Eagle Hill Institute

POTENTIAL IMPACTS OF THE INVASIVE EXOTIC SHRUB *RHAMNUS FRANGULA* L. (GLOSSY BUCKTHORN) ON FORESTS OF SOUTHERN NEW HAMPSHIRE

BRIAN FRAPPIER[1,*], ROBERT T. ECKERT[1,2], AND THOMAS D. LEE[1,3]

ABSTRACT - This paper investigated the potential for the exotic shrub *Rhamnus frangula* L. (glossy buckthorn) to alter native plant community composition in southeastern New Hampshire. Stratified random sampling was performed with 2 m x 2 m plots randomly located in 5 m intervals along three 50 m transects in four even-aged *Pinus*-mixed hardwood forests, three of which were managed stands. The associations between *R. frangula* and the measured species abundances and environmental variables were investigated using linear, least-squares multiple regression and Non-metric Multidimensional Scaling Ordination. Plot basal area of *R. frangula* was inversely related to woody seedling density ($p < 0.001$), herb cover ($p < 0.05$), and species richness ($p < 0.01$). The relative contribution of *R. frangula* to explaining variance in seedling density was greater than canopy openness, soil pH, soil clay, or soil sand. Abundance of *R. frangula* was a statistically significant predictor ($p < 0.05$) of individual herb species abundances for all study sites. This evidence supports the hypothesis that *R. frangula* causes a decline in seedling density and alters native ground level plant species abundances. Furthermore, the patterns agree with the suppression of ground level plant species abundances by *R. frangula* found in removal experiments.

INTRODUCTION

The United States has seen a dramatic increase in the number of naturalized exotic species over the past 100 years (United States Congress 1993), probably due to exponentially increasing transport opportunities (Di Castri 1989). Within New England, an estimated 30% of the flora is exotic (Ricketts et al. 1999). Impacts from exotic species are now listed as either the greatest (Czech and Krausman 1997) or the second greatest threat to Federally listed "endangered" species (Wilcove et al. 1998). Alteration of native species recruitment due to exotic species can lead to changes in community composition (Macdonald et al. 1989). Such effects have been demonstrated for exotic species such as *Mimosa pigra* L. in Australia (Braithwaite et al. 1989), *Melaleuca quinquenervia* (Cav.) Blake in southern Florida (Myers 1983), and *Myrica faya* Aiton in Hawai'i (Vitousek and Walker 1989). Beyond direct effects on species, some invasive species have the capacity to alter ecosystem functions such as fire frequency, nutrient cycling,

[1]Department of Natural Resources, University of New Hampshire, 215 James Hall, Durham, NH 03857. [2]rteckert@cisunix.unh.edu. [3]tom.lee@unh.edu. [*]Corresponding author - frappier@cisunix.unh.edu.

and water availability (Ewel 1986, Mack et al. 2000, Ramakrishnan and Vitousek 1989, Vitousek 1986).

Some exotic plant species have exhibited the capacity to invade relatively undisturbed ecosystems (Ewel 1986, Mooney and Drake 1989, Ramakrishnan and Vitousek 1989). Brothers and Spingarn (1991) found 47 exotic species in strictly protected, albeit fragmented, forest reserves in Indiana; three species were able to establish within the reserve centers. Such nature reserves require that both ecosystem structure and function remain intact (Noss and Cooperrider 1994). Thus, the threat of community alteration by the interaction of exotic plant species with the biotic and abiotic environment warrants attention in areas specifically protected for their community composition.

Indiscriminate control of an abundant exotic species, regardless of whether evidence of an impact exists, is not an effective strategy for managing invasions. The limited resources of most conservation efforts necessitates that we prioritize control and focus on those exotic species having an impact and, subsequently, on those having the most dramatic impacts (Macdonald et al. 1989). Control efforts may also have adverse impacts on native species, some of which may be rare or threatened (Usher 1987, Westman 1990). If the individualistic model of community assemblage is assumed, then each invasive species could have different impacts and those impacts may differ with the invaded community considered (Westman 1990). Therefore, in cases where an exotic species attains substantial abundance, direct experimental and/or comparative investigation is both justified and necessary to prioritize control and avoid unnecessary harmful impacts.

The objective of this research was to investigate the potential of the exotic shrub *Rhamnus frangula* L. (glossy buckthorn; Rhamnaceae) to alter plant community composition in southern New Hampshire *Pinus*-mixed hardwood forests. Originally native to Europe (Gleason and Cronquist 1983), *R. frangula* has naturalized throughout the northeastern United States. Its current range in North America extends from Nova Scotia south to Pennsylvania, west to Illinois with some spotty distribution in Minnesota and Wisconsin (Converse 1984). The earliest confirmed collections in North America are from London, Ontario in 1898 and Ottawa in 1899. The period of most rapid expansion in Canada appears to be between the 1970s and 1980s (Catling and Porebski 1994). Howell and Blackwell (1977) report the likely establishment of *R. frangula* in Ohio between 1914 and 1932. Its range will likely continue to expand in North America, the species becoming abundant in open and semi-open wetlands and some upland woodlands (Catling and Porebski 1994).

Rhamnus frangula inhabits a wide range of soil types and soil moisture conditions (Converse 1984) but prefers moist to wet sites that are not fully flooded. In some fens in its native European habitats, plant

species diversity below mature stands of *R. frangula* was found to be extremely low compared to that before stand maturation (Godwin 1936, Godwin et al. 1974). Conspecific seedling density below parent plants has been reported to be on the order of 100 seedlings m^{-2} (Converse 1984, Godwin 1943). Growth rates as high as 0.5 cm diameter growth per year (Godwin 1943) and 4 meters of height in 5 years (Converse 1984) have been recorded for this species.

It is possible, given such high conspecific seedlings numbers and consequent growth rate, that *R. frangula*, once established, could modify or displace native plant communities both in the short and long term. There is a small amount of evidence indicating that this may be the case in certain habitats in the United States. Taft and Solecki (1990) report that *R. frangula* has been established in Gavin Bog, Illinois, since at least the 1950s. In that location, it appears to be displacing *Ilex verticillata* in the tall shrub zone and advancing into the low shrub zone, possibly shading the typical low shrub community (Taft and Solecki 1990). Some managers have considered *R. frangula* enough of a threat to investigate the effectiveness of various control techniques (Converse 1984, Post et al. 1989, Reinartz 1997).

We hypothesized that dense stands of *R. frangula* have the capacity to alter plant species composition. Specifically, it was predicted that *R. frangula* abundance would be inversely correlated with the densities and richness of woody seedlings and herbs in *Pinus*-mixed hardwood forests of New Hampshire. We also hypothesize that after other possibly explanatory variables (soil texture and pH, canopy cover, and canopy basal area) had been controlled for using multivariate analysis, *R. frangula* abundance would continue to explain a significant amount of variance within any observed pattern. Lastly, the factors associated with greater *R. frangula* abundance were examined.

METHODS

Study sites - Four field sites, described below, were used in this study. All sites were former old-field even-aged *Pinus*-mixed hardwood stands located in southeastern New Hampshire. Three of the stands were managed for pine timber.

1. *College Woods* is a 131 ha forest located in the town of Durham and owned by the University of New Hampshire (UNH). A 2.5 ha stand of even-aged *Pinus strobus* L. (eastern white pine) and *P. resinosa* Aiton (red pine), the result of re-planting after construction of an adjacent reservoir in the 1930s, was sampled in this study. Girdled trees were present indicating that some management and thinning had occurred. One soil series, Buxton silt loam (Inceptisol: fine, illitic, frigid Aquic Dystric Eutrudepts), was mapped on this site. The site sloped slightly to the south.

2. *MacDonald Lot* is also a UNH holding in Durham. Most of the 3 ha stand is on a gentle south-facing slope that extends down to the Oyster River. This even-aged stand was dominated by *Pinus strobus* and most likely was the result of farm abandonment in the first half of the 20th century. Girdled trees were present indicating that some management and thinning had occurred. The sample area was on Suffield silt loam (Inceptisol: coarse-silty over clayey, mixed, active, mesic Dystric Eutrudepts). The site was on a slight northeastern facing slope.

3. *Rye Recreation Area* is held by the Town of Rye and managed as a recreation area with both managed forested sections and playing fields. The section used in this study was a continuous forest dominated by even-aged *P. strobus*, though with a larger component of hardwood species than the previous two sites. The sample area was 6.2 ha and had sandy loam Scituate (Inceptisol: coarse-loamy, mixed, active, mesic Oxyaquic Dystrudepts) and Newfields (Inceptisol: coarse-loamy over sandy or sandy-skeletal, mixed, active, mesic Oxyaquic Dystrudepts) soils in a closely intermingled complex. There was no substantial topography.

4. *Channel 11 Forest Compartment* is an approximately 4 ha stand located on UNH owned land in Durham. In contrast to the other stands, this stand occurs on an upland site. Topography is flat and gentle. The stand is a mix of even-aged *P. strobus* and mid-successional hardwoods on Buxton silt loam (Inceptisol: fine, illitic, frigid Aquic Dystric Eutrudepts) and Hollis (Inceptisol: loamy, mixed, active, mesic Lithic Dystrudepts) fine sandy loam soils. No evidence for active management was found.

Except for *R. frangula*, there was no apparent shrub-sapling layer in the forests studied. Whether this is due to forest management activities or canopy suppression is unknown.

In College Woods, aging of cut stems indicated that *R. frangula* appears to have invaded the stand approximately 36 years ago. Spatial analysis of stem size and age indicated that the invasion spread in an advancing front pattern from the reservoir at the rate of 6.2 m per year (Frappier et al. submitted). The age and pattern of invasion was not determined for the other stands. However, the size distribution of *R. frangula* seemed approximately the same in the other stands as in College Woods, indicating that the time of initial invasion may be similar (Frappier, pers. observ).

Field methods - Sampling was performed in the summer of 2000. Three 50 m transects were established in each study site. Transects were placed along the slope contour, avoiding forest edges and canopy gaps and placed so as to include as much variation in *R. frangula* cover as possible. A stratified random sampling scheme was employed with 2 m x 2 m sample plots randomly located at 5 m intervals along each transect; each plot center was situated on the transect line.

The following data were recorded from each plot: density and basal diameter of *R. frangula* stems; herb cover by species (cover classes of 0%, < 1%, 1–3%, 3–10% and subsequent increments of 10% were used); density of tree, shrub, and vine individuals under 1 m in height by species, density of tree, shrub, and vine individuals by species between 1 and 2 m in height; and cover of non-soil surface area. Non-soil surface area included exposed rocks and downed logs. For each plot, a soil sample from just below the litter layer was taken. Using a Nikon 950 digital camera fitted with a Nikon 950 fish-eye lens, a digital hemi-spherical photograph was taken of the canopy directly above any *R. frangula* cover, at 2.5 m in height, within each plot. Lastly, the basal diameter by species of all trees greater than 5 cm in basal diameter and within 5 m of the plot center was recorded.

To ensure that the full range of variation in *R. frangula* cover was sampled, four additional 2 m x 2 m plots were located off of the transects in each study area. Two of these plots were randomly located in ran-domly chosen areas that contained no *R. frangula* cover and two addi-tional plots were randomly located in randomly chosen areas with greater than 90% *R. frangula* cover. The same data that were recorded in the transect plots were recorded in these additional sample plots. These data were combined with the transect data for subsequent analyses. In total, 136 plots, 34 at each study site, were surveyed.

Laboratory Methods - Soil analyses were performed to determine the particle size distribution and pH of collected soil samples. Soil samples were air-dried for 24 hours. Particle size analysis was performed using the gravimetric method (Gee and Bauder 1986). Soil pH was determined using the slurry method suggested by Thomas (1996).

Data analysis - Canopy basal area was calculated as the total basal area for all canopy species in m^2 per m^2 of each 5 m radius overstory plot. Basal area of *R. frangula* was expressed as m^2 per m^2 of each 4 m^2 understory plot area. Percent canopy openness was determined from digital hemispherical photos using the Gap Light Analyzer imaging software (Frazer et al. 1999). The digital pixels were classified as "sky" and "non-sky" based on a light threshold, tolerance value. The tolerance value best able to correctly classify sky pixels was determined using the subjective best fit from a subsample of 10 photographs and was kept constant throughout the analyses.

The following variables were transformed to correct for negatively skewed distributions according to the recommendations in Zar (1999). *Rhamnus frangula* basal area, number of *R. frangula* stems, and canopy basal area were square-root-transformed. Seedling density was log-transformed. Percent herb covers by species and total herb cover were arcsine-transformed. The transformed variables were used in all subse-quent statistical tests.

All statistical analyses were performed using SPSS version 9 statistical software for Microsoft Windows. Differences between study areas were tested using a Multivariate Analysis of Variance (MANOVA) with study site as the independent variable. The combined dependent variables were herb cover, woody seedling density, and ground level plant species richness.

A linear least-squares multiple regression with backward selection of dependent variables (p-to-enter of 0.1 and a p-to-remove of 0.15) was used to investigate the environmental attributes and canopy species associated with *R. frangula* basal area (m^2/m^2; dependent variable). The predictor variables were percent canopy openness, percent soil clay, percent soil sand, soil pH, and individual canopy species basal areas in the overstory plots.

To examine relationships between *R. frangula* basal area and the dependent variables seedling density, herb cover, and ground level plant richness, separate linear standard multiple regressions were performed for each dependent variable. The independent variables in each model were *R. frangula* basal area, percent canopy openness, canopy basal area, percent soil clay, percent soil sand, and soil pH. These additional independent variables were included to control for their explanatory ability and ascertain the relative contribution of *R. frangula* abundance to predicting seedling density, herb cover, and ground level plant richness.

An indirect gradient analysis of herb species cover and woody plant species densities in the 2 m x 2 m plots was performed using Non-Metric Multidimensional Scaling. Only species that occurred in at least three plots were used in the ordination. To explore the relationships between environmental variables and the arrangement of plots in the ordination, separate linear least-squares regressions with backward selection of independent variables (p-to-enter of 0.1 and p-to-remove of 0.15) were performed for each dimension using the resulting plot dimension scores as the dependent variable. The predictor variables were percent canopy openness, canopy basal area, percent soil clay, percent soil sand, and soil pH. Individual canopy species basal areas were not used because our sample size was too small to allow backward multiple regressions. Canonical Correspondence Analysis was not used because of the high uncertainty in the predictive ability of chosen environmental variables prior to analysis (McCune 1997).

RESULTS

Rhamnus frangula basal area and number of stems were similar predictors in most tests. However, *R. frangula* basal area was usually significant at lower p-values. Therefore, the square root of basal area was used as the preferred measure of *R. frangula* abundance in all reported statistical tests.

Shrubs and small trees in the 1-2 m height category were recorded from only 9 plots and no plot had greater than 2 stems. As expected from visual inspection of the stands, shrubs and small trees in this height category were mostly absent in the forests studied. Thus, vegetation in the 1–2 m height category was not included in any subsequent analyses.

Study site comparisons - The study areas differed significantly (Wilks' Lambda = 0.069, $p < 0.001$) on the combined dependent variables herb cover, woody seedling density, ground level plant species richness, non-soil cover, canopy basal area, canopy openness, percent sand, percent clay, soil pH, and *R. frangula* basal area. Subsequent univariate comparisons indicated that the variables herb cover (F = 36.976, $p < 0.001$), woody seedling density (F = 12.427, $p < 0.001$), non-soil cover (F = 2.759, $p = 0.048$), percent clay (F = 8.108, $p < 0.001$), percent sand (F = 44.521, $p < 0.001$), and soil pH (F = 24.379, $p < 0.001$) differed significantly between the study sites. There were no differences observed for canopy basal area, canopy openness, or *R. frangula* basal area.

All sites were dominated by *Pinus strobus*. Unique to the College Woods site was the presence of *P. resinosa* as a major canopy component. In the Rye site, *Acer rubrum* L. (red maple) accounted for about 23% of the canopy basal area (Table 1). Compared to the other sites, species richness, herb cover, and seedling densities were depauperate in

Table 1. A summary of untransformed canopy basal area by tree species (m²/ha), physical environmental parameters, and select plant community attributes for each New Hampshire forest calculated from 136 5 m radius plots. Canopy species with less than 0.1 m²/ha basal area were grouped into an "other" category. *Rhamnus frangula* basal area was calculated from 136 4 m² plots. Note that the area coverage expressed in this table differs from the statistical analyses in that the values are expressed in m² per ha.

	Channel Eleven		College Woods		MacDonald Lot		Rye	
	$\overline{\chi}$	S*	$\overline{\chi}$	S*	$\overline{\chi}$	S*	$\overline{\chi}$	S*
Pinus strobus	50.31	33.26	26.55	27.97	38.77	26.03	31.15	30.75
Pinus resinosa	0.08	7.95	16.91	24.19	0	-	0	-
Acer rubrum	0.29	0.35	0.56	0.01	3.78	10.78	9.72	9.68
Fraxinus americana	0.18	0.61	0.19	0.27	0.03	0.15	0.05	0.26
Quercus rubra	0.60	2.01	0.06	3.46	1.80	3.41	0.52	1.19
Prunus serotina	0.20	0.25	0.07	0.15	0.10	0.35	0.11	0.28
Other	0.25	-	0.05	-	0.12	-	0.17	-
Total basal area	51.91	32.48	44.39	22.20	44.61	23.73	41.72	27.66
R. frangula basal area	7.01	5.02	6.54	2.98	4.09	2.02	5.30	2.35
Total herb cover (%)	31.35	21.80	3.46	17.27	45.38	27.00	42.83	20.31
Total seedlings <1 m	8.59	9.41	4.94	8.05	14.88	19.28	19.15	11.82
Herb richness	5.47	2.06	1.38	3.19	6.21	2.09	4.35	1.48
Seedling richness	2.85	1.58	1.26	1.30	3.44	1.35	3.44	1.50
Clay (%)	9.22	3.61	12.24	4.94	5.50	2.63	8.13	2.99
Sand (%)	69.26	8.82	61.28	10.42	79.50	4.30	83.01	5.57
Soil pH	4.30	0.24	4.67	0.33	3.98	0.24	4.33	0.21
Canopy openness (%)	14.32	2.33	13.81	1.88	14.77	2.67	15.20	3.22
Non-soil cover (%)	1.99	2.39	0.88	2.24	3.57	4.16	2.97	2.86

* Standard error

College Woods. Non-soil cover constituted only a small percentage (< 5%) of ground cover in all of the sites (Table 1). *Rhamnus frangula* accounted for a substantial percentage of total stand basal area ranging from 9.3% in MacDonald Lot to 14.7% in College Woods.

Predictors of R. frangula abundance - The final backward regression model significantly predicted the basal area of *R. frangula* (Adj. R^2 = 0.128, $p < 0.001$). *Rhamnus frangula* basal area was inversely related to *Fraxinus americana* basal area ($sr^2 = 0.029$, $p = 0.035$) and *Quercus rubra* basal area ($sr^2 = 0.058$, $p = 0.003$). Canopy openness was positively related to *R. frangula* basal area ($sr^2 = 0.055$, $p = 0.004$). Neither the remaining canopy species basal areas nor soil clay, soil sand, or soil pH were significantly related to *R. frangula* basal area at the $p < 0.01$ level.

Predictors of native species abundance and diversity - To further control for spurious correlations between *R. frangula* and ground level plant species abundance and diversity, canopy basal area was replaced with canopy basal areas for *Q. rubra* and *F. americana*, the two canopy species negatively related to *R. frangula* basal area. Total canopy basal area was dropped from these analyses to reduce the degree of multicollinearity between the predictor variables in the multiple regressions that follow.

The multivariate regression model predicting seedling density was highly significant (Adj. R^2 = 0.262, $p < 0.001$). Seedling density was inversely related to *R. frangula* basal area ($sr^2 = 0.168$, $p < 0.001$) (Fig. 1a) and positively related to soil sand content ($sr^2 = 0.031$, $p = 0.019$). Soil clay, soil pH, canopy openness, *F. americana* basal area, and *Q. rubra* basal area were not significantly related to seedling density when all variables were accounted for in the multiple regression. The predictor variables exhibited a low degree of multicollinearity as indicated by tolerance values greater than 0.667 (Table 2a).

The multivariate regression model predicting percent herb cover was highly significant (Adj. R^2 = 0.186, $p < 0.001$). Herb cover was inversely related to soil pH ($sr^2 = 0.059$, $p = 0.002$) and *R. frangula* basal area (sr^2 = 0.024, $p = 0.048$) (Fig. 1b). Soil clay, soil sand, soil pH, *F. americana* basal area, and *Q. rubra* basal area were not significantly related to herb cover when all variables were accounted for in the multiple regression The predictor variables exhibited a low degree of multicollinearity as indicated by tolerance values greater than 0.667 (Table 2b).

The multivariate regression model predicting ground level plant species richness was highly significant (Adj. R^2 = 0.279, $p < 0.001$). Species richness was inversely related to soil pH ($sr^2 = 0.085$, $p < 0.001$) and *R. frangula* basal area ($sr^2 = 0.037$, $p = 0.010$) (Fig. 1c). In addition, species richness increased with increasing *Q. rubra* basal area ($sr^2 = 0.021$, $p = 0.050$). Soil clay, soil sand, soil pH, canopy openness, and *F. americana*
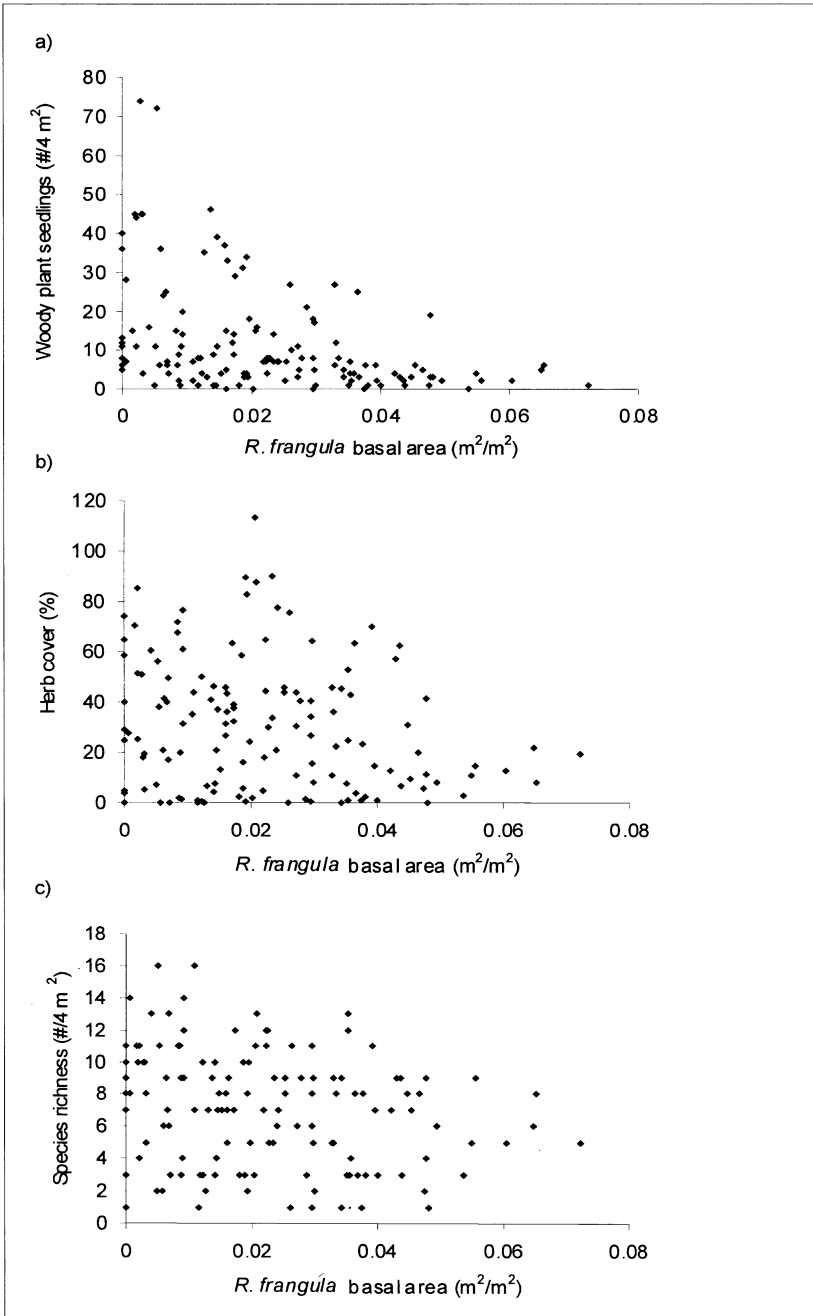
Figure 1. Untransformed relationships between *Rhamnus frangula* basal area (m²/m) and (a) seedling density, (b) total percent herb cover, and (c) total species richness in 4 m² plots.

basal area were not significantly related to ground level plant species richness when all variables were controlled for in the multiple regression. The predictor variables exhibited a low degree of multicollinearity as indicated by tolerance values greater than 0.667 (Table 2c).

Herb and woody seedling species abundance ordinations - Because previously described MANOVA testing for site differences indicated that the study sites differed significantly ($p < 0.05$) in herb cover, woody seedling density, and ground level plant species richness, separate indirect gradient tests were performed for each study area.

An NMS ordination of herb cover and seedling densities was obtained for Channel Eleven (Fig. 2). Visual examination of the NMS scree plot indicated that two dimensions parsimoniously fit the dis-

Table 2. Results of separate multiple regressions of several environmental factors and *Rhamnus frangula* basal area on the dependent variables (a) woody seedling density, (b) percent herb cover, and (c) ground level plant species richness.

(a) Woody seedling density (Adj. $R^2 = 0.262$, $p < 0.001$)

Predictor	Std. Coeff.	p	sr^2*	Tolerance**
Soil clay	-0.038	0.674	0.001	0.690
Soil sand	0.215	0.019	0.031	0.667
Soil pH	-0.111	0.157	0.011	0.907
Canopy openness	-0.046	0.561	0.002	0.877
R. frangula basal area	-0.446	0.000	0.168	0.843
F. americana basal area	-0.123	0.111	0.014	0.927
Q. rubra basal area	-0.042	0.597	0.002	0.885

(b) Percent herb cover (Adj. $R^2 = 0.186$, $p < 0.001$)

Predictor	Std. Coeff.	p	sr^2*	Tolerance**
Soil clay	-0.099	0.290	0.007	0.690
Soil sand	0.182	0.058	0.022	0.667
Soil pH	-0.255	0.002	0.059	0.907
Canopy openness	0.127	0.129	0.014	0.877
R. frangula basal area	-0.169	0.048	0.024	0.843
F. americana basal area	-0.027	0.737	0.001	0.927
Q. rubra basal area	0.033	0.686	0.001	0.885

(c) Ground level plant species richness (Adj. $R^2 = 0.279$, $p < 0.001$)

Predictor	Std. Coeff.	p	sr^2*	Tolerance**
Soil clay	-0.158	0.076	0.017	0.690
Soil sand	0.066	0.460	0.003	0.667
Soil pH	-0.306	0.000	0.085	0.907
Canopy openness	0.122	0.121	0.013	0.877
R. frangula basal area	-0.209	0.010	0.037	0.843
F. americana basal area	-0.135	0.077	0.017	0.927
Q. rubra basal area	0.154	0.050	0.021	0.885

*sr^2 = the squared semi-partial correlation.
**Tolerance = 1 - the squared multiple correlation of the variable with the other independent variables.
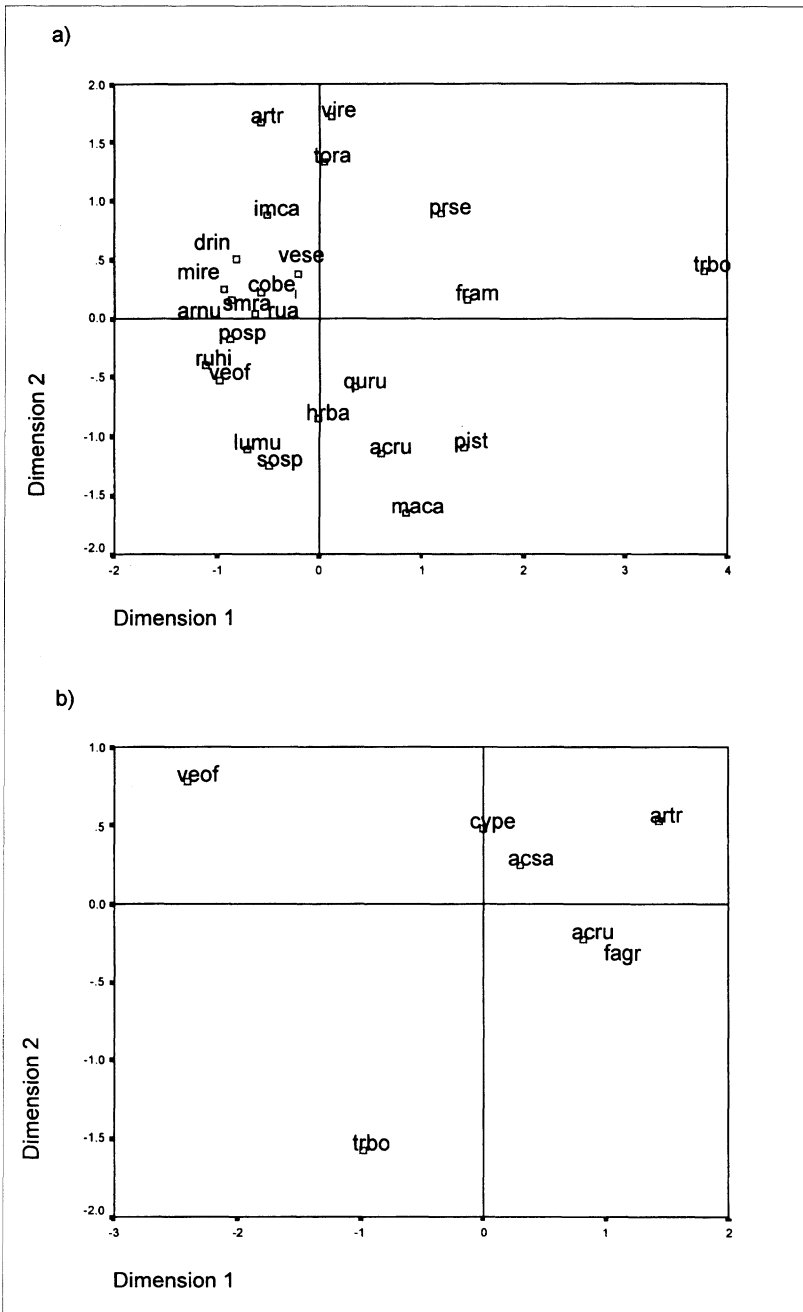
Figure 2. NMS Ordination diagrams for the southeastern New Hampshire study forests (a) Channel Eleven and (b) College Woods. Species abundances were standardized to a maximum magnitude of 1 by dividing each abundance value for each species in every plot by the maximum value attained for that species in all of the plots. See Table 4 for results of backward stepwise regression of environmental variables on each dimension.

tances in the data matrix. The first two NMS dimensions accounted for 59% of the variability in the data (axis 1 = 34%, axis 2 = 25%; final stress = 25.72).

The final regression model of plot dimension scores versus vegetation and stand predictor variables for the first dimension was significant but was only weakly correlated with the plot scores (Adj. $R^2 = 0.079$, $p = 0.004$). The first dimension was negatively correlated with *R. frangula* basal area ($sr^2 = 0.089$, $p = 0.004$; Table 4). No other variables were significantly correlated with dimension 1. The regression model predicting plot scores on dimension 2 for Channel Eleven was also significant but again was only weakly correlated with the plot scores (Adj. $R^2 = 0.051$, $p = 0.017$). Plot scores on dimension 2 were correlated with increasing *R. frangula* basal area ($sr^2 = 0.061$, $p = 0.017$; Table 4).

An NMS ordination of herb cover and seedling densities was obtained for College Woods (Fig. 2). Visual examination of the NMS scree plot indicated that two dimensions parsimoniously fit the distances in the data matrix. The first two NMS dimensions accounted for 73% of the variability in the data (axis 1 = 43%, axis 2 = 30%; final stress = 19.50).

Table 3. Labels used for herb and seedling species in NMS ordination diagrams.

Species	Label
Acer rubrum	acru
Acer saccharum	acsa
Aralia nudicaulis	arnu
Arisaema triphyllum	artr
Carya ovata	caov
Clintonia borealis	clbo
Cyperaceae	cype
Dryopteris intermedia	drin
Fagus grandifolia	fagr
Fraxinus amercana	fram
Impatiens capensis	imca
Juniperus communis	juco
Luzula multiflora	lumu
Lycopodia spp.	lyco
Maianthemum canadensis	maca
Mitchella repens	mire
Onoclea sensibilis	onse
Pinus strobus	pist
Poaceae	poac
Potentilla spp.	posp
Prunus serotina	prse
Quercus rubra	quru
Rubus hispidus	ruhi
Smilacina racemosa	smra
Solidago spp.	sosp
Toxicodenron radicans	tora
Trientalis borealis	trbo
Unknown herb A	hrba
Veronica officinalis	veof
Viburnum recognitum	vire

The final regression model of plot dimension scores versus vegetation and stand predictor variables for the first dimension was significant but was only weakly correlated with the plot scores (Adj. $R^2 = 0.114, p = 0.008$). The first dimension was negatively correlated with pH ($sr^2 = 0.131, p = 0.008$; Table 4). The regression model predicting plot scores on dimension 2 for College Woods was not significant at the $p < 0.05$ level (Adj. $R^2 = 0.051, p = 0.114$). The second dimension may represent a very weak gradient of increasing *R. frangula* basal area ($sr^2 = 0.041, p = 0.114$; Table 4).

An NMS ordination of herb cover and seedling densities was obtained for MacDonald Lot (Fig. 3). Visual examination of the NMS scree plot indicated that two dimensions parsimoniously fit the distances in the data matrix. The first two NMS dimensions accounted for 52% of the variability in the data (axis 1 = 21%, axis 2 = 31%; final stress = 27.11).

The final regression model of plot scores on the first dimension was highly significant (Adj. $R^2 = 0.500, p < 0.001$). The dimension represented a complex gradient of decreasing soil sand ($sr^2 = 0.328, p < 0.001$), canopy basal area ($sr^2 = 0.490, p < 0.001$), soil clay ($sr^2 = 0.203, p = 0.002$), canopy openness ($sr^2 = 0.124, p = 0.010$), and *R. frangula* basal area ($sr^2 = 0.138, p = 0.007$) and increasing non-soil cover ($sr^2 = 0.071, p = 0.047$; Table 4). The regression model predicting plot scores on dimension 2 for MacDonald Lot was also significant (Adj. $R^2 = 0.129, p = 0.029$) and represented a gradient of increasing soil clay ($sr^2 = 0.150, p = 0.029$; Table 4).

Table 4. Results of a backwards stepwise multiple regressions of several environmental variables and *R. frangula* basal area against plot scores from NMS ordinations of plant species abundances in 4 m² plots in the four New Hampshire *Pinus*-mixed hardwood forests studied. Results for the overall regression model for each site precede the results for each predictor variable. All variables were significant at the $p < 0.1$ level.

| Site	Dimension	Adj. model R^2	Model p	Predictor	Std. Coeff.	sr^{2*}
Channel Eleven	1	0.079	0.004	*R. frangula*	-0.298	0.089
	2	0.051	0.017	*R. frangula*	0.247	0.061
College Woods	1	0.114	0.008	pH	-0.362	0.131
	2	0.023	0.114	*R. frangula*	0.203	0.041
MacDonald Lot	1	0.500	<0.001	Soil sand	-1.613	0.328
				Canopy basal area	-1.304	0.490
				Soil clay	-0.939	0.203
				Canopy openness	-0.648	0.124
				R. frangula	-0.423	0.138
				Percent non-soil	0.324	0.071
	2	0.122	0.029	Soil clay	0.387	0.150
Rye	1	0.203	<0.001	pH	-0.331	0.095
				Soil clay	0.245	0.057
				R. frangula	0.237	0.055
	2	0.268	<0.001	Percent non-soil	0.363	0.130
				Soil clay	0.310	0.075
				R. frangula	0.270	0.069
				Canopy openness	0.212	0.034

* Squared semi-partial correlation.
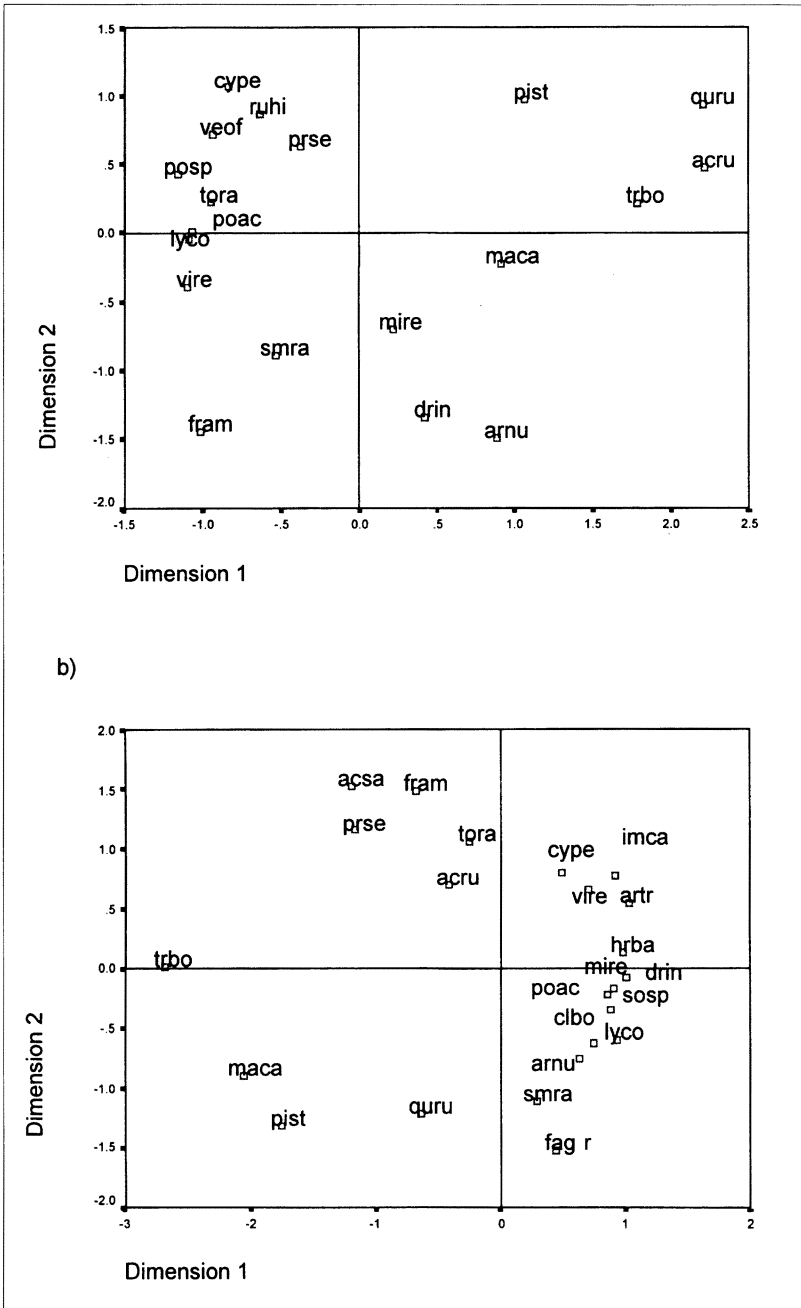
Figure 3. NMS Ordination diagrams for the southeastern New Hampshire study forests (a) MacDonald Lot and (b) Rye. Species abundances were standardized to a maximum magnitude of 1 by dividing each abundance value for each species in every plot by the maximum value attained for that species in all of the plots. See Table 4 for results of backward stepwise regression of environmental variables on each dimension.

An NMS ordination of herb cover and seedling densities was obtained for Rye (Fig. 3). Visual examination of the NMS scree plot indicated that two dimensions parsimoniously fit the distances in the data matrix. The first two NMS dimensions accounted for 85% of the variability in the data (axis 1 = 65%, axis 2 = 20%; final stress = 14.80).

The final regression model of plot scores on the first dimension for this site was significant (Adj. R^2 = 0.203, p < 0.001). This dimension represented a complex gradient of decreasing soil pH (sr^2 = 0.095, p < 0.001) and increasing soil clay (sr^2 = 0.057, p = 0.002) and *R. frangula* basal area (sr^2 = 0.055, p = 0.004; Table 4). The regression model predicting plot scores on dimension 2 for Rye was also significant (Adj. R^2 = 0.268, p < 0.001). The second dimension was a complex gradient of increasing non-soil cover (sr^2 = 0.130, p < 0.001), soil clay (sr^2 = 0.075, p < 0.001), *R. frangula* basal area (sr^2 = 0.069, p < 0.001), and canopy openness (sr^2 = 0.034, p < 0.013; Table 4).

Basal area of *R. frangula* was correlated with species associations on the first dimension of NMS ordinations for all study sites except College Woods; in College Woods, it was the sole correlate with the second dimension (Table 4). There was a low degree of multicollinearity between *Rhamnus frangula* basal area and the other predictor variables (tolerance values > 0.770). Thus, the relative contribution of *R. frangula* basal area to explaining variance was mostly independent of the other predictor variables in these regression models of NMS plot scores.

An association between *R. frangula* abundance and clonal species such as *Mitchella repens* L. (partridgeberry), *Toxicodendron radicans* (L.) Kuntze. (common poison-ivy)*,* and *Veronica officinalis* L. (common speedwell) was observed in Channel Eleven, Rye, and MacDonald Lot. However, another clonal species, *Maianthemum canadense* Desf. (wild lily-of-the-valley) appeared to be associated with areas of low *R. frangula* basal area in the same sites.

Species adapted to growth in early spring, such as *Dryopteris intermedia* and the mosses, were also associated with high *R. frangula* basal area (Figs. 2 and 3). These species are generally associated with wetter habitats; because *R. frangula* is also known to prefer wet sites (Converse 1984, Godwin 1943), these relationships could reflect an unmeasured set of correlations with water availability. The forest herb *Trientalis borealis* Raf. (northern starflower) was negatively associated with *R. frangula* in all sites. In addition, herb species normally associated with areas of increased light availability, such as *Rubus hispidus* L. (swamp dewberry), *Solidago* spp., and *Potentilla* spp., were inversely correlated with *R. frangula* (Figs. 2 and 3).

Seedlings of *Fraxinus americana* L. were consistently associated with high *R. frangula* basal area. Additionally, *Viburnum recognitum* Fern. seedlings were positively associated with *R. frangula* basal area

in Channel Eleven and Rye. These two species are also associated with wet areas. *Quercus rubra* L. and *A. rubrum* seedlings displayed a weak inverse correlation with *R. frangula* abundance. Both *Q. rubra* and *A. rubrum* are only mildly shade tolerant and may be responding to a decrease in light levels with high *R. frangula* abundance (Figs. 2 and 3). However, *R. frangula* was also inversely correlated with *Q. rubra* in the canopy (Table 2) implying that the relationship with the seedlings of this species may be a function of propagule availability. There was no consistent pattern to the response of other species' seedlings.

DISCUSSION

Rhamnus frangula was associated with areas of low woody seedling density, low herb cover, and low species richness in our four southeastern New Hampshire even-aged *Pinus*-mixed hardwood forests. There appeared to be a decrease in variability in seedling density, herb cover, and ground level plant species richness as *R. frangula* basal area increased. In contrast, high variability occurred where R. frangula was low in abundance. This pattern was most pronounced for seedling density (Fig. 1a).

Rhamnus frangula consistently had a low correlation with the other independent variables used in the statistical models predicting woody seedling densities, herb cover, and ground level plant species richness. It is unlikely that another plant species occupying the same stratum could be similarly correlated with ground level plant species distributions and abundances given the absence of a native shrub-sapling layer in the forests studied. However, it is clear that soil moisture may be playing a role in determining species abundances. Species generally associated with wetter sites [e.g. *Toxicodendron radicans* (L.) Kuntze. (common poison-ivy), *Arisaema triphyllum* (L.) Schott (jack-in-the-pulpit), and *Dryopteris intermedia* (Muhl. ex Willd.) Gray (intermediate wood fern)] clustered together in the ordinations. In addition, soil clay content, a possible surrogate measure for soil moisture capacity, was correlated with species abundances in the species ordinations in two of the sites (MacDonald Lot and Rye; Table 4). *Rhamnus frangula* abundance may be responding inversely to a moisture or nutrient gradient compared to other species and invading areas of low diversity and native species abundance or potentially suppressing these species.

While it is not possible to conclude with any certainty that *R. frangula* is causing the observed suppression of seedling density, percent herb cover, and species richness, we believe this evidence strongly supports the hypothesis. Two experiments found that plant

species richness, herb cover, and seedling densities were higher in areas where *R. frangula* had been previously removed compared to areas where *R. frangula* was allowed to remain (Sinclair and Catling 1999, Frappier et al. in press). Thus, both pattern and experiment appear to agree on the issue that high *R. frangula* abundance suppresses the natural variability in native species growth and/or recruitment. Species richness may be lowered by a decrease in abundance and consequent exclusion of non-clonal or late spring sprouting forbs due to resource competition.

It should be explicitly cautioned that these results are based on *Pinus*-mixed hardwood stands from a small area in New Hampshire. These results may not generalize to other community types where *R. frangula* invades such as bogs or open fields or to other geographic areas. Differing environmental variables combined with differing species interactions may alter the relationship of native species to *R. frangula* abundance.

These patterns described here are consistent with those found for other woody exotic plants in northeastern United States forests. Woods (1993) found an inverse relationship between *Lonicera tatarica* L. (tatarian honeysuckle) cover and seedling density and herb cover in southern New England. Similarly, Hutchinson and Vankat (1996) reported that *L. maackii* (Rupr.) Maxim. cover depressed seedling number, herb cover, and species richness. Wyckoff and Webb (1996) observed that fewer native saplings occurred below canopies of *Acer platanoides* L. (Norway maple) than below canopies of native species.

While the idea that an exotic species may not necessarily impact native species may be justified for exotic species remaining low in abundance, it is unlikely to be true for species that achieve significant abundance (Woods 1997). Resource limitation of some sort operates in most natural communities. Thus, while only a small percentage of exotic species with a pathway for introduction naturalize and spread (Williamson and Fitter 1996), a consistent pattern is emerging in the literature where woody invaders attaining appreciable biomass are negatively impacting species recruitment and richness in the native communities they invade (Braithwaite et al. 1989, Hutchinson and Vankat 1996, Myers 1983, Vitousek and Walker 1989, Woods 1993, Wyckoff and Webb 1996).

ACKNOWLEDGMENTS

LITERATURE CITED

Braithwaite, R.W., W.M. Lonsdale, and J.A. Estbergs. 1989. Alien Vegetation and native biota in Tropical Australia: The spread and impact of *Mimosa pigra*. Biological Conservation 48:189–210.

Brothers, T.S., and A. Spingarn. 1991. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology 6:91–99.

Catling, P.M. and Z.S. Porebski. 1994. The history of invasion and current status of glossy buckthorn, *Rhamnus frangula*, in southern Ontario. Canadian Field-Naturalist 108:305–310.

Converse, C.K. 1984. *Rhamnus cathartica* and *Rhamnus frangula*. Element Stewardship Abstract, The Nature Conservancy. 17 pp.

Czech, B., and P.R. Krausman. 1997. Distribution and causes of species endangerment in the United States. Science 277:1116.

Di Castri, F. 1989. History of biological invasions with special emphasis on the Old World. Pp. 1–30, *In* J.A. Drake, H.A. Mooney, F. DiCastri, R.H. Groves, F.J. Krueger, M. Rejmanek, and M. Williamson (Eds.). Biological Invasions: A Global Perspective. Wiley, New York, NY. 526 pp.

Ewel, J.J. 1986. Invasibility: lessons from south Florida. Pp. 214–229, *In* H.A. Mooney and J.A. Drake (Eds.). Ecology of Biological Invasions of North America and Hawaii. Ecological Studies 58. Springer-Verlag, New York, NY. 321 pp.

Frappier, B., Eckert, R.T., and Lee, T.D. In press. Experimental removal of the non-indigenous shrub *Rhamnus frangula* L. (glossy buckthorn): Effects on tree seedlings and herbs. Natural Areas Journal.

Frazer, G.W., C.D. Canham, and K.P. Lertzman. 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs. Copyright © 1999: Simon Fraser University, Burnaby, BC, and the Institute of Ecosystem Studies, Millbrook, NY.

Gee, G.W. and J.W. Bauder. 1986. Particle-size analysis. Pp.383–412, *In* A. Klute, (Ed.). Methods of Soil Analysis, Part 1. American Society of Agronomy, Madison, WI.

Gleason, H.A., and Crouquist, A. 1983. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Van Nostrand Reinhold Co., New York, NY. 810 pp.

Godwin, H. 1936. Studies in the ecology of Wicken Fen: III. The establishment and development of fen scrub. Journal of Ecology 24:82–116.

Godwin, H. 1943. *Frangula alnus* Mill. (*Rhamnus frangula*, L.). Journal of Ecology 31:77–92.

Godwin, H., D.R. Clowes, and B. Huntley. 1974. Studies in the ecology of Wicken Fen V. Development of fen carr. Journal of Ecology 62:197–214.

Howell, J.A., and W.H. Blackwell, Jr. 1977. The history of *Rhamnus frangula* (glossy buckthorn) in the Ohio flora. Castanea 42:111–115.

Hutchinson, T.F., and J.L. Vankat. 1997. Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. Conservation Biology 11:117–1124.

MacDonald, I.A., L.L. Loope, M.B. Usher, and O.H. Hamann. 1989. Invasive species in nature reserves. Pp. 215–255, *In* J.A. Drake, H.A. Mooney, F. DiCastri, R.H. Groves, F.J. Krueger, M. Rejmanek, and M. Williamson (Eds.). Biological Invasions: A Global Perspective. Wiley, New York, NY. 526 pp.

Mack, R.N., D. Simberloff, W.M. Lonsdale, H. Evans, M. Clout, and F.A. Bazzaz. 2000. Biotic Invasions: Causes, epidemiology, global consequences, and control. Ecological Applications 10:689–710.

McCune, B. 1997. Influence of noisy environmental data on Canonical Correspondence Analysis. Ecology 78:2617–2623.

Mooney, H.A., and J.A. Drake. 1989. Summary and conclusions. Pp. 493–502, *In* J.A. Drake, H.A. Mooney, F. DiCastri, R.H. Groves, F.J. Krueger, M. Rejmanek, and M. Williamson (Eds.). Biological Invasions: A Global Perspective. Wiley, New York, NY. 526 pp.

Myers, R.L. 1983. Site susceptibility to invasion by the exotic tree *Melaleuca quiquenervia* in southern Florida. Journal of Applied Ecology 20:645–658.

Noss, R.F., and A.Y. Cooperrider. 1994. Saving Nature's Legacy: Protecting and Restoring Biodiversity. Island Press, Washington, DC. 416 pp.

Post, T.W., E. McCloskey, and K.F. Klick. 1989. Two-year study of fire effects on *Rhamnus frangula* L. Natural Areas Journal 9:175–176.

Ramakrishnan, P.S., and P.M. Vitousek. 1989. Ecosystem level processes and the consequences of biological invasions. Pp. 281–300, *In* J.A. Drake, H.A. Mooney, F. DiCastri, R.H. Groves, F.J. Krueger, M. Rejmanek, and M. Williamson (Eds.). Biological Invasions: A Global Perspective. Wiley, New York, NY. 526 pp.

Reinartz, J. A. 1997. Controlling glossy buckthorn (*Rhamnus frangula* L.) with winter herbicide treatments of cut stumps. Natural Areas Journal 17:38–41.

Ricketts, T.H., E. Dinerstein, D.M. Olson, and C.J. Loucks (Eds.). 1999. Terrestrial Ecoregions of North America: A Conservation Assessment. Island Press, Washnigton, DC. 485 pp.

Sinclair, A. and P.M. Catling. 1999. The value of cutting in the management of glossy buckthorn (*Rhamnus frangula* L.). The Wetland Journal 11:25–27.

Taft, J.B., and M.K. Solecki. 1990. Vascular flora of the wetland and prairie communities of Gavin Bog and Prairie Nature Preserve, Lake County, Illinois. Rhodora 92:142–165.

Thomas, G.W. 1996. Soil pH and soil acidity. Pp. 475-490, *In* D.L. Sparks, et al., Methods of Soil Analysis, Part 3, Chemical Methods. Soil Science Society of America, Madison, WI.

United States Congress, Office Of Technology Assessment. 1993. Harmful nonindigenous species in the United States. OTA-F-565. U.S. Government Printing Office, Washington, DC.

Usher, M.B. 1987. Invasibility and wildlife conservation: Invasive species on nature reserves. Philisophical Transactions of the Royal Society London B 314:695–710.

Vitousek, P.M. 1986. Biological invasions and ecosystem properties: can species make a difference. Pp. 163–176, *In* H.A. Mooney and J.A. Drake (Eds.). Ecology of Biological Invasions of North America and Hawaii. Ecological Studies 58. Springer-Verlag, New York, NY. 321 pp.

Vitousek, P.M., and L.R. Walker. 1989. Biological invasion by *Myrica faya* in Hawaii: Plant demography, nitrogen fixation, ecosystem effects. Ecological Monographs 59:247–265.

Westman, W.E. 1990. Park management of exotic plant species: problems and issues. Conservation Biology 4:251–260.

Wilcove, D.S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience 48:607–615.

Williamson, M.H., and A. Fitter. 1996. The varying success of invaders. Ecology 77:1666–1670.

Woods, K.A. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. American Midland Naturalist 130:62–74.

Wyckoff, P.H., and S.L. Webb. 1996. Understory influence of the invasive Norway maple (*Acer platanoides*). Bulletin of the Torrey Botanical Club 123:197-205.

Zar, J.H. 1999. Biostatistical Analysis, 4th ed. Prentice-Hall, Upper Saddle River, NJ. 663 pp.