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# Fire indirectly benefits fitness in two invasive species

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**Abstract** Ecosystems perturbed from their natural disturbance regimes are more vulnerable to establishment and dominance of exotic plant species. Restoration efforts that reintroduce fire have achieved mixed success in reducing the abundance of exotic plants. The responses of many native species to fire are well known; fire-adapted species respond directly (heat and smoke cue germination) and indirectly (post-fire environment benefits seedling survivorship and growth) to fire. However, the direct and indirect effects of fire are unknown for most exotic plant species. We tested the direct and indirect effects of fire on two exotic invaders of Asian origin, *Ailanthus altissima* and *Lonicera maackii*, in North American woodlands. To quantify the direct effects of fire, we

compared germination rates of seeds exposed to varying levels of heat and smoke in a laboratory and placed at different soil depths during a prescribed fire in the field. We examined the indirect effects of fire by comparing seedling recruitment in burned and unburned woodland plots. Results indicate that neither *A. altissima* nor *L. maackii* have germination cues associated with fire. However, both species have greater seedling recruitment in burned as compared to unburned areas in the field. Although seeds of these invasive species are not specifically adapted to fire, they still benefit from post-fire environments and pose a challenge to restoration of fire-maintained ecosystems. Future studies using our approach will allow land managers to better predict how communities will respond to restoration efforts and to understand variability observed in past restoration projects.

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**Keywords** *Ailanthus altissima* · Fire · Germination · Heat · Invasive species · *Lonicera maackii* · Seedling recruitment · Smoke

## Introduction

Invasive species are one of the most pervasive threats to natural ecosystems, displacing native species and altering ecosystem structure and function (Brooks et al. 2005; Vilà et al. 2011; Powell et al. 2013; Simberloff et al. 2013; Jeschke et al. 2014).

Ecosystems that are perturbed from their natural disturbance regimes are particularly vulnerable to the invasion of and subsequent dominance by exotic plant species (Parepa et al. 2013; MacDougall et al. 2013; Murphy and Romanuk 2014). In woodlands of North America, the first step in restoring these invaded habitats is often to reintroduce the historic fire regime (Pyke et al. 2010; Ryan et al. 2013; Stambaugh et al. 2015). The success of restoration using fire is varied; sometimes reintroducing fire reduces exotic abundances and favors natives, and sometimes it does not (Pyke et al. 2010). Restoration projects typically have incomplete knowledge of the effects of fire on exotic plants and the variation observed in the success of these projects might depend on whether exotic species are adapted to fire.

Species that are adapted to the direct and indirect effects of fire, particularly in their seed ecology, will benefit from a fire regime (Pausas and Keeley 2014). Fire directly influences seeds of fire-adapted species by cueing germination via physical scarification, heat shock, and/or chemical stimulation by smoke (Brown et al. 2003; Flematti et al. 2004; Ooi et al. 2014). Additionally, seeds and seedlings may experience positive, indirect effects of fire, such as increased light attenuation at the soil surface, release from competition, increased nutrient cycling, and reduced seed herbivory (Tyler 1995; Keeley and Fotheringham 2000). Often the direct and indirect effects of fire work in concert to enhance seedling recruitment of fire-adapted species.

Fire has been shown to increase germination and seedling recruitment in a number of native species (Moreira et al. 2010; Keeley et al. 2011; Bargmann et al. 2014). However, the literature largely lacks studies combining information on both the direct and indirect effects of fire on exotic invaders (but see Vermeire and Rinella 2009; Emery et al. 2011). It is possible that the inconsistent success of using fire as a restoration tool in invaded habitats is due to variation in the responses of exotic species to different effects of fire. For example, population growth of the invasive grass, *Microstegium vimineum*, increases greatly after fires even though its seeds do not directly benefit from heat and smoke (Emery et al. 2011; Flory et al. 2015). This invasive increases fire intensity, which in turn inhibits the survival and recruitment of coexisting native species, thus providing an open, competition-free environment that indirectly benefits its own germination and seedling establishment (Emery et al.

2011; Wagner and Fraterrigo 2015). Projects aimed at restoring invaded habitats will increase their success rate if the adaptations of invaders to both the direct and indirect effects are considered prior to using fire for restoration.

Most studies examining the direct and indirect effects of fire on the fitness of plant species focus on early life stage vital rates, such as germination and seedling establishment rates, and assume that the effects of fire on these vital rates will be important to plant population dynamics. This assumption might be reasonable for many plant species for two reasons. First, the population growth rates of plants are sensitive to early life stage vital rates in most short-lived plant species (Silvertown et al. 1993), and in long lived plants that have rapid population growth rates, such as invasive perennials (Ramula et al. 2008; Schutzenhofer et al. 2009; Burns et al. 2013). Second, even vital rates with low sensitivity can alter plant population dynamics if those vital rates are changed dramatically enough by the environmental conditions (e.g., Pardini et al. 2015). Fire can often have dramatic effects on the germination and seedling establishment rates of plants.

This study aims to determine the direct, indirect, and net effects of fire on the germination and seedling recruitment of two woody species, *Lonicera maackii* and *Ailanthus altissima*, both of which are common invaders of mesic forests in North America (Luken and Thieret 1995; Kasson et al. 2013) and have rapidly growing populations at our study site (Crandall and Knight, personal observations). Specifically, we evaluated (1) germination rates after exposure to heat and smoke in the laboratory, (2) germination rates of seeds burned using a prescribed fire after burying them at different soil depths, and (3) seedling recruitment in burned and unburned field plots. A more complete understanding of the net effects of fire, both direct and indirect combined, on the seeds of exotic species should help elucidate the role of fire as a restoration tool in invaded ecosystems.

## Materials and methods

### Site description

The field studies were conducted at the Tyson Research Center, which is owned and managed by

Washington University in St. Louis (38.526578 N, -90.560322 W). The site is an oak-hickory woodland ecosystem within the Missouri Ozarks with a history of invasion by exotic species. Lightning-ignited fires occur during the summer when hot, humid conditions prevail and droughts are common, but most prescribed fires are lit during the dormant season between snow events when conditions are cold and dry (Sutherland 1997). Prior to colonial settlement in the 1840s, Native American groups set widespread fires throughout large portions of the Ozarks region every 4–6 years to maintain savanna-like conditions (Cutter and Guyette 1994; Hart and Buchanan 2012; Stambaugh et al. 2015). The prevalence of wildland fire in today's Ozarks has been greatly reduced, though prescribed burns have been sporadically reintroduced to the region as a restoration technique.

Fires in mesic, deciduous forests of North America where our sites are located are not as intense as those in other fire-dominated habitats (i.e., prairies, U.S. Western forests, Mediterranean Chaparral). Fuels are typically leaf litter and woody debris, which do not burn as hot or fast as fine fuels, such as dead grasses or pine needles. Fires move slowly through the understory and only heat the soil surface for extended periods of time in localized areas with high concentrations of woody debris (Hodgkinson and Oxley 1990; Cole et al. 1992). Average soil surface temperatures during prescribed fires in oak-hickory forests of the Midwestern U.S. have been reported between 157 and 210 °C depending on weather conditions (Boerner 2000), which is significantly lower than those reported for other systems (Gibson et al. 1990). Because fires are of lower intensity in mesic, deciduous forests, it is possible that fewer native species are adapted to the direct effects of fire compared to other habitats with more intense fires (but see Emery et al. 2011). Instead, these species might benefit more from a post-fire environment with less competition, increased soil nutrients, and greater light availability (Boerner et al. 2004).

### Study species

Both *L. maackii* (Amur honeysuckle) and *A. altissima* (tree-of-heaven) are management concerns in North American forests. *Lonicera maackii* is an upright, deciduous shrub with bird-dispersed fruits native to northeast China, Korea, eastern Siberia, and Japan that was introduced to North America in 1896 (Ingold and

Craycraft 1983; Luken and Thieret 1995, 1996). *Ailanthus altissima* is a deciduous tree producing many wind-borne seeds also originating from China and spreading to North America in the eighteenth century (Hu 1979). While fires are infrequent across much of Asia (Page et al. 2009), some habitats (e.g., lowland tropical areas) have a long history of frequent natural and human-induced fires (Stott et al. 1990). Because *L. maackii* and *A. altissima* have wide distributions across Asia, it is likely that they have at least periodically experienced fire during their evolutionary history. Both *L. maackii* and *A. altissima* were initially introduced to North America as ornamental plants, but have spread beyond their initial distribution and are classified as invasive species across most of their invaded range (Luken and Thieret 1995). Both species thrive in open and forest habitats with a history of human disturbance (Knapp and Canham 2000). *Lonicera maackii* has plastic stem growth that allows it to utilize both shady and high light environments (Luken et al. 1995). Further, *L. maackii* experiences less herbivory than many native woody species, promoting its competitive ability (Trisel and Gorchov 1994). *Ailanthus altissima*, though not shade tolerant like *L. maackii*, nevertheless has extremely rapid growth that allows it to take advantage of canopy gaps (Knapp and Canham 2000).

Although the effects of fire on the seeds of these species have not been studied, their germination requirements are known. *Lonicera maackii* seedlings will germinate and establish in a wide range of light conditions, allowing the species to establish in forest edges and interiors. With a minimal delay between dispersal and germination, *L. maackii* lacks a persistent seed bank (Luken and Goessling 1995). Conversely, *A. altissima* has a persistent seed bank, is shade-intolerant, and requires high light for germination. In closed canopy conditions seedlings may germinate but are unlikely to establish (Knapp and Canham 2000). Because both of these species have high population growth rates when colonizing new areas (Crandall and Knight, personal observations), it is likely that germination and seedling recruitment are important vital rates (see Schutzenhofer et al. 2009).

### Experimental methods

A laboratory experiment was used to test the direct effects of heat and smoke on the germination of

*L. maackii* and *A. altissima*. Seeds of each species were collected from multiple sites at the Tyson Research Center during the fall of 2012. Seeds of *L. maackii* were immediately removed from fruits, washed with tap water, and dried at room temperature before being placed in cold storage. Seeds of *A. altissima* were collected and placed immediately into cold storage. Seeds remained in cold storage at 4 °C for at least 3 months for cold stratification.

Seeds were subjected to different levels of heat and smoke using a protocol similar to other studies (see Keeley and Fotheringham 1998; Lindon and Menges 2008). Thus our results should be comparable to results from native species. Three heat treatments, 60, 100 and 140 °C, were used to simulate the temperature conditions seeds would experience in low intensity, moderate intensity, and high intensity fire (e.g., Cushwa et al. 1968; Mott et al. 1982; Loucks et al. 2008). These three heat treatments were applied in a drying oven for zero (controls), 1, 5 or 10 min, again designed to simulate the duration of time seeds might experience fire-associated temperatures during slow-moving understory fires with the longer temperatures representing microsites with greater woody debris (e.g., Herranz et al. 1998). The heat treatments were further delineated by the application of either wet or dry heat. As the heat treatments were applied and the seeds oven-heated, wet heat was created by filling the oven with steam, simulating fire conditions in moist woodland areas (e.g., Martin et al. 1975). Additionally, half of the seeds were also subjected to smoke for a period of 5 min to test germination cues initiated by chemicals in smoke, such as butenolid (Dixon et al. 1995; Nelson et al. 2009; Flematti et al. 2001, 2004; Ooi et al. 2014). The smoke treatment was applied by placing seeds in an aquarium filled with smoking leaf litter collected from Tyson Research Center. Each treatment combination was tested on 30 seeds and replicated three times. Once treatments were applied, the seeds were germinated in a greenhouse and seedlings were counted until no seeds germinated for a period of 2 weeks. The proportions of seeds that germinated were compared between treatments using ANOVAs and Tukey pairwise comparisons. Smoke and wet/dry heat did not have a significant effect on germination within each heat temperature and time combination, thus they were combined for final analyses.

A field experiment was used to assess the effects of seed burial depth on the germination of the two study

species in burned and unburned plots. For the first field experiment, 30 seeds of each species were placed in metal mesh packets and buried at depths of 0 (i.e., soil surface), 3 and 6 cm in three different burn units. Once buried, seeds were either unburned or subjected to a dormant season prescribed burn. Microsite conditions varied between plots with different invasive species, which affected the proportion of area burned. The average area burned by site for *A. altissima* was  $99.2 \pm 2.9\%$  and for *L. maackii* was  $85.1 \pm 18.5\%$ . Following the burns, the three replicates were sowed in a greenhouse and monitored until no seeds germinated for a period of 2 weeks. The effects of seed depth and fire presence on the proportion of seeds that germinated were assessed using ANOVAs and Tukey pairwise comparisons.

A second field experiment surveyed the indirect effects of prescribed fire on seedling recruitment. Plots of  $4 \text{ m}^2$  were systematically selected such that each plot had approximately the same density. *Ailanthus altissima* plots had approximately ten non-reproductive stems and were situated near a large, reproducing adult to increase the probability seeds would disperse into them. *Lonicera maackii* plots had 4–6 reproducing adults per plot. Seedling density was sampled before and after fire; *A. altissima* plots were sampled in June 2012 and 2013, and *L. maackii* plots were sampled in July 2012 and 2013. There were a total of 48 plots for each species distributed between three sites with 24 of the plots burned. Seedling response was determined by subtracting the number of seedlings in each plot after treatments (2013 survey) from the number present pre-treatment (2012 survey). Data were normalized using a square root transformation and then analyzed using a *t* test. All data in this study were analyzed using R Statistics (R core team 2014).

Both of the field experiments had similar fire conditions, including fuel loads. The burn day, February 15 of 2013, was proceeded by at least 5 days with no precipitation. On the day of the burns, relative humidity was between 40 and 50 and wind speeds did not exceed 16 kph. All fires were lit with a head fire after establishing a black line with a backing fire. Thus, the seedling plots and buried seed packets experienced a slow-moving head fire characteristic of mesic, deciduous forests. Fuel loads did not vary significantly between plots within species, so fire heterogeneity likely resulted from subtle differences in fuel moisture and topography. Fuels consisted

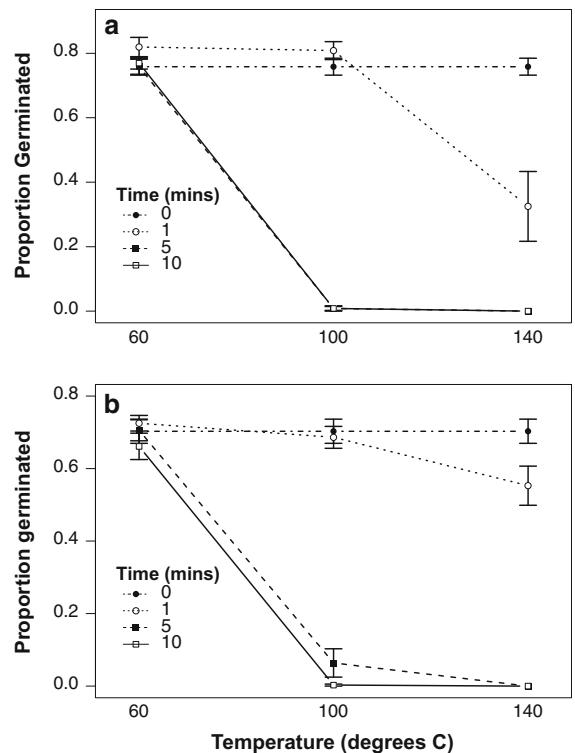
primarily of downed twigs and leaves of the invasive species in our study, *Quercus* spp., *Carya* spp., *Fraxinus* spp., and *Acer* spp. Understory species were sparse but when present consisted of *Ageratina altissima*, *Galium circaeans*, *Muhlenbergia sobolifera*, *Parthenocissus quinquefolia*, *Sanicula canadensis*, and woody seedlings. Neither *A. altissima* nor *L. maackii* are known to alter fire intensity or resident time.

## Results

Simulated direct effects of fire alter germination in both *A. altissima* and *L. maackii*. Smoke and whether the heat was wet or dry had no affect on germination and thus were excluded from graphs and analyses ( $P > 0.05$  for all comparisons). There were main and interactive effects of heat temperature and duration (all  $P$ 's  $< 0.001$ ) on germination of both *A. altissima* and *L. maackii* (Fig. 1a, b). Temperatures of 60 °C had no significant effect on germination, with seeds at all heat times showing similar rates of germination ( $P > 0.8$  for both species). However, temperatures of 100 °C significantly decreased germination for seeds exposed to heat for 5 or 10 min, but not for seeds exposed for only 1 min. At 140 °C, germination was significantly inhibited after as little as 1 min of heat, and no seeds germinated after exposure for more than 1 min.

Burning and burying seeds had different effects on germination of *A. altissima* and *L. maackii*. There were no main (burn:  $P = 0.275$ ; burial depth:  $P = 0.571$ ) or interaction ( $P = 0.086$ ) effects of burning and burying seeds on germination of *L. maackii* ( $P > 0.05$  for all comparisons; Fig. 2a), but two of the three replicates in the burned and soil surface (0 cm) treatment had very low germination. This decrease in germination was likely not significant as result of variation in natural fire temperatures. There was a significant interaction between burning and seed burial for *A. altissima* ( $P = 0.014$ ; Fig. 2b). Burial depth had no significant effect on germination where fire was absent ( $P = 0.108$ ). In contrast, the presence of fire significantly decreased germination at a depth of 0 cm ( $P = 0.024$ ), while depths of 3 and 6 cm caused no change in germination as compared to unburned seeds buried at the same depths.

The survey of seedlings in the field before and after prescribed burns revealed that fire indirectly increase

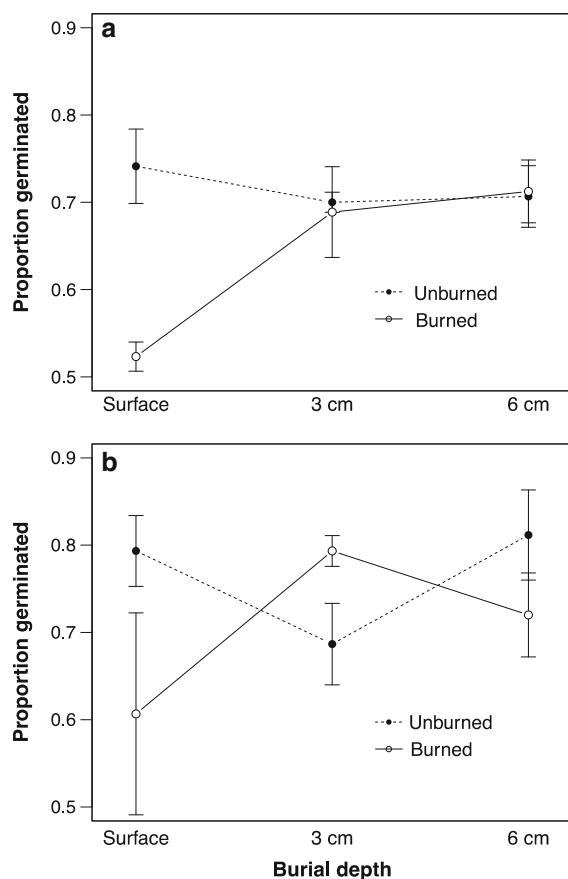


**Fig. 1** Proportion of seeds germinated for **a** *A. altissima* and **b** *L. maackii* after exposure to heat treatments for varying times ( $n = 144$  for each species). Both species exhibited main effects of temperature and heat time. Exposure to temperatures above 100° for longer than 1 min significantly inhibits germination of both species. Bars are standard error

seedling establishment of *A. altissima* ( $P = 0.016$ ) and *L. maackii* ( $P = 0.054$ ; Fig. 3). The number of seedlings increased in plots with prescribed fire as compared to plots that did not experience fire. Since we used a response variable that accounted for the number of seedlings prior to treatment, the difference in seedlings between years was likely the result of the treatment and not variation in yearly environmental conditions or propagule pressure between treatments within plots.

## Discussion

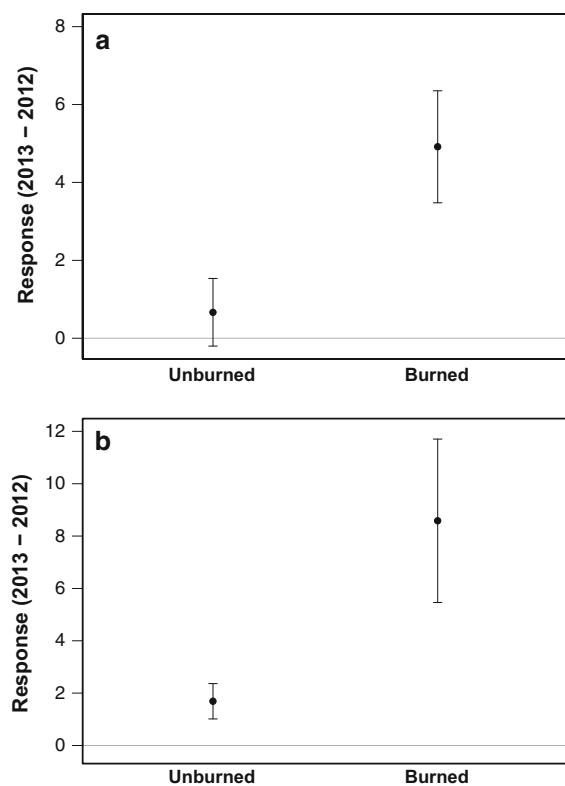
The direct and indirect effects of fire produce different effects on two woody exotic species, *A. altissima* and *L. maackii*, common in unmanaged, mesic, deciduous forests. Neither species demonstrated fire-related germination cues, and the seeds of both exotics are



**Fig. 2** Germination of **a** *A. altissima* and **b** *L. maackii* after burial in the field with and without prescribed fire ( $n = 18$  for each species). *Ailanthus altissima* exhibited a significant interaction between burial depth and burning (low germination for seeds in the burned and soil surface treatment). *Lonicera maackii* had no significant difference in germination between treatments. Bars are standard error

negatively affected by prolonged exposure to heat ( $>1$  min). Thus, seeds are unlikely to survive in fires when they are located on the soil surface or in a microsite with longer-burning woody debris. Furthermore, the presence of prescribed burns in the field increased seedling recruitment for both species indicating that they benefit from the indirect effects of fire. The combined results from the laboratory and field studies indicate that the indirect effect of fire are more important than the direct effects in governing recruitment of these two species.

Across many ecosystems, including Midwest U.S. prairies and Mediterranean chaparral, researchers have found that plant species of fire-dominated ecosystems



**Fig. 3** Survey of **a** *A. altissima* and **b** *L. maackii* seedlings in burned and unburned field plots ( $n = 48$  for each species). Response was calculated as the difference in seedling abundance before (2012) and after (2013) burn or no burn treatments. Burning significantly increased seedling recruitment in *A. altissima* plots as compared to unburned plots. There is some evidence that burning also increased seedling recruitment in *L. maackii* plots. Bars are standard error

rely on the direct effects of fire for germination cues (Keeley et al. 2011; Moreira et al. 2010; Vandvik et al. 2014). In contrast to these findings, germination of *A. altissima* and *L. maackii* was inhibited by the application of heat treatments greater than 60 °C for more than 1 min and unaffected by the application of smoke. Although these species likely experienced fires during their evolutionary history (e.g., Stott et al. 1990), our results suggest that they do not have direct, fire-related germination cues like those of other invasive species that have evolved in fire-dominated ecosystems (e.g., Flory et al. 2015). To our knowledge, there are a limited number of studies that examine plant adaptations to the direct effects of fire in Asian ecosystems, and as such research becomes available in the future it will help us to place our results into the larger context of Asian plant

invasions into fire-suppressed North American landscapes.

Seeds experience the greatest direct effects of fire on the soil surface where temperatures and desiccation potential are high (Cheplick and Quinn 1987; Auld and Denham 2006). Several studies have shown that burial, even by a depth of a few centimeters, protects seeds from the most extreme effects of fire (Tozer and Auld 2006). Our results for *A. altissima* show a similar pattern, wherein seeds on the soil surface during a fire had significantly lower germination. In contrast, germination of seeds of *L. maackii* did not significantly differ by burial depth. Fire heterogeneity and associated differences in local fire temperatures and resident times likely explain the large variance, and thus lack of significance, observed between *L. maackii* replicates. Across the landscape, it is likely that some locations experienced hotter fires, while other locations acted as refugia in which the direct effects of fire are less extreme or even absent (Clarke 2002; Schwilk and Keeley 2006; Crandall and Platt 2012).

For fire-adapted plants, the combined direct and indirect effects of fire result in an increase in seedlings post-fire (Keeley and Fotheringham 2000; Måren et al. 2010; Santana et al. 2009). Heat and/or smoke is key to breaking seed dormancy of many species and increasing the number of seedlings (Moreira et al. 2010; Måren et al. 2010; Vandvik et al. 2014). The indirect effects of fire further promote recruitment, with reductions in competition and herbivory contributing to the post-burn flush of seedlings (Tyler 1995; Knight and Holt 2005). In our study, the number of seedlings of both *L. maackii* and *A. altissima* increased after fire as compared to unburned sites. This result exposes an interesting contradiction between our laboratory and field results. Laboratory studies show that these species experience negative direct effects of fire, whereas field studies show that both species benefit from the indirect effects of fire, suggesting the post-fire environment provides strong advantages.

To gain a complete picture of plant responses to prescribed fire, it is important to combine laboratory studies that test for direct effects of fire on germination with field studies that examine seedling recruitment resulting from both direct and indirect effects of fire (see Keeley and Fotheringham 1998). If the heat and smoke from fire increases germination (a direct effect of fire), there will only be an increase in seedling recruitment if the post-fire environment is suitable for

seedling survival. In contrast, the direct effects of fire might increase seed mortality, but if the post-fire environment were suitable as found in our study, there could still be an increase in seedling recruitment resulting from greater seedling survival. Thus, the cumulative effects on germination and seedling recruitment are likely more important than one effect or the other in isolation.

Beneficial, indirect effects of fire on seed and seedling vital rates of rapidly-growing populations of exotic species pose a challenge for restoration of fire-maintained ecosystems. Because *A. ailanthus* and *L. maackii* benefit from a post-fire environment, the use of fire to restore ecosystems invaded by these species should be performed with caution, as both of these invasive species have the potential to respond strongly following fire, and these responses are likely to translate into increases in the growth rate of the population and density of the species. Land managers often reintroduce fires in habitats that are fire suppressed and contain exotic species with the goal of increasing the dominance and diversity of native plant species. However, such restoration will only be successful if native plant species respond more positively to fire and/or if native plant species have a competitive advantage over exotic species in the post-fire environment. Our study thus highlights the need to examine both the direct and indirect effects of fire on both native and invasive species prior to using fire for restoration of degraded ecosystems.

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