

VASCULAR PLANTS OF ADJACENT SERPENTINE AND
GRANITE OUTCROPS ON THE DEER ISLES, MAINE, U.S.A.

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ABSTRACT. We performed a comparative study of the vascular flora of a serpentine outcrop, Pine Hill, and that of a granite outcrop, Settlement Quarry, from Little Deer Isle and Deer Isle, respectively, Hancock County, Maine. We established four transects along a gradient from exposed to forested areas within each outcrop. Plants were recorded for presence and percent cover from circular plots along each transect. Soil and tissue samples were collected to examine soil-tissue elemental relations. One hundred thirty-two taxa were recorded from serpentine and 89 from granite. Fifty-seven taxa were shared by both sites. Species richness (α diversity) and diversity indices (Shannon-Weaver and Simpson) suggested significant differences between sites and within sites. Principle Component Analysis suggested substrates differed significantly between sites and between exposures within sites. Tissue analyses suggested intraspecific variation with respect to tissue elemental concentrations, especially in *Achillea millefolium*, *Oenothera biennis*, *Prunus virginiana*, *Selaginella rupestris*, *Spiraea alba* var. *latifolia*, and *Vaccinium angustifolium*. Serpentine populations of many taxa showed low tissue Ca:Mg ratios (< 1) and high Ni concentrations. Two-way ANOVA showed significant substrate \times species effects for several elements, including those that typically characterize serpentine substrates (Ca, Mg, Cr, Ni), suggesting significant genetic variation within species with respect to substrate. Finally, we compared our species list for Pine Hill with a plant survey done at Pine Hill and five additional serpentine sites of Maine in 1977 and provide a list of 285 vascular plant taxa from 62 families for serpentine in Maine.

Key Words: serpentine ecology, forest ecology, species diversity, geoecology, plant-soil relations

Serpentine habitats are found on peridotite and related ultramafic rocks, and the soils derived from such rocks provide harsh conditions for plant growth (Brady et al. 2005). The unique biogeochemistry of serpentine soil, characterized by key nutrient

deficiencies and imbalances, is responsible for the prevalence of rare native species, exclusion of alien species, and ecotype formation within those species that do not readily grow on serpentine soil (Alexander et al. 2007). Serpentine soils generally have a near-neutral pH, are high in metals such as Ni, Co, and Cr, and are low in many essential nutrients such as P, K, and Mo (Kruckeberg 1984; Walker 2001). Although serpentine soils have often been considered poor in N (Kruckeberg 2002), this trend generally applies only to serpentine barrens with little or no vegetation (Alexander et al. 2007). Further, increased input of nutrients, including N, from atmospheric sources has altered the nutrient status on serpentine (Weiss 1999) in recent years, with nutrient enrichment leading to drastic changes in species composition and interactions (Harrison and Viers 2007; Zavaleta et al. 2003). Ratios of Ca:Mg, often considered the prime determinant of serpentine tolerance (Gabrielli et al. 1990; Grace et al. 2007; Harrison 1999a,b), are generally <1 in serpentine soils and 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, often with a reduced capacity for moisture retention (Kruckeberg 2002). Given the extreme nature of these soils, their biota is often uniquely adapted and frequently restricted to such habitats (Rajakaruna and Boyd 2008).

The study of serpentine soils and associated vegetation in eastern North America has been minimal compared to that of western North America (Rajakaruna, Harris, and Alexander 2009). Despite the relative lack of attention, serpentine outcrops occur sporadically along Appalachian range from Newfoundland to Alabama, with considerable latitudinal variation related to climate and soil development (Alexander 2009; Rajakaruna, Harris, and Alexander 2009). *Cerastium velutinum* var. *villosissimum* (Caryophyllaceae) is the only recognized serpentine endemic plant for eastern North America while *Symphiotrichum depauperatum* (Asteraceae) is largely restricted to the substrate (Rajakaruna, Harris, and Alexander 2009). Harris and Rajakaruna (2009) recommended that *Adiantum viridimontanum* (Pteridaceae), *Aspidotis densa* (Pteridaceae), *Minuartia marcescens* (Caryophyllaceae), and *Symphiotrichum rhiannon* be considered endemic to serpentine of eastern

North America. Compared to western North America's 176 serpentine endemics (Safford et al. 2005), serpentine endemism is strikingly low in eastern North America (Harris and Rajakaruna 2009).

Having been glaciated as recently as approximately 13,000 years ago (Alexander 2009; Roberts 1992), the relative youth of serpentine outcrops in the northern part of the Appalachians may be responsible for the indistinctness of the region's serpentine flora compared to that of western North America (Rajakaruna, Harris, and Alexander 2009). The addition of glacial till may further ameliorate the generally stressful conditions of serpentine by buffering vegetation from heavy metal toxicity, increasing nutrient levels, and adding organic matter content, thereby increasing the water retention capacity of the soil (Rajakaruna, Harris, and Alexander 2009).

In Maine, serpentine occurs scattered in the coastal regions and along the Appalachian orogen (Alexander 2009). The only systematic examination of Maine's serpentine flora is the unpublished thesis of Carter (1979), who performed a phytogeographical survey of selected serpentine areas in Maine, including Little Deer Isle and Deer Isle (Hancock County), Bowmantown (Oxford County), White Cap Mountain (two sites, east and west; Franklin County), and Little Spencer Stream (Somerset County). The serpentine sites of Maine range from exposed outcrops with fine layers of glacial till to forested areas with much glacial till and few exposed boulders (Carter 1979). Edaphic heterogeneity has led to rocky outcrop vegetation, typical of serpentine outcrops worldwide, alongside forested habitats characteristic of regional forests (Carter 1979; Rajakaruna, Harris, and Alexander 2009). The vegetation demonstrates a variety of regional affinities including Arctic, Boreal, Canadian-Alleghanian, and Alleghanian (Carter 1979). Carter's list includes 242 taxa of currently recognized vascular plants from 59 families for the six serpentine areas he examined.

The goal of the current study was to perform a systematic survey of the vascular plants of the Pine Hill serpentine outcrop on Little Deer Isle, Maine, and compare it to the flora of Settlement Quarry, a nearby granite quarry of similar aspect, climate, and land-use history, to elucidate the effect of substrate on resident vegetation. Given that both serpentine and granitic outcrops consisted of exposed and forested habitats, we also explored the effect of

exposure on plant diversity at each outcrop. In addition, we analyzed elemental concentrations for soil and plant tissue to characterize the soil chemistry and reveal the effect of soil elemental differences upon select species at both Pine Hill and Settlement Quarry. We hypothesized that (a) substrates will show significant differences in soil characteristics, (b) substrates will be distinct between forested and exposed regions at both sites as well as within sites due to the differences relating to vegetation cover and soil depth, (c) such differences in substrate will lead to distinct floristic compositions between and within sites, and (d) tissue elemental concentrations of taxa on and off of serpentine will vary with respect to substrate. We also compared our species list to that of Carter (1979) to better document the taxa associated with serpentine habitats in Maine. Finally, we examined the similarity of taxa among the six serpentine sites.

MATERIALS AND METHODS

Site descriptions. Vascular plants were collected from May to September, 2007, from Pine Hill and Settlement Quarry on Little Deer Isle and Deer Isle, respectively, in Hancock County, Maine, U.S.A. Pine Hill is a former peridotite (herein serpentine) quarry on Little Deer Isle ($44^{\circ}17'07.3''\text{N}$, $68^{\circ}42'06.7''\text{W}$, WGS 84). The site is approximately 0.16 km^2 and located approximately 0.8 km inland from Penobscot Bay. See Harris et al. (2007) for a detailed description of the site and history of quarry activities.

Settlement Quarry is a former granite quarry on adjacent Deer Isle ($44^{\circ}10'37.6''\text{N}$, $68^{\circ}38'20.7''\text{W}$, WGS 84), otherwise having aspect, altitude, climate, and land-use history similar to Pine Hill. The area of the quarry is approximately 4–5 times greater than Pine Hill, although the outcrop itself is located a similar distance inland from Penobscot Bay. See Briscoe et al. (2009) for a detailed description of the site and history of quarry activities.

Vegetation sampling. Four 135 m parallel transects running north-south were placed on each site on a gradient from exposed to forested areas. Circular plots were placed at 30 m intervals along each transect for a total of five plots per transect. Each plot had an area of 168 m^2 and contained three nested 1 m^2 subplots. The plots were derived from the Beyond NAWMA plots developed by the National Institute of Invasive Species Science (Stohlgren et al. 2005)

and were similar to widely used Modified-Whittaker plots (Changwe and Balkwill 2003; Stohlgren et al. 1995). Within each circular plot, all vascular species were identified and voucher specimens collected. Within each subplot, percent cover and number of individuals per species were recorded.

Plants were identified using Haines and Vining (1998) and Magee and Ahles (2007). Nomenclature follows Integrated Taxonomic Information System [website (<http://www.itis.gov>); accessed Nov 2007]. Voucher specimens were deposited at the herbarium of College of the Atlantic, Bar Harbor, Maine (HCOA). Using the species lists generated by Carter (1979) and the current study, we explored trends in species richness and similarities among coastal and inland serpentine sites in Maine.

Soil sampling and analysis. Three one-liter soil samples were collected from the soil surface to 10 cm depth from each subplot using a plastic trowel. Samples were pooled by plot for a total of five samples per transect. Samples were air dried in the laboratory for one week and stored in plastic bags. Analyses were carried out on the 2 mm fraction obtained using a brass sieve. Values for pH were obtained following Kalra and Maynard (1991) using the 1:2 soil-to-solution method with distilled water and 0.01M CaCl₂. Exchangeable acidity was measured by titration using an extraction in 1M KCl (Burt 2004). Electrical conductivity (EC) was measured using a saturated paste extraction with distilled water (Gavlak et al. 2003). Soils were analyzed for Al, Cd, Cr, Cu, Fe, Mn, Mo, Ni, Pb, and Zn by extraction with 0.005M diethylene triamine pentaacetic acid (DTPA) buffered with triethanolamine to pH 7.3 (Lindsay and Norvell 1978) for two hours and subsequent detection by ICP-OES using matrix-matched calibration standards. Soils were analyzed for exchangeable cations (Ca, K, Mg, and Na) by extraction with 1M neutral ammonium acetate (Kalra and Maynard 1991) and concentrations determined by ICP-OES analysis. Cation exchange capacity (CEC) was calculated by summation of milliequivalent levels of exchangeable cations and acidity. Metal and nutrient analyses were conducted by the Analytical Laboratory of the University of Maine at Orono (UMO).

Tissue collection and analysis. Three to five leaves were collected from three widely separated individuals of *Achillea millefolium*, *Ambrosia artemisiifolia*, *Cerastium fontanum*, *Festuca filiformis*, *Fragaria virginiana*, *Hieracium caespitosum*, *H. pilosella*, *Hypericum*

perforatum, *Morella pensylvanica*, *Oenothera biennis*, *Onoclea sensibilis*, *Prunus virginiana*, *Rosa virginiana*, *Selaginella rupestris*, *Spiraea alba* var. *latifolia*, *Vaccinium angustifolium*, and *Woodсия ilvensis* on Pine Hill for analysis of total Al, Ca, Cd, Cr, Cu, Fe, K, Mg, Mn, Mo, N, Na, Ni, P, and Zn tissue concentrations. Specimens of the same species (except *A. artemisiifolia*, *C. fontanum*, and *W. ilvensis*) were collected from Settlement Quarry in a similar fashion and analyzed for tissue elemental concentrations to provide a contrast to Pine Hill. Leaves were rinsed with distilled water in the field until rid of visible dust and other debris. Samples were then stirred in 100 ml distilled water for one minute in the laboratory at medium speed using a standard magnetic stirrer, strained with a small sieve, air dried for three days in paper towels before being dried at 110°C in a forced draft oven for 48 hours. Dried samples were placed in a desiccation chamber for 24 hours before being ground in a mortar with liquid nitrogen or in a coffee grinder. Tissue elemental concentrations for all elements but N were determined by dry ashing at 450°C for five hours, digesting in 50% HCl, and using inductively coupled plasmaspectroscopy (ICP-OES). Total tissue N was estimated by direct combustion analysis at 1150°C in pure oxygen with subsequent detection by thermal conductivity in the combustion gases. All analyses were conducted at the Analytical Laboratory of UMO.

Statistical analysis. All plots were separated into binary groups based on substrate (serpentine vs. granite) and exposure (forested vs. exposed). Plots were considered forested if they occurred under the canopy of a stand of adult trees and possessed low light at ground level; plots were otherwise considered exposed. Diversity indices were calculated for each plot based on pooled subplot data using the Shannon-Weaver Index (Shannon and Weaver 1949) and the Simpson Index (Simpson 1949). Corollary evenness values were recorded for the Shannon-Weaver Index. Species richness was also calculated for each plot. Diversity indices and richness values were compared between substrates and exposure types by two-way ANOVA.

Soil data for 18 soil chemical features were compared between Pine Hill and Settlement Quarry using one-way ANOVA, with regard for exposure within substrates (i.e., forested vs. exposed granite) and between substrates (i.e., forested granite vs. forested serpentine). Principal Component Analysis (PCA) was used to

cluster plots based on soil variables, and the results were plotted on two-axis scatter plots (Gotelli and Ellison 2004). The axes were extracted so that the first axis explained the greatest amount of variance in the original variables and the second axis explained much of the remaining variance.

Tissue elemental concentrations were compared between Pine Hill and Settlement Quarry using one-way ANOVA. Two-way ANOVA was used to examine relationships between species (except *Ambrosia artemisiifolia*, *Cerastium fontanum*, and *Woodsia ilvensis*) and substrate on element accumulation patterns for all elements except N. The three species were excluded because they were not collected from the granitic site, and N was excluded due to several samples with insufficient tissue for N analysis. All analyses were performed with SYSTAT 12 (SYSTAT Software Inc., San José, CA) using log-transformed data. Natural log transformations satisfied the assumptions for parametric tests. Results were considered significant at $P < 0.05$.

RESULTS

Floristics. The Appendix lists the vascular plants collected from Pine Hill and Settlement Quarry and five serpentine sites, including Pine Hill, surveyed by Carter (1979). During the current study, 132 taxa from 41 families were recorded from Pine Hill, and 89 taxa from 36 families were recorded from Settlement Quarry. Fifty-seven taxa were shared by both sites. At Pine Hill, families with the most genera and species included Asteraceae (14 genera, 22 species), Poaceae (11 genera, 16 species), and Rosaceae (eight genera, 12 species). At Settlement Quarry, those families included Rosaceae (nine genera, 13 species), Asteraceae (seven genera, 12 species), and Poaceae (six genera, nine species). At Pine Hill, the most speciose genera were *Carex* (11 species), *Solidago* (six species) and *Trifolium* (four species). At Settlement Quarry, the most speciose genera were *Carex* and *Hieracium* with four species each.

Carter (1979) recorded 100 taxa in 32 families for Pine Hill; 67 of those taxa were also found by us (Appendix). Sixty-four taxa were unique to our study while 30 were unique to the survey by Carter. The two studies have documented a total 162 taxa from 44 families from serpentine at Pine Hill. A total of 285 plants from 62 families are reported for the six serpentine sites of Maine. One taxon, *Abies balsamea*, was shared by all six sites; five taxa, *Betula papyrifera*

var. *papyrifera*, *Clintonia borealis*, *Gymnocarpium dryopteris*, *Monotropa uniflora*, and *Oxalis montana*, were shared by five sites; 11 taxa were shared by four sites; 24 taxa were shared by three sites; 56 taxa were shared by 2 sites; and 180 taxa were found at only one site. In order of their species richness the sites were Little Deer Isle (162 species), Deer Isle (100 species), Bowmantown (71 species), Little Spencer Stream (62 species), White Cap Mountain East (36 species), and White Cap Mountain West (23 species). The two coastal serpentine sites, Little Deer Isle and Deer Isle, harbored more species (211 taxa) than the remaining four inland serpentine sites (131 taxa).

Richness and diversity indices. A two-way ANOVA indicated that species richness (α diversity) and diversity indices (Shannon-Weaver and Simpson) were significantly different between sites and within sites. Species richness was significantly higher on exposed plots on serpentine (24.3 ± 2.5) than exposed plots on granite (15.5 ± 1.8) while forested plots on serpentine (15.9 ± 1.3) were significantly less species rich than forested plots on granite (23 ± 2.2). All diversity indices showed significantly greater diversity for exposed serpentine and forested granite than for forested serpentine and exposed granite, respectively. Species richness and diversity indices were also significantly different between exposed and forested sites within each substrate. A significant interaction between substrate and exposure was observed for species richness and diversity indices.

Soil analysis. A Principle Component Analysis (PCA) based on 16 soil variables (Al, Ca, Cd, Cr, Cu, Fe, K, Mg, Mn, Na, Ni, Pb, Zn, acidity, ECEC, and pH) suggested substrates differed significantly between sites and between exposures within sites (Tables 1, 2; Figure 1). The PCA Axis 1 is strongly correlated with variables Cd, ECEC, Na, Cr, K, Mg, Fe, and Mn while Axis 2 shows strong correlation to pH (Table 2). Axis 1 and Axis 2 describe 47.4% and 20.6%, respectively, of the variation seen between the sites. The cumulative variance between sites explained by the soil variables tested is 68%. Forested plots from serpentine and granite were edaphically more similar to each other than exposed plots of the two substrates (Figure 1). The forested plots between serpentine and granite differed significantly in ECEC, pH (0.01 M CaCl₂), Ca:Mg, Cd, Cr, Fe, Mg, and Ni while the exposed plots between the two substrates differed significantly in ECEC, pH

Table 1. Soil features for serpentine and granitic soils collected from Pine Hill and Settlement Quarry, respectively. At each site, soil samples were collected from exposed and forested sites. All values are means \pm SE. Elemental concentrations are reported as ppm ($\mu\text{g/g}$ dry soil). Exchangeable acidity (Acidity) was measured by titration using an extraction in 1 M KCl. Effective cation exchange capacity (ECEC) was measured in meq/100 g. Significant ($P < 0.05$) differences between exposed and forested sites within substrate are in bold. Means with * represent values significantly different between exposed sites of serpentine and granite. Means with ** represent values significantly different between forested sites of serpentine and granite.

Soil Feature	Serpentine		Granite	
	Exposed (n=6)	Forested (n=14)	Exposed (n=13)	Forested (n=6)
Acidity	0.81 (± 0.3)	3.6 (± 0.8)	0.95 (± 0.13)	5.0 (± 1.3)
ECEC	21.6* (± 3.6)	25.2** (± 3.2)	1.8* (± 0.3)	9.7** (± 2.1)
pH (H ₂ O)	5.9 (± 0.4)	4.9 (± 0.17)	4.97 (± 0.08)	4.4 (± 0.14)
pH (0.01M CaCl ₂)	5.3* (± 0.4)	3.96** (± 0.18)	4.1* (± 0.07)	3.3** (± 0.13)
Al	91.9 (± 33.8)	108.9 (± 12.4)	60.8 (± 8.6)	111.1 (± 22.6)
Ca	1183.7* (± 297.6)	1513.5 (± 306.3)	104.9* (± 21.1)	519.3 (± 184.4)
Ca:Mg	0.9* (± 0.2)	1.1** (± 0.3)	4.9 (± 0.5)	2.97** (± 0.6)
Cd	0.4* (± 0.07)	0.4** (± 0.04)	0.04* (± 0.01)	0.21** (± 0.04)
Cr	0.34* (± 0.08)	0.41** (± 0.04)	0.02* (± 0.001)	0.07** (± 0.01)
Cu	51.6 (± 47.9)	4.9 (± 1.5)	1.7 (± 0.4)	1.72 (± 0.4)
Fe	301.3 (± 95.6)	579.6** (± 54.9)	65.4 (± 10.9)	380.8** (± 66.3)
K	137.9* (± 30.4)	219.3 (± 26.4)	33.5* (± 6.8)	156.6 (± 52.7)
Mg	1740.5* (± 374)	1578.6** (± 309)	24.7* (± 6.7)	174.4** (± 56.4)
Na	47.8* (± 12.3)	97.5 (± 10.6)	15.3* (± 1.7)	64.6 (± 13.1)
Ni	38.8* (± 7.5)	30.7** (± 6.8)	0.09* (± 0.03)	0.7** (± 0.13)
Mn	52.5 (± 19)	84.7 (± 16.6)	8.3 (± 3.2)	47.7 (± 21.9)
Pb	26.5 (± 6.7)	41.6 (± 10.6)	13.9 (± 8.6)	26.4 (± 7.3)
Zn	12.5* (± 2)	40.7 (± 27.8)	1.6* (± 0.5)	24.7 (± 13.1)

Table 2. Principal Component Analysis (PCA) results for soil data from serpentine and granitic soils collected from Pine Hill and Settlement Quarry, Maine. Results are based on the analysis of 18 soil variables: elemental concentrations, exchangeable acidity, effective cation exchange capacity (ECEC), Ca:Mg, and pH.

	PCA Axis 1	PCA Axis 2
Eigenvalues	8.535	3.707
% Variance	47.418	20.597
Cumulative % variance	47.418	68.015
Al	0.409	-0.581
Cd	0.964	0.109
Cr	0.884	-0.004
Cu	-0.081	0.427
Fe	0.851	-0.310
Mn	0.809	0.073
Ni	0.799	0.430
Pb	0.414	0.025
Zn	0.313	-0.242
Ca	0.760	0.368
K	0.884	-0.157
Mg	0.850	0.399
Na	0.886	-0.264
Acidity	0.293	-0.815
ECEC	0.955	0.234
Ca:Mg	-0.699	0.005
pH (H ₂ O)	-0.107	0.918
pH (CaCl ₂)	-0.035	0.937

(0.01 M CaCl₂), Ca, Ca:Mg, Cd, Cr, K, Mg, Na, Ni, and Zn (Table 1). Forested and exposed plots were edaphically more distinct for granite than serpentine (Figure 1). Within serpentine, exposed and forested habitats differed significantly in exchangeable acidity, pH, Fe, and Na while for granite, exposed and forested habitats differed significantly in exchangeable acidity, ECEC, pH, Al, Cd, Cr, Mg, Fe, Na, and Ni (Table 1).

Tissue analysis. Plant tissue analyses suggested intraspecific variation with respect to tissue elemental concentrations (Table 3), especially in *Achillea millefolium*, *Oenothera biennis*, *Prunus virginiana*, *Selaginella rupestris*, *Spiraea alba* var. *latifolia*, and *Vaccinium angustifolium* found at both sites. The ratio of Ca:Mg was low (< 1) in tissue of serpentine populations, including significant differences in *A. millefolium*, *Festuca filiformis*, *Hieracium caespitosum*, *H. pilosella*, *O. biennis*, *S. rupestris*, and *S. alba*

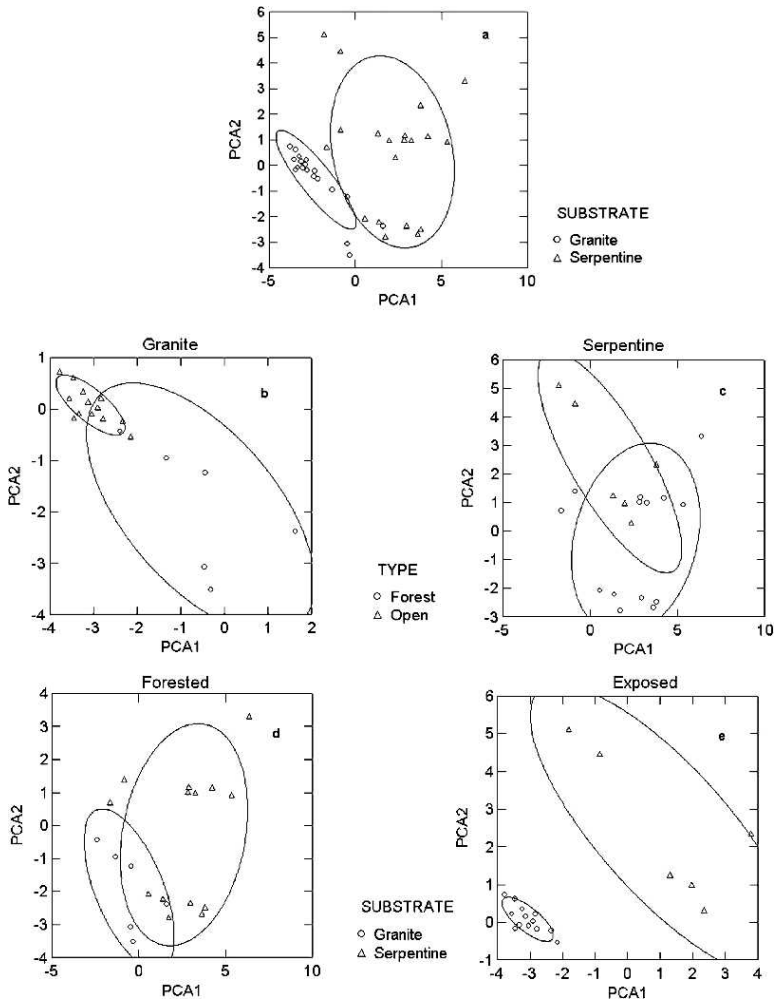


Figure 1. A Principal Component Analysis based on 18 soil variables of soil samples collected from Pine Hill (serpentine) and Settlement Quarry (granite). Percent variance explained by X-Axis is 47.4; Y-Axis is 20.6 (Table 2 lists accompanying eigenvalues, variance explained, and component loading for all soil variables tested). The plots represent (a) serpentine and granite, (b) exposed and forested plots within granite, (c) exposed and forested plots within serpentine, (d) forested plots between serpentine and granite, and (e) exposed plots between serpentine and granite.

Table 3. Continued.

SF ¹	Site	Species																
		Am	Aa	Cf	Ff	Fv	Hc	Hp	Hy	Mp	Ob	Os	Pv	Rv	Sa	Sr	Va	Wi
Ca	PH	0.42	1.1	0.2	0.06	0.76	0.33	0.31	0.5	0.7	0.9	0.9	1.4	0.7	0.2	0.03	0.7	0.1
		±	±		±	±	±	±	±	±	±	±	±	±	±	±	±	±
SQ	SQ	0.03	0.04	N/A	0.01	0.3	0.09	0.04	0.2	0.06	0.1	0.19	0.14	0.2	0.01	0.01	0.09	0.03
		±	N/A		0.12	0.92	0.98	0.86	0.4	0.6	1.3	0.7	1.9	0.8	0.4	0.2	0.7	N/A
Ca:Mg	PH	0.03			0.03	0.25	0.08	0.13	0.06	0.15	0.2	0.14	0.3	0.05	0.06	0.01	0.07	
		±	0.7	0.3	0.7	1.7	0.5	0.4	1.1	2	0.6	1.4	1.3	1.5	0.3	0.1	1.06	0.3
SQ	SQ	0.05	0.05	N/A	0.3	1.04	0.2	0.1	0.6	0.2	0.03	0.4	0.1	0.5	0.03	0.01	0.02	0.07
		±	N/A		2.2	3.6	3.3	2.2	1.2	3.3	8.8	2.4	4.3	2.7	2.7	2.1	2.6	N/A
Cd	PH	0.3			0.03	1.5	0.14	0.3	0.17	0.3	1.8	0.96	0.5	0.8	0.5	0.3	0.4	
		±	0.73	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	1.05	0.67	<0.5	<0.5
SQ	SQ	0.24	0.12	N/A	0.54	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	<0.5	0.07	0.2	<0.5	N/A
		±	N/A		±										±	±	±	±
		0.07			0.05									0.9	0.09			

Table 3. Continued.

SF ¹	Site	Species																
		Am	Aa	Cf	Ff	Fv	Hc	Hp	Hy	Mp	Ob	Os	Pv	Rv	Sa	Sr	Va	Wi
Cr	PH	2.7	4.4	3.3	1.3	2.2	5.4	3.9	2	1.3	5.7	2.5	2.8	2	1.9	2.8	2.9	1.8
		±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
SQ	SQ	0.35	0.1	N/A	0.4	0.3	2.5	0.4	0.3	0.13	0.8	0.3	0.12	0.12	0.1	0.9	0.6	0.1
		1.2	N/A	N/A	13.2	1.6	2.2	2.7	1.8	1.5	1.4	1.7	2.1	1.6	1.2	2.7	1.7	N/A
Cu	PH	±	0.05		±	±	±	±	±	±	±	±	±	±	±	±	±	±
		14.1	12.6	6.6	1	4.6	6	6.8	7.7	5.7	4.2	6.5	3.5	3.5	3.6	2.2	3.7	4.4
K	PH	1.96	2.1		0.2	1.3	0.5	1.2	1.3	1.6	1.03	0.8	0.3	0.3	0.3	0.5	0.5	1
		20.4	N/A	N/A	3.1	5	8.9	8.5	9.6	11.2	6.7	7.6	6.2	3.7	5.1	13.2	5.6	N/A
SQ	SQ	±			±	±	±	±	±	±	±	±	±	±	±	±	±	±
		1.3			2.2	0.6	0.1	0.3	0.81	3.7	2.8	2.4	0.7	0.8	0.3	2.1	0.9	
K	PH	1.9	1.5	0.4	0.3	0.97	2.9	2.2	0.8	0.4	0.7	1.8	0.4	0.5	0.3	0.5	0.2	1.02
		±	±		±	±	±	±	±	±	±	±	±	±	±	±	±	±
SQ	SQ	0.16	0.2		0.02	0.3	0.3	0.2	0.2	0.05	0.3	0.32	0.05	0.2	0.01	0.13	0.01	0.1
		2.5	N/A	N/A	0.4	1.2	3.6	2.7	1.1	0.6	1.4	1.8	1.8	0.9	1	0.6	0.3	0.4
		±			±	±	±	±	±	±	±	±	±	±	±	±	±	±
		0.4			0.02	0.08	0.01	0.19	0.06	0.06	0.1	0.07	0.09	0.08	0.07	0.03	0.02	

Table 3. Continued.

SF ¹	Site	Species																
		Am	Aa	Cf	Ff	Fv	Hc	Hp	Hy	Mp	Ob	Os	Pv	Rv	Sa	Sr	Va	Wi
Ni	PH	29.7	23.8	12.6	13.2	8.1	10.9	24.6	18.2	6.8	46.6	9.2	25.7	10.4	8.1	18.4	8.4	24.2
		±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
SQ	SQ	1.99	1.8		2	1.4	4.6	0.63	4.2	0.8	13.8	3.4	4	3.3	0.3	12.3	0.3	7.5
		±	N/A	N/A	46.9	3.6	2.7	2.5	4	7.5	3.2	5.2	4.9	3.1	2.4	9.2	3.8	N/A
P	PH	0.6			35	1.14	0.2	0.01	1.5	3.6	0.1	0.51	1.2	0.4	0.05	6.7	0.9	
		±	0.19	0.21	0.07	0.31	0.3	0.29	0.37	0.06	0.21	0.19	0.12	0.11	0.09	0.11	0.07	0.13
SQ	SQ	0.01	±		0.02	0.09	0.09	0.06	0.14	0.001	0.03	0.03	0.01	0.02	0.003	0.02	0.002	0.03
		0.18	N/A	N/A	0.07	0.15	0.24	0.25	0.28	0.09	0.15	0.21	0.14	0.22	0.09	0.08	0.09	N/A
Zn	PH	0.02			±	±	±	±	±	±	±	±	±	±	±	±	±	
		14.1	78.4	10.2	10.9	17.3	34.2	17.9	47.2	13.4	6.6	13.6	6.7	8.96	52.2	75.1	9.7	31.8
SQ	SQ	2.4	20.6		1.8	8.2	5.5	2	6	0.6	1.4	3.5	0.4	1.2	5.5	21.4	0.8	4.5
		53.9	N/A	N/A	24.1	29.2	61.4	153	158	15.5	34.5	31.9	56.8	8.8	145	139	13.3	N/A
		±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	
		12.1			6.1	3	7.2	31	55	0.53	13	5.7	13.7	1.5	1.9	19	1.5	

var. *latifolia*. Heavy metal content, especially Ni, was high in serpentine populations, with significantly higher means recorded for *A. millefolium*, *Hypericum perforatum*, *H. pilosella*, *O. biennis*, *P. virginiana*, *S. alba* var. *latifolia*, and *V. angustifolium*. Two-way ANOVA examining the relationships between species and substrate (independent variables) on element accumulation (dependent variable) in tissue samples indicated that the species variable was significant for 15 tissue variables tested (all but Cr). The substrate variable was significant for 14 variables tested (all but P, Cd). A significant interaction between these two source variables was observed for 13 dependent variables (all but P, Cd, Na), including those critical for serpentine tolerance such as Ca, Mg, Ni, and Cr.

DISCUSSION

Despite their recent glaciation (ca. 13,000 years ago) and the addition of glacial till, the serpentine soils at Pine Hill were chemically distinct from granitic soils found at Settlement Quarry (Table 1; Figure 1a); however, these differences were more pronounced in soils found on exposed rock than those from forested settings (Figure 1d, e). Pine Hill, despite its smaller area relative to Settlement Quarry, harbored 43 more taxa (Appendix). Although none of the taxa at Pine Hill are rare in New England, several regionally patchy species were frequent, including *Asplenium trichomanes* var. *trichomanes*, *Selaginella rupestris*, and *Woodсия ilvensis*. Although *S. rupestris* was also located at Settlement Quarry, the taxon was much more abundant at Pine Hill. *Asplenium trichomanes* var. *trichomanes* was represented by a single individual restricted to a shady, moist rocky ledge on the western slope of the serpentine outcrop. Extensive searches in the area failed to locate other individuals of this taxon. *Asplenium trichomanes* var. *trichomanes* is a known metal accumulator and has shown high accumulation of Sc, Cr, and Co (Ozaki et al. 2000). Although this taxon is not state or federally listed, given there was only one individual at this site, we did not collect tissue for elemental analysis.

Certain species, such as *Alnus incana* subsp. *rugosa*, *Lechea intermedia*, *Sibbaldiopsis tridentata*, and *Solidago puberula*, were ubiquitous at Settlement Quarry but did not occur at Pine Hill. These species are regionally common and their absence from Pine Hill may be due to their intolerance of serpentine. *Sibbaldiopsis*

tridentata was of particular interest as it is a common feature of many granitic outcrops in the region, including Settlement Quarry; its absence from Pine Hill suggests the importance of the edaphic factor in determining plant distributions.

Interesting in its absence from Pine Hill is *Adiantum viridimontanum*, an allotetraploid hybrid of *A. aleuticum* and *A. pedatum* (Paris 1991). Once thought restricted to serpentine soils in Vermont and Québec (Paris 1991; Ruesink 2001; Tyndall and Hull 1999), the species was recently found in Maine on nearby Deer Isle, growing on serpentine as a small population of about 15 individuals (Harris and Rajakaruna 2009). Previously reported by us as *A. aleuticum* (Rajakaruna, Harris, and Alexander 2009), it was confirmed as *A. viridimontanum* during a visit to the site in June, 2008 (A. Haines, New England Wild Flower Society and G. Hall, Appalachian Corridor Appalachien, pers. comm.). The species is not found at Pine Hill despite its close proximity to the Deer Isle population and areas within the site seemingly suited for the growth of the species.

While our study points to substrate effects on the flora of Deer Isles, the study by Carter (1979) provides a better understanding of the composition of the serpentine flora for Maine. Carter's survey of inland and coastal sites, combined with our study, show that the two coastal serpentine sites host more species (211) than the four inland sites (131). Only one taxon is shared by all six serpentine sites and almost 75% of the taxa recorded for serpentine in Maine are unique to only one site. The highly localized distribution pattern of serpentine tolerant taxa in Maine suggests that conservation of each site is critical to preserve the genetic variation that may exist in the serpentine tolerant populations.

Although serpentine had higher species numbers and plant families overall, similar to the pattern for bryophytes from the same two sites (Briscoe et al. 2009), the differences with respect to species richness and diversity indices are distinct based on substrate exposure, a feature we didn't explore in our previous floristic studies (Briscoe et al. 2009; Harris et al. 2007). Exposed serpentine harbored a significantly greater number of species compared to exposed granite; however, the pattern was reversed under forested settings. Overall, exposed serpentine and forested granite were more diverse (richness and evenness) than forested serpentine and exposed granite, respectively. The patterns of higher diversity on exposed serpentine compared to forested serpentine were consistent with soil features within the outcrop (Table 1). Exposed serpentine

soils are more “serpentine-like” than forested serpentine sites, characterized by Ca:Mg ratios < 1 , higher pH, and greater concentrations of heavy metals. Further, the exposed sites are rocky, with shallow soils that generally dry out early in the growing season. Early onset of moisture stress and chemical adversities are often reflected in the early flowering of taxa such as *Achillea millefolium* and *Fragaria virginiana* at Pine Hill compared to these taxa at Settlement Quarry (N. Rajakaruna, pers. obs.). Harsher growing conditions on exposed serpentine can provide a refuge for serpentine tolerant species or ecotypes of those species predisposed to colonize the substrate (Kruckeberg 1986; Rajakaruna 2004), leading to greater diversity of tolerant taxa. Thus, exposed serpentine provides a refugium for tolerant taxa as plants able to tolerate serpentine factors can remain on the exposed areas with less competition from intolerant species.

The forested serpentine sites, due to higher organic matter content and deeper soils, have a diluted “serpentine effect.” There, soils are characterized by lower pH and Ca:Mg ratio > 1 , typical of regional forest soils. Further, the shade provided by dense canopy in the forested sites is not conducive to the establishment of a dense herbaceous understory, resulting in a species-poor conifer forest typical of acidic soils in the region. These factors may have led to the lower species diversity observed within forested serpentine plots compared to exposed serpentine plots. However, the serpentine effect was still apparent in the forested plots (Table 1) due to *in situ* weathering and leaching of heavy metals from serpentine parental rocks within the forested sites. All heavy metals characteristic of serpentine soils (Cd, Cr, and Ni) were significantly higher and the Ca:Mg ratio was significantly lower in the forested serpentine than forested granite plots (Table 1). Thus, the serpentine effect, although diluted, may have led to lower diversity in the forested serpentine plots relative to the more benign soils of the forested granite plots.

Exposed and forested granite plots also differed in patterns of diversity. The exposed granite plots had little soil development ($< 1\text{--}4$ cm). When present in quantities suitable for plant growth, the soils had high sand content and virtually no organic matter. Results from the soil analyses (Table 1) are consistent with the observations on soil texture and organic matter content, pointing to lowest exchangeable cation exchange capacities and nutrient element concentrations for soils from exposed granite relative to

forested granite. Shallow and exposed soils are also prone to high evaporation leading to intense water stress, another possible reason for the low diversity of plants on the exposed granite. Thus, lack of soil suitable for plant establishment and growth may have led to the low species numbers found on the exposed granite relative to the well-developed forests on deeper, shaded soils of the forested granite. Even exposed serpentine had greater soil depths (5–12 cm) and soil development relative to exposed granite (1–4 cm). Greater soil depth and soil development, leading to a more favorable exchangeable cation exchange capacity and other chemical attributes (Table 1), may have resulted in the higher species composition on exposed serpentine compared to exposed granite. Overall, the lowest species diversity was found on the exposed granite, a pattern consistent with our results showing lack of soils and/or soil conditions favorable for plant establishment and growth.

The patterns we observed for species richness and diversity on granite and serpentine with respect to outcrop exposure have not been evaluated in previous work on plant-soil relations of rock outcrops in eastern North America (Rajakaruna, Harris, and Alexander 2009). Further, there is limited work worldwide examining plant diversity across serpentine and nonserpentine substrates based on soil exposure/forest cover (Alexander et al. 2007; Brooks 1987). Our findings suggest that soil exposure can lead to significant ecological heterogeneity within rock outcrops in recently glaciated regions such as those found in Maine. Further, our findings point to the importance of habitat heterogeneity, especially with respect to exposure. It is critical that any future conservation planning associated with rock outcrop plant communities consider outcrop exposure as a key determinant of floristic diversity. Studies exploring causes of variation within seemingly identical habitats are crucial for sound conservation planning of biota found on serpentine and other rock outcrops (Grace et al. 2007).

None of the 17 species examined for tissue elemental concentrations accumulated unusual amounts of any element (i.e., hyperaccumulation; Reeves 2003), although many serpentine taxa showed characteristically low Ca:Mg ratios and high Ni and Cr concentrations (Table 3). Ability to selectively accumulate Ca over Mg appears to be the most important physiological feature conveying greater tolerance to serpentine (Brady et al. 2005; Kazakou et al. 2008). Recent studies on *Achillea millefolium* populations collected from serpentine and nonserpentine habitats

from a number of locations worldwide, including Pine Hill and Settlement Quarry, have shown that populations from on and off serpentine differ in their Ca:Mg physiology (O'Dell and Claassen 2006; R. O'Dell, Bureau of Land Management, Hollister, CA, unpubl. results). Several taxa from our study, in addition to *A. millefolium*, showed significant differences with respect to elemental accumulation and may be worth examining for differential ion tolerance and/or local adaptation. They include *Oenothera biennis*, *Prunus virginiana*, *Selaginella rupestris*, *Spiraea alba* var. *latifolia*, and *Vaccinium angustifolium* (Table 3).

The two-way ANOVA model showed significant species \times substrate effects for several tissue variables, including the critical elements of serpentine (Ca, Mg, Ni, Cr), showing that for these elements there was significant genetic variation among species with respect to substrate. Given the importance of Ca:Mg ratios in serpentine tolerance, it would be useful to further explore these differences under laboratory or greenhouse settings to determine if there is evidence for genetic differentiation with respect to these important elements.

This study concludes a series of three papers exploring the serpentine plant-soil relations of Pine Hill on Little Deer Isle, Maine. Although we did not perform a comparative study for lichens (Harris et al. 2007), our work has shown that Pine Hill, a small serpentine outcrop barely 0.2 km² in size, harbors both a unique bryophyte (Briscoe et al. 2009) and vascular flora (this study), relative to an adjacent granite outcrop. Our work suggests a unique serpentine substrate effect on the regional flora at taxonomic, physiological, and community levels. Further, our research highlights the need to better document the floras of other under-explored geodaphic islands of the region, including limestone, dolomite, gypsum, and soils overlying metal-enriched geologies, including mine tailings and waste rock piles. Such geodaphic islands can provide unique habitats for regional floras, often leading to distinct plant communities like those we have described for serpentine at Pine Hill and guano deposits of bird nesting areas of Mount Desert Rock, Maine (Rajakaruna, Pope, Orozco, and Harris 2009).

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APPENDIX
SERPENTINE PLANTS OF MAINE

Serpentine plants recorded for Pine Hill, Little Deer Isle (PH), Deer Isle (DI), Bowmantown (BT), Little Spencer Stream (LS), White Cap Mountain East (WCE), and White Cap Mountain West (WCW) based on Carter (1979) and the current study. PH was surveyed in 1977 by Carter (1979) and in 2007 in the current study; all other sites were surveyed exclusively by Carter (1979). PH taxa collected exclusively by Carter (1979) denoted by *; taxa collected exclusively in the current study denoted by ^. Plants collected from Settlement Quarry (SQ; granite) during the current study are also listed. X = presence; - = absence.

Taxon	PH	DI	BT	LS	WCE	WCW	SQ
ACERACEAE							
<i>Acer rubrum</i> L.	X	X	-	-	-	-	X
<i>Acer saccharum</i> Marshall	-	-	X	-	-	-	-
<i>Acer spicatum</i> Lam.	-	X	X	-	X	-	-
ANACARDIACEAE							
^ <i>Rhus hirta</i> L.	X	-	-	-	-	-	-
^ <i>Toxicodendron radicans</i> (L.) Kuntze	X	-	-	-	-	-	-
APIACEAE							
* <i>Cicuta maculata</i> L.	X	X	-	-	-	-	-
<i>Heracleum maximum</i> Bartr.	-	-	X	-	-	-	-
<i>Ligusticum scoticum</i> L.	-	X	-	-	-	-	-
AQUIFOLIACEAE							
<i>Ilex verticillata</i> (L.) A. Gray	-	-	-	-	-	-	X
ARACEAE							
^ <i>Arisaema triphyllum</i> (L.) Schott var. <i>triphyllum</i>	X	-	-	-	-	-	-
^ <i>Symplocarpus foetidus</i> (L.) Nutt.	X	X	-	-	-	-	-
ARALIACEAE							
<i>Aralia hispida</i> Vent.	-	-	-	-	-	-	X
^ <i>Aralia nudicaulis</i> L.	X	X	-	X	-	-	-
ASPLENIACEAE							
^ <i>Asplenium trichomanes</i> L. var. <i>trichomanes</i>	X	-	-	-	-	-	-
<i>Asplenium trichomanes-ramosum</i> L.	-	-	-	X	-	-	-
ASTERACEAE							
<i>Achillea millefolium</i> L.	X	X	X	-	-	-	X
<i>Ambrosia artemisiifolia</i> L.	X	-	-	-	-	-	-
<i>Anaphalis margaritacea</i> (L.) Benth. & Hook. f.	-	-	-	X	-	-	X

Appendix. Continued.

Taxon	PH	DI	BT	LS	WCE	WCW	SQ
<i>Antennaria howellii</i> Greene subsp. <i>canadensis</i> (Greene) Bayer	–	–	–	–	–	–	X
<i>Antennaria neglecta</i> Greene	X	–	–	–	–	–	–
<i>Antennaria plantaginifolia</i> (L.) Hook.	–	X	–	–	–	–	–
<i>Cirsium muticum</i> Michx.	–	–	X	–	–	–	–
^ <i>Cirsium vulgare</i> (Savi) Ten.	X	–	–	–	–	–	–
^ <i>Conyza canadensis</i> (L.) Cronq. var. <i>canadensis</i>	X	–	–	–	–	–	–
^ <i>Doellingeria umbellata</i> (Mill.) Nees var. <i>umbellata</i>	X	X	X	–	–	–	–
* <i>Erigeron strigosus</i> Willd.	X	–	–	–	–	–	–
<i>Eupatorium maculatum</i> L.	–	–	X	–	–	–	–
* <i>Eupatorium perfoliatum</i> L.	X	–	–	–	–	–	–
^ <i>Euthamia graminifolia</i> (L.) Nutt. var. <i>graminifolia</i>	X	–	–	–	–	–	X
<i>Hieracium aurantiacum</i> L.	–	–	X	–	–	–	X
^ <i>Hieracium caespitosum</i> Dumort.	X	X	–	–	–	–	X
* <i>Hieracium canadense</i> Michx. var. <i>canadense</i>	X	–	–	–	–	–	X
<i>Hieracium pilosella</i> L.	X	–	–	X	–	–	X
* <i>Hieracium piloselloides</i> Vill.	X	–	–	–	–	–	–
* <i>Hieracium pratense</i> Tausch	X	–	–	–	–	–	–
^ <i>Hieracium scabrum</i> Michx. var. <i>scabrum</i>	X	–	–	–	–	–	–
^ <i>Hypochaeris glabra</i> L.	X	–	–	–	–	–	–
^ <i>Lactuca hirsuta</i> Nutt. var. <i>hirsuta</i>	X	–	–	–	–	–	–
<i>Leucanthemum vulgare</i> Lam.	X	–	–	–	–	–	–
<i>Oclemena acuminata</i> (Michx.) Greene	–	X	X	X	X	–	–
<i>Prenanthes altissima</i> L.	–	–	X	–	X	–	–
<i>Prenanthes trifoliata</i> (Cass.) Fernald	X	X	–	–	–	–	–
<i>Senecio sylvaticus</i> L.	–	X	–	–	–	–	–
<i>Solidago bicolor</i> L.	X	–	–	–	–	–	–
<i>Solidago canadensis</i> L.	X	–	–	–	–	–	–
<i>Solidago juncea</i> Aiton	X	–	–	–	–	–	X
<i>Solidago macrophylla</i> Pursh	–	–	X	X	X	–	–
<i>Solidago nemoralis</i> Aiton	X	–	–	–	–	–	–
<i>Solidago puberula</i> Nutt.	–	–	–	–	–	–	X
<i>Solidago rugosa</i> Mill. subsp. <i>rugosa</i> var. <i>rugosa</i>	X	–	X	–	–	–	X
<i>Solidago sempervirens</i> L.	–	X	–	–	–	–	–
* <i>Solidago ulmifolia</i> Willd.	X	–	–	–	–	–	–
<i>Sonchus arvensis</i> L.	–	X	–	–	–	–	–
^ <i>Symphotrichum lateriflorum</i> (L.) A. & D. Löve var. <i>lateriflorum</i>	X	–	–	–	–	–	–

Appendix. Continued.

Taxon	PH	DI	BT	LS	WCE	WCW	SQ
<i>Symphytotrichum novi-belgii</i> (L.) G.L. Nesom var. <i>novi-belgii</i>	X	-	-	-	-	-	X
* <i>Symphytotrichum puniceum</i> (L.) A. & D. Löve var. <i>puniceum</i>	-	X	-	-	-	-	-
* <i>Symphytotrichum tradescantii</i> (L.) G.L. Nesom	X	-	-	-	-	-	-
<i>Taraxacum officinale</i> F.H. Wigg.	X	-	-	X	-	-	-
BALSAMINACEAE							
* <i>Impatiens capensis</i> Meerb.	X	X	X	-	-	-	-
BERBERIDACEAE							
<i>Berberis thunbergii</i> DC.	-	-	-	-	-	-	X
<i>Berberis vulgaris</i> L.	-	X	-	-	-	-	-
BETULACEAE							
<i>Alnus incana</i> (L.) Moench subsp. <i>rugosa</i> (Du Roi) R.T. Clausen	-	-	-	-	-	-	X
* <i>Alnus viridis</i> (Chaix) DC. subsp. <i>crispa</i> (Aiton) Turrill	X	X	-	-	-	-	-
<i>Betula alleghaniensis</i> Britton	X	-	-	-	-	-	-
<i>Betula papyrifera</i> var. <i>cordifolia</i> (Regel) Fernald	-	-	-	-	X	X	-
<i>Betula papyrifera</i> Marshall var. <i>papyrifera</i>	X	X	X	X	-	X	X
<i>Betula populifolia</i> Marshall	-	-	-	-	-	-	X
BRASSICACEAE							
<i>Cardamine diphylla</i> (Michx.) Alph. Wood	-	-	X	-	-	-	-
<i>Cardamine pensylvanica</i> Willd.	-	-	X	-	-	-	-
CAMPANULACEAE							
<i>Campanula rotundifolia</i> L.	-	-	-	X	-	-	-
CAPRIFOLIACEAE							
<i>Diervilla lonicera</i> Mill.	X	X	-	X	X	-	X
<i>Linnaea borealis</i> L. subsp. <i>americana</i> (Forbes) Clausen	X	X	-	X	-	-	-
<i>Lonicera canadensis</i> Marshall	-	-	-	X	-	-	-
<i>Lonicera morrowii</i> A. Gray	-	-	-	-	-	-	X
<i>Lonicera villosa</i> (Michx.) Schult.	-	X	-	-	-	-	-
<i>Sambucus racemosa</i> L. var. <i>racemosa</i>	X	X	-	-	X	-	X
<i>Viburnum nudum</i> L. var. <i>cassinoides</i> (L.) Torr. & A. Gray	-	-	-	-	-	-	X

Appendix. Continued.

Taxon	PH	DI	BT	LS	WCE	WCW	SQ
CARYOPHYLLACEAE							
<i>Cerastium arvense</i> L.	–	–	–	–	–	X	–
^ <i>Cerastium fontanum</i> Baumg. subsp. <i>vulgare</i> (Hartm.) Greuter & Burdet	X	X	–	–	–	–	–
<i>Minuartia groenlandica</i> (Retz.) Ostenf.	–	–	–	–	–	–	X
^ <i>Moehringia lateriflora</i> (L.) Fenzl	X	–	–	–	–	–	–
^ <i>Stellaria graminea</i> L.	X	–	–	–	–	–	–
CELASTRACEAE							
^ <i>Celastrus orbiculatus</i> Thunb.	X	–	–	–	–	–	–
CHENOPODIACEAE							
<i>Atriplex prostrata</i> DC.	–	X	–	–	–	–	–
<i>Suaeda maritima</i> (L.) Dumort.	–	X	–	–	–	–	–
CISTACEAE							
<i>Lechea intermedia</i> Britton var. <i>juniperina</i> (Bickn.) B.L. Robins.	–	–	–	–	–	–	X
CLUSIACEAE							
^ <i>Hypericum canadense</i> L.	X	–	–	–	–	–	X
<i>Hypericum gentianoides</i> (L.) Britton, Sterns & Poggenb.	–	–	–	–	–	–	X
<i>Hypericum perforatum</i> L.	X	–	–	–	–	–	X
CONVOLVULACEAE							
<i>Calystegia sepium</i> (L.) R. Br. subsp. <i>sepium</i>	–	X	–	–	–	–	–
CORNACEAE							
<i>Cornus canadensis</i> L.	–	X	–	X	X	–	X
^ <i>Cornus sericea</i> L. subsp. <i>sericea</i>	X	–	–	–	–	–	–
CUPRESSACEAE							
^ <i>Juniperus communis</i> L. var. <i>depressa</i> Pursh	X	–	–	–	–	–	X
<i>Thuja occidentalis</i> L.	X	X	–	X	–	–	–
CYPERACEAE							
^ <i>Carex albicans</i> Willd. ex Spreng. var. <i>emmonsii</i> (Torr.) Rettig	X	–	–	–	–	–	X
<i>Carex arctata</i> Hook.	–	X	–	–	–	–	–
^ <i>Carex arctata</i> Hook.	X	–	–	–	–	–	–
<i>Carex brunnescens</i> (Pers.) Poir.	X	–	X	–	X	–	–
^ <i>Carex communis</i> L.H. Bailey	X	X	–	X	X	–	–
<i>Carex conoidea</i> Willd.	–	X	–	–	–	–	–
<i>Carex crinita</i> Lam.	–	–	X	–	–	–	–

Appendix. Continued.

Taxon	PH	DI	BT	LS	WCE	WCW	SQ
[^] <i>Carex debilis</i> Michx. var. <i>strictior</i> L.H. Bailey	X	-	-	-	-	-	X
* <i>Carex deflexa</i> Hornem. var. <i>deflexa</i>	X	-	-	-	-	-	X
<i>Carex intumescens</i> Rudge	-	X	X	-	X	-	-
<i>Carex laxiflora</i> Lam.	-	-	X	-	X	-	-
<i>Carex nigra</i> (L.) Reichard	X	-	-	-	-	-	-
[^] <i>Carex novae-angliae</i> Schwein.	X	X	-	-	-	-	-
<i>Carex paleacea</i> Wahlenb.	-	X	-	-	-	-	-
[^] <i>Carex pallescens</i> L.	X	-	-	-	-	-	-
* <i>Carex pseudocyperus</i> L.	X	-	-	-	-	-	-
[^] <i>Carex scoparia</i> Willd. var. <i>scoparia</i>	X	-	-	-	-	-	X
<i>Carex stipata</i> Willd.	-	-	X	-	-	-	-
[^] <i>Carex trisperma</i> Dewey var. <i>trisperma</i>	X	-	-	-	-	-	-
<i>Carex umbellata</i> Willd.	X	-	-	-	-	-	-
<i>Schoenoplectus maritimus</i> (L.) Lye	-	X	-	-	-	-	-
* <i>Scirpus cyperinus</i> (L.) Kunth	X	-	-	-	-	-	-
[^] <i>Scirpus hattorianus</i> Makino	X	-	-	-	-	-	-
DENNSTAEDTIACEAE							
[^] <i>Pteridium aquilinum</i> (L.) Kuhn var. <i>latiusculum</i> (Desv.) A. Heller	X	-	-	X	-	-	X
DRYOPTERIDACEAE							
<i>Cystopteris fragilis</i> (L.) Bernh.	-	-	-	X	-	-	-
<i>Dryopteris campyloptera</i> Clarkson	-	-	-	X	X	-	-
[^] <i>Dryopteris carthusiana</i> (Vill.) H.P. Fuchs	X	X	X	-	-	X	X
<i>Dryopteris intermedia</i> (Willd.) A. Gray	-	X	X	-	X	-	-
<i>Dryopteris marginalis</i> (L.) A. Gray	X	X	-	X	-	-	-
<i>Dryopteris</i> × <i>triploidea</i> Wherry	-	-	-	X	-	X	-
[^] <i>Gymnocarpium dryopteris</i> (L.) Newman	X	X	X	X	X	-	-
<i>Matteuccia struthiopteris</i> (L.) Todaro	-	-	X	-	-	-	-
<i>Onoclea sensibilis</i> L.	X	X	-	-	-	-	X
<i>Woodsia ilvensis</i> (L.) R. Br.	X	-	-	-	-	-	-
EQUISETACEAE							
* <i>Equisetum arvense</i> L.	X	X	-	-	-	-	-
<i>Equisetum sylvaticum</i> L.	-	X	X	-	-	-	-
ERICACEAE							
<i>Epigaea repens</i> L.	-	-	-	X	-	-	-
<i>Gaultheria hispida</i> (L.) Muhl. ex Bigelow	-	-	-	X	X	X	-
<i>Gaultheria procumbens</i> L.	-	-	-	X	-	-	-

Appendix. Continued.

Taxon	PH	DI	BT	LS	WCE	WCW	SQ
<i>Gaylussacia baccata</i> (Wangenh.) K. Koch	–	–	–	–	–	–	X
<i>Kalmia angustifolia</i> L.	–	–	–	X	–	–	–
<i>Kalmia polifolia</i> Wangenh.	–	–	–	–	–	X	–
<i>Ledum groenlandicum</i> Oeder	–	–	–	X	–	X	–
<i>Rhododendron canadense</i> (L.) Torr.	–	–	–	X	–	X	–
<i>Vaccinium angustifolium</i> Aiton	X	–	–	X	–	–	X
<i>Vaccinium cespitosum</i> Michx.	–	–	–	–	–	X	–
<i>Vaccinium corymbosum</i> L.	–	X	–	–	–	–	–
<i>Vaccinium myrtilloides</i> Michx.	–	–	–	X	X	X	–
<i>Vaccinium vitis-idaea</i> L. subsp. <i>minus</i> (Lodd.) Hultén	X	–	–	–	–	X	X
FABACEAE							
<i>Lathyrus japonicus</i> Willd. var. <i>maritimus</i> (L.) Kartesz & Gandhi	–	X	–	–	–	–	–
<i>Lathyrus palustris</i> L.	–	X	–	–	–	–	–
<i>Trifolium arvense</i> L.	X	–	–	–	–	–	–
^ <i>Trifolium campestre</i> Schreb.	X	–	–	–	–	–	–
<i>Trifolium pratense</i> L.	X	–	–	–	–	–	X
<i>Trifolium repens</i> L.	X	–	–	–	–	–	–
^ <i>Vicia cracca</i> L.	X	–	–	–	–	–	–
FAGACEAE							
^ <i>Quercus rubra</i> L.	X	X	–	–	–	–	X
FUMARIACEAE							
<i>Corydalis sempervirens</i> (L.) Pers.	–	–	–	X	–	–	X
<i>Dicentra canadensis</i> (Goldie) Walp.	–	–	X	–	–	–	–
GROSSULARIACEAE							
<i>Ribes cynosbati</i> L.	X	X	–	–	–	–	–
<i>Ribes glandulosum</i> Grauer	–	X	–	–	–	–	X
<i>Ribes lacustre</i> (Pers.) Poir.	–	–	X	X	–	–	–
<i>Ribes triste</i> Pall.	–	–	X	–	–	–	–
IRIDACEAE							
<i>Iris versicolor</i> L.	X	–	–	–	–	–	–
<i>Sisyrinchium montanum</i> Greene var. <i>crebrum</i> Fernald	X	–	–	–	–	–	X
JUNCACEAE							
<i>Juncus balticus</i> Willd. var. <i>littoralis</i> Engelm.	–	X	–	–	–	–	–
<i>Juncus brevicaudatus</i> (Engelm.) Fernald	–	–	X	–	–	–	–

Appendix. Continued.

Taxon	PH	DI	BT	LS	WCE	WCW	SQ
* <i>Juncus effusus</i> L. var. <i>conglomeratus</i> (L.) Engelm.	X	-	-	-	-	-	-
^ <i>Juncus tenuis</i> Willd.	X	-	-	-	-	-	X
^ <i>Luzula multiflora</i> (Ehrh.) Lej. subsp. <i>multiflora</i>	X	-	-	-	-	-	X
<i>Luzula multiflora</i> subsp. <i>frigida</i> (Buch.) Krecz.	-	X	-	-	-	-	-
JUNCAGINACEAE							
<i>Triglochin palustris</i> L.	-	X	-	-	-	-	-
LAMIACEAE							
^ <i>Galeopsis bifida</i> Boenn.	X	-	-	-	-	-	-
<i>Galeopsis tetrahit</i> L.	-	-	X	-	-	-	-
* <i>Lycopus virginicus</i> L.	X	-	X	-	-	-	-
^ <i>Mentha arvensis</i> L.	X	-	X	-	-	-	-
* <i>Prunella vulgaris</i> L. subsp. <i>lanceolata</i> (W. Bartram) Hultén	X	-	X	-	-	-	-
<i>Scutellaria galericulata</i> L.	-	X	-	-	-	-	-
<i>Scutellaria lateriflora</i> L.	-	-	X	-	-	-	-
LILIACEAE							
<i>Clintonia borealis</i> (Aiton) Raf.	-	X	X	X	X	X	X
<i>Erythronium americanum</i> Ker-Gawl.	-	-	X	-	-	-	-
<i>Hemerocallis fulva</i> L.	X	-	-	-	-	-	-
<i>Maianthemum canadense</i> Desf.	X	X	-	X	X	-	X
<i>Streptopus lanceolatus</i> (Aiton) Reveal var. <i>lanceolatus</i>	-	X	X	X	X	-	-
<i>Trillium erectum</i> L.	-	-	X	X	-	-	-
<i>Veratrum viride</i> Aiton	-	-	X	-	-	-	-
LYCOPODIACEAE							
<i>Huperzia lucidula</i> (Michx.) Trevis.	-	X	X	X	X	-	-
<i>Lycopodium clavatum</i> L.	-	X	-	X	-	-	-
<i>Lycopodium obscurum</i> L.	-	X	-	-	X	-	-
MONOTROPACEAE							
<i>Monotropa uniflora</i> L.	X	-	X	X	X	X	-
MYRICACEAE							
<i>Morella pensylvanica</i> (Mirb.) Kartesz	X	-	-	-	-	-	X
<i>Myrica gale</i> L.	-	X	-	-	-	-	-
ONAGRACEAE							
<i>Chamerion angustifolium</i> (L.) Holub subsp. <i>angustifolium</i>	-	-	-	-	-	-	X
<i>Circaea alpina</i> L.	-	-	X	-	-	-	-

Appendix. Continued.

Taxon	PH	DI	BT	LS	WCE	WCW	SQ
<i>Epilobium ciliatum</i> Raf. subsp. <i>glandulosum</i> (Lehm.) Hoch & Raven	-	-	X	-	-	-	-
<i>Oenothera biennis</i> L.	X	-	-	-	-	-	X
^ <i>Oenothera perennis</i> L.	X	-	-	-	-	-	-
OPHIOGLOSSACEAE							
<i>Botrychium virginianum</i> (L.) Sw.	-	-	-	X	-	-	-
ORCHIDACEAE							
<i>Goodyera tessellata</i> Lodd.	-	-	-	X	-	-	-
<i>Platanthera dilatata</i> (Pursh) Beck var. <i>dilatata</i>	-	-	X	-	-	-	-
OSMUNDACEAE							
^ <i>Osmunda cinnamomea</i> L.	X	X	-	-	-	-	-
<i>Osmunda claytoniana</i> L.	-	-	-	X	X	-	X
OXALIDACEAE							
^ <i>Oxalis montana</i> Raf.	X	-	X	X	X	X	-
^ <i>Oxalis stricta</i> L.	X	-	-	-	-	-	-
PINACEAE							
<i>Abies balsamea</i> (L.) Mill.	X	X	X	X	X	X	X
<i>Larix laricina</i> (Du Roi) K. Koch	-	-	-	X	-	-	-
<i>Picea glauca</i> (Moench) Voss	X	-	X	-	-	-	X
<i>Picea mariana</i> (Mill.) Britton, Sterns & Poggenb.	-	-	-	-	-	X	-
<i>Picea rubens</i> Sarg.	X	X	-	X	-	-	X
<i>Pinus resinosa</i> Soland.	-	-	-	X	-	-	-
<i>Pinus strobus</i> L.	X	X	-	X	-	-	-
PLANTAGINACEAE							
<i>Plantago maritima</i> L. var. <i>juncoides</i> (Lam.) A. Gray	-	X	-	-	-	-	-
PLUMBAGINACEAE							
<i>Limonium carolinianum</i> (Walter) Britton	-	X	-	-	-	-	-
POACEAE							
^ <i>Agrostis canina</i> L.	X	-	-	-	-	-	-
^ <i>Agrostis capillaris</i> L.	X	X	-	-	-	-	X
* <i>Agrostis perennans</i> (Walter) Tuck.	X	X	X	X	-	-	-
<i>Agrostis scabra</i> Willd.	-	-	-	-	-	-	X
^ <i>Anthoxanthum odoratum</i> L. subsp. <i>odoratum</i>	X	-	-	-	-	-	-
<i>Bromus ciliatus</i> L.	-	-	X	-	-	-	-

Appendix. Continued.

Taxon	PH	DI	BT	LS	WCE	WCW	SQ
<i>^Calamagrostis canadensis</i> (Michx.) P. Beauv.	X	X	-	-	-	-	-
<i>Cinna latifolia</i> (Goepp.) Griseb.	-	-	X	-	X	-	-
<i>Danthonia spicata</i> (L.) Roem. & Schult.	X	-	-	X	-	-	X
<i>Deschampsia flexuosa</i> (L.) Trin.	X	X	-	-	X	X	-
<i>Dichantherium acuminatum</i> (Sw.) Gould & C.A. Clark subsp. <i>fasciculatum</i> (Torr.) Freckmann	X	-	-	-	-	-	X
<i>^Elymus repens</i> (L.) Gould	X	X	-	-	-	-	X
<i>^Elymus trachycaulus</i> (Link) Shinners subsp. <i>trachycaulus</i>	X	-	-	-	-	-	-
<i>Elymus virginicus</i> L.	-	X	-	-	-	-	-
<i>Festuca filiformis</i> Pourret	X	-	-	-	-	-	X
<i>^Festuca rubra</i> L. subsp. <i>rubra</i>	X	X	-	-	-	-	X
<i>Glyceria melicaria</i> (Michx.) F.T. Hubb.	-	-	X	-	-	-	-
<i>Glyceria striata</i> (Lam.) Hitchc.	X	-	-	-	-	-	-
<i>*Leptochloa panicea</i> (Retz.) Ohwi subsp. <i>brachiata</i> (Steudl.) N. Snow	X	-	-	-	-	-	-
<i>*Lolium pratense</i> (Huds.) S.J. Darbyshire	X	-	-	-	-	-	-
<i>Oryzopsis asperifolia</i> Michx.	X	-	-	X	-	-	-
<i>Phalaris arundinacea</i> L.	-	-	X	-	-	-	-
<i>^Poa compressa</i> L.	X	-	-	-	-	-	X
<i>Poa palustris</i> L.	X	-	X	X	-	-	X
<i>Poa pratensis</i> L.	X	X	-	-	-	-	-
<i>Puccinellia maritima</i> (Huds.) Parl.	-	X	-	-	-	-	-
<i>Puccinellia tenella</i> (Lange) Holmb. subsp. <i>alascana</i> (Scribn. & Merr.) Tzvelev	-	X	-	-	-	-	-
<i>Schizachne purpurascens</i> (Torr.) Swallen	-	-	-	X	X	-	-
<i>*Setaria pumila</i> (Poir) Roem. & Schult. subsp. <i>pallidifusca</i> (Schumach.) B.K. Simon	X	-	-	-	-	-	-
<i>Spartina pectinata</i> Link	-	X	-	-	-	-	-
POLYGONACEAE							
<i>Polygonum cilinode</i> Michx.	-	X	-	-	-	-	-
<i>Polygonum cuspidatum</i> Siebold & Zucc.	X	-	-	-	-	-	-
<i>*Polygonum persicaria</i> L.	X	-	X	-	-	-	-
<i>Polygonum sagittatum</i> L.	-	-	X	-	-	-	-
<i>^Rumex acetosella</i> L.	X	-	-	X	-	-	X

Appendix. Continued.

Taxon	PH	DI	BT	LS	WCE	WCW	SQ
* <i>Rumex crispus</i> L.	X	X	-	-	-	-	-
POLYPODIACEAE							
<i>Athyrium filix-femina</i> (L.) Roth	-	X	X	X	X	-	-
<i>Polypodium virginianum</i> L.	X	X	-	X	-	-	-
<i>Polystichum braunii</i> (Spenner) Fée	-	-	X	-	-	-	-
PORTULACACEAE							
<i>Claytonia caroliniana</i> Michx.	-	-	X	-	-	-	-
PRIMULACEAE							
<i>Glaux maritima</i> L.	-	X	-	-	-	-	-
* <i>Lysimachia terrestris</i> (L.) Britton, Sterns & Poggenb.	X	-	-	-	-	-	-
<i>Trientalis borealis</i> Raf. subsp. <i>borealis</i>	X	X	-	-	X	-	X
PTERIDACEAE							
<i>Adiantum aleuticum</i> (Rupr.) C.A. Paris	-	-	-	-	-	X	-
<i>Adiantum pedatum</i> L.	-	X	-	X	-	-	-
PYROLACEAE							
<i>Chimaphila umbellata</i> W. Bartram subsp. <i>cisatlantica</i> (S.F. Blake) Hultén	-	-	-	X	-	-	-
RANUNCULACEAE							
<i>Actaea rubra</i> (Aiton) Willd.	-	-	X	-	-	-	-
<i>Coptis trifolia</i> (L.) Salisb.	-	X	X	-	X	X	-
<i>Ranunculus abortivus</i> L.	-	-	X	-	-	-	-
^ <i>Ranunculus acris</i> L. var. <i>acris</i>	X	-	-	-	-	-	-
<i>Thalictrum pubescens</i> Pursh	-	X	X	-	-	-	-
ROSACEAE							
<i>Amelanchier arborea</i> (Michx. f.) Fernald var. <i>arborea</i>	X	X	-	-	-	-	X
<i>Amelanchier bartramiana</i> (Tausch) M. Roem.	-	-	-	X	X	X	-
<i>Dalibarda repens</i> L.	-	-	-	X	-	-	-
<i>Fragaria virginiana</i> Duchesne var. <i>virginiana</i>	X	X	-	-	-	-	X
<i>Malus sylvestris</i> Mill.	X	-	-	-	-	-	-
<i>Photinia melanocarpa</i> (Michx.) Robertson & Phipps	-	-	-	-	-	-	X
^ <i>Potentilla argentea</i> L. var. <i>argentea</i>	X	-	-	-	-	-	-
^ <i>Potentilla norvegica</i> L.	X	-	-	-	-	-	X
<i>Potentilla simplex</i> Michx.	X	-	-	-	-	-	X
<i>Prunus pensylvanica</i> L. f.	X	-	-	-	-	-	X

Appendix. Continued.

Taxon	PH	DI	BT	LS	WCE	WCW	SQ
<i>Prunus virginiana</i> L. var. <i>virginiana</i>	X	X	-	-	-	-	X
* <i>Rosa carolina</i> L.	X	-	-	-	-	-	-
<i>Rosa virginiana</i> Mill.	X	X	-	-	-	-	X
<i>Rubus allegheniensis</i> Porter	-	-	-	-	-	-	X
<i>Rubus hispidus</i> L.	X	-	-	-	-	-	X
<i>Rubus idaeus</i> L. subsp. <i>strigosus</i> (Michx.) Focke	X	X	-	-	-	-	X
<i>Rubus pubescens</i> Raf.	-	X	-	-	-	-	-
<i>Sibbaldiopsis tridentata</i> (Aiton) Rydb.	-	-	-	-	-	-	X
<i>Sorbus americana</i> Marshall	-	-	-	-	-	X	-
<i>Sorbus decora</i> (Sarg.) C.K. Schneid.	-	-	-	X	-	-	-
<i>Sorbus groenlandica</i> (C.K. Schneid.) A. & D. Löve	-	-	-	-	X	-	-
<i>Spiraea alba</i> Du Roi var. <i>latifolia</i> (Aiton) Dippel	X	X	-	-	-	-	X
RUBIACEAE							
<i>Galium asprellum</i> Michx.	-	-	X	-	-	-	-
^ <i>Galium triflorum</i> Michx.	X	X	-	-	X	-	-
^ <i>Houstonia caerulea</i> L.	X	-	-	-	-	-	-
<i>Viburnum lantanoides</i> Michx.	-	X	X	-	X	-	-
SALICACEAE							
^ <i>Populus grandidentata</i> Michx.	X	-	-	-	-	-	X
<i>Populus tremuloides</i> Michx.	X	X	-	-	-	-	X
* <i>Salix discolor</i> Muhl.	X	-	-	-	-	-	-
<i>Salix humilis</i> Marshall var. <i>tristis</i> (Aiton) Griggs	-	-	-	-	-	-	X
SAXIFRAGACEAE							
<i>Chrysosplenium americanum</i> Hook.	-	-	X	-	-	-	-
<i>Tiarella cordifolia</i> L.	-	-	X	-	-	-	-
SCROPHULARIACEAE							
<i>Chelone glabra</i> L.	-	-	X	-	-	-	-
* <i>Euphrasia nemorosa</i> (Pers.) Wallr.	X	-	-	-	-	-	-
<i>Melampyrum lineare</i> Lam.	-	-	-	X	-	X	-
^ <i>Nuttallanthus canadensis</i> (L.) D.A. Sutton	X	-	-	-	-	-	X
<i>Rhinanthus minor</i> L. subsp. <i>minor</i>	X	-	-	-	-	-	-
* <i>Verbascum thapsus</i> L.	X	-	-	-	-	-	-
<i>Veronica americana</i> Benth.	-	-	X	-	-	-	-
^ <i>Veronica officinalis</i> L.	X	-	-	-	-	-	X
^ <i>Veronica serpyllifolia</i> L. subsp. <i>serpyllifolia</i>	X	-	-	-	-	-	-

Appendix. Continued.

Taxon	PH	DI	BT	LS	WCE	WCW	SQ
SELAGINELLACEAE							
<i>Selaginella rupestris</i> (L.) Spring	X	-	-	-	-	-	X
SOLANACEAE							
<i>Solanum dulcamara</i> L.	X	-	-	-	-	-	-
THELYPTERIDACEAE							
<i>Phegopteris connectilis</i> (Michx.) Watt	-	X	X	X	-	-	-
<i>Thelypteris noveboracensis</i> (L.) Nieuwl.	-	-	-	-	-	-	X
VIOLACEAE							
<i>Viola blanda</i> var. <i>palustriformis</i> A. Gray	-	-	X	-	-	-	-
<i>Viola lanceolata</i> L.	-	-	-	-	-	-	X
* <i>Viola macloskeyi</i> F.E. Lloyd subsp. <i>pallens</i> (Ging) M.S. Baker	X	X	-	-	-	-	-
<i>Viola sagittata</i> Aiton var. <i>ovata</i> (Nutt.) Torr. & A. Gray	-	-	-	-	-	-	X
* <i>Viola sororia</i> Willd.	X	X	-	-	-	-	-