

POPULATION-LEVEL EFFECTS OF AUGMENTED HERBIVORY ON *LESPEDEZA CUNEATA*: IMPLICATIONS FOR BIOLOGICAL CONTROL

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Abstract. Invasive species pose significant ecological costs, and therefore successful management techniques are important. One commonly employed method is biological control. The success of biological control depends largely on whether additional inflicted damage can successfully reduce the fitness and population growth rate of a target species. Here, we simulate herbivory on the invasive *Lespedeza cuneata* and create stage-structured projection models to determine if augmented herbivory by a leaf-chewing biological control agent would regulate the population growth rate of this species. We found that augmented herbivory influenced stage transitions of plants in the smallest stage class, causing higher mortality and reduced growth. No other effect was found on stage transitions or fecundities, despite manipulation of herbivory at exceptionally high levels (up to 80% leaf loss). None of the clipping treatments significantly reduced the population growth rate of *L. cuneata*. We conclude that biological control by a leaf chewing herbivore would not likely be successful, even if an exceptionally large amount of each plant were consumed. We suggest that this approach, a combination of simulated herbivory and demographic modeling, will provide essential information for understanding the utility of biological control to curb the population growth of invasive plant species.

Key words: biological control; compensation; demography; elasticity analysis; enemy release; fitness; growth rate; invasive; *Lespedeza cuneata*; matrix modeling; simulated herbivory; tolerance.

One of the most prominent hypotheses used to explain the success of invasive species is the enemy release hypothesis (Keane and Crawley 2002, Colautti et al. 2004). This hypothesis posits that invasive species are released from their natural enemies and are therefore able to attain large populations and become successful invaders. This concept implicitly underlies the premise of biological control programs, which introduce an invasive species' specialist enemy (e.g., herbivore) with the aim of regulating population growth (Debach 1974). A majority of biological control research aims at identifying appropriate specialist herbivores to introduce (Buckingham 1994, Julien and Griffiths 1998). However, much less attention has been given to investigating whether herbivore damage will regulate invasive plant populations and what level of herbivory would cause invasive populations to decline (Raghu and Dhileepan 2005).

Many studies have found that herbivores can drastically reduce fitness (Crawley 1997, Bigger and Marvier 1998) and affect population dynamics (Knight 2004, Leimu and Lehtilä 2006, Steets et al. 2007). However, some plants have a very high tolerance to herbivory, and increasing levels of herbivory have minimal effects on

fitness (Strauss and Agrawal 1999, Stowe et al. 2000). Some plants may even be able to increase growth in response to herbivory, resulting in positive effects of herbivory on fitness (e.g., Paige et al. 2001). The net effect of herbivory on plant population dynamics depends both on the magnitude of the effects of herbivores on plant vital rates (components of fitness) as well as the sensitivity of the population growth rate to these vital rates (Knight 2004, Ehrlén et al. 2005).

Biological control is controversial in nature and can be a risky endeavor for several reasons (Messing and Wright 2006). Biological control programs can be costly and can take years to successfully develop (McFadyen 1998). Out of all of the attempted introductions, less than one-fifth have accomplished the task of completely controlling the targeted invasive (Hall et al. 1980, Myers 1984). Furthermore, biological control agents can sometimes have unintended negative effects on non-target organisms (e.g., Pearson and Callaway 2003, Louda and Stiling 2004). In order to maximize the potential for successful biological control, it is crucial to determine if herbivory by the control agent will effectively reduce the population growth of the target species.

Several studies have investigated how enhanced herbivory affects various fitness components in invasive species. For example, enhanced herbivory was found to only have weak effects on *Lonicera japonica* (Schierenbeck et al. 1994) and Chinese tallow (*Sapium*

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sebifurum; Siemann and Rogers 2003). In contrast, Pratt et al. (2005) found that leaf loss had a strong negative effect on short-term reproduction in *Melaleuca quinquinervia*. However, investigating the effect of increased herbivory on various fitness components is only the first step in understanding how herbivory affects the population dynamics of an invasive plant species.

Here, we present the first study to examine how enhanced herbivory affects fitness components and population dynamics of a widespread noxious invader, *Lespedeza cuneata* (Fabaceae), to assess the potential for biological control. Specifically, we quantified the stage-specific effects of enhanced (simulated) herbivory on seed set, growth, and survival of each stage class. We incorporated these results into a stage-structured demographic matrix model to project the effect of herbivory on population growth rate, λ . Perturbation analyses (elasticity analysis) were used to quantify the sensitivity of λ to each underlying vital rate and to ultimately identify the vital rates that should be targeted by biological control efforts.

METHODS

Study system

Lespedeza cuneata, a native to Asia, is a perennial legume that invades meadows, prairies, open woodlands, old fields, and rangelands, establishing dense stands that can shade out native species (Eddy and Moore 1998). *Lespedeza cuneata* was first introduced to the United States in 1896 and has been deliberately planted across the United States for erosion control and forage (Hoveland and Donnelly 1985). Since then, *L. cuneata* has spread across the entire eastern half of the United States from Maryland to Kansas and is currently listed by several states as a noxious weed (Sheley et al. 1999). Since large stands of *L. cuneata* are not effectively controlled with mowing or chemical means, and because *L. cuneata* poses a large threat to the ranching industry and to tall-grass-prairie natural areas, biological control is being considered as a feasible alternative (E. Delfosse, personal communication).

Lespedeza cuneata exhibits a heteromorphic flowering system, whereby it produces both chasmogamous (CH) and cleistogamous (CL) flowers (see Plate 1). CH flowers are ~75% cross-pollinated by insects (Ansley 1960), whereas CL flowers are self-pollinated. Donnelly (1955) found that CH individuals achieved higher fitness (biomass and seed production) than CL individuals. However, CH flowers are more costly to produce, and a study in another heteromorphic flowering species found that herbivory reduces CH flower production (Steets and Ashman 2004).

Experimental design

To examine the effects of herbivory on stage-specific vital rates, we located naturally occurring *L. cuneata* individuals in old fields at Washington University's Tyson Research Center (Eureka, Missouri, USA). In

May 2005, we tagged individual plants and classified them into one of four stage classes based on number of branches per plant: small (1 branch); medium (2–5 branches); large (6–10 branches); extra large (>10 branches). Each monitored plant was a minimum of 10 cm from other conspecifics. We randomly selected individuals of each stage class for one of five treatments: ambient herbivory (control), 20%, 40%, 60%, and 80% enhanced herbivory (see Plate 1). We enhanced herbivory by removing the indicated percentage of leaflets by hand in May of 2005. It was not necessary to simultaneously consider the effects of natural herbivory since ambient levels of herbivory on *L. cuneata* are very low (range from 0–6%; unpublished data). We monitored 15 plants per treatment and stage.

In our study, we use simulated herbivory rather than manipulating natural herbivory to examine the effects of leaf loss on the fitness (survival, growth, reproduction) of *L. cuneata* (see Plate 1). Simulated herbivory allowed us to manipulate magnitude, timing, and type of damage in a simple and efficient experimental design (Hjalten 2004). We acknowledge that artificial herbivory may not induce natural plant responses, particularly in physiological and phytochemical traits (Lehtilä and Boalt 2004). However, many studies have found that simulated herbivory and natural herbivory have similar effects on growth and reproduction (Lehtilä and Boalt 2004), which were our response variables.

At the completion of the growing season, October 2005, we counted the number of fruits, and classified them as being either a CL or CH fruit, based on morphology (McKee and Hyland 1941). Each fruit contained a single seed. In May 2006, we relocated tagged individuals to determine the proportion that survived and the stage class of those survivors.

To determine germination rate of CH and CL seeds, we planted each type into seed baskets in early November 2005. Baskets were buried plastic pots (5 cm in diameter) filled with soil from the site, which was sieved to ensure that no other *L. cuneata* seeds were present. We planted a total of 25 baskets for each seed type (CH and CL), with 25 seeds/basket (1250 total seeds). In May of 2006, we recorded the number of germinants in each basket. All baskets were then destructively harvested to obtain any remaining seeds. The remaining seeds were then tested for viability using Tetrazolium. Because germination rates of CH and CL seeds differed (see *Results*), our population projection model explicitly considers these seed types.

Matrix model

We created a population projection matrix for each species using demographic transitions collected from 2005–2006 (Fig. 1). Our model explicitly considers differences in germination between the CH and CL seed types (see *Results*); however, once these seeds germinate, our model assumes that they do not differ in their vital rates. Our model incorporates a 1-yr seed bank. We

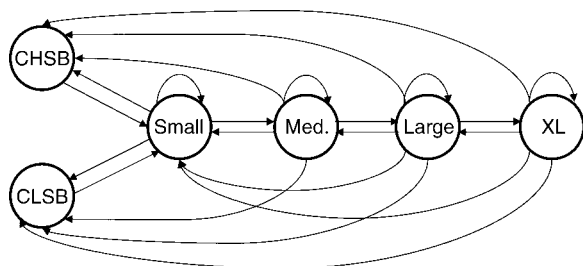


FIG. 1. Annual life cycle graph of *Lespedeza cuneata*, explicitly incorporating the mating system (cleistogamous and chasmogamous seed types). Each circle represents a stage class, and arrows represent vital rates (fecundity, stage transitions) from one year to the next. For example, the arrow going from extra large (XL) to cleistogamous seed bank (CLSB) is the product of the number of CL seeds produced per extra-large plant, the viability of CL seeds, and the proportion of viable CL seeds that enter the seed bank (1 – germination rate); all of these occur within a one-year time step. CHSB represents the chasmogamous seed bank.

assume the viability and germination rates of seeds in the seed bank are the same as those of fresh seeds. *Lespedeza cuneata* may have a longer-lived seed bank, and therefore this model may underestimate the survivorship of seeds in the seed bank. However, the population growth rate was very insensitive to changes in the vital rates of seeds in the seed bank (see *Results*), and thus our simple model should agree well with a more complicated model that includes a long-lived seed bank. We calculated a separate matrix for each clipping treatment. The dominant eigenvalue of the matrix gives the asymptotic population growth rate, λ . Calculation of λ determines whether a population can persist ($\lambda \geq 1$) or not ($\lambda < 1$).

For each clipping treatment, we calculated 95% bootstrap confidence intervals around λ (Caswell 2001). A bootstrap data set was calculated for a given clipping treatment by resampling individuals with replacement. The sample size of a bootstrap data set was identical to the original data set. This process of generating a bootstrap data set was repeated 1000 times. We then used the bootstrap data sets to generate 1000 values of λ , from which we calculated the mean and 95% confidence intervals. To determine whether λ was significantly altered by the clipping treatments, we performed randomization tests ($N = 1000$ runs for each pairwise combination; Caswell 2001).

To determine how sensitive the population dynamics of *L. cuneata* are to changes in each matrix element, we calculated the elasticities for the matrix elements of control plants. Elasticities measure the proportional change in λ that would result from a small proportional change in each annual matrix element (de Kroon et al. 1986, Caswell 2001). Elasticities provide a measure of the relative importance of each matrix element; changes in matrix elements with large elasticities will cause larger changes in λ than changes in those with smaller elasticities.

Retrospective analyses, such as life table response experiments (LTREs) allow one to quantify the contribution of each vital rate (or groups of vital rates, i.e., fertility, stage transitions of plants in a single stage class) to the difference in λ observed between experimental treatments (Caswell 2001). However, we found that only one group of vital rates was significantly altered by our clipping treatments (see *Results*), and thus we did not conduct retrospective analyses.

RESULTS

Differences in germination of heteromorphic seeds

We found that CH seeds had a higher germination rate (26.26%; $N = 575$) than CL seeds (16.15%; $N = 650$; t test, $P = 0.006$). In addition, viability did not differ between the seed types ($\chi^2 = 1.3$, $P = 0.246$); 20/20 recovered CH seeds and 118/126 recovered CL seeds were viable using Tetrazolium tests.

Effects of clipping treatments on vital rates

Clipping treatments altered the stage transitions of plants in the smallest (1 branch) stage class (Tables 1 and 2, Fig. 2A) but did not affect the stage transitions of plants in any of the other stage classes (Tables 1 and 2). As clipping increased, small plants were more likely to die or remain in the small stage class and less likely to advance to the medium stage class (Table 2, Fig. 2A). Clipping treatments in 2005 did not affect the number of CH or CL seeds produced by plants in any stage class in 2005 (Table 3).

Effects of clipping treatments on population dynamics

The population growth rate of control plants was extraordinarily high ($\lambda = 25.1$), corresponding to a population able to increase 25 times in abundance from one year to the next. The clipping treatments did not significantly decrease the population growth rate of this

TABLE 1. Mean stage transitions of plants in the small, medium, large, and extra-large size classes.

Stage transition	Mean proportion of plants (across all treatments)	χ^2	df	P
Small–dead	0.318	16.024	8	0.042
Small–small	0.242			
Small–medium	0.439	7.661	12	0.811
Medium–dead	0.111			
Medium–small	0.056	10.251	12	0.594
Medium–medium	0.805			
Medium–large	0.028	2.510	4	0.643
Large–dead	0.029			
Large–medium	0.382	0.717		
Large–large	0.485			
Large–extra large	0.103			
Extra large–large	0.283			
Extra large–extra large	0.717			

Note: Chi-square results are shown for each stage class to test for differences in stage transitions across clipping treatments (control vs. 20%, 40%, 60%, and 80% clipped).

TABLE 2. Matrix of *Lespedeza cuneata*, where each value represents the stage-specific transition probabilities from 2005 to 2006.

Stage at time $t + 1$	Mating system†		Stage at time t								
			Small, by clipping treatment					Medium	Large	Extra large	
	CHSB	CLSB	Control	20%	40%	60%	80%				
CHSB	0	0	0.361						0.505	3.86	4.96
CLSB	0	0	23.118						58.681	145.001	217.929
Small	0.263	0.168	23.366	23.525	23.833	23.448	23.525		56.081	158.15	231.339
Medium	0	0	0.643	0.615	0.308	0.385	0.231		0.805	0.382	0
Large	0	0	0						0.028	0.485	0.283
Extra large	0	0	0						0	0.103	0.717

Notes: The probabilities of small plants remaining small or transitioning into medium plants are listed for all clipping treatments to present how clipping affects the vital rates of *L. cuneata*. Clipping treatments did not significantly affect any other vital rates. † CHSB represents chasmogamous seed bank; CLSB represents cleistogamous seed bank.

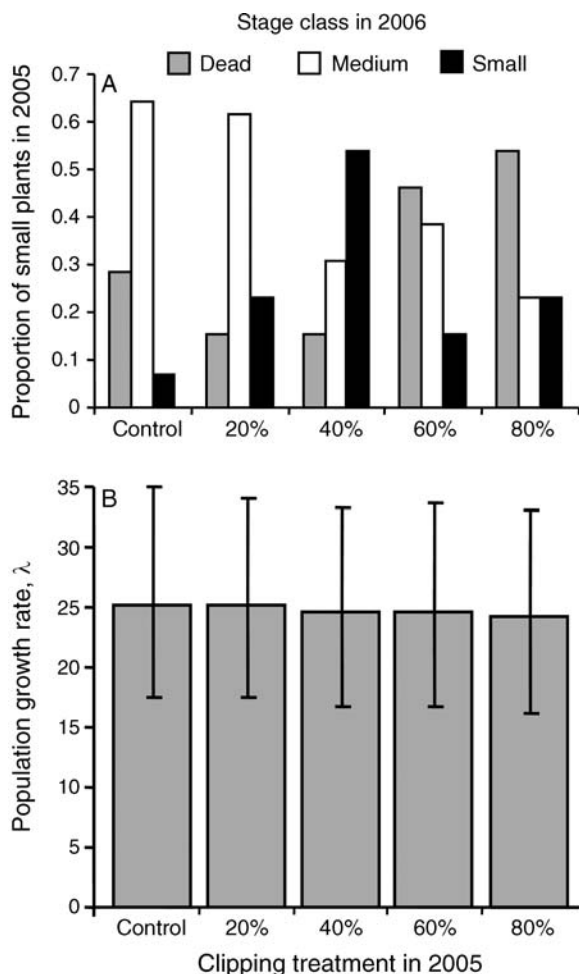


FIG. 2. The effects of each clipping treatment (control vs. 20–80% clipped) on (A) stage transitions of small (one branch) plants from 2005–2006. For stage transition results, all plants were in the small stage class in 2005, and bars show the proportion in each stage class in 2006. (B) Population growth rates (λ) are shown for clipping treatments in 2005. Error bars show 95% bootstrap confidence intervals. The population growth rate of control plants was extraordinarily high ($\lambda = 25.1$), indicating a population able to increase 25 times in abundance from one year to the next.

species (all pairwise randomization tests $P > 0.10$; Fig. 2B). Results from our elasticity analysis indicate that this *L. cuneata* population is disproportionately sensitive to the fecundity of plants in the small stage class (summed elasticity for CH and CL seed production = 0.8791). λ is relatively insensitive to all other vital rates (Table 4).

DISCUSSION

Our results demonstrate that biological control via a leaf-chewing herbivore is unlikely to effectively control *L. cuneata*. Indeed, even when we experimentally augmented leaf herbivory to 80%, the population growth rate was still enormous: 24.2. This was primarily because our elasticity analyses revealed that population growth rate was relatively insensitive to changes in the only vital rates that were affected by clipping: the stage transitions of small plants.

We found that *L. cuneata* was tolerant to large amounts of leaf loss early in its growing season. The fecundity of all stage classes and the stage transitions (growth, survival) of plants in the medium, large, and extra-large stage classes were unaffected by augmented leaf loss from 20–80%. These results correspond with those of other studies (Schierenbeck et al. 1994, Siemann and Rogers 2003), which found that herbivory had weak effects on fitness and add to a growing literature on the tolerance of non-native plant species.

Our study only examined the potential for leaf-chewing insects to affect fitness components and population growth rate, λ . However, other types of plant enemies, including seed predators and pathogens, need to be investigated as well. λ was most sensitive to changes in the fecundity of small plants, and therefore enemies that can reduce fecundity may reduce the population growth of this species. This suggests that biological control using a floral or seed predator may be more effective at targeting *L. cuneata*'s growth rate than a leaf chewer. Alternatively, if recruitment is limited by germination sites in this species (Crawley 1989), then reductions in seed production (i.e., by a seed predator) may be counteracted by increases in the germination rate (because these fewer seeds are more likely to find a

TABLE 3. Means and standard errors for cleistogamous (CL) and chasmogamous (CH) seed production of plants in each stage class.

Stage class	CL seed production			CH seed production		
	Mean no. seeds per plant	SE	<i>P</i>	Mean no. seeds per plant	SE	<i>P</i>
Small	134.7	29.7	0.65	9.3	4.2	0.77
Medium	351.7	60.9	0.53	23.8	6.8	0.28
Large	768.0	101.1	0.21	110.9	23.3	0.29
Extra large	1143.6	195.0	0.29	138.8	32.0	0.18

Notes: *P* values are shown from ANOVAs, which tested for differences in seed production among plants in different clipping treatments (tests were conducted separately for each stage class and for CL vs. CH seed types).

safe site; Myers and Risley 2000). Future research is necessary to determine if recruitment is limited by safe sites or by seed production.

In general, perennial plant species have been shown to be less sensitive to annual fecundity and more sensitive to changes in the fates of individuals in the largest stage classes (Silvertown et al. 1993). However, in *L. cuneata*, we find that the population growth rate was most sensitive to the fecundity of small plants and least sensitive to changes in the fate of plants in the large and extra-large stage classes. The discrepancy between our results and the more general results (Silvertown et al. 1993) can most likely be explained by the extraordinary high rate of population growth of *L. cuneata*. For such a rapidly growing population, growth rate is most sensitive to reproduction early in life, since this allows for a rapid generation time.

It is important to note that the experiment and model developed here is relatively simple in a variety of ways. However, in many cases we do not expect that more complicated models would alter our qualitative results. For example, we only conducted our clipping treatments once and measured the response to herbivory over a short time interval (one year). Our measured effects of herbivory may be an underestimate if some fitness consequences take multiple years to manifest or if continuous bouts of herbivory have non-additive consequences for plants. One way that fitness consequences could take multiple years to manifest is if herbivory influenced the belowground but not aboveground size of *L. cuneata* during our study interval. However, because aboveground size is generally correlated with belowground storage in perennial herbs (Cahill 2002), it is unlikely that unmeasured belowground effects of herbivory were significantly greater than our measured aboveground effects. Our model assumes that stage class predicts fitness; however, if plants with prior bouts of herbivory are more affected by future bouts of herbivory than other members of the same stage class, then our model will underestimate the population-level effects of herbivory. In addition, our study only considered a single transition year. While the environmental conditions in this year were typical for this area, temporal variation in environmental conditions could influence plant responses to herbivory (e.g.,

Bastrenta et al. 1995). Because of empirical limitations, our model assumes the seed bank only lasts a single year, even though *L. cuneata* may have a longer-lived seed bank. However, our elasticity analysis revealed that the population growth rate is highly insensitive to changes in the survivorship of seeds in the seed bank. Finally, our model and empirical data collection method ignores density dependence, and our experimental enhanced herbivory treatments may have differing effects (i.e., increased mortality, lower fertility) on plants suffering from density dependence. However, since herbivory fails to regulate growth during the exponential phase of population dynamics, as evinced by the λ of 24.2 we found at herbivory levels of 80%, it is still evident that a leaf chewing biological control agent would not suppress populations of *L. cuneata*. It is critical that management plans are developed rapidly for invasive species. Our study demonstrates how a simple model can be created and empirically parameterized in a brief time period (see also Shea and Kelly 1998, Parker 2000) and then used to determine the vital rates that should be targeted for control as well as the likely effectiveness of a biological control agent.

Invasive species costs the United States alone over \$137 billion each year (Pimentel et al. 2000), including costs associated with biological control research. Fur-

TABLE 4. Elasticity analysis for *L. cuneata* plants in the control treatment.

Summed vital rates	Elasticity
Fertility	
Small	0.8791
Medium	0.0560
Large	0.0002
Extra large	0.0000
Transitions	
CH seed bank	0.0001
CL seed bank	0.0062
Small	0.0562
Medium	0.0021
Large	0.0000
Extra large	0.0000

Notes: For each stage class, the elasticity of fertility considers the summed elasticities for CH and CL seed types, and the elasticity of stage transitions considers the summed elasticities of all possible stage transitions.



PLATE 1. (Top left) Chasmogamous flowers of *Lespedeza cuneata*. Photo credit: M. Schutzenhofer. (Top right) Two chasmogamous fruits of *L. cuneata*. Photo credit: M. Schutzenhofer. (Bottom left) A medium-sized *L. cuneata* individual in the control (ambient herbivory) treatment. Photo credit: T. Knight. (Bottom right) A medium-sized *L. cuneata* individual in the 80% augmented herbivory treatment. Photo credit: T. Knight.

thermore, biological control can have unintended consequences (e.g., Pearson and Callaway 2003, Louda and Stiling 2004). Therefore, investigating the likelihood that biological control will be effective is of primary importance. Simulating enhanced herbivory and using demographic modeling can rapidly assess the likely effectiveness of a biological control agent and pinpoint the vital rates on which biological control should focus. Information gathered from these methods may help to increase the success rate of biological control and reduce the ecological and economic risk associated with introducing biological control agents.

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