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RESEARCH ARTICLE

Increased light availability due to forestry mowing of invasive European buckthorn promotes its regeneration

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The invasive shrub *Rhamnus cathartica* L. (common buckthorn) dominates the understory of many temperate forests of eastern North America. Common buckthorn outcompetes native understory species for light, forming monospecific stands that suppress plant and animal diversity. Removing common buckthorn is a common management priority within its invasive range. In recent years, forestry mowing has become popular in removing common buckthorn. This control method removes a midstory of common buckthorn, increasing light availability to the lower understory (which could favor buckthorn regeneration) and creating a layer of mulch on the forest floor (which could suppress buckthorn regeneration). Here we investigate whether and how increased light availability and increased ground cover (mulch) resulting from forestry mowing affects buckthorn regeneration from the seed bank. We evaluated buckthorn germination, survival, and early growth in response to a factorial combination of shading treatments and buckthorn mulch depth treatments in an oak forest in Minnesota, U.S.A. Increased light availability increased buckthorn seedling survival and growth, whereas increased mulch depth did not significantly affect the number of buckthorn establishing from seed over one growing season and winter. Thus, removing buckthorn by forestry mowing (or any other method) is likely to facilitate buckthorn reestablishment by increasing light availability at the ground.

Key words: forest, forestry mowing, germination, light, mulch, removal, *Rhamnus cathartica*

Implications for Practice

- Increased light availability associated with forestry mowing stimulates germination and growth of invasive shrubs and facilitates their regeneration, potentially at higher densities than existed prior to management.
- By optimizing light and moisture conditions, thin layers of forestry mower mulch can stimulate germination, but this effect is mitigated by low overwinter survival of resulting seedlings. Mulch reduces microsite availability which may reduce establishment of other species from seed such that mulched areas are likely to exhibit lower diversity and cover of native plants.
- Restoring forest communities likely requires a combination of herbicides and revegetation following forestry mowing to limit reinvasion and to reestablish native communities.

Introduction

Invasive species degrade ecosystem function and contribute to global declines in biodiversity, making the control and removal of invasive species a common management priority (Levine et al. 2003; Ehrenfeld 2010; Simberloff 2011). Removing invasive species impacts the environmental conditions that at least partially regulate plant community assembly after invasive species removal (Bergstrom et al. 2009; Wittmer et al. 2013). Depending on the extent and nature of an invasion, removing an established invasive species can even leave an area prone to greater degradation or invasion than with the invasion intact (Zavaleta et al. 2001). The invasive tall shrub *Rhamnus cathartica* L. (common buckthorn) commonly dominates the understory of many oak forests and open-canopy woodlands in central and northeastern North America. Its dominance has severe impacts on forest biodiversity and ecosystem function (Archibold et al. 1997; Knight et al. 2007; Mascaro & Schnitzer 2007), and many of the challenges presented in buckthorn management exist in management of other invasive shrubs globally.

Like many understory and midstory invaders, buckthorn outcompetes native understory species for light and forms monospecific stands that suppress plant and animal diversity (Knight et al. 2007). Buckthorn is moderately shade tolerant

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and can establish seedlings under 1–2% midsummer light availability, especially in deciduous forests where spring light availability is higher (Knight 2006). Moreover, buckthorn grows more quickly than species with similar levels of shade tolerance, even under relatively high light availability (Harrington et al. 1989; Grubb et al. 1996). Buckthorn produces calcium- and nitrogen-rich leaf litter that accelerates ecosystem leaf litter decomposition, and hosts major agricultural pests and pathogens (Heneghan et al. 2002; Knight et al. 2007; Heimpel et al. 2010). These impacts are part of a positive feedback loop involving earthworms, wherein both buckthorn and earthworms facilitate the other's success through niche-construction mechanisms (i.e. invasional meltdown; Simberloff & Von Holle 1999; Simberloff 2006; Roth et al. 2015). Buckthorn has the greatest success in forest gaps or edges, with a moist but not saturated soil (Kurylo et al. 2007). Buckthorn also produces a prolific amount of highly viable seed that accumulates in soil and remains viable for up to 5 years (Archibold et al. 1997; Knight et al. 2007). These combined impacts of buckthorn leave invaded forests with abundant residual propagule pressure from buckthorn with little-to-no native species present to resist buckthorn reestablishment (Naeem et al. 2000; Klionsky et al. 2011; Rejmánek 2014). Therefore, emergence from the seedbank poses a significant threat to forest restoration (Iannone et al. 2013). Management plans following buckthorn removal must account for continued propagule pressure from the seedbank despite the absence of fruiting individuals nearby.

A diverse set of tools exist to control and remove buckthorn from forest communities (Delanoy & Archibold 2007). These tools include both mechanical (saws, weed wrenches, forestry mowers) and chemical (glyphosate, triclopyr, fosamine) methods of removal that can be combined in a wide array of methodologies (basal bark application, foliar spray, cut-and-treat). Most buckthorn removals combine cutting stems and treating stems with herbicide (Gale 2000). Due to the lack of profit in the harvest of buckthorn and the high time cost of removing dense stands, methods outside of this "cut and treat" approach have been sought (Provencher et al. 2001).

Forestry mowers (all-terrain vehicles with a front-mounted spinning serrated drum that shred the stems of woody understory species) are one such tool. These tools are increasingly popular among land managers and contractors because they quickly clear entire stands of buckthorn and can serve as a more cost-effective alternative to other buckthorn removal methods (Stanturf & Madsen 2002; Stanturf et al. 2003). It is also commonly assumed by managers that forestry mowing has an advantage of producing buckthorn mulch that could suppress germination of buckthorn seeds (A. M. Roth 2019, Friends of the Mississippi River, personal communication).

Forestry mowers have distinct impacts on the environmental conditions faced by remnant vegetation and establishing propagules. By shredding buckthorn and other woody understory and midstory species, forestry mowing both increases light availability in the understory and creates a layer of mulch on the forest floor. Whereas increased light availability is likely to favor buckthorn growth (Knight 2006; Kurylo et al. 2007), mulch can suppress plant regeneration by physically obstructing the hypocotyl of germinating seeds and preventing light from reaching the soil surface. However, some species can resprout multiple stems and can reestablish at a higher stem density compared to pre-removal conditions over only a few years (Brockway et al. 2009). In an attempt to reduce resprouts, forestry mowers are often driven down against buckthorn stumps with the goal of shattering the root crown from which resprouts are derived. While this can be successful, it can also significantly disturb the surrounding soils. Soil conditions are also affected by the presence of the mulch created by forestry mowers. Mulch has been shown to increase soil moisture retention and also to retard the growth of herbaceous species in agricultural experiments (Ramakrishna et al. 2006). In sum, forestry mowing likely has legacy effects on buckthorn regeneration that vary over time as mulch depth, light, and soil moisture change. Indeed in a multi-year study of germinant, yearling, and resprouting buckthorn, Iannone et al. (2013) found that surface application of buckthorn mulch led to transient decreases in buckthorn reinvasion, but that mulch had no lasting impact on buckthorn reinvasion. However, this is the only experimental test of the effects of mulch on buckthorn performance to our knowledge, and it is unclear whether these results are constrained by the depth of mulch used or how these results may be dependent on changes in light conditions caused by buckthorn removal.

In an experiment where we manipulated understory light availability using shade cloth and varied mulch depth by placing exogenous buckthorn mulch on top of bare ground plots in an oak forest, we evaluated buckthorn germination, survival, and early growth in response to experimentally varied depth of buckthorn mulch cover and light availability. Specifically, we addressed three questions: (1) How does forestry mower mulch depth influence buckthorn germination and seedling survival? (2) How does light availability impact these same metrics, as well as seedling growth? (3) How does the impact of mulch on buckthorn vary with light availability? This experiment builds upon findings of Iannone et al. (2013) by evaluating buckthorn performance across a gradient of mulch depths that are likely to occur with forestry mowing and by contextualizing the influence of mulch within concurrent changes in light availability.

Methods

Experimental Design

To ensure realistic growing conditions for *Rhamnus cathartica*, we selected an 8 m × 5 m area in oak canopy forest previously invaded by *R. cathartica* in Rice Creek Regional Park near Minneapolis, MN, U.S.A. (45.110184 N, 93.179663 W). Buckthorn was removed from the site in spring 2016 by hand-cutting stems at ground level and applying triclopyr on cut stems. Because forestry mowers were not used at this site, we are able to isolate the effects of forestry mower mulch from the soil disturbance that is sometimes associated with forestry mowers and ensure more uniform conditions across experimental plots. Within this area, twelve 1.5 m × 1.5 m plots were established in July 2017 (Fig. 1). These plots were weeded of woody and herbaceous cover, largely consisting of *R. cathartica*, *Alliaria*

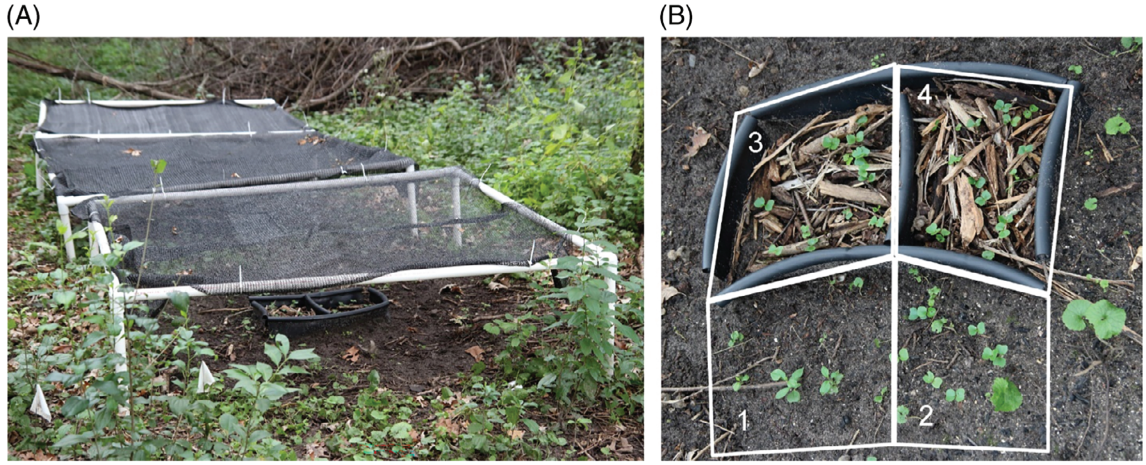

Figure 1. Photographs of (A) 3 of the 12 shading plots, receiving additional shade cloth shading (the 1, 3, and 5% light availability treatments all looked similar to this), and (B) 1 of the 12 shading plots receiving the 10% light availability treatment, that is, tree canopy shading without additional shade cloth shading. Each shading plot had three mulching subplots, shown in panel B: (1, 2) zero mulch; (3) thin mulch (1.3 cm); (4) thick mulch (3.8 cm). Into one of the zero mulch subplots (1), we transplanted three buckthorn germinants (seedlings) and measured their height. Into each of the other three subplots (2–4), we planted 20 buckthorn seeds.

petiolata (garlic mustard), and *Galeopsis tetrahit* (brittlestem hemp nettle). This was done to ensure that variation among plots in plant cover did not introduce variation in availability of soil resources or light. There was no litter layer present at the experimental site, likely due to the history of buckthorn invasion and persistent, severe invasion by earthworms (Heneghan et al. 2002; Suárez et al. 2006; Roth et al. 2015). Once the plots were reduced to bare soil, a 0.5 m × 0.5 m sampling area was divided into four subplots using plastic garden dividers (Fig. 1B). We then planted 20 buckthorn seeds in three of the four subplots and transplanted three buckthorn germinants (seedlings) into the fourth subplot. Seeds were collected from Elk River, Minnesota in January 2017 (allowing for in situ cold stratification). Seeds were separated from buckthorn fruits within 2 weeks of collection and stored in damp sand at 35°F until transplanted. Germinant transplants (identified as new seedlings that retained both cotyledons) were haphazardly selected from Marine on St. Croix, Minnesota in July 2017. All germinant subplots were given 100 mL of water to mitigate transplant shock.

To test the potential effects of forestry mower-created buckthorn mulch on buckthorn germination, we imposed three levels of mulch depth on seed subplots to represent increasing severity of buckthorn invasion at a mulched site. Sites with fewer and/or smaller buckthorn result in thinner mulch layers, whereas sites with more and/or larger buckthorn produce thicker mulch layers. Mulch was collected from a buckthorn-invaded oak forest in Marine on St. Croix, Minnesota, that had been forestry mowed during the previous winter. Within each plot, 0 cm (no mulch), 1.3 cm (thin mulch), and 3.8 cm (thick mulch) of mulch were placed on top of the three subplots that contained buckthorn seeds. These levels were designed to simulate differing levels of mulch found in nearby sites where forestry mowers had been used (personal observation).

Effects of light availability were tested by placing 1.5 m × 1.5 m shading structures over 9 of the 12 experimental plots (Fig. 1A). Structures were 0.5 m tall and built using polyvinyl chloride (PVC) and shading cloths of varying densities. We determined that the canopy over the experimental area was creating approximately 10% light availability by measuring the subcanopy light levels using a quantum light sensor and LI-250A reader (LI-COR Biosciences, Lincoln, NE, U.S.A.), while simultaneously measuring open light availability in a field 100 m away from the experimental area using a quantum sensor and LI-1000 logger (LI-COR Biosciences). Therefore, we aimed to create 1, 3, and 5% light availability treatments by covering structures with 90, 70, and 50% exclusion shade cloth, respectively. We also used an ambient control that was only subjected to the shading of the canopy (10% light). Light levels below the shading structures were measured in each plot, relative to light in the same open field, using the same instruments used to determine canopy shading. Realized light levels (mean ± SE) for the 1, 3, 5, and 10% treatments were: 0.5 ± 0.03%, 3.3 ± 0.09%, 5.5 ± 0.04%, and 11.8 ± 0.58%, respectively. Three plots were assigned to each level of shading. For comparison, light levels in an adjacent area (70 m away from the experimental plots) with a similar oak canopy, an intact buckthorn midstory, and very little ground cover (typical of buckthorn invasions) averaged (± SE) 2.0 ± 0.22% at chest height and 1.7 ± 0.14% at ground level ($n = 7$).

Data Collection

Starting on 4 August, 2017 (1 week after transplanting), we monitored buckthorn performance in each plot every 30 days for 3 months. Heights of transplanted germinants were measured to the base of the highest leaf and the number of living germinants in each seeded subplot was counted. Soil volumetric water

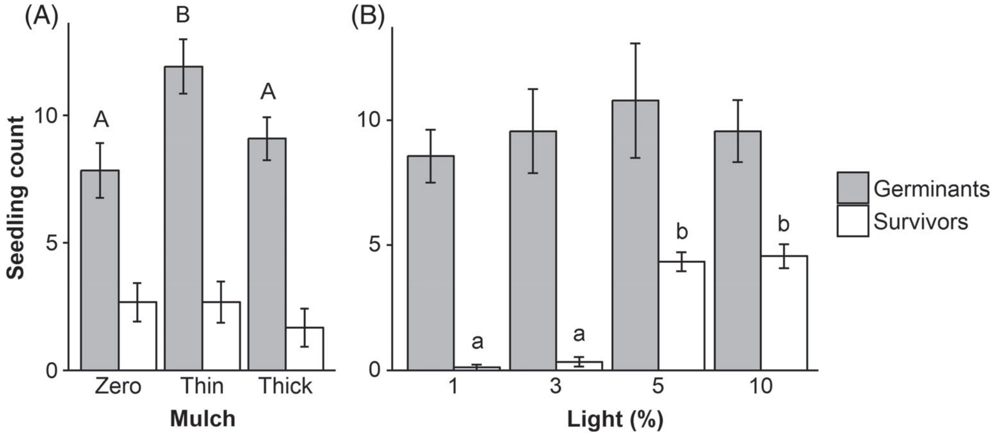

Figure 2. Impact of mulch depth (A) and light availability (B) on germination (gray) and survival into the following spring (white) of buckthorn. Values are the mean (± SE) number of individuals counted in subplots at the end of the growing season and during the following spring. The number of germinants varied significantly with mulch depth (A), whereas the number of spring survivors varied significantly with light treatment (B); within these, letters indicate which treatment levels differ significantly from each other ($p < 0.05$). No letters indicate non-significant differences across treatment levels.

content was measured to a depth of 6 cm in each seeded subplot, using a Thetaprobe SM300 (Delta-T Devices).

Data Analysis

Germination rate was calculated as the proportion of the 20 seeds that gave rise to buckthorn germinants within each subplot. We analyzed germination rate using a generalized linear mixed model with mulch and light treatment as categorical fixed effects, a binomial error distribution, plot as a random intercept to account for non-independence of the mulch treatment subplots within each light treatment plot, and subplot as an observation-level random effect to account for overdispersion (Gelman & Hill 2007, pp. 320–326). The number of seedlings found in fall 2017 was the number of "successes" and the number of seeds planted that did not result in seedlings was the number of "failures."

To analyze overwinter survival without confounding it with germination rate, we used a generalized linear mixed model like that above with the number of seedlings found in spring 2018 as the number of "successes" and the number of seedlings that germinated in 2017 and did not survive to spring 2018 as the number of "failures." The 1% light treatment had zero survival whereas all other treatments had non-zero survival, resulting in the statistical problem of separation and wildly inflated standard errors (Gelman & Hill 2007), so we added one survivor to one of the plots in that treatment to allow analysis.

To examine the number of survived seedlings integrating over both germination and overwinter survival rates, we used a third generalized linear mixed model like those above but with the number of seedlings found in spring 2018 as the number of "successes" and the number of seeds planted that did not result in seedlings found in spring 2018 as the number of "failures."

We calculated mean germinant growth for each plot as the mean difference between initial and final heights of the three germinants transplanted into that plot. We analyzed germinant growth as a function of light treatment using linear model analysis of variance (ANOVA).

We analyzed effects of mulch and light on soil volumetric water content using a linear mixed model with mulch and light treatment as categorical fixed effects and plot and subplot as random intercepts. We analyzed effects of volumetric water content on germination rate and survival using volumetric water content as the fixed effect, and the same random effects and binomial error distributions used to analyze effects of mulch and light on germination rate and survival.

All analyses were done using R version 3.4.2 (R Core Team 2014). Mixed models were analyzed using R package *lme4* (Bates et al. 2015). We report tests of coefficients using Wald χ^2 statistics from Type II ANOVAs that assess effects after accounting for all other non-interaction effects using R package *car* (Fox 2013 #8954). For treatments with significant ($p < 0.05$) Wald χ^2 tests for the treatment as a whole, we show results of Tukey multiple comparisons on the graphs using letters that indicate which treatment levels differ significantly from each other. For all models that included both mulch and light, interactions between mulch and light levels were not statistically significant and were excluded from the final models.

Results

Germination

Across all plots, germination rate was $48 \pm 3\%$ (mean ± SE). Germination responded to mulch depth ($\chi^2 = 13.24$, $df = 2$, $p = 0.001$, Fig. 2A, Table S1) such that the highest germination rates were observed at an intermediate mulch depth and lower germination rates were observed under bare ground conditions or with thick mulch. Subplots with thin mulch had 40% more germinants than bare soil subplots and 30% more germinants than thick mulch subplots. Germination rate did not respond significantly to changes in light availability ($\chi^2 = 1.39$, $df = 3$, $p = 0.708$, Fig. 2B, Table S1).

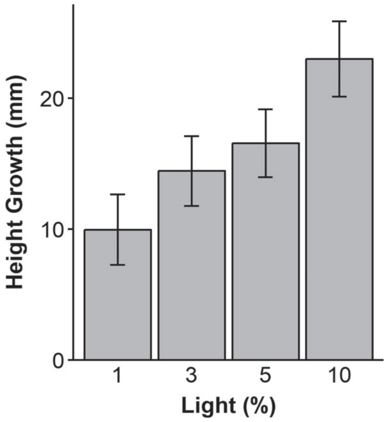

Figure 3. Mean (± SE) growth of transplanted germinants grown under each light availability treatment.

Overwinter survival of germinants into spring was strongly affected by both light availability and mulch depth. Overwinter survival of germinants into spring showed marked differences between lower light availability treatments and higher light availability treatments ($\chi^2 = 37.59$, $df = 3$, $p < 0.001$, Fig. 2B, Table S2). None of the germinants in the 1% light treatment survived into spring, and only 3.5% of germinants in the 3% light treatment survived into spring. In contrast, survival rates under 5% light and 10% light treatments were 40 and 48%, a 10- and 13-fold increase in survival compared to the 3% light treatment, respectively (Fig. 2B).

Overwinter survival was negatively affected by increasing mulch depth ($\chi^2 = 7.99$, $df = 2$, $p = 0.019$, Fig. 2A, Table S2). Plants in bare soil had an overwinter survival rate of 33%, those in thin mulch had an overwinter survival rate of 22%, and those in thick mulch had an overwinter survival rate of 18%. These differences in overwinter survival rate offset differences in germination rates. Consequently, the total number of living germinants at the end of the experimental period did not differ significantly between mulch treatments ($\chi^2 = 4.00$, $df = 2$, $p = 0.136$, Table S3).

Germinant Growth

The average growth of transplanted germinants in each plot across the 3-month time span was positively associated with light availability (Fig. 3; $F_{3,8} = 4.009$, $p = 0.052$, Table S4). Transplanted germinants increased in height 2.3 times more under the 10% light treatment compared to the 1% treatment.

Soil Moisture

Soil volumetric water content (moisture) did not vary consistently across light treatments ($\chi^2 = 6.41$, $df = 3$, $p = 0.093$, Fig. 4A), but greater mulch depth enhanced soil moisture ($\chi^2 = 10.41$, $df = 2$, $p = 0.005$, Fig. 4B, Table S5). However, when we replaced these treatments with soil moisture in our analyses, soil moisture did not significantly affect buckthorn germination ($\chi^2 = 0.01$, $df = 1$, $p = 0.932$, Table S6) nor survival ($\chi^2 = 0.93$, $df = 1$, $p = 0.336$, Table S7).

Discussion

Light Effects

While light availability had no significant effect on germination rates or soil moisture, it strongly facilitated survival and growth. Our data show that buckthorn germination occurs in as low as 1% light availability but that survival at 1 or 3% light (comparable with light levels below adjacent intact buckthorn stands) is markedly lower than the 5 or 10% light levels that result from removing buckthorn at this site. Buckthorn seedlings

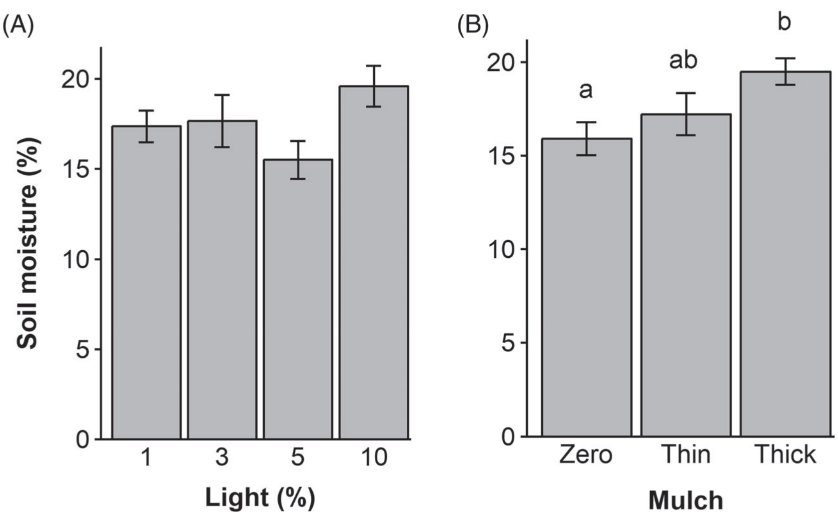

Figure 4. Effects of (A) light availability and (B) mulch depth on mean (± SE) volumetric water content within experimental plots. Water content varied significantly with mulch depth (B); letters indicate which treatment levels differ significantly from each other ($p < 0.05$). No letters indicate non-significant differences across treatment levels.

have been reported as having context-dependent survival at light levels similar to those examined here with survivorship varying by seedling age and proximity to mature trees (Knight 2006). However, we observed complete failure of buckthorn (i.e. 0% survival) in the 1% light availability plots. Considering that these sites were recently dominated by buckthorn and may retain soil legacies of that invasion, it is not surprising that our results resemble those of Knight (2006), where buckthorn grown at comparable light levels near mature buckthorn trees also had 0% survival. The sharp drop-off in survival from 5 to 3% light treatments that we observed suggests that there could be a threshold near this light level that is critical to the success of buckthorn as an invader. Again, these results are consistent with those of Knight (2006), but our findings here narrow the range of potential thresholds. Further work is needed to pinpoint a discrete light threshold for buckthorn; if found, this threshold could aid in identifying forests that are most and least at risk of invasion by buckthorn.

Mulch Effects

Our results indicate a nonlinear response of buckthorn to mulch that could result in forestry mowing unintentionally enhancing buckthorn germination rates in sites with intermediate buckthorn density and consequently intermediate mulch depth. The unimodal germination results may reflect a tradeoff between mulch enhancing soil moisture retention and thus germination, and physically obstructing emergence, and detection, following germination (Brockway et al. 2009; Roth et al. 2015). This tradeoff and consequent unimodal response have not been reported in the context of forestry mower mulch, but literature on leaf litter layers suggests that similar mechanisms could be responsible for similar trends with respect to leaf litter depth (Kostel-Hughes et al. 2005; Roth et al. 2015). In the absence of mulch, a germinant receives maximum light availability (restricted only by canopy shading) and grows without obstruction, but does not receive any of the water retention or herbaceous competitor reduction benefits that mulch may provide (Ramakrishna et al. 2006). Buckthorn germinating under a thin (1.3 cm) layer of mulch must navigate near-surface light obstruction from mulch but may face less competition from herbs and are insulated from desiccation by mulch (Gardiner & Hodges 1998). Indeed, we observed greater soil moisture under mulch. Thick mulch (3.8 cm) further increases soil water retention and may more strongly suppress herbaceous species, but buckthorn germinants must expend more resources to grow through the thicker mulch layer before they are able to start photosynthesizing. Therefore, as mulch depth increases, facilitation apparently gives way to suppression and abundance of buckthorn germinants decrease.

Differences in buckthorn germinant abundance between mulch depths did not persist through winter. Germinants that established in mulched plots had lower survival rates until the following spring than those established in control plots. This may reflect the increased carbon expenditure and the consequent photosynthetic opportunity cost associated with growing through mulch. We speculate that germinants growing through mulch were unable to accumulate enough carbon to support overwinter maintenance and therefore had lower overwinter survival rates. As a result, the number of germinants alive in spring did not differ between mulch depths, and the effects of mulch on buckthorn germinants were transient. These results are similar to those of Iannone et al. (2013), who found mulch to suppress buckthorn only for an 8-week period, although that period fell fully within the growing season. Despite differences in buckthorn germination rates, it is therefore unlikely that forestry mowing mulch will directly promote or inhibit buckthorn establishment.

Indirect impacts of forestry mower mulch on buckthorn performance could influence the rate of buckthorn reestablishment over larger temporal and spatial scales. Seeds present within the seedbank benefit from priority effects in the years following forestry mulching (Körner et al. 2008). Since buckthorn is often a dominant component of seedbanks in heavily invaded systems (Ogden & Rejmanek 2005; Delanoy & Archibold 2007; Greet 2016), these priority effects likely disproportionately promote the reestablishment of buckthorn over native species (Dickson et al. 2012). Dispersal of native seed into the system or active revegetation by managers could at least partially counteract this advantage, but the establishment of new seed dispersed into forestry-mowed areas is likely to be reduced by intervening mulch layers (Chambers 2000; Pan et al. 2004). If forestry mower mulch inhibits herbaceous species following buckthorn removal, surviving buckthorn germinants could face lower competition for light and nutrients in areas with forestry mower mulch compared to mulch-free areas (Teasdale & Mohler 2000; Brockway et al. 2009). Thus, we urge future studies to consider how priority effects resulting from forestry mower mulch could indirectly facilitate buckthorn germinants (Teasdale & Mohler 2000).

By increasing light levels, forestry mowing promotes buckthorn seedling survival and growth, despite creating a layer of mulch that is conventionally assumed to inhibit establishment. Consequently, land managers must contend with several years of stimulated buckthorn seedling performance (in addition to resprouts from cut stems) following forestry mowing if they wish to effectively control the invasion. A variety of methods exist for managing buckthorn within this context. Glyphosate and triclopyr are highly effective herbicides with widespread use in controlling buckthorn (Delanoy & Archibold 2007). Foliar herbicide application may offer the most reliable control option aside from mechanical removal (e.g. hand pulling). Additional methods can be used in conjunction with—or in limited cases, in lieu of—herbicide application. For instance, controlled burns may be able to inhibit establishment of buckthorn in systems with sufficient fuel loads (Gale 2000). However, buckthorn-invaded systems commonly lack ground cover or sufficient litter layers to carry flame (Knight et al. 2007), making burning challenging in many systems. If forestry mower mulch further reduces fine fuel loads created by herbaceous species, burning could be even less successful in forestry-mowed systems, but this has not been evaluated. Finally, active restoration via revegetation of native plant species has been an effective tool in restricting growth of invasive plants in other systems (primarily grasslands), but to what extent revegetation can impede the growth of buckthorn or many other woody invaders is unknown (Schuster et al. 2018). Revegetation may also produce greater fuel loads and outcompete small buckthorn missed by chemical herbicides, suggesting synergistic efficacy of revegetation when used in combination with other methods. Utilizing multiple approaches to managing buckthorn likely offers the greatest chance of successful control of buckthorn following forestry mowing.

Although we focus on buckthorn in this experiment, our findings may be generalizable to the management of other woody understory invaders. Glossy buckthorn (*Frangula alnus*) is a similar species to common buckthorn that has severe impact on forest understory communities (Frappier et al. 2003) and is often controlled using the same methods. However, the response of *F. alnus* to the conditions simulated here has not been evaluated. Some other, less closely related forest invaders have been considered in forestry mower studies, however. For example, *Lonicera maackii* and *Alliaria petiolata* have both been shown to be stimulated following shallow forestry mowing with more negative impacts on *L. maackii* accruing with deeper forestry mowing (Frank et al. 2018), but this is largely a function of disturbance caused by the forestry mower itself—something not included in our experimental design—and not the depth of resulting mulch. We speculate that mechanisms similar to the ones that led to our results would lead to comparable effects in other species, but this remains to be tested.

Forestry mowers create both increased light availability and varied depths of mulch. While forestry mowing provides a cost-effective method of clearing dense stands of buckthorn, we did not find evidence that mulching suppresses buckthorn regeneration. If forestry mower mulch suppresses herbaceous species, it could increase buckthorn's competitive advantage. Overall, despite creating a layer of mulch, forestry mowing has the potential to facilitate buckthorn reestablishment by increasing light availability. This highlights the need for follow-up control measures after forestry mowing—potentially including foliar herbicide, burning, and native revegetation, depending on site conditions—to prevent rapid reestablishment of buckthorn.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Summary of a statistical model relating germination to mulch and light treatments.

Table S2. Summary of a statistical model relating seedling survival (from fall 2017 until apring 2018) to mulch and light treatments.

Table S3. Summary of a statistical model relating the number of buckthorn seedlings present in spring 2018 to mulch and light treatments.

Table S4. Summary of a statistical model relating height growth increment of buckthorn seedlings planted as germinants to light treatment.

Table S5. Summary of a statistical model relating soil volumetric water content to mulch and light treatments.

Table S6. Summary of a statistical model relating germination to soil volumetric water content.

Table S7. Summary of a statistical model relating seedling survival from fall 2017 until spring 2018 to soil volumetric water content.

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