



Impact of the invasive shrub glossy buckthorn (*Rhamnus frangula* L.) on juvenile recruitment by canopy trees

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Abstract

The invasion of forests in the northeastern USA by glossy buckthorn (*Rhamnus frangula* L.) has resulted in a dense, non-native shrub layer that frequently dominates the understory. We investigated the effects of buckthorn on the survival and growth of juvenile canopy trees spanning a wide range of shade tolerance (sugar maple, *Acer saccharum* Marsh.; red maple, *Acer rubrum* L.; white ash, *Fraxinus americana* L.; and white pine, *Pinus strobus* L.), in a stand dominated by white pine. First, we measured the effect of buckthorn on sapling growth in a field study. Second, we inferred effects on sapling survivorship from age data and from published relationships between radial growth and mortality rate. Third, we evaluated the effects of buckthorn on seedling growth and survival in canopy openings, by felling trees to create experimental gaps.

Buckthorn reduced the growth and survival of saplings of all species, and altered the relative abundance of seedlings in favor of shade-tolerant species. Estimates of sapling survival implied that <10% of tree saplings can survive to grow through high density buckthorn under closed canopies. This reduces the probability that understory saplings will survive to recruit into all newly formed canopy gaps. The experimental results suggest that tree seedlings are most likely to recruit in canopy gaps, despite the generally high buckthorn cover in gaps. Thus, recruitment of tree seedlings in gaps (even under buckthorn) may become the main source of canopy recruits. The increasing dominance of glossy buckthorn in New England pine forests is likely to change the relative abundance of tree species in the forest canopy, and may delay the filling of canopy gaps.

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1. Introduction

Invasions of non-native plant species are a world-wide problem, causing dramatic changes in the species composition of communities (Parker et al., 1999; Schmitz et al., 1997; Farnsworth and Ellis, 2001), shifts in ecosystem processes (fire: D'antonio and Vitousek, 1992; nutrient cycling: Gordon, 1998;

Ehrenfeld et al., 2001; hydrology: Gordon, 1998), and even species extinctions (D'antonio and Vitousek, 1992). Such invasions are a problem for resource managers, causing at least 148 million dollars in lost revenue each year in the USA alone (Pimentel et al., 2000). Research on invasive plants commonly focuses on species that reach high densities (often forming monocultures) in their new habitat (Farnsworth and Ellis, 2001; Parker et al., 1999). However, some invasive plants that reach high density do not completely replace native species. Their impact on the community is then less obvious.

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The rapid invasion of several species of shade-tolerant, non-native shrubs into eastern forests (Hunter and Mattice, 2002) has had negative effects on forest tree seedlings, reducing survival and growth (Gorchov and Trisel, 2003) as well as local density and species richness (Woods, 1993; Silander and Klepeis, 1999; Hutchinson and Vankat, 1997; Frappier et al., 2002; Collier et al., 2002). If non-native shrubs change the relative abundance of tree species at the seedling stage, the relative abundances of recruits to the canopy could change accordingly. However, the effects of shrubs on juvenile trees may continue through the sapling stage and beyond. Thus, the effects of non-native shrubs on canopy recruitment cannot be determined from seedling studies alone.

To date, a direct impact of understory shrubs on canopy recruitment has been shown only for native shrubs occurring at locally high density. Some shade-tolerant native shrubs can cause complete failures in local canopy tree recruitment; these include *Rhododendron* spp. (Beckage et al., 2000; Baker and Van Lear, 1998), vine maple (*Acer circinatum* Pursh; Wardman and Schmidt, 1998), and bamboo (*Chusquea* spp.: Veblen, 1982; *Sasa* spp.: Yamamoto et al., 1995).

In this study, we investigate the impact of an invasive shrub, glossy buckthorn (*Rhamnus frangula* L.), on the performance (defined as survival and growth) of both seedlings and saplings of canopy tree species spanning a wide range of shade tolerance. We are aware of no previous study examining whether non-native shrubs influence tree sapling recruitment through the shrub layer. We hypothesized that negative effects of buckthorn would be greatest on the most shade-intolerant species.

The invasion of glossy buckthorn into forests and riparian areas in the Northeast has alarmed foresters and conservationists (Reinartz, 1997; Post et al., 1989; Converse, 1984). Buckthorn attains high cover in the understory of closed white pine (*Pinus strobus* L.) forests, especially in gaps. It is a tall, shade-tolerant shrub, commonly reaching 3 m in height in the understory and 4–5 m in gaps and open areas (Converse, 1984). In the understory, tree seedling density and diversity are known to be inversely related to buckthorn basal area, implying that buckthorn lowers the survival or germination rates of tree seedlings (Frappier et al., 2002). Fast-growing and bird-dispersed,

buckthorn has spread into many pine forests in the northeastern US and southeastern Canada in the last 20–30 years (Frappier et al., 2002; Catling and Porcowski, 1994).

Forests dominated by white pine are common throughout New England and are economically important sources of timber. Because buckthorn has frequent seed crops in sunny areas and can form seed banks in nearby forests (Frappier et al., 2002), it is likely to continue increasing in pine forests in the northeastern US for the foreseeable future. White pine does not regenerate under a closed canopy. We focused on the impact of buckthorn on the tree species that will replace the white pine canopy over time, in stands that are not silviculturally manipulated to promote white pine regeneration. The effects of shade-tolerant, invasive shrubs on juvenile recruitment may reduce the profitability of timber operations in invaded forests (Hutchinson and Vankat, 1997). Specifically, white pine forests with understories dominated by buckthorn may not remain economically viable for logging if buckthorn interferes with canopy replacement (delaying timber production) or shifts future canopy dominance to species with low timber value.

If buckthorn affects tree juvenile performance, the impact on canopy recruitment depends on how those effects vary with juvenile size, tree species, and canopy openness (gaps versus understory). We investigated the effects of buckthorn on the survival and growth of juvenile canopy trees of sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.), and white pine (*P. strobus* L.). First, we measured the effect of buckthorn on sapling growth in a field study. Second, we inferred effects on sapling survivorship from age data and from published relationships between radial growth and mortality rate. Third, we evaluated the effects of buckthorn on seedling growth and survival in canopy openings, by felling trees to create experimental gaps.

2. Methods

2.1. Study site

This was a privately owned 2.5 ha stand at Signal Hill, Lebanon, New Hampshire, USA (43°39'N,

72°14'W), between 240 and 360 m in elevation, on a gentle (10–20°) slope with a west-southwest aspect. The stand was chosen and delimited so that its overstory was dominated by white pine (>75% basal area), with glossy buckthorn present in the understory at densities >4 stems/100 m². The stand was ca. 50 years old, originating from cattle pasture (F. Hatch, long-time landowner, pers. commun.). Management since reversion to forest has been limited to scattered tree girdling and felling in 1981–1982. Buckthorn invaded the forest and surrounding wetlands in the early 1980s (F. Hatch, pers. commun.). Soils were shallow, rocky glacial till, with occasional granitic bedrock extrusions. The canopy was mostly white pine (*P. strobus*, 75–80% of canopy trees), with lower densities of red maple, sugar maple, and white ash, and occasional *Quercus rubra* L., *Prunus americana* Ehrh., and *Pyrus malus* L.

Although dominated by glossy buckthorn, the understory contained saplings of red maple, sugar maple, and white ash. Buckthorn cover was high in most areas, often reaching 100%, especially in canopy gaps. Over the study site, high density buckthorn (>50% cover) occurred in 41% of the area (unpublished data). Areas in or near large natural gaps (i.e. within 10 m of a gap >100 m² in area), or dominated (>75% cover) by ferns or other species of non-native shrubs, were excluded from our study. Rather, we

assessed juvenile tree performance in understory areas with high buckthorn cover, and in controlled (experimental) gaps. Areas in and near canopy gaps occupied 41% of the study site; areas dominated by ferns or other non-native shrubs occupied ca. 5% (unpublished data).

2.2. Sapling growth

From September to December 2002, we censused the entire 2.5 ha study site (except for excluded areas, as described above) for saplings (height 1.3–5 m) of sugar maple, red maple, and white ash. These species spanned a range of shade tolerance (sugar maple > red maple > white ash; Baker, 1949; Caspersen and Kobe, 2001). We included all tree saplings that fell into one of three buckthorn cover categories: subordinate, open, or emergent. Subordinate saplings were covered and surrounded by buckthorn, open saplings were free of buckthorn cover but occurred within 3 m of buckthorn, and emergent saplings had crowns above the buckthorn but were surrounded by buckthorn. Each sapling was assigned to one of these categories using the density of neighboring buckthorn stems and a crown illumination index CII (Clark and Clark, 1992; defined in Table 1) to estimate buckthorn cover. See Table 2 for sapling category definitions.

Table 1
Two indices of canopy openness defined for individual saplings

(A) Canopy cover class value	Definition
4	Direct small gap light: in a 90° arc above the sapling's crown, there is a canopy gap (>25 m ²) to the south, east, or west
3	Diffuse small gap light: in a 90° arc above the sapling's crown, there is a canopy gap (>25 m ²) to the north
2	Open canopy: in a 90° arc above the sapling's crown, there are 1 or more canopy breaks totaling 9–25 m ² in area
1	Completely closed canopy: in a 90° arc above the sapling's crown, there are no canopy breaks totaling >9 m ² in area
(B) Crown illumination index (CII) Definition	
5	Crown free of cover in 90° arc above it, and on all sides
4	Crown free of cover only immediately above it (in cylindrical projection)
3	Crown covered <90% above
2.5	Crown covered >90% above, with large gaps to the side (>50% surrounding area)
2	Crown covered >90% above, and one or more medium gaps to the side (26–50% surrounding area)
1.5	Crown covered >90% above, and only one small gap to the side (<25% surrounding area)
1	Crown has >90% cover above and is covered on all sides

(A) Canopy (overstory) cover codes. (B) Crown illumination index used for understory cover above and around saplings (adapted from Clark and Clark (1992)).

Table 2

Definitions of sapling categories relative to buckthorn cover, using crown illumination index and buckthorn stem density (see text for details)

			Approximate Scale:
	Subordinate	Open	Emergent
CII	2.5 or lower	4 or higher	4 or higher
Buckthorn stem density	One large stem (>1.3 m) within 1 m of sapling	No large stems within 1 m, one large stem within 3 m	One large stem (>1.3 m) within 1 m of sapling

For each species, in each buckthorn cover category (open, subordinate, or emergent), we randomly selected 30 saplings (except where the total number was <30) for measurement. To minimize spatial dependence in the data, only two saplings of each species were used in each 100 m² area. On each chosen sapling, we measured height, buckthorn cover category, basal diameter at 10 cm and percentage of buds browsed (by cervids). We also estimated both buckthorn-only and total (all vegetation) cover around each sapling, using CII, and overstory canopy code (defined in Table 1). Percentage of buds browsed was measured because most saplings showed evidence of minor cervid browsing and because shrub cover may influence browsing damage to seedlings (Gorchov and Trisel, 2003). In December 2002, saplings were cut at 10 cm above ground, for measurement in the laboratory.

On each individual, we measured annual extension growth (using bud scale scars) and radial growth. Extension growth could be measured reliably up to 9 years in the past. Age and radial growth were measured at 10 cm height on each sapling, by scanning stem cross-sections and measuring annual ring widths using WinDendro software (Regent Instruments, Inc.). Mean extension growth prior to 9 years ago was then estimated as (height 9 years ago – 10 cm)/(age – 9). Ring width measurements were made on the longest radius from pith to edge (bark excluded) and on a radius perpendicular to the longest radius; the mean of these two measurements was used in the growth analyses. So that sapling mortality could be estimated using published relationships between mortality and radial

growth (see below), radial growth was also measured a second time following the methods of Kobe et al. (1995). Kobe et al. (1995) measured the five most recent annual rings on a representative radius (the radius bisecting the angle formed by the longest and short radii of the stem cross-section). For consistency, we also used a 5-year interval to compare patterns of mean radial growth among sapling categories and species.

We analyzed differences among tree species and among sapling categories (emergent, open, and subordinate) in current height, height in 1993, overstory canopy code (Table 1), and percentage of buds browsed, using two-way ANOVAs. We analyzed the effect of species and buckthorn cover (open and subordinate) on mean extension growth (past years 1–9) and mean radial growth (past years 1–5) in three-way ANOVAs that used sapling size as a covariate. We then used three-way repeated-measures MANOVAs to determine how annual extension and radial growth changed from year to year. Extension and radial growth for each year were log-transformed to equalize the variance among sub-canopy categories and to normalize the residuals.

2.3. Sapling mortality

We used our radial growth data, along with published relationships between mortality rate and sapling radial growth (Kobe et al., 1995; Caspersen and Kobe, 2001), to estimate sapling mortality rates, for both open and subordinate saplings. Kobe et al. (1995) found that sapling mortality was related to radial growth by an approximately negative exponential

curve. For each species, we estimated three sapling mortality rates, based on the published parameter means and their high and low 95% confidence limits (Kobe et al., 1995). For each set of mortality parameters (mean, high and low), *t*-tests were used to evaluate differences in mortality rate between sapling categories (open and subordinate).

We estimated the time necessary for each tree species to grow through the buckthorn layer by taking the difference between minimum sapling height (1.3 m) and the mean height of emergent saplings (3.1 m) and dividing the result by the mean annual extension growth of subordinate saplings. We then used the estimated sapling mortality rates to project the density of subordinate saplings that would remain when they emerged from the buckthorn layer.

2.4. Experimental gaps and seedling performance

In October 2000, seven 10 m × 10 m plots were randomly located across the study site, subject to the criteria that they contain >50% buckthorn cover, at least 100 buckthorn stems >1.3 m in height, and occur under closed canopy. From November 2000 to March 2001, all trees in three of these plots were cut and moved outside the plots. Experimental gaps were limited to three at the landowner's request. The remaining four plots served as understory controls. Canopy openings ranged from ca. 100 to 300 m² in area, due to variation in the sizes of cut trees, and in the damage outside plots caused by tree felling. This variation in gap size probably contributed to variability in experimental results, by generating variation in resource availability. However, effects were measured entirely within the central 10 m × 10 m open areas.

In June 2002, a sample of seedlings of three species (sugar maple, red maple, and white pine) was tagged in each plot. These were the most common tree species occurring as seedlings under buckthorn canopies, and they covered a range of shade tolerance (sugar maple > red maple > white pine; Baker, 1949). In each 10 m × 10 m plot, seedlings <20 cm tall were tagged in 21 randomly selected 1 m² subplots, stratified across three buckthorn density classes: high (>1 buckthorn stem, >1.3 m tall), medium (one stem, >1.3 m tall), and low (no stems, >1.3 m in height). Seedlings were tagged in sequence, south to north, omitting those within 10 cm of already tagged seedlings. With this

protocol, seedling crowns did not touch, and seedlings were assumed to be independent within plots.

On each tagged seedling, we measured stem height, current-year extension growth, basal diameter, age, and finally the estimated CII for both buckthorn cover and cover from all understory vegetation (see Table 1 for categories). Seedlings were measured in June and September; plots were visited in random sequence, alternating by canopy treatment (gaps versus understory).

We used ANOVAs to determine if seedling extension growth (measured in August) and survival (over the period June–September) differed among species, or was affected by gap creation or by differences in understory cover (either total cover or buckthorn cover). Extension growth was log-transformed to normalize residuals. Individual size (basal diameter) was highly correlated with extension growth and was used as a covariate in the analysis. Buckthorn cover and total understory cover (both evaluated as CII) were strongly associated (78% of seedlings had the same cover code in both). Because buckthorn cover was of central interest, and explained more variation in seedling performance than did total understory cover in all analyses (higher *R*²), we present the results for buckthorn cover. The two metrics gave qualitatively similar results. In the growth analysis, CII values were binned into four classes to increase sample sizes: high buckthorn cover (CII 2 or lower), overhead buckthorn cover (CII of 2.5), partial cover (CII of 3), or low cover (CII of 4 or higher). In the survival analysis, CII was binned into two classes to increase sample size: high buckthorn cover (CII 2.5 or lower) and low buckthorn cover (CII 3 or higher). Survival data were arcsine-transformed.

Because sugar maple did not occur in control plots containing white pine and red maple, sugar maple response was analyzed separately from that of the other species.

3. Results

3.1. Sapling growth

Saplings under buckthorn had lower mean extension growth for the last 9 years (*P* < 0.0001) and lower mean radial growth for the last 5 years (Fig. 1,

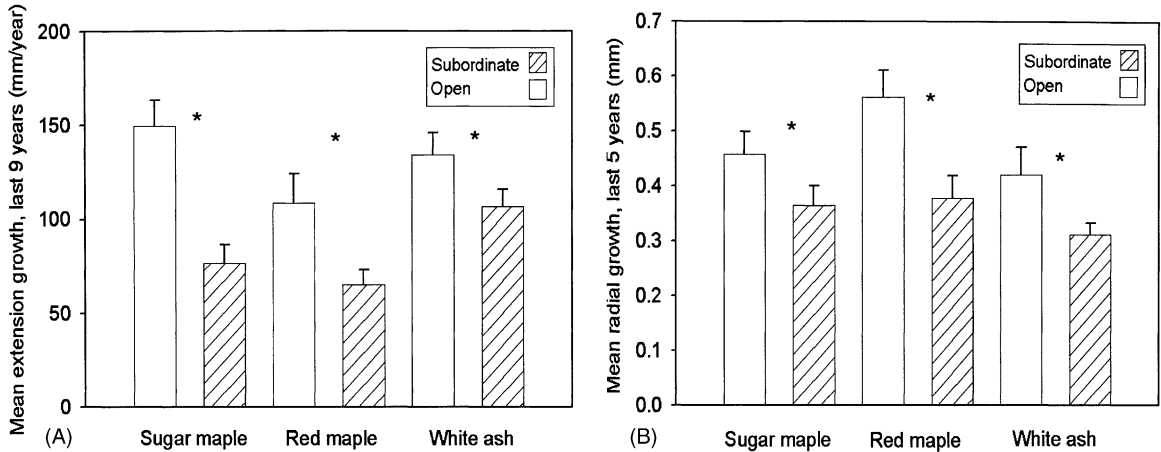


Fig. 1. Comparison of recent radial and extension growth between open (not under glossy buckthorn subcanopy) and subordinate (under glossy buckthorn subcanopy) saplings for three species (see text for details). Values are: (A) means \pm 1 S.E.) of the last 9 years of extension growth and (B) means \pm 1 S.E.) of the last 5 years of radial growth, for each sapling. Asterisks denote significant differences ($P < 0.05$) between open and subordinate saplings, within species (ANOVA).

$P < 0.0001$) than open saplings. This effect did not differ among sapling species; the species \times buckthorn cover interaction term was not significant for either extension ($P = 0.23$) or radial growth ($P = 0.26$). This reduction in sapling growth rate under buckthorn appeared in the last 8 years for extension growth and in the last 3 years for radial growth (Figs. 2–4). Repeated-measures MANOVAs showed that the effect

of buckthorn cover changed over time (i.e., a time \times buckthorn cover effect) for both radial growth ($P = 0.049$) and extension growth ($P = 0.0002$, years 1–9+). Prior to year 9, currently subordinate saplings often had growth at least equal to that of currently open saplings (Figs. 2–4).

Subordinate saplings, by definition, experienced high buckthorn cover in the understory. However,

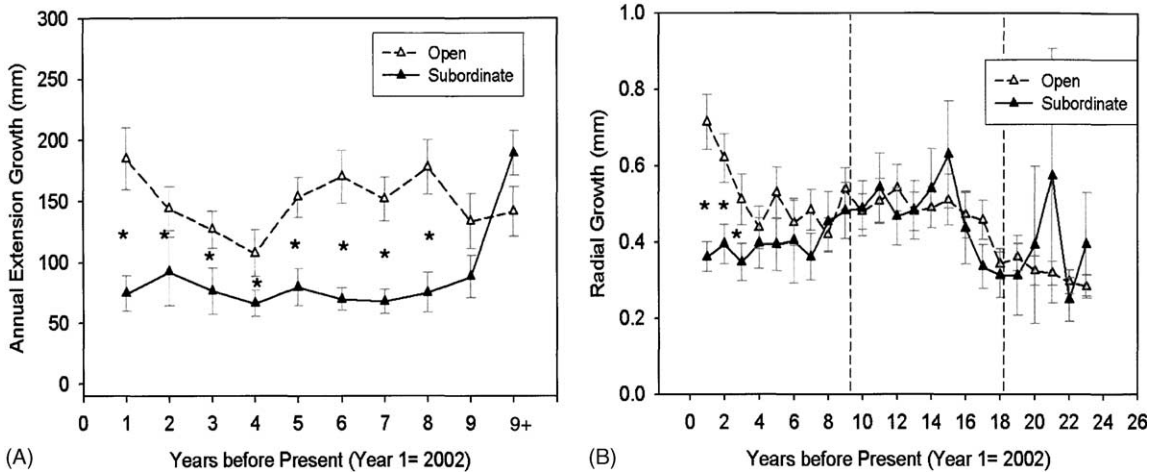


Fig. 2. Trends (means \pm 1 S.E.) in extension (A) and radial growth (B) of sugar maple, in open (not under glossy buckthorn subcanopy) and subordinate (under glossy buckthorn subcanopy) saplings (see text for details). Asterisks indicate significant differences between open and subordinate saplings ($P < 0.05$, t -tests). Values of extension growth for year 9+ are means over all previous years for each sapling. Radial growth is shown through year 23 (1980), but statistical analysis did not extend beyond year 18 due to reduced sample sizes.

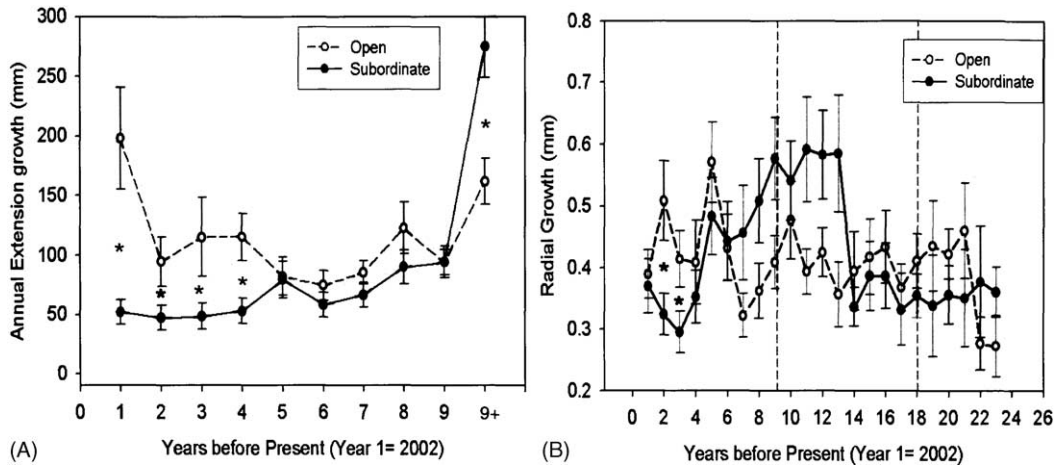


Fig. 3. Trends (means \pm 1 S.E.) in extension (A) and radial growth (B) of red maple, in open (not under glossy buckthorn subcanopy) and subordinate (under glossy buckthorn subcanopy) saplings (see text for details). Asterisks indicate significant differences between open and subordinate saplings ($P < 0.05$, t -tests). Values of extension growth for year 9+ are means over all previous years for each sapling. Radial growth is shown through year 23 (1980), but statistical analysis did not extend beyond year 18 due to reduced sample sizes.

subordinate saplings were less shaded by the upper (tree) canopy than open or emergent saplings (mean canopy cover class; subordinate 2.93, open 2.31, emergent 2.63, $P = 0.0005$). Emergents (mean height 3.09 m) were much taller than either open (2.59 m) or subordinate saplings (2.14 m) at the time of sampling (ANOVA, $P < 0.0001$). Subordinate saplings (mean height 2.14 m) were shorter than open saplings

(2.59 m, $P = 0.001$) at the time of sampling. However, this difference developed recently; their heights were similar 9 years ago ($P = 0.79$). Sapling species also differed in overall mean height (red maple 2.71 m, sugar maple 2.29 m, white ash 2.09 m; $P = 0.0007$). Percentage of buds browsed did not differ between open and subordinate saplings ($P = 0.16$) or among species ($P = 0.16$).

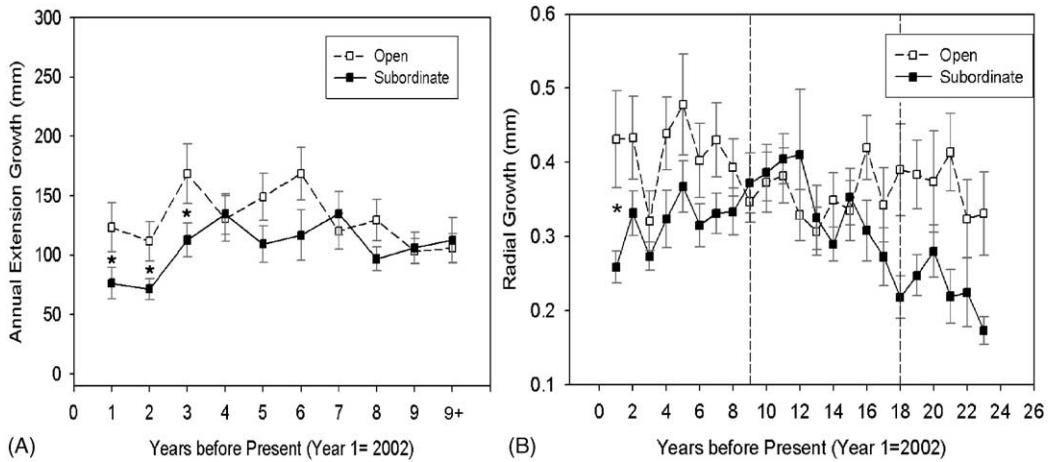


Fig. 4. Trends (means \pm 1 S.E.) in extension (A) and radial growth (B) of white ash, in open (not under glossy buckthorn subcanopy) and subordinate (under glossy buckthorn subcanopy) saplings (see text for details). Asterisks indicate significant differences between open and subordinate saplings ($P < 0.05$, t -tests). Values of extension growth for year 9+ are means over all previous years for each sapling. Radial growth is shown through year 23 (1980), but statistical analysis did not extend beyond year 18 due to reduced sample sizes.

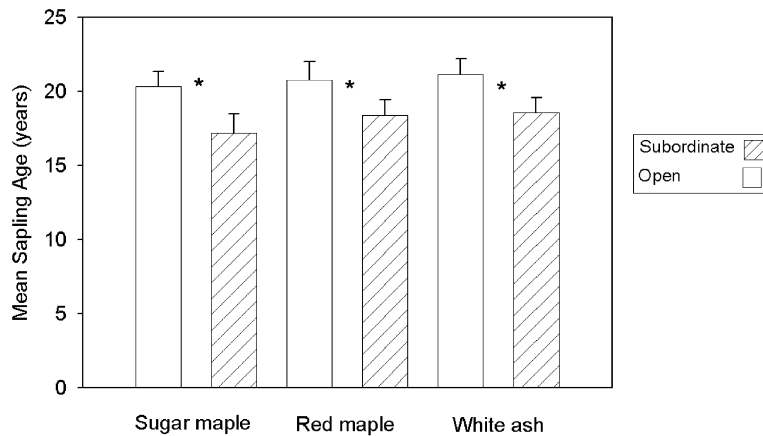


Fig. 5. Comparison of sapling ages (means \pm 1 S.E.) between open (not under glossy buckthorn subcanopy) and subordinate (under glossy buckthorn subcanopy) saplings of three tree species (see text for details). Asterisks denote significant differences for each species. Subordinate saplings were on average 2.5 years younger than open saplings ($P = 0.069$).

Tree canopy cover had no significant effects on sapling performance in these analyses and was dropped from the final model, in the results reported above.

3.2. Sapling age and mortality

Subordinate saplings were, on average, 2.52 years younger than open saplings ($P = 0.069$, Fig. 5). The relation between buckthorn cover and age was similar for all species (species \times buckthorn cover interaction, $P = 0.96$). Estimates of mortality from our radial growth data, using published growth–mortality relationships (Kobe et al., 1995), indicated that buckthorn reduces sapling survival substantially ($P < 0.05$, mean annual mortality open, 5.0%; subordinate, 10.4%). However, we cannot infer species differences in estimated mortality rate because of wide, overlapping prediction intervals in the growth–mortality relationships. For the three species of saplings we studied (sugar maple, red maple and white ash), growth–mortality curves on acidic, mesic soils (similar to those at our study site) did not differ greatly among species or geographic regions (Connecticut versus Michigan; Kobe et al., 1995; Caspersen and Kobe, 2001). In fact, the parameter estimates for the curve did not differ significantly among these species in one study (Kobe et al., 1995).

Projection of subordinate survival and growth indicates that few individuals can survive the many years of low growth and survival required to grow through

buckthorn. Saplings growing at the mean observed extension growth rate under buckthorn (8.50 cm per year) would take 22 years to grow from 1.3 m height (the beginning of the sapling height class) to 3.1 m (the mean height of emergent saplings). Estimated survival of open saplings over 22 years was much greater than that of subordinate saplings ($P < 0.05$, mean projection: 32.2% versus 8.9%, Fig. 6). Open sapling survival was always significantly higher than that of subordinate saplings, regardless of whether the mean or the upper or lower confidence limits of the mortality parameters were used (see Section 2; $P < 0.05$, Fig. 6).

3.3. Experimental gaps and seedling performance

Sugar maple seedling growth did not respond significantly to either artificial gaps or buckthorn cover ($P = 0.11$, Fig. 7). However, growth of both red maple and white pine was higher in canopy gaps ($P = 0.0003$), and red maple growth increased more in gaps than white pine ($P = 0.0015$, species \times treatment interaction). In the experimental gaps, growth of red maple and white pine was lower when under buckthorn (Tukey HSD, $P < 0.05$), but the effect of buckthorn was not significant in the understory (Tukey HSD, $P > 0.05$, gap \times buckthorn cover interaction, $P = 0.053$, Fig. 7). For sugar maple, seedling survival, like growth, was unresponsive to either buckthorn cover or artificial gaps ($P = 0.18$, Fig. 8). The survival of red maple and white pine was lower when under high

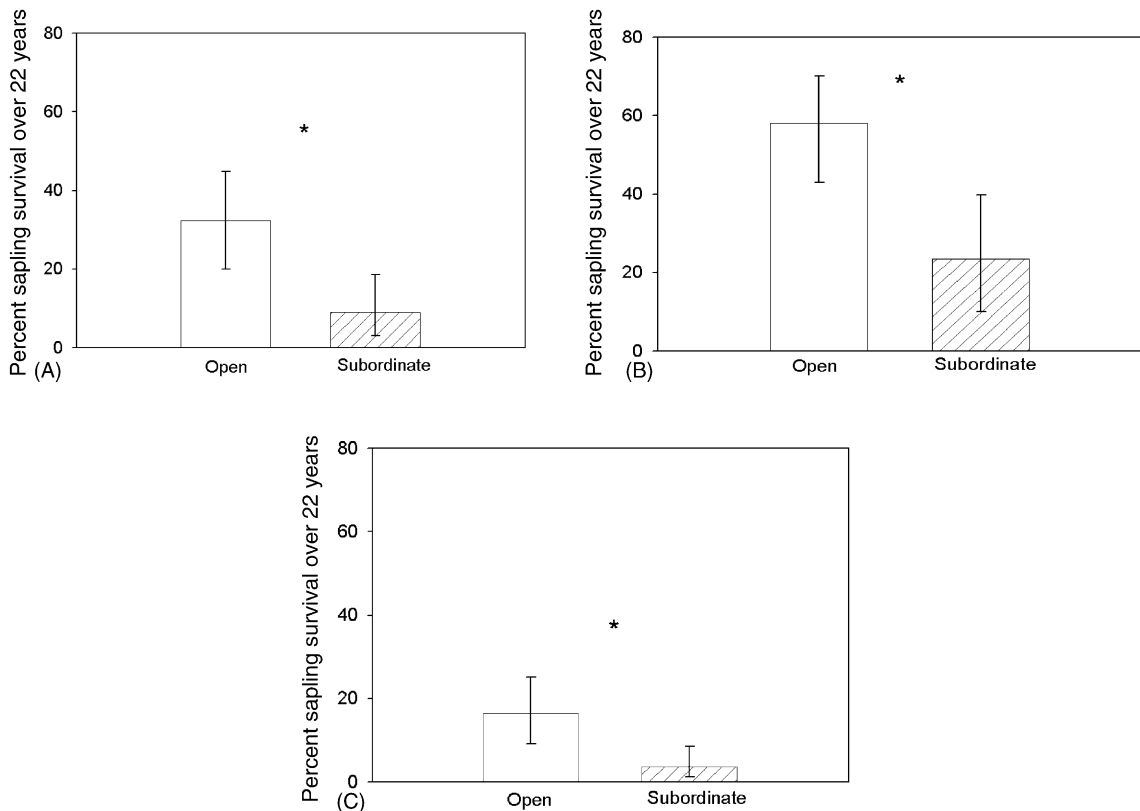


Fig. 6. Projected survival of subordinate (under glossy buckthorn) saplings to emergence from buckthorn cover. Survival was estimated from radial growth measures (this study) and published relationships between radial growth and sapling survival (Kobe et al., 1995). Estimates are shown for the mean (A), the upper (B) and lower (C) 95% confidence limits of mortality parameters, pooled for sugar maple, red maple and white ash. Values are percent estimated survival over 22 years, the mean time required for subordinate saplings to grow from 1.3 m (beginning of the sapling size class) to 3.1 m, the mean height of emergent (above buckthorn canopy) saplings. See text for details. Predicted survival of open (not under glossy buckthorn) saplings to year 22 is shown for comparison. Asterisks indicate significant differences ($P < 0.05$, t -tests).

buckthorn cover ($P = 0.029$, main effect), but only in the understory ($P = 0.072$, buckthorn cover \times gap interaction, Tukey HSD, $P < 0.05$). White pine survival was increased by artificial gaps (Tukey HSD, $P < 0.05$), but red maple survival did not differ between gaps and the understory (Tukey HSD, $P > 0.05$, species \times gap interaction, $P = 0.0015$, Fig. 8).

Of the seedlings that died, most had wilted (87%).

4. Discussion

4.1. Sapling growth

Glossy buckthorn in the forest understory clearly reduced the extension and radial growth of saplings of

all species (Fig. 1). Effects of buckthorn on growth appeared recently, and earlier for extension growth (3–9 years ago) than for radial growth (1–3 years ago). These trends imply that buckthorn either recently invaded the interior of the stand or recently increased in cover. The invasion first became apparent 20 years ago (F. Hatch, landowner, pers. commun.). Saplings appear to respond to competition in the understory by reducing allocation first to extension growth, then to radial growth; growing taller in deep shade may be a risky strategy for plants (Messier et al., 1999). Thus, extension growth appears to be a more sensitive measure than radial growth for evaluating the response of tree saplings to competition from non-native shrubs.

Differences among species in shade tolerance that were expressed in the seedling stage (red maple versus

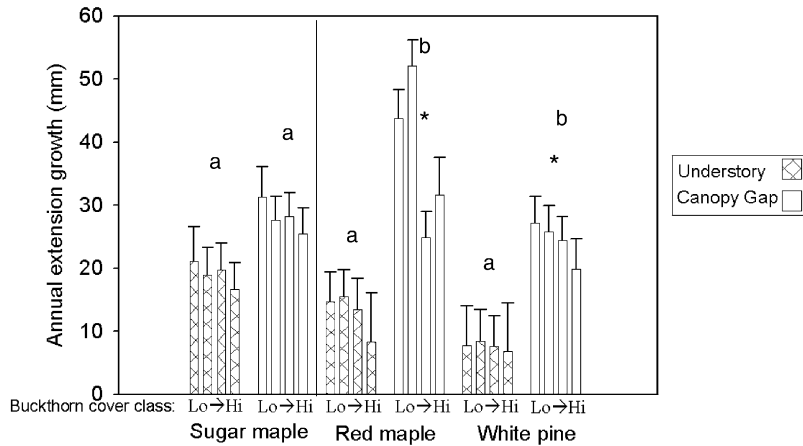


Fig. 7. Comparison of tree seedling extension growth (means \pm 1 S.E.) between experimental canopy gaps and understory, among buckthorn cover classes, and among tree species. Sugar maple was analyzed separately from red maple and white pine (see text for explanation). Letters denote significant differences between the understory and gaps, within species ($P < 0.05$, ANOVA). Asterisks denote significant effects of buckthorn cover on growth, within species and within gap or understory treatments ($P < 0.05$, ANOVA). See text for definition of buckthorn cover classes.

sugar maple, Figs. 7 and 8) were not apparent in the sapling stage (sugar maple versus red maple and white ash, Figs. 1–4 and 6). In general, tree juveniles are thought to become less tolerant of shading as their size (and therefore their respiratory demand relative to photosynthetic capacity) increases (Givnish, 1988). Red maple saplings were on average larger than sugar maple and were significantly larger than white ash;

these size differences may have obscured species differences in shade tolerance (Givnish, 1988; Messier et al., 1999).

Although light is believed to be the dominant limiting resource in the understory of temperate forest ecosystems (Canham et al., 1996), the availability of other resources has been shown to alter the effect of shading on juvenile tree performance (soil moisture,

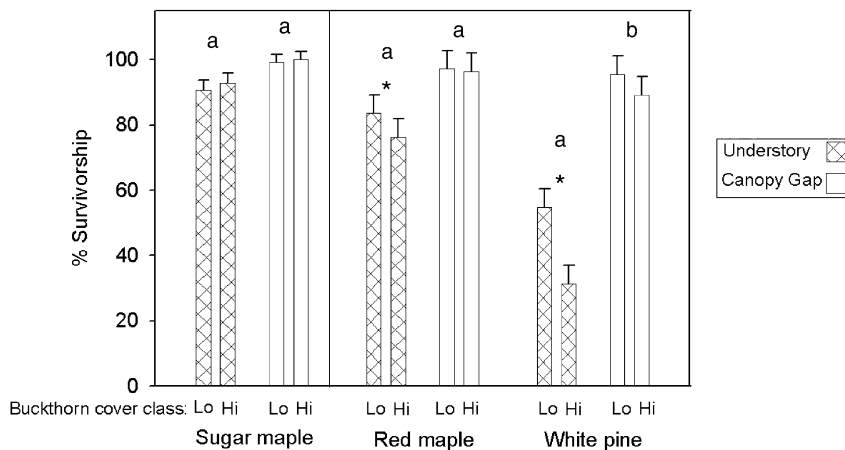


Fig. 8. Comparison of tree seedling survival (means \pm 1 S.E.) between experimental canopy gaps and understory, between buckthorn cover classes, and among tree species. Sugar maple was analyzed separately from red maple and white pine (see text for explanation). Letters denote significant differences between the understory and gaps, within species ($P < 0.05$, ANOVA). Asterisks denote significant effects of buckthorn cover on survival, within species and within gap or understory treatments ($P < 0.05$, ANOVA). See text for definition of buckthorn cover classes.

Caspersen and Kobe, 2001; nitrogen, Canham et al., 1996). In our experimental gaps, nutrient and water availability were probably affected, along with the large increase in light.

Glossy buckthorn has an extensive shallow root system (M.E. Fagan, pers. obs.) and may be a strong below-ground competitor. Japanese barberry (*Berberis thunbergii* DC.), another invasive shrub, has been shown to change soil pH and nutrient availability dramatically (Ehrenfeld et al., 2001). A mild drought during the late summer of 2002 probably contributed to the observed wilting in the seedlings that died under buckthorn, and may have affected sapling growth as well. Such short droughts are common in New England (Dupigny-Giroux, 2001).

Depending partly on variation in rainfall, below-ground competition may contribute to the overall effect of buckthorn on juvenile tree performance, causing responses that are not directly related to species' shade-tolerance. Subordinate saplings were likely affected by both above-ground and below-ground competition from buckthorn, emergent saplings by mostly below-ground competition, while open saplings were probably not subject to either. However, because these sapling classes also differed in height, we did not attempt to draw inferences in the results regarding the relative importance of above- and below-ground competition. In an experimental study of the effects of another non-native shrub, *Lonicera maackii*, both above- and below-ground effects were demonstrated, but above-ground competitive effects were strongest (Gorchov and Trisel, 2003). Overall, our main purpose in this study was to ascertain the effects of buckthorn on juvenile tree performance; we do not have evidence to discriminate rigorously among the mechanisms responsible for those effects.

4.2. Sapling age and mortality

The mean age of subordinate saplings was less than that of open saplings for all species (Fig. 5), implying that either recruitment or survival was reduced by buckthorn cover. Since buckthorn is unlikely to affect seed fall, it probably reduced the survival of all tree species in the juvenile stages, potentially including effects on seed germination.

Estimates of sapling mortality also indicate strong negative effects of buckthorn. Mean sapling mortality

under buckthorn was estimated as more than twice that of open saplings (10.4% versus 5.0% per year). We cannot estimate species differences in mortality with confidence because the parameters relating mortality to growth estimated by Kobe et al. (1995) and Caspersen and Kobe (2001) did not differ significantly among our study species.

We used estimates of mean sapling survival (all species) to project how many saplings would survive to the time taken to grow from the size of a small sapling to that of an emergent sapling. Estimated surviving sapling densities were 3.6 times greater for open saplings than for subordinate saplings (Fig. 6, mean projection: 32.3% versus 8.9% surviving). Thus, fewer than 10% of tree saplings are expected to be able to penetrate a buckthorn canopy. This increases the likelihood that saplings will fail to capture new canopy gaps when they form above dense buckthorn. Gaps with no saplings will fill more slowly from subsequent seedling recruitment (Messier et al., 1999). Such delays in canopy gap filling may increase the abundance of buckthorn in areas adjacent to gaps, due to protracted exposure to light (Frappier et al., 2002). Furthermore, delayed gap filling can itself alter the relative abundance of canopy recruits, because it favors light-demanding species that do not form seedling banks (Abe et al., 2002).

Overall, our estimates of sapling mortality and measures of sapling age support the conclusion that glossy buckthorn substantially reduces survival of all sapling species, dramatically reducing the density of potential recruits to the canopy.

4.3. Experimental gaps and seedling performance

Because high buckthorn cover reduces sapling densities in the understory, recruitment of seedlings in gaps may become the main source for canopy recruits. Although buckthorn reduced growth of shade-intermediate (red maple) and shade-intolerant (white pine) seedlings in gaps, seedling survivorship and growth rates were still higher in gaps than in the understory, even under buckthorn (Figs. 7 and 8). Canopy gaps in a shrub-dominated forest could thus be critical for successful recruitment of tree seedlings. However, if subsequent seedling performance is reduced sufficiently by understory competition, recruitment of canopy trees into gaps could nevertheless be "stalled"

for unknown lengths of time (Beckage et al., 2000; Wardman and Schmidt, 1998; Abe et al., 2002). It is likely that increases in buckthorn stature and density following gap formation will increase the negative effects of buckthorn in gaps over time.

Glossy buckthorn altered the relative abundance of seedlings towards a shade-tolerant species (sugar maple). Buckthorn reduced the performance (growth and/or survival) of all tree seedlings, except for sugar maple (Figs. 7 and 8). The survival of the most shade-intolerant species, white pine, was so reduced by buckthorn cover (Fig. 8) that pine survival to sapling size beneath buckthorn is highly unlikely. The short-term (6 months) seedling responses in this experiment showed large differences in performance among tree species that match expectations based on shade tolerance (e.g., Walters and Reich, 1996; Baker, 1949). Removal experiments and surveys by Frappier et al. (2002) also indicate that glossy buckthorn reduces the diversity and density of tree seedlings.

Our measures of seedling performance in the understory and experimental gaps provide more evidence for species-specific effects than do the results for saplings. However, we interpret these short-term results for seedlings cautiously. While buckthorn greatly reduced white pine survival in the understory, shade-intolerant white pine does not commonly form understory seedling banks, even in the absence of buckthorn (Burgess and Wetzel, 2002). The effect of buckthorn on red maple survival is more ecologically significant, although smaller in magnitude.

4.4. Management implications

Experimental studies investigating conditions for white pine regeneration (Burgess and Wetzel, 2002) indicate that seedling growth increases with both moderate thinning (one-crown spacing between crowns) and brush control by herbicide. Those experiments were apparently done in areas without heavy cover by non-native shrubs. However, experimental logging increased white pine seedling performance in our study as well, even under buckthorn cover. Thus, similar silvicultural practices to those described by Burgess and Wetzel (2002) for white pine regeneration may be effective where buckthorn invasion has occurred in the understory. Sufficiently aggressive herbicide treatments may control the tendency for

buckthorn to increase after canopy opening. Without such treatment, logging of stands already invaded by buckthorn, or in areas subject to substantial buckthorn seed input, should be considered carefully.

The following comments apply to the case where regeneration is by hardwood species, rather than white pine. Buckthorn in the understory is likely to favor other, less valuable shade-tolerant species, in addition to sugar maple (e.g., hemlock, beech, and Norway maple). Further, extended delays in canopy recruitment because of low sapling densities may reduce economic returns from timber management in forests invaded by buckthorn. The increasing understory dominance of glossy buckthorn in pine forests in the northeastern US is likely to change the species composition and rate of replacement of the forest canopy. If other invasive shrubs have similar effects, as seems plausible, the ecological impact of these invasions will extend beyond the understory to the forest canopy. Existing invasions of buckthorn and other shade-tolerant, non-native shrub species into forests in the eastern USA should be monitored, and new invasions should be prevented, if economic control measures can be found.

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