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Influence of Silvicultural Treatment, Site Characteristics, and Land Use History on Native and Nonnative Forest Understory Plant Composition on the Penobscot Experimental Forest in Maine

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INFLUENCE OF SILVICULTURAL TREATMENT, SITE CHARACTERISTICS, AND LAND USE HISTORY ON NATIVE AND NONNATIVE FOREST UNDERSTORY PLANT COMPOSITION ON THE PENOBSCOT EXPERIMENTAL FOREST IN MAINE

By

Elizabeth Bryce

B.S. Temple University, 2003

A THESIS

Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Science
(in Ecology and Environmental Science)

The Graduate School
The University of Maine
August, 2009

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By Elizabeth Bryce

Thesis Advisor: Dr. Laura S. Kenefic

An Abstract of the Thesis Presented
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This study investigates forest understory plant diversity and composition in managed and unmanaged stands within the context of a long-term silvicultural experiment in the Acadian Forest of Maine. I examined the effects of silvicultural intensity and past land use on understory plant species diversity and composition. Silvicultural treatments include three variants of the selection system, three variants of the shelterwood system, modified and fixed diameter-limit cutting, and an unregulated harvest. Two types of unmanaged stands were studied: a continuously forested natural area and secondary forest stands on old fields.

Chapter 1 presents analysis of understory plant diversity and composition in managed and unmanaged stands; patterns were examined in relation to site history, current management or use, and environmental factors such as overstory composition, basal area, canopy openness, and soil drainage. A total of 234 species were found in 317 plots. The old field stands had a richer and more diverse understory than all other

treatments. In continuously forested managed and unmanaged treatments, understory species richness and diversity generally declined with decreasing silvicultural intensity. Stands without an agricultural history were more similar in understory composition than old field stands. Differences in diversity and composition of understory plants appear to be related to canopy composition and forest floor disturbance. Old field stands were characterized by an overstory dominated by hardwoods and had greater mineral soil cover, while all other treatments were conifer-dominated and had greater basal area and more softwood litter cover. Softwood basal area was the best predictor of understory species diversity and richness in the continuously forested areas of the PEF.

All continuously forested stands, including those treated with silviculture, were composed of native forest plant species typical of the Acadian Forest, though plots in the natural area and unregulated harvest treatment included a few nonnative invasive plant seedlings. The understory composition of the old fields contained 13 nonnative species, nine nonnative invasive species, and a greater component of early successional ruderals than the continuously forested stands. While silvicultural treatments are associated with understory plant compositional changes, these differences are slight in comparison to the effects of an agricultural past. Continued monitoring of the understory vegetation is needed to understand the short- and long-term responses of understory plant populations to silvicultural treatment.

In Chapter 2, I further explore the pattern of nonnative invasive plant abundance and distribution on the PEF. Multivariate ordination of data from the old field stands revealed positive associations between invasive plants and exposed mineral soil and percent hardwood basal area. Spearman correlation analysis indicated the percent cover of invasive plants was negatively correlated with distance from a roadside, hardwood litter cover, and organic horizon thickness. Glossy buckthorn (*Frangula alnus)* was the most frequent invasive species in the old field stands, and its distribution was not correlated with any of the observed environmental variables.

An investigation of invasive plant occurrences in the silvicultural experiment area of the PEF assessed invasive plant encroachment. Meander surveys revealed that invasive plants were infrequent and were most often found close to woods roads and trails. *Frangula alnus* was the most frequent invasive plant in the silvicultural experiment area. The majority of invasive plant occurrences were in two locations: one replicate of the unregulated harvest and the natural area. These two areas are in close proximity to large invasive seed sources, and both areas have a greater degree of recreational or silvicultural disturbance, which is associated with invasive plant presence.

Monitoring of the nonnative invasive plants will yield needed information about their patterns of establishment in a conifer-dominated Acadian Forest. The prevalence of invasive species in the old fields warrants immediate action to prevent their spread into the managed areas of the PEF. An invasive species management plan should be implemented to protect the integrity of the long-term experiment and biodiversity at the PEF. A successful and cost-effective control strategy can only occur if applied while invasive plant populations are still small and sparse.

DEDICATION

To my parents and grandparents,

for your continuous

support and encouragement.

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Many people gave of their time and talents to make this work a success. My graduate committee was exceptional; I appreciate their great ideas during our meetings and their excitement about this project. Warm thanks to my thesis advisor, Laura Kenefic, who had faith in me from the beginning despite my inexperience with forestry. She allowed me to work independently, yet she was always available and gave sound advice throughout the entire process. Alison Dibble was an encouraging and patient teacher as I began my botanical journey.

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I have been privileged to have the opportunity to work with and learn from so many wonderful individuals at the University of Maine. The hard work and dedication I've witnessed in the students and faculty in the School of Forest Resources has been truly inspirational. Tremendous thanks to my fiancé, Matthew Olson, who has provided never-ending encouragement and moral support. Your stimulating conversation and thoughtful advice kept me going. I hope we continue to have those end-of-the-field-day, what-we-saw-in-the-woods talks for many happy years to come.

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Chapter 1

RELATIONSHIPS AMONG UNDERSTORY VEGETATION, SILVICULTURAL TREATMENT, AND LAND USE HISTORY ON THE PENOBSCOT EXPERIMENTAL FOREST IN MAINE

Introduction

Maintaining native plant diversity is often a key aspect in modern forest management plans, and herbaceous understory plants in temperate forests can often account for most of the plant diversity (Gracia et al. 2007). Therefore, increasing our understanding of understory plant species and their response to forest manipulations is integral. For example, specific understory species can determine tree regeneration success or failure, such as hay-scented fern (*Dennstaedtia punctilobula*) which has inhibited tree regeneration in temperate hardwood forests in Pennsylvania (Royo and Carson 2006), and nonnative Japanese stiltgrass (*Microstegium vimineum*) which has decreased the density and diversity of native woody seedlings in Tennessee (Oswalt et al. 2007). Forest herbs are sensitive to soil moisture and can be considered for use as site indicators (Lookingbill et al. 2004). The bryophyte community can indicate potential regeneration seedbeds (Dibble et al. 1999) and changes in air quality (Geiser and Reynolds 2002). Despite their importance, few understory plant species have been thoroughly studied in much detail. Some common species could be vulnerable to global warming or impacts due to timber harvest. Their various roles in the forest ecosystem are not yet fully understood.

Silvicultural treatments and associated harvest operations may change the composition and diversity of understory vegetation (North et al. 2005). Canopy removal changes the microclimate of the understory by potentially increasing soil moisture, nutrients, light, and temperature (Bergstedt and Milberg 2001), thereby affecting understory plant composition. By reducing overstory density, harvesting reduces the competitive influence of the canopy on understory plants and also leads to a shift in competitiveness among understory species (Bergstedt and Milberg 2001). Over time, understory species composition changes (Grandin 2004) as some individuals die, others take advantage of newly available resources and spread, and new individuals may establish from seed. Intolerant species often increase in abundance following canopy disturbance (North et al. 2005).

The intensity of silvicultural treatment determines the extent of changes in understory vegetation. Silvicultural treatments can mimic natural disturbances to which understory plants may be adapted. Many native understory species in the forests of Maine and adjacent Canada (i.e., the Acadian Region) are adapted to gap phase dynamics (Moore and Vankat 1986); their response to disturbances of this intensity may vary, but they remain a part of the forest community. More severe disturbances cause dramatic shifts in species composition. The New England landscape was extensively deforested and cultivated during the eighteenth century (Foster 1995). Many native forest herbs are slow to recolonize after the land has been tilled (Whitney and Foster 1988) or pastured (Niering 1998). Deforestation begins to effect changes in the soil horizons relatively quickly, especially on the spodosols that are common in the Acadian Region. Agricultural activities further change the physical and chemical properties of soils (Dupouey et al.

2002). With the forest cover absent, the A-horizon becomes less acidic and rates of decomposition increase (Buol et al. 1997). Agricultural activities such as plowing, fertilization, and livestock grazing can mix soil horizons, increase the concentration of soil nutrients or cause leaching of nutrients, increase aeration, or cause compaction of soil particles (Buol et al. 1997). These effects influence soils to the extent that the composition of secondary forests is often floristically different from forests on similar sites that were never in agriculture (Gachet et al. 2007).

Forestry applications in Maine are widespread and of varying intensities, from large exploitive harvests to small partial cuts (Seymour 1994). Forest understory vegetation response to harvesting has been studied in forests with an understory flora similar to that of the PEF in New Brunswick (Ramovs and Roberts 2005), Quebec (Haeussler et al. 2002), and Michigan (Buckley 2003). In Maine, research on understory response to harvest has included gap harvesting (Schofield 2003, Schumann et al. 2003), clearcuts with patch retention (Whitman and Hagan 2000), and a gradient of harvest intensity including large commercial clearcuts (Dibble et al. 1999). This study was initiated to help increase our understanding of patterns of forest understory plant diversity and composition in managed and unmanaged northern conifer forest stands that have undergone various types and intensities of harvesting and historical land use. Specific questions addressed were: (1) do understory species richness, diversity, and evenness differ with silvicultural treatment? (2) what environmental factors (soil drainage; canopy openness; overstory basal area) influence understory species richness, diversity, and composition? (3) how does understory species composition differ in forests with an agricultural history? and, (4) are native shade-tolerant understory species less abundant in more intensely harvested treatment areas?

Methods

Study Site

All research was conducted on the Penobscot Experimental Forest (PEF), a 1,540-ha forest located in Bradley, Maine (44°52′44″N, -68°39′12″W) (Figure 1.1). The PEF was established in 1950; its purpose is to "afford a setting for long-term research…to enhance forestry education of students and the public, and to demonstrate how the timber needs of society are met from a working forest" (Adams et al. 2004). The history of the property prior to 1950 is not well documented. Some partial harvesting occurred in the 18th and 19th centuries, but the forest had not been harvested since about 1900 (Kenefic et al. 2006). In addition, portions of the area now encompassed by the PEF had previously been cleared for agriculture, but the silvicultural treatments (described below) were not located on old fields.

The PEF is in the Acadian Forest, an ecotone between the eastern broadleaf forests to the south and the boreal forests to the north (Sendak et al. 2003). The PEF is dominated by mixed northern conifers including red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), eastern hemlock (*Tsuga canadensis*), northern white-cedar (*Thuja occidentalis*), and eastern white pine (*Pinus strobus*). White spruce (*Picea glauca*), black spruce (*P. mariana*), tamarack (*Larix laricina*), and red pine (*Pinus resinosa*) occur less frequently. The most common hardwoods are red maple (*Acer rubrum*), paper birch (*Betula papyrifera*), gray birch (*B. populifolia*), quaking aspen (*Populus tremuloides*), and bigtooth aspen (*P. grandidentata*). Also found on the PEF are American beech

(*Fagus grandifolia*), white ash (*Fraxinus americana*), northern red oak (*Quercus rubra*), and sugar maple (*Acer saccharum*) (Sendak et al. 2003).

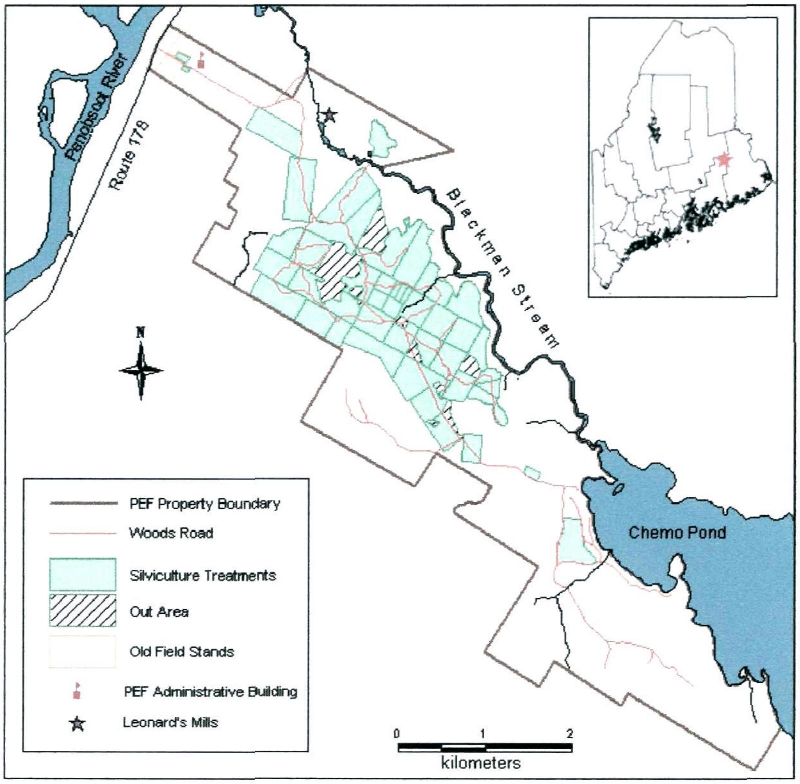

Figure 1.1. Map of the Penobscot Experimental Forest (PEF).

The natural disturbance regime is characterized by small-scale disturbances caused by downbursts and northwesterly storms (Foster 1995) which create small canopy gaps. These small gaps average approximately 50 m^2, and have a return interval ranging from 50 to 200 years (Seymour 1992). Periodically, hurricanes, ice storms, wildfire, and insect outbreaks – especially the spruce budworm (*Choristoneura fumiferana*) – have also shaped northern forests (Niering 1998), though the return interval for stand-replacing natural disturbances is 250-800 years (Lorimer 1977).

Soils on the PEF are Wisconsin glacial till derived from fine-grained sedimentary rock. The study area is predominantly spruce-fir flat, characterized by thin, shallow, often wet soils. Low glacial till "ridges" were formed from well-drained Plaisted loams and stony loams and moderately well-drained Howland loams and sandy loams. Poorly and very poorly drained Monarda and Burnham loams and silt loams occupy flat till areas between the ridges (Safford et al. 1969). In our study area, most soils were derived from Wisconsin till, though some formed from marine and lacustrine deposits of silt and clay (USDA 2007). A small portion (~5 ha) of our study area was in agriculture prior to 1950; physical differences in the soils include the absence of upper horizons and fewer rocks.

A 170-ha long-term silvicultural experiment was installed on the PEF by the U.S. Forest Service, Northern Research Station between 1952 and 1957. Eight twice-replicated treatments were randomly assigned to one of eighteen 6.6- to 17.5-ha experimental units, called compartments. Treatments include five-, ten-, and twenty-year selection systems (S05, S10, S20), two- and three-stage uniform shelterwood systems (SW2, SW3), fixed and modified diameter-limit harvests (FDL, MDL), and an unregulated harvest (URH). In the early 1980s, the three-stage shelterwood treatment was divided to investigate the influence of precommercial thinning on stand development (SW3sp). One of the compartments was set aside in 1954 as an unmanaged natural area; this area has received no harvesting or silvicultural activities. It was later subdivided after having developed into two distinct stands, and serves as a replicated reference treatment; it is referred to as the natural area (NAT). A detailed account of silvicultural treatments and outcomes can be found in Sendak et al. (2003).

Table 1.1a. Basal area. Current mean basal area (BA, m^2/ha) ± SE of trees inventoried on CFI plots, by diameter class and treatment. All plots were inventoried between 1998 and 2005.

Treatment	Basal Area		
	DBH 1.3 - 11.2 cm	DBH 11.3 - 21.3 cm	DBH ≥ 21.4 cm
Unregulated Harvest (URH)	13.4 ± 1.2	3.7 ± 0.3	1.1 ± 0.9
Fixed Diameter-limit (FDL)	9.7 ± 4.0	5.4 ± 0.9	4.1 ± 0.1
Modified Diameter-limit (MDL)	7.5 ± 0.5	6.2 ± 0.4	15.3 ± 1.1
20-yr Selection (S20)	9.0 ± 1.8	3.4 ± 0.4	13.4 ± 1.6
10-yr Selection (S10)	8.3 ± 1.0	5.2 ± 0.4	14.6 ± 1.7
5-yr Selection (S05)	3.8 ± 0.3	5.1 ± 0.5	17.7 ± 0.0
2-stage Shelterwood (SW2)	17.4 ± 0.6	11.9 ± 0.4	7.3 ± 1.8
3-stage Shelterwood with precommercial thinning (SW3sp)	10.0 ± 0.1	15.8 ± 1.0	3.8 ± 1.3
3-stage Shelterwood (SW3)	25.4 ± 3.6	11.0 ± 3.6	0.9 ± 0.3
Natural Area (NAT)	5.9 ± 5.3	6.7 ± 0.1	30.1 ± 12.4

Table 1.1b. Percent basal area. Current percent basal area in silvicultural treatments by tree species and species groups. *Picea* includes *Picea rubens, P. glauca,* and *P. mariana*; "Other conifers" includes *L. laricina* and *T. occidentalis*. Treatment codes are given in Table 1.1a.

Treatment	*Picea*	*Abies balsamea*	*Tsuga canadensis*	*Pinus strobus*	Other conifers	Hard-woods
URH	6	36	3	2	7	46
FDL	13	26	28	1	11	20
MDL	23	17	33	3	6	17
S20	26	18	34	1	6	14
S10	31	27	17	2	7	16
S05	22	18	42	3	4	10
SW2	11	41	14	4	7	22
SW3sp	40	40	4	3	0	14
SW3	20	45	4	17	0	14
NAT	8	16	29	25	3	19

Table 1.1c. Basal area removed. Total number of harvests for each silvicultural treatment since 1950 and percent of basal area removed in the most recent harvest.

Treatment	Compartment	Total number of harvests	Year of last harvest	% basal area removed in the last harvest
URH	22	2	1988	82.5
URH	8	2	1983	89.4
FDL	15	3	2001	59.3
FDL	4	3	1994	60.3
MDL	28	3	1997	21.1
MDL	24	3	1996	35.9
S20	27	3	1997	16.9
S20	17	3	1994	35.0
S10	20	5	1998	7.9
S10	12	5	1994	15.0
S05	16	10	2001	9.0
S05	9	10	1998	6.9
SW2	21	2	1967	70.0
SW2	30	2	1967	84.5
SW3sp[1]	23a	5	2002	6.4
SW3sp	29a	4	1972	77.8
SW3	29b	3	1983	94.7
SW3	23b	3	1974	94.7
NAT[2]	32a	N/A	N/A	N/A
NAT	32b	N/A	N/A	N/A

[1] Portions of Compartment 23a were commercially thinned in 2002; the replicate (29a) has not yet received this treatment. [2] The natural area (NAT) was not harvested.

Both replicates of the ten silvicultural treatments are inventoried regularly using permanent sample plots, called "continuous forest inventory" (CFI) plots. Across the experiment, there are an average of 8 to 21 CFI plots per compartment. Measurements have been recorded before and after each harvest and approximately every five years between entries. Inventory data include species and diameter at breast height (DBH, 1.37 m) of trees >1.3 cm DBH. See Table 1.1 for the current overstory composition of silvicultural treatments by size class (Table 1.1a) and species (Table 1.1b), and the percent of basal area removed in the most recent harvests (Table 1.1c). CFI plots are

0.081-, 0.020-, and 0.008-ha nested circular sample plots. Tree regeneration measurements (stocking and density by species and height class) are obtained from three 4.05-m^2 subplots within each CFI plot (Figure 1.2).

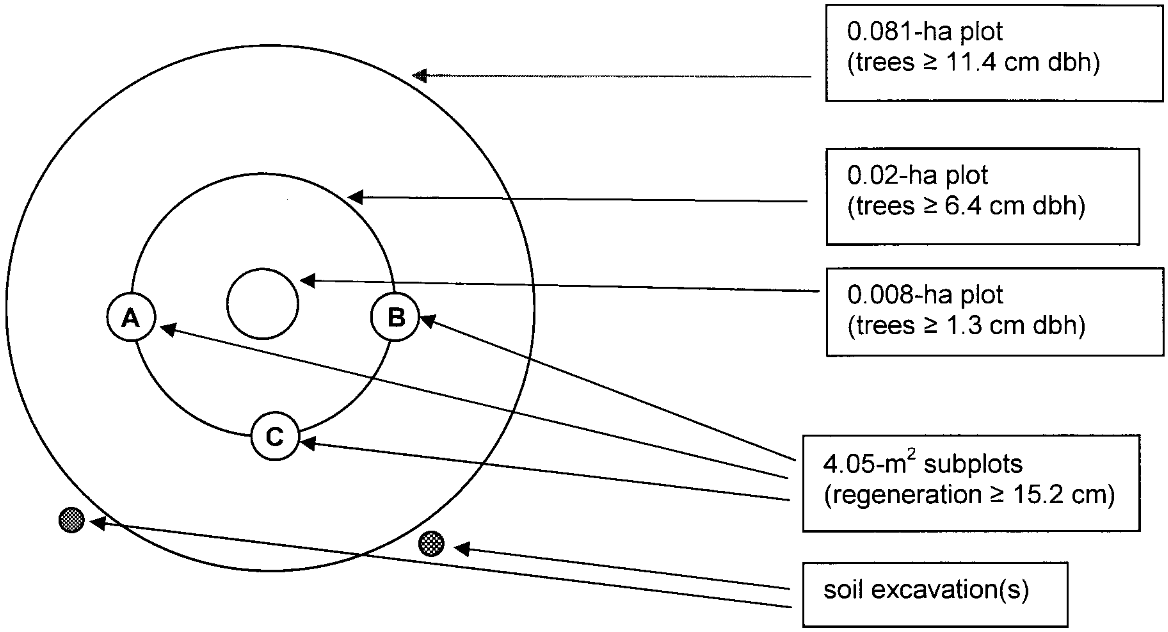

Figure 1.2. CFI plot design. Nested CFI plot design used on the PEF. Text boxes describe the overstory and tree regeneration data collected during periodic inventories (soil pits are not part of regular inventories).

In addition to comparing the effects of silvicultural treatments, comparisons with formerly cultivated sites would be useful to evaluate other differences in the understory plant diversity and composition. Abandoned old fields are located within the PEF near the entrance from Route 178; this approximately 5-ha area is bisected by Government Road (Figure 1.1). The old fields have developed into forest stands dominated by *Populus tremuloides*, *Betula populifera*, *Acer rubrum*, apple (*Malus sylvestris*), and cherry (*Prunus* sp.). Historical use of this land is mostly unknown; however, soils show signs of cultivation, and grazing is also likely to have occurred. Because this area was not included in the long-term silvicultural experiment, there are no historical data.

Portions of the PEF outside of the old field stands and the silvicultural experiment described above contain reserves defined by wetland and shoreland zoning, working forest managed by the University of Maine, administrative sites, and silvicultural experiments more recently initiated by the University of Maine; these areas were not included in the present study.

Data Collection

Sampling was conducted between June and August in 2006 and 2007. I sampled the CFI plots in each of the nine silvicultural experiment areas and the natural area (described above); the nine silvicultural treatments and the natural area will be collectively referred to as the "continuously forested treatments." Two unmanaged old field stands were also sampled.

At each CFI plot, I sampled the understory vegetation on subplots A and B (Figure 1.2). Because the old field stands were not part of the silvicultural experiment, they did not have CFI plots. Therefore, new plots modeled after the CFI plots were established in the old fields. Distances between the new plots in the old fields were chosen using a random number generator constrained by the observed distances between CFI plots.

Percent cover was estimated for all understory species using a modified version of the Braun–Blanquet scale: 1 = less than 5% and rare, 2 = less than 5% and uncommon, 3 = less than 5% and common, 4 = 5 to 25%, 5 = 26 to 50%, 6 = 51 to 75%, and 7 = 76 to 100%. Because percent cover was estimated for each species individually and stems were vertically stratified, the total cover of a subplot often sums to greater than 100%. Error was reduced by having one person estimate percent cover. Cryptogams (bryophytes and lichens) were identified to genus or group; *Lycopodium* and *Equisetum* were identified to genus. Reproductive features were usually unavailable for *Galium* and *Viola*, so these were grouped to the genus level for analysis. Tree seedlings and shrubs ≤0.6 m tall were assigned a cover class. I noted the presence of trees and shrubs >0.6 meters tall, but percent cover was not assessed (Burkman 2005). Plots were revisited in an effort to observe unknown plants in flower. Some plant species could not be identified in the field; in this case a specimen outside the subplot was collected and identified at the University of Maine herbarium.

So that vegetation data could be related to possible explanatory features, additional site variables were collected for each subplot; these included the percent cover of exposed rock, mineral soil, coarse woody material, and broadleaf and needle litter. Percent cover estimates were made using the same cover scale as above. Data regarding basal area (BA, m^2/ha of trees > 1.3 cm dbh) and density of overstory trees were obtained from the Forest Service long-term dataset.

To determine soil drainage, a soil pit was excavated outside the perimeter of each CFI plot. If the average slope across the plot was ≥5%, two soil pits were dug and the measurements averaged. Thickness of the organic horizon, thickness of the eluvial horizon, and depth to redoximorphic features (mottling) were measured to the nearest 0.5 cm. Drainage class and Briggs site class (Briggs 1994) at each plot were determined using these measurements.

As a surrogate for the measurement of light in the understory, a digital image of the canopy above each subplot was taken using a Sigma 8-mm 180° fisheye lens attached to a Canon EOS Digital Rebel camera. The camera was attached to a tripod, the camera lens was positioned 0.6 m above the forest floor, and a level was used to ensure that the lens was standardized in orientation. Images were captured in July and August of 2006 and 2007, between 5:30 and 8:00 a.m., and 4:00 and 8:00 p.m. to avoid direct sunlight. The images were processed using Microsoft® Picture It! (Microsoft 2002) software to increase the contrast between vegetation and sky. Gap Light Analyzer (Frazer et al. 1999) was used to obtain a value for percent canopy openness.

Data Preparation

Understory species were categorized as native or nonnative to North America based on Fernald (1987). Nonnative plants were further categorized as invasive based on IPANE records (Mehrhoff et al. 2003). Species were also classified as obligate wetland (≥99% probability of occurrence in wetlands) or facultative wetland (67-98% probability of occurrence in wetlands) (USDA 2008).

Cover class values for vegetation and environmental variables from the two subplots were converted to the cover class midpoint and averaged into a mean percent cover for each plot (Archer et al. 2007). Understory species were categorized into eight growth habit groups (Stevens 2001): bryophytes and lichens, graminoids, ferns and fern allies, herbs, subshrubs, shrubs, tree seedlings, and vines. Percent cover for growth habit groups was calculated by converting the cover class of each species to the percent cover midpoint (Archer et al. 2007) and then summing for all species in the group (Jenkins and Parker 2000).

Diversity indices for the understory plants, including bryophyte groups, were calculated by averaging plot-level data to obtain a mean for each replicate. I calculated species richness (S), species evenness (E), Shannon-Weiner diversity index (H'), and Hill's first and second order numbers (N_1, N_2).

I used a modified version of Hill's evenness ratio as proposed by Alatalo (1981):

$$E = (N_2 - 1) / (N_1 - 1)$$

Where N_1 and N_2 are Hill's first and second order numbers (defined below). Hill's evenness ratio was used because it is relatively unaffected by species richness and tends to be independent of sample size (Alatalo 1981); it is recommended by ecologists as the least ambiguous measure of evenness (Alatalo 1981, Hill 1973, Peet 1974).

Hill's numbers are considered by some to be the most interpretable measures of species diversity (Hill 1973, Jost 2006, MacArthur 1965, Peet 1974). Hill's first order number (N_1) is the number of species that are "abundant" in a community; Hill's second order number (N_2) is the number of species that are "very abundant" in the community:

$$N_1 = \exp(H')$$

$$N_2 = \frac{1}{\sum (n_i/N)^2)}$$

where N is the total number of individuals for all species (S) in the population, i = 1,2,3,…, S, and n_i is the number of individuals of the i^{th} species. While richness will vary with sample size, Hill's numbers are stable over a wide range of sample sizes (Hill 1973).

Statistical Analyses

Mixed model, one-way analysis of variance (ANOVA) was used to test the hypothesis that the treatments are associated with differing species richness, Shannon's H', evenness, and Hill's N_1 and N_2 of the understory vascular plants. Differences in the abundance (measured as total percent cover) of growth habit groups was also tested with mixed model ANOVA. Data were checked for violations of normality and homoscedasticity; variables were Box-Cox transformed to improve normality (Legendre and Legendre 1983). I used Tukey's honestly significant difference (HSD) with $\alpha = 0.10$ (due to low replication, see Sendak et al. 2003) to perform pairwise comparisons among the treatments. All ANOVA tests were carried out using SAS, version 9.1.3 (SAS 2002).

Linear regression was used to test the hypothesis that understory vascular species richness and diversity would vary as a function of overstory basal area, canopy openness, soil drainage, and other measured environmental characteristics. Understory vascular plant richness, cover, and diversity (H') were the dependent factors. Independent variables were selected based on examination of pairwise scatter plots, Pearson's correlation matrix, and multivariate ordination results (described below). I tested the reduced set of variables in simple linear regressions. The strongest independent variables were then tested in multiple regressions in order to investigate their model significance in combination. Independent variables were not used in combination if they were correlated at $r \geq 0.3$ (Weaver 2007). Data were checked for violations of normality and homoscedasticity. Box-Cox transformations of variables were used as needed to meet model assumptions (Legendre and Legendre 1983). Linear regression analysis and significance tests were carried out using the R statistical package (R Development Core Team 2007).

I used non-metric multidimensional scaling ordination (NMS) in PC-ORD version 4.07 (McCune and Mefford 1999) to examine the relationships among the understory species and between the species abundances and environmental variables. Sorensen's distance measure was used because it retains sensitivity in heterogeneous datasets and gives less weight to outliers (McCune and Mefford 1999). I chose the medium autopilot setting in PCORD, which performed the ordination using 15 runs with real data and 30 runs with randomized data (maximum of 200 iterations per run, McCune and Mefford 1999).

Cover values by species were square-root transformed to reduce the influence of the most abundant species (O'Connor and Crowe 2005). Plots in the species matrix were standardized to plot totals; this procedure is also called 'stand normalization' (Kenkel and Orloci 1986) or 'general relativization' of sites (McCune and Mefford 1999). Stand normalization sums the abundances for each species and divides each abundance by the total; this corrects for the total plant biomass found on the plot (Jongman et al. 1995). Uncommon species (those found on <5 plots) were omitted from NMS ordination because they are not likely to be placed accurately in ordination space (McGarigal et al. 2000). These adjustments reduced the stress, a measure of 'badness-of-fit,' of the NMS ordination.

Results

Understory Plant Diversity

On the PEF, gamma diversity of all plots sampled was 234 species in 162 genera and 81 families. The understory flora was typical of the Acadian Forest. No rare, threatened, or endangered species (MNAP 2009) were found. Total richness per stand ranged from approximately 28 species in the three-stage shelterwood treatment to 100 species in the old field stands (Table 1.2). Most species were relatively infrequent; approximately 75% of species were found on fewer than 10% of plots; approximately 63% of species were found on fewer than 5% of plots. In all, 4.7% of vascular plants recorded on plots could not be identified to species due to missing reproductive parts; these were mostly graminoids (2.3%) and members of the Asteraceae (1.1%).

The old field stands had the most nonnative and invasive species, as well as the most obligate wetland species (Table 1.3). Twenty-one nonnative species were recorded in the old field stands, nine of which are invasive in New England. Glossy buckthorn (*Frangula alnus*) and shrub honeysuckle (*Lonicera* spp.) were the most frequent invasive species in the old field stands (86% and 59% of plots, respectively), followed by Oriental bittersweet (*Celastrus orbiculata*) (41% of plots). Few invasive species were found in the silviculture treatment areas or in the natural area. *F. alnus* was found in five plots in four treatments: the unregulated harvest, 10-year selection, two-stage shelterwood, and the natural area. *Lonicera* spp. was found in one plot in an unregulated harvest replicate. Additionally, one seedling of *C. orbiculata* was seen in a modified diameter-limit replicate, and one 2 m tall Japanese barberry (*Berberis thunbergii*) was found in an unregulated harvest replicate. Species in wetland categories were found in all treatments

(Table 1.4). Three-seeded sedge (*Carex trisperma*), northern bugleweed (*Lycopus uniflorus*), and with-rod (*Viburnum nudum*) were the most frequent obligate wetland species.

Table 1.2. Species richness. Total understory vascular plant richness by treatment (± SE). Treatment codes are given in Table 1.1a. AG = old field stands.

Treatment	# plots	# species
AG	22	100.1 ± 3.1
URH	41	89.4 ± 5.4
FDL	33	70.2 ± 3.6
MDL	31	59.5 ± 0.5
S20	37	55.8 ± 7.7
S10	35	72.2 ± 7.9
S05	33	51.9 ± 8.5
SW2	30	52.7 ± 7.8
SW3sp	18	40.8 ± 3.2
SW3	17	31.6 ± 4.5
NAT	20	28.4 ± 1.6

Note: Due to unequal number of plots per replicate, a comparison of raw counts of total richness among treatment areas is inaccurate based on the species-area relationship (Hill 1973, MacArthur and Wilson 1967, Peet 1974). Many researchers suggest standardizing the data to an equal number of individuals or equal-sized areas before comparisons are made (Berger and Peuttmann 2000, James and Rathbun 1981). For comparisons in this table only, I standardized the data to the smallest area sampled in a compartment (8 plots per compartment). The program EstimateS was used to obtain a value for the total number of species observed based on equal sampling effort for each treatment area; it employs a bootstrapping method which randomly re-samples the data from all plots (Gotelli and Colwell 2001).

Table 1.3. Nonnative, invasive, and wetland plants. Numbers of nonnative, invasive, and wetland vascular plant species recorded on sampled plots. Treatment codes are given in Table 1.1a. AG = old field stands.

Treatment	Nonnative (not invasive)	Nonnative Invasive	Facultative wetland	Obligate wetland
AG	4	9	22	15
URH	1	2	25	8
FDL	2	0	22	6
MDL	0	0	15	5
S20	1	0	15	5
S10	2	1	20	9
S05	1	0	12	8
SW2	0	1	9	4
SW3sp	0	0	3	0
SW3	0	0	2	0
NAT	0	1	2	1

Table 1.4. Plant growth habit categories. Number of understory plant species recorded in plots by growth habit.

Growth Habit	**# of species**[1]
Bryophytes & lichens	15
Ferns & fern allies	18
Graminoids	39
Herbs	84
Subshrubs	11
Shrubs	35
Tree seedlings	27
Vines	5
Total	234

[1]Note: Bryophytes and lichens were identified to genus or group, not to species.

The old field stands contained 49 species not encountered in the silvicultural treatments or in the natural area, many of which are nonnative species commonly found in fields, early successional forests, and open woods such as witch's moneybags (*Hylotelephium telephium*), brittlestem hempnettle (*Galeopsis tetrahit*), European crabapple (*Malus sylvestris*), and hawthorn (*Crataegus* sp.). The unregulated harvest and the fixed diameter-limit treatments contained many species not found in other silvicultural treatments. Twenty-one species occurred in the unregulated harvest areas but not in any other silvicultural treatment. Many of these were native herbs such as arctic sweet coltsfoot (*Petasites frigidus*), rattlesnake root (*Prenanthes* sp.), Lindley's aster (*Symphyotrichum ciliolatum*), purplestem aster (*Symphyotrichum puniceum*), and blisterwort (*Ranunculus recurvatus*).

Treatment Effects

Pairwise comparisons using Tukey's HSD showed that species richness and diversity in each treatment was significantly different from that of at least one other treatment (Table 1.5). The old field stands, unregulated harvest, and fixed diameter-limit treatments were the richest and most diverse. The old field stands had an average of 27.3 vascular plant species per plot, this was 20.7 more species per plot than the three-stage shelterwood, which had the lowest species richness. The three-stage shelterwood was the least species-rich, with an average of 6.6 vascular species per plot, and was significantly different from all treatments except for the two-stage shelterwood, three-stage shelterwood with precommercial thinning, and the natural area (Table 1.5). I found fewer differences for diversity than richness among the treatments. For instance, while the 10-year selection was less rich than the old field stands, unregulated harvest, and fixed diameter-limit, it was similar in diversity. The 5-year selection was richer than the shelterwoods and natural area, but was similar in diversity.

Table 1.5. ANOVA results. Least square means (per plot), ± standard errors, and ANOVA results for species richness, Shannon's diversity index, evenness, and Hill's N_1 and N_2 in 11 treatments. Only vascular plants were included. Values within rows with different letters were significantly different among treatments using Tukey's pairwise comparisons ($\alpha = 0.10$). Treatments are: AG=old field stands, URH=unregulated harvest, FDL=fixed diameter-limit, MDL=modified diameter-limit, S20=20 year selection, S10=10 year selection, S05=5 year selection, SW2=2-stage shelterwood, SW3sp=3-stage shelterwood with pre-commercial thinning, SW3=3-stage shelterwood, NAT=natural area. n=number of replicates per treatment or area; see Table 1.2 for number of plots per treatment.

Parameter	**Treatment**											**ANOVA results**	
	AG n=2	**URH** n=2	**FDL** n=2	**MDL** n=2	**S20** n=2	**S10** n=2	**S05** n=2	**SW2** n=2	**SW3sp** n=2	**SW3** n=2	**NAT** n=2	***F***	***p***
Richness	26.68 ±0.01 a	20.44 ±0.01 ab	17.71 ±0.01 abc	13.49 ±0.01 bcde	11.56 ±0.01 cde	15.36 ±0.01 bcd	11.54 ±0.01 cde	9.79 ±0.01 cdef	9.04 ±0.01 def	5.06 ±0.01 f	6.74 ±0.01 ef	12.38	0.0001
Diversity (*H'*)	2.74 ±0.48 a	2.53 ±0.41 ab	2.37 ±0.43 abc	2.18 ±0.44 bcd	2.13 ±0.42 bcd	2.42 ±0.43 abc	2.1 ±0.43 cde	2.09 ±0.44 cde	2.04 ±0.5 cde	1.55 ±0.5 e	1.69 ±0.49 de	11.08	0.0002
Evenness	0.63 ±0.06 d	0.67 ±0.05 cd	0.7 ±0.05 bcd	0.69 ±0.05 bcd	0.78 ±0.05 abcd	0.79 ±0.05 abc	0.76 ±0.05 abcd	0.86 ±0.05 a	0.86 ±0.06 a	0.77 ±0.06 abcd	0.82 ±0.06 ab	6.83	0.0019
Hill's N_1	15.59 ±0.001 a	12.55 ±0.00 ab	10.72 ±0.001 ab	8.81 ±0.001 bc	8.46 ±0.00 bc	11.27 ±0.001 ab	8.15 ±0.001 bc	8.16 ±0.001 bc	7.74 ±0.001 bcd	3.67 ±0.001 d	5.39 ±0.001 cd	8.34	0.0008
Hill's N_2	10.49 ±0.003 a	8.76 ±0.001 ab	7.81 ±0.002 ab	6.38 ±0.002 bcd	6.67 ±0.002 bc	8.92 ±0.002 ab	6.42 ±0.002 bcd	6.98 ±0.002 abc	6.71 ±0.004 abcd	3.7 ±0.004 d	4.59 ±0.004 cd	8.73	0.0006

Significant differences were found in the number of abundant species (N_1) and the number of very abundant species (N_2). The old field stands, unregulated harvest, fixed diameter-limit, and 10-year selection had the greatest number of abundant and very abundant species (Table 1.5). Hill's numbers are a measure of diversity, but because they are actual numbers of species (not an index of diversity, as with Shannon's *H'*), they can be used to determine the magnitude of change in diversity between treatments (Jost 2006). For instance, the old field stands had 15.6 abundant species and the three-stage shelterwood had 3.7 abundant species; therefore, the old field was almost four times as diverse as the three-stage shelterwood.

Few differences were found in evenness among treatments. In general, the treatments with lower species richness were more even, and the more species-rich treatments were the least even. The old fields were the least even due to many uncommon and infrequent species. The two-stage shelterwood and three-stage shelterwood with precommercial thinning treatments were the most even, and were significantly different from the old field stands, unregulated harvest, fixed diameter-limit, and modified diameter-limit (Table 1.5).

There were significant differences in the percent cover of growth habits among treatments (Figure 1.3). Most habit groups had highest abundance in treatments where richness and diversity were high, and lowest abundance in species-poor and less diverse treatments. However, tree seedlings and bryophytes did not follow this trend; these two groups were most abundant in the selection treatments, which were intermediate in richness and diversity. Bryophyte and lichen cover was similar in all managed stands, but differences existed between managed stands and unmanaged stands. Tree seedlings obtained highest cover in the 5-year selection, but this was only significantly different from the two-stage shelterwood (Figure 1.3).

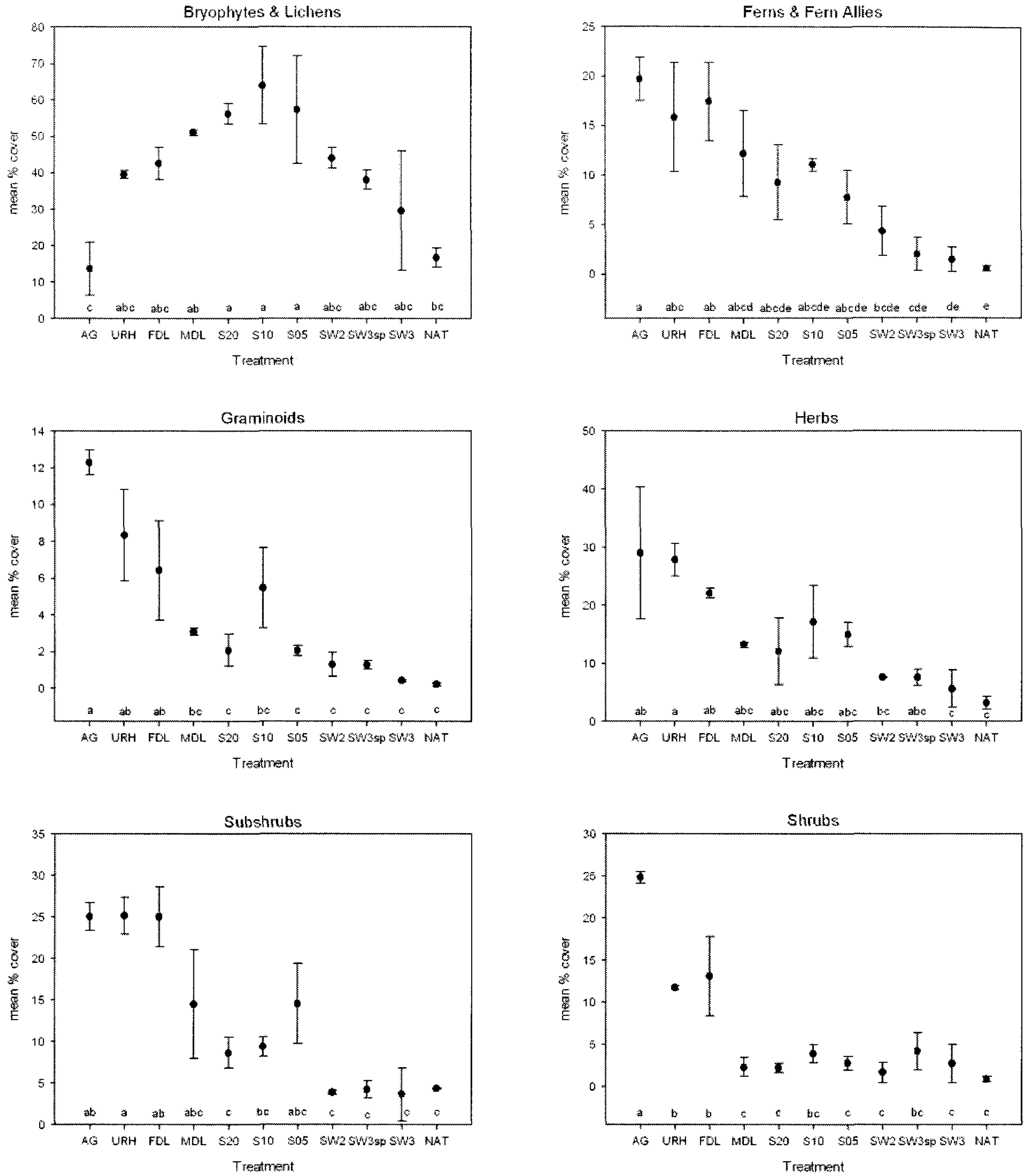

Figure 1.3. Percent cover of growth habit groups. Mean percent cover (raw means) of growth habit groups per plot. Bars are standard errors. Different letters (a-e) denote significant differences among treatments using Tukey's pairwise comparisons ($\alpha = 0.10$).

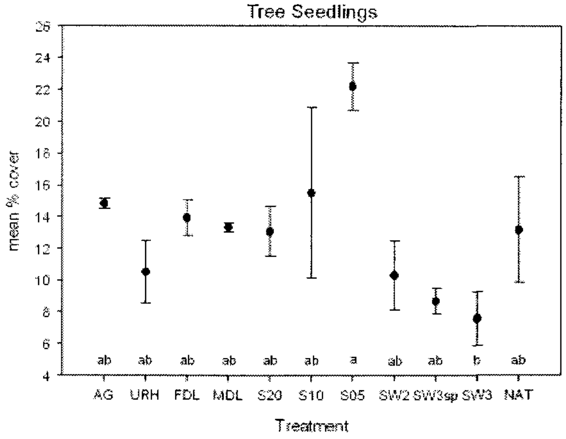

Figure 1.3 (continued). Percent cover of growth habit groups. Mean abundance (percent cover) of growth habit groups per plot. Bars are standard errors. Letters denote significant differences among treatments.

Linear Models

Understory species richness, diversity, and total percent cover were significantly related to five independent variables: total basal area, softwood basal area, softwood litter, canopy openness, and soil drainage (measured as depth to mottling) (Table 1.6). Total basal area and softwood basal area consistently explained the most variation in all three response variables. Canopy openness and soil drainage had significant relationships to the response variables, but did not explain much variation.

Softwood basal area had the strongest relationship to richness ($R^2=0.39$ $p < 0.001$), followed by total basal area ($R^2=0.34$ $p < 0.001$), and softwood litter cover ($R^2=0.30$ $p < 0.001$) (Table 1.6a). These three variables are highly correlated. A linear model using canopy openness and softwood basal area to describe the variation in species richness was highly significant ($p < 0.001$) and explained 43.66% of the variation in the data (Model a_6, Table 1.6b).

Softwood basal area alone was the best predictor of understory species diversity ($R^2=0.29$ $p < 0.001$) (Table 1.6a), though soil drainage and softwood litter cover described diversity almost as well ($R^2=0.27$ $p < 0.001$) (Model b_6, Table 1.6b).

Total basal area, softwood basal area, and softwood litter all performed well in linear models to describe percent understory cover ($R^2=0.39$, 0.38 and 0.36), but these three variables were highly correlated (Table 1.6a). The best model to describe variation in percent cover included softwood basal area and canopy openness ($R^2=0.48$ $p < 0.001$) (Model c_6, Table 1.6b).

Table 1.6 a. Simple linear regression results. Models used 317 plots in 11 treatments. BA= total basal area; swBA= % softwood basal area; SWL= % cover softwood litter cover; SD= soil drainage; CO= % canopy openness.

Model	y	b_o	b_1x	R^2_{adj}	p
a_1	richness	2.89223	-0.0056 BA	0.34	< 0.001
a_2	richness	3.1557	-0.0071 swBA	0.39	< 0.001
a_3	richness	3.27103	-0.0119 SWL	0.30	< 0.001
a_4	richness	2.85224	-0.0124 SD	0.12	< 0.001
a_5	richness	1.7061	+0.8760 CO	0.12	< 0.001
b_1	diversity (*H'*)	5.66634	-0.0160 BA	0.25	< 0.001
b_2	diversity (*H'*)	5.24441	-0.0161 swBA	0.29	< 0.001
b_3	diversity (*H'*)	4.83186	-0.0220 SWL	0.20	< 0.001
b_4	diversity (*H'*)	4.54334	-0.0321 SD	0.11	< 0.001
b_5	diversity (*H'*)	2.2449	+1.6650 CO	0.06	< 0.001
c_1	total percent cover	3.73126	-0.0089 BA	0.39	< 0.001
c_2	total percent cover	3.42717	-0.0081 swBA	0.38	< 0.001
c_3	total percent cover	4.10961	-0.0181 SWL	0.36	< 0.001
c_4	total percent cover	2.94153	-0.0103 SD	0.06	< 0.001
c_5	total percent cover	1.5634	+1.5849 CO	0.19	< 0.001

Table 1.6b. Multiple linear regression results. Models used 317 plots in 11 treatments.

Model	y	b_o	b_1x	b_2x	R^2_{adj}	p
a_6	richness	2.66441	-0.007 swBA	+0.6205 CO	0.44	< 0.001
b_6	diversity (*H'*)	5.29415	-0.0195 SWL	-0.0248 SD	0.27	< 0.001
c_6	total percent cover	2.9292	-0.0102 swBA	+1.3364 CO	0.48	< 0.001

Multivariate Analysis

NMS Ordination – All Plots

Using the complete dataset (317 plots in 11 treatments), a low stress, two-dimensional solution was found which described 81.8% of the dataset variation (Figure 1.4, Table 1.7). Plots in the silvicultural treatments and the natural area (the continuously forested plots) were grouped in the upper portion of the biplot. They are characterized by greater total basal area, softwood basal area, and softwood litter cover. Plots found in the old field stands were grouped in the lower right section of this biplot, and were characterized by greater hardwood basal area and exposed mineral soil.

The results of this ordination show clearly that the continuously forested plots were different in understory composition from the plots in the old fields. This separation of plots in ordination space based on land use history is not unusual (Jenkins and Parker 2000). There was a high degree of species turnover between the old field and the continuously forested plots; approximately 30% of all the species recorded in the former agricultural plots were not recorded in other treatment areas. In this situation, multivariate ordination is less able to recover data structure (Kenkel 1986) Therefore, the continuously forested plots and the old field plots were analyzed separately using multivariate ordination.

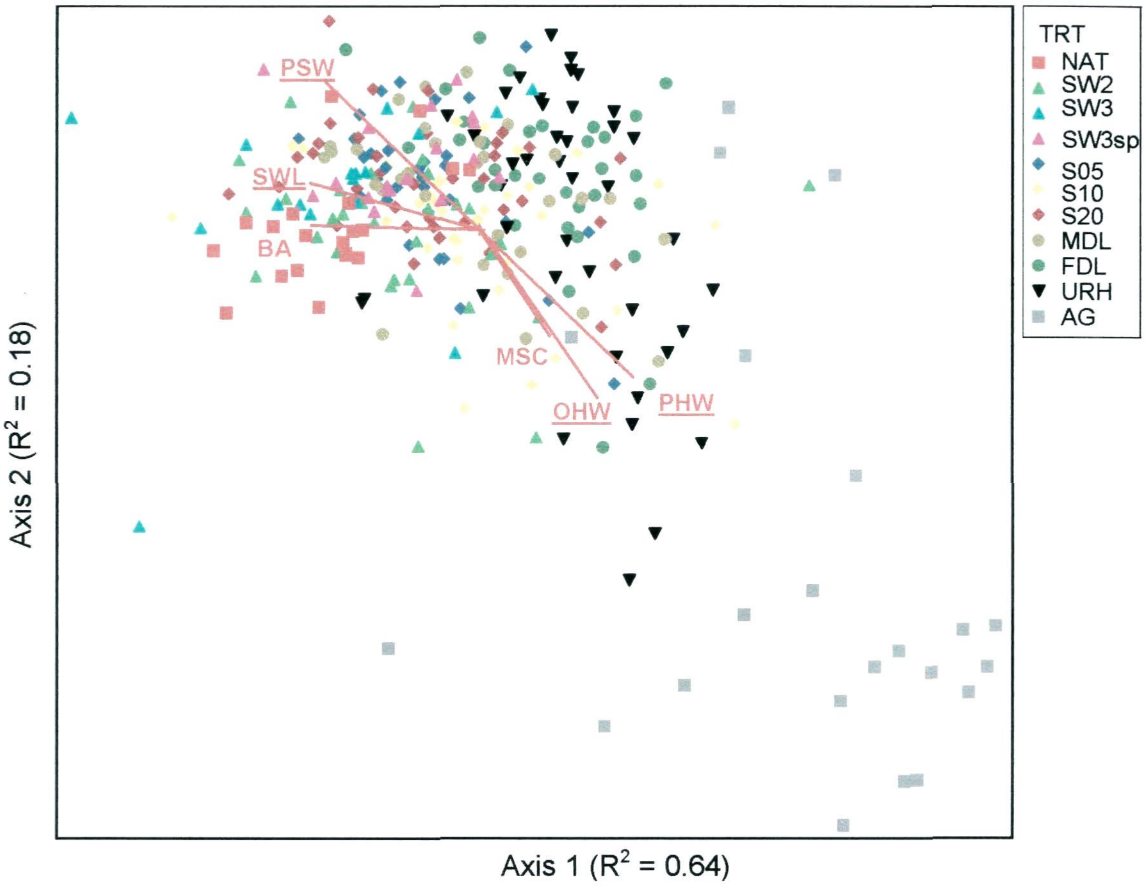

Figure 1.4. NMS results – all treatments. Biplot shows plots in species space. Dataset included all 317 plots. BA=basal area; PSW=% softwood basal area; PHW=% hardwood basal area; SWL=% softwood litter cover; MSC=% mineral soil cover; OHWD=% other hardwood basal area. 'Hardwood basal area' includes *Acer rubrum* and *Betula papyrifera*; 'other hardwood basal area' includes all other hardwood tree species.

Table 1.7. Pearson correlations – all treatments. Pearson correlations *(r)* between environmental variables and (NMS) ordination axes (see Figure 1.4).

Environmental variables	**Axis 1**	**Axis 2**
% Softwood litter cover (SWL)	-0.368	0.101
Total basal area (BA)	-0.366	0.008
% Hardwood basal area (PHW)	0.334	-0.324
% Softwood basal area (PSW)	-0.334	0.324
% Other hardwood basal area (OHWD)	0.259	-0.375
% Mineral soil cover (MSC)	0.175	-0.258

NMS Ordination – Continuously Forested Plots

NMS ordination of the continuously forested plots (295 plots in 10 treatments) resulted in a low stress, three dimensional solution representing approximately 84% of the dataset variation (Figure 1.5). The mean site scores for each treatment are plotted along with their 95% confidence intervals; similarities in understory composition among treatments are shown by overlap of confidence interval ellipses (Figure 1.5). Understory plant composition in the unregulated harvest and fixed diameter-limit treatments were similar, and together they were different from all other treatments. Confidence ellipses of the three selection treatments and the modified diameter-limit treatment showed considerable overlap. The confidence ellipses for the three-stage shelterwood and three-stage shelterwood with precommercial thinning do not overlap with any other treatment ellipses; their understory composition is different from that of other treatments (Figure 1.5).

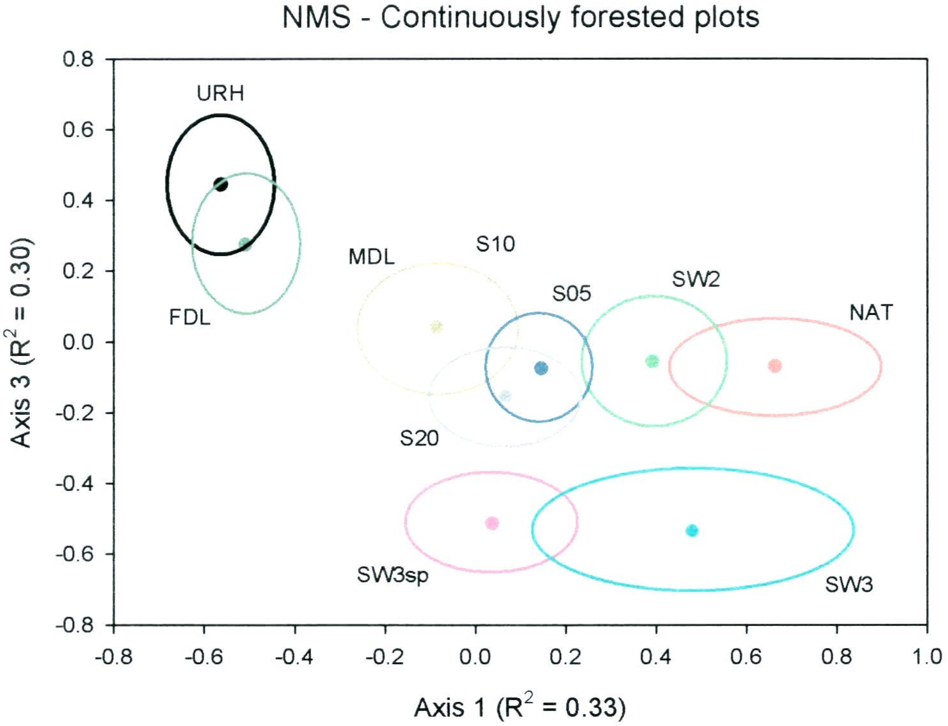

Figure 1.5. NMS results – continuously forested treatments. Biplot of the ten continuously forested treatments (295 plots). Points represent mean scores for treatments, and ellipses encompass 95% confidence intervals about the means. See Table 1.1a for explanation of treatment codes

In another run of the NMS ordination, I investigated the placement of species in plot space. PC-ORD displays vectors on the ordination biplot for those environmental variables that are most influential (Pearson's $r \geq 0.40$ for any axis) to the understory composition. Total basal area, basal area of *Pinus strobus*, and softwood litter cover were positively correlated with axis 1 (Table 1.8). Basal area of *Picea rubens* was positively correlated with axis 3. Soil drainage and canopy openness were not as strongly correlated with the ordination axes (Table 1.8), although the biplot reveals reveals a pattern of species groups according to their tolerance for shade (Figure 1.6a). Species that are typical of more open habitat conditions are on the lower end of axis 2; these include hawkweeds (*Hieracium* sp.) (Goldblum 1997, Roberts and Gilliam 1995), red raspberry

(*Rubus idaeus*), sweet fern (*Comptonia peregrina*), goldenrods (*Solidago* sp.) (Ramovs and Roberts 2005), calico aster (*Symphyotrichum lateriflorum*), Virginia strawberry (*Fragaria virginiana*) (Roberts and Gilliam 1995), and northern bush honeysuckle (*Diervilla lonicera*) (Roberts and Gilliam 1995). Many species classified as facultative or obligate wetlands species (USDA 2008) are also grouped together. These include blue skullcap (*Scutellaria lateriflora*), sensitive fern (*Onoclea sensibilis*), crested woodfern (*Dryopteris cristata*), dwarf red blackberry (*Rubus pubescens*), greater bladder sedge (*Carex intumescens*), and northern bugleweed (*Lycopus uniflorus*) (Figures1.6a and 1.6b). See Table 1.9 for explaination of species codes used in ordination biplots.

Table 1.8. Pearson correlations – continuously forested treatments. Pearson correlations (*r*) between environmental variables and NMS ordination axes (see Figures 1.6a and 1.6b).

Environmental variable	**Axis 1**	**Axis 2**	**Axis 3**
Total basal area (BA)	-0.07	0.57	0.51
Pinus strobus basal area (PIST)	0.16	0.27	0.43
% Softwood litter cover (SWL)	-0.12	0.31	0.51
Picea rubens basal area (PIRU)	-0.47	0.14	0.17
Depth to mottling (DTM)	-0.13	0.07	0.39
% Canopy openness (CO)	0.09	-0.33	-0.28

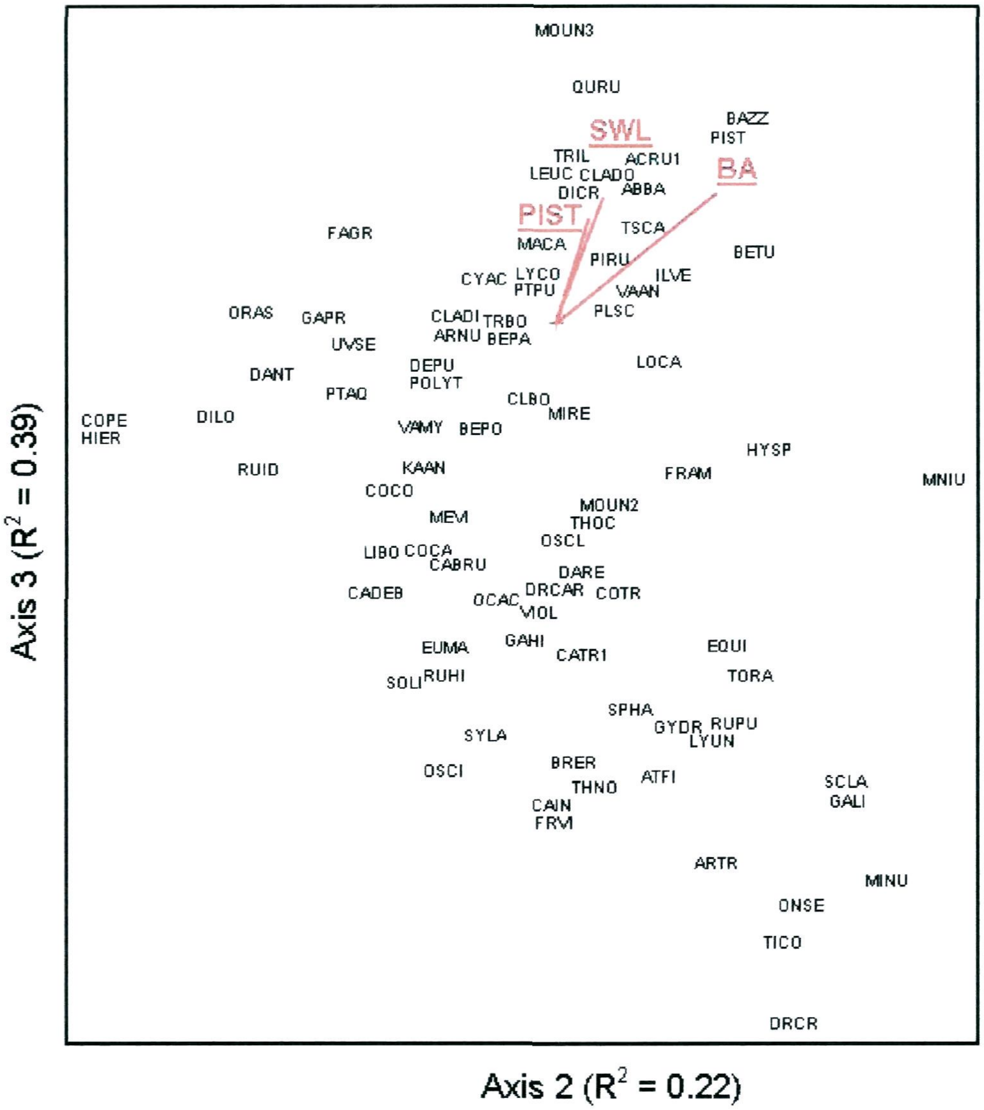

Figure 1.6 a. NMS results – species (axes 2 and 3). Species matrix included 295 continuously forested plots and 84 species. Plots in the old field were not included. Species that occurred in fewer than 5 plots were not included BA=total basal area; SWL= % softwood litter cover; PIST= % *Pinus strobus* basal area. See Table 1.9 for species codes.

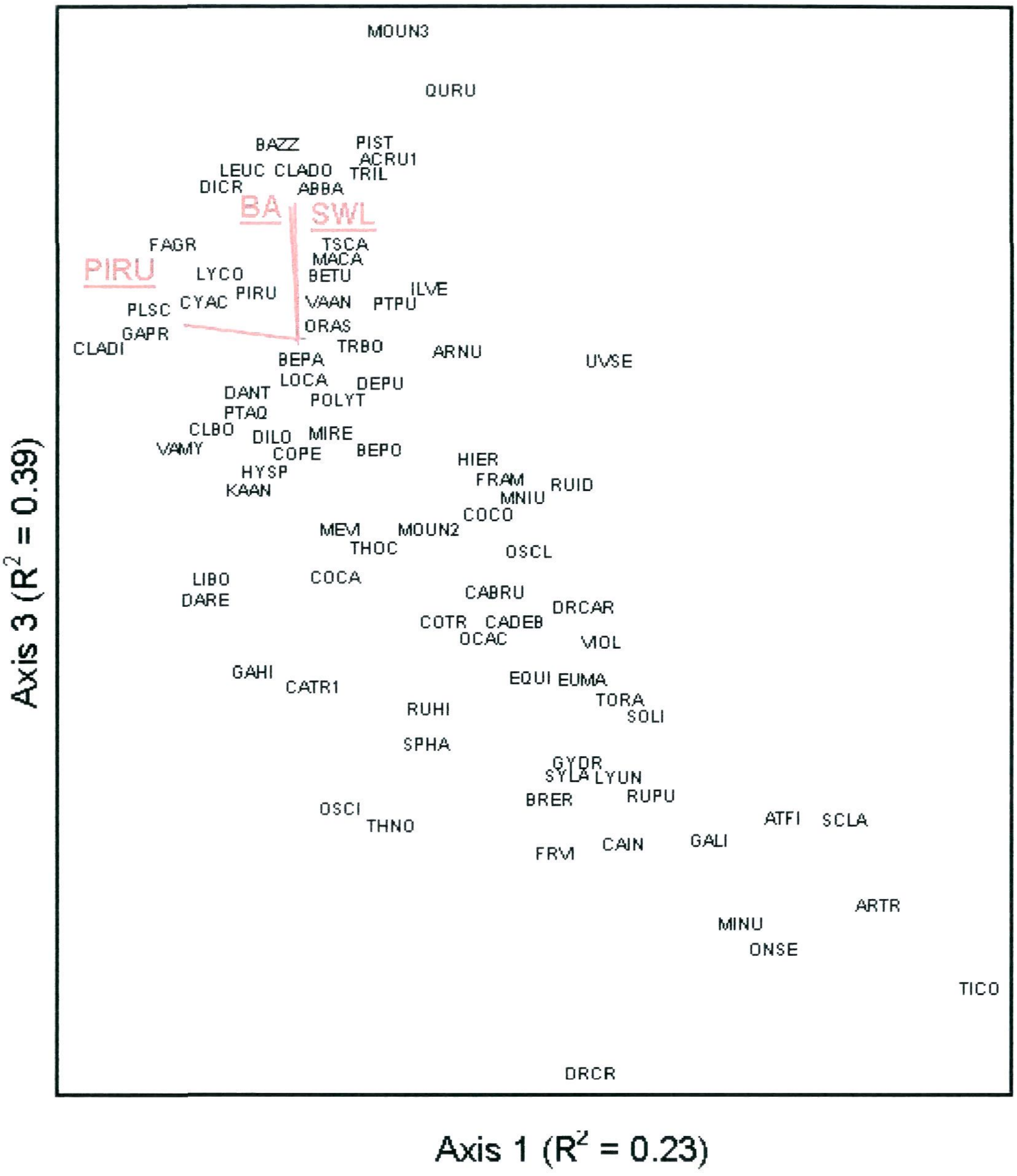

Figure 1.6b. NMS results – species (axes 1 and 3). Species matrix included 295 CFI plots and 84 species. Plots in the old field were not included. Species that occurred in fewer than 5 plots were not included. BA= total basal area; SWL= % softwood litter cover; PIRU= % *Picea rubens* basal area. See Table 1.9 for species codes.

Table 1.9. Plant species used in NMS ordinations. Species codes, genus and specific epithet, and common names of plant species on the PEF (see Figures 1.6a, 1.6b, and 1.7).

Code	Common name	Code	Common name
ABBA	*Abies balsamea* balsam fir	CORNU	*Cornus* sp. dogwood
ACPL	*Acer platanoides* Norway maple	COAL	*Cornus alternifolia* alternateleaf dogwood
ACRU1	*Acer rubrum* red maple	COCA	*Cornus canadensis* bunchberry
AGRO	*Agrostis* sp. bentgrass	COCO	*Corylus cornuta* beaked hazelnut
ALIN	*Alnus incana* speckled alder	COPE	*Coptonia peregrina* sweet fern
AMEL	*Amelanchier* spp. serviceberry	COTR	*Coptis trifolia* threeleaf goldthread
ANOD	*Anthoxanthum odoratum* sweet vernalgrass	CYAC	*Cypripedium acaule* pink lady's slipper
ANQU	*Anemone quinquefolia* wood anemone	DANT	*Danthonia* spp. oatgrass
ARNU	*Aralia nudicaulis* wild sarsaparilla	DARE	*Dalibarda repens* dewberry
ARTR	*Arisaema triphyllum* Jack in the pulpit	DEPU	*Dennstaedtia punctilobula* hayscented fern
ATFI	*Athyrium filix-femina* common ladyfern	DICR	*Dicranum* spp. dicranum moss
BAZZ	*Bazzania* spp. Bazzania moss	DILO	*Diervilla lonicera* n. bush honeysuckle
BEPA	*Betula papyrifera* paper birch	DOUM	*Doellingeria umbellata* parasol whitetop
BEPO	*Betula populifolia* gray birch	DRCAR	*Dryopteris carthusiana* spinulose woodfern
BETU	*Betula* spp. birch	DRCR	*Dryopteris cristata* crested woodfern
BRER	*Brachyelytrum erectum* bearded shorthusk	EPHE	*Epipactis helleborine* broadleaf helleborine
CABRU	*Carex brunnescens* brownish sedge	EQUI	*Equisetum* spp. horsetail
CADEB	*Carex debilis* white edge sedge	EUMA	*Eurybia macrophylla* bigleaf aster
CAGR	*Carex gracillima* graceful sedge	FAGR	*Fagus grandifolia* American beech
CAIN	*Carex intumescens* greater bladder sedge	FRAL	*Frangula alnus* glossy buckthorn
CATE	*Carex tenera* quill sedge	FRAM	*Fraxinus americana* white ash
CATR1	*Carex trisperma* threeseeded sedge	FRVI	*Fragaria virginiana* Virginia strawberry
CEOR	*Celastrus orbiculata* Oriental bittersweet	GAHI	*Gaultheria hispidula* creeping snowberry
CIRC	*Circaea* spp. enchanter's nightshade	GALI	*Galium* spp. bedstraw
CLADI	*Cladina* spp. reindeer lichen	GAPR	*Gaultheria procumbens* eastern teaberry
CLADO	*Cladonia* spp. cup lichen	GATE	*Galeopsis tetrahit* brittlestem hempnettle
CLBO	*Clintonia borealis* bluebead lily	GEUM	*Geum* spp. avens

Table 1.9 continued. Plant species used in NMS ordinations.

Code	Common name
GLST	*Glyceria striata* fowl mannagrass
GYDR	*Gymnocarpium dryopteris* oakfern
HIER	*Hieracium* sp. Hawkweed
HYSP	*Hylocomium splendens* stairstep moss
HYTE	*Hylotelephium telephium* witch's moneybags
ILVE	*Ilex verticillata* common winterberry
IMCA	*Impatiens capensis* jewelweed
KAAN	*Kalmia angustifolia* sheep laurel
LEUC	*Leucobryum* sp. leucobryum moss
LIBO	*Linnaea borealis* twinflower
LOCA	*Lonicera canadensis* Am. fly honeysuckle
LONI	*Lonicera* spp. honeysuckle
LYCO	*Lycopodium* spp. clubmoss
LYUN	*Lycopus uniflorus* northern bugleweed
MACA	*Maianthemum canadense* Canada mayflower
MASY	*Malus sylvestris* european crab apple
MEVI	*Medeola virginiana* Indian cucumber
MINU	*Mitella nuda* naked miterwort
MIRE	*Mitchell repens* partridgeberry
MNIU	*Mnium* spp. mnium moss
MOUN2	*Moneses uniflora* one-flowered pyrola
MOUN3	*Monotropa uniflora* Indianpipe
OCAC	*Oclemena acuminata* whorled wood aster
ONSE	*Onoclea sensibilis* sensitive fern
ORAS	*Oryzopsis asperifolia* roughleaf ricegrass
OSCI	*Osmunda cinnamomea* cinnamon fern
OSCL	*Osmunda claytoniana* interrupted fern
OXAL	*Oxalis stricta* common yellow woodsorrel
PAQU	*Parthenocissus quinquefolia* Virginia creeper
PIRU	*Picea rubens* red spruce
PIST	*Pinus strobus* eastern white pine
PLSC	*Pleurebium schrebii* big red stem moss
POLY	*Polytrichum* sp. polytrichum moss
POLYT	*Polytrichum* polytrichum moss
PONE	*Poa nemoralis* wood bluegrass
POTE	*Potentilla simplex* cinquefoil
POTR	*Populus tremuloides* quaking aspen
PRSE	*Prunus serotina* black cherry
PRVI	*Prunus virginiana* chokecherry
PRVU	*Prunella vulgaris* common selfheal
PTAQ	*Pteridium aquilinium* western brackenfern
PTPU	*Ptilidium pulcherrimum* Naugehyde moss
QURU	*Quercus rubra* northern red oak
RANU	*Ranunculus* buttercup
RHCA	*Rhamnus cathartica* common buckthorn
RIBE	*Ribes* spp. currant
RUHI	*Rubus hispidus* bristly dewberry
RUID	*Rubus idaeus* red raspberry
RUPU	*Rubus pubescens* dwarf red blackberry
RUVE	*Rubus vermontanus* Vermont blackberry
SCLA	blue skullcap
SODU	*Solanum dulcamara* climbing nightshade
SOLI	*Solidago* spp. goldenrod
SPAL	*Spiraea alba* white meadowsweet
SPHA	*Sphagnum* spp. sphagnum moss
SYLA	*Symphyotrichum lateriflorum* calico aster
THNO	*Thelypteris noveboracensis* New York fern
THOC	*Thuja occidentalis* cedar/arborvitae

Table 1.9 continued. Plant species used in NMS ordinations.

Code	Common name	Code	Common name
TICO	*Tiarella cordifolia* heartleaf foamflower	VAAN	*Vaccinium angustifolium* lowbush blueberry
TORA	*Toxicodendron radicans* eastern poison ivy	VAMY	*Vaccinium myrtilloides* velvetleaf blueberry
TRBO	*Trientalis borealis* starflower	VEOF	*Veronica officinalis* common speedwell
TRIL	*Trillium* spp. trillium	VIDE	*Viburnum dentatum* southern arrowwood
TSCA	*Tsuga canadensis* eastern hemlock	VIOL	*Viola* spp. violet
UVSE	*Uvularia sessilifolia* sessileleaf bellwort		

NMS Ordination – Old Field Stands

NMS ordination using the 22 plots in the old field stands resulted in a low stress, two dimensional solution representing 92% of the dataset variation (Figure 1.7, Table 1.10). The understory species formed two groups in this ordination biplot. The upper left area of the biplot represents portions of the old field stands where hardwoods dominated the canopy; these were predominantly early successional species like *Populus tremuloides* and *Betula populifolia* along with *Malus* spp. and *Prunus* spp. Herbaceous plants such as brittlestem hempnettle (*Galeopsis tetrahit)*, and common cinquefoil (*Potentilla simplex*) were also characteristic of these portions of the old field. Most of the invasive species are located in this part of the biplot with the exception of Norway maple (*Acer platanoides*) and *Frangula alnus*. Hardwood litter cover and organic horizon development were minimal, and there was a relatively greater amount of surficial mineral soil.

The lower right of the biplot contains understory species characteristic of primary northern conifer forests such as eastern teaberry (*Gaultheria procumbens*), bunchberry

(*Cornus canadensis*), and starflower (*Trientalis borealis*). These species were associated with greater overstory basal area, particularly of *Acer rubrum* and the late-successional *Tsuga canadensis*, and greater litter cover and thicker organic horizon. The condition of the forest floor, soils, and plant indicate that these plots fell in areas that were not affected by cultivation or grazing.

Figure 1.7. NMS results – Old field stands. Species matrix included 22 old field plots and 74 species. A 'b' after the species code indicates it was a woody plant > 0.6 m tall. Native species occurring in fewer than 3 plots and nonnative species occurring in fewer than 2 plots were not included. PHW= % hardwood basal area; MSC= % mineral soil cover; BA= total basal area; TSCA= % *Tsuga canadensis* basal area; HWL= % hardwood litter; OH= thickness of organic horizon; Dist= distance from plot to road; ACRU= % *Acer rubrum* basal area. See Table 1.9 for species codes.

Table 1.10. Pearson correlations – Old field stands. Pearson correlations (*r*) between environmental variables and NMS ordination axes (see Figure 1.7).

Environmental variables	Axis 1	Axis 2
Distance to road (DIST)[1]	0.62	-0.56
Basal area (BA)	0.32	-0.44
% Hardwood basal area (PHW)	-0.35	0.54
% *Tsuga canadensis* basal area (TSCA)	0.33	-0.46
% *Acer rubrum* basal area (ACRU)	0.50	-0.38
% Mineral soil cover (MSC)	-0.53	0.35
Organic horizon thickness (OH)	0.60	-0.57
% Hardwood litter (HWL)	0.61	-0.66

[1] Not measured in the continuously forested areas.

Discussion

Treatment Effects

Despite the lack of historical data regarding the understory composition of the PEF, my results suggest clear differences in understory diversity and composition that are associated with silvicultural treatment and differences in land use history. The continuously forested areas on the PEF used for this study were similar in overstory composition prior to treatment installation (Sendak et al. 2003). Treatments were applied with the main goals of increasing the softwood component of stands, increasing the proportion of *Picea* spp. relative to *Abies balsamea*, and favoring *Picea*, *A. balsamea*, and *Pinus strobus* over *Tsuga canadensis* and *Thuja occidentalis* (Sendak et al. 2003). Understory composition and diversity likely shifted in direct response to the change in canopy composition as has been reported for other forests (Bergstedt and Milberg 2001, Brosofske et al. 2001). Nevertheless, local seed source is also recognized as having an effect on species distribution (Lord and Lee 2001). In addition, the legacy of prior understory compositional differences may still be apparent (McKenzie et al. 2000).

The cover of understory vegetation often increases proportionally to the intensity of silvicultural treatment (Zenner et al. 2006). On the PEF, most habit groups attained highest cover in the old field, unregulated harvest, and fixed and modified diameter-limit treatments. Exceptions were cryptogams (bryophytes and lichens) and tree seedlings. Forest bryophytes are shade tolerant and sensitive to harvest intensity (Fenton and Bergeron 2007). On the PEF, bryophyte and lichen cover was highest in the selection treatments, and this was significantly different from the old field stands and the natural area. The large amount of overstory removed in the unregulated harvest, both diameter-limits, and the three shelterwood treatments could have a negative effect on bryophyte cover. The natural area is not harvested, but Sendak et al. (2003) mention substantial mortality occurred in the natural area; this created canopy openings that may have affected the bryophyte community. Low bryophyte cover in the unregulated harvest and fixed diameter-limit treatments may also be attributed to the relatively large proportion of hardwood basal area in those treatments; broadleaf litter can smother low-growing vegetation (Whitney and Foster 1988) and prevent extensive carpeting of bryophytes on the forest floor.

The continuously forested treatment plots group together in ordination space in a way that mirrors similarities in their silvicultural treatment history. The confidence interval ellipses of the unregulated harvest and fixed diameter-limit treatments overlap because they are similar in understory composition. These two treatments are the most exploitive harvest methods on the PEF (Kenefic et al. 2004). The two variants of three-stage shelterwood harvesting group together; these stands share a similar history and were only recently divided into precommercially thinned and unthinned replicates. The three types of selection treatments are similar because they each contain multiple stages of stand development (Oliver and Larson 1996). The modified diameter-limit treatment is more similar to the selection cuts because larger diameter *Picea*, *Pinus strobus*, *Tsuga canadensis*, *Larix laricina*, and *Betula papyrifera* were retained (Sendak et al. 2003). This resulted in a greater abundance of trees in the higher DBH classes in the modified diameter-limit stands than in the fixed diameter-limit treatment, and a canopy structure more similar to the selection treatments (Kenefic et al. 2004).

Of special interest were native forest understory species that are associated with shade or are thought to be sensitive to harvest intensity (although low abundances and frequencies precluded statistical analysis of individual understory species). For instance, trillium (*Trillium* sp.) and fringed polygala (*Polygala paucifolia)* were not recorded in the unregulated harvest; their absence is noted because they may be sensitive to harvest intensity due to a reliance on vegetative spread. Shade associated understory species may respond to the effects of harvesting in different ways. Canopy gaps can provide an opportunity for some forest herbs to expand in cover and fruit more prolifically than they would in less disturbed microhabitats (Dunn et al. 1983, Rankin and Tramer 2002), but other species may not be able to survive the increased light intensity, temperatures, and soil moisture that accompany canopy removal (Meier et al. 1995).

The frequency and abundance of native shade-associated understory species in silviculture treatments on the PEF are informative, but data here are not always consistent with that from similar forests. For example, one-flowered pyrola (*Moneses uniflora)* presence decreased with increasing disturbance in British Columbia (Beese and Bryant 1999); on the PEF it had greatest frequency in the fixed diameter-limit, and lowest frequency in the unregulated harvest and two-stage shelterwood. Eastern teaberry (*Gaultheria procumbens)* is sensitive to disturbance in some forests (Whitney and Foster 1988), but on the PEF it attained highest cover and frequency in the diameter limit and unregulated harvest treatments. Partridgeberry (*Mitchella repens)* and Indian cucumber (*Medeola virginiana)* are shade tolerant and may increace cover in gaps (Rankin and Tramer 2002). On the PEF, *M. repens* had greatest cover in the diameter-limit treatment, though it was most frequent in less intense treatments. *M. virginiana* was most frequent in the ten-year selection, followed by the fixed diameter-limit and unregulated harvest. Other native forest herbs that had greatest cover in the more exploitive treatments were pink lady's slipper (*Cypripedium acaule),* bluebead *(Clintonia borealis),* and goldthread (*Coptis trifolia).* Forest herbs that were more frequent in more exploitive treatments were *C. acaule*, twinflower (*Linnaea borealis*), and Indian pipe (*Monotropa uniflora*).

Data collected for this study were baseline measurements; therefore it cannot be determined whether particular species have declined due to the effects of silvicultural treatment. Shade tolerant understory species were present in all treatments. On the PEF, the unregulated harvest treatment is not a true silvicultural clearcut with plans for regeneration; in practice, it is a commercial clearcut in which only merchantable stems are removed, resulting in a degree of spatial patchiness in the remaining stand. The diameter-limit and selection treatments also result in a heterogeneous understory with the potential for many different microhabitats whereby native forest herbs may find refugia for survival. Future inventories after subsequent harvests are required to determine the responses of specific understory species to silviculture treatments.

Environmental Influences

Ordination and regression analyses revealed similar patterns of environmental and canopy characteristics influencing the understory. Consistently, the basal area of canopy tree species – especially softwood basal area -- and the amount of surficial materials (litter and soil cover, and organic horizon thickness) were the most important to understory diversity and composition. I sought evidence that soil drainage and canopy openness play important roles in structuring understory flora, but on the PEF these variables were secondary to basal area, litter and soil cover, and organic horizon thickness.

In continuously forested areas, total basal area, percent cover of softwood litter, and the basal area of *Pinus strobus* and *Picea rubens* were the most important measured environmental variables to the composition of the understory. Basal area is often negatively correlated with understory plant species cover (Fredericksen et al. 1999, McKenzie et al. 2000, Nagaike et al. 1999), though relationships vary with stand developmental stage, life history traits of specific species (McKenzie et al. 2000), and traits of plant guilds (Zenner et al. 2006). Partial cutting that reduced basal area by > 50% resulted in significant differences in understory structure in forests in southeast Alaska (Deal 2001). In Pennsylvania, a decrease in basal area was related to understory plant percent cover, but not to richness or diversity of the understory plants (Fredericksen et al. 1999).

Changes in the understory environment (amount of light, nutrients, and moisture) are influenced by overstory canopy type (Frelich et al. 2003, Legare et al. 2001). Canopy species may influence understory vegetation by influencing soil nutrient availability, soil pH, light transmittance (Legare et al. 2001) and precipitation throughfall (Beall 1934, Muoghalu 2000). Brosofske et al. (2001) found that relationships between understory plant diversity and other environmental variables became stronger when analyzed within similar overstory species composition, suggesting that canopy type has greater control over the understory vegetation than other environmental variables.

In the multivariate analysis, I explored the associations between the basal area of each overstory tree species and understory composition. For the continuously forested treatments, basal area of *Pinus strobus* and *Picea rubens* were consistently associated with understory composition. *Picea* spp. may shape the forest understory by reducing light levels to a greater degree than other canopy types (Macdonald and Fenniak 2007), or by direct root competition in the litter layer (Hannam et al. 2004). *P. strobus* is more intolerant of shade than the other conifers on the PEF, and more light is able to penetrate its canopy (Canham and Burbank 1994). Therefore, its influence on the understory is likely not due to the shade it casts, but may be due to the effects of its litter (addressed below). Also, *P. strobus* may be indicative of better site quality on the PEF, as it requires better drained soils (Seymour 1992). *Tsuga canadensis* is often associated with understory composition because it is a late-successional species and casts very dense shade. However, my analyses revealed *T. canadensis*-understory associations only in the old field area where it grew outside the area affected by past cultivation.

Percent canopy openness described a relatively small proportion of the variance in the data. Analysis of the hemispherical digital images enabled a quantitative analysis of the visible gaps in the forest canopy, but this is only a partial measure of the light environment. Additional light sources come from transmission by leaves and beam radiation reflected by leaves and stems (Canham et al. 1990). Analyses here were limited to light quantity; however, plant species respond differently to changes in light quality across the red to far red spectrum (Canham et al. 1990). Despite these limitations, the ordination biplot of continuously forested plots reveals a pattern of species groups according to their tolerance for shade. The commercial clearcut and the fixed diameter-limit treatments had the greatest frequency of understory species that are relatively intolerant of shade. These included grasses such as oatgrass (*Danthonia* spp.), bentgrass (*Agrostis perennans*), and fowl mannagrass (*Glyceria striata*), and herbs like Virginia strawberry (*Fragaria*), red raspberry (*Rubus idaeus*), and hawkweed (*Hieracium* spp.).

Litter cover can be a strong determinant of understory composition (Brosofske et al. 2001, Legare et al. 2001, Whitney and Foster 1988). Softwood litter cover was revealed by ordination to be an important factor in the composition of the understory on the PEF. Conifer litter differs from hardwood litter chemically and physically (Whitney and Foster 1988). *Tsuga canadensis* and *Pinus* sp. litter have low pH, high C/N ratios, and high iron concentrations, which allow ericaceous species such as lowbush blueberry (*Vaccinium angustifolium),* velvetleaf blueberry *(Vaccinium myrtilloides), Gaultheria procumbens*, and sheep laurel (*Kalmia angustifolium)* to do well under conifer canopies (Whitney and Foster 1988). Low-growing and prostrate herbs such as *Linnaea borealis* and *Mitchella repens* may be favored in conifer-dominated woods with small needle litter, as they can be smothered by hardwood litter.

Soil drainage was not strongly associated with the axes in the multivariate analysis presented here, although many species classified as facultative or obligate wetlands species (USDA 2008) are grouped together in the ordination biplot of the continuously forested plots. Common winterberry (*Ilex verticilata)* is a facultative wetland species, but in the ordination of the continuously forested treatments it was associated with better drained areas of the PEF. This may be explained by the prevalence of *I. verticilata* seedlings in the natural area where low-lying wet areas near Blackman Stream are in close proximity to upland areas dominated by *Pinus strobus*. The fleshy fruits of *I. verticilata* may be transported by animals from parent plants near the stream to drier upland areas where the young seedlings were recorded in sample plots.

Multivariate analysis of the continuously forested treatments showed most of the tree seedlings and bryophytes grouped together, and were separated from most of the herbaceous vegetation. This pattern may be indicative of the competition between tree seedlings and herbaceous vegetation. Tree seedlings often decrease in cover with increasing harvest intensity even when other life forms increase (Zenner et al. 2006). A direct association between tree seedlings and bryophytes may exist, as many tree species find an ideal seedbed in a patch of moss which can provide moisture during dry periods (Maguire and Forman 1983). In Maine forests, *P. rubens* seedlings are associated with *Bazzania trilobata*, a liverwort (Dibble et al. 1999).

Land Use History

Historical land use significantly affected the richness and diversity of understory plants. The old field stands were the most diverse and species rich, but low in evenness due to many infrequent species. Richness was due in part to the presence of many ruderal species and nonnative plants including invasive species; 21 nonnative species were recorded there, 15 of which were not found in continuously forested treatments. Research comparing abandoned old fields to managed stands in Indiana also found the greatest richness on agricultural plots, but lower diversity due to dominance by a few species

(Jenkins and Parker 2000). Secondary forests on previously cultivated land in Indiana have greater frequency of nonnative species (Jenkins and Parker 2000).

Commonly, forests on previously cultivated land are more diverse and differ compositionally from forests on land than has never been cultivated (Dupouey et al. 2002, Gachet et al. 2007, Howard and Lee 2002, Jenkins and Parker 2000). On the PEF, although the unregulated harvest and fixed diameter-limit treatments were similar to the old field stands in richness and diversity, the old fields were fundamentally different in terms of understory species composition. Cultivation is a severe disturbance that changes soil chemical and physical properties, and has long-term effects on plant diversity and composition (Dupouey et al. 2002). Some native herbs such as *Medeola virginiana* and *Mitchella repens* – both found on the PEF – do not typically seed bank and do not have mechanisms for far or fast dispersal. Instead, they tend to rely on vegetative spread, have slow rhizome growth, low rates of colonization, and low seed production. Thus, recolonization after cultivation is a slow process and they are unlikely to be found in old field stands (Whitney and Foster 1988).

Nonnative plant species are often associated with old fields and can also influence forest succession. Naturalized weedy species tend to appear after canopy removal and soil exposure (Dunn et al. 1983). Research by Whitney and Foster (1988) in primary woodlands and forested secondary old fields in Massachusetts and New Hampshire found that aggressive weedy species dominated secondary old-fields. They compete for resources and are often better adapted to take advantage of open site conditions through fast spread and long range dispersal mechanisms. On the PEF, a similar trend was apparent in the old fields, where nonnative and invasive species were abundant.

Conclusion

Results from this study indicate that historical land use has played an important role in shaping the forest understory vegetation on the PEF. The influence of prior land use is reflected in the greater richness and diversity in old field stands, and compositional differences between the continuously forested parts of the PEF and the old fields. Stands formerly in agriculture were compositionally different due a greater abundance of nonnative and invasive species and fewer native forest herbs.

Managed and unmanaged stands without an agricultural history were more similar in understory composition than they were to previously cultivated stands. Silvicultural treatments affected understory vegetation through changes in stand basal area. Total basal area, basal area of *Pinus strobus* and *Picea rubens*, and softwood litter cover were most important to determining understory composition in continuously forested plots. To a lesser degree, canopy openness and soil drainage had positive relationships with richness, diversity, and plant cover, and explained patterns in understory composition.

Silvicultural treatments have not dramatically shifted understory plant composition away from that expected in native forests in the Acadian Region. Native forest herbs were common in all treatments; many attained greatest cover in the more exploitive treatments. Frequency of nonnative and invasive species on plots was greatest in the unregulated harvest treatment, but did not exceed a few seedlings. Continued monitoring of the understory is needed to determine treatment effects on species dynamics.

Chapter 2

NONNATIVE INVASIVE PLANTS ON THE PENOBSCOT EXPERIMENTAL FOREST IN MAINE

Introduction

Nonnative invasive plants compromise the integrity of natural and managed ecosystems. They disrupt ecosystem processes such as succession, net primary production, biomass accumulation, nutrient cycling, and disturbance regimes (Vitousek 1996, 1990). Nonnative invasive plants can suppress native woody and herbaceous plant populations and reduce native plant diversity (Frappier et al. 2003, Gould & Gorchov 2000, Miller & Gorchov 2004).

Woody invasive plants cause considerable harm in forests managed for timber resources. Invasive woody vines such as oriental bittersweet (*Celastrus orbiculata)*, Japanese honeysuckle (*Lonicera japonica*) and kudzu (*Pueraria* m*ontana*) overtop and girdle trees (Greenberg et al. 2001, McNab & Meeker 1987, Niering 1998). Nonnative invasive shrubs can form dense thickets that prevent tree regeneration through allelopathy (Madritch & Lindroth 2009) and resource competition (Frappier et al. 2002, Miller & Gorchov 2004). Nonnative invasive shrubs may become dominant in early successional habitats (Frappier and Eckert 2003), limiting the recruitment of native plants (Hutchinson and Vankat, 1997) and slowing succession from field to forest. Invasive shrubs of concern in the Northeast include glossy buckthorn (*Frangula alnus*), Asian shrub honeysuckles (*Lonicera* spp.), Japanese barberry (*Berberis thunbergii*), and multiflora rose (*Rosa multiflora*) (Silander & Klepeis 1999).

The encroachment of invasive species is often facilitated by disturbance (Elton 1958), whether natural as in the case of blowdowns or wildfire, or anthropogenic as in the case of agriculture, road building, and forest harvesting. The reduction of native plant populations may give invasive species a competitive advantage on disturbed sites (Byers 2002). Additionally, an increase in available resources such as light and soil nutrients following a disturbance may create novel microhabitats to which nonnative species are better adapted than native species. (Greenberg et al. 2001).

Many nonnative invasive species can persist in undisturbed natural habitats (Horvitz et al. 1998). Plants that are able to establish in mature forests often exhibit a ‘sit and wait’ strategy whereby their shade tolerance allows for their survival as small seedlings under a closed canopy (Greenberg et al. 2001). Disturbances caused by logging (Brothers and Spingarn 1992, Silveri et al. 2001) and associated roads and trails (Parendes and Jones 2000) can trigger rapid invasive plant population expansion. Nonnative seedlings respond to the increased resources by accelerating their growth vegetatively and through clonal spread (Greenberg et al. 2001), often outcompeting native tree seedlings for valuable resources. When an invasion does occur, it usually causes a profound shift in the structure, composition, and function of forest ecosystems (Webster et al. 2006).

The U.S. Forest Service’s experimental forests are a valuable resource, providing long-term monitoring and experimental data on a wide range of ecological, silvicultural, wildlife, and climate research (Crawford 2006). In recent years, scientists at the Penobscot Experimental Forest (PEF) in Bradley, Maine have observed populations of invasive plants near the government administrative buildings, which are next to successional forest stands that were formerly in agriculture. A history of agriculture is often associated with the presence of invasive species (Niering 1998), as farmers commonly used exotic species when planting hedgerows (McDonald et al. 2008). The proximity of nonnative invasive populations increases the risk of invasive encroachment into the experimental forest. Because nonnative invasive plants have the potential to drastically change the forest composition and ecosystem processes, allowing their presence to continue unchecked could jeopardize the integrity of the PEF, which has a mission to "afford a setting for long-term research...to enhance forestry education of students and the public, and to demonstrate how the timber needs of society are met from a working forest" (Adams et al. 2004).

The purpose of this study was to investigate nonnative invasive plant populations on the PEF, to relate this information to environmental and stand characteristics, and to ascertain whether managed areas of the PEF are at risk from these invasive plants. We quantified factors that have been associated with invasive plants such as soil moisture (Davis 2000, McDonald 2008, Robertson 1994), stand composition, and canopy openness (Robertson et al. 1994). Hereafter, I will use the term 'invasive' to describe nonnative plants that have been classified as invasive in Maine by the Invasive Plant Atlas of New England (IPANE) (Mehrhoff et al. 2003). Native invasive plants are not addressed in this study.

Methods

Study Site

All research was conducted on the PEF, a 1,540-ha forest located in Bradley, Maine (44°52′44″N, -68°39′12″W) (Figure 2.1) Although the history of the PEF is not completely known, some partial cutting occurred on the forest between the late 1700s and early 1900s. In 1950 the land was purchased by nine pulp and paper land-holding companies. These companies leased the land to the U.S. Forest Service, Northern Research Station, as a site for long-term forest management research. In 1994, the PEF was donated to the University of Maine Foundation, though the Forest Service retained control of its long-term experiment (Kenefic et al. 2006).

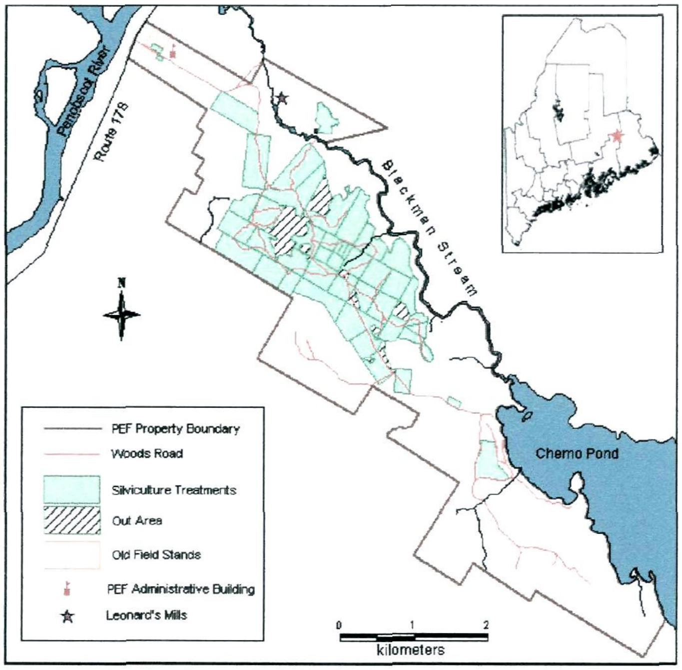

Fig 2.1. Map of the Penobscot Experimental Forest (PEF).

The PEF is in the Acadian Forest, an ecotone between the eastern broadleaf forests to the south and the boreal forests to the north (Sendak et al. 2003). The PEF is dominated by mixed northern conifers including red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), eastern hemlock (*Tsuga canadensis)*, northern white-cedar (*Thuja occidentalis*), and eastern white pine (*Pinus strobus*). White spruce (*Picea glauca*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), and red pine (*Pinus resinosa*) occur less frequently. The most common hardwoods are red maple (*Acer rubrum*), paper birch (*Betula papyrifera*), gray birch (*Betula populifolia*), quaking aspen (*Populus tremuloides*), and bigtooth aspen (*Populus grandidentata*). Also found on the PEF are American beech (*Fagus grandifolia*), white ash (*Fraxinus americana*), northern red oak (*Quercus rubra*), and sugar maple (*Acer saccharum*) (Sendak et al. 2003).

Soils on the PEF are predominantly Wisconsin glacial till derived from fine-grained sedimentary rock (Safford et al. 1969); many soils also formed from glacial outwash, and marine and lacustrine deposits of silt and clay (USDA 1963). The natural disturbance regime of the Acadian Forest is characterized by small-scale disturbances caused by downbursts and northwesterly storms (Foster 1995) which create small canopy gaps. These small gaps average approximately 50 m^2, and have a return interval ranging from 50 to 200 years (Seymour 1992). Periodic hurricanes, icestorms, wildfire, and insect outbreaks have also shaped northern forests (Niering 1998), though the return interval for natural stand-replacing disturbances is 250-800 years (Lorimer 1977).

An approximately 169-ha long-term silvicultural experiment was installed on the PEF by the U.S. Forest Service, Northern Research Station between 1952 and 1957. Silvicultural treatments are twice-replicated and include five-, ten-, and twenty-year selection systems, two- and three-stage uniform shelterwood systems, precommercially thinned three-stage shelterwood, fixed and modified diameter-limit harvests, and an unregulated harvest (commercial clearcut). The PEF also includes a natural area that has received no harvesting or silvicultural activities for over 60 years, and serves as a replicated reference treatment. A detailed account of silvicultural treatments and outcomes can be found in Sendak et al. (2003).

Both replicates of the ten silvicultural treatments are inventoried regularly using permanent sample plots, called "continuous forest inventory" (CFI) plots. Across the experiment, there are an average of 8 to 21 CFI plots per treatment replicate. Measurements have been recorded before and after each harvest and approximately every five years between entries. Inventory data include species and diameter at breast height (DBH, 1.37 m) of trees >1.3 cm DBH. CFI plots are 0.081-, 0.020-, and 0.008-ha nested circular sample plots. Tree regeneration measurements are obtained from three 4.05-m^2 subplots within each CFI plot.

In addition to natural and silvicultural disturbances, parts of the PEF were affected by human settlement and cultivation. A small area (~5 ha) in the northwestern portion of the PEF was cleared by prior landowners. This area is located near the entrance to the PEF from Route 178 and is bisected by Government Rd (Figure 2.1). Aerial photographs from 1956 show that this area was cleared of trees (S. Brodbeck, personal communication), and maps made as recently as 1980 labeled this area 'Field.' Soils show signs of cultivation and grazing (I. Fernandez, personal communication). The old fields have developed into forest stands dominated by *P. grandidentata*, *B. populifolia*, *A. rubrum*, European crabapple (*Malus sylvestris*), and cherry (*Prunus* spp.). *Lonicera* spp. (*L. morrowii* and *L. x bella*) appear to have been planted for ornamental purposes along the roadside (personal observation). The old fields of the PEF were not included in the long-term silvicultural experiment and there are no historical stand inventory data.

Another important aspect to the PEF is Leonard's Mills, a reconstructed eighteenth century logging settlement (Kenefic, in review) owned and operated by the Maine Forest and Logging Museum (MFLM). Each year, approximately 5,000 people visit to learn about Maine's forestry and logging history (MFLM 2007). Self-guided nature trails lead from the Leonard's Mills museum grounds through the Forest Service's nearby natural area. *Frangula alnus* seedlings are prevalent on the property, and *Lonicera* spp. appear to have been planted for ornamental purposes on the museum grounds (personal observation).

Data Collection

Data were collected in two old field stands during July and August of 2007. Six transects were laid perpendicular to the old field-road edge. At the time of data collection, the exact boundaries of the old fields were not mapped, so transects began at the old field-road edge and ended at the PEF property line. Twenty-two plots were established along six transects. This study was designed so that data could be analyzed in conjunction with the PEF long-term dataset; therefore, the plot layout in the old field stands was modeled after the CFI plots in the PEF silvicultural experiment areas (described above). Distances between plots were chosen using a random number generator, constrained by observed distances between CFI plots. The understory was sampled on two circular 4.05-m^2 subplots. Subplots were 8.02 m from plot center, and were located 180° from each other (Figure 2.2).

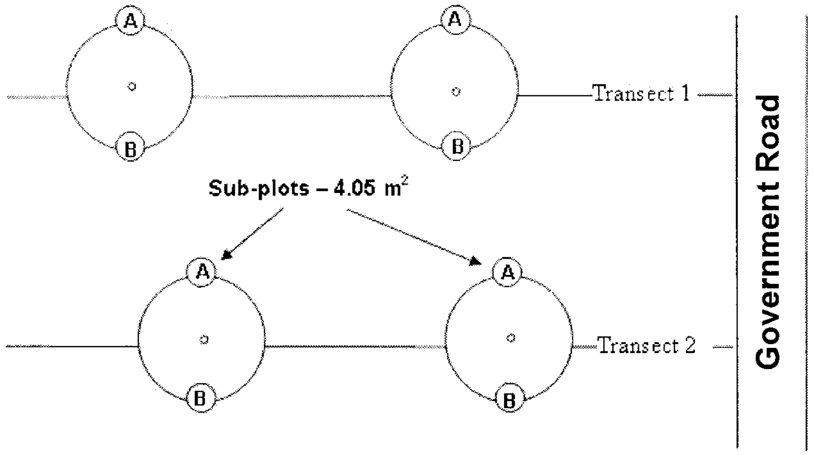

Figure 2.2. Sampling plot layout. Using a random number table, the distance from the roadside to the first plot in each transect was between 20 to 50 meters, distances between plots were 30 to 100 meters, and distances between transects were 60 to 100 meters.

Percent cover was estimated for all understory species using a modified version of the Braun–Blanquet scale: 1 = less than 5% and rare, 2 = less than 5% and uncommon, 3 = less than 5% and common, 4 = 5 to 25%, 5 = 26 to 50%, 6 = 51 to 75%, and 7 = 76 to 100%. Because percent cover was estimated for each species individually and stems were vertically stratified, the total cover of all plants often summed to greater than 100%. Tree seedlings and shrubs ≤0.6 meters tall were assigned a cover class; trees and shrubs >0.6 meters tall were counted, but not assigned a cover class (Burkman 2005). Error was reduced by having one person estimate percent cover on all plots, and plots were revisited in an effort to observe unknown plants in flower. Plant species that could not be identified in the field were collected and identified at the University of Maine Herbarium.

So that vegetation data could be related to possible explanatory features, I measured additional site variables for each subplot; these included exposed rock, exposed mineral soil, coarse woody material, and broadleaf and conifer litter. Percent cover was estimated using the same cover scale as above. Basal area (BA, m^2/ha) was measured at each plot center using a 10-BAF prism; results were converted to metric units. To determine soil drainage, a soil pit was excavated at the plot center. Thickness of the organic horizon, thickness of the eluvial horizon, and depth to redoximorphic features (mottling) were measured to the nearest 0.5 cm. Drainage class and Briggs site class (Briggs 1994) at each plot were determined using these measurements.

As a surrogate for the measurement of light in the understory, a digital image of the canopy above each subplot was taken using a Sigma 8-mm 180° fisheye lens attached to a Canon EOS Digital Rebel camera. The camera was attached to a tripod, the camera lens was positioned 0.6 meters above the forest floor, and a level was used to ensure that the lens was standardized in orientation. Images were captured in August 2007, between 5:30 and 8:00 a.m., and between 4:00 and 8:00 p.m. to avoid direct sunlight. The digital images were processed using Microsoft® Picture It! software to increase the contrast between vegetation and sky. Gap Light Analyzer (Frazer et al. 1999) software was used to obtain a value for percent canopy openness.

During the summers of 2006 and 2007, the forest understory plants in the Forest Service's silvicultural experiment stands (called compartments) were sampled in the same manner as the old fields (see Chapter 1). During this data collection, workers recorded the presence of invasive species both within the CFI plots and throughout the compartments; GPS coordinates were obtained for each invasive plant sighting. Overstory data including basal area by species was calculated from the Forest Service long-term dataset.

In order to ascertain the full extent of the invasive species' populations around the old field stands, a meander survey was conducted using a handheld GPS unit. Workers walked systematically through the old fields and adjacent forest taking notes and recording GPS coordinates at the locations of invasive plants. Using MapInfo® software, the approximate perimeter of the most abundant invasive species' ranges was mapped. Due to time constraints, the entire PEF property was not inventoried; this study only included the old field stands and the long-term U.S. Forest Service compartment study.

Analyses

Cover class values for each plant species and environmental variables from the two subplots were converted to the cover class midpoint and averaged into a mean percent cover for each plot (Archer, 2007). Horsetails (*Equisetum* spp.), bedstraw (*Galium* spp.) and goldenrods (*Solidago* spp.) were each grouped to the genus level for analysis.

Non-metric multidimensional scaling (NMS) ordination in PC-ORD version 4.07 (McCune and Mefford 1999) was used to examine the relationships among the understory species, and between understory species and environmental variables. Sorensen's distance measure was used because it retains sensitivity in heterogeneous datasets and gives less weight to outliers. I chose the 'slow and thorough' autopilot setting in PCORD, which performed the ordination using 40 runs with real data and 50 runs with randomized data (maximum of 400 iterations per run) (McCune and Mefford 1999).

Species' cover values were square-root transformed to reduce the influence of the most abundant species (O'Connor and Crowe 2005). Plots in the species matrix were standardized to plot totals; this procedure is also called 'stand normalization' (Kenkel and

Orloci 1986) or 'general relativization' of sites (McCune and Mefford 1999). Stand normalization sums the abundances for each species and divides each abundance by the total; this corrects for the total plant biomass found on the plot (Jongman et al. 1995). Species with low frequency in the old field plots were omitted from the NMS ordination because they are not likely to be accurately placed in ordination space (McGarigal 2000). These included three invasive species that each occurred in only one plot: multiflora rose (*Rosa multiflora*), garden valerian (*Valeriana officinalis*) and purple loosestrife (*Lythrum salicaria*). These adjustments reduced the stress, a measure of 'badness-of-fit,' of the NMS ordination.

Spearman rank correlation was used to investigate the relationships among invasive species, overstory composition, and environmental variables in the old field stands. Only two invasive species – *Frangula alnus* and *Lonicera* spp. – occurred frequently enough to be analyzed individually. The richness and percent cover of all invasive species recorded in each plot were totaled and analyzed as a group. Correlation tests were carried out using the R statistical package (R Development Core Team 2007).

On the PEF, invasive species were infrequently recorded on the CFI plots; when encountered, they were usually very small seedlings. This low density and abundance precluded formal analysis, yet the proximity of invasive plants to an important long-term experiment warranted further investigation. In a non-statistical, qualitative assessment of the data, I explored environmental commonalities associated with the presence of invasive species in the old field stands and the CFI plots.

Results

Old Fields

Twenty-one nonnative species (15.8%) were recorded in the old field plots, nine of which are listed invasive in New England (Table 2.1). *Frangula alnus* and *Lonicera* spp. were the most frequent invasive species sampled on the old field plots, occurring in 86 and 59% of plots, respectively. The invasive vine *Celastrus orbiculata* was found in 41% of plots; it was usually seen as small seedlings less than 30 cm tall, though in one plot it had grown into the canopy.

Table 2.1. Nonnative invasive species recorded in old field plots. Frequency is the percent of plots (n = 22) in which each species was recorded.

Latin name	Common name	Code	Growth habit	Frequency
Acer platanoides	Norway maple	ACPL	tree	13.6
Celastrus orbiculata	Oriental bittersweet	CEOR	vine	40.9
Frangula alnus	glossy buckthorn	FRAL	shrub	86.4
Lonicera spp.	shrub honeysuckle	LONI	shrub	59.1
Lythrum salicaria	purple loosestrife	LYSA	herb	4.6
Rhamnus cathartica	common buckthorn	RHCA	shrub	22.7
Rosa multiflora	multiflora rose	ROMU	shrub	4.6
Solanum dulcamara	climbing nightshade	SODU	vine	9.1
Valeriana officinalis	garden valerian	VAOF	herb	4.6

The meander survey of the old fields and adjacent forest yielded data regarding the extent of invasive species. Using this data, I created a map of the approximate perimeters of the invasive plant populations (Figure 2.3). *Frangula alnus* had the largest range. *Lonicera* spp. had the second largest range; often the shrubs had grown into tall, dense thickets. *Celastrus orbiculata* was seen occasionally; when present it had often climbed high into the canopy. *Rosa multiflora* and *Lythrum salicaria* were also present but were infrequent. One large (approx. 2-m tall) *R. multiflora* shrub was found, but other seedlings were less than 0.3 m tall. *L. salicaria* occurred in small groups along a small stream that winds through the southwest section of the old fields.

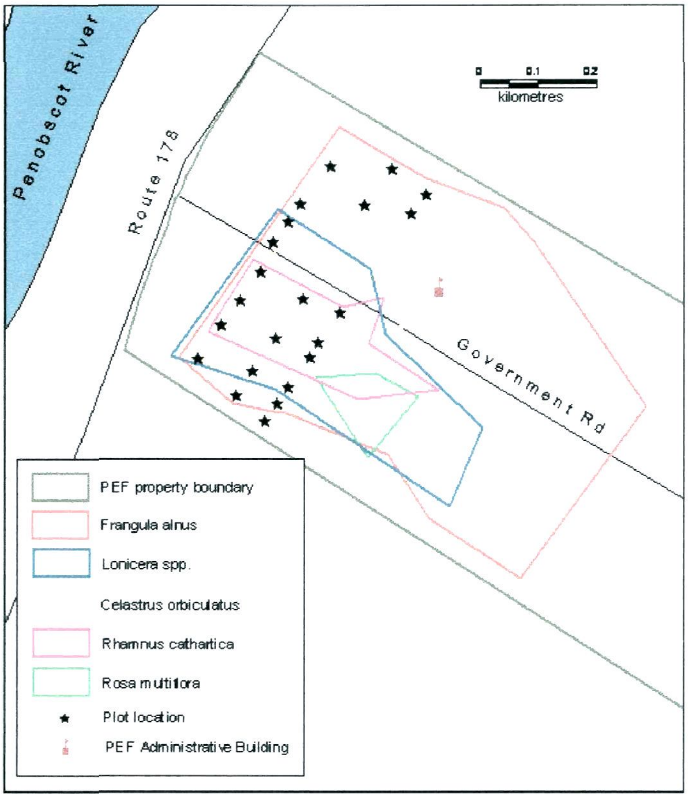

Figure 2.3. Map of the old field area. Plot locations in the PEF old field stands and approximate range of invasive species.

NMS ordination using the plots in the old fields (n = 22) resulted in a low stress, two dimensional solution representing 93% of the dataset variation (Figure 2.4). The understory species formed two groups in this ordination biplot. The upper left area of the biplot represents portions of the old field stands where hardwoods dominated the canopy;

these were predominantly early successional species like *Populus tremuloides* and *Betula populifolia* along with *Malus* spp. and *Prunus* spp. Herbaceous plants such as brittlestem hempnettle (*Galeopsis tetrahit)*, and common cinquefoil (*Potentilla simplex*) were also characteristic of these portions of the old field. Most of the invasive species are located in this part of the biplot with the exception of Norway maple (*Acer platanoides*) and *Frangula alnus*. Hardwood litter cover and organic horizon development were minimal, and there was a relatively greater amount of surficial mineral soil.

The lower right of the biplot contains understory species characteristic of primary northern conifer forests such as eastern teaberry (*Gaultheria procumbens*), bunchberry (*Cornus canadensis*), and starflower (*Trientalis borealis*). These species were associated with greater overstory basal area, particularly of *Acer rubrum* and the late-successional *Tsuga canadensis*, greater litter cover, and thicker organic horizon (Figure 2.4). The condition of the forest floor, soils, and plant composition lead to the conclusion that these plots fell in areas that were likely not affected by cultivation or grazing. Greater distance to the road was associated with these portions of the old fields.

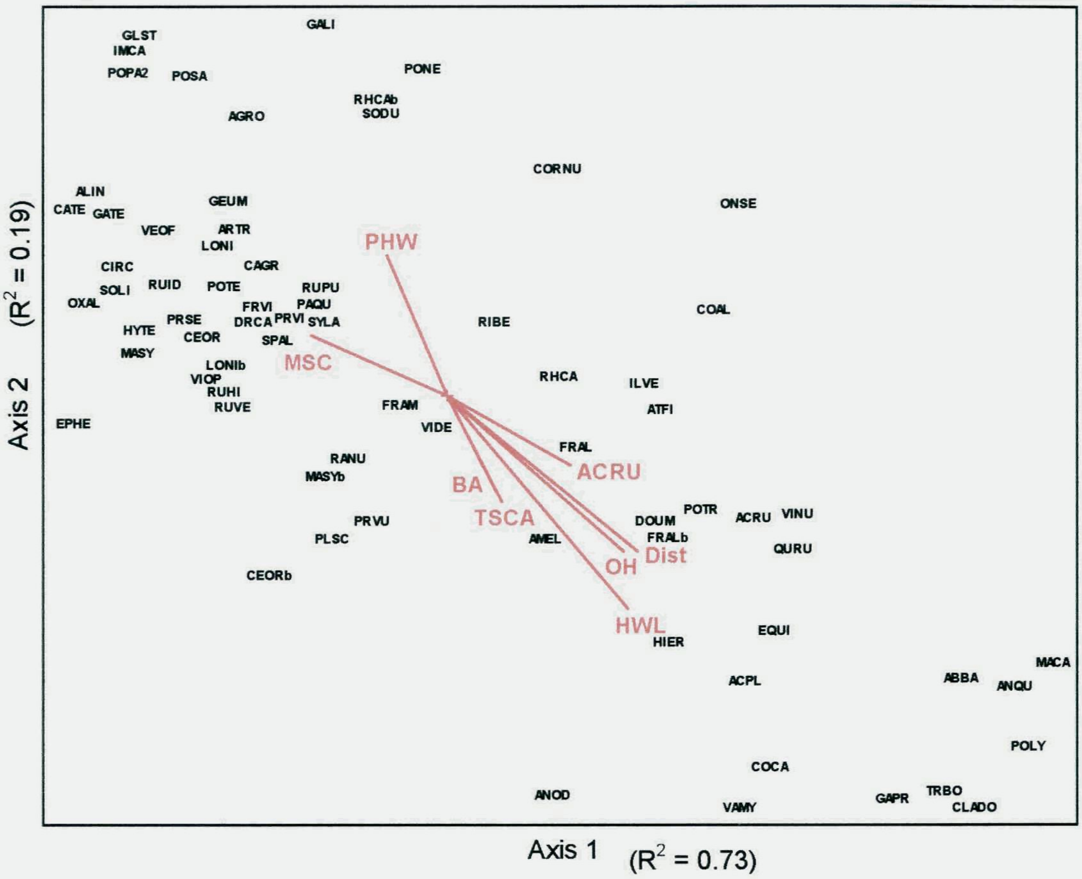

Figure 2.4. NMS results. See Table 2.2 for species codes. Species codes followed by a 'b' indicate a woody plant >0.6m tall. BA, total basal area; PHW, percent hardwood basal area; TSCA, *Tsuga canadensis* basal area; ACRU, *Acer rubrum* basal area; MSC, mineral soil cover; OH, organic horizon thickness; HWL, hardwood litter cover; Dist, Distance to Government road.

Table 2.2 Plant species used in the NMS analysis.

Code	Common name
ABBA	*Abies balsamea* balsam fir
ACPL	*Acer platanoides* Norway maple
ACRU	*Acer rubrum* red maple
AGRO	*Agrostis* spp. bentgrass
ALIN	*Alnus incana* speckled alder
AMEL	*Amelanchier* spp. serviceberry
ANOD	*Anthoxanthum odoratum* sweet vernalgrass
ANQU	*Anemone quinquefolia* wood anemone
ARTR	*Arisaema triphyllum* Jack in the pulpit
ATFI	*Athyrium filix-femina* ladyfern
CAGR	*Carex gracillima* graceful sedge
CATE	*Carex tenera* quill sedge
CEOR	*Celastrus orbiculata* Oriental bittersweet
CIRC	*Circaea* spp. enchanter's nightshade
CLADO	*Cladonia* spp. cup lichen
COAL	*Cornus alternifolia* alternateleaf dogwood
COCA	*Cornus canadensis* bunchberry
CORNU	*Cornus* spp. dogwood
DOUM	*Doellingeria umbellata* parasol whitetop
DRCAR	*Dryopteris carthusiana* spinulose woodfern
EPHE	*Epipactis helleborine* broadleaf helleborine
EQUI	*Equisetum* spp. horsetail
FRAL	*Frangula alnus* glossy buckthorn
FRAM	*Fraxinus americana* white ash
FRVI	*Fragaria virginiana* Virginia strawberry
GALI	*Galium* spp. bedstraw
GAPR	*Gaultheria procumbens* eastern teaberry
GATE	*Galeopsis tetrahit* brittlestem hempnettle
GEUM	*Geum* spp. avens
GLST	*Glyceria striata* fowl mannagrass
HIER	*Hieracium* sp. Hawkweed
HYTE	*Hylotelephium telephium* witch's moneybags
ILVE	*Ilex verticillata* common winterberry
IMCA	*Impatiens capensis* jewelweed
LONI	*Lonicera* spp. honeysuckle
MACA	*Maianthemum canadense* Canada mayflower
MASY	*Malus sylvestris* european crab apple
ONSE	*Onoclea sensibilis* sensitive fern
OXAL	*Oxalis stricta* common yellow woodsorrel
PAQU	*Parthenocissus quinquefolia* Virginia creeper
POLY	*Polytrichum* sp. polytrichum moss
PONE	*Poa nemoralis* wood bluegrass
POTE	*Potentilla simplex* cinquefoil
POTR	*Populus tremuloides* quaking aspen
PRSE	*Prunus serotina* black cherry
PRVI	*Prunus virginiana* chokecherry
PRVU	*Prunella vulgaris* common selfheal
QURU	*Quercus rubra* northern red oak
RANU	*Ranunculus* buttercup
RHCA	*Rhamnus cathartica* common buckthorn
RIBE	*Ribes* sp. currant
RUHI	*Rubus hispidus* bristly dewberry
RUID	*Rubus idaeus* red raspberry
RUPU	*Rubus pubescens* dwarf red blackberry
RUVE	*Rubus vermontanus* Vermont blackberry
SODU	*Solanum dulcamara* climbing nightshade
SOLI	*Solidago* spp. goldenrod
SPAL	*Spiraea alba* white meadowsweet
SYLA	*Symphyotrichum lateriflorum* calico aster
TRBO	*Trientalis borealis* starflower
VAMY	*Vaccinium myrtilloides* velvetleaf blueberry
VEOF	*Veronica officinalis* common speedwell
VIDE	*Viburnum dentatum* southern arrowwood

Results from the multivariate and correlation analyses indicate that canopy openness and soil drainage were not important environmental variables explaining the presence of invasive plants in the old fields on the PEF. Three variables describing forest floor conditions – organic horizon thickness, hardwood litter cover, and mineral soil cover – were associated with invasive plant richness and cover. Invasive plant cover was negatively correlated with organic horizon thickness and positively correlated with exposed mineral soil (Table 2.3). The percent cover of *Frangula alnus* was not strongly correlated with any of the observed environmental variables, although it was somewhat positively correlated with basal area (Table 2.3). Its central position in the biplot shows that it is not strongly associated with any of the environmental vectors in the ordination (Figure 2.4).

Table 2.3. Spearman correlations. DIST, distance to road; HWL, hardwood litter cover; MSC, mineral soil cover; OH, organic horizon thickness; BA, basal area; PHW, percent hardwood basal area.

	DIST	HWL	MSC	OH	BA	PHW
Total nonnative invasive plant richness	-0.58	-0.43	0.33	-0.32	-0.11	0.19
Total nonnative invasive plant cover	-0.54	-0.27	0.54	-0.48	-0.03	0.18
Frangula alnus cover	-0.03	0.24	-0.08	0.07	0.36	-0.16
Lonicera spp. cover	-0.59	-0.44	0.44	-0.47	-0.35	0.35

Silvicultural Treatments

The understory inventory of the CFI plots in the silviculture compartment study (Chapter 1) yielded a few occurrences of invasive species on the managed forest (Figure 2.5, Table 2.4). *Frangula alnus* was the most frequent invasive species; it was found on five plots in four compartments. In the silvicultural treatment areas, *F. alnus* was found growing on a thick organic horizon and under dense conifer shade. These environmental conditions are very different from those typical of the old fields where many invasive plant species were abundant. Meander surveys revealed nine additional *F. alnus* seedlings around the perimeter of the natural area.

Lonicera spp. was found on one plot in an unregulated harvest replicate; a few small plants were growing in a skid trail where the organic horizon and litter cover were below average for the stand. One *Celastrus orbiculata* seedling was found in a modified diameter-limit replicate. A *Bergeris thunbergii* shrub originally found by a graduate student in 2005 was relocated in 2007. This 2-m tall shrub was growing in a small treefall gap in an unregulated harvest replicate. A search of the surrounding area did not reveal other barberry seedlings. Except for the *B. thunbergii* shrub, all nonnative seedlings found in the managed areas of the PEF were small, ranging in height from 0.1 to 0.3 m.

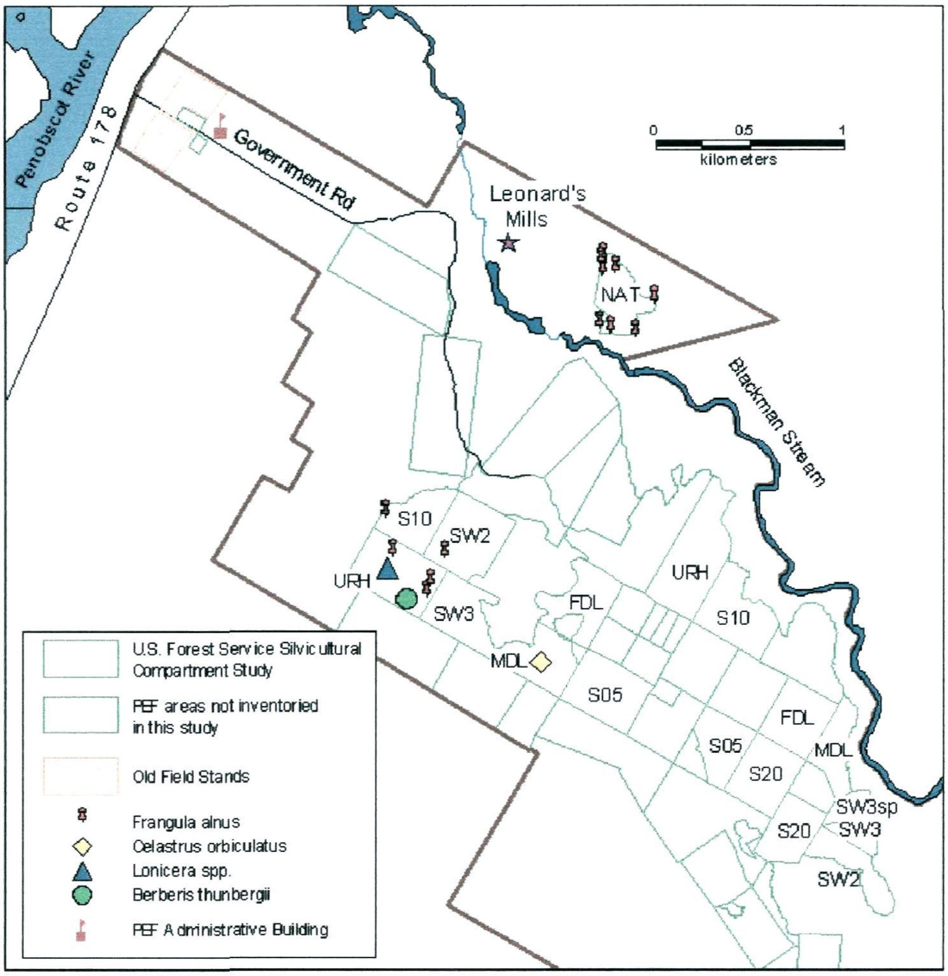

Figure 2.5. Map of invasive plant locations in experimental areas. Silviculture treatment codes are: NAT, natural area; URH, unregulated harvest; S05, 5-yr selection; S10, 10-yr selection; S20, 20-yr selection; FDL, fixed diameter-limit; MDL, modified diameter-limit; SW2, 2-stage shelterwood; SW3, 3-stage shelterwood; SW3sp, 3-stage shelterwood with pre-commercial thinning.

Variables associated with invasive plants in the old fields were not consistently similar to the conditions found in the silvicultural experiment areas where invasive plants were found (Table 2.4). For instance, although mineral soil cover was one of the most important factors associated with invasive plants in the old field plots, this association was not seen in the managed forest. Exposed mineral soil within the silvicultural treatment areas tended to occur with seasonal streams (personal observation). Invasive plants were not found on the 7.6% of CFI plots that did have exposed mineral soil (data not shown); CFI plots with invasive species did not have exposed mineral soil. Invasive plants were associated with a thin organic horizon in the old fields; however, in the CFI plots where invasives were present, the organic horizon was at least twice as thick (0.64 to 5.08 cm) as in the old field.

Table 2.4. Invasive plant species in silvicultural treatment areas. Plot-level data for the invasive plant species found in the silvicultural experiment areas. *Celastrus orbiculata* and *Berberis thunbergii* were not in CFI plots, therefore no environmental measurements were recorded (N/A).

Treatment	Compartment number	Species	O-Horizon (cm)	Mineral Soil Cover	Hardwood Litter Cover	Softwood Litter Cover	Notes
Unregulated Harvest	22	*Frangula alnus*	2.54	0.00	63.00	26.75	adjacent to a canopy gap
Unregulated Harvest	22	*Frangula alnus*	2.54	0.00	63.00	45.50	under low, dense conifer shade
Unregulated Harvest	22	*Lonicera* sp.	1.27	0.00	75.50	33.00	adjacent skid trail
Unregulated Harvest	22	*Berberis thunbergii*	N/A	N/A	N/A	N/A	in a canopy gap
10-yr Selection	20	*Frangula alnus*	2.54	0.00	51.75	63.00	plot in northwest of compartment, close to old fields & unmanaged area
2-stage Shelterwood	21	*Frangula alnus*	5.08	0.00	88.00	75.50	adjacent woods road
Natural Area	32	*Frangula alnus*	3.18	0.00	15.50	88.00	adjacent hiking path
Modified Diameter-limit	24	*Celastrus orbiculata*	N/A	N/A	N/A	N/A	

Discussion

Invasive plants were abundant in the PEF old fields. Many nonnative invasive plants were initially introduced in the United States for use as ornamentals and wildlife habitat (Webster et al. 2006). This was likely the intent of the original plantings of *Frangula alnus* and *Lonicera* spp. along the Government Road-old field edge and on the Leonard's Mills museum grounds. After the old fields were abandoned, these shrubs were able to spread from the roadside (and perhaps from other local sources). *F. alnus* and *Lonicera* spp. were most abundant in areas proximate to the roadside plantings.

Records of land use by prior landowners were not found, but examination of the soils indicated that grazing and plowing likely occurred. Agricultural practices induce chemical and physical changes in the soil, giving a competitive advantage to ruderal and invasive species (Dupouey et al. 2002). Agriculture can also decimate the native seed bank, making re-colonization of the original native plant composition a slow process (Dupouey et al. 2002, Jenkins and Parker 2000). In the PEF old fields, invasive plants were associated with exposed mineral soil. Invasive plants are often associated with soil disturbance (Robertson et al. 1994) due to an increase in nutrients or reduction of other plant competition (Hobbs and Huenneke 1992). McDonald et al. (2008) also found that plowed and pastured soils were more likely to support invasive plants, but allow that invasion success may have more to do with the naturally higher nutrient content of soils that were chosen for cultivation.

The success of invasive species is often linked to their multiple and effective methods for reproduction and dispersal. Animal-dispersed fleshy fruits are a successful dispersal mechanism for many invasive plants (Drummond 2005). Avian frugivores usually leave their foraging site soon after feeding (Malmborg and Willson 1988), potentially spreading seed into forest interiors far from the parent plants (Brothers and Spingarn 1992). This enables invasive species to establish populations independent of planted sources (Barton et al. 2004), rapidly increasing their distribution. Frugivorous birds are abundant on the PEF (Hartley 2003) and are probably the main dispersal agents of the invasive plant seed, though small mammals such as chipmunks, squirrels, and fox also consume and disperse fruit seeds (Aldous 1941, Fleming and Sosa 1994).

Despite a dense local population of invasive plants and abundant dispersal agents, few invasive plants were found in the silvicultural experiment areas of the PEF. My findings are consistent with those of Jenkins and Parker (2000) who found more nonnative plants on abandoned agricultural land than in silvicultural treatment areas. I did not find evidence for the hypothesis that CFI plots harboring invasive seedlings had similar environmental or stand conditions to the old field stands. Instead, the current distribution of invasive plants within the managed areas of the PEF is best explained by proximity to abundant seed source coupled with a higher degree of anthropogenic disturbance. The experimental areas that had the highest abundance of invasive plant seedlings were one replicate of the unregulated harvest (compartment 22) and the natural area (compartment 32). Both of these locations on the PEF are relatively close to the old fields and have a heightened level of harvesting or recreational disturbance.

Compartment 22 had more invasive plants than other silvicultural experiment areas. Since 1950 it has been harvested twice as an unregulated harvest, or commercial clearcut. This is one of the most intense harvesting treatment on the PEF; approximately 85% of the basal area was removed from compartment 22 during the most recent harvest in 1988. Compartment 22 is also closer to the old fields than most other treatment areas that I sampled, and is adjacent to a heavily cut property off the PEF (J. Brissette, personal communication). This combination of intense disturbance and proximity to the invasive plant populations in the old fields likely influenced the current presence of invasive plants in that stand.

Compartment 20 – a 10-year selection treatment – borders compartment 22 and is also close to the old fields, but only one invasive plant seedling was found in compartment 20. The 10-year selection is a less intense treatment than the unregulated harvest; basal area removed from compartment 20 has averaged 20% in each of the 5 entries over the last 50 years. The most recent harvest in 1998 removed only 8% of basal area. Proximity to invasive plant seed sources did not promote as much invasive seedling establishment as in the unregulated harvest; the lower level of canopy disturbance resulted in fewer resources available for new plants to establish. My findings are similar to those of Jenkins and Parker (2000), who found that nonnative cover decreased with decreasing silvicultural disturbance.

The unmanaged natural area was second to the unregulated harvest in the number of invasive species occurrences. Relatively undisturbed forests usually contain fewer invasive plants than more heavily disturbed areas (Selmants and Knight 2003). However, the nearby Leonard's Mills logging museum and the walking trails leading from the museum area through the natural area provide continuous public traffic. This intensity of public use is a type of disturbance that has been associated with an increase in the abundance of invasive species (Lundgren et al. 2004), and may help explain the higher frequency of invasive seedlings. The natural area is also in close proximity to an invasive seed source of *Lonicera* spp. and *Frangula alnus* on the Leonard's Mills Museum site.

Many occurrences of invasive species in the silvicultural experiment areas of the PEF coincided with a skid trail or roadside (see Table 2.3 notes). Roads and trails that accompany logging operations may harbor significantly more invasive species than the forest matrix (Buckley 2003). Environmental conditions on forest roads and trails include increased light, forest floor disturbance, soil compaction, reduced drainage, and changes in soil nutrient content and organic matter (Lundgren et al. 2004). Though roads and trails generally constitute a small percent of forest land area, they can be pathways for invasive plants into forest interiors (Buckley 2003). The spread of *Frangula alnus* into the natural area may be attributed to the aforementioned nature trails that lead from the museum grounds and wind through the stands. *F. alnus* seedlings were frequently seen along the trail that leads from the Leonard's Mills area toward the natural area (personal observation).

Factors influential to community invasion include the susceptibility to invasion and propagule pressure (Davis et al. 2000, Eschtruth and Battles 2009). Susceptibility to invasion is not a static property of a community; it is an emergent property that changes over time, and increases as resources increase (Davis et al. 2000). On the PEF there is an abundant source of nonnative invasive species, and regular silvicultural disturbances on the forest cause resource release which increase susceptibility to invasive plant establishment. The interaction of canopy disturbance and propagule pressure has been shown to significantly increase invasibility (Eschtruth and Battles 2009).

As the most frequent invasive species both in the old fields and the silvicultural treatment areas, *Frangula alnus* seems to have the advantage of being able to establish in a wide range of overstory and forest floor conditions on the PEF. *Lonicera* spp. seems to be more limited in its spread. It may require exposed mineral soil for successful germination; this is suggested by its correlations with leaf litter, organic horizon, and mineral soil in the old field stands. However, in over 60 years, these invasive plants have not expanded their populations into the experimental treatment areas beyond a few scattered seedlings.

The initial stage of an invasion is characterized by low abundance; therefore, when trying to predict the invasive potential of any species in a specific locale, current patterns are often not reliable estimates of future abundance (Hunter and Mattice 2002), because there may be a long lag time from the introduction of a species to it becoming invasive. Moody and Mack (1988) describe the spatial spread of plant invasions as multiple independent foci radiating into adjacent habitat. The growth of multiple small plant populations exceed the growing rate of a single large population, and control efforts that ignore outlier populations will not be successful in the long term (Moody and Mack 1988).

All effort should be taken to protect the original purpose of the PEF to provide examples of silvicultural practices and outcomes in the Acadian Forest. The early stage of invasive encroachment on the PEF provides an opportunity for the initiation of "early detection and rapid response" invasive control methods (Mehrhoff et al. 2003). To stem the spread of invasive species throughout the managed forest, field workers who conduct the regular treatment inventories should be trained to identify invasive species and instructed to remove all invasive plant seedlings encountered on the forest.

Conclusion

The threat to the PEF long-term silvicultural experiment posed by its proximity to thriving populations of invasive species should not be ignored. The fleshy fruits borne by most of these plants are dispersed widely by frugivorous birds. Presence of invasive seedlings within treatment areas indicates that the managed forest contains hospitable microsites for establishment, and the continued disturbances associated with harvesting will likely promote their spread in the future.

The combined influences of an agricultural past and proximity to roadside plantings contributed to the abundance of nonnative invasive plants in the old fields on the PEF. While *Frangula alnus* was not associated with the measured environmental variables, *Lonicera* spp. was associated with (and therefore may be limited by) specific forest floor characteristics including low leaf litter cover, thin organic horizon, and high mineral soil cover.

Few seedlings of invasive plants were found in the silvicultural experiment areas of the PEF. Sites in the silvicultural experiment area that currently support invasive plant seedlings are not sufficiently similar to the old field to explain invasives presence due to environmental or stand characteristics alone. Two treatment areas on the PEF had the majority of invasive seedlings: the unregulated harvest and the natural area. This pattern is attributed to local disturbances coinciding with proximity to an abundant propagule supply. Invasive species do not appear to have interrupted or influenced the PEF long-term silvicultural experiment at this time. However, continued monitoring of the invasive species populations is recommended, as this will yield needed information about their patterns of establishment in a conifer-dominated Acadian Forest.

The prevalence of invasive species in the old fields warrants immediate action to prevent their spread into the managed areas of the PEF. An invasive species management plan should be implemented to protect the integrity of the long-term experiment and biodiversity of the PEF. A successful and cost-effective control strategy can only occur if applied when invasive plant populations are still small and sparse. Control methods may include the removal by hand of all small invasive seedlings, mechanical removal of larger invasive plants, and herbicide treatment of the old fields to destroy the invasive plant infestation there. Coordination with property owners adjacent to the PEF would be useful to limit outside sources of invasive seed. The PEF is an interesting forest that is host to a large and important long-term experiment; protecting this resource now will benefit generations of foresters and landowners well into the future.

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Appendix A: Species List

Table A.1. Penobscot Experimental Forest Understory Plant Species List

Family	Code	Scientific name	Common name
Bryophytes & Lichens			
Cladoniaceae	CLADI	*Cladina* (Nyl.) Nyl	reindeer lichen
Cladoniaceae	CLADO	*Cladonia* P. Browne	cup lichen
Climaciaceae	CLDE	*Climacium dendroides* (Hedw.) Web. & Mohr	tree climacium moss
Climaciaceae	CLIM	*Climacium* F. Weber & D. Mohr ex Mohr	climacium moss
Dicranaceae	DICR	*Dicranum* Hedw.	dicranum moss
Hylocomiaceae	HYSP	*Hylocomium splendens* (Hedw.) Schimp. in B.S.G.	stairstep moss
Hylocomiaceae	PLSC	*Pleurozium schreberi* (Brid.) Mitt.	big red stem moss
Lepidoziaceae	BAZZ	*Bazzania* Gray nom. cons.	
Leucobryaceae	LEUC	*Leucobryum* Hampe	leucobryum moss
Mniaceae	MNIU	*Mnium* Hedw.	mnium calcareous moss
Polytrichaceae	ATRI	*Atrichum* P. Beauv.	atrichum moss
Polytrichaceae	POLYT	*Polytrichum* Hedw.	polytrichum moss
Ptilidiaceae	PTPU	*Ptilidium pulcherrimum* (Weber) Vainio	Naugehyde
Sphagnaceae	SPHA	*Sphagnum* L.	sphagnum
Ferns & fern allies			
Dennstaedtiaceae	DEPU	*Dennstaedtia punctilobula* (Michx.) T. Moore	eastern hayscented fern
Dennstaedtiaceae	PTAQ	*Pteridium aquilinum* (L.) Kuhn	western brackenfern
Dryopteridaceae	ATFI	*Athyrium filix-femina* (L.) Roth ssp.*angustum* (Willd.) Clausen	common ladyfern
Dryopteridaceae	DRYO	*Dryopteris* Adans.	
Dryopteridaceae	DRCAR	*Dryopteris carthusiana* (Vill.) H.P. Fuchs	spinulose woodfern
Dryopteridaceae	DRCL	*Dryopteris clintoniana* (D.C. Eaton) Dowell	Clinton's woodfern
Dryopteridaceae	DRCR	*Dryopteris cristata* (L.) Gray	crested woodfern
Dryopteridaceae	DRIN	*Dryopteris intermedia* (Muhl. ex Willd.) Gray	intermediate woodfern
Dryopteridaceae	DRMA	*Dryopteris marginalis* (L.) Gray	marginal woodfern
Dryopteridaceae	GYDR	*Gymnocarpium dryopteris* (L.) Newman	western oakfern

Family	Code	Scientific name	Common name
Dryopteridaceae	ONSE	*Onoclea sensibilis* L.	sensitive fern
Equisetaceae	EQUI	*Equisetum* L.	horsetail
Lycopodiaceae	LYCL	*Lycopodium clavatum* L.	running clubmoss
Lycopodiaceae	LYCO	*Lycopodium* L.	clubmoss
Osmundaceae	OSCI	*Osmunda cinnamomea* L.	cinnamon fern
Osmundaceae	OSCL	*Osmunda claytoniana* L.	interrupted fern
Thelypteridaceae	PHCO	*Phegopteris connectilis* (Michx.) Watt	beech fern
Thelypteridaceae	THNO	*Thelypteris noveboracensis* (L.) Nieuwl.	New York fern
Thelypteridaceae	THPA	*Thelypteris palustris* Schott	eastern marsh fern
Graminoids			
Cyperaceae	CAAR	*Carex arctata* Boott ex Hook.	drooping woodland sedge
Cyperaceae	CABRO	*Carex bromoides* Schkuhr ex Willd.	brome-like sedge
Cyperaceae	CABRU	*Carex brunnescens* (Pers.) Poir.	brownish sedge
Cyperaceae	CACO	*Carex communis* L.H. Bailey	fibrousroot sedge
Cyperaceae	CADEB	*Carex debilis* Michx.	white edge sedge
Cyperaceae	CADEW	*Carex deweyana* Schwein.	Dewey sedge
Cyperaceae	CADI	*Carex disperma* Dewey	softleaf sedge
Cyperaceae	CAGR	*Carex gracillima* Schwein.	graceful sedge
Cyperaceae	CAGY	*Carex gynandra* Schwein.	nodding sedge
Cyperaceae	CAIN	*Carex intumescens* Rudge	greater bladder sedge
Cyperaceae	CALA	*Carex lacustris* Willd.	hairy sedge
Cyperaceae	CALE	*Carex leptalea* Wahlenb.	bristlystalked sedge
Cyperaceae	CALUC	*Carex lucorum* Willd. ex Link	Blue Ridge sedge
Cyperaceae	CALUR	*Carex lurida* Wahlenb.	shallow sedge
Cyperaceae	CANO	*Carex normalis* Mackenzie	greater straw sedge
Cyperaceae	CAPR	*Carex projecta* Mackenzie	necklace sedge
Cyperaceae	CASC	*Carex scoparia* Schkuhr ex Willd.	broom sedge
Cyperaceae	CAST	*Carex stipata* Muhl. ex Willd.	owlfruit sedge
Cyperaceae	CATE	*Carex tenera* Dewey	quill sedge
Cyperaceae	CATR2	*Carex tribuloides* Wahlenb.	blunt broom sedge
Cyperaceae	CATR1	*Carex trisperma* Dewey	threeseeded sedge
Cyperaceae	SCCY	*Scirpus cyperinus* (L.) Kunth	woolgrass

Family	Code	Scientific name	Common name
Cyperaceae	SCHA	*Scirpus hattorianus* Makino	mosquito bulrush
Juncaceae	JUEF	*Juncus effusus* L.	common rush
Juncaceae	LUAC	*Luzula acuminata* Raf.	hairy woodrush
Juncaceae	LUZU	*Luzula* DC.	woodrush
Juncaceae	LUMU	*Luzula multiflora* (Ehrh.) Lej.	common woodrush
Poaceae	AGRO	*Agrostis L.*	bentgrass
Poaceae	AGPE	*Agrostis perennans* (Walt.) Tuckerman	upland bentgrass
Poaceae	ANOD	*Anthoxanthum odoratum* L.	sweet vernalgrass
Poaceae	BRER	*Brachyelytrum erectum* (Schreb. ex Spreng.) Beauv.	bearded shorthusk
Poaceae	CACA	*Calamagrostis canadensis* (Michx.) Beauv.	bluejoint
Poaceae	CILA	*Cinna latifolia* (Trevis. ex Goepp.) Griseb.	drooping woodreed
Poaceae	DACO	*Danthonia compressa* Austin	flattened oatgrass
Poaceae	DANT	*Danthonia* DC.	oatgrass
Poaceae	DASP	*Danthonia spicata* (L.) Beauv. ex Roemer & J.A. Schultes	poverty oatgrass
Poaceae	DIAC	*Dichanthelium acuminatum* (Sw.) Gould & C.A. Clark	tapered rosette grass
Poaceae	GLST	*Glyceria striata* (Lam.) Hitchc.	fowl mannagrass
Poaceae	ORAS	*Oryzopsis asperifolia* Michx.	roughleaf ricegrass
Poaceae	PONE	*Poa nemoralis* L.	wood bluegrass
Poaceae	POPAL	*Poa palustris* L.	fowl bluegrass
Herbs			
Alismataceae	SALA	*Sagittaria latifolia* Willd.	broadleaf arrowhead
Apiaceae	SISU	*Sium suave* Walter	hemlock waterparsnip
Araceae	ARTR	*Arisaema triphyllum* (L.) Schott	Jack in the pulpit
Araceae	CAPA1	*Calla palustris* L.	water arum
Asteraceae	ACMI	*Achillea millefolium L.*	common yarrow
Asteraceae	ANMA	*Anaphalis margaritacea* (L.) Benth.	pearly everlasting
Asteraceae	BIDE	*Bidens* L.	beggarticks
Asteraceae	DOUM	*Doellingeria umbellata* (P. Mill.) Nees	parasol whitetop
Asteraceae	EUMA	*Eurybia macrophylla* (L.) Cass.	bigleaf aster
Asteraceae	EUGR	*Euthamia graminifolia* (L.) Nutt.	flat-top goldentop
Asteraceae	HIER	*Hieracium* L.	hawkweed
Asteraceae	OCAC	*Oclemena acuminata (Michx.) Greene*	whorled wood aster

Family	Code	Scientific name	Common name
Asteraceae	PEFR	*Petasites frigidus* (L.) Fr.	arctic sweet coltsfoot
Asteraceae	PREN	*Prenanthes* L.	rattlesnakeroot
Asteraceae	SOCA	*Solidago canadensis* L.	Canada goldenrod
Asteraceae	SONE	*Solidago nemoralis* Ait.	gray goldenrod
Asteraceae	SORU	*Solidago rugosa* P. Mill.	wrinkleleaf goldenrod
Asteraceae	SYCI	*Symphyotrichum ciliolatum* (Lindl.) A. Löve & D. Löve	Lindley's aster
Asteraceae	SYLA	*Symphyotrichum lateriflorum* (L.) A.& D. Löve	calico aster
Asteraceae	SYPU	*Symphyotrichum puniceum* (L.) A. Löve & D. Löve	purplestem aster
Asteraceae	TAOF	*Taraxacum officinale* G.H. Weber ex Wiggers	common dandelion
Balsaminaceae	IMCA	*Impatiens capensis* Meerb.	jewelweed
Callitrichaceae	CAPA2	*Callitriche palustris* L.	vernal water-starwort
Caryophyllaceae	MOLA	*Moehringia lateriflora* (L.) Fenzl	bluntleaf sandwort
Crassulaceae	HYTE	*Hylotelephium telephium* (L.) H. Ohba ssp. *telephium*	witch's moneybags
Fabaceae	LOCO	*Lotus corniculatus* L.	birdsfoot-trefoil
Fabaceae	TRRE	*Trifolium repens* L.	white clover
Geraniaceae	GERA	*Geranium* L.	geranium
Iridaceae	IRVE	*Iris versicolor* L.	harlequin blueflag
Lamiaceae	GATE	*Galeopsis tetrahit* L.	brittlestem hempnettle
Lamiaceae	LYUN	*Lycopus uniflorus* Michx.	northern bugleweed
Lamiaceae	PRVU	*Prunella vulgaris* L.	common selfheal
Lamiaceae	SCGA	*Scutellaria galericulata* L.	marsh skullcap
Lamiaceae	SCLA	*Scutellaria lateriflora* L.	blue skullcap
Liliaceae	CLBO	*Clintonia borealis* (Ait.) Raf.	bluebead
Liliaceae	MACA	*Maianthemum canadense* Desf.	Canada mayflower
Liliaceae	MEVI	*Medeola virginiana* L.	Indian cucumber
Liliaceae	POPU	*Polygonatum pubescens* (Willd.) Pursh	hairy Solomon's seal
Liliaceae	TRIL	*Trillium* L.	trillium
Liliaceae	UVSE	*Uvularia sessilifolia* L.	sessileleaf bellwort
Lythraceae	LYSA	*Lythrum salicaria* L.	purple loosestrife
Monotropaceae	MOUN3	*Monotropa uniflora* L.	Indianpipe
Onagraceae	CHAN	*Chamerion angustifolium* (L.) Holub ssp. *angustifolium*	fireweed, great willow herb
Onagraceae	CIAL	*Circaea alpina* L.	small enchanter's nightshade

Family	**Code**	**Scientific name**	**Common name**
Onagraceae	CIRC	*Circaea* L.	enchanter's nightshade
Onagraceae	CILU	*Circaea lutetiana* L.	broadleaf enchanter's nightshade
Onagraceae	EPCI	*Epilobium ciliatum* Raf.	fringed willowherb
Onagraceae	EPCO	*Epilobium coloratum* Biehler	purpleleaf willowherb
Onagraceae	EPIL	*Epilobium* L.	willowherb
Onagraceae	LUPA	*Ludwigia palustris* (L.) Elliot	marsh seedbox
Onagraceae	OEPE	*Oenothera perennis* L.	little evening primrose
Orchidaceae	CYAC	*Cypripedium acaule* Ait.	pink lady's slipper
Orchidaceae	EPHE	*Epipactis helleborine* (L.) Crantz	broadleaf helleborine
Oxalidaceae	OXAL	*Oxalis* L.	woodsorrel
Polygalaceae	POPAU	*Polygala paucifolia* Willd.	finged polygala/gaywings
Polygonaceae	POLYG	*Polygonum* L.	knotweed
Polygonaceae	RUOR	*Rumex orbiculata* A. Gray	greater water dock
Primulaceae	LYTE	*Lysimachia terrestris* (L.) Britton, Sterns & Poggenb.	earth loosestrife
Primulaceae	TRBO	*Trientalis borealis* Raf.	starflower
Pyrolaceae	MOUN2	*Moneses uniflora* (L.) Gray	one-flowered pyrola
Pyrolaceae	PYRO	*Pyrola* L.	wintergreen
Ranunculaceae	ACRU2	*Actaea rubra* (Aiton) Willd.	red baneberry
Ranunculaceae	ANQU	*Anemone quinquefolia* L.	wood anemone
Ranunculaceae	COTR	*Coptis trifolia* (L.) Salisb.	threeleaf goldthread
Ranunculaceae	RANU	*Ranunculus* L.	buttercup
Ranunculaceae	RARE	*Ranunculus recurvatus* Poir.	blisterwort
Ranunculaceae	THPU	*Thalictrum pubescens* Pursh	king of the meadow
Rosaceae	DARE	*Dalibarda repens* L.	robin runaway/dewberry
Rosaceae	FRVI	*Fragaria virginiana* Duchesne	Virginia strawberry
Rosaceae	GEUM	*Geum* L.	avens
Rosaceae	GELA	*Geum laciniatum* Murray	rough avens
Rosaceae	GELAL	*Geum laciniatum* Murray var. *laciniatum*	rough avens
Rosaceae	GELAT	*Geum laciniatum* Murray var. *trichocarpum* Fernald	rough avens
Rosaceae	POTE	*Potentilla* L.	cinquefoil
Rosaceae	POSI	*Potentilla simplex* Michx.	common cinquefoil
Rubiaceae	GALI	*Galium* L.	bedstraw

Family	Code	Scientific name	Common name
Rubiaceae	GATR	*Galium triflorum* Michx.	fragrant bedstraw
Rubiaceae	HOCA	*Houstonia caerulea* L.	azure bluet
Saxifragaceae	MINU	*Mitella nuda* L.	naked miterwort
Saxifragaceae	TICO	*Tiarella cordifolia* L.	heartleaf foamflower
Scrophulariaceae	CHGL	*Chelone glabra* L.	white turtlehead
Scrophulariaceae	MELI	*Melampyrum lineare* Desr.	narrowleaf cowwheat
Scrophulariaceae	VEOF	*Veronica officinalis* L.	common speedwell
Scrophulariaceae	VESE	*Veronica serpyllifolia* L.	thymeleaf speedwell
Sparganiaceae	SPAR	*Sparganium* L.	bur-reed
Valerianaceae	VAOF	*Valeriana officinalis* L.	garden valerian
Violaceae	VIBL	*Viola blanda* Willd.	sweet white violet
Violaceae	VIOL	*Viola* L.	violet
Violaceae	VIPU	*Viola pubescens* Aiton	downy yellow violet
Shrubs			
Aquifoliaceae	ILMU	*Ilex mucronata* (L.) Powell, Savolainen & Andrews	catberry/mountain holly
Aquifoliaceae	ILVE	*Ilex verticillata* (L.) Gray	common winterberry
Betulaceae	ALIN	*Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) R.T. Clausen	speckled alder
Betulaceae	COCO	*Corylus cornuta* Marsh.	beaked hazelnut
Caprifoliaceae	DILO	*Diervilla lonicera* P. Mill.	northern bush honeysuckle
Caprifoliaceae	LOCA	*Lonicera canadensis* Bartr. ex Marsh.	American fly honeysuckle
Caprifoliaceae	LONI	*Lonicera* L.	honeysuckle
Caprifoliaceae	VIAC	*Viburnum acerifolium* L.	mapleleaf viburnum
Caprifoliaceae	VIDE	*Viburnum dentatum* L.	southern arrowwood
Caprifoliaceae	VINU	*Viburnum nudum* L. var. *cassinoides* (L.) Torr. & A. Gray	withe-rod
Caprifoliaceae	VIOP	*Viburnum opulus* L.	European cranberrybush
Caprifoliaceae	VIOPO	*Viburnum opulus* L. var. *opulus*	European cranberrybush
Cornaceae	COAL	*Cornus alternifolia* L. f.	alternateleaf dogwood
Cornaceae	CORN	*Cornus* L.	dogwood
Cornaceae	CORU	*Cornus rugosa* Lam.	roundleaf dogwood
Ericaceae	KAAN	*Kalmia angustifolia* L.	sheep laurel
Ericaceae	LEGR	*Ledum groenlandicum* Oeder	Labrador tea
Ericaceae	VAAN	*Vaccinium angustifolium* Ait.	lowbush blueberry

Family	Code	Scientific name	Common name
Ericaceae	VACO	*Vaccinium corymbosum* L.	highbush blueberry
Ericaceae	VAMY	*Vaccinium myrtilloides* Michx.	velvetleaf blueberry
Grossulariaceae	RIBE	*Ribes* L.	currant
Hamamelidaceae	HAVI	*Hamamelis virginiana* L.	American witchhazel
Myricaceae	COPE	*Comptonia peregrina* (L.) Coult.	sweet fern
Rhamnaceae	FRAL	*Frangula alnus* P. Mill.	glossy buckthorn
Rhamnaceae	RHCA	*Rhamnus cathartica* L.	common buckthorn
Rosaceae	AMEL	*Amelanchier* Medik.	serviceberry
Rosaceae	PHME	*Photinia melanocarpa* (Michx.) K.R. Robertson & Phipps	black chockberry
Rosaceae	ROSA	*Rosa* L.	rose
Rosaceae	ROMU	*Rosa multiflora* Thunb.	multiflora rose
Rosaceae	RUVE	*Rubus* cf. *vermontanus* Blanch.	Vermont blackberry
Rosaceae	RUID	*Rubus idaeus* L.	American red raspberry
Rosaceae	SPAL	*Spiraea alba* Du Roi	white meadowsweet
Rosaceae	SPTO	*Spiraea tomentosa* L.	steeplebush
Salicaceae	SADI	*Salix discolor* Muhl.	pussy willow
Salicaceae	SAER	*Salix eriocephala* Michx.	Missouri River willow
Sub-shrubs			
Anacardiaceae	TORA	*Toxicodendron radicans* (L.) Kuntze	eastern poison ivy
Araliaceae	ARHI	*Aralia hispida* Vent.	bristly sarsaparilla
Araliaceae	ARNU	*Aralia nudicaulis* L.	wild sarsaparilla
Caprifoliaceae	LIBO	*Linnaea borealis* L.	twinflower
Cornaceae	COCA	*Cornus canadensis* L.	bunchberry dogwood
Ericaceae	EPRE	*Epigaea repens* L.	trailing arbutus
Ericaceae	GAHI	*Gaultheria hispidula* (L.) Muhl. ex Bigelow	creeping snowberry
Ericaceae	GAPR	*Gaultheria procumbens* L.	eastern teaberry
Rosaceae	RUHI	*Rubus hispidus* L.	bristly dewberry
Rosaceae	RUPU	*Rubus pubescens* Raf.	dwarf red blackberry
Rubiaceae	MIRE	*Mitchella repens* L.	partridgeberry
Trees			
Betulaceae	BEAL	*Betula alleghaniensis* Britt.	yellow birch
Betulaceae	BETU	*Betula* L.	birch

Family	**Code**	**Scientific name**	**Common name**
Betulaceae	BEPA	*Betula papyrifera* Marsh.	paper birch
Betulaceae	BEPO	*Betula populifolia* Marsh.	gray birch
Betulaceae	OSVI	*Ostrya virginiana* (Mill.) K. Koch	hophornbeam
Cupressaceae	THOC	*Thuja occidentalis* L.	cedar/arborvitae
Fagaceae	FAGR	*Fagus grandifolia* Ehrh.	American beech
Fagaceae	QURU	*Quercus rubra* L.	northern red oak
Oleaceae	FRAM	*Fraxinum americana* L.	white ash
Oleaceae	FRPE	*Fraxinus pennsylvanica* Marsh.	green ash
Pinaceae	ABBA	*Abies balsamea* (L.) P. Mill.	balsam fir
Pinaceae	LALA	*Larix laricina* (Du Roi) K. Koch	tamarack
Pinaceae	PIGL	*Picea glauca* (Moench) Voss	white spruce
Pinaceae	PIRU	*Picea rubens* Sarg.	red spruce
Pinaceae	PIST	*Pinus strobus* L.	eastern white pine
Pinaceae	TSCA	*Tsuga canadensis* (L.) Carr.	eastern hemlock
Rosaceae	CRAT	*Crataegus* L.	Hawthorn
Rosaceae	MASY	*Malus sylvestris* (L.) Mill.	european crab apple
Rosaceae	PRPE	*Prunus pensylvanica* L. f.	pin cherry
Rosaceae	PRSE	*Prunus serotina* Ehrh.	black cherry
Rosaceae	PRVI	*Prunus virginiana* L.	chokecherry
Rosaceae	SORB	*Sorbus* L.	mountain ash
Salicaceae	POGR	*Populus grandidentata* Michx.	bigtooth aspen
Salicaceae	POTR	*Populus tremuloides* Michx.	quaking aspen
Sapindaceae	ACPE	*Acer pensylvanicum* L.	striped maple
Sapindaceae	ACPL	*Acer platanoides* L.	Norway maple
Sapindaceae	ACRU1	*Acer rubrum* L.	red maple
Sapindaceae	ACSA	*Acer saccharum* Marsh.	sugar maple
Vines			
Celastraceae	CEOR	*Celastrus orbiculata* Thunb.	Oriental bittersweet
Cucurbitaceae	ECLO	*Echinocystis lobata* (Michx.) Torr. & Gray	wild cucumber
Polygonaceae	POSA	*Polygonum sagittatum* L.	arrowleaf tearthumb
Solanaceae	SODU	*Solanum dulcamara* L.	climbing nightshade
Vitaceae	PAQU	*Parthenocissus quinquefolia* (L.) Planch.	Virginia creeper

Appendix B: Species Frequency Table

Table B.1. Understory plants recorded on the PEF in 2006 and 2007; frequency (% of plots) of occurrence by treatment.

Genus & Species	Common name	AG n=22	URH n=41	FDL n=33	MDL n=31	S20 n=37	S10 n=35	S05 n=33	SW2 n=30	SW3sp n=18	SW3 n=17	NAT n=20
Abies balsamea	balsam fir	0.18	0.98	0.91	0.94	0.89	0.97	0.97	0.97	1.00	0.94	0.90
Acer pensylvanicum	striped maple	0.05	0.02	0.00	0.00	0.00	0.00	0.06	0.03	0.00	0.00	0.00
Acer platanoides	Norway maple	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Acer rubrum	red maple	0.73	0.98	0.97	0.84	0.86	0.91	0.85	0.93	0.94	0.88	1.00
Acer saccharum	sugar maple	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Achillea millefolium	common yarrow	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Actaea rubra	red baneberry	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Agrostis perennans	upland bentgrass	0.09	0.07	0.00	0.03	0.00	0.03	0.00	0.00	0.06	0.00	0.00
Agrostis sp.	bentgrass	0.05	0.02	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Alnus incana	speckled alder	0.14	0.12	0.06	0.03	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Amelanchier sp.	serviceberry	0.45	0.02	0.03	0.03	0.05	0.00	0.00	0.00	0.00	0.00	0.00
Anaphalis margaritacea	pearly everlasting	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Genus & Species	Common name	AG n=22	URH n=41	FDL n=33	MDL n=31	S20 n=37	S10 n=35	S05 n=33	SW2 n=30	SW3sp n=18	SW3 n=17	NAT n=20
Anemone quinquefolia	wood anemone	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Anthoxanthum odoratum	sweet vernalgrass	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Aralia hispida	bristly sarsaparilla	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Aralia nudicaulis	wild sarsaparilla	0.09	0.76	0.85	0.61	0.51	0.66	0.55	0.37	0.28	0.06	0.50
Arisaema triphyllum	jack in the pulpit	0.64	0.07	0.00	0.03	0.03	0.06	0.00	0.00	0.00	0.00	0.00
Athyrium filix-femina	common ladyfern	0.27	0.17	0.09	0.10	0.03	0.11	0.03	0.07	0.00	0.00	0.00
Atrichum sp.	atrichum moss	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bazzania sp.		0.05	0.44	0.58	0.77	0.89	0.86	0.85	0.87	0.83	0.76	0.95
Betula alleghaniensis	yellow birch	0.00	0.00	0.06	0.03	0.05	0.00	0.00	0.00	0.00	0.00	0.00
Betula papyrifera	paper birch	0.00	0.15	0.52	0.13	0.14	0.11	0.06	0.13	0.11	0.18	0.00
Betula populifolia	gray birch	0.09	0.22	0.24	0.03	0.11	0.03	0.00	0.07	0.06	0.12	0.05
Betula sp.	birch	0.05	0.12	0.06	0.13	0.11	0.11	0.06	0.30	0.06	0.12	0.20
Bidens sp.	beggarticks	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Genus & Species	Common name	AG n=22	URH n=41	FDL n=33	MDL n=31	S20 n=37	S10 n=35	S05 n=33	SW2 n=30	SW3sp n=18	SW3 n=17	NAT n=20
Brachyelytrum erectum	bearded shorthusk	0.00	0.24	0.00	0.10	0.03	0.20	0.03	0.07	0.06	0.00	0.00
Calamagrostis canadensis	bluejoint	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Calla palustris	water arum	0.05	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Callitriche palustris	vernal water-starwort	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carex arctata	drooping woodland sedge	0.09	0.05	0.03	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Carex bromoides	brome-like sedge	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carex brunnescens	brownish sedge	0.05	0.07	0.21	0.06	0.05	0.03	0.03	0.00	0.00	0.00	0.00
Carex communis	fibrousroot sedge	0.00	0.02	0.03	0.00	0.03	0.00	0.03	0.00	0.06	0.06	0.00
Carex debilis	white edge sedge	0.09	0.10	0.15	0.03	0.00	0.03	0.00	0.00	0.00	0.06	0.00
Carex deweyana	Dewey sedge	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carex disperma	softleaf sedge	0.00	0.02	0.00	0.03	0.00	0.00	0.06	0.00	0.00	0.00	0.00
Carex gracillima	graceful sedge	0.32	0.05	0.03	0.03	0.00	0.03	0.03	0.00	0.00	0.00	0.00
Carex gynandra	nodding sedge	0.00	0.02	0.03	0.00	0.00	0.03	0.00	0.03	0.00	0.00	0.00

Genus & Species	Common name	AG n=22	URH n=41	FDL n=33	MDL n=31	S20 n=37	S10 n=35	S05 n=33	SW2 n=30	SW3sp n=18	SW3 n=17	NAT n=20
Carex leptalea	bristlystalked sedge	0.00	0.15	0.03	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Carex lucorum	Blue Ridge sedge	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carex lurida	shallow sedge	0.09	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Carex normalis	greater straw sedge	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carex projecta	necklace sedge	0.05	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carex scoparia	broom sedge	0.00	0.00	0.03	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Carex stipata	owlfruit sedge	0.05	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carex tenera	quill sedge	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carex tribuloides	blunt broom sedge	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carex trisperma	threeseeded sedge	0.00	0.07	0.09	0.16	0.08	0.09	0.00	0.03	0.00	0.00	0.00
Celastrus orbiculata	Oriental bittersweet	0.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chamerion angustifolium	fireweed, great willow herb	0.00	0.00	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chelone glabra	white turtlehead	0.05	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00
Cinna latifolia	drooping woodreed	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00

Genus & Species	Common name	AG n=22	URH n=41	FDL n=33	MDL n=31	S20 n=37	S10 n=35	S05 n=33	SW2 n=30	SW3sp n=18	SW3 n=17	NAT n=20
Circaea alpina	small enchanter's nightshade	0.05	0.00	0.03	0.00	0.03	0.03	0.03	0.00	0.00	0.00	0.00
Circaea lutetiana	broadleaf enchanter's nightshade	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Circaea sp.	enchanter's nightshade	0.32	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cladina sp.	reindeer lichen	0.00	0.29	0.21	0.13	0.32	0.11	0.12	0.10	0.33	0.18	0.00
Cladonia sp.	cup lichen	0.18	0.98	0.97	0.97	0.86	0.86	0.94	0.93	0.94	0.76	0.75
Climacium dendroides	tree climacium moss	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Climacium sp.	climacium moss	0.00	0.02	0.00	0.00	0.03	0.03	0.00	0.00	0.00	0.00	0.00
Clintonia borealis	bluebead	0.00	0.29	0.27	0.39	0.38	0.40	0.33	0.23	0.22	0.06	0.05
Comptonia peregrine	sweet fern	0.00	0.20	0.09	0.03	0.03	0.03	0.00	0.00	0.00	0.06	0.00
Coptis trifolia	threeleaf goldthread	0.09	0.34	0.24	0.19	0.22	0.43	0.09	0.27	0.17	0.00	0.15
Cornus alternifolia	alternateleaf dogwood	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cornus canadensis	bunchberry dogwood	0.23	0.73	0.67	0.48	0.43	0.71	0.33	0.27	0.39	0.24	0.10

Genus & Species	Common name	AG n=22	URH n=41	FDL n=33	MDL n=31	S20 n=37	S10 n=35	S05 n=33	SW2 n=30	SW3sp n=18	SW3 n=17	NAT n=20
Cornus rugosa	roundleaf dogwood	0.00	0.02	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cornus sp.	dogwood	0.14	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Corylus cornuta	beaked hazelnut	0.09	0.56	0.21	0.10	0.03	0.29	0.12	0.00	0.00	0.00	0.00
Crataegus sp.	Hawthorn	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cypripedium acaule	pink lady's slipper	0.00	0.10	0.15	0.23	0.19	0.11	0.27	0.03	0.11	0.18	0.00
Dalibarda repens	robin runaway/dewberry	0.05	0.07	0.12	0.00	0.19	0.17	0.06	0.03	0.06	0.00	0.00
Danthonia compressa	flattened oatgrass	0.00	0.05	0.03	0.03	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Danthonia sp.	oatgrass	0.09	0.12	0.03	0.03	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Danthonia spicata	poverty oatgrass	0.00	0.15	0.03	0.03	0.05	0.09	0.00	0.00	0.00	0.06	0.00
Dennstaedtia punctilobula	eastern hayscented fern	0.00	0.02	0.03	0.23	0.08	0.03	0.00	0.10	0.06	0.00	0.00
Dichanthelium acuminatum	tapered rosette grass	0.00	0.00	0.00	0.03	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Dicranum polysetum	dicranum moss	0.00	0.05	0.06	0.00	0.05	0.03	0.09	0.07	0.11	0.00	0.00

Genus & Species	Common name	AG n=22	URH n=41	FDL n=33	MDL n=31	S20 n=37	S10 n=35	S05 n=33	SW2 n=30	SW3sp n=18	SW3 n=17	NAT n=20
Diervilla lonicera	northern bush honeysuckle	0.00	0.44	0.18	0.00	0.11	0.00	0.03	0.00	0.28	0.12	0.00
Doellingeria umbellata	parasol whitetop	0.23	0.15	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00
Dryopteris carthusiana	spinulose woodfern	0.55	0.29	0.21	0.29	0.16	0.17	0.06	0.03	0.00	0.06	0.00
Dryopteris clintoniana	Clinton's woodfern	0.05	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dryopteris cristata	crested woodfern	0.05	0.12	0.06	0.03	0.00	0.03	0.00	0.03	0.00	0.00	0.00
Dryopteris intermedia	intermediate woodfern	0.05	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00
Dryopteris marginalis	marginal woodfern	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Dryopteris sp.		0.05	0.10	0.06	0.06	0.03	0.14	0.18	0.10	0.11	0.06	0.05
Echinocystis lobata	wild cucumber	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Epigaea repens	trailing arbutus	0.00	0.02	0.00	0.03	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Epilobium ciliatum	fringed willowherb	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Epilobium coloratum	purpleleaf willowherb	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00

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Epipactis helleborine	broadleaf helleborine	0.14	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Equisetum sp.	horsetail	0.14	0.32	0.09	0.06	0.27	0.23	0.00	0.23	0.00	0.06	0.00
Eurybia macrophylla	bigleaf aster	0.00	0.17	0.03	0.00	0.03	0.06	0.00	0.00	0.00	0.00	0.00
Euthamia graminifolia	flat-top goldentop	0.00	0.07	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fagus grandifolia	American beech	0.00	0.05	0.09	0.06	0.03	0.00	0.03	0.00	0.06	0.00	0.00
Fragaria virginiana	Virginia strawberry	0.77	0.37	0.18	0.06	0.03	0.20	0.06	0.00	0.00	0.00	0.00
Frangula alnus	glossy buckthorn	0.86	0.05	0.00	0.00	0.00	0.03	0.00	0.03	0.00	0.00	0.05
Fraxinus Americana	white ash	0.41	0.07	0.27	0.13	0.05	0.03	0.12	0.13	0.06	0.06	0.00
Fraxinus pennsylvanica	green ash	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fraxinus sp.	ash	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Galeopsis tetrahit	brittlestem hempnettle	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Galium sp.	bedstraw	0.23	0.17	0.09	0.03	0.05	0.11	0.06	0.07	0.00	0.00	0.00
Galium triflorum	fragrant bedstraw	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Genus & Species	**Common name**	**AG n=22**	**URH n=41**	**FDL n=33**	**MDL n=31**	**S20 n=37**	**S10 n=35**	**S05 n=33**	**SW2 n=30**	**SW3sp n=18**	**SW3 n=17**	**NAT n=20**
Gaultheria hispidula	creeping snowberry	0.00	0.07	0.06	0.06	0.05	0.11	0.00	0.03	0.00	0.06	0.00
Gaultheria procumbens	eastern teaberry	0.23	0.20	0.24	0.10	0.05	0.17	0.18	0.00	0.06	0.06	0.00
Geranium sp.	geranium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Geum laciniatum	rough avens	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Geum laciniatum var. *laciniatum*	rough avens	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Geum laciniatum var. trichocarpum	rough avens	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Geum sp.	avens	0.45	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Glyceria striata	fowl mannagrass	0.18	0.07	0.03	0.00	0.00	0.03	0.03	0.00	0.00	0.00	0.00
Gymnocarpium dryopteris	western oakfern	0.00	0.15	0.06	0.06	0.00	0.06	0.09	0.00	0.00	0.00	0.00
Hamamelis virginiana	American witchhazel	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.07	0.00	0.00	0.00
Hieracium sp.	hawkweed	0.23	0.12	0.12	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Houstonia caerulea	azure bluet	0.00	0.00	0.00	0.03	0.03	0.06	0.03	0.00	0.00	0.00	0.00

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Hylocomium splendens	stairstep moss	0.00	0.29	0.15	0.23	0.41	0.40	0.33	0.40	0.22	0.24	0.10
Hylotelephium telephium	witch's moneybags	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ilex mucronata	catberry/mountain holly	0.05	0.00	0.09	0.03	0.03	0.03	0.03	0.00	0.00	0.00	0.00
Ilex verticillata	common winterberry	0.14	0.17	0.09	0.10	0.16	0.06	0.03	0.17	0.06	0.00	0.25
Impatiens capensis	jewelweed	0.14	0.00	0.00	0.03	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Iris versicolor	harlequin blueflag	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Juncus effuses	common rush	0.05	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Kalmia angustifolia	sheep laurel	0.09	0.22	0.27	0.13	0.16	0.11	0.15	0.07	0.06	0.00	0.05
Larix laricina	tamarack	0.00	0.02	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ledum groenlandicum	Labrador tea	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Leucobryum sp.	leucobryum moss	0.05	0.15	0.21	0.23	0.11	0.09	0.42	0.17	0.28	0.35	0.05
Linnaea borealis	twinflower	0.00	0.17	0.21	0.06	0.16	0.11	0.15	0.03	0.11	0.06	0.05
Lonicera canadensis	American fly honeysuckle	0.00	0.17	0.09	0.00	0.14	0.23	0.27	0.00	0.17	0.00	0.05

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Lotus corniculatus	birdsfoot-trefoil	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Ludwigia palustris	marsh seedbox	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Luzula acuminate	hairy woodrush	0.05	0.02	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Luzula multiflora	common woodrush	0.05	0.00	0.00	0.00	0.03	0.03	0.00	0.00	0.00	0.00	0.00
Luzula sp.	woodrush	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lycopodium clavatum	running clubmoss	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Lycopodium sp.	clubmoss	0.00	0.10	0.06	0.13	0.08	0.06	0.00	0.10	0.22	0.12	0.00
Lycopus uniflorus	northern bugleweed	0.00	0.12	0.09	0.00	0.00	0.11	0.06	0.03	0.00	0.00	0.00
Lysimachia terrestris	earth loosestrife	0.00	0.00	0.00	0.03	0.03	0.06	0.03	0.03	0.00	0.00	0.00
Lythrum salicaria	purple loosestrife	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Maianthemum canadense	Canada mayflower	0.27	0.98	1.00	1.00	0.97	0.97	1.00	0.87	1.00	0.82	0.75
Malus sylvestris	european crab apple	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

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Medeola virginiana	Indian cucumber	0.00	0.10	0.12	0.06	0.05	0.14	0.00	0.07	0.00	0.00	0.00
Melampyrum lineare	narrowleaf cowwheat	0.00	0.02	0.00	0.03	0.03	0.00	0.00	0.00	0.06	0.00	0.00
Mitchella repens	partridgeberry	0.09	0.12	0.21	0.19	0.19	0.11	0.21	0.17	0.00	0.00	0.00
Mitella nuda	naked miterwort	0.00	0.05	0.00	0.00	0.03	0.06	0.06	0.00	0.00	0.00	0.00
Mnium sp.	mnium calcareous moss	0.00	0.10	0.03	0.06	0.00	0.06	0.09	0.13	0.00	0.00	0.15
Moehringia lateriflora	bluntleaf sandwort	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Moneses uniflora	one-flowered pyrola	0.00	0.02	0.15	0.00	0.00	0.09	0.06	0.03	0.06	0.00	0.00
Monotropa uniflora	Indianpipe	0.00	0.07	0.12	0.03	0.05	0.11	0.00	0.07	0.00	0.00	0.00
Oclemena acuminate	whorled wood aster	0.00	0.29	0.27	0.26	0.22	0.26	0.00	0.17	0.06	0.00	0.00
Oenothera perennis	little evening primrose	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Onoclea sensibilis	sensitive fern	0.55	0.22	0.06	0.06	0.05	0.17	0.09	0.13	0.00	0.00	0.00
Oryzopsis asperifolia	roughleaf ricegrass	0.00	0.41	0.33	0.16	0.14	0.09	0.12	0.00	0.06	0.06	0.05

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Osmunda cinnamomea	cinnamon fern	0.05	0.02	0.12	0.00	0.05	0.09	0.03	0.00	0.00	0.00	0.00
Osmunda claytoniana	interrupted fern	0.05	0.10	0.12	0.06	0.05	0.09	0.03	0.07	0.00	0.00	0.00
Osmunda sp.	osmunda	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Ostrya virginiana	hophornbeam	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Oxalis sp.	woodsorrel	0.27	0.00	0.00	0.06	0.03	0.06	0.00	0.00	0.00	0.00	0.00
Parthenocissus quinquefolia	Virginia creeper	0.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Petasites frigidus	arctic sweet coltsfoot	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Phegopteris connectilis	beech fern	0.00	0.00	0.03	0.06	0.03	0.03	0.03	0.00	0.00	0.00	0.00
Photinia melanocarpa	black chockberry	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Picea glauca	white spruce	0.09	0.05	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00
Picea rubens	red spruce	0.00	0.24	0.33	0.71	0.62	0.71	0.73	0.20	0.33	0.29	0.30
Picea sp.	spruce	0.00	0.00	0.00	0.00	0.03	0.03	0.03	0.00	0.00	0.00	0.00
Pinus strobus	eastern white pine	0.09	0.15	0.03	0.26	0.19	0.17	0.27	0.20	0.11	0.06	0.55

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Poa nemoralis	wood bluegrass	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Poa palustris	fowl bluegrass	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polygala paucifolia	finged polygala	0.00	0.00	0.00	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Polygonatum pubescens	hairy Solomon's seal	0.05	0.02	0.00	0.00	0.03	0.03	0.00	0.00	0.00	0.00	0.00
Polygonum sagittatum	arrowleaf tearthumb	0.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polygonum sp.	knotweed	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polytrichum sp.	polytrichum moss	0.18	0.66	0.73	0.45	0.46	0.29	0.09	0.33	0.56	0.35	0.30
Populus grandidentata	bigtooth aspen	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10
Populus tremuloides	quaking aspen	0.50	0.02	0.03	0.00	0.00	0.03	0.00	0.03	0.00	0.00	0.15
Potentilla simplex	common cinquefoil	0.64	0.02	0.03	0.03	0.03	0.06	0.00	0.03	0.00	0.00	0.00
Potentilla sp.	cinquefoil	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.00	0.00
Prenanthes sp.	rattlesnakeroot	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Prunella vulgaris	common selfheal	0.09	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00

Genus & Species	Common name	AG n=22	URH n=41	FDL n=33	MDL n=31	S20 n=37	S10 n=35	S05 n=33	SW2 n=30	SW3sp n=18	SW3 n=17	NAT n=20
Prunus serotina	black cherry	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Prunus virginiana	chokecherry	0.77	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Pteridium aquilinum	western brackenfern	0.05	0.39	0.64	0.42	0.49	0.34	0.36	0.07	0.22	0.06	0.05
Ptilidium pulcherrimum	Naugehyde	0.00	0.07	0.03	0.13	0.03	0.00	0.00	0.00	0.00	0.00	0.05
Pyrola sp.	wintergreen	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Quercus rubra	northern red oak	0.59	0.07	0.09	0.03	0.05	0.03	0.00	0.00	0.00	0.00	0.30
Ranunculus recurvatus	blisterwort	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ranunculus sp.	buttercup	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhamnus cathartica	common buckthorn	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ribes sp.	currant	0.23	0.02	0.00	0.00	0.00	0.03	0.00	0.03	0.00	0.06	0.00
Rosa multiflora	multiflora rose	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rosa sp.	rose	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rubus cf. *vermontanus*	Vermont blackberry	0.36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rubus hispidus	bristly dewberry	0.27	0.20	0.06	0.13	0.00	0.06	0.03	0.00	0.00	0.00	0.00

Genus & Species	Common name	AG n=22	URH n=41	FDL n=33	MDL n=31	S20 n=37	S10 n=35	S05 n=33	SW2 n=30	SW3sp n=18	SW3 n=17	NAT n=20
Rubus idaeus	American red raspberry	0.55	0.12	0.61	0.10	0.05	0.03	0.03	0.00	0.11	0.00	0.00
Rubus pubescens	dwarf red blackberry	0.77	0.39	0.09	0.06	0.08	0.20	0.15	0.17	0.06	0.06	0.00
Rubus sp.	blackberry	0.00	0.05	0.00	0.00	0.03	0.03	0.00	0.03	0.00	0.00	0.00
Rumex orbiculata	greater water dock	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sagittaria latifolia	broadleaf arrowhead	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Salix discolor	pussy willow	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Salix eriocephala	Missouri River willow	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus cyperinus	woolgrass	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Scirpus hattorianus	mosquito bulrush	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Scutellaria galericulata	marsh skullcap	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Scutellaria lateriflora	blue skullcap	0.00	0.05	0.06	0.03	0.03	0.09	0.00	0.07	0.00	0.00	0.00
Sium suave	hemlock waterparsnip	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Genus & Species	Common name	AG n=22	URH n=41	FDL n=33	MDL n=31	S20 n=37	S10 n=35	S05 n=33	SW2 n=30	SW3sp n=18	SW3 n=17	NAT n=20
Solanum dulcamara	climbing nightshade	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Solidago canadensis	Canada goldenrod	0.23	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Solidago nemoralis	gray goldenrod	0.00	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Solidago rugosa	wrinkleleaf goldenrod	0.09	0.10	0.09	0.06	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Sorbus sp.	mountain ash	0.05	0.12	0.00	0.00	0.03	0.03	0.03	0.00	0.00	0.00	0.05
Sparganium sp.	bur-reed	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sphagnum sp.	sphagnum	0.05	0.46	0.27	0.19	0.35	0.46	0.18	0.23	0.00	0.06	0.00
Spiraea alba	white meadowsweet	0.50	0.07	0.03	0.00	0.00	0.03	0.03	0.03	0.00	0.00	0.00
Spiraea tomentosa	steeplebush	0.00	0.05	0.03	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Symphyotrichum ciliolatum	Lindley's aster	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Symphyotrichum lateriflorum	calico aster	0.59	0.17	0.09	0.13	0.03	0.11	0.06	0.00	0.00	0.00	0.00
Symphyotrichum puniceum	purplestem aster	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Genus & Species	Common name	AG n=22	URH n=41	FDL n=33	MDL n=31	S20 n=37	S10 n=35	S05 n=33	SW2 n=30	SW3sp n=18	SW3 n=17	NAT n=20
Thalictrum pubescens	king of the meadow	0.09	0.02	0.00	0.03	0.00	0.06	0.00	0.00	0.00	0.00	0.00
Thelypteris noveboracensis	New York fern	0.00	0.07	0.06	0.03	0.00	0.00	0.06	0.07	0.00	0.00	0.00
Thelypteris palustris	eastern marsh fern	0.00	0.02	0.03	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Thuja occidentalis	cedar/arborvitae	0.05	0.24	0.48	0.19	0.35	0.31	0.27	0.10	0.00	0.00	0.00
Tiarella cordifolia	heartleaf foamflower	0.05	0.10	0.00	0.00	0.00	0.03	0.03	0.03	0.00	0.00	0.00
Toxicodendron radicans	eastern poison ivy	0.05	0.10	0.03	0.06	0.03	0.11	0.00	0.00	0.00	0.06	0.00
Trientalis borealis	starflower	0.23	1.00	0.94	0.87	0.73	0.83	0.94	0.70	0.61	0.24	0.30
Trifolium repens	white clover	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Trillium sp.	trillium	0.00	0.00	0.03	0.03	0.00	0.00	0.03	0.07	0.00	0.00	0.00
Tsuga canadensis	eastern hemlock	0.09	0.17	0.82	1.00	0.84	0.63	0.94	0.50	0.11	0.18	0.45
Uvularia sessilifolia	sessileleaf bellwort	0.00	0.15	0.03	0.03	0.00	0.09	0.00	0.00	0.00	0.00	0.00
Vaccinium angustifolium	lowbush blueberry	0.09	0.22	0.12	0.10	0.08	0.23	0.03	0.07	0.06	0.12	0.10

Genus & Species	Common name	AG n=22	URH n=41	FDL n=33	MDL n=31	S20 n=37	S10 n=35	S05 n=33	SW2 n=30	SW3sp n=18	SW3 n=17	NAT n=20
Vaccinium corymbosum	highbush blueberry	0.00	0.05	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.06	0.00
Vaccinium myrtilloides	velvetleaf blueberry	0.18	0.34	0.09	0.10	0.05	0.17	0.09	0.13	0.44	0.24	0.00
Vaccinium sp.	blueberry	0.05	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
Valeriana officinalis	garden valerian	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Veronica officinalis	common speedwell	0.18	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Veronica serpyllifolia	thymeleaf speedwell	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Viburnum acerifolium	mapleleaf viburnum	0.09	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Viburnum dentatum	southern arrowwood	0.86	0.07	0.03	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.05
Viburnum nudum	withe-rod	0.64	0.00	0.00	0.03	0.03	0.06	0.03	0.03	0.00	0.00	0.05
Viburnum opulus var. *opulus*	Guelder rose	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Viola blanda	sweet white violet	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Genus & Species	**Common name**	**AG n=22**	**URH n=41**	**FDL n=33**	**MDL n=31**	**S20 n=37**	**S10 n=35**	**S05 n=33**	**SW2 n=30**	**SW3sp n=18**	**SW3 n=17**	**NAT n=20**
Viola sp.	violet	0.09	0.37	0.24	0.19	0.05	0.11	0.06	0.10	0.06	0.00	0.00

Appendix C: Compartment Means

Table C.1. Compartment/Replicate means and standard errors for measured environmental variables.

Treatment	Compartment ID (n=#plots)		BA m^2/ha	#trees/ha	%BA Hardwood	%BA Softwood	% Canopy Openness	Moss %Cover	HW Litter % Cover	SW Litter % Cover	Mineral Soil % Cover	O-Horizon (cm)	Mottling (cm)	Briggs Class
AG	**N**	Mean	19.80	-	73.89	26.11	9.41	43.16	73.47	17.66	8.44	1.12	19.53	4
	n=8	SE	1.50	-	10.11	10.11	1.10	6.08	6.29	8.80	4.15	0.64	2.41	-
AG	**S**	Mean	19.02	-	96.12	3.88	9.25	26.27	53.18	3.80	7.05	0.23	18.14	4
	n=14	SE	2.12	-	2.30	2.30	1.04	5.62	8.51	3.25	1.52	0.13	1.17	-
URH	**22**	Mean	20.69	1559.35	42.65	57.35	9.48	35.75	64.94	17.84	1.65	2.18	13.72	4
	n=20	SE	1.76	174.73	5.72	5.72	0.98	3.43	4.50	3.63	1.57	0.20	1.73	-
URH	**8**	Mean	15.85	1391.64	51.81	48.19	8.47	36.04	69.55	29.24	0.00	2.13	18.92	4
	n=21	SE	0.87	68.19	5.38	5.38	0.77	3.37	4.67	5.20	0.00	0.18	2.84	-
FDL	**15**	Mean	12.65	702.23	14.76	85.24	21.11	46.44	44.75	42.24	0.85	2.18	20.75	3
	n=20	SE	0.96	117.66	2.21	2.21	2.44	4.45	5.32	5.47	0.53	0.18	2.82	-
FDL	**4**	Mean	14.43	764.23	27.79	72.21	13.55	35.29	55.21	39.15	0.60	2.62	20.37	3
	n=13	SE	1.07	107.88	3.59	3.59	1.91	7.47	5.53	7.73	0.60	0.28	2.46	-
MDL	**28**	Mean	28.04	1107.03	20.15	79.85	8.48	49.38	51.61	59.71	2.47	2.51	20.09	4
	n=19	SE	1.09	128.76	2.97	2.97	1.02	6.57	7.26	6.18	2.31	0.20	4.60	-
MDL	**24**	Mean	30.06	953.03	15.07	84.93	11.44	45.08	58.73	64.98	0.00	3.00	34.87	3
	n=12	SE	1.08	195.24	2.72	2.72	1.65	6.02	6.40	6.75	0.00	0.25	3.63	-
S20	**27**	Mean	26.37	1520.65	15.23	84.77	6.90	51.91	45.76	65.99	0.26	2.31	22.35	3
	n=23	SE	1.03	142.16	2.22	2.22	0.50	4.10	4.85	4.98	0.12	0.20	3.45	-
S20	**17**	Mean	25.13	993.36	11.99	88.01	9.94	49.52	43.88	43.09	0.55	1.75	23.14	3
	n=14	SE	1.36	173.95	2.06	2.06	1.33	6.04	5.65	5.91	0.55	0.25	3.20	-
S10	**20**	Mean	27.71	1176.77	17.64	82.36	8.21	50.98	51.79	59.07	0.07	2.24	12.98	4
	n=21	SE	1.43	179.75	2.74	2.74	0.97	5.47	6.51	4.33	0.07	0.23	1.52	-

Treatment	Compartment ID (n=#plots)		BA m^2/ha	#trees/ha	%BA Hardwood	%BA Softwood	% Canopy Openness	Moss %Cover	HW Litter % Cover	SW Litter % Cover	Mineral Soil % Cover	O-Horizon (cm)	Mottling (cm)	Briggs Class
S10	**12**	Mean	28.40	952.31	12.80	87.20	9.42	59.96	36.93	49.25	0.66	2.21	9.80	5
	n=14	SE	1.42	176.94	2.62	2.62	1.12	5.88	7.45	8.53	0.56	0.30	2.31	-
S05	**16**	Mean	27.35	496.75	8.08	91.92	8.61	51.00	34.43	38.31	0.00	2.97	41.78	2
	n=20	SE	1.21	88.65	1.50	1.50	0.95	6.11	5.96	5.11	0.00	0.20	1.91	-
S05	**9**	Mean	25.83	468.50	13.26	86.74	8.69	43.29	48.00	52.71	0.00	4.09	25.55	3
	n=13	SE	1.54	98.12	2.23	2.23	1.14	6.00	7.60	9.89	0.00	0.48	3.40	-
SW2	**30**	Mean	37.37	1405.68	20.49	79.51	8.16	33.00	55.81	53.81	0.00	1.85	30.94	3
	n=20	SE	1.72	156.44	3.05	3.05	0.80	6.70	5.81	6.79	0.00	0.15	3.96	-
SW2	**21**	Mean	35.77	1771.92	26.19	73.81	9.61	38.50	62.38	56.88	0.78	3.28	14.61	4
	n=10	SE	2.32	202.94	4.30	4.30	1.70	6.41	9.45	10.16	0.78	0.53	1.88	-
SW3sp	**29a**	Mean	27.20	980.86	10.00	90.00	6.48	43.47	46.75	60.34	0.00	1.96	26.04	3
	n=8	SE	1.06	125.90	2.02	2.02	0.76	6.79	10.73	5.99	0.00	0.20	5.28	-
SW3sp	**23a**	Mean	32.10	1020.62	15.42	84.58	11.96	30.63	46.38	41.13	0.00	3.05	34.24	3
	n=10	SE	2.18	149.38	2.96	2.96	3.10	5.59	6.99	6.91	0.00	0.46	3.84	-
SW3	**29b**	Mean	29.80	2048.72	19.14	80.86	8.20	38.47	45.19	57.38	0.00	1.98	31.39	3
	n=8	SE	1.87	382.06	6.51	6.51	1.07	8.51	6.91	7.17	0.00	0.38	7.24	-
SW3	**23b**	Mean	44.92	1794.78	12.93	87.07	7.06	13.63	47.22	69.41	0.00	2.34	41.28	2
	n=9	SE	1.79	149.44	4.94	4.94	0.54	5.32	10.44	7.71	0.00	0.56	3.15	-
NAT	**32b**	Mean	49.75	139.82	11.85	88.15	8.64	10.35	31.88	84.25	0.00	1.40	45.47	2
	n=10	SE	2.09	9.57	1.73	1.73	0.95	1.83	5.33	2.67	0.00	0.23	5.05	-
NAT	**32a**	Mean	35.69	1667.91	30.44	69.56	7.78	17.50	70.50	59.75	0.00	2.90	12.75	4
	n=10	SE	2.09	308.37	4.45	4.45	0.53	3.26	3.33	7.45	0.00	0.33	3.76	-

Appendix D: Treatment Means

Table D.1. Treatment means and standard errors for measured environmental variables.

Treatment (n=# plots)		BA (m^2/ha)	% Hardwood BA	% Softwood BA	# trees/ha	% Canopy Openness	Total Moss % Cover	HW Litter % Cover	SW Litter % Cover	Mineral Soil % Cover	O-Horizon (cm)	Mottling (cm)	Briggs Site Class
AG	Mean	19.30	88.04	11.96	-	9.31	32.70	60.56	8.84	7.56	0.5588	18.64	4
n=22	SE	1.43	4.46	4.46	-	0.76	4.48	6.15	3.96	1.74	0.254	1.12	-
URH	Mean	18.21	47.34	52.66	1473.45	8.96	35.90	67.30	23.68	0.80	2.159	16.38	4
n=41	SE	1.03	3.94	3.94	91.87	0.62	2.37	3.23	3.28	0.77	0.127	1.7	-
FDL	Mean	13.35	19.89	80.11	726.66	18.13	42.05	48.87	41.02	0.75	2.3622	20.57	3
n=33	SE	0.72	2.22	2.22	82.03	1.76	4.04	3.94	4.43	0.39	0.1524	1.91	-
MDL	Mean	28.82	18.18	81.82	1047.42	9.63	47.72	54.36	61.75	1.52	2.7178	26.01	3
n=31	SE	0.79	2.12	2.12	108.14	0.92	4.60	5.06	4.56	1.42	0.1524	3.35	-
S20	Mean	25.90	14.00	86.00	1321.13	8.05	51.01	45.05	57.32	0.37	2.0828	22.66	3
n=37	SE	0.82	1.59	1.59	116.74	0.63	3.38	3.65	4.20	0.22	0.1524	2.41	-
S10	Mean	27.99	15.71	84.29	1086.99	8.70	54.57	45.84	55.14	0.31	2.2098	11.68	4
n=35	SE	1.02	1.97	1.97	128.64	0.73	4.05	5.00	4.29	0.23	0.1778	1.32	-
S05	Mean	26.75	10.12	89.88	485.62	8.64	47.96	39.77	43.98	0.00	3.4036	35.69	3
n=33	SE	0.95	1.32	1.32	65.24	0.72	4.38	4.76	5.04	0.00	0.254	2.21	-
SW2	Mean	36.83	22.39	77.61	1527.76	8.65	34.83	58.00	54.83	0.26	2.286	25.86	3
n=30	SE	1.37	2.50	2.50	126.40	0.77	4.91	4.93	5.56	0.26	0.2286	3.1	-
SW3sp	Mean	29.92	13.01	86.99	1002.95	9.53	36.33	46.54	49.67	0.00	2.5654	30.58	3
n=18	SE	1.40	1.94	1.94	97.40	1.84	4.48	5.95	5.10	0.00	0.3048	3.23	-
SW3	Mean	37.81	15.85	84.15	1914.28	7.59	26.05	46.20	63.39	0.00	2.159	36.96	3
n=17	SE	2.26	3.97	3.97	192.27	0.58	5.82	6.05	5.32	0.00	0.3302	3.71	-
NAT	Mean	42.72	21.15	78.85	903.87	8.21	13.93	51.19	72.00	0.00	2.1336	29.11	3
n=20	SE	2.16	3.15	3.15	230.80	0.54	1.99	5.38	4.77	0.00	0.254	4.85	-

Appendix E: Wetland Indicator Plants

Table E.1. Wetland Indicator Status of Understory Species on the PEF.

OBL=Obligate Wetland (99% estimated probability of occurrence in wetlands).
FACW=Facultative Wetland (67-99% estimated probability of occurrence in wetlands).
FAC=Facultative (34-66% estimated probability of occurrence in wetlands).
FACU=Facultative Upland (1-33% estimated probability of occurrence in wetlands).
UPL=Obligate Upland (almost always occurs in non-wetlands; occurs in wetlands in another region).

Species	Common name	Code	Growth Habit
OBL			
Calla palustris	water arum	CAPA1	herb
Callitriche palustris	vernal water-starwort	CAPA2	herb
Carex arctata	drooping woodland sedge	CAAR	graminoid
Carex lacustris	hairy sedge	CALA	graminoid
Carex leptalea	bristlystalked sedge	CALE	graminoid
Carex lurida	shallow sedge	CALUR	graminoid
Carex stipata	owlfruit sedge	CAST	graminoid
Carex trisperma	threeseeded sedge	CATR1	graminoid
Chelone glabra	white turtlehead	CHGL	herb
Epilobium coloratum	purpleleaf willowherb	EPCO	herb
Glyceria striata	fowl mannagrass	GLST	graminoid
Ilex mucronata	catberry/mountain holly	ILMU	shrub
Iris versicolor	harlequin blueflag	IRVE	herb
Ledum groenlandicum	Labrador tea	LEGR	shrub
Ludwigia palustris	marsh seedbox	LUPA	herb
Lycopus uniflorus	northern bugleweed	LYUN	herb
Lysimachia terrestris	earth loosestrife	LYTE	herb
Penthorum sedoides	ditch stonecrop	PESE	herb
Polygonum sagittatum	arrowleaf tearthumb	POSA	vine
Rhamnus alnifolia	alderleaf buckthorn	RHAL	shrub
Rumex orbiculata	greater water dock	RUOR	herb
Sagittaria latifolia	broadleaf arrowhead	SALA	herb
Scutellaria galericulata	marsh skullcap	SCGA	herb
Sium suave	hemlock waterparsnip	SISU	herb
Viburnum nudum	withe-rod	VINU	shrub
FACW			
Arisaema triphyllum	Jack in the pulpit	ARTR	herb
Calamagrostis canadensis	bluejoint	CACA	graminoid
Carex bromoides	brome-like sedge	CABRO	graminoid
Carex brunnescens	brownish sedge	CABRU	graminoid
Carex disperma	softleaf sedge	CADI	graminoid
Carex intumescens	greater bladder sedge	CAIN	graminoid
Carex projecta	necklace sedge	CAPR	graminoid
Carex scoparia	broom sedge	CASC	graminoid
Carex tribuloides	blunt broom sedge	CATR2	graminoid

Species	Common name	Code	Growth Habit
Cinna latifolia	drooping woodreed	CILA	graminoid
Circaea alpina	small enchanter's nightshade	CIAL	herb
Coptis trifolia	threeleaf goldthread	COTR	herb
Dryopteris clintoniana	Clinton's woodfern	DRCL	fern
Dryopteris cristata	crested woodfern	DRCR	fern
Fraxinus pennsylvanica	green ash	FRPE	tree
Gaultheria hispidula	creeping snowberry	GAHI	subshrub
Ilex verticillata	common winterberry	ILVE	shrub
Impatiens capensis	jewelweed	IMCA	herb
Juncus effusus	common rush	JUEF	graminoid
Larix laricina	tamarack	LALA	tree
Lythrum salicaria	purple loosestrife	LYSA	herb
Mitella nuda	naked miterwort	MINU	herb
Onoclea sensibilis	sensitive fern	ONSE	fern
Osmunda cinnamomea	cinnamon fern	OSCI	fern
Petasites frigidus	arctic sweet coltsfoot	PEFR	herb
Poa palustris	fowl bluegrass	POPAL	graminoid
Populus balsamifera	balsam poplar	POBA	tree
Ranunculus abortivus	littleleaf buttercup	RAAB	herb
Rubus hispidus	bristly dewberry	RUHI	subshrub
Rubus pubescens	dwarf red blackberry	RUPU	subshrub
Salix discolor	pussy willow	SADI	shrub
Salix eriocephala	Missouri River willow	SAER	shrub
Scirpus cyperinus	woolgrass	SCCY	graminoid
Scutellaria lateriflora	blue skullcap	SCLA	herb
Spiraea alba	white meadowsweet	SPAL	shrub
Spiraea tomentosa	steeplebush	SPTO	shrub
Symphyotrichum lateriflorum	calico aster	SYLA	herb
Symphyotrichum puniceum	purplestem aster	SYPU	herb
Thalictrum pubescens	king of the meadow	THPU	herb
Thuja occidentalis	cedar/arborvitae	THOC	tree
Ulmus americana	American elm	ULAM	tree
Vaccinium corymbosum	highbush blueberry	VACO	shrub
Viola blanda	sweet white violet	VIBL	herb
FAC			
Abies balsamea	balsam fir	ABBA	tree
Acer rubrum	red maple	ACRU1	tree
Athyrium filix-femina	common ladyfern	ATFI	fern
Betula alleghaniensis	yellow birch	BEAL	tree
Betula populifolia	gray birch	BEPO	tree
Carex debilis	white edge sedge	CADEB	graminoid
Carex tenera	quill sedge	CATE	graminoid
Clintonia borealis	bluebead	CLBO	herb
Cornus canadensis	bunchberry dogwood	COCA	subshrub
Dalibarda repens	dewberry	DARE	herb
Dichanthelium acuminatum	tapered rosette grass	DIAC	graminoid
Dryopteris carthusiana	spinulose woodfern	DRCAR	fern
Echinocystis lobata	wild cucumber	ECLO	vine
Epilobium ciliatum	fringed willowherb	EPCI	herb

Species	Common name	Code	Growth Habit
Euthamia graminifolia	flat-top goldentop	EUGR	herb
Frangula alnus	glossy buckthorn	FRAL	shrub
Geum laciniatum	rough avens	GELA	herb
Geum laciniatum	rough avens	GELAL	herb
Geum laciniatum	rough avens	GELAT	herb
Hamamelis virginiana	American witchhazel	HAVI	shrub
Juncus tenuis	poverty rush	JUTE	graminoid
Kalmia angustifolia	sheep laurel	KAAN	shrub
Linnaea borealis	twinflower	LIBO	subshrub
Luzula acuminata	hairy woodrush	LUAC	graminoid
Lycopodium clavatum	running clubmoss	LYCL	fern
Maianthemum canadense	Canada mayflower	MACA	herb
Moehringia lateriflora	bluntleaf sandwort	MOLA	herb
Moneses uniflora	one-flowered pyrola	MOUN2	herb
Oenothera perennis	little evening primrose	OEPE	herb
Osmunda claytoniana	interrupted fern	OSCL	fern
Photinia melanocarpa	black chockberry	PHME	shrub
Poa nemoralis	wood bluegrass	PONE	graminoid
Ranunculus acris	tall buttercup	RAAC	herb
Ranunculus recurvatus	blisterwort	RARE	herb
Rubus idaeus	American red raspberry	RUID	shrub
Solanum dulcamara	climbing nightshade	SODU	vine
Solidago rugosa	wrinkleleaf goldenrod	SORU	herb
Thelypteris noveboracensis	New York fern	THNO	fern
Tiarella cordifolia	heartleaf foamflower	TICO	herb
Toxicodendron radicans	eastern poison ivy	TORA	subshrub
Trientalis borealis	starflower	TRBO	herb
Vaccinium myrtilloides	velvetleaf blueberry	VAMY	shrub
Veronica serpyllifolia	thymeleaf speedwell	VESE	herb
Viburnum dentatum	southern arrowwood	VIDE	shrub
FACU			
Acer pensylvanicum	striped maple	ACPE	tree
Acer saccharum	sugar maple	ACSA	tree
Achillea millefolium	common yarrow	ACMI	herb
Agrostis perennans	upland bentgrass	AGPE	graminoid
Anemone quinquefolia	wood anemone	ANQU	herb
Anthoxanthum odoratum	sweet vernalgrass	ANOD	graminoid
Aralia nudicaulis	wild sarsaparilla	ARNU	subshrub
Betula papyrifera	paper birch	BEPA	tree
Carex deweyana	Dewey sedge	CADEW	graminoid
Carex gracillima	graceful sedge	CAGR	graminoid
Carex normalis	greater straw sedge	CANO	graminoid
Circaea lutetiana	broadleaf enchanter's nightshade	CILU	herb
Corylus cornuta	beaked hazelnut	COCO	shrub
Cypripedium acaule	moccasin flower	CYAC	herb
Danthonia compressa	flattened oatgrass	DACO	graminoid
Dryopteris intermedia	intermediate woodfern	DRIN	fern
Dryopteris marginalis	marginal woodfern	DRMA	fern
Fagus grandifolia	American beech	FAGR	tree

Species	Common name	Code	Growth Habit
Fragaria virginiana	Virginia strawberry	FRVI	herb
Fraxinus americana	white ash	FRAM	tree
Galium triflorum	fragrant bedstraw	GATR	herb
Gaultheria procumbens	eastern teaberry	GAPR	subshrub
Gaylussacia baccata	black huckleberry	GABA	shrub
Goodyera cf. repens	rattlesnake plantain	GOOD	herb
Houstonia caerulea	azure bluet	HOCA	herb
Lonicera ×bella	showy fly honeysuckle	LOBE	shrub
Lonicera canadensis	American fly honeysuckle	LOCA	shrub
Lotus corniculatus	birdsfoot-trefoil	LOCO	herb
Luzula multiflora	common woodrush	LUMU	graminoid
Mitchella repens	partridgeberry	MIRE	subshrub
Monotropa uniflora	Indianpipe	MOUN3	herb
Ostrya virginiana	hophornbeam	OSVI	tree
Parthenocissus quinquefolia	Virginia creeper	PAQU	vine
Picea glauca	white spruce	PIGL	tree
Picea rubens	red spruce	PIRU	tree
Pinus strobus	eastern white pine	PIST	tree
Polygala paucifolia	finged polygala	POPAU	herb
Polystichum acrostichoides	Christmas fern	POAC	fern
Populus grandidentata	bigtooth aspen	POGR	tree
Potentilla simplex	common cinquefoil	POSI	herb
Prunella vulgaris	common selfheal	PRVU	herb
Prunus pensylvanica	pin cherry	PRPE	tree
Prunus serotina	black cherry	PRSE	tree
Prunus virginiana	chokecherry	PRVI	tree
Pteridium aquilinum	western brackenfern	PTAQ	fern
Quercus rubra	northern red oak	QURU	tree
Rosa multiflora	multiflora rose	ROMU	shrub
Solidago canadensis	Canada goldenrod	SOCA	herb
Taraxacum officinale	common dandelion	TAOF	herb
Trifolium repens	white clover	TRRE	herb
Trillium erectum	red trillium	TRER	herb
Tsuga canadensis	eastern hemlock	TSCA	tree
Uvularia sessilifolia	sessileleaf bellwort	UVSE	herb
Vaccinium angustifolium	lowbush blueberry	VAAN	shrub
Viola pubescens	downy yellow violet	VIPU	herb
UPL			
Gymnocarpium dryopteris	western oakfern	GYDR	fern
Rhamnus cathartica	common buckthorn	RHCA	shrub
Viburnum acerifolium	mapleleaf viburnum	VIAC	shrub

Data from http://plants.usda.gov, for the Northeast Region (CT, DE, KY, MA, MD, ME, NH, NJ, NY, OH, PA, RI, VA, VT, WV).

BIOGRAPHY OF THE AUTHOR

Elizabeth Bryce was born on November 14, 1977. Liz went to Temple University in Philadelphia, PA, with the help of an Outstanding Achievement Scholarship. Though initially undecided on a major, she felt passionate about conservation issues, and was drawn to classes in ecology and earth sciences. Liz gravitated toward the newly formed Environmental Studies program at Temple, majored in Environmental Sciences with a minor in Biology, and graduated in 2003.

After college, Liz worked for the Green Mountain Club as a summit caretaker on Mount Mansfield in Vermont, and as a campground environmental educator in Sequoia National Forest in California. But it was in volunteering for a post-doctoral scientist at the Academy of Natural Sciences that she was inspired to begin a path toward a career in plant ecology.

Liz resides in Orono, Maine with her fiancé Matthew Olson. She is a candidate for the Master of Science degree in Ecology and Environmental Science at the University of Maine in August, 2009.