Forest Ecology and Management 354 (2015) 170–176

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

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ARTICLE INFO

Article history:
Received 22 April 2015
Received in revised form 12 June 2015
Accepted 18 June 2015
Available online 22 June 2015

Keywords:
Exotic species
Fire behavior
Japanese stiltgrass
Microstegium vimineum
Plant invasion
Prescribed fire
Soil moisture

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.

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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http://dx.doi.org/10.1016/j.foreco.2015.06.024
0378-1127/

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