Crawford Co., Grantsburg, C. C. Deam 27,825 8 Jun 1919 (MICH); Fountain Co., Portland Arch Nature Preserve, A. W. Cusick 25,321 3 Jun 1986 (MICH); Marion Co., Harrison, H. H. Bartlett s.n. 9 Jun 1903 (MICH); Montgomery Co., Shades, D. Beal s.n. 25 Aug 1890 (MSC).

Kentucky: Bath Co., Pergram Creek, R. Hannan 6527 26 May 1981 (EKY); Bell Co., Pineville, R. Naczi 6700 25 Jun 1997 (NKY); Carter Co., Grahn, A. W. Cusick 26,526 10 Jun 1987 (VDB); Clay Co., Bush, A. A. Reznicek 9479 28 May 1993 (MICH); Clay Co., Manchester, John W. Thieret 55266 23 Jun 1984 (NKY); Cumberland Co., Burkesville, R. Naczi 7413 17 Jun 1998 (MICH); Elliott Co., Bruin, A. W. Cusick 30211 15 May 1992 (VPI); Estill Co., Lily Mountain, R. Hannan 6993 10 Jun 1981 (EKY); Estill Co., Irvine, R. Naczi 7816 12 May 1999 (MICH); Fulton Co., Wilson Hill, R. Athey 2306 24 May 1973 (VDB); Garrard Co., Maywoods Environmental and Educational Laboratory, D. A. Godbey 161 26 May 1983 (EKY); Hardin Co., Summit, R. Cranfill 717 26 May 1978 (MICH); Hardin Co., Elizabethtown, R. Naczi 6514 15 Jun 1997 (NKY); Hardin Co., Muldraught's Hill, R. Cranfill 689 26 May 1978 (MICH); Harlan Co., Big Black Mt., T. H. Kearney, Jr. s.n. (MTMG); Harlan Co., Harlan, Landon E. McKinney 5003 20 May 1992 (NKY); Harlan Co., Harlan, R. Naczi 6735 26 Jun 1997 (NKY); Harlan Co., Pine Mt., L. E. McKinney 5003 20 May 1992 (EKY); Laurel Co., Boone National Forest, L. E. McKinney 2192 31 May 1986 (VDB); Laurel Co., Rock Creek Gorge and Uplands, R. L. Thompson 89-1410 4 Jul 1989 (EKY); Lawrence Co., Webbville, John W. Thieret 53343 23 May 1993 (NKY); Lee Co., Hwy 11, Landon E. McKinney 5054 23 May 1992 (NKY); Lee Co., Cathedral Domain, T. J. Weckman 322 28 May 1993 (EKY); Letcher Co., Cornett Woods Appalachian Ecological Research Station, J. D. Sole 750 12 May 1979 (EKY); Letcher Co., Lilley Cornett Woods Appalachian Ecological Research Station, J. D. Sole 286 7 Jun 1978 (EKY); Lewis Co., M. E. Wharton 5482 2 Jul 1940 (MICH); McCreary Co., Honeybee, R. Naczi 6568 19 Jun 1997 (NKY); Meade Co., Brandenburg, R. C. Hoskinson 108 10 Jul 1950 (NCU); Pike Co., Marrowbone Creek, F. Levy s.n. 3 Oct 1982 (NCU); Pike Co., Couper Mt., F. Levy s.n. 13 Sep 1982 (NCU); Pike Co., Varney, F. Levy s.n. 14 Aug 1982 (NCU); Powell Co., Clay City, R. Naczi 7670 19 Sep 1998 (NKY); Powell Co., Natural Bridge State Nature Preserve, R. Naczi 6657 22 Jun 1997 (NKY); Powell Co., Red River Gorge, P. D. Higgins 1451 11 Jun 1969 (NCU); Powell Co., Clay City, M. E. Wharton 2041 6 May 1938 (MICH); Pulaski Co., Hwy 80, L. E. McKinney 2189 31 May 1986 (VDB); Rowan Co., Morehead, John W. Thieret 51149 4 Aug 1979 (NKY); Taylor Co., Campbellsville, R. Naczi 7432 18 Jun 1998 (USCH); Wolfe Co., Pine Ridge, J. Conrad 548 23 Jul 1969 (NCU).

Maine: Cumberland Co., Falmouth, E. B. Chamberlain 412 7 Jul 1902 (GH); Knox Co., Mt.
Megunticook, R. C. Bean 13542 13 Aug 1913 (GH); Knox Co., Mt. Megunticook, Camden, M. L.
Fernald 9042 13 Aug 1913 (GH); York Co., Cornish, M. L. Fernald s.n. 21 Jul 1891 (GH); York
Co., Seabury, F. T. Hubbard s.n. 5 Aug 1901 (GH); York Co., Tatnic, J. Parlin s.n. 11 Jul 1891
(GH); York Co., York River, M. L. Fernald 13052 9 Aug 1916 (GH).

Maryland: Baltimore Co., Perry Hall, C. Lea 1803 29 May 2000 (MARY); Carroll Co., Patapsco River, C. Lea 1544 13 May 2000 (MARY); Frederick Co., Point of Rocks, C. Lea 1716 28 May 2000 (MARY); Frederick Co., Catoctin Mt., F. J. Hermann 13753 13 Jul 1957 (MICH); Frederick Co., Catoctin Mt. Park, C. J. Hickey II 69 22 Jul 1972 (NCU); Frederick Co., Foxville Tower, E. Bolton 678 28 Aug 1955 (MARY); Garrett Co., Allegheny Plateau, C. T. Frye 1076 23 Jun 1998 (TAWES); Garrett Co., Kelso Gap, Earl L. Core s.n. 24 Jun 1931 (WV); Harford Co., Rocks SP, C. Lea 1854 29 May 2000 (MARY); Harford Co., Winter's Run, W. D. Longbottom 3128 15 Jun 1992 (MARY); Howard Co., Burtonville, W. H. Wagner Jr. 1071 17 Jun 1942 (MARY); Howard Co., Savage Mills, W. D. Longbottom 3067 4 Jun 1992 (MARY); Montgomery Co., Burtonsville, J. E. Benedict 4944 30 Jun 1940 (MARY); Montgomery Co., Forest Glen, Agnes Chase s.n. 4 Jul 1904 (WIS); Montgomery Co., Forest Glenn, Agnes Chase 19502 4 Jul 1904 (WIS); Montgomery Co., Potomac Gorge, Vaso Island, C. Lea 434 7 May 1995 (TAWES); Montgomery Co., Potomac Valley, A. Chase 2434 4 Jul 1904 (MICH); Washington Co., Washington Monument SP, C. Lea 1756 28 May 2000 (MARY).

Massachusetts: Berkshire Co., North Cedars, H. D. House 25881 16 Jul 1938 (NYS); Franklin Co., Conway, H. E. Ahles 64641 14 Sep 1966 (NCU); Franklin Co., North Sugarloaf, Anonymous s.n. 1 Jul 1817 (MSC); Hampshire Co., Hatfield, H. E. Ahles 77713 7 Jul 1973 (TAES); Hampshire Co., Middlefield, Merritt L. Fernald 9040 26 Jun 1913 (KANU); Norfolk Co., Blue Hills Reservation, Nathaniel T Kidder s.n. 11 Aug 1919 (KANU); Norfolk Co., Blue Hills Reservation, Nathaniel T Kidder s.n. 30 Jun 1920 (KANU); Norfolk Co., Blue Hills Reservation, Nathaniel T Kidder s.n. 30 Jun 1920 (KANU); Norfolk Co., Milton, F. F. Forbes s.n. 22 Jun 1902 (WIS); Norfolk Co., Milton, Geo. G. Kennedy s.n. 9 Jun 1908 (WIS); Worcester Co., Auburn, T. J. Rawinski 4401 31 Jul 1986 (VPI).

Michigan: Berrien Co., Bridgeman, J. Guidinger 7544 23 Jul 1985 (MICH); Berrien Co., Bridgeman, A. A. Reznicek 7120 16 Oct 1982 (MICH); Berrien Co., Chikaming Twp., G. W. Parmelee 1738 18 Aug 1950 (MSC); Berrien Co., Harbert, H. T. Darlington 1650 22 Aug 1917
(MSC); Berrien Co., Paw Paw, H. J. Darlington 1639 15 Aug 1917 (MSC); Kent Co., Grand Rapids,

E. J. Cole s.n. 15 Jul 1899 (MICH); Ottawa Co., Lake Shore Ave., M. R. Penskar 1006 14 Jun 1985 (MICH); Ottawa Co., Grand Haven, C. W. Bazuin 1432 30 Jun 1940 (MSC).

Mississippi: Tishomingo Co., Cave Spring, C. T. Bryson 4401 27 May 1986 (VDB).

Missouri: Cape Girardeau Co., Trail of Tears SP, A. A. Reznicek 10162 5 Jun 1996 (MICH); Iron Co., Dry Hollow Branch, A. E. Brant 3714 27 May 1997 (MO); Iron Co., Tom Sauk Mt. SP, P. M. McKenzie 1492 11 Aug 1994 (MICH); Iron Co., Tom Sauk Mt. SP, P. M. McKenzie 1495 11 Aug 1994 (MICH); Reynolds Co., Clark National Forest, D. Castaner 2415 24 Jun 1972 (NEB); Ste. Genevieve Co., Hickory Canyons Natural Area, B. Summers 10029 27 May 2003 (MO).

New Hampshire: Belknap Co., Center Harbor, A. R. Hodgdon 18119 19 Jun 1969 (GH); Carroll Co., Bald Mt., Albany, F. L. Steele s.n. 18 Aug 1948 (GH); Carroll Co., Tuftonboro, A. R. Hodgden 19471 9 Aug 1972 (GH); Carroll Co., White's Ledge, Bartlett, A. S. Pease 16631 8 Sep 1915 (GH); Cheshire Co., Surry, M. L. Fernald 243 23 Jul 1899 (GH); Cheshire Co., Surry, H. E. Ahles 75456 22 Jun 1972 (NCU); Cheshire Co., Walpole, R. G. Eaton 17159 19 Jun 1932 (GH); Cheshire Co., Westmoreland, R. J. Eaton s.n. 18 Jun 1932 (GH); Rockingham Co., Nottingham, A. R. Hodgdon 10446 22 Jul 1958 (GH); Strafford Co., Barrington, A. R. Hodgdon 3092 13 Sep 1936 (OKL); Strafford Co., Rollinsford, A. R. Hodgdon 11657 29 Jun 1960 (GH); Sullican Co., across from Hartland Vt., M. C. Cowden 1223 9 Aug 1962 (GH).

New Jersey: Burlington Co., Pemberton, B. Long 16212 14 Jun 1917 (VPI); Monmouth? Co., Hornerstown, R. R. Dreissbach 942 29 May 1922 (MICH); Morris Co., Parsippany, L. J. Mehrhoff 15740 1 Jul 1992 (MICH); Warren Co., Coopersville, R. L. Schaeffer 44310 27 Jul 1953 (KANU).

New York: Albany Co., Alcove, C. L. Shear s.n. 22 Jun 1892 (MSC); Albany Co., Town of Westerlo, G. C. Tucker 6075 17 Jun 1991 (NYS); Allegany Co., Alma Hill, R. T. Clausen 3921 18 Jun 1939 (NYS); Cattaraugus Co., Allegany SP, W. P. Alexander 13138 6 Aug 1926 (NYS); Cayuga Co., Chestnut Ridge, Moravia, C. Atwood s.n. 14 Aug 1881 (NYS); Chemung Co., Erin, R. T. Clausen 2626 27 Jun 1937 (NYS); Chemung Co., Far Rockaway, S. J. Smith 4173 18 Jun 1948 (NYS); Chemung Co., Ven Etten Jct., S. J. Smith 3241 21 Jun 1947 (NYS); Columbia Co., Hollowville, R. McVaugh 3764 29 Aug 1935 (NYS); Dutchess Co., Taconic SP, W. J. Crins 7616 10 Jun 1989 (NYS); Essex Co., Boxford, S. K. Harris 18543 11 Aug 1958 (NYS); Essex Co., Keene Valley, H. D. House 28060 5 Aug 1941 (NYS); Greene Co., Platte Cove, L. J. Mehrhoff 13435 22 Jun 1990 (MICH); Jefferson Co., Woodville, H. D. House 19882 14 Aug 1932 (NYS); Monroe Co., Greece, R. E. Shanks 766 3 Aug 1941 (VDB); Orange Co., Black Forest, H. M. Raup 7444 1 Jul 1936 (MICH); Orange Co., Black Forest, H. M. Raup 7339 26 Jun 1936 (MICH); Orange Co., Black Rock Forest, K. Barringer 5511 4 Aug 1992 (NYS); Orange Co., Harriman SP, J. G. Barbour 1383 13 Sep 1993 (NYS); Orange Co., Storm King Park, J. G. Barbour 3159 29 Jun 1996 (NYS); Oswego Co., Sandy Creek Township, N. Hotchkiss 3031 17 Jul 1928 (NYS); Putnam Co., East Mountain Trail, T. Weldy 1895 10 Jul 1997 (NYS); Putnam Co., McKeel Corners, T. Weldy 1886 9 Jul 1997 (NYS); Putnam Co., Philipstown, R. E. Zaremba 2649 22 Oct 1985 (NYS); Putnam Co., U. S. Military Academy Reservation: Constitution Island, J. G. Barbour 732 27 May 1993 (NYS); Rennsselaer Co., Petersburg, H. D. House 19544 19 Jul 1932 (NYS); Rensselaer Co., Town of Grafton, P. Weatherbee 4525 2 Jul 1997 (NYS); Rockland Co., Bear Mt. SP, J. G. Barbour 2071 22 Jun 1994 (NYS); Rockland Co., Harriman SP: Welch Pkwy., R. S. Mitchell 8806 15 Jun 1994 (NYS); Sullivan Co., Claryville, R. H. True 4494 9 Aug 1937 (NYS); Tompkins Co., Etna, A. J. Eames 9473 25 Jun 1918 (MICH); Ulster Co., Town of Olive, J. Bierhorst 176 14 Jun 1996 (NYS); Ulster Co., Town of Olive, J. Bierhorst 177 29 Jun 1996 (NYS); Warren Co., Lake George, H. D. House 26756 18 Jul 1939 (NYS); Washington Co., Lake George, H. D. House 28615 10 Jul 1943 (OKL); Washington Co., Lake George Region, S. H. Burnham s.n. 21 Jun 1897 (OKL); Washington Co., Putnam Mt., W. J. Crins 7995 16 Sep 1989 (NYS); Westchester Co., Cortlandt, R. E. Zaremba 2619 26 May 1986 (NYS).

North Carolina: Alleghany Co., Air Bellows Rd, P. D. McMillan 1865-b 30 Jun 1996 (CLEMS); Alleghany Co., Roaring Gap, J. R. Manhart 341 31 May 1981 (MICH); Alleghany Co., Blue Ridge Parkway, M. Denton 1417 24 May 1968 (MSC); Avery Co., Pyatte, H. E. Ahles 43668 17 Jun 1958 (NCU); Avery Co., Senia, H. E. Ahles 43537 17 Jun 1958 (NCU); Buncombe Co., Hickory Gap, W. W. Ashe 111 (NCU); Buncombe Co., Asheville, Charles T. Bryson 6776 27 Jul 1987 (WIS); Buncombe Co., Asheville, Phillip E. Hyatt 8808 28 Jul 1999 (NKY); Buncombe Co., Asheville vicinity, Phillip E. Hyatt 8810 28 Jul 1999 (MICH); Buncombe Co., Biltmore, W. W. Ashe 5241a 28 Jun 1897 (NCU); Buncombe Co., Blue Ridge, H. K. Svenson 13,024 4 Aug 1949 (SMU); Buncombe Co., Cedar Cliff, D. E. Boufford 14404 19 Jun 1974 (NCU); Caldwell Co., Blowing Rock, H. A. Ahles 43977 18 Jun 1958 (WV); Caldwell Co., Draco, A. E. Radford 15108 4 Aug 1956 (NCU); Clay Co., Buck Creek, H. E. Ahles 13663 2 Jun 1956 (NCU); Clay Co., Clay-Macon Co line, Harry E. Ahles 13663 2 Jun 1956 (KANU); Clay Co., Fires Creek, A. E. Radford 6161 5 Jun 1952 (NCU); Clay Co., Perry Gap, D. E. Boufford 14156 11 Jun 1974 (NCU); Clay Co., Perry Gap, D. E. Boufford 14210

11 Jun 1974 (NCU); Forsyth Co., Yadkin River Bridge, J. R. Manhart 352 30 May 1981 (MICH); Graham Co., Stecoach Gap, C. T. Bryson 6832 30 Jul 1987 (VDB); Graham Co., Round Top Mt., H. E. Ahles 13189 29 May 1956 (MICH); Graham Co., Round Top Mt., A. E. Radford 11842 29 May 1956 (SMU); Graham Co., Appalachian Trail, C. T. Bryson 6832 30 Jul 1987 (WIS); Graham Co., Robbinsville, J. A. Churchill 86232 5 Jul 1986 (WIS); Graham Co., Round Top Mt., H. E. Ahles 13189 29 May 1956 (NCU); Haywood Co., Crabtree, H. E. Ahles 46656 15 Jul 1958 (NCU); Haywood Co., Mt. Pisgah, G. S. Ramseur 4552 26 Jun 1958 (NCU); Haywood Co., Sunburst, D. E. Boufford 15049 23 May 1974 (NCU); Henderson Co., Fletcher Academy, V. E. McNeilus s.n. 19 Jul 1981 (WIS); Macon Co., Highlands, R. K. Godfrey 51430 21 Jul 1951 (MICH); Macon Co., Buck Creek, D. E. Boufford 13759 27 May 1974 (NCU); Macon Co., Coweeta, J. R. Manhart 297 16 May 1981 (MICH); Macon Co., Coweeta, J. R. Manhart 58 9 Jun 1980 (MICH); Macon Co., Coweeta Hydrologic Lab, *Phillip E. Hyatt 6643* 11 Jun 1995 (MICH); Macon Co., Coweeta Hydrologic Lab, Phillip E. Hyatt 6096 2 Jul 1994 (MICH); Macon Co., Coweeta Hydrologic Lab, James R. Manhart 297 16 May 1981 (WIS); Macon Co., Coweeta Hydrologic Lab, Phillip E. Hyatt 8622 28 May 1999 (USCH); Macon Co., Gneiss, A. E. Radford s.n. 31 May 1947 (NCU); Macon Co., Highlands, D. E. Boufford 16129 6 Jun 1975 (NCU); Macon Co., Hogback Gap, A. E. Radford 6116 3 Jun 1952 (NCU); Macon Co., Moore Knob, P. D. McMillan 4540 6 May 2000 (CLEMS); Macon Co., Nantahala, A. E. Radford 5253 7 Jun 1950 (NCU); Macon Co., Otto, Phillip E. Hyatt 8196 3 Jul 1998 (MICH); Madison Co., Big Laurel, H. E. Ahles 42615 6 Jun 1958 (VDB); McDowell Co., Mill Creek, C. R. Bell 3487 11 Jun 1956 (NCU); Mitchell Co., Spruce Pine, H. E. Ahles 43158 16 Jun 1958 (NCU); Polk Co., Melrose, D. C. Peattie 656 24 Jun 1921 (NCU); Polk Co., Tryon, F. R. Fosberg 18898 19 Jun 1942 (NCU); Polk Co., Tryon, D. C. Peattie 2207 20 May 1926 (NCU); Rutherford Co., Bat Cave Nature Preserve, H. McIver 28 16 Jul 1981 (NCU); Stokes Co., Hanging Rock SP, H. E. Ahles 59485 6 Jun 1965 (NCU); Surry Co., Low Gap, A. E. Radford 13148 23 Jun 1956 (NCU); Swain Co., Alarka, C. R. Bell 3265 6 Jun 1956 (NCU); Swain Co., Nantahala Gorge, D. E. Boufford 13667 26 May 1974 (NCU); Swain Co., Nantahala Gorge, D. E. Boufford 13688 26 May 1974 (NCU); Swain Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 27 Jun 1982 (WIS); Transylvania Co., Horsepasture Gorge, C. L. Rodgers 61397a 9 Jul 1961 (NCU); Transylvania Co., Pilot Cove, D. E. Boufford 16690 23 Jun 1975 (NCU); Transylvania Co., Pink Beds, D. E. Boufford 13487 21 May 1974 (NCU); Transylvania Co., Thompson River Gorge, D. M. E. Ware 3087 10 Jul 1970 (VDB); Transylvania Co., Thompson River Gorge, D. M. E. Ware 3142 13 Jul 1970 (VDB);

Watauga Co., Bethel, H. E. Ahles 43871 18 Jun 1958 (NCU); Watauga Co., Blowing Rock, M. L.
Smith 5861 7 Aug 1981 (VPI); Watauga Co., Hanging Rock, J. Rohrer 1934 10 Jun 1978 (NCU);
Yadkin Co., Yadkin River Bridge, J. R. Manhart 320 30 May 1981 (MICH); Yancey Co., Celo, H.
E. Ahles 46939 16 Jul 1958 (NCU); Yancey Co., Huntdale, H. E. Ahles 42818 7 Jun 1958 (NCU).

Ohio: Belmont Co., Rock Run, A. W. Cusick 22616 23 Jun 1983 (MICH); Belmont Co.,
Wayne twp., A. W. Cusick 9992 21 Jun 1969 (NCU); Erie Co., Cedar Point, G. B. Ashcroft s.n.
1 Jul 1997 (WIS); Holmes Co., Killbuck, A. W. Cusick 29,624 5 Jun 1991 (VDB); Jefferson Co.,
Yellow Creek, A. W. cusick 25,456 1 Jul 1986 (MICH); Lake Co., Painesville, H. C. Beardlee s.n.
(MSC); Lawrence Co., Lake Vesuvius Recreation Area, G. M. Silberhorn 2258 7 Jul 1968 (NCU).

Pennsylvania: Beaver Co., Moucea, J. Bright 6341 4 Jun 1932 (SMU); Beaver Co., Monaco, John Bright 6338 4 Jun 1932 (WIS); Bedford Co., Wolf Swamp Watershed, Homer Duppstadt s.n. 15 Jul 1970 (WV); Bedford Co., Bakers Summit, D. Berkheimer 5900 27 May 1945 (NCU); Bedford Co., Centerville, David Berkheimer 5927 28 May 1945 (KANU); Berks Co., Esterly, W. C. Brumbach 3550 27 Jun 1943 (VPI); Centre Co., Unionville, H. A. Wahl 988 2 Jun 1941 (NEB); Chester Co., Lenape, L. A. Standley 1526 21 Jun 1987 (MICH); Chester Co., Frazer, H. E. Stone s.n. 28 Jun 1925 (SMU); Chester Co., Landenberg, E. C. Earle 5110 27 Jun 1958 (SMU); Clarion Co., Driftwood, H. A. Wahl. s.n. 19 Jun 1934 (WIS); Clearfield Co., Penfield, E. B. Ehrle 1562 18 Sep 1955 (NYS); Delaware Co., Crum, F. J. Hermann 3090 29 May 1932 (MICH); Erie Co., Erie, John Bright s.n. 16 Jul 1927 (WV); Franklin Co., Tuscarora Summit, J. E. Benedict, Jr. 2859 5 Jul 1934 (VPI); Lackawanna Co., Ransom, P. E. Rothrock 350 3 Jun 1975 (NCU); Lancaster Co., Geiger's Quarry, Earl L. Core 6745 18 Jun 1938 (WV); Lehigh Co., Lehigh River, H. W. Pretz 8948 22 Jul 1917 (VDB); Lehigh Co., Emmaus, Harold W. Pretz 13772 22 Jun 1947 (KANU); Lehigh Co., Hosensack, W. M. Benner s.n. 17 Jun 1922 (GH); Lehigh Co., South Mountains, H. W. Pretz 6655 13 Jun 1914 (VDB); Northampton Co., Lower Saucon, R. L. Schaeffer, Jr. 14398 21 Jul 1941 (VPI); Northampton Co., 1.25 mi N of Lower Saucon, R. L. Schaeffer 14267 16 Jul 1941 (GH); Northampton Co., Wassergass, R. L. Schaeffer 9564 5 Aug 1940 (GH); Northampton Co., Easton, J. K. Small s.n. 4 Jul 1890 (NCU); Northampton Co., Easton, N. L. Britton s.n. 5 Jul 1889 (NEB); Northampton Co., Lower Saucon, R L Schaeffer 12460 11 Jun 1941 (KANU); Susquehanna Co., Susquehanna, J. A. Graves s.n. 1 Jul 1898 (NEB).

Rhode Island: Providence Co., Diamond Hill, Town of Cumberland, *E. J. Palmer* 45584 24 Aug 1941 (GH).

South Carolina: W. W. Ashe 152 16 Jul 1700 (NCU); Greenville Co., North Saluda Reservoir, John B. Nelson 16527 15 May 1995 (NKY); Greenville Co., North Saluda Reservoir, J. B. Nelson 16,527 15 May 1995 (MICH); Greenville Co., Bryant Mt., J. B. Nelson 16,522 15 May 1995 (MICH); Greenville Co., Table Rock Reservoir Watershed, S. R. Hill 23617 30 Jun 1992 (MICH); Greenville Co., Callahan/Hyde Mt., J. F. Townsend 2151 13 Jun 2000 (CLEMS); Greenville Co., Glassy Mt., C. N. Horn 5251 25 Jun 1992 (USCH); Greenville Co., Old Indian Mt., J. B. Nelson 16512 15 May 1995 (USCH); Greenville Co., Table Rock Reservoir, S. R. Hill 23492 22 Jun 1992 (CLEMS); Greenville Co., Table Rock Reservoir, S. R. Hill 23617 30 Jun 1992 (CLEMS); Oconee Co., Wright Creek, D. M. E. Ware 2942 8 May 1970 (VDB); Oconee Co., Chattooga Trail, L. L. Gaddy s.n. 26 May 1986 (CLEMS); Oconee Co., Oconee SP, A. Darr 1927 12 Jun 2003 (USCH); Oconee Co., Sumter National Forest, S. R. Hill 25048 22 May 1993 (MICH); Oconee Co., Sumter National Forest, A. A. Reznicek 8982 23 May 1992 (MICH); Oconee Co., Walhalla, A. E. Hodge 226 2 May 1982 (NCU); Pickens Co., Rt. 11, S. R. Hill 19275 9 May 1988 (VDB); Pickens Co., U. S. 178, C. R. Bell 3317 8 Jun 1956 (NCU); Pickens Co., U. S. 178, D. E. Boufford 20902 14 May 1979 (VDB); Pickens Co., U. S. 178, C. Horn 19275 9 May 1988 (MICH); Pickens Co., Rt. 178, S. R. Hill 19275 9 May 1988 (CLEMS); Pickens Co., Chimneytop Gap, A. Darr 1930 18 May 2004 (USCH); Pickens Co., Eastatoe Creek Gorge, D. E. Boufford 17371 18 Jul 1975 (NCU); Pickens Co., Howell Mt., P. D. McMillan 6345 12 May 2002 (CLEMS); Pickens Co., Pinnacle Mt., P. D. McMillan 7069 19 Jun 2003 (CLEMS); Pickens Co., Sassafras Mt., J. F. Townsend 2073 4 May 2000 (CLEMS); Pickens Co., Sassafras Mt., R. T. Clausen 3642 16 Sep 1938 (NYS); Pickens Co., Table Rock Reservoir, S. R. Hill 23692 10 Jul 1992 (CLEMS); Pickens Co., Wadakoe Mt., P. D. McMillan 6315 30 Apr 2002 (CLEMS); Pickens Co., Wadakoe Mt., P. D. McMillan 6392 11 May 2002 (CLEMS).

Tennessee: Thompson's, Anonymous 1002 1 May 1896 (NCU); Great Smoky Mts F. Rugel 107 1 May 1844 (VDB); Anderson Co., Norris Dam, V. E. McNeilus 90346 13 Jun 1990 (WIS); Anderson Co., Norris Dam, V. E. McNeilus 89-358 13 Jun 1989 (MICH); Anderson Co., Norris Dam, A. J. Sharp 2744 24 Jul 1934 (NCU); Anderson Co., Norris Dam SP, V. E. McNeilus 87-726 12 May 1987 (BRIT); Blount Co., Cades Cove, C. T. Bryson 10820 30 Jun 1991 (CLEMS); Blount Co., Cherokee NF, B. A. Ford 88926 17 May 1989 (NYS); Blount Co., Great Smoky Mt. NP, C. T. Bryson 10820 30 Jun 1991 (MICH); Blount Co., Great Smoky Mt. NP, S. Jones 4937 22 May 1990 (WIS); Blount Co., Great Smoky Mt. NP, R. Athey s.n. 15 May 1973 (VDB); Blount Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 6 Apr 1983 (WIS); Blount Co., Great Smokey Mt. NP, V. E. McNeilus s.n. 19 May 1984 (WIS); Carter Co., Watuga Lake, J. R. Manhart 328 31 May 1981 (MICH); Cheatham Co., Ashland City, R. Kral 26782 6 Jun 1966 (MICH); Cheatham Co., Ashland City, T. Smith s.n. 9 Jul 1982 (VDB); Clay Co., Celina, V. E. McNeilus 91-755 5 Aug 1991 (MICH); Clay Co., Celina, V. E. McNeilus 91-340 13 May 1991 (WIS); Coffee Co., Old Stone Fort SP, D. F. Brunton 10338 22 May 1991 (MICH); Cumberland Co., Brady Mt., R. Kral 83559 20 May 1994 (VDB); Cumberland Co., Brady Mt., R. Kral 83558 20 May 1994 (MICH); Davidson Co., TN 12, R. Kral 77671 22 May 1990 (VDB); Davidson Co., Joelton, J. M. Shaver 2475 9 May 1942 (VDB); Davidson Co., Vicinity of Long Hollow, B. Bowen BB95-016 1995 (VDB); Fentress Co., Clarkrange, A. W. Cusick 11,778 26 Jun 1971 (VDB); Franklin Co., Carter Mt., P. Somers 1132 21 May 1978 (VDB); Franklin Co., Wolf Cove, R. K. Clements 479 14 Aug 1985 (VDB); Greene Co., Carmel, J. A. Churchill 93163 13 Jun 1993 (WIS); Greene Co., Greene Mt., B. Boom 556 11 Jun 1980 (EKY); Grundy Co., Beershaba Springs, K. Rogers 43586 5 Jul 1969 (VDB); Grundy Co., Savage Creek Bridge, T. S. Patrick 380 21 Aug 1977 (EKY); Grundy Co., Monteagle Mt., R. Kral 65036 14 May 1980 (VDB); Grundy Co., Mt. View, R. Kral 68636 31 May 1982 (VDB); Grundy Co., Altamont, R. Kral 77744 29 May 1990 (VDB); Grundy Co., Monteagle, R. Kral 46503 17 May 1972 (WIS); Grundy Co., Savage Gulf Natural Area, T. S. Patrick 379 21 Aug 1977 (EKY); Grundy Co., Savage Gulf Natural Area, T. S. Patrick 202 8 Jun 1977 (VDB); Grundy Co., The Fiery Gizzard Gorges, R. C. Clark 964 26 Jun 1964 (NCU); Hamilton Co., Falling Water Falls State Natural Area, P. Somers 2095 21 Aug 1981 (VDB); Hawkins Co., Kyles Ford, P. Somers 1789 28 Jun 1979 (VDB); Jackson Co., Brimstone Creek Bridge, R. Kral 80520 14 May 1992 (VDB); Lawrence Co., Lawrenceburg, R. Kral 77463 5 May 1990 (VDB); Macon Co., K. E. Blum 3446 13 May 1969 (VDB); Monroe Co., Cherokee National Forest, D. E. Boufford 23607 18 May 1985 (VDB); Morgan Co., Stephen's, K. E. Rogers 44696 14 May 1966 (SMU); Morgan Co., Frozen Head SP, V. E. McNeilus s.n. 13 May 1984 (WIS); Morgan Co., Gatewood Bridge, V. E. McNeilus s.n. 20 Jun 1982 (WIS); Overton Co., Allred, V. E. McNeilus 93-1112 22 Jun 1993 (WIS); Polk Co., Hiawassee River, V. E. McNeilus s.n. 10 Apr 1984 (WIS); Polk Co., Wolf Creek, J. K. Underwood 41183 28 May 1966 (SMU); Putnam Co., I40, L. E. McKinney 2132 10 May 1986 (VDB); Rhea Co., Dayton, V. E. McNeilus 88-328 18 May 1988 (WIS); Rhea Co., Dayton, V. E. McNeilus s.n. 23 May 1982 (WIS); Roane Co., Clifty Creek, V. E. McNeilus 87727 13 May 1987 (WIS); Scott Co., Big South Fork Nat. Rec. area, V. E. McNeilus 87-728 6 May 1987 (MICH);

Scott Co., Big South Fork National Recreation Area, V. E. McNeilus 87530 27 Jun 1987 (WIS);
Scott Co., Big South Fork National River and Recreation Area, A. A. Reznicek 9556 22 Jun 1993 (MICH);
Sequatchie Co., Dunlap, R. Kral 77730 29 May 1990 (VDB);
Sevier Co., Gatlinburg, S. Jones 4933 22 May 1990 (VDB);
Sevier Co., Great Smoky Mt. NP, D. F. Brunton 7840 9 May 1988 (MICH);
Sevier Co., Great Smoky Mt. NP, D. F. Brunton 7840 9 May 1988 (MICH);
Sevier Co., Great Smoky Mt. NP, D. F. Brunton 7840 9 May 1988 (MICH);
Sevier Co., Greenbrier, A. J. Sharp 1981 5 Jul 1934 (NCU);
Sevier Co., Great Smoky Mt. NP, Co., Great Smoky Mt. NP, Laurel Falls,
V. E. McNeilus s.n. 24 May 1981 (WIS);
Sevier Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 29 Jun 1980 (WIS);
Sevier Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 29 Jun 1980 (WIS);
Sevier Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 29 Jun 1980 (WIS);
Sevier Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 29 May 1982 (WIS);
Sevier Co., Great Smoky Mt. NP, V. E. McNeilus s.n. 21 May 1982 (WIS);
Sevier Co., Sugarland, Ken Rogers 43617 29 Jun 1969 (WIS);
Sumner Co., Westmoreland, J. Alcorn 437
May 1975 (VDB);
Sumner Co., Taylor Hollow, R. Carter 1830 18 May 1979 (VDB);
Unicoi Co.,
Devil's Creek, B. Boom 543 10 Jun 1980 (EKY);
Unicoi Co., Unicoi, H. E. Ahles 54696 16 Jun 1961 (NCU);
Van Buren Co., Spenser, R. Kral 80571 19 May 1992 (VDB);
Williamson Co., Inman Branch , R. Kral 88609 2 Jun 1999 (VDB).

Vermont: Bennington Co., North Pownal, D. E. Boufford 17829 11 Aug 1975 (NCU); Bennington Co., North Pownal, E. W. Wood 2319 11 Aug 1975 (GH).

Virginia: Albermarle Co., Shenandoah NP, C. E. Stevens 3780 10 Jul 1971 (NCU); Alleghany
Co., Peters Mt., T. F. Wieboldt 6433 14 Jul 1987 (VPI); Appoxattox Co., Stonewall, A. M. Harvill 16845 8 Jul 1967 (NCU); Bath Co., Nimrod Hall, G. P. Fleming 13381 25 Jun 1997 (VPI);
Buchanan Co., Slate, T. F. Wieboldt 8559 20 May 1993 (VPI); Buchanon Co., Prater, J. A. Churchill 8284 16 Jun 1982 (WIS); Carroll Co., Burks Fork, D. W. Ogle 6383 30 May 1987 (VPI);
Carroll Co., Galax, G. B. Rossbach 2646 18 Jun 1961 (WV); Carroll Co., Va 694, L. J. Uttal 7168
4 Jun 1970 (VPI); Clarke Co., Buzzard Hill; Bluemont, G. P. Fleming 5465 25 May 1991 (VPI);
Craig Co., Potts Mt., T. L. Sharik SM77-5389 13 May 1977 (VPI); Dickinson Co., Bartlick, T. F. Wieboldt 4512 26 Aug 1982 (VPI); Fauquier Co., Bull Run Mountain, H. A. Allard 11909 15 Jun 1946 (WIS); Fauquier Co., Bull Run Mountains, H. A. Allard 19604 4 Jun 1950 (WV); Fauquier Co., Marshall, G. P. Fleming 2290 15 Jun 1986 (CLEMS); Fauquier Co., Western slope of Bull Run Mountains, H. A. Allard 5317 31 Jul 1938 (VPI); Fauquier Co., Hopewell Gap, H. A. Allard 406 26 May 1936 (VPI); Floyd Co., Rt. 648, G. P. Frank 616 17 Jul 1981 (VPI); Grayson Co., Bald Rock, D. W. Ogle 1291 28 Jul 1978 (VPI); Grayson Co., Bridle Creek, T. F. Wieboldt 6159 25 Jun 1986 (WIS); King George Co., Caledon Marsh, D. M. E. Ware 8520 6 Aug 1983 (VDB); King George

Co., Caledon Swamp, D. M. E. Ware 8186 8 Jun 1983 (CLEMS); Lee Co., Stone Mt., D. W. Ogle 5258 2 Jun 1984 (VPI); Madison Co., Stony Man Mt., H. D. House 4769 13 Sep 1948 (NYS); Montgomery Co., McCoy, R. Kral 10611 22 Jun 1960 (VDB); Morgan Co., Cacapon Mt. SP, T. F. Wieboldt 6211 13 Aug 1986 (WIS); Page Co., Big Meadows, J. A. Churchill s.n. 20 Jun 1957 (MSC); Page Co., Blue Ridge Mts, F. J. Hermann 11405 15 Oct 1944 (MICH); Page Co., Knob Mt., F. W. Hunnewell 19133 24 Jun 1949 (VPI); Patrick Co., Dodson, T. F. Wieboldt 9504 25 Jul 1996 (VPI); Patrick Co., Philpott Reservoir, T. F. Wieboldt 9504 25 Jul 1996 (MICH); Pulaski Co., Big Walker Mt., T. F. Wieboldt 9987 2 Jul 1998 (VPI); Pulaski Co., Rt. 606, J. A. Smith s.n. 8 Aug 1975 (VPI); Rappahannock Co., Shenandoah NP, F. R. Fosberg 41122 3 Aug 1960 (SMU); Rappahannock Co., Shenandoah NP, F. H. Sargent s.n. 16 Jun 1951 (WIS); Rappahannock Co., Shenandoah NP, F. R. Fosberg 48510 4 Jun 1967 (MICH); Rappahannock Co., Shenandoah NP, F. R. Fosberg 31000 17 Jul 1949 (VDB); Rappahannock Co., Shenandoah NP, F. R. Fosberg 45460 6 Jun 1964 (MICH); Rappahannock Co., Shenandoah NP, F. H. Sargent s.n. 16 Jun 1951 (SMU); Roanoke Co., Haven's WMA, Ft. Lewis Mt., N. A. Mason s.n. 15 Jun 1991 (VPI); Roanoke Co., Poor Mt., C. E. Stevens 2672 7 Sep 1970 (VPI); Scott Co., Fort Blackmore, R. Naczi 6889 15 Aug 1997 (NKY); Shenandoah Co., Big Schloss, C. E. Stevens 1231 21 Jul 1969 (VPI); Smyth Co., Marion, R. Kral 10900 2 Aug 1960 (SMU); Tazewell Co., Flattop Mt., L. J. Uttal 7130 28 May 1970 (VPI); Wise Co., Guest River Gorge, D. W. Ogle 5605 14 Sep 1984 (VPI).

West Virginia: Mamonon, John L. Sheldon s.n. 20 Jul 1918 (WV); Braxton Co., Strange Creek, W. V. University Biological Expedition s.n. 17 Jun 1941 (WV); Fayette Co., New River Gorge, Rodney L. Bartgis s.n. 5 Jun 1983 (WV); Fayette Co., Beckwith, Earl L. Core 4232 8 Jul 1932 (WV); Fayette Co., Clifftop, William N. Grafton s.n. 4 Jun 1995 (WV); Fayette Co., Short, Rodney L. Bartgis s.n. 5 Jun 1983 (WV); Grant Co., Dolly Sods, William N. Grafton s.n. 3 Jun 1999 (WV); Hampshire Co., Nathaniel Mt., Homer Duppstadtq s.n. 30 Jun 1977 (WV); Hancock Co., Tomlinson Run SP, J. Sumpstine s.n. 1 Jul 1939 (WV); Hardy Co., Lost River, H. A. Allard 6736 8 Jun 1939 (WV); Harrison Co., Turtletree Fork, William N. Grafton s.n. 5 Jun 1980 (WV); Jefferson Co., Avon Bend, Rodney Bartgis 1287 26 May 1989 (WV); Lewis Co., Camden, W. V. U. Botanical Expedition s.n. 15 Jun 1928 (WV); McDowell Co., Payton, William N. Grafton s.n. 9 Jun 1987 (WV); Monongalia Co., Chestnut Ridge Regional Park, William N. Grafton s.n. 28 Aug 1996 (WV); Monongalia Co., Dellslow, John L. Sheldon s.n. 10 Jun 1918 (WV); Morgan Co., Cacapon

Mt. SP., T. F. Wieboldt 6211 13 Aug 1986 (VPI); Nicholas Co., Nettie, William Basil Fox s.n. 21
Jun 1940 (WV); Pendleton Co., Seneca Rocks, H. A. Allard 20631 3 Jul 1952 (WV); Pendleton
Co., Seneca Rocks Trail, William N. Grafton s.n. 10 Aug 1997 (WV); Pendleton Co., Seneca, Earl
L. Core 6135 16 Jul 1937 (WV); Raleigh Co., Ivy Knob, William N. Grafton s.n. 30 Jun 1974
(WV); Ritchie Co., U. S. 50, William N. Grafton s.n. 8 Jun 1999 (WV); Roane Co., Hungry Beech
Preserve, Emily Grafton s.n. 23 Jun 1979 (WV); Tucker Co., Canaan Valley, H. A. Allard 19539 24
Jul 1949 (WV); Tyler Co., Sistersville, Earl L. Core 4133 24 Jun 1932 (WV); Upshur Co., Middle
Fork River, William N. Grafton s.n. 3 Aug 1995 (WV); Wayne Co., Buffalo Creek, Lewis Plymale
379 7 May 1938 (WV); Wetzel Co., Littleton, Oscar Haught 374 11 Jun 1931 (WV); Wood Co.,
U. S. 50, William N. Grafton s.n. 8 Jun 1999 (WV).

APPENDIX D

The geographic and ecological distribution of the Roan Mountain Sedge, Carex roanensis (Cyperaceae)

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This paper was previously published in the journal Castanea (volume 71, issue 1, pp. 45–53), and is reproduced here with permission.

Abstract

Carex roanensis is a globally rare species endemic in moderate to high elevation forests in the Southern Appalachian Mountains. All known collections were reviewed, including previously unpublished records from Pennsylvania, West Virginia, Virginia, North Carolina, and Tennessee, and an annotated distribution map is presented. A preliminary assessment of its ecological affinities is provided, especially with respect to the closely related *C. aestivalis* and *C. virescens*.

Introduction

Carex roanensis Hermann was described from a single 1936 collection from Roan Mountain, Carter County, Tennessee (Hermann 1947). Hermann placed *C. roanensis* in section *Gracillimae* (now included within § *Hymenochlaenae* — Waterway 2002). However, he noted some uncertainty regarding its true affinity. While it appeared to be very similar to *C. aestivaliformis* Mack. in section *Hymenochlaenae*, it also bore a strong resemblance to *C. virescens* Muhl. of section *Porocystis* (syn. = section *Virescentes*). The confusion arose in part because of the unnatural arrangement of these two sections. Recent molecular studies show that section *Porocystis* forms a natural group only when several species from sections *Hymenochlaenae*, *Longicaules*, *Hirtifoliae*, and *Hallerianae* are included within it (Waterway and Starr 2007). This new expanded *Porocystis* group includes *C. roanensis* as well as *C. aestivalis* Curtis. TWS and MJW are conducting molecular systematic studies to clarify this alignment.

Taxonomic confusion has confounded efforts to produce effective keys to distinguish *C. roanensis* from its closest presumed relatives. Hermann noted that it had long sheathing bracts, a character used to separate species of section *Hymenochlaenae* from those of section *Porocystis*. However, this character is variable within species and even within individuals (pers. obs.). As a result, specimens of *C. roanensis* have been misidentified as either *C. aestivalis* or *C. virescens*. Preliminary examination of morphological variation among these species suggests that *C. roanensis* is most readily distinguished from *C. aestivalis* by its pubescent perigynia (glabrous in *C. aestivalis*). In most cases, perigynium length is diagnostic between *C. roanensis* and *C. virescens*: the perigynia of *C. roanensis* are 2.6–3.5 mm long, while those of *C. virescens* are 1.9–2.6 mm. Another useful character is the density of perigynia at the base of the lowest spikelet. In *C. roanensis* there are 7 or fewer perigynia on the proximal centimeter of this spikelet, while in *C. virescens* there are 7 or more. These measurements are based on preliminary data; TWS is preparing a full analysis of morphological variation in these species.

Inadequate keys likely contributed to the scarcity of C. roanensis collections prior to the 1980's. John A. Churchill was the first to recognise *C. roanensis* in the field, discovering a small population at Spivey Falls, Unicoi County Tennessee in 1985 (Churchill and Wurdack 1986). More recently, additional records from Virginia, West Virginia (Wieboldt et al. 1998), and Kentucky (Naczi et al. 2002b) have been published. Unpublished reports note its occurrence in Georgia (NatureServe 2006). No comprehensive review of the geographic and ecological distribution of this species has been completed. The purpose of this paper is to provide such a review, based on new fieldwork and examination of herbarium collections.

Materials and Methods

The collections and observations of JTD, TFW, and GLK were made in the course of general collecting in the region. Data provided by TWS is part of an ongoing study of the taxonomy and ecology of *Carex roanensis* and allied species. The ecological generalizations were based on detailed vegetation surveys at nine populations and casual observations at six additional locations. This represents more than one third of the known sites and includes at least one population from each state in the range of *C. roanensis*, with the exception of the single population reported from extreme northern Georgia. The following herbarium collections were included in this study: VPI, KNK, NCU, USCH, CLEMS, GA, TENN, EKY, ETSU, VDB, MICH, MSC, WIS, WVA, BRIT, MTMG, dd (abbreviations follow Holmgren and Holmgren Holmgren and Holmgren 1990, except dd, the personal herbarium of David Danley).

Results

Ecology

Carex roanensis is most abundant on moderate to steep, often rocky, wooded slopes between 775 m and 1300 m elevation. It is associated with mesic hardwood communities ranging from rich cove to northern hardwood and mesic oak-hickory forest types. Typical canopy trees include Acer rubrum, A. saccharum, Aesculus flava, Fagus grandifolia, Fraxinus americana, Liriodendron tulipifera, Pinus strobus, Quercus montana, Q. rubra, Q. alba and Tilia americana. It favors areas with a relatively open understory and a relatively sparse- moderate herbaceous layer. Some of the North Carolina populations (particularly locations 22 and 24 below) occur in rich cove forests with a lush, diverse herbaceous layer. In these instances, C. roanensis is generally restricted to areas with sparser herbaceous growth, often along trails or on steeper slopes.

Carex virescens and *C. aestivalis* frequently co-occur with *C. roanensis*. In these situations, *C. virescens* is usually most abundant at lower elevations, and is gradually replaced by *C. roanensis* at intermediate elevations. *Carex roanensis* is replaced in turn by *C. aestivalis* at higher elevations. *Carex roanensis* flowers in mid- to late May, with fruits maturing by mid-June. Spikelets begin to shatter towards the end of July, but specimens with enough fruit remaining to allow identification have been taken as late as October. *Carex virescens* has a similar phenology, while *C. aestivalis* flowers and fruits about two weeks later.

Distribution

All known records for C. roanensis are plotted on Figure D.1. Vouchers for each numbered location are listed north to south by state, along with relevant notes in the text. The collections of TWS include normal vouchers, indicated with a collection number, and population samples (fruiting stems from 20 randomly selected individuals), indicated by "pop. sample" and a four-letter code which uniquely identifies the samples at MTMG. Many of the collections of JTD were made on behalf of private landowners, and the exact locations have been withheld to maintain their privacy.

Pennsylvania

- Fayette County: On slopes in mountain woods at Ohiopyle, 23 June 1929, John Bright 1841 (WVA); Ohiopyle State Park, Meadow Run Trail, very rare along trail in rocky woods, Acer rubrum dominant with Tsuga, Hamamelis, Polystichum, Dennstaedtia, Mediola virginiana, elev. 428 m, 21 June 2005, T. W. Smith 525 (MTMG); Ohiopyle State Park, occasional along the lower section of Beech trail, adjacent to Youghiogheny River trail and east of Kentuck campground, rocky wooded slopes under Acer saccharum, Liriodendron, Carya, Sassafras, Hamamelis, Magnolia, with Viola hastata, Polystichum, Parthenocissus, elev. 370 m, 21 June 2005, T. W. Smith 527 (MTMG); Ohiopyle State Park, Sugar Run trail between Jonathan Run and Mitchell Trail, occasional along rocky wooded slope, Maple-Beech forest with Liriodendron, Quercus rubra, Magnolia, 23 June 2005, T. W. Smith 529 & pop. sample PAFR (MTMG).
- Notes: Bright's collection was originally determined as *C. virescens*. The three new collections are separated by approximately 3 km, and so are treated as separate populations. *Carex roanensis* is very rare in this area, with less than 50 plants located in four days of intensive searching.

West Virginia

 Randolph County: Jeep trail through mixed hardwoods, NW slope of arm of Rich Mtn. above Birch Fork of Middle River, near Adolph, elev. 800 m, 15 August 1996, T. F. Wieboldt 9511 (VPI, reported in Wieboldt et al. 1998); W of Rich



Figure D.1: Distribution of *Carex roanensis*

Mtn. near Blue Rock Knob, 7.5 km SW of Adolph, Birch Fork watershed, elev. 1050 m, 6 June 2000, *T. F. Wieboldt 10447* (VPI).

- Notes: The 2000 collection is approximately 6 km from the site of the 1996 discovery, and are treated as two separate populations. Both records indicate that *C. roanensis* was growing in recently thinned hardwood forest. In 2003 the area was covered in dense regrowth and TWS could not relocate any *C. roanensis*.
- Pocahontas County: Moist shady road bank, Droop Mtn. Battlefield SP, 800 m W of U.S. Rt. 219, 16 August 2001, W. N. Grafton s.n. (WVA); Droop Mtn. Battlefield SP, patchy along park road, elev. 920 m, 12 July 2003 T. W. Smith pop. sample WVPR (MTMG).

Notes: The 2001 collection was originally determined as C. aestivalis.

Virginia

 Greene County: Hightop, south ridge, rocky oak and mixed hardwood forest on W-facing greenstone slope above Bacon Hollow, ca. 1.5 km SSE of Smith-Roach Gap, 7 km NNW of Dyke, elev. 800 m, 20 August 1996, *T. F. Wieboldt 9513 &* 9518 (VPI, reported in Wieboldt et al. 1998).

Notes: These two collections are from the same population.

- 5. Augusta County: Grassy swale, oak woods near ridge-crest, Bald Mtn. 400 m NNW of Little Bald Knob summit, ca. 3.3 km NNE of Camp Todd, elev. 1280 m, 13 July 1986, *T. F. Wieboldt 6131* (VPI, reported in Wieboldt et al. 1998); Level floodplain terrace, white pine stand now breaking up, likely an old field, between FR 95 and North River about 1.1 km SE of Camp Todd and ca. 10.1 km NNE of West Augusta, elev. 700 m, 6 June 2004, *T. Dierauf s.n.* (VPI).
- Notes: Two populations separated by about 4.8 km and 600 m elevation change. The first collection was originally determined as *C. virescens*; annotated as *C. roanensis* by C. T. Bryson, March 1987 (on duplicate).

- Augusta County: Rocky, N-facing slope under northern hardwoods, along Cold Spring Trail on NW flank of Elliott Knob, Great North Mtn., ca. 1.1 km WSW of the summit, 1.1 km N of Augusta Springs, occasional, elev. 1128 m, 6 July 1996, G. P. Fleming 11839 & B. A. Brodman (VPI, reported in Wieboldt et al. 1998).
- Patrick County: Rock Castle Gorge, under mixed hardwoods on slopes along Rock Castle Creek, Rocky Knob Recreation Area off Blue Ridge Parkway, SW of Tuggle Gap and W of Woolwine, 26 May 1996 & 4 June 1996, *R. Edwards s.n.* (VPI, reported in Wieboldt et al. 1998).

Notes: These two collections are from the same population.

 Floyd County: Buffalo Mtn., thin, dry hardwoods about mid-slope of S slope of mtn., ca. 7 km S of Willis, elev. 1067 m, 22 August 1991, *T. F. Wieboldt 7866 W T. J. Rawinski* (VPI, reported in Wieboldt et al., 1998 Wieboldt et al. 1998); Buffalo Mtn., common along access road, elev. 950 m, 8 July 2003, T. W. Smith pop. sample VAFR (MTMG).

Notes: The first collection was originally determined as C. virescens.

- Smyth County: Quebec, common along the Appalachian Trail where it crosses the Holston River and Rt. 670, elev. 775 m, 10 July 2003, T. W. Smith pop. sample VASR (MTMG)
- Smyth & Grayson Counties: Common along Mt. Rogers Trail between highway and Grindstone Campground on both sides of the county line, 7 July 2003, T. W. Smith 479 & 480 (MTMG).
- Note: Locations 9 and 10 are separated by ca. 9 km.
- Washington County: Cliffs on Little Mtn. just E of Tumbling Creek, 10 November 1984, D. W. Ogle, s.n. (VPI).
- Notes: Originally determined as C. virescens.

- 12. Wise County: Powell Mtn., dry, mesic, open hardwoods along top of limestone cliffs 2.2 km WNW of High Knob Lookout and 3.4 km SSW of Norton, elev. 914 m, 2 June 1988, *T. F. Wieboldt 6672* (VPI, reported in Wieboldt et al. 1998)
 Kentucky
- 13. Harlan County: Razor Fork area, Big Black Mtn., elev. 1060-1150 m, on S-facing slope, collected with Carex appalachica and Dryopteris carthusiana, 19 August 1998, R. L. Jones 8757 (EKY); Razor Fork area, Big Black Mtn., elev. 1060-1150 m, on S-facing slope, collected with Carex radiata and Ilex ambigua var. montana, 19 August 1998, R. L. Jones 8737b(EKY, reported in Naczi et al. 2002b); Black Mtn., abundant along roadcut outcrops and along steep wooded slopes, Hwy 160, 1.7 km from VA border, elev. 1000 m, 6 July 2003, T. W. Smith 478 & pop. sample KYHR (MTMG).
- Notes: *Carex roanensis* is locally very abundant at this location. These three collections are within 2 km of each other along the same slope of Black Mtn., and are considered to be a single population.

North Carolina

- 14. Ashe County: Oak-hickory woods on Bluff Mtn., 24 June 1961, A. E. Radford 44046 (NCU); Dry woods, Bluff Mtn., 7 July 1966, A. E. Radford 44907 (NCU); Rich woods on Bluff Mtn., 15 June 1968, A. E. Radford 45504 (NCU); Bluff Mtn., 14 July 1999, J. T. Donaldson 4349 (ETSU); Paddy Mtn., 12 October 1999, J. T. Donaldson 4451 (ETSU); Peak Mtn., 14 October 1999, J. T. Donaldson 4459 (ETSU); Three Top Mtn., 8 October 1999, J. T. Donaldson 4448 (ETSU).
- Notes: Four separate populations from adjacent mountains Bluff, Paddy, Peak and Three Top. The distances between populations range from 4 to 8 km. Radford's collections were originally determined as *C. virescens*.
- 15. Watauga County: Potato Hill, 5 October 1999, J. T. Donaldson 4447 (ETSU).

- Avery County: Maple-birch-magnolia (Cove) association, Frank olivine deposit,
 3.2 km S of Minneapolis, 11 July 1946, A. E. Radford s.n. (NCU); Wooded slope,
 1.6 km NNE of Pyatte on road to Mt. Pleasant, 17 June 1958, H. E. Ahles 43669 (NCU).
- Notes: These two collections represent separate populations, one north and one south of Mt. Pleasant and separated by ca. 5 km. Radford's collection was originally determined as *C. aestivalis*, subsequently annotated to *C. swanii*. Ahles' collection was first determined as *C. virescens*.
- Mitchell County: Bean Creek Rd., sparse along the road and on wooded slopes above, 8 June 2003, T. W. Smith 469 (MTMG).
- Notes: This location was first discovered by David Danley (National Forests in NC, pers. comm.).
- Mitchell County: Upland woods border, 3.7 km NNW of Spruce Pine on NC 26 along Bear Creek, 16 June 1958, *H. E. Ahles 43159* (NCU); Wooded slope, 0.8 km N of Penland, then 0.8 km W on road to Boonford, 23 July 1958, *H. E. Ahles 47170* (NCU).
- Notes: Both specimens were originally determined as C. virescens. The label data suggests that these collections were taken within 1 km of each other, and are treated as a single population.
- Mitchell and McDowell County: Spruce Pine, rocky banks of Lynn Gap Rd. about 0.4 km below Blue Ridge Parkway underpass, 25 June, 1986, J. A. Churchill 86094 (MSC); Little Switzerland, rocky woods along Ginseng Gorge Trail below Old Lynn Inn, 25 June 1986, J. A. Churchill 86093 (MSC);
- Notes: These two collections are from the same population, straddling the Mitchell-McDowell county line.

McDowell County: About 16 km N of Old Fort, along the Mountains to Sea Trail,
 0.8 km W of Hazel Nut Gap and the Blue Ridge Parkway, Grandfather Ranger District, Pisgah National Forest., elev. 1080 m, habitat montane oak-hickory forest, 19 June 2003, *David Danley 7250* (dd).

Notes: Locations 19 and 20 are ca. 12 km apart.

 Yancey County: Mtn. cove, 7 km N of Swiss, 16 July 1958, *H. E. Ahles* 46802 (NCU).

Notes: Originally determined as C. virescens.

- 22. Buncombe County: Razor Mtn., 4 June 2003, J. T. Donaldson 5354 (ETSU); Pisgah National Forest, Appalachian Ranger District,1000 m S of NC 197 and 250 m W of left fork of Straight Creek, northern hardwood forest dominated by Acersaccharum, Aesculus flava, Betula alleghaniensis and Fagus grandifolia,elev. 1150 m, 11 June 2003, G. Kauffman 1125 (dd); Sugarhouse Cove, sparse along old track at the edge of rich cove forest, elev. 950 m, 17 June 2003, T. W. Smith pop. sample NCBR (MTMG).
- Notes: These three populations are separated by 2 to 4 km. An additional sight record in the NC Natural Heritage Program database from Snake Den Rock is within a few kilometres of these populations (Misty Franklin, NC Natural Heritage Program, pers. comm.).
- 23. Buncombe County: Tanbark Ridge, NE of Asheville, W of Blue Ridge Parkway at mile marker 374.5 (Tanbark Tunnel). Up a ravine, ca. 400-800 m NW of tunnel, under mixed hardwood-conifer forest, rich mesic slopes, elev. 1030 m, 29 July 1987, C. T. Bryson 6807 (VPI).
- Notes: TWS relocated this population in 2003, but no additional collections were made.

- 24. Haywood County: Pisgah National Forest, Pisgah Ranger District, N of Middle Prong Wilderness, 120 m W of Middle Prong and 70 m N of Little Beartrap Branch, in rock-strewn, rich cove forest community dominated by *Liriodendron* tulipifera and minor amounts of Tilia americana, Acersaccharum, Aesculus flava, and Halesia tetraptera, elev. 1075 m, 19 June 2003, G. Kauffman 1133 (dd).
- Transylvania County: Fork River Ridge, 10 June 1962, A. E. Radford 44591 (NCU); Cove forest, Pisgah National Forest, ridges above Cove Creek, Liriodendron/Tsuga forest, elev. 970 m, 19 June 2003, T. W. Smith pop. sample NCTR (MTMG).
- Notes: The 1962 collection was originally determined as C. virescens.

Tennessee

- Johnson County: Beaverdam Creek, Wallace Rd, W of Snyder Lane, 7 October 2001, H. R. DeSelm 01-238 (TENN).
- Notes: A single *C. roanensis* plant was observed by JTD at the Nature Conservancy's John R. Dickey Birch Branch Sanctuary, but no voucher was taken. In addition, Joe McGuiness collected *C. roanensis* from Holston Mtn. in Sullivan County, but the voucher could not be located.
- Carter County: Walnut Mtn.: Fish Springs, on roadside bank just SSW of Firescald Knob on Rt. 39, C. virescens & C. aestivalis etc. absent, 5 August 1986, J. A. Churchill 86279, (TENN, MSC, VDB); J. T. Donaldson collections at ETSU: 29 July 1993, 644; 28 June 1993, 940; 28 June 1993, 941; 2 September 1995, 2307; 31 July 1999, 4377; 2 July 1999, 4319; Cherokee National Forest, Rt. 50, growing along road with C. virescens, 26 June 2003, T. W. Smith pop. sample TNCR (MTMG). Roan Mtn.: Rich moist soil under beech above toll road to Roan Mtn., 2 August 1936, D. M. Brown 255 (holotype at US, isotypes at MICH, ETSU, DUKE, Hermann 1947); Roan Mtn., elev. 1920 m, open moist

ground, 12 July 1964, Ken & Louise Rogers s.n. (TENN); Abundant along old Hack Rd., 1280 to 1460 m, northern hardwood forest, Roan Mtn., 5 August 1981, T. S. Patrick 3134 (WIS); About 1460 m, northern hardwoods along Hack Rd., Roan Mtn., 5 August 1981, T. S. Patrick 3136 (WIS). J. T. Donaldson collections at ETSU: 26 July 1993, 645; 29 June 1993, 939; 11 August 1994 1665; 29 September 1995, 2526; 26 June 1996, 2969; 15 September 1998, 3923; 15 September 1998, 3923A; 16 September 1998, 3929A; 16 September 1998, 3929B; 16 September 1998, 3929C; 16 September 1998, 3930; 15 September 1998, 3932; 1 October 2000, 4718; 1 October 2000, 4719; 1 October 2000, 4720; 1 October 2000, 4721; 1 October 2000, 4723; At the edge of a mown ditch beside the road up to Roan Mtn., on the upslope side of the road, steep slope, red and sugar maple, ash, 8 June 2004, T. W. Smith 470 (MTMG); Appalachian Trail at Carvers Gap Creek Rd. crossing on NC/TN border, growing with C. aestivalis, 27 June 2003, T. W. Smith pop. sample NCMiR (MTMG). Ripshin Ridge: 01-110 Stanley Rd. ca 1.6 km from Rt. 19E at Tiger Valley, 23 July 2001, H. R. DeSelm 01-110 (TENN). Clarke Mtn.: J. T. Donaldson collections at ETSU: 29 September 1995, 2506; 11 September 1998, 4007; 11 September 1998, 4008; 11 October 1998, 4009; 7 June 1999, 4283; 19 June 1999, 4301; 19 June 1999, 4302; Cherokee National Forest, up ridge about 90 m from parking area, Moffett Laurel, 7 June 1999, Carl Nordman s.n. (TENN); First knob north of parking area, Moffet Laurel, 7 June 1999, Carl Nordman s.n. (TENN)

Notes: *Carex roanensis* is very common in the vicinity of Roan Mountain, and is often locally more abundant than either *C. virescens* or *C. aestivalis*. We have divided these collections into four populations from NE to SW: Walnut Mtn. (including Little Pond Mtn., White Rocks Mtn., and Dennis Cove), Roan Mtn. (including Hughes Gap, Doll Flats, and George Creek), Ripshin Ridge and Clarke Mtn. (including Moffett Laurel Botanical Area). However, as these populations are more-or-less continuous across the upper slopes and ridges in the area it may be more appropriate to treat these as subpopulations of a single Roan Massif population. In addition to the vouchers listed here, there are sight records for all of these locations on file at the TN Division of Natural Heritage (Roger McCoy, TN Division of Natural Heritage, pers. comm.). JTD has observed C. roanensis on the NC side of Roan Massif, in Mitchell County (NC 261 ca. 3.2 km S of Carvers Gap) and Avery County (Big Yellow Mtn.).

- Unicoi County: Piney Grove, Piney Grove Rd. near County Line and near Grindstaff Lane, 9 June 2001, H. R. DeSelm 01-050 (TENN).
- 29. Unicoi County: On steep hardwood slope near beech tree ca. 200 m below Tumbling Brook Falls and 200 m above Chandler Cove Rd. at bridge, 15 June 1985, J. A. Churchill 85070 (MSC, VDB, WIS); On gneiss rock outcrop in rich black loam in ravine below falls of Spivey Creek above Chandler Hollow Rd., 01 August 1985, J. A. Churchill 85221 (MICH); At base of Spivey Falls on a large rock off Rt. 19W, 01 July 1988, J. A. Churchill 88051 (VPI).
- Notes: MJW with J. A. Churchill observed two plants of *C. roanensis* growing on a large boulder at this site in 1991, but no collections were made. TWS searched the area unsuccessfully in 2003. This is the location reported by Churchill and Wurdack (1986). They cited two specimens, *J.A. Churchill 85132 & 85221*, which were to be deposited at MSC, TENN, US, and VDB. However, 85221 could not be located in the collections from MSC, TENN, or VDB, but a duplicate was found at MICH. No *C. roanensis* specimen corresponding to 85132 could be found at any herbarium. An annotation on the *J. A. Churchill 85070* duplicate from MSC indicates it was used in preparing the illustrations for their paper, which suggests that the specimen referred to as 85132 is actually this sheet.

30. Polk County: Smith/Little Frog Mtn., Cherokee National Forest near Ducktown, elev. 580 m., mixed hardwood forest with Liriodendron, Sassafras, Nyssa, Robinia pseudoacacia, Aralia spinosa, Acer rubrum, Rubus allegheniensis, Smilax rotundifolia, Vitis aestivalis, Potentilla canadensis, Carex allegheniensis, C. virescens, Microstegium vimineum, and Dennstaedtia, 21 July 2005, J. T. Donaldson 6800 (ETSU).

Georgia

- 31. Rabun County: Clayton, draped over a large boulder above the upper reaches of Tallulah River about 1.6 km from road end and on W side of river, 4 July 1986, J. A. Churchill 86290 (MSC).
- Notes: MJW searched this location in 1991 and TWS searched it in 2003. Neither succeeded in finding *C. roanensis*.

Discussion

It is clear from this review that *C. roanensis* has been overlooked in the field, and further work is required to develop a more accurate picture of its rarity. The data available at present are consistent with a global conservation status ranking of G3, or vulnerable (NatureServe 2006), based on 44 populations. Population numbers within states suggest rankings of S1, critically imperilled, for Pennsylvania (3 populations), West Virginia (3), Kentucky (1), and Georgia (1), and S2, imperilled, for Virginia (10), Tennessee (8), and North Carolina (18). These should be considered preliminary assessments, as, with the exception of the Roan Massif populations, no population census data has been collected (Roger McCoy, TN Division of Natural Heritage, pers. comm.). Further investigation into the population dynamics and natural history of this species is required to fully assess its conservation status.