

Interactions between two co-dominant, invasive plants in the understory of a temperate deciduous forest

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Abstract

Negative interactions between non-indigenous and native species has been an important research topic of invasion biology. However, interactions between two or more invasive species may be as important in understanding biological invasions, but they have rarely been studied. In this paper, we describe three field experiments that investigated interactions between two non-indigenous plant species invasive in the eastern United States, *Lonicera japonica* (a perennial vine) and *Microstegium vimineum* (an annual grass). A press removal experiment conducted within a deciduous forest understory community indicated that *M. vimineum* was a superior competitor to *L. japonica*. We tested the hypothesis that the competitive success of *M. vimineum* was because it overgrew, and reduced light available to, *L. japonica*, by conducting a separate light gradient experiment within the same community. Shade cloth that simulated the *M. vimineum* canopy reduced the performance of *L. japonica*. In a third complementary experiment, we added experimental support hosts to test the hypothesis that the competitive ability of *L. japonica* is limited by support hosts, onto which *L. japonica* climbs to access light. We found that the abundance of climbing branches increased with the number of support hosts. Results of this experiment indicate that these two invasive species compete asymmetrically for resources, particularly light.

Abbreviations: ANOVA – Analysis of Variance; GLM – General Linear Model; MANOVAR – Multivariate Analysis of Variance with Repeated Measures; ORNERP – Oak Ridge Environmental Research Park; PPF – photosynthetic photon flux density; RCI – Relative Competition Index; TDR – time domain reflectometry; VWC – volumetric water content

Introduction

Interspecific interactions including competition, interference, and facilitation are important determinants of composition, distribution, and abundance of species within natural communities (Goldberg and Barton 1992; Callaway 1995; Keddy 2001). Mechanisms determining the nature of interspecific

interactions and how those interactions affect community structure are dependent on life history strategy, phenology, physiology, and morphology of potentially interacting species (Tilman 1987). Moreover, interactions between species change along biotic (e.g., presence of herbivores) and abiotic (e.g., resource availability) environmental gradients (Huston 1979; Wilson and Tilman

1991). The effect that resource availability has on species interactions, and how those interactions affect the structure and function of communities and ecosystems, has been a major topic of ecology (Darwin 1859; Clements et al. 1929; MacArthur and Wilson 1967; Tilman 1982; Keddy 2001).

Over the last several decades, ecologists have become increasingly interested in how invasions by non-indigenous organisms affect ecosystems (Elton 1958; Mack et al. 2000). Invasive species are considered one of the greatest threats to global biological diversity, second only to habitat destruction (Vitousek et al. 1997). Disturbance and resource availability may be the ultimate determinant of invasive plant establishment and success within ecosystems (Sher and Hyatt 1999; Davis et al. 2000) and invading species may possess novel traits, such as the ability to fix nitrogen, that allow them to use resources more efficiently than native species (Shea and Chesson 2002). In forests of eastern North America, non-indigenous species that invade understories are likely successful because they are shade-tolerant or respond positively to disturbance regimes that increase light availability (Luken 2003).

Asymmetric competition between non-indigenous and native species may also be an important factor determining invasions (Callaway and Aschehoug 2000; Call and Nilsen 2005) and their impact on native communities (Parker et al. 1999). In addition, positive interactions among two or more non-indigenous species may be an important determinant of the success and impact of invasive species (Elton 1958). Specifically, non-indigenous plants may facilitate other invasions (Simberloff and Von Holle 1999) by altering abiotic factors of ecosystems, such as fire regimes (Mack and D'Antonio 1998), water availability (Sala et al. 1996), or nitrogen cycling (Vitousek and Walker 1989). Alternatively, negative interactions between two or more non-indigenous species may limit the performance or spread of less competitive non-indigenous species, however, few studies have investigated such interactions (Simberloff and Von Holle 1999).

In this paper, we describe three experiments investigating interactions between two dissimilar co-occurring invasive species, *Lonicera japonica* Thunb. (Japanese honeysuckle), an invasive liana, and *Microstegium vimineum* (Trin.) A. Camus

(Japanese stiltgrass), an invasive annual grass, in a deciduous forest understory community. A native of east Asia, *Lonicera japonica* was intentionally introduced to the United States in 1862 and since its arrival has spread throughout most of the eastern US (Leatherman 1955; Spyreas et al. 2004). *L. japonica* competes with native species for both aboveground (Bruner 1967) and belowground resources (Whigham 1984) and can overtop small trees and shrubs impacting early successional and forest understory communities (Dillenburg et al. 1993). Also from Asia, *Microstegium vimineum* is an invasive annual grass and has invaded similar habitats throughout the eastern United States, often forming monocultures in understories of eastern forests (Barden 1987; Hunt and Zaremba 1992; Robertson et al. 1994; Redman 1995, Cole and Weltzin 2004). While few studies have documented its impact on native species, anecdotal and experimental evidence suggests that *M. vimineum* outcompetes native understory species (Fairbrothers and Gray 1972; Barden 1987) and may alter soil horizons (Kourtev et al. 1998) and nitrogen cycling (Ehrenfield et al. 2001).

L. japonica and *M. vimineum* are both considered by land managers and conservationists as serious threats to native plant communities and have been placed as high priorities for eradication and monitoring (Bowen et al. 2002). Both species are relatively shade tolerant (Carter and Teramura 1988; Horton and Neufeld 1998), share a similar range at regional and national scales (Bowen et al. 2002, Drake et al. 2003, USDA 2004), and can co-dominate forest understory communities. For example, *M. vimineum* and *L. japonica* comprised over 85% of the total production within a forest understory community located at the Oak Ridge National Environmental Research Park (ORNERP), Oak Ridge, Tennessee (Belote et al. 2004). *M. vimineum* and *L. japonica* are likely to determine community structure and diversity in the understories invaded by these species.

To investigate potential interactions, and to elucidate mechanisms determining interactions between *L. japonica* and *M. vimineum*, we established three separate experiments in 2001 and 2002 on the ORNERP. First, we conducted an *in situ* "press" removal experiment (Bender et al. 1984; Inouye 2001) in 2001 and 2002 to

investigate the interactions between *L. japonica* and *M. vimineum*. Within the plots of the removal experiment, we tested how soil water availability may effect competition between the two species by adding supplemental water to half of the plots and calculating relative competition indices. Data from the first growing season of the removal experiment suggested that *M. vimineum* interfered with *L. japonica* by overtopping it, regardless of soil moisture. *M. vimineum* can grow 40 cm tall with densities of up to 4000 individuals per m² during the peak of the growing season at this site (Belote 2003) and elsewhere on the ORNERP (Cole 2003). We hypothesized that *M. vimineum* was the superior competitor by reducing light to *L. japonica*, and established a separate light gradient experiment in 2002 to test this hypothesis. However, the invasiveness of *L. japonica* has been attributed to its climbing behavior (Larson 1999), which was limited by the design of the first two experiments (i.e., we removed woody tree seedlings and shrubs that could serve as support hosts to *L. japonica*). Therefore, in a third experiment in 2002 we added support hosts to *in situ* mixtures of *L. japonica* and *M. vimineum* to investigate the importance of the climbing growth strategy of *L. japonica* to its interactions with *M. vimineum*. We predicted that the addition of support hosts would increase the abundance of *L. japonica*.

This is one of the only mechanistic studies investigating interactions between two non-indigenous, invasive plants (Simberloff and Von Holle 1999). Throughout the paper we refer to non-indigenous species as those that have been introduced by human activities to a new region or continent. We reserve the term “invasive” or “invader” to describe those non-indigenous species that can dominate native communities and are of special conservation or management concern (Davis and Thompson 2000; 2001).

Materials and methods

Study site

Research was conducted in the understory of a sweetgum (*Liquidambar styraciflua* L.) plantation

established in 1988 on an old terrace of the Clinch River (elevation 230 m asl) at the Oak Ridge National Environmental Research Park, Oak Ridge, Tennessee (35°54' N; 84°20' W). The *L. styraciflua* trees are approximately 17 m tall, with a closed canopy that reduces the light in the understory by 70–95% during the growing season (Norby et al. 2002; Belote et al. 2004). The soil has a silty clay loam texture, is moderately well drained, and is slightly acidic (water pH approximately 5.5–6.0) (SCS 1967, van Miegroet et al. 1994). Precipitation is evenly distributed throughout the year with an annual mean of 1322 mm; mean annual temperature is 13.9 °C.

The understory plant cover is continuous and co-dominated by *L. japonica* and *M. vimineum*. On an average, *L. japonica* and *M. vimineum* account for approximately 50% and 40% understory biomass, respectively (Belote 2003), and together they contribute 88% to the total understory production (Belote et al. 2004). Other common understory taxa at the site include small clumps or scattered individuals of *Rubus* spp. L., *Solidago canadensis* L., and seedlings of *Acer negundo* L. Additional information about the climate and vegetation at the site are in Belote et al. (2004) and Norby et al. (2002).

Removal experiment

To investigate the interactions between *L. japonica* and *M. vimineum*, we initiated a 2-year removal experiment. In April 2001, we established 24 1-m² plots within the *L. styraciflua* understory, of which, the center 50 cm × 50 cm was used in all plant and environmental measurements to provide a 25 cm buffer from the surrounding community. We randomly assigned one of three vegetation treatments, and one of two watering treatments, to each plot. Vegetation treatments were established from the *in situ* plant community and included (1) monocultures of *L. japonica*, (2) monocultures of *M. vimineum*, and (3) mixtures of *L. japonica* and *M. vimineum*. Monocultures of *L. japonica* were established by pulling or clipping shoots of *M. vimineum* and all other taxa by hand. Monocultures of *M. vimineum* were established by removing *L. japonica* with a careful spot application of herbicide and some hand weeding in April. Mixture vegetation

treatments were established by removing all plant species other than *L. japonica* and *M. vimineum*, which were few, from each plot with spot applications of herbicide or by hand weeding. In the mixture plots, we carefully disturbed the soil with our hands to mimic the soil disturbance caused by vegetation removal in the monoculture plots. Plant species composition in all three vegetation treatments was maintained throughout the experiment by hand weeding as necessary.

Each vegetation treatment was randomly assigned one of two watering treatments that consisted of (1) ambient precipitation (=ambient) and (2) a weekly addition of water equivalent to a 27 mm precipitation event (=wet) between late April and mid-September (i.e., the growing season) in 2001 and 2002. Vegetation and watering treatment combinations were replicated four times in a fully crossed factorial design (3 vegetation treatments \times 2 watering treatments \times 4 replicates, $N=24$ plots).

Cover (%) of *L. japonica* and *M. vimineum* was visually estimated within each plot based on a modified Daubenmire cover class (Mueller-Dombois and Ellenberg 1974); we estimated cover prior to treatment initiation in April 2001 and again in June and September of 2001, and in May, June, and August of 2002. On each sample date, we also determined mean height of the *M. vimineum* canopy with a ruler at two random locations within each plot. At experiment termination in September 2002, we determined aboveground biomass (g/m^2) of both species by clipping them at ground level, drying them at 60 °C to constant mass, and weighing the samples.

Volumetric water content (VWC; %) in the top 15 cm of soil was recorded biweekly 4–6 days after watering events in all plots during the growing season with permanently placed time domain reflectometry (TDR) rods (Soil Moisture Equipment Corp., Santa Barbara, CA, USA). We measured photosynthetic photon flux density (PPFD; $\text{mol m}^{-2} \text{s}^{-1}$) 0.5 m above each plot at midday on clear days, thrice during each of the 2001 and 2002 growing seasons using a handheld line integrating ceptometer (AccuPAR, Decagon Devices, Inc., Pullman, WA, USA).

Light gradient experiment

We tested the effect that light reduction by *M. vimineum* might have on *L. japonica* cover and production by establishing a separate light gradient experiment adjacent to the competition experiment. We measured PPFD above and below the canopy of *M. vimineum* at random locations in the understory thrice during the 2001 growing season, and determined that *M. vimineum* reduced PPFD between 80% and 90%. Therefore in May 2002, we established 12 1-m^2 plots of *L. japonica* monoculture, and assigned each plot at random to one of three shade treatments created with shade cloth. First, monocultures of *L. japonica* were established and maintained as in the removal experiment. Commercially available shade cloth of different densities was erected 0.3 m above the top of the vegetation canopy within each plot to establish light treatments of (1) ambient understory PPFD (=non-shaded), (2) 40% of ambient PPFD (=medium), and (3) 2% of ambient PPFD (=dark). Plots with artificial shade were covered with $1.5\text{-m} \times 1.5\text{-m}$ squares of shade cloth to include a 0.25-m buffer around each plot. We clipped vegetation along the $1.5\text{ m} \times 1.5\text{ m}$ perimeter of each plot to prevent prostrate shoots of *L. japonica* from entering the plots. Light reduction treatments were verified to be accurately shading plots by determining PPFD above and below the shade cloth three times during the growing season.

We estimated cover of *L. japonica* at experiment initiation (May 2002) and again in June and July 2002 using the same technique as for the competition experiment. At experiment termination in August 2002, aboveground biomass of *L. japonica* was determined by clipping at ground level, drying at 60 °C to constant mass, and weighing. We determined VWC thrice during the growing season with a handheld TDR probe (Hydrosense; Decagon Devices, Inc., Pullman, WA, USA). Similar to the competition experiment, all vegetation and environmental data were recorded within the central $50\text{ cm} \times 50\text{ cm}$ area of each plot.

Support host experiment

In the absence of support hosts, *L. japonica* has a prostrate growth form and is unable to climb vertically (Larson 1999), which may limit its ability to acquire light when grown with *M. vimineum*. To test this hypothesis, we established an experiment in May 2001 wherein we added 1 mm diameter, 0.5 m tall wire stakes as experimental support hosts in mixtures of *L. japonica* and *M. vimineum*, which were established *in situ* by pulling all other species as in the removal experiment. Three densities of evenly placed support hosts were assigned at random to a total of 12 1 m² plots: (1) high density (81 hosts/m²), (2) medium density (16 hosts/m²), and (3) hosts absent (0 hosts/m²) ($n=4$). We determined vertical climbing behavior of *L. japonica* twice during the growing season (June and August) by counting the number of support hosts onto which *L. japonica* had twined. Aboveground biomass of each species was harvested within the central 50 cm × 50 cm area of each plot at experiment termination in August 2001, dried at 65 °C to constant mass, and weighed.

Statistical analysis

Removal experiment

We analyzed cover of *L. japonica*, and cover and height of *M. vimineum*, separately for main and interactive fixed effects of vegetation and watering treatments by year with a two-way analysis of variance with sampling date as the repeated measure (ANOVAR; procedure GLM; SAS Institute 1999). Biomass of *L. japonica* and *M. vimineum* were analyzed for main and interactive fixed effects of vegetation and watering treatments with a two-way analysis of variance (ANOVA; procedure GLM; SAS Institute 1999). VWC was analyzed by year for main and interactive effects of vegetation and watering treatments using a repeated measures multivariate ANOVA (MANOVAR; Pillai's Trace in SAS procedure GLM; SAS Institute 1999). Because *L. japonica* is evergreen and can grow during winter months, we used a paired *t*-test (procedure TTEST; SAS Institute 1999) to determine whether cover of *L. japonica* increased between

the September 2001 and May 2002 sampling dates.

We calculated relative competition indices (RCI) (Gurevitch et al. 2002) based on aboveground biomass of both species within each watering treatment to determine whether competition intensity differed between species and with water availability. RCI of each observation (*i*) was calculated as:

$$RCI_i = (B_{i\text{ monoculture}} - B_{\mu\text{ mixture}}) / B_{i\text{ monoculture}}$$

where $B_{i\text{ monoculture}}$ is the aboveground biomass of either *L. japonica* or *M. vimineum* grown in monoculture, and $B_{\mu\text{ mixture}}$ is the mean biomass of each species grown in mixture. Positive RCI values indicate detrimental effects by competing species on the species of interest when grown in mixture (i.e., a given species has greater biomass when grown in monoculture than in mixture). For example, an RCI value of 0.70 is interpreted as a 70% reduction in biomass of species *i* when grown in mixture relative to monoculture. In contrast, negative RCI values indicate facilitation or commensalism, where a given species has greater biomass when grown in mixture than in monoculture. We analyzed RCI for main and interactive effects of vegetation and watering treatment using a two-way ANOVA (procedure GLM; SAS Institute 1999).

Light gradient and support host experiments

Cover of *L. japonica*, and PPF and VWC data collected from the light gradient experiment were analyzed for each sampling date using a one-way ANOVA model (procedure GLM; SAS Institute 1999) to test for fixed effects of shade treatment. Similarly, we used a one-way ANOVA to analyze biomass of *L. japonica* at experiment termination.

We used a one-way ANOVA to analyze the number of support hosts used by *L. japonica*. Biomass of *L. japonica* and *M. vimineum* collected from the support host experiment were analyzed using separate one-way ANOVA models (procedure GLM; SAS Institute 1999) to test for fixed effects of density of support hosts.

Data from each of the three experiments were tested for normality and homogeneity of variance with the Shapiro–Wilk *W*-Statistic and Levene's test, respectively (Levene 1960; Shapiro and Wilk

1965); data that did not meet these assumptions were either log-transformed or arcsine-square root transformed before analysis as appropriate. Because cover values were converted to the midpoint of each class, they did not meet assumptions of normality and were rank-transformed before analysis (Zar 1999). The low number of replicates resulted in low statistical power, so we adopted a critical alpha level of 0.10.

Results

Competition experiment

Cover and biomass

Because there was a complex time \times vegetation \times water interaction affecting cover of *M. vimineum* in 2001 ($P=0.03$) but not in 2002 ($P=0.50$), we re-analyzed the cover data for main and interactive fixed effects of vegetation and watering treatments with a two-way model by sampling date for *M. vimineum*. No time \times vegetation \times water interaction for cover of *L. japonica* was observed for either year ($P \geq 0.12$), but we re-analyzed the cover data of *L. japonica* for main and interactive fixed effects of vegetation and watering treatment by date to compare both species' responses similarly. Predictably, cover of *L. japonica* and cover of *M. vimineum* did not differ between vegetation treatments prior to removal treatment initiation in April 2001

(Table 1, Figure 1). On all subsequent dates following press removal treatments, cover of *L. japonica* was greater in monoculture plots (without *M. vimineum*) than in mixture plots (with *M. vimineum*). However, on all but one sampling date, cover of *L. japonica* within vegetation treatment also depended on watering treatment (vegetation \times water interaction, Table 1). Specifically, cover of *L. japonica* in monoculture plots was greater in wet than ambient plots on three sampling dates, and cover of *L. japonica* in mixture plots was lower in wet than ambient plots on two sampling dates (Figure 1). Cover of *L. japonica* in mixture plots was greater in May 2002 than September 2001 (paired *t*-test; $P \leq 0.05$), but cover of *L. japonica* in the monoculture plots did not differ in this manner ($P \geq 0.18$).

Cover of *M. vimineum* differed little between vegetation treatments and watering treatments (Table 1, Figure 2). In June 2002, cover of *M. vimineum* in monoculture plots was less in wet than ambient treatments (Figure 2). Height of *M. vimineum* did not differ ($P \geq 0.53$) between treatments on any date (data not shown).

Biomass of *L. japonica* at experiment termination was 3 times greater in monoculture than when grown in mixture with *M. vimineum* ($P < 0.0001$), but did not differ between watering treatments ($P=0.72$, Figure 3; vegetation \times water interaction, $P=0.17$). Biomass of *M. vimineum* was 47% greater in monoculture than in mixture ($P=0.01$), and was 35% greater in wet than

Table 1. ANOVA *P*-values for main and interactive effects of vegetation treatments (monoculture vs. mixture) and watering treatments (ambient vs. wet) on cover (%) of *L. japonica* and *M. vimineum* in 2001 and 2002.

Species	Year	Source			
		Date	Vegetation	Water	Vegetation \times water
<i>L. japonica</i>	2001	April	0.81	0.84	0.27
		June	< 0.0001	0.56	0.05
		Sept.	< 0.0001	0.88	0.003
	2002	May	0.01	0.44	0.01
		June	< 0.0001	0.67	0.15
		Aug.	< 0.0001	0.52	0.04
<i>M. vimineum</i>	2001	April	0.29	0.45	0.36
		June	0.006	0.09	0.01
		Sept.	0.18	0.99	0.99
	2002	May	0.25	0.41	0.41
		June	0.57	0.57	0.57
		Aug.	0.29	0.05	0.99

Means are in Figures 1 and 2.

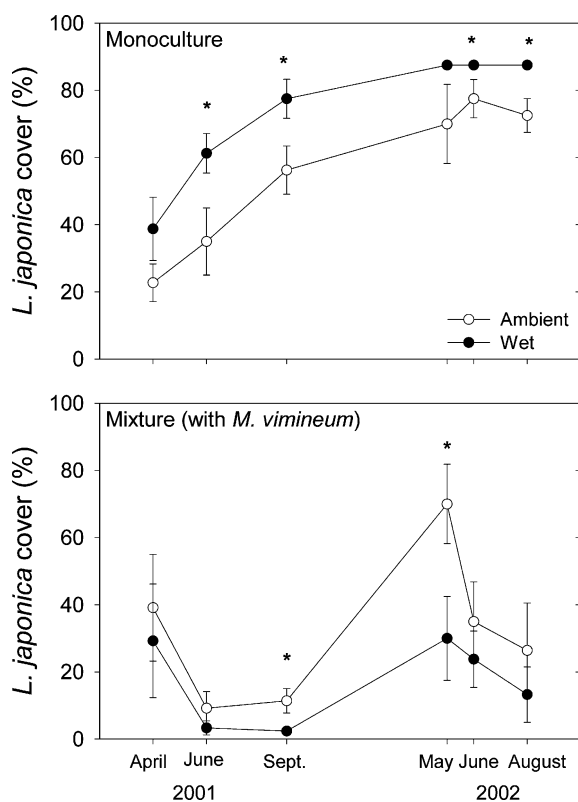


Figure 1. Cover of *L. japonica* (% \pm SE) in monoculture (top) and in mixture with *M. vimineum* (bottom) in two watering treatments at three sampling dates each in 2001 and 2002 (see Table 1). April 2001 data were recorded just prior to treatment initiation. For each date, asterisks indicate that means within vegetation treatment differed ($P < 0.05$) between water treatment; solid lines are included to emphasize intra- and inter-annual trends in evergreen *L. japonica*.

ambient precipitation plots ($P=0.03$, Figure 3; vegetation \times water interaction $P=0.83$).

RCI

RCI of *L. japonica* was greater than RCI of *M. vimineum* depending on watering treatment (water \times vegetation interaction, $P=0.01$). RCI of *L. japonica* was greater in wet mixture plots (0.74) than ambient mixture plots (0.53) ($P=0.01$). RCI of *M. vimineum* was greater in ambient mixture plots (0.38) than wet mixture plots (0.25) ($P=0.08$).

Soil moisture and PPFD

Soil VWC depended on watering treatment and time of year (water treatment \times time, $P \leq 0.0001$). On 9 of 10 dates in 2001, and all 7 dates

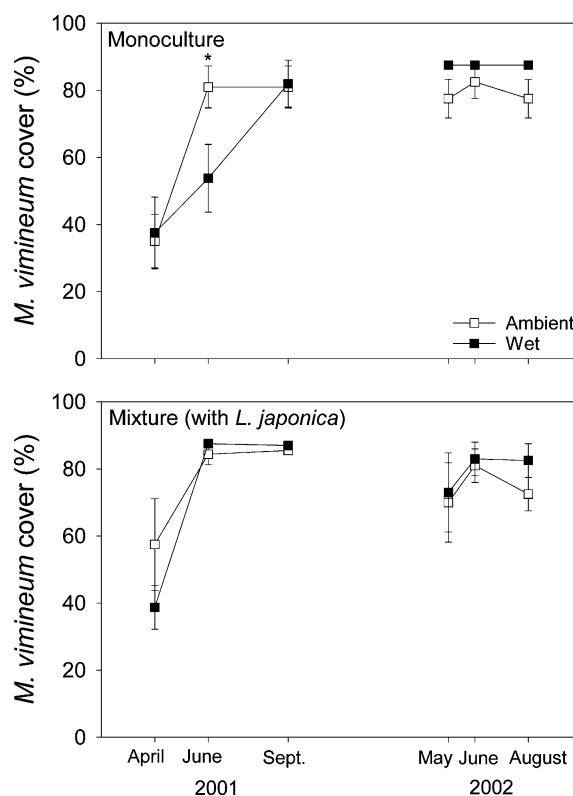


Figure 2. Cover of *M. vimineum* (% \pm SE) in monoculture (top) and in mixture with *L. japonica* (bottom) in two watering treatments at three sampling dates each in 2001 and 2002. April 2001 data were recorded just prior to treatment initiation. For each date, asterisks indicate that means within vegetation treatment differed ($P < 0.05$) between water treatment; solid lines are included to emphasize intra-annual trends.

in 2002, soil VWC after treatment initiation was greater in wet plots than ambient plots (Figure 4). In 2001, VWC peaked in May and August (time, $P=0.0001$), whereas in 2002 VWC peaked in May and declined throughout the growing season. PPFD did not differ ($P=0.49$) between treatments on any sampling date (data not shown).

Light gradient experiment

Cover of *L. japonica* did not differ between plots at the time the shade treatment was established in May 2002 (Figure 5). By June, cover of *L. japonica* was greater in non-shaded plots than plots that received the darkest treatment. By late July, *L. japonica* in the dark plots had lost most of its leaves, and cover of *L. japonica* in those plots was

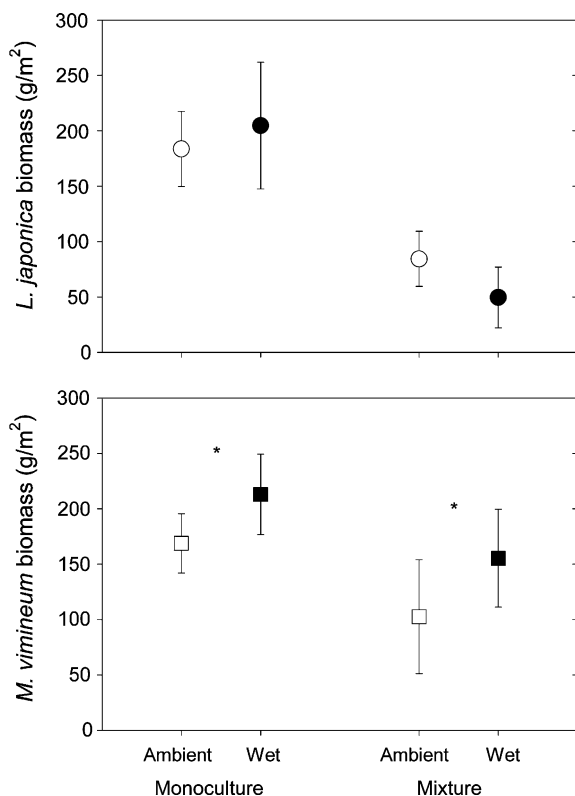


Figure 3. Biomass ($\text{g m}^{-2} \pm \text{SE}$) of *L. japonica* (top) and *M. vimineum* (bottom) within ambient and wet watering treatments in monoculture plots and in mixture plots. Within vegetation treatments, means that differed ($P < 0.05$) between water treatment are marked with an asterisk.

less than the medium and non-shaded plots; similarly, cover of *L. japonica* in plots with medium shade was lower than in plots with no shade. At experiment termination, aboveground biomass of *L. japonica* was lower ($P \leq 0.09$) in the dark shade treatment ($66 \pm 8 \text{ g/m}^2$) than the medium ($111 \pm 16 \text{ g/m}^2$) or non-shaded ($113 \pm 26 \text{ g/m}^2$) treatments, which did not differ ($P = 0.93$).

PPFD differed between treatments depending on date (Table 2). In May and June 2002, PPFD was greater in non-shaded plots than shaded plots, but did not differ between the medium and dark plots. In July, PPFD in the non-shaded plots did not differ from the medium shade plots, but they both had greater PPFD than the dark plots. Soil VWC did not differ between shade treatments on any date in 2002, i.e., May ($36\% \pm 1\%$; $P = 0.24$), June ($38\% \pm 1\%$; $P = 0.76$), or July ($28\% \pm 1\%$; $P = 0.65$).

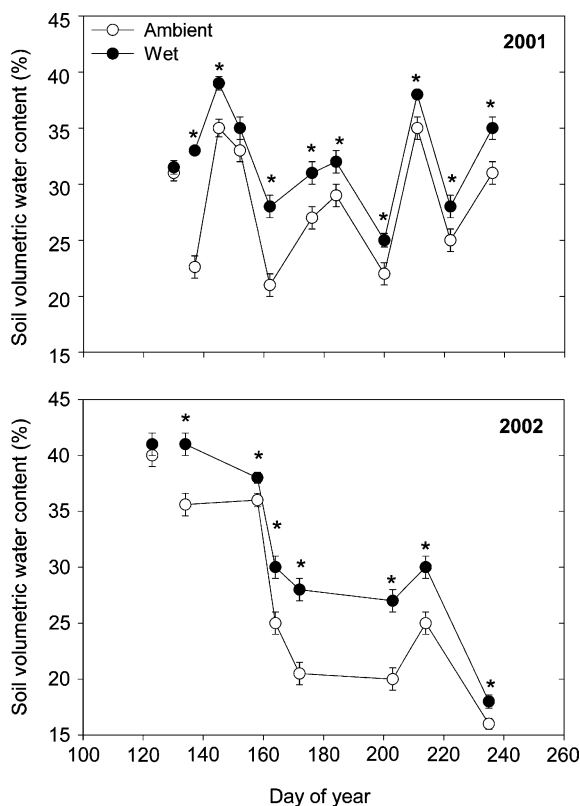


Figure 4. Soil volumetric water content (VWC; $\% \pm \text{SE}$) in ambient treatment (open circles) and wet treatment (closed circles) plots throughout the summer growing season in 2001 (top) and 2002 (bottom). The first sample date of each year was before initiation of weekly water additions; solid lines are included to emphasize intra-annual trends. Dates where VWC differed ($P < 0.05$) between watering treatments are indicated with asterisks.

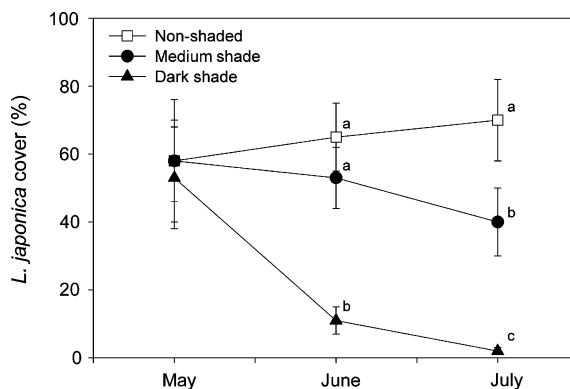


Figure 5. Cover of *L. japonica* ($\% \pm \text{SE}$) under three shade treatments: ambient (=Non-shaded), 40% of ambient understory (=Medium shade), and 2% of ambient understory (=Dark shade). On each date, means with different lowercase letters were different ($P < 0.05$).

Table 2. Mean (\pm SE) photosynthetic photon flux density (PPFD; $\mu\text{mol m}^{-2} \text{s}^{-1}$) in the *L. japonica* light gradient experiment during sampling periods, 2002.

Sampling period	Shade treatment		
	Non-shaded	Medium	Dark
May	45.2 \pm 17.5 ^a	11.2 \pm 2.2 ^b	1.3 \pm 0.1 ^b
June	27.2 \pm 7.9 ^a	6.1 \pm 0.4 ^b	1.4 \pm 0.2 ^b
July	33.8 \pm 2.2 ^a	24.9 \pm 12.7 ^a	2.5 \pm 0.5 ^b

Note. Within each sample period means with different superscript letters differed ($P < 0.05$).

Support host experiment

Experimental additions of support hosts increased circumnutation and vertical climbing behavior of *L. japonica*. The number of vertical climbing branches of *L. japonica* was greater ($P = 0.0004$) in plots with the high density of support hosts (13 ± 2) than plots with medium density of support hosts (9 ± 1). No climbing branches were observed in plots where support hosts were absent. However, additions of support hosts of either density did not affect biomass of *L. japonica* ($P = 0.17$) or *M. vimineum* ($P \geq 0.18$).

Discussion

Interpreting the nature of interactions between *L. japonica* and *M. vimineum* depends on the measure of abundance employed, a finding not uncommon to competition experiments (Gurevitch et al. 2002). Specifically, cover estimates demonstrated that *M. vimineum* interferes (i.e., amensalism) with *L. japonica*, whereas biomass data revealed a mutually detrimental relationship (i.e., competition) between the two species. However, it is clear that *M. vimineum* is a superior competitor to *L. japonica*, probably because reductions in light by *M. vimineum* negatively affected *L. japonica*. Moreover, *M. vimineum* more strongly interfered with *L. japonica* in plots that received weekly additions of water, because of increased reductions in the availability of light below the *M. vimineum* canopy. We explore these patterns and mechanisms further in the following paragraphs.

Based on cover, *M. vimineum* interfered with *L. japonica* but was unaffected by the presence

of *L. japonica*. In terms of biomass production, which is a more precise measure of abundance, interactions between *L. japonica* and *M. vimineum* were mutually detrimental, but still asymmetric in favor of *M. vimineum*. This supports findings that amensalistic interactions between non-indigenous species are probably rare (Simberloff and Von Holle 1999). *M. vimineum* performed better in wet than ambient plots regardless of the presence of *L. japonica*; the fact that *L. japonica* was not affected by the watering treatment when grown in mixture again illustrates the important nature of shading by *M. vimineum*.

Relative competition indices (based on biomass) for both species were positive, which indicates mutually detrimental interactions between the two species. However, the RCI for each species depended on the availability of water. For example, *L. japonica* was more detrimentally affected by *M. vimineum* in wet plots than ambient plots. Thus, additions of water did not release the two species from competition, but rather gave *M. vimineum* an added advantage over *L. japonica*. Therefore, we reject the hypothesis that interactions between these two species are caused by symmetric or asymmetric competition for water. In fact, this conclusion is consistent with the theory that increases in resource availability will likely benefit the better competitor (Huston 1979), which in this case is *M. vimineum*.

Mechanisms of species interaction

There are several mechanisms that explain the observed pattern of asymmetric competition between *M. vimineum* and *L. japonica*. First, the canopy of *M. vimineum* may reduce the availability of light to a point below the tolerance of *L. japonica*. Results from the light gradient experiment demonstrated that cover of *L. japonica* was reduced by shading commensurate with a canopy of *M. vimineum*. Based on these patterns, we cannot reject the hypothesis that light limits the abundance of *L. japonica* under the canopy of *M. vimineum*. In fact, this is the first study to provide experimental and mechanistic evidence of *M. vimineum*'s competitive ability and negative effects on other plant species within invaded communities.

Supplemental watering may have increased interception of light by the *M. vimineum* canopy within the wet plots. *M. vimineum* is known to increase its allocation to leaves and stems in shaded habitats with greater belowground resources (Claridge and Franklin 2002) which may increase its interception of light and competitive advantage over neighboring plants. While light interception was not specifically measured, this interpretation is supported by patterns of *M. vimineum* biomass, which was greater in wet plots, and supports the hypothesis that reduction in light by *M. vimineum* is the ultimate factor that limits co-occurring *L. japonica*.

The effect of resource availability on competitive intensity has long been a debated topic in ecology. The discussion centers on the interactions between belowground and aboveground resources and whether or not competition intensity increases with productivity (i.e., soil resource availability) (Grime 1973; Newman 1973; Tilman 1987; Keddy 2001). This study supports the theory that competition for aboveground resources (i.e., light) is more intense in areas of greater belowground resources (i.e., soil water availability). *M. vimineum* is often observed growing vigorously in wet shaded areas (e.g., along forest streams) and our results support the observation that higher soil water availability increases *M. vimineum*'s competitive ability and invasiveness in mesic areas (Claridge and Franklin 2002). However, *M. vimineum* is abundant on more xeric upland sites in the area (Cole 2003; Belote personal observation). Our data are limited with regard to the role of competition for belowground resources in unproductive sites, because soil moisture was not experimentally reduced to specifically test the effects of limited soil water availability. More data are needed to better understand mechanisms determining the abundance and distribution of *M. vimineum* and its competitive effects on other native and non-indigenous species.

While the debate on the importance of resource availability in determining the nature of competition has been a focus in ecology, the physiology and morphology of species may also explain the observed patterns of interactions (cf. Tilman 1987). In this case, the ability of *L. japonica* to use support hosts to acquire light has been pro-

posed as a mechanism by which *L. japonica* competes with other species (Dillenburg et al. 1993), and may be a factor related to its "invasiveness" (Larson 1999). Because other species were removed at the onset of all of our experiments, no support hosts were available to *L. japonica*. As a consequence, the prostrate growth form of *L. japonica* limited its ability to obtain light below the dense *M. vimineum* canopy, which it is not able to use as a support host because *M. vimineum*, though erect, has a weak culm. Similarly, other plants with prostrate growth forms are often overtopped by competitors because of their inability to acquire light resources (Grime 1965; Reader and Best 1989).

The addition of support hosts to mixtures of *L. japonica* and *M. vimineum* increased circumnutation activity and vertical climbing behavior of *L. japonica* after one growing season. Although biomass of *L. japonica* over this time period was unaffected by the addition of hosts, the duration of our experiment was probably insufficient to fully establish patterns. Over several growing seasons, the presence of support hosts may enable *L. japonica* to overtop *M. vimineum* and eventually exclude it or more symmetrically compete with it. *M. vimineum* cannot establish in areas where *L. japonica* has established thickets (Barden 1987), and shading by other plants has been shown to reduce performance of *M. vimineum* (Cole and Weltzin 2004). Because we cannot reject the hypothesis that *L. japonica* is limited by support hosts, more rigorous experimentation is needed to determine mechanisms governing this response.

Finally, *M. vimineum* may produce a phytotoxic substance that inhibits the growth of *L. japonica*. This hypothesis has yet to be tested, but in competition experiments between non-indigenous and native species allelopathic substances have been shown to be important determinants of invasive species interactions with co-occurring natives (Callaway and Ridenour 2004).

The importance of phenology

The different phenologies of *L. japonica* (an evergreen vine) and *M. vimineum* (an annual grass) are important in determining the interactions and coexistence of the two invasive species. Specifically, interactions between *L. japonica* and

M. vimineum depend on temporal variation in abundance of *M. vimineum*. *M. vimineum* canopy development during the summer reduces light to *L. japonica*. Litter of *M. vimineum* decomposes quickly after senescence at the end of the growing season (Ehrenfeld et al. 2001), and *L. japonica* is released from the negative effects of shading by *M. vimineum*. This explains the decrease in cover of *L. japonica* growing with *M. vimineum* throughout both summer growing seasons and the increase in cover of *L. japonica* between September 2001 and May 2002.

Thus, asymmetric competition between *M. vimineum* and *L. japonica* may result in temporal niche partitioning between the two species, which has been observed in other taxa (Carothers and Jaksic 1984). While some species have evolved life history strategies or phenologies to reduce negative interactions with competitors (Keddy 2001), *L. japonica* and *M. vimineum* have been sympatric in North America for only about 80 years, and we do not know if these species interact in their native ranges. Studying interactions between *L. japonica* and *M. vimineum* in their native range may provide interesting insights into the invasiveness of each species (Hierro et al. 2005).

Competition between invasive species

In a provocative article, Simberloff and Von Holle (1999) suggested that positive interactions (i.e., mutualism, commensalism, or facilitation) between non-indigenous species may facilitate further invasions and thus intensify the impact of invasive species on native ecosystems. Non-indigenous plants with novel traits that profoundly alter functions of ecosystems are the best example of invasive plants facilitating other invasive plants (e.g., *Myrica faya*, Vitousek and Walker 1989; *Tamarix ramosissima*, Sala et al. 1996), but little other evidence exists for facilitation among non-indigenous plants (Simberloff and Von Holle 1999). Results of this research indicate that interactions between *L. japonica* and *M. vimineum* are either amensalistic or competitive and are not mutualistic or facilitative. In this case, asymmetric competition between the two invasive species may actually limit the performance of each species, as well as the invasion by other non-indigenous species

and the establishment of native species (MacArthur and Wilson 1967). However, this study did not address the *process* of invasion, but rather the interactions of already co-dominant invaders. Our study did not track reproductive variables (e.g., flowering time and seed production), which may provide important insights into predicting longer-term population effects of interactions between these species. More mechanistic experiments need to be conducted to determine the long-term effects of competition to the success of each of the invasive species and the implications to native community diversity, structure, and function.

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