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Positive feedbacks between fire and non-native grass invasion in temperate deciduous forests

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ABSTRACT

Non-native grass invasions have the potential to change natural and prescribed fire regimes by altering fuels, which in turn may promote further invasion. We examined if invasion by *Microstegium vimineum*, a non-native annual grass, resulted in a positive invasion-fire feedback in eastern deciduous forests managed with prescribed fire and how this response varied across the landscape. Using paired invaded and uninvaded plots embedded in forest stands subjected to prescribed fire, we quantified differences in fire intensity and fuel loads, and fire effects on *M. vimineum* seedbank emergence, performance and spread. Invaded sites had less leaf litter and fine woody fuels, and increased fire intensity. Although fire reduced emergence of *M. vimineum* from the soil seedbank, sites subjected to prescribed fire had greater *M. vimineum* biomass and higher recruitment than unburned sites. Soil moisture strongly modulated *M. vimineum* response to fire, such that fire facilitated *M. vimineum* invasion more in wetter than drier sites. These findings indicate that deciduous forests are vulnerable to positive invasion-fire feedbacks, although the positive effect of fire may be less pronounced where soil moisture is limiting. The interaction between soil moisture and fire effects can inform management decisions regarding where to combine prescribed burning with intensive invasive control measures such as torching, hand pulling, and herbicide application.

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1. Introduction

Fire is an important process for maintaining species diversity and ecosystem function in many forest ecosystems across North America, including deciduous forests in the eastern US (Abrams, 1992; Royo et al., 2010; Stambaugh et al., 2015). Given its potential ecological benefits, prescribed burning has been widely implemented as tool for managing and restoring eastern deciduous forests with suppressed or altered fire regimes. Approximately one million ha are burned under prescription annually in the US (Ryan et al., 2013), with a substantial fraction occurring in eastern deciduous forests (Melvin, 2012).

While prescribed burning is useful for controlling woody understory growth, managing fuels and promoting native vegetation (Burton et al., 2011), the use of fire in eastern deciduous forests can also lead to less desirable changes (Matlack, 2013). Notably, prescribed burning can promote the recruitment of non-native invasive plant species (Glasgow and Matlack, 2007; Dibble et al., 2008; Kuppinger et al., 2010). Non-native invasive plant species with an established seedbank tend to respond positively to

post-fire conditions such as increased soil temperatures, increased light levels, reduction of the litter layer, reduced competition and increased available nitrogen. Once established, invasive plants can alter fire behavior by changing fuel characteristics, which in turn can promote further invasion (Brooks et al., 2004). The positive feedback between fire and invasion is well documented for non-native grasses (the grass-fire cycle; D'Antonio and Vitousek, 1992), and is attributable to their high flammability and tendency to recover from disturbance more quickly than native species. In seasonally dry woodlands in Hawaii, for example, invasion by the non-native grass *Schizachyrium condensatum* results in increased fire frequency and non-native grass cover after fire (Hughes et al., 1991). Similar impacts have been documented for non-native grass species in other ecosystems, including *Bromus tectorum* invasion in the US Great Basin (Balch et al., 2013), *Andropogon gayanus* in northern Australian savannah (Setterfield et al., 2010), and *Melinis minutiflora* at the Brazilian Cerrado savannah-forest ecotone (Hoffmann et al., 2004). In these grassland and dry woodland systems, non-native invasive grasses have altered fuel characteristics by either replacing less flammable, native vegetation or filling gaps between the naturally sparse vegetation to create more continuous fuels (D'Antonio and Vitousek, 1992).

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Although it is speculated that grass invasion of forests will increase flammability, few studies have investigated the interaction between grass invasion and fire in eastern deciduous forests (Dibble et al., 2008). The grass-fire cycle has predominantly been studied in dry woodlands and grasslands, which have different fuel characteristics than forests. Whereas grasses and forbs are the main fuel source in grassland communities, downed material from the overstory is the major contributor to the fuel load in most forest systems. Given this, understory grass invasion may have little influence on forest fire behavior, resulting in weak feedback between fire and invasion. At the same time, grasses have several unique characteristics that distinguish them from forest fuels, including a high surface area to volume ratio which allows for rapid drying, and low compactness which allows for more oxygen to mix with the fuel (DeBano et al., 1998). While both grasses and forest litter provide continuous horizontal fuels, the relatively slower drying that characterizes forest fuels can make them functionally discontinuous if the fuels are too wet to carry fire, whereas grass-invaded forests may have high functional continuity of fuels due to the rapid drying of grasses. As a result, grass invasion might contribute to changes in forest fire behavior despite the dominance of overstory fuels.

For this study, we investigate the interaction between fire and grass invasion of eastern deciduous forests using *Microstegium vimineum* (Trin.) A. Camus, an annual C4 species native to southeastern Asia (Fairbrothers and Gray, 1972). In its native range, *M. vimineum* occupies a variety of temperate habitats including forests, forest edges, and riparian areas, and fires are common during the dry winter months (Flory et al., 2011; Fischer et al., 2013). It occurs in similar habitats in the eastern US, and currently ranges from Texas to Massachusetts (USDA, 2015). By forming dense lawns in the forest understory, *M. vimineum* can significantly alter the understory community and suppress tree seedling growth (Oswalt et al., 2007; Marshall et al., 2009; Flory and Clay, 2010; Brewer, 2011). It can also affect ecosystem processes by altering microbial activities and accelerating nitrogen and carbon cycling (Ehrenfeld et al., 2001; Kourtev et al., 2003; Fraterrigo et al., 2011; Craig et al., 2015). Due its impacts on forest ecosystems, there is a need to characterize conditions that are facilitating the invasion success of *M. vimineum* and use this information to control established populations.

Generally, *M. vimineum* shows a positive response to disturbance, including fire, litter removal, and logging (Glasgow and Matlack, 2007; Oswalt and Oswalt, 2007; Nelson et al., 2009; Emery et al., 2013). Specifically, post-burn conditions have been shown to have a positive effect on *M. vimineum* growth (Glasgow and Matlack, 2007). Although *M. vimineum* germination and seedling density is reduced immediately following fire, these negative effects on stem density do not persist in the following growing season (Emery et al., 2013). In addition to responding positively to disturbance, *M. vimineum* performance is sensitive to resource gradients. *M. vimineum* growth and reproductive output is reduced in low light environments, under low nitrogen conditions, and in water-limited areas (Claridge and Franklin, 2002; Huebner, 2010a; Ross et al., 2011; Warren et al., 2011). These resource gradients may interact with fire regimes to amplify or weaken plant response to fire. By examining the interaction between fire and *M. vimineum* invasion across resource gradients, we can better identify areas where prescribed fire is more likely to promote invasion.

The overall objective of this study was to evaluate the interaction between fire and the invasion of a non-native annual grass, *M. vimineum*, in eastern deciduous forests across a range of environmental and fuel conditions. Specifically, we asked: (1) How does *M. vimineum* invasion influence fuels and fire intensity? and (2) How does prescribed fire affect emergence from the *M.*

vimineum seedbank and the performance and spread of *M. vimineum* across environmental gradients? We expected that grass invasion would increase fine fuel loads, and, in turn, increase fire intensity because of the high flammability of fine fuels. We further expected that fire would reduce emergence of *M. vimineum* from the seedbank, but that this negative effect would be outweighed by enhanced recruitment over the longer-term. Because *M. vimineum* performs better in mesic conditions, we predicted that low soil moisture would weaken the positive feedback between fire and *M. vimineum* invasion.

2. Methods

2.1. Study site

We conducted this work at the Shawnee National Forest (SNF) and Dixon Springs State Park (DSSP) located in the Central Hardwood Region between the Mississippi and Ohio rivers in far southern Illinois. In this unglaciated region, there are distinct landscape gradients from mesic, forested ravines to drier, upland forest. Mean temperature is 31 °C in the summer and 8 °C in the winter with a mean annual precipitation of 125 cm. During the study period (2011–2013), mean summer temperature was 26 °C and total annual precipitation ranged from 42 to 88 cm (http://www.ncdc.noaa.gov). The uplands in this region are dominated by mixed oak (*Quercus* sp.) and hickory (*Carya* sp.) forests and the mesic areas are comprised of a wide range of hardwoods including tulip poplar (*Liriodendron tulipifera*), beech (*Fagus grandifolia*), black walnut (*Juglans nigra*), bitternut hickory (*Carya cordiformis*), red oak (*Quercus rubra*), Kentucky coffee tree (*Gymnocladus dioicus*), Ohio buckeye (*Aesculus glabra*), honey locust (*Gleditsia triacanthos*), basswood (*Tilia americana*), white ash (*Fraxinus americana*), and sugar maple (*Acer saccharum*) (Mohlenbrock, 1982). In addition to the hardwood communities, the USDA Forest Service also maintains loblolly pine (*Pinus taeda*) and shortleaf pine (*Pinus echinata*) dominated stands. The USDA Forest Service regularly conducts prescribed burns at SNF to reduce fuels, stimulate the growth of native herbaceous plants and increase oak-hickory regeneration. Each year between October and April, an average of 2000 ha is burned. *M. vimineum* was first documented in the area prior to 1986 and frequently occurs near roads, trails, and streams, which are all common dispersal corridors for *M. vimineum* (Mohlenbrock, 1986; Christen and Matlack, 2009).

2.2. Study design

We evaluated the interaction between *M. vimineum* invasion and fire by conducting several detailed studies in multiple burn units and adjacent unburned forest stands. To determine fire effects on invasive grass performance, we compared grass recruitment, biomass, seed production, and advancement of the invasion front in burn units prior to burning and in adjacent unburned forest stands. In a subset of these burn units, we characterized pre- and post-burn fuel beds and measured fire residence times in paired invaded–uninvaded plots to determine how invasion influenced fuels and fire behavior. We also quantified seedbank emergence following burning to assess short-term fire effects on grass invasion. Collectively, the results of these studies provided insights into the pathways by which grass invasion and fire feedback to each other, allowing us to test the different components of the grass-fire cycle in eastern deciduous forests.

Burn units were selected to represent the range of variation in soil moisture conditions present in the study area, ranged in size from 15 to 1298 ha, and were between 4 and 41 km apart (Table A1). When the study began, the burn units had been last

burned in either 2009, 2010, or 2011; thus, performance and pre-burn fuel measurements were done 1–4 years since the last fire. Adjacent unburned areas were selected such that they were comparable to burn units with respect to elevation and terrain but lacked a history of management by fire. Detailed methods for each study are provided below.

2.2.1. M. vimineum performance and spread

To assess the influence of fire on *M. vimineum* performance, we established 17 plots in burn units and paired them with 17 plots in adjacent unburned stands ($n = 34$ plots total; Table A1). Approximately half of the plots were established in 2011 (nine in burn units and nine in unburned stands), with the remaining plots established in 2012. Although *M. vimineum* is a prolific seeder, local dispersal of *M. vimineum* populations is slow with populations spreading less than 25 cm annually (Rauschert et al., 2010). This slow spread coupled with high local recruitment results in discrete invasion edges. The study plots were installed near these discrete invasion edges to control for time since invasion. Each plot consisted of two parallel 3-m transects that began at a discrete invasion edge with 0.25×0.25-m subplots located 1, 2, and 3 m from the edge, moving into the invaded patch (*sensu* Warren et al., 2011).

In August of the year plots were established, the leaf litter, aboveground biomass of *M. vimineum*, and aboveground biomass of other herbaceous plants and woody seedlings were collected from the subplots along one of the two transects in each plot. Samples were dried to constant mass in a 60 °C oven and weighed. We counted flowering stems in the subplots of the unaltered transects during September of the year plots were established. In October, after seed set and before seed release, five randomly selected stalks were collected from the unaltered transects and seeds were counted in the lab to estimate seed production. In the following spring, we quantified recruitment by counting the number of new stems in all subplots along both harvested and unaltered transects. For all responses, subplot data were pooled, yielding one value per plot.

Prior to litter and biomass collection, we measured light and soil moisture along transects selected for destructive harvest. Light levels were measured over each subplot and under a reference full light condition using a LiC or quantum line sensor (LI-COR, Inc. Lincoln, Nebraska USA). The reference light measurement was used to calculate the percent of full sun for each subplot. Soil moisture was measured from three locations within each subplot using a Time Domain Reflectometry probe (Decagon 5TM Soil Moisture Sensor, Decagon Devices Inc., Pullman, WA, USA). All data were pooled by plot.

To determine fire effects on *M. vimineum* advancement, we installed three spread transects in each of the nine paired plots established in burn units and adjacent unburned stands in 2011 ($n = 18$ plots total). The spread transects were located within 10 m of the performance plots and consisted of 50-cm wide rows of pin flags starting at the invasion edge and moving perpendicular into the uninvaded area. The invasion edge was marked in July 2011, and advancement was measured from the marked edge to the farthest *M. vimineum* plant along each transect in August 2012. Distances were averaged by plot. We also determined the slope of each plot using a GIS and a 10-m DEM.

2.2.2. Forest fuels and fire intensity

In July–August of 2012, we measured fuels in 20 pairs of invaded and uninvaded plots ($n = 40$ plots total) distributed across seven of the burn units used in the performance study plus one additional site (DiSp; Table A1). Each fuel plot consisted of three 17-m fuel transects radiating from a central point at 0°, 120°, and 240° azimuths (Fig. A1). Along each transect, starting one

meter from the plot center, intersecting woody fuels were inventoried using Brown's line intercept method (Brown, 1974) with 1-h fuels (<0.64 cm in diameter) counted along two meters of the transect, 10-h fuels (0.64–2.5 cm in diameter) counted along four meters, 100-h fuels (2.5–7.6 cm in diameter) counted along eight meters, and 1000-h fuels (>7.6 cm) counted along 16 m of the transect. The diameters of all the 1000-h fuels were measured. Four subplots (25×25 cm) were established along each transect. Leaf litter (not including *M. vimineum* or other plants that were alive from July to August) and duff were harvested from these subplots, dried in a 60 °C oven, and weighed.

To determine what fuel types were consumed by prescribed fires, 11 sets of paired plots ($n = 22$ plots total) were resampled in spring of 2013 after burning using identical methods (Table A1). Prior to burning, data loggers and type K thermocouples were installed in all but two of these pairs ($n = 1$ per plot) (Table A1) to measure fire intensity. Thermocouples were placed at the soil surface, beneath the forest floor. Fire did not reach one of the invaded plots and this plot was not included in the analysis. Temperature was recorded every ten seconds and was used to calculate fire residence time, defined as the number of minutes over 60 °C. We used this temperature threshold because it is a temperature at which cell death can occur in plants (Levitt, 1980).

2.2.3. Seedbank emergence

We collected soil twice from each of 23 invaded plots in the spring of 2013 to assess the short-term effects of fire on the *M. vimineum* seedbank. Twelve plots were located in the burn units where fuels were measured (Table A1). In these plots, soil was collected before and within two days after burning. The remaining eleven plots were located in adjacent unburned areas and were sampled at the same time as the neighboring burn unit. For all plots, the time between sampling periods depended on when a burn took place and ranged from 7 to 22 d.

To account for spatial heterogeneity in the seedbank, we used a "many small samples" approach (Gross, 1990). This involved pooling 10 subsamples collected with a soil corer (6 cm diameter, 4 cm deep) in each plot. The first set of subsamples was collected along transects at 60 cm and 110 cm from the plot center at 0°, 18°, 36°, 54°, and 72° azimuths, and the second set of subsamples was collected at 70 cm and 220 cm at the same azimuths. Only the shallow seedbank was collected because low intensity prescribed fires typically do not heat the soil below a few centimeters (Heyward, 1938; DeBano et al., 1998; Iverson and Hutchinson, 2002). Composited seedbank samples were returned to the greenhouse and spread thinly over trays filled with sterile course sand. Trays were monitored weekly for emerging *M. vimineum* stems, and emerging stems were removed from the tray. Each tray was retained in the greenhouse after emergence peaked and two weeks had passed without new emerging individuals.

2.3. Data analysis

We used linear mixed models to evaluate differences in *M. vimineum* biomass, recruitment, and seed production with burn treatment, analyzing count data using generalized linear mixed models with a log-link function. In addition to burn treatment, *M. vimineum* performance models included soil moisture, litter mass, light, and all interactions as fixed effects. Pair was nested within burn unit and both pair and burn unit were incorporated as random effects. For models that included interactions with continuous covariates, the 1st and 3rd quantiles were used to estimate the interaction. These models were compared using AICc values for the mixed models and pseudo AICc values for the generalized linear mixed models. The models with the lowest AICc values were used as the best fit.

We tested for differences in *M. vimineum* advancement between burned and unburned plots using linear mixed models, with pair included as a random effect. Covariates included in these models as fixed effects were litter mass (determined from co-located performance plots), slope, and burn treatment. These models were compared with AICc values.

Pre-burn fuel composition was compared between invaded and uninvaded plots using generalized linear mixed models and a log-link function for count data. Random variables included the intercept and pair, which was nested within burn unit (also a random variable); invasion treatment was included as a fixed effect. To determine which fuel types were consumed and test for differences in fuel consumption between invaded and uninvaded plots, data from the fuel plots sampled before and after the spring 2013 burns were analyzed as a before–after control-impact design using a generalized linear mixed model with a log-link for count response variables (McDonald et al., 2000). Pair was nested within burn unit and both pair and burn unit were incorporated as random effects. For the before-after control-impact design, the fixed effects included invasion status, burn treatment (expressed as a before–after effect), and the interaction between invasion status and burn treatment. Because there are several variables that we would expect to contribute to fire intensity, we compared models which included invasion status, pre-burn fuels (separated by type), and slope as fixed effects.

Seed bank emergence was analyzed as a before-after control-impact design using a generalized linear mixed model with a log link (McDonald et al., 2000). Plot was nested in site and both plot and site were included as random effects. The fixed effects included the burn treatment, time (pre-burn vs. post-burn), and the interaction between burn treatment and time. All analyses were performed in SAS (SAS Institute Inc., 2013) using the proc glimmix or proc mixed functions.

3. Results

3.1. Fire effects on M. vimineum performance

M. vimineum performed better in stands managed with prescribed fire. *M. vimineum* biomass was significantly higher in burned plots ($F_{1,15} = 3.82$, $p = 0.07$) and areas of high soil moisture ($F_{1,15} = 19.9$, $p < 0.001$). A significant interaction between soil moisture and burn treatment indicated that soil moisture modulated the positive effects of burning on *M. vimineum* biomass ($F_{1,15} = 6.98$, $p = 0.02$). When estimated using soil moisture values for drier and wetter sites (1st and 3rd quantiles of the soil moisture data), *M. vimineum* biomass was 214% and 135% higher in burned and unburned plots (resp.) situated in wetter sites compared to drier sites (Fig. 1). Seed production per stalk did not vary with burn treatment ($F_{1,15} = 3.82$, $p = 0.10$); however, it was positively related to soil moisture in burned plots and unrelated to soil moisture in unburned plots ($F_{1,15} = 3.82$, $p = 0.06$; Fig. 2). There was no relationship between *M. vimineum* advancement and burn treatment or litter mass. There was, however, a positive relationship between slope and *M. vimineum* spread ($F_{1,8} = 24.5$, $p = 0.001$). Slope and burn treatment did not interact ($F_{1,6} = 0.04$, $p = 0.84$).

M. vimineum recruitment was significantly higher in burned plots, which had 37% more spring stems than unburned plots ($F_{1,49} = 174.8$, $p < 0.001$). Comparing recruitment in burned and unburned harvested plots enabled us to test for additive effects of fire on *M. vimineum* invasion; that is, effects of fire beyond those associated with removal of the litter layer and herbaceous understory. Burning plus litter and biomass removal had a minor but significant effect on spring stem emergence, which was 13% higher in
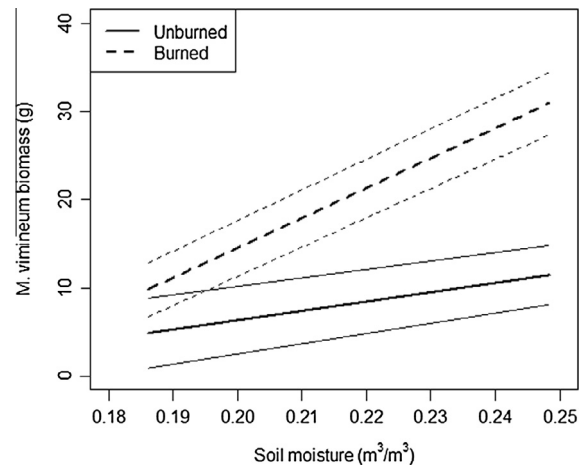

Fig. 1. The relationship between *M. vimineum* biomass and soil moisture by burn treatment. The thin lines show the SE around the mean.
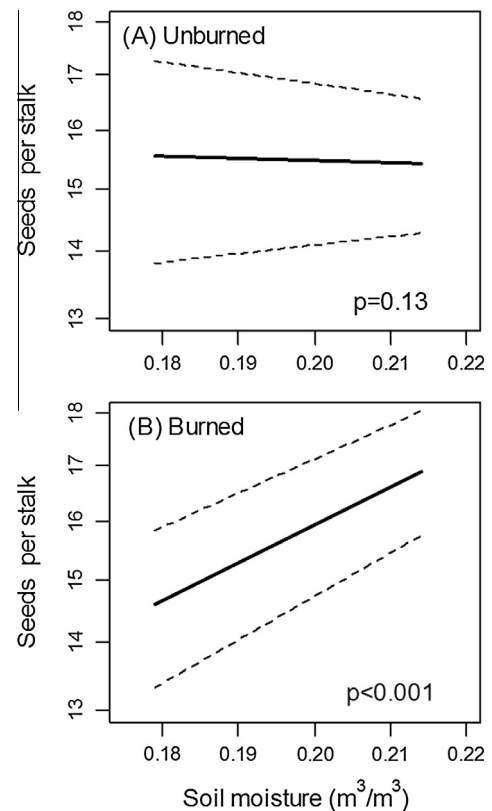

Fig. 2. The relationship between *M. vimineum* seed production and soil moisture by burn treatment. The dashed lines show the SE around the mean.

burned than unburned plots in the spring following harvest ($F_{1,49} = 30.9$, $p < 0.001$, Fig. 3).

The benefit of high spring emergence in burned plots persisted throughout the growing season. In August, the mean number of stems per plot was 93.9 (±15.2 SE) and 61.8 (±10.1 SE) in burned and unburned plots, respectively ($F_{1,17} = 137.5$, $p < 0.001$). In addition to burn treatment, the best model for the number of stems in August included soil moisture, litter mass, an interaction between soil moisture and litter mass, and an interaction between burn treatment and soil moisture. According to this model, the number of stems in August was positively related to soil moisture at burned sites ($F_{1,13} = 104.7$, $p < 0.001$) and unrelated at unburned sites. At wetter sites (3rd quantile of the soil moisture data), the number
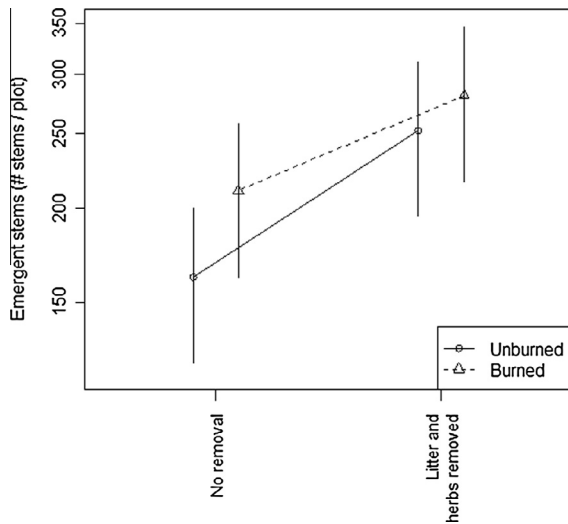
Fig. 3. Mean (±SE) *M. vimineum* recruitment with and without removal of litter and understory herbs, by burn treatment.

Table 1
Fuel loads (mean ± SE) for invaded and uninvaded plots before and after prescribed fire.

Fuel type	Pre-burn (Mg/ha)		Post-burn (Mg/ha)	
	Invaded plots	Uninvaded plots	Invaded plots	Uninvaded plots
Duff	1.58 ± 1.90	2.16 ± 2.11	3.21 ± 1.62	3.25 ± 1.26
Litter	5.83 ± 2.69	8.04 ± 2.44	4.96 ± 1.80	5.46 ± 1.36
1 h	0.45 ± 0.21	0.64 ± 0.27	0.31 ± 0.18	0.45 ± 0.27
10 h	0.60 ± 0.45	0.70 ± 0.42	0.42 ± 0.38	0.52 ± 0.41
100 h	4.11 ± 3.67	4.78 ± 3.71	3.74 ± 2.97	5.07 ± 3.88
1000 h	30.5 ± 32.8	20.8 ± 28.7	26.6 ± 30.5	33.4 ± 26.2
Total	38.5 ± 49.4	29.7 ± 40.6	33.9 ± 44.0	27.2 ± 37.1

of *M. vimineum* stems was 252% higher in burned than unburned plots. There was less of a difference between burned and unburned plots at drier sites (1st quantile of the soil moisture data) with 107% more stems in burned plots. There was a positive relationship between litter mass and the number of stems ($F_{1,13} = 6.39$, $p = 0.03$), and between litter mass and soil moisture ($F_{1,13} = 19.2$, $p < 0.001$).

3.2. Forest fuels and fire intensity

Prior to burning, fuel load averaged 40.1 Mg/ha (Table 1). The 1000-h fuels were the largest component of the fuel bed, comprising approximately 64% of the total fuel load. The 100-h fuels comprised approximately 11% of the total fuel load and litter comprised 17% of the total average fuel load. Fuel composition varied between invaded and uninvaded plots (Table 1). Invasion was associated with less litter mass and fine woody fuels, and more 1000-h fuels. In the uninvaded plots, there was 38% more leaf litter ($F_{1,19} = 27.2$, $p < 0.0001$) and 13% more 1-h fuels ($F_{1,19} = 24.4$, $p < 0.0001$). There was also a trend for 6% more 10-h fuels and 8% more 100-h fuels in uninvaded plots ($F_{1,19} = 3.25$, $p = 0.09$ and $F_{1,19} = 1.70$, $p = 0.05$, respectively). In contrast, there was 106% more 1000-h fuels based on count ($F_{1,19} = 6.11$, $p = 0.02$) and diameter ($F_{1,19} = 5.58$, $p = 0.03$) in the invaded plots with a trend for an average of 9.7 ± 6.5 SE Mg/ha more 1000-h fuels in the invaded plots ($F_{1,19} = 1.11$, $p = 0.30$).

Across all fuel types assessed, consumption did not vary between invaded and uninvaded plots (litter: $F_{1,30} = 1.9$, $p = 0.18$;
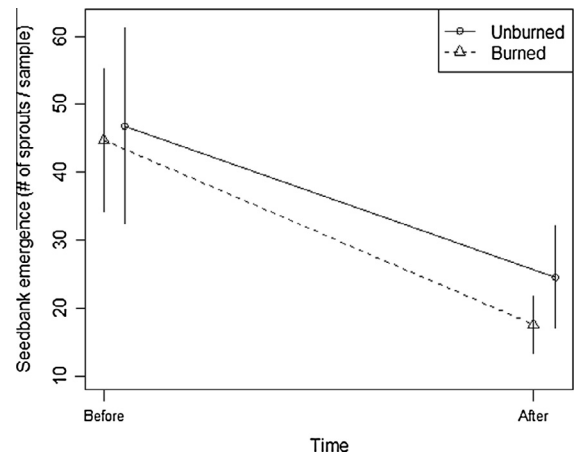
duff: $F_{1,30} = 0.01$, $p = 0.91$; 1-h: $F_{1,30} = 0.01$, $p = 0.94$; 10-h: $F_{1,30} = 0.66$, $p = 0.42$; 100-h: $F_{1,30} = 1.5$, $p = 0.23$; 1000-h: $F_{1,30} = 0.02$, $p = 0.90$). Leaf litter, 1-h, and 10-h fuels were reduced by 45–65% after burning, indicating that these fuel classes were combusted during the burn (litter: $F_{1,30} = 25.4$, $p < 0.001$; 1-h: $F_{1,30} = 82.9$, $p < 0.001$; 10-h: $F_{1,30} = 52.19$, $p < 0.001$).

Maximum recorded fire temperatures at the soil surface ranged from 75.7 °C to 299.8 °C, with an average of 407 s (± 143 SE) spent above 60 °C. Fire residence time over 60 °C was higher in invaded than uninvaded plots (invaded = 433 ± 50 s, uninvaded = 397 ± 44 s; $F_{1,5} = 26.9$, $p < 0.01$), but depended strongly on pre-burn litter mass ($F_{2,5} = 16.7$, $p < 0.01$). At invaded sites, fire residence times increased with increasing leaf litter mass, whereas in uninvaded areas, fire residence times decreased with increasing leaf litter mass ($F_{2,5} = 16.7$, $p < 0.01$).

3.3. Fire effects on seedbank emergence

Prior to fire, invaded study plots did not differ with respect to the number of *M. vimineum* seeds that emerged in the greenhouse (burned: mean = 44.8 ± 10.6; unburned: mean = 46.9 ± 14.5). After exposure to fire, however, 13% fewer seeds emerged from burned, invaded plots (burned: mean = 17.6 ± 4.2; unburned: mean = 24.6 ± 7.7) ($F_{1,25} = 8.50$, $p < 0.01$, Fig. 4).

4. Discussion and conclusions

A positive feedback between grass invasion and fire can accelerate the invasion process. Although the grass-fire cycle is well documented in grassland and dry woodland systems, it is unclear how this cycle operates in eastern deciduous forests where the tree community plays a dominant role in shaping the fuel characteristics. We found that fire had strong positive effects on *M. vimineum* biomass and recruitment, and a modest negative effect on emergence from the seedbank. Overall, this suggests that fire promotes the invasion of *M. vimineum* in eastern deciduous forests. We also found that *M. vimineum* invasion increases fire residence times, which supports the idea that there is a positive feedback between fire and invasion by *M. vimineum* in eastern deciduous forests.

Invaded plots had lower amounts of fine fuels, particularly leaf litter, which likely initially promoted *M. vimineum* establishment. Other studies have found that leaf litter can serve as a physical barrier to *M. vimineum* establishment (Oswalt and Oswalt, 2007). Invaded plots also had higher amounts of 1000-h fuels, which

Fig. 4. Mean (±SE) number of emerging *M. vimineum* sprouts from the seedbank of burned and unburned stands. Seedbank samples were collected before and after prescribed burn in the burned stands.

corresponded with the number of rotten and solid downed logs. Canopy disturbances that increase light availability can influence the invasibility of an area (Davis and Pelsor, 2001), and *M. vimineum* has been shown to respond positively to increased light (Nelson et al., 2009; Cheplick, 2010). Therefore, it is likely that the increased 1000-h fuels in invaded plots are indicative of canopy disturbance.

Although invasion was not associated with higher fine fuel loads, we observed an increase in fire residence times in invaded stands. Similarly, Emery et al. (2011) found that invasion by *M. vimineum* increased fire temperatures by 300–400 °C at an extensively invaded forest in central Indiana, USA. The effect size was not as large at SNF possibly because SNF is less productive overall than the site where Emery et al. (2011) worked. In our study, fire residence time was positively related to litter mass at invaded sites while fire intensity was negatively related to litter mass at uninvaded sites. Since there was no difference in fuel consumption between invaded and uninvaded plots, and uninvaded plots had more pre-burn litter, the negative relationship between litter depth and fire intensity at the soil surface in uninvaded plots is likely an artifact of remaining unburned litter insulating the soil surface where the temperature sensors were located. Despite the reduced litter layer and fine woody fuels in the invaded plots, we still found an increase in fire intensity in the invaded plots which, as suggested by Dibble et al. (2007), could be linked to the characteristics of *M. vimineum* as a fuel that is continuous and easily ignitable.

Despite the relatively low fire intensities measured during prescribed fires at SNF, temperatures at the soil surface were elevated enough to reduce *M. vimineum* emergence by 13%. This finding is consistent with previous studies showing that exposure to direct flame and high fire temperatures inhibit *M. vimineum* germination (Emery et al., 2011, 2013; Ward and Mervosh, 2012). Emery et al. (2013) found an approximately 80% reduction in *M. vimineum* germination the year following a spring burn compared to the subsequent year, which suggests that increased fire intensity can lead to increased seed mortality.

Despite lower emergence from the seedbank in the spring following prescribed fire, burned areas showed improved *M. vimineum* performance in terms of biomass, recruitment, and seed production. Emery et al. (2013) also found that *M. vimineum* performance improved following fire and overwhelmed the negative effects of fire on germination. Removing litter and herbaceous competitors had only a small effect on recruitment in burned sites compared to unburned sites. This suggests that fire facilitates invasion primarily by reducing barriers to recruitment, consistent with other studies showing that litter removal strongly promotes *M. vimineum* establishment (Glasgow and Matlack, 2007; Oswalt and Oswalt, 2007; Marshall and Buckley, 2008). In contrast, *M. vimineum* spread was predicted by slope. Other studies have shown that *M. vimineum* is more prevalent downslope from roads, a common dispersal corridor (Kuhman et al., 2010), and that spread is slow due to dispersal limitation and not strongly correlated to resource gradients such as soil moisture and light (Christen and Matlack, 2009; Huebner, 2010b; Rauschert et al., 2010).

To persist after fire, plant species use various strategies that include evading, resisting, and enduring fire. In the case of *M. vimineum*, we have shown that seeds which are exposed to fire have a reduced probability of emerging; however, post-burn litter reduction promotes establishment. Warren et al. (2012) showed that *M. vimineum* overcomes seed limitation by having high per capita seed production, and it is likely that the high propagule pressure combined with a reduced litter layer could be allowing *M. vimineum* to overcome the 13% reduction in emergence from the seedbank post-fire. The timing of seed arrival in relationship to fire is another mechanism which can influence post-fire invasion (DeGasperis and Motzkin, 2007). Previous studies highlight the importance of propagule arrival on *M. vimineum* success after prescribed fire. When seeds were sown after a burn treatment, Glasgow and Matlack (2007) found that germination increased. Additionally, Flory and Lewis (2009) found that *M. vimineum* germination could be reduced by timing prescribed fire to coincide with seed production. Overall, the positive influence of fire on establishment outweighs the direct negative effect on emergence from the seedbank, favoring the growth of *M. vimineum* populations. Consistent with this conclusion, demographic modeling shows that one year after prescribed fire there was no effect of burning on *M. vimineum* population growth despite a reduction in population growth immediately following the fire (Emery et al., 2013).

By demonstrating that *M. vimineum* increases fire intensity and responds positively to burning, our study supports the existence of the grass-fire cycle and a positive feedback between fire and invasion in eastern deciduous forests. However, because *M. vimineum*'s response to fire varies with soil moisture, the strength of this feedback will differ across forested landscapes. Previous studies have shown that soil moisture has a positive influence on *M. vimineum* performance (Touchette and Romanello, 2010; Warren et al., 2011). In addition to detecting a positive relationship between soil moisture and *M. vimineum* performance, we found that soil moisture interacted with burn treatments such that seed production was positively related to soil moisture at burned sites and unrelated to soil moisture at unburned sites. The weak response of *M. vimineum* to soil moisture gradients at unburned sites suggests that another resource or a biological interaction is limiting *M. vimineum* growth at the unburned sites. Considering that fire can increase light, reduce competition, and temporarily increase available nitrogen, and considering that *M. vimineum* performance can be limited by light, nitrogen, and competition (Huebner, 2010a; Ross et al., 2011; Fraterrigo et al., 2014), it is likely that one or more of these factors is limiting *M. vimineum* more than soil moisture at unburned sites. Furthermore, fire generally reduces soil moisture in forests through various mechanisms, including increased evaporative water loss due to the reduced litter layer, darkened soil, and increased amount of radiant energy reaching the forest floor (Neary et al., 1999). Consequently, burning in drier areas may lead to greater water limitation of plant growth. This finding has important implications for balancing prescribed burning objectives and control of *M. vimineum* invasion. Given that prescribed fire is a useful and cost effective way to manage fuels, promote native vegetation, and improve timber resources (Abrams, 1992; Burton et al., 2011), it is unrealistic to recommend that this tool not be used due to the negative impacts of fire on *M. vimineum* control. Within one management area, burning at drier sites will not give *M. vimineum* the same advantage as burning wetter sites, allowing managers to focus labor intensive invasive control methods, such as hand pulling, torching, and herbicide applications, in the wetter areas.

Acknowledgements

Appendix A. Supplementary data

Descriptive information for experimental plots and schematic of the fuel characterization transects. Supplementary data associated

with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.06.024.

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