

Similar biotic factors affect early establishment and abundance of an invasive plant species across spatial scales

Lara Souza · Windy A. Bunn · Jake F. Weltzin · Nathan J. Sanders

Received: 27 August 2009 / Accepted: 17 June 2010 / Published online: 30 June 2010
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Abstract Research in community invasibility has focused on biotic and abiotic factors that influence the establishment of invasive species and whether such factors vary with spatial scale. Here, we investigate the role of both biotic and abiotic factors associated with the initial establishment of *Lespedeza cuneata* (*L. cuneata*) and its abundance at three spatial scales: neighborhoods (9-m² plots), communities (50-m² transect) and old fields (5,000–70,000 m²). We asked: (1) Do resource availability and community structure

affect the establishment of *L. cuneata*?, and (2) Are resource availability and community structure associated with patterns of *L. cuneata* abundance from neighborhood scales to old-field scales? To investigate the first question, we manipulated soil nitrogen (N) availability at three levels in an existing old-field community and tracked emergence and persistence of *L. cuneata* seedlings, as well as total plant biomass of the community, availability of light, and soil moisture content. To address the second question, we performed surveys in which we estimated *L. cuneata* foliar cover at community scales (50-m² belt transects) and old-field scales (total area of 28 ha), and assessed the same biotic and abiotic variables as in the field experiment. The experiment revealed that establishment and persistence by *L. cuneata* seedlings were 15× and 5× lower in N-added plots than in N-reduced plots. Total plant community biomass was 30% greater in N-added plots than in N-reduced plots. Conversely, light and soil moisture were 60 and 20% lower in N-added plots than in N-reduced plots. Surveys of old fields indicated that community biomass was positively associated with *L. cuneata* cover at old-field scales likely resulting from greater soil N input from nitrogen fixation in fields with greater *L. cuneata* cover. In sum, these results indicate that biotic factors associated with establishment of a Rank 1 invasive plant species at the community scale are also related to its distribution at the old-field scale, but the direction of such associations changed across scales.

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Keywords Resource availability · Invasibility · Spatial scale · Establishment · *Lespedeza cuneata* · Invasive species · Abundance

Introduction

Biological invasions can alter the structure and function of native communities (Mack et al. 2000; Levine et al. 2003; Mack and D'Antonio 2003). Thus, understanding the factors that limit invasions at different stages of invasion (Reichard and Hamilton 1997; Rejmanek and Richardson 1996; Sakai et al. 2001; Kolar and Lodge 2002; Sexton et al. 2002; Levine et al. 2004; Dietz and Edwards 2006), and among spatial scales (Stohlgren et al. 1999, 2006; Dietz and Edwards 2006; Pauchard and Shea 2006; Fridley et al. 2007) is critical to predicting future plant invasions and their consequences. Dietz and Edwards (2006) provided a conceptual framework that allows invasion ecologists to predict more accurately the course of plant invasions by incorporating both ecological and evolutionary processes operating during different stages of invasion and at different spatial scales. Specifically, they proposed that the relative importance of species traits, habitat characteristics and propagule pressure change from initial to late invasion stages (Dietz and Edwards 2006). As an example, during the initial stages of plant invasions, propagule pressure and ruderal life-history traits likely promote successful invasion. But during late stages of plant invasions, stress-tolerant and/or competitive life history strategies along with habitat characteristics likely determine plant invasions. Additionally, a recent synthesis by Fridley et al. (2007) found that the factors which regulate invasion success vary with spatial scale: at neighborhood and community scales, where environments are homogenous, biotic interactions can influence invasions, but at larger scales where environments are heterogenous, abiotic extrinsic factors (such as propagule pressure and disturbance) will determine plant invasions.

The availability of resources can both positively and negatively influence the success of exotic species across stages of invasion and spatial scales (Davis et al. 2000; Hobbs and Atkins 1988; Huenneke et al. 1990; Wedin and Tilman 1996). The proposed mechanism for the positive effects of resources on

the growth of exotic populations is that increases in nutrient availability relieve exotic species from competitive effects imposed by native species (Davis et al. 2000). Negative effects of resource additions might arise when native species positively respond to increases in a given resource, reducing the availability of other resources (e.g., light, soil moisture), thus creating a barrier for successful colonization by exotics. This discrepancy among studies suggests that more experimental studies, coupled with observational studies across landscapes, are necessary to understand whether and how resource availability and community structure limits invasions at various stages of invasion (i.e., establishment and population growth) and across spatial scales. Here, we focus on how resources, with a particular focus on soil nitrogen, influence the establishment and abundance of *Lespedeza cuneata* (hereafter *Lespedeza*) in old-field ecosystems in East Tennessee, USA.

Lespedeza, a perennial nitrogen-fixer, was introduced into the United States from eastern and central Asia, and is now widespread in old fields, oak savannas and prairie communities (Eddy and Moore 1998). *Lespedeza* is considered a Rank 1 invasive species in several US states because of its negative effects on community structure and ecosystem function (Price and Weltzin 2003; Brandon et al. 2004; Garten et al. 2008). Dominance by *Lespedeza* has been associated with reductions in evenness and diversity of native plant species, as well as reductions in total aboveground biomass production (Price and Weltzin 2003). Moreover, N₂-fixation by *Lespedeza* has been shown to contribute to the nitrogen pools in old-field communities, thus altering species composition and nitrogen cycling (Garten et al. 2008).

Resource availability, in particular soil N, can control the population growth of *Lespedeza* species at small spatial scales (Ritchie and Tilman 1995; Brandon et al. 2004; Sanders et al. 2007). For example, in an old field in East Tennessee, Sanders et al. (2007) found that foliar cover and density of *Lespedeza* was lower in plots that received supplemental N, but only when abundance of insects was experimentally reduced. Similarly, Ritchie and Tilman (1995) found that amendments of soil macronutrients reduced cover of *Lespedeza capitata* in old-field communities in Minnesota. No studies, however, have addressed the role of resource availability on establishment and persistence of *Lespedeza*

seedlings. While seedling dynamics constitute only the initial steps in invasion success, their importance in affecting the distribution of species in grassland systems has been confirmed by several studies (Gross and Werner 1982; Foster et al. 2002).

In this study, we asked: (1) Does resource availability and community structure affect the establishment of *Lespedeza*? and (2) Are resource availability and community structure associated with patterns of *Lespedeza* abundance from community scales (e.g., 50-m²) to old-field scales (0.5–7 ha)? To address these questions, we experimentally manipulated soil N availability within extant communities, and tracked the establishment and persistence of *Lespedeza* added as seed over two growing seasons. We simultaneously assessed community biomass, soil moisture, and availability of light within the experimental plots. We conducted a survey for foliar cover of *Lespedeza* across 50 50-m² transects nested within 17 old-field plant communities, while simultaneously assessing resource availability and community and compartmental plant biomass.

Methods

Experimental study

Study site

The experiment was conducted in an old field at Oak Ridge National Environmental Research Park, near Oak Ridge, Tennessee (35° 58' N 84° 17' W). The old field was used for agriculture until 1943 and has been mowed annually each spring since 2001. The soil has a silty clay loam texture and is classified as Typic Hapludult. Mean annual rainfall is 1322 mm and air temperature ranges from 2.7°C (in January) to 31.2°C (in July). Dominant plant species at this site, and also across old fields in the area, include *Solidago altissima*, *Verbesina occidentalis* and *V. virginica*, which together comprise about 40% of total aboveground biomass in this system (Souza et al. In Review). In addition, about 60 subordinate herbaceous and woody native and introduced plant species, including *Lespedeza*, occur at the study site and make up the remainder of the total aboveground biomass. We chose *Lespedeza* as our focal species because it is the most common exotic species in old fields near our

site and is the fourth most abundant species in local old-field communities (Garten et al. 2008; Souza et al. In Review). Additional details about the site can be found in Sanders et al. (2007).

Experimental design

In a completely randomized design within an existing old-field plant community, we used 18 3 m × 3 m plots spaced with 2-m walkways (as part of a larger study described in Sanders et al. 2007). A 3-m tall fence to exclude deer surrounded all plots. In 2004 and 2005, we manipulated soil nitrogen (N) availability at three levels ($n = 6$ replicates): control (no manipulation), soil N-addition (application of urea fertilizer at a rate of 10 g N per m² year⁻¹ in one application in spring of each year), and soil N-reduction (application of carbon in the form of sucrose at a rate of 1,000 g C per m² in three equal applications during the course of the growing season). 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. These rates are consistent with other studies investigating controls of N and C on grassland and old-field ecosystems (e.g., McLendon and Redente 1992; Siemann 1998). To measure soil nitrogen availability, we used mixed-bed ion-exchange resin bags placed at the top 5-cm of the soil from May through September. We found that treatments increased ($P < 0.0001$) availability of soil nitrogen in N-added plots five-fold relative to control plots and 20-fold relative to N-reduced plots by 2005 (Sanders et al. 2007).

Establishment of Lespedeza

To control for potential propagule limitation, approximately 1,730 *Lespedeza* seeds per m² (obtained and recommended by Ernst Conservation Seeds, Meadville, PA) were broadcasted to each plot in the spring (March) of 2004, 2005 and 2006. Although *Lespedeza* plants produce seeds in the fall, seeds likely “disperse” across old fields in the spring as fields are mowed. We then established two permanent 0.4 m × 0.4 m (0.16 m²) subplots at random locations within each of the 18 plots with the constraint that they be situated 0.5 m from the edge of the plot to facilitate monitoring. Individual *Lespedeza* seedlings

were marked with painted stainless steel nails as they emerged. Four times during the 2005 growing season, and three times during the 2006 growing season, we recorded the number of seedlings that emerged and died within each subplot (i.e., establishment), and quantified the persistence of seedlings of the 2005 cohort into 2006 by calculating the proportion of seedlings that resprouted the following year. Seedling persistence after 1 year may not indicate long-term persistence of plant species. Nonetheless, literature addressing “nursery and field practice” of *Lespedeza cuneata* indicates that approximately 95% of 1-year-old seedlings can be easily transplanted into the field (Segelquist 1971; Martin et al. 1975).

Adult *Lespedeza* individuals can be an additional source of propagules, which should be considered when tracking *Lespedeza* seedling emergence and establishment. In fact, adult *Lespedeza* individuals can produce between 340–670 kg of seeds per hectare each year (771,000 seeds/kg) (Guernsey et al. 1970). We therefore estimated the foliar cover of adult *Lespedeza* individuals (as a percent of the total area of the plot) using a modified Braun-Blanquet cover class scale (Braun-Blanquet 1932) in September of both 2005 and 2006. The modified Braun-Blanquet scale included six categories: 1 = <1%, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75%, 6 = 75–100%.

Community-level responses

To determine whether the extant plant community responded to the nutrient amendments, with potential effects on establishment of *Lespedeza*, we quantified plant community aboveground biomass in September of 2005 and 2006. We determined total aboveground biomass by clipping to ground level all plants within a 0.5 m × 1 m quadrat randomly located within each 3 m × 3 m plot and at least 0.5 m from the seedling monitoring subplots. We categorized each clipped stem into one of the following groups: *Solidago* species, *Verbesina* species, *Lespedeza*, N-fixer, and total biomass. Clipped biomass was oven-dried at 60°C for 48 h, then weighed.

Environmental variables

We estimated light availability and soil volumetric water content (VWC) throughout the 2005 and 2006 growing seasons. We used a line-integrating

ceptometer (Decagon Accupar, Decagon Devices, Pullman, WA) to measure light availability (photosynthetic photon flux density, PPFD; $\mu\text{mol photons m}^{-2}\text{s}^{-1}$) below the canopy two cm from the soil surface at four locations within the 3 m × 3 m plots monthly in 2005 and 2006. To measure soil VWC, we installed two time domain reflectometers (TDR 100, Campbell Scientific, UK) at random locations within each 3 m × 3 m plot, and recorded VWC (% v/v) monthly in both 2005 and 2006. The reason why PPFD and soil VWC data were not collected in the same time periods in 2005 and 2006 was because in 2006 we were collecting data in experimental and observational studies.

Statistical analysis

We tested for the effects of soil N treatment on *Lespedeza* seedling emergence (i.e., establishment) and persistence (re-emergence of previous year’s seedlings) of *Lespedeza* using a one-way analysis of variance (ANOVA), with N treatment as the main factor in the model. We also used date as the repeated factor in a repeated measures ANOVA testing for the effects of the soil nitrogen amendments, time and their interaction on *Lespedeza* seedling establishment in 2005 and 2006.

We also built analysis of covariance (ANCOVA) models with soil nitrogen amendment as the main factor along with several biotic and abiotic covariates that might affect *Lespedeza* seedling establishment. In order to select relevant biotic and abiotic covariates for our model, we generated a correlation matrix among biotic and abiotic covariates and *Lespedeza* seedling establishment across all months. We included biotic (*Verbesina* biomass, *Solidago* biomass, total aboveground biomass, adult *Lespedeza* cover and cover and biomass of other N-fixing species) and abiotic (light, soil moisture, soil nitrogen) factors in our correlation matrix that were likely affected by soil N manipulation and subsequently likely affected early establishment by *Lespedeza*. If predictor variables (i.e., biotic and/or abiotic factors) were correlated ($P < 0.05$) with *Lespedeza* seedling establishment, then they were included in the ANCOVA as important covariates in the model.

We tested for the effects of soil N treatment on both biotic and abiotic community response variables. We used adult *Lespedeza* cover, cover and

abundance of other N-fixer species, and total aboveground biomass, as well as light and soil moisture availability, as response variables, with N treatment as the main factor in the model. We also ran randomization tests to further investigate the role of soil N manipulation on *Lespedeza* seedling dynamics and found qualitatively the same results. Therefore, we report only the results from the more traditional parametric analyses. For all analyses, we tested for normality of the residuals resulting from general linear models and applied transformations to variables that did not meet normality assumptions. We log-transformed seedling density in 2005 and applied a natural log transformation to adult *Lespedeza* foliar cover for both 2005 and 2006 prior to ANOVA and ANCOVA analyses. All mean values presented in tables and figures are un-transformed values. We used SAS 9.1.3, JMP 6.0, and EcoSim7 for all statistical analyses (Gotelli and Entsminger 2009).

Observational study

Study sites

We randomly chose 17 old fields at Oak Ridge National Environmental Research Park, all within 5 km of the experimental study site. The old fields ranged in size from 0.5 to 7.0 ha based on the presence of well-defined boundaries such as forests or roadcuts. All fields were abandoned from agriculture in 1943. We selected fields that had similar site histories (e.g., limited grazing if any, age since last plowed, limited crop use since abandonment). We randomly placed two to six (proportional to field area) 50-m² transects in each field. Along each transect, we placed five 1-m² plots spaced 10 m apart.

Lespedeza cover and community-level measurements

In each 1-m² plot, we estimated the foliar cover of *Lespedeza* in July 2006 using a modified Braun-Blanquet scale (Braun-Blanquet 1932). We also estimated total aboveground biomass in a randomly placed 0.5 m × 1 m subplot within each 1-m² plot. To estimate total aboveground biomass, we clipped all individuals rooted inside the sampling quadrats to approximately 1 cm from the soil surface and sorted the biomass into *Solidago* biomass, *Verbesina* biomass, other N-fixer biomass, and total aboveground

biomass. We then oven-dried the samples for 48 h at 65°C and quantified their weight. For each 1-m² plot, we enumerated all species, and used these data to calculate species richness, excluding *Lespedeza*.

Environmental variables

We estimated light availability and percent volumetric water content, at the peak of the growing season, in each of the 1-m² plots using the same methods as described above for the experimental study. We also collected a 10-cm soil core from the center of each 1-m² plot to quantify potential net mineralization of nitrogen (NO₃⁻, NH₄⁺ and total N). To estimate potential net nitrogen mineralization, we incubated soil sub-samples from each 1-m² plot for 33 days and compared nitrogen availability of the incubated sub-samples with that of sub-samples extracted prior to incubation (Elliot et al. 1999).

To assess availability of NO₃⁻ and NH₄⁺ in the soil solution, we used 2 M KCl for extractions. The extracts were then filtered on Whatman no. 1 filter paper after rinsing with deionized water and frozen prior to analysis for concentration of NO₃⁻ and NH₄⁺. Pool sizes of NO₃⁻ and NH₄⁺ were analyzed on a Lachat AE Flow Injection Autoanalyzer (Lachat Quikchem 8000, Hach Corporation, Loveland, OH), using the indophenol-blue (Lachat Instruments, Inc. 1990) and cadmium reduction-diazotization (Lachat Instruments, Inc. 1992) methods, respectively. All values of NO₃⁻, NH₄⁺ and total N are based on air-dried resins.

Statistical analyses

To test the biotic and abiotic factors associated with *Lespedeza* abundance in the observational study, we built multiple regression models at each spatial scale and used all possible regressions for variable selection. We used the Akaike Information Criterion adjusted for small sample size (AIC_c; Anderson and Burnham 2002) to evaluate multiple regression models accounting for variation in *Lespedeza* abundance. Prior to regression analysis, we tested for significant correlations between all predictor variables using Pearson's correlation coefficient. Predictor variables with significant pairwise correlation coefficients ($r > 0.751$) were not used in the same model (Kumar et al. 2006). All regression analyses

were performed using SAS 9.1.3 (SAS Institute, Inc., Cary, NC).

At the 50-m² transect and old-field scales, we included the measured biotic (*Solidago* biomass, *Verbesina* biomass, N-fixer biomass, total above-ground biomass) and abiotic variables (light availability, soil moisture, and potential net nitrogen mineralization) in our model selection procedures. For 50-m² transects, biotic variables were calculated as the sum of 1-m² plots within each transect. On the other hand, abiotic variables were calculated as the sum and average respectively of 1-m² plots within 50-m² each transect. Similarly, at the old-field scale, biotic and abiotic variables were calculated as the sum and average respectively of 50-m² transects within each field. Once the final models were built, we obtained the residuals and tested whether they were normally distributed using a Shapiro-Wilk test. We found that residuals of *Lespedeza* foliar cover model at the 50-m² transect scale were not normally distributed and therefore we applied a log transformation ($\ln(y + 1)$).

Results

Experimental study

The effects of the treatment alone in 2005 and 2006 were strong: seedling establishment in N-reduced and

control plots always exceeded ($P < 0.05$) that of N-added plots (Fig. 1). *Lespedeza* seedling establishment was, on average, 15× lower in N-added plots than in N-reduced and control plots during two growing seasons. In 2005, time (Wilks' $\lambda = 0.49$, $df = 2,15$, $P = 0.02$), but no time × nutrient interaction (Wilks' $\lambda = 0.58$, $df = 2,15$, $P = 0.29$) affected *Lespedeza* seedling establishment. In 2006, neither time (Wilks' $\lambda = 0.75$, $df = 2,15$, $P = 0.13$) nor the time × nutrient interaction (Wilks' $\lambda = 0.80$, $df = 2,15$, $P = 0.53$) affected seedling establishment. In 2005, N-added plots contained ~9 seedlings m⁻² compared to ~93 and ~83 seedlings m⁻² in N-reduced and control plots, respectively (Fig. 1). Likewise, in 2006, N-reduced plots had 90 *Lespedeza* seedlings m⁻² whereas N-added plots averaged only 1 seedling m⁻² (Fig. 1).

Lespedeza seedling persistence was also lower in N-added plots compared to N-reduced plots only. *Lespedeza* seedling persistence was 76% lower in N-added plots compared to N-reduced plots ($F = 4.43$, $P = 0.03$), but seedling persistence did not differ between control and N-added and N-reduced plots ($P > 0.05$) (Fig. 2).

The abundances of *Lespedeza* and other N-fixing species was lower in N-added than in N-reduced plots, but did not differ from controls. In 2005, foliar cover of adult *Lespedeza* was 8× lower in N-added plots than in control plots and 4× lower in N-added plots than in N-reduced plots (Table 1). By 2006, soil

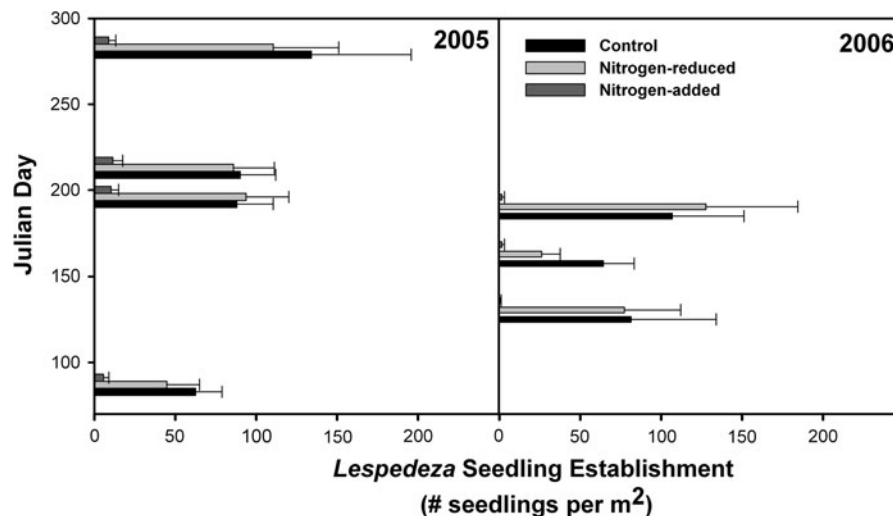


Fig. 1 *Lespedeza* seedling establishment (seedlings per m²) at each level of soil nitrogen availability in 2005 and 2006. Values are means and \pm SE

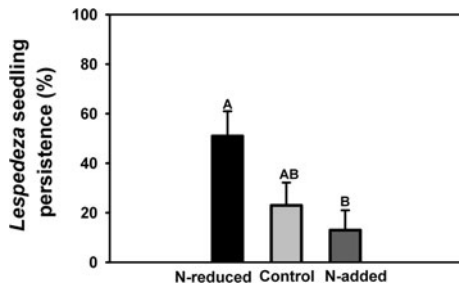


Fig. 2 *Lespedeza* seedling persistence (seedlings per m²) at each level of soil nitrogen availability in 2006. Values are means and \pm SE. Different letters represent statistical difference at alpha = 0.05 using Tukey’s HSD means separation test

Table 1 ANOVA results for cover of established adult *Lespedeza* and other N-fixer species in 2005 and for established adult *Lespedeza* cover and biomass of other N-fixer species 2006

	Mean	SE	F	P
2005				
Adult <i>Lespedeza</i> cover				
Control	16.5 ^a	5.6	5.58	0.008
N-added	2.6 ^b	1.2		
N-reduced	8.4 ^a	3.1		
Other N-fixer cover				
Control	53.3 ^a	7.2	6.95	0.007
N-added	15.0 ^b	6.2		
N-reduced	41.5 ^a	8.7		
2006				
Adult <i>Lespedeza</i> cover				
Control	2.2 ^a	0.3	1.68	0.219
N-added	3.8 ^a	2.3		
N-reduced	10.4 ^a	5.6		
Other N-fixer biomass				
Control	64.1 ^a	40.8	2.92	0.080
N-added	8.5 ^a	6.4		
N-reduced	117.6 ^a	36.8		

Values are untransformed mean and standard error (SE). Bold P-values are statistically significant. Superscripts indicate which means differed from one another

nitrogen had no effect ($P > 0.05$) on adult *Lespedeza* foliar cover (Table 1). Likewise, cover and biomass of other N-fixing plants were lower ($P < 0.05$) in N-added plots than in N-reduced plots in 2005 and 2006 respectively (Table 1).

N-added plots had on average 30% lower light availability than did control or N-reduced plots in both 2005 and 2006 (Appendix A1). In 2005, light

availability depended on time (Wilks’ $\lambda = 0.21$, $df = 2,15$, $P < 0.0001$) and the time \times nutrient interaction (Wilks’ $\lambda = 0.39$, $df = 2,15$, $P = 0.04$). In fact, light availability was $\sim 14\%$ lower in N-added plots than controls and 47% lower than in N-reduced plots. By 2006, only time (Wilks’ $\lambda = 0.05$, $df = 2,15$, $P < 0.0001$) affected light availability, though the time \times nutrient interaction (Wilks’ $\lambda = 0.53$, $df = 2,15$, $P = 0.20$) was no longer significant (Appendix A1). In fact, in 2006, N-added plots had on average 35% less light than did controls and 40% less available light than did N-reduced plots in 2006 (Appendix A1).

Soil moisture availability was 15% lower in N-added plots than N-reduced plots during both growing seasons. In 2005, time (Wilks’ $\lambda = 0.02$, $df = 2,15$, $P < 0.0001$), but no time \times nutrient interaction (Wilks’ $\lambda = 0.50$, $df = 2,15$, $P = 0.18$) affected soil moisture in this old-field community (Appendix A1). In fact, volumetric water content was 5% lower in N-added plots than in control plots and light availability was 15% lower in N-reduced plots than in control plots (Appendix A1). By 2006, soil moisture depended on both time (Wilks’ $\lambda = 0.04$, $df = 2,15$, $P < 0.0001$) and the time \times nutrient interaction (Wilks’ $\lambda = 0.43$, $df = 2,15$, $P = 0.06$). N-added plots had on average 10% lower soil moisture availability than did controls and 24% lower soil moisture availability than N-reduced plots.

Light availability and abundance of other N-fixer species, as well as of adult *Lespedeza* individuals, were the only factors associated with *Lespedeza* seedling establishment in both 2005 and 2006 (Appendix B1). In fact, higher light availability, early in the growing season, ($0.49 > r < 0.60$, $P < 0.01$) along with higher abundances of both N-fixers and adult *Lespedeza* individuals (Appendix B1), promoted *Lespedeza* seedling establishment in both 2005 and 2006. On the other hand, only light availability and biomass of other N fixers were important biotic covariates in predicting *Lespedeza* seedling establishment in 2005 and 2006 (Table 2).

Greater soil nitrogen stimulated total aboveground biomass later in the experiment, reducing both light availability and soil moisture. While N treatment did not affect total aboveground biomass in 2005 ($P > 0.05$), by 2006 N-added plots had 40% greater biomass than N-reduced plots, but did not differ from control plots ($F = 5.2$, $P = 0.02$). Consequently, total aboveground biomass was negatively correlated

Table 2 ANCOVA table of the effects of soil N treatment and biotic (adult *Lespedeza* and the abundance of other N-fixers) and abiotic (light availability) covariates on *Lespedeza* seedling establishment

Variables	DF	<i>Lespedeza</i> May		<i>Lespedeza</i> June		<i>Lespedeza</i> August		<i>Lespedeza</i> October	
		F	P	F	P	F	P	F	P
2005									
Soil nitrogen	2	0.157	0.86	0.984	0.40	0.374	0.70	1.852	0.20
Adult <i>Lespedeza</i>	1	0.090	0.76	0.911	0.36	2.012	0.18	3.393	0.09
Light availability	1	1.900	0.19	2.635	0.13	1.530	0.24	6.116	0.03
Other N-fixer cover	1	2.291	0.16	2.572	0.13	3.536	0.08	4.146	0.06
Variables	DF	<i>Lespedeza</i> March		<i>Lespedeza</i> May		<i>Lespedeza</i> June			
		F	P	F	P	F	P		
2006									
Soil nitrogen	2	0.548	0.59	1.170	0.34	1.590	0.24		
Adult <i>Lespedeza</i>	1	2.518	0.14	0.258	0.62	0.240	0.64		
Light availability	1	2.253	0.16	2.400	0.15	2.230	0.16		
Other N-fixer biomass	1	0.008	0.93	0.001	0.98	1.350	0.05		

Values in bold are statistically significant ($P < 0.05$)

with light availability ($R^2 = 0.30$, $P = 0.02$) in 2006, but not in 2005 ($R^2 = 0.01$, $P = 0.71$).

Observational study

Overall, multiple regression models predicting *Lespedeza* cover at the old-field scale accounted for more variation (69%) in *Lespedeza* abundance than did multiple regression models at the 50-m² transect (15%) (Table 3). Additionally, only biotic variables were important in predicting *Lespedeza* abundance across spatial scales, suggesting that resource availability was not directly associated with the successful establishment of *Lespedeza*.

The abundance of other N-fixing species was the biotic variable most consistently associated with *Lespedeza* abundance across the both the community and old-field scales. Across 50-m² transects and old fields, as the aboveground biomass of other N-fixing species increased, foliar cover of *Lespedeza* decreased (Table 3; Fig. 3). In turn, 50-m² transects and old fields with lower aboveground biomass of other N-fixers were more invaded by *Lespedeza*. Total biomass was also associated with *Lespedeza* cover, but only at the old-field scale. At the old-field scale, we found that old fields with greater biomass of other N-fixing species had lower foliar cover of *Lespedeza* (Table 3).

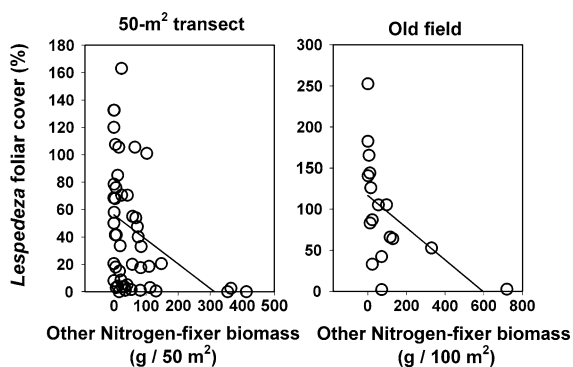
Discussion

Resource availability and *Lespedeza* seedling establishment

Lespedeza seedling establishment and persistence were lower in plots where soil N was added than in plots where soil N was reduced. Other studies have found that increasing soil nitrogen (Sanders et al. 2007) or increasing soil macronutrients (Ritchie and Tilman 1995) had a negative impact on *Lespedeza* cover and stem density. One proposed mechanism is that increases in soil N availability directly stimulate the production of resident plant species (native community), consequently altering the abiotic environment (i.e., soil moisture, light or macronutrient limitation). Such alteration of microhabitat can decrease community invasibility if change in conditions or reduction in resources is limiting for invaders. For example, increases in aboveground biomass can affect *Lespedeza* establishment in two ways at the neighborhood scale. First, greater biomass production can result in lower soil moisture and/or light availability limiting seedling survival and subsequent persistence (Davis and Pelsor 2001). Second, greater aboveground biomass can result in greater litter accumulation, which serves as a physical barrier to the establishment and/or persistence of

Table 3 Best multiple regression models explaining the variation of *Lespedeza* abundance at two spatial scales: 50-m² transects, and old fields

Variable	DF	Parameter	P	Partial R ²	Model R ²	P
Old field						
Intercept	1	0.4085	0.1242		0.69	0.001
Total aboveground biomass	1	0.0007	0.0014	0.39		
N-fixer aboveground biomass	1	-0.0021	0.0156	0.22		
<i>Solidago</i> aboveground biomass	1	0.0009	0.0249	0.08		
50-m ² transect						
Intercept	1	0.4058	<0.0001		0.15	<0.0001
N-fixer aboveground biomass	1	-0.0012	0.0055	0.15		

**Fig. 3** Linear relationship between *Lespedeza* foliar cover (%) and N-fixer aboveground biomass summed across 50-m² transects (a), and old fields (b) in 2006

Lespedeza seedlings (Facelli and Facelli 1993; Rasan et al. 2007).

Resource availability and community structure

Total aboveground biomass was higher in N-added plots compared to N-reduced plots, but not different from control plots. In our experiment, both soil moisture and light availability were lower in N-added plots than in N-reduced plots. Similar to our study, Davis and Pelsor (2001) found that increases in resource availability (soil moisture) resulted in greater aboveground biomass of the resident old-field community in Minnesota. Moreover, communities with greater aboveground biomass had lower light availability and were less invaded by native forbs.

Although light availability, adult *Lespedeza* cover, and abundance (i.e., foliar cover and aboveground biomass) of other adult N-fixer species were all

correlated with *Lespedeza* seedling establishment in both growing seasons, only light availability and other N-fixer abundance were important covariates in the ANCOVA model. Greater light availability for N-fixation and greater amounts of soil rhizobia surrounding N-fixer rhizosphere (Acharya et al. 2006) can promote *Lespedeza* seedling survival by stimulating seedling growth rates.

Community structure and *Lespedeza* abundance across scales

In contrast with the findings from the experiment (neighborhood scale), plant-available soil nitrogen, light availability, and soil moisture were not directly related to the abundance of *Lespedeza* at the community and old-field scales. Instead, similar biotic predictors to *Lespedeza* seedling establishment were strongly associated with the abundance patterns by *Lespedeza* at both community and old-field scales. For example, the abundance of other N-fixing species was consistently negatively associated with *Lespedeza* abundance at both spatial scales. It is likely that across 50-m² transects and old fields, greater N-fixer abundance may deter invasion by *Lespedeza* because established N-fixers are as well adapted to low N environments as *Lespedeza* is and are potentially competitively superior. Alternatively, *Lespedeza*, especially at greater abundance, can lower light availability limiting the abundance and distribution of shade-intolerant species, such as other N-fixing species (Tilman 1987). In fact, *Lespedeza* has been found to negatively impact native communities by displacing native species once it is well established (Price and Weltzin 2003; Brandon et al. 2004). Further,

it maybe that native N-fixers and *Lespedeza* may change their association depending on the stage of invasion. For example, during the initial stage of invasion (establishment stage), N-fixers may facilitate *Lespedeza* emergence and early persistence (as in our experimental study) by providing soil symbionts for N-fixation of *Lespedeza* seedlings. On the other hand, during later stages of invasion (as in the observational study where we looked at growth and spread of *Lespedeza*), interspecific competition between native N-fixers and *Lespedeza* rather than facilitation, may dominate interactions between *Lespedeza* and native N-fixers. In fact, Dietz and Edwards (2006) have suggested that mechanisms that promote and/or halt plant invasions during initial stages differ from those operating at later stages.

Old fields with greater total aboveground biomass exhibited higher *Lespedeza* abundance than did old fields with lower total aboveground biomass. In fact, total old-field biomass accounted for 40% of the variation in *Lespedeza* cover. We found in the experimental study, in small plots (0.16-m² quadrats) that productivity was negatively related to establishment by *Lespedeza*. However, for entire old fields, ranging in size from 5,000 to 70,000 m² we found that establishment was positively correlated with productivity. This seemingly paradoxical result is akin to the ‘invasion paradox’ reviewed by Fridley et al. (2007), in which they show that success of invasive species seems to be negatively correlated with native species richness at small spatial scales, but positively at larger spatial scales. Our results are reconcilable with the hypothesis that, at local, neighborhood scales, productivity of the native community limits invasion, perhaps because of reduced space, light, or water availability. But at larger spatial scales, sites that are productive (i.e. favorable environments) are good places for invasive species, just as they are for native species. Taken together, these results show that the factors that limit invasion at one scale may actually promote invasion at another spatial scale.

Future studies should focus on better understanding the population dynamics of *Lespedeza* and other invasive species across spatial scales in order to better predict and manage overall population growth rates. For example, Schutzenhofer and Knight (2007) found that isolating particular demographic stages associated with higher fitness can successfully target

management efforts rather than attempting to control every demographic stage.

Conclusions

Overall, we found that increases in resource availability, such as soil N, could deter initial invasion by a Rank 1 invasive species, *Lespedeza cuneata*, in old-field communities. Greater community biomass, lower light and soil moisture availability, as well as lower foliar abundance of N-fixing species (including adult *Lespedeza* individuals) in N-added plots, all likely reduced *Lespedeza* seedling establishment. Similar biotic factors as in our experimental study also accounted for patterns of *Lespedeza* abundance across spatial scales, but in some counterintuitive ways. Greater aboveground biomass was positively associated with *Lespedeza* abundance in the observational study while negatively associated with the establishment of *Lespedeza* in the experimental study. The contradictions in our findings likely result from commonly documented ‘scale dependent paradox’ whereby favorable environments hinder invasions at small spatial scales, yet promote invasions at large spatial scales. Additionally, N-fixer biomass was negatively associated with *Lespedeza* abundance in the observational study while positively associated with the establishment of *Lespedeza* in the experimental study. Again, interactions between native N-fixers and *Lespedeza* likely change with stages of invasion ranging from facilitation during early invasion and interspecific competition during late stages of invasion. The management of *Lespedeza* will depend on both stage of invasion and spatial scale of management efforts. Variation in resource availability will be a key factor guiding management efforts directed at controlling *Lespedeza* seedling emergence (early establishment) at small spatial scales. On the other hand, community properties (total biomass, other N-fixer biomass) are associated with *Lespedeza* patterns of abundance (later establishment) across spatial scales.

Acknowledgments We thank Emily Austin, Courtney Campany, Cayenne Engel, John Evans, William Farrell, Emmi Felker-Quinn, Elizabeth Ferguson, Onike Mnzava, Zach Kiershman, Katherine Sides, and Joanne Ledford for help in the field and lab. Additionally, lab work would not have been possible without protocols provided by Aimée Classen, as well as laboratory space and supplies provided by Department of Energy, Grant No. DE-FG02-02ER63366. James Evans

facilitated field logistics. Aimée Classen, Martin Nuñez and Daniel Simberloff provided insightful comments on earlier versions of this manuscript. The Department of Ecology and Evolutionary Biology at the University of Tennessee provided funding to LS through a Summer Research Award.

Appendix

See Tables 4, 5

Table 4 ANOVA results for light and soil moisture availability in 2005 and 2006

2005		Light availability ($\mu\text{mol photons m}^2 \text{ s}^{-1}$)				2006		Light availability ($\mu\text{mol photons m}^2 \text{ s}^{-1}$)			
		Mean	SE	F	P			Mean	SE	F	P
May	Control	314.5	33.4	3.33	0.0634	April	1239.5 ^a	67.5	6.94	0.0074	
	N-added	136.9	73.2				780.9 ^b	119.6			
	N-reduced	541.8	66.5				1231.3 ^a	104.5			
June	Control	139.7 ^a	29.4	17.18	0.0001	May	104.7 ^{ab}	22.1	7.47	0.0056	
	N-added	359.7 ^a	89.1				51.2 ^a	14.4			
	N-reduced	140.7 ^b	18.1				150.9 ^b	15.1			
July	Control	105.9 ^a	26	5.29	0.0183	June	92.4 ^{ab}	6.9	5.73	0.014	
	N-added	143.7 ^b	33.5				44.5 ^a	12.5			
	N-reduced	155.0 ^a	39.7				113.8 ^a	21.3			
August	Control	89.3	12.2	0.59	0.57	July	119.1	23	0.81	0.46	
	N-added	90.9	14.7				98.3	18.6			
	N-reduced	121.8	23.5				146.8	36.1			
2005		Soil volumetric water content (%)				2006		Soil volumetric water content (%)			
		Mean	SE	F	P			Mean	SE	F	P
June	Control	8.5 ^a	0.7	5.95	0.0135	April	19.6	1	1.79	0.2009	
	N-added	8.5 ^a	0.4				20.2	0.5			
	N-reduced	9.8 ^b	0.6				21.7	0.8			
August	Control	12.6	1.1	1.8	0.1995	May	17.7 ^{ab}	0.4	6.76	0.0081	
	N-added	11.9	0.6				16.1 ^b	0.8			
	N-reduced	13.7	0.7				20.1 ^a	1			
September	Control	6.1	0.6	1.11	0.3553	June	11.2 ^a	0.8	18.97	<0.0001	
	N-added	5.2	0.4				9.9 ^a	0.7			
	N-reduced	5.9	0.5				17.3 ^b	1.1			
						July	8	1	1.8	0.1994	
							7.2	0.9			
							9.6	0.8			

Values are mean and standard error (SE) of untransformed variables. Bold *P*-values are statistically significant. Superscripts indicate which means differed from one another

Table 5 Correlation matrix of biotic (*Solidago biomass*, *Verbesina biomass*, Total biomass, Adult *Lespedeza* cover) and abiotic (light and soil moisture availability) variables against *Lespedeza* seedling establishment through time (March–October) in 2005 and 2006

2005 Variable	May		June		August		October	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Light May	0.49	0.002	0.5	0.002	0.49	0.002	0.6	0.001
Light June	−0.17	0.335	−0.15	0.371	−0.14	0.425	−0.07	0.669
Light July	0	0.988	−0.01	0.936	0.01	0.95	−0.03	0.839

Table 5 continued

2005 Variable	May		June		August		October	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Light August	0.06	0.746	0.05	0.785	0.11	0.535	0.21	0.21
Soil moisture May	0.25	0.148	0.19	0.264	0.21	0.237	0.17	0.339
Soil moisture June	0.2	0.233	0.22	0.205	0.19	0.272	0.25	0.139
Soil moisture July	0.27	0.118	0.34	0.04	0.31	0.067	0.4	0.015
Soil moisture September	0.14	0.419	0.23	0.186	0.21	0.228	0.3	0.078
Total biomass	-0.17	0.313	-0.24	0.163	-0.25	0.144	-0.3	0.077
<i>Solidago</i> biomass	-0.19	0.265	-0.23	0.171	-0.25	0.144	-0.27	0.106
<i>Verbesina</i> biomass	0.04	0.818	0.04	0.799	0.04	0.839	0.01	0.971
<i>Lespedeza</i> cover	0.63	<0.001	0.62	<0.001	0.57	<0.001	0.52	0.001
Other N-fixer cover	0.46	0.057	0.54	0.021	0.6	0.009	0.39	0.107
2006 Variable	March		May		June			
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>		
Light April	0.42	0.081	0.3	0.233	0.48	0.043	-	-
Light May	0.74	0	0.47	0.051	0.59	0.01	-	-
Light June	0.54	0.02	0.66	0.003	0.64	0.004	-	-
Soil moisture April	0.17	0.501	0.19	0.439	-0.12	0.625	-	-
Soil moisture May	0.46	0.052	0.37	0.126	0.33	0.183	-	-
Soil moisture June	0.41	0.088	0.49	0.037	0.36	0.141	-	-
Total biomass	-0.16	0.533	-0.04	0.888	-0.29	0.247	-	-
<i>Solidago</i> biomass	-0.38	0.116	-0.33	0.175	-0.49	0.04	-	-
<i>Verbesina</i> biomass	0.04	0.864	-0.28	0.266	-0.17	0.493	-	-
<i>Lespedeza</i> cover	0.57	0.015	0.37	0.126	0.45	0.063	-	-
Other N-fixer biomass	0.45	0.063	0.5	0.035	0.7	0.001	-	-

Values in bold are statistically significant ($P < 0.05$)

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