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Canopy gaps facilitate establishment, growth, and reproduction of invasive *Frangula alnus* in a *Tsuga canadensis* dominated forest

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Abstract The primary objective of this study was to determine whether the exotic, invasive shrub, glossy buckthorn (*Frangula alnus*), is more abundant in canopy gaps created by logging than in uncut forests. Secondary objectives were to determine whether buckthorn abundance in gaps is related to gap size, and whether or not buckthorn exhibits advanced regeneration. The abundance of glossy buckthorn was estimated in five patch cuts and three single-tree cuts in a 90 year old eastern hemlock–eastern white pine–sweet birch forest at the Woodman Horticultural Farm in Durham, NH, USA. Glossy buckthorn was 96 times more abundant in logged areas than in uncut control plots. The three largest but youngest gaps (>0.08 ha; 5 years old) had the greatest proportion of tall (>2 m), reproductively mature glossy buckthorn individuals, with 18.4% fruiting. The older, medium-sized gaps (ca. 0.03 ha; 10 years old) contained the highest overall densities of glossy buckthorn, but few stems were flowering (∼2%) and none were fruiting at the time of sampling. Small gaps (<0.01 ha; 10 years old) appeared to be sinks for glossy buckthorn, as all individuals were <0.5 m tall and none were >4 years old. As age and size of gaps were correlated, it was difficult to determine which factor played a larger role in the establishment and persistence of glossy buckthorn. However, the greater proportion of individuals >2 m tall and greater reproductive vigor of glossy buckthorn in large gaps relative to small gaps—despite fewer years available for growth—suggest that larger disturbances lead to more resources available for buckthorn growth, survival, and reproduction. Individuals <0.5 m tall were observed in uncut control plots at low density (<30 stems/ha) and 5% of stems in large gaps were older than the gaps themselves, suggesting that gap formation released previously established glossy buckthorn individuals (i.e., advanced regeneration).

Abbreviations

ABA	Absolute basal area
DBH	Diameter at breast height
RBA	Relative basal area

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Introduction

Non-native invasive plants threaten native forest ecosystems. Eastern US forests have been invaded by >20 non-native woody species and these may be significantly altering ecosystem structure and function

(Johnson et al. 2006; Webster et al. 2006). Webster et al. (2006) noted that woody invasives have the ability to inhibit regeneration of desired native plant species and that the alteration of natural plant communities by invasives may have unforeseen cascading consequences that diminish the ecological services provided by forests.

Forest disturbance is usually followed by colonization of early successional species (Howard and Lee 2002; Livingston and Allessio 1968; Webb et al. 2001) and may increase the potential for colonization by invasive species (Belote et al. 2008; Hobbs and Huenneke 1992; Lundgren et al. 2004; Searcy et al. 2006). Rejmánek (1989) remarked that pioneer communities exhibit a higher number of invasive species than more mature stands, suggesting that invasive species thrive on disturbance, and that open space created by biomass destruction may be the only general factor responsible for colonization of invasive species. Many invasives, in fact, were purposefully introduced to colonize disturbed areas (i.e., roadsides and eroded areas, Lundgren et al. 2004). The success of invasives after disturbance may be attributed to their ability to colonize as fast as, or faster than, native species (Lundgren et al. 2004) and to form dense stands, which prevent tree regeneration and depress forest herb populations (Fagan and Peart 2004; Frappier et al. 2003; Hartman and McCarthy 2008; Woods 1993).

Logging is a common disturbance that can facilitate invasion of forests by exotic plants. Indeed, some studies have demonstrated increased abundance or species richness of exotic plants after logging (e.g., Gray 2005; Selmants and Knight 2003; West and Chilcote 1968) although others have reported no or minimal effects (Dodson et al. 2008; Griffis et al. 2001; Kern et al. 2006; Roberts and Zhu 2002; Stapanian et al. 1998). In some cases, logging facilitates invasion only when accompanied by scarification or burning (Dodson et al. 2008; Griffis et al. 2001; Haeussler et al. 2002). The intensity of tree harvest may influence the degree of invasive success (Rejmánek 1989) as large gaps receive more light and perhaps provide more soil resources for recruiting plants (Baret et al. 2008; Denslow et al. 1998; Scharenbroch and Bockheim 2007). There is, in fact, some evidence that the species richness and abundance of invasive plants increases with the fraction of tree basal area harvested or the size of canopy gaps

(Baret et al. 2008; Belote et al. 2008; Totland et al. 2005).

Few studies have examined the effects of logging on the success of woody invasive plants in forests of the northeast USA. An extensive correlative study of invasive shrubs in central and western Massachusetts found that the presence of non-native *Berberis thunbergii* and *Rosa multiflora* was related to logging intensity, while the presence of *Frangula alnus* was not (McDonald et al. 2008a). A related study found that, on soils with low C/N, five invasive shrub species, including *F. alnus*, were associated with high intensity logging (McDonald et al. 2008b). DeGasperis and Motzkin (2007), however, found that historical land use better predicted the distribution and abundance of non-native *Berberis thunbergii* than did forest harvesting.

Abundant in the northeastern United States, glossy buckthorn (*Frangula alnus* P. Mill.; also *Rhamnus frangula* L.; hereafter 'buckthorn') is a non-native invader of both open areas and young forests—often forming dense thickets (Fagan and Peart 2004; Frappier et al. 2003; Johnson et al. 2006; Webster et al. 2006; Wingard 2007). Buckthorn grows in a wide range of soils but prefers moist to wet, nutrient rich sites (Frappier et al. 2003; Godwin 1943; McDonald et al. 2008a; Wingard 2007). Buckthorn can attain high cover in the understory of young eastern white pine (*Pinus strobus* L.)—mixed hardwood forests and is considered to be moderately shade tolerant (Cunard and Lee 2009). Like most other invasive species, buckthorn can influence species composition in communities, shift ecosystem processes, and may even cause local species extinctions (Fagan and Peart 2004; Frappier et al. 2004).

Although some research has been carried out on the ecology of buckthorn in the northeast USA (e.g., Cunard and Lee 2009; Fagan and Peart 2004; Frappier et al. 2003, 2004; Sanford et al. 2003; Wingard 2007), only McDonald et al. (2008a, b) have reported on the ability of buckthorn to colonize areas disturbed by logging and these studies offered contrasting results (see above). More detailed information on the relationship between logging intensity and the extent of buckthorn colonization would be valuable for forest management. There is no known "silver bullet" for buckthorn eradication; however, extensive knowledge of its ecology may lead to better management practices and possibly effective control methods.

Our research was conducted in New Hampshire, the second most forested state in the USA with 84% of its total land area covered by trees (Levesque 2007). Tree harvesting is a multi-billion dollar NH industry with 55.7 million board feet[3] of hardwood sawlogs and 173.9 million board feet[3] of softwood sawlogs harvested in 2005 (Levesque 2007). Harvest techniques used in the state's mixed deciduous-evergreen forest include single tree selection, group selection, and clear-cutting (Ward et al. 2006). New Hampshire also relies heavily on forest-related recreation and tourism, which was a billion dollar industry in 2005 (Levesque 2007). Clearly, the integrity of NH forests is essential for many different industries and thus sustainable management of these resources is vital.

Specific objectives of this study were to determine whether buckthorn is more abundant in gaps created by logging than in uncut forests, whether buckthorn abundance in gaps is related to gap size, and whether or not buckthorn can establish and persist under a forest canopy (i.e., advanced regeneration).

Methods

In an eastern hemlock–eastern white pine–sweet birch (*Tsuga canadensis–Pinus strobus–Betula lenta* L.) forest at the University of New Hampshire (UNH) owned Woodman Horticultural Farm, Durham, NH (43°09′04″N, 70°56′12″W), eight canopy gaps were created by tree harvest between 1998 and 2004. All eight gaps were created by the UNH Office of Woodlands and Natural Areas either for revenue generation or to demonstrate standard harvest methods. The three largest gaps (>0.08 ha) were cut in the winter of 2003–2004 and were 5 years old at the time of our study. Three small (≤0.01 ha) and two medium (ca. 0.03 ha) gaps were cut in the winter of 1998–1999, and were 10 years old at the time of the study. We established five control plots, each 20 × 50 m (0.1 ha), in the same stand as the gaps but in areas that had no evidence of recent logging or other human disturbance. To select control plots, a grid was established over areas of undisturbed forest and coordinates for control plots were randomly selected. Location of control plots was constrained such that they were not adjacent to one another; however, diagonal corners could be shared. All

vegetation sampling of gaps and control plots took place between June 1 and July 14, 2008.

Gaps were surveyed to accurately estimate total gap area. Horizontal distance between boles of adjacent margin trees was measured using a metric tape and azimuths were taken with a SUUNTO KB-20 Vista handbearing compass. Distances and azimuths were used to determine horizontal gap area via standard planar surveying methods.

A soil auger was used to examine soil profiles from at least two locations within each gap. Mineral horizons were hand-textured. As soil type in our study area varies with topographic position (Vieira and Bond 1973), we sampled different slope positions when they were present within a gap or plot. Soil samples were classified based on Vieira and Bond (1973).

We estimated basal areas of live trees in uncut control plots and cut trees in gaps. In control plots, the diameter at breast height (DBH, breast height = 1.4 m above the ground) of each live tree ≥10 cm in diameter was measured with calipers. In gaps, the diameter of each stump at the height of cut (just above ground level) was measured using calipers or diameter tape and these data were used to estimate DBH by the method of Wharton (1984). Basal area of each tree (cut and live) was estimated from DBH, and both relative basal area and absolute basal area (the latter in $m^2 ha^{-1}$) were calculated for each species in each gap and control plot.

In gaps, the line intercept method was used to estimate percent cover of herbaceous plant species and shrubs. In each gap, a center baseline running true east–west was established and transects were placed 5 m apart, perpendicular to the baseline. Transects ran true north–south, starting and ending at the gap margin. Each transect was divided into 10 m increments and, within each increment, one 5 m section was randomly chosen for sampling (Fig. 1). Each selected 5 m segment was broken up into 1 m units and percent cover of each species was estimated within these units. This was done by placing a metric tape along the transect and determining the length (cm) of one edge of the tape covered (in vertical projection) by foliage or stems of each species. A species was considered to have continuous coverage if there were no gaps >1 cm in plant cover along the line. The actual number of 5 m long segments sampled varied with gap size, where the maximum was 20 and the minimum was 1.

A Gap

B Uncut control plot
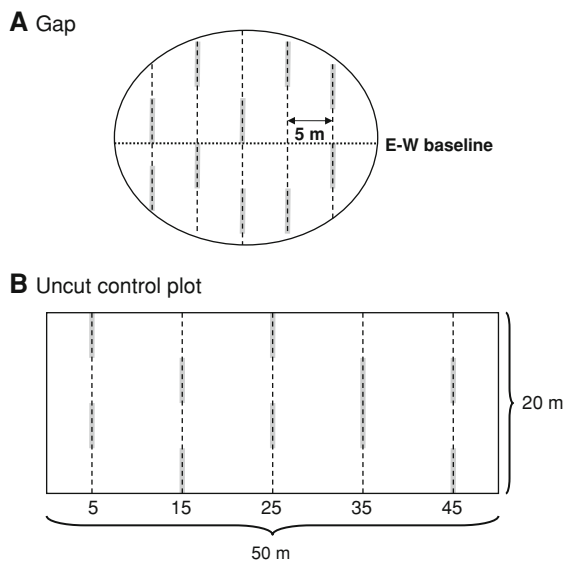
Fig. 1 Sample design for **a** a gap and **b** an uncut control plot. In the gap, transects (*dashed lines*) were 5 m apart along the east-west baseline (*dotted line*) and for every 10 m of transect, one randomly chosen 5 m segment (*shaded areas*) was sampled for plant cover. In control plots, 5, 20 m transects (*dashed lines*) paralleled the short axis of the plot. On each transect, two randomly chosen 5 m long segments (shaded areas) were sampled for plant cover. Woody stems were censused throughout gaps and control plots

The densities of trees between 0.5 and 8 m tall, and of all invasive shrubs regardless of height, were determined by census in each gap. Each individual tree or shrub (native and invasive) was identified to species and placed in a height class (0.5–1, 1–2, 2–4, 4–6, or 6–8 m). Invasive shrub species were also tallied in the 0–0.5 m class.

Vegetation sampling for uncut control plots was conducted using the same methods described for gaps. However, for percent cover estimation, 5, 20 m long transects were set parallel to the short axis of each plot. Transects were located 5 m from each end of the plot and 10 m apart throughout the central part of the plot. Each 20 m transect was divided into two 10 m increments and, within each of these 10 m increments, one 5 m section was randomly chosen to sample (Fig. 1). Cover estimation proceeded as in gaps. The densities of trees between 0.5 and 8 m tall, and of all invasive shrubs by species and regardless of height, were estimated by census in plots as described above for gaps.

Increment cores (from just above the root crown) were extracted from the largest eastern white pine and

the largest eastern hemlock in each control plot in order to approximate the age of the uncut stand. Tree ages were estimated by the number of individual wood rings between the pith and vascular cambium of each core.

All buckthorn individuals in uncut control plots and gaps were removed from the ground (including roots) and assessed as to reproductive status (fruiting and/or flowering). Up to 30 individuals per gap or plot were randomly chosen for age estimation. If multiple stems existed on the same plant, only the largest stem was sampled. The age of each sampled stem was then estimated (using a dissecting microscope or hand lens) by counting the number of wood rings observed between pith and cambium at the basal end of the cut stem segment. The wood of buckthorn is "semi-ring porous" and produces "distinct annual rings" (Schweingruber and Landolt 2005). We found that wood rings were most easily observed after allowing stems to dry for 1–2 days and making a transverse cut with a sharp craft knife or razor blade. Sanding with fine sandpaper clogged vessels with sawdust and obscured ring boundaries. Our decision to age only the largest stem per individual was based on a sample of randomly-selected, multiple-stemmed individuals (10 individuals each from two sites within 2 km of the Woodman Horticultural Farm); in 17 of these 20 individuals, the stem with greatest basal diameter had an equal or greater number of wood rings than the stem with a smaller diameter (T. D. Lee, unpublished data).

Dependent variables were compared across gap size/age classes and the control using one-way parametric analysis of variance (ANOVA). Prior to analyses, proportions were arcsine square root transformed and data sets with mean and variance correlated were log or square root transformed. Tukey's test was used to make paired comparisons. For all tests, null hypotheses were rejected when $P \leq 0.05$. When data did not meet assumptions of parametric analysis we compared gap classes and controls using a non-parametric Kruskal–Wallis test.

Results

Site characteristics

Surveying determined that all gaps were between 0.007 and 0.138 ha in area (Table 1). These precise

Table 1 Areas, gap classes, years since cut, and soil types of gaps and uncut control plots at the Woodman Horticultural Farm, Durham, NH

Gap or plot	Area (ha)	Gap class	Years since cut	Soil type
Gap 1	0.082	Large	5	H–C, B
Gap 2	0.138	Large	5	H–C
Gap 3	0.096	Large	5	H–C
Gap 4	0.037	Medium	10	H–C, B
Gap 5	0.030	Medium	10	H–C
Gap 6	0.007	Small	10	H–C
Gap 7	0.008	Small	10	H–C
Gap 8	0.008	Small	10	B
Control 1	0.1	Uncut	–	H–C, B
Control 2	0.1	Uncut	–	H–C, regolith
Control 3	0.1	Uncut	–	H–C
Control 4	0.1	Uncut	–	H–C
Control 5	0.1	Uncut	–	H–C, B

Soil types were determined using a soil auger at two locations within each gap and control plot (see text). Key to soil types: H–C = Hollis–Charlton very rocky fine sandy loam, B = Buxton silt-loam, regolith = exposed bedrock

area estimates confirmed our initial classification of gaps as large (gaps 1, 2, and 3), medium (gaps 4 and 5), and small (gaps 6, 7, and 8). Average gap area was 0.051 ha.

Study sites were underlain by three soil types: Hollis–Charlton very rocky fine sandy loam, Buxton silt loam (Vieira and Bond 1973; Table 1), and regolith (exposed rock). Hollis–Charlton soils, which typify uplands in the study area, predominated in both the gaps and control plots. There was no association of soil type with gap class or gap versus control plot.

Based on the increment cores from canopy trees, each uncut control plot contained at least one eastern hemlock or eastern white pine >92 years, suggesting that these plots had been forested for at least that long. Of the 10 trees cored, the oldest was 119 years and the youngest was 80 years. All stumps observed in control plots were well decomposed, which suggests that there had been no recent disturbances.

Tree basal area

To assess the similarity of the forest in control plots to that in gaps prior to cutting, we compared basal areas estimated from cut stumps in gaps with those from

live trees ($\geq$10 cm in diameter) in controls. Total absolute basal area (ABA) was similar in control plots, large gaps, and medium gaps (45.6–52.8 m^2 ha^{-1}), but was greater in small gaps (131.7 m^2 ha^{-1}; Table 2). Statistical analysis showed that while small gaps (10 years old) had significantly greater total ABA than control plots, none of the other paired comparisons were different (one-way parametric ANOVA on log-transformed data; $F = 5.07$; $df = 3,9$; $P = 0.025$; $R^2 = 0.628$; followed by Tukey's test). The mean relative basal areas (RBA) of individual tree species harvested from the gaps were similar to those of live trees in control plots; in all gap size classes and control plots eastern hemlock RBA was greatest, eastern white pine second, and sweet birch was either third or absent (small gaps only; Table 2). The RBA of eastern hemlock, eastern white pine, or sweet birch did not vary significantly across gap size classes and control plots (one-way parametric ANOVA on arcsine square root transformed data, $P > 0.05$).

Vegetation

Mean percent herb cover was greatest (16.1%) in medium gaps (10 years old), somewhat less in large gaps (5 years old), and sparse (<2%) in small gaps (10 years old) and control plots (Fig. 2). Herb cover was significantly different among treatments (one-way parametric ANOVA on arcsine transformed data: $F = 7.497$; $df = 3,9$; $P < 0.008$; $R^2 = 0.714$) and all treatments, except small gaps and control plots, were different from one another (Tukey's test, $P < 0.05$).

Mean total shrub cover (native and non-native species) exceeded that of herbs only in large gaps (5 years old, Fig. 2). Here, over 90% of total shrub cover was comprised of blackberry (*Rubus allegheniensis* T.C. Porter) and red raspberry (*Rubus idaeus* L. var. *strigosus*, Michx.), which together covered 42.5% of the ground. Total shrub cover was low (<4%, Fig. 2) in all other treatments. There was a significant difference in *Rubus* spp., cover among treatments (one-way parametric ANOVA on arcsine square root transformed data: $F = 51.37$; $df = 3,9$; $P < 0.001$; $R^2 = 0.945$). Control plots and small gaps were the only treatments found to have similar *Rubus* spp. cover. Besides *Rubus* spp., cover of all other shrub species was low in all gap classes and controls (Fig. 2).

Table 2 Basal areas (at breast height, 1.4 m above ground) of trees harvested to create canopy gaps and of live trees ($\geq$10 cm DBH) from uncut, control plots in Durham, NH

Treatment	Total absolute basal area (m^2 ha^{-1})	Relative basal area (proportion)			
		Eastern hemlock	Eastern white pine	Sweet birch	Other species
Uncut	45.6[b]	0.529	0.357	0.087	0.027
Large gaps (5 years)	52.8[ab]	0.480	0.347	0.171	0.002
Medium gaps (10 years)	46.0[ab]	0.615	0.323	0.061	0.000
Small gaps (10 year)	131.7[a]	0.810	0.190	0.000	0.000

For harvested trees, basal area was estimated at breast height using measurements on cut stumps (see text). Total absolute basal area (m^2 ha^{-1}, all species combined) and relative basal areas of individual species are presented for three size classes of canopy gaps (large, 0.08–0.14 ha; medium, 0.03–0.04 ha; small, <0.01 ha) and uncut control plots (0.10 ha). Values with the same letter superscript are not different at $P = 0.05$ (Tukey's test)
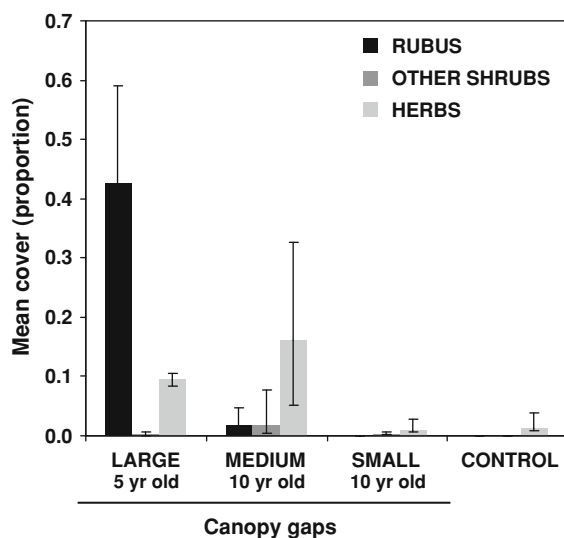
Fig. 2 Mean percent cover of *Rubus* spp., all other shrubs (native and nonnative), and all herbs in forest canopy gaps (*large*, 0.08–0.14 ha; *medium*, 0.03–0.04 ha; *small*, <0.01 ha) and control plots (0.1 ha), in Durham, NH. *Error bars* are back-transformed arcsine square root transformed standard deviations

Of the trees (>0.5 m tall and <10 cm DBH), only sweet birch and eastern hemlock had densities high enough to reveal patterns among the gap classes and controls (Table 3). Large (5 years old) and medium (10 years old) gaps contained >1,800 sweet birch stems/ha, while small gaps and control plots had few sweet birch individuals (<100 stems/ha). There was a significant difference in densities among treatments (one-way parametric ANOVA on square root transformed densities; $F = 49.42$, $df = 3,9$; $P < 0.001$; $R^2 = 0.943$), but Tukey's test showed no significant difference between large (5 years old) and medium

gaps (10 years old) or between small gaps and control plots. Eastern hemlock density was greatest in control plots, significantly lower in large gaps, and significantly lower still in medium and small gaps (Table 3, one-way parametric ANOVA on square root transformed densities; $F = 4.209$, $df = 3,9$; $P < 0.041$; $R^2 = 0.584$; followed by Tukey's test).
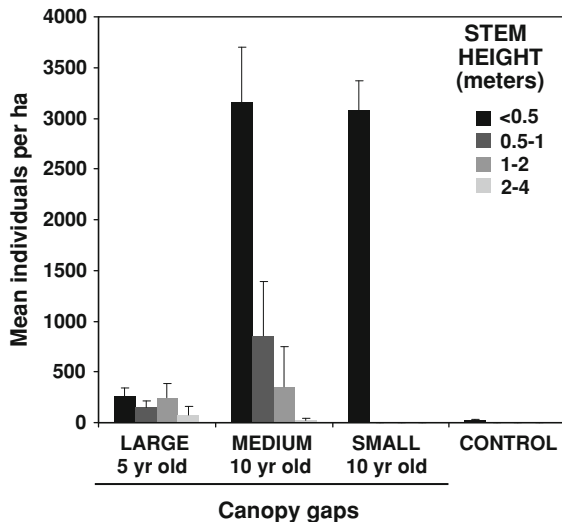
Glossy buckthorn

Glossy buckthorn was present in every gap and uncut control plot, but its mean total density (including all height classes) across all 7 gaps was over 96 times greater than its mean density in the uncut controls (Table 3). In control plots, mean density was always below 30 stems ha^{-1}, while densities in gaps ranged from 722 to 4,380 stems ha^{-1}. Total buckthorn density varied significantly among treatments (Table 3; one-way parametric ANOVA on square root transformed densities; $F = 237.5$, $df = 3,9$; $P < 0.001$; $R^2 = 0.988$) with all gap classes having greater density than control plots and the older medium and small gaps having greater density than large gaps (5 years, Table 3, Tukey's test $P < 0.05$). The medium and small gap classes were not statistically different from one another (Tukey's test $P > 0.05$).

Buckthorn height and the proportion of reproducing stems also differed between gaps and controls and among gap classes. The density of buckthorn individuals >2 m in height differed significantly among gap classes and control plots (Kruskal–Wallis test statistic = 9.131, $df = 3$, $P = 0.028$). In small gaps and control plots, stems were always <0.5 m tall. In both large and medium gaps, buckthorn was found up to 4 m tall, though these taller stems (2–4 m) occurred at

Table 3 Means and standard deviations for density (stems ha^{-1}) of sweet birch ($\geq$0.5 m tall, <10 cm DBH), eastern hemlock ($\geq$0.5 m tall, <10 cm DBH), and glossy buckthorn (all heights and diameters) in large, medium, and small gaps and in uncut control plots at the Woodman Horticultural Farm, Durham, NH

Gap or plot	Sweet birch	Eastern hemlock	Glossy buckthorn
Large gaps (5 year)	1,841 $\pm$ 785[a]	1,146 $\pm$ 1,070[b]	722 $\pm$ 330[b]
Medium gaps (10 year)	3,567 $\pm$ 338[a]	134 $\pm$ 0.63[c]	4,380 $\pm$ 395[a]
Small gaps (10 year)	43 $\pm$ 74[b]	327 $\pm$ 286[c]	3,075 $\pm$ 291[a]
Control	88 $\pm$ 75[b]	2,478 $\pm$ 1,601[a]	26 $\pm$ 11[c]

Letter superscripts (a, b, c) represent statistical differences (within species) found using Tukey's test

Fig. 3 Mean glossy buckthorn density (stems ha^{-1}) by size-age class in forest canopy gaps (*large*, 0.08–0.14 ha; *medium*, 0.03–0.04 ha; *small*, <0.01 ha) and control plots (0.1 ha) in Durham, NH. *Error bars* are one standard deviation

Fig. 4 Mean proportion of glossy buckthorn individuals in each 1 year age class, by gap size-age class (*large*, 0.08–0.14 ha; *medium*, 0.03–0.04 ha; *small*, <0.01 ha) in Durham, NH. 0 year = new seedlings (originating in 2008), 1 year = originating in 2007, etc. *Error bars* are back-transformed arcsine square root transformed standard deviations

lower densities than smaller stems, especially in medium gaps (Fig. 3). The proportion of stems 2–4 m in height was greater in all three large gaps (mean = 7.9%) than in the medium gaps (mean = 0.4%). Buckthorn was observed to be flowering only in large and medium gaps (30.5 and 2.1% of individuals, respectively), while fruiting occurred *only* in the three large gaps (16, 18 and 21% of individuals fruiting; mean = 18.4%).

Based on wood ring counts, buckthorn ages ranged from "0", i.e., seedlings originating in 2008, the year we sampled, to "7", individuals with 7 complete annual rings (and part of an 8th) and originating in 2001 (Fig. 4). Five percent of the individuals collected from large gaps were greater than 5 years old, and thus older than the gaps. Large and medium gaps

contained all age classes while small gaps only contained individuals up to 4 years old.

Discussion

Consistent with our first hypothesis, glossy buckthorn was 96 times more abundant in disturbed areas (gaps) than in undisturbed forest. Buckthorn not only had low density in uncut control areas, but these few stems were all <0.5 m in height, in contrast to medium and large gaps, where maximum stem height exceeded 2 m. Thus, tree harvest in eastern hemlock–eastern white pine–sweet birch forest appeared to promote invasion of buckthorn.

These results are consistent with a vast literature indicating that, in forests, the establishment and persistence of some species are dependent on canopy gaps. Removal of canopy trees reduces competition and allows poorer competitors to successfully colonize and, for a time, avoid competitive exclusion (e.g., Forcier 1975; Henry and Swan 1974; Leak and Filip 1975; McClure and Lee 1993). Our results are also consistent with a growing literature inferring that timber harvest promotes invasion by non-native species that might otherwise be excluded by competition (Baret et al. 2008; Belote et al. 2008; Gray 2005; Rejmánek 1989; Totland et al. 2005; West and Chilcote 1968). There are few studies of logging effects on invasive shrubs in the northeastern USA, and their results are not consistent. Webb et al. (2001) found that harvest of invasive Norway maple (*Acer platanoides*) in a mature deciduous forest in New Jersey increased the species richness and abundance of other non-native plants, including glossy buckthorn. In western Massachusetts, McDonald et al. (2008b) found that, on soils with low carbon-to-nitrogen ratios, five invasive shrub species, including glossy buckthorn, were associated with high intensity logging (McDonald et al. 2008b). Working in the same area, however, McDonald et al. (2008a) reported that the presence of Japanese barberry (*Berberis thunbergii*) and multiflora rose (*Rosa multiflora*), but *not* glossy buckthorn, was related to logging intensity. In some cases, land use history or soil characteristics are better predictors of invasive presence than the occurrence of recent logging (DeGasperis and Motzkin 2007; McDonald et al. 2008a).

Some invasive plants, such as Norway maple (Martin and Marks 2006) and perhaps Japanese barberry (DeGasperis and Motzkin 2007) may be sufficiently shade tolerant to persist indefinitely under a closed canopy. Glossy buckthorn invades and persists in early and mid-successional forest stands, even without canopy disturbance, but declines in late successional stands, apparently due to reduced light levels associated with canopy dominance by shade-tolerant trees (Cunard and Lee 2009). Over time, buckthorn's intolerance of deep shade might result in its exclusion from late successional stands. Our data suggest that canopy gaps might reverse buckthorn decline and allow its long-term persistence in northeastern forests.

Specific gap characteristics, such as size and time since logging, likely played important roles in the post-logging plant community and in glossy buckthorn establishment in gaps at Woodman Horticultural Farm. As gap size and age were perfectly correlated in our study (small and medium gaps were 5 years older than large gaps), it was difficult to determine which of these two variables played the greater role in determining patterns of buckthorn abundance, height, and reproduction among gaps. As we explain below, it is likely that both factors—age and size—played important roles.

The greater density of buckthorn in the older (medium and small) gaps may have been the result of additional time available for colonization. Despite more time for growth, however, the majority of stems in these medium and small gaps were small (<0.5 m) relative to those in large gaps. At other locations buckthorn has been observed to grow at rates as high as 0.5 cm diameter per year (Godwin 1943) and up to 4 m tall in 5 years (Converse 1984)—rates that are consistent with results for our large gaps but not for small gaps. Our patterns of buckthorn reproduction reflected those of height growth; while stems in our small and medium (10 years old) gaps had not initiated fruits by mid-summer (though they may have done so later in the season), 18.4% of those in the large (5 years old) gaps were fruiting and almost a third were flowering. The greater proportion of tall plants and greater reproductive vigor of plants in large gaps, relative to small and medium gaps—despite fewer years available for growth—suggests that individuals in smaller gaps were more light-limited (and perhaps more nutrient-limited) than those in the large gaps. Moreover, that buckthorn individuals were younger (had fewer wood rings) in the small (10 years) gaps than in the medium (10 years) and larger (5 years) gaps, suggests lower survival in the smaller gaps and is consistent with the hypothesis of greater stress there.

Collectively, patterns of buckthorn height, reproduction, and age suggest that small gaps (<0.01 ha, typically created under single tree selection) in eastern hemlock–eastern white pine–sweet birch forest will be sinks (sensu Pulliam 1988) for buckthorn and will not, by themselves, allow long-term persistence of buckthorn (although overall buckthorn abundance *is* greater in small gaps). Like many other forest species,

buckthorn may be adapted to successfully colonize gaps larger than a certain size (Forcier 1975; McClure and Lee 1993; Runkle 1981), and given that natural or anthropogenic openings meet this size criterion, buckthorn may be able to persist in these forests. Increased gap size is known to increase the abundance of two woody invaders of tropical forests, *Rubus alceifolius* (Baret et al. 2008) and *Lantana camera* (Totland et al. 2005).

There is an alternative hypothesis to explain the higher density of buckthorn in the older (small and medium) gaps as compared with the younger (larger) ones. A large buckthorn population was located ca. 100 m northeast of three of the five medium and small gaps, while the remaining small and medium gaps and all three larger gaps were farther from this population. Because of the close proximity of some of the medium and small gaps to this potential source of colonists, these gaps may have been more frequently and repeatedly colonized over the past 10 years, resulting in higher density than the more remote gaps. This, perhaps combined with the likely low survival of buckthorn seedlings in small gaps, may also explain why small gaps had only buckthorn individuals <4 years in age despite the gaps having existed for 10 years.

Our control plots had been forested for at least 90 years. At the time of sampling, the forest canopy of every control plot was dominated by eastern hemlock, eastern white pine, and sweet birch, and these canopies were continuous (free of openings caused by canopy tree death). Levels of photosynthetically active radiation in the understories of these plots were likely very low (Howard and Lee 2002). Thus, the existence of a few buckthorn individuals under these dense eastern hemlock–dominated canopies suggests that buckthorn is moderately tolerant of shade and is able to survive, at least for some undetermined time period (perhaps just a few years), under light-limitation. This view is in agreement with the work of Frappier et al. (2003) and Cunard and Lee (2009). Such 'advanced regeneration' suggests that buckthorn forms 'seedling banks,' cohorts of suppressed seedlings that can take immediate advantage of canopy openings. Such opportunism is known for native forest trees such as shade-tolerant sugar maple (*Acer saccharum* Marshall; Canham 1985; McClure et al. 2000) and American beech (*Fagus grandifolia* Ehrh.; McClure et al. 2000), although buckthorn is probably unable to withstand suppression for as long a time as these species. Successful advanced regeneration of buckthorn in our study is supported by the fact that 5% of stems in the large gaps were estimated to be 1–3 years older than the gaps themselves; these stems must have established prior to gap formation and likely withstood a period of suppression prior to gap formation.

It is possible that variation in buckthorn abundance, size, reproduction, and age among gap classes and control plots was influenced by factors other than gap size and age. Gaps and control plots may have differed in soils or micro-climate. Our field observations, however, indicated that soils did not vary greatly among sites. Moreover, the abundances of canopy tree species, which typically change in response to soil and micro-climate characteristics (e.g., Leak 1978), did not differ among gap classes and control plots. Total absolute basal area (ABA of all species) was greater in small gaps than in uncut controls, but this was likely the result of loggers selecting one to several particularly large trees for harvest. In medium and large gaps, which resulted from group selection, trees of various sizes were removed and total ABA was not distinguishable from that of control plots. We concluded that the species composition and structure of the forest that occupied the gaps prior to cutting was generally similar to that in control plots.

Another factor potentially influencing the abundance and population structure of buckthorn in canopy gaps was competing vegetation. The large (younger) gaps had 42.5% *Rubus* spp. cover, while medium (older) gaps had little shrub cover and modest herb cover, and the small gaps had little plant cover of any kind. Our data showed that the high *Rubus* spp. percent cover in large gaps was complemented by low buckthorn density, especially in the smaller height classes. High *Rubus* spp. cover in the large gaps, perhaps combined with higher hemlock densities than in other gap classes (see below), may have decreased buckthorn germination and establishment there, especially in recent years as *Rubus* proliferated. The herbs in medium (older) gaps did not appear to have had the same effect on buckthorn. At present, it is impossible to decipher this because we do not know whether buckthorn readily competes with herbs or other shrubs during initial post-logging succession.

There were distinct abundance patterns observed across all treatments for sweet birch and eastern hemlock stems. Sweet birch was abundant in large

and medium gaps but nearly absent in small and control treatments. Sweet birch is a well known gap colonizer (Henry and Swan 1974) and probably utilized light and nutrients released after gap creation. It is likely that there was not enough biomass destruction in the small gaps to allow sufficient sunlight for sweet birch colonization. Conversely, eastern hemlock was most abundant in large gaps and in the understory in the control plots, and this was most likely due to advanced regeneration. Low eastern hemlock density in small and medium gaps may have been a result of chance absence of advanced regeneration there, or mortality caused by skidder activity, dragging of timber, or slash deposition during harvest.

The ability of glossy buckthorn to successfully invade medium and large canopy openings in concert with its ability to inhibit tree regeneration (Fagan and Peart 2004; Frappier et al. 2004) poses a problem for forest management. In New Hampshire and elsewhere in New England, foresters use a mix of silvicultural systems, ranging from single tree selection, which creates small canopy gaps, through group selection and clear-cutting, which leave larger openings (Leak and Filip 1975; Ward et al. 2006). Our results suggest that buckthorn invasion in eastern hemlock-dominated stands might be minimized through the use of single tree selection. Unfortunately, in hemlock stands, single tree selection tends to regenerate less valuable shade-tolerant species such as hemlock and American beech (Ward et al. 2006). Group selection and clear-cutting regenerate mid-tolerant and intolerant species, such as the birches and oaks (Leak and Filip 1975; McClure and Lee 1993; Ward et al. 2006), which are economically more desirable. Consequently, when managing for less tolerant species in areas where buckthorn is abundant, maximum tree regeneration may depend on buckthorn removal several years after logging. Silvicultural system is less an issue in successional ("old-field") white pine-dominated stands in our area, as buckthorn is capable of invading these stands regardless of disturbance regime (Cunard and Lee 2009).

Conclusion

Glossy buckthorn (*Frangula alnus*) was 96 times more abundant in disturbed (logged) areas than in undisturbed eastern hemlock dominated forests. The size of the disturbance, however, seemed to play an important role in the establishment and persistence of this invasive shrub. Larger gaps allowed for the establishment of buckthorn and the growth of some individuals to maturity; medium gaps allowed for individuals to mature, at much slower rates, perhaps due to light limitation; and small gaps allowed for the establishment of buckthorn but not for long-term persistence. Buckthorn was able to establish seedlings at low densities under a closed eastern hemlock-dominated canopy, which suggests that it may be capable of colonizing gaps by means of advanced regeneration. Harvesting trees via single tree selection may minimize interference of buckthorn with tree regeneration, but may not regenerate desired tree species.

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