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Effects of roads and forest successional age on experimental plant invasions

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ABSTRACT

Anthropogenic activities can promote plant invasions by changing habitat conditions and the dispersal of invasive plant propagules. Invasions are often more common near roads and in young habitats than in interior and mature habitats, but it is unknown if these patterns are due to differences in habitat conditions or to dispersal limitation. We tested if reduced colonization of interior and mature forests by invasive plants is due to unfavorable habitat conditions. We experimentally introduced seeds and seedlings of three invasive and three native species at six distances from roads in a series of young and mature forests. Seed germination and seedling survival, growth, and herbivore damage were quantified over three years. Exotics had higher germination rates than natives with the greatest difference in mature forests. Both native and exotic seedling growth declined with increasing distance from roads. Overall, seedling growth was much greater in young compared to mature forests. Despite growth rate differences, more than 75% of exotic and native seedlings survived over the experiment. Native species suffered significantly more herbivory than exotic species, suggesting that their growth may be suppressed by herbivory. In general, conditions along roads and in young forests promoted invasive shrub growth but invasions were not entirely limited by conditions in interior and mature forests. Our results show that two common landscape features, roads, and successional age heterogeneity, can influence the distribution of plant invasions. To better manage these invasive species, mature forests should be maintained and disturbances such as road-building should be avoided.

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1. Introduction

Invasions of exotic species, fragmentation, and habitat loss are the primary causes of biodiversity declines and alteration of ecosystem processes (Mack et al., 2000; Pimentel et al., 2000). Predicting patterns of invasions across fragmented habitats is necessary for effective invasive species management and conservation of native species. Theories of invasive plant spread suggest that landscape patterns of invasions are determined by two main factors: habitat conditions that affect population growth, and patterns of dispersal (With, 2002). For many ecosystem types, the relative importance of these two causal factors for predicting community susceptibility to invasions is unknown. Roads are an example of a widespread landscape feature that fragment habitats and create edges with high resource availability that can act as conduits for plant dispersal (Cadenasso et al., 1997; Forman and Alexander, 1998; Matlack, 1993). Many forests have been heavily fragmented by roads (Riitters and Wickham, 2003), resulting in reduced habitat quality and biodiversity (Forman et al., 2003), and more frequent and higher density plant invasions along roads than at interior sites (e.g., Flory and Clay, 2006; Parendes and Jones, 2000; Pauchard and Alaback, 2006; Watkins et al., 2003).

The presence of roads can increase soil moisture, soil disturbance, nutrient runoff, sun exposure, and temperature (Delgado et al., 2001; Forman, 2000; Parendes and Jones, 2000; Rentch et al., 2005), factors which can promote plant invasions independent of roads (Davis et al., 2000; With, 2002). Correspondingly, sites far from roads may be resistant to invasions due to different abiotic conditions such as reduced disturbance frequency or resource availability (Gelbard and Harrison, 2003). Invasive species success can also be promoted by release from herbivore pressure (DeWalt et al., 2004; Keane and Crawley, 2002) and edge habitat conditions along roads such as increased light or temperature may enhance herbivore activity (Cadenasso and Pickett, 2000; Fortin and Mauffette, 2001). The release of exotic species from herbivory combined with enhanced herbivory on native species may facilitate exotic success along roads. The potential role of herbivore preferences facilitating invasive success might be independent of, or correlated with, other mechanisms such as enhanced dispersal or habitat differences. Roads can also act as dispersal corridors where seeds can be spread by vehicles, water, and by birds and other animals that use roadways as travel paths (Buckley et al., 2003; Lonsdale and Lane, 1994; Von der Lippe and Kowarik, 2007). Determining how roads affect habitat conditions and the dispersal of seeds will help determine whether exotic species will remain largely restricted to roadsides or whether interior sites are also at risk from invasions.

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Independent of roads, successional age can influence patterns of plant invasions with young systems being more susceptible to invasions than mature systems (Blumenthal et al., 2003; Fierke and Kauffman, 2006; Flory and Clay, 2006; Thiele and Otte, 2006, but see Domenech and Vila, 2006). Secondary succession follows disturbances such as tree blow-downs, even-aged tree harvests, or abandonment of agricultural fields, resulting in exposed soil, greater light availability, and reduced competition for resources (Bonan, 2002). In early successional habitats, species that disperse large numbers of small seeds, grow quickly, and reproduce early are often most successful. Many exotic invaders exhibit these traits (Grotkopp and Rejmanek, 2007; Rejmanek and Richardson, 1996), suggesting that habitat conditions present in early successional systems are more favorable for plant invasions than mature systems. Preferential dispersal of invasive plant seeds to early successional communities occurs when animals, including birds that disperse fleshy-fruited species, favor those areas for feeding, nesting habitat, or cover (Gosper et al., 2005). Prediction and management of plant invasions will be influenced by patterns of exotic species dispersal and habitat conditions across successional forest systems.

The distribution of native species may also be responsive to proximity to roads and successional age (Gosper et al., 2005; Spooner, 2005; Spooner et al., 2004). The success of native species may be constrained by conditions along roads and in young systems if animals that commonly disperse some native species avoid such areas (Gelbard and Harrison, 2003; Turner, 1996). For example, Tomimatsu and Ohara (2004) found that recruitment of native understory species was significantly reduced near forest edges due to altered microclimate conditions. Because native species can provide “biotic resistance” to invasions by competing with introduced species (Levine et al., 2004; Von Holle, 2005), a better understanding of the response of both native and invasive species to roads and the successional age of systems will help explain the distribution of plant invaders.

One of the greatest threats to eastern deciduous forests in the USA is invasion by the exotic shrubs *Elaeagnus umbellata* (autumn olive), *Ligustrum obtusifolium* (privet), and *Lonicera maackii* (bush honeysuckle). These shrubs have been shown to reduce forest overstory productivity (Hartman and McCarthy, 2007), inhibit tree regeneration (Gorchov and Trisel, 2003; Merriam and Feil, 2002; Orr et al., 2005), and suppress native herbaceous species (Gould and Gorchov, 2000). Previously, we reported that invasive shrubs occur at higher densities along roads than in interior forests and in young and mid-successional forests than mature forests in central and southern Indiana (Flory and Clay, 2006). Specifically, the density of *L. maackii* declined significantly as distance from road increased and *E. umbellata* declines with increasing distance from roads approached significance ($P = 0.07$). *L. obtusifolium* densities were not significantly affected by distance from road (Flory and Clay, 2006). In the present study, we tested the hypothesis that the distribution of these invasive shrubs is restricted to roadsides and young forests due to habitat conditions rather than seed dispersal limitation. We experimentally initiated invasions of *Elaeagnus*, *Ligustrum*, and *Lonicera* at six distances from roads in young and mature forests in two independent experiments. In the first experiment we planted seed to test the effects of distance from roads and forest age on seed germination. In the second experiment we planted seedlings and measured their survival, growth, and herbivore damage over three years. To determine if these exotic species have unique responses to roads and forest successional age or if native species react similarly, we also planted seed and seedlings of three common native understory species in the same locations. If invasions of these shrubs are limited to roadsides and early successional forests because of habitat conditions, then exotic seed germination and

seedling survival would be reduced at interior and mature sites relative to native species. Alternatively, if distance from road and forest age does not affect exotic germination or seedling success, then dispersal to interior and mature forests could result in widespread shrub invasions.

2. Methods

2.1. Study area

We conducted this study in southern Indiana USA. Historically, the region was contiguous deciduous forest but much of it was harvested for timber or cleared for agriculture by the early 1900s. Due to steep topography and poor soils, many areas were abandoned for agricultural purposes and have been reforested, resulting in a mixture of forests of varying successional ages. Forests are a combination of mixed oak–hickory (*Quercus–Carya*) and beech–maple (*Fagus–Acer*) stands (Woodall et al., 2005) depending on the local land-use history, environmental conditions, and forest successional age. The climate is temperate with relatively hot, dry summers, cold winters, and above-average precipitation during the spring and fall months. On average, the region receives 102 cm of precipitation per year and daily maximum temperature during the summer months is 29 °C (Noble et al., 1990).

2.2. Site selection

In June 2004, we selected six mature (defined as >60 years old) and six young (defined as <40 years old) forest sites within 30 km of Bloomington, Indiana (Fig. 1). Sites were located 200 m–40 km apart to ensure independence of observations. Forest successional age was determined by average tree dbh (diameter in breast height), dated aerial photographs, and personal communication with landowners and property managers. We selected sites that bordered paved, two-lane public roads, but did not have confounding topographic features such as ravines, drainage ditches, or steep slopes within 60 m of the road. Sites included state forests, private forests, and two properties of the Indiana University Research and Teaching Preserve.

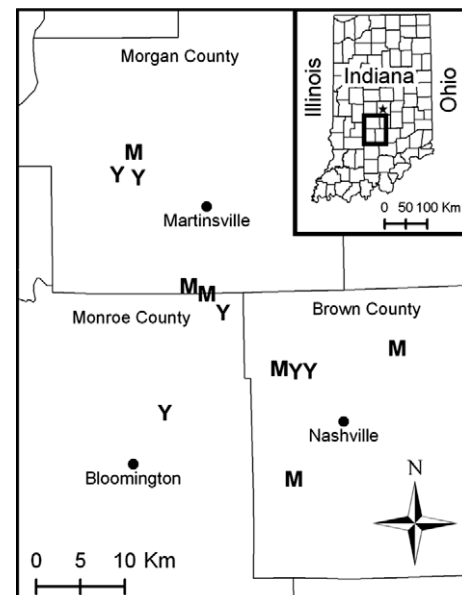


Fig. 1. Research sites. Map of south central Indiana, USA showing the six mature (M), and six young (Y) forest sites used in the experiment.

2.3. Habitat conditions

To characterize environmental conditions at the study sites, we collected data on light availability and soil moisture in summer 2005. At 0 m, 5 m, 10 m, 20 m, 40 m, and 60 m from the road at each site, we established a 5 m long transect running parallel to the road. At five locations approximately 1 m apart along the transect, we measured photosynthetically active radiation (PAR) and calculated percent available light by comparing PAR values to measurements taken in open sun (AccuPAR Linear PAR/LAI ceptometer, Decagon Devices, Inc., Pullman, WA). We also collected a 125 cm³ sample of mineral soil at the center of each transect to evaluate gravimetric water content. We quantified the amount of leaf litter at each of the six distances from roads at each site by collecting all litter from within a 25 cm × 25 cm PVC frame in December 2008. Litter was dried to constant mass and weighed.

We evaluated the forest structure along the transect at each site by quantifying average tree dbh, tree basal area, and species dominance. At 0 m, 5 m, 10 m, 20 m, 40 m, and 60 m from the road at each site we used a wedge prism to quantify tree basal area (Grenier et al., 1991). We then identified and measured the dbh of the five nearest trees at each of the six distances from roads that were included in the measurement of tree basal area.

2.4. Experimental design

To evaluate the effects of distance from roads and forest age on seed germination of the three native and three exotic species, we established a germination experiment in October 2004. At each of the 12 field sites, we randomly chose a point along the road that was at least 100 m from confounding landscape features such as creeks, other roads, or ravines. We then established a 60 m transect extending perpendicular to the road into the forest. There was a 1–3 m wide strip maintained by mowing along each road, so transects started where the mowed strip met the forest edge. At 0 m, 5 m, 10 m, 20 m, 40 m, and 60 m from the road we placed 10 seeds of each of three native and three exotic species together within 10 cm × 10 cm mesh bags constructed of military-grade green mosquito netting (0.09 mm² openings). We chose to evaluate these distances from roads because our previous work (Flory and Clay, 2006) showed that there were strong effects of distance from roads in the first 10 m and that the effects extended at least 30 m into the forest. Seeds were collected from all species in natural areas near Bloomington, Indiana and were cleaned and air dried. Bags were protected from rodent herbivory by folding a 15 cm × 30 cm piece of galvanized steel hardware cloth (5 mm × 5 mm openings) around each bag. Bags within hardware cloth were placed below any leaf litter and were held to the soil surface by two landscaping staples. We used the three most common woody invasive species based on a previous survey of 14 forested sites in Indiana: *E. umbellata* (autumn olive), *L. obtusifolium* (privet), and *L. maackii* (bush honeysuckle; Flory and Clay, 2006), plus three common native understory species: *Cercis canadensis* (redbud), *Lindera benzoin* (spicebush), and *Cornus florida* (flowering dogwood).

To determine how distance from roads and forest age affected native and exotic seedlings, we established a second experiment in June 2004. We planted four replicate seedlings of each of the above six native and exotic species in random locations within an 8 × 3 grid (144 total seedlings per transect) at 0 m, 5 m, 10 m, 20 m, 40 m, and 60 m from roads. There was one transect established per site at 12 total sites. The long axis of each grid was oriented parallel to the road and adjacent seedlings were planted 0.4 m apart. Seedlings were initially reared in the Indiana University greenhouse from either cuttings or seed and were eight weeks old at planting. Seedlings of all species were approximately uniform in height (10–15 cm) when planted. Seedlings that died with-

in two weeks of planting were replaced but no further treatments were applied. We used seedlings because seedling survival and growth are relatively easy to evaluate, and because seedlings are more likely to show survival and growth responses than larger individuals.

2.5. Data collection

Seed germination bags were collected in late June 2005. Seeds were evaluated for germination and were scored as germinated if the seed coat was broken and the root radical had emerged. Although bags were enclosed within hardware cloth, some bags were still damaged by rodents. The proportion of seeds germinated was calculated as the number germinated out of the number recovered.

In September 2004, 2005, and 2006 we evaluated seedling survival and scored each surviving seedling for herbivory on a scale of 0–5 by visually estimating leaf area consumption such that 0 = no herbivory, 1 = ≤25% leaf loss, 2 = 26–50%, 3 = 51–75%, 4 = >76%, and 5 = 100% of leaves removed by herbivores. In September 2006, we harvested the above-ground portion of all surviving seedlings and measured total height and basal diameter. Seedlings were then dried at 60 °C to constant mass and weighed. To prevent further plant invasions, we removed all seedlings before they reached reproductive age and surveyed all plots one year later in 2007 to confirm that no seedlings had survived past the end of the experiment.

2.6. Data analysis

We used ANOVA to analyse the fixed effects of distance from road, forest successional age, and site (nested within age) on percent available light, percent soil moisture, tree dbh, tree basal area, and litter mass. We averaged the replicate light and dbh measurements for each distance from the road at each site. We used a fixed effects model because we were specifically interested in how these three important invasive species are affected by distance from road and forest successional age. We also used ANOVA to evaluate the fixed effects of distance from road, forest successional age, native/exotic origin, species (nested within origin), site (nested within age), and their interactions on the proportion of seeds germinated, and seedling survival, growth (height, diameter, and biomass), and herbivory (Proc GLM, SAS Institute Inc., 2002). We averaged the survival, growth measurements, and herbivore damage of the four replicate individuals of each species planted at each location to simplify the statistical analyses. Individual-based statistical analyses of survival and growth yielded qualitatively identical results. There were no differences among years for herbivore damage so measures of herbivory were averaged across all three years. Data were log-transformed to improve normality (Shapiro–Wilks test) and equality of variances (Levene's test) when necessary. If invasions by these species are limited to roadsides and young forests due to habitat conditions, we would expect higher exotic seed germination and seedling survival along roads that in interior sites and greater germination and survival in young compared to mature forests relative to native species.

3. Results

3.1. Habitat conditions

There was no effect of distance from roads or forest age on percent light or percent soil moisture (Table 1, Fig. 2a and b). There was also no effect of distance from roads on tree dbh, tree basal area, or litter mass. However, there were significant effects of

Table 1
ANOVA results for the effects of distance from roads, forest age, and site on percent light, percent soil moisture, tree diameter at breast height (dbh), tree basal area, and litter mass.

Source	df	Percent light		Percent soil moisture		dbh		Basal area		Litter mass	
		F	P	F	P	F	P	F	P	F	P
Distance	5	0.88	0.50	1.25	0.30	0.53	0.75	1.08	0.38	0.30	0.91
Age	1	0.03	0.87	1.08	0.31	340.04	<0.0001	104.93	<0.0001	19.72	<0.0001
Dist × age	5	1.28	0.29	1.28	0.29	2.54	0.04	2.84	0.03	1.47	0.22
Site (age)	10	1.80	0.09	2.83	0.007	4.20	0.0003	3.18	0.003	2.12	0.04

Note: P-values listed in bold are <0.05.

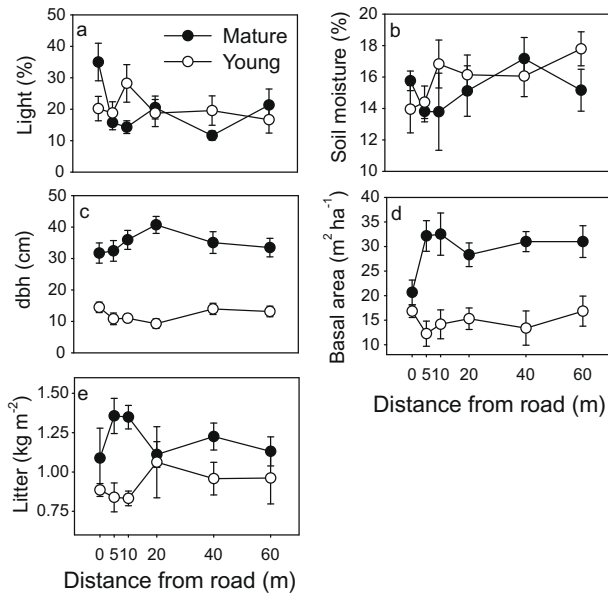


Fig. 2. Habitat conditions. Average (\pm SE) percent light (a), percent soil moisture (b), tree diameter at breast height (dbh, c), tree basal area (d), and litter mass (e) at six distances from roads at six mature and six young forest sites.

forest age on tree dbh, tree basal area, and litter mass (Table 1, Fig. 2c–e). On average, tree dbh in mature forests (mean \pm SE, 34.27 ± 1.23 cm) was nearly three times that of trees in young forests (11.90 ± 0.92 cm). The average basal area of trees in mature forests (29.27 ± 1.34 m² ha⁻¹) was significantly greater than young forests (14.80 ± 1.05 m² ha⁻¹). There was a significant distance by age interaction for both dbh and basal area with an effect of distance from roads in mature but not young forests (Table 1, Fig. 2c and d). On average, leaf litter mass in mature forests (1.21 ± 0.05 kg m⁻²) was 32% higher than in young forests

(0.92 ± 0.05 kg m⁻²), but did not vary with distance from road (Table 1, Fig. 2e).

We identified 180 trees at mature forest sites and 174 trees at young forest sites. The dominant trees at the mature sites were *Quercus rubra* (22% of identified trees), *Acer saccharum* (14%), *Liriodendron tulipifera* (14%), *Quercus alba* (11%), and *Sassafras albidum* (10%). The young sites were dominated by *S. albidum* (23%), *Acer rubrum* (15%), *L. tulipifera* (11%), *Rhus* spp. (10%), and *Prunus serotina* (5%).

3.2. Germination

Seed germination was affected by distance from roads, forest age, and native/exotic origin. Overall, the percent exotic germination (mean \pm SE, $29.9 \pm 2.4\%$) was more than three times that of native species ($9.3 \pm 1.4\%$). In mature forests, percent germination ($24.0 \pm 2.2\%$) was significantly greater than in young forests ($16.3 \pm 2.1\%$, Table 2, Fig. 3). There was a significant statistical interaction between age and origin with exotic germination being relatively greater in mature forests (Table 2, Fig. 3).

3.3. Seedling survival

Seedling survival was unrelated to the main effects of distance from road, forest successional age, and native/exotic origin (Table 2). However, there was a significant age \times origin interaction on seedling survival (Table 2, Fig. 4). In mature forests, the average percent native seedling survival for three years (mean \pm SE; $79.9 \pm 2.9\%$) was 3.4% greater than exotic seedling survival ($76.5 \pm 3.4\%$), but in young forests exotic survival ($79.6 \pm 3.1\%$) was 9.5% greater than native survival ($70.1 \pm 3.4\%$; Fig. 4).

3.4. Seedling growth

Distance from road, forest age, and native/exotic origin all affected seedling growth. Exotic and native seedlings were taller near roads than at the interior locations but the effect was only

Table 2
ANOVA results for the effects of distance from roads, forest age, native/exotic origin, and their interactions on seed germination and seedling survival, height, diameter, biomass, and herbivory.

Source	df	Germination		Survival		Height		Diameter		Biomass		Herbivory	
		F	P	F	P	F	P	F	P	F	P	F	P
Distance	1	3.28	0.0065	0.24	0.9427	2.03	0.0735	4.63	0.0004	5.58	<0.0001	0.42	0.8374
Age	5	11.60	0.0007	0.82	0.3646	45.89	<0.0001	56.61	<0.0001	37.36	<0.0001	1.29	0.2578
Origin	1	195.09	<0.0001	1.51	0.2203	1.89	0.1695	12.69	0.0004	13.18	0.0003	205.70	<0.0001
Dist × age	5	2.84	0.0159	1.83	0.1061	1.34	0.2464	1.85	0.1031	1.84	0.1040	3.84	0.0021
Dist × origin	5	1.22	0.3	1.43	0.2123	0.40	0.8456	0.37	0.8664	0.94	0.4518	1.28	0.2706
Age × origin	1	5.37	0.0210	6.99	0.0085	5.35	0.0213	0.03	0.8566	0.59	0.4433	0.96	0.3273
Dist × age × origin	5	1.43	0.2117	0.40	0.8492	0.37	0.8662	0.69	0.6280	0.35	0.8823	1.12	0.3509
Site (age)	10	4.72	<0.0001	8.17	<0.0001	4.56	<0.0001	7.78	<0.0001	6.49	<0.0001	3.17	0.0007
Species (origin)	4	32.20	<0.0001	58.55	<0.0001	3.86	0.0043	2.09	0.0821	1.62	0.1693	39.19	<0.0001

Note: P-values listed in bold are <0.05.

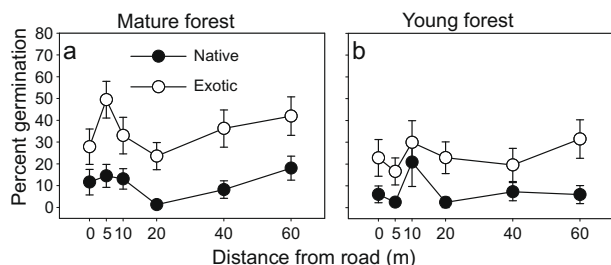


Fig. 3. Seed germination. Average (\pm SE) percent seed germination for three native and three exotic species at six distances from roads in mature (a) and young (b) forests.

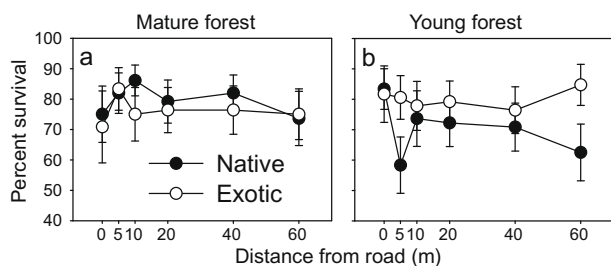


Fig. 4. Seedling survival. Average (\pm SE) percent survival of native and exotic seedlings at six distances from roads in mature (a) and young (b) forests over the three year experiment.

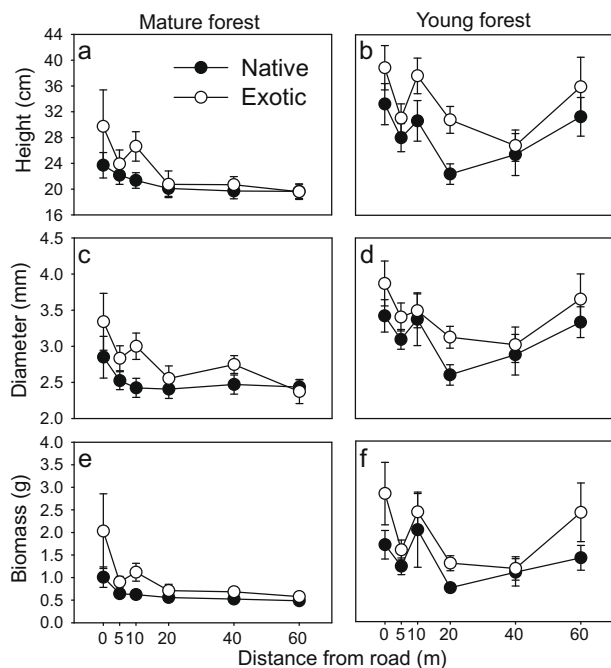


Fig. 5. Seedling growth. Average (\pm SE) height (a, b), diameter (c, d), and biomass (e, f) of native and exotic seedlings alive at the end of the experiment for six distances from roads in mature and young forests.

marginally significant (Table 2, Fig. 5a and b). On average, seedling height for native and exotic species in young forests (mean \pm SE; 31.04 ± 0.89 cm) was 41% greater than in mature forests (22.02 ± 0.56 cm). There was also an age \times origin interaction with exotic seedlings relatively taller than native seedlings in young forests (Table 2, Fig. 5a and b). Distance from road, forest age, and na-

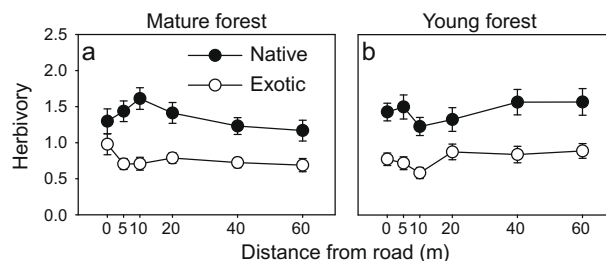


Fig. 6. Seedling herbivory. Average (\pm SE) herbivory experienced by native and exotic seedlings at six distances from roads in mature (a) and young (b) forests.

tive/exotic origin all significantly affected basal stem diameter but there were no interactions among the main effects (Table 2, Fig. 2c and d). Seedlings had greater basal diameter near roads than at interior locations and 24% greater basal diameter in young (3.27 ± 0.07 cm) compared to mature (2.63 ± 0.05 cm) forests (Table 2, Fig. 5c and d). On average, exotic species had 11% larger diameters (3.12 ± 0.07 mm) than native species (2.82 ± 0.06 mm; Table 2, Fig. 5c and d). Seedling biomass was affected by distance from road, forest age, and native/exotic origin (Table 2, Fig. 2e and f). On average, the seedling biomass near roads was nearly twice the biomass of those at the three most interior locations. Seedlings had 117% greater biomass in young (1.67 ± 0.13 g) compared to mature (0.77 ± 0.06 g) forests. Overall, the three exotic species (1.49 ± 0.12 g) had 48% greater biomass than the native (1.01 ± 0.09 g) species, but both native and exotic species reacted similarly to distance from road and forest age (Table 2, Fig. 5e and f).

3.5. Herbivory

Native seedlings suffered an average of 82% more herbivore damage than exotic seedlings (native mean \pm SE; 1.40 ± 0.04 , exotic 0.77 ± 0.03 ; Table 2, Fig. 6) but distance from road and forest age had no effect on native or exotic seedling herbivory (Table 2). There was a distance \times age interaction with a decrease in herbivory as distance from road increased in mature forests but an increase in herbivory at greater distances from roads in young forests (Table 2, Fig. 6). Most observed herbivory was by insects and small mammals.

4. Discussion

Our results demonstrate significant differences in the performance of exotic versus native species in relation to distance from roads and successional age of the habitat. Seeds of the three exotic species germinated at higher rates than the native species overall, and the relative difference in germination was more pronounced in mature forests. However, habitat conditions near roads did not promote exotic seed germination. Seedlings of all species grew more near roads and in young forests relative to interior and mature sites, corresponding to previous observations of established exotic shrubs (Flory and Clay, 2006). This suggests that invasions are partly limited at interior and mature forest sites by habitat conditions. Because seeds of the three exotic species germinated at high rates in interior and mature sites and because there were no effects of distance from road or forest age on exotic seedling survival (more than 75% of seedlings survived at interior and mature sites over the three years of the study), invasions may also be limited, in part, by lack of dispersal. In general, our results demonstrate that invasions of the exotic shrubs *E. umbellata*, *L. obtusifolium*, and *L. maackii* may become more widespread if seeds are dispersed to interior locations and mature forests,

particularly if seed dispersal coincides with changes in habitat conditions that promote their growth.

Habitat conditions conducive to plant colonization are often more favorable along roads and in early successional forests (Bonan, 2002; Forman and Alexander, 1998). In our previous study we found that exotic shrubs occurred at higher densities near roads than at interior sites (Flory and Clay, 2006), leading to the hypothesis that seed germination would be greater near roads and in young forests. However, we found no effect of distance from road or forest age on percent available light or soil moisture. Young forests had significantly smaller trees, less tree basal area, and less litter. Reduced competition from established trees may enhance exotic seedling growth and reduced litter may promote exotic seed germination. While distance from road and forest age did affect seed germination, it was not in the direction that we expected. Germination of the three exotic species was higher at intermediate distances from roads, interior sites, and in mature forests, suggesting that patterns of natural invasions are not predicted by patterns of seed germination.

Distance from road affected seedling growth but not seedling survival. At interior sites, habitat conditions reduced seedling growth, especially in mature forests, but the majority (>75%) of all seedlings survived the duration of the experiment. It is not clear how long these exotic species could continue to persist without substantial growth. If seedlings can survive for relatively long time periods under unfavorable conditions, then seedling populations at interior and mature sites will steadily increase. For example, when canopy gaps with high light penetration and nutrient availability are created (Bonan, 2002), rapidly growing exotic seedlings may quickly come to dominate a community. Such invasions could result in suppressed forest regeneration and persistent invasions (Gorchov and Trisell, 2003; Hartman and McCarthy, 2007). Even though this experiment was conducted over an extended time frame, much longer demographic studies are needed to determine if survival or growth is regulating the population dynamics of invasive shrubs. In addition, it is unclear which specific habitat factors are regulating population growth. With greater replication of sites with particular physical and biological characteristics we could possibly determine the specific factors that explain invasive success, or how the roles of differential herbivory, dispersal limitation and environmental conditions might vary with site characteristics.

Our results show that seeds of three invasive shrubs can germinate at interior and mature sites and that exotic seedlings can survive for years at those locations. However, significantly more natural invasions occur along roads and in young forests (Flory and Clay, 2006). All three exotic and two of the three native species used in the experiments presented here have bird-dispersed fruits. Many frugivorous birds preferentially feed along edges and in gaps, and fruit removal occurs more rapidly in such sites (reviewed by Gosper et al., 2005). Thus, those areas should receive proportionally more seeds than interior and mature forests. Although habitat conditions along roads are often relatively favorable for invasive plant growth compared to interior sites (e.g., Parendes and Jones, 2000; Rentch et al., 2005), our results demonstrate that the three exotic shrub species examined here are not excluded from interior and mature forests due to reduced seed germination or seedling survival.

Native species can provide biotic resistance to invasions by competing with introduced species for resources such as light, water, and nutrients (Levine et al., 2004). Greater survival and growth of native vs. exotic species in interior and mature forests would suggest that these native species might provide resistance to invasions. We observed higher germination for exotic than native species and there was an age by origin interaction with relatively greater exotic seed germination in mature forests. While there were no differences in growth between native and exotic

species with distance from road, there was a significant interaction between forest age and native/exotic origin for seedling survival. Native species survival was higher in mature forests and exotic survival was higher in young forests, but differences in survival between native and exotic species were not large (i.e. 3% in young forests and 10% in mature forests). In a previous field survey, we found about 70% more invasive shrubs in young and mid-successional forests than mature forests and over four times more invasive shrubs near roads than at sites 30 m from roads (Flory and Clay, 2006). It is unknown how small differences in survival over the three years of this experiment might contribute to the large differences in patterns of invasion over many years.

There were significantly higher rates of herbivory on native than exotic seedlings and native species had much lower average growth rates than exotic species. The native species received over 80% more herbivore damage than exotic species, which would result in significantly less photosynthate production for native vs. exotic species. Release from natural enemies has been shown to influence invasive plant population dynamics in other systems (e.g., Dietz et al., 2004; Liu et al., 2007). For example, application of pesticides to the neotropical shrub *Clidemia hirta* significantly increased its survival and growth where it was native but not where it was introduced, demonstrating that its success in the introduced range was partly due to release from its natural enemies (DeWalt et al., 2004). Invasions of *E. umbellata*, *L. obtusifolium*, and *L. maackii* may be promoted by differences in rates of herbivory but other factors such as differences in disease risk or physiology could also contribute to differences in seedling growth rates. These species may be invasive simply because they have exceptionally high growth rates as a result of artificial selection for horticultural purposes. Alternatively, they may have evolved to grow more rapidly in the absence of their natural enemies following their introduction to the USA (Zou et al., 2008).

4.1. Conclusions and management implications

In summary, our results show that patterns of seed germination for three exotic shrub species do not coincide with patterns of natural invasions, indicating that germination rates do not control invasions. The growth of exotic seedlings was greater along roads and in young forests than in interior and mature forests. Exotic seedling survival was relatively high in interior and mature forests, suggesting that if seeds are dispersed to those sites they may be vulnerable to invasion, especially following disturbances. There were no differences in available light or soil moisture between young and mature forests or among different distances from roads but forest community structure strongly differed between forest ages. Mature forests had larger trees, more tree basal area, and more leaf litter, characteristics that may have inhibited exotic seedling growth. Fragmentation and disturbance of forests due to agriculture, timber harvests, and road-building can promote invasions by altering habitat conditions and the dispersal of invasive plant propagules. The response of the native and exotic species examined here to roads and successional age was qualitatively similar, but exotic species suffered less herbivore damage and grew faster. More generally, our results demonstrate that two common landscape features, roads, and forest age heterogeneity, alter the growth of three invasive shrub species. If habitats are altered and there is less mature forest far from roads, the overall vulnerability of forests to invasions may increase.

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