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Research Article

Understory Revegetation Enhances Efficacy of Prescribed Burning after Common Buckthorn (*Rhamnus cathartica*) Management

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ABSTRACT

The use of prescribed burns to suppress woody invasive species like common buckthorn (*Rhamnus cathartica*) in temperate deciduous forests is often limited by fine fuel availability. This is particularly problematic in the period following mechanical removal of buckthorn, when fire has the greatest probability of preventing buckthorn from re-establishing dominance through remaining small individuals, resprouts, or seeds. Here, we test whether revegetating by seeding C_3 grasses and forbs enhances fine fuel availability and subsequent spread and impact of prescribed burns in two semi-open forests (8–24% tree canopy light transmission) in Minnesota. We found seeding increased cover of grass litter by more than 12-fold and decreased bare ground by 73%. Consequently, seeded areas enhanced fire spread by 85% and resulted in a three-fold increase in the proportion of wood pyrometers fully consumed. One year after burning, seeded plots had 72% less woody cover compared to adjacent unseeded plots, and burned subplots had 33% less woody cover compared to adjacent subplots that were not burned. Our findings support the use of herbaceous seeding (particularly of *Elymus* grasses) in buckthorn removal projects. The positive effects of seeding on burn performance via increased fine fuel quantity outweighed potential negative effects of understory phenology on fuel moisture content and flammability. Thus, a combined approach of seeding and burning is likely to offer enhanced control of small buckthorn stems compared to either passive restoration or seeding alone.

Index terms: Elymus spp.; fire; fuel; grass; invasion; understory; restoration; revegetation; seeding

INTRODUCTION

Prescribed burning is commonly used to suppress woody plant species in savannas and open woodlands, and can be an effective method of invasive plant control in temperate deciduous forests (Boudreau and Willson 1992; Heisler et al. 2003; Glasgow and Matlack 2007; Bond 2008). In particular, management approaches that utilize a combination of mechanical removal and burning can sometimes effectively suppress invasive trees or shrubs like *Rhamnus cathartica* (common buckthorn) and promote native understory plants (Pearson and Gillette 2001; Bisikwa et al. 2020). In these cases, burning may offer managers a tool to effectively limit re-establishment of buckthorn after initial chemical or mechanical treatment. Initial removal efforts significantly increase availability of light and other resources (Heneghan et al. 2002; Anfang et al. 2020) and remaining buckthorn propagules experience little competition from native species due to depleted native seedbanks (Lamb et al. 2022). Therefore buckthorn often rapidly re-establishes dominance through a combination of resprouting stems, remaining small stems, and new germination (Knight et al. 2007; Wragg et al. 2021). Burning may be an effective method of controlling these remaining small stems, but the efficacy of burning in forest understories invaded by buckthorn is unclear.

Managers often implement annual or periodic burning to control buckthorn seedlings within the first 5 y following buckthorn removal in communities with near continuous herbaceous groundcover, such as savannas or open woodlands (Pearson and Gillette 2001; Bisikwa 2005). This can be successful because first-year buckthorn seedlings rarely survive burning and larger stems may lose vigor and/or be killed by repeated burning or other follow-up management (Richburg 2005; Bowles et al. 2007). However, competitive exclusion of native ground cover by buckthorn (Knight et al. 2007; Klionsky et al. 2011), the rapid decomposition of buckthorn leaf litter (Heneghan et al. 2002; Ashton et al. 2005), low density of native understory cover due to overstory shade, and/or positive feedbacks between buckthorn and exotic earthworms (Hale et al. 2006; Roth 2015) result in high proportions of bare ground and the loss of fine fuels in many buckthorn-invaded woodlands and forests (Kollmann and Grubb 1999; Heneghan et al. 2004). Buckthorn also produces leaf litter that decomposes quickly (Ashton et al. 2005) and is less combustible than most native tree species (Dibble et al. 2007). Fine fuel loads in buckthorn-invaded forests and woodlands are largely composed of overstory canopy leaf litter and rarely persist beyond early summer (Ashton et al. 2005; Roth 2015). Similar shifts in fuel dynamics have created self-sustaining feedbacks toward reduced fire frequency and severity in many eastern deciduous forests of North America (Abrams 2005) and limit the use of prescribed fires to manage buckthorn invasions in those systems (Frelich et al. 2015).

Revegetation seeding can in some contexts effectively increase cover of fast-growing, highly combustible grasses and forbs (Vander Yacht et al. 2020; Wragg et al. 2021; Schuster et al. 2022; Kaul et al. 2023). In particular, senesced grasses can be slow to decompose and contribute significantly to fine fuel loads in the fall and the following spring (Elder et al. 2011; Wagner and Fraterrigo 2015; Prior et al. 2017). Seeding native herbaceous species in a semi-open forest context has also been shown to reduce invasion of buckthorn seedlings by 51% over 4 y (Schuster et al. 2022). Although this reduction in buckthorn abundance is meaningful, herbaceous seeding alone is insufficient to prevent buckthorn re-establishment. Revegetating understories following combined mechanical removal and chemical treatment of buckthorn may simultaneously reduce buckthorn re-establishment and augment fine fuel loads to facilitate the use of fire for greater control of buckthorn seedlings.

Differences in plant functional group dominance and phenology likely complicate the relationship between revegetation and the efficacy of fire in buckthorn management. The literature that suggests revegetation seeding is likely to increase fuel abundance—particularly fine grass fuel—and therefore increase fire spread and severity is largely based on the ecology of fire-adapted native C_4 grasses in grasslands (Briggs et al. 2002; Bond et al. 2005; Vander Yacht et al. 2020) and invasive C_3 grasses in shrublands (D'Antonio and Vitousek 1992; Fusco et al. 2019). However, revegetation of temperate deciduous forests is commonly performed using mixtures of native C_3 grasses (particularly *Elymus* spp. and *Bromus* spp.) and forbs adapted for low fire frequencies (Frelich et al. 2017) and understory conditions (Wragg et al. 2021; Schuster et al. 2022). In particular, understory phenology that entails early spring emergence and late fall senescence (Augspurger and Bartlett 2003) may increase overall ground layer moisture levels and inhibit fire spread and intensity despite overall increased fine fuel loads (McGranahan et al. 2012). Standard fuel models used to assess how vegetation composition and structure impacts flammability lack these fine distinctions in phenology and structure that are crucial to understanding the effects of seeding on understory fires (Ottmar et al. 2007; Riccardi et al. 2007; Sandberg et al. 2007), leaving the net effect of seeding on fire spread and severity in forest understories unknown.

Here, we test the hypothesis that herbaceous revegetation increases fine fuel abundance and continuity in forest understories and consequently increases the spread, severity (i.e., the damage done to woody stems by fire), and potential impact of a single prescribed burn on buckthorn seedlings. We also characterize understory plant community composition in the year following burning to evaluate burn effects on herbaceous plants.

METHODS

We tested our hypothesis by burning small portions of plots established as part of a larger revegetation experiment located in deciduous forests of Minnesota, USA. That experiment was designed to compare buckthorn re-establishment from resprouts and seedlings in understories that had undergone revegetation seeding and areas that were left unseeded following initial mechanical buckthorn removal with follow-up foliar herbicide. We burned nine pairs of seeded and unseeded plots across two sites (Elk River, Minnesota, and Marine on St. Croix, Minnesota) and evaluated how revegetation seeding impacts burn efficacy.

Experimental Design and Measurements

We utilized two sites that had previously had understory communities dominated by buckthorn and had undergone initial mechanical removal of buckthorn via mastication (forestry mower) in January 2017. The Marine on St. Croix site (45.171437°N, 92.765094°W) was an oak-aspen (*Quercus* spp. and *Populus tremuloides* canopy) forest composed of both upland and lowland areas. Canopy light transmission at the Marine on St. Croix site ranged 13–23% across experimental blocks (mean 17%) as measured using paired quantum sensors (described in Schuster et al. 2022). The Elk River site (45.303173°N, 93.579193°W) was an open-canopy floodplain dominated by *Quercus* spp. (oak) but with *Celtis occidentalis* (hackberry), *Fraxinus pennsylvanica* (green ash), and *Ulmus americana* (American elm) being common members of the canopy as well. Canopy light transmission at the Elk River site ranged 8–24% across experimental blocks (mean 18%). In February 2017, we established four experimental blocks at the Marine on St. Croix site and five experimental blocks at the Elk River site. Each block consisted of two 30 m × 12 m plots that were randomly assigned to either be seeded or unseeded. In seeded plots, we then hand broadcast a seed mixture (Table 1) containing 9 native grasses (including one C_4 grass: *Sorghastrum nutans*), 2 native sedges, 22 native forbs, and 2 cover crop graminoids at a rate of 40.4 kg ha^{-1}. Unseeded plots received no seeds.

In July 2017, foliar herbicide was applied to all plots to control buckthorn resprouting from cut stems and potentially improve establishment of seeded species. We applied a foliar herbicide (3.5% fosamine ammonium mixed with water) to all plots at a rate of 300 L ha^{-1} via high-volume pistol grip sprayers (described in Schuster et al. 2020). We had anticipated this herbicide to primarily affect woody stems, and while fosamine ammonium exerted strong control against buckthorn, we also observed some nontarget damage to seeded grass species (Schuster et al. 2020). To compensate for potential long-lasting nontarget impacts on seeded grasses, we conducted supplemental seeding (Table 1) of three native grasses and one cover crop graminoid at a rate of 104 kg ha^{-1} in February 2018. We then allowed seeds to establish through 2019 in preparation for burns, and selectively treated buckthorn stems with fosamine ammonium in autumn of 2019.

Table 1.—Composition of seed mixtures applied in the spring of 2017 and 2018. All species are native to the study site except for the two agricultural cover crop species, *Triticum aestivum* and *Lolium multiflorum.* All species utilize C_3 photosynthesis except for *Sorghastrum nutans* (C_4).

		Seeds m^{-2}	
Scientific Name	Common Name	2017	2018
Bouteloua curtipendula	Sideoats Grama	11.8	0
Bromus pubescens	Hairy Woodland Brome	23.7	0
Elymus canadensis	Canada Wildrye	53.8	329.4
Elymus villosus	Silky Wildrye	32.3	332.6
Elymus virginicus	Virginia Wildrye	66.7	0
Hystrix patula	Bottlebrush Grass	15.1	0
Muhlenbergia mexicana	Mexican Muhly	138.9	609.2
Panicum virgatum	Switchgrass	28.0	0
Sorghastrum nutans	Indian Grass	23.7	0
Carex brevior	Plains Oval Sedge	46.3	0
Carex radiata	Eastern Star Sedge	32.3	0
Lolium multiflorum	Annual Rye	165.8	0
Triticum aestivum	Spring Wheat	54.9	163.6
Agastache scrophulariaefolia	Purple Giant Hyssop	11.8	0
Aquilegia canadensis	Red Columbine	4.3	0
Aster cordifolius	Heart-leaved Aster	17.2	0
Aster laevis	Smooth Blue Aster	6.5	0
Aster macrophyllus	Large Leaf Aster	4.3	0
Aster sagittifolius	Arrow-leaved Aster	16.1	0
Campanula americana	Tall Bellflower	5.4	0
Clematis virginiana	Virgin's Bower	5.4	0
Desmodium canadense	Showy Tick-trefoil	1.1	0
Eupatorium purpureum	Purple Joe Pye Weed	4.3	0
Ageratina altissima	White Snakeroot	74.3	0
Geranium maculatum	Wild Geranium	1.1	0
Hydrophyllum virginianum	Viginia Waterleaf	1.1	0
Hypericum pyrimidatum	Great St. Johnswort	11.8	0
Monarda fistulosa	Wild Bergamot	31.2	0
Rudbeckia hirta	Black-eyed Susan	36.6	0
Rudbeckia laciniata	Green Coneflower	2.2	0
Rudbeckia triloba	Brown-eyed Susan	50.6	0
Scrophularia lanceolata	Figwort	29.1	0
Thalictrum dasycarpum	Tall Meadow Rue	10.8	0
Verbena hastata	Blue Vervain	22.6	0
Zizia aurea	Golden Alexanders	11.8	0
TOTAL		1052.7	1434.8

We burned a 4 m × 4 m subplot within each seeded and unseeded plot to evaluate potential consequences of revegetation seeding for an initial prescribed fire (Supplemental Figures S1, S2). Subplots were located at one end of adjacent seed and unseeded plots to avoid interfering with other experimental work in the central portions of the larger plots. Following initial buckthorn management (in this case, by forestry mower in 2017), fine fuel loads were largely absent, but revegetation rapidly reintroduced fine fuel–producing C_3 grasses. To characterize fuel availability within each subplot, we visually estimated cover of graminoid litter, green living graminoids, tree leaf litter, and bare ground prior to fire ignition. Estimates were conducted by two trained observers independently and recording the mean of the two independent estimates to reduce the influence of each observer's bias. Our decision to measure fuel availability via cover is unlikely to have influenced our results compared to other potential metrics (e.g., biomass) because the majority of fine fuel in our experimental areas were composed of grasses and grass litter, and in grasslands fuel cover correlates with fuel biomass and is also strongly predictive of burn spread (Wragg et al. 2018; Cardoso et al. 2022). Although we performed estimates of graminoid litter and green graminoids including both grasses and sedges, grasses were more common and contributed more strongly to fuel loads. Therefore, we refer to these estimates as "grass litter" and "green grass" covers from this point onward. We performed the same estimates for living woody fuel and dead woody fuel cover but found that they were too scarce to contribute to our analyses (see Statistical Analyses).

Burn subplots were prepared for burning by raking a 1 m wide fire break around them and then initiating a ring burn ignition via drip torch. The use of a ring burn at this small scale precluded us from observing some elements of fire behavior that occur at larger scales (more often performed as strip backing fires) but is sensitive to the large differences in overall fuel quality and availability associated with our treatments (see Results; Kral et al. 2015). After ignition, subplots were monitored until fire self-extinguished (either due to consuming all fuel or failing to spread). We only provided a single ignition around each subplot and once fires extinguished, we did not impose additional ignition attempts. Marine on St. Croix subplots were burned on 7 May 2019 and Elk River subplots were burned on 27 April 2021. Equipment failure prevented us from recording site-specific conditions, but data from regional weather stations suggest that temperature was approximately 17°C and 7°C, relative humidity was approximately 30% and 80%, and wind speed was 2–5 ms^{-1} and 4–5 ms^{-1} for the Marine on St. Croix and Elk River site burns, respectively.

We quantified the spread and severity of fire in each subplot using a combination of pyrometers, visual estimates, and buckthorn seedlings (Supplemental Figure S3). First, we placed 13 pairs of bamboo skewers (4 mm diameter, 203 mm tall) and toothpicks (2 mm diameter, 51 mm tall) in the ground inside each subplot immediately prior to ignition to serve as pyrometers representing buckthorn stems of different sizes. Pyrometers (both skewers and toothpicks) were placed in a cross pattern with a pair in the center of the subplot and 3 pairs extending in each cardinal direction spaced 50 cm apart (i.e., 150 cm in each direction). Skewers and toothpicks were spaced 3 cm apart at each position. Immediately after the burn, we scored the condition of each pyrometer using a 5 point scale: 0 = unburned; 1 = darkened, but unburned; 2 = burned, but not consumed; 3 = partially consumed by the burn; 4 = completely consumed by the burn. We also visually estimated fire spread as the proportion of the subplot area that showed visual indicators of burning.

To evaluate how well our pyrometers reflected the impacts of a single burn on buckthorn, we identified up to 5 buckthorn stems within each subplot (75 total since some subplots contained fewer than 5 buckthorn) and placed additional pairs of pyrometers next to them. Buckthorn stems ranged from 0.6 mm to 7.4 mm diameter (Supplemental Table S1). We then scored the post-burn condition of both buckthorn and pyrometers using the same scale as other pyrometers.

We returned to our experimental plots in July of the year after burning (14 months after burning) and surveyed plant community composition in both burned and not burned portions of each plot. We visually estimated total woody cover, total herbaceous cover, cover of graminoid species, and cover of forb species in two diagonally adjacent 1 m × 1 m quadrats positioned northwest and southeast of the center of each burned subplot (whether seeded or unseeded). We also repeated these cover estimates in two 1 m × 1 m quadrats that were systematically positioned 2 m outside of burned subplots and 5 m apart within the larger 30 m × 12 m plot. By conducting sampling in this way, we were able to collect cover data for a factorial combination of seeding and burning.

Statistical Analyses

We used a series of general linear mixed models to test our hypotheses. All analyses included block as a random factor nested within site (analyses of plant community composition also included plot nested within block). Analyses were performed using SAS 9.4 (SAS Institute, Cary, North Carolina, USA). Full statistical results are presented in Supplemental Tables S2–S6.

Effect of Seeding on Fuel Loads

To evaluate effects of seeding on fuel load, we analyzed cover of green grass, grass litter, tree litter, and bare ground as a function of seeding (seeded or unseeded), site (Marine on St. Croix or Elk River), and the interaction of seeding and site. Cover estimates were transformed into proportions and analyzed using PROC GLIMMIX with a beta error distribution and logit link function.

To evaluate drivers of burn spread, we analyzed burn area (as a proportion) and the number of toothpicks affected (burn scores >0) as functions of site and one of four additional factors (seeding, natural log-transformed grass litter cover, natural log-transformed green grass cover, and natural log-transformed tree litter cover), as well as the interaction of site and those factors, each in a separate model. These additional factors needed to be considered separately since they are highly correlated with each other. Analyses of burn area were conducted using PROC GLIMMIX with a beta error distribution and logit link function. Analyses of the number of toothpicks affected were conducted using PROC MIXED.

Effect of Fuel Loads on Fire Spread and Severity

To evaluate drivers of burn severity, we analyzed burn scores of skewer pyrometers as a function of seeding, site, and the interaction of seeding and site in PROC MIXED. To disentangle effects of seeding on burn severity from burn spread, we only considered skewers that were paired with toothpicks that had been affected by burning in this analysis (i.e., had burn scores >0). Similar to our investigation of drivers of burn spread, we repeated this analysis by replacing seeding with either natural log-transformed grass litter cover, natural log-transformed green grass cover, or natural log-transformed tree litter cover. We also performed a χ^2 test on the distribution of burn scores across all skewer pyrometers (comparing seeded and unseeded plots regardless of pick scores, $n = 234$ skewers) to evaluate how seeding affected fire severity overall (including seeding effects on spread).

To evaluate whether our pyrometers accurately represented immediate impacts of burning on buckthorn stems, we characterized the relationship between flammability of our pyrometers and actual buckthorn stems in PROC MIXED. We analyzed buckthorn burn score as a function of each buckthorn's paired skewer pyrometer score, the buckthorn's basal diameter, site, and all possible interactions between the three factors.

Effect of Fire and Seeding on Community Composition

To evaluate impacts of burning and seeding on understory plant community composition in the year following burning (14 months later), we natural log-transformed each cover estimate (total woody cover, total herbaceous cover, graminoid cover, and forb cover) and analyzed it using PROC MIXED as a function of seeding, burning, and site. All possible two- and three-way interactions were included in each model.

RESULTS

Effect of Seeding on Fuel Loads

Herbaceous seeding increased green and senesced grass cover with the latter leading to increased fire spread and intensity (Table 2). Seeding more than doubled estimated cover of green grasses (from 10% to 25% on average; $P = 0.01$) and increased grass litter cover by more than 12-fold (Figure 1; from 2% to 29% on average; $P < 0.01$). Seeding also reduced bare ground (from 2.11% to 0.56% on average; $P = 0.03$) and decreased visible tree leaf litter (from 86% to 70% on average; $P < 0.01$). Green grass cover was higher at the Elk River site compared to the Marine on St. Croix site ($P = 0.03$). Differences in ambient (unseeded) green grass cover between the sites also led to seeding being marginally more effective at increasing green grass cover in Marine on St. Croix compared to Elk River ($P = 0.07$). Overall, fuel load estimated immediately before burning was largely determined by seeding treatment.

Effect of Fuel Loads on Fire Spread and Severity

Herbaceous seeding almost doubled the estimated burned area (Table 2; from an average of 51% in unseeded areas to 94% in seeded areas; $P < 0.01$). Similar effects were observed for toothpick pyrometers, which we used as a complementary, less-subjective metric of burn spread. The proportion of toothpick pyrometers affected by fire (i.e., had a burn score >0) more than doubled with herbaceous seeding (Table 2; from 0.45 to 0.94, on average; $P < 0.01$).

Fires were more extensive in areas with greater herbaceous fuel cover. Estimated burned area and proportion of toothpick pyrometers burned were higher in seeded plots (Figure 1, Table 2). Greater grass litter cover enhanced both area burned (Figure 1A;

Table 2.—Mean ± SE estimates of green grass, grass litter, tree leaf litter, and bare ground cover (%) in experimental subplots immediately prior to burning. Also mean ± SE estimates of area burned and the percentage of toothpick pyrometers affected by fire (burn score >0) immediately after burn. Grass cover includes sedges.

	Elk River		Marine on St. Croix	
	Unseeded	Seeded	Unseeded	Seeded
Cover Estimates (%)				
Green grass	17 ± 6	27 ± 4	1 ± 0	22 ± 5
Grass litter	4 ± 3	28 ± 10	0 ± 0	30 ± 15
Tree leaf litter	78 ± 5	74 ± 4	96 ± 2	64 ± 15
Bare ground	2 ± 1	1 ± 0	3 ± 2	1 ± 0
Fire Extent (%)				
Burn area	42 ± 8	91 ± 5	62 ± 19	98 ± 1
Toothpick pyrometers affected	38 ± 11	92 ± 4	54 ± 25	96 ± 2

$P < 0.01$) and toothpick pyrometers burned (Figure 1B; $P < 0.01$). Conversely, area burned ($P = 0.02$) and the number of toothpick pyrometers burned ($P = 0.05$) were both lower in subplots with greater bare ground. Cover of green grasses and tree litter did not significantly affect either estimated burn area or the number of toothpick pyrometers affected by fire.

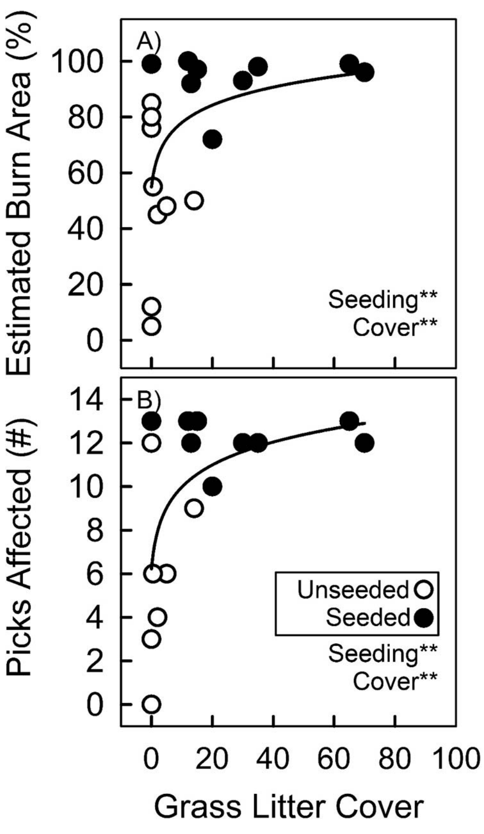

Figure 1.—Relationships between grass litter cover (%) and two measures of fire spread in burn subplots—(A) visually estimated burn area (%) and (B) the number of toothpick pyrometers (13 per subplot) that showed visual signs of burn damage (i.e., burn score >0)—in seeded (closed) and unseeded (open) plots. Curved lines represent the back-transformed modeled relationships. * indicates $P < 0.05$; ** indicates $P < 0.01$. Interaction terms were not significant.

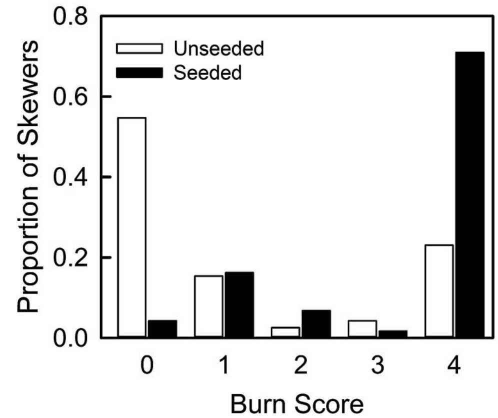

Figure 2.—Proportion of all skewer pyrometers ($n = 234$) found in each burn score category in burned subplots within unseeded (white) and seeded (black) plots. Burn scores: 0 = unburned; 1 = darkened, but unburned; 2 = burned, but not consumed; 3 = partially consumed by the burn; 4 = completely consumed by the burn.

Skewer pyrometers were generally accurate indicators of the flammability of buckthorn seedlings. Burn scores of skewers were generally indicative of burn scores for adjacent buckthorn ($P < 0.01$). Skewers had a mean burn score of 2.25 (± 0.20 SE) whereas buckthorn seedlings had a mean burn score of 1.69 (± 0.17 SE). Burning impacts on buckthorn were not significantly affected by seedling diameter.

Burns tended to be more severe (as measured by burn scores of those skewer pyrometers that had adjacent toothpick pyrometers with positive burn scores) in seeded plots compared to unseeded plots ($P = 0.10$). Herbaceous seeding increased mean skewer burn score from 2.77 (± 0.19 SE) in unseeded areas that had burned ($n = 53$) to 3.36 (± 0.11 SE) in seeded areas that had burned ($n = 110$). Severity (again, as measured by burn scores of skewer pyrometers whose adjacent toothpick pyrometers had positive burn scores) was not significantly affected by cover of green grass, grass litter, or tree leaf litter.

Considering all skewer pyrometers deployed across the experiment (regardless of the burn score of their adjacent toothpick pyrometer; $n = 234$), seeding shifted the distribution of burn scores to be more severe (Figure 2; $\chi^2 = 82.5$, d.f. = 4, $P < 0.01$). This reflects the combined impacts of seeding on fire spread and intensity. Seeding decreased the proportion of skewers that were unaffected by fire (i.e., burn score = 0) by 93% (from 0.55 to 0.04) and increased the proportion of skewers consumed (i.e., burn score = 4) more than three-fold (from 0.23 to 0.71).

Effect of Fire and Seeding on Community Composition

We found strong influences of seeding and burning on plant community composition one year post-burn (Table 3). Across both sites, grass cover in seeded plots was more than three-fold that of unseeded plots (49% compared to 15%; $P < 0.01$). The stimulatory effect of seeding on grass cover remained after burning (seeding × burning: $P = 0.10$).

Table 3.—Mean ± SE estimates of total combined herbaceous, grass, forb, and woody cover (%) in experimental subplots, estimated 14 months after burns. Total herbaceous cover was estimated independently of grass and forb cover. Grass cover includes sedges. Letters indicate statistically similar groups (Tukey HSD) within cover type.

	Unseeded		Seeded	
Cover Type	Not burned	Burned	Not burned	Burned
Total Herbaceous	39 ± 6 a	52 ± 7 ab	60 ± 6 b	63 ± 5 b
Grasses	18 ± 6 a	11 ± 4 a	45 ± 6 b	54 ± 5 b
Forbs	26 ± 4 ab	43 ± 7 a	19 ± 2 b	15 ± 2 b
Total Woody	13 ± 3 a	9 ± 2 a	4 ± 1 b	2 ± 1 b

Subplots that were both seeded and burned had the greatest grass cover (54 ± 5%; mean ± SE) on average. Increases in grass cover with seeding led to 36% greater total herbaceous cover as well (from 46% to 62% cover on average; $P < 0.01$), despite forb cover being 51% less in seeded plots compared to unseeded plots (from 34% to 17% cover on average; $P < 0.01$). Total herbaceous cover, grass cover, and forb cover did not differ significantly between sites, although seeding tended to have a larger impact on grass cover at Marine on St. Croix compared to Elk River ($P = 0.07$), as we saw also for fuel load. In contrast, woody cover was four-fold greater in the Elk River site compared to the Marine on St. Croix site ($P < 0.01$), due to the greater abundance of buckthorn and other woody species (*Fraxinus pennsylvanica*, *Celtis occidentalis*, and *Rubus* spp.) at Elk River. Both seeding (Figure 3A; $P < 0.01$) and burning (Figure 3B; $P = 0.04$) reduced woody cover (72% and 33% reduction due to seeding and burning, respectively) across the experiment. We did not detect any significant interactions between seeding and burning on woody cover ($P = 0.77$).

DISCUSSION

We evaluated the impacts of revegetation seeding on the potential use of prescribed fire to suppress buckthorn re-establishment after initial removal in two tree communities with relatively closed canopies based on most standards (Hanberry et al. 2018, 2020). We found broad support for our hypothesis that seeding increases cover of grass litter and

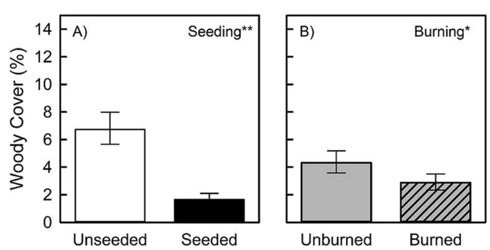

Figure 3.—Visually estimated woody cover (mean ± SE) in (A) unseeded (open) and seeded (closed) plots and (B) not burned (gray) and burned (hashed) subplots. * indicates $P < 0.05$; ** indicates $P < 0.01$.

increases fire spread compared to adjacent unseeded areas. However, impacts of seeding were largely confined to affecting burn spread and not burn severity. Although burn scores were higher in seeded subplots compared to unseeded subplots, this effect was only marginally significant and the relationship between grass litter cover (the largest pool of fine fuel in our systems; Elder et al. 2011; Prior et al. 2017) and burn scores was even weaker (Supplemental Information). This is likely an artifact from the scale of our experiment. We burned small subplots (4 m × 4 m) that did not allow for larger-scale aspects of fire behavior to develop. For example, at larger scales, preheating of fuels from nearby fire can lead to synergistic impacts of fuel loading on fire intensity and severity (Beer 1991). Had we conducted this experiment at larger scales, we may have detected more robust relationships between grass litter cover and burn scores in addition to the consistent impacts of seeding and grass litter cover on burn spread. Our results illustrate how herbaceous seeding (primarily composed of native C_3 grasses—C_4 and nonnative graminoids were not present in any burn subplots) can increase fine fuel loads even in relatively closed-canopy forests (<20% canopy openness) and allow for effective burning.

Overall, our findings suggest that a combined management approach including the mechanical removal of buckthorn, immediately followed by herbaceous seeding and any required follow-up control of large buckthorn resprouts, and then burning after grass establishment, may offer enhanced suppression of small buckthorn. Our findings complement those of earlier observational (Wragg et al. 2021) and experimental (Schuster et al. 2022) studies showing that revegetation seeding can reduce the size and abundance of buckthorn seedlings. Reduced performance of buckthorn after seeding is a useful component of achieving management goals and increases the vulnerability of remaining stems to further management. Remaining stems are more effectively treated by herbicides (Bisikwa et al. 2020) and can be more easily controlled with additional burning (Franklin et al. 2003; Lawes et al. 2011). The low spread of fire we observed in unseeded areas was associated with low cover of senesced grasses even if total herbaceous cover was relatively high (due largely to higher forb abundance in unseeded plots). Seeding facilitated fire spread by increasing the availability of fine fuels and led to more consistently severe burn impacts on pyrometers. Based on the correlation between skewer pyrometer scores and buckthorn seedling scores, we infer seeding would also enhance burning of buckthorn stems.

The impacts of revegetation seeding on fine fuel loads is likely to vary with canopy conditions. In this study, we observed strong impacts of seeding on the abundance of grasses and grass litter in two sites that spanned a range of relatively dark conditions (8–24% canopy light transmission). However, Schuster et al. (2022) evaluated the same seed mixture under more varied light conditions (4–57% canopy light transmission). There, cover of seeded species (primarily *Elymus* spp. as in this experiment) was positively correlated with canopy openness, reaching 100% cover in areas with more than 45% canopy light transmission. Conversely, areas with low canopy light transmission supported less cover of seeded species and seeded species were virtually absent from the darkest areas. Our sites occupied relatively moderate light conditions along the gradient examined by Schuster et al. (2022) and thus were able to support moderate cover of seeded species. Fine fuel loads are likely to be less affected by seeding in systems with progressively less light availability but increasingly augmented in woodlands with greater light availability. However, systems with ample existing fine fuel loads prior to revegetation (e.g., savannas or grasslands) may be less affected by seeding since fine fuels are ambiently abundant.

The relatively high levels of skewer pyrometer consumption by fire that we observed in seeded plots suggests that burns conducted following seeding are also likely to consume buckthorn seedlings and small resprouting stems. This largely matches the types of impacts commonly observed for woody plants in other settings (O'Connor et al. 2020), but like other observations of burn impacts on woody vegetation, some of the plants affected by fire could have maintained living roots (Boudreau and Willson 1992). However, the capacity for any one individual to resprout is constrained by stored carbohydrates, and seedlings are less likely to hold sufficient reserves to support resprouting. Indeed, when we returned to resurvey community composition one year post-burn at the Elk River site, the only living buckthorn we observed were those that had escaped burning (burn score = 0) or had been only mildly damaged (burn score = 1). Whereas all of the 20 relocatable buckthorn seedlings in unseeded subplots at the Elk River site were visibly alive one year after burning, only 9 of the 16 relocatable buckthorn seedlings in seeded plots were visibly alive at that same time (PDW, pers. obs.), consistent with the increased spread and severity of fire in seeded plots. Hence, repeated burning may offer sustained and more effective control of buckthorn (Richburg 2005; Bowles et al. 2007). Comparable grass cover between burned and unburned areas in the year after a burn suggests that repeated burning is feasible for the communities considered here. Had we observed significant decreases in grass cover associated with burning, it would have been unlikely that grass productivity would have supported additional burns. We also did not observe noticeable changes in herbaceous community composition: native C_3 grasses dominated seeded areas both before and after burning. The grasses used in this seeding experiment remained highly productive even after burning, suggesting that future burns are likely to be at least as—if not more (see Reich et al. 2001)—intense, in areas where those grasses establish. The potential for repeated burns in revegetated areas may facilitate improved control of buckthorn over time as resprouts become more established and new seedlings emerge.

Previously it was unclear whether the traits of dominant Midwest understory grass functional groups would allow use of fire as a viable tool. The stimulatory impacts of seeding on burning were strong enough to overcome potential suppressive effects caused by the phenology and moisture content of C_3 grasses. C_3 grasses often produce litter that is less flammable than C_4 grasses (McGranahan et al. 2012) and, in our experiment, C_3 grasses also emerged from dormancy sufficiently early to overlap with our spring burning treatments, strongly increasing the cover of green vegetation in seeded plots. Both of these factors likely dampened the effect of fire in our experiment (Fosberg 1971; Dimitrakopoulos and Papaioannou 2001). Yet, the benefits of increased fine fuel loading were strong enough to override these potentially inhibitory effects and resulted in increased spread and impact of fire in seeded plots. We observed positive effects of seeding on fuel loading and fire behavior in both sites despite the different environmental contexts of the two sites and burns. The Elk River burn took place 2 y later than the Marine on St. Croix burn and consequently had a more developed herbaceous layer (Table 2) that might otherwise dampen effects of seeding. Yet, we found consistent impacts of seeding and no significant interactions between seeding (or cover) and site—suggesting the effects of seeding were robust to the different environments considered here. It is likely that the net effect of seeding on fire behavior could be amplified if burns were conducted when grasses were dormant or when fuel moisture levels were less, either as a result of burning later in the season or environmental stochasticity. Although our results support the use of seeding to facilitate burning, they also highlight the need for manager planning and seizing opportunities to burn when conditions are most favorable.

Our findings suggest seeding C_3 grasses and forbs can produce sufficient fine fuel to effectively promote the use of prescribed burns as part of a multifaceted approach to management of buckthorn and other woody invaders in forests and woodlands with moderate light availability. Overall, seeding may allow for larger and more frequent controlled burns—at least in semi-open forests—that reduce the amount of follow-up mechanical and chemical removal needed to manage buckthorn.

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