BIOGEOGRAPHY, ECOLOGY, AND EVOLUTION OF THE ENDEMIC VASCULAR FLORA OF THE GLACIATED GREAT LAKES REGION: A CASE STUDY OF THE *SOLIDAGO SIMPLEX* SPECIES COMPLEX

by

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DEDICATION

To Andy and Sequoia, whose countless hours of help, encouragement, and fetch made this all worthwhile.

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BIOGEOGRAPHY, ECOLOGY, AND EVOLUTION OF THE ENDEMIC VASCULAR FLORA OF THE GLACIATED GREAT LAKES REGION: A CASE STUDY OF THE *SOLIDAGO SIMPLEX* SPECIES COMPLEX

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Pleistocene glacial activity transformed the Great Lakes basin into a natural laboratory where the effects of past glaciation on the development of the regional flora and the evolution of endemic species can be readily examined. This dissertation focuses specifically on the ecology and evolution of the endemic flora of the Great Lakes region. Chapter II characterizes biogeographic and ecological patterns of the 60 endemic vascular plants that have been described from the region. The majority of these plants are restricted to specialized habitats in the northern Great Lakes region. Many of these endemics have been hypothesized to be recently evolved edaphic specialists, but the evolution of the vast majority remains unstudied. Chapters III, IV, and V examine cytogeographic, phylogeographic, and ecological patterns in *Solidago simplex* across North America and in the Great Lakes region. Cytogeographic studies revealed patterns that were more complex than previously realized. This data combined with phylogeographic analyses of cpDNA suggest that 1) tetraploids within *Solidago simplex* formed multiple times, 2) the Great Lakes region was populated by migrants from multiple glacial refugia, 3) the southeastern United States and Beringia were not primary sources of postglacial migrants into the Great Lakes region, and 4) there is a significant biogeographic connection between the Great Lakes region and the Rocky Mountains. Field and herbarium studies revealed that *Solidago simplex* populations in the Great Lakes region are separated by a combination of cytological, ecogeographic, morphological, and phenological differences. These data suggest that the Great Lakes region harbors at least three reproductively isolated species. Diploid plants in the northern Great Lakes region are referable to *Solidago simplex* var. *simplex*. The sand dune endemic, *S. simplex* var. *gillmanii*, is ecologically and morphologically distinct from all other entities in the region and should be elevated to species status. Tetraploid rock outcrop plants, normally recognized as *S. simplex* var. *ontarioensis*, represent at least two distinct entities. Their evolution and circumscription require additional study. Overall, this research indicates that a complex Pleistocene history and adaptation to specialized habitats has driven diversification and speciation in *Solidago simplex* and likely the broader endemic flora as well.

CHAPTER I

INTRODUCTION

Phylogeographic and paleoecological studies indicate that Pleistocene glacial cycles caused pronounced changes in species distributions and greatly altered the genetic structure within species-populations (Hewitt 1996, 2000). The direct effects of glaciation are most obvious at northern latitudes where species had to repopulate the landscape following glacial retreat. The classical view of North American Pleistocene biogeography posits that repeated continental glaciations caused mass extinctions of the biota of the northern latitudes and forced species to retreat to southern-latitude refugia during glacial periods. Species subsequently migrated out of these southern survivia and expanded their ranges during interglacial periods (Davis 1983; Huntley and Webb 1989; Hewitt 1996). Several recent studies of North American temperate species, however, seem to support earlier hypotheses (e.g., those of Gleason 1923; Braun 1928) that proposed that many species survived glacial periods in cryptic refugia closer to the glacial boundary (McLachlan and Clark 2004; McLachlan et al. 2005; King et al. 2009). At present, however, the population histories of most North American plant species and the overall effects of glaciation on population distribution and divergence remain woefully understudied. This is especially true for northern temperate species, herbaceous plants, and species restricted to specialized habitats.

The major objective of this dissertation is to develop a framework that can be used to address hypotheses concerning the origins and evolution of floristic diversity in glaciated North America. My dissertation research has focused specifically on the ecology and evolution of the endemic vascular flora of the glaciated Great Lakes region. The dissertation is divided into four primary chapters. Chapter II characterizes biogeographic and ecological patterns in the endemic vascular flora of the Great Lakes region. In chapters III, IV, and V, I used the *Solidago simplex* species complex (with two endemic varieties in the Great Lakes region) as a model system to address specific biogeographic and evolutionary hypotheses. These chapters examine cytogeographic, phylogeographic, and ecological patterns in *Solidago simplex* (and four closely related species in *Solidago* subsect. *Humiles*) across North America and in the Great Lakes region. The last chapter synthesizes the research on the endemic flora of the Great Lakes region and *Solidago simplex* and discusses the broader impacts of the work and possible future directions.

Chapter II. Evolutionary and ecological biogeography of the endemic flora of the glaciated Great Lakes region. The Great Lakes basin lies entirely within the limits of Pleistocene glaciation. Continental ice sheets invaded the region at least six times during the Pleistocene, most recently during the Wisconsinan glaciation that ended roughly 15,000 YBP (Larson and Schaetzl 2001). Species returned to the region only after recession of the ice sheets. Thus in geological terms, the flora of the Great Lakes region is extremely young. Therefore, the presence of endemic plant species (e.g., *Cirsium pitcheri*, *Iris lacustris*, *Solidago houghtonii*, and numerous less well-characterized taxa) in this recently glaciated landscape raises a number of questions. Did these species evolve during the Pleistocene, migrate into the region following deglaciation, and subsequently become restricted to the region (i.e., are they relicts of previously more widespread taxa)? Or conversely did these species evolve *in situ* since the end of the last glacial period? What biogeographic and ecological factors have been important to their evolution and persistence within the region?

To date, the endemic flora of the Great Lakes region has not been well characterized and answers to the above-stated questions have gone largely unstudied. In this chapter I compiled a comprehensive list of the endemic vascular plant taxa that have been described from the Great Lakes region. I then used specimen data and literature reports to characterize the geographic and habitat distributions of the described endemics within the region. Lastly, I reviewed and synthesized the available biogeographic, ecological, evolutionary, and taxonomic information available for each of the described endemics to evaluate the support for the above-stated questions.

Chapter III. Polyploidy, speciation, and infraspecific cytotype variation in goldenrods: the cytogeography of Solidago subsection Humiles. *Solidago simplex* has traditionally been divided into two subspecies that are defined exclusively along lines of infraspecific cytotype variation (Ringius 1986; Semple and Cook 2006). Both subspecies occur in the Great Lakes region, the only part of North America where they are regionally sympatric. In the 1980's, Gordon Ringius proposed that tetraploid populations of *S. simplex* in eastern North America (which he recognized as subsp. *randii*) had evolved from a single migration and subsequent polyploidization of diploid *S. simplex* from western North America sometime during the Wisconsinan glacial period (Ringius 1986; Ringius and Semple 1987). The recent discovery in the southeastern United States of three closely related species in *Solidago* subsect. *Humiles* (which were not considered in the earlier studies) raises doubts over the rather simple biogeographic hypotheses outlined by Ringius. In addition, the more widespread occurrence of presumably diploid populations in the northern Great Lakes region (occurrence first noted by Zimmerman 1956; distribution discussed by Voss 1996) suggests that the cytogeography of *S. simplex* in the Great Lakes region has not been adequately characterized.

In this chapter, I used DNA ploidy determinations from flow cytometry, chromosome counts, and published data to examine cytogeographic patterns in *Solidago* subsect. *Humiles* (*S. simplex* and four closely related species) across North America with expanded taxon and geographic sampling in the southeastern United States and the Great Lakes region. I then evaluated previous biogeographic and taxonomic hypotheses in light of the cytogeographic patterns and infraspecific cytotype variation recovered in *S.* subsect. *Humiles* (in a framework similar to that described by Soltis et al. 2007). Lastly, I compared patterns of infraspecific cytotype variation found in *S. simplex* to those found in other *Solidago* species.

Chapter IV. Phylogeographic patterns in Solidago simplex in North America.

There have been few phylogeographic studies of widespread northern species, herbaceous species, and species restricted to extreme environments in North America. Our understanding of broad scale phylogeographic patterns in northern temperate parts of the continent is therefore incomplete. *Solidago simplex* has a widespread transcontinental distribution (with a significant west to east disjunction), and the species complex likely survived glaciation in multiple Pleistocene refugia. In this chapter, I conducted a phylogeographic study of *Solidago* subsect. *Humiles* across its North American range. This study examines biogeographic patterns and glacial history across the entire continent and provides an opportunity to uncover phylogeographic patterns that are likely different from those recovered from plant species that are restricted the southeastern United States.

I examined the population-level structuring of chloroplast genetic diversity in *Solidago simplex* and four other species in *Solidago* subsect. *Humiles* across their entire North America distribution. The recovered phylogeography will not only allow me to test specific biogeographic and evolutionary hypotheses in *S. simplex*, but will also provide a framework from which we can examine hypotheses concerning 1) the floristic connectivity of western and eastern North America during the Pleistocene, 2) the complexity of the glacial histories of widespread North American species, and 3) the dual roles of historical glaciation and recent microevolution in shaping North American biodiversity.

Chapter V. Disjunction, habitat specificity, and flowering phenology: the influences of geography and ecology on reproductive isolation and speciation in Great Lakes populations of Solidago simplex. My review in Chapter II uncovered 60 endemic plant taxa that have been described from the Great Lakes region. Thirty-two of these taxa appeared to be distinct entities and were characterized well enough that their geographic and habitat distributions in the region could be examined in detail. Analysis of this data revealed that nearly all of these endemics occurred in open, non-forested habitats in the northern part of the Great Lakes region, and 53% of the endemics were restricted to habitats along the shores of the Great Lakes. The data suggest that adaptation of plants to different specialized habitats in the recently glaciated landscape has likely driven the evolution of edaphic endemism and ecological speciation.

In this chapter, I used the *Solidago simplex* species complex as a model group in which to examine fine-scale patterns of ecological differentiation across the Great Lakes region. Historical data from herbarium specimens, field data from natural populations, and data from a common garden were used to address the following questions: 1) What population-, habitat-, and taxon-level differences in ecology and flowering phenology are present in *S. simplex* populations across their range in the Great Lakes region? 2) Are the differences environmentally or genetically based (e.g., are they maintained in a common garden)? 3) Do these data suggest that *S. simplex* taxa in the Great Lakes region are reproductively isolated and behaving as biological species?

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CHAPTER II

EVOLUTIONARY AND ECOLOGICAL BIOGEOGRAPHY OF THE ENDEMIC FLORA OF THE GLACIATED GREAT LAKES REGION

The Great Lakes basin lies entirely within the limits of Pleistocene glaciation (Fig. 2.1). Continental ice sheets invaded the region at least six times during the Pleistocene, each time exterminating the biota of the region and drastically reshaping the landscape (Larson and Schaetzl 2001). The most recent glacial interval, the Wisconsinan, ended roughly 15,000 YBP. Unlike species in some northern regions of North America that likely survived glacial periods *in situ* (e.g., species in Beringia or coastal regions of the Pacific Northwest, New England, and the Maritime Provinces of Canada; reviewed in Pielou 1991; Abbott et al. 2000), species inhabiting the Great Lakes region colonized only after recession of the ice sheets (despite assertions to the contrary by Fernald 1925, 1935). Thus in geologic terms, the contemporary flora of the Great Lakes region is extremely young, having assembled within the last 10,000 to 15,000 years.

The majority of the native flora (ca. 2500 species) consists of wide-ranging species that inhabit the basic vegetation formations of the region (e.g., temperate and mixed forest, wetlands). Biogeographic data have long suggested that this flora is composed of species with decidedly different floristic affinities (Gleason 1923; Fernald 1935). Gleason (1923) proposed that the flora of the upper Midwest migrated into the region from five primary sources, the southern Appalachians, the southern Coastal Plain, the Ozark Mountains, the Great Plains, and eastern Canada. Remington (1968) noted similar patterns in the bird fauna of the region and included the Great Lakes basin as one of his suture zones (areas of secondary contact between species that survived glaciation in different refugia). A number of recent studies (e.g., Dobes et al. 2004; Swenson and Howard 2005; Placyk et al. 2007) have lent support to the view that the Great Lakes region is indeed a zone of secondary contact for a number of different species.

In addition to the more-or-less widespread elements of the flora, a small number of endemic plant species have been described from the region as well. Many of these described Great Lakes region endemics, however, have not received wide recognition as distinct taxonomic entities. This was highlighted by Loehle (2006), when he concluded that the evolution of endemic species generally takes a long time, and that many endemics described from glaciated regions are likely taxonomic artifacts. Recent studies from arctic regions, however, suggest that substantial amounts of biological species diversity at northern latitudes has previously gone unrecognized (reviewed in Brochmann and Brysting 2008). And a number of empirical and theoretical studies suggest that ecological speciation (e.g., edaphic differentiation) can occur on relatively short timescales (Levin 1993, 2004; Rundle and Nosil 2005; Hendry et al. 2007).

The presence of endemic plant species (e.g., *Cirsium pitcheri*, *Iris lacustris*, *Solidago houghtonii*, and numerous less well-characterized taxa) in this recently glaciated landscape raises a number of questions. Did these species evolve during the Pleistocene, migrate into the region following deglaciation, and subsequently become restricted to the region (i.e., are they paleoendemics or relicts of previously more widespread taxa)? Or conversely did these species evolve *in situ* since the end of the last glacial period? If so, what biogeographic and ecological factors have been important to their evolution and persistence within the region?

Objectives. These elements of the flora may retain some signal of past evolutionary and biogeographic events that may help elucidate the history of the flora as a whole as well as shed light on the evolutionary processes operative in recently glaciated lowland environments. To date, however, the endemic flora of the Great Lakes region has not been well characterized and the above-stated questions have largely gone unstudied. The primary objectives of this study were to 1) search the literature and compile a comprehensive list of endemic vascular plant taxa that have been described from the Great Lakes region, 2) use specimen data and reports from the literature to characterize the geographic and habitat distributions of the described endemics to the extent possible, and 3) synthesize the available biogeographic, ecological, evolutionary, and taxonomic information for each of the described endemics to evaluate the support for the above-stated questions.

MATERIALS AND METHODS

Study Region. The glaciated Great Lakes region of North America is located in the interior, northeastern part of the continent between latitudes 41.0° N and 50.5° N and longitudes 75.8° W and 92.5° W (Fig. 2.1). The region is centered around the five Laurentian Great Lakes, which together comprise the largest freshwater system on the planet (Schaetzl and Isard 2002). The region is bounded on the south and west by the states of Illinois, Indiana, Michigan, Minnesota, New York, Ohio, Pennsylvania, and Wisconsin and on the north and east by the province of Ontario. The surface area of the lakes and the drainage basin that surrounds them covers approximately 765,990 km^2 (Larson and Schaetzl 2001; Schaetzl and Isard 2002). The elevation of the region ranges from a maximum of ca. 701 m above sea level at Eagle Mountain in Cook Co., Minnesota to a minimum of ca. 75 m above sea level at the outlet of Lake Ontario. The present-day Great Lakes drain via the St. Lawrence River into the Gulf of St. Lawrence and northern Atlantic Ocean.

The Great Lakes basin lies entirely within the limits of Pleistocene glaciation (Dorr and Eschman 1970; Williams et al. 1998). Continental ice sheets invaded the region at least six times during the Pleistocene, most recently during the Wisconsinan glaciation that ended roughly 15,000 YBP (Larson and Schaetzl 2001). During each glacial period, the ice sheets scoured the landscape, deepened the lake basins, and depressed the earth's crust under their massive weight. The present-day surficial characteristics of the region are the aftermath of those repeated glaciations. Glacial deposits of the most recent Wisconsinan glaciation and the erosional processes that followed deglaciation dominate the landscape of the Great Lakes basin and have acted together to form the mosaic of landforms and habitats present across the region today.

The Great Lakes region has generally been divided into two broad physiographic provinces based on topography and underlying bedrock geology (Larson and Schaetzl 2001). The northern and western parts of the Great Lakes region are part of the Laurentian (or Superior) Uplands. This area is the southwestern-most extension of the Canadian Shield, an area of crystalline Precambrian rocks that covers most of eastern Canada. The granite hills of the Laurentian Uplands and rock outcrops along the shores of Lake Superior are remnants of an ancient mountain range that has worn away by some two billion years of erosion and glaciation. Soils in this region are typically thin and nutrient poor, and bedrock dominates much of the landscape. This area around the perimeter of Lake Superior forms the topographically most rugged and highest elevation part of the Great Lakes basin.

The southern and eastern extents of the basin form the Eastern Lakes section of the Central Lowlands province. This area is characterized by generally low relief and is underlain by calcareous, sedimentary bedrock of Paleozoic age. The glacially transported soils of the Eastern Lakes section are typically deep and fertile, as exemplified by the till plains that stretch across much of northern Indiana, northern Ohio, and southern Michigan. There are, however, extensive areas of glaciofluvial deposits in parts of northern and western Michigan and northern Wisconsin, which form broad, sandy (and often droughty) outwash plains. Along the northern boundary of the Eastern Lakes section, the resistant dolomite of the Niagara Escarpment forms a broad arc of cliffs and rock shores that run from the Niagara region of New York to the Bruce Peninsula and Manitoulin Island in Ontario through the Garden Peninsula of Michigan to the cliffs and outcrops of the Door Peninsula in Wisconsin. In the southern part of the region, glacial till covers most of the bedrock, however, limestone bedrock surfaces in several areas, where it forms the rocky islands and Marblehead Peninsula of western Lake Erie and the extensive alvar (limestone pavement) formations of the Napanee plain at the eastern end of Lake Ontario.

One of the most prominent and ecologically dynamic features of the Great Lakes region (aside from the lakes themselves) is the boundary between the lakes and the surrounding land surface. There are more miles of freshwater shoreline in the Great

Lakes region (ca. 16,900 km if island shorelines are included) than in any other region in the world. Shorelines range from the low, marsh-lined shores along Lakes Erie and Ontario, to the rocky shores and cliffs of Lakes Huron and Superior. Sand beaches and dunes are another major feature of the shores of the Great Lakes. Great Lakes sand dunes are best developed along the southern and eastern shores of Lake Michigan (e.g., Indiana Dunes, Sleeping Bear Dunes) and the southern shore of Lake Superior (e.g., Grand Sable Dunes), but all of the Great Lakes have active dunes of some extent.

Literature Review of Endemic Taxa. A preliminary list of endemic vascular plant taxa was generated by reviews of species and infraspecific taxa discussed in Fernald (1950), Argus and White (1982), Voss (1972, 1985, 1996), and the published volumes from the Flora of North America project. Additional floristic manuals, taxonomic treatments, and specimen databases were utilized during targeted searches for specific taxa.

Those taxa that were determined to be entirely restricted to the Great Lakes drainage basin (or restricted to the basin but with several populations immediately outside the drainage basin divide, usually along shorelines or drainage outlets of the glacial Great Lakes) were included in the list of endemic taxa. Species (or infraspecific taxa) whose distributions are predominantly within the glaciated Great Lakes region but also extend outside of the drainage basin (greater than 15% of populations outside the basin) were included in the list as "near endemics." Wider-ranging, upper Midwestern endemics, such as Hill's Oak (*Quercus ellipsoidalis*), were not included in the study. Endemic microspecies described in the genera *Antennaria*, *Crataegus* and *Rubus* (which typically represent distinctive, apomictic lineages) were also not included in the study.

Source Material and Biogeographic and Ecological Data. Distributional and habitat data for endemic taxa were obtained from a variety of sources, including a number of regional, state, and local floras, taxonomic treatments and monographs, rare species reports from federal, state, and local agencies, research articles, specimen databases, fieldwork by the author, and examination of herbarium specimens primarily at MICH, UMBS, and WAT.

RESULTS

The literature review uncovered a total of 60 endemic vascular plant taxa that have been described from the Great Lakes region (Tables 2.1-2.2). The endemic taxa are distributed among 29 families and 44 genera of flowering plants. The family with the greatest representation in the list was the Asteraceae with nine genera and 16 endemic taxa. The genus *Solidago* had the greatest individual representation in the list, with eight Great Lakes endemic taxa.

Most endemic vascular plants described from the Great Lakes region have not been widely or consistently recognized as distinct taxonomic entities and have not been closely studied (see discussion of individual endemics in Appendix 2.1). Review of herbarium specimens and the literature suggested that 32 of the endemic taxa were distinct enough to be tentatively recognized taxonomically (Table 2.1). The remaining 28 endemic taxa have not been widely recognized (Table 2.2). This last list included populations of four taxa (*Apocynum sibiricum* f. *arenarium*, *Erigeron philadelphicus* var. *provancheri*, *Symphyotrichum pilosum* var. *pringlei*, and *Schizachyrium littorale*) that potentially represent undescribed, incipient, regional endemics as opposed to disjunct occurrences of more wide-ranging taxa (Appendix 2.1).

Examination of occurrence data for the 32 tentatively recognized endemic vascular plants revealed that they were not evenly distributed throughout the Great Lakes region (examples of distributions shown in Figs. 2.2-2.10). At a lake-basin level, more endemics have been documented from the Lake Huron and Lake Michigan basins than the other basins (23 and 27 endemics each, respectively). The Lake Superior basin was second with 14 endemic taxa, while the Lake Erie and Lake Ontario basins harbored the lowest diversity of endemics with 11 and 6 taxa, respectively. Closer examination revealed that distributions were uneven within most individual lake basins as well (e.g., all endemics, except *Linum medium* var. *medium*, from the Lake Huron basin are restricted to the perimeter of the main lake basin and absent from the eastern Georgian Bay area). Overall, there was a pattern of higher endemic richness in the north-central part of the region (especially along the boundary of the Niagara Escarpment in Michigan and Ontario) and lower endemic richness in the extreme northern (Lake Superior) and extreme southern and eastern (Lake Erie and Lake Ontario) portions of region.

Examination of habitat distributions also revealed major patterns within the region. The majority of the 32 tentatively recognized endemic vascular plants occur only or predominantly along the shores of the Great Lakes (ca. 17 species). Two of the wider ranging, near endemic species, *Hypericum kalmianum* and *Solidago ohioensis*, also occur frequently along the Great Lakes shores but occur frequently inland as well. Shoreline specialists occupy three broad types of shoreline habitats: active dune systems (9 species), rocky shorelines and/or alvar formations (10 species), and sandy beaches, calcareous shores, and interdunal meadows (9 species). Several of the endemic taxa that occur predominantly along the Great Lakes shores are sometimes present at inland sites as well, typically along shorelines of the glacial Great Lakes or in calcareous fen-like habitats that are presumably, ecologically analogous to Great Lakes shorelines. Thirteen endemic taxa have a primarily non-shoreline distribution. These taxa occur in a variety of habitats, including inland pine barrens and sand prairies, stabilized wooded dunes, and northern white-cedar swamps. Endemic taxa are almost entirely absent from the major vegetation formations of the region (e.g., southern deciduous forest, mixed and boreal forest, widespread wetland habitats, floodplains).

DISCUSSION

Endemic vascular plants have traditionally been classified as either paleoendemics, which are relict species that were once more widespread but now persist as small, remnant populations, or neoendemics, which are species that evolved more recently and have not expanded their ranges (following Stebbins and Major 1965). Stebbins and Major (1965) admitted that this dichotomy of endemics is idealized, and a spectrum of intermediate scenarios could be envisioned. A scenario in which a species originated in the distant past, underwent range contraction and fragmentation during the Pleistocene, and then differentiated into a number of narrowly distributed sibling taxa during the Holocene would combine elements of both models. Likewise, a recently evolved species could have been more widespread in the past (e.g., in early postglacial times) and due to climate change or competitive interactions could now be restricted to a few isolated locations.

There is evidence that some Great Lakes region endemics likely represent remnants of previously more widespread distributions. Phylogeographic work by Chung et al. (2004) suggested that *Oxytropis campestris* var. *chartacea* likely represents the southern remnant of a previously widespread species. Its closest relatives occur much further north in boreal and arctic regions of North America. *Polemonium occidentale* subsp. *lacustre* also likely represents a remnant of a previously more widespread distribution. These two species seem to comprise a variation of a more generalized biogeographic pattern in eastern North America, where species with predominantly western or boreal distributions are present in eastern North America as periglacial relicts (Olfelt et al. 1998; Cole and Kuchenreuther 2001). This pattern has not been very well studied.

The vast majority of described vascular plant endemics in the Great Lakes region appear to represent incipient edaphic endemics that are restricted to open, ecologically stressful habitats. Studies of edaphic endemics in other regions have concentrated overwhelmingly on taxa restricted to soils derived from serpentine or soils with high heavy metal content (Kruckeberg 1951; Mayer and Soltis 1994; Rajakaruna 2004; Harris and Rajakaruna 2009). But a number of habitats in the Great Lakes region, like limestone pavements (alvars), shoreline rock outcrops, active dune systems, and sand barrens can exert strong ecological selection pressures that could potentially drive the formation of local edaphic endemics (e.g., Maun 1994; Maun 1998). Studies of several Great Lakes endemics (e.g., *Cirsium pitcheri* and *Iris lacustris*) suggest that they represent incipient entities that evolved from more wide-ranging species that occur in unglaciated areas outside of the Great Lakes region (Loveless and Hamrick 1988; Hannan and Orick 2000).

Comparisons with Other North American Centers of Endemism. Jansson (2003) proposed that endemism is highest in regions with long, stable climatic histories and lowest in regions that have seen major climatic change in the recent past. Loehle's (2006) commentary on patterns of plant endemism in eastern North America supported this hypothesis and highlighted broad scale patterns in vascular plant endemism that have been documented by other major studies of North American endemism as well (e.g., Raven and Axelrod 1978; Gentry 1986; Sorrie and Weakley 2001; MacRoberts et al. 2002; Sorrie and Weakley 2006). Rates of endemism mirror patterns in total species diversity and are substantially higher in coastal, unglaciated areas of North America (Fig. 2.11). Interior, unglaciated regions of the continent (e.g., the Ozark Interior Highlands; Zollner et al. 2005), despite their geologic antiquity, do not have appreciably higher amounts of endemism than the Great Lakes region.

Thorough reviews of vascular plant endemism in adjacent areas of glaciated North America have not been performed, but it appears that the Great Lakes region harbors a larger number of endemic taxa than other northern, temperate areas of the continent. Harris and Rajakaruna (2009), however, suggested that inadequate knowledge of the flora and reluctance to recognize narrowly distributed edaphic endemics in glaciated regions have likely contributed to the idea that northeastern North America harbors few endemic taxa. Additional studies of vascular plant endemism in eastern North America are needed to shed light on patterns of endemism and species diversity in this part of the continent.

Summary. This review uncovered 60 endemic plant taxa that have been described from the Great Lakes region. Thirty-two of these taxa appear to be distinct entities and are characterized well enough that their geographic and habitat distributions in the region could be examined in detail. Analysis of this data revealed that nearly all of these endemics occurred in open, non-forested habitats in the northern part of the Great Lakes region, and 53% of the endemics were restricted to habitats along the shores of the Great Lakes. Considering that the Great Lakes region was largely forested (approximately 90-95% of the land surface) prior to European settlement, the endemic flora shows a marked affinity to regionally uncommon habitat types. These results suggest that adaptation of plants to different "extreme" habitats in the recently glaciated landscape has likely driven the evolution of edaphic endemism and ecological speciation.

Many of the described Great Lakes region endemics have not received wide recognition as distinct taxonomic entities. This is highlighted by the broad reviews of endemism by Gentry (1986) and Loehle (2006) discussed above. Loehle proposed that the evolution of endemic species takes a long time, and that many endemics described from glaciated regions are likely taxonomic artifacts. Recent studies from arctic regions, however, suggest that substantial amounts of biological species diversity at northern latitudes has previously gone unrecognized (reviewed in Brochmann and Brysting 2008). Additional studies of endemic plants in the Great Lakes region will be required to gain a better understanding of their evolution in this recently glaciated region.

Table 2.1. Geographic and habitat distributions of 32 endemic and near endemic vascular plant taxa from the glaciated Great Lakes region. Near endemic taxa have their distributions centered within the drainage basin but also have occurrences outside the drainage basin (ca. 15 percent or less). Taxa with only a few occurrences outside the drainage basin, primarily along drainage outlets of previous stages of the Great Lakes, are included with the endemics and are preceded by an asterisk (*). Geographic and habitat distributions were determined from specimen data and review of the literature.

	Geographic Distribution					Habitat Occurrence				
Endemic Taxon	Ontar.	Erie	Huron	Mich.	Super.	Dune	Rock, Alvar	Shore, Fen	Barren, Prairie	Other
1. Vascular Plant Taxa Endemic to the Great Lakes Basin										
Anacardiaceae										
Rhus aromatica var. *arenaria*	-	X	-	X	-	X	-	-	-	-
Asteraceae										
Cirsium pitcheri	-	-	X	X	X	X	-	-	-	-
Solidago hispida var. *huronensis*	-	-	X	-	X	X	-	-	-	-
Solidago houghtonii	X	-	X	X	-	-	X	X	-	-
Solidago simplex var. *gillmanii*	-	-	X	X	-	X	-	-	-	-
Solidago simplex var. *ontarioensis*	-	-	X	X	X	-	X	-	-	-
Solidago uliginosa (4*n*)	-	-	X	X	-	-	X	-	-	-
Solidago "vossii" (8*n*)	-	-	-	X	-	-	-	-	X	-
**Tetraneuris herbacea*	-	X	X	X	-	-	X	-	-	-
Brassicaceae										
Cakile endentula var. *lacustris*	X	X	X	X	X	-	-	X	-	-
Cyperaceae										
Carex scirpoidea subsp. *convoluta*	-	-	X	X	-	-	X	-	-	-
Fabaceae										
Oxytropis campestris var. *chartacea*	-	-	-	X	X	-	-	X	-	-
Iridaceae										
Iris lacustris	-	-	X	X	-	-	X	X	-	-
Linaceae										
Linum medium var. *medium*	-	-	X	-	-	-	-	X	-	-

Lycopodiaceae										
**Lycopodiella margueritae*	-	X	-	X	-	-	-	-	-	X
Lycopodiella subappressa	-	X	X	X	-	-	-	-	-	X
Ophioglossaceae										
Botrychium acuminatum	-	-	-	-	X	X	-	-	-	X
Botrychium pseudopinnatum	-	-	-	-	X	-	-	-	-	X
Poaceae										
Elymus lanceolatus subsp. psammophilus	-	-	X	X	X	X	-	-	-	-
Polemoniaceae										
Polemonium occidentale subsp. *lacustre*	-	-	-	-	X	-	-	-	-	X
Rosaceae										
Prunus alleghaniensis var. *davisii*	-	X	X	X	-	-	-	-	X	-
Prunus pumila var. *pumila*	X	X	X	X	X	X	-	-	-	-
Phrymaceae										
Mimulus michiganensis	-	-	X	X	-	-	-	X	-	X
Violaceae										
Viola novae-angliae subsp. *grisea*	-	-	-	X	-	-	-	-	X	-
Vitaceae										
Vitis riparia var. *syrticola*	X	X	X	X	-	X	X	-	-	-

2. Vascular Plant Taxa Endemic to the Great Lakes Basin and Upper Midwest (Near Endemics)

Asteraceae										
Solidago ohioensis	X	X	X	X	-	-	-	X	-	-
Solidago speciosa var. *jejunifolia*	-	-	X	X	X	-	-	-	X	-
Clusiaceae										
Hypericum kalmianum	X	X	X	X	-	-	X	X	-	-
Iridaceae										
Sisyrinchium strictum	-	-	-	X	X	-	X	-	X	X

Ophioglossaceae										
Botrychium mormo	-	-	X	X	X	-	-	-	-	X
Poaceae										
Calamovilfa longifolia var. *magna*	-	-	X	X	X	X	-	-	X	-
Valerianaceae										
Valeriana edulis var. *ciliata*	-	X	X	X	-	-	X	X	-	-

Table 2.2. Twenty-eight vascular plant taxa of uncertain biogeographic, evolutionary, and/or taxonomic status that 1) have been described as endemic to the glaciated Great Lakes region and/or 2) represent incipient taxa with convergent/parallel phenotypes similar to geographically disjunct taxa. The latter are preceded by an asterisk (*). The taxa have been divided into four categories that are not entirely mutually exclusive (e.g., 14 of the 27 taxa have a predominantly shoreline distribution, and most examples in this table have not been extensively studied).

1. Differentiated Populations from Sand Dunes and/or Great Lakes Shoreline Habitats

- **Apocynaceae**
  - *Apocynum sibiricum* forma *arenarium* (in part)
- **Asteraceae**
  - *Erigeron philadelphicus* var. *provancheri* (in part)
  - *Symphyotrichum pilosum* var. *pringlei* (in part)
- **Poaceae**
  - *Schizachyrium littorale* (in part)
- **Polygonaceae**
  - *Polygonum pensylvanicum* var. *eglandulosum*
- **Rutaceae**
  - *Ptelea trifoliata* var. *deamiana*
- **Salicaceae**
  - *Salix glaucophylloides* var. *albovestita*
  - *Salix glaucophylloides* var. *glaucophylla*
  - *Salix syrticola*

2. Disjunct but Apparently Undifferentiated Populations of more Wide-Ranging Taxa

- **Asteraceae**
  - *Arnica cordifolia* subsp. *whitneyi* - (*A. cordifolia* from western North America)
  - *Euthamia remota* - (*E. caroliniana* from the Atlantic Coastal Plain)
  - *Tanacetum huronense* var. *huronense* - (*T. bipinnatum* from arctic and western North America)
- **Cyperaceae**
  - *Eleocharis geniculata* var. *dispar* - (*E. geniculat*a from the southern United States)

3. Rare Taxa Known from Only One or Two Locations

- **Betulaceae**
  - *Betula murrayana* - (allopolyploid, known from single location)
- **Burmanniaceae**
  - *Thismia americana* - (unstudied, presumed extirpated)
- **Iridaceae**
  - *Sisyrinchium hastile* - (included in *S. albidum* in FNA, presumed extirpated)
- **Malvaceae**
  - *Iliamna remota* - (disjunct from Appalachians, two populations)

4. Taxa of Uncertain Taxonomic Distinction and/or Taxa not Extensively Studied

- **Asteraceae**
  - *Eupatorium rugosum* var. *tomentellum*
- **Betulaceae**
  - *Betula papyrifera* forma *coriacea*
  - *Betula pumila* var. *glabra*
  - *Betula* ×*purpusii*
- **Caprifoliaceae**
  - *Campanula rotundifolia* var. *velutina*

Diervilla lonicera var. *hypomalaca*
Cornaceae
Cornus baileyi
Grossulariaceae
Ribes cynosbati var. *atrox*
Lamiaceae
Stachys palustris var. *nipigonensis*
Primulaceae
Primula intercedens
Rosaceae
Amelanchier huronensis

Figure 2.1. Topographic relief map of the glaciated Great Lakes region of North America. The red line indicates the approximate boundary of the Great Lakes drainage basin divide. The dashed black line indicates the approximate maximum extent of the most recent, Wisconsinan glaciation. Map was modified from: Color North American Shaded Relief Map (USGS National Center for EROS, 2004).

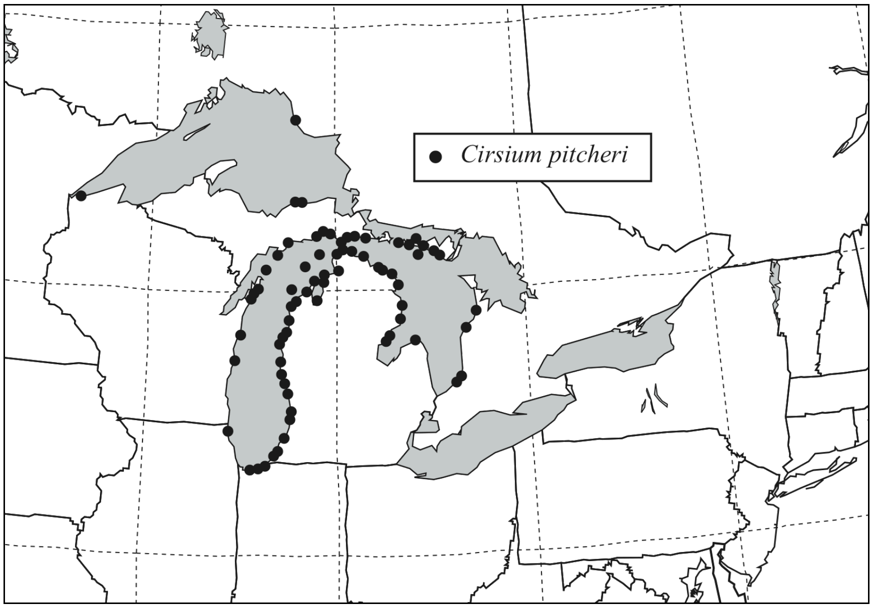

Figure 2.2. Great Lakes region distribution of *Cirsium pitcheri*. Based on Guire and Voss (1963), Keddy and Keddy (1984), and Morton and Venn (1984), supplemented by records in the Michigan Flora and Wisflora databases.

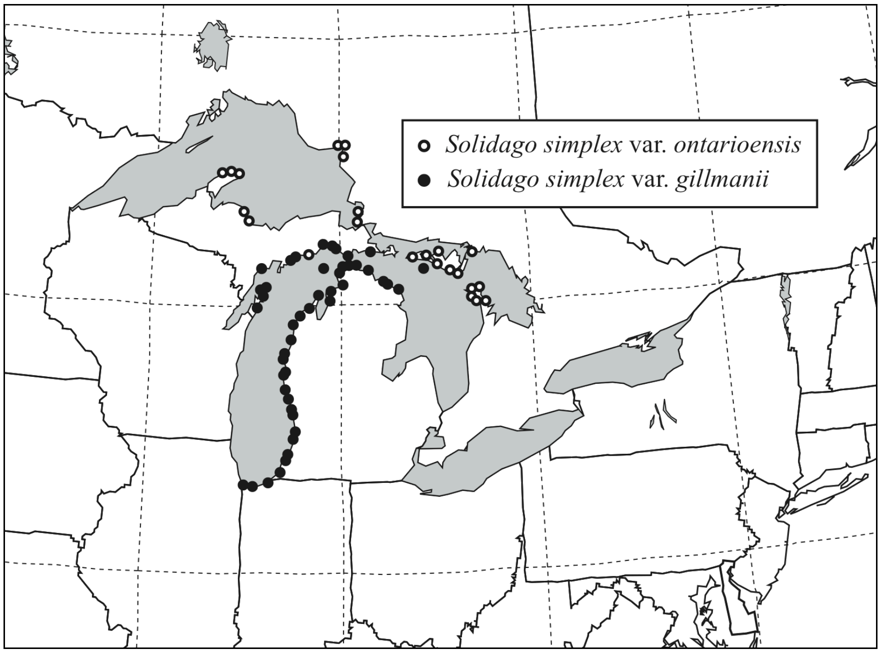

Figure 2.3. Great Lakes region distribution of *Solidago simplex* var. *gillmanii* and *S. simplex* var. *ontarioensis*. Based on examination of specimens at GH, MICH, MT, UMBS, and WAT, supplemented by records in the Michigan Flora and Wisflora databases, Morton and Venn (1984), Ringius (1986), and Semple et al. (1999).

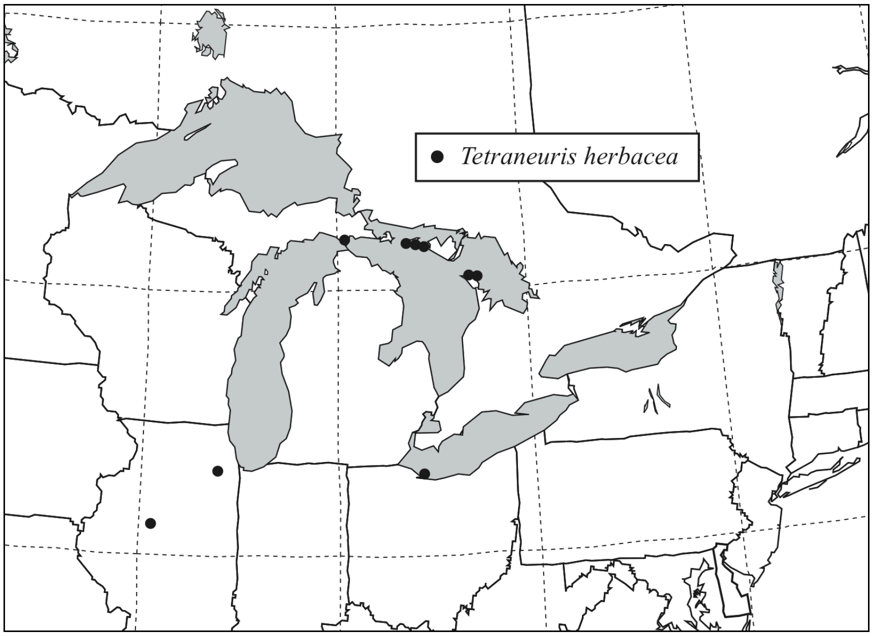

Figure 2.4. Great Lakes region distribution of *Tetraneuris herbacea*. Based on Voss (1935), Campbell et al. (2001), and Demauro (1993), supplemented by specimens in MICH.

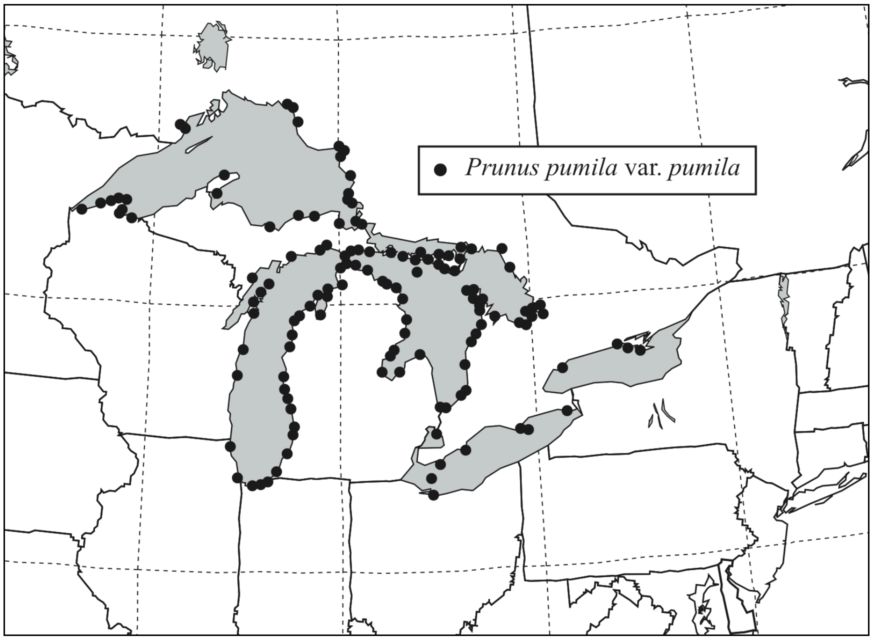

Figure 2.5. Great Lakes region distribution of *Prunus pumila* var. *pumila*. Based on Soper and Heimburger (1982), Catling and Larson (1997), and Rohrer (2000), supplemented by records in the Michigan Flora database.

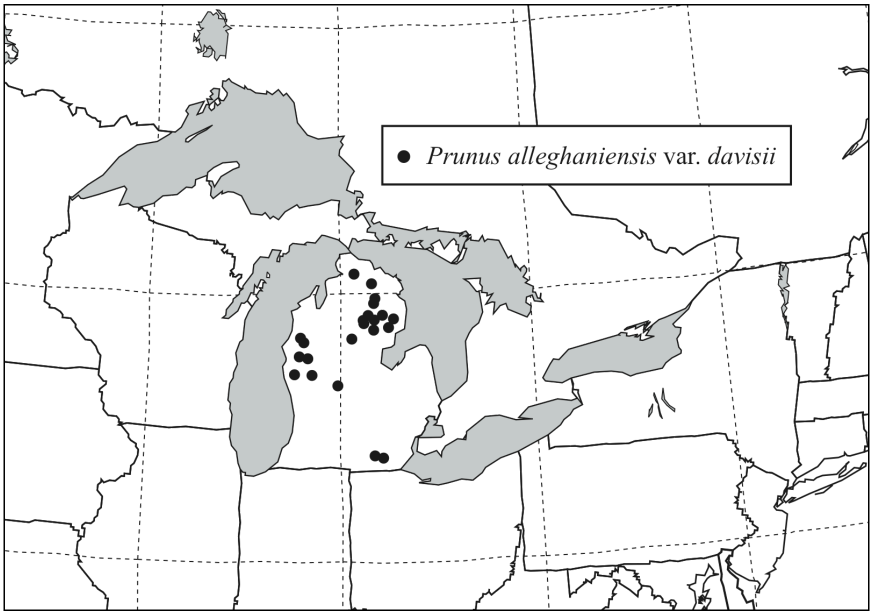

Figure 2.6. Great Lakes region distribution of *Prunus alleghaniensis* var. *davisii*. Based on Taylor (1990), supplemented by records in the Michigan Flora database.

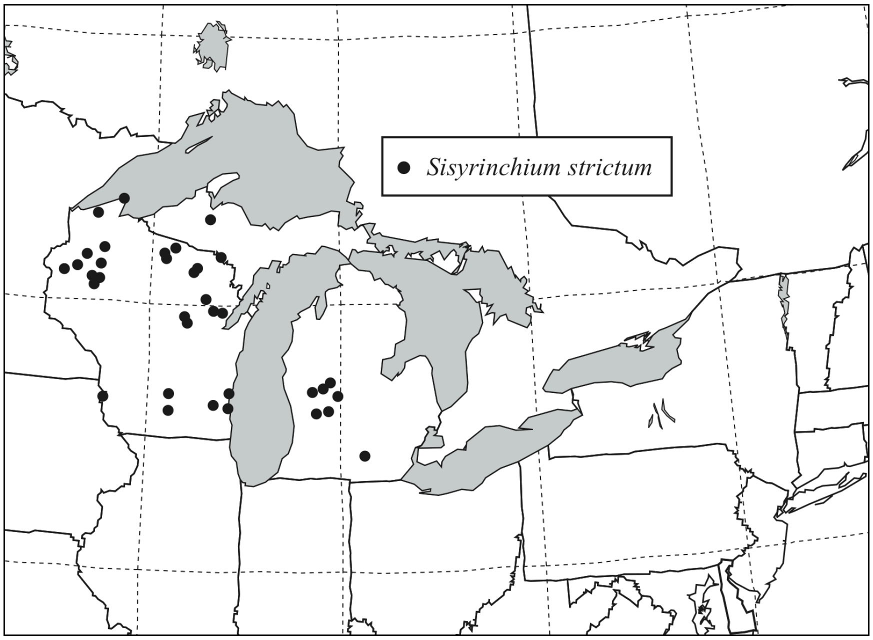

Figure 2.7. Great Lakes region distribution of *Sisyrinchium strictum*. Based on specimens in MICH, supplemented by records in the Michigan Flora and Wisflora databases.

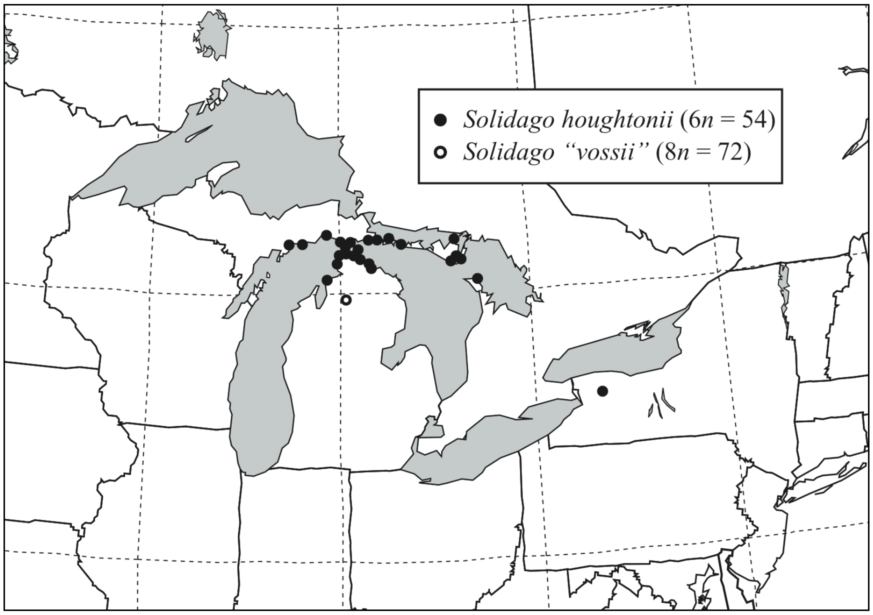

Figure 2.8. Great Lakes region distribution of *Solidago houghtonii* and *S. "vossii"*. Based on Guire and Voss (1963), Morton (1979), and Morton and Venn (1984), supplemented by records in the Michigan Flora database.

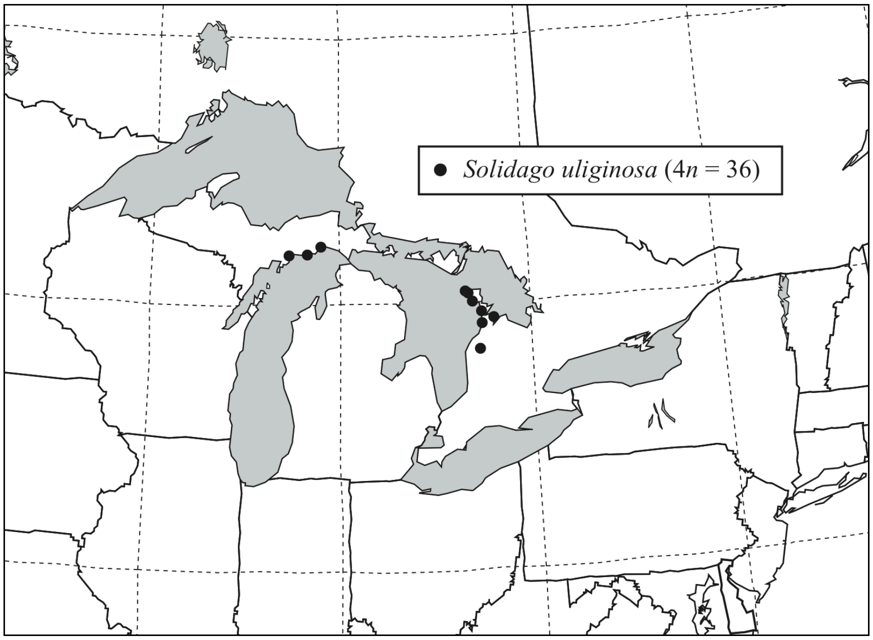

Figure 2.9. Great Lakes region distribution of tetraploid *Solidago uliginosa* (4*n* = 36). Based on Chmielewski et al. (1987).

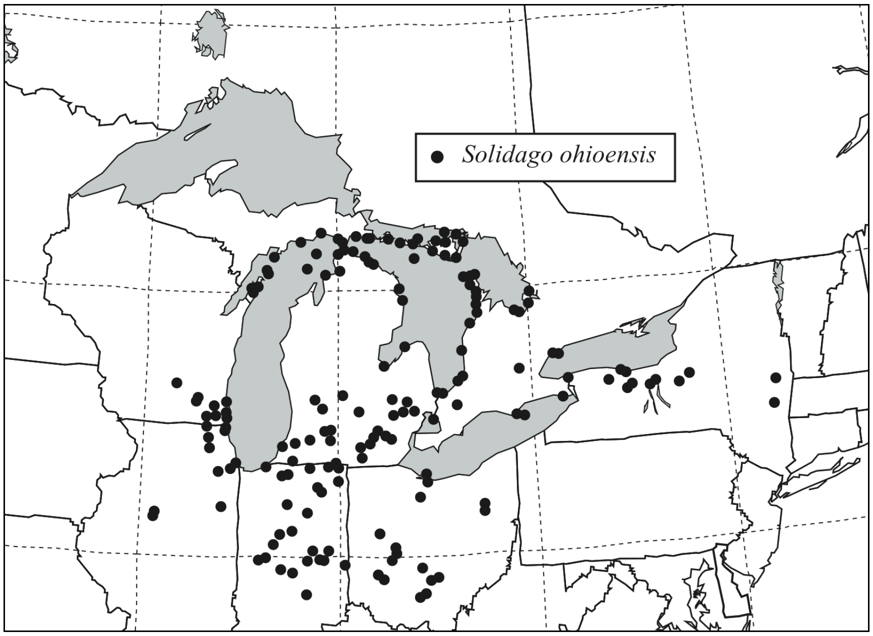

Figure 2.10. Great Lakes region distribution of *Solidago ohioensis*. Based on Pringle (1982), supplemented by specimens in MICH and records in the Wisflora database, Morton and Venn (1984), and Semple et al. (1999).

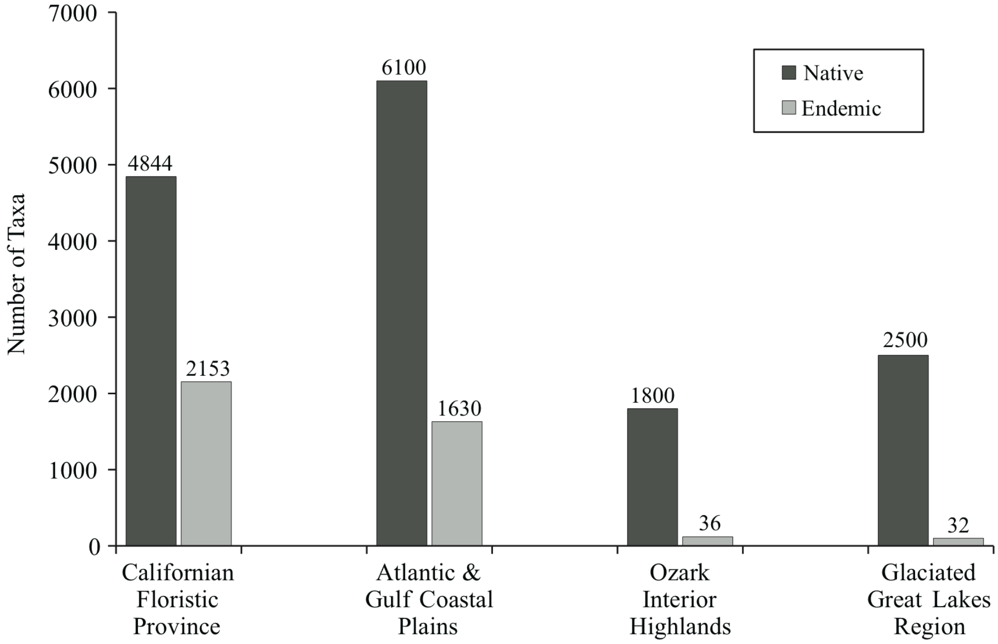

Figure 2.11. Comparison of vascular plant endemism in four studied regions of North America. Data from: this study, Hickman (1993), Raven and Axelrod (1978), Sorrie and Weakley (2001, 2006), and Zollner et al. (2005). Total numbers of native taxa (species in the case of the Californian Floristic Province) are approximations but serve to illustrate the overall patterns of endemism.

APPENDIX 1.1: ANNOTATED CHECKLIST OF THE ENDEMIC VASCULAR FLORA OF THE GREAT LAKES REGION

This appendix summarizes distributional, evolutionary, and taxonomic data for the 60 vascular plant taxa included in Tables 2.1-2.2 and discussed in the text. While a few of the taxa in this appendix have been intensively studied, many of the endemics summarized here have little information available aside from their original taxonomic descriptions and treatments in regional floristic works. Taxonomic authority and publication data for each taxon are provided. Brief discussions follow.

1. *Amelanchier huronensis* Wiegand -- Rhodora 22: 150 (1920). Wiegand (1920) described this calciphilic, large-flowered *Amelanchier* from sand dunes and limestone shores of Lakes Huron, Michigan, and Superior. Fernald (1950) recognized the species and attributed it to open woods, cliffs, and shores from northern Lake Huron to northern Michigan, Wisconsin and Minnesota. More recently, this species has not been widely recognized, and Voss (1985) included *A. huronensis* in the somewhat poorly understood *A. sanguinea* (Pursh) DC species complex.
2. *Apocynum sibiricum* Jacq. forma *arenarium* (F. C. Gates) Fernald -- Rhodora 37: 328 (1935). Schaffner (1910) first discussed the prostrate-growing, sand dune form of clasping-leaf dogbane from dunes at Cedar Point, Ohio. Gates (1911), while studying a similar sand dune form of *Dalea purpurea* Vent., named the plants forma *arenarium* (initially as *A. hypericifolium* Ait. f. *arenarium* F. C. Gates). Fernald (1935) recognized the taxon and stated that it was the common plant of sands and gravels of the Great Lakes region. This taxon has not been further studied.

3. *Arnica cordifolia* Hooker subsp. *whitneyi* (Fernald) Maguire -- Brittonia 4: 452 (1943). Fernald (1935) described eastern, disjunct occurrences of *A. cordifolia* on the Keweenaw Peninsula, Michigan as *Arnica whitneyi* Fernald. Maguire (1943) reduced *A. whitneyi* to a subspecies of the western *A. cordifolia*, stating "were it not for the geographical isolation, subsp. *whitneyi* would be with difficulty retained as a distinct entity." Recent works (e.g., Marquis and Voss 1981; Voss 1996; Wolf 2006) have recognized a broadly defined and broadly distributed *A. cordifolia*. Regardless of their taxonomic status, the Lake Superior populations are widely disjunct from the main range of the species in the western Cordillera and Black Hills of South Dakota.
4. *Betula murrayana* B. V. Barnes & Dancik -- Canadian Journal of Botany 63(2): 226 (1985). Barnes and Dancik (1985) described this fertile, allopolyploid birch from Third Sister Lake, Washtenaw Co., Michigan. They proposed that *B. murrayana* was an octoploid backcross of *B.* ×*purpusii* to *B. alleghaniensis* Britton. To date, this taxon has been found at only the type locality.
5. *Betula papyrifera* Marshall f. *coriacea* Fernald & Wiegand -- Rhodora 25: 209 (1923). Fernald and Wiegand (1923) described this thick-leaved form of paper birch from "sand dunes overlying Silurian shales and schists" from the shores of southern Lake Ontario. Fernald (1950) recognized f. *coriacea*, but more recent treatments have not recognized this endemic form of paper birch (Voss 1985; e.g., Gleason and Cronquist 1991). It has not been studied.
6. *Betula pumila* L. var. *glabra* Regel -- Pflanzenr. (Engler) 4, Fam. 61: 72. 1904. Fernald (1950) described this variety as local in Michigan and northern Indiana; no other mention could be found. It is possible that Fernald was referring to *B. pumila* f.

glabrescens H.J.P.Winkl. Regardless, Voss (1985) stated that *Betula pumila s.l.* is a polymorphic complex, with multiple varieties growing together in some locations in Michigan. The taxonomy of this complex remains poorly described.

7. *Betula ×purpusii* C. K. Schneid. -- Ill. Handb. Laubholzk. 1: 102 (1904). This taxon is the allopentaploid hybrid of *B. alleghaniensis* Britt. and *B. pumila* L. Fernald (1950) attributed it to *Larix* swamps from the Bruce Peninsula, Ontario to Michigan, northern Indiana, Illinois and Minnesota, and it has been widely recognized in regional floristic works (e.g., Braun 1961; Voss 1985; Gleason and Cronquist 1991). Dancik and Barnes (1972) determined that *B. ×purpusii* was represented almost entirely by F1 hybrids in the population they studied in southeastern Michigan. It has been implicated in the origins of *B. murrayana* (Barnes and Dancik 1985).
8. *Botrychium acuminatum* W. H. Wagner -- Contributions from the University of Michigan Herbarium 17: 321 (1990). Wagner and Wagner (1990) described *B. acuminatum* from Grand Sable Dunes on Lake Superior, where it occurs most frequently on open dunes and wooded slopes. It is known from several localities in the Lake Superior basin of Canada as well.
9. *Botrychium mormo* W. H. Wagner -- American Fern Journal 71(1): 26 (1981). Wagner and Wagner (1981) described this little moonwort from rich, northern hardwood forests in Minnesota. Its documented range is from northern Michigan and Wisconsin into Minnesota. Its small size and sporadic appearance make it very difficult to find (Wagner and Wagner 1981). Additional work is needed to better understand its geographic distribution.

10. *Botrychium pseudopinnatum* W. H. Wagner -- Contributions from the University of Michigan Herbarium 17: 322 (1990). Wagner and Wagner (1990) described *B. pseudopinnatum* from collections made at Angler Settlement on the north shore of Lake Superior, Ontario. It occurs in sandy habitats and is known only from the north and eastern shores of Lake Superior. *Botrychium pseudopinnatum* is the only known hexaploid (2*n* = 270) in subg. *Botrychium* (Wagner and Wagner 1990).
11. *Cakile edentula* (Bigelow) Hooker var. *lacustris* Fernald -- Rhodora 24: 23 (1922). Fernald (1922) distinguished populations of sea rocket growing on beaches of the Great Lakes as *C. edentula* var. *lacustris*, based primarily on differences in fruit morphology. Rodman (1974) recognized var. *lacustris* in his monograph of the genus and speculated that it evolved from the maritime *C. edentula* var. *edentula* sometime after the last glacial maximum. The biogeography and Pleistocene history of Great Lakes sea rocket have not been studied.
12. *Calamovilfa longifolia* (Hook.) Scribn. in Hack. var. *magna* Scribn. & Merr. -- Circ. Div. Agrostol. U.S.D.A. 35: 3 (1901). Lamson-Scribner and Merrill (1901) described *C. longifolia* var. *magna* from sand dunes of Lake Michigan near the mouth of the Kalamazoo River. This endemic is almost entirely restricted to active sand dunes along the shores of Lakes Huron, Michigan, and Superior but also has disjunct occurrences in sandy habitats in western Indiana, western Illinois, southern Wisconsin, and eastern Iowa (Thieret 1966). Thieret (1960) determined that var. *magna* differed from the western var. *longifolia* in its generally taller stature, wider, more open panicle, divergent panicle branches, and often densely pubescent sheaths. *Calamovilfa longifolia* var. *magna* is a characteristic and important component of

Great Lakes sand dunes, and Anwar Maun and his students intensively studied its ecology and population biology (e.g., Maun 1981; Maun 1989, 1994).

13. *Campanula rotundifolia* var. *velutina** Both Fernald (1950) and Voss (1996) mentioned the densely puberulent variety of *C. rotundifolia* described from Cheboygan County, Michigan, however, they provided different varietal names (Voss as *C. rotundifolia* var. *canescens* E. J. Hill). No additional information concerning either variety could be found. Other authors have not recognized the variety (e.g., Shetler 1982).
14. *Carex scirpoidea* Michx. subsp. *convoluta* (Kük.) D. A. Dunlop -- Novon 7(4): 355 (1997). Dunlop (1997) and Dunlop and Crow (1999) described *C. scirpoidea* subsp. *convoluta* as the most geographically restricted of the subspecies of *C. scirpoidea*. It occurs in alvar habitats along the dolomite shores of northern Lake Huron in Ontario and Michigan. They stated that subsp. *convoluta* represents a geographically based ecotype that differs in only a few characters from the other subspecies of *C. scirpoidea*.
15. *Cirsium pitcheri* Torr. & A. Gray -- Flora of North America (Torr. & A. Gray) 2: 456 (1843). *Cirsium pitcheri* is restricted to beaches and active sand dunes along the shores of Lakes Huron, Michigan and Superior (Guire and Voss 1963; Voss 1996). Loveless and Hamrick (1988) examined genetic structure in both *C. pitcheri* and the assumedly closely related *C. canescens*. They concluded that *C. pitcheri* most likely evolved as a disjunct derivative of *C. canescens* following glaciation. Kelch and Baldwin (2003) included *C. pitcheri* but not *C. canescens* in their phylogenetic study of North American *Cirsium*, thus its evolutionary relationships and broader

Pleistocene history remain unresolved. Due to its federal and state threatened species status, the ecology and population biology of *C. pitcheri* have been intensively studied. Investigations have focused on survivorship (D'Ulisse and Maun 1996), seed dormancy and germination ecology (Chen and Maun 1998; Hamze and Jolls 2000), reproductive biology and habitat (Keddy and Keddy 1984), and recovery and conservation issues (Bowles et al. 1993; Promaine 1999).

16. *Cornus baileyi* J. M. Coult. & W. H. Evans -- Bot. Gaz. 15: 37 (1890). Coulter and Evans (1890) differentiated *C. baileyi* from similar species (namely *C. stolonifera* Michx.) by its wooly pubescence on the lower leaf surface and compressed pit with prominently furrowed edge. They described its range as the shores of the Great Lakes and west to Wyoming but stated, "The range is very obscure as yet." Both Fosberg (1942) and Rickett (1944) recognized this entity as forma *baileyi* (Fosberg as *C. sericea* L. f. *baileyi* and Rickett as *C. stolonifera* f. *baileyi*) and regarded it as largely restricted to the Great Lakes region. Rickett (1944) suggested that disjunct western populations with the pubescence of f. *baileyi* likely represented variations of *C. stolonifera* f. *interior* Rickett. Voss (1985) indicated that f. *baileyi* occurs commonly on the shores of the Great Lakes but is also widespread elsewhere in the region. This somewhat cryptic endemic entity requires more study.
17. *Diervilla lonicera* Mill. var. *hypomalaca* Fernald -- Rhodora 42: 144 (1940). Fernald (1940) described this pubescent leaved variety of *D. lonicera* from the northern Great Lakes region in Ontario and Wisconsin. Voss (1996) mentioned the variety but did not further discuss its significance in Michigan or the Great Lakes region. It has not been studied.

18. *Eleocharis caribaea* (Rottb.) S. F. Blake var. *dispar* (E. J. Hill) S. F. Blake -- Rhodora 20: 24 (1918). Hill (1881) described this taxon (originally as *E. dispar*) from "sloughs" in Lake Co., Indiana. Blake (1918) subsequently reduced the disjunct populations in the southern Great Lakes region, which he distinguished by their purplish-colored scales and achenes, to a variety of the widespread, tropical and subtropical species, *E. caribaea*. The recognition of var. *dispar* has varied, and in the recent Flora of North America treatment it was synonymized under *E. geniculata* (L.) Roemer & Schultes (Smith et al. 2002).
19. *Elymus lanceolatus* (Scribn. & J. G. Sm.) Gould subsp. *psammophilus* (J. M. Gillett & H. Senn) Á. Löve -- Taxon 29: 167 (1980). Gillett and Senn (1961) described the morphologically distinct, disjunct *Agropyron* populations on the sandy shores of Lakes Huron and Michigan as a new, endemic species, *Agropyron psammophilum*. Great Lakes plants generally differ in a number of characters (e.g., more villous lemmas, more glaucous foliage, and less attenuate glumes) from the western *A. dasystachyum* (Hook.) Scribn (Voss 1972). Barkworth et al. (2007), however, recognized a broadly-defined *E. lanceolatus* subsp. *psammophilus* including the Great Lakes plants with morphologically similar individuals scattered throughout the western range of the species.
20. *Erigeron philadelphicus* L. var. *provancheri* (Vict. & J. Rousseau) B. Boivin -- Naturaliste Canad. 89: 72 (1962). Victorin and Rouseau described a small, glabrate, rock-outcrop fleabane, *E. provancheri* Vict. & J. Rousseau, from the tidal estuary of the St. Lawrence River near Quebec City, Quebec. It is known from only four locations, all widely disjunct, in eastern North America. Morton and Venn (1984)

documented *E. philadelphicus* var. *provancheri* on the dolomite shores of Lucas and Perseverance islands in Lake Huron, and Morton (1988) reported it from dolomite shores at the tip of the Bruce Peninsula as well. It is not clear if these disjunct populations represent a single taxon or are incipient ecological species. Further study is needed.

21. *Eupatorium rugosum* Kunth var. *tomentellum* (B. L. Rob.) S. F. Blake -- Rhodora 43: 557 (1941). Robinson (1911) described this short-pubescent, non-viscid variety of *E. rugosum* (originally as *E. urticaefolium* Reichard var. *tomentellum*) from specimens collected in Illinois, Michigan, and Wisconsin. Blake (1941) reported additional collections of var. *tomentellum* from coastal New Jersey, while Fernald (1950) restricted it to woods and thickets in the Great Lakes region. More recently, this taxon has not been widely recognized and was synonymized under *Ageratina altissima* (L.) King & H. Rob. var. *altissima* in Flora of North America.
22. *Euthamia remota* Greene -- Pittonia 5: 78 (1902). Greene (1902) described *E. remota* from the "rolling prairie country about Lake Michigan." Fernald (1950) attributed it to sandy woods, openings, and prairies from northwestern Ohio and southern Michigan to northeastern Illinois and Wisconsin. Sieren (1981) and Fisher (1988) included *E. remota* in a broadly-defined *E. gymnospermoides* Greene. Voss (1996) discussed the nomenclatural and taxonomic confusion surrounding *E. remota* and pointed out its similarity to the eastern *E. caroliniana* (L.) Porter & Britton (as opposed to the Great Plains *E. gymnospermoides*). Haines (2006) synonymized *E. remota* under the eastern coastal plain *E. caroliniana*.

23. *Hypericum kalmianum* L. -- Species Plantarum 2: 783 (1753). The distribution of *H. kalmianum* is centered on the Great Lakes region, but it occurs outside of the drainage basin in Wisconsin and the Ottawa River Valley of Canada (McLaughlin 1931; Guire and Voss 1963). McLaughlin (1931) argued that *H. kalmianum* was restricted to rocky/sandy soils, dunes, and calcareous interdunal hollows along shorelines of the current and glacial Great Lakes. He also proposed that the species survived glaciation in the Driftless Area of Wisconsin and quickly spread along shorelines as the ice margin receded. Adams (1962) allied *H. kalmianum* with the southern *H. lobocarpun* Gatt. No studies of *H. kalmianum* have been undertaken.
24. *Iliamna remota* Greene -- Leafl. Bot. Observ. Crit. i. 206 (1906). Greene described *I. remota* from what is now Langham Island in the Kankakee River, Illinois. This perplexing species was known only from the type locality until several populations were discovered in Virginia (sometimes segregated as *I. corei* Sherff) and near Elkhart, Indiana (Swinehart and Jacobs 1998). Boda Slotta and Porter (2006) found that the Illinois/Indiana and Virginia populations comprised distinct lineages, but the biogeography and evolution of this rare, disjunct species remain unresolved.
25. *Iris lacustris* Nutt. -- Gen. N. Amer. Pl. [Nuttall]. 1: 23 (1818). Nuttall described *I. lacustris* from collections made from the gravelly shores of Mackinac Island, Michigan (Voss 1972). This endemic is restricted to calcareous shores and limestone pavements of the Niagara Escarpment in the northern Lower Peninsula of Michigan, eastern Wisconsin, and Manitoulin Island and the Bruce Peninsula, Ontario (Guire and Voss 1963; Trick and Fewless 1984). Hannan and Orick (2000) proposed, based on isozyme data, that *I. lacustris* most likely evolved from a dispersal of the

southeastern *Iris cristata* Ait. into the Great Lakes region soon after deglaciation. No broader-scale evolutionary studies have been undertaken. Due in part to its federal and state threatened status, the ecology and reproductive biology of *I. lacustris* have been investigated in some detail. Studies have examined habitat and general ecology (e.g., Van Kley and Wujek 1993) and breeding system and pollination biology (e.g., Planisek 1983; Larson 1998).

26. *Linum medium* (Planch.) Britton var. *medium* -- Ill. Fl. N. U.S. (Britton & Brown) 2: 349 (1897). *Linum medium* var. *medium* was described from the shores of northern Lake Huron and is endemic to the Georgian Bay region of southern Ontario (Rogers 1963; Pringle 1995). Pringle (1995) referred older records of *L. medium* var. *medium* from the shores of Lakes Erie and Ontario to the diploid *L. medium* var. *texanum* (Planch.) Fernald. Harris (1968) proposed that the tetraploid *L. medium* var. *medium* ($2n = 72$) was possibly an allopolyploid hybrid of *L. medium* var. *texanum* and *L. virginianum* L. (each $2n = 36$). No additional work has been done on this endemic.
27. *Lycopodiella margueritae* J. G. Bruce, W. H. Wagner & J. Beitel -- Michigan Bot. 30(1): 9 (1991). Bruce et al. (1991) described this tetraploid species of bog clubmoss from fossil dune systems near the shores of Lake Michigan in southwestern Michigan. It has since been documented from fossil dunes near Lake Erie and Lake Huron. *Lycopodiella margueritae* and *L. subappressa* (both tetraploids with $2n = 312$) form fertile hybrids. Hybrids between *L. margueritae* and the diploid *L. inundata* (L.) Holub, however, are triploid and sterile. Little is known about the biology and evolution of this species.

28. *Lycopodiella subappressa* J. G. Bruce, W. H. Wagner & J. Beitel -- Michigan Bot. 30(1): 4 (1991). Bruce et al. (1991) described this tetraploid species of bog clubmoss from fossil dune systems near the shores of Lake Michigan in southwestern Michigan. As mentioned above, hybrids between this and the preceding species are fertile. Hybrids between *L. subappressa* and the diploid *L. inundata* (L.) Holub, however, are triploid and sterile. Little is known about the biology and evolution of this species.

29. *Mimulus michiganensis* (Pennell) Posto & Prather -- Syst. Bot. 28(1): 177 (2003). Pennell (1935) described this large-flowered Michigan endemic (originally as *Mimulus glabratus* subsp. *michiganensis*) from the "banks of Niger Creek near Topinabee, Cheboygan County, Michigan." It is currently known from about 20 populations in the Straits of Mackinac and Grand Traverse areas of Michigan (Voss 1996). Bliss (1986) determined that *M. michiganensis* was a vegetative apomict that produced aneuploid gametes. Posto and Prather (2003) concluded from molecular studies that *M. michiganensis* and *M. glabratus* var. *jamesii* were closely related yet distinct entities. They subsequently elevated the endemic to species status.

30. *Oxytropis campestris* DC. var. *chartacea* (Fassett) Barneby -- Proc. Calif. Acad. Sci. 4th ser. 27: 269 (1952). Fassett (1936) described this endemic (originally as *O. chartacea*) from the sandy shores of several calcareous lakes in central Wisconsin. Barneby (1952) reduced these disjunct Wisconsin populations to a variety of the circum-boreal *O. campestris* and proposed that it was most closely related to the northeastern North American *O. campestris* var. *johannensis* Fern. Recent phylogeographic work suggested that vars. *chartacea* and *johannensis* were

differentiated sister lineages that likely represented remnants of a previously widespread ancestor (Chung 2001; Chung et al. 2004).

31. *Polemonium occidentale* Greene subsp. *lacustre* Wherry -- Amer. Midl. Naturalist 34: 376 (1945). Wherry (1942) described disjunct occurrences of the western *P. occidentale* in northeastern Minnesota as subsp. *lacustre*, based on differences in several morphological characters. Solheim and Judziewicz (1984) documented the occurrence of the taxon in cedar swamps in northern Wisconsin. It is known from only a handful of sites in Minnesota and Wisconsin and has not been studied.
32. *Polygonum pensylvanicum* var. *eglandulosum* Myers -- Castanea 7(4-5): 74-75 (1942). Myers (1942) described this glabrous, eglandular smartweed as endemic to the limestone shores of the western Lake Erie islands. This taxon has not been closely studied and was synonymized under *Persicaria pensylvanica* in Flora of North America.
33. *Primula intercedens* Fernald -- Rhodora 30: 86 (1928). Fernald (1928) segregated plants from the upper Great Lakes region with (in his view) strongly angled and rugose seeds and a heavy wax coating on the leaves as the endemic *P. intercedens*, although he suggested at the same time that the specific differences were not fully convincing and that *P. intercedens* and *P. mistassinica* Michx. likely hybridized extensively. More recent authors have not recognized *P. intercedens* as a distinct entity (e.g., Vogelmann 1960; Guire and Voss 1963; Soper et al. 1965; Voss 1996).
34. *Prunus alleghaniensis* Porter var. *davisii* W. Wight -- in U. S. Dept. Agric. Bull. 179: 51 (1915). *Prunus alleghaniensis* is restricted to a small area of the Appalachian Mountains primarily from central Pennsylvania through West Virginia. Wight (1915)

distinguished disjunct occurrences in northern lower Michigan as *P. alleghaniensis* var. *davisii*. Taylor (1990) found that Alleghany Plum was restricted to open habitats (barrens, prairies, and roadsides) in areas of acidic Grayling sands in Michigan. Shaw and Small (2005) found that *P. alleghaniensis s.l.* shared a common, and geographically widespread chloroplast haplotype with other plums in the Chickasaw clade of *Prunus* section *Prunocerasus*.

35. *Prunus pumila* var. *pumila* L. -- Mant. Pl. 75 (1767). This variety of sand cherry is restricted to active sand dunes around the shores of the Great Lakes (Catling and Larson 1997; Rohrer 2000). It is one member of the taxonomically poorly understood *Prunus pumila* species complex. The four varieties in this complex have been variously treated and recognized as species by some authors (e.g., Fernald 1923; Fernald 1950). No intensive studies have examined genetic structuring and/or phylogenetic relationships within the complex.
36. *Ptelea trifoliata* L. var. *deamiana* Nieuwl. -- American Midland Naturalist 2: 179 (1912). Nieuwland (1912) segregated pubescent, sand dune plants of *P. trifoliata* growing along the southern shore of Lake Michigan as a new variety, *P. trifoliata* var. *deamiana.* He argued that these plants, delimited by their densely pubescent young branches and petioles, somewhat smaller and firmer leaves, and low habit, were distinct from the southern and western *T. trifoliata* var. *mollis* Torr. & A. Gray. Fernald (1950), however, included "dunes of L. Michigan" within the range of var. *mollis.* Bailey (1962), in her monograph of the genus, mapped all Great Lakes region plants as *P trifoliata* var. *trifoliata* but stated "to the dune shores of southern Lake Michigan" in her statement concerning the distribution of var. *mollis.* Voss (1985)

referred most Michigan plants to var. *trifoliata* but stated that var. *mollis* had been attributed to the state as well. These populations have not been well studied.

37. *Rhus aromatica* Aiton var. *arenaria* (Greene) Fernald -- Rhodora 43: 599 (1941). Greene (1903-1906) described the low, small-leaved, pubescent plants of fragrant sumac growing on sand dunes along the southern end of Lake Michigan as *Rhus arenaria*. Barkley (1937), in his monograph of the genus, recognized the dune plants of the southern Great Lakes as taxonomically distinct but reduced them to a variety of the small-leaved, western *R. trilobata* Nutt. Subsequently, Fernald (1941) argued that fruit characters clearly placed these plants in the eastern *R. aromatica*. Some later authors have recognized this endemic (e.g., Braun 1961; Gleason and Cronquist 1991), but as Spooner et al. (1983) aptly stated, "further research is needed to clarify the taxonomic status of the varieties of fragrant sumac."
38. *Ribes cynosbati* var. *atrox* Fernald -- Rhodora 37: 261 (1935). Fernald (1935) described this stout, heavily armed variety of *R. cynosbati* from dry woods on Manitoulin Island, Ontario. Morton and Venn (1984) indicated that heavily armed plants were scattered throughout the eastern part of the island. Thomson (1970) reported similar plants from the Bruce Peninsula, Ontario. Examination of specimens at MICH suggests that armed plants are scattered throughout the Great Lakes region.
39. *Salix glaucophylloides* Fernald var. *albovestita* (C. R. Ball) Fernald -- Rhodora 48: 45 (1946). Ball (1939) described this willow (originally as *S. glaucophylla* Bebb var. *albovestita*) from sand dunes along the southern shore of Lake Erie in Ohio and Pennsylvania. He separated it from other Great Lakes dune plants of *S. glaucophylla* by its more distinctly cordate leaf bases and densely white tomentose leaves and

branchlets. Fernald (1948) recognized this endemic as *S. glaucophylloides* var. *albovestita* and attributed it to "dunes of the Great Lakes from New York and southern Ontario to Michigan." In his study of *Salix* sect. *Cordatae*, Dorn (1995) included the Great Lakes plants in a more widely distributed *S. myricoides* var. *albovestita*, which is most common along the southern shore of James Bay.

40. *Salix glaucophylloides* Fernald var. *glaucophylla* (Bebb) Schneider -- J. Arnold Arbor. 1: 157 (1920). Bebb (in Wheeler and Smith 1881) described this endemic willow (originally as *S. glaucophylla*) from shoreline sand dunes of the Great Lakes region. Schneider (1920) included *S. glaucophylla* as a disjunct variety of the northeastern and maritime *S. glaucophylloides*. Some later authors recognized *S. glaucophylloides* var. *glaucophylla* (e.g., Fernald 1950; Braun 1961), but more often, dune plants of the Great Lakes region have been included in a broadly-defined *S. myricoides* var. *myricoides* (e.g., Voss 1985; Gleason and Cronquist 1991; Dorn 1995) that encompasses plants from the Great Lakes region and northeastern North America.

41. *Salix syrticola* Fernald -- Rhodora 9: 225 (1907). Fernald (1907) described this endemic species, which he noted was clearly related to the disjunct, far northern *S. cordata* Michx., from sand dunes around the Great Lakes. Some later works recognized *S. sytricola* (e.g., Fernald 1950; Braun 1961), but more often, dune plants of the Great Lakes region have been included in a broadly-defined *S. cordata* (e.g., Voss 1985; Gleason and Cronquist 1991; Dorn 1995).

42. *Schizachyrium littorale* E. P. Bicknell -- Bulletin of the Torrey Botanical Club 35: 182 (1908). This maritime grass (sometimes recognized as *S. scoparium* (Michx.)

Nash var. *littorale*) is restricted to active dune systems along the Atlantic and Gulf coasts of North America, with disjunct occurrences in the southern Great Lakes region (Wipff 2003). Examination of specimens of *S. scoparium* from sand dune systems in the northern Great Lakes region revealed that plants there often have decumbent culm bases and compressed lower internodes that root when buried by sand. It is unclear if populations in the Great Lakes region actually represent *S. littorale* or an incipient, regional dune race, or perhaps a combination of the two.

43. *Sisyrinchium hastile* E. P. Bicknell -- Bulletin of the Torrey Botanical Club 26: 297 (1899). Bicknell (1899) described this species from Farwell collections from the "sandy shores of Belle Isle, in the Detroit River, Michigan." Fernald (1950) stated that “very little is known; seeming unique among our species.” Voss (1972) questioned the origins of *S. hastile* and proposed that it may be an escape from cultivation. Known only from the type locality, it has not been recollected.
44. *Sisyrinchium strictum* E.P.Bicknell -- Bulletin of the Torrey Botanical Club 26: 299 (1899). Bicknell (1899) described this species from sandy plains in Montcalm Co., Michigan. Its taxonomic status has been questioned over the years, but Voss (1967, 1972) recognized *S. strictum*, arguing that it appeared as distinct as many species in the genus. *Sisyrinchium strictum* grows in a variety of habitats and is nearly endemic to the Great Lakes region, occurring only in Michigan and Wisconsin (where it extends west of the drainage basin on sandy outwash plains).
45. *Solidago hispida* Muhl. ex Willd. var. *huronensis* Semple -- University of Waterloo Biological Series 39: 36 (1999). Semple et al (1999) described this glabrous variety of *S. hispida* as endemic to sand dunes along the shores of Lake Huron. Ringius

(1986) previously indicated that glabrous sand dune plants of *S. hispida* occurred on the Keweenaw Peninsula in Michigan. Fieldwork and examination of herbarium specimens at MICH revealed that *S. hispida* var. *huronensis* is more widespread than Semple et al. described, also occurring on dunes along the southern and eastern shores of Lake Superior (e.g., *J.A. Peirson 627*, *M.J. Oldham 30892*).

46. *Solidago houghtonii* Torr. & A. Gray -- Manual (Gray) 211 (1848). Douglas Houghton first collected the large-headed *S. houghtonii* along the shores of northern Lake Michigan in Mackinaw Co., Michigan. This endemic is essentially confined to sandy and rocky shores from the Straits of Mackinac and northern Michigan along the northern edge of Lake Huron to the Bruce Peninsula, Ontario. Disjunct plants occur in Bergen Swamp, Genesee Co., New York (Guire and Voss 1963; Semple and Cook 2006). Morton (1979) proposed that *S. houghtonii* ($2n = 54$) was an allohexaploid derivative of a cross between *S. ohioensis* ($2n = 18$) and *S. ptarmicoides* ($2n = 18$) with a subsequent backcross to *S. ohioensis*. Semple et al. (1999) proposed that *S. riddellii* may be involved in its origin. Laureto and Barkman (2004, 2005) suggested, based on chloroplast DNA sequence data, that *S. gigantea* was the maternal parent. As of yet, no definitive conclusions have been reached.
47. *Solidago ohioensis* Riddell -- Western Journal of the Medical and Physical Sciences 8(32): 497 (1835). Riddell described *S. ohioensis* from wet prairies (fens) south of Columbus, Ohio. Throughout the southern part of its range in Illinois, Indiana, Ohio, Michigan, and Wisconsin, *S. ohioensis* is restricted to calcareous fens and wet meadows, while in the northern part of its range it is restricted to calcareous shorelines along the Niagara Escarpment in Michigan and Ontario (Pringle 1982).

Pringle (1982) proposed that *S. ohioensis* survived the Wisconsinan glaciation south of the ice margin in Ohio. This hypothesis has not been tested.

48. *Solidago simplex* Kunth var. *gillmanii* (A. Gray) G. S. Ringius -- Phytologia 70(6): 398 (1991). See next chapters for discussions of this endemic.
49. *Solidago simplex* Kunth var. *ontarioensis* (G. S. Ringius) G. S. Ringius -- Phytologia 70: 398 (1991). See next chapters for discussions of this endemic.
50. *Solidago speciosa* Nutt. var. *jejunifolia* (E. S. Steele) Cronquist -- Rhodora 49: 77 (1947). Steele (1913) described this taxon (originally as *S. jejunifolia*) from sand plains near Indian River, Cheboygan Co., MI. The geographic and morphologic circumscription and taxonomic status of this goldenrod have varied over the years (e.g., Voss 1996; Semple and Cook 2006), and it is currently included in a broadly defined *S. speciosa* var. *speciosa* (sensu Semple and Cook 2006). Plants of *S. speciosa* var. *jejunifolia* growing in northern Michigan pine barrens tend to be morphologically distinct from (i.e., smaller plants with fewer leaves, shorter involucres, and less dense arrays) and flower earlier than their non-barren counterparts. This near endemic has not been studied.
51. *Solidago uliginosa* Nutt. -- Journal of the Academy of Natural Sciences of Philadelphia 7:101 (1834). Diploid *S. uliginosa* ($2n = 18$) is widely distributed in wetland habitats across eastern North America (Semple and Cook 2006). Chmielewski et al. (1987) reported that two cytotypes occur in the Great Lakes region. The tetraploid cytotype ($4n = 36$) is essentially restricted to alvars and areas of thin soil over limestone bedrock along the northern boundary of the Niagara Escarpment in Ontario and Michigan; diploids are excluded from this habitat. Great

Lakes region tetraploids likely represent an incipient, ecologically and cytologically distinct species.

52. *Solidago "vossii"* - undescribed. Inland populations of what was originally thought to be *S. houghtonii* in Crawford County, MI represent a distinct species. This species occupies a different habitat, is more robust, has larger involucres and ray florets, and is octoploid ($2n = 72$). These populations have not been well studied.
53. *Stachys palustris* var. *nipigonensis* Jenn. -- Journal of the Washington Academy of Sciences 10: 459 (1920). Jennings (1920) described this variety of *S. palustris* from shores "along Ombabika and Orient bays, Lake Nipigon." Fernald (1950), however, stated the range of the taxon as widespread across much of North America, perhaps switching his discussions of *S. palustris* vars. *nipigonensis* and *macrocalyx* Jenn. Gill (1980) synonymized both varieties under *S. palustris* subsp. *palustris*. Mulligan et al. (1983) proposed that *S. palustris* was not native to North America, and subsequently Mulligan and Munro (1989) synonymized *S. palustris* var. *nipigonensis* under *S. pilosa* Nutt. The taxonomy of *Stachys* in northern North America remains unclear.
54. *Symphyotrichum pilosum* (Willd.) G.L.Nesom var. *pringlei* (A.Gray) G.L.Nesom -- Phytologia 77(3): 289 (1995). The *S. pilosum* polyploid complex is widespread throughout eastern North America (Brouillet et al. 2006). Glabrous plants have been variously treated over the years but are now generally combined into a broadly distributed *S. pilosum* var. *pringlei* (discussed in Chmielewski and Semple 2001; Semple et al. 2002; Brouillet et al. 2006). Examination of specimens at MICH and populations in the field suggested that the taxonomy of *S. pilosum* remains poorly understood; glabrous shoreline plants of var. *pringlei* in the Great Lakes region

appear to be subtly differentiated for glabrous inland populations. Additional research is needed.

55. *Tanacetum huronense* Nutt. -- Gen. N. Amer. Pl. 2: 141 (1818). Nuttall collected and described *T. huronense* from the shores of Lake Huron near the Straits of Mackinac in 1810 (Guire and Voss 1963). In the Great Lakes region it grows on sand dunes and sandy/rocky beaches on the shores of northern Lakes Huron and Michigan and southern Lake Superior. *Tanacetum huronense* is now usually included in a broadly-defined *T. bipinnatum* (L.) Sch. Bip., which ranges across the northern parts of continent.

56. *Tetraneuris herbacea* Greene -- Pittonia 3: 268 (1898). Greene (1898) recognized the disjunct populations of *Tetraneuris* from the Great Lakes region as a new species, *T. herbacea*, stating that they were "wholly removed from the rest of the genus both in habitat and in character." The species occurs sporadically in shoreline alvar and similar limestone habitats on the Marblehead Peninsula of western Lake Erie, the Bruce Peninsula and Manitoulin Island, Ontario, and in northern Michigan. It was historically known from several sites in northern Illinois, but those populations have since become extirpated (Voss 1935; Demauro 1993). Demauro (1993) found that *H. herbacea* was a reduced aneuploid ($n = 14$) with normal chromosome structure and meiotic behavior, thus separating it from the remainder of the genus that has a base chromosome number of $n = 15$. Cusick (1991) proposed that *T. herbacea* arose from a migration of a western ancestor during the Xerothermic period. No evolutionary hypotheses have been tested.

57. *Thismia americana* N. E. Pfeiffer -- Bot. Gaz. 57: 123 (1914). Pfeiffer (1914) described *T. americana* from her personal collections made from an open, lake plain prairie near Chicago, Illinois. Her initial collections and observations are the only documented evidence for the existence of this perplexing entity. Mass et al. (1986) concluded that *T. americana* is most-closely related to the Australian/New Zealand/Tasmanian *T. rodwayi* F. von Müller.

58. *Valeriana edulis* Nutt. var. *ciliata* (Torr. & A. Gray) Cronquist -- Manual of Vascular Plants of Northeastern U.S. and Canada 658 (1963). Torrey and Gray described *V. edulis* var. *ciliata* (originally as *V. ciliata*) from specimens collected by John Samples from a cedar swamp (fen) south of Urbana, Ohio (Stuckey 1966). This near endemic is almost entirely restricted to fens from central Ohio and southern Michigan through Wisconsin and Minnesota, with a few populations from limestone cliffs in southern Ontario. Meyer (1951) reduced *V. ciliata* to a disjunct subspecies of the western *V. edulis* and noted that morphologically the varieties are almost indistinguishable, but geographically and ecologically they are quite distinct. Aside from research by Jennifer Windus (e.g., Windus 1997; Faivre and Windus 2002), no studies of this rare Midwestern endemic have been undertaken.

59. *Viola novae-angliae* House subsp. *grisea* (Fernald) N. L. Gil-ad -- Boissiera 53: 68 (1997). *Viola novae-angliae s.l.* shows a marked disjunction between New England and the maritime provinces of Canada and the northwestern Great Lakes region in Ontario, Michigan, Minnesota, and Wisconsin (Ballard and Gawler 1994). Fernald (1935) segregated northern Michigan plants from sandy plains in Schoolcraft Co., Michigan as the endemic var. *grisea* (originally as *V. septentrionalis* Greene var.

grisea). Ballard (1994) and Ballard and Gawler (1994) synonymized *V. septentrionalis* var. *grisea* under *V. novae-angliae*, stating that too much intrapopulation and geographic variation existed to recognize a distinct entity. Gil-Ad (1997) subsequently resurrected the taxon as a subspecies of *V. novae-angliae*. Relationships and population history in *V. novae-angliae* remain unclear.

60. *Vitis riparia* Michx. var. *syrticola* (Fernald & Wiegand) Fernald -- Rhodora 41: 431 (1939). Fernald and Wiegund (1923) described this pubescent, dune-inhabiting grape (as a variety of *V. vulpina* L.) from shoreline dunes on Lakes Ontario and Michigan. Braun (1961) did not attribute the taxon to the Lake Erie dunes in northern Ohio, while Voss (1985) indicated that dune inhabiting plants of *V. riparia* in Michigan are often more pubescent but did not recognize any intraspecific taxa. Catling and Mitrow (2005) examined ecological, geographic, and morphological patterns in *V. riparia* in southern Ontario. They found that pubescent plants (referable to var. *syrticola)* had a predominantly shoreline, sand dune distribution but that there was no clear bimodal pattern of pubescence among the 623 specimens they examined. They suggested that pubescent plants of sand dunes should be referred to as the "dune race" and not given varietal rank.

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CHAPTER III

POLYPLOIDY, SPECIATION, AND INFRASPECIFIC CYTOTYPE VARIATION IN GOLDENRODS: THE CYTOGEOGRAPHY OF *SOLIDAGO* SUBSECTION *HUMILES*

Polyploidy (or the possession of more than two complete chromosome complements) has long been recognized as an important mechanism of plant evolution (Muntzing 1936; Stebbins 1971; Lewis 1980). As early as the 1930's and 1940's, results from field and greenhouse studies began to demonstrate that polyploid taxa were often ecologically distinct from their diploid relatives and often occupied at least partially separate geographic ranges (Muntzing 1936; Stebbins 1942; Löve and Löve 1943; Clausen et al. 1945; Haskell 1951). Recent studies have markedly broadened our understanding of the ecological and evolutionary dynamics of polyploidy in plants (Soltis and Soltis 2000; Soltis et al. 2004). It is now realized that many polyploid taxa (perhaps the majority) have formed recurrently (reviewed in Soltis and Soltis 1999), that polyploid plants often differ morphologically and phenologically from their diploid progenitors (reviewed in Ramsey and Schemske 2002), that polyploidy can have significant effects on the evolution of ecological interactions (Thompson et al. 2004; Halverson et al. 2008a), and that polyploidy is likely an important mechanism of plant speciation (Coyne and Orr 2004; Rieseberg and Willis 2007).

Despite some theoretical arguments that incipient polyploid formation and establishment should be rare (e.g., minority cytotype exclusion following Levin 1975;

Husband 2000), polyploidy is abundant in plants. Broad-scale estimates have suggested that 30-70% of flowering plants have some incidence of polyploidy in their histories (Stebbins 1950; Grant 1981; Masterson 1994), and even the most conservative models have estimated that between 2-4% of speciation events in angiosperms have involved a change in ploidy (Otto and Whitton 2000; Coyne and Orr 2004; Rieseberg and Willis 2007). In some groups in particular (e.g., the genera *Solidago* and *Symphyothrichum* in the Asteraceae) recurrent polyploidy appears to be ubiquitous and to have played a significant role in diversification and speciation.

Goldenrods, plants in the genus *Solidago*, have long been notorious for their complex patterns of morphological and ploidal variation. Cytological data extracted from the recent Flora of North America treatment of *Solidago* (Semple and Cook 2006) indicate that 11 species of goldenrods are strictly polyploid (i.e., they exist only at the tetraploid level or above). An additional 32% of North American species (25 out of 77 species) harbor infraspecific cytotype variation. In only a few instances have cytotypes been named; more often cytotypes have been included in broadly defined taxa.

While these statistics support the idea that polyploidy has occurred frequently in *Solidago*, at the same time they indicate that the majority of this ploidal variation has not been recognized taxonomically. Soltis et al. (2007) argued that even though most infraspecific cytotype variation has been ignored taxonomically (they were specifically reviewing autopolyploidy), many infraspecific chromosomal races meet the criteria of multiple species concepts. This raises a number of questions for genera, like *Solidago*, that harbor substantial amounts of taxonomically unrecognized cytotypic variation. How is this cytotypic variation partitioned within species complexes? Is it likely that polyploid cytotypes formed recurrently? Are cytotypes ecologically, geographically, or morphologically distinct? Are cytotypes largely reproductively isolated? In what cases should infraspecific cytotypes be recognized as good biological species?

This study seeks to examine a few of these questions, using cytogeographic patterns in *Solidago* subsect. *Humiles* (*S. simplex* and four closely-related species) as a model system. In the 1980's, Gordon Ringius proposed the hypothesis that tetraploid populations of *S. simplex* in eastern North America (which he recognized as subsp. *randii*) had evolved from a single migration and subsequent polyploidization of diploid *S. simplex* from western North America sometime during the Wisconsinan glacial period (Ringius 1986; Ringius and Semple 1987). Rare diploid populations in northeastern North America were thought to represent either relicts from a previously more widespread distribution (e.g., populations in Gaspé, Quebec) or recent, Holocene migrants from western North America (e.g., populations in the northern Great Lakes region). The subsequent description of two morphologically distinct yet closely-related species, *S. arenicola* and *S. kralii*, and rediscovery of *S. plumosa* (previously thought to be extinct) in potentially refugial areas in the southeastern United States has raised doubts over the simplistic biogeographic hypothesis outlined by Ringius (1986) and Ringius and Semple (1987). In addition, the widespread occurrence of previously undocumented, apparently diploid populations in the northern Great Lakes region (occurrence first noted by Zimmerman 1956; distribution discussed by Voss 1996) suggests that the cytogeography of *S. simplex* in the region has not been adequately characterized either.

Objectives. The objectives of this study were to 1) use DNA ploidy determinations from flow cytometry, chromosome counts, and published data to examine cytogeographic patterns in *Solidago* subsect. *Humiles* across North America with expanded taxon and geographic sampling in the southeastern United States and the Great Lakes region, 2) evaluate previous biogeographic and taxonomic hypotheses in light of the cytogeographic patterns and infraspecific cytotype variation recovered in *S.* subsect. *Humiles* (in a framework similar to that described by Soltis et al. 2007), and 3) compare patterns of infraspecific cytotype variation found in *S.* subsect. *Humiles* with those found in other *Solidago* species.

MATERIALS AND METHODS

Study Group. *Solidago* subsect. *Humiles* is composed of five morphologically similar and closely-related species: *S. arenicola*, *S. kralii*, *S. plumosa*, *S. simplex*, and *S. spathulata*. Goldenrods in *S.* subsect. *Humiles* are united by the presence of resinous glands on the foliage and involucral bracts that cause all members of the group to be glutinous or sticky. In addition, all species in the subsection have virgate to paniculiform arrays with non-secund capitula (Semple and Cook 2006).

The subsection occurs entirely in North America and is transcontinental in distribution. *Solidago arenicola*, *S. kralii*, and *S. plumosa* are narrowly distributed endemics in the southeastern United States (Fig. 3.1). *Solidago arenicola* is restricted to rocky or sandy riverbanks and floodplains in the Cumberland Plateau region of northern Alabama, Tennessee, and southern Kentucky. *S. kralii* is confined to sand hills along the Coastal Plain fall line in a small area of Georgia and South Carolina. *Solidago plumosa* is known from a single population on mafic rocks along the Yadkin River in Stanley Co., North Carolina. *Solidago spathulata* inhabits sand dunes along the Pacific coast from central California to northern Oregon. *Solidago simplex* is widespread and transcontinental in distribution but absent from the center of the continent (Fig. 3.1).

Ringius (1986) divided *S. simplex* into two subspecies. Diploid subsp. *simplex* (2*n*=18) is widespread yet patchily distributed in montane and alpine habitats throughout the western cordillera from Alaska to Mexico (Fig. 3.1). Disjunct, eastern diploid populations in the northern Great Lakes region and Gaspé, Quebec have also been placed in subspecies *simplex*. Tetraploid subsp. *randii* (2*n*=36) is restricted to the Great Lakes region and Appalachian Mountains in eastern North America. Four varieties are currently recognized in subsp. *randii*. *Solidago simplex* var. *racemosa* inhabits rocky riverbanks throughout the Appalachian Mountains, from Tennessee to New Brunswick, while *S. simplex* var. *monticola* is confined to barrens and serpentine soils in New England and southern Quebec. *Solidago simplex* vars. *ontarioensis* and *gillmanii* are endemic to the Great Lakes region, inhabiting rocky shores from the Bruce Peninsula, Ontario to southern and eastern Lake Superior and active dune systems along the shores of lakes Huron and Michigan, respectively.

Field Sampling. Because the overall aim of this study was to examine continental and regional cytogeographic patterns is *Solidago* subsect. *Humiles*, our sampling scheme was designed to fill in gaps in coverage (taxonomic and geographic) in previously underrepresented regions (e.g., the southeastern United States) and in regions with potentially complex cytogeographic patterns (e.g., the Great Lakes region). Members of *S.* subsect. *Humiles* were sampled from across their ranges in the Great Lakes region (Michigan and Ontario) and the southeastern United States (Alabama, Georgia, North Carolina, South Carolina, Tennessee, and West Virginia), with several additions from eastern and western North America (Oregon, Pennsylvania, and Vermont). Locality information for the 38 populations sampled in this study is presented in Table 3.1. At each site, rhizome cuttings from N = 1-9 widely spaced individuals (clones spaced > 3 m apart) were harvested in the field and transplanted to Matthaei Botanical Gardens at the University of Michigan or to the University of Waterloo North Campus Greenhouses. Flowering stems were harvested in the field (or from greenhouse-grown plants if not flowering in the field) and deposited as vouchers in the University of Michigan Herbarium (MICH) or the University of Waterloo Herbarium (WAT). Rhizomes/rootstocks were potted in standard potting soil and watered weekly to prevent desiccation.

Chromosome Number and DNA Ploidy Determination. Meiotic counts were made from pollen mother cells dissected from field-prepared buds fixed in Acetic Ethanol (3:1/EtOH:glacial acetic acid) and subsequently refrigerated in 70% EtOH. Mitotic counts from root tip preparations followed protocols outlined in Semple and Cook (2004). Root tips were harvested from actively growing greenhouse plants and immediately treated in 0.01% colchicine or saturated paradichlorobenzene (PDB) for 2-3 hr. After pretreatment in colchicine or PDB, root tips were fixed in Acetic Ethanol and then hydrolyzed in 1 N HCl for 30 min at 60°C before squashing. All squashes were stained with 1% acetic orcein, and all counts were made from fresh preparations. Permanent slides were made for most preparations as described by Semple et al. (1981) and are retained by J. C. Semple.

DNA ploidy (sensu Hiddeman et al. 1984) was determined by flow cytometry after the relative DNA content (from flow cytometry) was calibrated with previously determined chromosome numbers from a subset of populations in the study. At least one calibration/standardization was used for each recovered DNA ploidy level (2x, 4x, and 6x). Similar methodologies have been used successfully for a number plant species, including two other species of *Solidago* (Halverson et al. 2008b; Schlaepfer et al. 2008a).

Fresh *Solidago* leaf material was harvested from greenhouse-grown plants and stored in cool conditions for up to one week. For each sample, approximately one half of a young leaf was chopped with a clean razor blade in 0.8 ml ice-cold LB01 buffer (Dolezel et al. 1989) with 50 µg/ml propidium iodide and 50 µg/ml RNAse added. An approximately equal amount of fresh leaf from *Glycine max* (L.) Merr. ‘Polanka’ was co-chopped as an internal DNA content standard (2.5 pg/2c; cited in Dolezel et al. 1994; Dolezel et al. 2007). After chopping, each sample was filtered through a 30-µm filter into a microcentrifuge tube. Filtered samples were then centrifuged. The supernatant was subsequently removed, and the pellet was resuspended in 50 µg/ml propidium iodide and incubated at room temperature for 20-45 minutes. Samples were run on a BD FACSCalibur flow cytometer in the Department of Integrative Biology at the University of Guelph. Samples were run at medium pressure for 90 seconds, and data were acquired using CellQuest Pro software (BD Biosciences).

Most samples (128/140) were analyzed using Modfit software (Verity Software) to estimate peak means, CVs and nuclei number. Twelve samples in which the *Solidago* peak was very close to the *G. max* peak were measured using CellQuest Pro software, manually gating peaks. DNA content was calculated as:

$$\mathit{DNA\ Content} = 2.5 \times \frac{\mathit{Solidago\ mean}}{\mathit{Glycine\ max\ mean}}$$

where 2.5 equals the standardized mean genome size of *Glycine max* (in pg/2c) and the other mean values represent the experimentally determined values for each sample.

Literature Review and Mapping. Published chromosome counts were obtained through literature searches and through cross-referencing with Ringius and Semple (1987). Population data for literature reports accepted in this study is listed in Appendix 1. Cytovouchers for almost all literature reports were examined by at least one of the authors to confirm species determinations. All reports from the literature were compiled into a database and organized by locality. These populations from the literature were georeferenced and then pooled with data from this study to create cytogeographic maps representing all taxa in *S.* subsect. *Humiles*. Reports with the same locality description (within 1 km when georeferenced) were considered to be intrapopulation samples for mapping purposes.

RESULTS

Cytogeographic patterns in Solidago subsect. Humiles. Chromosome numbers and DNA ploidy determinations are reported for 336 individuals, including 146 new reports (Table 3.2). Of the 146 new reports, 140 were DNA ploidy determinations from flow cytometry analyses and six were direct counts using traditional cytological methods (Tables 3.1-3.2). Flow cytometry recovered three non-overlapping DNA ploidy groups that correspond to 2x, 4x, and 6x counts (Table 3.3). This data was consistent with literature reports and indicated that only three ploidy levels have been found in *S.* subsect. *Humiles*: diploid ($2n = 18$), tetraploid ($2n = 36$), and hexaploid ($2n = 54$). No odd ploidy individuals (e.g., triploid with $3n = 27$ or pentaploid with $5n = 45$) have been found in *S.* subsect. *Humiles*.

All currently recognized taxa within *Solidago* subsect. *Humiles* have at least one ploidy level report. Our diploid DNA ploidy determination represents the first published report for *S. plumosa* Small and is consistent with an unpublished count (Guy Nesom, pers. com.). Cytotypes within subsect. *Humiles* show significant geographic and taxonomic structuring (Fig. 3.2). All but one count of *S. simplex* var. *nana*, *S. simplex* var. *simplex*, and *S. spathulata* from western North America were diploid (2*n* = 18). Patterns in eastern North America were more complex at a regional scale and included counts of 2*n* = 18, 36, and 54. A single West Virginia population of *S. simplex* var. *racemosa* was found to be hexaploid (2*n* = 54).

Although multiple ploidal levels were found in eastern North America, almost no within-population variation was observed. Three mixed ploidy populations were uncovered in this study (mean number of intrapopulation samples = 5.33, minimum = 5, maximum = 6). In each case, a single tetraploid individual was recovered from an otherwise diploid population in the northern Great Lakes region. Beaudry (1969) reported a similar situation (one tetraploid and four diploid individuals) from the Yukon Territory, Canada. His counts, however, were all made from seedlings grown from a single maternal individual.

Rejected Reports. Sixteen literature reports were rejected due to initial taxon misidentification (Appendix 2). Diploid counts from the rocky eastern shore of Lake Superior (from Agawa Bay south to Batchewana Bay) and from the tip of the Bruce Peninsula were previously attributed to southward extensions of *S. simplex* var. *simplex* in the Great Lakes region (Morton 1981; Semple et al. 1981; Ringius and Semple 1987). Examination of cytovouchers (e.g., *Semple and Brammall 2860* MO! and *Semple and*

Brammall 2862 MO!, MT!) revealed that these specimens vary in stem, leaf, and peduncular pubescence (from essentially glabrous to very sparsely pubescent) and in cypsella pubescence (from glabrous to very slightly pubescent) and have relatively small capitula (3-4 mm). Overall form and vegetative appearance were superficially consistent with identification as *S. simplex*, but capitula and achene characteristics, lack of glutinosity, and growth form in a common garden align these specimens with *S. hispida* Willd. (see discussion for further explanation).

A report of diploid *S. simplex* var. *simplex* from Fort Saskatchewan, Alberta (Beaudry 55-276-5 MT!, cited in Beaudry and Chabot 1959) was upon examination determined to be *S. uliginosa* Nutt. A previous report of *S. simplex* var. *simplex* from South Dakota (Semple and Brammall 4476 WAT!, cited in Ringius and Semple 1987) was identified as *S. missouriensis* Nutt. Cytovouchers of *S. simplex* var. *simplex* from the Capitan Mountains in southeastern New Mexico (Soreng 1493 ASU!, MO!, cited in Ward and Spellenberg 1986) were suggestive of *S. spectabilis* (D.C. Eaton) A. Gray or another species in *S.* subsect. *Junceae* (Rydberg) G.L. Nesom. Due to this ambiguity, they were excluded from the cytogeographic maps.

DISCUSSION

This study confirmed a number of the patterns found by previous cytogeographic work on *S. simplex* and *S. spathulata* (Ringius 1986; Ringius and Semple 1987), but our increased taxon and population coverage allowed us to uncover additional patterns not previously documented (five species and 336 reports included in this study compared to two species and ca. 130 reports in Ringius and Semple 1987).

Patterns in western North America remain unchanged from earlier studies; the subsection is known only at the diploid level throughout its range from Alaska and northern Canada south through the Rocky Mountains. Disjunct populations in Mexico have been presumed to be diploid but have never been sampled for cytogeographic work.

Patterns in eastern North America are more complex than previously realized. Ringius and Semple (1987) reported diploid populations of *S. simplex* from the northern extremes of the distribution in the Lake Superior region and from Gaspé, Quebec. Diploid populations in the Great Lakes region are more widespread than previously thought. They occur throughout the northern Lower Peninsula of Michigan in xeric jack pine barrens. Diploid reports from the eastern shores of Lake Superior were rejected (see below). Our results also indicated that diploid populations are also present at the southeastern extreme of the distribution in Georgia and the Carolinas. Two of the southeastern endemics, *S. kralii* and *S. plumosa*, occur only at the diploid level. *Solidago arenicola* (the third southeastern endemic) is tetraploid throughout its limited range.

Ringius (1986) and Ringius and Semple (1987) did not sample any populations from the southeastern Unites States. Inclusion of the three southeastern endemics plus southern populations of *S. simplex* var. *racemosa* in West Virginia greatly increased our understanding of cytogeographic patterns in that region. Semple and Cook (2006) proposed that southern Appalachian populations of *S. simplex* var. *racemosa* might be hexaploid (based on a series of hexaploid counts from Valley Falls, West Virginia), but our analyses found that *S. simplex* var. *racemosa* is tetraploid throughout its range, except for the hexaploid population at Valley Falls.

Ringius and Semple (1987) proposed that two transcontinental migrations produced the current disjunct distribution of cytotypes in *Solidago simplex*. The first migration of diploid *S. simplex* from western North America occurred during the early-stages of the Wisconsinan glaciation and resulted in the formation of tetraploid *Solidago* subsp. *randii* in the Appalachian Mountains. The second migration occurred during the Holocene, when diploid *S. simplex* spread south from the Beringian refugium across western Canada to the northern Great Lakes region.

Patterns uncovered by this study and much recent work on the evolution of polyploid plant species (reviewed in Soltis and Soltis 1999; Soltis et al. 2004) suggest that the previous hypotheses proposed by Ringius and Semple are likely too simple. Their initial hypotheses proposed that tetraploid *S. simplex* subsp. *randii* was a monophyletic lineage that originated from a single polyploidization within the last 100,000 years. Numerous molecular studies have demonstrated that the recurrent formation of polyploid lineages is more likely the norm than the exception (e.g., Segraves et al. 1999), and Soltis et al. (1999) proposed that most polyploid species are probably polyphyletic. The presence of three members of *Solidago* subsect. *Humiles* in the southeastern United States (Keener and Kral 2003; Semple 2003; Semple and Cook 2006) also raises additional questions. *Solidago plumosa* ($2n = 18$) is ecologically and morphologically similar to some populations of *S. simplex* var. *racemosa* ($2n = 36$) from the Southern Appalachians, and Semple and Cook (2006) suggested that it may be very closely related to *S. simplex*. The presence of three distinct, narrowly endemic species in the southeastern United States suggests a longer history of allopatry and divergence within the subsection than previously proposed.

Polyploidy, Speciation, and Infraspecific Cytotype Variation in Solidago. Soltis et al. (2007) proposed that many infraspecific chromosomal races within taxonomically recognized species actually meet the criteria of multiple species concepts. This raises a number of questions for genera, like *Solidago*, that harbor substantial amounts of taxonomically unrecognized cytotypic variation. Examination of published data for eight species of *Solidago* indicated that infraspecific chromosomal races in a number of species meet the requirements of multiple species concepts (data summarized in Table 3.4).

Ringius and Semple (1987) pointed out that the geographic segregation of subspecies in *S. simplex* mirrored patterns in other *Solidago* species. Infraspecific chromosomal races in six of the eight species summarized in Table 3.4 have largely distinct geographic ranges. Tetraploid populations of *S. uliginosa* in the Great Lakes region, while not geographically segregated, are ecologically distinct from diploid populations in the region. Chmielewski et al. (1987) found that tetraploids were restricted to alvars habitats along the Niagara Escarpment, while diploids did not occur on this habitat.

The extensive body of traditional cytological work compiled for *Solidago* suggests that there are strong intrinsic barriers to intracytotype gene flow and that the formation of odd ploidy individuals (i.e., triploid or pentaploid) is an extremely rare event. Semple (1992) found that only 0.12% (8 out of 6908 records) of North American chromosome counts for asters and goldenrods were from odd ploidy individuals. Pollination studies have supported cytological findings, indicating that there is strong triploid block in *Solidago* and that interploidal crosses are overwhelmingly (almost entirely) unsuccessful (Melville and Morton 1982; Ringius 1986). Recent cytogeographic studies utilizing flow cytometry (with substantially larger sample sizes than traditional studies) have reached the same general conclusions, although minutely higher numbers of odd ploidy individuals have been uncovered (Halverson et al. 2008b; Schlaepfer et al. 2008a). This cumulative data suggests that there is no significant triploid or pentaploid bridge between cytotypes. Recent work on *S. altissima* (Halverson et al. 2008b), however, suggested that incipient tetraploid plants may form a bridge between diploid and hexaploid subspecies. It is not known if this pattern will turn out to be common in other goldenrods.

This study and cumulative cytological data from numerous other studies of *Solidago* strongly suggest that polyploidy has been an important factor in diversification in the genus. Patterns from a number of cytogeographic studies indicate that infraspecific cytotypes often (but not always) represent ecogeographically, morphologically, and reproductively isolated lineages. Possible recurrent origins of polyploid populations in some species (e.g., *S. altissima* and *S. nemoralis*) have possibly promoted intercytotype gene flow and prevented lineage divergence in those taxa, but additional genetic studies are needed to test hypotheses in these species. Substantial phenotypic variation within species and the predominant use of a traditional morphological species concept have contributed to the levels of infraspecific cytotype variation currently recognized in *Solidago*, despite the fact that many of these infraspecific cytotypes appear to represent biological species.

A New Endemic Solidago from Eastern Lake Superior? Previous cytological studies reported populations of diploid *S. simplex* var. *simplex* along the eastern shore of Lake Superior (from Agawa Bay south to Batchewana Bay) and from the tip of the Bruce Peninsula (Morton 1981; Semple et al. 1981; Ringius and Semple 1987). This study indicate that diploid *S. simplex* occurs along the north shore of Lake Superior to Terrace Bay but does not extend south along the eastern shore of Lake Superior or to the Bruce Peninsula. Examination of cytovouchers cited in previous studies and plants transplanted to the Matthaei Botanical Gardens for this study revealed that these populations do not represent *S. simplex* but are instead an as of yet undescribed taxon related to *S. hispida*. Superficially these plants are very similar in appearance to *S. simplex* (hence the confusion), but closer examination revealed that they are never glutinous (a characteristic of all plants in subsect. *Humiles*), the achenes and arrays are generally glabrate, and the capitula are generally small (3-4 mm). None of these characters indicates *S. simplex*. Diploid *S. simplex* from the northern shore of Lake Superior has glutinous foliage and flower heads, densely strigose achenes, and larger capitula (4-5 mm). Flow cytometry analyses indicated that the mean genome size of the undescribed Lake Superior plants was smaller than diploid *S. simplex* and more similar to that of *S. hispida* var. *huronenis* (Peirson, unpublished data). Sample sizes and sampling design were not set up to test this hypothesis more thoroughly however.

Examination of herbarium specimens from throughout the Lake Superior region indicated that diminutive rock outcrop plants of *S. hispida* (with varying degrees of pubescence) are quite common in a number of localities (e.g., the shores of Lake Superior and also Isle Royale National Park). It is unclear whether these plants have a common origin or represent independently derived ecological forms. Voss (1996) suggested that these populations may represent disjunct occurrences of *S. hispida* var. *tonsa*. This taxon is a localized, endemic from the maritime provinces of Canada, however, and doubtfully occurs in the Great Lakes region. These populations may represent a new endemic goldenrod from the Great Lakes region and deserve further study.

Summary. Chromosome numbers and DNA ploidy determinations from 336 individuals, including 146 new reports, revealed significant geographic and taxonomic structuring of cytotypic variation within *Solidago* subsect. *Humiles*. Counts of *S. simplex* subsp. *simplex* and *S. spathulata* from western North America were diploid ($2n = 18$), except for a single tetraploid count from the Yukon. Patterns in eastern North America were more complex and included ploidy determinations of $2n = 18$, 36, and 54. Although multiple cytotypes were found in eastern North America, there was significant geographic segregation and almost no within-population variation. Tetraploids occurred throughout the distribution in the east, while diploids occurred at the extremes of the range in the southeastern United States, northern Great Lakes region, and Gaspé Peninsula, Quebec.

The complex cytogeographic patterns recovered in *S.* subsect. *Humiles* cast doubt on the more simplistic scenario proposed by Ringius and Semple (1987) and suggest a longer history of allopatry and probable multiple origins of polyploids in the east. The patterns recovered and the paucity of within population variation, however, do not suggest widespread, repeated generation of polyploid individuals as in some other goldenrods (e.g., *S. altissima* and *S. nemoralis*). Examination of infraspecific cytotype variation in *S. simplex* (and in seven other species of *Solidago*) revealed that chromosomal races within a number of species, but not in all, appear to be behaving as distinct, reproductively isolated species. These results suggest that species diversity in *Solidago* is likely considerably higher than currently recognized taxonomically.

Table 3.1. Locality information and numbers of individuals sampled from 38 populations of *Solidago* subsect. *Humiles* included in this study. Nomenclature follows Semple and Cook (2006). Countries: U.S.A., United States; Can, Canada. Collector abbreviations are as follows: *JP*, J.A. Peirson; *S&S*, J.C. Semple and B. Semple; *Voss*, E.G. Voss; *Hr&St*, Hrusa and G.L. Stebbins. *JP* and *Voss* vouchers are deposited at MICH; *S&S* and *Hr&St* vouchers are deposited at WAT. The majority of ploidy determinations (2x, 4x, 6x) were inferred from flow cytometry analysis. Direct chromosome counts are indicated by an asterisk (*).

						No. of Individuals			
	Country	State	County	Latitude	Longitude	2x	4x	6x	Voucher(s)
Solidago arenicola									
Locust Creek at Rte 231	U.S.A.	Alabama	Blount	34.02	-86.57	-	2	-	*JP* 608
Swann Bridge	U.S.A.	Alabama	Blount	34.00	-86.60	-	1 + 1*	-	*JP* 609, *S&S* 11196
Lily Bridge	U.S.A.	Tennessee	Morgan	36.10	-84.72	-	4	-	*JP* 610
Solidago kralii									
Vaucluse	U.S.A.	South Carolina	Aiken	33.61	-81.82	1	-	-	*JP* 605
I-20 north of Graniteville	U.S.A.	South Carolina	Aiken	33.62	-81.83	1*	-	-	*S&S* 11218
Bowens Mill 1	U.S.A.	Georgia	Ben Hill	31.84	-83.21	1*	-	-	*S&S* 11212
Bowens Mill 2	U.S.A.	Georgia	Ben Hill	31.84	-83.21	1*	-	-	*S&S* 11216-B
Hartford	U.S.A.	Georgia	Pulaski	32.25	-83.40	1*	-	-	*S&S* 11208
Solidago plumosa									
Yadkin River	U.S.A.	North Carolina	Stanley	35.41	-80.09	3	0	0	*JP* 604
Solidago simplex* var. *gillmanii									
West of Detour Village	U.S.A.	Michigan	Chippewa	45.97	-84.06	0	7	0	*Voss* 16893
West of Manistique	U.S.A.	Michigan	Schoolcraft	45.91	-86.32	0	8	0	*JP* 590
Silver Lake State Park	U.S.A.	Michigan	Oceana	43.65	-86.54	0	2	0	*JP* 595
Wilderness State Park, Sturgeon Bay	U.S.A.	Michigan	Emmet	45.71	-84.95	0	7	0	*JP* 531

Thompson's Harbor State Park	U.S.A.	Michigan	Presque Isle	45.35	-83.57	0	5	0	*JP* 789
Warren Dunes State Park	U.S.A.	Michigan	Berrien	41.91	-86.60	0	4	0	*JP* 517
Solidago simplex* var. *monticola									
Falls of Lana	U.S.A.	Vermont	Addison	43.90	-73.06	0	2	0	*JP* 581
Solidago simplex* var. *ontarioensis									
Tobermory, Big Tub Lighthouse	Can	Ontario	Bruce	45.26	-81.67	0	5	0	*JP* 475
Georgian Bay	Can	Ontario	Bruce	45.25	-81.52	0	4	0	*JP* 560
Fort Wilkins State Park	U.S.A.	Michigan	Keweenaw	47.47	-87.86	0	5	0	*JP* 625
Tobermory, Elgin Street	Can	Ontario	Bruce	45.26	-81.64	0	6	0	*JP* 562
Government Dock	Can	Ontario	Algoma	47.94	-84.85	0	6	0	*JP* 557
South of Tobermory, Hay Bay Road	Can	Ontario	Bruce	45.24	-81.68	0	6	0	*JP* 563
Sand Beach	Can	Ontario	Algoma	47.96	-84.86	0	1	0	*JP* 555
Seul Choix Point	U.S.A.	Michigan	Schoolcraft	45.92	-85.91	0	9	0	*JP* 467
Solidago simplex* var. *racemosa									
Audra State Park	U.S.A.	West Virginia	Barbour	39.04	-80.07	0	4	0	*JP* 598
Below Carnifex Ferry Battlefield	U.S.A.	West Virginia	Nicholas	38.21	-80.94	0	3	0	*JP* 603
Holton Dam	U.S.A.	Pennsylvania	York	39.81	-76.33	0	4	0	*JP* 585
Valley Falls	U.S.A.	West Virginia	Marion	39.39	-80.09	0	0	5	*JP* 597
Solidago simplex* var. *simplex									
Rte 612 and Deward Road	U.S.A.	Michigan	Kalkaska	44.77	-84.85	3	0	0	*JP* 464
I-75 south of Gaylord	U.S.A.	Michigan	Otsego	44.97	-84.67	4	0	0	*JP* 647
Fletcher Road	U.S.A.	Michigan	Kalkaska	44.57	-85.06	1	0	0	*JP* 541
Big Creek Road	U.S.A.	Michigan	Oscoda	44.67	-84.28	3	0	0	*JP* 542

North of St. Helena	U.S.A.	Michigan	Roscommon	44.40	-84.41	4	1	0	*JP* 463
Rte 612 and I-75	U.S.A.	Michigan	Crawford	44.78	-84.72	7	0	0	*JP* 538
Staley Lake Road	U.S.A.	Michigan	Crawford	44.65	-84.64	4	1	0	*JP* 535
Terrace Bay	Can	Ontario	Thunder Bay	48.77	-87.11	5	1	0	*JP* 550
Solidago spathulata									
Gearhart/Seaside	U.S.A.	Oregon	Clatsop	46.02	-123.93	2	0	0	*JP* 636
Cavedale Rd east of Hwy-12	U.S.A.	California	Sonoma	38.38	-122.46	1*	0	0	*Hr&St* 11428

Table 3.2. Summary of chromosome counts and DNA ploidy determinations for *Solidago* subsect. *Humiles* from the literature and this study.

Taxon	Somatic chromosome #	DNA ploidy	# of dets. from literature	# of dets. this study	Total # of counts
S. arenicola	2n = 36	4x	1	8	9
S. kralii	2n = 18	2x	2	5	7
S. plumosa	2n = 18	2x	---	3	3
S. simplex	2n = 18, 36, 54	2x, 4x, 6x	175	127	302
subsp. *simplex*	2n = 18, 36	2x, 4x	94	34	128
var. *chlorolepis*	2n = 18	---	7	---	7
var. *nana*	2n = 18	---	1	---	1
var. *simplex*	2n = 18	2x	85	31	116
var. *simplex*	2n = 36	4x	1	3	4
subsp. *randii*	2n = 36, 54	4x, 6x	81	93	174
var. *gillmanii*	2n = 36	4x	15	33	48
var. *monticola*	2n = 36	4x	15	2	17
var. *ontarioensis*	2n = 36	4x	24	42	66
var. *racemosa*	2n = 36	4x	21	11	32
var. *racemosa*	2n = 54	6x	6	5	11
S. spathulata	2n = 18	2x	12	3	15
Totals			190	146	336

Table 3.3. Sample frequencies and relative DNA content as determined by flow cytometry analysis of fresh leaf tissue from species in *Solidago* subsect. *Humiles*. Populations with both diploid and tetraploid cytotypes were counted twice.

			Relative DNA Content		
Ploidy level	No. Populations	No. Individuals	Mean (± SD)	Min.	Max.
Diploid	11	37	2.30 (0.06)	2.21	2.50
Tetraploid	24	98	4.36 (0.11)	4.07	4.58
Hexaploid	1	5	6.08 (0.08)	5.96	6.17

Table 3.4. Species criteria applied to patterns of infraspecific cytotype variation in eight species of *Solidago*. In addition to the Flora of North America treatment of *Solidago* (Semple and Cook 2006), data for species were summarized from the following: *S. altissima* (Melville and Morton 1982; Halverson et al. 2008b), *S. curtissii* (Cook and Semple 2008; Cook et al. 2009), *S. flexicaulis* (Chmielewski and Semple 1985; Cook and Semple 2008; Cook et al. 2009), *S. gigantea* (Melville and Morton 1982; Schlaepfer et al. 2008a; Schlaepfer et al. 2008b), *S. nemoralis* (Brammall and Semple 1990; Semple et al. 1990), *S. rigida* (Heard and Semple 1988), *S. simplex* (Ringius 1986; Ringius and Semple 1987), *S. uliginosa* (Chmielewski et al. 1987).

	Species criterion				
Species	Biological	Evolutionary or Ecological	Phylogenetic apomorphic	Phylogenetic diagnosability	Taxonomic
S. altissima	Probably, but incipient tetraploids may form a bridge between diploid and hexaploid cytotypes in zone of sympatry	Yes, distinct lineages, distinct geographic ranges at continental scale, but local co-occurrence where cytotypes overlap	Unclear, intrapopulation cytotypes more closely related to each other (e.g., gene flow or lineage recombination)	Yes, chromosome number, capitula morphology	Yes, capitula size between diploids and hexaploids, tetraploids in zone of sympatry obscure pattern
S. curtisii	Unclear, recurrent within population polyploidy may act as a bridge between cytotypes	Unclear, within population variation, overlapping ranges, probable recurrent origins of polyploids	Unknown	Yes, chromosome number	No, varieties have distinct morphology, but infravarietal cytotypes not distinguishable
S. flexicaulis	Yes, triploids very rare	Yes, distinct lineages, largely distinct geographic ranges	Unknown	Yes, chromosome number, capitula and floral morphology	Yes, capitula size
S. gigantea	Yes, odd ploidies very rare, substantial triploid block, interploidal crosses unsuccessful	Probably, appear to be distinct lineages, largely distinct geographic ranges	Unclear, cpDNA suggests multiple origins of polyploids	Yes, chromosome number	No, apparently indistinguishable
S. nemoralis	Yes, triploids not reported	In part, diploid and tetraploid subsp. are distinct lineages, distinct geographic ranges	Unknown, but presumably multiple origins of polyploidy in subsp. *nemoralis*	Yes, chromosome number, involucral and floral morphology	Yes, capitula size, floral and achene characters, but sometimes difficult to distinguish

S. rigida	Yes, triploids not reported in areas of sympatry	Yes, distinct lineages, largely distinct geographic ranges	Unknown	Yes, chromosome number, distinct morphology	Yes, capitulescence and phyllary characteristics, vegetative pubescence, sometimes difficult to distinguish
S. simplex	Yes, no triploids reported, interploidal crosses failed, phenological separation in region of sympatry	Yes, appear to be distinct lineages, largely distinct geographic ranges, ecological separation	Unclear, considerable haplotype sharing between cytotypes, likely multiple origins of polyploids	Yes, chromosome number, morphology, but sometimes difficult to distinguish	Sometimes, plant size and capitula size but sometimes difficult to distinguish
S. uliginosa	Yes, triploids not reported, suggestion that phenologies differ on local scales	Probably, appear to be distinct lineages, ecological separation (in some regions)	Unknown, presumably multiple origins of polyploids	Yes, chromosome number	Unknown

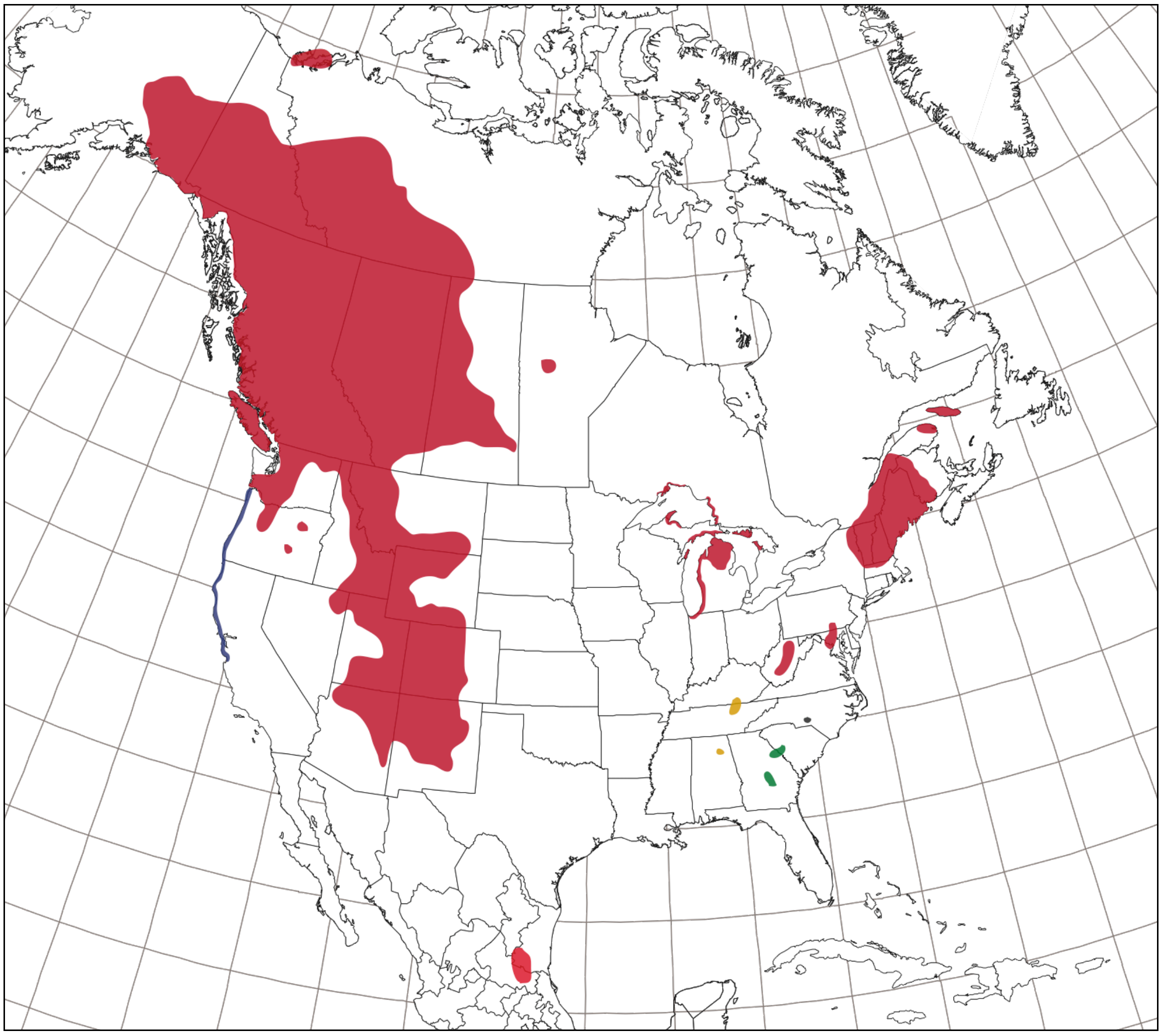

Figure 3.1. Generalized distribution of *Solidago* subsect. *Humiles* in North America: *S. arenicola* (yellow shading), *S. kralii* (green shading), *S. plumosa* (grey shading), *S. simplex* (red shading), *S. spathulata* (blue shading).

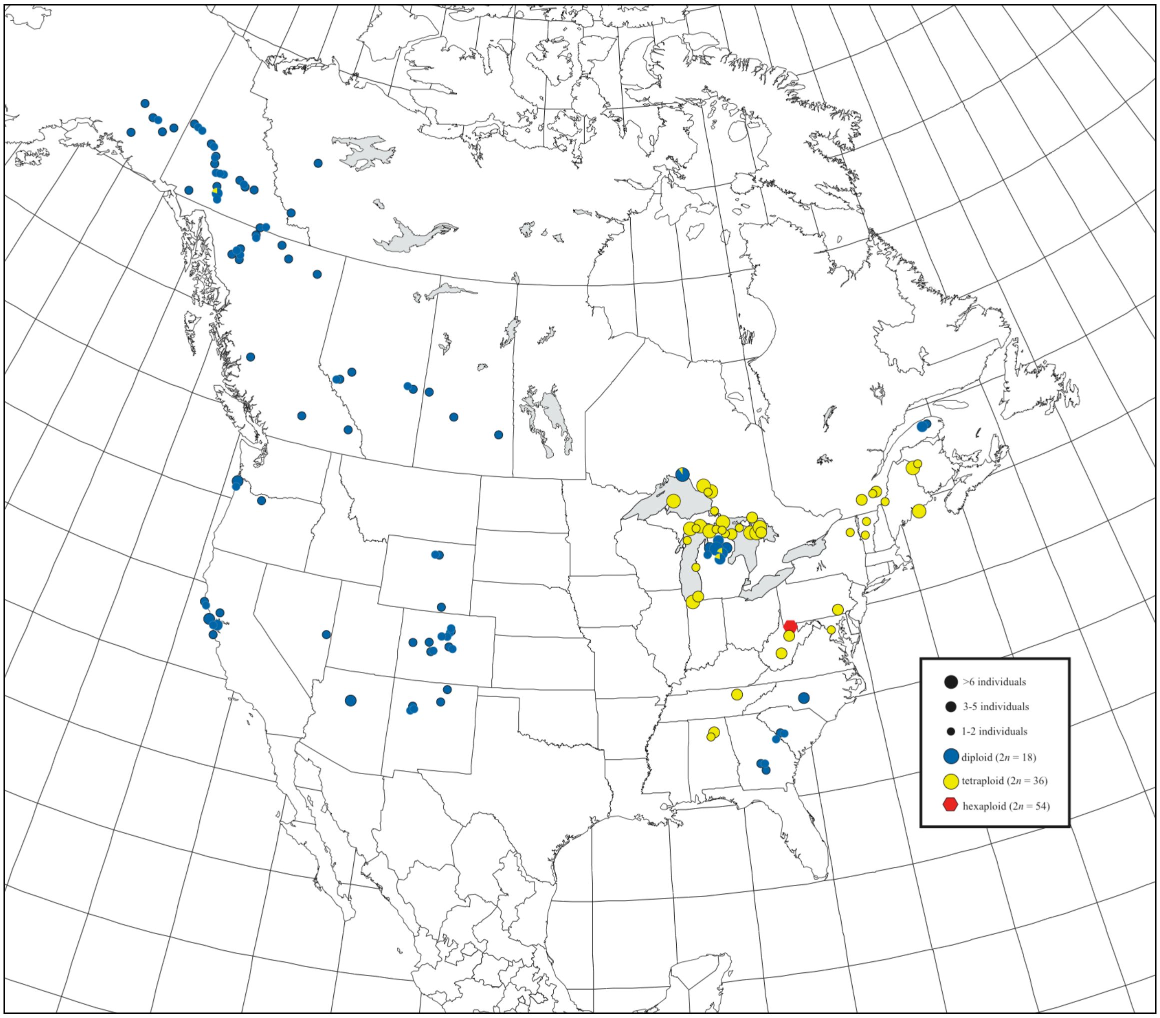

Figure 3.2. Distribution of cytotypes ($2n$ = 18, 36, 54) within *Solidago* subsect. *Humiles* based on data from this study and from confirmed literature reports. Pie diagrams represent the proportion of cytotypes in each sampled population and are scaled for sample sizes at each population.

APPENDIX 1

Table 3A1.1. Locality and cytovoucher information for 190 published chromosome counts from *Solidago* subsect. *Humiles*. Nomenclature follows Semple and Cook (2006). Rejected reports (n = 16) are presented in Appendix 2 and are discussed in the text. Countries are designated as follows: U.S.A., United States; Can, Canada. References for counts are indicated by superscripts as follows: a, Beaudry and Chabot (1959); b, Raven et al (1960); c, Beaudry (1963); d, Beaudry (1969); e, Mulligan et al (1972); f, Hartman (1977); g, Taylor and Taylor (1977); h, Keil and Pinkava (1979); i, Morton (1981); j, Semple et al (1981); k, Ward and Spellenberg (1986); l, Ringius and Semple (1987); m, Semple et al (1989); n, Semple et al (1992); o, Gervais et al (1999); p, Semple et al (2001); q, Semple (2003); r, Semple and Cook (2004).

Species/Location	Country	State/Prov.	County	Latitude	Longitude	Count	Herbarium	Voucher(s)
Solidago arenicola								
NW of Cleveland, woods near Locust Creek of Warrior River	U.S.A.	Alabama	Blount	34.02	-86.57	36[r]	WAT	S&S 11191
Solidago kralii								
S of Hartford, GA-230 1 km SE of US-341/GA-27	U.S.A.	Georgia	Pulaski	32.28	-83.45	18(9II)[q]	WAT	Cook et al 701
US-1, NE of Blythe, S of Ellis Pond.	U.S.A.	Georgia	Richmond	33.33	-82.18	18(9II)[q]	WAT	S&S 11217
Solidago simplex* var. *chlorolepis								
Mount St. Anne	Can	Quebec	Gaspe	49.00	-66.04	18[o]	QFA	Boudreau 96-175, Boudreau 96-176
Mount Albert, Gaspe Peninsula, near headwaters of Ruisseau de Diable	Can	Quebec	Gaspe	48.91	-66.18	18[l]	WAT	R 1691
Mount Albert, Vallee du diable	Can	Quebec	Gaspe	48.91	-66.18	18[o]	QFA	Lavoie et al 94-5
Mount Albert, Gaspe Peninsula	Can	Quebec	Gaspe	48.91	-66.18	18[l]	WAT	R 1690, R 1700, R 1702

Solidago simplex* var. *gillmanii								
Great Duck Island, Lake Huron	Can	Ontario	Manitoulin	45.69	-82.94	36[i]	WAT	Morton & Venn 9493
Mackinaw City	U.S.A.	Michigan	Emmet	45.78	-84.74	36[c]	MT	Voss 58-280, Voss 58-281
Rogers City	U.S.A.	Michigan	Presque Isle	45.42	-83.80	36[i]	WAT	Morton & Venn 10911
Indiana Dunes State Park	U.S.A.	Indiana	Porter	41.68	-87.02	36[l]	WAT	R 1511, R 1512, R 1513, R 1516, R 1517, R 1521
Huron Beach	U.S.A.	Michigan	Presque Isle	45.57	-84.14	36[l]	WAT	R 1818, R 1819
Manistique	U.S.A.	Michigan	Schoolcraft	45.91	-86.32	36[l]	WAT	R 1840
Baileys Harbor	U.S.A.	Wisconsin	Door	45.07	-87.11	36[l]	WAT	R 1845, R 1847
Solidago simplex* var. *monticola								
Black Lake	Can	Quebec	Megantic	46.03	-71.40	36[a]	MT	J. Beaudry & Cinq-Mars 56-433
Thetford Mines	Can	Quebec	Megantic	46.07	-71.30	36[l]	WAT	R 1805, R 1806, R 1808, R 1809
Whiteface Mountain	U.S.A.	New York	Essex	44.35	-73.86	36[c]	MT	Parker 58-19-2
Mount Mansfield	U.S.A.	Vermont	Chittenden	44.54	-72.81	36[c]	MT	J. Beaudry 58-246
Mount Desert Island	U.S.A.	Maine	Hancock	44.31	-68.34	36[l]	WAT	R 1743, R 1754, R 1757, R 1759, R 1762, R 1763, R 1768, R 1769
Solidago simplex* var. *nana								
Mt. Hood, Cooper Spur Trail below Eliot	U.S.A.	Oregon	Hood River	45.38	-121.65	18[p]	WAT	S&Xg 10270

Glacier								
Solidago simplex* var. *ontarioensis								
Old Woman Bay	Can	Ontario	Algoma District	47.79	-84.90	36[d]	MT?	Purchase 62-5-1, Purchase 62-5-2, Purchase 62-5-3, Purchase 62-5-4, Purchase 62-5-5
West of Sault St. Marie, Gros Cap	Can	Ontario	Algoma District	46.53	-84.59	36	WAT	S 11086
Gros Cap	Can	Ontario	Algoma District	46.53	-84.59	36[l]	WAT/MT	R 1448
Michipigoten Harbor	Can	Ontario	Algoma District	47.94	-84.85	36[l]	WAT	R 1987, R 1988, R 1989, R 1990
Old Woman Bay	Can	Ontario	Algoma District	47.79	-84.90	36[l]	WAT	R 2005, R 2006
Georgian Bay, near Cypress Lake Provincial Park	Can	Ontario	Bruce	45.25	-81.52	36[l]	WAT	R 2066
Killarney	Can	Ontario	Manitoulin	45.98	-81.46	36[l]	WAT/MT	R 2041, R 2042, R 2043, R 2045, R 2047
Tobermory, end of Elgin Street	Can	Ontario	Bruce	45.25	-81.68	36[j]	WAT/MO	S&B 2788
Tobermory, shore of Lake Huron	Can	Ontario	Bruce	45.25	-81.68	36[j]	WAT	S 2437
Tobermory, along Bay Street	Can	Ontario	Bruce	45.25	-81.68	36(18II)[j]	WAT/MO	S&B 2787
Tobermory, along Front Street	Can	Ontario	Bruce	45.26	-81.64	36(18II)[j]	WAT/MO	S&B 2780
Copper Harbor	U.S.A.	Michigan	Keweenaw	47.47	-87.86	36[l]	WAT	R 1887
Solidago simplex* var. *racemosa								
Aroostook River	Can	New Brunswick	Victoria	46.81	-67.77	36[l]	WAT	R 1631, R 1632, R 1633, R 1635, R 1637, R 1639, R 1640, R

								1642, R 1643, R 1646
Plaster Rock on Tobique River	Can	New Brunswick	Victoria	46.91	-67.39	36[l]	WAT	R 1780, R 1786, R 1787
Drummondville, St. Francis River	Can	Quebec	Drummond	45.89	-72.48	36[l]	WAT	R 1658, R 1659, R 1661, S&Bt 3407
Drummondville, St. Francis River	Can	Quebec	Drummond	45.89	-72.48	36[j]	WAT	S&Bt 3407
Valley Falls State Park	U.S.A.	West Virginia	Marion	39.39	-80.09	54[c]	MT	Core 57-661, Core 57-662, Core 57-663, Core 57-664, Core 57-667, Core 57-668
Great Falls on the Potomac River	U.S.A.	Maryland	Montgomery	39.00	-77.25	36[l]	WAT	JCS&R 7663
Arnold Pond	U.S.A.	Maine	Franklin	45.39	-70.79	36[l]	WAT	S&K 4621
PA 372 at Susquehanna River	U.S.A.	Pennsylvania	York	39.81	-76.33	36[l]	WAT	JCS&R 7612
Solidago simplex* var. *simplex								
Lac Laberge (seedlings)	Can	Yukon	--	60.99	-135.13	18[d]	MT?	Marsh 63-6-1, Marsh 63-6-3, Marsh 63-6-4, Marsh 63-6-5
Lac Laberge (seedling)	Can	Yukon	--	60.99	-135.13	36[d]	MT?	Marsh 63-6-2
Lake Jasper, Jasper National Park	Can	Alberta	--	53.11	-117.99	18[i]	WAT	Morton NA4600
Lavoy, East of Vegreville on Hwy. 16	Can	Alberta	--	53.47	-111.90	18[i]	WAT	Morton & Venn NA14175
Muncho Lake Provincial Park	Can	British Columbia	--	58.95	-125.77	18[i]	WAT	Morton & Venn NA14135
Saskatoon	Can	Saskatchewan	--	52.22	-106.75	18[i]	WAT	Morton NA2234

Watson Lake	Can	Yukon	--	60.06	-128.69	18[i]	WAT	Morton NA2005
Keele River	Can	Northwest Territories	Mackenzie District	64.37	-124.90	18(9II)[e]	DAO	Cody 19936
Nahanni National Park Reserve, Flat River Warden's Cabin	Can	Northwest Territories	--	61.42	-126.84	18	WAT	S 11156
Jasper National Park, Miette Hot Springs	Can	Alberta	--	53.13	-117.78	18[l]	WAT	S&Bt 4332
West of Mannville	Can	Alberta	--	53.33	-111.26	18[l]	WAT	S&Bt 4283
East of Obed Lake	Can	Alberta	--	53.54	-117.12	18[l]	WAT	S&Bt 4315
Kamloops	Can	British Columbia	--	50.65	-120.27	18[l]	WAT	CC 615A
North of Kinaskan Lake	Can	British Columbia	--	57.69	-130.04	18[l]	WAT	CC 2667
Windermere Lake	Can	British Columbia	--	50.46	-115.99	18[l]	WAT	S&Bt 4362
Terrace Bay	Can	Ontario	Thunder Bay District	48.77	-87.11	18[l]	WAT	R 1970, R 1972, R 1974, R 1977, R 1979
3 km west of the Ross River on Campbell Highway	Can	Yukon	--	61.99	-132.61	18[l]	WAT	CC 2307
West of Marshall	Can	Saskatchewan	--	53.22	-109.82	18[l]	WAT	S&Bt 4267
Springside	Can	Saskatchewan	--	51.34	-102.74	18[l]	WAT	S&Bt 4218
Dawson City	Can	Yukon	--	64.07	-139.42	18[l]	WAT	CC 2472
42 km west of Dawson City	Can	Yukon	--	64.23	-140.23	18[l]		CC 2469
7 km south of McQuesten River on Klondike Loop	Can	Yukon	--	63.54	-137.28	18[l]	WAT	CC 2662
18 km SW of Ross River on Campbell Highway	Can	Yukon	--	61.86	-132.36	18[l]		CC 2281
80 km SE of Ross River on Campbell Highway	Can	Yukon	--	61.75	-131.16	18[l]	WAT	CC 2265
Klondike Loop, 12 km S of Pelly Crossing near the 2nd lake	Can	Yukon	--	62.73	-136.69	18[m]	WAT	CC2665

Alaska Hwy, KP600, Testa River flats, just N of Testa service station	Can	British Columbia	--	58.79	-122.66	18[n]	WAT	Ch et al CC3773
Alaska Hwy, 21 km SE of Fireside	Can	British Columbia	--	59.61	-126.79	18[n]	WAT	Ch et al CC3783
Cassiar Hwy, 6 km N of Boya Lake Provincial Park turnoff	Can	British Columbia	--	59.42	-129.18	18[n]	WAT	Ch et al CC4720
Cassiar Hwy, KP729.8, at Yukon border	Can	British Columbia	--	60.00	-129.05	18[n]	WAT	Ch et al CC4709
12 km N of Iskut just N of Tsasbye Creek	Can	British Columbia	--	57.93	-130.05	18[n]	WAT	Ch et al CC4752
Telegraph Creek Rd., 1 km NE of Telegraph Creek	Can	British Columbia	--	57.91	-131.12	18[n]	WAT	Ch et al CC4738
Telegraph Creek Rd., 40 km S of Dease Lake	Can	British Columbia	--	58.26	-130.62	18[n]	WAT	Ch et al CC4735
Telegraph Creek Rd., 5 km S of Dease Lake	Can	British Columbia	--	58.41	-130.08	18[n]	WAT	Ch et al CC4731
Campbell Hwy, KP570, 21 km SE of Carmacks Junction	Can	Yukon	--	62.04	-135.90	18[n]	WAT	Ch et al CC4606
Campbell Hwy, KP560, just N of turnoff to Frenchman L. Gov't Campground	Can	Yukon	--	62.08	-135.65	18[n]	WAT	Ch et al CC4608
Campbell Hwy, KP539, N of turnoff to Frenchman L. Gov't Campground	Can	Yukon	--	62.10	-135.30	18[n]	WAT	Ch et al CC4610
Campbell Hwy, KP410, 10 km SE of Faro Junction	Can	Yukon	--	62.20	-133.52	18[n]	WAT	Ch et al CC4614
S of Whitehorse, Klondike Loop 2, KP108.3	Can	Yukon	--	60.59	-134.87	18[n]	WAT	Ch et al CC3883
Klondike Loop 2, 2 km N of MacGregor Creek, KP406-407	Can	Yukon	--	62.41	-136.59	18[n]	WAT	Ch et al CC4604
5 km S of Pelly Crossing, Klondike Loop, KP460	Can	Yukon	--	62.78	-136.58	18[n]	WAT	Ch et al CC4600

Dempster Hwy, KP12.2	Can	Yukon	--	64.03	-138.58	18[n]	WAT	Ch et al CC4561
Silver Trail Hwy, NE of Stewart Crossing, KP19	Can	Yukon	--	63.38	-136.65	18[n]	WAT	Ch et al CC4563
Cassiar Hwy. (Hwy. -37) 80 km S of Alaska Hwy, KP643.5, ca. 5 km N of Boya Lake	Can	British Columbia	--	59.45	-129.22	18[p]	WAT	S&S 10631
Alaska Hwy. just N of Haines Junction	Can	Yukon	--	60.76	-137.54	18[p]	WAT	S&S 10623
Klondike Loop (YT-2), KP270, N of Fox Lake	Can	Yukon	--	61.30	-135.55	18[p]	WAT	S&S 10626
Tweedsmuir Park, near lodge	Can	British Columbia	--	53.10	-125.88	18(9II)[g]	UBC	N. Turner 843
Snowy Range, 4 miles NW of Centennial	U.S.A.	Wyoming	Albany	41.35	-106.20	18[f]	RM	Hartman 3043
Inner Basin, San Francisco Peaks	U.S.A.	Arizona	Coconino	35.34	-111.66	18[h]	ASU	Keil 11724, Keil 11723, Reeves & Keil K11576
Slopes of Mt Fairplay, Taylor Highway	U.S.A.	Alaska	--	63.68	-142.26	18[i]	WAT	Morton NA2095
Sante Fe Basin	U.S.A.	New Mexico	Sante Fe	35.76	-105.82	18[i]	WAT	Morton & Venn NA7105
2 km west of Shaw Creek on Alaska Highway	U.S.A.	Alaska	--	64.26	-146.15	18[l]	WAT	CC 2442
55 km northeast of Slana on Glenn Highway	U.S.A.	Alaska	--	63.12	-143.29	18[l]		CC 2545
Nederland	U.S.A.	Colorado	Boulder	39.96	-105.52	18[l]	WAT	S 6548
US-50 west of Poncha Springs	U.S.A.	Colorado	Chaffee	38.54	-106.22	18[l]	WAT	S 7743
Echo Lake	U.S.A.	Colorado	Clear Creek	39.66	-105.60	18[l]	WAT	S 6600
Mount Evans	U.S.A.	Colorado	Clear Creek	39.59	-105.65	18[l]	WAT	S 6596, S 6597
South of Idaho Springs	U.S.A.	Colorado	Clear Creek	39.73	-105.53	18[l]	WAT	S 6604
South of Grand Mesa on CO-65	U.S.A.	Colorado	Delta	39.01	-107.99	18[l]	WAT	S 7790

West of Monarch Pass	U.S.A.	Colorado	Gunnison	38.50	-106.33	18[l]	WAT	S 7747
Keystone	U.S.A.	Colorado	Summit	39.61	-105.97	18[l]	WAT	S 6556
Florissant	U.S.A.	Colorado	Teller	38.95	-105.28	18[l]	WAT	S&Bt 7251
Pike's Peak	U.S.A.	Colorado	Teller	38.84	-105.04	18[l]	WAT	S 7722
Wheeler Peak	U.S.A.	Nevada	White Pine	38.98	-114.31	18[l]	WAT	S 5745
North of Gearhart	U.S.A.	Oregon	Clatsop	46.02	-123.93	18[l]	WAT	S&Bt 7113
Powder River Pass	U.S.A.	Wyoming	Johnson	44.16	-107.10	18[l]	WAT	S&Bt 4452
Alaska Hwy (MP1368), NW of Tok, 12 km NW of Dot Lake	U.S.A.	Alaska	--	63.70	-144.32	18[m]	WAT	CC2456
North of Dot Lake, Alaska Hwy, KP1367.5	U.S.A.	Alaska	--	63.67	-144.10	18[n]	WAT	Ch et al CC4470
Glenn Hwy, 1 km E of Tolsona Lake Rd.	U.S.A.	Alaska	--	62.10	-146.02	18[n]	WAT	Ch et al CC4102
CO-82 16 km E of Aspen, E of FR-106	U.S.A.	Colorado	Pitkin	39.13	-106.68	18[p]	WAT	S&Zh 10450
County line, SE of San Mateo, San Mateo Rd.	U.S.A.	New Mexico	McKinley/ Valencia	35.30	-107.60	18[p]	WAT	S,Su&Ah 9368
N of Grants, San Mateo Spring Canyon	U.S.A.	New Mexico	McKinley/ Valencia	35.32	-107.62	18[p]	WAT	S,Su&Ah 9370, S,Su&Ah 9372
Cebolleta Mts., Mt. Taylor	U.S.A.	New Mexico	Valencia	35.25	-107.59	18[p]	WAT	S,Su&Ah 9379
Cebolleta Mts., Mt. Taylor	U.S.A.	New Mexico	Valencia	35.25	-107.59	18[p]	WAT	S,Su&Ah 9380
W of Buffalo, US-16 between Pole Creek & Caribou Creek	U.S.A.	Wyoming	Johnson	44.19	-106.92	18[p]	WAT	S&Xg 10211
Wheeler Peak	U.S.A.	New Mexico	Taos	36.56	-105.42	18[k]	NMC	RWS 5822
Solidago spathulata								
Point Reyes	U.S.A.	California	Marin	38.00	-123.00	18[d]	MT?	Nobs 60-235-2, Rousi 60-25

Twin Peaks	U.S.A.	California	San Francisco	37.75	-122.45	18[d]	MT?	Beaudry et al 59-211, Beaudry et al 59-211-1, Beaudry et al 59-211-3
Lake Merced	U.S.A.	California	San Francisco	37.72	-122.50	18[d]	MT?	Beaudry et al 59-210-1, Beaudry et al 59-218-1
Point Reyes	U.S.A.	California	Marin	38.00	-123.00	18(9II)[b]	JEPS	Raven 13694
Pebble Beach	U.S.A.	California	San Mateo	37.24	-122.41	18[l]	WAT	R 1482
North of Sand Lake	U.S.A.	Oregon	Tillamook	45.33	-123.97	18[l]	WAT	S&Bt 7119
CA-1, just N of rd. to Point Arena Lighthouse	U.S.A.	California	Mendocino	38.96	-123.73	18[m]	WAT	S&H 8542
CA-1, N of Anchor Bay, ca. 11 km N of Sonoma Co. line	U.S.A.	California	Mendocino	38.84	-123.63	18(9II)[m]	WAT	S&H 8548

Table 3A1.2. Locality and cytovoucher information for 16 published chromosome counts from *Solidago* subsect. *Humiles* that were rejected in this study. Nomenclature follows Semple and Cook (2006). Countries are designated as follows: U.S.A., United States; Can, Canada. References for counts are indicated by the same superscripts as in Appendix 1.

Species	**Location**	**Country**	**State/Prov.**	**County**	**Count**	**Herbarium**	**Voucher(s)**
S. uliginosa	Fort Saskatchewan	Can	Alberta	--	18[a]	MT	G.H. Turner 55-276-3, G.H. Turner 55-276-4, G.H. Turner 55-276-5
S. cf. hispida	Perce Mt, Gaspe Peninsula	Can	Quebec	Gaspe	18[i]	WAT	Morton NA4142
S. cf. spectabilis	1 km NE of Capitan Peak	U.S.A.	New Mexico	Lincoln	18(9II)[k]	NMC/MO/ASU	RJS 1493
S. missouriensis	Black Hills	U.S.A.	South Dakota	Custer	18[l]	WAT	S&Bt 4476
S. hispida	18.8 km N of Pancake Bay Provincial Park	Can	Ontario	Algoma District	18[j,l]	WAT/MT/MO	S&Bt 2862
S. hispida	18.6 km S of Montreal River Harbor, rocky shore of Lake Superior	Can	Ontario	Algoma District	18(9II)[j]	WAT/MO	S&B 2860
S. hispida	North of Agawa Bay	Can	Ontario	Algoma District	18[l]	WAT	Ringius 2009, 2012
S. hispida	Mica Bay	Can	Ontario	Algoma District	18[l]	WAT	Ringius 2105, 2016, 2018
S. hispida	Pancake Bay	Can	Ontario	Algoma District	18[l]	WAT/MT	Ringius 1435
S. hispida	Lake Superior, west of Pancake Bay	Can	Ontario	Algoma District	18[i]	WAT	Morton NA2311
S. missouriensis	Bow Falls, Banff	Can	Alberta	--	36[i]	WAT	Morton NA3412

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CHAPTER IV

PHYLOGEOGRAPHIC PATTERNS IN *SOLIDAGO SIMPLEX* IN NORTH AMERICA

Quaternary climatic oscillations caused pronounced changes in species distributions and altered the genetic structure and diversity within species-populations across the northern hemisphere (Hewitt 1996, 2000). In North America, the direct effects of Pleistocene glacial cycles are most evident in the northern, glaciated portions of the continent, but all regions of the continent were ultimately affected by paleoclimatic cycles. Geologic evidence has produced a detailed chronological profile of the advance and retreat of the continental ice sheets of the most recent Wisconsinan glaciation, and paleoecological reconstructions have provided a broad picture of major vegetation changes since the last glacial maximum (Orme 2002). Presently, however, the population histories of the vast majority of temperate North American species and the overall effects of glaciation on population distribution and divergence remain largely unstudied.

Biogeographic Consequences of Glaciation in North America. The classical view of Pleistocene biogeography posits that repeated continental glaciations caused mass extinctions of the biota of northern latitudes and forced species to retreat to southern latitudes or refugia during glacial periods. Species migrated out of these southern survivia and expanded their ranges during interglacial periods (Davis 1983b; Huntley and Webb 1989; Hewitt 1996). In eastern North America, the majority of paleoecological reconstructions have suggested that during glacial maxima, tundra and boreal forest grew south of the ice margin, while temperate species were largely restricted to southern

Appalachian and Coastal Plain refugia (Wright 1970; Davis 1983a, b; Webb et al. 1983; Delcourt et al. 1984; Davis et al. 2000; Williams et al. 2000; Flakne 2003). Some early plant ecologists and biogeographers proposed, however, that temperate species in eastern North America likely persisted in cryptic refugia closer to the glacial margin (Gleason 1923; Braun 1928, 1955). Recent studies of several eastern North American species by J. S. McLachlan and others seem to support this scenario (McLachlan and Clark 2004; Rowe et al. 2004; McLachlan et al. 2005). In western North America, paleoecological research has recovered similar patterns of southward vegetation displacement (Whitlock and Bartlein 1997; Thompson and Anderson 2000), but unlike the east, it has also pointed to a major boreal/arctic refugium in Beringia (Pielou 1991; Abbott and Brochmann 2003; Brubaker et al. 2005).

Following the recession of the ice sheets, species migrated into the interior, glaciated parts of North America from refugia beyond the glacial boundary. Paleoecological studies suggest that postglacial recolonization was complex and that species responded individually to glaciation (Prentice 1986; Huntley and Webb 1989). Biogeographic data have long supported the idea that many modern communities in glaciated regions are composed of species with decidedly different floristic affinities. Gleason (1923) proposed that the flora of the Midwest migrated into the region from five primary sources, the southern Appalachians, the southern Coastal Plain, the Ozark Mountains, the Great Plains, and eastern Canada. In addition to these floristic elements, disjunct western and remnant arctic/alpine elements have also been identified in the northern Great Lakes region (Fernald 1935; Stebbins 1935). Marquis and Voss (1981) hypothesized that multiple, independent postglacial migrations from western North

America account for the current distributions of the western disjuncts.

Phylogeography and Genetic Consequences of Glaciation. Repeated episodes of isolation in glacial refugia and subsequent recolonization of glaciated territory altered the genetic structure and diversity within species-populations (Hewitt 1996). At the height of glacial periods, many species were hypothesized to be restricted to small, isolated refugia (Davis 1983a). Because only some lineages migrated into and survived in these refugia, the geographical structuring of genetic diversity within species-populations was drastically changed (Hewitt 1996, 2000). Reduced population size in small refugia enhanced the effects of genetic drift (Nei et al. 1975; Ellstrand and Elam 1993), fostering the establishment and divergence of independent lineages in different refugia.

Rare, long distance dispersal from these refugia has long been hypothesized as fundamental to the rapid postglacial colonization of glaciated North America (Cain et al. 1998; Cain et al. 2000). Some recent studies, however, have suggested that stepping-stone dispersal from cryptic refugia may have been more important than previously realized (Clark et al. 1998; Stewart and Lister 2001; McLachlan and Clark 2004; Brubaker et al. 2005). These modes of postglacial expansion have different population genetic and population dynamic consequences (Hewitt 1996; Ibrahim et al. 1996; Hewitt 2000), with recolonization through long distance dispersal expected to lead to the establishment of highly differentiated populations and greater spatial clustering beyond the main migration front. Work in Europe has shown that in some instances, admixture from multiple glacial refugia has created a geographic mosaic of haplotype lineages, with the highest amounts of haplotype diversity found in nonrefugial areas (Hewitt 1999; Petit et al. 2003).

Phylogeography, or the examination of intraspecific genealogical patterns over geographical space, has been used extensively to examine the genetic signature remaining from postglacial migration and from incipient lineage divergence (Schaal et al. 1998; Avise 2000). European botanists have used phylogeography to examine biogeographic hypotheses, trace postglacial migration routes, and locate refugial areas for alpine plants (e.g., Comes and Kadereit 2003; Stehlik 2003; Tribsch and Schonswetter 2003; Vargas 2003; Schonswetter et al. 2004), forest trees (e.g., Demesure et al. 1996; Lumaret et al. 2002; Petit et al. 2002a; Petit et al. 2002b), and Mediterranean species (e.g., Comes and Abbott 2001).

The numbers of phylogeographic studies in North America have generally lagged those in Europe. In addition, most phylogeographic studies of North American plant species have been regionally focused on the arctic, western North America, and the southeastern United States, thus our understanding of broad scale phylogeographic patterns over much of North America remains limited. The majority of studies in eastern North American have examined forest trees like *Fagus grandifolia*, (e.g., McLachlan et al. 2005; Morris et al. 2008b), *Liquidambar styraciflua* (Morris et al. 2008a), *Liriodendron tulipifera* (e.g., Parks et al. 1994; Sewell et al. 1996), *Picea* spp. (e.g., Hawley and DeHayes 1994; Jaramillo-Correa et al. 2004), and *Pinus* spp. (Walter and Epperson 2001; Godbout et al. 2005; Walter and Epperson 2005). Phylogeographic studies of herbaceous plant species in eastern North America are far fewer and have focused primarily on woodland herbs from the eastern and southeastern Unites States (e.g., *Trillium spp.*; Griffin and Barrett 2004b, a; Gonzales and Hamrick 2005; Gonzales et al. 2008). A review of plant phylogeography in unglaciated eastern North America has reinforced the paradigm that species' responses to glaciation were idiosyncratic (Soltis et al. 2006); patterns in unglaciated eastern North America were complex and not highly concordant among species.

Phylogeographic studies of widespread northern temperate and boreal species, herbaceous species, and species restricted to extreme habitats have been extremely limited in North America. We therefore know little concerning the Pleistocene history of northern species whose distributions lie largely in glaciated North America. We also have virtually no phylogeographic data on species (or species complexes) that show marked disjunctions from the western Cordillera to the Great Lakes region or northeastern North America. One of the few phylogeographic studies of a widespread montane and boreal group (the *Arabis drummondii* and *A. holboellii* complex; Dobes et al. 2004), suggested that the species complex survived glaciation in multiple refugia, including the Rocky Mountains, Beringia, and near the Great Lakes region. Whether this pattern is common among widely distributed northern species awaits additional study.

Objectives. In this study, we conducted a chloroplast DNA phylogeographic study of the *Solidago simplex* species complex. The complex has a transcontinental distribution in North America (with a significant west to east disjunction) and likely survived glaciation in multiple refugia. This provides an opportunity to examine biogeographic patterns and glacial history across the entire continent and to assess hypotheses concerning biotic connections between western and eastern North America. Because *Solidago* is an herbaceous perennial plant species, its life-history traits and dispersal capabilities differ from those of large-seeded, long-lived forest trees. Its response to glaciation, therefore, likely differed as well, and examination of its

Pleistocene biogeography provides an opportunity to uncover phylogeographic patterns that may be more generally characteristic of the flora of northern North America (since trees comprise only a small, specialized part).

We examined the population-level structuring of chloroplast genetic diversity in *Solidago simplex* and four other species in *Solidago* subsection *Humiles* across their entire North America distribution. The estimated phylogeographic history will not only allow us to test specific biogeographic and evolutionary hypotheses in *S. simplex*, but will also provide a framework from which we can examine hypotheses concerning 1) the floristic connectivity of western and eastern North America during the Pleistocene, 2) the complexity of the glacial histories of widespread North American species, and 3) the dual roles of historical glaciation and recent microevolution in shaping North American biodiversity.

Because the species range of *Solidago simplex* encompasses most of western, montane North America and discrete unglaciated and glaciated regions of eastern North America, numerous, distinct biogeographic hypotheses can be addressed in this study. Below are two specific phylogeographic hypotheses related to the scenario posited by Ringius and Semple that we address. **H_1:** Tetraploid subspecies *randii* evolved from a single migration of diploid *S. simplex* from western to eastern North America during the Wisconsin glacial period. With such a recent origin (less than 100,000 years) we would expect all varieties of subspecies *randii* to harbor a subset of the haplotype variation found in subspecies *simplex* and that any unique haplotypes would be recently evolved tip haplotypes. **H_2:** Diploid populations of *S. simplex* in the northern Great Lakes region represent a recent Holocene migration from western North America. If this hypothesis were correct, we would expect to recover contemporary western haplotypes from diploid populations in the northern Great Lakes region.

MATERIALS AND METHODS

Taxonomy and Biogeography of Solidago subsect. Humiles. *Solidago* (Asteraceae: Astereae) is a largely North American genus of ca. 100 species of rhizomatous, perennial herbs (Semple and Cook 2006). Goldenrods are self-incompatible, obligately outcrossing plants that are pollinated by a variety of insects including bees, wasps, and beetles. Seed dispersal in *Solidago* is amenochorous (via wind); the cypselae have a doube-layered bristly pappas that aids in wind dispersal (Hood and Semple 2003).

Solidago subsect. *Humiles* is composed of five morphologically similar and closely-related species: *S. arenicola*, *S. kralii*, *S. plumosa*, *S. simplex*, and *S. spathulata*. Goldenrods in *Solidago* subsect. *Humiles* are united by the presence of resinous glands on the foliage and involucral bracts that cause all members of the group to be glutinous or sticky. In addition, all species in the subsection have virgate to paniculiform arrays with non-secund capitula (Semple and Cook 2006). Molecular phylogenetic evaluation of relationships in *Solidago* is largely wanting, but early chloroplast PCR-RFLP work by Zhang (1996) placed *S. simplex* sister to *S. spathulata* (formerly often treated as *S. simplex* var. *spathulata*). These two members of subsect. *Humiles* were placed sister to the arctic/alpine *S. multiradiata* and Eurasian *S. virgaurea*.

Solidago subsect. *Humiles* is restricted to North America and is transcontinental in distribution. *Solidago arenicola*, *S. kralii*, and *S. plumosa* are narrowly distributed endemics in the southeastern United States (Fig. 4.1). *Solidago arenicola* is restricted to rocky or sandy riverbanks and floodplains in the Cumberland Plateau region of northern Alabama, Tennessee, and southern Kentucky. *Solidago kralii* is confined to sand hills along the Coastal Plain fall line in a small area of Georgia and South Carolina. *Solidago plumosa* is known from a single population on mafic rocks along the Yadkin River in Stanley Co., North Carolina. *Solidago spathulata* inhabits sand dunes along the Pacific coast from central California to northern Oregon. *Solidago simplex* is widespread and transcontinental in distribution but absent throughout the center of the continent.

Ringius (1986) divided *S. simplex* into two subspecies. Diploid subsp. *simplex* (2*n*=18) is widespread yet patchily distributed in montane and alpine habitats throughout the western cordillera from Alaska to Mexico (Fig. 4.1). Disjunct, eastern diploid populations in the northern Great Lakes region and Gaspé, Quebec have also been placed in subspecies *simplex*. Tetraploid subsp. *randii* (2*n*=36) is restricted to the Great Lakes region and Appalachian Mountains in eastern North America. Four varieties are currently recognized in subsp. *randii*. *Solidago simplex* var. *racemosa* inhabits rocky riverbanks throughout the Appalachian Mountains, from Tennessee to New Brunswick, while *S. simplex* var. *monticola* is confined to barrens and serpentine soils in New England and southern Quebec. *Solidago simplex* vars. *ontarioensis* and *gillmanii* are endemic to the Great Lakes region, inhabiting rocky shores from the Bruce Peninsula, Ontario to southern and eastern Lake Superior and active dune systems along the shores of lakes Huron and Michigan, respectively.

Ringius and Semple (1987) proposed that two transcontinental migrations produced the current disjunct distribution of cytotypes in *Solidago simplex*. The first migration of diploid *S. simplex* from western North America occurred early in the Wisconsinan glacial period and resulted in the formation of tetraploid subspecies *randii* in the Appalachian Mountains. The second migration occurred more recently during the Holocene when diploid *S. simplex* migrated out of the Beringian refugium across Canada to the northern Great Lakes region. According to this hypothesis, *S. simplex* is composed of two monophyletic lineages: diploid *S. simplex* subsp. *simplex* and tetraploid *S. simplex* subsp. *randii*.

Patterns uncovered by cytogeographic work (Chapter III) and much recent work on the evolution of polyploid plant species (reviewed in Soltis and Soltis 1999; Soltis et al. 2004) suggest that the previous hypotheses proposed by Ringius and Semple are likely too simple. Their initial hypotheses proposed that tetraploid *S. simplex* subsp. *randii* was a monophyletic lineage that originated from a single polyploidization within the last 100,000 years. Numerous molecular studies have demonstrated that the recurrent formation of polyploid lineages is more likely the norm than the exception (e.g., Segraves et al. 1999), and Soltis et al. (1999) proposed that most polyploid species are probably polyphyletic. The presence of three members of *Solidago* subsect. *Humiles* in the southeastern United States (Keener and Kral 2003; Semple 2003; Semple and Cook 2006) also raises additional questions. *Solidago plumosa* ($2n = 18$) is ecologically and morphologically similar to some populations of *S. simplex* var. *racemosa* ($2n = 36$) from the Southern Appalachians, and Semple and Cook (2006) suggested that it may be very closely related to *S. simplex*. Overall the presence of three distinct, narrowly endemic species in the southeastern United States suggests a longer history of allopatry and divergence within the subsection that previously proposed.

Taxon and Population Sampling. A total of 368 accessions of *Solidago* subsect. *Humiles* were collected from 72 populations (including 289 individuals from 57 populations of *Solidago simplex*) from throughout its North American range in the United States and Canada (Table 4.1). Samples were collected from the majority of the species' ranges as well as the locations of proposed glacial refugia. Sampling included all infraspecific taxa within *Solidago* subsect. *Humiles*, except for the very narrowly distributed *S. simplex* var. *nana* and *S. simplex* var. *chlorolepis* (Table 4.1). At each population, leaf samples from ca. 20 healthy plants (individual clones spaced at least two meters apart) were removed and stored separately in silica gel for preservation. Voucher herbarium specimens for all populations were collected and deposited at the University of Michigan Herbarium (MICH). In addition to the field-sampled populations, leaf material from two herbarium specimens of *Solidago simplex* (H2 and H5 in Table 4.1) was also included. H5 represents the only accession from the southern extreme of the distribution in Mexico.

Outgroup comparisons included the closely related genera *Petradoria* and *Oreochrysum* (following the classifications in Zhang 1996; Beck et al. 2004) and 24 populations of non-*Humiles Solidago*. Outgroup sampling within *Solidago* included representatives of six of the eleven currently recognized North American sections of the genus. Greater emphasis was placed on members of section *Multiradiatae* (e.g., seven populations of *S. multiradiata* from western North America and two populations of *S. leiocarpa* from New England) because previous work by Zhang (1996) suggested that sections *Multiradiatae* and *Humiles* were closely related.

DNA extraction, PCR amplification, and sequencing. Total genomic DNA was isolated from silica-dried leaf samples and herbarium specimens using the DNeasy Plant Mini Kit (Qiagen Corporation, Valencia, CA) following the manufacturer's protocols. Herbarium samples were extracted in the same manner as silica dried samples with the exception of an additional overnight incubation with β-mercaptoethanol. Ten silica-dried samples required additional purification of the genomic extract and were purified using glass milk technology (GeneClean, MP Biomedicals, Solon, OH) following the manufacturer's protocols. Extracted genomic DNA was stored at -80ºC.

Because plastids are maternally inherited and thus record patterns of seed dispersal and migration in *Solidago* (inheritance tested by Schlaepfer et al. 2008), sequences of chloroplast spacer regions were used to address hypotheses of Pleistocene biogeography and postglacial plant migration in *S. simplex*. In initial trials, eleven chloroplast intergenic spacers were screened for 10 species of *Solidago*. From those, two spacers (trnH-psbA and trnK-rps16) were chosen for the cpDNA phylogeographic study for their utilizable polymorphism and consistent amplification and sequencing. The trnH-psbA spacer was amplified and sequenced using the trnH-f and psbA-3f primers of Kress et al. (2005). The trnK-rps16 spacer was amplified and sequenced with primers trnK-F1 (GCCGCACTTAAAAGCCGAG) and rps16-R1 (CCCAATGAGCCGTCTATCG) designed specifically for this study.

The 20μL polymerase chain reaction (PCR) cocktails contained 2.5μL of 10X Buffer, 3.5 mM $MgCl_2$, 100 μM of each dNTP, 0.5μL of each primer, 0.3μL of Taq polymerase, 1.0 μL of 1/50 diluted template DNA, and 10.0μL of ddH_20. The thermal cycle for trnH-psbA was 94ºC for 3.0 min, followed by 40 cycles of 94ºC for 45 sec, 55ºC for 45 sec, and 72ºC for 3 min, with a final extension at 72ºC for 10 min. The thermal cycle for trnK-rps16 was 94ºC for 3.0 min, followed by 35 cycles of 94ºC for 45 sec, 55ºC for 1 min, and 72ºC for 3 min, with a final extension at 72ºC for 10 min. Negative controls were run with each PCR mix (using water instead of genomic DNA) to check for contamination. PCR products were purified using ExoSAP-IT (Affymetrix, Santa Clara, CA). Sequences were obtained using BigDye chemistry (Applied Biosystems Incorporated [ABI], Foster City, CA) on an ABI 3730 XL capillary sequencer. All sequencing was performed at the University of Michigan DNA Sequencing Core.

The sequencing strategy for *Solidago* subsect. *Humiles* was two-fold. First, single individuals from all 72 populations were sequenced to capture preliminary estimates of range-wide genetic diversity rather than to intensively examine intrapopulation variation (following Petit et al. 2005). Second, 37 of those populations from throughout the range were blindly selected and an additional eight individuals per population were sequenced to assess within population genetic diversity (at the same time making sure all taxa and regions were represented adequately).

DNA sequence alignment, indel scoring, and concatenation. Sequence files were edited in Sequencher 4.6 (Genecodes Corporation, Ann Arbor, MI) and aligned automatically in Clustal X version 2.0 (Larkin et al. 2007) using default parameters. Final alignments were done manually in Se-Al version 2.0a11 (available for download at http://evolve.zoo.ox.ac.uk/software.html) following recommendations for cpDNA spacer regions (Kelchner 2000; Borsch et al. 2003; Löhne and Borsch 2005). In the trnK-rps16 spacer, length variation (from 9-14bp) in a poly-A region was removed because of the potential for non-homologous repeat patterns. In the trnH-psbA spacer, a variable region of mostly TA repeats (hotspot region sensu Borsch et al. 2003; Schlaepfer et al. 2008) was excluded because of potential non-homology. Also in the trnH-psbA spacer, a 23 bp inversion and indel complex (in three samples from population S60) was reverse-complemented and scored as a single mutational event. All other indels were retained and coded as described below. The final alignment of the concatenated dataset (including indels) was 1482 bp.

Simulation studies by Simmons et al. (2007) indicated that inclusion of indel variation in phylogenetic analyses (they only considered parsimony analyses) was preferable to treating gaps as missing data or excluding gapped positions altogether (which is consistent with others studies such as Simmons et al. 2001). They found that simple indel coding (SIC sensu Simmons and Ochoterena 2000) and modified complex indel coding (MCIC sensu Müller 2006) were preferable to other coding methods (e.g., 5th state coding or excluding gapped positions entirely). In their parsimony analyses, SIC and MCIC performed comparably, but analyses of datasets with MCIC-coded gaps generally produced greater resolution and higher statistical support (presumably because SIC incorporates more missing data into the alignment when there are overlapping indels). Simmons et al (2007) ultimately recommended that MCIC be used when possible, but that SIC could be used when it was not feasible or possible to run analyses with MCIC.

Based on these recommendations, indels in the trnK-rps16 and trnH-psbA spacers were coded as single mutational events using two different coding methodologies. SIC was implemented using the program SeqState (Müller 2005, 2006). A variation of MCIC was implemented by manually condensing indels to single positions (or to the minimum number of positions required to fully represent regions when overlapping indels were present) and subsequently counting gaps as a fifth base in the analyses.

Because the chloroplast genome is transmitted as a single locus and recombination is thought to be very rare, plant phylogeographic studies have often concatenated different plastid regions into a single alignment file without checking for congruence (Petit and Vendramin 2007). We checked the congruence of the trnK-rps16 and trnH-psbA spacers with a partition homogeneity test (the incongruence length difference test of Farris et al. 1995) implemented in PAUP* version 4.0b10 (Sinauer Associates, Sunderland, MA). Because the test was not significant ($p = 0.45$), the trnK-rps16 and trnH-psbA spacers were concatenated into a single alignment file for all subsequent analyses.

Bayesian Phylogenetic Analyses. Prior to running phylogenetic analyses, the best-fit model of sequence evolution for the concatenated dataset was selected with the program MODELTEST version 3.7 (Posada and Crandall 1998) using both the Akaike information criterion and hierarchical likelihood ratio tests. MODELTEST selected the F81+G model for the two concatenated chloroplast spacers (the same model selected for chloroplast spacers by Schlaepfer et al. 2008).

Phylogenetic relationships among 55 haplotypes recovered from 395 accessions of *Solidago* subsect. *Humiles* and outgroup taxa were reconstructed using Bayesian analyses implemented in the program MRBAYES version 3.1.2 (Ronquist and Huelsenbeck 2003). Indel variation was included in the Bayesian analyses by appending the SIC data as a binary partition at the end of the data matrix. The SIC-coded dataset was analyzed using mixed models (F81+G model used for nucleotide data in partition 1; restriction model used for binary-scored indel data in partition 2). Two independent analyses with four Markov chains each and default heating parameters were run for 2.0×10^6 generations. Convergence of the two independent MCMC analyses was assessed by examining cumulative split frequency plots (using the cumulative function in AWTY; Nylander et al. 2008). Trees were sampled every 100 generations, resulting in 20,006 total trees. A total of 18,006 trees (after a burn-in of 2000 trees) were used to produce a majority-rule consensus tree. Clade credibility values were used to assess nodal support.

Network construction and phylogeographic analyses. Among closely related species or at intraspecific levels, network analyses have been shown to provide additional information and to better accommodate ancestral polymorphism and hybridization than traditional phylogenetic analyses (Clement et al. 2000; Posada and Crandall 2001; Jakob and Blattner 2006; Kiefer et al. 2009). For these reasons, chloroplast spacer sequence data for 368 individuals from 72 populations of *Solidago* subsect. *Humiles* was analyzed in a statistical parsimony framework using the program TCS 1.21 (Clement et al. 2000). Network reconstruction was carried out using the MCIC coded dataset with gaps treated as a fifth base. Connections between haplotypes were set at the default 95% limit. The Bayesian inference tree (from the last section) was used to check the overall structure of the network and to resolve any closed loops. Alternative connections were indicated by dashed lines.

Genetic diversity parameters, including haplotype diversity (h), indel diversity (π_I), and nucleotide diversity (π_S), for all taxa within *Solidago* subsection *Humiles* were calculated using DNASP 4.0 (Rozas et al. 2003). Spatial analysis of molecular variance

(SAMOVA, Dupanloup et al. 2002) was used to analyze the geographical structure of genetic variation in *Solidago* subsect. *Humiles*.

Dupanloup et al. (2002) proposed SAMOVA as an alternative to the AMOVA approach (Excoffier et al. 1992) when a priori group definitions are difficult or are not desired. The SAMOVA program defines geographically homogeneous groups of populations that are maximally differentiated from each other. The user selects the number of groups that will be analyzed (from K = 2 to 20), and the program uses 100 replicates of a simulated annealing procedure to maximize the between-group differentiation (F_{CT}). The number K that results in the highest F_{CT} value while at the same time minimizing singleton groups is generally preferred (following Heuertz et al. 2004; Tomimatsu et al. 2009). Because species in *Solidago* subsect. *Humiles* appear to be recently evolved (e.g., recovery of a star-shaped network and substantial haplotype sharing) and relationships within the group are unclear, this approach was chosen over a priori assignments. For the SAMOVA analysis, 37 populations of *Solidago* subsect. *Humiles* with intrapopulation sampling (n = 333 individuals) were analyzed. The program was run iteratively with user-specified groups of K = 2 to 15.

RESULTS

Phylogenetic analyses. Bayesian inference was used to reconstruct phylogenetic relationships among chloroplast haplotypes from the concatenated trnK-rps16 and trnH-psbA dataset. The concatenated dataset (with SIC indel scoring) was 1539 bp. Fifty-five chloroplast haplotypes were recovered from 395 individuals of *Solidago* subsect. *Humiles* and the outgroup taxa (Table 4A1.1). Phylogenetic analyses resolved a monophyletic

Solidago, but phylogenetic structure within *Solidago* was generally shallow (Fig. 4.2). *Oreochrysum parryi* (in the past sometimes treated as *Solidago parryi*) was a clear outgroup and distinct from the *Solidago* clade. Bayesian clade credibility values indicated high support for several haplotype clades, including a clade of 15 haplotypes from individuals from western North America and the northern Great Lakes region.

Bayesian phylogenetic analyses did not resolve a monophyletic *Solidago* subsect. *Humiles*. Outgroup *Solidago* species were distributed throughout the phylogeny. Analyses also indicated that 11 chloroplast haplotypes were shared among species.

Network construction and phylogeographic analyses. Statistical parsimony was used to reconstruct relationships among chloroplast haplotypes from the concatenated trnK-rps16 and trnH-psbA dataset. The concatenated dataset (with a variation of MCIC indel scoring) was 1295 bp. Forty-six chloroplast haplotypes were recovered from 368 individuals of *Solidago* subsect. *Humiles* (Table 4.2; Table 4A1.1; Fig. 4.3). The overall topology of the statistical parsimony network and recovered groupings of haplotypes were largely consistent with the expanded Bayesian analysis discussed in the last section.

Visual inspection of haplotype distributions indicated some geographic structuring of genetic diversity, but considerable haplotype sharing among species, ploidy levels, and regions was clearly evident (Figs. 4.3-4.5). Haplotype 15 and closely related haplotypes (which also formed a well-supported clade in the Bayesian analysis) are almost entirely confined to western North America except for three populations in the northern Great Lakes region.

Spatial analysis of molecular variance (SAMOVA) was used to more rigorously examine the geographic structuring of genetic diversity in *Solidago* subsect. *Humiles*.

Following recommendations by Heuertz et al. (2004), the group structure selected by the SAMOVA analysis comprised seven groups of populations (K = 7, F_{CT} = 0.51; Table 4.3). Overall, this level of partitioning revealed relatively low levels of geographic structuring but did segregate *S. spathulata* populations from the rest of *Solidago* subsect. *Humiles*. There were three singleton groups defined by this genetic structure, all from western North America. Two of the singleton groups consisted of disjunct (at least in terms of our sampling) populations of *S. simplex*: S169 from the White Mountains in southeastern Arizona, and S176 from western Alberta. The last singleton group consisted of a population of *S. spathulata* from northern Oregon. The remaining four groups contained multiple populations. Two clusters contained two populations each. One consisted of a population of *S. arenicola* from Kentucky (S104) and *S. plumosa* (S98). The other contained two populations of *S. spathulata* from northern California (S126 and S128). Two populations of *S. simplex* var. *gillmanii* from the northern Great Lakes region consistently clustered with two western *S. simplex* var. *simplex* populations from Wyoming and New Mexico. The remaining cluster contained 26 populations from across North America.

DISCUSSION

Our phylogenetic analyses confirmed results from several recent barcoding studies that have suggested that plastid sequence data cannot adequately distinguish individual *Solidago* species (Kress et al. 2005; Shaw et al. 2005; Fazekas et al. 2008). Most of these studies cite low levels of sequence variation as the primary impediment to species delimitation (which appears to be partially correct), but our results suggest that extensive haplotype sharing among species due to either retention of ancestral polymorphism or gene flow (chloroplast capture) among species will also likely be a significant impediment to future phylogenetic studies in *Solidago*. Schlaepfer et al. (2008) found similar patterns in their study of *S. gigantea*, despite the fact that their outgroup sampling was extremely limited.

In our broader analysis that included outgroup taxa, five species and sixty individuals of *Solidago* shared haplotype number four. This haplotype occupied the basal *Solidago* node in the Bayesian inference tree and the central haplotype in the statistical parsimony network. These data suggest that this haplotype represents an ancestral *Solidago* haplotype (because of its internal position and widespread occurrence). The other haplotypes that were shared among species were scattered across the phylogeny and parsimony network. The extensive haplotype sharing and star-shaped network recovered from statistical parsimony analyses suggests that divergence in *Solidago* was relatively recent (but divergence times have not been estimated). Our sampling was not specifically designed to attempt to distinguish between the retention of ancestral chloroplast polymorphism or gene flow between species. And although retention of ancestral polymorphism seems likely, it remains unclear as to which of these processes has driven the observed patterns in *Solidago*.

These findings raise serious doubts about any studies that attempt to use plastid DNA to examine specific evolutionary relationships within *Solidago*, even if extensive outgroup sampling and comparisons (both in terms of taxonomic diversity and population coverage) are included. Laureto and Barkman (2004, 2005) utilized cpDNA haplotype variation to study the hybrid origin of the allohexaploid Great Lakes endemic *Solidago* *houghtonii*. They recovered the surprising result that *S. gigantea*, a member of a strikingly different section of the genus, appeared to be the maternal parent of *S. houghtonii*. Semple and Cook (2006) subsequently discussed morphological features of *S. houghtonii* that might allude to its link with *S. gigantea*. In light of our molecular data, it seems far more plausible that incomplete lineage sorting and not hybridization caused the patterns observed in *S. houghtonii*.

Despite the lack of resolution in the Bayesian inference tree and extensive sharing of haplotypes among species and infraspecific taxa within *Solidago simplex*, we can still address several of the taxonomic hypotheses proposed by Ringius (1986) and Ringius and Semple (1987). They initially proposed that the eastern tetraploid *S. simplex* subsp. *randii* was a monophyletic lineage that originated from a single eastward migration of western diploid *S. simplex* during the Wisconsinan glacial period. The complex cytogeographic patterns in eastern North America uncovered in Chapter III suggest that their initial hypothesis was likely too simple. When we mapped chromosome number (ploidy level) onto the statistical parsimony network, it revealed that tetraploid individuals in *Solidago* subsect. *Humiles* are scattered across the network. Tetraploid individuals harbored 24 distinct haplotypes, 8 of which were shared with diploids and 16 of which were restricted to only tetraploids. Although we do not attempt to infer exactly how many polyploid events occurred in *S. simplex*, it is clear that a single origin of polyploidy cannot account for the pattern.

Similarly, Schlaepfer et al. (2008) inferred as many as seven independent origins for tetraploid *S. gigantea* in eastern North America. Together, these results for *Solidago* are fully consistent with numerous other studies that have shown that recurrent origins of polyploid taxa are expected (Soltis and Soltis 1999).

Phylogeographic Patterns in Solidago simplex. The level of partitioning used in the SAMOVA analyses (K = 7) indicated that there was relatively little geographical structuring of chloroplast diversity in *Solidago* subsect. *Humiles*. The analysis separated *S. spathulata* populations from the Pacific coast from other members of the subsection. It also grouped two populations from the northern Great Lakes region with two populations of *S. simplex* from western North America; these four populations were similar in that they were all nearly fixed for haplotype number six. Most populations, however, grouped together into one large cluster regardless of their geographic distribution.

Visual inspection of haplotype distributions, however, suggested that there was more geographic differentiation within *S.* subsect. *Humiles* than indicated by the seven-group SAMOVA analysis. A total of 14 haplotypes were recovered from both *S. simplex* populations in the Great Lakes region and from *Solidago* subsect. *Humiles* populations in the southeastern United States. While the regions harbored the same number of haplotypes, closer examination of haplotype distributions strongly suggested that the southeastern United States was not the primary source of postglacial migrants for the Great Lakes region. Only two haplotypes were shared between these regions. In addition, populations in the Great Lakes region harbored five private haplotypes that did not occur in any other region. Haplotype diversity in northeastern North America was considerably lower than in the Great Lakes region or the southeastern United States. Only seven haplotypes were recovered from populations there. Populations in western North America contained the highest number of haplotypes with 26. Populations in the Great Lakes region shared more haplotypes with populations in New England (n = 4) and western North America (n = 7) than they did with the southeast.

The haplotype complement in the Great Lakes region is more similar to the northern Rocky Mountains and northeastern North America than to the southeastern United States. The presence of haplotypes from the western clade in the northern Great Lakes region supports the earlier hypotheses of a biotic connection between the western Cordillera and the northern Great Lakes region. There is no evidence from our data that suggests that diploid *S. simplex* migrated into the Great Lakes region from a Beringian refugium, but increased sampling in western Canada and Alaska are needed to more fully address this hypothesis. Our data also indicate that there are a number of haplotypes that only occur in glaciated regions of eastern North America (some private to the Great Lakes region and one shared with northeastern populations). These data support the idea that Great Lakes region populations of *Solidago simplex* survived glaciation in a northern refugium closer to the ice margin and not the southern United States.

This raises the question of whether the recommendations of Heuertz et al. (2004) are applicable to this system. They were examining genetic structure within European Ash (*Fraxinus excelsior* L.), a large forest tree that presumably survived glaciation in only a few refugia in southern Europe. Their intent was to identify range-wide structuring that resulted from postglacial expansion out of only those few refugia. *Solidago* subsect. *Humiles* likely survived the Wisconsinan glaciation in numerous different refugia. It is also plausible that populations of *S. simplex* have been isolated from each other and from the main species range for a long period of time (e.g., populations at the southern extreme of the range in Arizona and New Mexico). The system examined by Heuertz et al. is likely much more similar to studies of forest trees and woodland herbs in the southeastern United States. In a widely distributed group like *Solidago* subsect. *Humiles*, it might be more informative to see which populations are geographically and genetically distinct enough to form singleton or small clusters in the SAMOVA analysis.

Higher levels of partitioning in the SAMOVA analysis (e.g., K = 14; Table 4.3), as expected, produced more singleton populations than lower levels of partitioning, and differentiation among groups also increased. Examination of the resultant clusters revealed patterns that more closely corresponded to the visual inspections of the data. Populations from the Great Lakes region showed multiple associations with populations from all other regions of North America. There were also two clusters of populations that contained only Great Lakes populations. Populations from northeastern North America generally clustered with populations from the Great Lakes region and the Appalachian Mountains. The general clustering of populations from western North America with populations throughout eastern North America that was present in the K = 7 analysis largely dissolved with the higher level of partitioning. Western populations formed a number of separate groups; the only significant connection to eastern North America occurred with populations from the northern Great Lakes region.

Plant Phylogeography in Eastern North America. Phylogeographic studies of plants in North America are just beginning to shed light on the patterns suggested by biogeographic and paleoecological studies. On a continental scale, patterns in North America appear to be more complex than those found in Europe (patterns in eastern North America reviewed by Soltis et al. 2006). This has been attributed to the north-south orientation of mountain ranges in North America, which allowed species to migrate more easily to refugia south of the ice margin. The east-west orientation of the Alps in Europe has often been cited as a major determinant of temperate tree species diversity and phylogeographic structure in European forests. Studies on both continents indicate that many species (especially large forest trees) survived glaciation in southern refugia (see reviews in Soltis et al. 2006; Petit and Vendramin 2007).

Studies of widespread northern temperate and boreal species have been relatively few in North America, and therefore broad generalizations cannot be made. This work on *S. simplex* and several other recent studies, however, suggest that cryptic northern refugia were more important contributors to postglacial colonization than previously realized (e.g., Stewart and Lister 2001; McLachlan et al. 2005; King et al. 2009). Additional studies are needed to see how common these emerging patterns actually are.

Table 4.1. North American sampling locations for *Solidago* subsect. *Humiles* and outgroup taxa sequenced for the molecular studies. Voucher specimens are deposited in the University of Michigan Herbarium (MICH) or University of Waterloo Herbarium (WAT). Isolated genomic DNA is maintained at the University of Michigan.

Population	n	Country	State or Province	Latitude	Longitude	Voucher number
Solidago arenicola						
S5	1	USA	Alabama	33.99	-86.60	Semple 11196-2
S100	1	USA	Alabama	34.02	-86.57	Peirson 608
S101	9	USA	Alabama	33.99	-86.60	Peirson 609
S102	9	USA	Tennessee	36.10	-84.72	Peirson 610
S103	1	USA	Tennessee	36.48	-84.67	Peirson 611
S104	9	USA	Kentucky	36.84	-84.34	Peirson 612
Solidago kralii						
S4	1	USA	Georgia	32.25	-83.40	Semple 11208-2
S99	9	USA	South Carolina	33.62	-81.82	Peirson 605
Solidago plumosa						
S98	9	USA	North Carolina	35.41	-80.09	Peirson 604
Solidago simplex						
S11	9	USA	Michigan	45.92	-85.91	Peirson 467
S112	9	USA	Michigan	47.47	-87.86	Peirson 625
S113	9	USA	Michigan	47.47	-88.06	Peirson 626
S12	1	USA	Michigan	46.10	-85.39	Peirson 589
S138	9	USA	Michigan	45.97	-84.06	Voss 16893
S140b	9	USA	Montana	47.87	-112.74	Peirson 660
S142	9	USA	Wyoming	44.85	-107.84	Peirson 662
S145	1	USA	Wyoming	44.24	-106.98	Peirson 665
S146	9	USA	Wyoming	44.16	-107.10	Peirson 666
S150	9	USA	Wyoming	41.19	-106.15	Peirson 670

S155	1	USA	Colorado	40.75	-106.56	Peirson 676
S156	1	USA	Colorado	40.22	-106.06	Peirson 677
S159	1	USA	Colorado	39.66	-105.88	Peirson 682
S16	9	Canada	Ontario	45.56	-82.01	Peirson 474
S162	9	USA	Colorado	39.08	-106.54	Peirson 686
S163	1	USA	Colorado	38.81	-106.39	Peirson 687
S164	1	USA	Colorado	37.48	-106.80	Peirson 688
S165	1	USA	Colorado	37.70	-107.78	Peirson 689
S167	9	USA	New Mexico	35.89	-106.66	Peirson 692
S169	9	USA	Arizona	33.77	-109.19	Peirson 694
S172	9	Canada	Brit. Columbia	50.11	-121.55	Peirson 781
S173	9	Canada	Brit. Columbia	51.26	-116.70	Peirson 782
S176	9	Canada	Alberta	51.12	-115.08	Peirson 786
S178	9	Canada	Yukon	62.21	-136.34	Bennett 08-515
S24	9	Canada	New Brunswick	45.96	-66.82	Peirson 490
S25	1	Canada	New Brunswick	46.81	-67.77	Peirson 493
S26	1	USA	Maine	44.33	-68.29	Peirson 495
S28	1	USA	Maine	44.39	-70.97	Peirson 498
S3	1	Canada	NW Territories	61.42	-126.84	Semple 11156-8
S37	1	USA	Michigan	42.24	-86.37	Peirson 518
S38	9	USA	Michigan	42.70	-86.21	Peirson 520
S50	1	USA	Michigan	44.78	-84.72	Peirson 538
S53	9	USA	Michigan	44.67	-84.28	Peirson 542
S57	9	USA	Michigan	45.15	-84.18	Peirson 549
S58	9	USA	Michigan	45.91	-86.32	Peirson 590
S60	9	Canada	Ontario	48.77	-87.11	Peirson 550
S63	9	Canada	Ontario	47.94	-84.85	Peirson 557
S65	1	Canada	Ontario	45.25	-81.52	Peirson 559

S67	1	Canada	Ontario	45.26	-81.64	Peirson 562
S68	1	Canada	Ontario	45.24	-81.68	Peirson 563
S70	1	Canada	Quebec	45.48	-71.94	Peirson 565
S71	9	Canada	Quebec	45.97	-71.37	Peirson 566
S73	1	Canada	Quebec	46.72	-71.28	Peirson 570
S74	9	Canada	Quebec	46.20	-70.75	Peirson 571
S77	1	USA	Maine	44.31	-68.34	no voucher
S8	1	USA	Michigan	44.40	-84.41	Peirson 463
S81	1	USA	Vermont	44.49	-73.19	Peirson 579
S83	9	USA	Vermont	43.90	-73.06	Peirson 581
S84	1	USA	Vermont	43.84	-72.96	Peirson 584
S85	9	USA	Pennsylvania	39.81	-76.33	Peirson 585
S86	1	USA	Maryland	39.00	-77.25	Peirson 586
S89	9	USA	Michigan	45.31	-85.31	Peirson 592
S94	1	USA	West Virginia	39.39	-80.09	Peirson 597
S96	1	USA	West Virginia	39.21	-79.99	Peirson 601
S97	9	USA	West Virginia	38.21	-80.94	Peirson 603
H2	1	USA	Colorado	38.96	-105.08	Ehlers 7751
H5	1	Mexico	Nuevo Leon	24.12	-99.66	Hinton 22120
Solidago spathulata						
S2	1	USA	California	38.39	-122.48	Hrusa 11428
S126	9	USA	California	38.58	-123.34	Peirson 629
S128	9	USA	California	40.77	-124.22	Peirson 631
S129	1	USA	California	41.00	-124.11	Peirson 632
S131	9	USA	Oregon	45.00	-104.00	Peirson 634
S133	1	USA	Oregon	46.02	-123.93	Peirson 636
Outgroup species						
Oreochrysum parryi						

S149	1	USA	Wyoming	41.18	-106.14	Peirson 669
S160a	1	USA	Colorado	39.62	-105.93	Peirson 684
Petradoria pumila						
S148	1	USA	Utah	40.87	-109.50	Peirson 668
Solidago flexicaulis						
S34	1	USA	Michigan	42.30	-83.75	Peirson 510
Solidago gigantea						
S31b	1	USA	Michigan	42.30	-83.75	Peirson 503
Solidago hispida						
S23	1	USA	Maine	45.22	-70.48	Peirson 489
S18	1	Canada	Ontario	44.66	-81.27	Peirson 477
S136	1	USA	Michigan	46.67	-85.56	Peirson 641
S64	1	Canada	Ontario	47.38	-84.70	Peirson 558
Solidago leiocarpa						
S29	2	USA	New Hampshire	44.28	-71.30	Peirson 501
S30	2	USA	New Hampshire	44.27	-71.30	Peirson 500
Solidago multiradiata						
S141	2	USA	Montana	45.01	-109.40	Peirson 661
S143	2	USA	Wyoming	44.76	-107.59	Peirson 663
S151a	2	USA	Wyoming	41.36	-106.23	Peirson 672
S174	2	Canada	Alberta	51.45	-116.26	Peirson 783
S6	1	Canada	NW Territories	62.37	-128.68	Semple 11165
TRAL1	1	USA	Alaska	61.10	-149.58	Reznicek 11695
TRAL4	1	USA	Alaska	61.40	-149.14	Reznicek 11728
Solidago nemoralis						
S33a	1	USA	Michigan	42.30	-83.75	Peirson 507
Solidago ptarmicoides						
S32	1	Canada	Ontario	42.55	-80.11	Peirson 505

Solidago rigida						
S33	1	USA	Michigan	42.30	-83.75	Peirson 506

Table 4.2. Chloroplast genetic diversity within *Solidago* subsect. *Humiles*. Number of sampled populations (N_P); number of sampled individuals (N_I); number of haplotypes (H_P); haplotype diversity (h); number of segregating indels (I); indel diversity (π_I); number of segregating sites (S); and nucleotide diversity (π_S) are indicated for each species and for infraspecific taxa within *Solidago simplex*.

Taxon	N_P	N_I	H_P	h	I	π_I	S	π_S
Solidago subsect. *Humiles*	72	368	46	0.9252	42	0.00232	28	0.00148
Solidago arenicola	6	30	7	0.8069	7	0.00187	4	0.00092
Solidago kralii	2	10	3	0.5111	2	0.00070	1	0.00015
Solidago plumosa	1	9	2	0.2222	3	0.00050	2	0.00034
Solidago simplex	57	289	35	0.8972	35	0.00205	23	0.00140
subsp. *simplex*	26	138	22	0.8940	28	0.00244	14	0.00151
var. *simplex* (W)	21	109	19	0.8639	28	0.00264	12	0.00149
var. *simplex* (E)	5	29	6	0.7365	8	0.00118	7	0.00121
subsp. *randii*	31	151	20	0.8525	20	0.00131	15	0.00135
var. *gillmanii*	6	38	5	0.7013	7	0.00150	4	0.00113
var. *ontarioensis*	8	48	9	0.8351	10	0.00156	8	0.00136
var. *monticola*	6	22	6	0.7403	5	0.00108	6	0.00070
var. *racemosa*	11	43	12	0.7929	10	0.00068	8	0.00125
Solidago spathulata	6	30	7	0.7563	6	0.00154	3	0.00035

Table 4.3. Fixation indices and number of singleton groups obtained from the spatial analyses of molecular variance (SAMOVA) of chloroplast sequence data from *Solidago* subsect. *Humiles*. Fixation indices as follows: F_{ST}, differentiation among populations; F_{CT}, differentiation among groups of populations; F_{SC}, differentiation among populations within groups.

	Number of K User-Defined Group													
	2	3	4	5	6	7	8	9	10	11	12	13	14	15
F_{ST}	0.77	0.75	0.76	0.74	0.76	0.75	0.74	0.71	0.71	0.71	0.70	0.70	0.68	0.68
F_{CT}	0.41	0.43	0.44	0.48	0.47	0.51	0.50	0.51	0.52	0.53	0.53	0.54	0.54	0.54
F_{SC}	0.62	0.55	0.56	0.51	0.55	0.49	0.48	0.41	0.40	0.39	0.36	0.36	0.31	0.30
Singletons	0	0	1	0	3	3	4	4	6	7	6	8	6	7

Figure 4.1. Generalized distribution of *Solidago* subsect. *Humiles* in North America: *S. arenicola* (yellow shading), *S. kralii* (green shading), *S. plumosa* (grey shading), *S. simplex* (red shading), *S. spathulata* (blue shading).

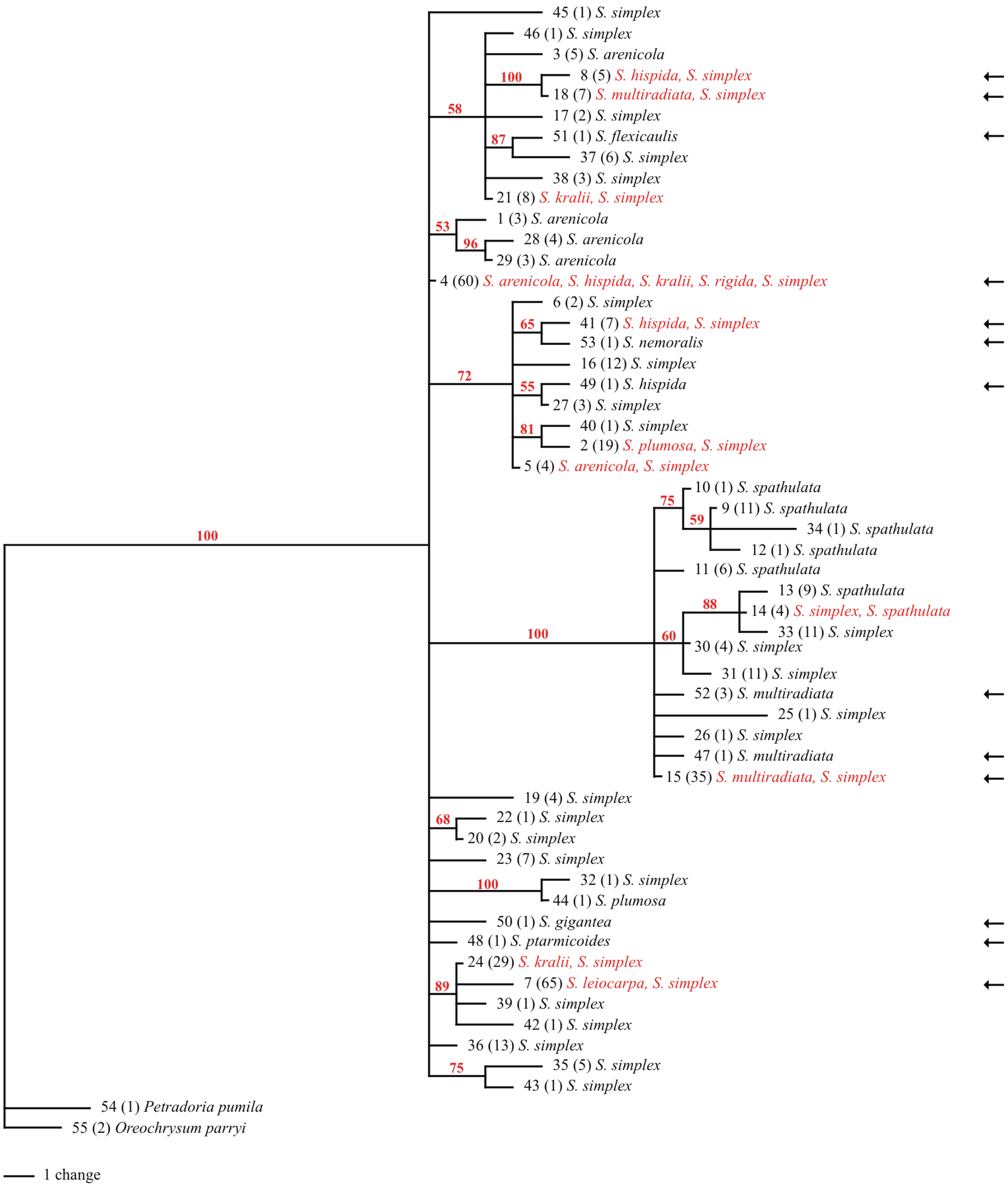

Figure 4.2. Bayesian phylogram from analysis of 55 cpDNA haplotypes recovered from 392 *Solidago* subsect. *Humiles* and three outgroup accessions. Numbers above branches are Bayesian posterior probabilities. Branches are labeled with the following information: haplotype number, number of accessions with haplotype in parentheses, species with haplotype. Haplotypes shared by more than one species are indicated with red text. Arrows indicate placement of non-*Humiles Solidago* in the phylogram.

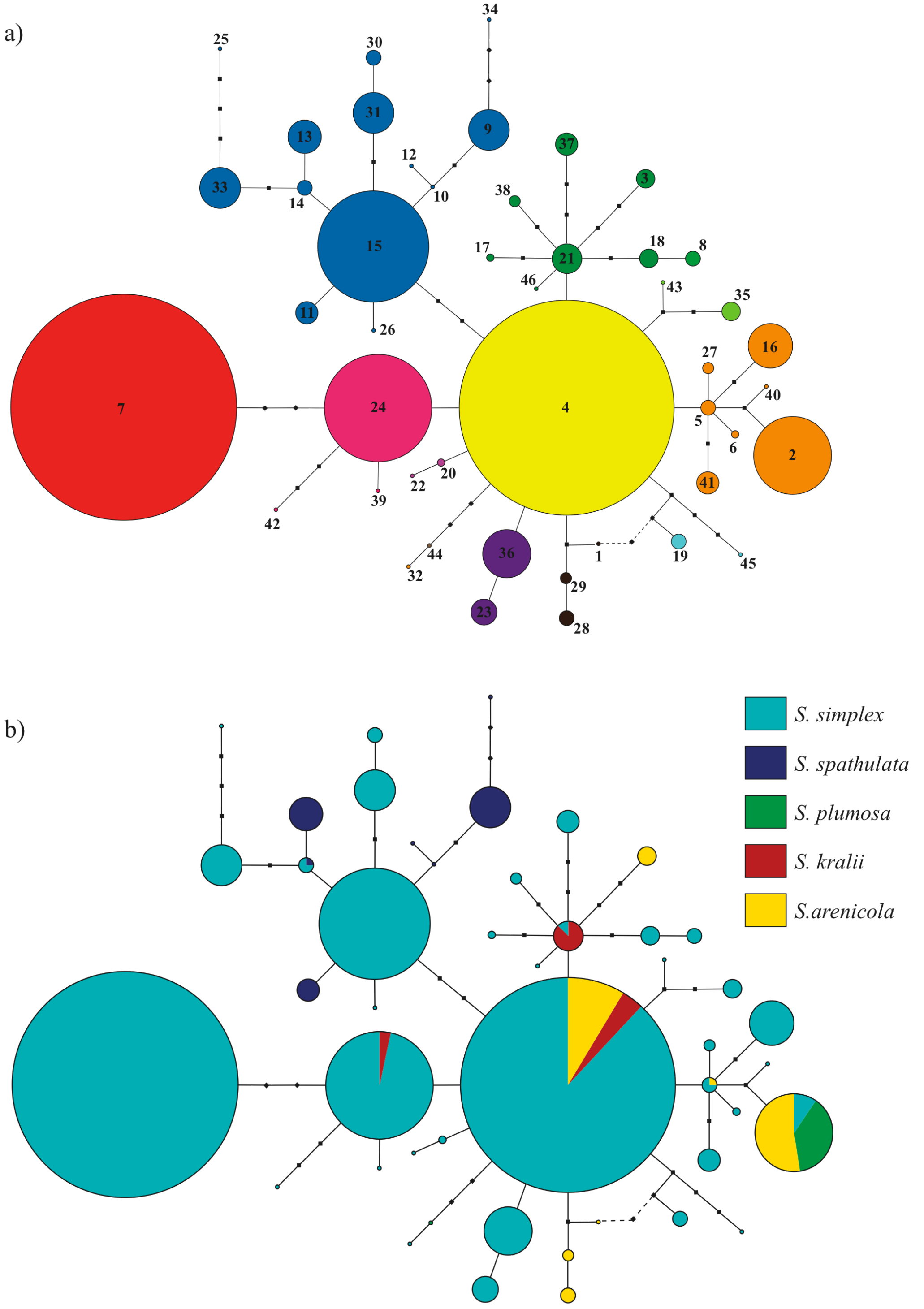

Figure 4.3. Statistical parsimony network of 46 cpDNA haplotypes recovered from 368 accessions of *Solidago* subsect. *Humiles*. Haplotypes were arbitrarily assigned numbers 1-46. Haplotypes were colored to indicate major groups (a) and species distributions (b).

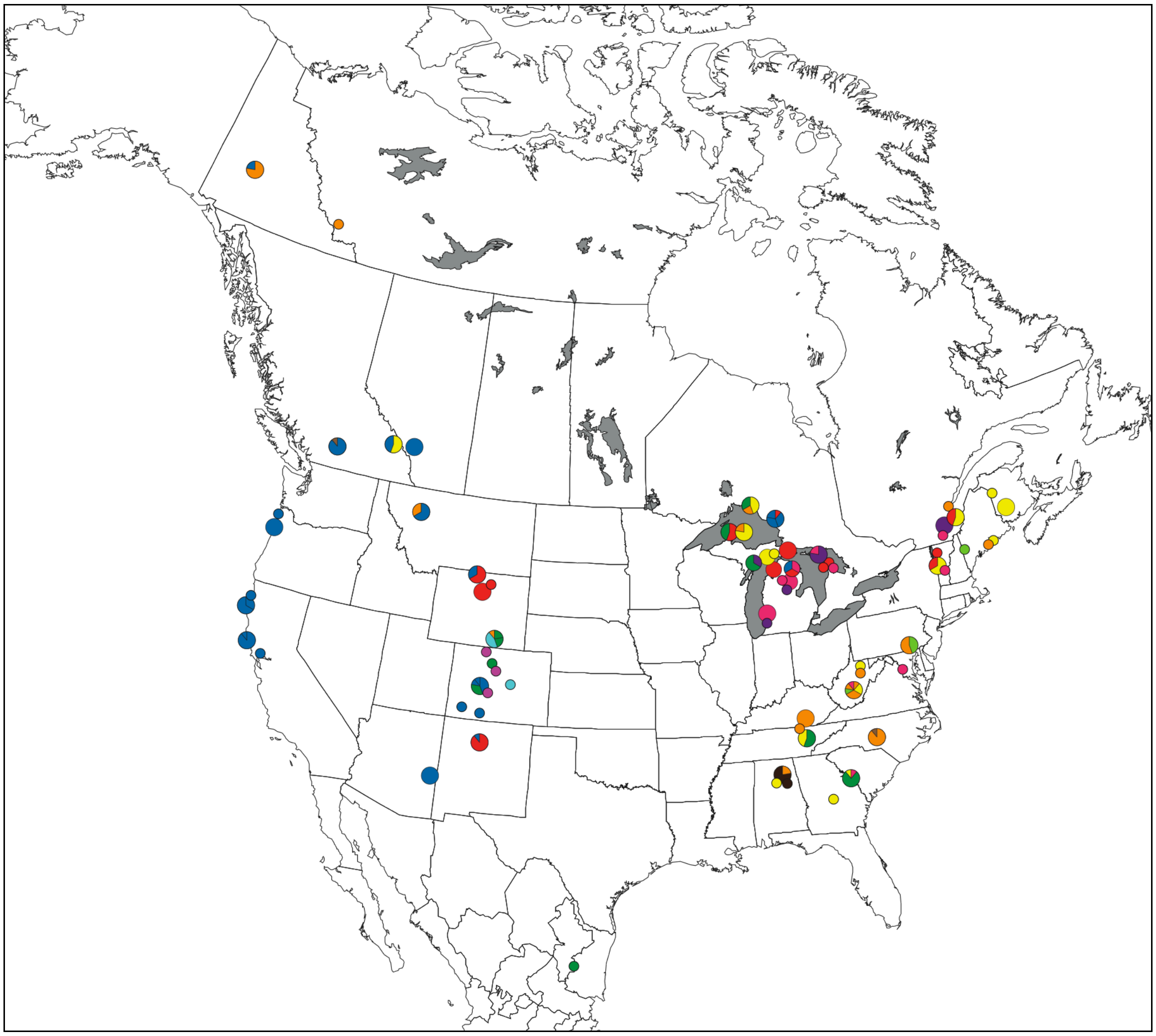

Figure 4.4. Distribution and frequency of *Solidago* subsect. *Humiles* chloroplast haplotypes in North America. Haplotype colors correspond to Fig. 3a.

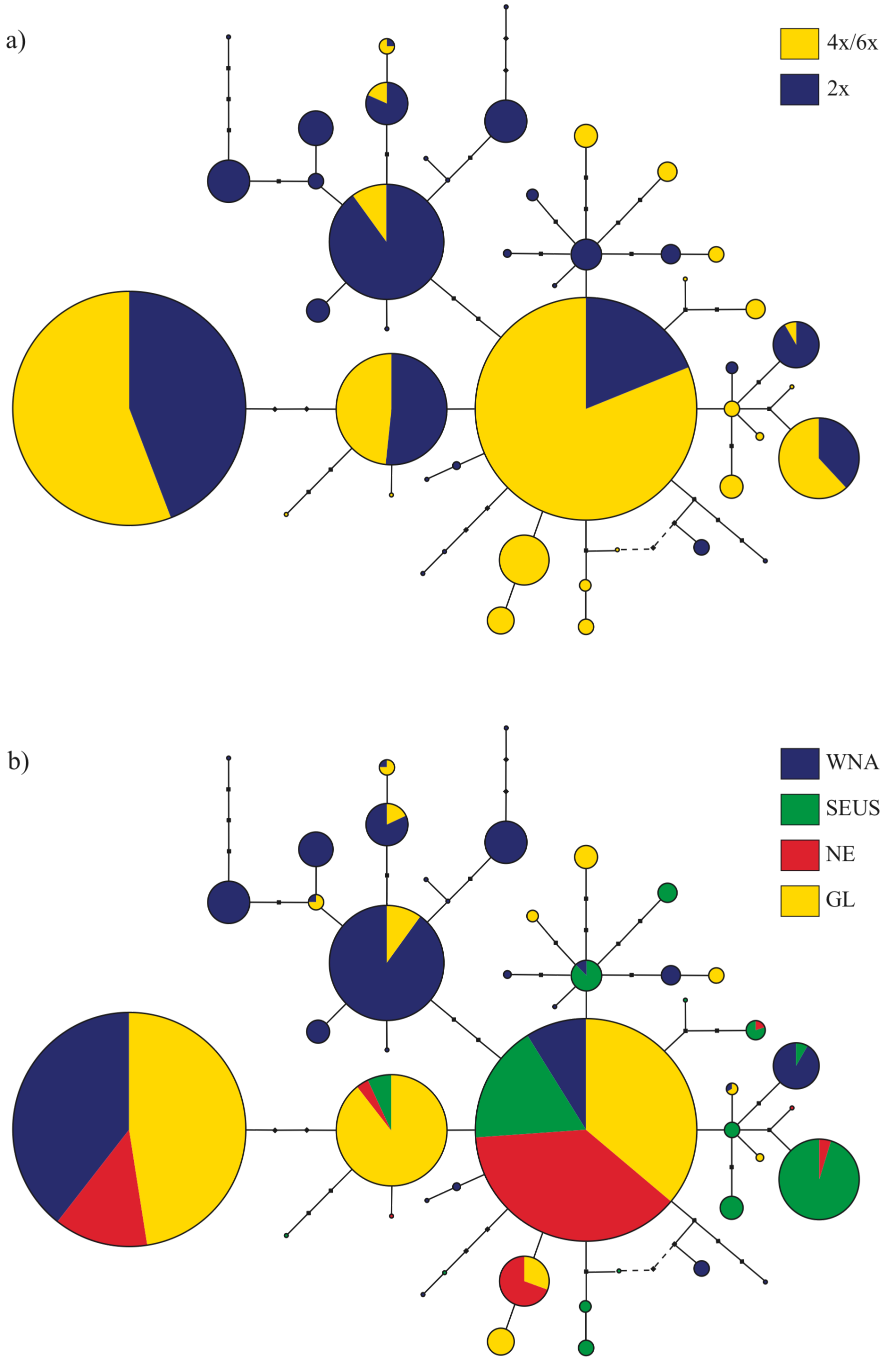

Figure 4.5. Statistical parsimony cpDNA haplotype networks for *Solidago* subsect. *Humiles* showing distribution of diploid vs. tetraploid/hexaploid cytotypes (a) and geographic distribution (b). Geographic regions shown are western North America (WNA), southeastern United States (SEUS), northeastern North America (NE), and the Great Lakes region (GL).

APPENDIX 1

Table 4A1.1. Haplotype distribution within *Solidago* subsect. *Humiles* and outgroup.

	Haplotypes																									
Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Solidago arenicola																										
S5				1																						
S100	1																									
S101		2																								
S102			5	4																						
S103					1																					
S104		9																								
Solidago kralii																										
S4				1																						
S99				1																	7			1		
Solidago plumosa																										
S98		8																								
Solidago simplex																										
S11				9																						
S112				7		2																				
S113							5	4																		
S12				1																						
S138							9																			
S140b															6	3										
S142							6								3											
S145							1																			
S146							9																			
S150																	2	2	4							
S155																				1						
S156																					1					
S159																						1				
S16																							7	2		
S162															4			3							1	1
S163																				1						
S164															1											
S165															1											
S167							8																			
S169																										
S172															8											
S173				5											4											
S176																										
S178																7										
S24				9																						
S25				1																						
S26		1																								
S28																										
S3																1										
S37																										
S38																								9		
S50																								1		
S53																								9		
S57							3							3										3		
S58																										
S60				4																						
S63							1								3											
S65																								1		
S67							1																			
S68							1																			
S70																										
S71																										
S73																										

Haplotypes																												
27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
	4	3																										
																	1											
1																												
			1																									
				9																								
					1																							
						9																						
						2																						
								1																				
									1																			
									3	6																		
2											3																	
			3	2																								
												1																
									9																			
													1															

	Haplotypes																									
Population	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
S74				5			4																			
S77				1																						
S8																								1		
S81							1																			
S83				6			3																			
S84																								1		
S85																										
S86																										
S89							9																			
S94				1																						
S96																1										
S97		1		2	3																			1		
H2																										
H5																										
Solidago spathulata																										
S2																										
S126									8	1																
S128									3		6															
S129												1														
S131													9													
S133														1												
Outgroup species																										
Oreochrysum parryi																										
S149																										
S160a																										
Petradoria pumila																										
S148																										
Solidago flexicaulis																										
S34																										
Solidago gigantea																										
S31b																										
Solidago hispida																										
S23																										
S18								1																		
S136																										
S64				1																						
Solidago leiocarpa																										
S29							2																			
S30							2																			
Solidago multiradiata																										
S141															1											
S143																										
S151a																		2								
S174															2											
S6																										
TRAL1															1											
TRAL4															1											
Solidago nemoralis																										
S33a																										
Solidago ptarmicoides																										
S32																										
Solidago rigida																										
S33				1																						

Haplotypes																												
27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
								4						5														
															1													
														1		1												
																		1										
																			1									
							1																					
																												1
																												1
																											1	
																								1				
																							1					
																						1						
														1														
																									1			
																									2			
																				1								
																										1		
																					1							

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CHAPTER V

DISJUNCTION, HABITAT SPECIFICITY, AND FLOWERING PHENOLOGY: THE INFLUENCES OF GEOGRAPHY AND ECOLOGY ON REPRODUCTIVE ISOLATION AND SPECIATION IN GREAT LAKES POPULATIONS OF *SOLIDAGO SIMPLEX*

Jansson (2003) proposed that regional glacial history (more precisely the magnitude of climatic change since the last glacial maximum) is one of the major predictors of global-scale patterns of endemism. In that light, northern glaciated regions are expected to harbor very few endemic species. Broad reviews of plant endemism in North America have generally supported this view, and few, if any, endemic plant taxa have been broadly recognized in glaciated areas of North America (Gentry 1986; Loehle 2006). Results discussed in Chapter II suggest that the flora of the glaciated Great Lakes region, despite its geologically young age, harbors a relatively large number of endemic plant taxa. This is most noticeable when the Great Lakes flora is compared to floras of adjacent regions of glaciated North America (e.g., the upper Midwest and/or northeastern North America) that have almost no described endemic plant taxa (but see Harris and Rajakaruna 2009 for a brief discussion of northeastern endemic taxa). Thus the Great Lakes region stands out as an anomaly in a generally endemic-poor part of North America.

My review in Chapter II uncovered 60 endemic plant taxa that have been described from the Great Lakes region. Thirty-two of these taxa appeared to be distinct entities and were characterized well enough that their geographic and habitat distributions in the region could be examined in detail. Analysis of this data revealed that nearly all of these endemics occurred in open, non-forested habitats in the northern part of the Great Lakes region, and 53% of the endemics were restricted to habitats along the shores of the Great Lakes. Considering that the Great Lakes region was largely forested (approximately 90-95% of the land surface) prior to European settlement, the endemic flora shows a marked affinity to regionally uncommon habitat types. These results suggest that adaptation of plants to specialized habitats in the recently glaciated landscape has likely driven the evolution of edaphic endemism and ecological speciation.

Many of the described Great Lakes region endemics have not received wide recognition as distinct taxonomic entities. This is highlighted by the broad reviews of endemism by Gentry (1986) and Loehle (2006) discussed above. Loehle proposed that the evolution of endemic species generally takes a long time, and that many endemics described from glaciated regions are likely taxonomic artifacts. This hypothesis runs counter to a plethora of theoretical and empirical studies of ecological speciation that have proposed that local adaptation to different habitats and the development of reproductive barriers (especially prezygotic barriers like temporal isolation) can occur over relatively short time periods (McNeilly and Antonovics 1968; Levin 1993; Schluter 1998; Eubanks et al. 2003; Levin 2003, 2004; Nosil et al. 2005; Rundle and Nosil 2005; Hendry et al. 2007). Recent studies from arctic regions suggest that substantial amounts of biological species diversity at northern latitudes has previously gone unrecognized (reviewed in Brochmann and Brysting 2008). Our understanding of the ecology and evolution of the vast majority of endemic plants described from the Great Lakes region is scant because few of the endemics have been closely studied since their initial taxonomic description. Do many of the endemic taxa in the Great Lakes region represent reproductively isolated species?

Objectives. In this chapter, I used the *Solidago simplex* species complex as a model group in which to examine fine-scale patterns of ecological differentiation across the Great Lakes region. Historical data from herbarium specimens, field data from natural populations, and data from a common garden were used to address the following questions: 1) What population-, habitat-, and taxon-level differences in ecology and flowering phenology are present in *S. simplex* populations across their range in the Great Lakes region? 2) Are the differences environmentally or genetically based (e.g., are they maintained in a common garden)? 3) Do these data suggest that *S. simplex* taxa in the Great Lakes region are reproductively isolated and behaving as good biological species?

MATERIALS AND METHODS

Study system. *Solidago* L. (Asteraceae: Astereae) is a predominantly North American genus of ca. 100 species of rhizomatous, perennial herbs (Semple and Cook 2006). Goldenrods are self-incompatible, obligately outcrossing plants that are pollinated by a variety of generalist pollinators including bees (e.g., *Apis mellifera* L. and *Bombus* L. spp.), wasps (e.g., *Polistes* spp.), and beetles (e.g., *Chauliognathus pennsylvanicus* DeGeer) (Mulligan and Findlay 1970; Gross and Werner 1983; Havercamp and Whitney 1983; Buchele et al. 1992). Seed dispersal in *Solidago* is amenochorous (via wind); the cypselae have a double-layered bristly pappus that aids in wind dispersal (Hood and Semple 2003).

Solidago simplex (sticky goldenrod) is currently placed in *Solidago* subsect.

Humiles (Rydberg) Semple along with four other species: *S. arenicola* Kenner & Kral, *S. kralii* Semple, *S. plumosa* Small, and *S. spathulata* de Candolle (Semple 2003; Semple and Cook 2006). It is transcontinental in distribution with a stark disjunction between the western Cordillera and eastern North America. It is absent across the central parts of the continent (see Fig. 3.1 in Chapter III; Ringius 1986; Semple et al. 1999). Based on cytological and morphometric studies, Ringius (1986) divided *S. simplex* (what he referred to as *S. glutinosa* Nutt.) into two subspecies. Diploid subsp. *simplex* ($2n = 18$) is widespread in montane and alpine habitats from Alaska to northern Mexico. Ringius assigned disjunct, diploid populations on the northern shore of Lake Superior and in Gaspé, Quebec to *S. simplex* subsp. *simplex*. Voss (1996) suggested that smaller-flowered, inland pine barren populations of *S. simplex* in northern Michigan might belong to the diploid subspecies as well, and recent cytogeographic work supported that conclusion (data presented in Chapter III). Following earlier treatments, tetraploid subsp. *randii* ($2n = 36$) is restricted to eastern North America with four varieties currently recognized (but see discussion in Chapter III). Varieties *monticola* and *racemosa* are restricted to rocky riverbanks and upland barrens in the Appalachian Mountains and northeastern North America. *Solidago simplex* vars. *ontarioensis* and *gillmanii* are Great Lakes region endemics, inhabiting rocky shores and active coastal sand dunes, respectively.

Study Region. The glaciated Great Lakes region of North America is located in the interior, northeastern part of the continent between latitudes 41.0° N and 50.5° N and longitudes 75.8° W and 92.5° W (Fig. 5.1). The region is centered around the five Laurentian Great Lakes, which together comprise the largest freshwater system on the planet (Schaetzl and Isard 2002). The region is bounded on the south and west by the states of Illinois, Indiana, Michigan, Minnesota, New York, Ohio, Pennsylvania, and Wisconsin and on the north and east by the province of Ontario. The surface area of the lakes and the drainage basin that surrounds them covers approximately 765,990 km^2 (Larson and Schaetzl 2001; Schaetzl and Isard 2002). The elevation of the region ranges from a maximum of ca. 701 m above sea level at Eagle Mountain in Cook Co., Minnesota to a minimum of ca. 75 m above sea level at the outlet of Lake Ontario. The present-day Great Lakes drain via the St. Lawrence River into the Gulf of St. Lawrence and northern Atlantic Ocean.

The Great Lakes basin lies entirely within the limits of Pleistocene glaciation. Continental ice sheets invaded the region at least six times during the Pleistocene, most recently during the Wisconsinan glaciation that ended roughly 15,000 YBP (Larson and Schaetzl 2001). During each glacial period, the ice sheets scoured the landscape, deepened the lake basins, and depressed the earth's crust under their massive weight. The present-day surficial characteristics of the region are the aftermath of those repeated glaciations. Glacial deposits of the most recent Wisconsinan glaciation and the erosional processes that followed deglaciation dominate the landscape of the Great Lakes basin and have acted together to form the mosaic of landforms and habitats present across the region today.

The Great Lakes region has generally been divided into two broad physiographic provinces based on topography and underlying bedrock geology (Larson and Schaetzl 2001). The northern and western parts of the Great Lakes region are part of the Laurentian (or Superior) Uplands. This area is the southwestern-most extension of the

Canadian Shield, an area of crystalline Precambrian rocks that covers most of eastern Canada. The granite hills of the Laurentian Uplands and rock outcrops along the shores of Lake Superior are remnants of an ancient mountain range that has worn away by some two billion years of erosion and glaciation. Soils in this region are typically thin and nutrient poor, and bedrock dominates much of the landscape. This area around the perimeter of Lake Superior forms the topographically most rugged and highest elevation part of the Great Lakes basin.

The southern and eastern extents of the basin form the Eastern Lakes section of the Central Lowlands province. This area is characterized by generally low relief and is underlain by calcareous, sedimentary bedrock of Paleozoic age. The glacially transported soils of the Eastern Lakes section are typically deep and fertile, as exemplified by the till plains that stretch across much of northern Indiana, northern Ohio, and southern Michigan. There are, however, extensive areas of glaciofluvial deposits in parts of northern and western Michigan and northern Wisconsin, which form broad, sandy (and often droughty) outwash plains. Along the northern boundary of the Eastern Lakes section, the resistant dolomite of the Niagara Escarpment forms a broad arc of cliffs and rock shores that run from the Niagara region of New York to the Bruce Peninsula and Manitoulin Island in Ontario through the Garden Peninsula of Michigan to the cliffs and outcrops of the Door Peninsula in Wisconsin. In the southern part of the region, glacial till covers most of the bedrock, however, limestone bedrock surfaces in several areas, where it forms the rocky islands and Marblehead Peninsula of western Lake Erie and the extensive alvar (limestone pavement) formations of the Napanee plain at the eastern end of Lake Ontario.

One of the most prominent and ecologically dynamic features of the Great Lakes region (aside from the lakes themselves) is the boundary between the lakes and the surrounding land surface. There are more miles of freshwater shoreline in the Great Lakes region (ca. 16,900 km if island shorelines are included) than in any other region in the world. Shorelines range from the low, marsh-lined shores along Lakes Erie and Ontario, to the rocky shores and cliffs of Lakes Huron and Superior. Sand beaches and dunes are another major feature of the shores of the Great Lakes. Great Lakes sand dunes are best developed along the southern and eastern shores of Lake Michigan (e.g., Indiana Dunes, Sleeping Bear Dunes) and the southern shore of Lake Superior (e.g., Grand Sable Dunes), but all of the Great Lakes have active dunes of some extent.

Herbarium data and analyses. Specimen data from herbarium sheets, the Michigan Flora and Wisflora databases, and verified published reports (e.g., from Ringius 1986; Semple et al. 1999) were analyzed to investigate distributional patterns and habitat specificity of *Solidago simplex* throughout the Great Lakes region. Herbarium specimens were initially identified to variety (*gillmanii*, *ontarioensis*, or *simplex*) using the taxonomic frameworks outlined in Ringius (1986), Ringius and Semple (1987), and Semple and Cook (2006). Information from the above-stated sources plus recent cytogeographic data (discussed in Chapter III) were used to assign a probable ploidy level ($2n = 18$ or $2n = 36$) to each herbarium specimen. Label data from specimens was used to georeference populations and to assign categorical habitat descriptors for each specimen. Four broad habitat descriptors were assigned: sand barren, sand dune, granite/basalt outcrop, and dolomite/limestone outcrop. Specimens that could not be identified to variety or that did not have specific location data were excluded from the study.

Specimen data (specifically collection date) from the Michigan Flora database and from herbarium collections of the author were used as proxies for preliminary estimates of regional flowering patterns of *S. simplex* populations throughout the Great Lakes states. Collection dates of flowering specimens were converted to standardized ordinal dates that represented the days after January 1st of each year. In this manner, collections for different years could be combined into a common framework. Specimens that were not flowering at the time of collection, specimens that did not have a specific collection date, and specimens that did not have a specific collection locality (to the city- or township-level) were excluded from the analyses.

Statistical analyses of flowering phenology were performed on a four-group circumscription of the specimens. The grouping scheme was based on a combination of taxonomic, ecological, and morphological characters, some of which became apparent only after field grown individuals had been transplanted to the common garden (see Appendix 1 for a detailed explanation of group circumscription). The four circumscribed groups were: "sand dune", "sand barren", "rock outcrop large-plant", and "rock outcrop small-plant". The "sand dune" category was composed of *S. simplex* var. *gillmanii* plants for active sand dunes. The "sand barren" category was composed of *S. simplex* var. *simplex* plants from inland pine barrens. The "rock outcrop large-plant" category was composed of large-statured plants of *S. simplex* var. *ontarioensis* from dolomite outcrops of the Niagara Escarpment. The "rock outcrop small-plant" category was composed of morphologically similar, small-statured plants of both tetraploid *S. simplex* var. *cf. ontarioensis* from dolomite shores of the Bruce Peninsula and granite shores of eastern

Lake Superior and diploid *S. simplex* var. *simplex* from the north shore of Lake Superior.

Differences in mean collection date (the proxy for flowering period) were analyzed using an analysis of variance framework to test the hypothesis that these four groups of *S. simplex* had differentiated phenologically. One-way analysis of variance followed by post hoc multiple comparisons tests were performed on each group.

Field data and analyses. In the summer of 2006, populations of *Solidago simplex* in sand barren and sand dune habitats were surveyed to assess their suitability for season-long field monitoring of flowering phenology. The basic criteria used to assess each population's suitability included the total number of plants present at the site (i.e., were there sufficient numbers of plants present?) and the density of plants and the areal extent of the population (i.e., was the population large enough to sample widely spaced patches of individuals?). In May-June 2007, field plots in two sand barren populations (Staley Lake Road barren and Rte 612 barren) and one sand dune population (Sturgeon Bay dunes) were established. In addition to the above-stated criteria, the Sturgeon Bay site was chosen because it was further north than the sand barren populations (thus serving to remove any confounding latitudinal gradient in flowering phenology) and because herbarium data suggested that plants there began flowering somewhat earlier (around mid July) than at other sand dune sites (e.g., *H.A. Gleason 95,* GH and *T.P. Marshall 687,* MSC).

At the Rte 612 and Sturgeon Bay sites, three widely spaced plots were established in areas with moderately high densities of *S. simplex* clones. In each plot, all plants were tagged and general demographic data recorded. Once plants had bolted but before anthesis occurred, 15 randomly distributed flowering plants per plot (a total of 45 plants per population) were chosen for phenological monitoring. At the Staley Lake Road site, 31 widely spaced individuals were tagged for phenological monitoring because the plants at that site occurred at densities too low to feasibly establish separate plots. Starting in late June and continuing through early October, populations were visited weekly, and the number of capitula buds, receptive capitula, and senesced capitula were recorded for the selected flowering plants.

Phenological differentiation among the three populations was analyzed with two different metrics. In the first analysis, the median flowering date of each individual plant was determined by calculating the date by which half of the total capitula had become receptive. When the median date fell between two actual observation dates, the midpoint was used. Differences in the median (peak) flowering date between the three populations were examined using analysis of variance. Post hoc multiple comparisons tests were performed to examine pairwise differences in peak flowering.

Differences in median (peak) flowering capture only one dimension of the potential variation in flowering phenology between species/populations (see discussions of temporal niche variation in Fleming and Partridge 1984). In order to obtain a more comprehensive estimation of phenological differentiation, pairwise overlaps in flowering phenology curves (i.e., overlaps in temporal niches) between the three populations were also calculated. The data used to represent the temporal niche was the population-level proportion of capitula that were receptive on a given observation date (i.e., individual data were pooled within populations). Because capitula could potentially be receptive on more than one observation data, the area under each phenological curve was standardized to equal one before overlap was calculated. Pianka's Niche Overlap Index (Pianka 1973) was calculated using the program EcoSim (Gotelli and Entsminger 2009). The formula used to calculate niche overlap was

$$O_{12} = O_{21} = \frac{\sum_{i=1}^{n} p_{2i} * p_{1i}}{\sqrt{\sum_{i=1}^{n} (p_{2i}^{2})(p_{1i}^{2})}}$$

where O_{12} and O_{21} are the symmetrical niche overlaps between a pair of populations, p_{1i} equals the proportion of receptive capitula for population one on the *i*th day, and p_{2i} equals the proportion of receptive capitula for population two on the *i*th day. Values for Pianka's Index can range from zero (no overlap) to one (complete overlap).

Common garden data and analyses. During the summer of 2005, rhizome cuttings were harvested from populations of *Solidago simplex* growing throughout the Great Lakes region and transplanted to the greenhouse at the University of Michigan's Matthaei Botanical Garden (location data for populations is provided in Table 1). Rhizomes were planted into Sunshine® potting medium in 24-cell greenhouse flats and watered regularly to induce rooting. After approximately one month, plugs were potted into standard greenhouse containers in a mixture of Sunshine® potting medium and Turface® in a 20:1 ratio by volume. Pots were moved outside for the remainder of the growing season. In December, after senescence of basal leaves from freezing temperatures, all pots were moved to a covered coldframe for overwintering. The coldframe was uncovered in late March/early April of 2006, and plants were moved back outside in early May. In 2006 and 2007, beginning in early June and continuing until the last plant died back from frost, the number of capitula buds, receptive capitula, and senesced capitula were recorded from each flowering plant on biweekly or weekly intervals.

For statistical analyses of phenological differentiation, plants in the common garden were circumscribed using the same four-taxon grouping scheme used for herbarium specimens (see Appendix 1 for an explanation of group circumscription). Phenological data from 2006 and 2007 were analyzed separately.

As with the field data, phenological differentiation in the common garden was analyzed using two different metrics. Differences in the median (peak) flowering date among the four circumscribed groups were examined in an analysis of variance framework. The median flowering date of each individual plant was determined by calculating the date by which half of the total capitula had become receptive. When the median date fell between two observation dates, the midpoint was used. One-way analysis of variance followed by post hoc multiple comparisons tests were performed on each group with the program SPSS 17.0.

In addition to analyzing differences in peak flowering among groups, 2006 and 2007 pairwise niche overlaps between the four circumscribed groups were calculated with the program Ecosim (Gotelli and Entsminger 2009) following the procedures described for the field data. Population-level niche overlaps for 2006 and 2007 common garden data were also calculated and are discussed in Appendix 2.

A number of niche overlap indices, including Pianka's (1973) index, have been criticized for their assumptions that the niche breadth data being analyzed have an underlying normal distribution. Mouillot et al. (2005) proposed a new, non-parametric approach to calculating niche overlap that makes no assumptions concerning the distribution of the data and that might better handle the variation of continuous measures of niche breadth (as opposed to categorical data). A comparison of 2006 common garden niche overlap estimates derived from the two different approaches is discussed in Appendix 2.

RESULTS

Herbarium Results. Examination of herbarium specimens revealed that *Solidago simplex* populations are restricted to four distinct, predominantly allopatric habitats in the Great Lakes region: dolomite and limestone shorelines/cliffs along the Niagara Escarpment, granite and basalt outcrops along the shores of Lake Superior, active sand dunes along the shores of Lakes Michigan and Huron, and inland jack pine barrens in northern lower Michigan (Figs. 5.2-5.3). *Solidago simplex* var. *gillmanii* is restricted to active coastal sand dunes, while the other varieties do not occur in this habitat. *Solidago simplex* var. *simplex* (as traditionally defined by ploidy - see Chapter III) has a disjunct distribution within the region. Along the north shore of Lake Superior and also Lake Nipigon the variety inhabits shoreline rock outcrops, but in the southern part of the region the variety is restricted to xeric, inland jack pine barrens. *Solidago simplex* var. *ontarioensis* (as traditionally circumscribed by ploidy) also occupies two habitats. It is restricted to dolomite/limestone shores along the Niagara Escarpment in Ontario and Michigan and granite/basalt shores along the eastern shore of Lake Superior and the Keweenaw Peninsula.

Specimen data also indicated that there is broad-scale phenological differentiation (as inferred from collection date) among *S. simplex* plants from throughout the Great Lakes region (Table 5.2; Fig 5.4). Pine barren and rock outcrop (small-plant) populations begin flowering before other *S. simplex* in late June and early July, peak (as inferred by mean collection date) in mid July, and finish flowering by late July. Peak flowering of rock outcrop (large-plant) populations was determined to be significantly later than both sand barren and rock outcrop (small-plant) populations in the ANOVA (mean collection date ca. 16 days later, $p < 0.001$). Rock outcrop (large-plant) individuals begin flowering in mid July, peak in early August, and finish in mid August. Peak flowering in sand dune plants was found to be significantly later than all other groups in the ANOVA ($p < 0.001$). Plants in this habitat generally begin flowering in early-mid August (although there are a some flowering herbarium collections from mid-late July), peak in early September, and continue flowering into October.

Field Results. Field surveys of two pine barren populations and one sand dune population were consistent with the overall patterns obtained from herbarium collection data but provided finer-scale resolution of phenological patterns within and among populations (Table 5.3; Figs. 5.5-5.6). Results from the ANOVA indicated that the median flowering date (here used to represent peak flowering) was significantly different for sand barren and sand dune populations, with peak flowering of the Sturgeon Bay population occurring approximately two months after the sand barren populations (separation of ca. 58 days, $p < 0.001$). The two sand barren populations began flowering in late June, peaked in early July, and finished flowering by mid-late July. The Sturgeon Bay dune population began flowering in early-mid August (exact start-date not determined), peaked in early September, and finished flowering in early October.

Estimates of temporal niche overlap were consistent with visual inspection of the phenological data and with the ANOVA results. Sand barren populations had high niche overlap (Pianka's Niche Overlap Index = 0.9875). The Sturgeon Bay dune population showed no temporal niche overlap with the two sand barren populations (Pianka's Niche Overlap Index = 0.0000).

Common Garden Results. Analyses of 2006 and 2007 common garden data were consistent across years and showed overall patterns that were consistent with results obtained from analyses of both the herbarium and field data (Tables 5.1,5.4; Figs. 5.7-5.10). One difference noted between the common garden and other data sets was an overall shift toward earlier flowering (by approximately 2-3 weeks) for all plants in the common garden. Pine barren and rock outcrop (small-plant) populations began flowering in early June before other *S. simplex* populations, reached peak flowering in mid-late June, and finished flowering by early-mid July. Peak flowering of rock outcrop (large-plant) populations was found to be significantly later than both sand barren and rock outcrop (small-plant) populations in the ANOVA (peak separation of ca. 14-19 days, $p < 0.001$). Rock outcrop (large-plant) individuals began flowering in mid June, peaked in mid July, and largely finished by mid August. Peak flowering of sand dune populations was found to be significantly later than all other groups in the ANOVA ($p < 0.001$). Sand dune plants in the common garden generally began flowering in late July, peaked in mid-late August, and continued flowering through October. Later flowering was most pronounced in the southern-most populations (below 44° N latitude).

Estimates of temporal niche overlap among garden grown plants were consistent with visual inspection of the phenology data and with the ANOVA results (Table 5.5; Appendix 5.2). Sand barren and rock outcrop (small-plant) populations displayed high levels of temporal niche overlap (Pianka's Niche Overlap Index: 2006 = 0.8339, 2007 =

0.8589). Both of these groups displayed moderate to high niche overlap with rock outcrop (large-plant) populations. Pianka's Niche Overlap Index ranged from 0.3199 (2007 sand barren) to 0.7820 (2006 rock outcrop small-plant). Sand dune populations had a consistently low temporal niche overlap with the other groups. There was almost no temporal overlap between dune populations and sand barren and rock outcrop (small-plant) populations (Pianka's Niche Overlap Index ranged from 0.0018 to 0.0219). There was slightly higher overlap between sand dune and rock outcrop (large-plant) populations, but overlap among these was also relatively small (Pianka's Niche Overlap Index: 2006 = 0.1705, 2007 = 0.1163).

DISCUSSION

Solidago simplex is represented by five distinct groups of populations in the Great Lakes region. Two allopatric groups of diploid *S. simplex* var. *simplex* occur in the northern Great Lakes region. One set of populations occurs around the shores of Lake Nipigon and east along the northern shore of Lake Superior to Terrace Bay, Ontario. The other set of populations occurs approximately 600 km further south in xeric jack pine barrens in northern lower Michigan. These two disjunct groups of *S. simplex* var. *simplex* are ecologically and morphologically distinct, although morphometric analyses have not yet been conducted. Their flowering phenology, however, overlapped completely in the common garden. Resolution from phylogeographic studies (discussed in Chapter IV) was not detailed enough to determine how many migrations likely account for these sets of populations in the Great Lakes region.

The third representative of *S. simplex* in the Great Lakes region is the sand dune endemic *S. simplex* var. *gillmanii*. This endemic occurs on active sand dunes along the shores of Lake Michigan and northwestern Lake Huron. Examination of herbarium specimens, plants in the field, and plants grown in the common garden indicated that populations of *S. simplex* var. *gillmanii* are ecologically, morphologically, and phenologically distinct from all the other members of *S. simplex* in the Great Lakes region. The sand dune habitat exerts strong selection on plants that grow there, and sand dune specialists often have specific adaptations to survive the extreme environment of the dune system (Maun 1994, 1998). *Solidago simplex* var. *gillmanii* produces long vertical rhizomes that allow it to tolerate sand burial. In fact, seedlings grown in the greenhouse (i.e., seedlings that have never experienced sand burial) also produce long vertical rhizomes (Peirson, unpub. data). No other taxa in *S. simplex* produce these vertical rhizomes, but *S. spathulata* that is endemic to dune systems along the Pacific coast does. Ringius (1986) used this morphological distinction as part of his justification for recognizing *S. spathulata* as a distinct species. In addition to these morphological distinctions, *S. simplex* var. *gillmanii* is also phenologically distinct from the other taxa in the region. It flowers considerably later than the other species. These data suggest that this morphologically distinct sand dune endemic is reproductively isolated from all other *S. simplex* by strong ecological and temporal barriers. I therefore propose that *S. simplex* var. *gillmanii* be elevated to species level (see conclusion for brief discussion concerning nomenclature).

Two morphologically distinct groups of tetraploid *Solidago simplex* occur on rock outcrops in the Great Lakes region. Large-statured plants occur on dolomite shores of northern Lake Huron and northern Lake Michigan along the boundary of the Niagara

Escarpment. Small-statured plants occur primarily on granite/basalt outcrops along the southern and eastern shores of Lake Superior, but one population of entirely small-statured plants was also found on dolomite shores at the tip of the Bruce Peninsula (approximately 3 km from populations of larger plants). The size groups of rock outcrop plants were phenologically distinct in the common garden, although there was a small amount of overlap in temporal niches. Phylogeographic data suggested that the small-statured plants might have a separate origin from the large-statured plants; the small-statured plants possessed haplotypes likely derived from western North American *S. simplex*. As discussed in Chapter IV, however, extensive haplotype sharing within *Solidago* subsect. *Humiles* precludes any concrete assessments of evolutionary relationships.

Similar Patterns in Other Great Lakes Region Endemic Goldenrods. In addition to the patterns of population differentiation uncovered in *S. simplex*, research for this study uncovered similar habitat-level complexity in other Great Lakes region species of *Solidago*. Initial examination of herbarium specimens of "*S. simplex* var. *gillmanii*" (e.g., *McVaugh 9586* MICH, *Voss 15011* MICH) from active dune systems along the south shore of Lake Superior indicated that populations there did not represent *S. simplex*. These dune plants had the overall form of *S. simplex* var. *gillmanii* but also appeared to have pubescent stems and foliage. Vegetative pubescence (outside of the floral arrays) is not found in *S. simplex*. Fieldwork along the south shore of Lake Superior confirmed the initial observations from herbarium collections. Plants in these populations were almost always pubescent and were never glutinous. Sticky leaves, stems, and capitula are defining characteristics of plants in *Solidago* subsect. *Humiles*. These large dune plants on the south shore of Lake Superior are an undescribed sand dune endemic that appears to be closely related to hairy goldenrod *S. hispida*.

Semple et al (1999) described *S. hispida* var. *huronensis*, a glabrous form of the species endemic to sand dunes along the shores of Lake Huron. Subsequent examination of herbarium specimens at MICH revealed that *S. hispida* var. *huronensis* is apparently more widespread than previously thought, also occurring on dunes along the southern and eastern shores of Lake Superior (e.g., *J.A. Peirson 627*, *M.J. Oldham 30892*). In Chapter III, I proposed that a number of previously reported diploid *S. simplex* occurrences along the eastern shore of Lake Superior actually represent miniature, glabrate, rock outcrop forms of *S. hispida*. Voss (1996) discussed the occurrence of these miniature rock outcrop plants on Michigan's Keweenaw Peninsula and Isle Royale and suggested that they may represent disjunct populations of the eastern maritime *S. hispida* var. *tonsa* Fern. Regardless of their current nomenclatural/taxonomic status, these small, glabrous rock outcrop plants are morphologically very similar to *S. hispida* var. *huronensis* (aside from overall plant stature). Flow cytometry data (Peirson, unpublished data) indicated that both of these entities are diploid ($2n = 18$) and have genomes of similar size. These two taxa are likely very closely related.

Flowering phenology in this apparent *S. hispida* species complex displays the same general pattern that was uncovered in *S. simplex*. Shoreline rock outcrop populations flower early, beginning in early-mid July, whereas sand dune populations from similar latitudes flower much later, in August and September. As in *S. simplex*, these differences in flowering phenology among *S. hispida* populations are maintained in the common garden (Peirson, unpublished data).

This small accumulation of data suggests that members of the *S. hispida* complex in the Great Lakes region have undergone a strikingly similar ecological radiation to that of *S. simplex*, however, the evolution of this population differentiation in *S. hispida* remains largely unstudied. Whether ecological selection in these different habitats was alone sufficient to drive population divergence or whether a complex Pleistocene history also contributed is unclear. The origin of the large tetraploid dune plants along the southern shore of Lake Superior also requires additional study. They could represent a series of autopolyploid *S. hispida* populations that have adapted to the active dune environment (typical, presumably diploid *S. hispida* plants grow nearby in sandy, open woods). They could alternatively represent allopolyploids that originated from the hybridization of *S. hispida* and another goldenrod, like *S. simplex*. Detailed cytogeographic, ecological, morphometric, and phylogeographic studies of *S. hispida* in the Great Lakes region and eastern North America will be required to test these and other hypotheses.

Summary. Cytological, ecogeographic, morphological, and phenological differences among Great Lakes populations of *S. simplex* suggest that the region harbors at least three distinct, reproductively isolated species. 1) Western, diploid *S. simplex* is a geographically distinct lineage; it is only sympatric with eastern members of *Solidago* subsect. *Humiles* in the Great Lakes region. In the Great Lakes region, diploid populations are ecogeographically and temporally isolated from the other taxa. 2) *Solidago simplex* var. *gillmanii* is ecologically distinct from other member of *S.* subsect. *Humiles* and possesses specific adaptations to its sand dune habitat. It is also temporally isolated from the other *S. simplex* in the region. Thus it meets the requirements of multiple species concepts. 3) Two morphologically distinct groups of tetraploid *Solidago simplex* occur on rock outcrops in the Great Lakes region. Phylogeographic data suggest that they likely had different origins, but no definitive conclusions can yet be drawn.

Parallel patterns of divergence in Great Lakes region populations of *S. hispida* (with specialized rock outcrop and sand dune taxa) support the hypothesis that adaptation to specialized habitats has been an important evolutionary driver of diversity in *Solidago*. These results are likely applicable to the broader endemic flora as well.

Table 5.1. Locality, habitat, ploidy, and flowering statistics for *Solidago simplex* populations analyzed in the common garden studies.

								No. of Samples and Median Flowering Date			
	Country	State/Prov	County/Dist.	Latitude	Longitude	Habitat	Ploidy	N_{2006}	Date$_{2006}$	N_{2007}	Date$_{2007}$
Solidago simplex* var. *gillmanii											
Indiana Dunes	U.S.A.	Indiana	Porter	41.68	-87.02	Dune	4x	-	-	3	278
Warren Dunes	U.S.A.	Michigan	Berrien	41.91	-86.60	Dune	4x	-	-	7	272
Charlevoix Dunes	U.S.A.	Michigan	Charlevoix	45.31	-85.31	Dune	4x	5	219	1	221
Sturgeon Bay Dunes	U.S.A.	Michigan	Emmet	45.71	-84.95	Dune	4x	24	230	7	232
Silver Lake Dunes	U.S.A.	Michigan	Oceana	43.65	-86.54	Dune	4x	2	280	2	265
Thompson's Harbor	U.S.A.	Michigan	Presque Isle	45.35	-83.57	Dune	4x	-	-	2	221
Dunes W of Manistique	U.S.A.	Michigan	Schoolcraft	45.91	-86.32	Dune	4x	17	228	3	242
Solidago simplex* var. *ontarioensis											
Government Dock	Can	Ontario	Algoma	47.94	-84.85	Metamorphic	4x	15	177	15	180
Sandy Beach	Can	Ontario	Algoma	47.96	-84.86	Metamorphic	4x	1	168	1	179
Big Tub Lighthouse	Can	Ontario	Bruce	45.26	-81.67	Limestone	4x	13	176	14	176
Bruce Peninsula Park	Can	Ontario	Bruce	45.25	-81.52	Limestone	4x	4	202	3	201
Elgin Street	Can	Ontario	Bruce	45.26	-81.64	Limestone	4x	15	186	7	199
Hay Bay Road	Can	Ontario	Bruce	45.24	-81.68	Limestone	4x	13	187	13	199
Seul Choix Point	U.S.A.	Michigan	Schoolcraft	45.92	-85.91	Limestone	4x	8	196	12	197

Solidago simplex* var. *simplex											
Terrace Bay	Can	Ontario	Thunder Bay	48.77	-87.11	Metamorphic	2x	7	172	6	183
Rte 612 & I-75	U.S.A.	Michigan	Crawford	44.78	-84.72	Barren	2x	8	171	5	173
Staley Lake Road	U.S.A.	Michigan	Crawford	44.65	-84.64	Barren	2x	11	177	4	179
Rte 612 & Deward Road	U.S.A.	Michigan	Kalkaska	44.77	-84.85	Barren	2x	-	-	2	175
Fletcher Road	U.S.A.	Michigan	Kalkaska	44.57	-85.06	Barren	2x	-	-	1	185
Big Creek Road	U.S.A.	Michigan	Oscoda	44.67	-84.28	Barren	2x	-	-	1	175
North of St. Helena	U.S.A.	Michigan	Roscommon	44.40	-84.41	Barren	2x	11	171	5	174

Table 5.2. Sample sizes, flowering statistics, and ANOVA post hoc multiple comparisons for *S. simplex* herbarium collections from the Great Lakes region. Mean collection (flowering) dates with the same superscript letter are not significantly different ($\alpha = 0.05$).

Habitat Group	No. of Samples	Mean Date (stand. dev.)	95% Confidence Interval	
			Lower	Upper
Sand Barren	61	199.9 ^{a} (9.6)	195.8	204.0
Rock Outcrop (small)	63	202.0 ^{a} (14.8)	197.9	206.0
Rock Outcrop (large)	25	218.2 ^{b} (6.7)	211.9	224.6
Sand Dune	172	240.4 ^{c} (19.2)	238.0	242.9

Table 5.3. Sample sizes, flowering statistics, and ANOVA post hoc multiple comparisons for field-surveyed *S. simplex* populations in northern Michigan. Population mean collection (flowering) dates with the same superscript letter are not significantly different ($\alpha = 0.05$).

Site	Habitat	No. of Samples	Mean Date (stand. dev.)	95% Confidence Interval	
				Lower	Upper
Rte 612 and I-75	Barren	45	185.8^{a} (4.5)	183.7	187.9
Staley Lake Road	Barren	31	186.9^{a} (5.4)	184.3	189.4
Sturgeon Bay	Dune	45	244.7^{b} (9.8)	242.6	246.8

Table 5.4. Sample sizes, flowering statistics, and ANOVA post hoc multiple comparisons for *S. simplex* plants grown in the common garden. Mean flowering dates with the same superscript letter are not significantly different ($\alpha = 0.05$).

Habitat Group	No. of Samples	Mean Date (stand. dev.)	95% Confidence Interval	
			Lower	Upper
2006				
Sand Barren	30	173.1 ^{a} (5.3)	168.9	177.3
Rock Outcrop (small)	36	175.3 ^{a} (7.4)	171.4	179.1
Rock Outcrop (large)	40	189.9 ^{b} (12.3)	186.3	193.6
Sand Dune	48	230.1 ^{c} (15.8)	226.8	233.5
2007				
Sand Barren	18	175.7 ^{a} (6.2)	168.8	182.7
Rock Outcrop (small)	36	178.9 ^{a} (7.0)	174.0	183.9
Rock Outcrop (large)	35	198.5 ^{b} (13.9)	193.5	203.5
Sand Dune	25	251.2 ^{c} (25.3)	245.3	257.1

Table 5.5. Pairwise niche overlaps for 2006 and 2007 common garden phenology data. Pianka's Niche Overlap Index was calculated using the program EcoSim (Gotelli and Entsminger 2009). Populations were grouped by habitat with rock outcrop plants divided into two groups as described in Appendix 2.

	Sand Barren	Rock Outcrop (small)	Rock Outcrop (large)	Sand Dune
2006				
Sand Barren	-	0.8339	0.5204	0.0018
Rock Outcrop (S)	-	-	0.7820	0.0219
Rock Outcrop (L)	-	-	-	0.1705
Sand Dune	-	-	-	-
2007				
Sand Barren	-	0.8589	0.3199	0.0040
Rock Outcrop (S)	-	-	0.6944	0.0183
Rock Outcrop (L)	-	-	-	0.1163
Sand Dune	-	-	-	-

Figure 5.1. Topographic relief map of the glaciated Great Lakes region of North America. The red line indicates the approximate boundary of the Great Lakes drainage basin divide. The dashed black line indicates the approximate maximum extent of the most recent, Wisconsinan glaciation. Map was modified from: Color North American Shaded Relief Map (USGS National Center for EROS, 2004).

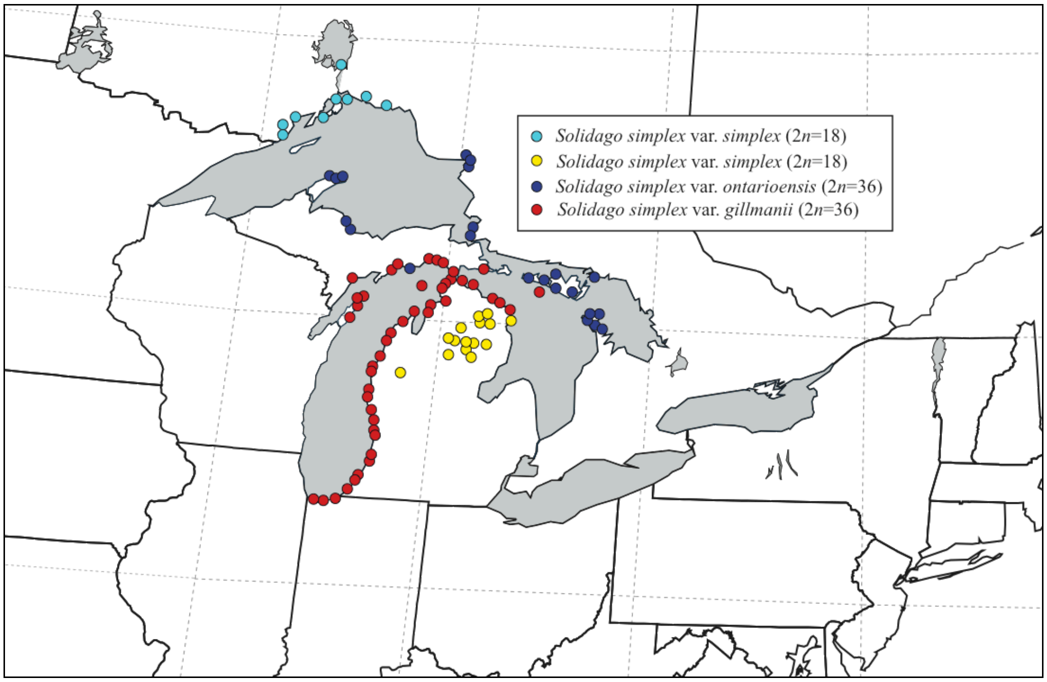


Figure 5.2. Distribution of *Solidago simplex* populations in the Great Lakes region of North America. Dots represent population localities based upon specimen data from the Michigan Flora and Wisflora databases; examination of herbarium specimens from GH, MICH, MO, MT, QFA, UMBS, and WAT; and distribution maps in Ringius (1986) and Semple et al (1999). Infraspecific taxon designations follow the Flora of North America treatment for *Solidago* (Semple and Cook 2006). Ploidy determinations follow the framework outlined in Chapter III. *Solidago simplex* var. *simplex* has been divided into two groups to highlight its disjunct distribution in the region. Some individual records are not shown on the map to avoid excessive overlapping of points.

Figure 5.3. Four characteristic habitats of *Solidago simplex* in the Great Lakes region: inland pine barren (upper left), dolomite/limestone shoreline (upper right), granite/basalt shoreline (lower left), and active coastal sand dune (lower right).

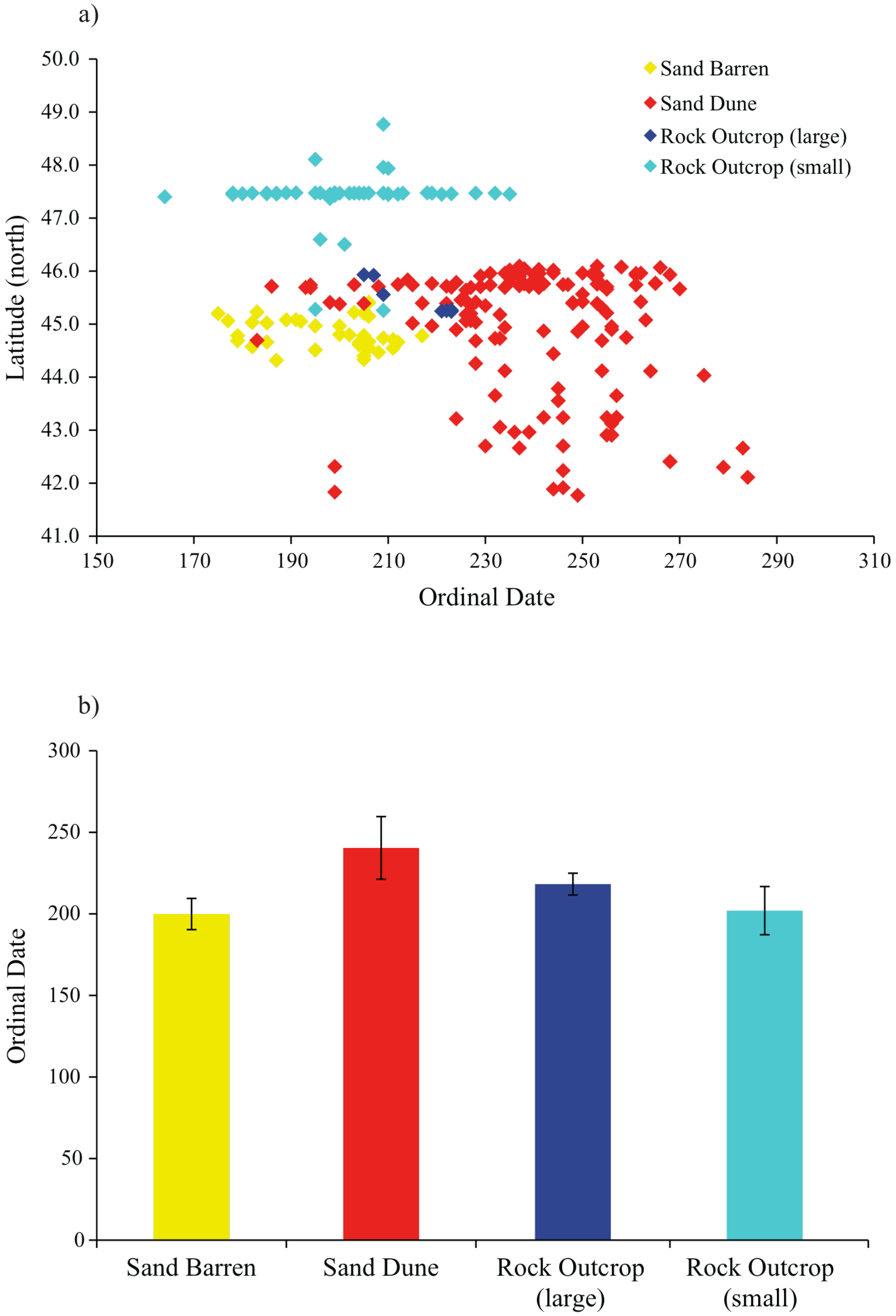


Figure 5.4. Collection date (as a proxy for flowering date) of *Solidago simplex* herbarium specimens from throughout the Great Lakes region. Individual collection date in relation to latitude (a). Mean collection date and standard deviation for groups (b). Plants were grouped by habitat with rock outcrop plants divided into two groups as described in Appendix 2. Collection date was converted to a standardized ordinal date.

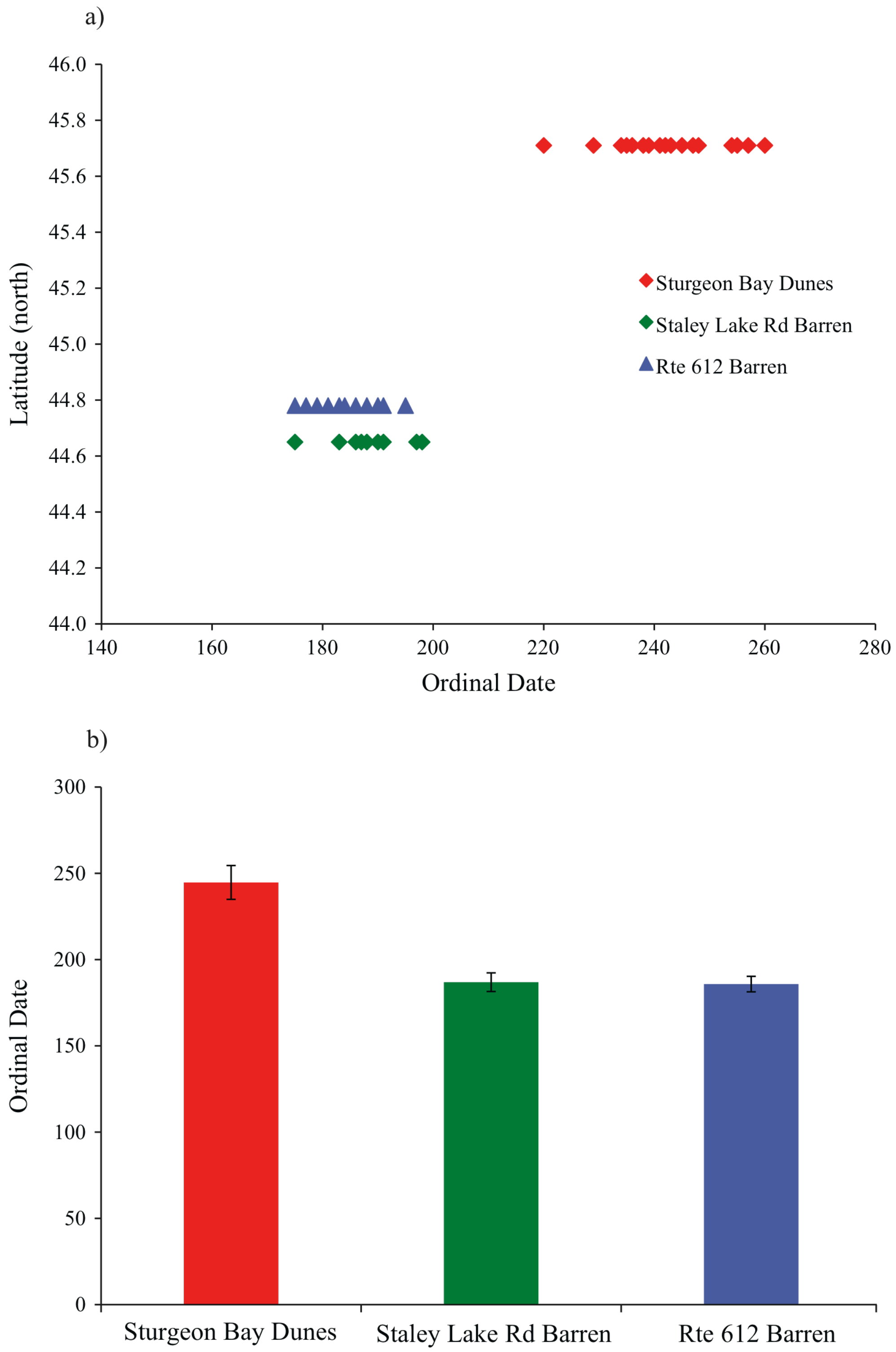


Figure 5.5. Median flowering date of three populations of *Solidago simplex* in the northern lower peninsula of Michigan in 2007: a) individual-level flowering and b) population-level flowering (by pooling all individuals within a population).

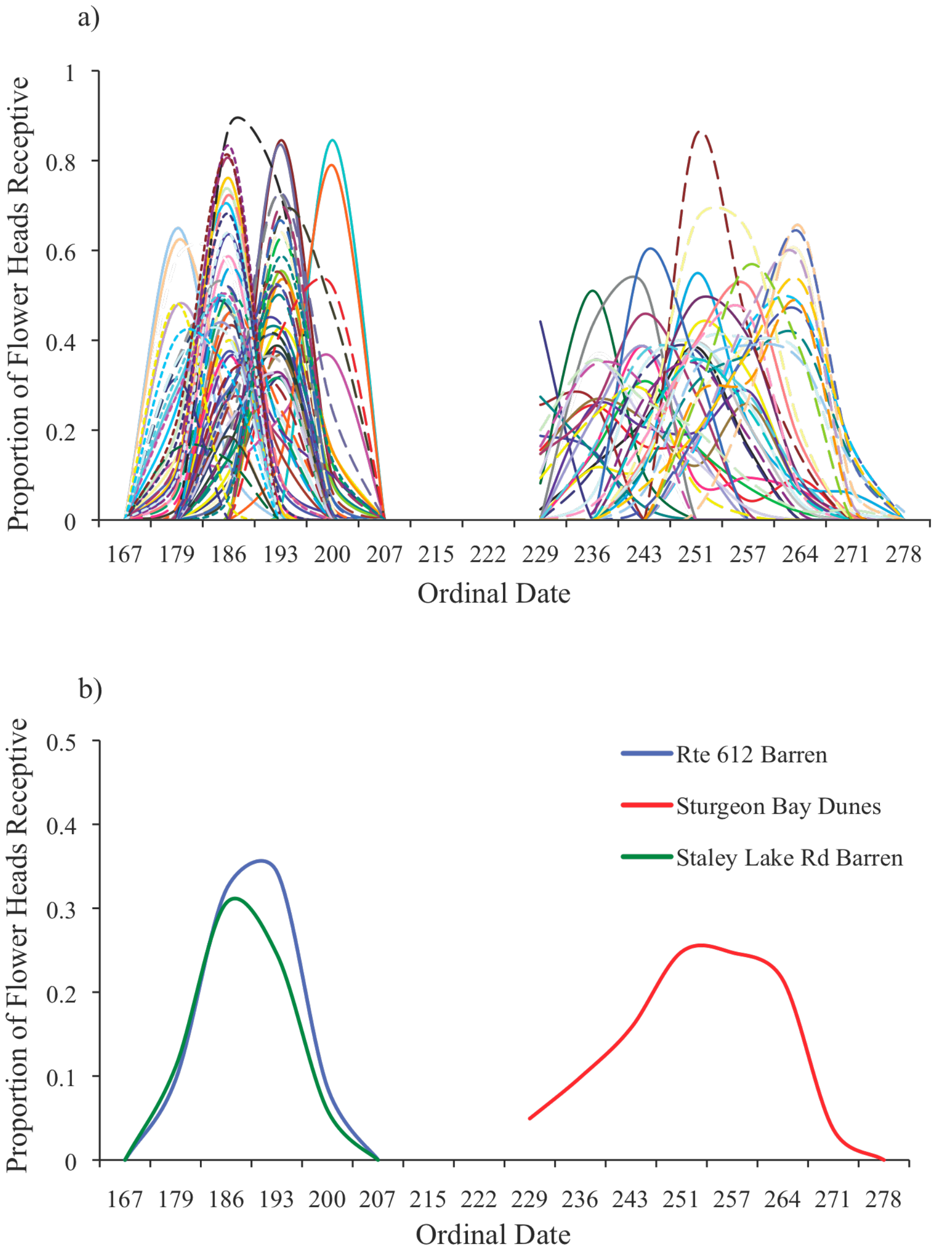


Figure 5.6. Flowering phenology curves of three populations of *Solidago simplex* in the northern lower peninsula of Michigan in 2007: a) individual-level flowering and b) population-level flowering (by pooling all individuals within a population).

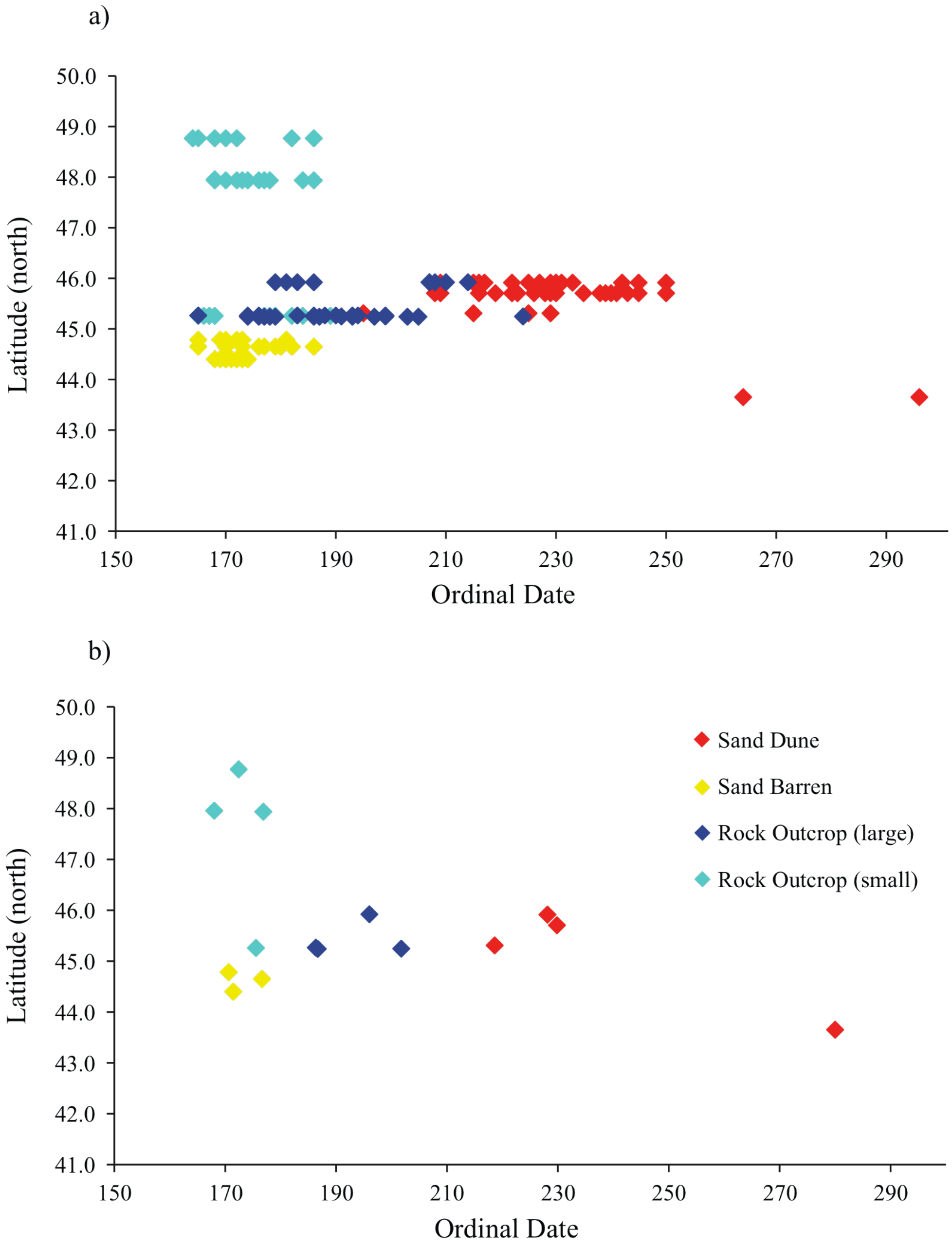


Figure 5.7. Median flowering date and population latitude for *Solidago simplex* plants grown in a common garden in 2006: a) individual-level flowering and b) mean population-level flowering. Groups are circumscribed by habitat with rock outcrop plants divided into two groups (as described in Appendix 2).

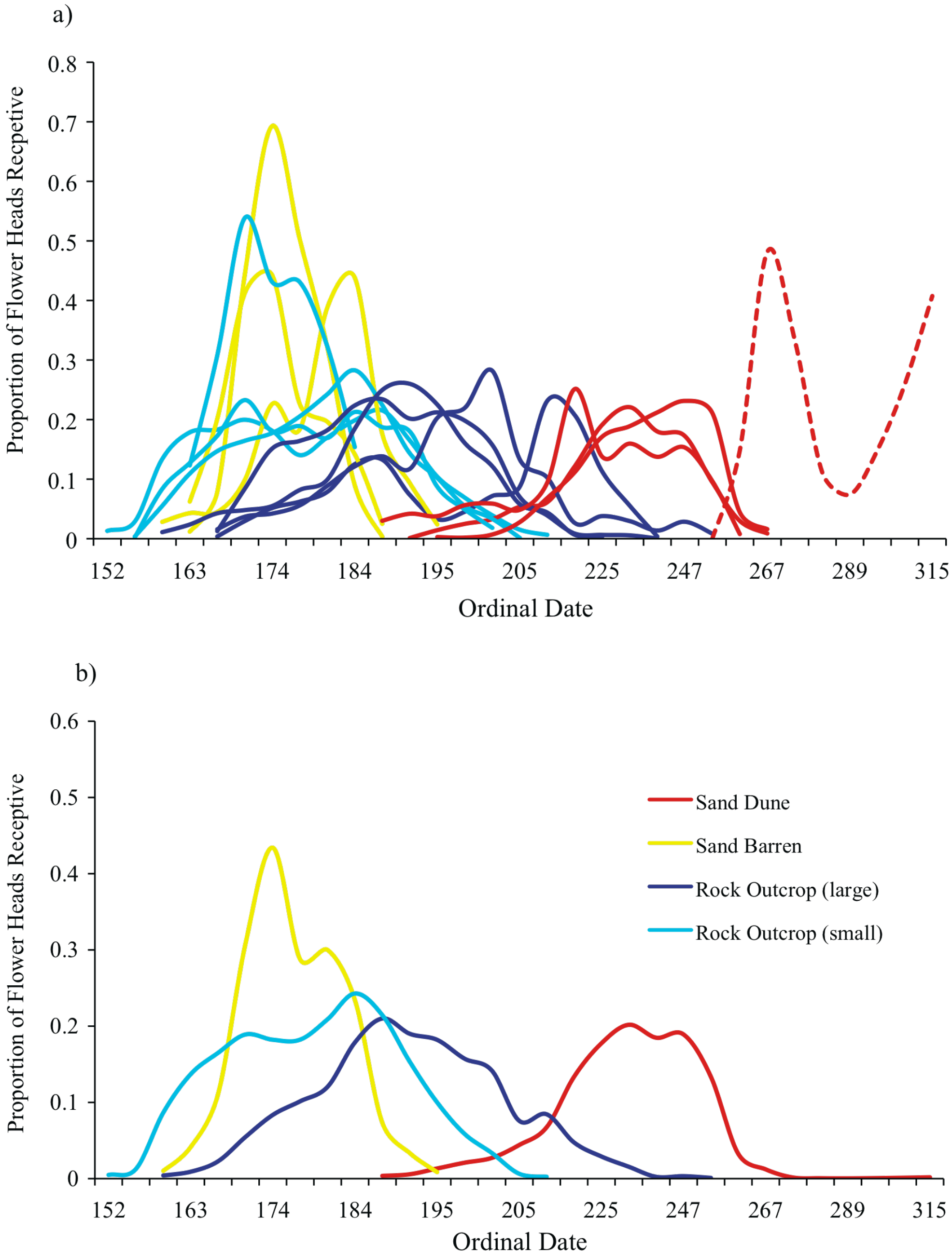


Figure 5.8. Flowering phenology curves of *Solidago simplex* plants grown in a common garden in 2006: a) population-level flowering and b) habitat-level flowering (by pooling populations from the same habitat type). Plants were grouped by habitat with rock outcrop plants divided into two groups (as described in Appendix 2).

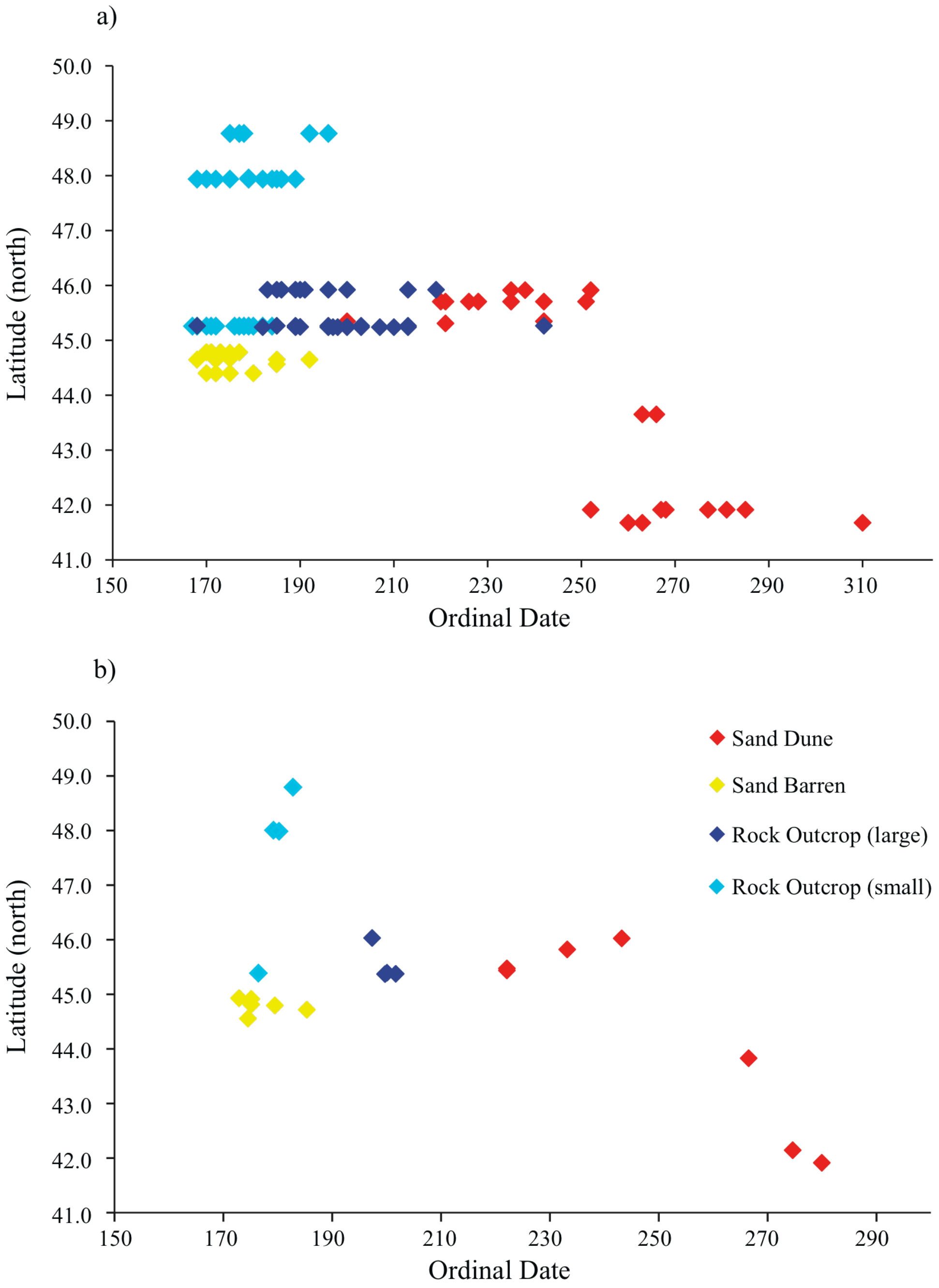


Figure 5.9. Median flowering date and population latitude for *Solidago simplex* plants grown in a common garden in 2007: a) individual-level flowering and b) mean population-level flowering. Plants were grouped by habitat with rock outcrop plants divided into two groups (as described in Appendix 2).

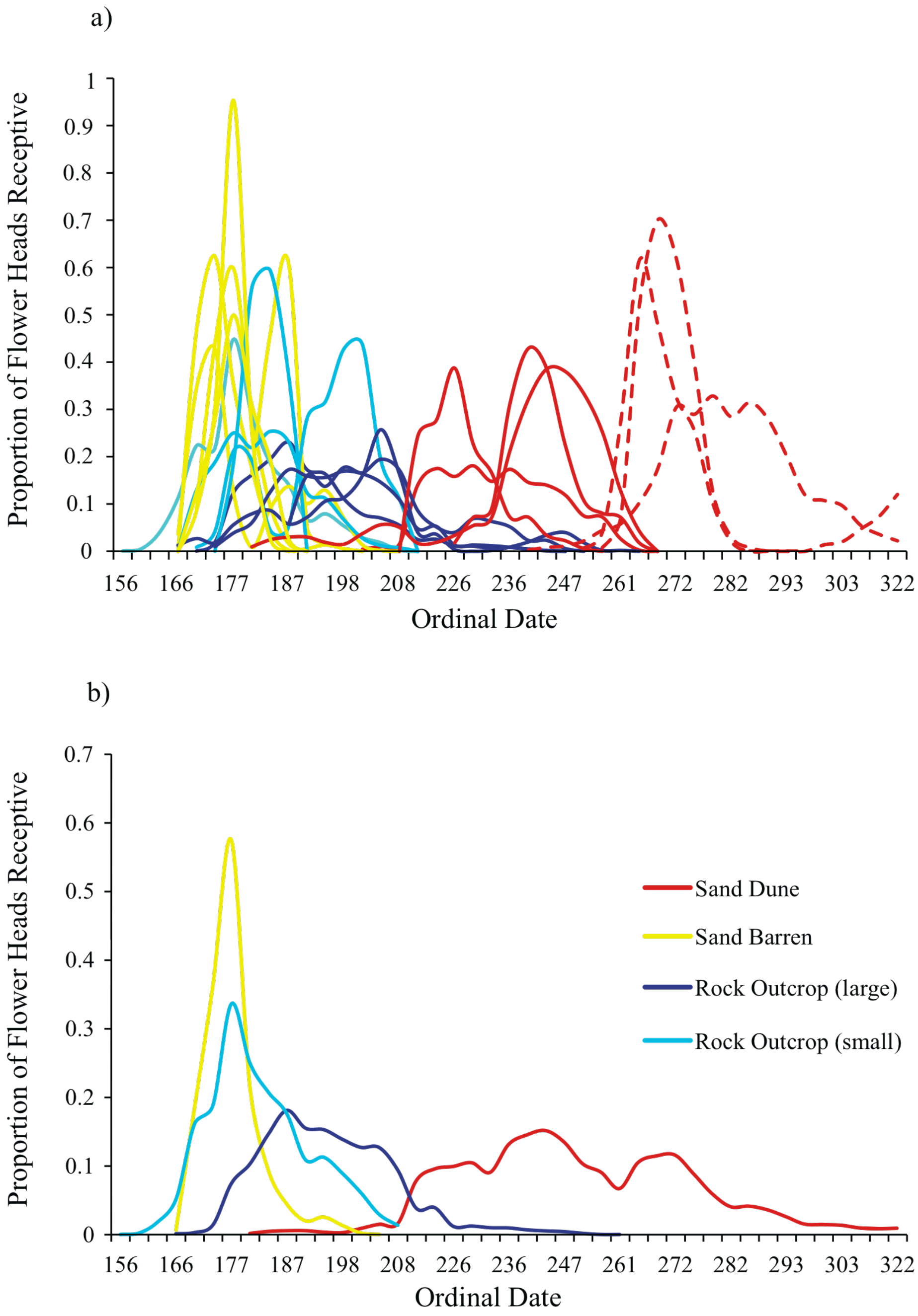


Figure 5.10. Flowering phenology curves of *Solidago simplex* plants grown in a common garden in 2007: a) population-level flowering and b) habitat-level flowering (by pooling populations from the same habitat type). Plants were grouped by habitat with rock outcrop plants divided into two groups (as described in Appendix 2).

APPENDIX 1

Three varieties of *Solidago simplex* have been attributed to the Great Lakes region (Ringius 1986; Voss 1996; Semple et al. 1999; Semple and Cook 2006). Examination of herbarium specimens, natural populations in the field, and plants grown in the common garden supported some of the previous circumscriptions but also suggested that there was additional population-level and habitat-level complexity in the region that had yet to be adequately addressed. This appendix provides a brief explanation of that complexity and the rationale for the four-taxon group circumscription used in the analysis of variance (ANOVA) and niche overlap calculations. It does not, however, serve as an exhaustive, monographic description of the ecological and morphological variation present in Great Lakes region populations of *S. simplex*. Additional field, garden, and morphometric studies are still needed to fully characterize this variation.

Sand Dune Plants. *Solidago simplex* var. *gillmanii* plants from active sand dunes along the shores of Lake Michigan and northern Lake Huron are ecologically and morphologically distinct from the other members of the species complex in the region and were treated as a separate group "sand dune" in all analyses. The group circumscription adopted for this study was consistent with treatments of *S. simplex* var. *gillmanii* by Ringius (1986) and Semple and Cook (2006). Voss (1996), however, included populations of sand dune adapted plants from the south shore of Lake Superior in a broadly defined *S. simplex* var. *gillmanii*. Those plants are not members of the *S. simplex* species complex and were not included in this study (their affinities are discussed in the text and elsewhere).

Sand Barren Plants. Inland populations of *S. simplex* in northern Michigan jack pine barrens are ecologically and morphologically distinct from other populations of *S. simplex* in the Great Lakes basin. These populations represent the only inland occurrences of *S. simplex* in the region and were treated as a separate group "sand barren" in all subsequent analyses. Ringius (1986) evidently saw only one specimen from these populations and suggested that it might represent an adventive individual of *S. simplex* var. *simplex* from western North America. Voss (1996) suggested that these populations might represent disjunct eastern extensions of *S. simplex* var. *simplex*. Flow cytometry data (discussed in Chapter III) confirmed that these populations were in fact diploid, which is consistent with their placement in *S. simplex* var. *simplex*. At the same time, however, these populations are morphologically distinct from (taller plants with smaller, more numerous capitula) and ca. 500 km south of diploid *S. simplex* var. *simplex* from northern Lake Superior rock outcrops. Their probable affinities to the other diploid populations in the Great Lakes region and to western North American populations are discussed in the text.

Rock Outcrop Plants. Previous treatments of *S. simplex* in the Great Lakes region have indicated that two varieties of the species, *S. simplex* var. *ontarioensis* and *S. simplex* var. *simplex*, inhabit shoreline rock outcrop communities. Observations of rock outcrop plants in the common garden in 2006 suggested that there were indeed two distinct groups of these plants present in the Great Lakes region. One group of populations was composed of plants that were consistently small in stature (ca. 30 cm tall or shorter) and began flowering very early. The other group of populations was composed of plants that were generally larger (ca. 35 cm tall or taller) and flowered later. These phenotypic groups corresponded reasonably well to habitat type. The smaller statured populations were almost entirely from granite/basalt outcrops along the northern and eastern shores of Lake Superior, except for one population from dolomite outcrops at the tip of the Bruce Peninsula (Big Tub Lighthouse). The populations of larger plants were all from dolomite outcrops of the Niagara Escarpment along the northern shores of Lakes Huron and Michigan.

To determine if these two groups of rock outcrop plants were morphologically distinct across multiple years in the common garden, two phenotypic characters, mean stem height and the mean number of capitula per stem, were recorded for each flowering plant at the time of peak anthesis in the common garden in 2007 and 2008. Mean stem height was statistically different between the two groups of plants in both 2007 and 2008 (Table 5A1.1). Visualization of both quantitative morphological measurements distinguished two largely exclusive clusters of rock outcrop plants in the common garden (Fig. 5A1.1). There was, however, phenotypic plasticity evident among the populations of large rock outcrop plants in the common garden. Plants from the Elgin Street population from Bruce Co., Ontario had been relatively large during 2006 (Peirson pers. obs.), but in 2007 many of the plants were considerably smaller. In 2008, plants from that population were again larger and clustered entirely with the other large rock outcrop plants. This type of phenotypic plasticity is not surprising in the large rock outcrop plants given that all rock outcrop plants were quite small (stunted) in the field, presumably due to stressful growing conditions in their rock outcrop habitats. When plants in the common garden are stressed (e.g., from heavy flowering in one year), it is conceivable that they would be smaller in stature the following year.

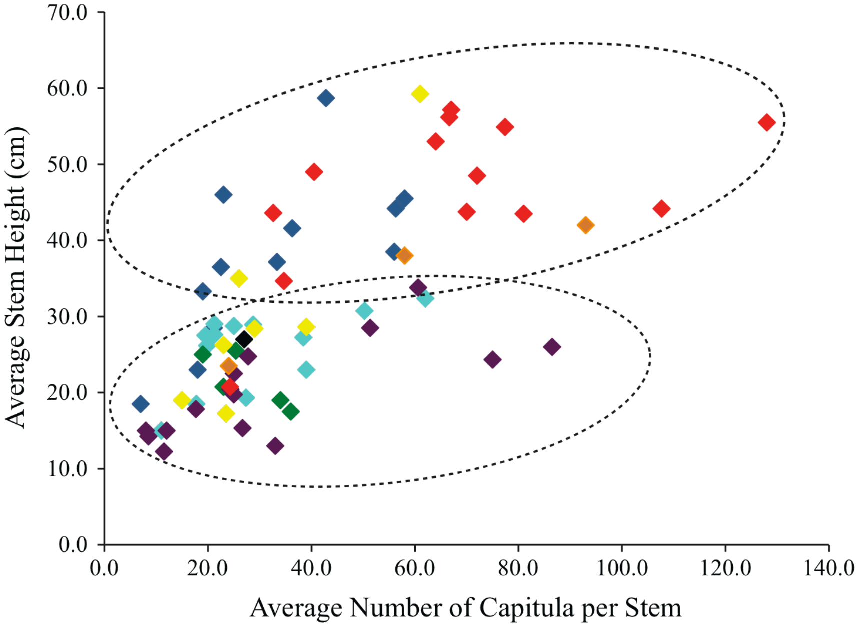
Based on the taxon descriptions in Ringius (1986) and Semple and Cook (2006), the two clusters of rock outcrop plants were initially interpreted as representing diploid *S. simplex* var. *simplex* (the populations of smaller plants) and tetraploid *S. simplex* var. *ontarioensis* (the populations of larger plants). Data from flow cytometry analyses (discussed in Chapter III), however, indicated that the two morphological groups did not correspond precisely to the previously described varieties. The populations of large plants from dolomite outcrops of the Niagara Escarpment were indeed found to be entirely tetraploid, which is cytologically consistent with their inclusion in *S. simplex* var. *ontarioensis*. The populations of small plants from both granite and dolomite rock shorelines, however, were also found to be largely tetraploid. The only exception was a diploid population from Terrace Bay on the north shore of Lake Superior.

Following traditional circumscriptions based on ploidy information, nearly all of the small tetraploid plants should be included in var. *ontarioensis*. Yet they have strong ecological, phenological, and phenotypic similarities to diploid *S. simplex* var. *simplex*. For subsequent phenological analyses, the rock outcrop populations were divided into two phenotypic groups, "small-plant" and "large-plant", instead of the traditionally recognized taxonomic varieties. In this way, the hypothesis that the two morphologic/phenotypic groups of rock outcrop plants were phenologically distinct could be more rigorously tested in all subsequent analyses.

Table 5A1.1. Samples sizes and flowering stem height statistics for rock outcrop plants of *Solidago simplex* grown in the common garden. Stem height was measured for each plant at peak anthesis.

	n	Mean Stem Height (cm)	S.D.	Min. Stem Height (cm)	Max. Stem Height (cm)	Sig.
2007						
Rock Outcrop (S)	35	22.6	5.9	12.5	33.8	< 0.001
Rock Outcrop (L)	35	39.2	12.5	17.3	59.3	< 0.001
2008						
Rock Outcrop (S)	19	19.9	4.0	12.6	26.7	= 0.002
Rock Outcrop (L)	25	46.3	13.1	22.7	74.7	= 0.002

a) 2007



b) 2008

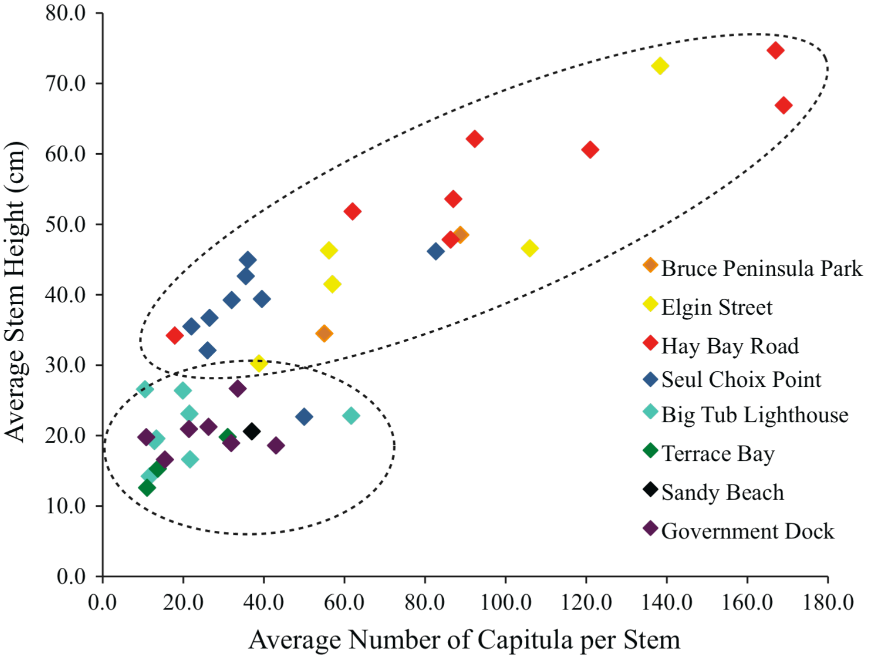


Figure 5A1.1. Scatter plot of two phenotypic characters measured on rock outcrop plants of *Solidago simplex* grown in the common garden. Each point represents a single individual. Stem height and number of capitula per stem were measured for each plant at peak anthesis in 2007 (a) and 2008 (b).

APPENDIX 2

This appendix provides additional niche overlap data and analyses that supplement the data already discussed in the text.

Population-level Differentiation. Pairwise population-level temporal niche overlap estimates for 2006 and 2007 common garden data are provided in Tables 5A2.1 and 5A2.2, respectively. Niche overlaps were estimated by calculating Pianka's Niche Overlap Index (Pianka 1973) with the program EcoSim (Gotelli and Entsminger 2009) following the methods described in the text. Pairwise population overlaps were consistent with habitat-level data discussed in the text, and indicated that there was substantial niche differentiation among a number of populations. Sand barren and rock outcrop (small) populations generally displayed high levels of overlap in both 2006 and 2007. Several populations that had extremely small sample sizes in 2007 (e.g., n = 1, n = 2), however, displayed very little overlap with other sand barren and rock outcrop (small) populations. This is most likely a sampling problem that does not indicate actual niche differentiation. As with the data presented in the text, rock outcrop (large-plant) populations showed moderate overlap with sand barren and rock outcrop (small-plant) populations in 2006 and 2007. In general, sand dune populations showed little to no overlap with sand barren and rock outcrop (small-plant) populations in 2006 and 2007, regardless of the latitude of the sand dune populations. The data indicate that there were moderate levels of temporal niche overlap between rock outcrop (large-plant) populations and northern sand dune populations. Southern sand dune populations (below 44° N latitude) showed almost no temporal niche overlap with any of the other populations.

Latitudinal Differentiation. Numerous studies have demonstrated that latitudinal gradients in climate and the length of the growing season can have pronounced effects on phenological patterns in many different taxa, including *Solidago* (e.g., Weber and Schmid 1998). The populations of *S. simplex* examined in the common garden spanned approximately 800 km of latitude, and visual inspection of the phenological data suggested that there was a general latitudinal trend in flowering phenology in the system. To make sure that pairwise niche differences were not simply an effect of latitude, the relationship between pairwise temporal niche overlap and pairwise latitudinal and geographic distance between populations was examined for 2006 and 2007 common garden data (Figs. 5A2.1, 5A2.2). Visual inspection suggested that there was no strong signal of "differentiation by distance" in the data. Additionally, linear regression indicated that the relationship between pairwise niche overlap and distance (either geographical or latitudinal) in both 2006 (latitudinal $R^2 = 0.000038$) and 2007 (latitudinal $R^2 = 0.04224$) data was weak. The slightly stronger signal in 2007 was likely driven by the flowering in that year of extreme southern populations of *S. simplex* var. *gillmanii* that are geographically distant from all other populations and flowered significantly later than all other populations. These data suggest that a general latitudinal gradient was not the major driver of pairwise temporal niche differentiation in the system (although they do not indicate that there is not a latitudinal trend in flowering phenology across the entire region).

Non-parametric Niche Overlap Estimates. A number of niche overlap indices, including Pianka's (1973) index, have been criticized for their assumptions that the niche breadth data being analyzed are either categorical in nature, or, if they are not, that they have an underlying normal distribution (see brief discussion in Mouillot et al. 2005).

Mouillot et al. (2005) proposed a new, non-parametric approach to calculating niche overlap that makes no assumptions concerning the distribution of the data and that better handles the variation of continuous measures of niche breadth (as opposed to categorical data). In their initial studies, Mouillot et al. (2005) found that traditional niche overlap indices generally overestimated the amount of pairwise niche overlap (as compared to their kernel-based method).

To compare the results of traditional niche overlap indices with those of the non-parametric method of Mouillot et al. (2005), pairwise niche overlap estimates for 2006 common garden data were estimated using a non-parametric kernel-based approach in the program R (R Team 2009). Overlaps are presented in Table 5A2.3. Comparison of the pairwise niche overlaps estimated in EcoSim and by the kernel-based approach indicated that the two niche overlap approaches obtained significantly different estimates of niche overlap (Fig. 5A2.3; Wilcoxon Signed Ranks Test on 105 paired comparisons, $p < 0.001$). The niche overlap estimates calculated from Pianka's Niche Overlap Index were generally higher than estimates obtained from the kernel-based approach (61 out of 105 pairwise estimates). The traditional method overestimated (in comparative terms) niche overlap when overlaps were moderate to high (above approximately 0.20). Alternatively, when niche overlap estimates were small (ca. 0.15 and below), traditional niche overlap estimates slightly underestimated the amount of niche overlap (ca. 36 out of 105 pairwise estimates).

These results indicate that if the kernel-based approach had been used for this study, that most populations of *S. simplex* would appear more temporally differentiated.

Table 5A2.1. Pairwise niche overlap for 2006 common garden data. Pianka's Niche Overlap Index was calculated using the program Ecosim (Gotelli and Entsminger 2009).

	R.B.	S.L.B.	612 B.	B.T.L.	T.B.O.	S.B.O.	G.D.O.	S.C.O.	B.O.	E.O.	H.B.O.	S.B.D.	M.D.	C.D.	S.L.D.
Roscommon Barren	-	0.65	0.94	0.63	0.70	0.92	0.68	0.27	0.22	0.28	0.50	0.00	0.00	0.00	0.00
Staley Lake Barren	-	-	0.67	0.78	0.82	0.67	0.91	0.48	0.43	0.62	0.75	0.00	0.00	0.03	0.00
Rte 612 Barren	-	-	-	0.74	0.80	0.97	0.74	0.28	0.24	0.32	0.50	0.00	0.00	0.00	0.00
Big Tub Lighthouse	-	-	-	-	0.98	0.75	0.95	0.47	0.55	0.76	0.79	0.02	0.01	0.10	0.00
Terrace Bay Outcrop	-	-	-	-	-	0.81	0.97	0.46	0.51	0.74	0.80	0.01	0.00	0.08	0.00
Sandy Beach Outcrop	-	-	-	-	-	-	0.76	0.27	0.24	0.32	0.50	0.00	0.00	0.00	0.00
Gov't Dock Outcrop	-	-	-	-	-	-	-	0.51	0.56	0.78	0.85	0.02	0.00	0.08	0.00
Seul Choix Outcrop	-	-	-					-	0.64	0.59	0.61	0.46	0.36	0.65	0.00
Bruce Outcrop	-	-	-	-	-	-	-	-	-	0.85	0.87	0.26	0.16	0.39	0.00
Elgin Outcrop	-	-	-	-	-	-	-	-	-	-	0.95	0.08	0.03	0.23	0.00
Hay Bay Outcrop	-	-	-	-	-	-	-	-	-	-	-	0.09	0.03	0.22	0.00
Sturgeon Bay Dunes	-	-	-	-	-	-	-	-	-	-	-	-	0.95	0.91	0.03
Manistique Dunes	-	-	-	-	-	-	-	-	-	-	-	-	-	0.86	0.04
Charlevoix Dunes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00
Silver Lake Dunes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 5A2.2. Pairwise niche overlap for 2007 common garden data. Pianka's Niche Overlap Index was calculated using the program Ecosim (Gotelli and Entsminger 2009).

	R.B.	S.L.B.	612B.	F.B.	K.B.	O.B.	B.T.L.	T.B.O.	S.B.O.	G.D.O.	S.C.O.	B.O.	E.O.	H.B.O.	M.D.	C.D.	S.B.D.	T.H.D.	S.L.D.	I.D.	W.D.
Roscommon Barren	-	0.62	0.82	0.16	0.94	0.97	0.89	0.31	0.46	0.74	0.18	0.00	0.22	0.17	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Staley Lake Barren	-	-	0.89	0.28	0.45	0.59	0.69	0.32	0.24	0.71	0.36	0.21	0.28	0.35	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Rte 612 Barren	-	-	-	0.07	0.68	0.78	0.77	0.20	0.24	0.65	0.10	0.01	0.17	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fletcher Rd Barren	-	-	-	-	0.07	0.29	0.42	0.16	0.83	0.69	0.63	0.13	0.28	0.53	0.00	0.00	0.00	0.05	0.00	0.00	0.00
Kalkaska Barren	-	-	-	-	-	0.92	0.84	0.31	0.35	0.64	0.11	0.00	0.19	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oscoda Barren	-	-	-	-	-	-	0.94	0.33	0.62	0.82	0.26	0.00	0.27	0.23	0.00	0.00	0.00	0.02	0.00	0.00	0.00
Big Tub Lighthouse	-	-	-	-	-	-	-	0.46	0.65	0.91	0.45	0.16	0.39	0.41	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Terrace Bay Outcrop	-	-	-	-	-	-	-	-	0.25	0.52	0.79	0.80	0.79	0.85	0.00	0.00	0.01	0.09	0.00	0.00	0.00
Sandy Beach Outcrop	-	-	-	-	-	-	-	-	-	0.79	0.57	0.05	0.33	0.44	0.00	0.00	0.00	0.04	0.00	0.00	0.00
Gov't Dock Outcrop	-	-	-	-	-	-	-	-	-	-	0.69	0.27	0.47	0.61	0.00	0.00	0.00	0.05	0.00	0.00	0.00
Seul Choix Outcrop	-	-	-	-	-	-	-	-	-	-	-	0.75	0.73	0.95	0.03	0.12	0.11	0.12	0.00	0.00	0.00
Bruce Outcrop	-	-	-	-	-	-	-	-	-	-	-	-	0.87	0.87	0.15	0.30	0.33	0.22	0.00	0.00	0.00
Elgin Outcrop	-	-	-	-	-	-	-	-	-	-	-	-	-	0.87	0.12	0.10	0.17	0.25	0.00	0.00	0.00
Hay Bay Outcrop	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.23	0.14	0.13	0.13	0.00	0.00	0.00
Manistique Dunes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.25	0.71	0.89	0.02	0.05	0.03
Charlevoix Dunes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.82	0.22	0.00	0.00	0.00

Sturgeon Bay Dunes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.68	0.01	0.03	0.02
Thompsons Harbor Dunes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.04	0.10	0.06
Silver Lake Dunes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.91	0.57
Indiana Dunes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.50
Warren Dunes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 5A2.3. Pairwise niche overlap for 2006 common garden data calculated using a kernel-based approach (following the methods described in Mouillot et al. 2005) implemented in the program R (R Team 2009).

	R.B.	S.L.B.	612 B.	B.T.L.	T.B.O.	S.B.O.	G.D.O.	S.C.O.	B.O.	E.O.	H.B.O.	S.B.D.	M.D.	C.D.	S.L.D.
Roscommon Barren	-	0.44	0.59	0.34	0.39	0.55	0.41	0.14	0.12	0.18	0.24	0.00	0.00	0.01	0.00
Staley Lake Barren	-	-	0.52	0.64	0.70	0.56	0.78	0.38	0.34	0.57	0.59	0.02	0.00	0.06	0.00
Rte 612 Barren	-	-	-	0.52	0.58	0.84	0.54	0.22	0.20	0.26	0.32	0.00	0.00	0.04	0.00
Big Tub Lighthouse	-	-	-	-	0.90	0.56	0.86	0.49	0.48	0.62	0.66	0.08	0.02	0.16	0.00
Terrace Bay Outcrop	-	-	-	-	-	0.63	0.90	0.46	0.45	0.58	0.65	0.05	0.01	0.13	0.00
Sandy Beach Outcrop	-	-	-	-	-	-	0.59	0.24	0.20	0.30	0.36	0.00	0.00	0.01	0.00
Gov't Dock Outcrop	-	-	-	-	-	-	-	0.48	0.45	0.62	0.69	0.06	0.01	0.15	0.00
Seul Choix Outcrop	-	-	-	-	-	-	-	-	0.67	0.58	0.58	0.40	0.31	0.57	0.00
Bruce Outcrop	-	-	-	-	-	-	-	-	-	0.76	0.75	0.25	0.17	0.36	0.01
Elgin Outcrop	-	-	-	-	-	-	-	-	-	-	0.86	0.14	0.07	0.24	0.00
Hay Bay Outcrop	-	-	-	-	-	-	-	-	-	-	-	0.14	0.07	0.25	0.00
Sturgeon Bay Dunes	-	-	-	-	-	-	-	-	-	-	-	-	0.85	0.81	0.09
Manistique Dunes	-	-	-	-	-	-	-	-	-	-	-	-	-	0.71	0.10
Charlevoix Dunes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.06
Silver Lake Dunes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

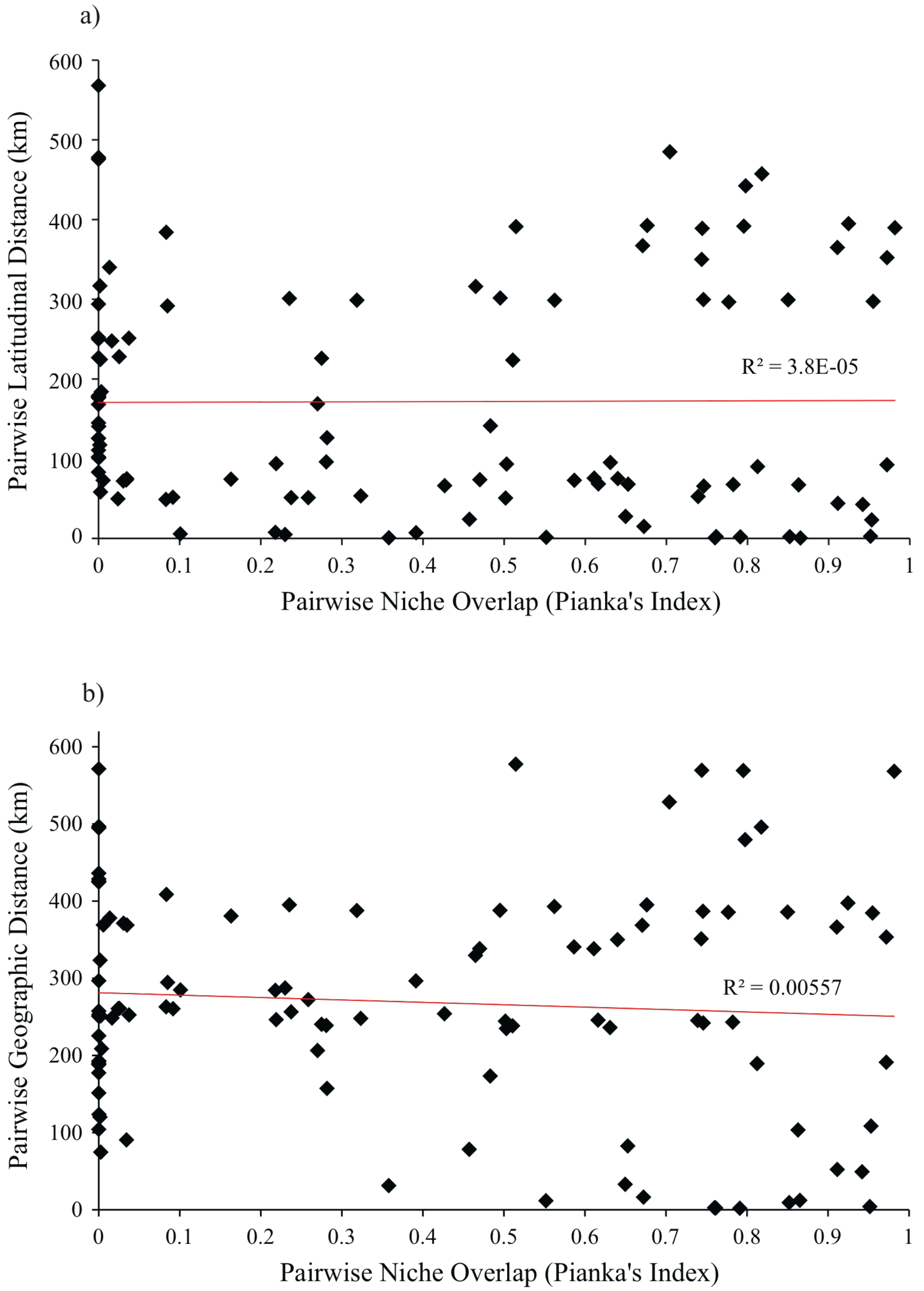
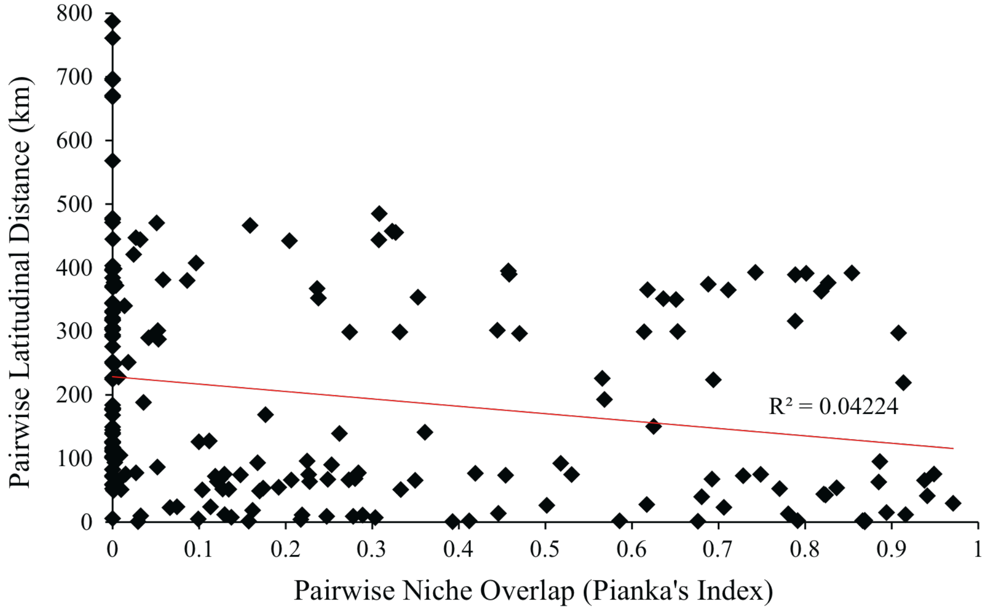


Figure 5A2.1. Correlation of pairwise latitudinal distance (a) and pairwise geographic distance (b) with pairwise population-level flowering overlap for *Solidago simplex* common garden data from 2006.

a)



b)

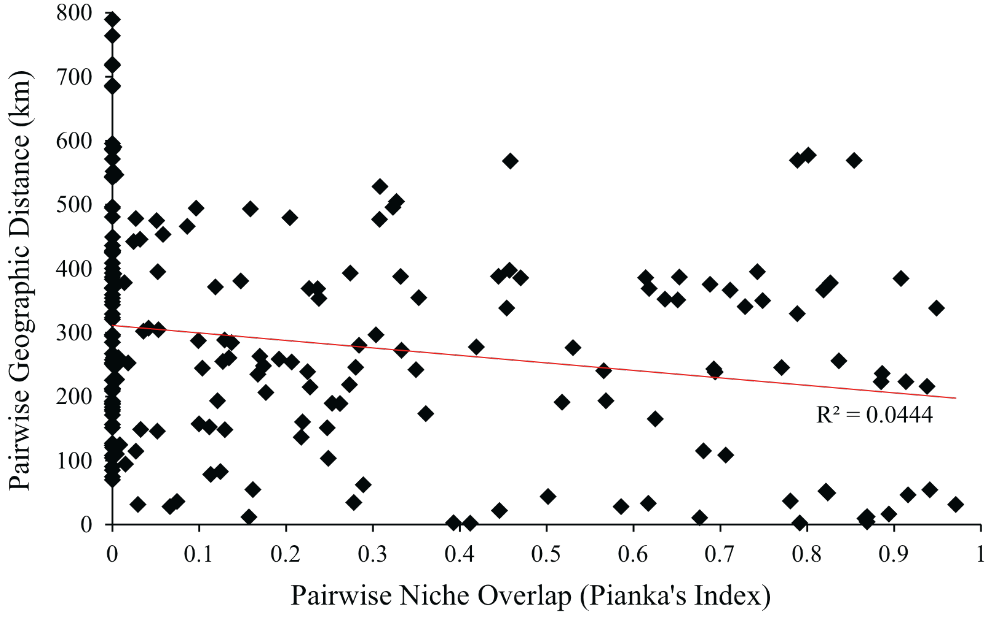


Figure 5A2.2. Correlation of pairwise latitudinal distance (a) and pairwise geographic distance (b) with pairwise population-level flowering overlap for *Solidago simplex* 2007 common garden data.

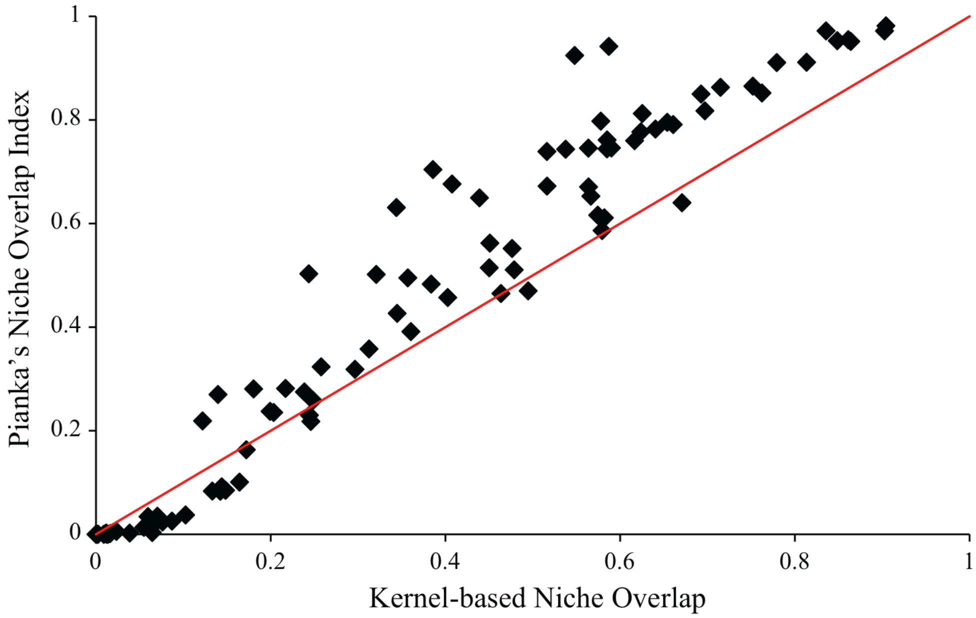


Figure 5A2.3. Comparison of Pianka's Niche Overlap Index calculated using the program EcoSim (Gotelli and Entsminger 2009) with a niche overlap estimate calculated using a kernel-based approach in the program R (R Team 2009) for 2006 common garden data. The red diagonal line represents equality between the two estimates.

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CHAPTER VI

CONCLUSION

Phylogeographic and paleoecological studies indicate that Pleistocene glacial cycles caused pronounced changes in species distributions and greatly altered the genetic structure within species-populations (Hewitt 1996, 2000). At present, however, the population histories of most North American plant species and the overall effects of glaciation on population distribution and divergence remain woefully understudied. This is especially true for northern temperate species, herbaceous plants, and species restricted to extreme habitats.

The major objective of my dissertation was to develop a framework that could be used to address hypotheses concerning the origins and evolution of floristic diversity in glaciated North America. Specifically I focused my dissertation research on the ecology and evolution of the endemic vascular flora of the glaciated Great Lakes region, and I used the *Solidago simplex* species complex (with one disjunct and two endemic varieties in the Great Lakes region) as a model system to address specific biogeographic and evolutionary hypotheses. Below I summarize the results of my four primary chapters.

Chapter II. Evolutionary and ecological biogeography of the endemic flora of the glaciated Great Lakes region. The Great Lakes basin lies entirely within the limits of Pleistocene glaciation. Continental ice sheets invaded the region at least six times during the Pleistocene, most recently during the Wisconsinan glaciation that ended roughly 15,000 YBP (Larson and Schaetzl 2001). Species returned to the region only after recession of the ice sheets. Thus in geological terms, the flora of the Great Lakes region is extremely young.

The presence of endemic plant species in this recently glaciated landscape raises a number of questions. Did these species evolve during the Pleistocene, migrate into the region following deglaciation, and subsequently become restricted to the region (i.e., are they relicts of previously more widespread taxa)? Or conversely did these species evolve *in situ* since the end of the last glacial period? What biogeographic and ecological factors have been important to their evolution and persistence within the region?

This review uncovered 60 endemic plant taxa that have been described from the Great Lakes region. Thirty-two of these taxa appear to be distinct entities and are characterized well enough that their geographic and habitat distributions in the region could be examined in detail. Analysis of this data revealed that nearly all of these endemics occurred in open, non-forested habitats in the northern part of the Great Lakes region, and 53% of the endemics were restricted to habitats along the shores of the Great Lakes. Considering that the Great Lakes region was largely forested (approximately 90-95% of the land surface) prior to European settlement, the endemic flora shows a marked affinity to regionally uncommon habitat types. These results suggest that adaptation of plants to different "extreme" habitats in the recently glaciated landscape has likely driven the evolution of edaphic endemism and ecological speciation.

Many of the described Great Lakes region endemics have not received wide recognition as distinct taxonomic entities. This is highlighted by the broad reviews of endemism by Gentry (1986) and Loehle (2006) discussed above. Loehle proposed that the evolution of endemic species takes a long time, and that many endemics described from glaciated regions are likely taxonomic artifacts. Recent studies from arctic regions, however, suggest that substantial amounts of biological species diversity at northern latitudes has previously gone unrecognized (reviewed in Brochmann and Brysting 2008). Additional studies of endemic plants in the Great Lakes region will be required to gain a better understanding of their evolution in this recently glaciated region.

Chapter III. Polyploidy, speciation, and infraspecific cytotype variation in goldenrods: the cytogeography of Solidago subsection Humiles. *Solidago simplex* has traditionally been divided into two subspecies that are defined exclusively along lines of infraspecific cytotype variation (Ringius 1986; Semple and Cook 2006). Both subspecies occur in the Great Lakes region, the only part of North America where they are regionally sympatric. In the 1980's, Gordon Ringius proposed that tetraploid populations of *S. simplex* in eastern North America (which he recognized as subsp. *randii*) had evolved from a single migration and subsequent polyploidization of diploid *S. simplex* from western North America sometime during the Wisconsinan glacial period (Ringius 1986; Ringius and Semple 1987). The recent discovery in the southeastern United States of three closely related species in *Solidago* subsect. *Humiles* (which were not considered in the earlier studies) raises doubts over the simplistic biogeographic hypotheses outlined by Ringius. In addition, the more widespread occurrence of presumably diploid populations in the northern Great Lakes region (occurrence first noted by Zimmerman 1956; distribution discussed by Voss 1996) suggests that the cytogeography of *S. simplex* in the Great Lakes region has not been adequately characterized.

Chromosome numbers and DNA ploidy determinations from 336 individuals, including 146 new reports, revealed significant geographic and taxonomic structuring of cytotypic variation within *Solidago* subsect. *Humiles*. Counts of *S. simplex* subsp. *simplex* and *S. spathulata* from western North America were diploid (2n = 18), except for a single tetraploid count from the Yukon. Patterns in eastern North America were more complex and included ploidy determinations of 2n = 18, 36, and 54. Although multiple cytotypes were found in eastern North America, there was significant geographic segregation and almost no within-population variation. Tetraploids occurred throughout the distribution in the east, while diploids occurred at the extremes of the range in the southeastern United States, northern Great Lakes region, and Gaspé Peninsula, Quebec.

The complex cytogeographic patterns recovered in *S.* subsect. *Humiles* cast doubt on the more simplistic scenario proposed by Ringius and Semple (1987) and suggest a longer history of allopatry and probable multiple origins of polyploids in the east. The patterns recovered and the paucity of within population variation, however, do not suggest widespread, repeated generation of polyploid individuals as in some other goldenrods (e.g., *S. altissima* and *S. nemoralis*). Examination of infraspecific cytotype variation in *S. simplex* (and in seven other species of *Solidago*) revealed that chromosomal races within a number of species, but not in all, appear to be behaving as distinct, reproductively isolated species. These results suggest that actual species diversity in *Solidago* is likely considerably higher than currently recognized taxonomically.

Chapter IV. Phylogeographic patterns in Solidago simplex in North America.

There have been few phylogeographic studies of widespread northern species, herbaceous species, and species restricted to extreme environments in North America. Our understanding of broad scale phylogeographic patterns in northern temperate parts of the continent is therefore incomplete. *Solidago simplex* has a widespread transcontinental distribution (with a significant west to east disjunction), and the species complex likely survived glaciation in multiple Pleistocene refugia. In this chapter, I conducted a phylogeographic study of *Solidago* subsect. *Humiles* across its North American range. This study examines biogeographic patterns and glacial history across the entire continent and provides an opportunity to uncover phylogeographic patterns that are likely different from those recovered from plant species that are restricted the southeastern United States.

Phylogeographic analyses suggested that 1) tetraploid varieties within *S. simplex* formed repeatedly from diploids, 2) the southeastern United States was not a primary source of postglacial migrants into the Great Lakes region, 3) the Beringian refugium was not a source of postglacial recolonization for the Great Lakes region, and 4) there is a significant biogeographic connection between the Great Lakes region and the northern Rocky Mountains.

These phylogeographic results differ from other studies in eastern North America that have identified major Pleistocene refugia in the southeastern United States. This work on *S. simplex* and several other recent studies, however, suggest that cryptic northern refugia were more important contributors to postglacial colonization than previously realized (e.g., Stewart and Lister 2001; McLachlan et al. 2005; King et al.

2009). Additional studies are needed to see common these emerging patterns actually are.

Chapter V. Disjunction, habitat specificity, and flowering phenology: the influences of geography and ecology on reproductive isolation and speciation in Great Lakes populations of Solidago simplex. My review in Chapter II uncovered 60 endemic plant taxa that have been described from the Great Lakes region. Thirty-two of these taxa appeared to be distinct entities and were characterized well enough that their geographic and habitat distributions in the region could be examined in detail. Analysis of this data revealed that nearly all of these endemics occurred in open, non-forested habitats in the northern part of the Great Lakes region, and 53% of the endemics were restricted to habitats along the shores of the Great Lakes.

These data suggest that adaptation of plants to different "extreme" habitats in the recently glaciated landscape has likely driven the evolution of edaphic endemism and ecological speciation. At the same time, however, many of the described Great Lakes region endemics have not received wide recognition as distinct taxonomic entities. In this chapter, I examined fine-scale patterns of ecological differentiation in the *Solidago simplex* species complex in the Great Lakes region to ask the question: Do the endemic taxa in the Great Lakes region represent distinct reproductively isolated species?

Cytological, ecogeographic, morphological, and phenological differences among Great Lakes populations of *S. simplex* suggest that the varieties of *S. simplex* in the region are actually three distinct, reproductively isolated species. Results from Chapters III and IV indicated that diploid *S. simplex* is a geographically distinct lineage; it is only sympatric with eastern members of *Solidago* subsect *Humiles* in the Great Lakes region.

Diploid populations there, however, are ecogeographically and temporally isolated from the tetraploid taxa. Diploid *S. simplex* s.l. thus meets the requirements of multiple species concepts and should be recognized as a species distinct from the eastern tetraploid *Solidago* subsp. *randii*. The sand dune endemic, *S. simplex* var. *gillmanii*, is ecologically distinct from other member of *Solidago* subsect. *Humiles* and possesses specific adaptations to its sand dune habitat. It is also temporally isolated from other *S. simplex* in the region. Therefore, it also meets the requirements of multiple species concepts and should be elevated to species status. The last species in the region is represented by two morphologically distinct forms of the rock outcrop endemic, *Solidago simplex* var. *ontarioensis*. Phylogeographic data and common garden studies suggest that the two forms of tetraploid rock outcrop plants likely had different origins, but as of yet it is not clear if they should be regarded as distinct species or be retained in a broadly defined *S. simplex* subsp. *randii*. Additional studies will be needed to test these hypotheses.

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