Differential effects of two dominant plant species on community structure and invasibility in an old-field ecosystem

Lara Souza¹,* , Jake F. Weltzin² and Nathan J. Sanders¹

Abstract

Aims
In this study, we examined the effects of Solidago altissima (hereafter Solidago) and two species in the genus Verbesina, Verbesina virginica and Verbesina occidentalis (hereafter Verbesina), on the structure of an old-field plant community and establishment by an invasive plant species, Lespedeza cuneata (hereafter Lespedeza).

Methods
We removed Solidago, Verbesina and both Solidago and Verbesina from 4-m² plots in an intact old-field community during two growing seasons. We then quantified the effects of these removals on richness, evenness, diversity and composition of the subdominant plant community. We also measured the total aboveground biomass and the aboveground biomass of the subdominant community. To assess how these removals affected establishment by Lespedeza, we planted 20 seeds in each plot and tracked seedling emergence and survival for one growing season.

Important Findings
Subdominant community evenness and Shannon diversity were higher in plots from which Solidago and Verbesina were removed relative to control plots. However, there were no effects of dominant species removal on species richness or composition of the subdominant community. Total aboveground biomass was not affected by dominant species removal, suggesting that the community of subdominant species exhibited compensation. In fact, subdominant community biomass was greater when Solidago, but not Verbesina, was removed. Light availability was also greater in plots where Solidago was removed relative to control plots throughout the growing season. In addition, removal of dominant species, in particular Solidago, indirectly reduced the emergence, but not survival, of Lespedeza seedlings by directly promoting subdominant community biomass. Taken together, our results suggest that dominant old-field plant species affect subdominant community structure and indirectly promote establishment by Lespedeza.

Keywords: compensation • establishment • invasive • Lespedeza cuneata • Solidago • Verbesina

Received: 20 April 2010 Revised: 28 September 2010 Accepted: 29 September 2010

INTRODUCTION

Dominant species are those that comprise the greatest proportion of the production and/or resource uptake in local plant communities, thereby playing an important role in driving community dynamics and regulating ecosystem processes (Bazzaz 1996; Chapin et al. 2000; Dangles and Malmqvist 2004; Grime 2001; Goldberg and Barton 1992; Hector et al. 1999; Hooper 1998; Hooper and Vitousek 1997; Hooper et al. 2005; McNaughton and Wolf 1970; May 1978; Wardle et al. 1999; Whittaker 1972). When dominant species alter the structure of the subdominant community and affect ecosystem processes, they may also influence community invasibility (Bazzaz 1996; Hobbs and Huennekke 1992; Huston and Smith 1987; Meiners et al. 2002). For instance, there is some evidence that dominant plant species can hinder plant invasions in grasslands and old-field communities via resource competition for limiting nutrients and/or space (Crawley et al. 1999; Dukes 2002; Emery and Gross 2006, 2007; Smith and Knapp 1999; Smith et al. 2004; Wilsey and Polley 2002).
Of course, not all dominant species are equal and have equivalent effects on the rest of the community. That is, dominant species identity affects community structure and invasibility in a variety of ways. For example, Emery and Gross (2006) found that the effect of dominant species on invasibility varied among dominant species, with some dominant species having positive effects on the establishment by exotic species and others having negative effects. In their study, old-field communities that were dominated by exotic species, such as Bromus inermis and Centaurea maculosa, exhibited high susceptibility to invasion by native and nonnative seedlings, whereas communities dominated by the native species Andropogon virginicus had high resistance to invasion. Whether dominant plant species differentially affect structure of the subdominant community and invasibility in other systems remains an open question.

In this study, we examined whether the removal of dominant plant species in an old-field community affects community structure, ecosystem processes and invasion by a nonnative species. We removed the dominant forb species Solidago altissima (hereafter Solidago) and two species in the genus Verbesina (Verbesina occidentalis and Verbesina virgínica, hereafter Verbesina), which together comprise almost half of the aboveground biomass in these old fields. We did not differentiate between Verbesina species in the field as they have similar life history traits and morphologies. In fact, both Verbesina species are perennial and have similar phenologies and occur at similar abundances across local old-field communities (Souza and Bunn, unpublished data). Specifically, we made four predictions. First, the removal of dominant plant species would increase richness, evenness and Shannon diversity and alter the composition of the community of subdominant species via release from competitive effects resulting in greater resource availability. Second, the removal of dominant plant species would alter light and soil nitrogen availability shaping compensatory responses of the subdominant species. Third, the removal of dominant species would increase resource availability and therefore promote the emergence and survivorship of the exotic species Lespedeza, a Rank 1 invasive species via increases of resource availability or hinder emergence and survivorship of Lespedeza given strong compensatory responses of the subdominant community. Fourth, the effects of species removal would depend on the identity of the dominant species given that dominant species can vary in their resource use and effects on other species.

MATERIALS AND METHODS

Study site

In spring 2005, we initiated an experiment in an old field at Oak Ridge National Environmental Research Park, near Oak Ridge, TN (35° 58’N 84° 17’W). The old-field site was used for agriculture until 1943 and is mowed each spring. The soil has a silty clay loam texture and is classified as Typic Hapludult. Mean annual rainfall is 1322 mm and mean air temperature ranges from 2.7°C (January) to 31.2°C (July).

Solidago and Verbesina, which together comprise ~40% of total aboveground biomass, are the dominant species at this site and across old fields in the area. Solidago is an abundant and widespread species in old fields in the USA (Semple and Cook 2006). Solidago makes up, on average, 20% (range = 5–47%) of the aboveground biomass in old-field communities near our study site (Souza and Bunn, unpublished data). Additionally, previous work near our site has shown that Solidago can influence ecosystem processes such as productivity (Crutsinger et al. 2006) and the structure of associated arthropod communities (Crawford et al. 2007; Crutsinger et al. 2006, 2008). Verbesina makes up, on average, 18% (range = 0–73%) of the aboveground biomass in old-field communities near our study site (Souza and Bunn, unpublished data). However, little is known about the effects of Verbesina on communities and ecosystems, though it is a common genus in the eastern USA (Chappelka et al. 2003). In addition, ~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 (Souza and Bunn, unpublished data).

Experimental manipulation

Beginning in spring 2005, we manipulated the presence of Solidago and Verbesina in twenty-four 2 × 2-m plots in an existing old-field community. The plots were spaced 1 m from each other in a completely randomized plot design. The experiment was a 2 × 2 factorial design: Solidago (present or removed) and Verbesina (present or removed). We clipped the dominant species (to 1 cm from the ground) throughout the growing season (April–October), but during the peak of the growing season (July and August), target species were clipped as necessary at least every week.

On average, control plots (those from which neither Solidago nor Verbesina were removed) consisted of 156 g m⁻² of Solidago and 125 g m⁻² of Verbesina. Solidago made up, on average, 30% of the total biomass of control plots and Verbesina made up, on average, 20% of the total biomass of control plots. The removal of one codominant species did not affect the biomass or cover of the other (P ≥ 0.10 in all cases).

Community- and ecosystem-level responses

In each of the plots, we tallied plant species richness (S) and foliar cover of each plant species present at the beginning of the experiment (June 2005) and then at the peak of the growing season in August 2006, 1 year after the initiation of the experiment (see Supplementary table S1 for species-specific foliar cover across removal treatments). We estimated species-specific foliar cover using a modified Braun-Blanquet cover class scale (Braun-Blanquet 1932). The modified Braun-Blanquet scale included six categories: 1 = <1%, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75% and 6 = 75–100%. We also quantified the responses of different functional groups
(forbs, graminoids, nitrogen fixers, woody species) to the removal of dominant species (see Supplementary table S2 for average foliar cover of plant functional groups across removal treatments) by summing up the total foliar cover across individuals that belonged to each functional group. We calculated the Shannon diversity index ($H'$) from foliar cover data (August 2006) by using the median of each cover class category as our value of abundance (excluding foliar cover of Lespedeza, Verbesina and Solidago). We calculated evenness ($J'$) as $H' / \ln(n(S))$.

In August 2006, we estimated aboveground biomass by clipping to 1 cm aboveground level all plants within a randomly placed $0.5 \times 1$ m quadrat within each experimental plot. We categorized each clipped stem into one of the following groups: Solidago, Verbesina or subdominant species. Clipped biomass was oven-dried at 60°C for approximately 48 h and then weighed.

We measured photosynthetic photon flux density (PPFD, hereafter light availability) monthly from April to August in 2006 in each of the 24 experimental plots, as well as soil nitrogen availability. To estimate light availability, we used a line-integrating ceptometer (Decagon Accupar; Decagon Devices, Pullman, WA) with all light availability measurements made on clear days between 11 am and 2 pm. To assess the availability of NO$_3^{-}$ and NH$_4^+$ in the soil solution, we placed mixed-bed ion-exchange resin bags in nylon stockings (H-OH form, #R231-500; Fisher Scientific International Inc., Pittsburgh, PA) at 5-cm soil depth at two locations in each of the 24 experimental plots (Hart et al. 1994). Resins were then air-dried, and 2 g of resins from each plot were extracted with 2 M KCl. Pool sizes of NO$_3^{-}$ and NH$_4^+$ were analyzed on a Lachat AE Flow Injection Autoanalyzer (Lachat Quikchem 8000; Hach Corporation, Loveland, OH). All values expressed in this article are based on air-dried resins.

**Emergence and survivorship of Lespedeza seedlings**

In March 2006, we added 20 Lespedeza seeds (Ernst Conservation Seeds, Meadville, PA) to each of the 24 plots. Ten seeds were buried 1 mm deep at 7-cm spacing within each of two grids, within each plot, where each grid was located 0.5 m from the northern and southern edges of the plot. The location of each seed was marked with a painted nail so that we could track emergence and survivorship of seedlings over the course of the growing season. We censused emerged seedlings every 2 weeks between May and August 2006 and recorded both the number of seedlings that emerged and, of the seedlings that emerged, the number of seedlings that survived until August. Although seedling emergence and survival are only the first steps in invasion success, several studies support their importance in driving the distribution of species and invasions in grassland systems (Gross and Werner 1982; Foster et al. 2002).

**Statistical analyses**

To examine the effects of the removal of codominant species on plant community structure and on establishment by Lespedeza, and to investigate the potential mechanisms underlying those effects, we used a Multivariate Analysis of Variance (MANOVA) model followed by a series of generalized linear models (GLMs). The MANOVA allowed us to test whether there was an overall effect of the treatments on the linear combination of response variables as a whole. In the MANOVA and GLMs, the effects were (i) Solidago (at two levels: present or removed) and (ii) Verbesina (at two levels: present or removed). The response variables in the MANOVA and GLMs were subdominant species richness, subdominant species evenness, subdominant Shannon diversity, subdominant biomass, total biomass, light and soil N availability and Lespedeza seedling emergence and survival. We used Tukey’s HSD means separation test ($\alpha = 0.05$) to identify which treatment means differed from one another.

We used GLMs with Solidago and Verbesina as main factors and used the following covariates: biomass of the subdominant community, species richness, evenness (excluding Lespedeza, Verbesina and Solidago), light availability and the foliar cover of mature Lespedeza to test effects on emergence and survival of Lespedeza. We built a correlation matrix including covariates to test for significant pairwise correlations ($P < 0.05$). Finally, in the GLMs, we chose a Poisson distribution when analyzing count response variables such as subdominant species richness and Lespedeza seedling emergence. For proportion data such as Lespedeza seedling survival, we used a binomial distribution, and for the remainder variables, we used a normal distribution.

We used PRIMER (Plymouth Marine Laboratory, UK) to conduct an analysis of similarity (ANOSIM) followed by pairwise comparisons to examine the effects of dominant species on composition of the subdominant community. In the analysis, we created two main grouping factors: Solidago (present or removed) and Verbesina (present or removed). Based on species-specific foliar cover of each subdominant species, we constructed a nonmetric multidimensional scaling (NMDS) plot, a nonparametric approach, using Bray–Curtis similarity coefficients from a triangular matrix (Bray and Curtis 1957) of euclidean distances of samples within versus among removal treatments. Further, the NMDS plot can illustrate similarity and/or dissimilarity in composition between communities. We excluded one of the plots from all analyses because it contained a fast-growing autumn olive shrub (Elaeagnus umbellata) that was unique to that plot and substantially altered overall biomass and structure of that plot.

**RESULTS**

**Community- and ecosystem-level responses**

The MANOVA indicated that the removal treatments differed in their effects on community- and ecosystem-level processes (Wilks’ $\lambda = 0.163$, degrees of freedom [df] = 7, 13, $F = 9.49$, $P < 0.001$). Because the MANOVA indicated an overall effect of the treatments, we followed the MANOVA with subsequent GLMs.
The removal of the two dominant plant taxa affected some aspects of the structure of the subdominant community. Evenness and Shannon diversity of the subdominant community were both, on average, 20% greater in Solidago removal plots than in plots where Solidago was present. Likewise, subdominant community evenness and Shannon diversity were, on average, 30% greater in Verbesina removal plots than in plots where Verbesina was present (Table 1; Fig. 1). However, the removal of dominant taxa did not affect species richness of the subdominant community (Table 1), and the ANOSIM indicated that composition of the subdominant community was also not affected by the removal of either Solidago (global \( R = -0.084, P = 0.84 \), Supplementary table S3) or Verbesina (global \( R = -0.004, P = 0.47 \), Supplementary table S3).

The responses of individual taxa to the treatments (when both dominant species were removed vs. plots where both dominant species were present) varied dramatically: cover of Sorghum halepense was 11× greater in removal plots (5.4%) than in control plots (0.5%); Lonicera japonica was 31× greater in removal plots (15.4%) than in control plots (0.5%) and Elephantopus carolinianus (5.9% in removal plots), Rubus flavinanus (17.1% in removal plots) and Solidago gigantea (10.4% in removal plots) were all absent in control plots, but attained relatively high cover values in the removal plots. Yet, there were no main effects of Solidago or Verbesina removal treatments on the total abundance of exotic species, in terms of foliar cover (\( F = 0.61, P = 0.44 \), and \( F = 0.32, P = 0.58 \), respectively), as well as on the total abundance of native plant species (\( F = 1.16, P = 0.29 \), and \( F = 0.41, P = 0.53 \), respectively). We note that L. japonica, R. flavinanus and S. halepense are all exotic species in East Tennessee. Additionally, the abundance of woody species was 45% greater in Solidago removal plots than in plots where Solidago was present, whereas the abundance of forb species was 55% lower in Verbesina removal plots than in plots where Verbesina was present (Supplementary table S2).

Removal of dominant taxa led to compensatory responses by the subdominant species. Biomass of the subdominant community was 49% greater in plots from which Solidago was removed than in plots where Solidago was present, but did not differ in plots where Verbesina was removed compared to plots where Verbesina was present (Table 1; Fig. 2). However, there was no effect of dominant species removals on total community biomass (Table 1; Fig. 2), suggesting that subdominant species compensated for the removal of both dominant species. For instance, when both dominant species were present total community biomass was, on average, 544 g m\(^{-2}\). When both

### Table 1: results for GLMs of effects of dominant species removal on total community biomass, subdominant biomass, subdominant richness, subdominant evenness and subdominant diversity

<table>
<thead>
<tr>
<th>Treatment</th>
<th>df</th>
<th>Chi square</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total community biomass</td>
<td>1, 19</td>
<td>0.5971</td>
<td>0.4397</td>
</tr>
<tr>
<td>Solidago removal</td>
<td>1, 19</td>
<td>0.2685</td>
<td>0.6043</td>
</tr>
<tr>
<td>Verbesina removal</td>
<td>1, 19</td>
<td>1.5363</td>
<td>0.2151</td>
</tr>
<tr>
<td>Solidago × Verbesina removal</td>
<td>1, 19</td>
<td>4.8260</td>
<td>0.0280</td>
</tr>
<tr>
<td>Subdominant community biomass</td>
<td>1, 19</td>
<td>0.0179</td>
<td>0.8935</td>
</tr>
<tr>
<td>Solidago removal</td>
<td>1, 19</td>
<td>1.2926</td>
<td>0.2489</td>
</tr>
<tr>
<td>Verbesina removal</td>
<td>1, 19</td>
<td>1.4207</td>
<td>0.2333</td>
</tr>
<tr>
<td>Solidago × Verbesina removal</td>
<td>1, 19</td>
<td>9.1966</td>
<td>0.0025</td>
</tr>
<tr>
<td>Subdominant community diversity</td>
<td>1, 19</td>
<td>14.6101</td>
<td>0.0001</td>
</tr>
<tr>
<td>Solidago removal</td>
<td>1, 19</td>
<td>1.6824</td>
<td>0.1946</td>
</tr>
<tr>
<td>Verbesina removal</td>
<td>1, 19</td>
<td>0.9592</td>
<td>0.3274</td>
</tr>
<tr>
<td>Solidago × Verbesina removal</td>
<td>1, 19</td>
<td>0.4538</td>
<td>0.5005</td>
</tr>
</tbody>
</table>

Significant variables (\( P < 0.05 \)) are in bold.

**Figure 1:** effect of dominant species removal on mean (±standard error, \( n = 6 \)) subdominant Shannon diversity (top panel) and subdominant Shannon evenness (bottom panel). Treatments: P = no removal and R = species removal; different letters represent statistical difference at alpha = 0.05 using Tukey’s HSD means separation test.
dominant species were removed, the biomass of the subdominant community was 586 g m\(^{-2}\) (t = 0.20, df = 19, P = 0.85).

Light availability (PPFD) was, on average, 35% greater in plots from which Solidago was removed when compared to plots where Solidago was present throughout the growing season (Table 2). Light availability in Verbesina removal plots differed from plots where Verbesina was present only during the peak of the growing season (July) (Table 2). Verbesina comprised a smaller proportion of the total community biomass (20%) than did Solidago (30%). As a result, light availability was greater in Solidago removal plots than in Verbesina removal plots when compared to plots where Solidago and Verbesina were present, respectively (because only 20% of the aboveground biomass was removed). Finally, soil nitrogen availability in the form of nitrate was not affected by the Solidago (P = 0.49) or Verbesina (P = 0.20) removal compared to plots where Solidago and Verbesina were present, respectively. Likewise, the removal of Solidago (P = 0.66) or Verbesina (P = 0.09) did not alter soil ammonium compared to plots where Solidago and Verbesina were present.

**Emergence and survivorship of Lespedeza seedlings**

Dominant species removal did not directly affect emergence or survival of Lespedeza seedlings. However, richness of subdominant species, biomass of the subdominant community and cover of mature Lespedeza were important covariates for seedling emergence, but not survival (Table 3). Subdominant community and biomass was negatively related to both emergence (Fig. 3) and marginally negatively related to survival (Fig. 3) of Lespedeza seedlings, while mature Lespedeza cover was positively related to seedling emergence but not survival. Finally, total community biomass was not related to the emergence of Lespedeza seedlings (P = 0.52, F = 5.2) but was negatively related to Lespedeza seedling survival (P = 0.02, F = 6.47).

**DISCUSSION**

**Dominant species affect subdominant community structure**

Both Solidago and Verbesina affected the structure of the subdominant plant community in this old-field ecosystem. In particular, evenness and Shannon diversity of the subdominant community were higher when either Solidago or Verbesina were removed relative to control plots where both species were present. The removal of each dominant species led to an increase in equitability of the remaining subdominant species, at least over the course of this experiment. Furthermore, forbs and woody plant species responded to the removal of
dominant species to a greater extent than did grasses and N-fixers, and their responses depended on which dominant species was removed. This indicates that when *Solidago* or *Verbena* are present, they will suppress woody species (greater resource use overlap) or facilitate forb species perhaps more than they do subdominant species such as grasses and N-fixers (Supplementary table S2). The lack of responses by functionally dissimilar species, grasses and N-fixers to dominant species removal was not surprising, yet the contingency of responses by similar functional groups, woody species and forbs to dominant species removal was indeed an unexpected result.

Though the removal of dominant species affected Shannon diversity and evenness of the subdominant community, subdominant community richness and composition were not affected by either *Solidago* or *Verbena* removal. These two community metrics, richness and composition, might take longer to respond to the removal of dominant species. If our experiment continued for several years, recruitment by new species might have been higher in the removal plots than in the control plots. Similar to our study, Schmitz (2003) found that subdominant species richness did not differ in plots where *Solidago rugosa* was abundant compared to plots where *Solidago rugosa* was low. Additionally, Munson and Lauenroth (2009) found that dominant species influenced the composition of rare subdominant species but only after 8 years of removal treatments.

Biomass of the subdominant community was affected only by removal of *Solidago*, not removal of *Verbena*. Competition theory predicts that when a dominant species is removed from a community, the biomass of the rest of the community should increase (Tilman 1987; Whittaker 1965). In our system, the compensatory responses of the subdominant community were consistent with such a hypothesis but contingent upon the identity of the dominant species which was removed. In fact, total community biomass did not differ in either *Solidago* or *Verbena* removals relative to controls, further supporting compensatory responses by subdominant community biomass. Although the biomass of the subdominant community did not show compensatory responses to *Verbena* removal, we speculate that the lack of differences in total community biomass in *Verbena* present and *Verbena* removal plots may be due to the minimal effect of *Verbena* species in this old-field community.

Other studies have documented similar compensatory responses (Polley et al. 2007; Suding et al. 2006; Symstad and Tilman 2001; Wardle et al. 1999). For instance, Polley et al. (2007) found that removing annual species in a prairie ecosystem led to compensatory responses of the subdominant species and consequently total community biomass did not differ between removal plots and controls. Furthermore, Suding et al. (2006) found that the removal of one codominant alpine species, *Deschampsia caespitosa*, altered the structure of the

| Table 3: summary of GLMs for effects of *Solidago* and *Verbena* and covariates on emergence and survival of *Lespedeza* seedlings |

<table>
<thead>
<tr>
<th>Seedling emergence</th>
<th>Seedling survival</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>df</strong></td>
<td><strong>Estimate</strong></td>
</tr>
<tr>
<td>-------------------</td>
<td>------------------</td>
</tr>
<tr>
<td><em>Verbena</em> removal</td>
<td>7, 15</td>
</tr>
<tr>
<td><em>Solidago</em> removal</td>
<td>7, 15</td>
</tr>
<tr>
<td>Subdominant evenness</td>
<td>7, 15</td>
</tr>
<tr>
<td>Subdominant richness</td>
<td>7, 15</td>
</tr>
<tr>
<td>Subdominant biomass</td>
<td>7, 15</td>
</tr>
<tr>
<td>Light availability</td>
<td>7, 15</td>
</tr>
<tr>
<td><em>Lespedeza</em> foliar cover</td>
<td>7, 15</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Seedling emergence</th>
<th>Seedling survival</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>df</strong></td>
<td><strong>Estimate</strong></td>
</tr>
<tr>
<td>-------------------</td>
<td>------------------</td>
</tr>
<tr>
<td><em>Verbena</em> removal</td>
<td>7, 15</td>
</tr>
<tr>
<td><em>Solidago</em> removal</td>
<td>7, 15</td>
</tr>
<tr>
<td>Subdominant evenness</td>
<td>7, 15</td>
</tr>
<tr>
<td>Subdominant richness</td>
<td>7, 15</td>
</tr>
<tr>
<td>Subdominant biomass</td>
<td>7, 15</td>
</tr>
<tr>
<td>Light availability</td>
<td>7, 15</td>
</tr>
<tr>
<td><em>Lespedeza</em> foliar cover</td>
<td>7, 15</td>
</tr>
</tbody>
</table>

*P*-values $\leq 0.05$ are in bold.

Figure 3: a plot of the residuals of *Lespedeza* emergence (top panel) and survival (bottom panel) from the GLM including the main effects (Control, *Solidago* removal, *Verbena* removal, *Solidago* and *Verbena* removal) and the covariates (subdominant richness and evenness and foliar cover of *Lespedeza*) against biomass of the subdominant community. The line is the best-fit linear regression. Symbols: C = control, V = *Verbena* removed, S = *Solidago* removed and B = *Solidago* and *Verbena* removed.
subdominant community (removal increased evenness) and subdominant biomass partitioning. This suggests that the subdominant communities of plants in the tall grass prairies, alpine meadow systems and old fields are able to compensate for species loss.

**Solidago indirectly limits Lespedeza establishment**

Solidago removal led to compensatory responses of the subdominant community, which in turn negatively affected both seedling emergence and survival of Lespedeza. Biomass of the subdominant community was higher in Solidago removal plots than in plots where Solidago was present. In turn, total community biomass was not affected by the removal of either dominant plant species as the subdominant community compensated for dominant species loss. Previous studies (Hector et al. 1999; Hooper 1998; Naeem et al. 1994; Tilman 1996) along with ecological theory (Tilman 2004) have suggested that high-productivity communities have greater resource use complementarity than low productivity communities and are less likely to be invaded than are low productivity communities. We found that biomass of the community of subdominant species was negatively associated with invasibility. This suggests that the suite of subdominant species in this system directly compete, most likely for space rather than light availability (i.e. not statistically significant covariate in GLM model), with potential colonizing species.

Mature Lespedeza cover and subdominant richness were positively associated with Lespedeza seedling emergence but not survival. Rhizobium inoculum can certainly be beneficial for seedling emergence, and plots with greater mature Lespedeza foliar cover potentially had higher densities of soil rhizobia than did plots with few mature Lespedeza individuals (Acharya et al. 2006). Since Lespedeza is a common species in this system, the potential for facilitative effects of adults on seedlings is likely. Finally, subdominant communities with greater richness also promoted Lespedeza seedling emergence. This finding may indicate that factors that promote subdominant richness also promote the early establishment by Lespedeza.

Of course, Lespedeza is only one species among many non-native invasive species in this system. Lespedeza is a Rank 1 invasive species across many US states (Eddy and Moore 1998; Hoveland and Donnelly 1985; Shely et al. 1999) and has been shown to alter native communities (Brandon et al. 2004; Garten et al. 2008; Price and Weltzin 2003). Moreover Lespedeza is the most common invasive species in this system (Souza et al., in review), and previous and ongoing work in this system has focused on Lespedeza (Sanders et al. 2007; Souza et al., in review). However, experiments similar to ours, focusing on the effects of dominant species on other invasive species, would be enlightening especially with a focus on the identity of dominant species. Additionally, experiments addressing the role of dominant species on community structure, ecosystem processes and invasibility could be conducted over longer temporal scales so we can make further generalizations of underlying processes structuring communities and shaping ecosystem processes and susceptibility to biological invasions.

In sum, our study, combined with other recent species removal studies, suggests that the consequences of species loss from plant communities may be contingent on the identity of the dominant species which results in differential responses of the subdominant plant community (Bret-Harte et al. 2004; Diaz et al. 2003; Emery and Gross 2006; Suding et al. 2006; Wardle et al. 1999). Compensatory responses by the subdominant community can be a function of the identity of the dominant species. Additionally, compensatory responses by the subdominant community can shape biological invasions. Although our findings suggest that Solidago and Verbesina might promote the early establishment by Lespedeza, they may limit the invasion dynamics of other exotic species. In particular, the cover of three exotic species (L. japonica, R. flavinanus and S. halepense) was significantly higher when the dominant species were removed. Future studies on the potentially diverse and differential effects of dominant species on plant community structure and function, as well as invasion dynamics, might identify generalities among ecosystems and the contingent effects of dominant species.

**SUPPLEMENTARY MATERIAL**

Supplementary tables S1–S3 is available at Journal of Plant Ecology online.

**FUNDING**

The Department of Ecology and Evolutionary Biology at the University of Tennessee (Summer Research Award to L.S.).

**ACKNOWLEDGEMENTS**

We thank Philip Allen, Rita Amaral, Windy Bunn, E. Cayenne Engel, John Evans, Elizabeth Ferguson, William Farrell, Zack Kiershmann, Kristin Lane and Onike Mnzawa for their great help during field work. We would like to thank Tara Sackett, Martin Nunez and the UTK community ecology group for helpful comments. James Evans from Tennessee Wildlife Resource Agency facilitated field logistics

Conflict of interest statement. None declared.

**REFERENCES**


