Serpentine Geoecology of Eastern North America: A Review

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ABSTRACT. Serpentine outcrops are model habitats for geoecological studies. While much attention has been paid to serpentine outcrops worldwide, the literature on eastern North American serpentine and associated biota is scant. This review examines the available literature, published and unpublished, on geoecological studies conducted on serpentine in eastern North America, from Newfoundland through Québec and New England south to Alabama. Most serpentine outcrops in the region have been mapped, but there have been few intensive mineralogical and pedological investigations. The limited soil analyses available suggest elevated levels of heavy metals such as Ni, near-neutral pH values, and Ca:Mg ratios <1, characteristic of serpentine soils worldwide. Botanical studies to date have largely focused on floristic surveys and the influence of fire exclusion and grazing on indigenous vegetation. To date, 750 taxa of vascular plants belonging to 92 families have been reported from serpentine outcrops in the region. Two taxa, *Agalinis acuta* and *Schwalbea americana*, are federally endangered in the United States while many others are listed as rare, endangered, or imperiled in one or more states or provinces. Globally, six species, *Adiantum viridimontanum*, *Minuartia marcescens*, *Pycnanthemum torrei*, *S. americana*, *Scirpus longii*, and *Symphyotrichum depauperatum* are listed as imperiled (G2) while one species, *A. acuta*, is listed as critically imperiled (G1). *Cerastium velutinum* var. *villosissimum* is the only recognized serpentine endemic plant for eastern North America while *A.viridimontanum*, *Aspidotis densa*, *M. marcescens*, and *S. depauperatum* are largely restricted to the substrate. Based on current distributions, we propose that *A.viridimontanum* and *M. marcescens* be considered endemic to serpentine substrates in eastern North America. Studies on cryptogams list 163 species of lichens and 146 species of bryophytes for the region. None of the species found appear to be restricted to the substrate. Compared to other regions of the world, ecophysiological and evolutionary investigations are scant. Biosystematic investigations are restricted to the taxa *Adiantum aleuticum*, *C. velutinum* var. *villosissimum*, and *S. depauperatum*. Plant-soil relations, especially the capacity to hyperaccumulate metals such as Ni and the ecological consequences of metal accumulation, are also under explored. One report from eastern Canada lists *Arenaria humifusa*, *M. marcescens*, *Packera paupercula*, and *Solidago hispida* as hyperacumulating Ni although the findings have yet to be confirmed by subsequent investigations. Overall, serpentine geoecology in eastern North America remains largely unexplored.

Key Words: Ca:Mg, edaphic endemism, geobotany, heavy metal-hyperaccumulation, nickel, rare plants, serpentine soil, serpentine endemism, ultramafic ecology

Within a given climatic regime, geology plays a central role in the distribution and ecology of plant species and their associated biota (Jenny 1941, 1980). The most significant causes of localized or unusual plant distributions are discontinuities in geology and edaphics—geoedaphics (Kruckeberg 1986). Extreme edaphic conditions as often seen on limestone (Lloyd and Mitchell 1973; Lousley 1950; Shimizu 1962, 1963), gypsum (Turner and Powell 1979), dolomite (Kruckeberg 2002; Lloyd and Mitchell 1973), granite (Ornduff 1986; Walters and Wyatt 1982; Wyatt and Fowler 1977), guano deposits (Gillham 1956; Ornduff 1965; Vasey 1985), vernal pools (Holland and Jain 1977, 1981), salt marshes (Flowers et al. 1986), and even mine tailings (Antonovics et al. 1971; Shaw 1990a), provide ideal settings for examining the role of the edaphic factor in the distribution and ecology of plants and their associated biota.

Serpentine outcrops have long provided model habitats for the study of geobotany worldwide (Brooks 1987; Kruckeberg 2002; Roberts and Proctor 1992). The word *serpentine* is applied in a general sense to describe soils rich in iron magnesium silicates derived from a range of ultramafic rocks (Coleman and Jove 1992; Wyllie 1979a). Serpentine more accurately refers to a group of hydrous magnesium phyllosilicate minerals, including antigorite, chrysotile and lizardite, in hydrothermally altered ultramafic rocks (Brooks 1987; Kruckeberg 1984). Nevertheless, researchers worldwide, us included, use the term *serpentine* loosely to describe rocks, soils, vegetation, and other biota associated with ultramafic outcrops.

Soils derived from serpentine outcrops provide harsh conditions for plant growth (Brady et al. 2005). These soils generally have a near-neutral pH, are high in metals such as Ni, Co, and Cr, and low in many essential nutrients such as P, K, and Mo (Kruckeberg 1984; Walker 2001). Although serpentine soils have often been considered to be poor in N (Kruckeberg 2002), this generally applies only to serpentine barrens with little or no vegetation (Alexander et al. 2007). Calcium:magnesium ratios are generally <1 which are unfavorable for plant growth (Bradshaw 2005; Brady et al. 2005; Skinner 2005). Although physical features of serpentine soils can vary considerably from site to site (Alexander et al. 2007) and within a site (Rajakaruna and Bohm 1999), serpentine outcrops are often found in open, steep landscapes with soils that are generally shallow and rocky with a reduced capacity for moisture retention (Kruckeberg 2002). See Alexander et al. (2007) for a broader and more balanced perspective on available-water capacity in serpentine soil across more diverse landscapes. Given the extreme nature of these soils, their biota is often uniquely adapted and frequently restricted to such habitats.

Serpentine outcrops worldwide are known to harbor high rates of endemic plant species with rates of endemism generally increasing toward the equator (Alexander et al. 2007; Brooks 1987; Kruckeberg 2002). Of the 1410 species endemic to California, 176 (12.5%) are restricted to serpentine (Hickman 1993). This is a remarkably high number given only 670 taxa are associated with serpentine soils in California, a substrate covering less than 1.5% of the state (Safford et al. 2005). Thus, it is no surprise that serpentine floras are well-studied in California and other parts of western North America (Alexander et al. 2007; Harrison and Viers 2007; Kruckeberg 1984, 1992; Safford et al. 2005), not only for their taxonomic value but also for their usefulness in testing ecological (Harrison, Davies, Safford, and Viers 2006; Harrison, Davies, Grace, Safford, and Viers 2006; Harrison, Safford, Grace, Viers, and Davies 2006; Safford and Harrison

2004) and evolutionary scenarios (Baldwin 2005; Bradshaw 2005; Patterson and Givnish 2004; Rajakaruna et al. 2003; Rajakaruna and Whitton 2004; Wright et al. 2006; Wright and Stanton 2007). The tropical islands of New Caledonia and Cuba also provide remarkable cases of serpentine endemism (Boyd et al. 2004; Brooks 1987; Kruckeberg 2002). In New Caledonia, 3178 taxa, approximately 50% of the native flora, are endemic to serpentine soils (Jaffré 1992). In Cuba, 920 species, approximately one-third of the taxa endemic to Cuba, have developed solely on serpentine soils (Borhidi 1992). Similar restrictions and notable floristic associations are also found in serpentine areas of the Mediterranean, Africa, Australia-New Zealand, and Asia (Baker et al. 1992; Balkwill 2001; Boyd et al. 2004; Brooks 1987; Chiarucci and Baker 2007; Jaffré et al. 1997).

Little attention has been paid to biota on serpentine outcrops in eastern North America despite its patchy occurrence along the Appalachian orogen, spreading south from Newfoundland and Quebec to New Brunswick, Maine, Vermont, New York, Pennsylvania, New Jersey, Delaware, Maryland, Virginia, North Carolina, South Carolina, Georgia, and Alabama (Figure 1a, b). Although these outcrops have attracted some attention, resulting in unpublished theses (Carter 1979; Sirois 1984), conference proceedings (Roberts 1992), book chapters (Brooks 1987; Sirois and Grandtner 1992; Tyndall and Hull 1999), and numerous papers in regional journals, no extensive review has appeared to date for the region. An account of the natural history of serpentine outcrops in eastern North America is found in a book by Dann (1988). Similarly, Reed (1986) provides an extensive treatment of the floras of the serpentine outcrops in eastern North America.

This review is the first attempt to highlight the geoecology of serpentine outcrops of eastern North America, focusing on all unpublished and published reports we have been able to locate from the early 1900s to present. It is our hope that this review will generate renewed interest in the under-explored serpentine outcrops of the region and lead to much-needed geobotanical and geoecological investigations and conservation efforts.

GEOLOGY AND SOILS OF SERPENTINE OUTCROPS OF EASTERN NORTH AMERICA

The sharply demarcated boundaries of vegetation commonly found with geologic boundaries between serpentine and other substrates are nothing less than striking (Figure 2). This remarkable biological phenomenon seen at a local geographic scale is controlled primarily by geology and is a fitting reminder that the "plant world exists by geologic consent" (Kruckeberg 2002, pg. ix).

Ultramafic rocks are chemically similar to the mantle of Earth (MacGregor 1979). The chemistry of the mantle is drastically different from that of the continental crust, the mantle being primarily composed of Mg-silicates whereas Ca is more abundant than Mg in the crust (Alexander et al. 2007). Relatively few plants are adapted to soils derived from rocks of the mantle (Brooks 1987), however, upon adaptation they often become specialized and restricted to such soils (Kruckeberg 1986; Rajakaruna and Whitton 2004; Rajakaruna and Boyd, in press). Most of the serpentine found in eastern North America originated in the formation of the ocean floor. Mantle rocks are produced along ocean ridges where partial melting in the upper mantle produces reservoirs of gabbro melt, or magma, that feed basalt lava flows from ocean ridges. As fresh melt is added, lava spreads from the ridges where it cools to form rocks (Wyllie 1979b). The succession of rocks produced from this melting and cooling, from bottom to top, is peridotite (modified mantle), gabbro, and basalt—a sequence called ophiolite. Most ophiolite is subducted, sinking back into the mantle, but some is incorporated into continental crust (Coleman and Jove 1992; Wyllie 1979b).

The ultramafic outcrops of eastern North America have an interesting history that spans millions of years (Roberts 1996; Williams and Hatcher 1982, 1983; Williams and Talkington 1977). The fragmentation of the super-continent Rhodina, formed during the Proterozoic Era over 0.5 Ga ago, left an ocean off the coast of a large continental mass from which North America would eventually emerge. Volcanic deposits, ophiolites, and sediments that accumulated in this ocean were pushed against the margin of the precursor of the North American continent several times during the Paleozoic Era, from about 500 to 250 Ma ago; each time some of the foreign materials were accreted onto the continent. Accreted peridotites have been altered to various degrees, with the most completely altered rocks becoming serpentinite, composed of the serpentine group of minerals (antigorite, chrysotile, and lizardite). Chemically, serpentinite is similar to peridotite (olivine and pyroxene minerals), except for the addition of water, which increases its volume by about one-third. Because serpentinite is so chemically similar to peridotite, most plants do not discriminate between soils derived from these two rocks.

Paleozoic accreted terranes were added to the North American continent as far inland as the Brevard Zone in the Blue Ridge Mountains of the southern Appalachians and to the Baie Verte-Brompton (BV-B) line in the northern Appalachians (Williams and

St. Julien 1982). Some foreign, or allochthonous, rocks (for example, the Hare Bay allochthon in Newfoundland) were pushed beyond the Brevard Zone and the BV-B line and deposited over rocks that had formed on the preaccretionary Proterozoic continent. The most well known of these is the Bay of Islands ophiolite in western Newfoundland. It is one of the most complete ophiolites exposed anywhere in the world (Coleman and Jove 1992). Ophiolites, with some ultramafic rocks in them, cover about 3% (318,000 ha) of Newfoundland's 106,000 km^2 (Roberts 1992), where they are more concentrated than in any other Appalachian area (Figure 1a). Besides in the ophiolites of western and northern Newfoundland and the Baltimore complex of the mid-Appalachian orogeny in Maryland and southeastern Pennsylvania, serpentine rocks are most concentrated along the BV-B line in the northern Appalachians, along the Brevard Zone from Alabama to North Carolina, and in the Albemarle-Nelson Soap-Stone Belt in Virginia, with small scattered serpentine exposures southeast of these lineaments and in the Blue Ridge Mountains. The ophiolite of Boil Mountain in western Maine (Caldwell 1998; Figure 1a) is a prominent exposure southeast of the BV-B line.

Unlike serpentine regions of western North America, serpentine areas of the northern Appalachian region south to Long Island were covered by ice during the Pleistocene glaciation (Dyke 2004). There may have been some unglaciated nunataks on Newfoundland and the Gaspé Peninsula. For some time after the Laurentide continental glacier had melted, icecaps persisted on Newfoundland and the Gaspé Peninsula. Ice cover slowly disappeared from the Gaspé Peninsula between 10 and 13.5 ka ago (Dyke 2004). As such, the length of exposure to the forces of weathering and soil formation for these outcrops is short in comparison to outcrops from unglaciated regions such as the Piedmont, south of the limit of glaciation in central New Jersey and eastern Pennsylvania.

Chemically, serpentine rocks differ from other rocks in having very high Mg and low Ca, K, and P levels. They have relatively high concentrations of elements 23 through 28 (V, Cr, Mn, Fe, Co, and Ni; Coles 1979). It is generally believed that the low ratio of exchangeable Ca:Mg found in soils derived from serpentine rock is the most limiting factor for plant growth, although high Ni levels in some serpentine soils may be toxic to many plants (Brady et al. 2005). Exchangeable Ca:Mg ratios are considerably >1 in most soils but are <1 (mostly <0.7) in serpentine soils and much lower in serpentine subsoils (Alexander et al. 2007; Brooks 1987).

The serpentine soils of the northern Appalachians are weakly developed, namely Entisols, Inceptisols, and Mollisols (Soil Survey Staff 1999), or Regosols, Brunisols, and Gleysols, respectively, in Canada (Roberts 1980, 1992; Sirois and Grandtner 1992). There are also several occurences of poorly drained serpentine organic soils in Canada termed Humisols (or Terric Cryosaprists in Soil Taxonomy; Soil Survey Staff 1999). Serpentine soils of the southern Appalachian orogen, beyond the limit of the Pleistocene glaciation, commonly have subsoil clay accumulations referred to as argillic horizons (Ogg and Smith 1993; Rabenhorst et al. 1982). These are Alfisols, or, where intensively leached, Ultisols. Physically the serpentine soils in the northern Appalachian region are similar to those of nonserpentine soils in the region, except that none of the serpentine soils have the bleached E horizons that form in Spodosols, which are more acid than the serpentine soils. Although many serpentine soils south of the continental glacial limit have argillic horizons, they are lacking in serpentine soils north of there.

Serpentine soils cover a considerable extent of eastern Canada. Approximately 318,000 ha of ophiolite is found in Newfoundland (Roberts 1992), including 7,700 ha with serpentine soils in the western part of the province (Roberts 1980). Québec's Mt. Albert region in the Gaspésie consists of at least 6,400 ha of ultramafics (Sirois et al. 1988; L. Sirois, pers. comm.) while the Eastern Townships have approximately 250,000 ha (Brooks 1987), contributing to the majority of the serpentine in the province. Estimates by E. B. Alexander from soil surveys in the Appalachian region of the United States suggest that there are approximately 6,900 ha in Pennsylvania, 23,600 ha in Maryland, and at least 243 ha of serpentine soils in North Carolina. Although New Brunswick, Maine, Vermont, New York, New Jersey, Delaware, Virginia, South Carolina, Georgia, and Alabama also have small but appreciable amounts of serpentine (Brooks 1987; Reed 1986; Tyndall and Hull 1999), the total for the eastern United States is probably on the order of 40,000 ha. In comparison, California has 600,000 ha of serpentine (Safford et al. 2005), although estimates by E. B. Alexander based on soil surveys point to about half this area for both California and southwestern Oregon.

Serpentine is clearly more extensive in accreted terranes along the western coast of North America, and the greater variety of climates found there has contributed to a greater variety of soils (Alexander et al. 2007). This wide range of soils derived from ultramafic rocks has led to a remarkable array of plant species endemic to this region (Alexander et al. 2007; Kruckeberg 1984, 2002). The range of serpentine soils in eastern North America, from very cold Entisols and Histosols to cold Inceptisols, cool Alfisols, and warm Ultisols, has similarly given rise to a unique flora and associated biota worthy of appreciation, study, and conservation. Table 1 compares the pH, exchangeable Ca:Mg ratio, and Ni concentration of serpentine soils from Jasper Ridge Biological Preserve, San Mateo County, California (Rajakaruna and Bohm 1999) with those reported from serpentine soils in Newfoundland (Roberts 1992), Maine (L. R. Briscoe et al. unpubl. data), New York (Parisio 1981), Maryland (Cumming and Kelly 2007), Pennsylvania (Miller and Cumming 2000), and Buck Creek, North Carolina (Mansberg and Wentworth 1984). While the geographically separated outcrops differ in their length of exposure to the forces of weathering and soil formation, the soils collected 0-10 or 15 cm from surface are surprisingly similar with respect to exchangeable Ca:Mg ratio (Table 1; all < 1, except in organic Histic epipedons in Newfoundland). Table 1 also shows that when compared to adjacent non-serpentine soils, the serpentine soils, regardless of geographical origin, have generally higher values of exchangeable Ni (8.5-116 $\mu g\ g^{-1}$ dry soil for serpentine vs 0.13-0.4 $\mu g\ g^{-1}$ dry soil for nonserpentine) and pH (6.2-6.74 for serpentine vs 4.2-5.25 for nonserpentine), and lower values of exchangeable Ca:Mg (0.025-0.56 for inorganic serpentine layers vs 1.55-4.34 for nonserpentine).

PLANT LIFE ON SERPENTINE OUTCROPS OF EASTERN NORTH AMERICA

Although few in comparison to other regions of the world, there are several descriptive and experimental studies highlighting aspects of the floristic associations and ecological relations of serpentine outcrops in eastern North America. These studies include floristic surveys of lichens, bryophytes, algae, microbes, and vascular plants; ecophysiological studies focusing on plant-heavy metal relations; evolutionary studies focusing on cross-kingdom interactions and the role of edaphics in plant speciation; ecological studies concentrating on plant adaptation; and applied ecological studies exploring avenues for the remediation of previously mined serpentine habitats and the implications of fire, grazing, and land-use practices on the maintenance of native vegetation.

STUDIES ON LICHENS, BRYOPHYTES, ALGAE, MICROBES

The intimate and often inseparable relationship between cryptogams such as lichens and their substrates suggests a strong possibility of substrate effects for such species associated with extreme geoedaphic habitats (Brodo 1974). Worldwide, however, there have been relatively few studies of lichens on serpentine soils (Favero-Longo et al. 2004), and only two published studies have examined lichens on serpentine soils in eastern North America (Harris et al. 2007; Sirois et al. 1988). Sirois et al. (1988) listed 202 lichen taxa associated with serpentine substrates on Mt. Albert, Gaspésian Provincial Park, Québec, Canada (Figure 1a); of these taxa, 36 were recorded for the first time in Québec; 16 were new to Canada, and 11 to North America. The 11 species listed for the first time from North America include *Belonia russula* (Physciaceae), *Buellia tergestina* (Physciaceae), *Cladonia stricta* var. *uliginosa* (Cladoniaceae), *Dactylospora urceolata* (Dactylosporaceae), *Endococcus propinquus* (Agyriaceae), *E. rugulosus* (Agryriaceae), *Lecidea plumbeoatra* (Agyriaceae), *Lithographa tesserata* (Agyriaceae), *Polyblastia melaspora* (Lecanoraceae), *Rinodina mniaraea* var. *mniaraeiza* (as *Rinodina mniaraeiza*; Lecanoraceae), and *Scoliciosporum umbrinum* var. *compacta* (Lecanoraceae). They concluded that the ecological influences of serpentine on the lichens were, in many aspects, similar to those observed on vascular plants in the region (Rune 1954), where many taxa are largely restricted to areas with serpentinized rocks. A recent study by Harris et al. (2007) explored the lichen flora of a serpentine outcrop from Deer Isle, Hancock County, Maine, USA (Figure 1a). Sixty-three species were found, comprising 35 genera. Two species, *Buellia ocellata* (Physciaceae) and *Cladonia symphycarpa* (Cladoniaceae), were new reports for New England. Twenty species, including one genus, *Lobaria* (Lobariaceae), were new reports for serpentine substrates worldwide (Favero-Longo et al. 2004). These studies suggest that there may be a serpentine substrate effect for lichens in eastern North America and that further study may reveal new species or interesting floristic associations even for outcrops that have only been exposed for less than 10,000 years since the retreat of the Pleistocene glaciers (Dyke 2004). Table 2 lists 163 lichen species recorded from serpentine outcrops in eastern North America as reported by Harris et al. (2007) and Sirois et al. (1988).

Little work has been undertaken for bryophytes growing on serpentine soils worldwide. The limited number of studies to date focus on British Columbia (Lewis et al. 2004), Québec (Belland 1987; Sirois 1984), and Newfoundland (Belland and Brassard 1988; Roberts 1992) in Canada; California (Sigal 1975), Maine (L.R. Briscoe et al. unpubl. data), and Maryland (Shaw and Albright 1990) in the United States, the British Isles (Bates 1978), Cuba (Marín et al. 2004; Pócs 1988), Japan (Takaki 1968), and Poland (Samecka-Cymerman and Kempers 1994; Samecka-Cymerman et al. 2002). Sirois (1984) lists 115 species of bryophytes for serpentine substrates on Mt. Albert. Robinson (1966) described the moss *Bryum reedii* (Bryaceae) as a new species first collected from serpentine in Maryland (Anderson et al. 1990). It was subsequently found by C. F. Reed on a granite outcrop in Delaware (J. Spence, National Park Service, pers. comm.). Briscoe et al. (unpubl. data) compared the bryophyte floras of a serpentine and a granite outcrop from Deer Isles, Hancock County, Maine, USA (Figure 1a) and examined tissue elemental concentrations for select species collected from both sites. Fifty-five species were found, 43 on serpentine and 26 on granite. Fourteen (25.5%) of these species were found at both sites. Out of the 43 species collected from serpentine soils 31 were previously reported to occur on such soils worldwide (L. R. Briscoe et al., unpubl. data). Of the 43 species collected from serpentine on Deer Isle, 12 were shared with the 115 species collected from serpentinized areas of Mt. Albert (Sirois 1984). The tissue of mosses collected from the serpentine site had higher Mg, Ni and Cr concentrations and lower Ca:Mg ratios than the tissue of those collected from the granite site. This trend is similar to that observed for vascular plants collected from serpentine soils worldwide (Brady et al. 2005; Brooks 1987). Table 3 lists 147 bryophyte species recorded from serpentine outcrops in eastern North America as reported by Belland and Brassard (1988), L. R. Briscoe et al. (unpubl. data), Roberts (1992), Robinson (1966), Shaw and Albright (1990), Shaw (1991), and Sirois (1984).

Unlike vascular plants, there are few records of serpentine endemism for cryptogamic species worldwide. Cryptogamic species appear to be broadly tolerant of substrate and show wide geographic distributions and range disjunctions that frequently span more than one continent (Schuster 1983). Thus, very few of these species are endemic to specific substrates, a pattern that has led some to argue that cryptogams such as bryophytes evolve more slowly or are genetically depauperate (Crum 1972) although recent molecular (Fernandez et al. 2006) and eco-physiological (Shaw 1990b) studies suggest otherwise. We were unable to locate examples of lichens endemic to serpentine soils; Favero-Longo et al. (2004) concluded that although several lichen species have been historically recorded as endemic to serpentine substrates, all such species have also been found on other non-mafic yet basic siliceous substrates. A similar scenario exists for bryophytes; of the 15 species of bryophytes listed as endemic to Cuba and occurring on serpentine, none are restricted to serpentine (Marín et al. 2004). One moss species, *Pseudoleskeella serpentinensis* (Leskeaceae), however, is thought to be endemic to serpentine in western North America (Shevock 2003). Given the high percentage of serpentine endemism among vascular plants, the low percentage among cryptogams is intriguing and is a topic worthy of investigation.

Only one study has examined algal diversity on serpentine soils in eastern North America. Terlizza and Karlander (1979) described algae from serpentine soils at Soldiers Delight, Maryland (Figure 1b). The algae were found to be of the phyllum Cyanophycota (as Cyanophyta; some of which fix nitrogen) and the divisions Chlorophyta and Chrysophyta. At these taxonomic levels, however, the soil algal composition was similar to that of non-serpentine soils. One study has also examined the microbe populations on an asbestos mine associated with a serpentine outcrop in southeastern Québec, Canada (Moore and Zimmermann 1977). Although the tailings were devoid of vegetation they supported significant microbe populations, although less than in normal agricultural soil. A 12-year old tailing was found to contain 7.4×10^4 aerobic, heterotrophic bacteria; 6.9×10^3 actinomycetes; and 3.4×10^2 fungi per gram of tailings.

STUDIES ON VASCULAR PLANTS: FLORISTICS

Table 4 lists 750 taxa of vascular plants belonging to 92 families documented from serpentine outcrops in eastern North America, noting those species listed as rare, endangered, or threatened in Canada or the United States and those with global protection status (Atlantic Canada Conservation Data Center 2007; Center for Plant Conservation 2007; Centre de données sur le patrimoine naturel du Québec 2007; NatureServe 2007; USDA, NRCS 2007). Serpentine outcrops of eastern North America harbor many taxa with localized distribution patterns, including many that are threatened in several states across the United States and imperiled in Newfoundland and Québec, Canada (Atlantic Canada Conservation Data Center 2007; Centre de données sur le patrimoine naturel du Québec 2007). Two taxa, *Agalinis acuta* and *Schwalbea americana* (Scrophulariaceae), found on serpentine outcrops in eastern North America (Hay et al. 1992; Tyndall and Hull 1999), are federally listed as endangered in the United States (Center for Plant Conservation 2007; NatureServe 2007). Globally, six species, *Adiantum viridimontanum* (Pteridaceae), *Minuartia marcescens* (Caryophyllaceae), *Pycnanthemum torrei* (Lamiaceae), *S. americana, Scirpus longii* (Cyperaceae), and *Symphyotrichum depauperatum* (Asteraceae) are listed as imperiled (G2) while *A. acuta* is listed as critically imperiled (G1). *Cerastium velutinum* var. *villosissimum* (as *C. arvense* var. *villosissimum*; Caryophyllaceae) is the only recognized serpentine endemic plant for eastern North America (Gustafson et al. 2003; Morton 2004) while *A. viridimontanum, Aspidotis densa* (Pteridaceae), *M. marcescens,* and *S. depauperatum* are largely restricted to the substrate (Brooks 1987; Roberts 1992; Tyndall and Hull 1999). *Symphyotrichum depauperatum*, once thought to be endemic to serpentine, was recently collected from mafic diabase glades in North Carolina (Gustafson and Latham 2005; Hart 1990; Levy and Wilbur 1990). Based on current distributions, we propose that *A. viridimontanum* and *M. marcescens* should be considered endemic to serpentine substrates from eastern

North America. *Aspidotis densa*, a strong serpentine indicator in western North America, appears to be restricted to serpentine outcrops in eastern North America (Kruckeberg 2002). While this taxon is abundant in western North America and is sometimes found off serpentine outcrops there, it appears to be endemic to the substrate in eastern North America. Even with the addition of these taxa, the number of serpentine-endemic species in eastern North America is in sharp contrast to the 176 species endemic to serpentine in California alone (Safford et al. 2005). Because many serpentinized areas in eastern North America were under ice during the last glaciation, limiting the extent of soil development and length of plant colonization (Roberts 1992), it is likely that the plants associated with these young soils have not had adequate time to diverge and specialize as on similar soils in non-glaciated, lower latitudes of the world.

Floristic surveys have been conducted on many of the prominent serpentine sites in eastern North America (Figure 1a, b), including the exhaustive surveys by Reed (1986) on many key serpentine sites across eastern North America. The serpentine barrens of Maryland are perhaps the best studied serpentine outcrops in the eastern United States (Tyndall 2005; Tyndall and Farr 1989, 1990; Tyndall and Hull 1999). Serpentine areas in Maryland, including the renowned Soldiers Delight site, host a number of rare species (Tyndall 1992a; Tyndall and Hull 1999): *Agalinis acuta*, *Carex hystericina* (Cyperaceae), *C. richardsonii* (Cyperaceae), *Desmodium obtusum* (as *D. rigidum*; Poaceae), *Dichanthelium oligosanthes* var. *oligosanthes* (as *Panicum oligosanthes*; Poaceae) *Gentiana andrewsii* (Gentianaceae), *Gentianopsis crinita* (Gentianaceae), *Linum sulcatum* (Linaceae), *Panicum flexile* (Poaceae), *P. torrei*, *Sporobolus heterolepis*

(Poaceae), *Symphyotrichum depauperatum* (as *Aster depauperatus*), and *Talinum teretifolium* (Portulaceae).

Serpentine areas of Delaware (Tyndall and Hull 1999), Georgia (Radford 1948), Maine (Carter 1979; N. Pope and N. Rajakaruna, unpubl. data), New York (Reed 1986), North Carolina (Mansberg and Wentworth 1984; Milton and Purdy 1988; Radford 1948), Pennsylvania (Latham 1993; Pennell 1910, 1912, 1930; Wherry 1963), and Vermont (Zika and Dann 1985) have also been exposed to restricted floristic explorations (see approximate locations of study sites in Figure 1a, b); however, much less is known about these floras than is known of the serpentine flora of Maryland.

Zika and Dann (1985) explored several serpentine outcrops in Vermont (Figure 1a) and found several rare and one possibly threatened plant species for the state. The rare species included *Adiantum pedatum* var. *aleuticum* (Pteridaceae), *Agrostis borealis* (Poaceae), *Asplenium trichomanes-ramosum* (as *A. viride*; Aspleniaceae), *Carex scirpoidea* (Cyperaceae), *Dryopteris fragrans* (Dryopteridaceae), *Empetrum nigrum* (Ericaceae), *M. marcescens* (as *Arenaria marcescens*), *Scirpus caespitosus* (Cyperaceae), *Thelypteris simulata* (Cyperaceae), *Vaccinium uliginosum* (Ericaceae), and *V. vitis-idaea* (Ericaceae). *Lycopodium selago* (Lycopodiaceae) was recommended to be listed as threatened in Vermont (Zika and Dann 1985). They also found this taxon on non-serpentine substrates in two small alpine zones where it was threatened by heavy foot traffic. It was listed as rare throughout New England by Crow et al. (1981). Similarly, Crow et al. (1981) suggested *A. pedatum* var. *aleuticum*, *A. trichomanes-ramosum* (as *A. viride*), *M. marcescens* (as *Arenaria marcescens*), and *Moehringia macrophylla* (as *Arenaria macrophylla*; Caryophyllaceae) be listed as threatened or endangered in New

England. Currently, the serpentine-associated species state listed as threatened in Vermont are *A. trichomanes-ramosum, M. marcescens*, and *A. viridimontanum* (Vermont Department of Fish and Wildlife 2005).

In a detailed floristic and phytogeographical analysis of several serpentine sites in Maine, Carter (1979) documented 250 taxa and concluded that although there was no overriding continuity in the composition of the serpentine flora in the state, the generally stunted vegetation reflected the presence of serpentine soils. The collection of *Oryzopsis asperifolia* (Poaceae) was a new record for Somerset County, while *A. trichomanes-ramosum* (as *A. viride*), also collected from Somerset County, had been recorded from only one other site in the state. *Adiantum pedatum* var. *aleuticum* from Franklin County was listed as a new record for the state. The two fern species are currently state listed as S1 (highly rare statewide) with a global rarity status of G4 and G5, respectively (Maine Natural Areas Program 2005). Recent studies on serpentine on Deer Isle, Maine (N. Pope and N. Rajakaruna unpubl. data) also suggest interesting floristic associations, with known serpentine species such as *A. trichomanes* and *A. aleuticum* restricted to the Island's serpentine substrates.

Adiantum aleuticum from the eastern North American serpentine sites has been exposed to rigorous biosystematic studies (Paris 1991; Paris and Windham 1988; Rugg 1922). The *A. aleuticum* complex includes *A. pedatum* subsp. *calderi* and *A. pedatum* var. *aleuticum* and is genetically divergent from the common eastern woodland maidenhair fern, *A. pedatum sensu stricto* (Paris 1991; Paris and Windham 1988). The allotetraploid derivative of *A. pedatum* and *A. aleuticum*, *A. viridimontanum*, is known only from a few serpentine outcrops in Vermont (Paris 1991) and is listed as threatened there (Vermont

Department of Fish and Wildlife 2005). The parental taxa are found on several serpentine outcrops in southeastern Canada and northeastern United States and are often considered rare where they are found (Carter 1979; Cody 1983; Paris 1991; Zika and Dann 1985).

Serpentine outcrops in eastern Canada have had a long history of botanical exploration (e.g., Fernald 1907, 1911, 1926, 1933). Outcrops in Québec (Bouchard et al. 1983; Legault and Blais 1968; Rune 1954; Sirois and Grandtner 1992) and Newfoundland (Bouchard et al. 1978, 1991; Damman 1965; Dearden 1977, 1979; Hay et al. 1992, 1994; Robertson and Roberts 1982) have been extensively botanized. As mentioned previously, *Aspidotis densa* (as *Cheilanthes siliquosa*) and *Minuartia marcescens* (as *Arenaria marcescens*), are listed as threatened in Québec (Développement durable, Environnement et Parcs Québec 2007). A recent report by the Canadian Legal Information Institute (2008) also lists *Polystichum scopulinum* (Dryopteridaceae), *Salix chlorolepis* (Salicaceae), and *Solidago simplex* subsp. *simplex* var. *chlorolepis* (Asteraceae), all associated with serpentine on Mount Albert in the Gaspésie, as threatened in Québec. Several other rare species have been documented on serpentine in eastern Canada including *Danthonia intermedia* (Poaceae), *Eleocharis nitida* (Cyperaceae), *Festuca altaica* (Poaceae), *Salix arctica*, and three species of Caryophyllaceae: *Minuartia biflora*, *Sagina caespitosa*, and *S. saginoides*, all fairly recent additions to the flora of Newfoundland (Hay et al. 1994). Given their occurrence in mostly high altitude serpentine sites, including Table Mountain and the White Hill Mountains (Newfoundland) and Mt. Silver and Mt. Albert (Québec; Figure 1a), these plants are prone not only to the typical physio-chemical stresses of serpentine soils but also to physical stresses such as drought, wind, snow, and cryoturbation (Roberts 1980, 1992).

ECOPHYSIOLOGICAL AND EVOLUTIONARY STUDIES

Serpentine habitats have long provided a model for ecophysiological and evolutionary studies (Brady et al. 2005; Roberts and Proctor 1992). While many long-term studies exist for other regions of the world, especially in California (Alexander et al. 2007; Kruckeberg 1984, 1992, 2002), few such rigorous studies have been conducted in eastern North America. The following is a summary of key studies focusing on ecological and evolutionary aspects of serpentine habitats, their plants, and associated biota in eastern North America.

Plant Heavy-Metal Relations. Heavy metal accumulation in plants is an intriguing phenomenon and much work has been conducted to determine its physiological and genetic basis (Pollard et al. 2002) as well as the adaptive significance (Boyd 2004, 2007) of this unusual physiological process. Heavy metal hyperaccumulation can be found in plants growing on a range of metalliferous soils (Brooks 1998), and the hyperaccumulation of heavy metals, notably Ni, is a phenomenon commonly found in vascular plants from serpentine soils (Reeves 2003). Hyperaccumulation is defined as the accumulation of over 0.1% of leaf dry weight in a metal (1000 $\mu g\ g^{-1}$ dry leaf tissue) for most metals, including Ni, although the level is over 1% for metals such as Zn and Mn. Only 320 Ni hyperaccumulators have been discovered world-wide, belonging to mostly the Brassicaceae and Euphorbiaceae (Reeves 2003). About two-thirds of the known Ni hyperaccumulators are found in the tropics, with the islands of New Caledonia and Cuba harboring the majority of such species. There are only two verified reports of Ni hyperaccumulators in the United States: *Thlaspi montanum* (Brassicaceae; Heath et al. 1997; Reeves et al. 1983) and *Streptanthus polygaloides* (Brassicaceae; Reeves et al. 1981), both restricted to western North America. *Thlaspi montanum* consists of three varieties (var. *montanum*, var. *siskiyouense*, and var. *californicum*) in western North America, all of which were found to hyperaccumulate Ni (Reeves et al. 1983). A third taxon, *Minuartia rubella* (as *Arenaria rubella*; Caryophyllaceae), has also been reported to hyperaccumulate Ni (Kruckeberg et al. 1993). Further investigation of this species from the original site, however, has cast doubt on the validity of the reported data (R. R. Reeves, pers. comm.). The only proposed hyperaccumulators of Ni from eastern North America—*Arenaria humifusa* (Caryophyllaceae), *Minuartia marcescens* (Caryophllaceae), *Packera paupercula* (as *Senecio pauperculus*; Asteraceae), and *Solidago hispida* (Asteraceae)—occur in Newfoundland (Roberts 1992). These reports have yet to be verified (R. R. Reeves, pers. comm.); however, the Asteraceae and Caryophyllaceae are families with known Ni hyperaccumulators elsewhere (Brooks 1998). Brooks (l987) lists these four species as the only proposed Ni hyperaccumulators to be found in previously-glaciated regions of the world.

Milton and Purdy (1988) sampled the foliage from several species of trees growing on serpentine soils in the Buck Creek and Webster-Addie districts in the Blue Ridge Mountains, North Carolina. White oak (*Quercus alba*; Fagaceae) leaves accumulated the most Ni, about 400 to 700 $\mu g\ g^{-1}$ dry leaf tissue from five sites at Buck Creek, but <200 $\mu g\ g^{-1}$ from sites at Webster-Addie. A recent study by L. R. Briscoe et al. (unpub. data) demonstrated higher levels of Ni in mosses collected from serpentine soil compared to those collected from nonserpentine soil. *Polytrichum juniperinum* and *P. piliferum* (Polytrichaceae), found on and off of serpentine soil, contained 26.3 and 129 μg g^{-1} Ni in dry leaf tissue, respectively, on serpentine, compared to < 1.5 and 3.69 μg g^{-1} Ni in dry leaf tissue, respectively, from nonserpentine soils. *Weissia controversa* (Pottiaceae), a species known to inhabit metal-contaminated sites worldwide (Porley and Hodgetts 2005; Shaw et al. 1987), accumulated the highest levels of Ni (363 μg g^{-1} Ni in dry leaf tissue) among all species sampled. Levels of metal accumulation have not been determined for the many serpentine taxa thus far listed for eastern North America (Tables 2, 3, 4). Intense study should be directed at taxa with known accumulators, especially in the families Asteraceae, Brassicaceae, and Caryophyllaceae known to harbor a disproportionately high number of species worldwide with the capacity to hyperacumulate Ni and other metals (Brooks 1998; Reeves 2003).

Cross Kingdom Interactions. Due to the harsh conditions ruling serpentine habitats, plants growing on serpentine and their associated biota—ranging from mutualistic organisms such as mycorrhizae, pollinators, and seed dispersers to antagonistic organisms such as pathogens and herbivores—show unique adaptations or biotic associations (Alexander et al. 2007; Kruckeberg 1984). Some animals are dependent on serpentine soils and their plants while many others spend at least some part of their lives on serpentine soils. Much of the work exploring serpentine plants and their cross-kingdom interactions has been conducted in western North America and other parts of the world (Boyd 2007). Notable studies include those on ants (Fisher 1997), butterflies (Gervais and Shapiro 1999; Harrison and Shapiro 1988), daddy long-leg spiders (Alexander et al. 2007), leaf beetles (Mesjasz-Przybylowicz and Przybylowicz 2001), and pocket gophers (Hobbs and Mooney 1995; Proctor and Whitten 1971).

In the only study of its kind from eastern North America, Wheeler (1988) found a beetle (*Diabrotica crista*; Chrysomelidae)—seldom found along the Atlantic coast but common farther west—to be abundant on the Goat Hill and Nottingham barrens and present at Soldiers Delight. The main host-plant for the larvae is big bluestem (*Andropogon gerardii*; Poaceae) in the Midwest and assumed to be little bluestem (*Schizachyrium scoparium*; Poaceae) on serpentine prairies and savannas of the Baltimore complex. Although much work has been done elsewhere on insects and arthropods associated with plants that grow on serpentine soils, including their potential for metal accumulation (Boyd 2007; Boyd, Davis, Wall, and Balkwill 2006; Boyd, Wall, and Jaffré 2006); this area is clearly under-explored in eastern North America.

Microbe-soil relations of serpentine outcrops have been investigated by several groups worldwide (Balkwill 2001; Boyd et al. 2004). A number of researchers have examined mycorrhizae on serpentine soils in California (Hopkins 1987; Moser et al. 2005) and found distinct differences in taxa found on serpentine soils. In eastern North America, Panaccione et al. (2001) found a lower diversity of ectomycorrhizal fungi on serpentine plots at Soldiers Delight than on nearby non-serpentine soil. They collected *Cenococcum geophilum* (Ascomycota) isolates from *Pinus virginiana* (Pinaceae) seedlings in both serpentine and non-serpentine soils and found that the *C. geophilum* isolates from serpentine sites were genetically more similar to each other than to isolates from both local and distant non-serpentine sites. A study conducted in Virginia by Sheets et al. (2000) showed that the diversity of basidiocarps, mycorrhizas, and mycorrhizal inocula was lower on serpentine soil than on non-serpentine soil. Castelli and Casper (2003) demonstrated both inter- and intra-specific arbuscular mycorrhizal (AM) fungal variation among the dominant grass species in a serpentine community in Pennsylvania. Gustafson and Casper (2004) examined the impact of nutrient addition on AM fungal performance and expression of plant/fungal community feedback in three serpentine grasses found on the Goat Hill and Nottingham serpentine barrens in Chester County, Pennsylvania. Their study suggested implications for decoupling of plant/fungal community feedback by anthropogenic nutrient enrichment. Serpentine grasslands often harbor plants with shallow root systems and brief life cycles and mycorrhizae appear to play an important role in plant nutrition and adaptation under such conditions (Hopkins 1987); improper management of such soils combined with atmospheric deposition of nutrients (Weiss 1999) may have unfavorable effects on plants and their microbe communities. Thiet and Boerner (2007) examined the role of soil ectomycorrhizal (ECM) fungal inoculum in the invasion of *P. virginiana* at Soldiers Delight in Maryland. They suggested that ECM fungi facilitate rapid pine colonization from bordering mature pine forests and current management practices should incorporate methods to kill or disrupt hyphal mats attached to mature pines to halt pine invasion to serpentine barrens. Cumming and Kelly (2007) investigated the effects of *P. virginiana* invasion at Soldiers Delight on soil properties, AM fungi, and native plant growth. They found drastic changes in soil pH (a drop from 6.2 to 4) and other changes in soil chemistry, AM fungal community structure, and plant growth, although varying in impact among serpentine grassland, savannah, and woodland habitats. This study has important implications for the management and restoration of serpentine habitats.

Plant Ecology. Serpentine outcrops have long provided natural laboratories for exploring ecological theory (Alexander et al. 2007; Harrison, Davies, Safford, and Viers 2006; Harrison, Davies, Grace, Safford, and Viers 2006; Harrison, Safford, Grace, Viers, and Davies 2006) and evolutionary processes (Kruckeberg 2002; Rajakaruna 2004). Such studies in eastern North America are limited in number and scope.

Dearden (1979) examined factors influencing plant community location and composition on serpentine bedrock in western Newfoundland. He identified six plant community types and concluded that species composition was significantly correlated with available Ca, an element generally low in serpentine soils, and topography. The community types showing the greatest similarity to adjacent non-serpentine soils were found on soils with highest available Ca, lowest available Mg, and lowest total Ni concentrations.

It was once commonly thought that the availability of soil water was the main factor limiting plant growth on the serpentine soils (Hughes et al. 2001; Proctor 1999). Hull and Wood (1984) examined plant water relations to determine if water availability was a limiting factor in the distribution of *Quercus* species on serpentine soils in Maryland. Although pre-dawn xylem water potentials were similar for the serpentine oaks (*Q. stellata*, *Q. marilandica*) and the non-serpentine oaks (*Q. alba*, *Q. velutina*) early in the growing season, by late summer they were higher for the serpentine species; however, the trend was not consistent for all species across the two substrates. Despite differences in their responses to water availability, they concluded that water alone is not responsible for the distributional pattern of these species in Maryland.

Wood (1984) investigated plant-soil relationships for several elements known to vary significantly in concentration between serpentine and non-serpentine soils. There were no differences in heavy metal or Ca concentrations in the plants and soils tested; however, Mg concentrations differed significantly, suggesting an important role for Mg, especially in the distribution of oak species found on serpentine (*Q. stellata* and *Q. marilandica*) and off serpentine (*Q. alba* and *Q. velutina*) in Maryland. The Ca:Mg ratio is now considered a major factor controlling plant growth and diversity on serpentine soils (Brady et al. 2005).

Hart (1980) examined the mechanisms by which serpentine-restricted taxa and their weedy congeners coexist on serpentine soils in southeastern Pennsylvania. He documented contrasting strategies for the congeneric pairs, with the weeds generally having higher potential growth rate, more mesic leaf structures, lower seedling mortality (on normal soils), lower Ca uptake, and earlier or more abundant seed production. He concluded that the most significant factors allowing weeds to persist on serpentine appear to be rapid growth when conditions are favorable and some reproduction early in the life cycle. The presence of early flowering times for several bodenvag species (Kruckeberg 1986) suggests that this is also true for certain weedy species on the serpentine outcrops on Deer Isle, Maine (N. Pope and N. Rajakaruna, unpubl. data). The serpentine-restricted congeners appear to allocate biomass not to rapid growth or early reproduction but to organs that enhance growth and survival during severe stress (Hart 1980). This study suggests that both weeds and their serpentine-restricted congeners can co-exist when both moisture and nutrient availability are found within a particular range; when moisture and nutrients are found in abundance weeds grow faster and when low, serpentine-restricted taxa are favored. A similar trend was observed for edaphic races of *Lasthenia californica* (Asteraceae) in California (Rajakaruna and Bohm 1999).

Arabas (2000) examined the spatial and temporal patterns of disturbance and vegetation change in the Nottingham Barrens of Pennsylvania over the past 150 years. The study points to the importance of fire in maintaining the serpentine savannah conditions that support many rare and endemic serpentine taxa. Less frequent fires allow the savannahs and open woodlands to convert to closed hardwood forests with immediate consequences on native plant diversity. Soil depth is also an important factor influencing rate and direction of succession; where soils are shallow, indigenous species have a competitive edge. This study, examining the inter-relationships among fire frequency, vegetation, and soil depth of a serpentine barren, has important implications for land management.

Fire clearly plays a critical role in maintaining the vegetation of serpentine habitats in fire-prone regions (Harrison et al. 2003; Safford and Harrison 2004) and improper management of these sites can have dire consequences on plants uniquely adapted to grow there (Tyndall 1994). Tyndall and Hull (1999) provided a useful summary of pre- and post-settlement land-use history for both Maryland and Pennsylvania showing how fire suppression and livestock grazing have drastically altered the floristic composition of the serpentine barrens since the mid-1900s. In a study exploring succession patterns following fire on a serpentine barren in Pennsylvania, Miller (1981) suggested that the post-fire flora and succession patterns on serpentine are distinct from those on nonserpentine and that the dominant species on serpentine are well-adapted to the occurrence of fires. In an exhaustive study of the role of fire on serpentine chaparral in California, Safford and Harrison (2004) reported that the effects of fire on less productive plant communities like serpentine chaparral may be longer lasting than the effects of fire on similar but more productive communities found off serpentine. All these studies point to the key role fires play in maintaining the diversity and ecology of serpentine habitats.

Only a handful of studies have examined the nature of ecotypic variation and divergence in response to serpentine soils in eastern North America despite many such studies elsewhere (Alexander et al. 2007; Brady et al. 2005). Ware and Pinion (1990) found little evidence of local adaptation to serpentine soils in serpentine populations of the bodenvag taxon, *Talinum teretifolium* (Portulaceae; Kruckeberg 1984), found on granite from Virginia to Georgia, on serpentine in the northern portion of its range in Maryland and Pennsylvania, and on sandstone on the western and southern extreme of its range. Serpentine plants performed similarly on all substrates, showing no evidence of local adaptation to serpentine soils, but developed chlorosis when grown on limestone soils. Despite slow growth, plants on serpentine soils remained healthy, persisting in the generally competition-free, shallow soils found there. Miller and Cumming (2000) examined the potential for ecotypic differentiation in *Pinus virginiana*, an invasive species on serpentine barrens. They tested the effects of exchangeable Ca:Mg and Ni on growth, foliar pigment concentrations, and nutrient status of seedlings from serpentine and nonserpentine soils in Pennsylvania. They found that seedlings from trees currently growing on serpentine were no different in their response to Ca:Mg and Ni than those from off serpentine. This study implies that no ecotypic differentiation has occurred in this species with respect to key serpentine soil factors.

Habitat Restoration and Management Studies. Serpentine outcrops have long been subjected to mining for the extraction of heavy metals such as Ni and Cr as well as minerals such as asbestos (Brooks 1998; Kruckeberg 1984, 2002). Moore and Zimmermann (1977) tested the revegetation potential of 23 species tolerant of asbestos tailings in Québec and found that the grasses (Poaceae) *Bromus inermis, Elymus junceus, Lolium perenne*, and *Poa pratensis* and the legumes (Fabaceae) *Medicago sativa*, *Melilotus alba*, and *Trifolium hybridum* could be successful at revegetating the site. The cost of revegetation and the availability of seed from local populations were cited as obstacles to the revegetation effort.

Long-term suppression of fire and changes in grazing patterns have led to the rapid spread of *Pinus virginiana* and *Juniperus virginiana* (Cupressaceae), both fire-intolerant conifers, as well as *Frangula alnus* (as *Rhamnus frangula*; Rhamnaceae), fast-replacing the native herbaceous plants restricted to the serpentine barrens of Maryland (Tyndall 1992a, b; Tyndall and Hull 1999). Native oaks, *Q. stellata* and *Q. marilandica*, are also affected by the fast-growing conifers, although *P. virginiana* succession appears to be inhibited to some extent by drought (Tyndall and Farr 1990). Barton and Wallenstein (1997) concluded that *P. virginiana* stands tend to increase soil depth (both mineral soil and litter depth), promoting suitable conditions for forests typical of non-serpentine sites in the region. Without immediate and proper management all remaining serpentine barrens in Maryland are at risk of developing into conifer forests, representing a loss of habitat for the rare species living there (Knox 1984; Tyndall 1992b, 1994, 2005).

CRITICAL INFORMATION GAPS AND FUTURE DIRECTIONS

Serpentine outcrops provide unique opportunities for ecologists to explore the critical role of geology on biota worldwide. While there appears to be a dearth of such studies in eastern North America relative to other parts of the world, our review points to a number of detailed studies examining the taxonomic and experimental aspects of biota on serpentine outcrops in the region. While the descriptive work has pointed to several interesting taxa, floristic associations, cross-kingdom interactions, possible impacts of soils on the divergence of species, and implications for management of these unique habitats, there is still much work needed to reveal the geoecology and best management practices of serpentine outcrops in the region. While we report geoecological studies from Newfoundland, Québec, Maine, Vermont, New York, Delaware, Virginia, North Carolina, and Georgia, we failed to locate any published literature on serpentine geoecology from New Brunswick, New Jersey, South Carolina, and Alabama. We identify several areas where further research would significantly enhance the knowledgebase for serpentine geoecology in eastern North America.

As is evident from the limited geographical knowledge, a more rigorous attempt at mapping the geologic extent of serpentine in eastern North America is greatly needed. Studies to characterize the mineralogy, pedology, and soil characteristics of serpentinized areas across eastern North America are also needed (R. G. Coleman, pers. comm.). While a few larger outcrops in Newfoundland (Dearden 1979; Roberts 1980, 1992), Québec (De

Kimpe et al. 1973; Laurent 1975), Maryland (Rabenhorst and Foss 1981), and Pennsylvania (Miller and Cumming 2000) have received some attention (Brooks 1987; Tyndall and Hull 1999), smaller outcrops in New Brunswick, Maine, Vermont, New York, New Jersey, Delaware, Virginia, North Carolina, South Carolina, Georgia, and Alabama have gone largely unnoticed. Studies to date have shown that the soil chemical features, especially concentrations of heavy metals such as Ni and nutrient ratios such as exchangeable Ca:Mg, are comparable to those found in serpentine soils from California (Table 1) and other regions of the world (Alexander et al. 2007; Brooks 1987). A better understanding of the soils, especially from the rhizosphere of plants, would reveal the nature of soil-related stressors as well as specific tissue-ion relations for plants found on serpentine in the region.

Additional surveys should be conducted on floristics, including detailed studies of vascular plants, non-vascular plants, and lichens. While several studies have addressed the diversity of serpentine-associated vascular plants of the region (Table 4), especially in Newfoundland, Québec, Maryland, Pennsylvania, and North Carolina, there are still many under-explored serpentine outcrops across eastern North America including in Maine, Vermont, New York, Delaware, and Virginia. We were unable to find any detailed floristic surveys for serpentine in New Jersey, Delaware, Virginia, North Carolina, South Carolina, Georgia, or Alabama other than those listed in Reed (1986). A better understanding of floristics can reveal taxa with site-associated variation, leading to experimental investigations on ecotypic or species-level divergence (Rajakaruna 2004). Currently, such biosystematic investigations exist for only three serpentine-associated taxa, *Adiantum aleuticum* (Paris and Windham 1988), *Cerastium arvense var. villosum*

(Gustafson et al. 2003), and *Symphytotrichum depauperatum* (Gustafson and Latham 2005), compared to a plethora of such investigations from California (Alexander et al. 2007; Rice and Espeland 2007). *Aspidotis densa*, which shows an intriguing disjunct distribution on serpentine between western and eastern North America (Kruckeberg 2002), and the two proposed narrow endemics, *Adiantum viridimontanum* and *Minuartia marcescens*, would be taxa worthy of investigation in this respect. To date only a handful of investigations have focused on lichens in Québec and Maine (Table 2) and bryophytes in Québec, Maine, and Maryland (Table 3). This information is lacking for Newfoundland, New Brunswick, Vermont, New Jersey, New York, Delaware, Virginia, North Carolina, South Carolina, Georgia, and Alabama.

Studies of plant-metal relations are lacking compared to studies of this nature in other regions where outcrops occur (Alexander et al. 2007; Reeves 2003). The discovery of only a handful of species with the potential to accumulate high levels of Ni (Roberts 1992) may result from under-study of soil-tissue relations for the region. Even the currently proposed Ni hyperaccumulators (Roberts 1992) have not been verified (R. R. Reeves, pers. comm.). Given that plant-available soil Ni levels in the region are comparable to levels found in areas such as California (Table 1), it is possible that additional taxa may be found with the capacity to accumulate this metal. Detailed studies of tissue analyses should be conducted in outcrops across the region as only two studies to date have examined aspects of heavy metal tolerance and accumulation, one in North Carolina (Milton and Purdy 1988) and the other in Maine (L. R. Briscoe et al. unpubl. data). Intense study could reveal additional taxa with the unusual capacity to hyperaccumulate Ni and other metals as well as reveal any unique relations plants may have with respect to other soil elements, particularly nutrients such as Ca and Mg. If such investigations do not reveal new hyperaccumulators or confirm the currently listed hyperacumulators (Roberts 1992), they may provide the basis to explore the intriguing question as to why there are so few hyperacumulators in North America and other temperate regions compared to tropical areas (Reeves 2003).

Studies of cross-kingdom interactions are lacking, especially those that examine herbivores and pathogens associated with serpentine plants (Boyd 2004). While many such studies exist for California and other tropical serpentine outcrops (Boyd 2007), the studies to date in eastern North America have focused on mycorrhizal associations on serpentine soil in only Maryland (Cumming and Kelly 2007; Panaccione et al. 2001; Thiet and Boerner 2007), Pennsylvania (Castelli and Casper 2003; Gustafson and Casper 2004), and Virginia (Sheets et al. 2000). Only one study from Pennsylvania and Maryland has examined a plant-insect association on serpentine in eastern North America (Wheeler 1988). Studies of cross-kingdom interactions do not exist for any of the other states or provinces. Investigations on the potential for metal transfer to higher trophic levels, key to examining how these metal-rich habitats could influence ecosystem health (Boyd, Davis, Wall, and Balkwill 2006; Boyd, Wall, and Jaffré 2006; Wall and Boyd 2002), do not exist for any state or province where serpentine occurs in eastern North America.

Ecological and evolutionary studies are also at a foundational level. Serpentine outcrops provide model habitats to test ecological and evolutionary theory, as clearly documented from detailed geoecological studies in other parts of the world (Alexander et al. 2007; Baker et al. 1992; Boyd et al. 2004; Brooks 1987; Harrison and Viers 2007).

There is much opportunity to conduct studies of the ecology, physiology, and evolution of particular taxa associated with serpentine soils including those that appear to be endemic or largely restricted to the substrate. Studies on the evolutionary ecology of such taxa could reveal the nature of serpentine tolerance, direction and strength of selection imposed by serpentine factors, and factors and mechanisms responsible for divergence. Finally, studies focusing on soil remediation and site restoration are minimal. Although Ni mining has been considered largely economically unattractive in the eastern United States, extensive prospecting of Ni and other heavy metals has occurred in Virginia, North Carolina, Georgia, and Alabama (Worthington 1964) and other parts of eastern North America (Cannon 1971; Wickland 1990). Serpentine outcrops that have undergone mining operations, such as those found in eastern Canada (Moore and Zimmermann 1977), can provide model habitats to investigate the potential for phytoremediation and phytomining using metal accumulating serpentine plants. Both of these practices are quickly gaining recognition as environmentally friendly, low-cost technologies for the remediation of metal-contaminated sites worldwide (Angle and Linacre 2005; Boominathan et al. 2004; Brooks 1998; Pilon-Smits 2005). Plants associated with serpentine soils are not merely biological novelties suited for taxonomic, ecological, physiological, and evolutionary investigations; they also hold great potential as tools for the restoration of metal-contaminated sites around the world (Whiting et al. 2004). While eastern North American serpentine outcrops provide a wealth of opportunities for geoecological investigations, ever-expanding agriculture, forestry, and mining activity, fire suppression, and urbanization have drastically affected the biota of many eastern North American serpentinized areas. This is especially of concern as six of the serpentine taxa found in the region are globally imperiled (G2) and one taxon is listed as globally critically imperiled (G1). Recent years have seen the declaration of several preserves worldwide, set aside for their unique edaphic habitats and associated biota. Although spotty in their distribution and inadequate in number on a global scale, several preserves in the states of California, Oregon, and Washington, and in Cuba, Italy, New Caledonia, New Zealand, South Africa, and Sri Lanka have led the way in raising awareness of the immediate need for the conservation of these unique biotas (Kruckeberg 2002, 2004; Rajakaruna and Bohm 2002). There are several preserves in eastern North America, including the well-known Mt. Albert, Gaspésian Provincial Park, Québec, Canada (Kruckeberg 2004); Table Mountain, Gros Morne National Park, Newfoundland, Canada (Belland and Brassard 1988; Bouchard et al. 1986; Roberts 1992); State-Line Serpentine Barrens in Pennsylvania (Nature Conservancy 2007); Soldiers Delight Natural Environment Area in Maryland (Flanagan-Brown 2001; Soldiers Delight Conservation, Inc. 2007); and Pine Hill Preserve, Deer Isle, Maine (Harris et al. 2007) set aside to preserve the unique biota associated with such sites. Preservation of such sites will assist in the conservation of rare and/or physiologically distinct species and provide avenues for much-needed long-term studies as well as opportunities to educate the general public of the role extreme geologic settings play in maintaining and generating biotic diversity. It is our hope that this review will generate renewed interest in serpentine geoecology as a fruitful field with much promise for future research in eastern North America.

ACKNOWLEDGMENTS. The authors thank Nathaniel Pope and two anonymous reviewers for commenting on the manuscript; Jose Perez-Orozco, Josephine Rassat, Leslie Heimer, Madeline Helser, and Kathleen Tompkins for assistance in the literature review and preparation of tables; Apoorv Gehlot, Jose Perez-Orozco and Gordon Longsworth for assistance in preparing the figures; and College of the Atlantic, Maine Space Grant Consortium, and Maine Sea Grant for funding provided to NR and TBH during the process of writing this paper.

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Table 1. Soil surface chemical analyses for serpentine soil samples (S) collected from Jasper Ridge, CA (Rajakaruna and Bohm 1999); Soldier's Delight, MD (Cumming and Kelly 2007); Newfoundland, Canada (Roberts 1992); Deer Isles, ME (L. R. Briscoe et al. unpubl. data); Conowingo Barrens, PA (Miller and Cumming 2000); Staten Island, NY (Parisio 1981); and Buck Creek, NC (Mansberg and Wentworth 1984) along with values for adjacent nonserpentine soils samples (NS). Some of the Newfoundland soils have surface organic layers > 20 cm thick (Histic epipedons); these are listed separately from soils lacking thick surface organic layers (inorganic epipedons). Nickel was extracted by several different methods [DPTA, exchangeable (neutral ammonium acetate), Mehlich-3, and total dissolution with concentrated acids], some of which are not comparable. Values listed are means ± standard errors.

Site	pH (soil water)	Exchangeable Ca:Mg	Ni µg g^{-1}
Jasper Ridge, CA (S) (n=123)	6.74 ± 0.03	0.21 ± 0.01	116.45 ± 3.95 DPTA
Soldier's Delight, MD (S) (n=3)	6.2 ± 0.1	0.56 ± 0.12	66.1 ± 6.6 Mehlich-3
Newfoundland, Canada (S) (organic layer, n=5)	6.1 ± 0.6	1.39 ± 0.69	21.9 ± 8.1 exchangeable 842± 294 total
Newfoundland, Canada (S) (inorganic layer, n=6)	6.7 ± 0.3	0.025 ± 0.008	20.8 ± 23.0 exchangeable 2949± 512 total
Little Deer Isle, ME (S) (n=18)	6.5 ± 0.2	0.45 ± 0.05	44.8 ± 5.6 DPTA

Conowingo Barrens, PA (S) (n=4)	6.6 ± 0.1	0.17 ± 0.01	21 ± 6 Mehlich-3
Staten Island, NY (S) (n=1)	6.9	0.17	8.5 exchangeable
Buck Creek, NC (S) (n=11)	6.1 ± 0.3	0.09 ± 0.03	—
Deer Isle, ME (NS) (n=15)	5.25 ± 0.08	4.34 ± 0.4	0.13 ± 0.02 DPTA
Conowingo Barrens, PA (NS) (n=3)	4.2 ± 0.1	2 ± 0.01	0.4 ± 0.3 Mehlich-3
Buck Creek, NC (NS) (n=5)	4.7 ± 0.3	1.55 ± 0.44	—

Table 2. Lichen species reported from serpentine substrates in eastern North America based on studies by Harris et al. (2007; Maine, USA = ME) and Sirois et al. (1988; Québec, Canada = QC). Names standardized using Index Fungorum (Index Fungorum Partnership) (http://www.indexfungorum.org; accessed 28 Jan 2008), Integrated Taxonomic Information System (http://www.itis.gov; accessed 23 Jan 2008), and USDA, NRCS (2008).

Species	**Occurrence**
Acarospora fuscata (Nyl.) Arnold	ME
Alectoria nigricans (Ach.) Nyl.	QC
A. ochroleuca (Hoffm.) A. Massal.	QC
Amygdalaria panaeola (Ach.) Hertel & Brodo	QC
Anaptychia palmulata (Michx.) Vain.	ME
Arctoparmelia centrifuga (L.) Hale	QC
A. incurva (Pers.) Hale	QC
Aspicilia cinerea (L.) Körb.	ME; QC
Bacidia sabuletorum (Schreb.) Lettau	QC
Baeomyces carneus Flörke	QC

B. rufus (Huds.) Rebent.	QC
Bellemerea cinereorufescens (Ach.) Clauzade & Cl. Roux	QC
Belonia russula Nyl.	QC
Biatora vernalis (L.) Fr.	QC
Bryocaulon divergens (Ach.) Kärnefelt	QC
Bryoria nitidula (Th. Fr.) Brodo & D. Hawksw.	QC
Buellia dispersa A. Massal.	QC
B. leptocline (Flot.) A. Massal.	QC
B. ocellata (Flot.) Körb.	ME
B. papillata (Sommerf.) Tuck.	QC
Caloplaca ammiospila (Wahlenb.) H. Olivier	QC
C. holocarpa (Hoffm.) A.E. Wade	QC
C. lithophila H. Magn.	ME
C. microthallina (Wedd.) Zahlbr.	ME
C. scopularis (Nyl.) Lettau	ME
C. sinapisperma (Lam. & DC.) Maheu & A. Gillet	QC

C. tetraspora (Nyl.) H. Olivier	QC
Candelariella aurella (Hoffm.) Zahlbr.	ME
C. vitellina (Hoffm.) Müll. Arg.	ME; QC
Carbonea vorticosa (Flörke) Hertel	QC
Catillaria lenticularis (Ach.) Th. Fr.	ME
C. muscicola Lynge	QC
Catolechia wahlenbergii (Ach.) Körb.	QC
Cetraria cucullata (Bellardi) Ach.	QC
C. delisei (Schaer.) Nyl.	QC
C. ericetorum subsp. *ericetorum* Opiz	QC
C. hepatizon (Ach.) Vain.	QC
C. islandica (L.) Ach. subsp. *crispiformis* (Räsänen) Kärnefelt	QC
C. islandica (L.) Ach. subsp. *islandica*	QC
C. laevigata Rass.	QC
C. nivalis (L.) Ach.	QC
C. tilessi Ach.	QC

Cladina mitis (Sandst.) W.L. Culb.	QC
C. rangiferina (L.) Nyl.	QC
C. stellaris (Opiz) Brodo	QC
Cladonia acuminata (Ach.) Norrl.	ME; QC
C. amaurocraea (Flörke) Schaer.	QC
C. boryi Tuck.	ME
C. cariosa (Ach.) Spreng.	ME
C. carneola (Fr.) Fr.	QC
C. cenotea (Ach.) Schaer.	QC
C. chlorophaea (Sommerf.) Spreng.	QC
C. coccifera (L.) Willd.	QC
C. coniocraea (Flörke) Spreng.	QC
C. crispata (Ach.) Flot.	QC
C. cristatella Tuck.	ME; QC
C. cyanipes (Sommerf.) Nyl.	QC
C. decorticata (Flörke) Spreng.	QC

C. *deformis* (L.) Hoffm.	QC
C. *digitata* (L.) Hoffm.	QC
C. *ecmocyna* Leight. subsp. *ecmocyna*	QC
C. *furcata* (Huds.) Schrad.	QC
C. *glauca* Flörke	QC
C. *gracilis* (L.) Willd. subsp. *gracilis*	QC
C. *macilenta* Hoffm.	ME
C. *macilenta* Hoffm. var. *bacillaris* (Genth) Schaer.	QC
C. *macroceras* (Delise) Ahti	QC
C. *macrophylla* (Schaer.) Stenh.	QC
C. *maxima* (Asahina) Ahti	QC
C. *mitis* Sandst.	ME
C. *multiformis* G. Merr.	QC
C. *phyllophora* Hoffm.	QC
C. *pleurota* (Flörke) Schaer.	ME; QC
C. *polycarpoides* Nyl.	ME

C. pyxidata (L.) Hoffm.	ME; QC
C. rangiferina (L.) F.H. Wigg.	ME
C. rei Schaer.	ME
C. scabriuscula (Delise) Leight.	QC
C. squamosa (Scop.) Hoffm.	ME; QC
C. stricta (Nyl.) Nyl. var. *uliginosa* Ahti	QC
C. subulata (L.) F.H. Wigg.	QC
C. sulphurina (Michx.) Fr.	QC
C. symphycarpia (Flörke) Fr.	ME
C. turgida Hoffm.	ME; QC
C. uncialis (L.) F.H. Wigg.	ME; QC
C. wainioi Savicz	QC
Coelocaulon aculeatum (Schreb.) Link	QC
Collema subflaccidum Degel.	ME
Dactylospora urceolata (Th. Fr.) Arnold	QC
Dermatocarpon luridum (With.) J.R. Laundon	QC

D. miniatum (L.) W. Mann	ME
D. rivulorum (Arnold) Dalla Torre & Sarnth.	QC
Dibaeis baeomyces (L. f.) Rambold & Hertel	ME
Diploschistes scruposus (Schreb.) Norman	QC
Endococcus propinquus (Körb.) D. Hawksw.	QC
E. rugulosus (Leight.) Nyl.	QC
Ephebe lanata (L.) Vain.	QC
Flavoparmelia caperata (L.) Hale	ME
Fuscidea kochiana (Hepp) V. Wirth & Vězda	QC
F. lowensis (H. Magn.) R.A. Anderson & Hertel	QC
Fuscopannaria praetermissa (Nyl.) P.M. Jørg.	ME
Hypogymnia physodes (L.) Nyl.	QC
H. tubulosa (Schaer.) Hav.	QC
H. vittata (Ach.) Parrique	QC
Icmadophila ericetorum (L.) Zahlbr.	QC
Imshaugia aleurites (Ach.) S.L.F. Mey.	QC

Ionaspis odora (Ach.) Th. Fr.	QC
Lecanora argentea Oksner & Volkova	ME
L. dispersa (Pers.) Röhl.	ME
L. epibryon (Ach.) Ach.	QC
L. hagenii (Ach.) Ach.	QC
L. placidensis (H. Magn.) Knoph, Leuckert & Rambold	QC
L. polytropa (Hoffm.) Rabenh.	ME; QC
Lecidea brunneofusca H. Magn.	QC
L. pycnocarpa (Körb.) Ohlert	QC
L. tessellata Flörke	QC
L. umbonata (Hepp) Mudd	QC
Lecidella carpathica Körb.	QC
L. euphorea (Flörke) Hertel	QC
L. stigmatea (Ach.) Hertel & Leuckert	ME; QC
L. wulfenii (Ach.) Körb.	QC
Lecidoma demissum (Rutstr.) Gotth. Schneid. & Hertel	QC

Lepraria caesioalba (de Lesd.) J.R. Laundon	ME
L. incana (L.) Ach.	QC
L. neglecta (Nyl.) Erichsen	ME
L. normandinoides Lendemer & R. C. Harris	ME
Leptogium cyanescens (Pers.) Körb.	ME
Lithographa tesserata (DC.) Nyl.	QC
Lobaria pulmonaria (L.) Hoffm.	ME
Melanelia stygia (L.) Essl.	QC
Miriquidica leucophaea (Rabenh.) Hertel & Rambold	QC
M. plumbeoatra (Vain.) A.J. Schwab & Rambold	QC
Muellerella lichenicola (Sommerf.) D. Hawksw.	QC
Mycobilimbia berengeriana (A. Massal.) Hafellner & V. Wirth	QC
M. hypnorum (Lib.) Kalb & Hafellner	QC
Mycoblastus alpinus (Fr.) Hellb.	QC
M. sanguinarius (L.) Norman	QC
Nephroma parile (Ach.) Ach.	ME

Omphalina hudsoniana (H.S. Jenn.) H.E. Bigelow	QC
Ophioparma lapponica (Räsänen) Hafellner & R.W. Rogers	QC
Pannaria rubiginosa (Thunb.) Delise	ME
Parmelia saxatilis (L.) Ach.	ME
P. sulcata Taylor	ME
Parmotrema crinitum (Ach.) M. Choisy	ME
Peltigera didactyla (With.) J.R. Laundon	ME
P. rufescens (Weiss) Humb.	ME
Pertusaria amara (Ach.) Nyl.	ME
Phaeophyscia adiastola (Essl.) Essl.	ME
P. rubropulchra (Degel.) Moberg	ME
P. sciastra (Ach.) Moberg	ME
Physcia caesia (Hoffm.) Fürnr.	ME
Placynthiella icmalea (Ach.) Coppins & P. James	ME
Porpidia subsimplex (H. Magn.) Fryday	ME
Psorula rufonigra (Tuck.) Gotth. Schneid.	ME

Rhizocarpon geminatum Körb.	ME
R. obscuratum (Ach.) A. Massal.	ME
Scoliciosporum umbrinum (Ach.) Arnold	ME
Spilonema revertens Nyl.	ME
Stereocaulon glaucescens Tuck.	ME
Xanthoparmelia cumberlandia (Gyeln.) Hale	ME
X. plittii (Gyeln.) Hale	ME
Xanthoria elegans (Link) Th. Fr.	ME
X. parietina (L.) Th. Fr.	ME

Table 3. List of mosses (Bryophyta) and liverworts (Marchantiophyta) recorded for serpentine soils in eastern North America. Occurrences based on Belland and Brassard (1988), Roberts (1992) for Newfoundland, Canada (NL); L. R. Briscoe et al. (unpubl. data) for Maine, USA (ME); Sirois (1984) for Québec, Canada (QC); Shaw and Albright (1990), Shaw (1991), and Robinson (1966) for Maryland, USA (MD). Names standardized using Integrated Taxonomic Information System (http://www.itis.gov; accessed 28 Jan 2008).

Species	**Occurrence**
BRYOPHYTA	
Amblystegium serpens (Hedw.) Schimp.	ME
Anastrophyllum minutum (Schreb.) Schust.	QC
A. saxicola (Schrad.) Schust.	QC
Andreaea rothii var. *rothii* Web. & Mohr	QC
Anomodon rostratus (Hedw.) Schimp.	ME
Aulacomnium androgynum (Hedw.) Schwaegr.	ME
A. palustre (Hedw.) Schwaegr.	QC
Bartramia pomiformis Hedw.	ME
Brachythecium calcareum Kindb.	QC
B. oedipodium (Mitt.) Jaeg.	QC
B. populeum (Hedw.) Schimp.	QC
B. reflexum (Starke) Schimp.	QC
B. rutabulum (Hedw.) BSG.	ME; QC
B. velutinum (Hedw.) BSG.	ME; QC

Bryum amblyodon C. Muell.	QC
B. argenteum Hedw.	MD; QC
B. knowltonii Barnes	QC
B. lisae var. *cuspidatum* (Bruch & Schimp.) Marg.	QC
B. pseudotriquetrum (Hedw.) G. Gaertn., B. Mey. & Scherb.	QC
B. reedii Robins.	MD
Callicladium haldanianum (Grev.) Crum	ME
Calliergon stramineum (Brid.) Kindb.	QC
Campylium chrysophyllum (Brid.) J. Lange	ME
C. hispidulum (Brid.) Mitt.	QC
C. stellatum (Hedw.) C. Jens.	QC
Catoscopium nigritum (Hedw.) Brid.	NL
Ceratodon purpureus (Hedw.) Brid.	ME; QC
Cirriphyllum piliferum (Hedw.) Grout	QC
Cynodontium alpestre (Wahlenb.) Milde	QC
Dicranum acutifolium (Lindb. & Arnell.) Weinm.	QC
D. bonjeanii De Not.	QC
D. elongatum Schwaegr.	QC
D. fragilifolium Lindb.	QC
D. fuscescens Turn.	QC
D. majus Sm.	QC

D. montanum Hedw.	ME; QC
D. ontariense Peters.	QC
D. polysetum Sw.	ME; QC
D. scoparium Hedw.	ME; QC
Funaria flavicans Michx.	MD
F. hygrometrica Hedw.	ME
Hedwigia ciliata (Hedw.) P. Beauv.	ME
Herzogiella striatella (Brid.) Iwats.	ME
Hylocomiastrum pyrenaicum (Spruce) Fleisch.	QC
H. umbratum (Hedw.) Fleisch.	QC
Hylocomium splendens (Hedw.) Schimp.	NL; QC
Hymenostylium recurvirostre (Hedw.) Dix.	QC
Hypnum mammillatum (Brid.) Loeske	ME
H. cupressiforme Hedw.	ME
H. imponens Hedw.	ME
H. pallescens (Hedw.) P. Beauv.	ME; QC
Isopterygiopsis pulchella (Hedw.) Iwats.	QC
Isothecium myosuroides Brid.	ME
Kiaeria glacialis (Berggr.) Hag.	QC
Lejeunea cavifolia (Ehrh.) Lindb. Emend. Buch	NL
Leucobryum glaucum (Hedw.) Angstr.	ME
Limprichtia revolvens (Sw.) Loeske	QC

Loeskeobryum brevirostre (Brid.) Fleisch.	QC
Paludella squarrosa (Hedw.) Brid.	QC
Paraleucobryum longifolium (Hedw.) Loeske	QC
Philonotis fontana (Hedw.) Brid.	QC
Plagiothecium laetum Schimp.	QC
Platygyrium repens (Brid.) Schimp.	ME
Pleurozium schreberi (Brid.) Mitt.	ME; NL; QC
Pohlia cruda (Hedw.) Lindb.	QC
P. nutans (Hedw.) Lindb.	QC
P. sphagnicola (Bruch & Schimp.) Lindb. & Arnell	QC
Polytrichastrum alpinum var. *alpinum* (Hedw.) G. L. Sm.	QC
Polytrichum commune Hedw.	QC
P. formosum Hedw.	QC
P. juniperinum Hedw.	ME; QC
P. longisetum Brid.	QC
P. piliferum Hedw.	ME
P. strictum Brid.	QC
Pterigynandrum filiforme Hedw.	ME
Ptilium crista-castrensis (Hedw.) De Not.	QC
Pylaisiella polyantha (Hedw.) Grout	QC
Rhacomitrium heterostichum (Hedw.) Brid.	QC
R. lanuginosis (Hedw.) Brid.	NL; QC

Rhytidiadelphus squarrosus (Hedw.) Warnst.	QC
R. triquetrus (Hedw.) Warnst.	ME
Rhytidium rugosum (Hedw.) Kindb.	QC
Sanionia uncinata var. *uncinata* (Hedw.) Loeske	QC
Schistidium apocarpum (Hedw.) Bruch & Schimp.	QC
Sphagnum angustifolium (Russ.) C. Jens.	QC
S. capillifolium (Ehrh.) Hedw.	QC
S. centrale C. Jens.	QC
S. fuscum (Schimp.) Klinggr.	QC
S. girgensohnii Russ.	QC
S. lindbergii Schimp.	QC
S. rubellum Wils.	QC
S. russowii Warnst.	QC
S. teres (Schimp.) Ångstr.	QC
S. warnstorfii Russ.	QC
Splachnum sphaericum Hedw.	QC
Tetraphis pellucida Hedw.	QC
Tetraplodon angustatus (Hedw.) Bruch & Schimp.	NL
T. mnioides (Hedw.) Bruch & Schimp.	QC
Thuidium recognitum (Hedw.) Lindb.	ME
Tomenthypnum nitens (Hedw.) Loeske	QC

Ulota hutchinsiae (Sm.) Hammar	ME
Warnstorfia exannulata var. *exannulata* (Schimp.) Loeske	QC
Weissia controversa Hedw.	ME; QC
MARCHANTIOPHYTA	
Anastrophyllum minutum (Schreb.) Schust.	ME
Barbilophozia atlantica (Kaal.) K. Mull.	QC
B. attenuata (Mart.) Loeske	QC
B. barbata (Schreb.) Loeske	ME
B. floerkei (Web. & Mohr) Loeske	QC
B. hatcheri (Evans) Loeske	QC
B. kunzeana (Hub.) Gams	QC
B. lycopodioides (Wallr.) Loeske	QC
Blepharostoma trichophyllum (L.) Dum.	QC
Calypogeia sphagnicola (Arnell & J. Perss.) Warnst. & Loeske	QC
Cephalozia connivens (Dicks.) Lindb.	QC
C. lunulifolia (Dum.) Dum.	QC
C. pleniceps (Aust.) Lindb.	QC
Cephaloziella hampeana (Nees.) Schiffn.	ME
C. rubella (Nees) Warnst.	QC
Chandonanthus setiformis (Ehrh.) Lindb.	QC
Cladopodiella fluitans (Nees) Joerg.	QC
Cololejeunea biddlecomiae (Aust.) Evans	ME

Frullania tamarisci subsp. *asagrayana* (Mont.) Hatt.	ME
Gymnocolea inflata (Huds.) Dum.	QC
Harpanthus flotovianus (Nees) Nees	QC
Lejeunea lamacerina (Steph.) Schiffn. subsp. *geminata* Schust.	ME
L. cavifolia (Ehrh.) Lindb. Emend. Buch	ME
Lophocolea heterophylla (Schrad.) Dum.	ME
Lophozia alpestris (Web.) Evans	QC
L. ascendens (Warnst.) Schust.	QC
L. bicrenata (Hoffm.) Dum.	QC
L. ventricosa (Dicks.) Dum.	QC
Metzgeria conjugata Lindb.	ME
M. furcata (L.) Dumort.	ME
Mylia anomala (Hook.) S. Gray	QC
Odontoschisma elongatum (Lindb.) A.W. Evans	QC
O. denudatum (Mart.) Dumort.	QC
O. macounii (Aust.) Underw.	QC
Pellia endiviifolia (Dicks.) Dumort.	QC
Ptilidium ciliare (L.) Nees	ME; QC
P. pulcherrimum (G. Web.) Hampe	QC
Radula complanata (L.) Dum.	ME
Scapania curta (Mart.) Dum.	QC

S. irrigua (Nees) Gottsche & Lindenb. & Nees	QC
S. irrigua (Nees) Gottsche & Lindenb. & Nees subsp. *rufescens* (Loeske) Schust.	QC
S. paludosa (K. Mull.) K. Mull.	QC
Tritomaria quinquedentata (Huds.) Buch	QC

Table 4. Vascular plant species recorded from serpentine outcrops in eastern North America. Names standardized using Integrated Taxonomic Information System (http://www.itis.gov; accessed 23 Jan 2008), International Plant Names Index (http://www.ipni.org; accessed 23 Jan 2008), and USDA, NRCS (2008). Federal (USA), State (standard state abbreviations), and Global (G1=critically imperilled, G2=imperilled) protected status data from USDA, NRCS (2008), Center for Plant Conservation (http://www.centerforplantconservation.org; accessed 28 Jan 2008), and NatureServe (http://www.natureserve.org; accessed 28 Jan 2008); E=endangered, EV=exploitably vulnerable, H=historical, PREX=probably extirpated, PRX =presumed extirpated, PX=possibly extirpated, T=threatened, R=rare, S=sensitive, SC=special concern, and X=extirpated. Rarity data for Newfoundland (NL), Canada from Atlantic Canada Conservation Data Center (http://www.accdc.com/products/ranking.html; accessed 24 Jan 2008) and Québec, Canada (QC) from Centre de données sur le patrimoine naturel du Québec (http://www.cdpnq.gouv.qc.ca/produits-en.htm; accessed 23 Jan 2008); S1= critically imperiled, S2= imperiled, S3= vulnerable, S4=apparently secure, S5=secure, SX=extinct, and SH=possibly extinct.

Family, Species	Citation	Global, Federal, State/Province Protected Status
ACERACEAE		
Acer rubrum L.	Brooks 1987 Carter 1979 Dearden 1979 Mansberg and Wentworth 1984 Miller 1981 Tyndall and Farr 1990 Zika and Dann 1985 Wherry 1963	—

A. saccharum Marshall	Brooks 1987 Carter 1979	—
A. spicatum Lam.	Brooks 1987 Carter 1979	KY (E)
ADOXACEAE		
Viburnum acerifolium L.	Miller 1981	—
V. lantanoides Michx.	Carter 1979	KY (E), NJ (E)
V. nudum var. *cassinoides* (L.) Torr. & A.Gray	Brooks 1987 Mansberg and Wentworth 1984 Zika and Dann 1985	IN (E)
V. prunifolium L.	Wherry 1963	CT (SC)
AGAVACEAE		
Yucca constricta Buckley	Maoui 1966	—
ANACARDIACEAE		
Rhus copallina L.	Miller 1981 Wherry 1963	—
R. glabra L.	Tyndall and Hull 1999 Wherry 1963	QC (SH)
R. hirta L.	Miller 1981 Wherry 1963	—
Robinia pseudoacacia L.	Brooks 1987 Miller 1981	—
Toxicodendron radicans subsp. *radicans* (L.) Kuntze	Tyndall and Hull 1999 Wherry 1963	—
APIACEAE		
Angelica venenosa (Greenway) Fernald	Wherry 1963	CT (SC)
Cicuta maculata L.	Carter 1979 Wherry 1963	—
Conioselinum chinense Britton, Sterns & Poggenb.	Dearden 1979	IL (E), IN (E), MA (SC), NJ (E), NC (E), PA (E), WI (E)
Heracleum maximum Bartr.	Carter 1979	KY (E),TN (SC)
Ligusticum scoticum L. subsp. *hultenii* (Fernald) Calder & Roy L.Taylor	Carter 1979	—
Sanicula marilandica L.	Wherry 1963	WA (S)
Thaspium trifoliatum (L.) A.Gray	Mansberg and Wentworth 1984	MD (E)
Zizia aptera (A.Gray) Fernald	Wherry 1963	CT (E), IN (R), MI (T), RI (H)
Z. aurea Koch	Wherry 1963	—
APOCYNACEAE		
Apocynum cannabinum L.	Brooks 1987	—
A. × *floribundum* Greene	Wherry 1963	—
AQUIFOLIACEAE		

Ilex ambigua Elliott	Brooks 1987	—
Nemopanthus mucronatus (L.) Trel.	Brooks 1987 Dearden 1979	—
ARACEAE		
Symplocarpus foetidus (L.) W. P. C.Barton	Carter 1979	TN (E)
ARALIACEAE		
Aralia nudicaulis L.	Brooks 1987 Carter 1979	—
ARISTOLOCHIACEAE		
Hexastylis arifolia Small var. *ruthii* (Ashe) H.L.Blomq.	Mansberg and Wentworth 1984 Tyndall and Hull 1999	FL (T)
ASCLEPIADACEAE		
Asclepias purpurascens L.	Wherry 1963	CT (SC), MA (E), RI (H), TN (SC), WI (E)
A. syriaca L.	Wherry 1963	
A. verticillata L.	Brooks 1987 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Wherry 1963	MA (T)
A. viridiflora Pursh	Brooks 1987 Tyndall 1992b Tyndall 1994 Wherry 1963	CT (SC), FL (E), NY (T)
ASPLENIACEAE		
Asplenium platyneuron (L.) Britton, Sterns, Poggenb.	Tyndall and Farr 1990 Wherry 1963	ME (SC), NY (EV), QC (S2)
A. trichomanes L.	Zika and Dann 1985	MN (T), NY (EV)
A. trichomanes-ramosum L.	Carter 1979 Zika and Dann 1985	ME (T), MI (T), NY (E), VT (T), WI (E)
ASTERACEAE		
Achillea millefolium L.	Carter 1979 Miller 1981 Tyndall and Farr 1990 Zika and Dann 1985	—
A. millefolium L. var. *borealis* (Bong.) Farw.	Pennell 1930	ME (SC)
Ageratina aromatica var. *aromatica* (L.) Spach	Tyndall and Farr 1990 Wherry 1963	MA (E)
Ambrosia artemisiifolia L.	Carter 1979 Wherry 1963	—
Anaphalis margaritacea (L.) Benth. & Hook.f.	Carter 1979	—
Antennaria howellii Greene subsp. *neodioica* (Greene) Bayer	Wherry 1963	—
A. neglecta Greene	Carter 1979	—

	Wherry 1963	
A. plantaginifolia (L.) Hook.	Carter 1979 Wherry 1963	—
Artemisia campestris (L.) subsp. *borealis* (Pall) H.M.Hall & Clem.	Brooks 1987	ME (PX), MA (E), NY (E)
Aster umbellatus Mill.	Carter 1979	—
Cirsium discolor (Willd.) Spreng.	Wherry 1963	
C. muticum Michx.	Carter 1979 Wherry 1963	AR (T)
C. pumilum Spreng.	Wherry 1963	—
C. vulgare (Savi) Ten.	Miller 1981	—
Erechtites hieracifolia (L.) DC.	Tyndall 2005 Wherry 1963	—
Erigeron strigosus Willd.	Brooks 1987 Carter 1979	—
Eupatorium maculatum L.	Carter 1979	—
E. perfoliatum L.	Brooks 1987 Carter 1979 Wherry 1963	—
E. purpureum L.	Wherry 1963	—
E. rotundifolium L. var. *ovatum* (Bigelow) Torr.	Wherry 1963	NH (E), NY (E)
Eurybia radula (Aiton) G. L.Nesom	Brooks 1987	CT (E), KY (E), MD (E), NJ (E), NY (E)
Euthamia graminifolia var. *graminifolia* (L.) Nutt.	Carter 1979	—
E. graminifolia (L.) Nutt. var. *nuttallii* (Greene) W. Stone	Wherry 1963	—
Helianthus divaricatus L.	Wherry 1963	QC (S3)
H. giganteus L.	Wherry 1963	IL (E)
Heliopsis helianthoides Sweet	Wherry 1963	—
Hieracium aurantiacum L.	Carter 1979	—
H. caespitosum Dumort.	Carter 1979	—
H. canadense Michx.	Carter 1979	—
H. gronovii L.	Wherry 1963	—
H. pilosella L.	Carter 1979	—
H. piloselloides Vill.	Carter 1979	—
H. venosum L.	Brooks 1987 Wherry 1963	ME (E)
Krigia virginica Willd.	Wherry 1963	IA (E), ME (PX), OH (T)
Lactuca biennis (Moench) Fernald	Wherry 1963	—
L. canadensis L.	Pennell 1930 Tyndall and Hull 1999	—
Leucanthemum vulgare Lam.	Carter 1979	—

Liatris pilosa var. *pilosa* Willd.	Brooks 1987	—
L. spicata Willd.	Wherry 1963	—
Oclemena acuminata (Michx.) Greene	Carter 1979	KY (T), OH (PRX)
Omalotheca sylvatica (L.) Sch. Bip. & F. W. Schultz	Brooks 1987	ME (SC), MI (T), NY (E), VT (E)
Packera anonyma (Wood) W.A. Weber & Á. Löve	Brooks 1987 Pennell 1930 Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	PA (R)
P. paupercula (Michx.) Á. Löve & D. Löve	Brooks 1987 Pennell 1930 Roberts 1980 Roberts 1992	CT (E), NH (T), OH (T)
P. plattensis (Nutt.) W.A.Weber & Á.Löve	Mansberg and Wentworth 1984 Tyndall and Hull 1999	PA (X)
Prenanthes alba L.	Wherry 1963	KY (E)
P. altissima L.	Carter 1979	—
P. nana (Bigelow) DC.	Brooks 1987	ME (E), NY (E)
P. serpentaria Pursh	Wherry 1963	MA (E)
P. trifoliata (Cass.) Fernald	Carter 1979	OH (E)
Pseudognaphalium obtusifolium subsp. *obtusifolium* (L.) Hilliard & B. L. Burtt	Tyndall 2005 Wherry 1963	—
Senecio sylvaticus DC.	Carter 1979	—
Sericocarpus asteroides Britton, Sterns & Poggenb.	Brooks 1987 Wherry 1963	ME (E)
Solidago bicolor L.	Carter 1979 Wherry 1963	—
S. caesia L.	Wherry 1963	WI (E)
S. caesia L. var. *curtisii* (Torr. & A.Gray)	Mansberg and Wentworth 1984	—
S. canadensis L.	Brooks 1987 Carter 1979	—
S. canadensis L. var. *scabra* (Willd.) Torr. & A.Gray	Wherry 1963	—
S. hispida Willd.	Brooks 1987 Dearden 1979 Roberts 1992	MD (E, X)
S. juncea Aiton	Brooks 1987 Wherry 1963	—
S. macrophylla Pursh.	Carter 1979	MA (T)

S. multiradiata Aiton	Brooks 1987	ME (T)
S. nemoralis Aiton	Carter 1979 Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	—
S. rugosa Mill.	Carter 1979 Wherry 1963	—
S. sempervirens L.	Carter 1979	—
S. simplex Kunth var. *randii* (Porter) Kartesz & Gandhi	Brooks 1987	KY (SC), MA (E), TN (T)
S. uliginosa Nutt. var. *linoides* (Torr. & A. Gray) Fernald	Brooks 1987	NH (T)
Sonchus arvensis L.	Carter 1979	—
Symphyotrichum cordifolium (L.) G. L. Nesom	Wherry 1963	—
S. depauperatum (Fernald) G. L. Nesom	Brooks 1987 Gustafson and Latham 2005 Hart 1980 Miller 1981 Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	G2, MD (E), PA (T)
S. dumosum var. *dumosum* (L.) G. L. Nesom	Wherry 1963	IA (E), OH (T)
S. ericoides var. *ericoides* (L.) G. L. Nesom	Brooks 1987	TN (T)
S. foliaceum var. *foliaceum* (DC.) G. L. Nesom	Brooks 1987	—
S. laeve (L.) Á. Löve & D. Löve var. *concinnum* (Willd.) G. L. Nesom	Tyndall and Hull 1999	MD (E, X), NY (E)
S. laeve var. laeve (L.) Á. Löve & D. Löve	Tyndall and Hull 1999 Wherry 1963	—
S. lateriflorum var. *lateriflorum* (L.) Á. Löve & D. Löve	Asteraceae	NY (E)
S. novi-belgii var. *novi-belgii* (L.) G. L. Nesom	Brooks 1987 Carter 1979	PA (T)
S. novi-belgii (L.) G. L. Nesom var. *villicaule* (A. Gray) Labrecque & Brouillet	Brooks 1987	QC (S1)
S. patens var. *patens* (Aiton) G. L. Nesom	Wherry 1963	ME (PX), NH (T)
S. pilosum var. *pilosum* (Willd.) Nesom	Hart 1980	
S. pilosum var. *pringlei* (Gray) G. L. Nesom	Wherry 1963	NY (T), QC (S1)
S. puniceum var. *puniceum* (L.) A.& D. Löve	Carter 1979	NJ (E), NY (E), PA (T)

	Wherry 1963	
S. undulatum (L.) G. L. Nesom	Mansberg and Wentworth 1984 Wherry 1963	—
Taraxacum officinale F. H. Wigg.	Carter 1979 Tyndall and Farr 1990	—
Vernonia glauca (L.) Willd.	Wherry 1963	NJ (E), PA (E)
V. noveboracensis (L.) Michx.	Brooks 1987 Wherry 1963	KY (SC), OH (PRX)
Xanthium strumarium L.	Tyndall and Farr 1990	—
BALSAMINACEAE		
Impatiens capensis Meerb.	Carter 1979 Wherry 1963	—
BERBERIDACEAE		
Berberis vulgaris L.	Carter 1979	—
Mahonia trifoliolata Fedde	Maoui 1966	—
BETULACEAE		
Alnus incana (L.) Moench subsp. *rugosa* (Du Roi) R.T.Clausen	Brooks 1987	IL (E)
A. serrulata (Aiton) Willd.	Wherry 1963	QC (S1)
A. viridis (Chaix) DC. subsp. *crispa* (Aiton) Turrill	Carter 1979 Dearden 1979	MA (T), PA (E), TN (SC)
Betula alleghaniensis var. *alleghaniensis* Britton	Brooks 1987 Mansberg and Wentworth 1984	IL (E)
B. nana L.	Brooks 1987 Dearden 1979	—
B. papyrifera Marshall	Brooks 1987 Carter 1979 Dearden 1979 Tyndall and Hull 1999 Zika and Dann 1985	—
B. papyrifera Marsh. var. *cordifolia* (Regel) Fernald	Carter 1979	TN (E)
B. pubescens Ehrh. subsp. *borealis* (Spach) A. Löve & D. Löve	Zika and Dann 1985	—
B. pumila L.	Brooks 1987 Dearden 1979 Roberts 1980	CT (SC), IA (T), ME (SC), MA (E), NH (E), NY (T), OH (T)
Carpinus caroliniana Walter subsp. *virginiana* (Marsh.) Furlow	Wherry 1963	—
Corylus americana Walter	Tyndall and Hull 1999 Wherry 1963	QC (SH)
BRASSICACEAE		

Arabis alpina L.	Ryan 1988	—
A. lyrata L.	Brooks 1987 Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	OH (T), VT (T)
Cardamine bellidifolia L.	Hay et al. 1992	ME (E), NH (E), NL (S1)
C. diphylla (Michx.) Alph. Wood	Carter 1979	QC (S4)
C. pensylvanica Willd.	Carter 1979	—
CAMPANULACEAE		
Campanula rotundifolia L.	Brooks 1987 Tyndall and Hull 1999 Zika and Dann 1985	NY (EV), OH (E)
Lobelia inflata L.	Brooks 1987	—
L. spicata Lam.	Tyndall and Farr 1990 Wherry 1963	—
L. spicata Lam. var. *scaposa* McVaugh	Brooks 1987	—
CAPRIFOLIACEAE		
Diervilla lonicera Mill.	Carter 1979	IN (R), TN (T)
Linnaea borealis L.	Dearden 1979	IN (X), IA (T), MD (E, X), NJ (E), OH (PRX), PA (T), RI (H), TN (PX, E)
Lonicera canadensis Marshall	Carter 1979	IN (X), MD (E), NJ (E), TN (SC)
L. japonica Thunb.	Miller 1981 Wherry 1963	—
L. sempervirens L.	Wherry 1963	ME (E)
L. villosa (Michx.) Schult.	Carter 1979 Dearden 1979	OH (PRX), PA (E)
L. villosa (Michx.) Schult. var. *calvescens* (Fernald & Wieg.) Fernald	Brooks 1987	—
Sambucus nigra L. subsp. *canadensis* (L.) R. Bolli	Wherry 1963	—
S. racemosa var. *racemosa* A.Gray	Carter 1979	IL (E), KY (E), RI (H)
CARYOPHYLLACEAE		
Arenaria humifusa Linden & Planch	Brooks 1987 Dearden 1979 Roberts 1980 Roberts 1992	—
A. serpyllifolia L.	Wherry 1963	—
Cerastium alpinum L.	Roberts 1980	—

C. arvense L.	Carter 1979 Zika and Dann 1985	—
C. arvense L. subsp. *strictum* (L.) Ugborogho	Hay et al. 1994	—
C. arvense L. *var. velutinum* (Raf.) Britton	Gustafson and Latham 2005 Hay et al. 1994	TN (E)
C. arvense L. var. *villosum* (Darl.) Hollick & Britton	Brooks 1987 Hart 1980 Pennell 1930 Ryan 1988 Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	PA (E)
C. velutinum Rafinesque var. *villossissimum* (Pennell) J. K. Morton as *C. arvense* L. var. *villosissimum* Pennell	Latham 1993 Gustafson et al. 2003 Morton 2004	PA (E)
C. beeringianum Cham. & Schlecht.	Brooks 1987 Dearden 1979 Roberts 1980	—
C. fontanum Baumg. subsp. *vulgare* (Hartm.) Greuter & Burdet	Carter 1979 Hart 1980	—
C. terrae-novae Fernald & Wiegand	Brooks 1987 Dearden 1979 Hay et al. 1994 Tyndall and Hull 1999	—
Dianthus armeria L.	Brooks 1987	—
Lychnis alpina L.	Brooks 1987	—
L. alpina L. var. *americana* Fernald	Dearden 1979	—
Minuartia biflora (L.) Schinz & Thell.	Brooks 1987 Hay et al. 1994 Tyndall and Hull 1999	NL (S1)
M. marcescens ((Fernald) House	Brooks 1987 Dearden 1979 Roberts 1980 Roberts 1992 Sirois et al. 1988 Tyndall and Hull 1999 Zika and Dann 1985	G2, VT (T), NL (S2, S3), QC (S2)
M. michauxii var. michauxii (Fenzl) Farw.	Zika and Dann 1985 Wherry 1963	IN (R), NJ (E), RI (E)
M. rubella (Wahlenb.) Hiern.	Brooks 1987 Sirois et al. 1988	ME (T), VT (T)

Moehringia macrophylla (Hook.) Fenzl	Tyndall and Hull 1999 Zika and Dann 1985	MA (E), MN (T), WI (E), CT (E), MI (T), QC (S3)
Sagina caespitosa (J. Vahl) Lange	Tyndall and Hull 1999 Hay et al. 1994	NL (SH)
S. nodosa (L.) E. Mey.	Brooks 1987 Dearden 1979	MI (T)
S. saginoides (L.) Karst.	Tyndall and Hull 1999 Hay et al. 1994	NL (S1)
Silene acaulis L.	Dearden 1979 Roberts 1980	ME (PX)
S. acaulis (L.) Jacq. var. *exscapa* (All.) DC.	Brooks 1987	NH (T)
S. stellata (L.) W. T. Aiton	Wherry 1963	CT (SC), MI (T), RI (H)
Spergularia rubra J. Presl & C. Presl	Brooks 1987	—
CELASTRACEAE		
Celastrus scandens L.	Wherry 1963	NY (EV)
CHENOPODIACEAE		
Atriplex prostrata R. Br.	Carter 1979	—
Suaeda maritima (L.) Dumort.	Carter 1979	—
CISTACEAE		
Helianthemum bicknellii Fernald	Wherry 1963	KY (T), MD (E), OH (T), PA (E), TN (PX, E), VT (T)
Lechea minor L.	Wherry 1963	OH (T)
L. pulchella var. *pulchella* Raf.	Wherry 1963	MI (T), OH (T), TN (E)
L. racemulosa Michx.	Wherry 1963	IN (E), NY (R)
CLUSIACEAE		
Hypericum gentianoides (L.) Britton, Sterns & Poggenb.	Brooks 1987 Miller 1981 Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	IA (E)
H. hypericoides subsp. *hypericoides* (L.) Crantz	Wherry 1963	—
H. perforatum L.	Brooks 1987 Carter 1979	—
H. punctatum Lam.	Brooks 1987 Wherry 1963	—
COMMELINACEAE		
Tradescantia virginiana L.	Wherry 1963	—
CONVOLVULACEAE		
Calystegia sepium subsp. *sepium* (L.) R. Br.	Carter 1979	—
C. spithamaea subsp. *spithamaea* (L.) Pursh	Wherry 1963	NH (T)

CORNACEAE		
Cornus alternifolia L. f.	Wherry 1963	FL (E)
C. canadensis L.	Brooks 1987 Carter 1979 Dearden 1979	IL (E), IN (E), IA (T), MD (E), OH (T)
C. florida L.	Mansberg and Wentworth 1984	ME (E), NY (EV), VT (T)
CUPRESSACEAE		
Juniperus communis L.	Brooks 1987 Dearden 1979 Roberts 1980 Tyndall and Hull 1999 Zika and Dann 1985	IL (T), IN (R), MD (E, X), OH (E)
J. communis L. var. *depressa* Pursh	Brooks 1987	KY (T); NL (S4, S5)
J. horizontalis Moench	Brooks 1987 Dearden 1979 Roberts 1980	IL (E), IA (T), NH (E), NY (E), VT (T), NL (S5)
J. virginiana L.	Miller 1981 Tyndall and Farr 1990 Tyndall and Hull 1999 Wherry 1963	—
Thuja occidentalis L.	Carter 1979	CT (T), IL (T), IN (E), KY (T), MD (T), MA (E), NJ (E), TN (SC)
CYPERACEAE		
Bulbostylis capillaris (Elliott) Fernald	Wherry 1963	—
Carex annectens E. P. Bicknell	Wherry 1963	—
C. arctata Hook.	Carter 1979	IN (E), NJ (E), OH (E)
C. atlantica subsp. *atlantica* L. H. Bailey	Wherry 1963	IN (T)
C. atratiformis Britton	Sirois et al. 1988	ME (SC), MI (T), NY (E), VT (T)
C. bicknellii Britton	Wherry 1963	ME (PX), NY (T), OH (T), PA (E)
C. brunnescens (Pers.) Poir. subsp. *sphaerostachya* (Tuck.) Kalela	Carter 1979	IL (E), IN (E), NJ (E), OH (T)
C. bushii Mack.	Wherry 1963	CT (SC), IN (E), ME (PX), MA (E), NJ (E), OH (E)
C. buxbaumii Wahlenb.	Brooks 1987 Dearden 1979	CT (E), KY (H), MD (T), NH (E), NY (T), PA (R), TN (SC), VT (E), WA (S)
C. capitata L. var. *arctogena* (Harry Sm.) Hiitonen	Sirois et al. 1988	NH (T)
C. cephalophora Willd.	Wherry 1963	QC (S2)

C. communis L. H. Bailey	Carter 1979	IL (T)
C. conoidea Willd.	Carter 1979 Sirois et al. 1988	IN (E), MD (E), NC (T), OH (T)
C. deflexa Hornem.	Carter 1979	—
C. echinata Murray	Brooks 1987 Dearden 1979 Wherry 1963	IL (E), IN (E), OH (E)
C. exilis Dewey	Brooks 1987 Dearden 1979	CT (E), MD (E), NH (T), NC (T), WI (T)
C. flaccosperma Dewey var. *glaucodea* (Olney) Kükenth.	Wherry 1963	—
C. flava L.	Sirois et al. 1988	IN (T), PA (T), WA (S)
C. glaucodea Tuck.	Brooks 1987	MA (E)
C. granularis Willd.	Wherry 1963	NH (E)
C. gynandra Schwein.	Carter 1979	—
C. hirsutella Mack.	Wherry 1963	CT (SC), NH (E), QC (S2)
C. hystericina Willd.	Tyndall and Hull 1999 Wherry 1963	KY (H), MD (E), WA (S)
C. interior L. H. Bailey	Wherry 1963	—
C. intumescens Rudge	Carter 1979	IL (T)
C. lachenalii Schkuhr	Brooks 1987	—
C. laxiculmis Schwein.	Wherry 1963	ME (E), MN (T), QC (S1)
C. laxiflora Lam.	Carter 1979	—
C. lenticularis var. *lenticularis* Michx.	Sirois et al. 1988	MA (T), WI (T)
C. limosa L.	Dearden 1979	CT (E), IN (E), NJ (E), OH (E), PA (T), RI (H)
C. lurida Wahlenb.	Wherry 1963	—
C. magellanica Lam. subsp. *irrigua* (Wahlenb.) Hultén	Brooks 1987 Dearden 1979	WA (S)
C. nigra All.	Carter 1979	MI (E), NY (E)
C. nigromarginata Schwein.	Wherry 1963	CT (SC), IL (E), NY (E)
C. normalis Mack.	Wherry 1963	—
C. novae-angliae Schwein.	Carter 1979	CT (SC), MI (T)
C. paleacea Wahlenb.	Carter 1979	—
C. pellita Willd.	Wherry 1963	KY (E), TN (PX, E)
C. pensylvanica Lam.	Wherry 1963	
C. pseudocyperus L.	Carter 1979	CT (E), IN (E), NJ (E), OH (E), PA (E)
C. retroflexa Willd.	Wherry 1963	NH (T), NY (E)
C. richardsonii R. Br.	Sirois et al. 1988 Tyndall 1994 Tyndall and Hull 1999	IN (E), OH (PRX), PA (E), VT (E), QC (S1)

C. rosea Willd.	Wherry 1963	—
C. scirpoidea Michx.	Brooks 1987 Dearden 1979 Zika and Dann 1985	ME (T), MI (T), NH (T), NY (E), WA (S)
C. scoparia Schkuhr	Wherry 1963	—
C. stipata Willd.	Carter 1979 Wherry 1963	—
C. straminea Willd.	Wherry 1963	IN (T), KY (T), MI (E), NY (E)
C. stricta Lam.	Wherry 1963	—
C. umbellata Willd.	Carter 1979 Ryan 1988 Tyndall 1992b Tyndall 1994 Tyndall and Farr 1990 Tyndall 2005 Wherry 1963	NH (E)
C. vestita Willd.	Wherry 1963	ME (E), MD (E), TN (PX, E)
C. vulpinoidea Michx.	Wherry 1963	—
C. willdenowii Schkuhr	Wherry 1963	CT (SC), IL (T), NY (T)
Cyperus bipartitus Torr.	Wherry 1963	WA (S)
C. lupulinus (Spreng.) Marcks subsp. *macilentus* (Fernald) Marcks	Wherry 1963	QC (S2)
C. squarrosus L.	Wherry 1963	ME (PX), NH (T), RI (E)
C. strigosus L.	Wherry 1963	—
Dulichium arundinaceum Britton	Wherry 1963	—
Eleocharis erythropoda Steud.	Wherry 1963	—
E. melanocarpa Torr.	Tyndall and Farr 1990	IN (T), MD (E), NJ (E), RI (E)
E. nitida Fernald	Hay et al. 1994 Tyndall and Hull 1999	MI (E), MN (T), WI (E), NL (S1)
E. palustris (L.) Roem. & Schult.	Wherry 1963	—
E. tenuis (Willd.) Schult.	Brooks 1987 Wherry 1963	NJ (E), NY (E), PA (E)
Fimbristylis annua (All.) Roem. & Schult.	Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	PA (T)
F. autumnalis (L.) Roem. & Schult.	Brooks 1987	ME (T), VT (E), QC (S2)
Rhynchospora capitellata (Michx.) Vahl	Wherry 1963	QC (S2)
Schoenoplectus maritimus (L.) Lye	Carter 1979	CT (SC), IL (E), NJ

		(E), NY (E)
S. tabernaemontani (C. C. Gmel.) Palla	Wherry 1963	—
Scirpus atrovirens Muhl.	Wherry 1963	—
S. caespitosus (R.Br.) Poir.	Dearden 1979 Zika and Dann 1985	—
S. cyperinus (L.) Kunth.	Carter 1979 Wherry 1963	—
S. hudsonianus Fernald	Brooks 1987 Dearden 1979	—
S. longii Fernald	Hay et al. 1992	G2, CT (SC), ME (T), MA (T), NJ (E), RI (E)
Scleria pauciflora Willd.	Brooks 1987 Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall 2005	MA (E), MI (E), OH (T), PA (T)
S. pauciflora Willd. var. *caroliniana* (Willd.) Alph. Wood	Wherry 1963	CT (E), NY (E)
S. triglomerata Michx.	Wherry 1963	—
Trichophorum caespitosum (L.) Hartman as *Scirpus caespitosus* (R.Br.) Poir. var. *callosus* Bigelow	Brooks 1987	—
DENNSTAEDTIACEAE		
Dennstaedtia punctilobula (Michx.) T. Moore	Wherry 1963	IL (E), MI (PREX)
Pteridium aquilinum (L.) Kuhn	Zika and Dann 1985	—
P. aquilinum (L.) Kuhn var. *latiusculum* (Desv.) A. Heller	Carter 1979 Wherry 1963	—
P. aquilinum (L.) Kuhn var. *pubescens* Underw.	Brooks 1987	—
DIAPENSIACEAE		
Diapensia lapponica L.	Brooks 1987 Dearden 1979	ME (SC), NH (T), NY (T), VT (E)
DRYOPTERIDACEAE		
Cystopteris fragilis (L.) Bernh.	Carter 1979	NY (EV), OH (PRX)
Dryopteris campyloptera Clarkson	Carter 1979	CT (E), MD (E), NY (EV), PA (E)
D. carthusiana (Vill.) H.P. Fuchs	Carter 1979	AR (T), KY (SC), NY (EV), TN (T)
D. fragrans (L.) Schott	Zika and Dann 1985	ME (SC), NH (T), NY (E)
D. intermedia (Willd.) A. Gray	Carter 1979	IA (T), NY (EV)
D. marginalis (L.) A. Gray	Carter 1979 Wherry 1963	IA (T), MN (T), NY (EV)
D. × *triploidea* Wherry	Carter 1979	—

Gymnocarpium dryopteris (L.) Newman	Carter 1979	IL (E), IA (T), MD (E), NY (EV), OH (T)
Matteuccia struthiopteris (L.) Todaro	Carter 1979	IN (R), NY (EV)
Onoclea sensibilis L.	Carter 1979	—
Polystichum acrostichoides (Michx.) Schott	Tyndall and Farr 1990 Wherry 1963	MN (T), NY (EV)
P. braunii (Spenn.) Fée	Carter 1979 Rugg 1922	MA (E), MN (E), NY (EV), PA (E), WI (T)
P. scopulinum (D. C. Eaton) Maxon	Brooks 1987 Cody 1983	—
Woodsia ilvensis (L.) R. Br.	Carter 1979	IL (E), IA (E), MD (T), NY (EV), OH (PRX), RI (H)
EBENACEAE		
Diospyros texana Scheele	Maoui 1966	—
D. virginiana L.	Wherry 1963	CT (SC), NY (T)
EMPETRACEAE		
Empetrum nigrum L.	Zika and Dann 1985 Dearden 1979	MI (T), MN (E)
EQUISETACEAE		
Equisetum arvense L.	Carter, 1979	—
E. sylvaticum L.	Carter, 1979 Wherry 1963	IL (E), IA (T), MD (E)
ERICACEAE		
Andromeda polifolia L. var. *glaucophylla* (Link) DC.	Brooks 1987 Dearden 1979 Roberts 1980	CT (T), IN (R), NJ (E), OH (PRX), RI (E)
Epigaea repens L.	Brooks 1987 Dearden 1979 Zika and Dann 1985 Wherry 1963	FL (E), NY (EV)
Gaultheria hispidula Muhl.	Brooks 1987 Dearden 1979	CT (T), MD (E), NJ (E), OH (PRX), PA (R), WA (S)
G. procumbens L.	Carter 1979 Mansberg and Wentworth 1984 Zika and Dann 1985	IL (E)
Gaylussacia baccata (Wangenh.) K. Koch	Miller 1981 Tyndall and Hull 1999 Wherry 1963	IA (T)
G. dumosa Torr. & A. Gray	Brooks 1987 Dearden 1979	PA (E), TN (T), CT (T), NH (T), NY (E)
Harrimanella hypnoides (L.) Coville	Hay et al. 1994 Sirois et al. 1988	ME (T), NL (S2)

Kalmia angustifolia L.	Carter 1979 Zika and Dann 1985	NY (EV)
K. latifolia L.	Mansberg and Wentworth 1984 Tyndall and Hull 1999 Zika and Dann 1985 Wherry 1963	FL (T), ME (SC), NY (EV)
K. polifolia Wangenh.	Brooks 1987 Dearden 1979	NJ (E), NY (EV)
Ledum groenlandicum Oeder	Brooks 1987 Dearden 1979 Roberts 1980 Zika and Dann 1985	CT (T), OH (E), PA (R)
Lyonia ligustrina (L.) DC.	Wherry 1963	OH (PRX)
L. mariana (L.) D. Don	Wherry 1963	CT (SC), PA (E), RI (H)
Oxydendrum arboreum (L.) DC.	Brooks 1987	IN (T), MD (E)
Phyllodoce caerulea (L.) Bab.	Sirois et al. 1988	ME (T), NH (T)
Rhododendron calendulaceum (Michx.) Torr.	Mansberg and Wentworth 1984	OH (E), PA (X)
R. canadense (L.) Torr.	Brooks 1987 Carter 1979 Dearden 1979	NJ (E), NY (T)
R. lapponicum (L.) Wahlenb.	Brooks 1987 Dearden 1979 Sirois et al. 1988	ME (T), NY (E), WI (E)
R. maximum L.	Mansberg and Wentworth 1984	ME (T), MA (T), NY (EV), OH (T), VT (T)
R. periclymenoides (Michx.) Shinners	Miller 1981 Wherry 1963	NH (E), NY (EV), OH (T)
R. viscosum (L.) Torr.	Brooks 1987 Mansberg and Wentworth 1984 Wherry 1963	ME (E), NH (T), NY (EV)
Vaccinium angustifolium Aiton	Brooks 1987 Carter 1979 Dearden 1979 Wherry 1963	IA (T)
V. caespitosum Michx.	Carter 1979	MI (T), NY (E), WI (E)
V. corymbosum L.	Carter 1979 Wherry 1963	IL (E)
V. fuscatum Aiton	Wherry 1963	—
V. macrocarpon Aiton	Brooks 1987 Dearden 1979	IL (E), TN (T)
V. myrtilloides Michx.	Carter 1979 Zika and Dann 1985	CT (SC), IN (E), IA (T), OH (T), WA (S)

V. oxycoccus L.	Brooks 1987 Dearden 1979	IL (E), IN (T), MD (T), OH (T)
V. pallidum Aiton	Mansberg and Wentworth 1984 Miller 1981 Tyndall and Hull 1999 Wherry 1963	—
V. stamineum L.	Mansberg and Wentworth 1984 Miller 1981 Tyndall 2005 Wherry 1963	VT (E)
V. uliginosum L.	Brooks 1987 Dearden 1979 Zika and Dann 1985	MI (T), MN (T), NY (R)
V. vitis-idaea L.	Brooks 1987 Dearden 1979 Zika and Dann 1985	MI (E)
EUPHORBIACEAE		
Chamaesyce maculata (L.) Small	Wherry 1963	—
C. nutans (Lag.) Small	Wherry 1963	—
Euphorbia corollata L.	Wherry 1963	—
FABACEAE		
Acacia greggii A.Gray	Maoui 1966	
Amphicarpa bracteata (L.) Fernald	Wherry 1963	NH (T)
Baptisia tinctoria (L.) R.Br.	Wherry 1963	KY (T), ME (E)
Chamaecrista fasciculata var. *fasciculata* (Michx.) Greene	Brooks 1987 Wherry 1963	—
C. nictitans var. *nictitans* Moench	Wherry 1963	NH (E)
Crotalaria sagittalis L.	Wherry 1963	NH (E), NY (E), VT (T)
Desmodium ciliare (Willd.) DC.	Wherry 1963	NY (T)
D. marilandicum (L.) DC.	Brooks 1987 Wherry 1963	NH (E)
D. obtusum (Willd.) DC.	Tyndall and Hull 1999 Wherry 1963	NY (E)
D. paniculatum (L.) DC.	Wherry 1963	QC (S1)
D. perplexum B. G. Schub.	Wherry 1963	—
Lathyrus japonicus Willd. var. *maritimus* (L.) Kartesz & Gandhi	Carter 1979	IL (E), VT (T), IN (E)
L. palustris L.	Carter 1979	KY (T), MD (E, X), PA (E), TN (SC), VT (T)
Lespedeza capitata Michx.	Wherry 1963	KY (SC)
L. hirta (L.) Hornem.	Wherry 1963	ME (PX), VT (T)

L. procumbens Michx.	Wherry 1963	MI (PREX), NH (E)
L. repens (L.) W. Bartram	Wherry 1963	CT (SC), NY (R)
L. violacea (L.) Pers.	Wherry 1963	NY (R), VT (T)
L. virginica (L.) Britton	Brooks 1987 Wherry 1963	NH (T), WI (T)
L. × *manniana* Mack. & Bush	Wherry 1963	—
Strophostyles umbellata (Willd.) Britton	Wherry 1963	NY (E)
Stylosanthes biflora Britton, Sterns & Poggenb.	Wherry 1963	PA (E)
Tephrosia virginiana (L.) Pers.	Wherry 1963	NH (E)
Trifolium arvense L.	Carter 1979	—
T. campestre Schreb.	Carter 1979	—
T. pratense L.	Carter 1979	—
T. repens L.	Carter 1979	—
FAGACEAE		
Castanea dentata (Marsh.) Borkh.	Mansberg and Wentworth 1984 Wherry 1963	KY (E), ME (SC), MI (E), TN (SC)
Quercus alba L.	Brooks 1987 Mansberg and Wentworth 1984 Milton and Purdy 1988 Tyndall and Hull 1999 Wherry 1963	QC (S3)
Q. coccinea Wangenh.	Brooks 1987 Mansberg and Wentworth 1984	ME (E)
Q. ilicifolia Wangenh.	Wherry 1963	VT (E)
Q. marilandica Münchh.	Brooks 1987 Hull and Wood 1984 Miller 1981 Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 2005 Wherry 1963	—
Q. palustris Du Roi	Wherry 1963	
Q. prinoides Willd.	Wherry 1963	IN (E)
Q. prinus L.	Brooks 1987 Wherry 1963	IL (T), ME (T)
Q. rubra L.	Brooks 1987 Wherry 1963	—
Q. stellata Wangenh.	Brooks 1987 Hull and Wood 1984 Miller 1981 Tyndall and Hull 1999 Tyndall 2005	—

	Wherry 1963	
Q. velutina Lam.	Tyndall and Hull 1999 Miller 1981 Wherry 1963	—
FUMARIACEAE		
Corydalis sempervirens Pers.	Carter 1979	IL (E), IN (E), IA (T), KY (SC), TN (E)
Dicentra canadensis Walp.	Carter 1979	CT (T), ME (T), NH (T), NJ (E)
GENTIANACEAE		
Gentiana andrewsii Griseb.	Tyndall and Hull 1999	MD (T), MA (T), NH (T), NY (EV), RI (H), VT (T)
G. villosa L.	Wherry 1963	IN (E), MD (E), OH (E), PA (E)
Gentianopsis crinita (Froel.) Ma	Tyndall and Hull 1999 Wherry 1963	GA (T), MD (E), NH (T), NY (EV), NC (SC, E), QC (S1)
Sabatia angularis (L.) Pursh	Brooks 1987 Tyndall 1994 Wherry 1963	MI (T), NY (E)
GERANIACEAE		
Geranium maculatum L.	Wherry 1963	QC (SX)
GROSSULARIACEAE		
Ribes cynosbati L.	Carter 1979	—
R. glandulosum Ruiz & Pav.	Carter 1979	CT (E), NJ (E), OH (PRX)
R. lacustre (Pers.) Poir.	Carter 1979	CT (SC), MA (SC), PA (E)
R. triste Pall.	Carter 1979	CT (E), OH (E), PA (T)
HAMAMELIDACEAE		
Hamamelis virginiana L.	Mansberg and Wentworth 1984	—
IRIDACEAE		
Hypoxis hirsuta Coville	Wherry 1963	ME (PX), NH (T)
Iris versicolor L.	Carter 1979	—
Sisyrinchium angustifolium Mill.	Wherry 1963	—
S. montanum Greene var. *crebrum* Fernald	Carter 1979	IL (E), IN (E), NJ (E), OH (E), WA (S)
S. mucronatum Michx.	Brooks 1987 Mansberg and Wentworth 1984 Tyndall and Farr 1990 Tyndall and Hull 1999	ME (SC), MA (E), NY (E), OH (E)

	Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	
JUGLANDACEAE		
Carya glabra (Mill.) Sweet	Brooks 1987	—
JUNCACEAE		
Juncus acuminatus Michx.	Wherry 1963	QC (S1)
J. balticus Willd.	Brooks 1987 Carter 1979	IN (R), MD (E, X), PA (T)
J. biflorus Elliott	Wherry 1963	NY (E), PA (T)
J. brevicaudatus (Engelm.) Fernald	Carter 1979	—
J. dichotomus Elliott	Brooks 1987 Wherry 1963	OH (E), PA (E)
J. dudleyi Wiegand	Brooks 1987	ME (SC)
J. effusus L.	Wherry 1963	—
J. effusus L. var. *conglomeratus* (L.) Engelm.	Carter 1979	—
J. marginatus Rostk.	Wherry 1963	—
J. secundus Poir.	Brooks 1987 Tyndall 1994 Tyndall and Farr 1990 Wherry 1963	IN (E), ME (SC), NH (E), OH (T), VT (E)
J. tenuis Willd.	Wherry 1963	—
J. trifidus L.	Brooks 1987 Dearden 1979	MD (E), NC (E), NY (T), TN (PX, E)
Luzula acuminata Raf.	Mansberg and Wentworth 1984	IL (E), IN (E), NJ (E)
L. bulbosa (Alph. Wood) Smyth & Smyth	Wherry 1963	OH (T), PA (E)
L. campestris (L.) DC.	Wherry 1963	—
L. multiflora (Ehrh.) Lej. subsp. *frigida* (Buchenau) Krecz.	Carter 1979	—
JUNCAGINACEAE		
Triglochin palustre L.	Carter 1979	IL (T), IN (T), IA (T), NY (T), PA (X), RI (H)
LAMIACEAE		
Cunila origanoides (L.) Britton	Brooks 1987 Wherry 1963	—
Galeopsis tetrahit L.	Carter 1979	—
Lycopus virginicus Michx.	Carter 1979	MI (T), QC (S2)
Mentha arvensis L.	Carter 1979	
Monarda punctata L.	Tyndall and Farr 1990	KY (H), OH (E), PA (E)
Prunella vulgaris L.	Brooks 1987 Mansberg and Wentworth 1984	—

P. vulgaris L. subsp. *lanceolata* (W. Bartram) Hultén	Carter 1979 Wherry 1963	—
Pycnanthemum flexuosum Britton, Sterns & Poggenb.	Brooks 1987 Miller 1981 Wherry 1963	—
P. tenuifolium Schrad.	Brooks 1987 Wherry 1963	—
P. torrei Benth.	Tyndall and Hull 1999	G2, CT (E), IL (E), MD (E), NH (E), NJ (E), NY (E), PA (E), TN (SC)
Scutellaria elliptica Epling	Mansberg and Wentworth 1984 Wherry 1963	—
S. galericulata L.	Carter 1979	—
S. integrifolia L.	Wherry 1963	CT (E), NY (E)
S. lateriflora L.	Carter 1979	
S. parvula Michx. var. *missouriensis* (Torr.) Goodman & C.A. Lawson	Wherry 1963	CT (E), MD (T), NJ (E)
Trichostema dichotomum L.	Wherry 1963	IN (R), MI (T), QC (SH)
LAURACEAE		
Lindera benzoin Blume	Wherry 1963	ME (SC)
Sassafras albidum (Nutt.) Nees.	Brooks 1987 Mansberg and Wentworth 1984 Miller 1981 Tyndall and Farr 1990 Tyndall and Hull 1999 Wherry 1963	ME (SC)
LILIACEAE		
Aletris farinosa L.	Wherry 1963	ME (PX), NY (T), PA (E)
Chamaelirium luteum A.Gray	Wherry 1963	CT (E), IN (E), MA (E), NY (T)
Clintonia borealis (Aiton) Raf.	Brooks 1987	IN (E), MD (T), OH (E), TN (SC)
Erythronium americanum Ker Gawl.	Carter 1979	—
Hemerocallis fulva L.	Carter 1979	—
Lilium philadelphicum L.	Wherry 1963	KY (T), MD (E, X), NM (E), NY (EV), OH (T), TN (E)
Maianthemum canadense Desf.	Brooks 1987 Dearden 1979	KY (T)

M. racemosum subsp. *racemosum* (L.) Link	Mansberg and Wentworth 1984 Wherry 1963	AZ (SR)
Polygonatum biflorum (Walter) Elliot var. *commutatum* (Schult. & Schult. f.) Morong	Wherry 1963	NH (E)
Streptopus lanceolatus var. *lanceolatus* (Aiton) Reveal	Carter 1979	KY (E)
Trillium erectum L.	Carter 1979	IL (E), NY (EV)
Uvularia perfoliata L.	Wherry 1963	IN (E), NH (E)
U. puberula Michx.	Mansberg and Wentworth 1984	NJ (E), NY (E), PA (R)
Veratrum viride Aiton	Carter 1979	—
LINACEAE		
Linum floridanum Trel.	Wherry 1963	MD (E, X)
L. intercursum E.P.Bicknell	Wherry 1963	CT (SC), IN (E), MD (T), MA (SC), NJ (E), NY (T), PA (E), RI (E)
L. medium (Planch.) Britton	Brooks 1987	NY (E)
L. medium (Planch.) Britton var. *texanum* (Planch.) Fernald	Wherry 1963	MA (T), NY (T)
L. sulcatum Riddell	Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall 2005	CT (SC), IN (R), MD (E), NJ (E), NY (T), PA (E), RI (H)
L. virginianum L.	Wherry 1963	MI (T)
LYCOPODIACEAE		
Huperzia lucidula (Michx.) Trevis.	Carter, 1979	NY (EV)
H. selago var. *selago* (L.) Schrank & Mart.	Tyndall and Hull 1999 Zika and Dann 1985	CT (SC), ME (T), MA (E), NY (E), PA (X),
Lycopodium alpinum L.	Hay et al. 1992	—
L. clavatum L.	Carter, 1979	IL (E), IA (E), KY (E), NY (EV)
L. digitatum A. Braun	Wherry 1963	NY (EV)
L. obscurum L.	Carter 1979	IN (R), NY (EV)
LYTHRACEAE		
Cuphea viscosissima Jacq.	Wherry 1963	—
MAGNOLIACEAE		
Liriodendron tulipifera L.	Miller 1981	—
MONOTROPACEAE		
Monotropa uniflora L.	Carter 1979	—
MYRICACEAE		
Comptonia peregrina (L.) J.M.Coult.	Wherry 1963	IL (E), KY (E), OH (T), TN (E)
Morella pensylvanica (Mirb.) Kartesz	Carter 1979	NY (EV), OH (E)
Myrica gale L.	Brooks 1987	NC (E), PA (T)

	Carter 1979	
NAJADACEAE		
Najas gracillima Morong	Zika and Dann 1985	IN (E), KY (SC), ME (SC), MD (E, X), OH (E), PA (T)
NYSSACEAE		
Nyssa sylvatica Marshall	Brooks 1987 Mansberg and Wentworth 1984 Miller 1981 Wherry 1963	—
ONAGRACEAE		
Circaea alpina L.	Brooks 1987 Dearden 1979	IL (E), IN (X), KY (SC)
Epilobium ciliatum Raf. subsp. *glandulosum* (Lehm.) Hoch & P.H. Raven	Carter 1979	NY (E)
Oenothera biennis L.	Carter 1979	—
O. fruticosa L.	Miller 1981 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall and Farr 1990 Tyndall 2005 Wherry 1963	CT (SC)
O. fruticosa subsp. *fruticosa* L.	Brooks 1987	—
O. fruticosa L. subsp. *glauca* (Michx.) Straley	Mansberg and Wentworth 1984	—
OPHIOGLOSSACEAE		
Botrychium dissectum Spreng.	Wherry 1963	NY (EV)
B. virginianum (L.) Sw.	Carter 1979	NY (EV)
ORCHIDACEAE		
Goodyera pubescens (Willd.) R. Br.	Mansberg and Wentworth 1984 Wherry 1963	FL (E), NY (EV), QC (S2)
G. tesselata Lodd.	Carter 1979	MD (E, X), NJ (E), NY (EV), OH (PRX), PA (T)
Liparis liliifolia (L.) Lindl.	Wherry 1963	CT (E), MA (T), NY (E), RI (E), VT (T)
L. loeselii (L.) Rich.	Wherry 1963	AR (T), KY (T), NH (T), NY (EV), TN (E), WA (E)
Malaxis unifolia Michx.	Wherry 1963	CT (E), FL (E), IN (E), NH (T), NY (EV), RI (E)
Platanthera dilatata var. *dilatata* (Pursh) Beck	Carter 1979	CT (SC), IN (E), MA

		(T), NY (EV), PA (E)
P. flava var. *flava* (L.) Lindl.	Wherry 1963	IL (E), IN (E), NJ (E), TN (SC)
Spiranthes lacera (Raf.) Raf. var. *gracilis* (Bigelow) Luer	Wherry 1963	ME (PX)
S. tuberosa Raf.	Wherry 1963	CT (SC), FL (T), NY (EV), PA (X), RI (E)
OSMUNDACEAE		
Osmunda cinnamomea L.	Carter 1979	FL (CE), IA (E), NY (EV)
O. claytoniana L.	Carter 1979	AR (T), NY (EV)
O. regalis L.	Wherry 1963	FL (CE), IA (T), NY (EV)
OXALIDACEAE		
Oxalis montana Raf.	Carter 1979	OH (PRX)
O. stricta L.	Brooks 1987 Wherry 1963	—
PINACEAE		
Abies balsamea (L.) Mill.	Brooks 1987 Carter 1979 Tyndall and Hull 1999	CT (E)
Larix laricina (Du Roi) K.Koch	Brooks 1987 Dearden 1979 Roberts 1980	IL (T), MD (E), NL (S5)
Picea glauca (Moench) Voss	Brooks 1987	—
P. glauca (Moench) Voss	Carter 1979	—
P. mariana Britton, Sterns & Poggenb.	Brooks 1987 Carter 1979 Roberts 1980	NL (S5)
P. rubens Sarg.	Zika and Dann 1985	CT (SC), NJ (E)
Pinus echinata	Tyndall and Hull 1999	
P. resinosa Mill.	Brooks 1987 Carter 1979	CT (E), IL (E), NJ (E)
P. rigida Mill.	Brooks 1987 Mansberg and Wentworth 1984 Miller 1981 Tyndall and Hull 1999 Wherry 1963	QC (S1)
P. strobus L.	Brooks 1987 Carter 1979 Zika and Dann 1985	IN (R)
P. virginiana Mill.	Brooks 1987 Miller 1981 Tyndall and Farr 1990	NY (E)

	Tyndall and Hull 1999 Tyndall 2005 Wherry 1963	
Tsuga canadensis Carrière	Brooks 1987 Mansberg and Wentworth 1984	—
PLANTAGINACEAE		
Plantago maritima L. var. *juncoides* (Lam.) A. Gray	Carter 1979	NY (T)
PLUMBAGINACEAE		
Armeria maritima (Mill.) Willd. subsp. *sibirica* (Boiss.) Nyman	Brooks 1987 Dearden 1979 Roberts 1980	—
Limonium carolinianum (Walter) Britton	Carter 1979	NY (EV)
POACEAE		
Agrostis capillaris L.	Carter 1979	—
A. hyemalis (Walter) Britton, Sterns & Poggenb.	Tyndall 2005 Wherry 1963	—
A. mertensii Trin.	Zika and Dann 1985	—
A. perennans (Walter) Tuck.	Brooks 1987 Carter 1979 Wherry 1963	—
A. stolonifera L.	Tyndall and Farr 1990	—
Andropogon gerardii Vitman	Mansberg and Wentworth 1984 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall 2005 Wheeler 1988 Wherry 1963	—
Anthoxanthum odoratum L.	Miller 1981	—
Aristida dichotoma Michx.	Brooks 1987 Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	MI (PREX)
A. longispica Poir.	Tyndall and Hull 1999 Wherry 1963	CT (SC), MI (T)
A. oligantha Michx.	Wherry 1963	—
A. purpurascens Poir.	Brooks 1987 Maoui 1966 Tyndall and Hull 1999	CT (SC), MA (T), PA (T)

	Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	
Bouteloua curtipendula (Michx.) Torr.	Brooks 1987 Nixon and McMillan 1964 Wherry 1963	CT (E), KY (SC), MI (T), NJ (E), NY (E), PA (T)
B. hirsute Lag.	Nixon and McMillan 1964	AR (E)
B. rigidiseta Hitchc.	Maoui 1966	AR (E)
Bromus ciliatus var. *ciliatus* L.	Carter 1979	MD (E, X)
Calamagrostis canadensis (Michx.) P. Beauv.	Carter 1979	—
Cinna latifolia Griseb.	Carter 1979	MD (T), NJ (E), OH (E)
Danthonia intermedia Vasey	Brooks 1987 Hay et al. 1994 Tyndall and Hull 1999	NL (S1,S2)
D. spicata (L.) Roem. & Schult.	Carter 1979 Mansberg and Wentworth 1984 Tyndall and Farr 1990 Tyndall 2005 Wherry 1963	—
Deschampsia alpina (L.) Roem. & Schult.	Brooks 1987	—
D. caespitosa (L.) P. Beauv.	Brooks 1987 Mansberg and Wentworth 1984 Roberts 1980 Wherry 1963 Zika and Dann 1985	CT (SC), IN (R), MD (E), KY (E), MA (E)
D. flexuosa (L.) Trin.	Carter 1979 Roberts 1980 Zika and Dann 1985	KY (T)
Dichanthelium acuminatum (Sw.) Gould & C.A. Clark var. *fasciculatum* (Torr.) Freckmann	Carter 1979 Wherry 1963	IN (X), TN (E)
D. acuminatum (Sw.) Gould & C.A. Clark var. *lindheimeri* (Nash) Gould & C. A. Clark	Wherry 1963	OH (E)
D. boscii (Poir.) Gould & C. A. Clark	Mansberg and Wentworth 1984 Wherry 1963	—
D. clandestinum (L.) Gould	Brooks 1987 Wherry 1963	—
D. depauperatum (Muhl.) Gould	Tyndall and Farr 1990 Tyndall and Hull 1999	—

	Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	
D. dichotomum var. *dichotomum* (L.) Gould	Brooks 1987 Mansberg and Wentworth 1984 Wherry 1963	MA (E), IN (E), PA (E), FL (T), IL (E), OH (E)
D. linearifolium (Scribn.) Gould	Brooks 1987 Wherry 1963	—
D. meridionale (Ashe) Freckmann	Wherry 1963	OH (T)
D. oligosanthes var. *oligosanthes* (Schult.) Gould	Tyndall and Hull 1999	NY (E)
D. oligosanthes (Schult.) Gould var. *scribnerianum* (Nash) Gould	Wherry 1963	NY (E), PA (E)
D. ovale (Elliot) Gould & C. A. Clark var. *addisonii* (Nash) Gould & C. A. Clark	Tyndall 2005 Wherry 1963	OH (E), PA (X), IN (R)
D. sphaerocarpon (Elliot) Gould var. *isophyllum* (Scribn.) Gould & C. A. Clark	Wherry 1963	MI (E)
D. sphaerocarpon var. *sphaerocarpon* (Elliot) Gould	Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	CT (SC), NH (E)
D. villosissimum var. villosissimum (Nash) Freckmann	Wherry 1963	MA (SC), OH (PRX)
Digitaria cognata (Schult.) Pilg.	Maoui 1966	PA (T)
D. filiformis (L.) Koeler	Wherry 1963	MI (PREX), NY (T), OH (PRX)
Elymus repens (L.) Gould	Carter 1979	
E. trachycaulus subsp. *trachycaulus* (Link) Gould	Brooks 1987 Mansberg and Wentworth 1984	MD (E, X)
E. virginicus L.	Carter 1979	—
Eragrostis intermedia Hitchc.	Maoui 1966	—
E. pectinacea (Michx.) Nees	Wherry 1963	—
E. spectabilis (Pursh) Steud.	Tyndall and Farr 1990 Tyndall 2005	—
Festuca altaica Trin.	Brooks 1987 Hay et al. 1994 Tyndall and Hull 1999	MI (T), NL (S2), QC (S2, S3)
F. filiformis Lam.	Carter 1979	—
F. rubra L.	Brooks 1987 Dearden 1979	ME (E), NH (E),

Glyceria melicaria (Michx.) F. T. Hubb.	Carter 1979	—
G. striata (Lam.) Hitchc.	Carter 1979 Wherry 1963	—
Hierochloe odorata (L.) P. Beauv.	Carter 1979	MD (E), NC (E), PA (E)
Hilaria belangeri (Steud.) Nash	Nixon and McMillan 1964	—
Leersia oryzoides (L.) Sw.	Wherry 1963	—
L. virginica Willd.	Wherry 1963	NH (T), WI (T)
Lolium pratense (Huds.) Darbysh.	Carter 1979	
Muhlenbergia glomerata Trin.	Brooks 1987 Mansberg and Wentworth 1984	WA (S)
M. mexicana Trin.	Wherry 1963	—
M. sylvatica Trin.	Wherry 1963	QC (S2)
Nassella leucotricha (Trin. & Rupr.) R. W. Pohl	Maoui 1966	—
Oryzopsis asperifolia Michx.	Brooks 1987 Carter 1979	IN (E), MD (T), NJ (E), OH (E)
Panicum anceps Michx.	Wherry 1963	—
P. capillare L.	Wherry 1963	—
P. dichotomiflorum Michx.	Wherry 1963	—
P. flexile Scribn.	Tyndall and Hull 1999	MD (E), NJ (E), NY (T), VT (E), QC (S2)
P. gattingeri Nash	Wherry 1963	MA (SC)
P. hallii Vasey	Maoui 1966	—
P. philadelphicum Trin.	Tyndall and Hull 1999 Wherry 1963	IA (T), MA (SC), NH (E), OH (T), PA (T), QC (S2)
P. virgatum L.	Nixon and McMillan 1964 Wherry 1963	QC (S1)
Paspalum laeve Michx.	Wherry 1963	CT (E), NY (E)
P. setaceum Michx.	Wherry 1963	CT (SC), NY (T)
Phalaris arundinacea L.	Carter 1979	—
Piptochaetium avenaceum (L.) Parodi	Tyndall and Hull 1999	IN (T), OH (PRX), PA (X)
Poa compressa L.	Tyndall 2005	—
P. palustris L.	Carter 1979	TN (E)
P. pratensis L.	Brooks 1987 Carter 1979 Wherry 1963	—
P. saltuensis Fernald & Wiegand	Mansberg and Wentworth 1984	KY (E), MD (E), NJ (E), OH (E), TN (SC), IL (E), MA (E), PA (T)
Puccinellia distans (Jacq.) Parl.	Brooks 1987	—

P. maritima Parl.	Carter 1979	—
P. tenella A. E. Porsild subsp. *alaskana* (Scribn. & Merr.) Tzvelev	Carter 1979	CT (SC), NH (E)
Schizachne purpurascens Swallen	Carter 1979	CT (SC), IL (E), IN (E), KY (T), MD (E), NJ (E), OH (E)
Schizachyrium scoparium (Michx.) Nash	Flanagan-Brown 2001 Nixon and McMillan 1964 Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall 2005	OH (E), PA (R)
S. scoparium var. *scoparium* (Michx.) Nash	Brooks1987 Mansberg and Wentworth 1984 Miller 1981 Wherry 1963	—
Setaria faberi Herrm.	Wherry 1963	—
S. parviflora (Poir.) Kerguélen	Wherry 1963	MA (SC), IN (E)
S. pumila (Poir.) Roem. & Schult. subsp. *pallidifusca* (Schumach.) B. K. Simon	Carter 1979	—
Sorghastrum nutans (L.) Nash.	Brooks 1987 Flanagan-Brown 2001 Nixon and McMillan 1964 Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 1994 Tyndall 2005 Wherry 1963	ME (E), QC (S3)
Spartina pectinata Link	Carter 1979	WA (S)
Sphenopholis obtusata (Michx.) Scribn.	Brooks 1987 Tyndall and Farr 1990 Wherry 1963	ME (PX), NH (E), NY (E), OH (T), VT (E)
Sporobolus cryptandrus A. Gray	Maoui 1966	CT (E), NH (T), PA (R), QC (S2)
S. heterolepis A.Gray	Brooks 1987 Mansberg and Wentworth 1984 Tyndall and Farr 1990 Tyndall and Hull 1999 Wherry 1963	CT (E), KY (E), MD (E), NY (T), NC (E), OH (T), PA (E), QC (S2)
S. vaginiflorus (A. Gray) Alph. Wood	Wherry 1963	—
Tridens flavus var. *flavus* Hitchc.	Wherry 1963	—

Vulpia octoflora (Walter) Rydb.var. *glauca* (Nutt.) Fernald	Wherry 1963	NH (E)
POLEMONIACEAE		
Phlox carolina L.	Mansberg and Wentworth 1984	MD (E, X)
P. subulata subsp. *subulata* L.	Brooks 1987 Tyndall 2005 Wherry 1963	TN (T)
POLYGALACEAE		
Polygala ambigua Nutt.	Wherry 1963	—
P. paucifolia Willd.	Brooks 1987 Mansberg and Wentworth 1984	IN (E), KY (E), OH (E)
P. sanguinea L.	Wherry 1963	—
P. senega L.	Wherry 1963	CT (E), ME (E), MD (T), NJ (E), QC (S2)
P. verticillata L.	Brooks 1987	—
POLYGONACEAE		
Polygonum aviculare L.	Hart 1980	—
P. cilinode Michx.	Carter 1979	IN (E), OH (E), TN (T)
P. cuspidatum Siebold & Zucc.	Carter 1979	—
P. persicaria L.	Carter 1979	MA (SC)
P. sagittatum L.	Carter 1979	—
P. tenue Michx.	Brooks 1987 Hart 1980 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall and Farr 1990	ME (PX), NH (E), NY (R)
Rumex acetosella L.	Carter 1979	—
R. crispus L.	Carter 1979	—
POLYPODIACEAE		
Athyrium filix-femina (L.) Roth	Carter 1979 Wherry 1963	FL (T), NY (EV)
Polypodium virginianum L.	Carter 1979 Rugg 1922 Zika and Dann 1985	NY (EV)
PORTULACACEAE		
Claytonia caroliniana Michx.	Carter 1979	—
Talinum teretifolium Pursh	Brooks 1987 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall and Farr 1990 Wherry 1963	—

PRIMULACEAE		
Androsace septentrionalis L.	Brooks1987 Dearden 1979	—
Glaux maritima L.	Carter 1979	MD (E, X), MN (E), NJ (E), RI (H)
Lysimachia quadrifolia L.	Mansberg and Wentworth 1984 Wherry 1963	NY (E), TN (SC)
L. terrestris Britton, Sterns & Poggenb.	Carter 1979	KY (E), TN (E)
Primula mistassinica Michx.	Dearden 1979	IL (E), ME (SC), NY (T), VT (T)
P. stricta Hornem.	Hay et al. 1994	NL (S1)
Trientalis borealis Raf.	Brooks 1987 Carter 1979 Dearden 1979 Zika and Dann 1985	GA (E), IL (T), KY (E), TN (T)
PTERIDACEAE		
Adiantum aleuticum (Rupr.) C.A.Paris	Paris 1991 Paris and Windham 1988 Tyndall and Hull 1999	ME (E), QC (S2)
A. aleuticum (Rupr.) C.A.Paris (as *A. pedatum* L. subsp. *calderi* Cody)	Cody 1983 Paris 1991 Paris and Windham 1988	—
A. aleuticum (Rupr.) C.A.Paris (as *A. pedatum* L. var. *aleuticum* Rupr.)	Brooks 1987 Carter 1979 Cody 1983 Dearden 1979 Paris 1991 Paris and Windham 1988 Rugg 1922 Tyndall and Hull 1999 Zika and Dann 1985	—
A. pedatum L.	Carter 1979 Wherry 1963	NY (EV), QC (S4)
A. viridimontanum C.A.Paris	Paris 1991 Tyndall and Hull 1999	G2, VT (T), QC (S3)
Aspidotis densa (Brack.) Lellinger	Brooks 1987 Tyndall and Hull 1999	QC (S1)
PYROLACEAE		
Chimaphila maculata (L.) Pursh	Mansberg and Wentworth 1984 Wherry 1963	IL (E), ME (E), NY (EV)
C. umbellata (L.) W. Bartram subsp. *cisatlantica*	Carter 1979	IN (T)

(S.F. Blake) Hultén	Wherry 1963	
Pyrola americana Sweet	Wherry 1963	IN (R), KY (H), TN (E)
P. elliptica Nutt.	Wherry 1963	—
RANUNCULACEAE		
Actaea rubra (Aiton) Willd.	Carter 1979	IN (R), OH (T)
Coptis trifolia Salisb.	Carter 1979	MD (E), WA (S)
Ranunculus abortivus L.	Carter 1979	—
R. lapponicus L.	Sirois et al. 1988	ME (T), MI (T), WI (E)
R. pedatifidus Sm. var. *affinis* (R. Br.) L.D. Benson	Hay et al. 1992	NL (S2)
Thalictrum alpinum L.	Brooks 1987 Dearden 1979	—
T. macrostylum Small & A.Heller	Brooks 1987 Mansberg and Wentworth 1984 Tyndall and Hull 1999	—
T. pubescens Pursh	Carter 1979	IN (T)
T. revolutum DC.	Hay et al. 1994 Wherry 1963	IA (E), RI (H), QC (S1)
T. thalictroides (L.) Eames & B.Boivin	Wherry 1963	FL (E), ME (PX), NH (T)
RHAMNACEAE		
Ceanothus americanus L.	Ryan 1988 Wherry 1963	ME (T), QC (S2)
Frangula alnus Mill.	Tyndall and Hull 1999	—
ROSACEAE		
Amelanchier arborea (F.Michx.) Fernald	Brooks 1987 Carter 1979 Miller 1981 Mansberg and Wentworth 1984 Wherry 1963	—
A. bartramiana (Tausch) M. Roem.	Carter 1979	MA (T), PA (E)
A. laevis Wiegand	Wherry 1963	
Dalibarda repens L.	Carter 1979	CT (E), MI (T), NJ (E), NC (E), OH (T), RI (E)
Fragaria virginiana Mill.	Carter 1979	
Malus coronaria var. *coronaria* (L.) Mill.	Wherry 1963	NY (E)
M. sylvestris Mill.	Carter 1979	—
Photinia melanocarpa (Michx.) K.R.Robertson & J.B.Phipps	Wherry 1963	IA (E)
Physocarpus opulifolius (L.) Maxim.	Mansberg and Wentworth 1984	FL (E)

Potentilla canadensis L.	Brooks 1987 Mansberg and Wentworth 1984 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	—
P. fruticosa L	Brooks 1987	—
P. simplex Michx.	Carter 1979	—
Prunus americana Marshall	Wherry 1963	NH (T), VT (T)
P. pensylvanica L. f.	Brooks 1987 Carter 1979	IN (R)
P. serotina Ehrh.	Miller 1981	—
P. virginiana L.	Carter 1979	TN (SC)
Rosa carolina L.	Carter 1979 Wherry 1973	
R. multiflora Murray	Miller 1981	—
R. virginiana Mill.	Brooks 1987 Carter 1979	—
Rubus allegheniensis Porter	Miller 1981	—
R. argutus Link	Wherry 1963	—
R. cuneifolius Pursh	Tyndall and Hull 1999	CT (SC), NH (E), NY (E), PA (E)
R. flagellaris Willd.	Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall and Farr 1990 Tyndall 2005 Wherry 1963	IN (E), QC (S2)
R. frondosus Bigel.	Wherry 1963	—
R. hispidus L.	Carter 1979	—
R. idaeus subsp. *strigosus* (Michx.) Focke	Carter 1979	—
R. occidentalis L.	Miller 1981 Wherry 1963	—
R. pensilvanicus Poir.	Wherry 1963	—
R. pubescens Raf.	Brooks 1987 Carter 1979 Dearden 1979	IL (T)
Sanguisorba canadensis L.	Brooks 1987 Wherry 1963	GA (T), IL (E), IN (E), KY (E), ME (T), MD (T), MI (T), RI (E), TN (E)
Sibbaldia procumbens L.	Hay et al. 1992	NH (E), NL (S1)
Sibbaldiopsis tridentata (Aiton) Rydb.	Roberts 1980	CT (E), GA (E), IA

		(E), NJ (E), PA (E), RI (H), TN (SC)
Sorbus americana Marshall	Carter 1979	IL (E)
S. decora C.K.Schneid.	Carter 1979	IN (X), MA (E), OH (E), PA (E)
S. groenlandica (C.K.Schneid.) Á.Löve & D.Löve	Carter 1979	—
Spiraea alba Du Roi var. *latifolia* (Aiton) Dippel	Zika and Dann 1985 Wherry 1963	OH (PRX)
RUBIACEAE		
Galium aparine L.	Miller 1981	—
G. asprellum Michx.	Carter 1979 Wherry 1963	TN (SC)
G. boreale L.	Tyndall and Hull 1999 Wherry 1963	—
G. pilosum Aiton	Wherry 1963	NH (E)
G. tinctorium L.	Wherry 1963	—
G. triflorum Michx.	Carter 1979 Wherry 1963	—
Houstonia caerulea L.	Brooks 1987 Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 1994 Tyndall 2005 Wherry 1963	—
H. serpyllifolia Michx.	Mansberg and Wentworth 1984	KY (E), PA (X)
Mitchella repens L.	Wherry 1963	IA (T)
SALICACEAE		
Populus grandidentata Michx.	Miller 1981 Wherry 1963	TN (SC)
P. tremuloides Michx.	Carter 1979 Miller 1981	—
Salix arctica Richardson	Brooks 1987 Dearden 1979 Hay et al. 1994 Roberts 1980 Tyndall and Hull 1999	NL (S2)
S. arctophila Cockerell	Hay et al. 1992	ME (E), NL (S2)
S. argyrocarpa Andersson	Hay et al. 1994	ME (E), NH (T), NL (S1)
S. brachycarpa Nutt.	Brooks 1987	—
S. calcicola Fernald & Wiegand	Hay et al. 1992	NL (S3)
S. cordata Muhl.	Hay et al. 1992	IL (E), NY (E), WI (E), NL (S1)

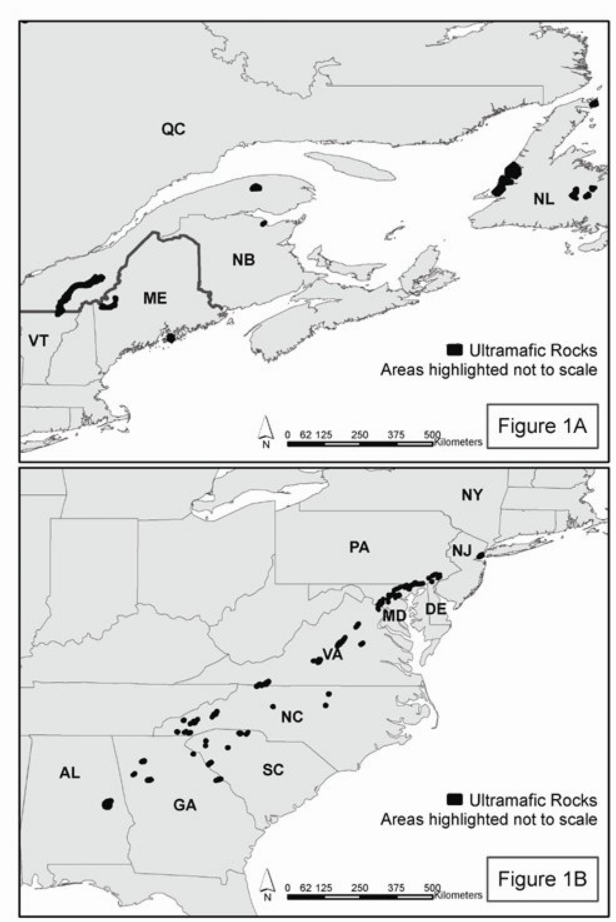
S. discolor Muhl.	Carter 1979	KY (H)
S. herbacea L.	Hay et al. 1992 Hay et al. 1994	ME (T), NH (T), NY (E), NL (S2)
S. humilis Marsh. var. *tristis* (Aiton) Griggs	Tyndall and Hull 1999 Wherry 1963	—
S. pedunculata Fernald	Hay et al. 1992	—
S. reticulata L.	Hay et al. 1992	—
S. × *wiegandii* Fernald	Hay et al. 1992	—
SANTALACEAE		
Comandra umbellata Nutt.	Wherry 1963	—
SAXIFRAGACEAE		
Chrysosplenium americanum Hook.	Carter 1979	IN (T), KY (E)
Parnassia grandifolia DC.	Brooks 1987	FL (E), KY (E), NC (T), TN (SC)
Saxifraga aizoides L.	Brooks 1987 Dearden 1979	NY (T)
S. oppositifolia L.	Brooks 1987 Dearden 1979	NY (E)
S. rivularis L.	Hay et al. 1992	NH (E), WA (S), NL (S2)
S. virginiensis Michx.	Brooks 1987 Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Wherry 1963 Zika and Dann 1985	IL (E), IN (R)
Tiarella cordifolia L.	Carter 1979	NJ (E), WI (E)
SCROPHULARIACEAE		
Agalinis acuta Pennell	Tyndall and Hull 1999 Tyndall 1994	G1, USA (E), CT (E), MD (E), MA (E), NY (E), RI (E)
A. obtusifolia Raf.	Brooks 1987	KY (E), MD (E)
A. paupercula (A. Gray) Britton var. *borealis* Pennell	Wherry 1963	OH (E), NY (T)
A. paupercula var. *paupercula* (A.Gray) Britton	Wherry 1963	PA (E)
A. tenuifolia var. *tenuifolia* (Vahl) Raf.	Wherry 1963	—
Aureolaria flava (L.) Farw.	Wherry 1963	—
A. pedicularia (L.) Raf.	Brooks 1987	IA (E), ME (SC), MN (T)
A. pedicularia var. *pedicularia* (L.) Raf.	Wherry 1963	OH (E)
Castilleja coccinea (L.) Spreng.	Brooks 1987 Mansberg and Wentworth 1984 Wherry 1963	CT (E), KY (E), ME (PX), MD (E), NY (E), RI (H)

C. septentrionalis Lindl.	Dearden 1979	ME (SC), MI (T), MN (E), NH (T), VT (T)
Chelone glabra L.	Wherry 1963	NY (EV)
Euphrasia nemorosa Pers.	Carter 1979	MI (T)
Linaria vulgaris Mill.	Brooks 1987	—
Melampyrum lineare Lam.	Brooks 1987 Carter 1979 Mansberg and Wentworth 1984	IN (R), OH (T)
Pedicularis canadensis L.	Mansberg and Wentworth 1984	—
Rhinanthus minor subsp. *minor* L.	Carter 1979	—
Schwalbea americana L.	Hay et al. 1992	G2, USA (E), CT (SC), FL (E), GA (E), KY (H), MD (E, X), NJ (E), NC (E), TN (PX, E)
Verbascum blattaria L.	Brooks 1987	—
V. thapsus L.	Carter 1979	—
Veronica americana Benth.	Carter 1979	IL (E), IN (X), KY (H), TN (SC)
Veronicastrum virginicum Farw.	Wherry 1963	MA (T), NY (T), VT (E)
SELAGINELLACEAE		
Selaginella rupestris (L.) Spring	Carter, 1979	IN (T), OH (PRX)
S. selaginoides (L.) Mart. & Schrank	Hay et al. 1992	ME (T), MN (E), WI (E), NL (S4, S5)
SMILACACEAE		
Smilax glauca Walter	Mansberg and Wentworth 1984 Miller 1981 Tyndall and Farr 1990 Wherry 1963	—
S. herbacea L.	Wherry 1963	—
S. rotundifolia L.	Hull and Wood 1984 Mansberg and Wentworth 1984 Miller 1981 Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	—
SOLANACEAE		

Solanum dulcamara L.	Carter 1979	—
THELYPTERIDACEAE		
Phegopteris connectilis (Michx.) Watt	Carter 1979	IL (E), IA (E), NY (EV), TN (SC)
P. hexagonoptera (Michx.) Fée	Wherry 1963	ME (SC), MN (T), NY (EV), QC (S2)
Thelypteris noveboracensis (L.) Nieuwl.	Mansberg and Wentworth 1984 Wherry 1963	IL (E), NY (EV)
T. simulata (Davenport) Nieuwl.	Tyndall and Hull 1999 Zika and Dann 1985	MD (T), NY (EV), NC (T), TN (PX, E), QC (SH)
TYPHACEAE		
Typha angustifolia L.	Wherry 1963	—
T. latifolia L.	Wherry 1963	—
URTICACEAE		
Boehmeria cylindrica (L.) Sw.	Wherry 1963	—
VIOLACEAE		
Viola blanda var. *palustriformis* A. Gray	Carter 1979	IL (E), IA (E)
V. conspersa Rchb.	Wherry 1963	—
V. macloskeyi subsp. *pallens* (Ging) M.S. Baker	Carter 1979	—
V. palmata L.	Wherry 1963	ME (PX), NH (E)
V. palustris L.	Hay et al. 1994	ME (E), NH (T), NL (S2, S3)
V. pedata L.	Brooks 1987 Wherry 1963	NH (T), NY (EV), OH (T)
V. sagittata Ait.	Pennell 1930 Tyndall and Farr 1990 Tyndall and Hull 1999 Tyndall 1992b Tyndall 1994 Tyndall 2005 Wherry 1963	—
V. sagittata var. *ovata* (Nutt.) Torr. & A. Gray	Brooks 1987 Pennell 1930	WI (E), QC (S1)
V. sororia Willd.	Carter 1979	—
VITACEAE		
Vitis aestivalis Michx.	Wherry 1963	ME (E)

Figure 1. Locations of ultramafic rock exposures in the northern (a) and southern (b) Appalachian regions. Localities based on Larrabee (1966) and E. B. Alexander (unpubl. data). Credit: Jose Perez-Orozco and Apoorv Gehlot

Figure 2. A sharply-demarcated floristic boundary under the control of an edaphic boundary at Jasper Ridge Biological Preserve, San Mateo County, California. The yellow-flowered *Lasthenia californica* (Asteraceae; in background) is restricted to serpentine soils. The boundary between *L. californica* and grasses is defined by a serpentine-sandstone transition. Credit: Bruce A. Bohm


QC
NL
NB
ME
VT
Ultramafic Rocks
Areas highlighted not to scale
0 62 125 250 375 500 Kilometers
N
Figure 1A
NY
PA
NJ
MD
DE
VA
NC
SC
AL
GA
Ultramafic Rocks
Areas highlighted not to scale
0 62 125 250 375 500 Kilometers
N
Figure 1B