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INVASION THROUGH QUANTITATIVE EFFECTS: INTENSE SHADE DRIVES NATIVE DECLINE AND INVASIVE SUCCESS

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Abstract. The effects of invasive nonnative species on community composition are well documented. However, few studies have determined the mechanisms by which invaders drive these changes. The literature indicates that many nonnative plant species alter light availability differently than natives in a given community, suggesting that shading may be such a mechanism. We compared light quantity (photosynthetically active radiation, PAR) and quality (red : far-red ratio, R:Fr) in riparian reaches heavily invaded by a nonnative tree (*Acer platanoides*) to that in an uninvaded forest and experimentally tested the effects of our measured differences in PAR and R:Fr on the survival, growth, and biomass allocation of seedlings of the dominant native species and *Acer platanoides*. Light conditions representative of the understory of *Acer platanoides*-invaded forest decreased survival of the native maple *Acer glabrum* by 28%; *Amelanchier alnifolia* by 32%; *Betula occidentalis* by 55%; *Elymus glaucus* by 46%; and *Sorbus aucuparia* by 52%, relative to seedlings growing in PAR similar to that of native understories. In contrast, *Acer platanoides* and the native shrub *Symphoricarpos albus* were not affected by reductions in PAR.

Acer platanoides seedlings and saplings are uniquely adapted to shade relative to native species. *Acer platanoides* was the only species tested that decreased allocation to roots relative to shoots in the invaded forest vs. the native forest light conditions. Therefore it was the only species to demonstrate an adaptive response to the particular light environment associated with *Acer platanoides* invasion as predicted by optimal partitioning theory.

The profound change in light quantity associated with *Acer platanoides* canopies appears to act as an important driver of native suppression and conspecific success in invaded riparian communities. Further research is necessary to determine whether the effect of nonnative plant-driven changes on light quantity and quality is a widespread mechanism negatively affecting resident species and facilitating invasion by nonnatives.

Key words: *Acer platanoides*; biological invasion; impact mechanism; quantitative effects; shading impact.

INTRODUCTION

Despite the wealth of general conceptual hypotheses for why some invaders have such striking effects on native communities, we know little about the basic mechanisms for how “strong invaders” suppress natives (Levine et al. 2003). Our limited understanding of these impact mechanisms affects our ability to predict the potential invasiveness of nonnative species (Rejmanek and Reichard 2001), their effects, or the vulnerability of individual systems to invasions (Elton 1958, Levine and D’Antonio 1999).

Invasive plant species with major effects on community composition and ecosystem-level processes often

appear to have traits that are qualitatively different from those of resident species, including novel mutualisms (Vitousek et al. 1987), means of acquiring resources (Chapin et al. 1994), allelopathic compounds (Callaway and Ridenour 2004), or establishing novel disturbance regimes (D’Antonio and Vitousek 1992). Furthermore, invasiveness has been linked to novelty in other studies (Ricciardi and Atkinson 2004). However, invaders may also succeed by quantitatively amplifying traits that natives possess (Levine et al. 2003).

Norway maple (*Acer platanoides* Linn.) has invaded northeastern forests of the United States (Wyckoff and Webb 1996, Martin 1999, Webster et al. 2005) and riparian and mesic montane forests of the northern Rocky Mountains (Reinhart et al. 2005, 2006). Reinhart et al. (2005) demonstrated that a riparian reach invaded by *Acer platanoides* (76% *A. platanoides* canopy coverage) had much lower understory species richness (69% fewer species) than reaches with low levels of *A. platanoides* invasion (0–11% *A. platanoides* canopy coverage). Plant diversity beneath solitary *A. platanoides* trees also declined as the size of the trees increased,

Manuscript received 22 December 2005; revised 17 March 2006; accepted 21 March 2006. Corresponding Editor: J. A. Antos.

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TABLE 1. Nonnative and invasive plants either suspected or known to alter light availability relative to resident species.

Genus	Reference(s)
Suspected	
<i>Acacia</i>	Holmes and Cowling (1997)
<i>Acer</i>	Wyckoff and Webb (1996), Bertin et al. (2005), Reinhart and VandeVoort (2006)
<i>Carpinus</i>	Kwiatkowska et al. (1997)
<i>Clematis</i>	Ogle et al. (2000)
Various grass species	D'Antonio et al. (1998)
<i>Lespedeza</i>	Brandon et al. (2004)
<i>Ligustrum</i>	Lavergne et al. (1999)
<i>Lonicera</i>	Gould and Gorchoy (2000), Gorchov and Trisel (2003)
<i>Myrica</i>	Walker and Vitousek (1991)
<i>Pueraria</i>	Forseth and Innis (2004)
<i>Rhamnus</i>	Fagan and Peart (2004)
<i>Sapium</i>	Siemann and Rogers (2003a)
<i>Sargassum</i>	Staehr et al. (2000)
Various tropical vines	Horvitz and Koop (2001)
Known	
<i>Acer</i>	Reinhart et al. (2006)
<i>Falcataria</i>	Hughes and Denslow (2005)
<i>Melinis</i>	Lenz and Facelli (2003)
<i>Mimosa</i>	Braithwaite et al. (1989)
<i>Pinus</i>	Leege and Murphy (2001)
<i>Tradescantia</i>	Standish et al. (2001)

whereas the abundance of conspecifics increased with increasing age of *A. platanoides* trees. Furthermore, reciprocal transplants demonstrated that the growth of *A. platanoides* seedlings is improved by overstory conspecifics, but seedlings of the two dominant, native canopy tree species are highly suppressed by the invader. Although the mechanism(s) for these changes is unknown, a striking difference that we have observed in riparian forests invaded by *A. platanoides* is the deep shade cast by its canopy (see Plate 1 and images in the Supplement).

Shading affects community composition in natural forests (Pagès et al. 2003), and anecdotal observations often attribute reductions in native species abundance/diversity in a range of plant communities to shading by nonnative species (Table 1). Here we provide the first experiment testing the effect of simulated light environments representing conditions in understories of a native forest and a forest heavily invaded by *A. platanoides* on seedlings of abundant native and nonnative species while controlling for other differences between invaded and uninvaded sites (e.g., nutrient availability, allelopathy, etc.). We tested the effect of light quantity and quality associated with invaded and uninvaded riparian forests on the survival, growth, and resource allocation of seedlings of resident species and *A. platanoides*.

METHODS AND MATERIALS

Study area

We described the canopy structure and understory light of neighboring riparian reaches of mixed deciduous

forest along a 3.4-km section of the lower drainage of the Rattlesnake Creek, Montana, USA. Since riparian vegetation can vary naturally because of many factors (geological substrate, hydrology, disturbance history, etc.; Foote 1965), we sampled along a short (3.4 km) and topographically homogeneous section of the creek in order to minimize potentially confounding site effects. Research was conducted in two reaches that differed substantially in the abundance of *Acer platanoides* (see Supplement). One reach was heavily invaded by *A. platanoides* (76% *A. platanoides* canopy coverage; 46°52.644' N, 113°58.565' W), and one had low levels of invasion (0%; 46°53.969' N, 113°58.345' W) (Reinhart et al. 2005). We refer to the reach with low levels of *A. platanoides* invasion (0%) as being "native."

Black cottonwood (*Populus trichocarpa* T. & G.), ponderosa pine (*Pinus ponderosa* Dougl.), and Rocky Mountain maple (*Acer glabrum* Torr.) trees dominated the original native riparian community in our study area (Foote 1965). *Acer platanoides* is a large tree relative to the native congener *Acer glabrum*, which is a small tree to shrub, often with clumped stems. Riparian reaches with currently low levels of *Acer platanoides* invasion have understories dominated by grasses, forbs, and shrubs (Foote 1965, Reinhart et al. 2005). The 15 species with greatest cover in the understory of these reaches are (starting with the most abundant): *Symphoricarpos albus*, *Acer platanoides*, *Cynoglossum officinale*, *Populus trichocarpa*, *Osmorhiza chilensis*, *Elymus glaucus*, *Ame-lanchier alnifolia*, *Sorbus aucuparia*, *Galium triflorum*, *Acer glabrum*, *Rosa nutkana*, *Prunus virginiana*, *Solanum dulcamara*, *Arctium lappa*, and *Equisetum hyemale* (Reinhart et al. 2005). Refer to Reinhart et al. (2005) for a more detailed description of the climate, soils, community composition of the reaches, etc.; and refer to Foote (1965) for a detailed description of the community composition prior to invasion by *Acer platanoides*.

Effect of *Acer platanoides* on canopy structure and understory light

We collected comparative data describing the canopy cover and understory light environments along a heavily invaded reach and native reach. We also compared the understory light environments between an invaded area (near *Populus trichocarpa* and *Acer platanoides*) and where *A. platanoides* had been selectively removed (near *P. trichocarpa* trees). For further details on this portion of the methodology refer to the Appendix.

Effect of light quantity and quality on seedlings

Because community composition in the understory of *Acer platanoides* is strikingly different than in native riparian forests (Reinhart et al. 2005), we compared in a greenhouse experiment the effect of light quantity and quality that we measured in the heavily invaded and native riparian reaches (Fig. 1, Table 2) on the survival, growth, and biomass allocation of native and nonnative species that occur in our study system. Six of the seven

FIG. 1. Light spectra in open patches, understories of native riparian forests, and understories of riparian forests invaded by *Acer platanoides*. Bars represent the maximum 95% CI for each curve. Vertical shaded bars represent the red (656–664 nm) and far-red (726–734 nm) portions of the spectrum. The visible portion of the spectrum is from 380 to 750 nm. Discussion of the methods is provided in the Appendix.

species used were among the 15 most abundant species in the understory of our study system and include: a native grass (*Elymus glaucus* Buckl.), native shrubs (*Amelanchier alnifolia* Nutt. and *Symphoricarpos albus* (L.) Blake), native trees (*Acer glabrum* and *Betula occidentalis* Hook.), and nonnative trees (*Acer platanoides* and *Sorbus aucuparia* L.).

The light quantity (photosynthetically active radiation, PAR) and light quality (ratio of red [656–664 nm of the electromagnetic spectrum] to far-red light [726–734 nm], R:Fr) associated with a heavily invaded (low PAR and low R:Fr) riparian reach and a native riparian reach (high PAR and high R:Fr) were determined (see Table 2 and the Appendix for a description of the methods). A 2 × 2 factorial design was used to simulate native and invaded conditions and test the effect of light quantity (low PAR, invaded condition; high PAR, native condition) and light quality (low R:Fr, invaded condition; high R:Fr, native condition) on seedling survival, growth, and allocation. To simulate the light quality that we measured in native and invaded forest understories (Table 2), we used green filters (Lee Filters, Burbank, California, USA). We used a Lee filter 88 to simulate R:Fr in the understory of a riparian forest invaded by *Acer platanoides* (R:Fr = 0.31 determined with spectroradiometer) and a Lee filter 122 to simulate light quality in the understory of a native riparian forest (R:Fr = 0.72).

Neutral light filters (Lee Filters) were used to reduce PAR to levels measured in the understories of native and invaded reaches (Table 2). Ideally, PAR would have remained exactly the same between R:Fr treatments; however, slight differences in the effects of the different R:Fr filters on PAR made this impossible. We made PAR differences between R:Fr treatments very closely comparable by combining neutral filters to produce

PAR levels for the invaded R:Fr treatments that were slightly higher (445 and 18 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and lower (412 and 10 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) than the levels of the native R:Fr treatments (PAR = 430 and 14 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $n = 8$ per treatment). Thus the mean PAR levels were comparable for R:Fr treatments within individual PAR treatments (i.e., 428.5 vs. 430 for the native PAR treatments and 14 vs. 14 for the invaded PAR treatments). Data for native R:Fr treatments were pooled in the invaded ($n = 16$) and native PAR treatments ($n = 16$).

Green and neutral filters were attached to the open top of a cardboard frame (61.00 × 45.75 cm [side facing north/south × side facing east/west]). The side to the south was 10 cm tall and the east/west sides sloped up from the south side at a 15° angle to maximize irradiance in the naturally lit greenhouse. We measured the PAR and temperature under each box to validate the treat-

TABLE 2. Canopy cover (leaf area index, LAI) and understory light quantity (photosynthetically active radiation, PAR, mean ± 95% CI) and quality (red:far-red, R:Fr) in open patches and in understories of a native riparian reach (0% *Acer platanoides* canopy coverage) and a reach heavily invaded by *Acer platanoides* (76% *Acer platanoides* canopy coverage).

Variables	LAI (m^2/m^2)	PAR ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	R:Fr
Full sun	0	~1800	1.74 ± 0.20
Native	1.88 ± 0.25	397.5 ± 93.22	0.64 ± 0.13
Invaded	4.21 ± 0.02	17.2 ± 7.67	0.27 ± 0.13

Notes: The data for the reach heavily invaded by *A. platanoides* appear in boldface type. Refer to the Appendix for a discussion of the methods corresponding with these data and other results substantiating the idea that *A. platanoides* invasion alters riparian forest structure and understory light quantity and quality.

TABLE 3. ANOVA results for the effect of light quantity (photosynthetically active radiation, PAR), light quality (red:far-red ratio, R:Fr), and interactions on the biomass, height, and root:mass ratio of seedlings of native shrub (*Amelanchier alnifolia* and *Symphoricarpos albus*) and tree species (*Acer glabrum*) and a nonnative tree species (*Acer platanoides*).

Species	PAR		R:Fr		PAR $\times$ R:Fr	
	F	P	F	P	F	P
<i>Acer platanoides</i> (df = 1, 42)						
Biomass (log[x])	54.07	<0.0005	0.27	0.61	0.84	0.37
Height	9.39	0.004	0.35	0.56	2.11	0.15
Root:mass ratio	11.68	0.001	5.46	0.02	10.18	0.003
<i>Acer glabrum</i> (df = 1, 39)						
Biomass ($\sin^{-1}\sqrt{[x]}$)	29.93	<0.0005	4.87	0.03	4.50	0.04
Height	7.07	0.01	3.34	0.08	3.58	0.06
Root:mass ratio	13.92	0.001	3.98	0.05	0.01	0.93
<i>Amelanchier alnifolia</i> (df = 1, 29)						
Biomass ($\sin^{-1}\sqrt{[x]}$)	18.82	<0.0005	1.02	0.32	1.05	0.32
Height	8.03	0.01	0.01	0.94	0.004	0.95
Root:mass ratio	5.71	0.02	2.36	0.14	1.40	0.25
<i>Symphoricarpos albus</i> (df = 1, 32)						
Biomass (log[x])	19.38	<0.005	2.00	0.17	1.74	0.20
Height (log[x])	41.29	<0.0005	0.15	0.71	0.002	0.96
Root:mass ratio	0.03	0.87	3.14	0.09	0.56	0.46

Note: Species followed by relevant transformation.

ments and identify any differences in temperature associated with the treatments. Tukey hsd post hoc analyses revealed no significant differences in temperature between treatments (data not shown).

All individuals of a species were collected as recently germinated seedlings from either the heavily invaded reach or a neighboring reach with intermediate levels of invasion (46°53.416' N, 113°58.254' W) in the spring of 2002. For a species, we collected individuals that were similar in size and then randomly assigned individuals to light treatments. Rocket pots (525 cm³) were filled with a 1:1 ratio of silica sand averaging 0.60–0.85 mm in diameter (20/30 grit; Lane Mountain, Valley City, Washington, USA) and potting soil (Hyponex; Scotts, Marysville, Ohio, USA). One seedling was planted in each pot, and pots were randomly arranged on racks in a naturally lit greenhouse (Dietert Gardens, University of Montana). After a two-week acclimation period, seedlings were randomly assigned to experimental light treatments ($n = 8$ for native R:Fr or 16 for invaded R:Fr treatments). Seedlings were watered once every 1–2 days and fertilized once at the beginning of the experiment with 4.5 mL/pot of Osmocote slow-release fertilizer (19-6-12 N-P-K, Scotts). Seedlings were grown for 85 days in the experimental light treatments and harvested on 25 September 2002. Seedling survival, biomass (i.e., root, shoot, and total biomass), and stem height were recorded. Survival data were compared for each species separately with a log-linear analysis designed to test the individual effect and interaction of PAR and R:Fr treatments using SAS version 8.0 (SAS Institute, Cary, North Carolina, USA). To maintain homogeneity of variances for these analyses, we transformed the biomass data (*Acer glabrum*, *Acer platanoides*, *Ame-*

lanchier alnifolia, and *Symphoricarpos albus*) and height data (*Symphoricarpos albus*) with either $\log_{10}[x]$ or $\sin^{-1}\sqrt{[x]}$ (see Table 3). Even after transformation, the biomass data continued to violate the homogeneity of variances assumption. Analysis of variance was still used, because it is robust to heterogeneity of variances (Underwood 2002). Species with no mortality in a treatment created “sampling zeros,” and the data for these species were transformed by adding a small constant ($X + 0.01$) (Agresti 2002). The biomass, height, and root:mass ratio (root mass $\div$ total biomass) data were analyzed for species that maintained relatively high survival across treatments (i.e., *Acer glabrum*, *Acer platanoides*, *Amelanchier alnifolia*, and *Symphoricarpos albus*) using a two-way ANOVA with PAR and R:Fr as fixed effects. We also tested for an effect of native (high PAR and high R:Fr) and nonnative conditions (low PAR and low R:Fr) on seedling survival with log-linear tests and on growth/allocation with t tests.

RESULTS

Effect of Acer platanoides on canopy structure and understory light

At the scale of entire reaches, native canopies dominated by *Populus trichocarpa* reduced total PAR to $\sim 400 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, or 20% of full sunlight (Fig. 1, Table 2). However, the riparian reach heavily invaded by *A. platanoides* had dramatically higher canopy cover and much lower light levels in the understory (Fig. 1). This reach had a mean PAR of $17 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, $<5\%$ that in the native riparian reach (Table 2). Leaf area index was 123% greater in the reach now dominated by *A. platanoides* than in a native riparian reach (Table 2).

FIG. 2. Effect of light quantity (photosynthetically active radiation, PAR) and quality (red:far-red ratio, R:Fr) on seedling survival. Seedling species include: *Acer glabrum*, *Acer platanoides*, *Amelanchier alnifolia*, *Betula occidentalis*, *Elymus glaucus*, *Sorbus aucuparia*, and *Symphoricarpos albus* ($n = 8$ seedlings for the low R:Fr treatment and 16 seedlings for the high R:Fr treatment). Different lowercase letters indicate a significant difference among the means ($P \leq 0.05$) in the native (high PAR and high R:Fr) and nonnative conditions (low PAR and low R:Fr) according to log-linear tests. Two-way log-linear results are reported in *Results*.

Not only did the heavily invaded reach have greater canopy cover and reduced energy flow (total PAR) to the understory, the R:Fr ratios were 58% lower than in the native riparian reach (Table 2). At the scale of individual trees, PAR under *A. platanoides* canopies ($40.02 \pm 15.53 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, mean $\pm$ SE) was 25% of that under *Populus trichocarpa* trees in areas where *A. platanoides* had been selectively removed ($163 \pm 67.74 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; t test, $t = -3.92$, $\text{df} = 34$, $P < 0.0005$).

Effect of light quantity and quality on seedlings

Across both R:Fr treatments, low PAR, comparable to that in invaded understories, decreased survival of the native maple *Acer glabrum* by 28%; *Amelanchier alnifolia* by 32%; *Betula occidentalis* by 55%; *Elymus glaucus* by 46%; and *Sorbus aucuparia* by 52% relative to seedlings growing in PAR similar to that of native understories (Fig. 2, log-linear analysis, *Acer glabrum*, χ^2

PLATE 1. Understory dominated by seedlings of *Acer platanoides* in a forest heavily invaded by this species. Photo credit: K. Reinhart.

$= 6.84$, $P = 0.009$; *Amelanchier alnifolia*, $\chi^2 = 6.88$, $P = 0.009$; *Betula occidentalis*, $\chi^2 = 6.31$, $P = 0.01$; *Elymus glaucus*, $\chi^2 = 6.89$, $P = 0.009$; *Sorbus aucuparia*, $\chi^2 = 6.85$, $P = 0.0088$; all $df = 1$). In contrast, *Acer platanoides* and the native shrub *Symphoricarpos albus* were not affected by reductions in PAR (decreased survival by 0% and 25%, respectively; Fig. 2, *Acer platanoides*, $\chi^2 = 0$, $P = 1.00$ and *Symphoricarpos albus*, $\chi^2 = 2.45$, $P = 0.12$; all $df = 1$).

The low PAR and low R:Fr levels associated with invaded forests relative to native riparian forest reduced the survival of most tested native and nonnative species common at our field sites, but it had no effect on *Acer platanoides* seedlings. When both light quantity and quality of invaded forests were mimicked (low PAR and low R:Fr) mortality of native species was much higher in invaded environments than native environments (high PAR and high R:Fr). *Acer glabrum* survival decreased by 38%, *Betula occidentalis* by 57%, *Elymus glaucus* by 57%, and *Sorbus aucuparia* seedlings by 53% (Fig. 2). Overall, *Acer platanoides* maintained the highest survival in invaded light conditions (87.5%, Fig. 2).

By itself, R:Fr had no effect on the seedling survival of most species (*Acer glabrum*, $\chi^2 = 0.07$, $P = 0.79$; *Acer platanoides*, $\chi^2 = 0.59$, $P = 0.44$; *Amelanchier alnifolia*, χ^2

$= 0.24$, $P = 0.63$; *Elymus glaucus*, $\chi^2 = 0.23$, $P = 0.63$; *Sorbus aucuparia*, $\chi^2 = 0.07$, $P = 0.79$; *Symphoricarpos albus*, $\chi^2 = 0.27$, $P = 0.60$; all $df = 1$). However, there was a marginally significant effect of R:Fr toward increasing the mortality of native *Betula occidentalis* seedlings ($\chi^2 = 3.20$, $P = 0.074$). There was no interaction in the effect of PAR and R:Fr on seedling survival (*Acer glabrum*, $\chi^2 = 0.07$, $P = 0.79$; *Acer platanoides*, $\chi^2 = 0.00$, $P = 1.00$; *Amelanchier alnifolia*, $\chi^2 = 0.23$, $P = 0.63$; *Elymus glaucus*, $\chi^2 = 0.23$, $P = 0.63$; *Sorbus aucuparia*, $\chi^2 = 0.07$, $P = 0.79$; *Symphoricarpos albus*, $\chi^2 = 0.27$, $P = 0.60$; all $df = 1$).

For the four species with the highest overall survival (*Acer glabrum*, *Acer platanoides*, *Amelanchier alnifolia*, and *Symphoricarpos albus*), reduction in light quantity mimicking *Acer platanoides* invasion reduced the height and biomass of all four tested species relative to seedlings grown in light quantities similar to those in native riparian areas (Fig. 3, Table 3). In contrast, R:Fr alone affected only *Acer glabrum*. There was no effect of R:Fr or PAR $\times$ R:Fr on the biomass of *Acer platanoides*, *Amelanchier alnifolia*, and *Symphoricarpos albus* or the height of the four tested species (Table 3). The biomass of *Acer glabrum* seedlings was 21% less in low R:Fr (conditions created by *Acer platanoides*) than high R:Fr

FIG. 3. Effect of light quantity (photosynthetically active radiation, PAR) and quality (red:far-red ratio, R:Fr) on the total biomass and height of *Acer glabrum*, *Acer platanoides*, *Amelanchier alnifolia*, and *Symphoricarpos albus* seedlings ($n = 5-8$ seedlings for the low R:Fr treatment and 9–16 seedlings for the high R:Fr treatment). Error bars represent $\pm$ SE, and different lowercase letters indicate a significant difference among the means ($P \leq 0.05$) in the native (high PAR and high R:Fr) and nonnative conditions (low PAR and low R:Fr) according to t tests. Two-way ANOVA results are reported in *Results*.

treatments (Table 3). *Acer glabrum* biomass was also $\geq 34\%$ greater in the treatment with high PAR and high R:Fr (light conditions under native canopies) relative to other treatments (Table 3). The height and biomass of all tested species were smaller when grown in the invaded (low PAR and low R:Fr) vs. native light environments (high PAR and high R:Fr) except for the height of *Amelanchier alnifolia*, which did not differ between simulated environments (Fig. 3).

Reductions in PAR elicited similar changes in the biomass allocation of native and *Acer platanoides* seedlings. However, the effect of R:Fr and the interactive effect of PAR and R:Fr on allocation were more complicated and often differed in unique ways between the invader and native species. Simulated *Acer platanoides*-driven reductions in PAR decreased the root:mass ratios of *A. platanoides* and two of three native species (*A. platanoides* by 22%, *Acer glabrum* by 28% and *Amelanchier alnifolia*

FIG. 4. Effect of light quantity (photosynthetically active radiation, PAR) and quality (red:far-red ratio, R:Fr) on the root:mass ratio (root mass divided by total biomass) of *Acer glabrum*, *Acer platanooides*, *Amelanchier alnifolia*, and *Symphoricarpos albus* seedlings. Error bars represent $\pm$ SE, and different lowercase letters indicate a significant difference among the means ($P \leq 0.05$) in the native (high PAR and high R:Fr) and nonnative conditions (low PAR and low R:Fr) according to t tests. Two-way ANOVA results are reported in *Results*.

seedlings by 19%) relative to seedlings in PAR levels similar to those found in native riparian forests (Fig. 4, Table 3). Thus, reductions in PAR triggered three of four species to allocate proportionally more resources to shoots than roots. The root:mass ratios of two native species were unresponsive to changes in R:Fr; however, experimental reductions in R:Fr increased the root:mass ratio of *Acer glabrum* seedlings by 18% (Table 3). In contrast, reductions in R:Fr decreased the root:mass ratio of *Acer platanooides* by 14% relative to seedlings in high R:Fr (Table 3).

There was an interactive effect of PAR and R:Fr on the biomass allocation of *Acer platanooides* (root:mass ratio) but not on native species (Fig. 4, Table 3). Furthermore, native species had similar root:mass ratios when grown in native (high PAR and high R:Fr) vs. invaded light environments (low PAR and low R:Fr; Fig. 4). In contrast, the invaded light environment caused a 38% reduction in the root:mass ratios of *A. platanooides* seedlings relative to plants grown in conditions similar to those in native riparian areas. Overall, *A. platanooides* was the only species tested to proportionally increase allocation to shoots in response to the combined reductions in PAR and R:Fr characteristic of *A. platanooides*-invaded forests.

DISCUSSION

Many nonnative species decrease the richness and alter the composition of the communities they invade (Selleck et al. 1962, Ridenour and Callaway 2001, Siemann and Rogers 2003b, Reinhart et al. 2005; refer to Levine et al. [2003] for 33 additional citations). In a review, Levine et al. (2003) reported that only 5% of studies explored the mechanisms causing these impacts. We observed profound changes in light quantity and quality associated with *Acer platanooides* invasion ($<5\%$ PAR in a native riparian area; Fig. 1, Table 2, and Supplement) and found that the reductions in light quantity appear to drive native suppression and *A. platanooides* success in invaded riparian communities in western Montana, USA. Our results indicate that *A. platanooides* simply creates a degree of shade atypical of the uninvaded riparian forests and support the idea that quantitative changes elicited by invasive species can lead to overwhelming dominance by the invader and strong inhibition of natives. Shade is not qualitatively novel. Shade affects most if not all ecological systems. However, the quantitative effects of *A. platanooides*, in a system relatively depauperate of shade-tolerant native woody species (Hansen et al. 1995), creates conditions that suppress other species and that favor its own offspring (Reinhart et al. 2005). Historically, distur-

bance in the form of flooding and fire played an important role in affecting the structure and composition of this riparian system. The recent alteration of these natural disturbance regimes (e.g., stream flow at study sites regulated by a dam established in 1905) has probably played an important role in facilitating the invasion of *A. platanoides* and the development of a system structurally and functionally similar to a late-successional deciduous forest. Reinstating either of these disturbance regimes may help favor native vs. nonnative species.

Changes in light quantity (PAR) regulate shade tolerance adaptations (Smith 1982, Lambers et al. 2000), while changes in R:Fr are thought to induce shade avoidance phenotypes (e.g., Morgan and Smith 1979, Gilbert et al. 2001). Although simulated *A. platanoides*-driven reductions in PAR had a negative effect on the growth of all species including *A. platanoides*, *A. platanoides* responded to changes in PAR and R:Fr by allocating resources in a novel and adaptive way relative to resident species. For example, low root:shoot ratios are a common developmental response to shading (e.g., Chapin 1980, Givnish 1988, Lei and Lechowicz 1998). As predicted by optimal partitioning theory (Chapin 1980), low PAR, mimicking that under *A. platanoides*, resulted in lower root:mass ratios for three of four species including *A. platanoides*. However, increases in overstory canopy cover in nature are generally associated with reductions in PAR and R:Fr (e.g., Frankland and Poo 1980). In our study, examining PAR alone provides an inflated estimate of the adaptive responses of native species to invasive light conditions. When comparing species responses to light quantity and quality together, *A. platanoides* was the only species tested that decreased allocation to roots relative to shoots in invaded conditions and therefore was the only species to demonstrate an adaptive response to the combined qualitative and quantitative light conditions associated with *A. platanoides* invasion. Thus, the relatively high survival of *A. platanoides* in invaded light environments (low PAR, low R:Fr) relative to native species appears to result from the invader's tolerance to deep shade produced by itself (i.e., low PAR and R:Fr). The shade tolerance of *A. platanoides* seedlings and saplings results in part from their ability to shift biomass allocation in varying light environments in a way that is consistent with optimal partitioning theory, deviates from natives, and includes altering root:mass ratios and increasing leaf area with stem height more rapidly than natives do in deep shade (see Appendix).

Reproductive strategies may play an important role in forest succession (Forcier 1975). Our study focused on the affect of altered light regimes on the early stages of seedling development. Resident species that can reproduce clonally (e.g., *Symphoricarpos albus*) may be more capable of persisting in deep shade. This may help explain why *Symphoricarpos albus* is the second

most abundant native species in the understory at the reach heavily invaded by *A. platanoides* (Reinhart et al. 2005). However, seedlings of this species appear relatively tolerant to shade (Fig. 2). Additional comparative experiments at the later stage of plant growth are necessary to determine whether resident native species continue to decline at low levels of light quantity.

We describe an effect of an invader on a resource that corresponds in part with Tilman's (1982) R^* theory for resource competition. If all species are limited by the same resource, then one species may displace its competitors if it has an R^* (resource level associated with that species grown in monoculture) that is lower than that of the other species. In riparian forests, trees of *A. platanoides* appear to draw resources in the understory down to a level that only its own seedlings can tolerate, essentially a positive feedback, which maintains "oskars" (a plant in a suppressed juvenile state in the understory of a forest; Silvertown 1987) ready to exploit forest gaps (Wyckoff and Webb 1996, Martin 1999, Reinhart et al. 2005).

Acer platanoides success in riparian communities of the northern Rocky Mountains may be enhanced by its effect on the light regime; however, it is unlikely that this same mechanism is the driver of *A. platanoides* invasion of forests in the northeastern United States. In these forests, other native canopy species (e.g., *Acer saccharum* and *Fagus grandifolia*) are functionally and structurally similar and decrease light to roughly similar levels as *A. platanoides* (K. O. Reinhart, *personal observation*), and many native species are as tolerant to shade as *A. platanoides* (Canham et al. 1994, Lei and Lechowicz 1998). In contrast, some researchers have argued that *A. platanoides* produces greater shade than native tree species in eastern deciduous forests in the United States (Wyckoff and Webb 1996, Bertin et al. 2005). Moreover, removal of *A. platanoides* trees in a northeastern forest was associated with increased recruitment of native species (Webb et al. 2001). Comparative experiments like the one performed here are necessary to determine whether shade production and tolerance explain the invasive success of *A. platanoides* in deciduous forests of the northeastern United States or whether the invasive success of *A. platanoides* depends on different mechanisms in different plant communities.

Other studies have suggested that some invasive nonnative species reduce light to levels that can suppress native species (Table 1) but few studies have tested this experimentally (Gorchov and Trisel 2003). We cannot say how important this mechanism is relative to other mechanisms, but accurate prediction of the impacts of nonnative species is an important goal of invasion biology and depends on understanding the manner in which nonnative species alter ecosystems and suppress natives.

ACKNOWLEDGMENTS

This research benefited from the helpful comments by two anonymous reviewers. We thank Bruce Mahall, Anna Sala, Carol Brewer, Tom Mitchell-Olds, John Maron, and John McKay for letting us borrow research equipment and facilities. We also thank Adam Collins, Julie Reinhart, and Giles Thelen for their tireless assistance in the field and laboratory. This research was funded in part by a Project IBS-CORE Undergraduate Research Fellowship awarded to J. Gurnee, provided by a grant from the Howard Hughes Medical Institute to the University of Montana, an FPI fellowship provided by the Spanish Minister of Education and Science awarded to R. Tirado, funding from the USDA to K. O. Reinhart (NRI 2003-02047) and funding from the National Science Foundation, the USDA, The Aldo Leopold Wilderness Center, and the Civilian Research and Development Foundation to R. M. Callaway.

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APPENDIX

Further details of methods used for measuring the effect of *Acer platanoides* on canopy structure and understory light and a table showing allometry of shrubs and saplings naturally occurring in shaded understories (*Ecological Archives* A016-060-A1).

SUPPLEMENT

Multirow spherical panoramas in QuickTime Virtual Reality (QTVR) format for depicting native riparian vegetation and riparian vegetation heavily invaded by *Acer platanoides* occurring adjacent to Rattlesnake Creek, Missoula, Montana, USA, in 2005 (*Ecological Archives* A016-060-S1).