Ecology, 88(9), 2007, pp. 2383–2391
© 2007 by the Ecological Society of America

INSECTS MEDIATE THE EFFECTS OF PROPAGULE SUPPLY AND RESOURCE AVAILABILITY ON A PLANT INVASION

NATHAN J. SANDERS,[1,4] JAKE F. WELTZIN,[1] GREGORY M. CRUTSINGER,[1] MATTHEW C. FITZPATRICK,[1] MARTIN A. NUÑEZ,[1] CHRISTOPHER M. OSWALT,[2] AND KRISTIN E. LANE[3]

[1]*Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996-1610 USA*
[2]*Department of Forestry, Wildlife, and Fisheries, University of Tennessee, Knoxville, Tennessee 37901-1071 USA*
[3]*Department of Biological Sciences, Humboldt State University, Arcata, California 95521 USA*

Abstract. Invasive species are a global threat to biodiversity and the functioning of natural ecosystems. Here, we report on a two-year experiment aimed at elucidating the combined and relative effects of three key controls on plant invasions: propagule supply, soil nitrogen (N) availability, and herbivory by native insects. We focus on the exotic species *Lespedeza cuneata*, a Rank 1 invasive species. Propagule supply and soil N-availability interacted to control the density and foliar cover of *L. cuneata*. In low N plots, density and foliar cover of *L. cuneata* were higher in the propagule addition plots than in the plots to which propagules were not added. Surprisingly, this interaction was significant only when the abundance of herbivores was experimentally reduced. This experiment provides evidence that native insect herbivores mediate the interactive effects of propagule supply and resources on invasion by a widespread invasive plant species.

Key words: biological invasion; dispersal; herbivory; invasive species; Lespedeza cuneata; *nutrients; plant–insect interactions.*

INTRODUCTION

Invasive exotic plant species threaten native biodiversity and alter the structure and function of ecosystems (Mack et al. 2000). As a result, identifying the factors that affect the establishment and spread of invasive species has emerged as a focal area of ecological research. The factors that determine whether a plant species will successfully establish and spread can be divided into three broad categories: resource availability, propagule supply, and ecological resistance (Lodge 1993, Davis et al. 2000, Levine et al. 2004, Lockwood et al. 2005).

Resource availability can alter invasion dynamics (e.g., Davis et al. 2000). For example, some invasive plant species might be more efficient than native species at exploiting limiting resources (D'Antonio et al. 1998, Suding et al. 2004). Several studies have demonstrated that increases in the availability of soil resources, particularly nitrogen, promote invasions in grasslands (Hobbs and Atkins 1988, Huenneke et al. 1990, Milchunas and Lauenroth 1995, Burke and Grime 1996, Wedin and Tilman 1996). The general idea is that nutrient addition acts to reduce the effects of competition by the native community, thereby facilitating the success of the invader. If the addition of limiting nutrients enhances the success of the invading species, a potential feedback could occur that further enables the invader to outcompete native species. Alternatively, the addition of limiting nutrients could have indirect deleterious effects on the invader if native species are able to preempt resources, perhaps leading to competition for another limiting resource (e.g., light or water).

Propagule supply, the number of individuals introduced to a resident community, should also influence invasibility. Surprisingly, few experimental studies have addressed the role of propagule supply on plant invasions (but see Levine 2000, Von Holle and Simberloff 2005, Cadotte 2006, Thomsen et al. 2006). Though sites might differ substantially in their suitability to an invasive species, their susceptibility to invasion cannot be examined without accounting for differences in propagule supply rate (Rouget and Richardson 2003).

The ecological resistance hypothesis posits that introduced plant species often fail to invade because strong interactions from members of the resident native community inhibit their establishment and spread (Elton 1958, Maron and Vilá 2001, Levine et al. 2004, Rogers and Siemann 2004). Most tests of the ecological resistance hypothesis have focused on competition from resident plant species only (Levine et al. 2004), despite the long-standing interest in how herbivory might regulate plant populations (Hairston et al. 1960, Crawley 1983, Louda et al. 1990, Louda and Potvin 1995). The few studies that have examined how herbivores might limit plant invasions (Levine et al. 2004, Rogers and Siemann 2004) have tended to focus on the "Enemy Release Hypothesis" (Keane and Crawley 2002, Agrawal et al. 2005, Joshi and Vrieling 2005). The Enemy Release Hypothesis suggests that exotic plant species escape the enemies that attacked

Manuscript received 3 September 2006; accepted 2 February 2007. Corresponding Editor: D. R. Strong.
[4] E-mail: nathan.sanders@utk.edu

them in their native range, and that the impact of enemies is greater on native species than on invasive species (Maron and Vila 2001, Keane and Crawley 2002). As a result, the probability of higher population growth rates or establishment is greater for nonnative than native organisms. Though the Enemy Release Hypothesis is frequently tested (Agrawal et al. 2005), few studies have experimentally excluded native insect herbivores to test whether herbivory affects the establishment of invasive plant species (reviewed in Levine et al. 2004 and Parker et al. 2006). For example, in the meta-analysis by Levine et al. (2004), only 12 of 52 studies examined the effects of native herbivores in natural systems on the establishment and performance of exotic plant species; of those 12, only two focused on herbivory by insects. Nevertheless, Levine et al. (2004) concluded that herbivory can have a strong and negative effect on invader establishment. Similarly, Parker et al. (2006) showed that native herbivores can decrease the abundance of exotic plants in natural communities. Thus, ecological resistance by native herbivores appears to be a potentially strong, but rarely examined, control on plant invasions.

Resource availability, propagule supply, and herbivory by native insects can interact to affect invasion dynamics (Mitchell et al. 2006). The conceptual model of D'Antonio et al. (2001; see also Thomsen et al. 2006) summarizes how propagule supply and both abiotic and biotic factors might interact to limit invasions. In particular, when the abiotic environment is completely unsuitable, or when ecological resistance by the native community is high, no amount of propagule supply will increase the probability of invasion success. However, as the abiotic environment becomes more suitable or ecological resistance is reduced, the importance of propagule supply increases. Finally, as resources increase to the point where other biotic or abiotic constraints become limiting, the importance of propagule supply again declines (Foster 2001, Foster and Dickson 2004). This conceptual model, though, remains little tested (Thomsen et al. 2006).

Because these factors can interact in complicated ways (Von Holle and Simberloff 2005, Thomsen et al. 2006), ecologists know little about whether high levels of propagule supply can counteract the effects of ecological resistance by the native community (e.g., Von Holle and Simberloff 2005), how ecological resistance might depend on resource availability (Olff et al. 1997), or whether nutrient availability can be so low that even high levels of propagule supply fail to lead to establishment. In this paper, we examine a suite of predictions about the interactions among resource availability, propagule supply, and ecological resistance by native herbivores as controls on invasion by *Lespedeza cuneata* in an old-field ecosystem. We conducted a field experiment in which we manipulated resource availability (levels of soil N), propagule supply (number of seeds), and ecological resistance by native herbivores (presence of insects) in a crossed factorial design within an old field in east Tennessee. We predicted that when resource availability is low, or when the abundance of native insect herbivores is high, then the addition of propagules will have no effect on invasions. In contrast, when resource availability is high, or the abundance of herbivores is low, then addition of propagules will positively affect invasions.

Materials and Methods

We established a field experiment in spring 2004 within a ~10-ha old field at Freels Bend at the Oak Ridge National Environmental Research Park (NERP) near Oak Ridge, Tennessee, USA (35°58′ N, 84°17′ W). The site was abandoned from agricultural use in 1943 and was managed for open-space and wildlife habitat until the end of 2003. The soil, classified as a Typic Hapludult, has a silty clay loam texture and is moderately well drained and slightly acidic. Precipitation is generally evenly distributed throughout the year with an annual mean of 1322 mm; the average July maximum temperature is 31.2°C and the average January minimum temperature is 2.7°C. Dominant plant species at the site and in adjacent old fields include *Verbesina occidentalis*, *V. virginica*, *Solidago altissima*, and *Rubus* spp. Sub-dominants include ~60 other herbaceous and woody species, including various invasive species which are patchily distributed at low densities throughout the site and in adjacent fields. The site has been mowed every few years, typically in early spring, for the last several decades.

The focal species in this study is *Lespedeza cuneata*, a nonnative invasive leguminous shrub widely distributed throughout the eastern United States. *Lespedeza cuneata* was recently classified as a "Rank 1" (Severe Threat) pest plant species by the Southeast Exotic Pest Plant Council (information *available online*),[5] because it can alter the composition and structure of communities of native old-field plants (Eddy and Moore 1998, Brandon et al. 2004). *Lespedeza cuneata* occurs at the study site at low densities, with an average foliar cover <1% (see *Results*).

In April 2004, we constructed 72 3 × 3 m plots, including a 0.5-m buffer around each plot, at a spacing of 2 m among plots, within existing vegetation at the site. Therefore, experimental plots were 3 m from one another. We erected a 3-m tall fence encircling the site to exclude deer. Soil nitrogen (N) availability (at three levels), insect abundance (at two levels), and propagule supply of *L. cuneata* (at two levels) were assigned to plots in a fully crossed, completely randomized design, with six replicates of each unique treatment combination ($3 \times 2 \times 2 \times 6 = 72$ plots). Availability of soil N was manipulated by (1) additions of N (supplied as urea fertilizer, at a rate of 10 g/m^2 in May of 2004 and

[5] ⟨http://www.se-eppc.org⟩

February 2005), (2) additions of carbon (C; applied as sucrose at a rate of 167 g C/m^2 in May and again in August each year), and (3) an unamended control. These rates are consistent with other studies investigating controls of N and C on population and community dynamics in grasslands and old fields (e.g., McLendon and Redente 1992, Siemann 1998). Application of sucrose, which is ~46% C in a molecular form readily available to microbes, results in immobilization of plant-available N in the soil solution. The addition of sucrose as a carbon source may have unintended consequences, especially if it attracts generalist predators such as ants. However, in extensive searching at the site, we rarely detected ants in any of the experimental plots (Lane 2006).

Propagule supply treatments included (1) addition of seeds and (2) an unseeded control. *Lespedeza cuneata* seeds were applied with a standard seed spreader (Handy Green II, Scotts Miracle-Gro, Marysville, Ohio, USA) in May 2004 and 2005 at a rate of 1730 seeds/m^2. This is the recommended seeding rate from the supplier (*L. cuneata* is readily available for purchase as a cover plant). The fact that *L. cuneata* occurs patchily and at low densities at the site does not confound our results because the treatment effects were so large.

The abundance of native insect herbivores was manipulated at two levels: (1) the reduction of insects, and (2) an unmanipulated control (where insects were not reduced). We reduced insects using a combination of vacuum sampling and a permethrin insecticide (Hi-Yield Kill-A-Bug, Voluntary Purchasing Group, Bonham, Texas, USA) applied with a backpack sprayer at a rate of 0.23 L/m^2 every 2–3 weeks during the growing season in 2004 and 2005. Permethrin is a synthetic pyrethroid-based insectide that is widely used in ecological studies (e.g., Root 1996, Lynch et al. 2006, Schmitz 2006). These treatments effectively reduced insect abundance. When we sampled the plots using a combination of sweep-netting, vacuum sampling, and visual scanning, insect abundance was, on average, four times lower ($P < 0.0001$) in the insect-reduced plots (6.6 ± 0.7 insects, mean ± SE) than in the control plots (28.4 ± 2.0 insects; Lane 2006). This reduction is comparable to that attained in other studies that have reduced insect abundance to assess the effects of insects on plant communities (e.g., Mulder et al. 1999). We identified all of the insects to the lowest taxonomic resolution (i.e., species in some cases, but morphospecies within families in most cases; Lane 2006). Based on two years of observations at the field site, and detailed studies on plant–insect interactions conducted at the site, we are confident that herbivores were by far the most abundant trophic group (Lane 2006). Moreover, most of the herbivores we encountered appeared to be generalists. Of the insect taxa that were most frequently detected in the insect-reduced plots, only one was an herbivore; this was an aphid that was difficult for us to remove or reduce using the insecticide treatment and vacuum sampling. However, we never detected this species on *L. cuneata*.

The use of insecticides in ecological studies has a number of potential limitations (Brown et al. 1987, Crawley 1989, Root 1996, Carson and Root 2000, Siemann et al. 2004); therefore, we used a pyrethroid insecticide because it is long-lived and shows low levels of phytotoxicity. Moreover, in 2005 we initiated a small-scale experiment to examine the effects of our insecticide on plant growth at the research site, and found no effect of insecticide application on biomass, growth, or seed production by *L. cuneata* (Caflisch 2006). The application of this insecticide is equivalent to a watering level two orders of magnitude lower than the average rainfall received at the site for the same period so it should not lead to a systematic watering bias or confounding factor. There should also be no "fertilization effect" associated with the application of this insecticide. The availability of NO_3-N and NH_4-N in the soil solution did not differ between plots to which we applied insecticide and control plots (t tests; $P > 0.45$ in all cases).

In October of 2004 and 2005 (i.e., near the end of the growing season in each year), we estimated foliar cover of each plant species, including *L. cuneata*, within each plot using a modified Braun-Blanquet cover class scale. We also estimated the density of *L. cuneata* in each plot by establishing a 0.5-m^2 quadrat at a random location within each plot and counting all individuals of *L. cuneata* within the quadrat. We estimated aboveground biomass of *L. cuneata,* and all other plant species combined, by clipping all individuals at ground level; plant samples were dried at 50°C for 36 hours and then weighed.

In each year, we monitored soil volumetric water content (VWC, %) to 20-cm depth approximately monthly during the growing season of each year by sampling calibrated time-domain reflectometry probes (TDR; TDR 100, Campbell Scientific, Logan, Utah, USA) permanently installed at two random locations within each plot. We also determined availability of light (photosynthetic photon flux density, PPFD; μmol per square meter per second) below the plant canopy (as percentage of PPFD at the top of the canopy), four times during the 2004 and 2005 growing seasons at three random locations within each plot using a handheld line integrating ceptometer (AccuPAR, Decagon Devices, Pullman, Washington, USA) coupled to a quantum sensor that obtained concurrent measurements of PPFD at the top of the canopy.

We used mixed-bed ion-exchange resin bags (H-OH form, number R231-500, Fisher Scientific International, Pittsburgh, Pennsylvania, USA) at 5-cm soil depth at two locations in each plot to assess temporal patterns of availability of NO_3-N and NH_4-N in the soil solution. Resin bags were placed in the plots each year in May and removed in September. Resins were air-dried and composited within plot; equal masses of resin were

TABLE 1. Results from 2005 of significance testing for effects of ecological resistance by insects, nutrient addition, propagule supply, and their interactions on the density, cover, and biomass of *Lespedeza cuneata*.

Factor	df	SS	*F*	*P*
Density				
Insects	1	2.97	1.40	0.24
Nutrients	2	64.20	15.10	0.001
Insects × nutrients	2	1.87	0.44	0.65
Propagules	1	25.79	12.13	0.001
Insects × propagules	1	0.42	0.20	0.66
Nutrients × propagules	2	27.74	6.52	0.003
Insects × nutrients × propagules	2	8.21	1.93	0.15
Error	60			
Cover				
Insects	1	42.01	1.14	0.29
Nutrients	2	371.30	5.04	0.01
Insects × nutrients	2	87.84	1.20	0.31
Propagules	1	78.13	2.12	0.15
Insects × propagules	1	78.13	2.12	0.15
Nutrients × propagules	2	130.65	1.77	0.18
Insects × nutrients × propagules	2	349.52	4.75	0.01
Error	60			
Biomass				
Insects	1	3.07	1.02	0.32
Nutrients	2	0.76	0.13	0.88
Insects × nutrients	2	8.25	1.37	0.26
Propagules	1	1.89	0.63	0.43
Insects × propagules	1	0.07	0.02	0.88
Nutrients × propagules	2	3.91	0.65	0.53
Insects × nutrients × propagules	2	14.73	2.45	0.10
Error	60			

extracted with 2 mol/L KCl (Keeney and Nelson 1982) prior to analysis for concentration of NO_3^- and NH_4^+ using an autoanalyzer (Lachat Quikchem 8000, Hach, Loveland, Ohio, USA).

In a companion study, Caflisch (2006) examined the effect of herbivore reduction on the growth and survival of *L. cuneata*. Thirty 8-L pots were filled with a 1:1 mixture of Premier Pro-Mix BX potting soil (Premier Horticulture, Quakertown, Pennsylvania, USA) and Nature's Helper Water Saver Soil Conditioner (Smith Garden Products, Cumming, Georgia, USA), and were buried flush with the ground. In May 2005, each pot was planted with 10 individual *L. cuneata* seedlings. Half of the pots received insecticide application (as described previously), and the other half were retained as a control. In October 2005, near the end of the growing season, foliar damage was scored on a scale of one to 10; damage scores reflected a combination of the proportion of damaged leaves and the approximate mean severity of the damage to the leaves, independent of plant height or total number of leaves. A score of one indicated an apparently undamaged plant, and a score of 10 indicated a bare (but living) stem. Dead plants were not given a damage score, even if aboveground tissue was still present. Individual plant shoot length and the number of surviving plants per pot were recorded as measures of performance.

Statistical analyses

We analyzed the density, biomass, and cover of *L. cuneata* separately for the main and interactive fixed effects of N availability, propagule supply, and ecological resistance by insects with separate three-way analysis of variance (ANOVA) models for both 2004 and 2005. Because of occasional three-way interactions among the factors, we also used separate two-way ANOVA models for each level of the insect reduction treatment to examine main and interactive effects of N availability and propagule supply.

We analyzed the environmental variables soil VWC and availability of light of the resident community for main and interactive fixed effects of the three treatments, with sampling date as the repeated measure, using separate repeated-measures multivariate ANOVA models (MANOVAR; Pillai's Trace in SAS procedure GLM; SAS Institute 1999). Availability of NO_3-N, NH_4-N, and total N (NO_3-N + NH_4-N) in the soil solution were analyzed with separate three-way ANOVA models. When second-order interactions were significant, we reanalyzed the data by insect reduction treatment.

For the the companion study designed to determine the effect of insect reduction on *L. cuneata* performance, we analyzed herbivory, shoot length, and survivorship of *L. cuneata* using separate *t* tests. All data were tested for normality with the Shapiro-Wilk *W* statistic. Data that did not meet these assumptions were log-transformed or arcsine square-root transformed before analysis as appropriate to meet the assumptions of the analyses. Non-transformed data are presented for ease of interpretation. We used Tukey post hoc tests to compare levels within factors for significant ($P < 0.05$) main effects and first-order interactions. Results for most response variables were either quantitatively or qualitatively similar between 2004 and 2005; thus, results presented are for 2005 unless otherwise noted.

RESULTS

Propagule supply, nutrient availability, and ecological resistance by insects interacted to affect foliar cover of *L. cuneata* (insect × propagule × nutrient interaction, $F_{2,60} = 4.75$, $P = 0.01$, Table 1). When insects were reduced, addition of propagules increased cover of *L. cuneata* about sevenfold in C-addition plots, but not in control or N-addition plots (propagule × nutrient interaction; $F_{2,60} = 4.62$, $P = 0.02$, Fig. 1). The interaction among propagule supply, nutrient availability, and ecological resistance by insects on density of *L. cuneata* was not significant ($F_{2,60} = 1.95$, $P = 0.15$, Table 1). However, when insects were present, there were independent, but not interactive, effects of nutrient addition ($F_{2,31} = 6.03$, $P = 0.006$) and propagules ($F_{1,31} = 3.80$, $P = 0.06$) on density (Fig. 1). When insects were reduced, addition of propagules increased the density of *L. cuneata* about threefold in C-addition plots, but not in control or N-addition plots (nutrient × propagule, $F_{2,31} = 9.85$, $P = 0.0005$).

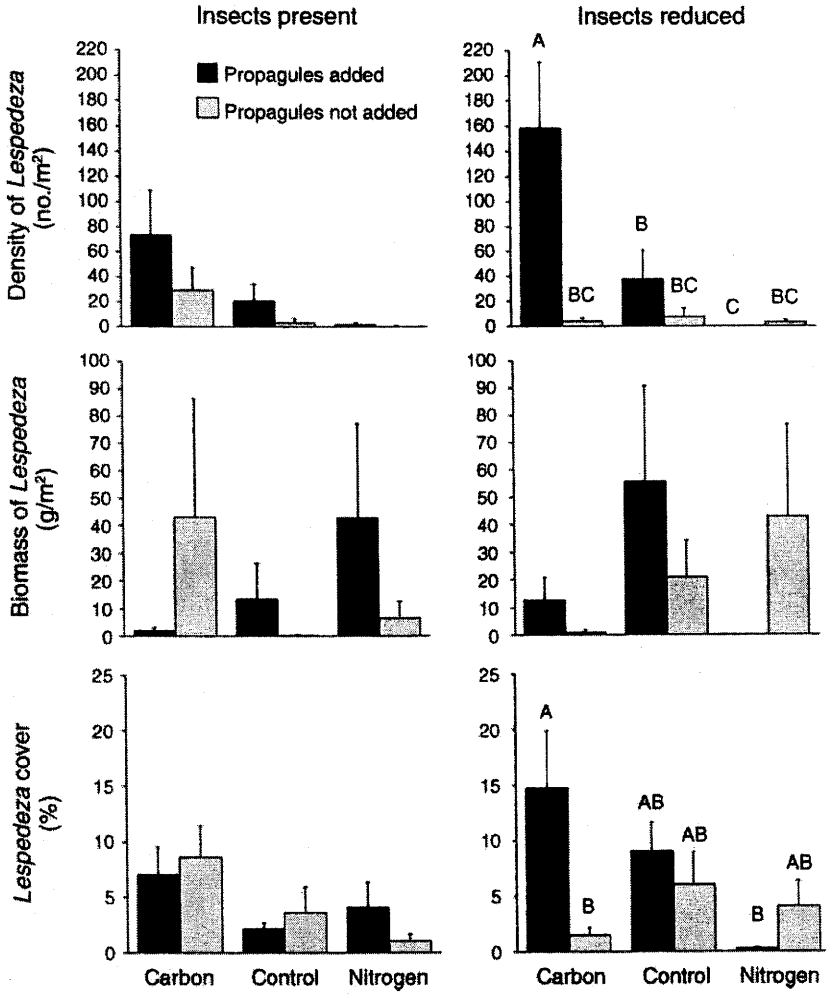

FIG. 1. The effects of insect reduction, propagule supply, and nutrient treatment on the density, biomass, and cover of the invasive plant *Lespedeza cuneata* in 2005. Insects were reduced by the application of insecticide. Propagules were added at a rate of 1730 seeds·m^{-2}·yr^{-1}. Nutrient treatments included additions of N (supplied as urea fertilizer, at a rate of 10 g/m^2), additions of carbon (C; applied as sucrose at a rate of 167 g C/m^2), and an unamended control. The panels on the left represent the 36 plots from which insects were not reduced, and the panels on the right represent the 36 plots from which insects were reduced. In each of the panels, the gray bars indicate the response (mean ± SE) of the plots to which propagules were not added, and the black bars indicate the response (mean ± SE) of the plots to which propagules were added. Different letters above bars indicate means that are statistically different from one another (Tukey's hsd, $P < 0.05$).

Biomass of *L. cuneata* did not differ among treatments (Table 1). When we explored further the interactive effects of propagule supply and nutrient availability using reduced model two-way analyses, neither propagule supply, resource addition, nor their interaction was significant.

Total aboveground biomass of all plant species other than *L. cuneata* did not differ among the treatments ($P > 0.09$). Light available below the plant canopy (percentage) in May was lower in N plots than in control or C plots, although availability of light below the canopy did not differ substantially between treatments later in the growing season (date × nutrient interaction, $P < 0.001$, Fig. 2). Soil volumetric water content (VWC, %) was generally lower in plots that received N than in plots that received C throughout the growing season (date × nutrient interaction, $P = 0.04$; Fig. 3).

In 2004, total N (NO_3-N + NH_4-N) in the soil solution was five times greater in the N plots, and three times lower in the C plots, than in the control plots ($P < 0.0001$). Additions of urea increased both NO_3-N and NH_4-N ($P < 0.0001$), whereas additions of C decreased NO_3-N ($P < 0.0001$) but not NH_4-N ($P = 0.50$). In 2005, total N in the soil solution was two times greater in the N plots, and six times lower in the C plots, than in the control plots ($P < 0.0001$). Additions of urea increased both NO_3-N and NH_4-N ($P < 0.0001$), whereas additions of C decreased NO_3-N ($P < 0.0001$) but not NH_4-N ($P = 0.50$).

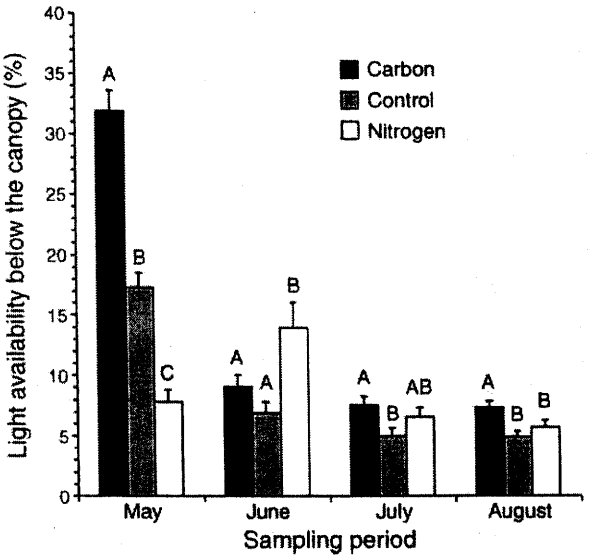

FIG. 2. The effect of nutrient treatment on the availability of light (mean ± SE; photosynthetic photon flux density, [PPFD]) below the canopy (as a percentage of PPFD above the canopy) during the 2005 growing season. Nutrient treatments are as in Fig. 1. For each date, means with different letters differed among nutrient treatments ($P < 0.05$).

In the companion study, insecticide application did not affect shoot length ($F_{1,28} = 0.23$, $P = 0.63$) or survivorship ($F_{1,28} = 0.33$, $P = 0.57$) of *L. cuneata*.

DISCUSSION

Ecological resistance is conferred by insect herbivores

Our results from the manipulative field experiment highlight the key role that insect herbivores may play in shaping plant communities (Olff and Ritchie 1998) and plant invasions (Kuijper et al. 2004, Levine et al. 2004, Rogers and Siemann 2004). Our results indicate that the presence of insect herbivores mediates the interactive effects of propagule supply and nutrient availability on this particular plant species.

Insects may limit the establishment and early success of *L. cuneata*, and hence patterns of invasion, in several ways. First, native insect herbivores may attack *L. cuneata* seedlings and limit recruitment, though it is unclear which life history stage of *L. cuneata* (i.e., seeds vs. seedlings) may have been affected by the presence of insects. Because legumes are often more nitrogen-rich than nonlegumes, they may experience higher rates of herbivory (Knops et al. 2000). Ritchie and Tilman (1995), for example, showed that the abundance of legumes increased dramatically when herbivores were excluded. However, our results indicate that the effect of insects seems to matter only in nutrient poor (i.e., C-addition and ambient) plots, counter to the prediction that herbivory should be more important in nutrient-rich sites (Grover 1995, Kuijper et al. 2004). Other studies have shown that site characteristics, especially those associated with low productivity, can influence the impact of herbivores on plant species (e.g., Maschinski and Whitham 1989, Siemann and Rogers 2003), and perhaps such site-specific effects also occur in our system. A more likely explanation is that the quality of *L. cuneata* leaf tissue relative to the rest of the plant community is even greater in the low N plots, thus making *L. cuneata* an even more likely target for selective herbivory.

Second, because we applied a broad-base insecticide, several trophic levels of arthropods could have been affected. For example, in plots where insecticide was not applied, herbivores may have relied on *L. cuneata* seedlings in the understory to escape top predators and parasitoids in the overstory (Schmitz 2004). Our insect surveys at the site (Lane 2006) suggest that herbivores are the most abundant insect trophic group, and that herbivores are greatly reduced by the application of the insecticide. Third, it is possible that the insecticide affected non-arthropod herbivores, such as snails or rodents, both of which can have important effects on plant invasions (Levine et al. 2004). However, effects of permethrin insecticide on snails and rodents have been little studied.

How might we explain the significant three-way interaction among insects, propagule supply, and resource availability? For generalist, native insect herbivores to regulate an invasion, they must attack plants that often occur at high densities (Root 1973). In our system, this occurs only in the C-addition and ambient plots in which propagules were added. It could also be that the influence of insects on *L. cuneata* is strongest in the C-addition and control plots because the quality of the other plant species might be considerably lower than *L. cuneata* in these treatments. Thus, the

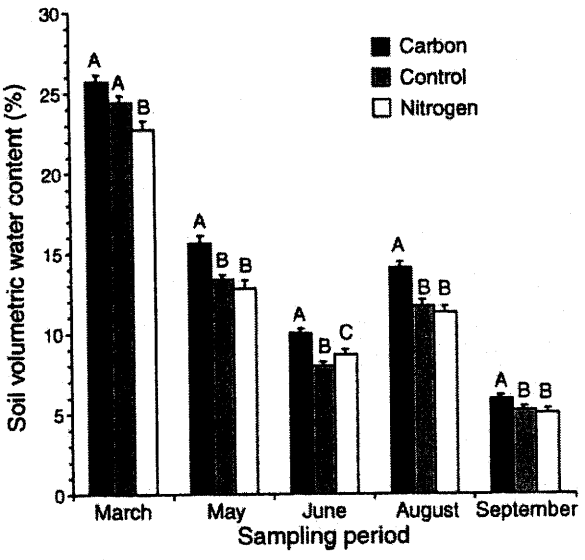

FIG. 3. The effect of nutrient treatment on soil volumetric water content (VWC; mean ± SE) at 0–20 cm soil depth during the 2005 growing season. Nutrient treatments are as in Fig. 1. For each date, means with different letters differed among nutrient treatments ($P < 0.05$).

counterintuitive interpretation is that herbivory by native insects matters only when the density of the invader is high (i.e., when propagules are added) and the quality of host plants in the resident community is low (i.e., in C-addition or ambient plots). This interpretation has some parallels to the conceptual model proposed by D'Antonio and colleagues (D'Antonio et al. 2001, Thomsen et al. 2006) in that a certain threshold of propagule supply has to be met before ecological resistance (in our case herbivory by native insects) affects this invasive species. In this system, the threshold for control by insects might be sufficient food to support a collection of herbivores. The companion experiment which examined the effects of insect reduction on the growth and survivorship of *L. cuneata* found no treatment effects (Caflisch 2006). This agrees with the results of the larger experiment because our data suggest herbivores limit *L. cuneata* only when it is a high quality resource (in low N plots). In the companion experiment, it was the only resource available to herbivores.

Our interpretation contrasts almost exactly an earlier proposition for when herbivores might limit invasions (Maron and Vila 2001). Maron and Vila (2001) suggested that generalist herbivores might limit plant invasions only when the density of the exotic plant is below some critical density. But when density rises above some minimum threshold, perhaps because of increased propagule supply, herbivores no longer limit the invasion. Future experiments should focus on determining whether ecological resistance by insect herbivores limits invasions, and under gradients of propagule supply.

Nitrogen addition indirectly limits this invasion

There are several reasons why there might not be direct effects of nutrients on *L. cuneata* establishment and early success. First, the effect of nutrient addition might act indirectly to limit *L. cuneata*. For example, availability of light below the canopy was greater in C-addition and ambient plots than in N plots early in the growing season, when emerging seedlings might be light-limited. This hypothesis is supported by a companion greenhouse experiment, which showed that survivorship of *L. cuneata* seedlings increased as availability of light increased (J. F. Weltzin et al., *unpublished data*). Further, soil moisture was typically greater in plots with C additions than in plots with N additions; in the absence of herbivores, this soil moisture differential could favor *L. cuneata* in plots with C addition.

Second, several studies have shown how increased N addition might actually promote invasions (e.g., Davis and Pelsor 2001), or that increased C might hinder invasions (Ridenour and Callaway 2001). Addition of N might not promote invasion by *L. cuneata* for the simple reason that *L. cuneata* is a legume capable of atmospheric N fixation. Moreover, previous studies have found that addition of N can lower the competitive advantage of legumes (Ritchie and Tilman 1995, Brandon et al. 2004). As such, in the control and C-addition plots, *L. cuneata* may have been at a competitive advantage, whereas in the N-addition plots, it may have been at a competitive disadvantage.

The effect of propagule supply matters only in suitable habitats

Several recent studies have shown that recruitment limitation may be more important than competitive interactions or escape from natural enemies in determining invasion dynamics and the composition of plant communities (D'Antonio et al. 2001, Siemann and Rogers 2003, Gross et al. 2005, Von Holle and Simberloff 2005). In our study, we found that the density and cover of *L. cuneata* were greater in seeded than unseeded plots (when availability of N was relatively low). This result is not that surprising: more individuals being released into a community should buffer the population from potential demographic accidents or marginal environments (Lockwood et al. 2005). What is somewhat surprising, though, is that the addition of propagules did not seem to influence the establishment of *L. cuneata* in high nitrogen environments. This suggests that the effect of propagule supply, at least for this species, matters only in relatively low N environments, whereas high N environments may be unsuitable for establishment of *L. cuneata*, regardless of propagule supply. Indeed, the abundance of a plant species (whether native or nonnative) in a local community is likely regulated by both propagule supply and subsequent success of seedlings: individuals first have to reach a suitable habitat, then persist once there (Levine 2000, D'Antonio et al. 2001). This dual requirement suggests that both propagule supply and the conditions in the recipient community interact to drive invasions; other studies have reached similar conclusions (e.g., Grime 1979, Huston 1999, Zobel et al. 2000, D'Antonio et al. 2001). For example, two recent studies (Foster 2001, Foster and Dickson 2004) showed that the role of propagule supply in structuring native plant communities declined as habitat productivity increased. Our findings are in general accord with theirs in that increased propagule supply was most important at low and ambient resource availability, and least important at high resource levels. Siemann and Rogers (2003), who worked at spatial scales much larger than ours, showed that higher levels of propagule supply increased the probability of establishment, and that the effect of propagule supply varied among habitats. Taken together, these results suggest that the role of propagule supply in plant communities generally, and plant invasions specifically, can be mediated by other factors.

Conclusions

In conclusion, it is clear that many mechanisms are involved in controlling the spread of invasive plant species, and, more generally, the assembly of plant communities. The results from this experiment provide

evidence that native insect herbivores mediate the interactive effects of propagule supply and resources on invasion by a widespread invasive plant species. Much of the initial research on biological invasions aimed to identify "the" factor that regulates biological invasions (e.g., Drake et al. 1989). Even today, arguments about the importance of ecological resistance (deRivera et al. 2005), resources (Davis and Pelsor 2001, Stevens and Carson 2002, Gross et al. 2005, Walker et al. 2005), and propagule supply (Levine 2000, Foster 2001) tend to ignore the likelihood that resources, ecological resistance, and propagule supply act together to determine invasibility. In contrast, our work and a growing number of recent studies highlight how multiple interacting factors shape the dynamics of plant invasions (e.g., Maron and Vilá 2001, Scherber et al. 2003, Siemann and Rogers 2003, Kellogg and Bridgham 2004, DeWalt et al. 2004, Gross et al. 2005, Von Holle and Simberloff 2005, Lambrinos 2006, Mitchell et al. 2006, Thomsen et al. 2006). Understanding the ecological circumstances under which particular factors regulate invasions, or how such factors interact, could help predict the spread and potential impact of invasive plant species in natural ecosystems.

Acknowledgments

Much of the research presented here was conducted and synthesized as part of the Fall 2004 course in Community Ecology at the University of Tennessee. We thank Adam Fuller, Catie Stewart, Cayenne Engel, John Evans, Caroline DeVan, and especially Lara Souza for providing field and laboratory help with many aspects of the project. We also thank Jim Evans, Pat Parr, and Harry Quarles for facilitating this research. This manuscript was improved by comments from Aimée Classen and Rob Dunn.

Literature Cited

Agrawal, A. A., P. M. Kotanen, C. E. Mitchell, A. G. Power, W. Godsoe, and J. Klironomos. 2005. Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. Ecology 86:2979–2989.

Brandon, A. L., D. J. Gibson, and B. A. Middleton. 2004. Mechanisms for dominance in an early sucessional old field by the invasive non-native *Lespedeza cuneata* (Dum. Cours.) G. Don. Biological Invasions 6:483–493.

Brown, V. K., M. Leijn, and C. S. A. Stinson. 1987. The experimental manipulation of insect herbivore load by the use of an insecticide (malathion): the effect of application on plant growth. Oecologia 72:377–381.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology 77:776–790.

Cadotte, M. W. 2006. Dispersal and species diversity: a meta-analysis. American Naturalist 167:913–924.

Caflisch, M. G. 2006. A test of the enemy release hypothesis using a congeric pair of *Lespedeza* species. Thesis. University of Tennessee, Knoxville, Tennessee, USA.

Carson, W. P., and R. B. Root. 2000. Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. Ecological Monographs 70:73–99.

Crawley, M. J. 1983. Herbivory: the dynamics of animal–plant interactions. University of California Press, Berkeley, California, USA.

Crawley, M. J. 1989. Insect herbivores and plant-population dynamics. Annual Review of Entomology 34:531–564.

D'Antonio, C. M., R. F. Hughes, M. Mack, D. Hitchcock, and P. M. Vitousek. 1998. The response of native grasses to the removal of invasive exotic grasses in the seasonally dry Hawaiian woodland. Journal of Vegetation Science 9:699–712.

D'Antonio, C. M., J. M. Levine, and M. Thomson. 2001. Ecosystem resistance to invasion and the role of propagule supply: a California perspective. Journal of Mediterranean Ecology 27:233–245.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528–534.

Davis, M. A., and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecology Letters 4:421–428.

deRivera, C. E., G. M. Ruiz, A. H. Hines, and P. Jivoff. 2005. Native predator limits abundance and distribution of an introduced crab. Ecology 86:3364–3376.

DeWalt, S. J., J. S. Denslow, and K. Ickes. 2004. Natural-enemy release facilitates habitat expansion of an invasive shrub, *Clidemia hirta*. Ecology 85:471–483.

Drake, J. A., H. A. Mooney, F. D. Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. 1989. Biological invasions: a global perspective. Wiley, Chichester, UK.

Eddy, T. A., and C. M. Moore. 1998. Effects of sericea lespedeza (*Lespedeza cuneata* (Dumont) G. Don) invasion on oak savannas in Kansas. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 86:57–62.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Wiley, New York, New York, USA.

Foster, B. L. 2001. Constraints on colonization and species richness along a grassland productivity gradient: the role of propagule availability. Ecology Letters 4:530–535.

Foster, B. L., and T. L. Dickson. 2004. Grassland diversity and productivity: the interplay of resource availability and propagule pools. Ecology 85:1541–1547.

Grime, J. P. 1979. Plant strategies and vegetation processes. Wiley, Chichester, UK.

Gross, K. L., G. G. Mittelbach, and H. L. Reynolds. 2005. Grassland invasibility and diversity: responses to nutrients, seed input, and disturbance. Ecology 86:476–486.

Grover, J. P. 1995. Competition, herbivory and enrichment: nutrient-based models for edible and inedible algae. American Naturalist 145:746–774.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 44:421–425.

Hobbs, R. J., and L. Atkins. 1988. The effect of disturbance and nutrient addition on native and introduced annuals in the Western Australian wheatbelt. Australian Journal of Ecology 13:171–179.

Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology 71:478–491.

Huston, M. A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos 86:393–401.

Joshi, J., and K. Vrieling. 2005. The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. Ecology Letters 8:704–714.

Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. Trends in Ecology and Evolution 17:164–170.

Keeney, D. R., and D. W. Nelson. 1982. Nitrogen: inorganic forms. Pages 643–698 *in* A. L. Page, R. H. Miller, and D. R. Keeney, editors. Methods of soil analysis: part 2. American Society of Agronomy. Madison, Wisconsin, USA.

Kellogg, C. H., and S. D. Bridgham. 2004. Disturbance, herbivory, and propagule dispersal control dominance of an invasive grass. Biological Invasions 6:319–329.

Knops, J. M. H., M. Ritchie, and D. Tilman. 2000. Selective herbivory on a nitrogen fixing legume (*Lathyrus venosus*)

influences productivity and ecosystem nitrogen pools in an oak savanna. Ecoscience 7:166–174.
Kuijper, D. P. J., D. J. Nijhoff, and J. P. Bakker. 2004. Herbivory and competition slow down invasion of a tall grass along a productivity gradient. Oecologia 141:452–459.
Lambrinos, J. G. 2006. Spatially variable propagule pressure and herbivory influence invasion of chaparral shrubland by an exotic grass. Oecologia 147:327–334.
Lane, K. E. 2006. The structure and dynamics of arthropod communities in an old-field ecosystem. Thesis. Humboldt State University, Arcata, California, USA.
Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science 288:852–854.
Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 7:975–989.
Lockwood, J. L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology and Evolution 20:223–228.
Lodge, D. M. 1993. Biological invasions: lessons from ecology. Trends in Ecology and Evolution 8:133–136.
Louda, S. M., K. H. Keeler, and R. D. Holt. 1990. Herbivore influences on plant performance and competitive interactions. Pages 413–444 *in* J. B. Grace and D. Tilman, editors. Perspectives on plant competition. Academic Press, San Diego, California, USA.
Louda, S. M., and M. A. Potvin. 1995. Effect of inflorescence-feeding insects in the demography and lifetime fitness of a native plant. Ecology 76:229–245.
Lynch, M. E., I. Kaplan, G. P. Dively, and R. F. Denno. 2006. Host-plant mediated competition via induced resistance: interations between pest herbivores on potatoes. Ecological Applications 16:855–864.
Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10:689–710.
Maron, J. L., and M. Vilá. 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. Oikos 95:361–373.
Maschinski, J., and T. G. Whitham. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. American Naturalist 134:1–19.
McLendon, T., and E. F. Redente. 1992. Effects of nitrogen limitation on species replacement dynamics during early secondary succession on a semiarid sagebrush site. Oecologia 91:312–317.
Milchunas, D. G., and W. K. Lauenroth. 1995. Inertia in plant community structure: state changes after cessation of nutrient-enrichment stress. Oecologia 5:452–458.
Mitchell, C. E., et al. 2006. Biotic interactions and plant invasions. Ecology Letters 9:726–740.
Mulder, C. P. H., J. Koricheva, K. Huss-Danell, P. Hogberge, and J. Joshi. 1999. Insects affect relationships between plant species richness and ecosystem process. Ecology Letters 2: 237–246.
Olff, H., J. De Leeuw, J. P. Bakker, R. J. Platerink, H. J. Van Wijnen, and W. De Munck. 1997. Vegetation succession and herbivory in a salt marsh: changes induced by sea level rise and silt deposition along an elevational gradient. Journal of Ecology 85:799–814.
Olff, H., and M. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in Ecology and Evolution 13:261–265.
Parker, J. D., D. E. Burkepile, and M. E. Hay. 2006. Opposing effects of native and exotic herbivores on plant invasions. Science 311:1459–1461.
Ridenour, W. M., and R. M. Callaway. 2001. The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. Oecologia 126:444–450.
Ritchie, M. E., and D. Tilman. 1995. Responses of legumes to herbivores and nutrients during succession on a nitrogen-poor soil. Ecology 76:2648–2655.
Rogers, W. E., and E. Siemann. 2004. The role of herbivores in alien plant invasions: insights using a combination of methods to enhance or reduce herbivory. Pages 329–356 *in* W. W. Weisser and E. Siemann, editors. Insects and ecosystem function. Springer-Verlag, Heidelberg, Germany.
Root, R. B. 1973. Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs 43:95–120.
Root, R. B. 1996. Herbivore pressure on goldenrods (*Solidago altissima*): its variation and cumulative effects. Ecology 77: 1074–1087.
Rouget, M., and D. M. Richardson. 2003. Understanding patterns of plant invasion at different spatial scales: quantifying the roles of environment and propagule pressure. Pages 3–15 *in* L. E. Child, J. H. Brock, G. Brundu, K. Prach, P. Pysek, P. M. Wade, and M. Williams, editors. Plant invasions: ecological threats and management solutions. Backhuys Publishers, Leiden, The Netherlands.
SAS Institute. 1999. The SAS system for Windows. Version 8e. SAS Institute, Cary, North Carolina, USA.
Scherber, C., M. J. Crawley, and S. Porembski. 2003. The effects of herbivory and competition on the invasive alien plant *Senecio inaequidens* (Asteraceae). Diversity and Distributions 9:415–426.
Schmitz, O. J. 2004. From mesocosms to the field: the role and value of cage experiments in understanding top-down effects in ecosystems. Pages 277–302 *in* W. W. Weisser and E. Siemann, editors. Insects and ecosystem function. Springer-Verlag, Heidelberg, Germany.
Schmitz, O. J. 2006. Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. Ecology 87:1432–1437.
Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. Ecology 79:2057–2070.
Siemann, E., W. P. Carson, W. E. Rogers, and W. W. Weisser. 2004. Reducing herbivory using insecticides. Pages 303–328 *in* W. W. Weisser and E. Siemann, editors. Insects and ecosystem function. Springer-Verlag, Heidelberg, Germany.
Siemann, E., and W. E. Rogers. 2003. Herbivory, disease, recruitment limitation, and success of alien and native tree species. Ecology 84:1489–1505.
Stevens, M. H. H., and W. P. Carson. 2002. Resource quantity, not resource heterogeneity, controls diversity. Ecology Letters 5:420–426.
Suding, K., K. LeJeune, and T. Seastedt. 2004. Competitive impacts and responses of an invasive weed: dependencies on nitrogen and phosphorous availability. Oecologia 14:526–535.
Thomsen, M. A., C. M. D'Antonio, K. B. Suttle, and W. P. Sousa. 2006. Ecological resistance, seed density and their interactions determine patterns of invasion in a California coastal grassland. Ecology Letters 9:160–170.
Von Holle, B., and D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology 86:3212–3218.
Walker, S., J. B. Wilson, and W. G. Lee. 2005. Does fluctuating resource availability increase invasibility? Evidence from field experiments in New Zealand short tussock grassland. Biological Invasions 7:195–211.
Wedin, D., and D. Tilman. 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. Science 274:1130–1132.
Zobel, M., M. Otsus, J. Liira, M. Moora, and T. Möls. 2000. Is small-scale species richness limited by seed availability or microsite availability? Ecology 81:3274–3282.