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Author(s): Catherine Owen Koning , Rhine Singleton
Source: Natural Areas Journal, 33(3):256-263. 2013.
Published By: Natural Areas Association
DOI: http://dx.doi.org/10.3375/043.033.0304
URL: http://www.bioone.org/doi/full/10.3375/043.033.0304

RESEARCH ARTICLE

Effects of Moderate Densities of Glossy Buckthorn on Forested Plant Communities in Southwest New Hampshire, USA

Catherine Owen Koning[1,2]

[1]Franklin Pierce University
40 University Drive
Rindge NH 03461

Rhine Singleton[1]

[2] Corresponding author: koningc@franklin-pierce.edu; 603-899-4322

Natural Areas Journal 33:256–263

ABSTRACT: To investigate the hypothesis that *Frangula alnus*, glossy buckthorn, is causing a decrease in native plant diversity in forested plant communities of southwest New Hampshire, thirty nine 20-m x 20-m plots were established in five different forest types, and all buckthorn saplings and seedlings were removed from 15 of the plots. A nested plot design was used to sample shrubs and herbs. Treatment plots were kept free of buckthorn for five years. There was a positive relationship between pre-treatment buckthorn density and percent openness of the forest canopy, and with basal area of white pine (*Pinus strobus*), but not with soil wetness indicators. No significant changes in overall plant diversity or stem density were detected after buckthorn was removed, although stem density of woody plants, and seedlings of *Acer rubrum* did show significant increases in the treatment plots when compared to controls, but these effects were only seen in areas with the highest densities of buckthorn. No effects of buckthorn were observed below an average of 8.25 stems per m2. Compared to other areas of the northeastern United States, the densities of buckthorn were very low. Buckthorn seedling densities showed small increases in the control and monitoring plots, perhaps indicating a slow build-up to a "threshold" density, beyond which greater impacts on native species may be seen.

Index terms: forest management, *Frangula alnus*, glossy buckthorn, invasive species

INTRODUCTION

Invasive species can wreak economic, social, and ecological havoc on scales ranging from local to global (Mack et al. 2000). Impacts can include decreased biomass of native species, local extinction of species, loss of community relationships, and complete alteration of ecosystem structure and function (Sandlund et al. 1999; Mack et al. 2000; Christian 2001; Ludsin and Wolfe 2001; Heneghan et al. 2002). In addition, alien species generate huge economic costs, in terms of lost harvestable value, lost ecosystem services, and cost of control (Mooney 1999; Mack et al. 2000; Jenkins 2002). This cost has been estimated at $138 billion in the United States alone (Mack et al. 2000).

While the impacts of some invasive species have been clearly documented, it is common for severe negative impacts to be inferred without adequate quantification. In a detailed review of the scientific literature in 1995, Anderson pointed out that several assumptions about the impact of the invasive purple loosestrife (*Lythrum salicaria)* on native species had very little scientific information to support them. Since then, a number of studies have demonstrated more clearly negative effects (e.g., Gaudet and Keddy 1995; Weihe and Neely 1997; Farnsworth and Ellis 2001).

When an invasive plant occurs at low densities but high frequencies, conservationists tend to assume the presence of the biological equivalent of a ticking time bomb. Some invasive species have persisted at low levels of abundance for decades, and then spread aggressively over a relatively short period of time (Sandlund et al. 1999; Mack et al. 2000). These 'lag times' are presumed to result from low initial population density, researchers' inability to detect the exotics, climatic shifts, addition of atmospheric pollutants, lack of dispersers that can recognize and use the propagules, presence of predators, or lack of available habitat in the beginning, particularly in areas that later become disturbed (Crooks and Soule 1999).

Once an exotic species becomes established, managers need to remove and control the spread of these plants. The difficulty of complete eradication in many cases has led to the recent realization that the goal may be reduction of the target population to a "non-threatening level" (Mack et al. 2000). However, a "non-threatening level" has yet to be defined for most invasive species. For the land manager, the presence of an invasive species leads to several questions: Is the invasive species pushing out native species; is it increasing in abundance beyond that "non-threatening level;" and will management activities be cost-effective?

This study focuses on one invasive plant species, the woody shrub glossy buckthorn (*Frangula alnus* Mill., formerly known as *Rhamnus frangula* L.), in mature second-growth forests of southwestern New Hampshire, USA. A European species, glossy buckthorn's original point of introduction to North America has not been identified. Glossy buckthorn was reported in Ontario, Canada, before 1900, where it was known to have escaped from cultivation. It did not spread widely beyond the originally reported areas until 1970. Since that time, it has become a dominant plant in wetlands and in those mesic habitats where it receives enough light (Catling and Porebski 1994). In the northern Allegheny Plateau riparian savanna, invasion by buckthorn reduced percent cover and changed the dominant species composition of the herbaceous layer (Possessky et al. 2000), although it did not affect herbaceous species richness overall. An undisturbed native bog community in Wisconsin was invaded by buckthorn in 1955. After those colonizers reached maturity and began to produce fruit, about 12 years later, the glossy buckthorn biomass in the bog increased logarithmically, resulting in a dense tall shrub canopy, which competed aggressively with native vegetation (Reinartz 1997; Reinartz and Kline 1998). Other studies found that exotic shrub species such as buckthorn had no greater dominance in the community, or effect on diversity, than native species did (Houlahan and Findlay 2004).

Although the U.S. Forest Service classifies buckthorn in its highest category for invasiveness in the Northeastern U.S. (U.S. Forest Service 1999), it varies in abundance throughout the region and is not as prevalent in northern New England as in areas further south (Magee and Ahles 1999). Nevertheless, in white pine (*Pinus strobus*) dominated forests of southeastern New Hampshire, Frappier et al. (2003) reported that woody seedling density, herb cover, and species richness were all negatively correlated with buckthorn density. In addition, experimental removal of buckthorn resulted in an increase in first year tree seedling density suggesting that buckthorn does have a negative effect on native forest plant species (Frappier et al. 2004).

In the forests of southwestern New Hampshire, buckthorn is one of very few invasive plant species (New Hampshire Dept. of Resources and Economic Development 2011). Although it reaches its highest density in wet or highly disturbed areas (e.g., Houlahan and Findlay 2004), it is present at lower density in most upland communities, including mixed hardwood and mixed coniferous forests. The focus of this study is to determine whether buckthorn has already surpassed the "non-threatening level" in these areas. Specifically, the goals are to: (1) assess the impact of glossy buckthorn on forested plant communities, (2) determine if densities of buckthorn in unmanaged forests are changing, and (3) determine if management efforts can reverse the effects of buckthorn.

METHODS

Study location, design, and data collection

All study areas are located on land owned by Franklin Pierce University in Rindge, New Hampshire (42.78°N, 72.06°W), at elevations ranging from 310 – 360 m AMSL. A stratified random sampling design was used. Forested areas were categorized by former land use, based on historical records and on landscape features (stonewalls, presence/absence of barbed wire, soil microtopography, presence/absence of stumps indicating logging), and by dominant tree species. In each of five forest types (coded A through E, Table 1), one set of three 20-m x 20-m plots was established in each of three different forest stands. In the C plots, one of the forest stands was destroyed, resulting in an n = 2 for that forest type. In each set, pre-treatment data were collected on buckthorn density; the plot with less than 5 stems of buckthorn (0.03 stems per m^2) became the monitoring plot, the purpose of which was to determine whether buckthorn density was changing (the D forest had no areas of low buckthorn density, so no monitoring plots were established). The monitoring plots had no apparent differences from the other areas, and did not stand out in the subsequent ordination analyses. Of the two remaining plots, one plot was randomly chosen to be the treatment plot (all buckthorn removed), and one was chosen to be the control plot. A nested plot design was used, with five 5-m x 5-m shrub plots located within each quadrant and center of each 20-m x 20-m plot, and 1-m x 1-m herb layer plots within each shrub plot. Data from these subplots were averaged within each 20-m x 20-m plot for analysis. Pre-treatment data were collected in June of 2003 on percent cover and stem density for all vascular plant species, and percent cover for mosses. In the 1-m x 1-m herb plots, only herbaceous plants and woody seedlings were considered (individuals were considered saplings if they were greater than 1 m tall or 0.5 m for short-statured species such as *Vaccinium angustifolia*). In the shrub plots, all saplings and shrubs were identified and counted. In the 20-m x 20-m plots, all trees (≥ 10 cm dbh) were identified and tagged, and the diameter at breast height was measured (dbh = 1.3 m above the forest floor).

Canopy photographs were used to assess overall light levels in each of the forest types. A Nikon Coolpix 995 camera with a fisheye FC–E8 lens was used to photograph the canopy at a height of 2 m above the ground in the center of each of the 5-m x 5-m shrub plots. A level was used to ensure that the camera was pointed vertically. Photos were checked for blooming (excessive light making vegetation appear white; Leblanc et al. 2005) and re-taken if necessary. Photographs were analyzed using the software Hemisfer to calculate canopy openness, a measure of the percent area of the canopy open to sky (Schleppi et al. 2007). Threshold, the cutoff light level that is used to determine whether each pixel is considered vegetation or sky, was determined automatically by Hemisfer using the procedure of Nobis and Hunziker (2005).

Soil moisture in each plot was evaluated indirectly using a wet soil metric based on a system of wetland plant indicators developed by the U.S. Fish and Wildlife Service (USFWS 1996). In this system, used reliably across the U.S. in delineating jurisdictional wetlands, each plant species has been assigned a region-specific indicator status based on its affinity to wetlands: obligate species are those that are found in wetlands 99% of the time (in the wettest of the wetlands), facultative-wetland species are found in wetlands 67% – 98% of the time, facultative species are those that are found in wetlands 33% – 66% of the time, facultative-upland species are

Table 1. **Characteristics of forest communities sampled. 1 = Three of the initial nine plots in the C forest type were destroyed for development in 2004 so were omitted; 2 = D plots had no monitoring plots.**

	Forest Type									
	A		B		C		D		E	
	Mixed pine/hard-woods		Mixed hard-woods		Mixed conifer/red maple		White pine forest		Spruce wetland	
# of forest stands	3		3		2		3		3	
# of 20 m x 20 m plots	3		3		3		2		3	
Land-use history	Cultivation; logging		Pasture; logging		Pasture; logging		Pasture; logging		Logging	
Tree species (basal area/m^2)	mean	s.d	mean	s.d	mean	s.d	mean	s.d	mean	s.d
Pinbus strobus L.	12.99	10.51	1.22	2.33	10.81	4.51	31.81	11.54	6.61	11.62
Acer rubrum L.	8.34	6.40	13.36	7.86	11.71	4.21	8.14	2.73	5.64	5.82
Picea sp.	0.11	0.33	0.00	-	1.76	1.37	0.00	-	23.05	6.09
Tsuga canadensis (L.) Carrière	0.24	0.47	0.97	1.07	12.77	6.68	0.00	-	0.41	0.74
Prunus serotina Ehrh.	0.09	0.28	0.00	0.00	1.18	1.84	7.46	3.72	0.00	-
Fraxinus americana L.	2.66	2.49	2.20	2.63	0.00	0.00	0.00	-	0.00	-
Acer saccharum Marsh.	1.14	1.93	3.23	3.64	0.00	0.00	0.00	-	0.00	-
Betula alleghaniensis Britton	0.32	0.89	2.88	4.86	0.00	0.00	0.00	-	0.00	-
Quercus rubra L.	0.07	0.14	0.91	1.48	1.04	1.30	0.54	1.21	0.00	-
Betula papyrifera Marsh.	1.62	2.17	0.22	0.48	0.32	0.79	0.33	0.75	0.00	-
Abies balsamea (L.) Mill.	0.00	-	0.24	0.39	0.79	0.64	0.00	-	1.20	2.12
Betula lenta L.	0.70	1.23	0.52	1.00	0.00	0.00	0.00	-	0.00	-
Fagus grandifolia Ehrh.	0.08	0.25	0.77	1.58	0.05	0.13	0.05	0.12	0.00	-
Other	0.00	-	0.38	-	0.00	-	0.11	-	0.15	-
Total	28.36		26.88		40.43		48.44		37.06	
Total Herb cover per m^2	8.85	11.20	18.25	17.23	10.03	12.15	28.78	16.71	53.53	27.43
Species richness	5.36	2.70	5.40	1.98	8.43	3.56	8.60	2.24	10.42	3.19
Diversity H	0.93	0.50	0.70	0.47	1.22	0.48	0.93	0.45	0.77	0.49
% Canopy openness	8.76	0.46	8.99	0.60	10.68	0.59	10.83	0.75	10.17	0.71
Shrub plot pre-treatment buck-thorn seedling density per m^2	0.79	1.37	0.04	0.05	0.16	0.37	7.03	3.72	0.68	0.60
Shrub plot pre-treatment buck-thorn sapling density per m^2	0.19	0.42	0.01	0.03	0.04	0.12	1.22	0.83	0.09	0 .16

found in wetlands 2% – 32% of the time, and upland species are found in wetlands only 1% of the time. Each species found in the plot was assigned a wetland indicator status from 1–5 (1 = obligate wetland species, 5 = upland species); this number was weighted by the proportion of the total percent cover for that species. Each species' weighted wetland indicator status numbers were then averaged for each plot to obtain the wetness indicator metric for each plot.

After data collection, all buckthorn trees, saplings, and seedlings were removed from the 20-m x 20-m treatment plots. Smaller individuals were removed by hand. Most were cut and a 50.2% solution of glyphosate (Roundup brand) was applied immediately to the cut stump. Treatment plots were "weeded" to keep the buckthorn out in 2005 and 2006. In 2008, data were collected in all plots using the same methods described earlier.

Data analysis

Non metric multidimensional scaling (NMS) was used to ordinate the relative stem density data for the 39 plots, averaging the subplot data first, using the program PC–ORD (McCune and Medford 1999), and following the recommendations in McCune and Grace (2002). The distance measure used was Sorensen, with a random starting configuration, 10 runs with real data, 200 iterations, choosing a 3-dimensional solution with final stability of 0.00042, and final stress of 10.09 for the ordination of 2003 data. The hypothesis that communities with more light availability and wetter conditions will have greater buckthorn density was tested using linear regression and multiple regression models and with environmental variable overlays using NMS.

Differences in pre-treatment buckthorn density, and differences in change in buckthorn stem density among different forest types and between treatment types in the herb and shrub plots, were tested using ANOVA with Bon Ferroni post-hoc testing. In addition, linear regression was used to test for a possible relationship between buckthorn density and basal area of white pine, and between buckthorn density and canopy openness and wetland indicator metric. All stem density data were $\log_{10}$ transformed to approach normal distributions (Zar 1999); data distributions were checked for each transformation. Percent cover data were transformed using the arcsine transformation.

A repeated measures ANOVA was used to test for the effect of buckthorn removal on herb diversity (based on the Shannon-Wiener index) and on herb species richness, total herb stem density, and total percent herb cover. To test for treatment effects on individual species in each forest type, the change in stem density in each herb plot or shrub plot was calculated by subtracting stem density before treatment (2003) from stem density after treatment (2008). The change in stem density in the control plots was then compared to the treatment plots in each forest type using a t-test. Only species that had a frequency of 10% or more across all herb or shrub plots in each forest type were tested, and only plots which had the species either before or after treatment were used. Percent cover data were treated similarly to stem density but were only analyzed for species with no stem counts (e.g., mosses and clubmosses). Microsoft Excel and PASW statistics Ver. 13 (SPSS 2009) were used for the statistical analyses.

RESULTS

A total of 101 vascular plant species were found in the herb plots and 29 woody shrub or sapling species in the shrub plots. The NMS ordination of plots into species space for the before-treatment data is shown in Figure 1. Axes 1, 2, and 3 explained 39.3%, 16.9%, and 34.0% of the variation respectively, for a cumulative of 90.3% of the variation. The two environmental parameters, wetland indicator status and percent canopy openness, showed the strongest correlation with Axis 3 ($r^2 = 0.232$ and 0.407 respectively). This ordination shows a fairly clear separation among the five forest types, except for some overlap between the C plots (mixed conifer forest on former pasture) and the D plots (white pine forest on former pasture). The species with the highest correlations with axis 1 were white pine trees ($r^2 = 0.603$), buckthorn saplings ($r^2 = .576$), and with axis 2 black birch (*Betula lenta*) saplings ($r^2 = .424$) and hay-scented fern (*Dennstaedia punctilobula*) ($r^2 = .361$), and for axis 3, the goldthread (*Coptis trifolia*) and spruce (*Picea*) trees showed the highest correlations ($r^2 = 0.583$ and 0.484).

Factors Influencing Buckthorn Abundance

Pre-treatment buckthorn seedling density in the herb plots was significantly different among the five forest types (df = 4, F = 22.67, $p < 0.001$); the white pine forest D plots had the highest density, and were significantly different from all the other forest types ($p < 0.001$). Buckthorn was significantly more abundant in plots with higher light levels as measured by canopy openness. Figure 2 shows that buckthorn density from the 5-m x 5-m sample plots

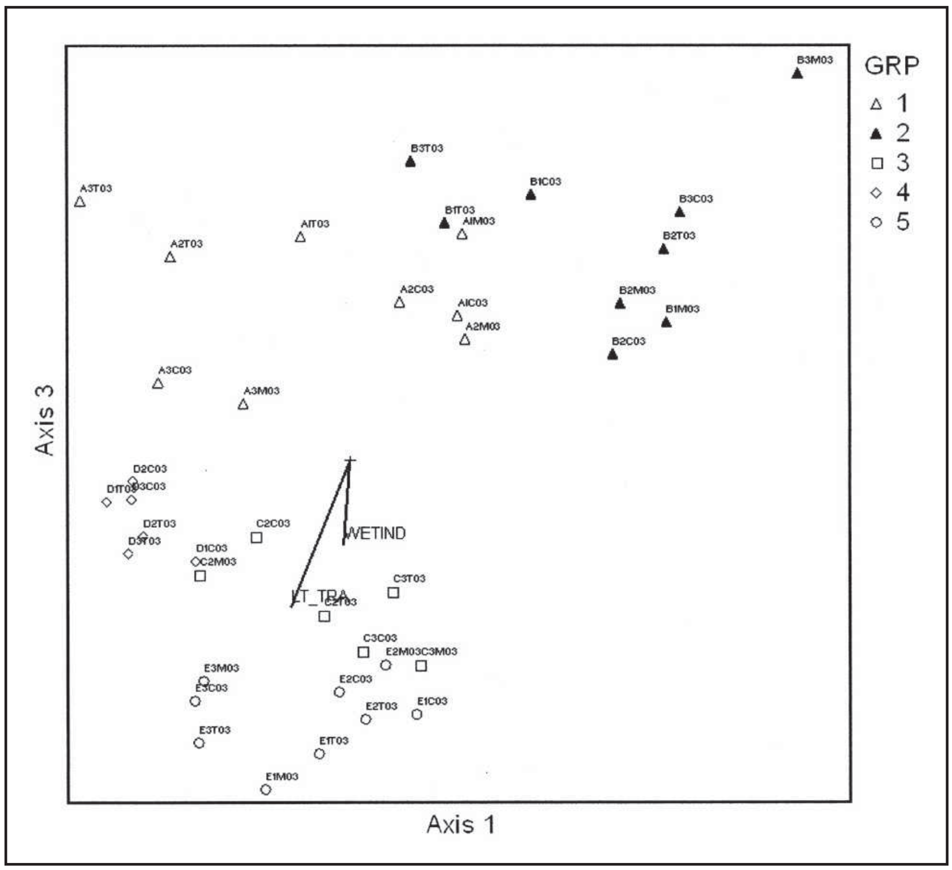

Figure 1. NMS ordination of plots in species space. A = mixed pine/hardwoods on formerly cultivated land; B = mixed hardwoods on former pasture; C = conifers on former pasture; D = white pine on former pasture; E = Spruce wetland on formerly logged areas. LT_TRA = Light transmission; WETIND = Wetness indicators.

averaged across the 20-m x 20-m plots was greater when the canopy was more open (df = 38, p = 0.0043, $r^2 = 0.20$). This increase in buckthorn density with light was also true for the 1-m x 1-m herb plots averaged across the 20-m x 20-m plots (df = 38, p = 0.0056, $r^2 = 0.19$).

There was no significant relationship between buckthorn stem density and soil wetness indicators (df = 38, p-value = 0.68, $r^2 = 0.0047$). A multiple regression of buckthorn density vs. canopy openness and wetness indicator species was consistent with the results from the individual simple regression analyses (df = 38, p = 0.0069, $r^2 = 0.24$, p light = 0.0019, p wetind = 0.172).

A regression of average buckthorn density in the 20-m x 20-m plots vs. total basal area of white pine revealed a significant positive relationship between these two variables (Figure 3, df = 38, p = $1.28\text{x}10^{-7}$, $r^2 = 0.534$).

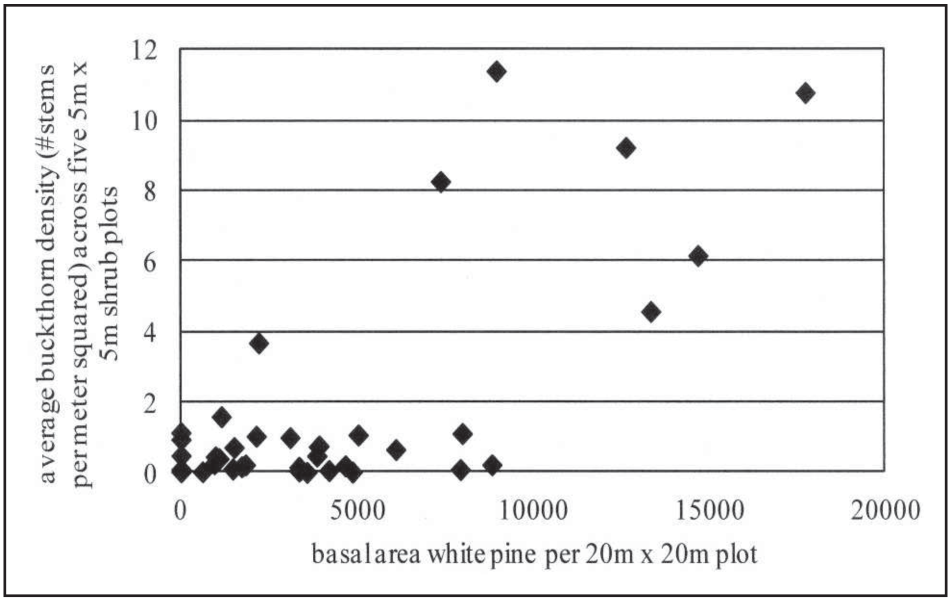

Figure 3. Buckthorn density (number of seedlings and saplings per meter squared) as a function of white pine basal area. Density is averaged across the five 5-m x 5-m shrub plots nested within the 20-m x 20-m plots.

Regression analysis showed that pre-treatment buckthorn density (seedlings plus saplings averaged across the 1-m^2 herb plots within the 20-m x 20-m plots) was not significantly related to the Shannon-Wiener diversity index (H) (df = 38 p = 0.66, $r^2 = 0.0053$) or species richness (df = 38, p = 0.73, $r^2 = 0.0033$). There also was no significant relationship between pre-treatment buckthorn stem density in the herb plots and total stem density per m^2 (df = 38, p = 0.46, $r^2 = 0.015$), woody stem density (df = 38, p = 0.81, $r^2 = 0.0015$), or herb stem density (df = 38, p = 0.45, $r^2 = 0.016$).

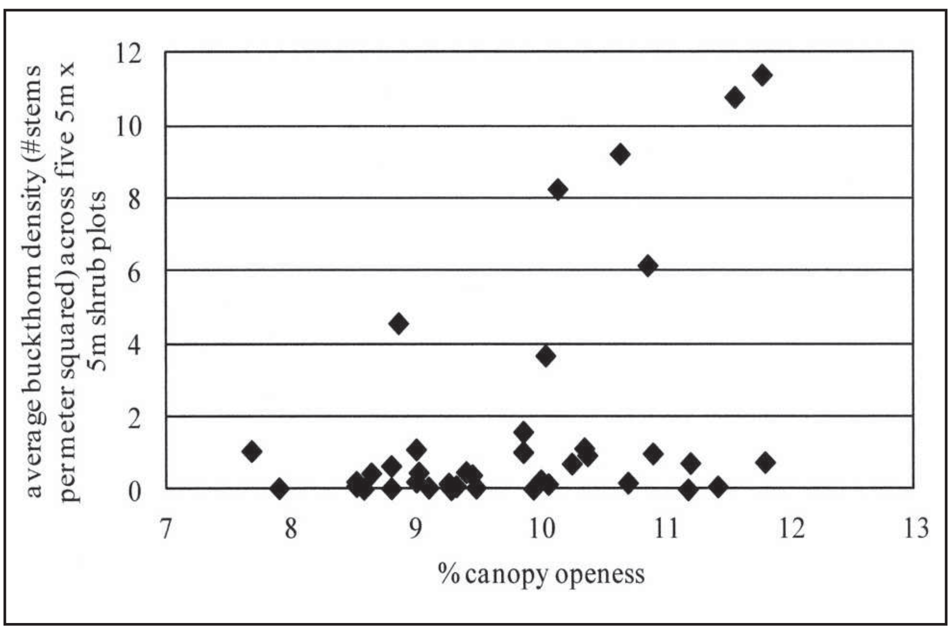

Figure 2. Buckthorn density (number of saplings and seedlings per meter squared) as a function of % canopy openness in the 5-m x 5-m shrub plots. Density is averaged across the five 5-m x 5-m shrub plots nested within the 20-m x 20-m plots.

Effects of buckthorn removal

After treatment, buckthorn seedling density in the herb plots increased in the control plots by a mean of 0.26 stems per m^2 (s.d. = 0.83) over the 5-year study period, averaged over all forest types, and in the monitoring plots by 0.29 stems per m^2 (s.d. = 1.04), but decreased in the treatment plots, as expected, by an average of 2.51 stems per m^2 (s.d. = 5.88). A paired t-test showed no significant difference between the pre- and post-treatment stem densities in the control and monitoring plots; but, not surprisingly, there was a significant difference in the treatment plots (df = 13, $p < 0.05$). Buckthorn sapling density in the 5-m x 5-m plots also did not change significantly in either the control or monitoring plots, but did decrease in the treatment plots, again as expected as the result of the removal.

A repeated measures ANOVA comparing all treated herb plots to control herb plots found no significant treatment effect of buckthorn removal on the total number of non-buckthorn stems (df = 1, F = 0.048, p = 0.828), plot richness (df = 1, F = 0.491, p = 0.485), and Shannon-Wiener Diversity (df = 1, F = 0.499, p = 0.481). Time and forest type did have a significant effect on all three variables ($p < 0.001$).

Eighteen individual native species in each forest type occurred frequently enough in the 1-m x 1-m herb plots for statistical testing. Significant differences were found only in the white pine forests (D forests), which had the highest buckthorn stem density (Table 2). Red maple (*Acer rubrum*) increased in the treatment plots, but decreased in the control plots. All woody species together also showed a significant difference in the treatments vs. the control plots in the D forest, with the control plots showing an average decrease of 10.27 stems per plot from 2003 to 2008, while the controls only showed an average decrease of 1.93 woody stems per plot.

Red maple, hazelnut (*Corylus cornuta*), balsam fir (*Abies balsamea*), and white pine were the only species occurring frequently enough as saplings in the 5-m x 5-m plots to be tested for an effect of buckthorn removal. For these species, the change in stem density from 2003 to 2008 in the treatment plots was not significantly different than the change in the control plots. In addition, the change in total sapling density across all species was not different in the treatment than in the control plots.

DISCUSSION

Glossy buckthorn frequently invades in disturbed and wet areas (e.g., Reinartz 1997; Reinartz and Kline 1998), but relatively little is known about its role in second-growth forests that have not been recently altered. In this study, the white pine forest on formerly pastured land had the highest density of buckthorn stems, while the mixed hardwood, later successional forests on former pasture, had the lowest. Canopy openness was positively correlated with buckthorn density and may be a significant factor in determining which areas were the most invaded, while soil wetness indicators were not.

In this study, buckthorn affected only one individual species, and only in the white pine forest on former pasture (D forest), which had the highest densities of buckthorn. However, buckthorn removal had a significant positive effect on all woody species, considered collectively, in the white pine D forest. The results of this study support those reported by Frappier et al. (2004), who found that buckthorn was having a strong suppressive effect on the first-year seedlings of several native trees, including *Acer rubrum*, *Fraxinus americana*, *Pinus strobus,* and *Quercus rubra*. However, they did not detect any effects on other species, despite the fact that their studies were conducted only in white pine forests with 90% or more buckthorn cover. The buckthorn density in this study is much lower, leading us to suggest that the buckthorn densities we experienced in the A, B, C, and E forests are still below the "non-threatening" level. Thus we can posit that the "threshold" or "non-threatening" level of buckthorn is higher than 1.5 seedlings and saplings stems per m^2 (the highest average density in the A, B, C, and E forests), but less than 8.25 stems per m^2 (the density in the white pine D forests).

Sanders (1993) also found that pine forests with lower overstory density had higher glossy buckthorn densities. In her study, a marked increase in glossy buckthorn seemed to be the result of the presence of many fruiting-aged individuals at the time of self-pruning of the 30 – 45 year old overstory pines; presumably the loss of the lower pine branches with age allowed greater light levels required for the seeds to germinate. She also found that buckthorn seed production was lowest in the smallest height class, while 89% – 100% of the plants in the medium and tall height classes produced seeds. Sanders (1993) also speculated that the preference of birds to use pines as a roosting site may explain the increased frequency of glossy buckthorn in pine stands relative to the mixed deciduous stands.

In this part of New England, white pine forests usually succeed into mixed hardwood forest communities, such as the B forest type in this study. In these mature second-growth forests, an important factor to consider is the possibility that buckthorn is competitively excluded as succession proceeds. In mid-successional secondary forests in southeastern New Hampshire, Cunard and Lee (2009) found that dead buckthorn shrubs were associated with greater basal area of shade tolerant trees and lower light levels than live buckthorn shrubs. Sanford et al. (2003) also found that glossy buckthorn exhibited low survival in the forest understory. In our study, when all forest types were considered together, buckthorn density in the control and monitoring plots did not show any statistically significant change.

We did observe natural mortality of buckthorn saplings in some of our A plots where light gaps were filling in, which is consistent with Cunard and Lee's (2009) conclusion that "patience is a virtue," because buckthorn density declines as forest succession proceeds. Future study in the monitoring and control plots will determine whether buckthorn density is increasing or decreasing as forests mature.

While it remains to be seen whether patience is a virtue, or if we are sitting on a ticking time bomb, it is easy to remove occasional stems of buckthorn, so our advice to our own land managers is to err on the side of caution and remove the buckthorn in the less invaded forests before it becomes a problem.

ACKNOWLEDGMENT

This research was supported by Faculty Research Funds from Franklin Pierce University. The authors thank their many field assistants, including Virgil Wetmore, Tracy Gora, Catrina Capucci, Eric Feldbaum, Tim Foley, Jerry Breault, and Neel Patel.

Catherine Owen Koning is a wetland scientist and Professor of Environmental Science at Franklin Pierce University.

Rhine Singleton is a forest ecologist and Associate Professor of Environmental Science and Biology at Franklin Pierce University.

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Table 2. Changes in number of stems in each herb plot (change in stems = #stems in 2008 - #stems in 2003). * = significant difference between control and treatment plots at p < 0.05, ** = significant at p < 0.01. ID = Insufficient data (not enough occurrences of that species in that forest type; a minimum of 14 herb plots was required). 1 = seedlings only; 2 = percent cover; 3 = not including *Frangula alnus*.

		A		B		C		D		E	
		Mixed pine/hard-woods		Mixed hardwoods		Mixed conifer/red maple		White pine forest		Spruce wetland	
		mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.	mean	s.d.
Abies balsamea (L.) Mill.[1]	ctrl	ID	ID	ID	ID	-1.40	1.13	ID	ID	-2.73	3.59
	trt	ID	ID	ID	ID	-0.20	0.28	ID	ID	-3.80	5.74
Acer rubrum L.[1]	ctrl	-1.35	0.96	-5.33	6.65	-0.60	0.85	**-1.00****	0.80	8.13	4.45
	trt	-0.33	2.84	-3.60	4.10	-0.80	1.98	**2.00****	0.60	3.00	7.12
Ácer sáccharum [1] Marsh.	ctrl	-3.78	6.04	ID	ID	ID	ID	ID	ID	ID	ID
	trt	-2.47	4.27	ID	ID	ID	ID	ID	ID	ID	ID
Coptis groenlandica Salisb.	ctrl	ID	ID	ID	ID	-17.00	24.04	-8.07	21.09	-31.13	31.13
	trt	ID	ID	ID	ID	-26.40	14.71	7.60	14.03	-21.67	10.51
Cornus canadensis L.	ctrl	ID	ID	ID	ID	ID	ID	ID	ID	-4.53	8.89
	trt	ID	ID	ID	ID	ID	ID	ID	ID	-1.60	1.22
Dennstaedtia punctilobula	ctrl	ID	ID	-6.73	2.12	ID	ID	ID	ID	ID	ID
(Michx.)	trt	ID	ID	-4.27	4.35	ID	ID	ID	ID	ID	ID
Frangula alnus Mill.[1]	ctrl	0.75	1.30	0.00	0.00	-0.40	0.57	0.67	1.40	0.20	0.53
	trt	-1.47	2.54	0.00	0.00	-0.90	0.71	-9.33	8.49	-0.33	0.23
Fraxinus americana L.[1]	ctrl	-0.83	0.85	ID	ID	ID	ID	ID	ID	ID	ID
	trt	2.47	2.14	ID	ID	ID	ID	ID	ID	ID	ID
Gaultheria procumbens L.	ctrl	ID	ID	ID	ID	-5.40	7.64	-3.93	6.81	ID	ID
	trt	ID	ID	ID	ID	-1.70	2.12	-3.60	6.24	ID	ID
Ilex verticillata (L.) A.	ctrl	ID	ID	ID	ID	ID	ID	ID	ID	-0.27	0.50
Gray [1]	trt	ID	ID	ID	ID	ID	ID	ID	ID	-0.33	0.64
Lycopodium clavatum L.[1]	ctrl	ID	ID	ID	ID	-0.14	0.14	1.05	1.34	ID	ID
	trt	ID	ID	ID	ID	0.71	1.26	-5.66	4.99	ID	ID
Maianthemum canadense	ctrl	-3.82	3.34	-4.13	6.99	-1.50	4.38	-4.33	7.37	2.60	2.60
Desf.	trt	1.40	1.22	-15.27	18.46	-1.60	0.85	1.47	6.85	-0.80	0.35
Mitchella repens L.	ctrl	ID	ID	ID	ID	ID	ID	ID	ID	-2.13	3.35
	trt	ID	ID	ID	ID	ID	ID	ID	ID	-0.87	1.03
Osmunda cinnamomea L.	ctrl	ID	ID	ID	ID	ID	ID	ID	ID	-0.40	0.60
	trt	ID	ID	ID	ID	ID	ID	ID	ID	1.20	1.44
Picea spp.[1]	ctrl	ID	ID	ID	ID	ID	ID	ID	ID	-1.47	1.14
	trt	ID	ID	ID	ID	ID	ID	ID	ID	-1.33	6.31
Pinus strobus L.[1]	ctrl	ID	ID	ID	ID	-1.90	1.27	-0.47	0.23	-0.67	1.55
	trt	ID	ID	ID	ID	-2.70	3.25	1.20	1.20	-2.33	1.03
Prunus Serotina Ehrh.[1]	ctrl	0.32	0.39	ID	ID	ID	ID	-3.33	4.46	ID	ID
	trt	-0.33	0.58	ID	ID	ID	ID	-0.80	0.35	ID	ID
Trientalis borealis Raf.	ctrl	2.08	4.50	ID	ID	1.30	1.56	4.73	0.61	-1.73	2.00
	trt	-1.67	3.42	ID	ID	-1.10	2.12	5.53	8.72	-0.27	0.61
Vaccinium angustifolium	ctrl	ID	ID	ID	ID	ID	ID	1.93	8.41	-0.47	1.33
Aiton [1]	trt	ID	ID	ID	ID	ID	ID	0.40	5.13	-2.20	2.99
Total number of woody	ctrl	-2.82	4.35	-6.00	5.05	-5.60	1.98	**-10.27***	1.75	2.00	8.43
species[3]	trt	-4.53	2.60	-4.93	3.50	-3.90	3.82	**-1.93***	3.44	-7.67	5.46
Total number of stems (all	ctrl	21.05	18.23	9.47	41.17	-34.80	10.47	-41.73	29.22	-45.27	21.30
species) [3]	trt	53.00	59.26	15.27	61.73	-43.30	27.01	-3.80	34.47	-39.93	18.96

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