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# Insect herbivores change the outcome of plant competition through both inter- and intraspecific processes

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*Abstract*. Insect herbivores can affect plant abundance and community composition, and theory suggests that herbivores influence plant communities by altering interspecific interactions among plants. Because the outcome of interspecific interactions is influenced by the per capita competitive ability of plants, density dependence, and intrinsic rates of increase, measuring herbivore effects on all these processes is necessary to understand the mechanisms by which herbivores influence plant communities. We fit alternative competition models to data from a response surface experiment conducted over four years to examine how herbivores affected the outcome of competition between two perennial plants, *Solidago altissima* and *Solanum carolinense*. Within a growing season, herbivores reduced *S. carolinense* plant size but did not affect the size of *S. altissima*, which exhibited compensatory growth. Across seasons, herbivores did not affect *S. carolinense* density or biomass but reduced both the density and population growth of *S. altissima*. The best-fit models indicated that the effects of herbivores varied with year. In some years, herbivores increased the per capita competitive effect of *S. altissima* on *S. carolinense*; in other years, herbivores influenced the intrinsic rate of increase of *S. altissima*. We examined possible herbivore effects on the longer-term outcome of competition (over the time scale of a typical old-field habitat), using simulations based on the best-fit models. In the absence of herbivores, plant coexistence was observed. In the presence of herbivores, *S. carolinense* was excluded by *S. altissima* in 72.3% of the simulations. We demonstrate that herbivores can influence the outcome of competition through changes in both per capita competitive effects and intrinsic rates of increase. We discuss the implications of these results for ecological succession and biocontrol.

*Key words: biocontrol; coexistence; competition; density dependence; insect herbivory; intrinsic rate of increase; model selection; old-field communities; plant–insect interactions; response surface;* Solanum carolinense; Solidago altissima.

## Introduction

Numerous studies have documented herbivore effects on plant abundance and community composition (Brown and Heske 1990, Carson and Root 2000). Because herbivory rarely results in plant mortality, theory suggests that herbivores influence plant community structure by altering the competitive ability (i.e., ability to acquire resources) of one species with another (e.g., Crawley 1983, Louda et al. 1990). For example, herbivores could mediate coexistence by feeding on dominant plant species, weakening their competitive effects on others and leading to higher diversity. Alternatively, if herbivores selectively feed on inferior competitors, this could exacerbate the negative effects of competition, accelerating rates of competitive exclusion and reducing plant diversity. Although, in theory, selective feeding can change plant community structure by influencing interspecific competition, empirical support for this particular mechanism is weak. Because herbivores also influence other processes important for determining the outcome of competition, such as intrinsic rates of growth (Maron and Crone 2006) and intraspecific competition (Underwood and Halpern 2012), herbivore effects on these processes must be considered as well.

Herbivores could affect the outcome of interspecific competition in at least two ways: through changes in the per capita interspecific competitive ability of plants and changes in their total population size. This can be illustrated with a simple equation describing the outcome of competition between two species, $X$ and $Y$:

$$X_{t+1} = f(X_t) - \beta Y_t. \qquad (1)$$

The dynamics of species $X$ are a function of intraspecific interactions, $f(X_t)$, and interspecific competition, $\beta Y_t$ (for simplicity, the analogous equation for species $Y_{t+1}$ is not shown). The net competitive effect of species $Y$ on $X$ is the product of two components: the per capita competitive ability of species $Y$ on $X$ ($\beta$) and the total population size of $Y$, both of which can be influenced by herbivores (Louda et al. 1990, Chase et al. 2002). Many interspecific competition studies have examined the

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effect of herbivores on the per capita interspecific competitive ability of plants (reviewed by Hambäck and Beckerman 2003). Per capita effects are typically measured in terms of traits associated with resource intake, such as individual plant size, growth rates, or fitness, across one or two growing seasons (reviewed by Goldberg and Barton 1992). It is generally thought that herbivores decrease the interspecific competitive ability of plants by consuming plant tissue (thus reducing resource intake), making resources more available to undamaged plants (Crawley 1983, Louda et al. 1990). However, resource intake can sometimes increase following damage through compensatory growth or increased photosynthesis (i.e., tolerance to herbivory; Whitham et al. 1991, Strauss and Agrawal 1999), leaving fewer resources for undamaged plants.

Although several studies examine herbivore effects on the per capita interspecific competitive ability of plants, it is unclear how changes in per capita interspecific competitive ability alone (ignoring intraspecific processes) relate to changes in the outcome of interspecific competition and, thus, plant community structure. To our knowledge no empirical studies have examined how herbivory might affect the outcome of interspecific competition through changes in intraspecific processes, yet many population-level studies do suggest that herbivore effects on these processes can affect plant demography (Maron and Crone 2006). Changes in the intrinsic rate of increase have been documented in plant populations following release from herbivory (Fagan and Bishop 2000) and may explain how nonnative plants spread in novel environments (enemy release hypothesis; Keane and Crawley 2002). Recent work suggests that herbivores can also change intraspecific density dependence in plant populations, and that the strength and form of herbivore effects on plants may vary with plant size (Underwood and Halpern 2012). Because the outcome of interspecific competition is determined by both the per capita interspecific competitive ability of plants and their population sizes, measuring herbivore effects at both of these levels is necessary to separate the contributions of these different mechanisms.

To measure per capita interspecific competitive ability, intrinsic rate of increase, and density dependence simultaneously, mathematical models of competitive population dynamics must be fit to data so that parameters for each of these processes can be estimated. A comparison of model parameters estimated in the presence and absence of herbivores would then disentangle the mechanisms by which herbivores influence plant communities. These models would also allow results from experiments conducted over a few seasons to be extrapolated across many seasons, the time scale necessary to observe community dynamics. Measuring inter- and intraspecific processes requires experimental designs that simultaneously manipulate both plant densities and frequencies. Previous experimental studies have examined herbivore effects across a limited range of plant densities (examples in Hambäck and Beckerman 2003) so that density-dependent processes cannot be estimated for both plant species. These experiments have also confounded inter- and intraspecific density effects on plant growth (Inouye 2001). The necessary data for dissecting different mechanisms for herbivore effects on plant communities can be gathered using response surface experimental designs that simultaneously vary the densities and frequencies of both plant species over a wide range of values (Law and Watkinson 1987, Inouye 2001).

The goal of our study was to examine how insect herbivores affect a simple two-species plant community. We asked whether herbivore effects on the relative abundance of these two plant species are mediated through changes in their per capita interspecific competitive ability and/or through other processes (i.e., intrinsic rate of increase or strength of density dependence). We carried out a response surface field experiment over four years, allowing us to include the effects of herbivores on processes that occur only across years and to estimate across-year variance due to ontogeny or environmental variation. We measured plant densities across years in the presence and absence of insect herbivores and fit competition models to our experimental data (1) to identify which processes (i.e., per capita interspecific competition, intrinsic rate of increase, and strength of density dependence) were most influenced by herbivores, and (2) to determine how herbivore effects on processes varied with time. We used parameterized competition models (3) to simulate how herbivore-mediated changes to these processes might play out over time scales longer than the length of the experiment.

## METHODS

### *Study system*

*Solanum carolinense* and *Solidago altissima* are perennial herbaceous plants native to the eastern United States (Werner et al. 1980, Wise and Cummins 2006). Both species reproduce vegetatively and by seed, and co-occur in disturbed areas and early-successional agricultural fields. Both *S. carolinense* and *S. altissima* support generalist and specialist herbivores, including leaf chewers, phloem feeders, gall makers, and leaf miners. Herbivores are known to influence the performance (Root 1996, Wise and Sacchi 1996), population growth (Carson and Root 1999, Underwood and Halpern 2012), and natural selection (Meyer 1993, Wise and Cummins 2006) of both plant species.

In May 2007, *S. carolinense* and *S. altissima* root cuttings were planted at the Mission Road Research Facility at Florida State University (Tallahassee, Florida, USA; 30.52° N, 84.4° W). Cuttings (1.5 ± 0.2 g) were taken from greenhouse-grown plants collected from natural populations in north Florida and south Georgia between 2001 and 2007. Each cutting was placed in a 530-mL nursery pot with a 3:1 mixture of

Fafard 3 soil (Conrad Fafard, Agawam, Massachusetts, USA) to coarse sand, and was kept in a greenhouse for approximately six weeks (plant heights ~12–17 cm).

### *Experimental design and data collection*

In June 2007, *S. carolinense* and *S. altissima* were transplanted into 1-m$^2$ field quadrats, each with a particular combination of plant densities. A response surface experiment with 17 density combinations of *S. carolinense* and *S. altissima* were planted (densities were 1, 6, 12, and 18 individuals per 1-m$^2$ quadrat in various combinations; see Appendix A). We crossed each density treatment with the presence/absence of insect herbivores. Densities were chosen to span the range of natural densities (T. Kim, *unpublished data*). The 17 treatments within the response surface design (hereafter referred to as a set) were clustered together spatially (quadrats were separated by 1.5 m of weed mat). There were six replicate sets arranged as three pairs (paired sets were separated by 5–7 m of weed mat, and each pair was separated by 12–30 m). Thus the experiment encompassed a total of 102 1-m$^2$ quadrats, arranged in three spatial blocks, each block consisting of a pair of sets, each set comprising 17 density treatments (1092 planted individuals).

To manipulate the presence of herbivores, one of the sets in each block was sprayed once every two weeks with a nonsystemic insecticide, N-methyl carbamate (Sevin, GardenTech, Lexington, Kentucky, USA) to greatly reduce insect damage (20 mL Sevin/3.14 L water); control sets were sprayed with equal amounts of water throughout the growing season (May–October). Sevin has been shown to have little or no effect on plant growth or reproduction in other systems (Lau and Strauss 2005), and does not reduce pollinator visits or pollen germination of *S. carolinense* in the field in north Florida (A. Winn and K. Kilcourse, *unpublished data*). To ensure that competition occurred only between *S. carolinense* and *S. altissima*, other plant species were gently removed by hand. For grass culms not easily removed by hand, the broad-spectrum herbicide Glyphosate (Roundup, Scotts, Marysville, Ohio, USA) was applied using a sponge or paint brush. To confine roots, we trenched the perimeter of each 1-m$^2$ quadrat once per month using a shovel. We measured the number of stems of each species in each 1-m$^2$ quadrat from 2007 to 2010 in June when most stems (including seedlings) had emerged from the soil. To determine whether spray treatment was effective at reducing leaf damage and biomass, we measured plant damage (percentage of leaf area removed) on all leaves of all plants. For internal-feeding insects (mostly gall makers) on *S. altissima*, we also assessed gall damage as the proportion of *S. altissima* plants within each quadrat attacked by gall-makers. As a proxy for plant biomass, we also measured the total stem lengths for each plant. Total stem length was positively correlated with the total above- and belowground biomass of each plant species ($r^2 = 0.80$ for *S. carolinense* and $r^2 = 0.66$ for *S. altissima*; T. Kim, *unpublished data*). Correlations were obtained from nonexperimental plants grown in similar competitive environments. These nonexperimental plants were harvested at various times throughout the growing season between 2007 and 2010 and oven-dried; correlations between oven-dried mass and total length of stems were determined. A nondestructive measure of plant biomass was necessary to allow continued plant growth in the experiment.

### *Data analysis and fitting competition models to data*

To provide an overview of herbivore effects across years on plant damage and biomass, repeated-measures ANOVAs were used (PROC MIXED, SAS Institute 2010; see Appendix B for details). Repeated-measures ANOVAs also were performed to test for the effects of spraying and initial planting densities of *S. carolinense* and *S. altissima* on the final densities of *S. carolinense* and *S. altissima* stems in each year (PROC MIXED, SAS Institute 2010; see Appendix B for details). In all these cases, separate analyses were performed for *S. carolinense* and *S. altissima*.

Although ANOVA results provide an overview of the significance of herbivory and/or competition, they tell us little about the mechanism by which herbivores influence the outcome of competition, and do not allow us to make long-term predictions. To achieve these ends, we fit competition models to our data. Model-fitting was a two-step process: finding the most appropriate competition model and then incorporating herbivore effects. First, from a set of five standard competition models, we selected one model that best described interactions between *S. carolinense* and *S. altissima*. These models all have been commonly applied in ecology and include both linear (Ricker 1954, May 1974) and nonlinear (Leslie 1958, Hassell and Comins 1976, Law and Watkinson 1987) density effects (Appendix C). The response variable was stem recruitment in the next generation (i.e., total number of stems of each plant species in each quadrat; hereafter, stem density) and thus included stems from both asexual and sexual reproduction. Our model assumed that all stems contributed equally to population sizes regardless of reproductive origin and size. Model-fitting was performed in R version 2.12 using the bbmle package (Bolker 2010, R Development Core Team 2010). The model parameters were estimated using maximum likelihood and two error distributions (normal and Poisson). Because the strength of per capita competition and demographic processes could vary over the course of our four-year experiment, we divided our data set into three transition periods (change in densities from 2007 to 2008, 2008 to 2009, and 2009 to 2010). For each transition period, we fit the models pooling stem densities from sprayed and unsprayed treatments. We determined the second-order Akaike Information Criterion (AIC$_c$) for each model and used $\Delta$AIC$_c$ to select the best-fit models. $\mathrm{AIC_c}$ weights ($w$), which sum to 1, were used to indicate the relative support for each model (Burnham and Anderson 2002). Preliminary analyses (results not shown) indicated that the normal error distribution was a much better fit to the data, probably because stem densities remained high in most treatments and data variance did not meet Poisson assumptions (Fig. 1). The model that received the highest average support across the three transition periods was the Law and Watkinson (1987) competition model ($\bar{w} = 0.25$ for *S. carolinense* and $\bar{w} = 0.29$ for *S. altissima*; Appendix C); this model was therefore used in the following analyses.

Our second step involved incorporating herbivore effects into the Law and Watkinson competition model to determine which, and to what extent, model parameters were affected by herbivores:

$$X_{t+1} = X_t \lambda \frac{1}{1 + c(X_t + \beta_{XY} Y_t)}. \qquad (2)$$

The parameters in this model are the intrinsic rate of increase $\lambda$ (per capita growth rate at low densities), the competition coefficient $\beta_{XY}$ (per capita effect of species $Y$ on species $X$), and a constant that describes the response of species $X$ to both inter- and intraspecific densities, $c$ (strength of density dependence). We introduced herbivory terms ($\gamma$) into the model, adding a unique $\gamma$ to each of the model parameters (including the standard deviation, $\sigma$, in stem densities), either alone or in all possible combinations with others, creating a series of 16 alternative models embodying different ways in which herbivores might affect plant populations (Table 1). Models were fit to stem density data for each transition period separately. We used $\Delta\mathrm{AIC_c}$ and $\mathrm{AIC_c}$ weights ($w$) to select the best-fit model. In cases where multiple models had similar fits ($\Delta\mathrm{AIC_c} < 2$), we selected the most parsimonious model (Burnham and Anderson 2002). To determine the relative importance of each herbivory term ($\gamma$) across all models, importance weights ($w+$) of each $\gamma$ parameter were calculated by summing $\mathrm{AIC_c}$ weights across all models in which each $\gamma$ parameter occurred (Burnham and Anderson 2002). Unlike $\mathrm{AIC_c}$ weights, these importance weights ($w+$) sum to $>1$ because some models contained multiple $\gamma$ parameters; thus the $\mathrm{AIC_c}$ weights of these models were counted multiple times.

### *Simulating herbivore effects on the outcome of competition*

To examine how herbivore effects might play out over periods longer than the length of this experiment, we ran stochastic simulations (see Supplement) using the best-fit competition models with herbivore effects, chosen in step two. Simulations ran for 50 time steps, an appropriate time scale for examining *S. carolinense* and *S. altissima* persistence in old fields (Hartnett and Bazzaz 1985). We calculated 95% confidence intervals (CI) for each parameter in each transition period using *profile* and *confint* functions in R (Table 2). For the first time step, all parameter values were drawn from a distribution covering the 95% CIs of parameters estimated in transition 1, because processes associated with initial establishment in the field occurred during this transition period. In subsequent time steps, parameter values were all randomly drawn from their distributions in transition 2 or in transition 3, with equal probability, reflecting environmental and ontogenetic variability. Based on the likelihood contours for each pairwise combination of parameters within each transition period, the estimates for $\lambda$ and $c$ were positively correlated, whereas estimates for other pairs of parameters were uncorrelated or very weakly correlated (results not shown). We used independent draws from uniform distributions covering the 95% confidence intervals for all parameter values and induced positive correlations for $\lambda$ and $c$. We recorded the mean densities of *S. carolinense* and *S. altissima* in the last 25 times steps of each simulation, a period in which densities appeared to stabilize (hereafter referred to as final densities). Separate simulations were run using parameter estimates from the best-fit models in the presence and absence of herbivores; each of these scenarios was replicated 10 000 times.

## RESULTS

The spray treatment was effective in reducing leaf damage on both plant species, but the strength of spraying varied with year (interaction between year and spray treatment, $F_{3,228} = 4.32$, $P < 0.0001$ for *S. carolinense*; $F_{3,228} = 15.88$, $P < 0.0001$ for *S. altissima*; Fig. 1A, B; see Appendix B). In control plots, leaf damage was generally higher on *S. carolinense* than *S. altissima* (Fig. 1A). *S. carolinense* was frequently attacked by leaf-chewing insects such as *Manduca sexta*, *Leptinotarsa juncta*, and *Spodoptera exigua* throughout the growing season, with a mean of 22.3% leaf tissue loss averaged across years. In contrast, leaf damage on *S. altissima* was low (7.1% leaf tissue loss averaged across years), but attacks by aphids (*Uroleucon* sp.) and gall-forming flies (*Eurosta solidaginis*, *Rhopalomyia solidaginis*) were observed (27.8% of *S. altissima* individuals, averaged across years, had galls).

Herbivores had varying effects on growth in biomass and stem densities. Spray treatment increased *S. carolinense* biomass in the first year of the experiment, but had no effects in later years (interaction between year and spray treatment, $F_{3,228} = 6.47$, $P = 0.0003$; Fig. 1C). Spray treatment had no effect on the densities of *S. carolinense* across years (interaction between year and spray treatment, $F_{3,222} = 1.05$, $P = 0.37$; Fig. 1E). In contrast, spray treatment had no effect on *S. altissima* biomass and densities except in the last year of the experiment (interaction between spray and year on biomass, $F_{3,228} = 5.25$, $P = 0.0016$), interaction between spray and year on densities, $F_{3,222} = 9.24$, $P < 0.0001$; Fig. 1D, F).

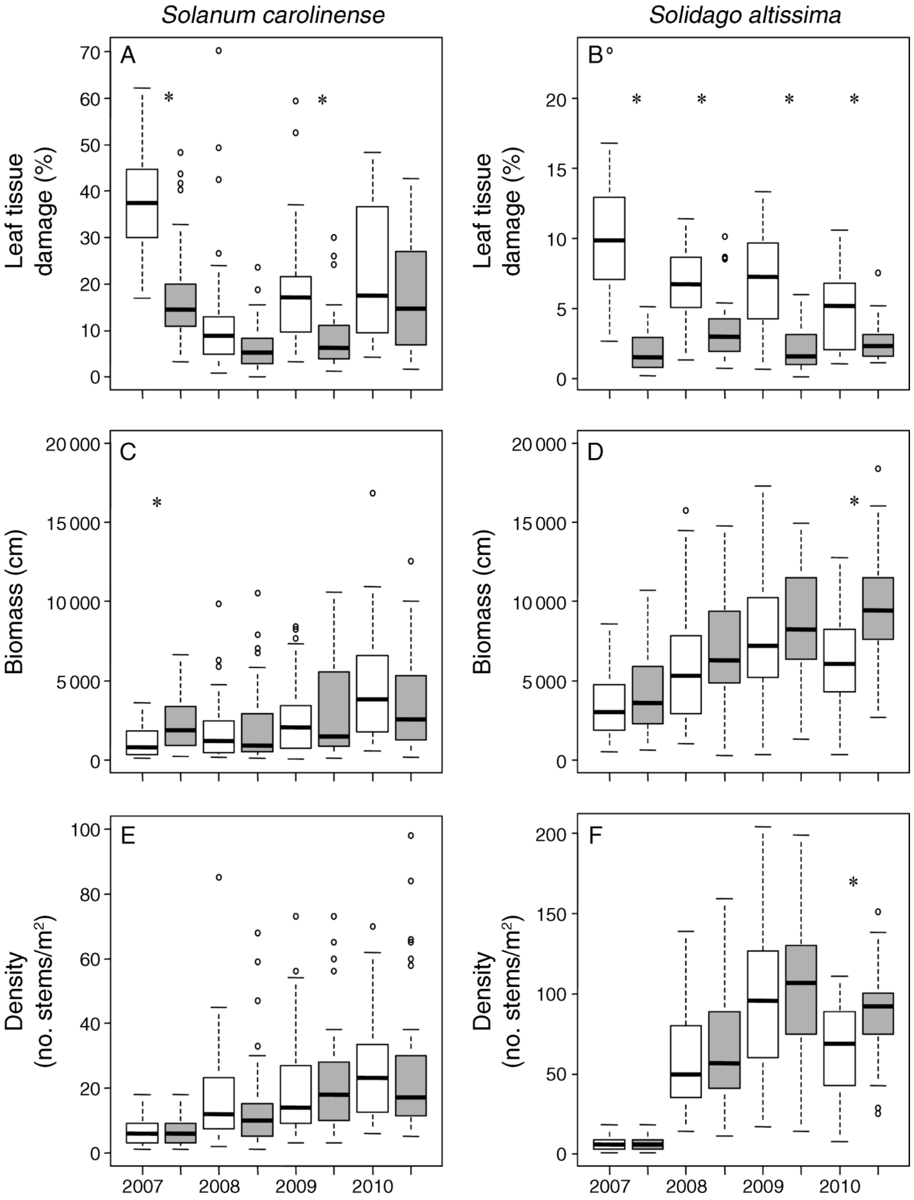

FIG. 1. Spray treatment effects on (A, B) leaf tissue damage, (C, D) biomass, and (E, F) stem density of *Solanum carolinense* and *Solidago altissima*. White boxes represent herbivores present (unsprayed control); gray boxes represent herbivores absent (sprayed with insecticide). Thick horizontal lines indicate medians, and whiskers encompass 1.5 times the interquartile range from the boxes. Leaf damage was averaged for plants in each 1-$m^2$ quadrat. Biomass was the sum of all stem lengths in each 1-$m^2$ quadrat. Stem densities for all 17 density treatments are included in the boxplots. Asterisks indicate significant ($P < 0.05$) spray treatment effect within years (see Appendix B for details).

The densities of stems were also influenced by the initial planting densities of *S. carolinense* and *S. altissima* (Appendix B). Although stem densities in any given year were influenced by the initial planting densities of conspecifics (interaction between year and initial conspecific densities, $F_{3,222} = 20.76$, $P < 0.0001$ for *S. carolinense*; $F_{3,222} = 42.24$, $P < 0.0001$ for *S. altissima*; Appendix B), stem densities were also influenced by the initial planting densities of heterospecifics (interaction between year and initial heterospecific densities, $F_{3,222} = 5.03$, $P = 0.002$ for *S. carolinense*; $F_{3,222} = 5.45$, $P = 0.001$ for *S. altissima*; Appendix B). Competition between *S. carolinense* and *S. altissima* appeared asymmetric (Appendix D). *S. altissima* had negative effects on *S. carolinense* recruitment (although effects appeared to decline with time), but *S. carolinense* consistently had weak effects on *S. altissima* recruitment (Appendix D).

*Fitting competition models to* S. carolinense *data.*— The best-fit model varied among the transition periods

TABLE 1. $\Delta$AIC$_c$ and AIC$_c$ weights (in parentheses) for the 16 candidate LW (Law and Watkinson 1987) models.

| | | | | *Solanum carolinense* | | |
|---|---|---|---|---|---|---|
| No. | Model no. and equation(s) | $\gamma$ param | *K* | 2007–2008 | 2008–2009 | 2009–2010 |
| 1 | $X_{t+1} = (X_t\lambda_X)/[1 + c_x(X_t + \beta_{XY}Y_t)]$ | none | 4 | 3.2 (0.06) | 15.4 (<0.01) | **0.2 (0.21)**† |
| 2 | $X_{t+1} = (X_t\lambda_X)/[1 + c_x(X_t + [\beta_{XY} + \gamma_{\beta X}]Y_t)]$ | $\beta$ | 5 | 2.4 (0.10) | 2.3 (0.19) | 2.2 (0.08) |
| 3 | $X_{t+1} = X_t(\lambda_X + \gamma_{\lambda X})/[1 + c_x(X_t + [\beta_{XY} + \gamma_{\beta X}]Y_t)]$ | $\lambda$, $\beta$ | 6 | 18.0 (0.01) | 4.1 (0.08) | 4.3 (0.03) |
| 4 | $X_{t+1} = X_t(\lambda_X + \gamma_{\lambda X})/[1 + c_x(X_t + \beta_{XY}Y_t)]$ | $\lambda$ | 5 | 5.2 (0.02) | 13.1 (<0.01) | 2.2 (0.08) |
| 5 | $X_{t+1} = X_t\lambda_X/[1 + (\gamma_{cX} + c_x)(X_t + \beta_{XY}Y_t)]$ | *c* | 5 | 3.8 (0.05) | 13.4 (<0.01) | 2.1 (0.08) |
| 6 | $X_{t+1} = X_t(\lambda_X + \gamma_{cX})/[1 + (\gamma_c + c_x)(X_t + \beta_{XY}Y_t)]$ | $\lambda$, *c* | 6 | 18.5 (<0.01) | 13.9 (<0.01) | **0.0 (0.24)** |
| 7 | $X_{t+1} = (X_t\lambda_X)/[1 + (\gamma_{cX} + c_x)(X_t + [\beta_{XY} + \gamma_{\beta X}]Y_t)]$ | *c*, $\beta$ | 6 | 18.5 (<0.01) | 3.9 (0.09) | 4.1 (0.03) |
| 8 | $X_{t+1} = X_t(\lambda_X + \gamma_{\lambda X})/[1 + (\gamma_{cX} + c_x)(X_t + [\beta_{XY} + \gamma_{\beta X}]Y_t)]$ | $\lambda$, *c*, $\beta$ | 7 | 18.5 (<0.01) | 8.6 (0.01) | 3.8 (0.04) |
| 9 | $X_{t+1} = (X_t\lambda_X)/[1 + c_x(X_t + \beta_{XY}Y_t)]$ | $\sigma$ | 5 | **0.8 (0.22)**† | 11.8 (<0.01) | **1.9 (0.09)** |
| 10 | $X_{t+1} = (X_t\lambda_X)/[1 + c_x(X_t + [\beta_{XY} + \gamma_{\beta X}]Y_t)]$ | $\beta$, $\sigma$ | 6 | **0.0 (0.32)** | **0.0 (0.62)**† | 4.1 (0.03) |
| 11 | $X_{t+1} = X_t(\lambda_X + \gamma_{\lambda X})/[1 + c_x(X_t + [\beta_{XY} + \gamma_{\beta X}]Y_t)]$ | $\lambda$, $\beta$, $\sigma$ | 7 | 18.5 (<0.01) | 33.3 (<0.01) | 6.3 (0.01) |
| 12 | $X_{t+1} = X_t(\lambda_X + \gamma_{\lambda X})/[1 + c_x(X_t + \beta_{XY}Y_t)]$ | $\lambda$, $\sigma$ | 6 | 18.5 (<0.01) | 10.3 (<0.01) | 4.0 (0.03) |
| 13 | $X_{t+1} = X_t\lambda_X/[1 + (\gamma_{cX} + c_x)(X_t + \beta_{XY}Y_t)]$ | *c*, $\sigma$ | 6 | **1.6 (0.14)** | 11.1 (<0.01) | 4.0 (0.03) |
| 14 | $X_{t+1} = X_t(\lambda_X + \gamma_{\lambda X})/[1 + (\gamma_{cX} + c_x)(X_t + \beta_{XY}Y_t)]$ | $\lambda$, *c*, $\sigma$ | 7 | 18.5 (<0.01) | 10.4 (<0.01) | 5.0 (0.02) |
| 15 | $X_{t+1} = X_t\lambda_X/[1 + (\gamma_{cX} + c_x)(X_t + [\beta_{XY} + \gamma_{\beta X}]Y_t)]$ | *c*, $\beta$, $\sigma$ | 7 | 18.5 (<0.01) | 12.0 (<0.01) | 7.2 (0.01) |
| 16 | $X_{t+1} = X_t(\lambda_X + \gamma_{\lambda X})/[1 + (\gamma_{cX} + c_x)(X_t + [\beta_{XY} + \gamma_{\beta X}]Y_t)]$ | $\lambda$, *c*, $\beta$, $\sigma$ | 8 | 18.5 (<0.01) | 18.2 (<0.01) | 9.6 (<0.01) |

*Notes:* Models were fit to *Solanum carolinense* or *Solidago altissima* stem density recruitment data and were arranged by transition periods. Herbivore effects ($\gamma$) were incorporated into the LW models by modifying one or more model parameters ($\gamma$ param). Parameters include: *X*, focal plant densities; *Y*, competitor plant densities; $\beta_{XY}$, competition coefficient for effect of species *Y* on species *X*; $\lambda_X$, population growth rate of species *X* at low densities; $c_x$, the total density response. *K* is the number of parameters in a given model number. Parameters were estimated using maximum likelihood and assuming a normal error distribution, where the standard deviation ($\sigma$) was also an estimated parameter that could be influenced by herbivores (models 9–16). Values from best-fit models and models of similar fit ($\Delta$ACI$_c$ < 2) are in boldface. Model values with a dagger (†) were used in simulations.

(Table 1). In transition 1 (2007–2008), three models were similar in fit ($\Delta$AIC$_c$ < 2; in boldface in Table 1); we selected the most parsimonious of these as the best-fit model (Burnham and Anderson 2002). For transition 1, the presence of herbivores increased the standard deviation in stem densities ($w = 0.22$, model 9). For transition 2 (2008–2009), herbivores increased the per capita competitive effect of *S. altissima* on *S. carolinense*, and the standard deviation in *S. carolinense* stem densities ($w = 0.62$, model 16). For transition 3 (2009–2010), three models were similar in fit ($\Delta$AIC$_c$ < 2; Table 1). We therefore considered the most parsimonious model as the best-fit model. For this model, herbivores had no effects on model parameters ($w = 0.21$, model 1). The best-fit models captured 76–90% of the variation in the observed data (Appendix D). To ensure that the selected models best described herbivore effects on plant growth, we compared the importance of each herbivory parameter ($\gamma$) across all models using importance weights ($w^+$). The $\gamma$ parameters that collectively received the highest support across all models for each transition period match those found in the selected best-fit models (Appendix E).

*Fitting competition models to* S. altissima *data.*—For *S. altissima*, the best-fit models varied with transition period (Table 1). In transition 1 (2007–2008), the selection process indicated that herbivores increased the standard deviation in *S. altissima* stem density, but

TABLE 2. Point estimates and 95% confidence intervals (in parentheses) for parameters of best-fit models in Table 1.

| Parameter | 2007–2008 | 2008–2009 | 2009–2010 | Mean |
|---|---|---|---|---|
| A) *S. carolinense* | | | | |
| $\lambda_S$ | 1.99 (1.42 to 2.73) | 2.1 (1.75 to 2.51) | 1.14 (1.08 to 1.21) | 1.74 |
| $c_S$ | 0.01 (0.003 to 0.03) | 0.015 (0.01 to 0.02) | 0.00064 (0.0003 to 0.006) | 0.01 |
| $\beta_{SG}$ | 3.75 (0.65 to 5.15) | 0.006 (−0.22 to 0.22) | 1.22 (0.72 to 2.94) | 1.66 |
| $\sigma_S$ | 6.04 (5.02 to 7.46) | 6.64 (5.36 to 7.47) | 8.20 (7.19 to 9.47) | 6.96 |
| $\gamma_{\beta SG}$ | n/a | 0.59 (0.30 to 1.03) | n/a | |
| B) *S. altissima* | | | | |
| $\lambda_G$ | 11.07 (8.73 to 14.39) | 2.53 (2.11 to 3.09) | 1.67 (1.30 to 2.23) | 5.09 |
| $c_G$ | 0.03 (0.01 to 0.06) | 0.007 (0.004 to 0.01) | 0.008 (0.004 to 0.01) | 0.02 |
| $\beta_{GS}$ | 0.88 (0.32 to 2.21) | 0.66 (0.48 to 2.07) | 0.26 (0.13 to 1.42) | 0.60 |
| $\sigma_G$ | 12.94 (10.78 to 15.94) | 20.99 (18.41, 24.24) | 17.05 (14.96, 19.70) | 16.99 |
| $\gamma_{\lambda G}$ | −1.5 (−2.77 to−0.39) | n/a | −0.36 (−0.57 to −0.20) | n/a |

*Notes:* Parameters were estimated using stem density recruitment data for (A) *S. carolinense* (subscript S) and (B) *S. altissima* (subscript G) and arranged by transition periods; n/a means "not applicable" (parameters were not included in the models for a given year). See Table 1 for parameter definitions.

Table 1. Extended.

| *Solidago altissima* | | |
|---|---|---|
| 2007–2008 | 2008–2009 | 2009–2010 |
| 12.0 (<0.01) | **0.0 (0.26)†** | 21.9 (<0.01) |
| 11.8 (<0.01) | **1.3 (0.14)** | 20.2 (<0.01) |
| 9.0 (<0.01) | 3.2 (0.05) | **1.0 (0.20)** |
| 7.1 (0.01) | 2.0 (0.10) | **0.0 (0.33)†** |
| 7.2 (0.01) | 2.1 (0.09) | 2.2 (0.11) |
| 8.6 (0.01) | 3.6 (0.04) | 4.1 (0.04) |
| 10.1 (<0.01) | 3.0 (0.06) | 2.3 (0.11) |
| 10.2 (<0.01) | 5.9 (0.01) | 3.6 (0.06) |
| 6.5 (0.02) | 2.0 (0.10) | 23.8 (<0.01) |
| 6.3 (0.02) | 3.3 (0.05) | 22.1 (<0.01) |
| 3.7 (0.08) | 5.7 (0.02) | 3.5 (0.06) |
| **0.0 (0.45)†** | 4.0 (0.03) | 4.0 (0.05) |
| 2.2 (0.16) | 4.3 (0.03) | 4.3 (0.04) |
| 3.3 (0.09) | 9.3 (<0.01) | 8.7 (<0.01) |
| 2.7 (0.11) | 5.2 (0.02) | 6.5 (0.01) |
| 5.1 (0.04) | 8.5 (<0.01) | 10.7 (<0.01) |

reduced *S. altissima* growth rate ($w = 0.45$, model 9). In transition 2 (2008–2009), two models were of similar fit and we selected the most parsimonious model as the best-fit model ($w = 0.26$, model 1). In transition 2, herbivores had no effects on model parameters. Finally, in transition 3, herbivores reduced the growth rate of *S. altissima* ($w = 0.33$, model 4). The best-fit models captured 66.3–87.8% of the variation in the observed data (Appendix D). The $\gamma$ parameters that collectively received the highest support across all models for each transition period match those found in the selected best-fit models (Appendix E).

*Variation in model parameters*.—We compared the magnitude of parameters from the best-fit models among years and between plant species (Table 2). The magnitude of intrinsic rates of increase ($\lambda$) and density responses ($c$) decreased over time for both plant species. The magnitude of competition ($\beta$) also varied through time, but only for the effect of *S. altissima* (G) on *S. carolinense* (S), $\beta_{SG}$. When model parameters were averaged across transition periods, there were species-level differences. For *S. altissima*, the mean intrinsic rate of growth in the absence of herbivores was greater than for *S. carolinense* ($\bar{\lambda}_G = 5.09$ vs. $\bar{\lambda}_S = 1.74$). The competitive effect of *S. altissima* on *S. carolinense* was greater than 1 ($\bar{\beta}_{SG} = 1.66$), indicating that interspecific competition was stronger than intraspecific competition. On the other hand, the effect of *S. carolinense* on *S. altissima* was less than 1 ($\bar{\beta}_{GS} = 0.6$), indicating that intraspecific competition was stronger than interspecific competition. Also, the density response of *S. altissima* was twice as large as the response of *S. carolinense* ($\bar{c}_S = 0.01$, $\bar{c}_G = 0.02$), indicating that total density dependence (both conspecific and heterospecific) was stronger in *S. altissima* than in *S. carolinense*. Finally, *S. altissima* had a wider distribution of stem densities ($\bar{\sigma}_G = 16.99$) compared to *S. carolinense* ($\bar{\sigma}_S = 6.96$), which may be explained by the overall higher number of *S. altissma* stems (Fig. 1C, D).

*Simulation of herbivore effects on longer-term community dynamics*.—To examine how the effects of herbivory and competition might play out beyond the four years of our experiment, we performed simulations based on the best-fit models. By incorporating variation around parameter estimates and performing replicate simulations, we generated a range of competitive outcomes and the estimated probability of competitive exclusion over 50 years in the presence and absence of insect herbivores (Fig. 2). Our results should be interpreted cautiously because our sample of only a few years may not accurately estimate total year-to-year variation and would fail to capture long-term directional trends, such as those driven by climate change. Regardless, our simulations showed that herbivores significantly reduced the mean final densities of *S. carolinense* (50.1 stems/m$^2$ without herbivores; 0.7 stems/m$^2$ with herbivores), but had slight positive effects on mean final *S. altissima* densities (104.8 stems/m$^2$ without herbivores; 121.2 stems/m$^2$ with herbivores). Simulation results differ from the mean densities observed during the last year of the experiment, particularly in the presence of herbivores (Fig. 2), suggesting that a longer experiment is needed to observe the ultimate outcome of competition. Simulations also showed that herbivores influenced the probability of competitive exclusion. In the absence of herbivores, competitive exclusion was never observed. In the presence of herbivores, competitive exclusion (stem densities $<1/\text{m}^2$) of *S. carolinense* by *S. altissima* was observed in 72.3% of the simulations, and 98.2% of the mean final densities of *S. carolinense* were $<10$ stems/m$^2$.

## Discussion

Herbivores are known to influence plant community structure (reviewed by Huntly 1991), and these effects are thought to arise through changes to interspecific plant competition (Louda et al. 1990). Because herbivores can influence the per capita competitive ability of plants, intrinsic rates of increase, and strength of density dependence (all of which are important for determining population sizes), we need to consider how herbivores influence all of these processes to understand and predict the long-term consequences of herbivory for plant communities. Over the course of our experiment, herbivores reduced stem densities of *S. altissima* but had little effect on *S. carolinense*, despite high leaf damage and reduction in plant biomass. Models fit to our experimental data showed that herbivores influenced different model parameters in different years. In some years (transition 1, 2007–2008; transition 3, 2009–2010), herbivores reduced the population growth rate of *S. altissima*, whereas in other years (transition 2, 2008–2009) herbivores increased the competitive effect of *S. altissima* on *S. carolinense* (Table 2). Herbivores also

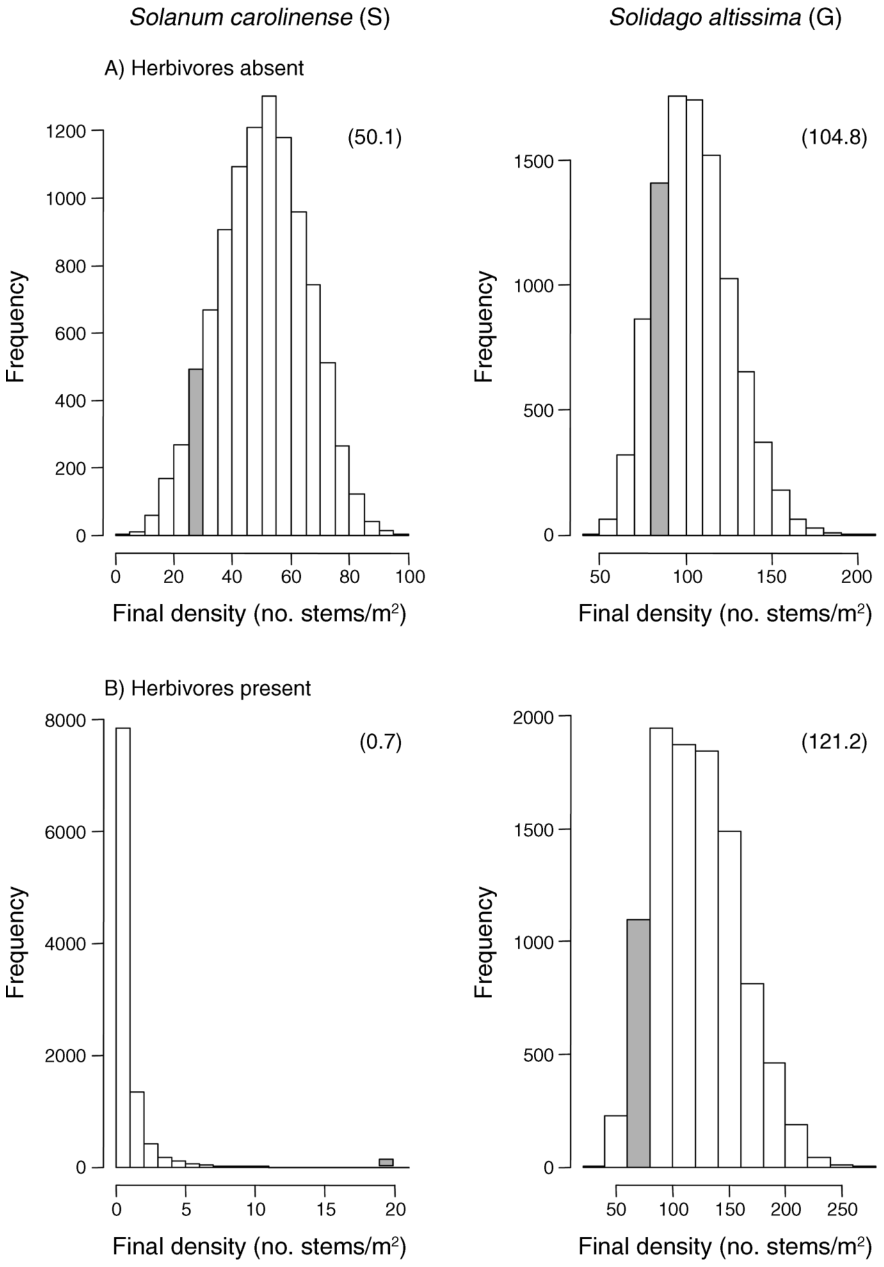

FIG. 2. Frequency distribution of *S. carolinense* and *S. altissima* mean final densities in the (A) absence or (B) presence of herbivores from replicate simulations ($n = 10\,000$) of best-fit competition models (Table 1). For details, see *Methods: Simulating herbivore effects on the outcome of competition*. Model parameters were drawn randomly from a uniform distribution encompassing the 95% CIs of parameter estimates (Table 2). Numbers in parentheses represent final densities averaged across all 10 000 simulations. Gray bars indicate bin locations of the mean densities of *S. carolinense* and *S. altissima* at the end of the four-year study.

increased the standard deviation in stem densities for both *S. altissima* and *S. carolinense*, suggesting that plots varied in the density or impact of herbivores. Our simulations show that herbivore-mediated changes to model parameters can influence the outcome of interspecific competition and coexistence, and decrease the final population sizes of both plant species. These simulations suggest that the presence of insect herbivores increases the probability of competitive exclusion of *S. carolinense* by *S. altissima*.

*Herbivore effects on model parameters*.—In our study, herbivores affected the model parameters of the dominant plant species, *S. altissima*. Herbivores lowered population growth at low densities ($\lambda_G$) for *S. altissima* but also increased the per capita competitive effect of *S. altissima* on *S. carolinense* ($\beta_{SG}$). We speculate that overcompensation in *S. altissima* growth may have led to changes in model parameters. The apical meristem of *S. altissima* was frequently attacked by gall makers, often resulting in overcompensation in total stem length through the production on lateral stems (Fig. 1B). Overcompensation in *S. altissima* biomass has been reported in other studies (Schmid et al. 1988, Meyer 1998). The cost of compensatory growth could reduce stem numbers in following years, resulting in a reduction in $\lambda$ when herbivores are present. The production of lateral stems following damage could, in turn, increase the competitive effect of *S. altissima* on *S. carolinense*, as larger plants can reduce the amount of light reaching *S. carolinense* in the understory (T. Kim, *unpublished data*), leaving *S. carolinense* with less light for growth. We also observed increased variation in stem densities in the presence of herbivores for both *S. altissima* and *S. carolinense*. Damaged (control) plants did not experience the same level of damage across density treatments; damage varied according to the initial planting treatments (Appendix B). This context-dependent herbivory could have increased the variation in plant responses (including stem production) to herbivory compared to undamaged plants.

*Long-term effects of herbivores*.—Although consumers (including herbivores) can facilitate coexistence (predator-mediated coexistence; Caswell 1978, Ishii and Crawley 2011), there is no general consensus as to whether consumers should increase, decrease, or have no effects on the probability of competitive exclusion (Chase et al. 2002, Chesson and Kuang 2008). This is perhaps because, in theory, coexistence depends on both the competition coefficients and carrying capacities of the competing species; both parameters can be affected by consumers in different ways. In this study, herbivores lowered population growth of the dominant plant species, *S. altissima* ($\lambda_G$). For the Law and Watkinson (1987) model, the single-species carrying capacity is determined by the ratio $(\lambda-1)/c$; therefore a reduction in the growth rate of *S. altissima* (the dominant plant species) should, in theory, favor (predator-mediated) coexistence by serving as another limiting factor for population growth and decreasing the carrying capacity of *S. altissima*. However, our results also showed an increase in the per capita competitive effect of *S. altissima* on *S. carolinense* ($\beta_{SG}$) in the presence of herbivores, which would favor competitive exclusion. These opposing effects of herbivores have very different consequences for coexistence. In our simulations, we found that, in the presence of herbivores, competitive exclusion of *S. carolinense* by *S. altissima* was frequently predicted to occur within 50 years or less, whereas in the absence of herbivores, coexistence was predicted (Fig. 2). This suggests that herbivore effects on the per capita competitive ability of *S. altissima* outweighed the negative effects on *S. altissima* intrinsic rates of growth, resulting in a net negative effect on *S. carolinense* for coexistence. In nature, we might expect similar outcomes to occur in environments where competition for resources is strong (e.g., nutrient-poor or late-successional environments, populations near carrying capacity). Alternatively, in environments where competition is less fierce (e.g., following disturbance, invasion fronts), the negative effects of herbivores on intrinsic rates of growth may supersede their effects on competitive interactions for determining the outcome of competition.

Our results could have large implications for invasion and biocontrol. Both *S. altissima* and *S. carolinense* are considered invasive in parts of the United States, Asia, and Europe, and biocontrol might be considered as a tool for decreasing their population sizes or reducing their spread (Weber and Schmid 1998, Follak and Strauss 2010). If biocontrol agents such as herbivores are to be used to reduce population sizes of *S. altissima* or *S. carolinense*, examining herbivore effects on plant intrinsic population growth rates alone may not be effective in predicting plant population sizes in the long term. Because many invasive plants are competing with other (often native) plants, management strategies should also consider the effects of biocontrol on competitive interactions. The goal of reducing invasive plant populations is often coupled with increasing neighboring native plant populations (Mack et al. 2000). Therefore examining the effects of biocontrol on multiple aspects of plant performance may be needed to avoid unintended consequences of biocontrol.

In our experimental system, *S. carolinense* and *S. altissima* were the only two species present; nontarget species were removed. Although the results from our simulations suggest competitive exclusion by *S. altissma*, natural old fields are successional habitats where *S. carolinense* and *S. altissima* are eventually outcompeted by woody plants unless recurring disturbance allows them to persist. Nevertheless, our results can offer insight into how herbivores might influence rates of succession. *Solidago altissima* is a dominant plant in old fields and can form dense, monospecific stands with thick litter layers (Hartnett and Bazzaz 1985). It has been suggested that *S. altissima* stands inhibit colonization of woody species, thereby slowing rates of succession (Carson and Root 1999). In our study, herbivores decreased the population growth rates of *S. altissima* in some years, but increased its competitive ability against *S. carolinense* in other years, resulting in competitive exclusion of *S. carolinense* by *S. altissima*. These results suggest that herbivores reduce the time required for *S. altissima* to become dominant (typically 5–20 years after establishment), facilitating the formation of dense *S. altissima* stands and potentially slowing rates of succession.

*Conclusions*.—In the 1960–1970s, herbivores were thought to be unimportant for structuring plant communities (Hairston et al. 1960). Since then, empirical studies have documented herbivore effects across a wide range of systems and various herbivore taxa (Huntly 1991), yet it remains unclear how herbivores influence plant community structure. Because herbivory rarely results in immediate plant mortality, the prevailing theory is that herbivores influence plant communities by affecting interspecific plant competition (Crawley 1983). However, surprisingly, few empirical studies have thoroughly examined the mechanisms leading to changes in plant communities, as was pointed out over a decade ago by Louda et al. (1990) and Hulme (1996). To our knowledge, ours is the first experimental study to tease apart how herbivores might affect plant communities by simultaneously measuring herbivore effects on per capita interspecific competitive effects, intrinsic rates of increase, and density dependence. In our two-species plant community, the presence of herbivores affected the abundance of both plant species through changes in per capita interspecific competitive effects and intrinsic rates of population increase. The effects of herbivores on intraspecific processes have been largely ignored when examining herbivore effects on plant communities (Louda et al. 1990, Hulme 1996); studies have focused instead on how herbivores change the per capita interspecific competitive ability of plants. Because our results show that per capita interspecific competition is not the only factor important for mediating herbivore effects on the outcome of competition, future studies should also examine herbivore effects on intraspecific processes to fully understand how herbivores influence plant communities.

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## Supplemental Material

### Appendix A

Response surface experimental design with varying densities of *Solanum carolinense* and *Solidago altissima* (*Ecological Archives* E094-159-A1).

### Appendix B

Detailed description of statistical methods and tables (*Ecological Archives* E094-159-A2).

### Appendix C

AIC weights (*w*) for five standard competition models using stem density recruitment data (*Ecological Archives* E094-159-A3).

### Appendix D

Observed and predicted recruitment data for *Solanum carolinense* and *Solidago altissima* (*Ecological Archives* E094-159-A4).

### Appendix E

Importance weights of herbivore effects on $\lambda$, $\beta$, and $c$ using $\mathrm{AIC_c}$ weights ($w$) from the 16 candidate Law and Watkinson (1978) competition models (*Ecological Archives* E094-159-A5).

### Supplement

R code for simulating the long-term outcome of competition between *Solanum carolinense* (S) and *Solidago altissima* (G) in the presence or absence of herbivores (*Ecological Archives* E094-159-S1).