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Germination, survival, and early growth of three invasive plants in response to five forest management regimes common to US northeastern deciduous forests

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ABSTRACT

The association between invasive plants and disturbance is well-documented. Most forest management regimes include disturbance (i.e., harvesting and fire) to improve regeneration of native plants, such as oaks. There is a need for land managers of northeastern forests to foster regeneration of native species without promoting invasive species establishment. We evaluated the germination, first-year survival, and growth of three exotic plants (*Ailanthus altissima*, *Alliaria petiolata*, and *Microstegium vimineum*) in 56 uninvaded forest stands located in five management regimes (control, single burn, repeat burn, diameter limit cut, and shelterwood) across two provinces (Appalachian Plateau, AP, and Ridge and Valley, RV) and two slope aspects (north-to-east facing, NE, and south-to-west facing, SW). These results were compared with the native *Quercus rubra* survival and growth under the same conditions. Two-hundred-fifty seeds and 30 transplants for each species were planted at each site. Germination, survival, and growth were measured three times over one growing season and analyzed using generalized linear mixed models.

RV sites had more open canopies, lower soil fertility, and lower plant species richness than AP sites; NE aspects had higher soil fertility and plant species richness than SW aspects. The shelterwood sites had the most open canopies. Germination rates were below 25%, but lowest in the control sites and higher in the RV and on NE aspects for all three species. Survival was above 70% for *A. altissima*, *M. vimineum*, and *Q. rubra* but below 20% for *A. petiolata*, with little difference among province, aspect, or management regime for all three species. Survival decreased significantly between measurements. *Microstegium vimineum* grew the most of the three species. *Microstegium vimineum* and *A. petiolata* grew best in shelterwoods and better in the RV and on NE aspects. *Ailanthus altissima* had more root growth in the RV than the AP and the least root growth in the control sites. *Quercus rubra* survived better in the RV and best in the harvested sites, though growth did not differ among the management regimes. These invasive species are similar to many native species during the early stages of colonization; their germination, survival and growth are initially precarious and dependent on adequate resources (NE aspects) with minimal competition (RV province). Our results suggest that the likelihood of colonization by invasive plants could be reduced by keeping canopy openings below 15% and encouraging native understory competition with deer exclusion and artificial regeneration where native seed sources are depleted.

1. Introduction

The opening of a forest canopy after a disturbance, such as a harvest or fire, may result in invasion by exotic plant species, given a seed source (Hobbs, 1991; Hobbs and Huenneke, 1992; Eschtruth and Battles, 2009; Driscoll et al., 2016). Successful invasion of nonnative invasive plants in disturbed areas is further dependent, in part, on available resources, with mesic and nutrient-rich sites invaded more frequently than xeric sites (Davis et al., 2000; Huebner and Tobin, 2006). When making predictions about invasion by nonnative plants into forests, it is important to distinguish between invasion at the early colonization stage and invasion as measured in terms of the probability

Abbreviations: *AiAl*, *Ailanthus altissima*; *AlPe*,, *Alliaria petiolata*; AP,, Appalachian plateau; C, control; dbh, diameter at breast height; DLC, diameter limit cut; *MiVi*, *microstegium vimineum*; *QuRu*, *quercus rubra*; RB, repeat burn; RV, Ridge and Valley; SB, single burn; SHW, shelterwood

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of dominance and spread. For instance, Huston (2004) concluded that the probability of dominance is highest under productive conditions, whereas early establishment is more likely under unproductive, undisturbed site conditions or disturbed, productive site conditions. Theoretically, one could reduce invasion likelihood by manipulating the degree of disturbance or site productivity (Huston, 2004).

Successful oak regeneration in northeastern US forests is associated with forest management defined by disturbances that increase the amount of light reaching the forest floor and decrease competition with other plants. Historically, fire sustained some oak forests (Abrams, 1992) and current National Forest Plans in the Eastern US propose increasing the use of fire and/or shelterwood harvest treatments to sustain or restore oak ecosystems (Wayne National Forest Management Plan, 2006; Monongahela National Forest Management Plan, 2011). Shelterwoods are usually conducted with a first-removal harvest to open the canopy enough (anywhere between 30 and 70% residual basal area) to stimulate regeneration, followed by a second harvest that removes the remaining canopy trees (Loftis, 1990). Diameter limit cut (DLC) harvests are commonly carried out on private nonindustrial lands in the eastern US, which includes 75.5% of northeastern forests (Oswalt et al., 2014). Although DLC harvests usually result in a profit for both buyer and seller with harvests every 15–20 years, they may lead to a loss of valuable species and diminishing economic return on harvests over time (Nyland, 1992; Nyland, 2005; Kenefic et al., 2005). Regeneration prescriptions involving shelterwood harvests have been used by the US Forest Service, some state forests, and some large industrial forestry companies, but are less common on private lands because it usually takes 5–10 years before adequate regeneration is achieved and a more complete overstory harvest can be conducted to yield additional revenue (Brose et al., 1999a; 1999b). If a stand is not dominated by trees with diameters meeting the diameter limit or larger, DLC harvests may have lower or similar light levels reaching the understory than would be found in a first-removal shelterwood.

Fires used for oak regeneration in northeastern forests are generally low-intensity burns that open the subcanopy, reducing competition from shade-tolerant species (Lorimer et al., 1994; Miller et al., 2004; Hutchinson et al., 2005b). Fire behavior and, thus, plant species' response to fire can vary substantially across microclimatic gradients (Iverson et al., 2004; Iverson et al., 2008). Fire effects on herbaceous species composition of northeastern forests are significant, but show minimal post-burn increases in nonnative invasive plants (Hutchinson et al., 2005a) mainly in unproductive areas with invasive plant seed sources (Marsh et al., 2005). Unlike fire, increased nutrient availability after harvesting will be due to reduced nutrient uptake (Boerner and Sutherland, 1997) and slash decomposition, but not as much as would be found in ash after a fire (Belleau et al., 2006). Light levels are also likely to be higher after a harvest than a fire (Miller et al., 2004). Nonetheless, both fire and harvesting treatments result in a mosaic of microclimates in the understory. In areas prone to acid deposition, fire, unlike harvesting, may have a positive effect on general plant growth by increasing soil Ca/Al ratios (Boerner et al., 2004).

The positive correlation between disturbance and invasion by nonnative plants suggests that managing for oak regeneration with disturbance may elevate the risk of invasion. Our research addresses this oak regeneration and invasive plant establishment dilemma by focusing on responses of three common nonnative invasive plants of northeastern forests to disturbance-induced changes in available resources (e.g., light, water, nutrients) over a gradient of existing environmental conditions (physiography and vegetation composition). These environmental conditions influence nonnative invasive plants' ability to become established. Relating invasive plant response to both existing physiographic characteristics and changes in resource availability caused by fire or harvesting will help managers prioritize sites for both oak and invasive plant management. Because the effects of disturbance tend to be site specific and potentially less important than site abiotic and biotic conditions (Moles et al., 2012), this project encompasses both landscape and microclimatic scales in order to make our results relevant to more land managers of northeastern forests. Our research links resource changes caused by common forest management regimes to nonnative invasive plant early establishment and productivity along both small-scale topographic and large-scale physiographic gradients. All in all, we address the possibility of manipulating disturbance severity or existing environmental conditions (perhaps by selecting certain site types over others) in such a way to reduce the risk of invasion in response to forest management regimes used to regenerate native species.

Microstegium vimineum (Japanese stiltgrass), hereafter referred to as *MiVi*, *Alliaria petiolata* (garlic mustard), hereafter referred to as *AlPe*, and *Ailanthus altissima* (tree of heaven), hereafter referred to as *AiAl*, are among the more aggressive nonnative plant invaders of northeastern forests of the US, but are also of international significance as invaders. *MiVi*, native to Asia, is also found as a nonnative species in Central America and the Caribbean (EPPO, 2015). *AlPe*, native to Europe, is also found as a nonnative plant in Canada and Australia (CABI, 2017). *AiAl,* native to north and central China, Taiwan, and North Korea, is considered a problematic exotic nationwide in the US and is now also present as a nonnative species in Canada, Europe, eastern Asia, Africa, Central America, South America and both Australia and New Zealand. (Q-Bank, 2017).

Both *MiVi*, an annual late-season grass, and *AlPe*, a biennial herb, are shade-tolerant species often found in closed-canopy conditions, making them a threat in highly disturbed and less disturbed forests. Though shade-tolerant, *MiVi* produces significantly less seed in shaded environments, primarily due to a smaller plant size (Huebner, 2011; Cheplick and Fox, 2011) and lower abundance (Beasley and McCarthy, 2011). *MiVi,* which uses C_4 photosynthesis, can rapidly grow and produce more seed in response to small increases in light, such as sunflecks or canopy gaps, but it can only use 25% of full sunlight (Winter et al., 1982; Horton and Neufeld, 1998). Glasgow and Matlack (2007) showed that *MiVi* abundance was significantly greater after a high-intensity burn than low-intensity burn or no-burn in mesic valleys but only under canopy gaps, suggesting that this species' local abundance is most dependent on light availability. *AlPe* flowers once in early spring of its second year, taking advantage of the relatively open forest canopy. Similar to *MiVi*, *AlPe* may be found in high-light and shaded areas. *AlPe* can be found at higher densities in closed canopy conditions, but its second year of growth and reproduction appears to be most stimulated by intermediate light levels (Byers and Quinn, 1998; Phillips-Mao et al., 2014). *AiAl* growth rates are significantly higher in high-light environments than in low light, though small seedlings and saplings will survive under a closed canopy and low-light conditions (Kota et al., 2007). Similar to *MiVi*, *AiAl* responds positively to an increase in light, and its response will be most evident in high-light conditions. Of the three species, both *MiVi* and *AlPe* appear to be relatively dependent on mesic conditions. *AiAl*, a dioecious tree, is relatively drought tolerant and may invade more xeric sites (Trifilo et al., 2004). Though most females of *AiAl* usually do not produce seed until they are small trees (Wickert et al., 2017), both sexes will spread prolifically via root sprouts. Vegetative growth of this species increases in response to stem and root damage (Kowarik and Säumel, 2007).

Both *AlPe* and *MiVi* have been documented to form seed banks (Gibson et al., 2002; Byers and Quinn, 1998), which are likely to respond positively to any increase in light and nutrients resulting from a fire or harvesting. *AiAl*'s high germination rates may explain a lack of a seed bank, but a seed bank has been found in several sites (Kostel-Hughes et al., 1998; Redwood et al. and Rebbeck unpublished data) where site conditions (lower temperatures) may affect germination as well as seed decomposition rates. Even without a long-lived seed bank, *AiAl*'s wind-dispersed seed may access new disturbed areas from as far away as 100 m (Landenberger et al., 2007), and once at these sites, may take advantage of the higher light and nutrient levels.

We asked the following question: How do *MiVi*, *AlPe*, and *AiAl*