Nonnative invasive plants in the Penobscot Experimental Forest in Maine, USA: Influence of site, silviculture, and land use history1,2

Article *in* The Journal of the Torrey Botanical Society · January 2012

DOI: 10.3159/TORREY-D-10-00019.1

4 authors, including:

Elizabeth Olson

Laura Kenefic
Northern Research Station, USDA Forest Service

Alison Dibble
University of Maine

Journal of the Torrey Botanical Society 138(4), 2011, pp. 453–464

Nonnative invasive plants in the Penobscot Experimental Forest in Maine, USA: Influence of site, silviculture, and land use history[1,2]

Elizabeth Olson[3]
University of Maine, School of Forest Resources, Orono, ME 04469-5755

Laura S. Kenefic
U.S. Forest Service, Northern Research Station, Bradley, ME 04411

Alison C. Dibble
Stewards LLC, Brooklin, ME 04616

John C. Brissette
U.S. Forest Service, Northern Research Station, Durham, NH 03824

OLSON, E. (University of Maine, School of Forest Resources, Orono, Maine 04469-5755), L.S. KENEFIC (U.S. Forest Service, Northern Research Station, Bradley, ME 04411), A.C. DIBBLE (Stewards LLC, P.O. Box 321, Brooklin, ME 04616), and J.C. BRISSETTE (U.S. Forest Service, Northern Research Station, Durham, NH 03824). Nonnative invasive plants in the Penobscot Experimental Forest in Maine, USA: influence of site, silviculture, and land use history. J. Torrey Bot. Soc. 138: 453–464. 2011.—We investigated the occurrence of nonnative invasive plants on approximately 175 ha comprising a long-term, 60-year-old U.S. Forest Service silvicultural experiment and old-field stands in the Penobscot Experimental Forest (PEF) in central Maine. Stands in the silvicultural experiment were never cleared for agriculture, but have been repeatedly partially cut. Our objectives were to determine the extent of nonnative invasive plant populations in the PEF, and to relate invasive plant abundance and distribution to management history and environmental factors (overstory composition and basal area, canopy openness, and soil characteristics). We found ten invasive plant species in the study area. Very few occurrences of these were in the silvicultural experiment; where present, invasive plants there appear to be associated with proximity to seed source, and a greater degree of recreational or silvicultural disturbance. Ordination showed that the environmental variables which were associated with invasive species in the old fields were not associated with the presence of invasives in the silvicultural treatments. In the old-field stands, invasive plant cover was positively related to exposed mineral soil and negatively related to organic horizon thickness; invasive plant richness was negatively related to hardwood litter cover. *Frangula alnus* was the most frequent invasive plant species in both the old-field stands and silvicultural experiment; its distribution was not correlated with observed environmental variables. Control measures are recommended to prevent further encroachment of invasive plants into the silvicultural experiment.

Key words: U.S. Forest Service experimental forests, invasive plant, old-field successional forest, *Frangula alnus*, *Lonicera*.

Nonnative invasive plants compromise the integrity of natural and managed ecosystems. The expansion of invasive plants is often facilitated by disturbances (Elton 1958), such as agriculture and forest harvesting, which reduce native plant populations and give nonnative invasive species a competitive advantage (Byers 2002). When such an expansion occurs, it often causes a profound shift in the structure, composition, and function of forest ecosystems (Webster et al. 2006).

Woody invasive plants can cause considerable harm in forests managed for timber resources. Disturbance 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 due to increased light, forest floor disturbance, soil compaction, reduced drainage, and changes in soil nutrient content and organic matter (Lundgren et al. 2004). Invasive woody vines often overtop (McNab and Meeker 1987, Niering 1998) and girdle trees (Greenberg et al.

[1] Funding was provided by the Northeastern States Research Cooperative (Theme 1) and the University of Maine, School of Forest Resources.

[2] We thank field workers Betsy Dionne, Catherine Amy Kropp, Matt Noone, and Mike Puleo. We appreciate help and support from Christopher S. Campbell, Arthur Haines, and the Josselyn Botanical Society. We are grateful for assistance from Rick Dionne and Tim Stone.

[3] Author for correspondence. Email: elizabetholson77@gmail.com.

2001). Nonnative invasive shrubs can form dense thickets that prevent tree regeneration (D'Appollonio 2006) through allelopathy (Madritch and Lindroth 2009) and resource competition (Frappier et al. 2003a, Miller and Gorchov 2004). Such plants 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 (Silveri et al. 2001). Invasive shrubs of concern in the Northeast include *Frangula alnus* P. Mill., *Lonicera* spp., and *Berberis thunbergii* DC. *Celastrus orbibulata* Thunb. is a regionally problematic invasive woody vine (Silander and Klepeis 1999).

Nonnative invasive plants have spread into a variety of forest types throughout New England. In New Hampshire, *Frangula alnus* has been associated with reduced woody seedling density, herb cover, and species richness (Frappier et al. 2003a). Woods (1993) reported that *Lonicera tatarica* L. was associated with reduced tree seedling density in four forests in Vermont and Massachusetts. Silveri et al. (2001) reported that logging operations contributed to the spread of *Celastrus orbiculata* in a mesic *Quercus*-conifer forest in Massachusetts.

Published research of terrestrial nonnative invasive plants in Maine has focused on relationships to fire, wildlife, and distribution. For example, Dibble et al. (2007) investigated ways in which invasive plants alter fuels in the Northeastern U.S., including Maine sites, and found wide variability in the combustion properties of invasive plants versus native counterparts. Dibble et al. (2008) included Maine in a review of invasive plants and fire in natural communities of the Northeastern U.S. Drummond (2005) compared wild bird selection of fruits – native versus those of invasive plants – in central Maine. Barton et al. (2004) investigated invasive plants around Farmington, Maine, but did not sample forest interiors, stating that invasive plants were rarely found in the forests of western Maine. *Berberis thunbergii* was previously believed to be limited from becoming invasive in northern New England by low temperature tolerance limits (Silander and Klepeis 1999), yet it has infested many forests in southern and coastal Maine (D' Appollonio 2006, Dibble and Rees 2005). *Frangula alnus* is common in the mid- and understory in mixed-conifer forests in east-central Maine (Bangor Land Trust 2009, Orono Land Trust 2011).

Since the 1920s, one of the most important sources of information about the management of northeastern forests has been the U.S. Forest Service experimental forests (Berven et al. in press). These forests, which are established by the Chief of the Forest Service, provide long-term data about the responses of ecosystems to management and natural disturbances (Adams et al. 2008). The Penobscot Experimental Forest (PEF) in east-central Maine is one of 22 experimental forests in the Northeast and Lake States, and provides critical information about the long-term dynamics of managed and unmanaged mixed northern conifers (Sendak et al. 2003).

In recent years, scientists at the PEF have observed populations of invasive plants in successional forest stands that were formerly in agriculture. Preliminary surveys suggested that there are vigorous populations of nonnative invasive plants in the PEF, including *Frangula alnus* and *Lonicera* spp. (shrub honeysuckles; the invasive vine *Lonicera japonica* Thunb. is not known to occur in the PEF), as well as small populations of *Lythrum salicaria* L., *Celastrus orbiculata*, and *Berberis thunbergii* (unpublished data on file, U.S. Forest Service). Past inventories of trees and shrubs in the PEF included observations of *B. thunbergii*, *F. alnus*, *Solanum dulcamara* L., and *Lonicera xylosteum* L. (Safford et al. 1969); a small herbarium of plants collected in the 1960s contains specimens of these with notes that they were found near the entrance to the PEF and at Leonard's Mills (see study site description below). Yet the extent of nonnative invasive populations or possible relationships to management activities or environmental factors had not been quantified. Moreover, it was not known to what extent these species had invaded the long-term Forest Service silvicultural study at the PEF. Silvicultural disturbances may increase susceptibility to invasive plant establishment because the new canopy openings provide opportunity for early-colonizing, wide-niche species through increased light and reduced competition (Silveri et al. 2001).

Objectives of this study were to investigate the extent of nonnative invasive plant populations in the PEF, and to relate invasive plant abundance and distribution to management history and environmental factors. We quantified factors that have been associated with invasive plants such as soil drainage (Robertson et al. 1994, Davis et al. 2000, McDonald et al. 2008), canopy openness, and overstory composition (e.g. total basal area, basal area by species, percent hardwood basal area, and percent softwood basal area) (Robertson et al. 1994). We use "invasive" to describe nonnative plants that have been classified as such by the Invasive Plant Atlas of New England (IPANE) (Mehrhoff et al. 2003). Species nomenclature follows the *Flora of Maine* (Haines and Vining 1998).

Materials and Methods. STUDY SITE. All research was conducted at the PEF, a 1,540-ha forest located in Bradley and Eddington, Maine (44°52′44″N, −68°39′12″W), approximately 16 km north of Bangor, Maine. The PEF is in the Acadian Forest, which lies 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 *Picea rubens* Sarg., *Abies balsamea* (L.) Mill., *Tsuga canadensis* (L.) Carr., *Thuja occidentalis* L., and *Pinus strobus* L. The most common hardwoods are *Acer rubrum* L., *Betula papyrifera* Marsh., *Betula populifolia* Marsh., *Populus tremuloides* Michx., and *Populus grandidentata* Michx. (Sendak et al. 2003). The soils in the PEF are predominantly Wisconsin glacial till derived from fine-grained sedimentary rock (Safford et al. 1969). The majority of the study area for the present research is located on poorly drained Monarda and Burnham loams and silt loams, and moderately well-drained Howland loams and sandy loams (USDA, SCS 1963; Sendak et al. 2003).

Although the history of the PEF is not completely known, some partial cutting occurred in the forest between the late 1700s and early 1900s. A long-term silvicultural experiment encompassing approximately 169 ha was initiated in the PEF by the Forest Service between 1952 and 1957. Stand-level silvicultural treatments are twice-replicated, with each replicate (called a "compartment") averaging 8 ha each. Most compartments in the silvicultural experiment have received repeated partial harvests. Treatments include the selection system with five-, ten-, and twenty-year cutting cycles, the uniform shelterwood system with two- and three-stage overstory removal, precommercial thinning (in the three-stage shelterwood), fixed and modified (flexible) diameter-limit harvests, and an unregulated harvest (commercial clearcut). The PEF also includes reference stands that have received no harvesting or silvicultural activities for over 60 years. A detailed account of silvicultural treatments and outcomes can be found in Sendak et al. (2003).

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 Road (Fig. 1). Soils show signs of cultivation and grazing; aerial photographs from 1956 show that this area was cleared of trees; and maps made as recently as 1980 labeled this area 'Field.' The old fields have developed into forest stands with an overstory dominated by *Populus grandidentata*, *Betula populifolia*, *Acer rubrum*, *Malus sylvestris* P. Mill., and *Prunus* spp. The shrub layer is dominated by several nonnative shrubs, including *Frangula alnus, Lonicera morrowii* A. Gray and *L.* ×*bella* Zabel. The old fields of the PEF were not included in the long-term silvicultural experiment and have no historical stand inventory data.

Leonard's Mills, a reconstructed eighteenth-century logging settlement owned and operated by the Maine Forest and Logging Museum (MFLM), is located on property within the PEF. Each year, approximately 5,000 people visit to learn about Maine's forest and logging history (MFLM 2007). Self-guided nature trails lead from the Leonard's Mills museum grounds through the Forest Service's nearby reference stands. *Frangula alnus* is prevalent on the property, and *Lonicera* spp. appear to have been introduced for "conservation wildlife plantings" or ornamental purposes on the museum grounds.

DATA COLLECTION. Vegetation in the PEF was sampled during the summers of 2006 and 2007. We inventoried 317 plots in 22 forest stands representing 10 silvicultural treatments (including the unharvested references) and the old fields (Table 1). The compartments in the silvicultural experiment were inventoried using permanent sample plots: 0.08-, 0.02-, and

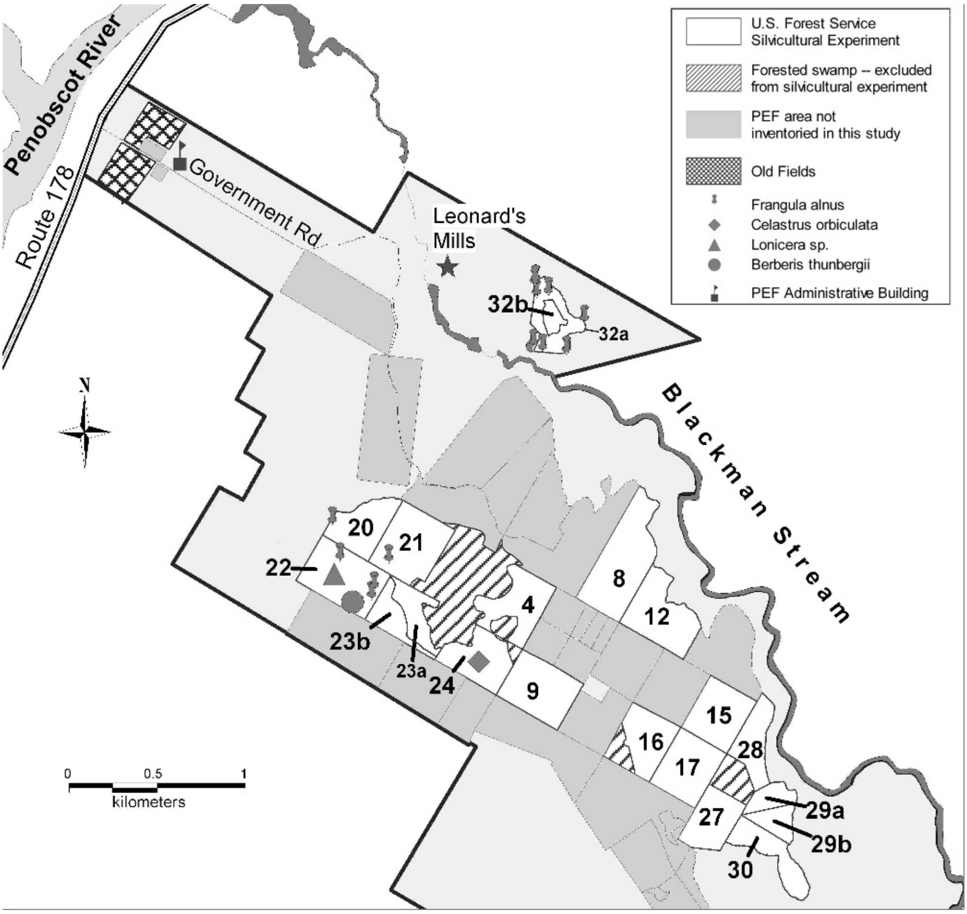

FIG. 1. Map of invasive plant locations in the silvicultural experiment.

0.008-ha nested circular plots used by the Forest Service for scheduled inventories. Understory plant measurements were obtained from two 4.05-m^2 subplots within each permanent sample plot.

Plot layout in the old-field stands was modeled after the permanent sample plots in the silvicultural experiment. We set up three transects in each of the two old-field stands, then established a total of 22 plots. Distances between plot centers were chosen using a random number generator, constrained by observed distances between permanent sample plots (i.e., no less than 30 m apart).

Percent ground cover was estimated for all herbaceous species and also for woody species $\leq$0.6 meters tall using the cover scale: $<$5%, 5 to 25%, 26 to 50%, 51 to 75%, and 76 to 100%. Basal area (BA, m^2ha^{-1}) of trees $>$1.3 cm in diameter at breast height (DBH, 1.37 m) was obtained from the most recent PEF inventory data. In the old fields, overstory basal area and species composition were measured at each plot center using a 10-BAF prism; results were converted to metric units.

So that vegetation data could be related to possible explanatory features, we estimated the percent cover of exposed mineral soil and hardwood and conifer litter at each subplot, using the same cover scale as above. To determine soil drainage (Briggs 1994), one soil pit was excavated at each plot; thickness of the organic horizon and depth to redoximorphic features (mottling) were measured to the nearest 0.5 cm.

As a surrogate for the measurement of light in the understory, a single 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 positioned on a tripod 0.6 meters above the forest floor. Gap Light Analyzer (Frazer et al.

Table 1. Silvicultural treatments and old fields, total number of harvests for each silvicultural treatment since 1950, and percent of basal area removed in the most recent harvest. [1]Portions of compartment 23a were commercially thinned in 2002; the replicate (29a) has not yet received this treatment. [2] The references were not harvested.

Treatment Name	Compartment number	Total number of harvests	Year of last harvest	% basal area removed	Number of Plots
Unregulated Harvest	22	2	1988	82.5	20
Unregulated Harvest	8	2	1983	89.4	21
Fixed Diameter-limit	15	3	2001	59.3	20
Fixed Diameter-limit	4	3	1994	60.3	13
Modified Diameter-limit	28	3	1997	21.1	19
Modified Diameter-limit	24	3	1996	35.9	12
20-yr Selection	27	3	1997	16.9	23
20-yr Selection	17	3	1994	35.0	14
10-yr Selection	20	5	1998	7.9	21
10-yr Selection	12	5	1994	15.0	14
5-yr Selection	16	10	2001	9.0	20
5-yr Selection	9	10	1998	6.9	13
2-stage Shelterwood	21	2	1967	70.0	10
2-stage Shelterwood	30	2	1967	84.5	20
3-stage Shelterwood with precommercial thinning	23a	5	2002	6.4	10
3-stage Shelterwood with precommercial thinning	29a	4	1983	77.8	8
3-stage Shelterwood	29b	3	1974	94.7	8
3-stage Shelterwood	23b	3	1972	94.7	9
Reference	32a	–	–	–	10
Reference	32b	–	–	–	10
Old Field	–	–	–	–	8
Old Field	–	–	–	–	14

1999) software was used to obtain a value for percent canopy openness.

To obtain a more complete understanding of the extent of invasive species in the PEF silvicultural experiment, we recorded the presence of invasive species both within the permanent sample plots and elsewhere in the compartments; GPS coordinates were obtained for the location of each invasive plant. A meander survey was conducted to ascertain the full extent of invasive species populations in the areas adjacent to the old fields. Workers walked systematically through the old fields and neighboring forest on the PEF recording GPS coordinates at the locations of invasive plants. Using GIS software (MapInfo 2007), we mapped the approximate perimeter of each population of the most abundant invasive species.

Analyses. Cover class values for each plant species in subplots were converted to the cover class midpoint for each abundance level and averaged into a mean percent cover by plot (Archer et al. 2007). The environmental variables were also averaged over the two subplots.

We used non-metric multidimensional scaling (NMS) ordination in PC-ORD version 4.07 (McCune and Mefford 1999), using all plots in the silvicultural experiment and the old fields, to examine similarities among plots that contained nonnative invasive plants. We also performed NMS analysis using data from the old fields alone to more closely examine relationships between invasive species and environmental variables; data from the silvicultural experiment were not included because invasive plants there were too infrequent. Sorensen's distance measure was used because it retains sensitivity in heterogeneous datasets and gives less weight to outliers (McCune and Mefford 1999).

Species or species groups with low frequency (fewer than three plots) were omitted from the NMS ordinations because they are not likely to be accurately placed in ordination space (McGarigal et al. 2000). Therefore, four invasive species were not included in the ordination: *Lythrum salicaria, Rosa multiflora, Solanum dulcamara* and *Valeriana officinalis* L. The environmental variables included were: canopy openness, depth to mottling, thickness of the organic horizon, mineral soil cover, softwood and hardwood litter cover, total basal area, percent hardwood basal area,

Table 2. Nonnative invasive species recorded in old-field plots. Frequency is the percent of plots (22 plots in N = 2 old-field stands) in which each species was recorded. Area is the approximate extent of each species' population; area was not calculated for all species.

Species	Growth habit	Frequency (±SD)	Area (hectares)
Frangula alnus P. Mill.	shrub	0.89 ± 0.15	32.63
Lonicera spp. (*L. morrowii* A. Gray and *L. xbella* Zabel)	shrub	0.52 ± 0.38	11.59
Celastrus orbiculata Thunb.	vine	0.35 ± 0.32	7.36
Rhamnus cathartica L.	shrub	0.23 ± 0.03	4.40
Acer platanoides L.	tree	0.16 ± 0.13	no data
Solanum dulcamara L.	vine	0.10 ± 0.04	no data
Lythrum salicaria L.	herb	0.07 ± 0.10	no data
Rosa multiflora Thunb. *ex* Murr.	shrub	0.06 ± 0.09	1.30
Valeriana officinalis L.	herb	0.04 ± 0.05	no data

percent softwood basal area, and basal area by species for trees >1.3 cm DBH.

Spearman rank correlation was used to investigate the relationships among total invasive species richness, total invasive species cover, and environmental variables in the old-field stands. The percent cover of invasive species that occurred in greater than 25% of the old-field plots was also used in the correlation analysis; these were *Frangula alnus*, *Lonicera* spp., *Celastrus orbiculata*, and *Rhamnus cathartica*. Correlation tests were carried out using the R statistical package (R 2007).

Results. SILVICULTURAL EXPERIMENT. The understory vegetation in the silvicultural experiment was typical of the Acadian Forest (Bryce 2009), and revealed few occurrences of invasive species (Fig. 1). *Frangula alnus* was found in five plots in four treatments: the unregulated harvest, 10-year selection, two-stage shelterwood, and reference. *Lonicera* sp. was found in one plot in the unregulated harvest. Meander surveys revealed nine additional *F. alnus* seedlings around the perimeter of the reference, one seedling of *Celastrus orbiculata* in the modified diameter-limit, and one *Berberis thunbergii* shrub in the unregulated harvest. Inspection of the map of invasive plants in the silvicultural experiment (Fig. 1) suggests that their occurrence may relate to proximity to seed source (i.e., the old fields and Leonard's Mills) and/or disturbance from harvesting or public trail use. All invasive plants were seedlings less than 0.5 m tall except for the *B. thunbergii* which was 2 m tall.

OLD FIELDS. Nine invasive plant species were found in the old-field plots (Table 2). *Frangula alnus* and *Lonicera* spp. (shrub honeysuckles: *L. morrowii* and *L. xbella* were both identified) were the most frequent invasive species found in the old fields; they occurred in 89% and 52% of plots, respectively. The invasive vine *Celastrus orbiculata* was found in 35% of plots.

The meander survey of the old-field stands and adjacent forest yielded data from which we created a map of the approximate perimeters of the invasive plant populations (Fig. 2). *Frangula alnus* occupied the largest area (Table 2). *Lonicera* spp. occupied the second largest area; often the shrubs had grown into tall, dense thickets. *Celastrus orbiculata* was seen occasionally and had often climbed high into the canopy. *Rosa multiflora* and *Lythrum salicaria* were also present but infrequent. One large (approx. 2-m tall) *R. multiflora* shrub was found, but all other *R. multiflora* seedlings were less than 0.3-m tall. *L. salicaria* occurred only as scattered individuals along a stream that winds through the southwest section of the old fields.

NON-METRIC MULTIDIMENSIONAL SCALING. Using all plots in the silvicultural experiment and in the old fields (n = 317), a low stress (19.1), two-dimensional solution was found which described 81.8% of the dataset variation (Fig. 3). Plots in the silvicultural experiment were grouped in the upper portion of the biplot, regardless of whether or not they contained invasive plants. These plots were characterized by greater total BA, softwood BA, and softwood litter cover. Old-field plots were grouped in the lower right section of this biplot, and were characterized by greater hardwood BA and exposed mineral soil. Treatment type was the most important factor structuring the ordination. One old-field plot did not contain any invasive plants; this plot

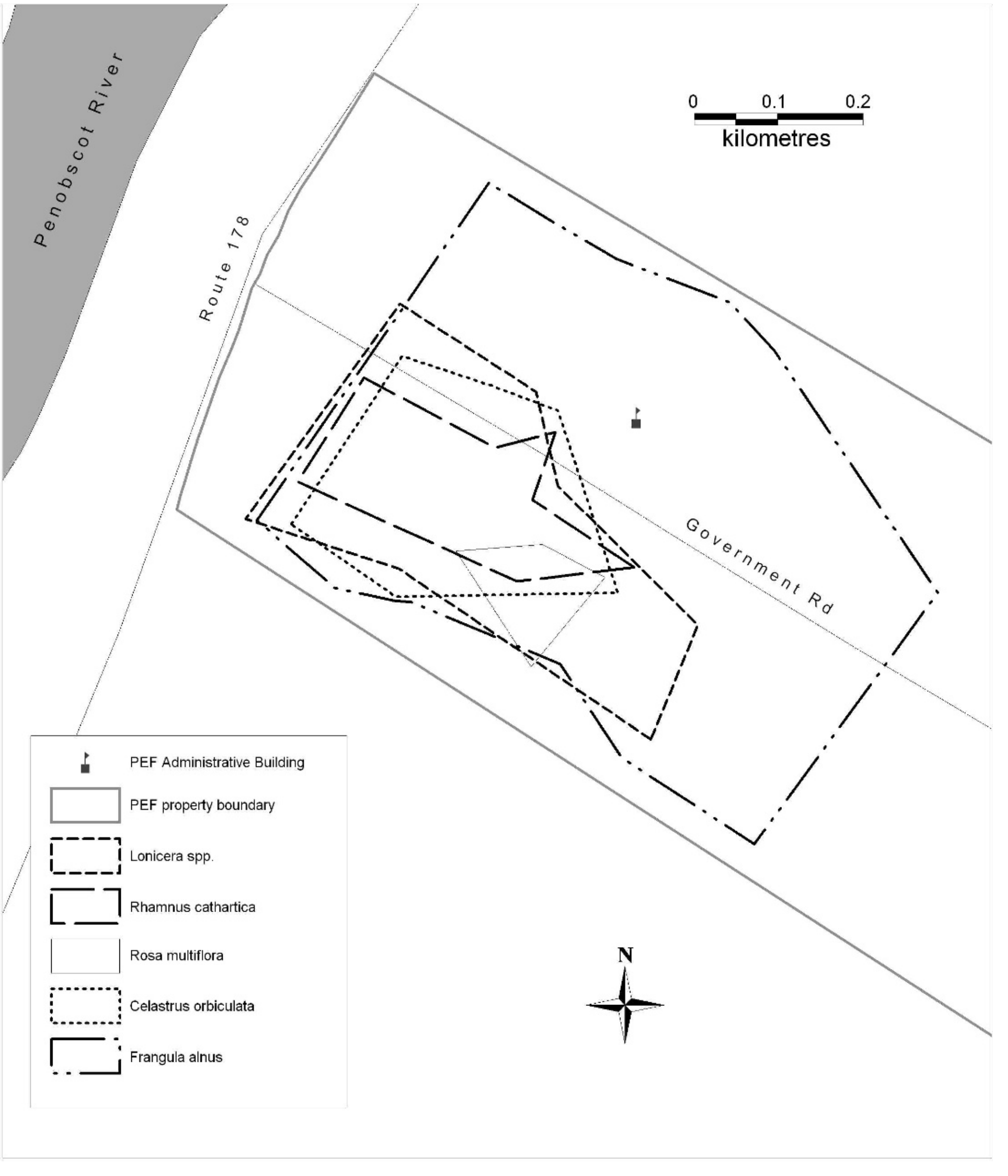

FIG. 2. Map of the old-field forest stands showing approximate range of the most abundant nonnative invasive plant populations.

was grouped with the other old-field plots (Fig. 3b). Plots in the silvicultural experiment that contained invasive species did not group with the old-field plots.

NMS ordination using data from the old-field plots (n = 22) resulted in a low stress (10.2), two-dimensional solution representing 93.1% of the dataset variation (Fig. 4). Plots from the silvicultural experiment were excluded from this portion of the analysis due to too few observations of invasive plants. *Lonicera* spp. and *Celastrus orbiculata* were located in the upper left section of the biplot. This area of the biplot represents portions of the old-field stands where mineral soil cover and the percent basal area of hardwoods were greatest. *Acer platanoides* is located on the lower right of the biplot; here, litter cover and organic

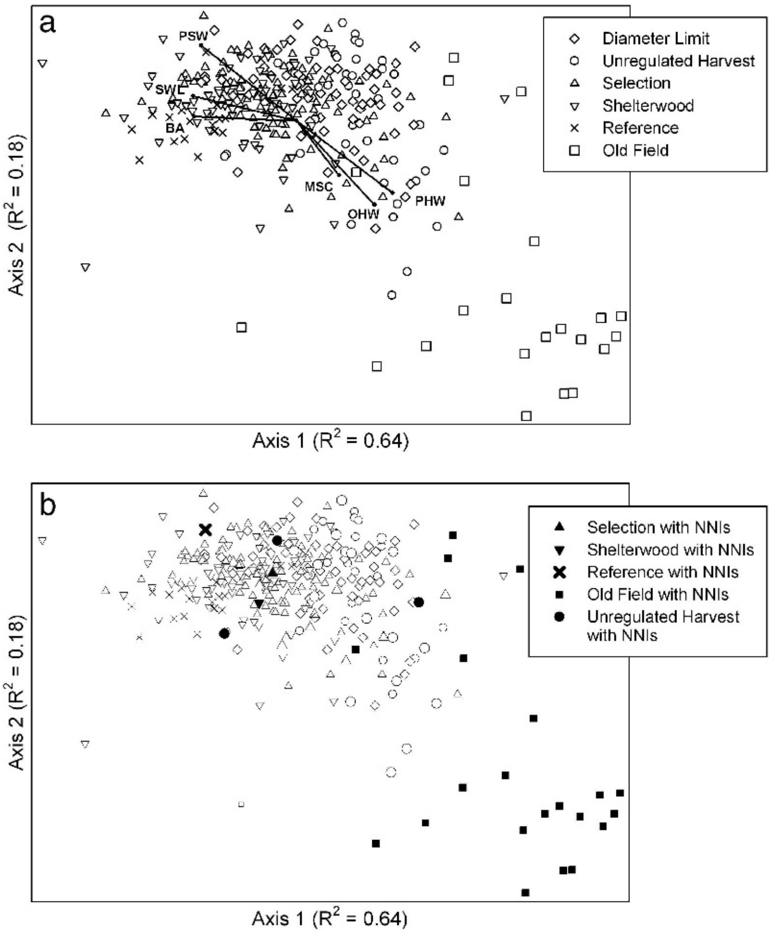

FIG. 3. NMS ordination of old fields and silvicultural experiment; a) the vectors designate the important environmental variables; BA, total basal area; PSW, percent softwood basal area; SWL, softwood litter cover; MSC, mineral soil cover; PHW, percent hardwood basal area; OHW, hardwoods basal area, and b) the boldface symbols are the plots in which nonnative species occurred.

horizon thickness are greatest, and basal area is dominated by conifers. *Frangula alnus* and *Rhamnus cathartica* were located at the center of the biplot, indicating that they were not associated with any of the measured environmental variables (Fig. 4).

CORRELATION. Spearman correlation analysis of the old-field data was similar to the ordination results. Canopy openness and soil drainage were not important environmental variables explaining the presence of invasive plants in the old fields in the PEF. Three variables describing the forest floor – organic horizon thickness, hardwood litter cover, and mineral soil cover – were associated with invasive plant richness and cover. Invasive plant richness was negatively correlated with hardwood litter; invasive plant cover was negatively correlated with organic horizon thickness and positively correlated with exposed mineral soil (Table 3). The percent cover of *Frangula alnus* was not strongly correlated with any of the observed environmental variables, though it was somewhat positively correlated with BA (Table 3).

Discussion. Invasive plants were abundant in the PEF old-field stands, but were uncommon in the silvicultural experiment. Our findings are consistent with those of Jenkins and Parker (2000) who found more nonnative plants on abandoned agricultural land than in silvicultural treatment areas. Despite a dense local population of invasive plants, few were

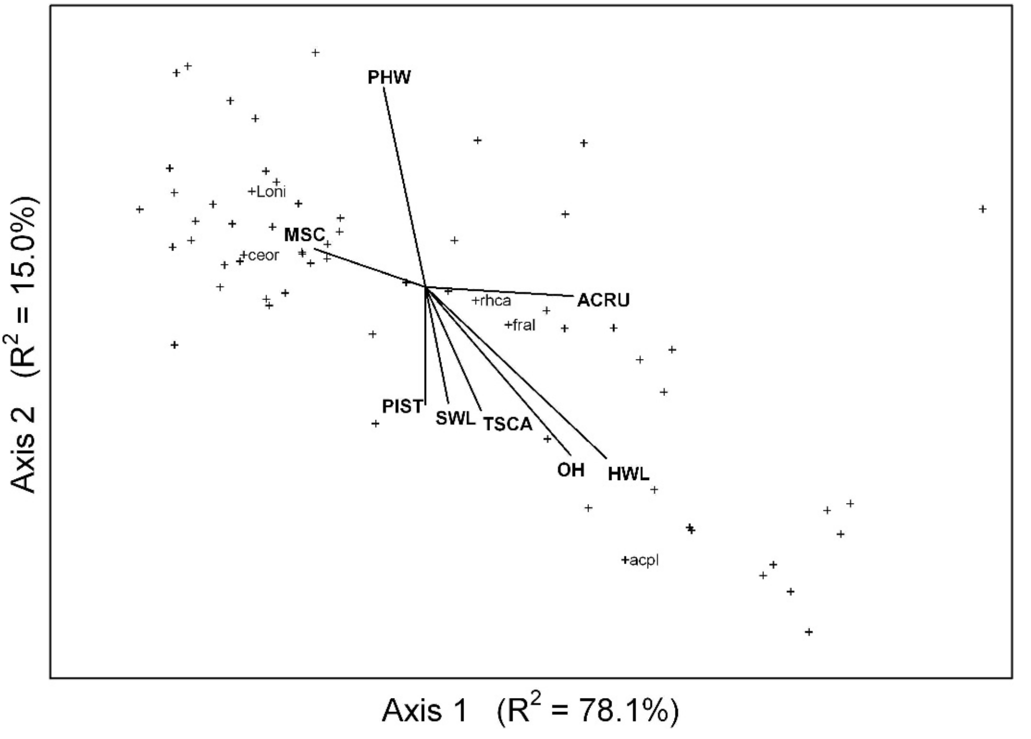

FIG. 4. NMS results. Environmental variables: PHW, percent hardwood basal area; PIST, *Pinus strobus* basal area; TSCA, *Tsuga canadensis* basal area; ACRU, *Acer rubrum* basal area; MSC, mineral soil cover; OH, organic horizon thickness; HWL, hardwood litter cover; SWL, softwood litter cover. Nonnative invasive species: acpl, *Acer platanoides*; ceor, *Celastrus orbiculata*; fral, *Frangula alnus*; Loni, *Lonicera* spp.; rhca, *Rhamnus cathartica*.

found in the silvicultural experiment of the PEF. We did not find evidence that silvicultural experiment plots harboring invasive seedlings were similar in environmental conditions to those in the old-field stands. Instead, the current distribution of invasive plants within the silvicultural experiment of the PEF appear to be related to proximity to seed source or a higher degree of disturbance in the form of harvesting or public trail use. Many of the occurrences of invasive species in the silvicultural experiment coincided with skid trails (personal observation). The interaction of canopy disturbance and propagule pressure has been shown to significantly increase invasibility (Eschtruth and Battles 2009).

In the old-field stands, invasive plants were positively associated with exposed mineral soil, and negatively associated with hardwood leaf litter and a thick organic horizon. 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.

The areas of the silvicultural experiment that had the highest abundance of invasive plant seedlings were the references (compartments 32a and 32b) and one compartment of the unregulated harvest (compartment 22). Compartment 22 had more invasive plants than other harvested compartments. Since 1950 it has been harvested twice as an unregulated harvest, or commercial clearcut. This is one of the most intense harvesting treatments in the PEF; approximately 85% of the basal area was removed from compartment 22 during the most recent treatment in 1988. Compartment 22 is also closer to the old fields than most other treatment areas that we sampled. 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.

Table 3. Results of Spearman correlation analysis. Relationships between richness and cover of invasive species, and environmental variables measured in 22 plots in the old fields. NNI rich, richness of nonnative invasive plants; NNI cover, percent cover of nonnative invasive plants; FRAL, *Frangula alnus*; LONIC, *Lonicera* spp.; CEOR, *Celastrus orbiculata*; RHCA, *Rhamnus cathartica*.

	NNI rich	NNI cover	FRAL	LONIC	CEOR	RHCA
Hardwood litter	**−0.433**	−0.274	0.236	**−0.436**	−0.209	0.077
(% cover)	***P* = 0.044**	*P* = 0.216	*P* = 0.289	***P* = 0.042**	*P* = 0.349	*P* = 0.731
Mineral Soil	0.329	**0.540**	−0.084	**0.437**	0.203	−0.291
(% cover)	*P* = 0.135	***P* = 0.01**	*P* = 0.708	***P* = 0.042**	*P* = 0.365	*P* = 0.189
O-horizon	−0.321	**−0.476**	0.070	**−0.469**	**−0.471**	−0.046
(cm depth)	*P* = 0.145	***P* = 0.025**	*P* = 0.756	***P* = 0.028**	***P* = 0.027**	*P* = 0.838
Total Basal Area	−0.109	−0.027	0.364	−0.354	0.111	0.282
	P = 0.627	*P* = 0.904	*P* = 0.096	*P* = 0.105	*P* = 0.621	*P* = 0.203
Hardwood Basal	0.188	0.176	−0.164	0.351	0.180	−0.193
Area (% of total)	*P* = 0.400	*P* = 0.433	*P* = 0.466	*P* = 0.109	*P* = 0.421	*P* = 0.389
Canopy Openness	−0.186	−0.003	−0.123	−0.149	0.143	−0.286
	P = 0.406	*P* = 0.988	*P* = 0.583	*P* = 0.508	*P* = 0.523	*P* = 0.196
Depth to Mottling	0.393	0.317	0.107	0.181	0.253	0.315
	P = 0.070	*P* = 0.151	*P* = 0.634	*P* = 0.418	*P* = 0.255	*P* = 0.153

Compartment 20 – a selection treatment with a 10-year cutting cycle – borders compartment 22 and is also close to the old fields, but only one invasive plant seedling was found there. 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 likely resulted in fewer resources available for new plants to establish. These findings are consistent with those of Jenkins and Parker (2000), who found that nonnative cover decreased with diminishing silvicultural disturbance.

Frangula alnus seedlings were found in seven locations in the unmanaged reference stands. Relatively undisturbed forests usually contain fewer invasive plants than more heavily disturbed areas (Selmants and Knight 2003). However, the references are in close proximity to invasive seed sources of *Lonicera* spp. and *Frangula alnus* at the Leonard's Mills Museum site. Walking trails leading from the museum grounds through the reference stands 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).

Ten nonnative invasive plant species were found in the old-field stands; however, none have expanded into the silvicultural experiment beyond a few scattered seedlings. *Frangula alnus* was the most frequent invasive species in the old fields and the silvicultural experiment, and was seen along the trail that leads from Leonard's Mills toward the references. It has established in a wide range of overstory and forest floor conditions in the PEF. *Lonicera* seems to be more limited in its spread and may require exposed mineral soil for successful germination; this is suggested by its positive correlations with percent cover of mineral soil in the old-field stands.

There may be a long lag time from the introduction of a species to it becoming invasive (Frappier et al. 2003b). The initial stage of an encroachment is characterized by low abundance; therefore, when trying to predict the invasive potential of any species in a specific locale, observed patterns are often not reliable estimates of future abundance (Hunter and Mattice 2002). Observations since measurements were collected for this study suggest that *Lythrum salicaria* and *Valeriana officinalis* populations are expanding in drainage ditches along forest roads in the PEF. Invasive plant control measures should be taken to protect the PEF and its mission to provide examples of silvicultural practices and outcomes in the Acadian Forest.

Conclusions. A history of agriculture appears to be an important factor in nonnative invasive plant species abundance in the PEF. Invasive plants were abundant in old-field stands, yet few were found in the silvicultural experiment. Presence of invasive plants in the silvicultural experiment plots was not associated with the measured environmental variables. Instead, invasive plant presence there may be the result of disturbances of harvesting and highly trafficked public trails and roads.

This indicates that the managed forest contains many sites equally suitable for establishment, and continued disturbances, both natural and associated with harvesting, will likely promote the spread of invasive plants in the future. Invasive species have not influenced the PEF long-term silvicultural experiment at this time, yet the proximity to thriving populations of invasive species indicates that a plan to address the potential expansion of invasive plants may be necessary in the near future. If the invasive plants are ignored, they could eventually impact forest regeneration and the interpretation of results of the long-term experiments.

Literature Cited

Adams, M. B., L. Loughry, and L. Plaugher. 2008. Experimental Forests and Ranges of the USDA Forest Service. General Technical Report NE-321 Revised. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 178 p.

Archer, J. K., D. L. Miller, and G. W. Tanner. 2007. Changes in understory vegetation and soil characteristics following silvicultural activities in a southeastern mixed pine forest. J. Torr. Bot. Soc. 134(4): 489–504.

Bangor Land Trust. 2009. Bangor Land Trust Newsletter. Retrieved June 1, 2011 from Bangor Land Trust. <http://www.bangorlandtrust.org/assets/publication_summer09.pdf>

Barton, A. M., L. B. Brewster, A. N. Cox, and N. K. Prentiss. 2004. Non-indigenous woody invasive plants in a rural New England town. Biol. Invas. 6: 205–211.

Berven, K., L. Kenefic, A. Weiskittel, M. Twery, and J. Wilson. In press. The lost research of early northeastern spruce-fir experimental forests: A tale of lost opportunities. In: Irland, L., ed., Long-term silvicultural and ecological studies, volume 2. Yale University, Global Institute of Sustainable Forestry.

Briggs, R. D. 1994. Site classification field guide. Cooperative Forestry Research Unit Technical Note 6, Maine Agricultural and Forest Experiment Station Misc. Pub. 724. Univ. of Maine, Orono, ME. 15 p.

Brothers, T. S. and A. Spingarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conserv. Biol. 6(1): 91–100.

Bryce, E. 2009. 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. M.S. thesis. University of Maine, Orono, ME. 123 p.

Byers, J. E. 2002. Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos 97(3): 449–458.

D'Appollonio, J. 2006. Regeneration strategies of Japanese barberry (*Berberis thunbergii* DC.) in coastal forests of Maine. M.S. thesis. University of Maine, Orono, ME. 93 p.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. J. Ecology 88: 528–534.

Dibble, A. C. and C. A. Rees. 2005. Does the lack of reference ecosystems limit our science? A case study in nonnnative invasive plants as forest fuels. J. Forestry. 103(7): 329–338.

Dibble, A. C., K. Zouhar, and J. Kapler-Smith. 2008. Chapter 5. Northeastern bioregion. In: Zouhar, K., Smith, J. Kapler, Brooks, M. L., and Sutherland, S. [eds.], Wildland fire in ecosystems: fire and nonnative invasive plants. Gen. Tech. Rep. RMRS-GTR-42-vol. 6. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Dibble, A. C., R. H. White, and P. K. Lebow. 2007. Combustion characteristics of north-eastern USA vegetation tested in the cone calorimeter: invasive versus non-invasive plants. International Journal of Wildland Fire 16(4): 1–20.

Drummond, Brie. 2005. The selection of native and invasive plants by frugivorous birds in Maine. Northeast. Nat. 12(1): 33–44.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Chicago and London: The University of Chicago Press, 181 p.

Eschtruth, A. K. and J. J. Battles. 2009. Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. Ecol. Monogr. 79(2): 265–280.

Frappier, B. and R. T. Eckert. 2003. Utilizing the USDA PLANTS database to predict exotic woody plant invasiveness in New Hampshire. For. Ecol. Manage. 185: 207–215.

Frappier, B., R. T. Eckert, and T. D. Lee. 2003a. Potential impacts of the invasive exotic shrub *Rhamnus frangula* L. (glossy buckthorn) on forests of southern New Hampshire. Northeast. Nat. 10(3): 277–296.

Frappier, B., T. D. Lee, K. F. Olson, and R. T. Eckert. 2003b. Small-scale invasion pattern, spread rate, and lag-phase behavior of *Rhamnus frangula* L. For. Ecol. Manage. 186: 1–6.

Frazer, G. W., C. D. Canham, P. Sallaway, and D. Marinakis. 1999. Gap Light Analyzer, Version 2.0. Simon Fraser University & Institute of Ecosystem Studies, Burnaby, British Columbia and Millbrook, New York.

Greenberg, C. H., L. M. Smith, and D. J. Levey. 2001. Fruit fate, seed germination, and growth of an invasive vine – an experimental test of 'sit and wait' strategy. Biol. Invas. 3: 363–372.

Haines, A. and T. F. Vining. 1998. Flora of Maine. Bar Harbor, ME, V. F. Vining Co. 847 p.

Hobbs, R. J. and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conserv. Biol. 6(3): 324–337.

Hunter, J. C. and J. A. Mattice. 2002. The spread of woody exotics into the forests of a northeastern landscape, 1938–1999. J. Torr. Bot. Soc. 129(3): 220–227.

Hutchinson, T. F. and J. L. Vankat. 1997. Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. Conserv. Biol. 11(5): 1117–1124.

JENKINS, M. A. AND G. R. PARKER. 2000. The response of herbaceous-layer vegetation to anthropogenic disturbance in intermittent stream bottomland forests of southern Indiana, USA. Plant Ecol. 151: 223–237.

LUNDGREN, M. R., C. J. SMALL, AND G. D. DREYER. 2004. Influence of land use and site characteristics on invasive plant abundance in the Quinebaug Highlands of Southern New England. Northeast. Nat. 11(3): 313–332.

MADRITCH, M. D. AND R. L. LINDROTH. 2009. Removal of invasive shrubs reduces exotic earthworm populations. Biol. Invas. 11: 663–671.

MAINE FOREST AND LOGGING MUSEUM. 2007. Maine Forest and Logging Museum at Leonard's Mills Historic Settlement. Retrieved June 23, 2009 from the Maine Forest and Logging Museum. <http://www.leonardsmills.com/mission.html>

MAPINFO. 2007. MapInfo Professional, Version 9.0.2. MapInfo Corporation, New York, USA.

MCCUNE, B. AND M. J. MEFFORD. 1999. PC-ORD for Windows. Multivariate Analysis of Ecological Data. Version 4.07. Gleneden Beach, Oregon, USA: MjM Software.

MCDONALD, R. I., G. MOTZKIN, AND D. R. FOSTER. 2008. Assessing the influence of historical factors, contemporary processes, and environmental conditions on the distribution of invasive species. J. Torr. Bot. Soc. 135(2): 260–271.

MCGARIGAL, K., S. CUSHMAN, AND S. STAFFORD. 2000. Multivariate Statistics for Wildlife and Ecology Research. New York: Springer. 283 p.

MCNAB, W. H. AND M. MEEKER. 1987. Oriental bitterweeet: a growing threat to hardwood silviculture in the Appalachians. N. J. Appl. For. 4: 174–177.

MEHRHOFF, L. J., J. A. SILANDER, S. A. LEICHT, E. S. MOSHER, AND N. M. TABAK. 2003. IPANE: Invasive Plant Atlas of New England. Retrieved on June 8, 2010 from the Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA. http://nbii-nin.ciesin.columbia.edu/ipane/

MICROSOFT PICTURE IT! 2002. Microsoft Picture It! Photo 7.0, Version 7.0.716.0. Microsoft Corp.

MILLER, K. E. AND D. L. GORCHOV. 2004. The invasive shrub, *Lonicera maackii*, reduces growth and fecundity of perennial forest herbs. Oecologia 139(3): 359–375.

NIERING, W. A. 1998. Forces that shaped the forests of the Northeastern United States. Northeast. Nat. 5(2): 99–110.

ORONO LAND TRUST. 2011. Orono Land Trust Newsletter, 2010–2011. Retrieved June 1, 2011 from Orono Land Trust. <http://www.oronolandtrust.org/newsletters/vol91.pdf>

PARENDES, L. A. AND J. A. JONES. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. Conserv. Biol. 14(1): 64–75.

R. 2007. R: A language and environment for statistical computing, Version 2.6.1. The R Foundation for Statistical Computing. R Development Core Team, Vienna, Austria.

ROBERTSON, D. J., M. C. ROBERTSON, AND T. TAGUE. 1994. Colonization dynamics of four exotic plants in a Northern Piedmont natural area. Bull. Torr. Bot. Club 121(2): 107–118.

SAFFORD, L. O., R. M. FRANK, AND E. L. LITTLE, JR. 1969. Trees and shrubs of the Penobscot Experimental Forest, Penobscot County, Maine. Research Paper NE-128. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 32 p.

SELMANTS, P. C. AND D. H. KNIGHT. 2003. Understory plant species composition 30–50 years after clearcutting in southeastern Wyoming coniferous forests. For. Ecol. Manage. 185: 275–289.

SENDAK, P. E., J. C. BRISSETTE, AND R. M. FRANK. 2003. Silviculture affects composition, growth, and yield in mixed northern conifers: 40-year results from the Penobscot Experimental Forest. Can. J. For. Res. 33: 2116–2128.

SILANDER, J. A. AND D. M. KLEPEIS. 1999. The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. Biol. Invas. 1: 189–201.

SILVERI, A., P. W. DUNWIDDIE, AND H. J. MICHAELS. 2001. Logging and edaphic factors in the invasion of an Asian woody vine in a mesic North American forest. Biol. Invas. 3: 379–389.

UNITED STATES DEPARTMENT OF AGRICULTURE, SOIL CONSERVATION SERVICE. 1963. Soil Survey of Penobscot County, Maine. Washington, D.C.: United States Department of Agriculture, Soil Conservation Service in cooperation with the University of Maine Agricultural Experiment Station, 1959, No. 28. 266 p.

WEBSTER, C. R., M. A. JENKINS, AND S. JOSE. 2006. Woody invaders and the challenges they pose to forest ecosystems in the Eastern United States. J. For. 104(7): 366–374.

WOODS, Kerry D. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. Amer. Midl. Nat. 130(1): 62–74.