FIRE AND NON-NATIVE GRASS INVASION ACROSS A HETEROGENEOUS LANDSCAPE IN THE CENTRAL HARDWOODS

BY

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THESIS

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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. I 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 with or without a history of prescribed fire, I quantified differences in fire intensity and fuel loads, and fire effects on *M. vimineum* seed bank emergence and performance. 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, plots with a history of prescribed fire exhibited higher *M. vimineum* biomass and recruitment than unburned plots the following growing season. Soil moisture strongly modulated *M. vimineum* response to fire, such that the positive response of *M. vimineum* to soil moisture was greater at sites which were burned. 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 eastern deciduous forests (Abrams 1992, Brose et al. 2001, McEwan et al. 2007, Boerner et al. 2008, Royo et al. 2010). Given the potential ecological benefits of fire, prescribed burning has been widely implemented as tool for managing and restoring forest lands (Bowman et al. 2009). Approximately one million ha are burned under prescription annually in the US (Ryan et al. 2013). While prescribed burning is useful for controlling woody understory growth, managing fuels and promoting native vegetation (Burton et al. 2011), the practice has recently come under scrutiny because it can lead to undesirable changes in forest ecosystems (Matlack 2013).

Notably, prescribed burning can promote the recruitment of invasive plant species (Huebner 2006, Glasgow and Matlack 2007, Dibble et al. 2008, Kuppinger et al. 2010). For example, invasive plants which have an established seed bank can respond positively to post-fire conditions such as increased soil temperatures, increased light levels, a reduction in 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 exotic grasses (the grass-fire cycle; D'Antonio and Vitousek 1992), which have high flammability and tend to recover from disturbance more quickly than native species. In seasonally dry woodlands in Hawaii, for example, invasion by the exotic grass *Schizachyrium condensatum* resulted in increased fire frequency and exotic grass cover after fire (Hughes et al. 1991). Similar impacts have been documented for various exotic grasses 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

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Brazilian Cerrado savannah-forest ecotone (Hoffmann et al. 2004). In these grassland and dry woodland systems, 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).

Although it has been speculated that the continuous fuel bed created by grass invasion in eastern deciduous forests might 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 predominately been studied in savannahs 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 that temperate forest fuels are a composite of overstory and understory material, the influence of understory invasion on fire behavior might not be as apparent in forests, and the grass-fire cycle might not apply. However, grasses have several unique characteristics that distinguish them from the forest fuels including high surface area to volume ratios which allow for rapid drying and low compactness which allows for more oxygen to mix with the fuel. Although 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. Conversely, grass-invaded forests might have more functionally continuous fuels due to the rapid drying of grasses. Given that grass is a unique fuel, grass invasion in forests might contribute to changes in fire behavior despite the presence of fuel from the forest overstory.

For this study, I evaluated the interaction between fire and invasion of *Microstegium vimineum* (Trin.) A. Camus, an annual C4 grass native to southeastern Asia (Fairbrothers and

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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). *M. vimineum*'s adaptability to low light environments, large area of occurrence (26 eastern and two western U.S. states), competitive ability and effects on ecosystem processes has made this non-native invasive a top priority for control efforts (Warren et al. 2011b). By forming dense lawns in the forest understory, *M. vimineum* significantly alters the understory community and suppresses tree seedling growth (Adams and Engelhardt 2009, Marshall et al. 2009, Flory and Clay 2010, Brewer 2011). *M. vimineum* also has a significant impact on ecosystem processes by altering microbial activities and accelerating nitrogen and carbon cycling (Ehrenfeld et al. 2001, Kourtev et al. 2003, Fraterrigo et al. 2011, Strickland et al. 2011, Craig et al. 2015). Due to these 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, Webster et al. 2008, Huebner 2010a, Ross et al. 2011, Warren et al. 2011a). These resource gradients can 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, *Microstegium vimineum*, in eastern deciduous forests across a range of soil moisture and fuel conditions. Specifically, I asked: (1) How does *M. vimineum* invasion influence fuels and fire intensity? (2) How does prescribed fire affect emergence from the *M. vimineum* seedbank? And (3) How does burn history influence *M. vimineum* performance across a soil moisture gradient?

2. Methods

2.1 Study Site

This work was conducted 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 (Schwegman et al. 1973). Mean temperature is 31° C in the summer and 8° C in the winter with a mean annual precipitation of 125 cm. The uplands in this region are dominated by mixed oak (*Quercus sp.*) and hickory (*Carya sp.*) woodlands 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 manage fuels, stimulate the growth of native herbaceous plants and increase oak-hickory regeneration. Each year between October and April, an average of 2,000 ha are burned. *M. vimineum* was first documented in the area prior to 1986 and mostly 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

    2.2.1 Forest fuels and fire intensity plots

To quantify forest fuels in invaded and uninvaded areas, I established 20 paired invaded-uninvaded plots across eight burn units. Burn units were selected to represent the range of variation in soil moisture conditions present in the study area (Table 1). The burn units ranged in size from 15 to 1298 ha, and were between 4 and 41 km apart. Only burn units which were adjacent to an unburned area, were invaded by *M. vimineum*, and had been burned in FY2009 or FY2010 were used. Each fuel plot consisted of three 17-m fuel transects radiating from a central point at 0°, 120°, and 240° azimuths (see appendix for plot diagram). 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-hour fuels (< 0.64 cm in diameter) counted along two meters of the transect, 10-hour fuels (0.64-2.5 cm in diameter) counted along four meters, 100-hour fuels (2.5-7.6 cm in diameter) counted along eight meters, and 1000-hour fuels (>7.6 cm) counted along 16 meters of the transect. The diameters of all the 1000-hour fuels were measured. Four subplots (25 × 25 cm) were established along each transect. Leaf litter (not including *M. vimineum* or other plants which were alive from July to August) and duff were harvested from these subplots, dried, and weighed. All 20 paired plots were sampled in July-August of 2012 to determine differences in fuel load in invaded and uninvaded areas. To determine what fuel types were consumed by the prescribed fires, 11 paired plots, which were burned in the spring of 2013, were resampled in July-August of 2013. During the spring 2013 burns, data loggers and type K thermocouples were installed (n=1 per plot) to measure fire temperatures at the soil surface in invaded and uninvaded fuel types. Nine paired, invaded and uninvaded plots had data loggers installed; however, fire did not reach one of the invaded plots and this plot was removed from the dataset. Temperature was recorded every ten seconds and was used to calculate the number of

minutes over 60° C. I used this temperature threshold because it is a temperature at which cell death can occur in plants (Levitt 1980).

2.2.2 Seed bank plots

To assess the effects of fire on the seed bank, soil was collected from 23 invaded plots (n=12 burned, n=11 unburned) before and after the spring 2013 prescribed burn. Plots were located in or near the burn units used for the fuel plots (Table 1). All post-burn samples were collected within two days of the burn and the time between before and after samples ranged from 7 - 22 days. To account for the spatial heterogeneity in the seed bank, the samples were collected using a "many small samples" approach and collecting 10 cores (6 cm in diameter, 4 cm deep) in each location (Gross 1990). The pre-burn subsamples were collected along a transect at 60 cm and 110 cm from the plot center at 0°, 18°, 36°, 54°, and 72° azimuths, and the post burn samples were collected at 70 cm and 220 cm at the same azimuths (see appendix for plot diagram). Only the shallow seed bank 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). Seed bank 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.

2.2.3 *M. vimineum* performance plots

To assess the influence of burn history on *M. vimineum* performance, I established 18 paired plots (10 established in 2011 and 8 established in 2012) in adjacent burned and unburned stands. These plots were established across ten burn units, a portion of which occurred in the same burn units as the fuel and seed bank plots (Table 1). Only burn units which were adjacent to an

unburned area, were invaded by *M. vimineum*, and were part of a regular burn rotation with the most recent burn occurring within the last 2 years were used. Although *M. vimineum* is a prolific seeder, local dispersal on *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 consists of two 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 invasion edge. One of these transects was used for the destructive harvest plot, and one was not altered (Fig. 1). 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. After being dried to constant mass, these samples were weighed. Light and soil moisture were also measured in each subplot. Soil moisture was measured using a Time Domain Reflectometry probe (Decagon 5TM Soil Moisture Sensor, Decagon Devices Inc., Pullman, WA, USA); to control for microscale variation, soil moisture was measured in three locations within each subplot and pooled. Light levels were measured over each subplot and under a reference full light condition using a LiCor 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. In the paired undisturbed plots, the flowering stems were counted in September of the year plots were established. In October, after seed set and before seed release, five randomly selected stalks were collected and seeds were counted in the lab. In the spring of the following year, the number of new stems was quantified in both the subplot where all vegetation and litter had been removed and in the paired subplot located 0.25 m from the destructive harvest subplot.

2.2.4 *M. vimineum* spread transects

To determine the impact of burn history on spread, I installed three spread transects each within 10 m of the ten burned and eight unburned performance plots in July of 2011. The spread transects consisted of pin flags marking 50-cm transects starting at the invasion edge and moving perpendicular into the uninvaded area. In August of 2012, these invasion boundary transects were measured for progression of the invasion front by measuring from the marked 2011 invasion edge to the farthest *M. vimineum* plant along the transect.

2.3 Data Analysis

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 each plot pair which was nested within burn unit (also a random variable); the invasion treatment was 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). Each plot pair was nested within site and was incorporated as a random effect. For the before-after control-impact design, the fixed effects included the invasion treatment, the burn treatment (expressed as a before-after effect), and the interaction between invasion and burn treatments. Because there are several variables that I would expect to contribute to fire intensity, I compared models which included the effect of invasion, pre-burn fuels (separated by type), and slope.

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). The plots were treated as a random effect within the burned and unburned treatment groups. The fixed effects included the burn treatment categorical data, the time categorical data (preburn vs. postburn), and the interaction between burn treatment and time. *M. vimineum* biomass, recruitment, and seed production were analyzed using linear mixed models, and all count data were analyzed using generalized linear mixed models using 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. For models which 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, and the models with the lowest values were used as the best fit. *M. vimineum* spread was analyzed using linear mixed models where each plot pair was a random effect. Covariates included in these models as fixed effects were litter biomass, slope, burn treatment, and if the plot was burned between sampling. These models were compared with AICc values. All analyses were performed in SAS (SAS Institute 2013) using the proc glimmix and proc mixed functions.

3. Results

3.1 Forest fuels and fire intensity

Prior to burning, preburn fuel load averaged 40.1 Mg/ha (Table 2). The 1000-hour fuels were the largest component of the fuel bed, comprising approximately 64% of the total fuel load. The 100-hour 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 2). Invasion was associated with less litter and fine woody fuels, and more 1000-hour fuels. In the uninvaded plots, there was 38% more leaf litter ($F_{1,19} = 27.2$, $p < 0.0001$) and 13% more 1-hour fuels ($F_{1,19} = 24.4$, $p < 0.0001$). There was also a trend for 6% more 10-hour fuels and 8% more 100-hour 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-hour 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 $\pm$ 6.5 SE Mg/ha more 1000-hour 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-hour: $F_{1,30} = 0.01$, $p = 0.94$; 10-hour: $F_{1,30} = 0.66$, $p = 0.42$; 100-hour: $F_{1,30} = 1.5$, $p = 0.23$; 1000-hour: $F_{1,30} = 0.02$, $p = 0.90$). Leaf litter, 1-hour, and 10-hour 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-hour: $F_{1,30} = 82.9$, $p < 0.001$; 10-hour: $F_{1,30} = 52.19$, $p < 0.001$).

Maximum recorded fire temperatures at the soil surface ranged from 75.7° C to 299.8° C, with the average time above 60° C = 407 s $\pm$ 143 s. Fire residence time over 60° C was higher in invaded than uninvaded plots (invaded = 433 s $\pm$ 50, uninvaded = 397 s $\pm$ 44; $F_{1,5} = 26.9$, $p < 0.01$), but depended strongly on preburn litter mass ($F_{2,5} = 16.7$, $p < 0.01$; Fig 2). At invaded

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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; Fig 2).

3.2 Fire effects on seed bank 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 sites: mean = 44.8 ± 10.6; unburned sites: mean = 46.9 ± 14.5). After exposure to fire, however, 13% (burned sites: mean = 17.6 ± 4.2; unburned sites: mean = 24.6 ± 7.7) fewer seeds emerged from burned, invaded plots ($F_{1,25}$ = 8.50, p < 0.01, Fig. 3).

3.3 Burn history and *M. vimineum* performance

Despite the negative impact of fire on seed bank emergence, *M. vimineum* performed better in stands managed with prescribed fire. Burned plots had 37% more spring stems than unburned plots ($F_{1,49}$ = 174.8, p < 0.001). Litter disturbance also increased the number of *M. vimineum* stems ($F_{1,49}$ = 706.0, p < 0.001). Although the effects of litter removal were stronger in unburned ($F_{1,49}$ = 37.0, p < 0.001) than burned plots ($F_{1,49}$ = 2.6, p = 0.11), spring stem emergence was 13% higher in burned plots than unburned plots following litter removal ($F_{1,49}$ = 30.9, p < 0.001, Fig. 4).

The benefit of high spring emergence in burned plots persisted throughout the growing season. In August, the mean number of stems 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 burn sites and unrelated at unburned sites ($F_{1,13}$ = 104.7, p <0.001). At wetter sites (3rd quantile of the soil moisture data), the number of *M. vimineum* stems was 252% higher in burned areas than at unburned areas; there was less of a difference between burn treatment at drier sites (1st quantile of the soil moisture data) with 107% more stems at burned sites. 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).

By the end of the growing season, *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 history 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% higher in burned and 135% higher in unburned plots situated in wetter sites compared to drier sites (Fig. 5). Seed production per stalk did not vary with burn history ($F_{1,15}$ = 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 = 0.060; Fig. 6). There was no relationship between *M. vimineum* spread and burn history (both long term and the 2011-2012 burn season) or litter biomass. There was a positive relationship between slope and *M. vimineum* spread ($F_{1,8}$ = 24.5, p = 0.001); however, there was no interaction between slope and burn treatment ($F_{1,6}$ = 0.04, p = 0.84).

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 savannah 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. I found that fire had positive effects on *M. vimineum* recruitment and biomass, and a modest negative effect on emergence from the seed bank. Overall, this suggests that fire promotes the invasion of *M. vimineum* in eastern deciduous forests. I 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.

Site conditions significantly influenced the relationship between invasion and fuel composition. 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-hr fuels, which 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-hour fuels in invaded plots are indicative of canopy disturbance.

Although invasion was not associated with higher fine fuel loads, I 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 my 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 change 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 was 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, Ward and Mervosh 2012, Emery et al. 2013). 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 seed bank in the spring following prescribed fire, areas with a burn history had improved *M. vimineum* performance in terms of spring emergence, number of stems, biomass accumulation, 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. While other studies support the finding that litter removal promotes *M. vimineum* establishment (Glasgow and Matlack 2007, Oswalt and Oswalt 2007, Marshall and

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Buckley 2008), I found that litter removal treatments interacted with burn treatments resulting in higher spring emergence in the burned plots with litter removed as compared to unburned plots with litter removed. This additive effect of fire and litter removal on recruitment might be due to differences in propagule pressure; there were 152% more stems contributing to seed production in the burned areas in our study. Thus, although litter removal in unburned areas has a larger effect on *M. vimineum* establishment than litter removal in burned areas, litter disturbance in burned areas is likely to enhance invasion intensity. In contrast, *M. vimineum* spread was predicted by slope. Other studies have shown that *M. vimineum* was more prevalent downslope from roads, a common dispersal corridor (Kuhman et al. 2011), 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). Thus, fire does not directly facilitate spread but rather contributes to invasion by reducing barriers to recruitment.

To persist after fire, plant species can use various strategies which include evading, resisting, and enduring fire (Huebner 2006). In the case of *M. vimineum*, I have shown that the seeds which are exposed to fire have a reduced probability of emerging; however, the post-burn litter reduction provides an ideal place for 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 seed bank post-fire. The timing of seed arrival in relationship to fire is another mechanism which can influence post-fire invasion (DeGasperis and Motzkin 2007). Other 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 seed production. Overall, the positive influence of fire on establishment outweighs the direct negative effect on emergence from the seed bank, 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).

This study demonstrates that *M. vimineum* increases fire intensity and responds positively to burning, and thus supports the existence of the grass-fire cycle and a positive feedback loop for invasion in eastern deciduous forests. However, because *M. vimineum*'s response to fire varies with soil moisture, the strength of this positive feedback will differ across forested landscapes. Previous studies have shown that soil moisture has a positive influence on *M. vimineum* performance (Webster et al. 2008, Huebner 2011). In addition to detecting a positive relationship between soil moisture and *M. vimineum* performance in this study, 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 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* response to soil moisture gradients at the unburned sites. Furthermore, fire generally reduces soil moisture through various mechanisms including increased evaporative water loss in forest stands by reducing the litter layer and increasing the amount of radiant energy reaching the

forest floor (Neary et al. 1999). Consequently, burning in drier areas may lead to 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.

5. Tables and Figures

Table 1. Summary of burn units and experimental plots.

Burn unit	Summary of experimental plots (number of pairs)							Overstory	Burn year	Average light ± SD (percent of full sun)	Average soil moisture ± SD (m^3/m^3)	Mean herbaceous biomass (excluding *M. vimineum*) ± SD (g)
	Fire intensity	Fuel (pre-burn)	Fuel (post-burn)	Seed bank (burned)	Seed bank (unburned)	Perfor-mance	Spread					
AsTr	0	0	0	0	0	1	1	Black locust	2012	8.1 ± 3.2	0.20 ± 0.01	0.34 ± 0.35
DiSp	0	1	0	0	0	0	0	Mixed oak and ash	2012	not measured	not measured	not measured
CeGr	0	1	1	1	1	1	1	Mixed oak and shortleaf pine	2013	19.1 ± 10.0	0.17 ± 0.03	2.92 ± 2.76
ClHo	0	0	0	0	0	1	0	Mixed oak-hickory and shortleaf pine	2013	4.0 ± 0.7	0.20 ± 0.03	3.56 ± 4.41
LeMi	0	1	1	1	1	1	0	Mixed oak and shortleaf pine	2013	19.1 ± 1.3	0.15 ± 0.01	0.45 ± 0.44
NeHo	0	3	0	0	0	1	0	Mixed oak and shortleaf pine	2013	9.6 ± 1.9	0.18 ± 0.03	0.79 ± 0.82
OnGa	3	5	2	2	7	5	2	Mixed oak-hickory, mixed oak, and shortleaf pine	2013	14.5 ± 6.6	0.18 ± 0.04	2.52 ± 4.96
ReHo	0	0	0	0	0	1	1	Mixed oak	2012	11.5 ± 8.0	0.17 ± 0.01	0.75 ± 0.62
TePo	4	4	4	4	0	3	2	Mixed oak-hickory and shortleaf pine	2013	18.9 ±7.3	0.18 ± 0.03	1.25 ± 1.12
TrTo	0	1	0	0	3	1	0	Mixed oak-hickory and shortleaf pine	2011	11.7 ±2.8	0.20 ± 0.01	2.24 ± 3.52
WhSi	2*	2	2	3	0	2	2	Mixed oak-hickory and ash/cherry/ poplar	2013	17.7 ± 11.8	0.18 ± 0.05	1.34 ± 1.55

Table 2. Summary of mean fuel levels (Mg/ha) ± SE for invaded and uninvaded plots before and after the prescribed fire.

Fuel Type	Pre-burn		Post-burn	
	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 hour	0.45 ± 0.21	0.64 ± 0.27	0.31 ± 0.18	0.45 ± 0.27
10 hour	0.60 ± 0.45	0.70 ± 0.42	0.42 ± 0.38	0.52 ± 0.41
100 hour	4.11 ± 3.67	4.78 ± 3.71	3.74 ± 2.97	5.07 ± 3.88
1000 hour	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

Figure 1. Burn history plot design adapted from Warren et al. (2011b).
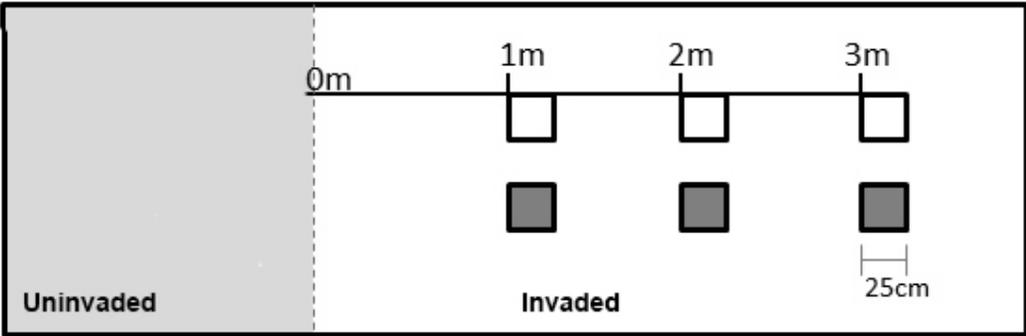
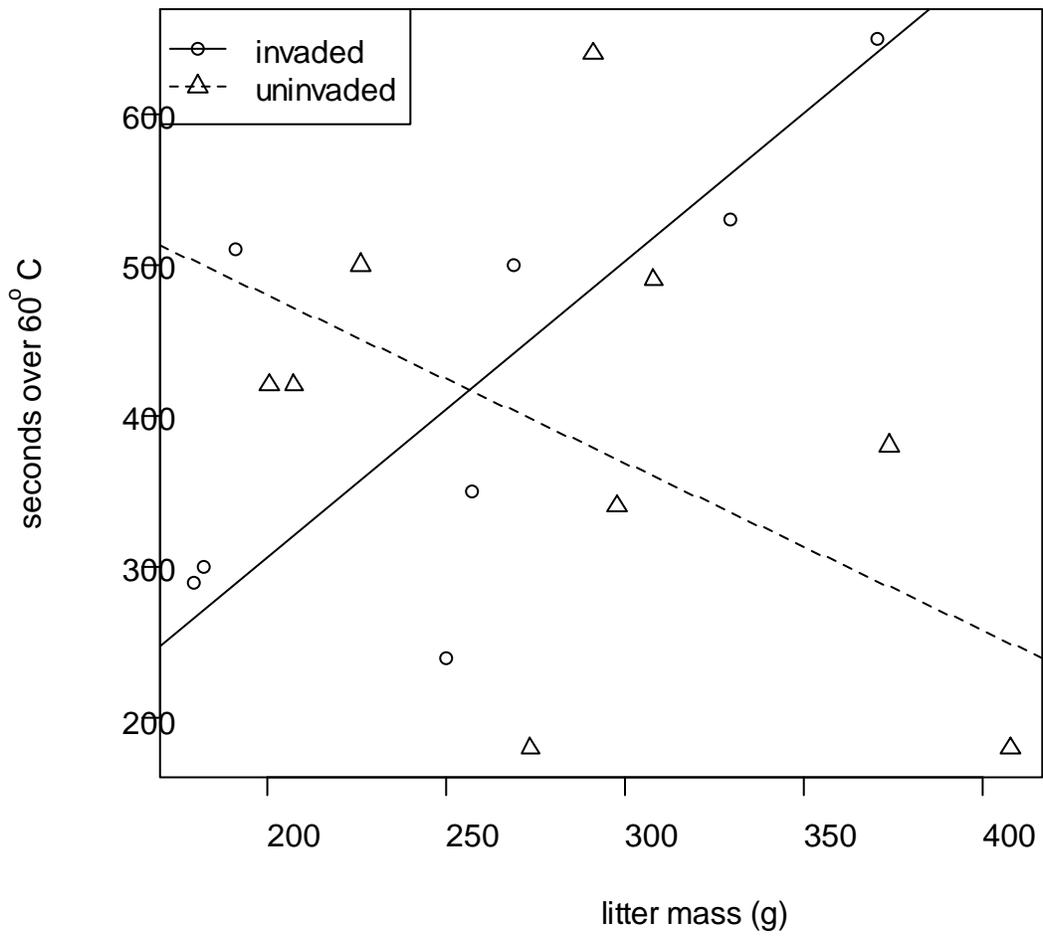Figure 2. The relationship between fire intensity and leaf litter mass in invaded and uninvaded plots.

Figure 3. The mean number of emerging *M. vimineum* sprouts from the seed bank ± SE for the

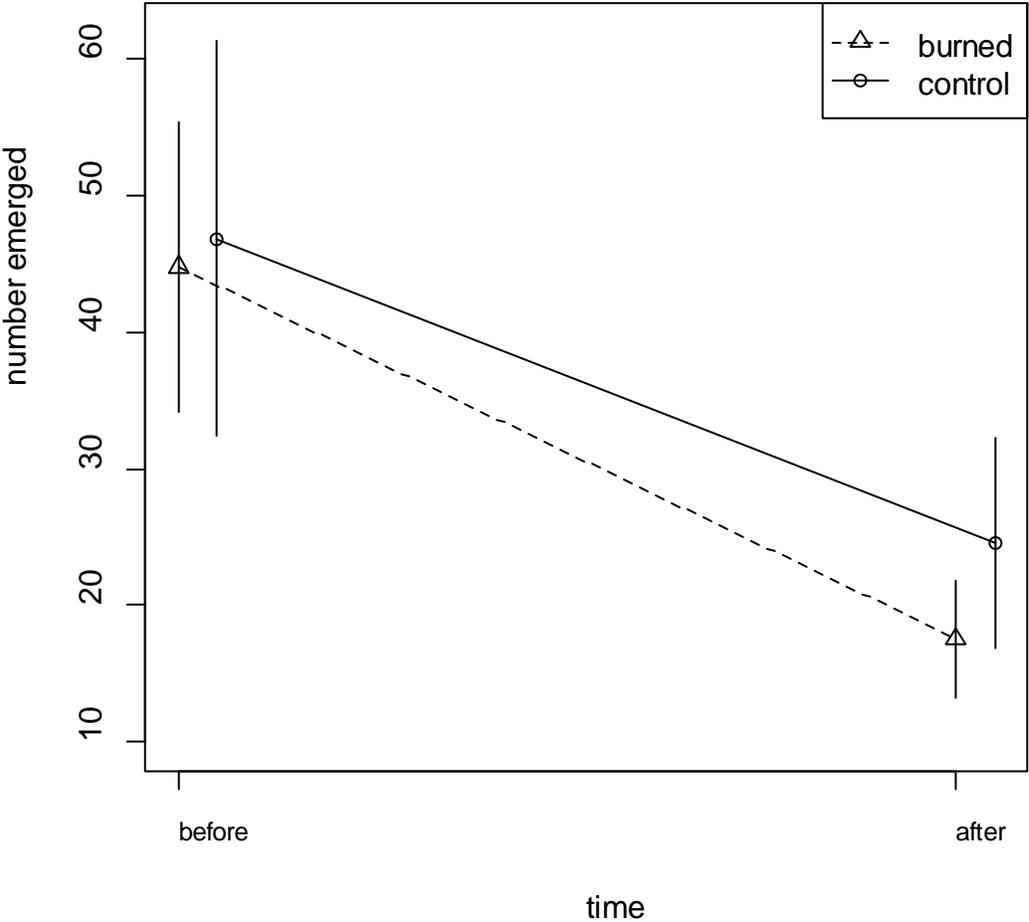burned and control treatments each collected before and after the prescribed burn.

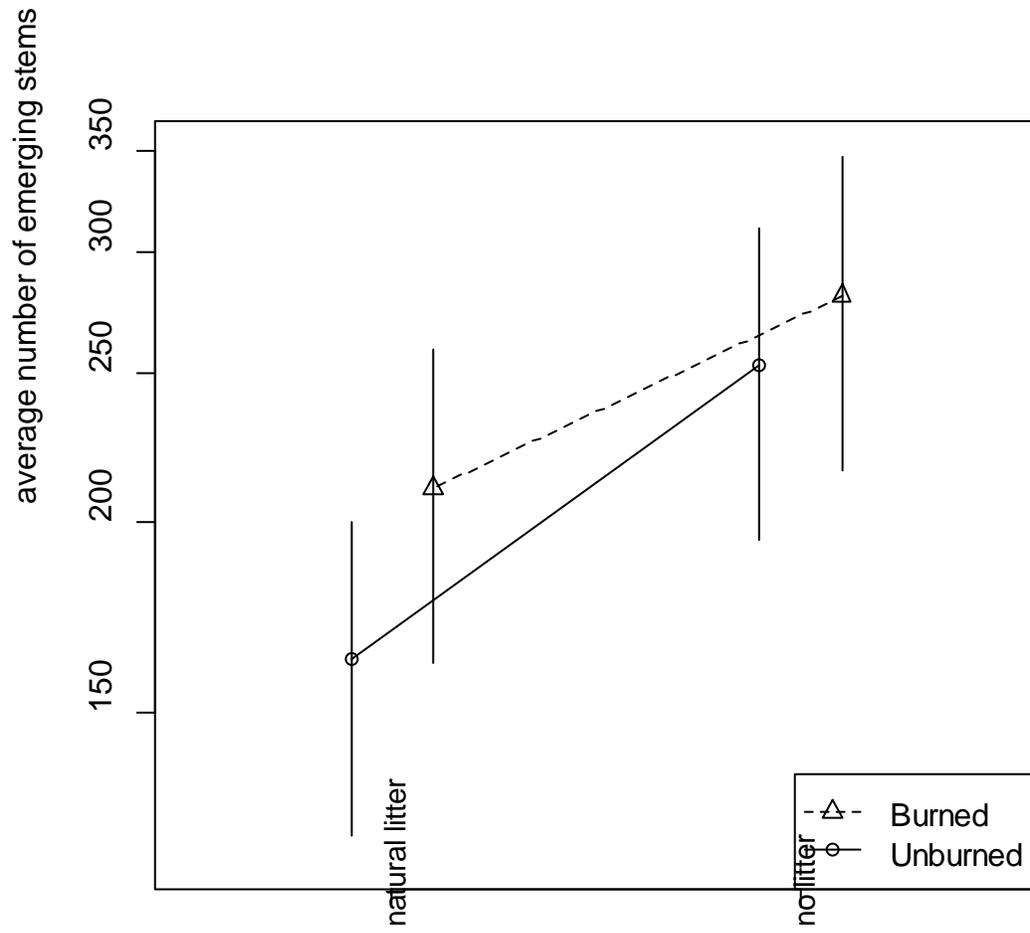Figure 4. Mean *M. vimineum* recruitment ± SE under natural and reduced litter treatments and burn treatments.

Figure 5. The relationship between *M. vimineum* biomass and soil moisture. The thin lines show the SE around the mean.
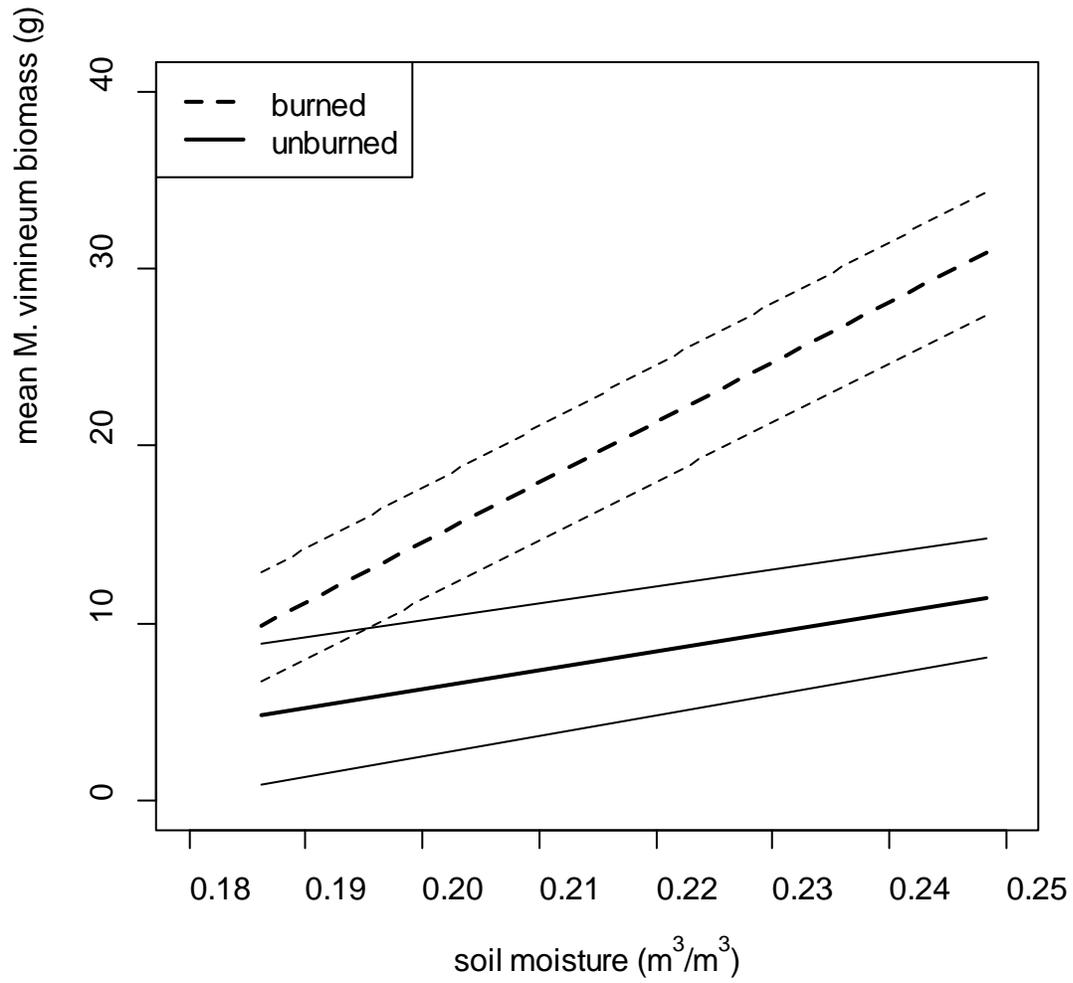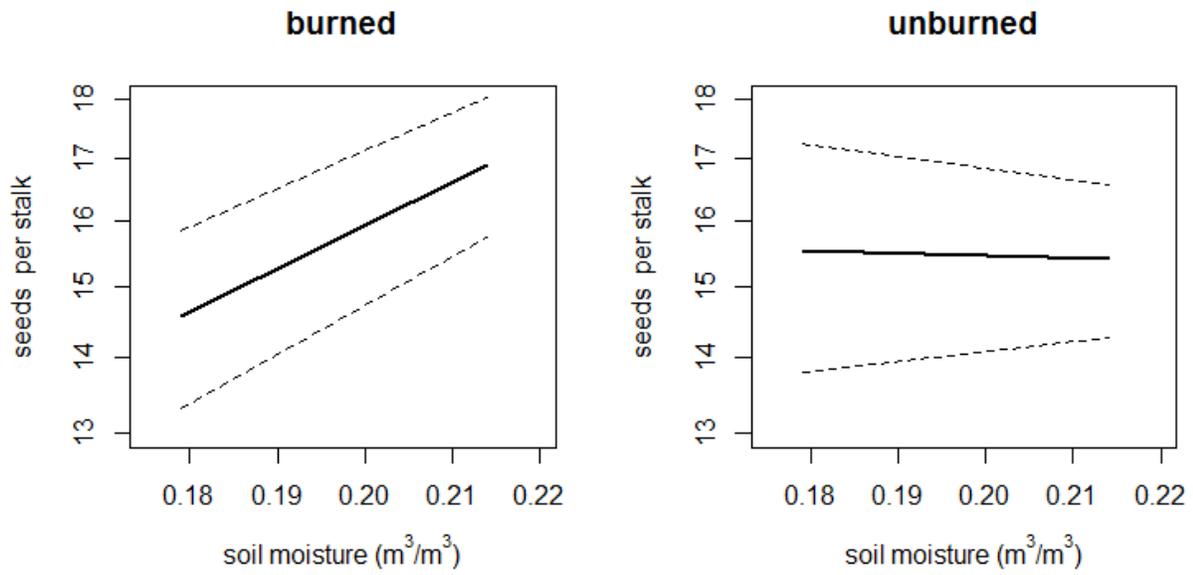
Figure 6. The relationship between *M. vimineum* seeds per stalk and soil moisture by burn treatment. The dashed lines show the SE around the mean.

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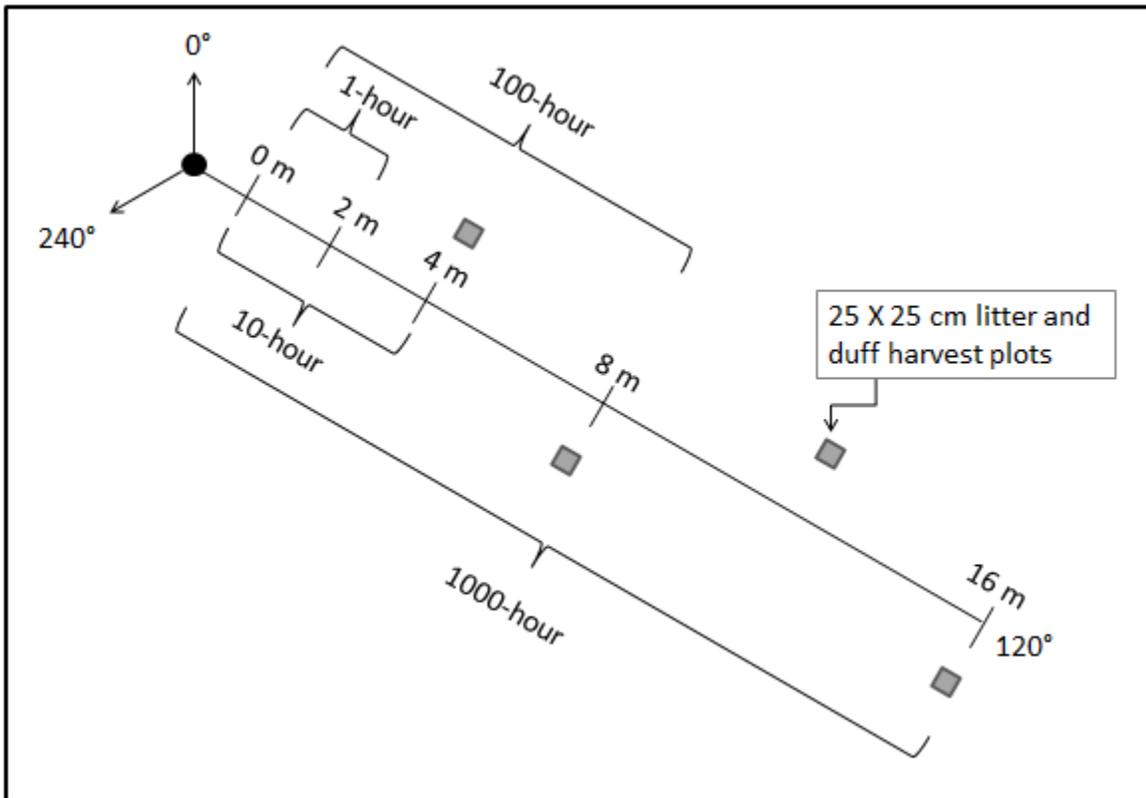
Appendix: Supplemental plot diagrams

Diagram 1. Fuel characterization plots.

Diagram 2. Seed bank plots.