Using plants to control buckthorn (*Rhamnus cathartica*): Improved biotic resistance of forests through revegetation

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ABSTRACT

Woody invaders of temperate forest understories reduce native diversity worldwide. Common buckthorn *Rhamnus cathartica*, is among the most widespread of such invaders in North America. Invaded communities often have seedbanks largely comprised of the dominant invader - with few native species remaining - and therefore lack the capacity to build biotic resistance against re-invasion following invader removal. Consequently, invaders, including buckthorn, often quickly re-establish in the absence of continued management. We investigated the capacity of native plant revegetation to inhibit buckthorn re-establishment from seedbanks in the understories of three forests of Minnesota, USA. Specifically, we established experimental plots subjected to seeding of 35 native species, planting of Pennsylvania sedge (*Carex pensylvanica*) plugs, or bare-root plantings of either mixed shrubs (*Sambucus canadensis, Sambucus racemosa, Corylus americana,* and *Cornus racemosa*) or mixed trees (*Abies balsamea* and *Acer saccharum*). We then measured buckthorn germinant establishment, growth, and survival for the following four growing seasons. We observed consistent impacts of revegetation on ground-level light availability and associated buckthorn performance. Compared to unplanted understory controls beneath the mature tree canopy, shrub plantings were the most impactful. Shrubs reduced light availability to buckthorn seedlings by 67% relative to unplanted controls (to <2% total light by the third year) and led to 51% lower year-over-year survival of buckthorn by the end of the experiment. Revegetation also suppressed buckthorn seedling growth. After four years, shrub plantings resulted in buckthorn that were 53% shorter and had 38% fewer leaves than buckthorn grown in unplanted controls. Considering the combined impacts on survival and growth, planted shrubs, trees, and sedges reduced buckthorn invasion by 89%, 81%, and 66%, respectively; and seeding alone reduced invasion by 51%. Our findings indicate that revegetating forests, particularly with shrubs and trees, can greatly reduce invasion by buckthorn and potentially other species. Greater adoption of revegetation by land managers may therefore increase native biodiversity, reduce herbicide applications, and improve the overall health and value of forests.

1. Introduction

Invasive plant species commonly alter ecosystem structure and function in ways that jeopardize restoration efforts (Ehrenfeld, 2010). Although initial control of invasive plants is a priority for many land managers, legacies of invasion can leave communities vulnerable to re-invasion (Weidlich et al., 2020). This is a common problem in forest understories of North America invaded by *Rhamnus cathartica* L.

(common buckthorn). Buckthorn is routinely removed by chemical or mechanical means (Delanoy and Archibold, 2007) but quickly re-establishes, necessitating repeated management (Anfang et al., 2020; Knight et al., 2007). Revegetating native communities can reduce invasion in grasslands, but the efficacy of revegetation in forests is poorly understood (Schuster et al., 2018) and its effects against buckthorn invasion are untested.

The biology of buckthorn undermines native plant regeneration and

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biotic resistance, leaving forests primed for rapid re-establishment of buckthorn after initial management efforts. Following buckthorn removal, light availability at the soil surface commonly increases by over tenfold (Anfang et al., 2020) and the management-related disturbance elevates nutrient availability (Heneghan et al., 2002). These conditions favor plant establishment (Gurevitch et al., 2008). Yet, native species are rarely able to exploit these abundant resources (Ibáñez et al., 2021) due to legacies of buckthorn invasion (Lamb et al., 2022). Buckthorn readily resprouts from the stem, allowing a plant to rapidly regrow and outcompete newly-establishing plants (Wragg et al., 2021) if it has been cut or non-lethally treated with herbicide (Delanoy and Archibold, 2007; Schuster et al., 2020a). Buckthorn also produces a prolific amount of seed (Knight et al., 2007) that can result in continuous cover of seedlings (Delanoy and Archibold, 2007; Qaderi et al., 2009). In contrast, most native plant species can be excluded by buckthorn and few plants persist under dense buckthorn cover (Lamb et al., 2022; Larkin et al., 2014; Qaderi et al., 2009). Native seedbanks are also depleted following buckthorn invasion and consequent intense shading (Plue et al., 2010), and natural regeneration of native species following buckthorn removal is often limited, especially in sites with dense canopies (Larkin et al., 2014; Wragg et al., 2021). These factors result in strong priority effects that favor buckthorn over other species (Stuble and Souza, 2016; Young et al., 2005). Consequently, forests that have undergone buckthorn management have low biotic resistance and rapidly transition back into buckthorn dominance if left unmanaged (Wragg et al., 2021).

Establishing native cover soon after disturbance reduces the competitive advantage many invasive plants gain through abundant seedbanks and legacy effects on resource availability (Young et al., 2017). Buckthorn survival declines rapidly under canopies with <10% light transmission but only fails under <3% light transmission (Anfang et al., 2020; Schuster et al., 2020b), indicating that dense shading from native species is likely necessary to prevent buckthorn re-establishment. Furthermore, buckthorn depends on an extended leaf phenology that allows it to photosynthesize when many native species are dormant and the canopy is thinning (Fridley, 2012). To successfully limit buckthorn, revegetation treatments likely need to maintain cover late in autumn and mitigate buckthorn's phenological advantage (Schuster et al., 2021). As a consequence, land managers may need to consider novel plant communities to effectively suppress buckthorn (Jackson and Hobbs, 2009).

Here, we evaluate the ability of five revegetation treatments to suppress buckthorn arising from seed in three oak forests in Minnesota, USA. These revegetation treatments were designed to reflect a spectrum of land manager effort and plant functional traits. In general, we hypothesize that revegetation treatments reduce buckthorn growth and survival by limiting light availability to new buckthorn arising from seed, and that site conditions will interact with revegetated species' niches to determine overall treatment performance. More specifically, we ask: 1) how are the realized cover and composition of each revegetation treatment affected by canopy openness? 2) how are buckthorn germination and survival affected by revegetation and associated changes in light availability? 3) how is buckthorn growth affected by revegetation and associated changes in light availability?

2. Methods

2.1. Experimental design

We conducted revegetation experiments in three sites varying in canopy light interception and composition, topography, and soil conditions where dense stands of buckthorn had previously formed continuous cover. All three sites had been heavily invaded for at least a decade prior to the start of the experiment. The first site was located in a lowland oak-aspen (*Quercus* spp. and *Populus tremuloides* canopy) woodland near Marine on St. Croix, Minnesota (45.1713, −92.7654)

where buckthorn had been cleared by forestry mower in early 2017. The second and third sites were located in upland oak forests (*Quercus* spp. canopy) in Circle Pines, Minnesota (45.1100, −93.1802) and Savage, Minnesota (44.7158, −93.3346). At the Circle Pines site, buckthorn was removed by hand-cutting and treating cut stumps with Triclopyr (Garlon 4) in 2017. At the Savage site, buckthorn was removed in 2014 by forestry mowing with follow-up foliar herbicide in 2015 and burning in 2016. These three sites reflect common conditions in our region. Our treatments ranged from passive restoration (i.e. natural recruitment of native species) to densely planting bare root trees and shrubs. We selected these treatments to span a range of management options and used native species that we hypothesized would offer strong competition to establishing buckthorn due to high shade tolerance, extended leaf phenology, and/or high growth rate.

We seeded subsets of each site with a diverse mixture of 11 grasses, 2 sedges, and 22 forbs (see Supporting Information for full list of species) at a rate of 1053 seeds m^{-2} in February 2017. The seed mix (which was the same for all three sites) included species with a range of shade tolerance and growth rates to accommodate variable conditions within and between sites. The seed mix contained many species commonly used in revegetation (PB personal observation) and emphasized those that we expected to compete strongly for light against buckthorn either by producing dense vegetative cover (e.g., *Rudbeckia* spp. and *Ageratina altissima*) and/or by creating shade in autumn (e.g., senesced *Elymus* spp. leaving a layer of thatch). At each site, we then established 30 plots within six experimental blocks in April 2017. Each block consisted of five 1.2 × 1.2 m plots.

One plot (the unseeded control) was positioned in an area that was left unseeded and four plots were positioned in a seeded area. One seeded plot was left without any additional planting. The three remaining plots in the seeded area were planted with one of three additional revegetation treatments: shrubs, trees, or sedges.

The shrub treatment was planted with 30–45 cm tall bare root shrubs (an even mixture of *Sambucus canadensis*, *Sambucus racemosa*, *Corylus americana*, and *Cornus racemosa*). All four species are common in our region, but were largely absent from our experimental areas at the start of the experiment. These species were selected due to expected high niche-overlap with buckthorn (Hess et al., 2020), including (for *Sambucus* spp.) their extended autumn phenology (Schuster et al., 2021).

The tree treatment was planted with 30–45 cm tall bare root trees (an even mixture of *Abies balsamea* and *Acer saccharum*). *A. saccharum* is highly shade-tolerant and produces dense canopy cover, and *A. balsamea* is a fast-growing evergreen conifer. Sites dominated by either species have been shown to be less heavily invaded than those with more open canopies (Kurylo et al., 2007; Schuster et al., 2020b).

The sedge treatment was planted with plugs of *Carex pensylvanica*. *C. pensylvanica* is a common, fast-growing sedge that can create dense ground cover and also compete strongly for soil resources (Randall and Walters, 2019).

In all three planting treatments, plants were spaced 20–24 cm apart (the equivalent of 208,000 stems ha^{-1}). Each block was fenced with wildlife netting to exclude large herbivores. Buckthorn resprouting from cut stems were cut at ground level in July 2017–2020 to mimic thorough follow-up control of the original buckthorn invasion and prevent our small plots from being overwhelmed by resprouting buckthorn.

2.2. Measurements

We monitored the composition of experimental plots in late July or early August 2017–2019. Composition was determined via visual estimates of cover, considering only the top-most layer of vegetation, by identifying the cover type at each of 100 grid points formed by the intersections of strings in a frame placed over each plot (the sum of all cover types within a plot always equaled 100%). Observers looked directly downwards over each grid point. We determined the proportion of cover of each plot comprised by each planted species, as well as total

cover of seeded species (Supporting Information) total cover of species that were neither seeded nor planted, and area with no living vegetation (i.e. bare ground).

We measured light availability in each plot in late July or early August of 2017, 2018, and 2019 using an AccuPAR LP-80 (METER, Pullman, WA, USA). At each sampling date, we measured light availability 2 m above the ground and again at ground level (averaging two readings taken either side of the plot midline) in each plot under diffuse light conditions. We compared these measurements to each other and to simultaneous "open sky" readings taken in nearby fields using a LI-190R quantum sensor (LI-COR Biosciencecs, Lincoln, NE, USA).

Canopy light penetration (the fraction of incoming light that passed through the canopy) was calculated as the fraction of light detected above plots relative to light detected in the open. Similarly, we calculated understory light penetration (the fraction of incoming light that passed through the understory) as the fraction of light detected at ground-level relative to light detected above the understory in each plot. Finally, we calculated ground-level light availability (the fraction of incoming light that passed through both the canopy and the understory) as the fraction of light detected at ground-level relative to light detected in the open.

We utilized four cohorts of buckthorn seedlings as controlled indicators of buckthorn performance. We transplanted three first-year buckthorn seedlings into each plot in June 2017. These seedlings (the "transplant" cohort) were collected from the area surrounding the Marine on St. Croix site. Because naturally-occurring buckthorn would arise from seed, we also planted three sets of eight buckthorn seeds within each plot in May of 2017, and two additional sets of eight buckthorn seeds within each plot in both May 2018 and May 2019 (comprising the 2017, 2018, and 2019 cohorts respectively). Measurements from the individuals within each cohort within a plot were averaged for statistical analyses. Buckthorn seeds were collected from fruit on mature buckthorn trees in March 2017–2020, then cleaned and stored at 5 °C until they were planted.

We assessed the germinant establishment, growth and survival of buckthorn within plots annually in September. For each set of eight buckthorn seeds planted earlier that year, we recorded the number of seedlings that had emerged, and identified the seedling of median height. We marked this seedling for future observation and recorded its height and the number of true leaves present. We then harvested the aboveground biomass of all other seedlings arising from that cohort, dried them at 65 °C, and weighed them. We repeated height and leaf measurements for all surviving marked buckthorn that were planted in earlier years (either as seed or as a first-year seedling). If a buckthorn could not be located or had no leaves, we determined that it had died.

2.3. Statistical analyses

We used a series of linear mixed models, or generalized linear mixed models where Normal error distributions were not appropriate, to explore our four guiding research questions.

How are the cover and composition of each revegetation treatment affected by canopy openness?

We analyzed vegetation cover types separately for each treatment. For seeded and control plots, we considered three cover types: species that we seeded into plots, species that we did not seed into plots, and bare ground. For all other treatments, we also considered additional cover types: *C. pensylvanica* in sedge plots; *Sambucus* spp*., C. americana*, and *C. racemosa* in shrub plots; and *A. balsamea* and *A. saccharum* in tree plots. For each treatment, we analyzed cover as a function of cover type (3–6 levels), year (3 levels), canopy light penetration, and all their interactions, using a logit link function with beta error distribution and zero-inflation.

How are buckthorn germination and survival affected by revegetation and associated light availability?

To test the productivity and shading capacity of our planting

treatments and resulting light conditions experienced by buckthorn seedlings, we analyzed understory light penetration as a function of treatment, year, and canopy light penetration, and all possible interactions of those three variables. We also performed the same analysis with ground-level light availability as the response variable to evaluate the light conditions experienced by buckthorn seedlings.

We analyzed buckthorn germinant establishment using generalized linear mixed models. These models used a binomial error distribution and logit link function to analyze the number of seeds that germinated in the summer after they were planted. An observation-level random effect accounted for overdispersion.

Buckthorn survival was analyzed using a discrete-time survival model, incorporating survival at the end of every growing season for the marked buckthorn of each cohort. These survival models were fit using binomial error distributions with complementary log-log link functions, which resulted in coefficients that we back-transformed to estimates of annual survival probabilities (Austin, 2017). Each model included interval (year) as an additional fixed effect.

In each model, we analyzed each buckthorn response metric as a function of ground-level light availability, seedling cohort (2017 transplant, 2017 seed, 2018 seed, or 2019 seed), and their interaction. We also analyzed each buckthorn response metric as a function of planting treatment (control, seeded, sedges, trees, or shrubs), canopy light penetration, cohort, and all their interactions.

How is buckthorn growth affected by revegetation and associated light availability?

We leveraged our two oldest buckthorn cohorts (2017 seeds and transplants) to understand how our treatments affected buckthorn performance after four growing seasons. For these cohorts only, we analyzed the height (mm) and the number of leaves on all living marked buckthorn, as well as the cumulative growth of buckthorn at the end of the fourth growing season (2020).

Cumulative growth was calculated as the biomass (g) of marked buckthorn seedlings in each plot relative to the number of marked seedlings in that plot at the end of the first year of the experiment (2017). We first used the following allometric relationship based on buckthorn seedlings harvested from our experimental area to estimate biomass non-destructively:

$$ln\,(\mathrm{M}) = -10.452 + (1.4197^{*}\,ln\,[\mathrm{H}]\,) + (0.7506^{*}\,ln[\mathrm{L}+1]\,)$$

Where M is the estimated mass (g), H is the height (mm), and L is the number of leaves of a buckthorn seedling. We then calculated the product of survival through 2020 (surviving seedlings per 2017 seedling) and the mean estimated biomass of surviving seedlings in each plot. This metric, which we call "cumulative buckthorn growth," quantifies the amount of buckthorn biomass produced per seedling that existed in 2017 in an integrative way that considers both growing conditions and likelihood of survival.

We analyzed each buckthorn response metric as a function of ground-level light availability (averaged over all years) and cohort. We also analyzed each buckthorn response metric as a function of planting treatment (control, seeded, sedges, trees, or shrubs) and seedling cohort (transplant or 2017). We used a log link function with gamma error distribution for analyses of leaf count and cumulative buckthorn growth (and also zero-inflation for the latter).

2.4. Model fitting

Each model included plot nested within block nested within site as a random factor; discrete time survival analyses additionally included cohort nested within plot as a random factor. All models were fit using R package glmmTMB (Brooks et al., 2017); model assumptions were checked for all models using R package DHARMa (Hartig, 2021). To meet model assumptions about the distributions of residuals (assumed to be Normal except where other error distributions are specified above),

we log-transformed light metrics and seedling height. We report tests of the significance of fixed effects using Wald χ^2 tests from Type II Analysis of Deviance tables constructed for each statistical model. (Type II means that tests of main effects are conditional on other main effects but not on interaction effects.)

3. Results

How are the cover and composition of each revegetation treatment affected by canopy openness?

Cover within control plots was comprised mostly by non-seeded and non-planted species ($\chi^2 = 23.64$, df $= 2$, p < 0.001, Table 1). However, even though we did not seed into control plots, species that were seeded into other plots became increasingly prominent in control plots over time, especially in those with greater canopy light penetration ($\chi^2 = 13.26$, df $= 4$, p $= 0.010$).

Although seeded species were abundant within seeded plots (24% cover on average), seeded plots remained dominated by non-seeded species on average ($\chi^2 = 12.50$, df $= 2$, p $= 0.002$). Seeded species were more abundant in plots with greater canopy light penetration, reaching up to 100% cover in one plot with 45% canopy light penetration ($\chi^2 = 18.99$, df $= 2$, p < 0.001). Conversely, bare ground and non-seeded cover was sharply lower at sites with higher canopy light penetration.

The planted species, *C. pensylvanica*, dominated sedge plots and had the highest mean cover of the considered categories ($\chi^2 = 45.53$, df $= 3$, p < 0.001), and tended to be greater in plots with higher canopy light penetration ($\chi^2 = 40.15$, df $= 3$, p < 0.001). Remaining cover varied between seeded and non-seeded species over time ($\chi^2 = 42.01$, df $= 6$, p < 0.001). Bare ground remained a relatively minor constituent of sedge plots over time.

Tree plot cover was dominated by *A. saccharum* ($\chi^2 = 26.93$, df $= 4$, p < 0.001), especially in later years ($\chi^2 = 31.99$, df $= 8$, p < 0.001), reaching approximately 40% cover on average in 2019. *A. saccharum* cover declined where canopy light penetration was higher, whereas seeded herbaceous species were more abundant in plots with higher canopy light penetration ($\chi^2 = 31.74$, df $= 4$, p < 0.001). *A. balsamea* remained relatively stable throughout our experiment (22% cover on average). Cover of herbaceous seeded and non-seeded species tended to decline over time.

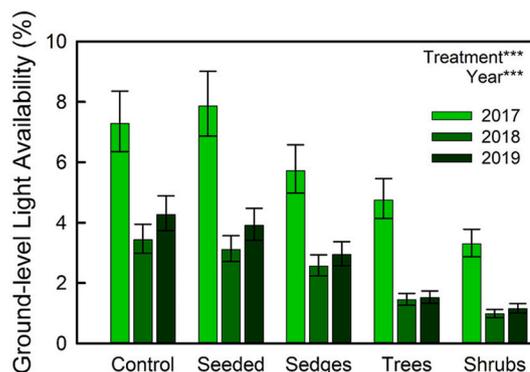Shrub plots were dominated by *Sambucus* spp. ($\chi^2 = 290.10$, df $= 5$, p

< 0.001), which became increasingly dominant over time ($\chi^2 = 42.80$, df $= 10$, p < 0.001), reaching 80% cover on average in 2019. Other shrub species constituted relatively small proportions of cover ($<10\%$), and *C. americana* was less common in plots with higher canopy light penetration. Combined seeded and non-seeded herbaceous species became increasingly scarce over time (only 4% cover total in 2019). There was no significant impact of canopy light penetration on any cover type in this treatment ($\chi^2 = 6.43$, df $= 5$, p $= 0.267$).

How are buckthorn germination and survival affected by revegetation and associated light availability?

The ground-level light availability experienced by buckthorn seedlings (the fraction of light at ground-level relative to light in the open) varied across treatments ($\chi^2 = 243.84$, df $= 4$, p < 0.001), year ($\chi^2 = 249.89$, df $= 2$, p < 0.001), and canopy light penetration ($\chi^2 = 72.38$, df $= 1$, p < 0.001). Ground-level light availability was greatest in control plots, and was lowest in shrub plots where total light penetration was 67% lower than in controls when averaged across years (Fig. 1). Differences in ground-level light availability were caused by reduced transmission of light through the understory in tree (16%) and shrub (12%) plots ($\chi^2 = 243.85$, df $= 4$, p < 0.001) relative to controls (36%, averaged across years). Ground-level light availability declined steeply after the first year, starting at an average of 5.5% in 2017 and declining to 2.4% by 2019 ($\chi^2 = 249.89$, df $= 2$, p < 0.001), consistent with increasing productivity of plots – including unplanted controls – over time.

Averaged across the entire experiment, 28% of the buckthorn seeds germinated in their first year after planting. However, there was five-fold variation in germinant establishment across seed cohorts ($\chi^2 = 354.16$, df $= 2$, p < 0.001), with the greatest germinant establishment in 2017 (51%) and the lowest in 2018 (9%). Germinant establishment increased with increasing ground-level light availability ($\chi^2 = 44.95$, df $= 1$, p < 0.001). Differences in cohort germinant establishment were most apparent in the darkest plots under the densest overstory canopies ($\chi^2 = 14.20$, df $= 2$, p < 0.001), whereas lighter plots tended to have more similar germinant establishment across cohorts. Consequently, mean germinant establishment over the experiment varied significantly across planting treatments (Fig. 2; $\chi^2 = 37.35$, df $= 4$, p < 0.001). We observed the greatest mean germinant establishment (34%) in the control plots (which had the highest light levels) and lowest (22%) in shrub plots (which had the lowest light levels). Seeding alone or sedge planting did not significantly reduce germinant establishment compared to control plots, but tree planting provided comparable germinant establishment to shrubs (Fig. 2).

Considering annual survival analyzed across all available years for all cohorts (both seeds and transplanted buckthorn), transplanted

Table 1
Mean (%) and standard error (s.e.) of percent cover values for each planting treatment in 2017, 2018, and 2019.

Treatment	Cover type	2017 Mean	s.e.	2018 Mean	s.e.	2019 Mean	s.e.
Control	seeded	3	2	8	6	13	3
	non-seeded	50	7	59	7	55	7
	bare	47	7	32	6	33	6
Seeded	seeded	15	3	32	8	23	6
	non-seeded	49	7	40	7	46	7
	bare	35	6	28	5	31	7
Sedge	*C. pensylvanica*	43	7	37	5	48	5
	seeded	6	3	34	7	12	3
	non-seeded	42	8	18	3	21	4
	bare	8	4	11	3	19	5
Tree	*A. balsamea*	23	2	19	2	24	4
	A. saccharum	19	3	33	6	41	8
	seeded	7	4	22	9	4	2
	non-seeded	35	5	14	3	23	7
	bare	16	4	11	3	9	3
Shrub	*Sambucus* spp.	56	4	74	7	80	6
	C. racemosa	5	1	2	1	3	2
	C. americana	18	1	8	2	8	3
	seeded	2	1	10	6	2	2
	non-seeded	12	3	2	1	2	1
	bare	7	2	5	2	5	3

Fig. 1. Mean ($\pm$ s.e.) ground-level light availability, back-transformed from least squared means from a statistical model. Values were recorded under each revegetation plot in the first three years of the study (2017–2019). Ground-level light availability was measured mid-summer and was calculated as the percentage of total incoming light (measured in the open without a tree canopy) reaching the soil surface. *** indicates p ≤ 0.001.
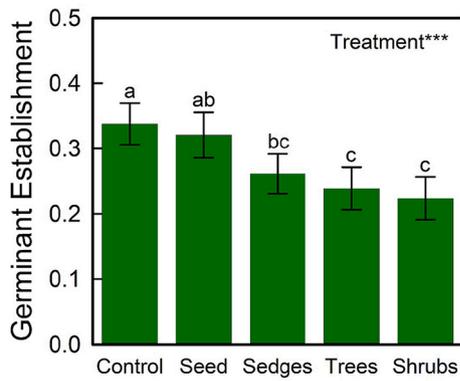
Fig. 2. Mean (± s.e.) fraction of buckthorn seeds germinating (and surviving until the end of their first growing season, when they were surveyed) across all cohorts in each revegetation treatment. Values back-transformed from model output. Letters indicate statistically-similar groups (Tukey method). *** indicates p ≤ 0.001.

buckthorn had greater annual survival (63% survival) than individuals that grew from seed that were also planted in 2017 (53%). Each consecutive seed cohort experienced lower annual survival rates ($\chi^2 = 37.25$, df = 3, p < 0.001), down to only 28% in the 2019 cohort. Annual survival was also lower where there was lower light availability at the ground (Fig. 3; $\chi^2 = 57.43$, df = 1, p < 0.001). As with germinant establishment, the relationship between buckthorn survival and light availability corresponded with significant differences in annual survival across planting treatments ($\chi^2 = 42.07$, df = 4, p < 0.001). Buckthorn annual survival was comparable between control plots (71%) and seeded plots (74%), but was reduced by half or more by planting trees (29%) or shrubs (36%), when averaged across all cohorts (Fig. 4). Sedges also reduced buckthorn survival, to a lesser extent (to 56%). These differences in annual survival compounded into even stronger differences in 4-year survival. For instance, the 2017 seed cohort in control plots averaged 53% survival through 2020, whereas those grown in shrub plots had 8% survival (85% reduction).

How is buckthorn growth affected by revegetation and associated light availability?

In this section we consider only the oldest cohorts of buckthorn, those planted as seedling transplants or seeds in 2017.

Surviving buckthorn seedlings grew to an average height of 253 mm by 2020. Seedlings grown under higher ground-level light availability experienced greater height growth ($\chi^2 = 8.66$, df = 1, p = 0.003). Accordingly, there were large differences in buckthorn height across treatments ($\chi^2 = 21.99$, df = 4, p < 0.001). Buckthorn seedlings were
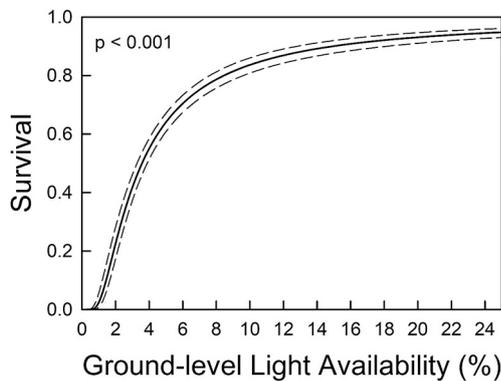

Fig. 3. Modelled relationship between mean (± s.e.) annual buckthorn seedling survival and ground-level light availability based on discrete-time survival model output. Ground-level light availability was measured each summer and calculated as the percentage of total incoming light reaching the soil surface.
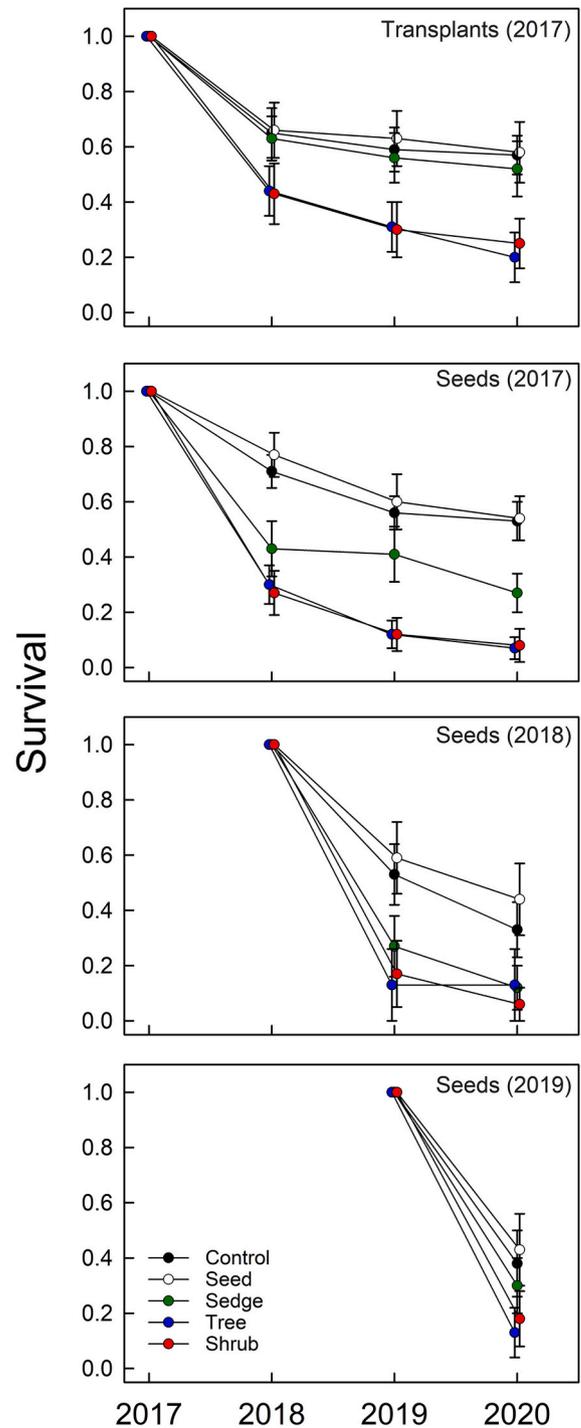
Fig. 4. Mean (± s.e.) fraction of buckthorn seedlings surviving in each year for each cohort in each revegetation treatment.

tallest in control plots, and were 20%, 26%, 40% and 53% shorter in the seeded, sedge, tree, and shrub plots respectively (Fig. 5A). Transplanted seedlings grew to be 30% taller than seedlings arising from planted seeds ($\chi^2 = 12.14$, df = 1, p < 0.001).

Buckthorn seedlings produced a variable number of leaves by 2020 based on the treatment in which they were grown (Fig. 5B; $\chi^2 = 28.63$, df = 4, p < 0.001). On average, buckthorn grown in control plots produced the greatest number of leaves (26 ± 4; mean ± s.e.). Relative to control plots, buckthorn grown in seeded, sedge, tree, and shrub plots had 18%, 20%, 26%, and 38% fewer leaves by the end of the 2020 growing season. Buckthorn grown in plots with greater ground-level
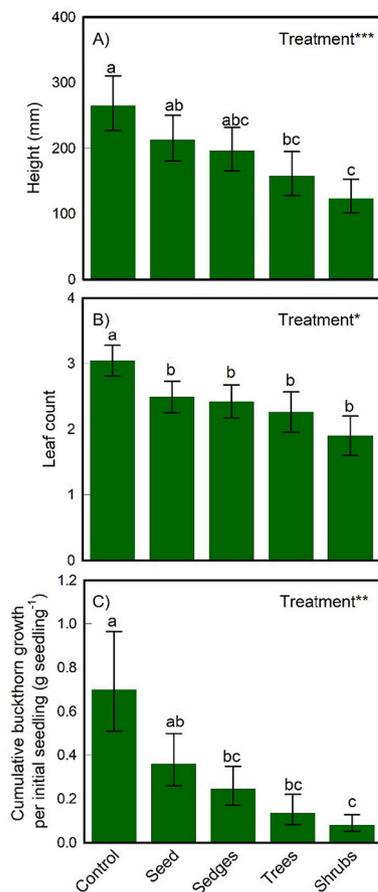
Fig. 5. Mean (± s.e.) of A) height, B) leaf count, and C) estimated cumulative buckthorn growth per initial seedling for 2017 buckthorn cohorts measured at the end of the 2020 growing season in each revegetation treatment. Values back-transformed from model output. Letters indicate statistically-similar groups (Tukey method). * indicates $p \leq 0.05$, ** indicates $p \leq 0.01$, and *** indicates $p \leq 0.001$.

light availability tended to produce more leaves ($\chi^2 = 7.98$, df = 1, p = 0.005). Leaf production of buckthorn seedlings did not differ between transplanted seedlings and seedlings grown from seed ($\chi^2 = 3.21$, df = 1, p = 0.073).

Treatment effects on buckthorn seedling performance were compounded when considering integrated growth and survival over three years ($\chi^2 = 32.06$, df = 4, p < 0.001). Control plots had the greatest cumulative buckthorn growth per initial seedling (Fig. 5C). Seeding alone reduced cumulative growth by 51%. Planting sedges reduced cumulative growth by 66%. The greatest reduction in cumulative growth was found in tree or shrub plots, which reduced cumulative growth by 81% and 89%, respectively (Fig. 5C). As with both height and survival, cumulative growth was greater with increasing ground-level light availability ($\chi^2 = 12.60$, df = 1, p < 0.001) and for transplanted seedlings than for seedlings arising from seed ($\chi^2 = 28.11$, df = 1, p < 0.001).

4. Discussion

Our revegetation treatments resulted in two- to ten-fold reductions in buckthorn re-invasion, measured as the compounded influences of our treatments on buckthorn seedling survival and growth. Buckthorn responses to competition from revegetation treatments were consistent with earlier work on buckthorn shade tolerance (Anfang et al., 2020; Harrington et al., 1989; Schuster et al., 2020b). The least effective treatment was herbaceous seeding; while buckthorn survival was not

impacted by seeding alone, buckthorn in seeded plots tended to be smaller and therefore more easily controlled by other management activities (e.g., prescribed burning, Michielsen et al., 2017). In contrast, we found dense plantings of trees and shrubs generated the most shade and offered the greatest levels of buckthorn suppression across a diverse set of temperate deciduous forests. Whereas all 18 control plots had at least one of the buckthorn seedlings from the 2017 cohorts survive through 2020, there were zero buckthorn from the 2017 cohorts surviving until 2020 in 10 of 18 tree plots and 11 of 18 shrub plots. Thus, the tree and shrub treatments were able to fully exclude buckthorn in the majority of cases.

The large suppressive effect of tree and shrub plantings are likely attributable to both treatments producing dense shade mid-summer, but also having an extended leaf phenology (see model comparisons in Appendix A). Buckthorn rarely loses its leaves due to senescence, but instead holds them until winter and loses them mostly as a consequence of frost damage. This extended leaf phenology allows for critical carbon gains that regulate buckthorn growth and survival (Harrington et al., 1989; Schuster et al., 2020b). However, both *Sambucus* spp. (deciduous) and *A. balsamea* (evergreen) display significant phenological overlap with buckthorn (Schuster et al., 2021). Native trees and shrubs are also likely to display other elements of niche overlap – including competing for light and nutrients in the same strata of the canopy and soil, respectively – due to sharing a woody growth habit with buckthorn (Hess et al., 2020). Therefore, revegetating with species that display a high degree of niche overlap with buckthorn likely stifles buckthorn carbon gains and suppresses buckthorn re-establishment (Knight et al., 2007; O'Connell and Savage, 2020; Schuster et al., 2021; Stuble and Young, 2020).

4.1. Implications for management

We have demonstrated the effectiveness of a broad range of revegetation strategies in suppressing buckthorn re-establishing from seed. Similarities in growth between buckthorn and other woody forest invaders suggest that they too may be effectively suppressed by revegetation. For instance, *Frangula alnus* and *Lonicera* spp. spread via seed, invade many of the same habitats, and have similar growth requirements as buckthorn (Schulte et al., 2011). However, these species are less shade-tolerant than buckthorn (Cunard and Lee, 2009; Kalkman et al., 2019; Schulte et al., 2011) and are likely to be more susceptible to the intense competition for light created by our tree and shrub treatments. The treatments used here may therefore offer a template for management of other invaders in other systems that can be adapted based on regional flora.

Which type of revegetation is most effective at suppressing invasion depends on site conditions, particularly canopy openness. Herbaceous species tended to become more abundant and even started to spread into unseeded areas where canopy openness was higher. In contrast, cover of the planted shrub species did not vary significantly with canopy openness. Both herbaceous seeding and shrub plantings may therefore be effective at producing cover in higher-light environments, whereas trees or shrubs are necessary to generate dense cover under darker conditions.

To be effective, woody revegetation may need to be protected from herbivory. Our experimental plots were small (1.2 m × 1.2 m) and were contained within a fenced area. Therefore, large herbivores (e.g. *Odocoileus virginianus,* white-tailed deer) were excluded from this experiment and their impact on revegetation efficacy (particularly in the tree or shrub treatments) is unclear. Deer often selectively browse palatable native species over unpalatable invasive ones (Aronson and Handel, 2011; Knight et al., 2009), hindering forest regeneration (Forrester et al., 2014; Tilghman, 1989) and likely slowing revegetation efforts. Therefore, young trees and shrubs may need to be protected from deer to maintain their efficacy against buckthorn depending on local deer populations.

Our revegetation treatments will likely need to be adapted by

managers based on their logistical and budgetary constraints. Woody plant restoration at larger scales is often financially challenging because seeding woody species is often ineffective and bare-root plants require ample funding (Ceccon et al., 2015). If our experiments had been established by contractors, plots seeded with herbaceous species would have cost <1% as much as plots planted with bare-root shrubs or trees or sedge plugs due to the price of propagules and the labor associated with planting versus seeding (PB personal observation). In order for our treatments to be operationalized for widespread use, further investigation into cost reduction strategies are therefore warranted. In particular, evaluating alternative methods for establishing woody species, such as seeding and associated site preparation techniques could provide a low-cost pathway toward establishing trees and shrubs at or near the densities used here (Ceccon et al., 2015). We observed self-thinning on our most productive woody plant plots, suggesting that lower planting densities could be equally effective at buckthorn suppression for a lower investment. Identifying density thresholds for bare root plantings would therefore also be valuable for operationalizing our shrub and tree treatments. Though herbaceous seeding is less costly, cost is still a barrier at large scale. Few of the more costly wildflowers in our seed mix established within our plots (MS, PW personal observation), implying that many of these species could likely be removed from the seed mix without losing efficacy (at least in the first few years after seeding).

We prioritized potential biotic resistance over historical community assemblages when selecting species to include in our revegetation treatments. Consequently, some land managers may not find all of the species considered here to be desirable in their particular system, especially those attempting to restore recognized remnant native plant communities. For example, the omission of *Quercus* in our treatments may be unpalatable to managers of oak woodlands. Yet, if managers are willing to embrace novel communities, even temporarily, they may help to resist invasion in the short-term and undesirable native species may then be thinned or removed gradually over time (Brancalion et al., 2020). Compounding influences of multiple global change factors – including invasion – also suggest that the maintenance of biodiversity and ecosystem function may require alternative, novel community assemblages (Jackson and Hobbs, 2009).

The types of revegetation considered in this study will often require additional management to fully prevent buckthorn re-establishment. Most importantly, existing buckthorn and their resprouts must be thoroughly controlled (e.g., via foliar herbicide, see Schuster et al., 2020a) since revegetated plants cannot establish quickly enough to compete against the rapid growth of resprouts (> 2 m in a single growing season for large trees; MS personal observation) (Wragg et al., 2021). Additionally, while some of our treatments often resulted in the complete exclusion of buckthorn (zero buckthorn seeds survived in the majority of replicates of the tree and shrub plantings), buckthorn responses to revegetation were variable. Some buckthorn survived, particularly in the seeded treatment. Thus, although we find that revegetation reduces the amount of buckthorn returning, it does not always eliminate buckthorn and does not make continued monitoring unnecessary. Follow-up control of resprouts and escaping buckthorn seedlings may be required of managers. For less-precise methods of follow-up control, avoiding non-target impacts on the revegetated plants requires careful planning. For example, foliar herbicide may be applied to buckthorn resprouts before planting native shrubs or trees but after allowing time for resprouts to emerge (typically one growing season). To what extent a delay in planting would affect the outcome of revegetation remains unclear. Yet, our data clearly demonstrate that revegetation can be an effective tool to reduce (and in some cases, eliminate) buckthorn re-establishment.

5. Conclusion

Buckthorn removal is often only effective in the short-term as deciduous forests quickly revert to a buckthorn-dominated state. Here, we have shown that a broad range of revegetation strategies can increase biotic resistance and successfully reduce growth and survival of buckthorn re-establishing from seed following buckthorn removal. Over a 4-year period, we detected a two- to ten-fold reduction in buckthorn invasion under herbaceous seeding and shrub planting treatments, respectively. Our findings demonstrate that forest managers can quickly build biotic resistance and reduce re-establishment of buckthorn by shifting priority effects to promote establishment of fast-growing native plant communities. The revegetation treatments designed and tested here can serve as a template for development of practical strategies to control buckthorn and potentially other invasive shrub and tree species. Ultimately, our findings endorse revegetation as an effective tool in reducing invasion that likely also improves forest health more broadly. By building long-term biotic resistance, revegetation may provide significant cost and labor savings to managers in the long run, reduce demand for herbicide applications, increase forest understory native plant diversity, and improve wildlife habitat. Such impacts would not only benefit the forests of today, but aid in their conservation for the foreseeable future.

Data availability statement

Data used in the analyses presented here have been uploaded to DRYAD: https://doi.org/10.5061/dryad.573n5tb9w

Authorship

MS, PW, AR, LF, and PR conceived the ideas; MS, PW, PB, and PR designed the experiment and methodology; MS, PW, and PB established the experimental plots; MS and PW collected the data; MS and PW analyzed the data; MS led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

CRediT authorship contribution statement

Michael J. Schuster: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Project administration, Funding acquisition. **Peter D. Wragg:** Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – review & editing, Project administration, Funding acquisition. **Alexander M. Roth:** Conceptualization, Resources, Writing – review & editing, Funding acquisition. **Paul Bockenstedt:** Conceptualization, Methodology, Resources, Writing – review & editing, Funding acquisition. **Lee E. Frelich:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition. **Peter B. Reich:** Conceptualization, Methodology, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare no conflict of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2022.106730.

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