

The Interactive Effects of Herbivory and Mixed Mating for the Population Dynamics of *Impatiens capensis*

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ABSTRACT: In this study, we examine the demographic consequences of mixed mating and explore the interactive effects of vegetative herbivory and mating system for population dynamics of *Impatiens capensis*, a species with an obligate mixed mating system (i.e., individuals produce both obligately selfing cleistogamous and facultatively outcrossing chasmogamous flowers). In two natural populations, we followed seeds derived from cleistogamous and chasmogamous flowers subject to different herbivory levels throughout their life cycle. Using a mating system–explicit projection matrix model, we found that mating system types differed in important vital rates. Cleistogamous individuals had higher rates of germination than did chasmogamous individuals, whereas chasmogamous individuals expressed a fecundity advantage over cleistogamous individuals. In addition, population growth was most sensitive to changes in vital rates of cleistogamous individuals, indicating the demographic importance of selfing for these populations. Herbivory also had demographic consequences; a 33%–49% reduction in herbivory caused the population growth rates to increase by 104%–132%, primarily because of effects on vital rates of selfed individuals. Our results not only uncover a novel consequence of mating system expression, that is, mating system influences population dynamics, but also shed light on the role of herbivores in maintaining mixed mating.

Keywords: cleistogamy, demography, outcrossing, population growth rate, selfing.

Both genetic factors and environmental conditions influence the structure of plant populations (Hamrick and Godt 1990; Linhart and Grant 1996) and thus are likely important regulators of population dynamics. Among genetic factors, the mating system (relative production of selfed and outcrossed individuals) is of utmost importance to population structure because it largely determines the amount of genetic variation observed in a population, whereas one of the primary ecological factors affecting plant populations is herbivory (Crawley 1989). This ubiquitous ecological interaction is known to affect numerous vital rates of plants, including growth, survivorship, and fecundity (reviewed in Crawley 1989; Huntly 1991), which can scale up to affect population dynamics and growth rate (e.g., Bastrenta et al. 1995; Ehrlén 1995, 2003; Rooney and Gross 2003; Knight 2004). In recent years, evidence has mounted that herbivory also has consequences for mating system expression (Elle and Hare 2002; Steets and Ashman 2004; Ivey and Carr 2005; Steets et al. 2006a, 2006b). Yet, to date, few empirical data exist on the effect of mating system for population dynamics (but see Le Corff and Horvitz 2005) and the consequence of herbivory-induced changes in mating system for population growth.

Although evolutionary biologists have long studied the consequences of selfing or outcrossing for individual fitness (Charlesworth and Charlesworth 1987), population genetic structure (Hamrick and Godt 1990), and speciation (Barrett 1990), the demographic significance of a mixed strategy (both outcrossing and selfing) has been largely ignored (but see Oostermeijer 2000; Le Corff and Horvitz 2005; Koslow and DeAngelis 2006). To have a greater understanding of the population-level consequences of mixed mating, we must first account for contributions of selfed and outcrossed individuals throughout the life cycle to population dynamics. For example, selfed individuals may germinate at a lower rate and experience reduced survival and fecundity compared with outcrossed individuals as a result of inbreeding depression (reviewed in Charlesworth and Charlesworth 1987). Alternatively, in highly structured populations, the opposite pattern may hold because of

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outbreeding depression (e.g., Pelabon et al. 2005). Although numerous researchers have compared vital rates (i.e., germination, survival, and fecundity) of selfed and outcrossed individuals (e.g., Waller 1984; Luijten et al. 2002), only one study has evaluated any of these vital rates in the context of a demographic model (Le Corff and Horvitz 2005). Le Corff and Horvitz (2005) found that population spread and growth rate of *Calathea micans* were most sensitive to changes in the production of seedlings derived from outcrossing flowers, compared with changes in the production of seedlings derived from selfing flowers. Although the model by Le Corff and Horvitz (2005) considered the dispersal ability and germination rate of progeny of selfed and outcrossed flowers separately, the model did not differentiate the survival or fecundity of these progeny types. Thus, a more complete evaluation that includes all vital rates of selfed and outcrossed individuals is essential to understand the demographic consequences of mating system to population dynamics and persistence.

Herbivores are an important aspect of the environment and are known to affect plant mating system expression and individual fitness (Elle and Hare 2002; Steets and Ashman 2004; Ivey and Carr 2005; Steets et al. 2006a, 2006b); thus, it is likely that herbivore pressure may influence plant population dynamics. In fact, there are several avenues for herbivory-induced changes in mating system to affect population dynamics. First, herbivory may affect the outcrossing rate by increasing (Steets and Ashman 2004; Ivey and Carr 2005; Steets et al. 2006b) or decreasing (Elle and Hare 2002; Steets et al. 2006a) the relative numbers of selfed versus outcrossed individuals produced. This, in turn, could have demographic effects if the vital rates of the mating types differ. Second, if herbivory increases the expression of inbreeding depression, as has been observed in a few species (Carr and Eubanks 2002; Hayes et al. 2004), it will further bias the relative contributions of selfed and outcrossed progeny to the next generation and potentially affect population dynamics. Finally, herbivory may have transgenerational effects (sensu Agrawal 2001) that alter the demographic value of selfed versus outcrossed seeds. For instance, if maternal herbivory reduces the provisioning and/or performance of selfed progeny more than outcrossed progeny (Steets and Ashman 2004), then outcrossed individuals may contribute more to population growth in the following generation than selfed individuals.

As a first step in understanding the avenues by which herbivory and mating system interact to affect population dynamics, we investigate the first two potential effects, that is, those that occur within a single generation, and leave the transgenerational aspect to a future study. Specifically, we address the demographic effects of mating system and herbivory in *Impatiens capensis*, a species with an obligate mixed mating system (i.e., individuals produce both selfing

cleistogamous [CL] and facultatively outcrossing chasmogamous [CH] flowers). In natural populations, we followed seeds derived from CL and CH flowers (hereafter, CL and CH individuals) subject to different herbivory levels throughout their life cycle to address the following questions. (1) How do mating system and herbivory affect vital rates (i.e., germination, survival, and fecundity)? (2) How does herbivory affect the population dynamics of *I. capensis*? (3) How sensitive are the population dynamics of *I. capensis* to cleistogamy and chasmogamy, and does herbivory change the relative contributions of CL and CH individuals to population growth? (4) What is the relative contribution of each vital rate to changes in population growth rate between herbivory levels?

Methods

Study System

Impatiens capensis Meerb. (Balsaminaceae) is an annual herb native to North America (Schemske 1978). This species reproduces only sexually, via CL and CH flowers. The flower types are easily distinguished by their positions on the plant and pedicel structure (Schemske 1978). The obligately self-pollinating CL flowers have reduced petals, anthers, and sepals and lack nectaries. In contrast, the CH flowers are showy and open to pollination by numerous species of bees (e.g., *Bombus* spp., *Apis mellifera*, *Dialictus rohweri*) as well as the ruby-throated hummingbird (*Archilochus colubris*; Steets et al. 2006a). The CH flowers are self-compatible, but strong protandry prevents autogamy. In the northwestern Pennsylvania populations studied here, outcrossing rates for CH flowers range between 0.29 and 1.00, and a significant portion of this variation is related to herbivore damage (Steets et al. 2006a). Plants usually emerge in the spring (March–May), begin production of CL flowers in early summer (mid-June) and CH flowers in late summer (August), and senesce in the fall (October). Seeds produced in the fall germinate the following spring; that is, there is no persistent seed bank (Antlfinger 1989).

Numerous insect species feed on the vegetative tissue of *I. capensis* (see Schemske 1978). In the populations we studied, vegetative herbivory averaged 50% of leaves damaged per plant but varied among individuals (0%–100%) and was primarily caused by chrysomelid beetles, leaf miners, grasshoppers, and katydids (J. A. Steets, personal observation).

Experimental Design

During the summer of 2003, we haphazardly collected CL and CH seeds from individuals in two *I. capensis* populations in Crawford County, Pennsylvania (L pop-

ulation: 41°38.6'N, 80°25.7'W; W population: 41°40.6'N, 80°25.6'W). Both populations occurred in deciduous forests in which the overstory predominately was composed of oak (*Quercus* spp.), beech (*Fagus sylvatica*), and maple (*Acer* spp.). In the L population, *I. capensis* occurred in monospecific stands, whereas in the flood-prone W population, *I. capensis* was found among other understory herbs, including skunk cabbage (*Symplocarpus foetidus*), jack-in-the-pulpit (*Arisaema* spp.), and large-flowered trillium (*Trillium grandiflorum*). Seeds were stored in distilled water at 4°C until November 2003, at which time they were planted into plots in their respective populations. Specifically, we randomly set out 12 1-m² plots in each population in locations where *I. capensis* occurred. Within each plot, we cleared other vegetation and planted 400 native seeds (200 CL and 200 CH seeds) in a randomized grid 5 cm apart, for a total of 2,400 CL and 2,400 CH seeds per population. This planting design produced a seed density that was similar to that found in natural *I. capensis* populations (Antlfinger 1989). Seeds were planted to a depth of 1 cm into sections of 1-cm-diameter plastic straws and covered with sand and leaf litter. Once seedlings emerged in the spring, plots were randomly assigned to either a reduced (RH) or an ambient (AH) herbivory treatment. Herbivory to plants in RH plots was reduced with biweekly applications of Conserve (active ingredient spinosad), an insecticide that reduces herbivory without affecting *I. capensis* growth, reproduction, or pollinator visitation (Steets 2005). Plants in AH plots were sprayed with water at the same frequency to serve as a control. In the W population, one RH plot was destroyed by early spring floods; thus, the sample size for this population was reduced to 11 plots (five RH plots and six AH plots). Vegetative herbivory was recorded once (mid-flowering season) as the percentage of leaves damaged per plant. To determine whether the insecticide spray reduced herbivory, we performed ANOVA (PROC GLM, SAS Institute) with herbivory treatment, population, seed type (CL, CH), and their interactions as fixed effects and plot mean percent leaf damage of seed types as the response variable. For each population, we report the standardized mean difference (i.e., effect size, d) between treatments in leaf damage (for calculation, see Gurevitch and Hedges 2001).

Ideally, to determine how mating system and herbivory interact to affect population dynamics, one would measure vital rates of known selfed and outcrossed seeds in different herbivory environments. However, obtaining sufficient sample size for such a demographic study would require thousands of controlled crosses to generate the seed types. In lieu of this, we took advantage of the heteromorphic flowering system of *I. capensis* and followed known selfed (i.e., CL seeds) and potentially outcrossed (i.e., CH seeds) seeds throughout their life cycle. However, we are confi-

dent that the majority of CH seeds used in this experiment were outcrossed because CH outcrossing rate was 60% and 82% in the L and W populations, respectively, during the summer we harvested seeds for this experiment (Steets et al. 2006a). In addition, data from another experiment conducted in the W population indicate that maternal effects (i.e., differential maternal resource provisioning to mating system types) are unlikely to explain the results obtained because seedling biomass does not differ between CL and CH individuals (J. A. Steets and T.-L. Ashman, unpublished data). Therefore, any difference that we observe between CL and CH vital rates is likely a result of the difference in inbreeding level of progeny derived from CL and CH flowers.

We recorded seedling germination and survival to reproduction and marked the peduncles of developing fruits with nontoxic paint weekly throughout the growing season (April 1–October 6, 2004). At the end of the season, we quantified CL and CH fruit production on all surviving plants in each plot by enumerating painted peduncles. To estimate seed production per plant, we collected up to three CL and CH fruits from each individual and enumerated the number of seeds per fruit. For each individual, total CL (or CH) fecundity was calculated as the product of CL (or CH) fruit production and mean CL (or CH) seed production per fruit. For the few plants for which we were unable to obtain seeds, we used plot mean CL or CH seed production per fruit for a CL or CH individual in the above calculation of fecundity. In each plot, an average of 354 seeds germinated (range: 286–400), 55 individuals survived to reproduce via cleistogamy (range: 13–95), and 10 individuals survived to reproduce via cleistogamy and chasmogamy (range: 0–26).

How Do Mating System and Herbivory Affect Vital Rates?

The basic model for projecting population growth of a structured population is $\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$, where \mathbf{n} is a vector with i rows representing the number of individuals in each life stage at times t and $t + 1$ and \mathbf{A} represents the annual projection matrix with i rows and j columns containing all life stage transition probabilities (a_{ij}). We constructed a two-stage (i.e., CL seed and CH seed) matrix model for *I. capensis* with four matrix elements (i.e., CL seed to CL seed [a_{11}], CL seed to CH seed [a_{21}], CH seed to CL seed [a_{12}], and CH seed to CH seed [a_{22}]; fig. 1A). The transition probabilities in \mathbf{A} are a multiplicative function of germination (g), survivorship (p), and fecundity (f) of CL and CH individuals. For each population, we calculated the matrix elements (a_{ij}) within each plot and then averaged across all plots within a treatment to generate a single \mathbf{A} matrix for each of the four herbivory level–population combinations. The matrix elements from the annual ma-

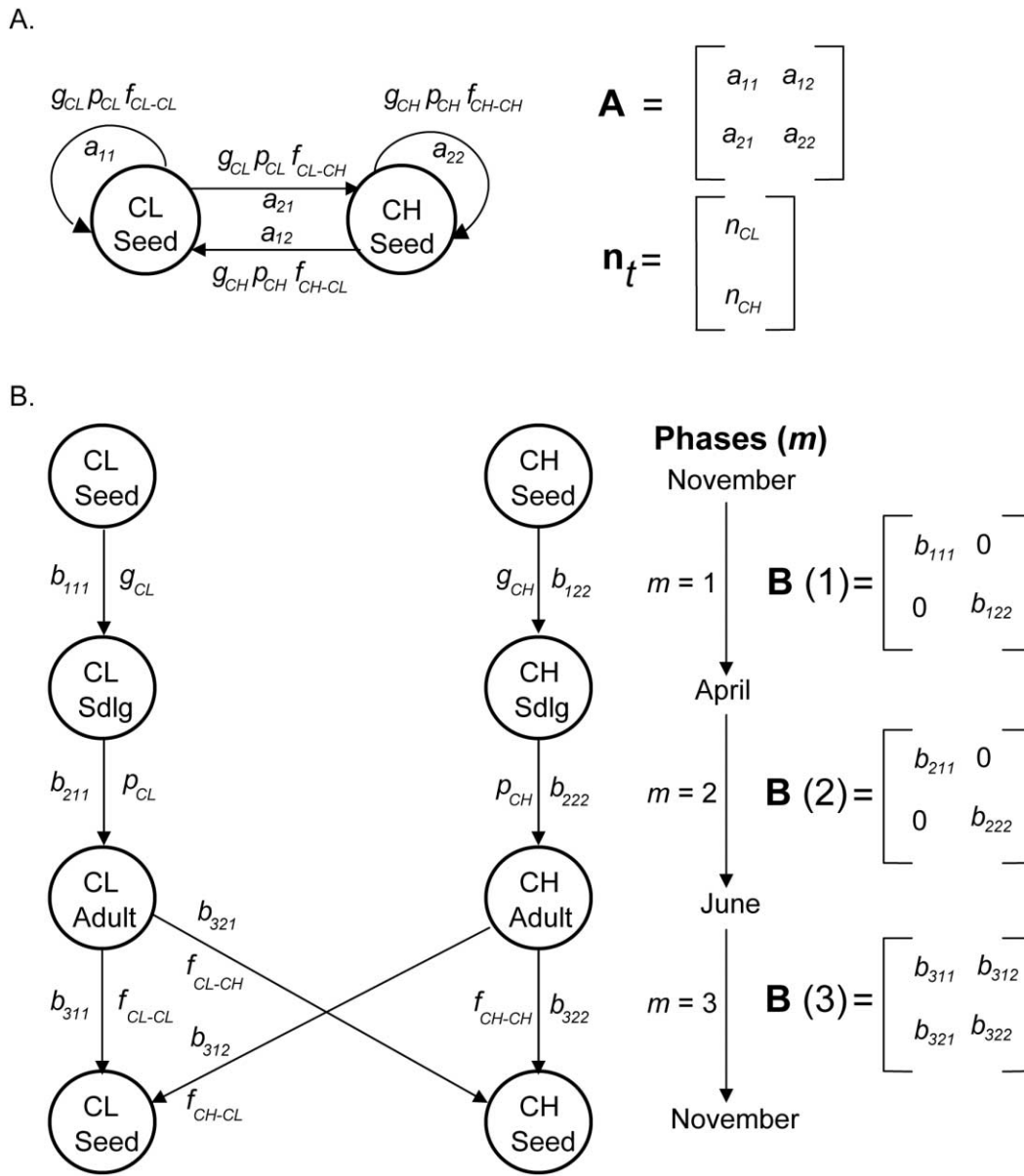


Figure 1: A, Annual life cycle graph and projection matrix model of *Impatiens capensis* incorporating mating system. The number of cleistogamous (CL) and chasmogamous (CH) individuals in the next generation (\mathbf{n}_{t+1}) can be calculated as $\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$, where \mathbf{A} represents the annual projection matrix with its four matrix elements, that is, CL seed to CL seed (a_{11}), CL seed to CH seed (a_{21}), CH seed to CL seed (a_{12}), and CH seed to CH seed (a_{22}). B, Periodic life cycle graph and projection matrix model of *I. capensis* incorporating mating system. The complete population cycle consists of three phases (m). The population projection matrices $\mathbf{B}(h)$ (where $h = 1, 2, \dots, m$) describe within-year variation in vital rates (b_{mij}). To describe the population dynamics over the entire cycle, we calculate the matrix product \mathbf{A} by taking the product of all the \mathbf{B} matrices (i.e., $\mathbf{A} = \mathbf{B}(3) \times \mathbf{B}(2) \times \mathbf{B}(1)$). Vital rates include CL germination (g_{CL}), CH germination (g_{CH}), CL survival (p_{CL}), CH survival (p_{CH}), CL adult CL fecundity (f_{CL-CL}), CL adult CH fecundity (f_{CL-CH}), CH adult CL fecundity (f_{CH-CL}), and CH adult CH fecundity (f_{CH-CH}).

trix model are presented in table A1 and will not be discussed further.

Because *I. capensis* is an annual plant, the above-outlined matrix model with a 1-year time step (i.e., fig. 1A) simultaneously considers many vital rates (germina-

tion, survival, fecundity) in a single transition probability, and thus it does not allow for examination of the effects of herbivory on population growth through these underlying vital rates. In contrast, periodic matrix models provide a framework for modeling the demography of annual

plants because they emphasize within-year temporal variation, allowing a larger proportion of the information available from demographic observations to be included (Caswell 2001). Thus, we additionally created a periodic matrix model that explicitly considers the mating system of *I. capensis* (fig. 1B). The complete population cycle consists of three phases (m ; fig. 1B). The first phase occurs from November to April and includes two vital rates, seed survival and germination of CL (g_{CL}) and CH (g_{CH}) seeds. The second phase occurs from April to June and includes the vital rates of CL (p_{CL}) and CH (p_{CH}) survival to reproduction. The final phase occurs from June to November and includes four fecundities: CL adult CL fecundity (f_{CL-CL}), CL adult CH fecundity (f_{CL-CH}), CH adult CL fecundity (f_{CH-CL}), and CH adult CH fecundity (f_{CH-CH}). The resultant periodic projection matrices $\mathbf{B}(h)$ (where $h = 1, 2, \dots, m$) describe within-year variation in these vital rates. To describe the population dynamics over the entire cycle, the matrix product \mathbf{A} is calculated by taking the product of all the \mathbf{B} matrices (i.e., $\mathbf{A} = \mathbf{B}(3) \times \mathbf{B}(2) \times \mathbf{B}(1)$). We quantified vital rates separately for each herbivory level and created a separate periodic matrix model for each herbivory level–population combination by first averaging vital rates within a plot and then averaging across plots within a population. Because there was no a priori expectation for germination to differ with herbivory levels, all plots in a population were averaged to estimate germination rates of CL and CH seeds.

Mean CL and CH germination rate and seedling survivorship (conditional on germination) were calculated for each plot. To determine the effects of population (L, W) and seed type (CH, CL) on germination rate, we conducted a fixed-effects ANOVA (PROC GLM, SAS Institute). Similarly, we performed a fixed-effects ANOVA to determine the effect of herbivory treatment, population, seed type, and their interactions on survival to reproduction. The CL and CH fecundity were quantified for individual plants within plots, and we performed a mixed-model ANOVA (PROC MIXED, SAS Institute) with population, herbivory treatment, seed type, and their interactions as fixed effects and plot nested within population and herbivory treatment designated as a random factor. Plot was not explicitly considered in the analyses for germination and survivorship because these vital rates were calculated at the plot level; plot was explicitly considered in the analyses for CL and CH fecundity because these vital rates were calculated for individuals within plots. Germination and survivorship were arcsine transformed, and CL and CH fecundity were log transformed before analysis to improve normality (Zar 1999).

How Does Herbivory Affect Population Dynamics of *I. capensis*?

To determine how herbivory affects population dynamics of *I. capensis*, we projected several population-level parameters from \mathbf{A} . First, we calculated population growth rate (λ) for each herbivory treatment within each population as the dominant eigenvalue of \mathbf{A} (Caswell 2001). We expected λ to be lower with herbivory because this antagonism dramatically reduces fecundity in *I. capensis* (Steets and Ashman 2004; Steets et al. 2006a, 2006b). In addition, for each herbivory level–population combination, we calculated the stable stage distribution (\mathbf{w}) as the right eigenvector of \mathbf{A} (Caswell 2001). The stable stage distribution is the proportion of individuals in each stage class (i.e., CL and CH individuals) once the population reaches equilibrium (Caswell 2001). Given that herbivory increases proportional production of CL seeds per plant (Steets and Ashman 2004; Steets et al. 2006a), we expected herbivory to shift the stable stage distribution in a similar way. Finally, we calculated the reproductive value (\mathbf{v}) as the left eigenvector of \mathbf{A} for each herbivory level–population combination (Caswell 2001). For *I. capensis*, the reproductive value can be interpreted as the present value of the future offspring produced by CH and CL individuals. Because herbivory increases the proportion of CL seeds produced by an individual (Steets and Ashman 2004; Steets et al. 2006a), we also expected the reproductive value to be altered by herbivory. To determine whether λ , \mathbf{w} , or \mathbf{v} differs between populations or herbivory treatments, we compared these population-level parameters using randomization tests (see “Confidence Intervals and Randomization Tests”). We further decomposed the differences in λ between herbivory treatments using retrospective analyses (i.e., life table response experiment [LTRE]).

How Sensitive Are the Population Dynamics of *I. capensis* to Cleistogamy and Chasmogamy, and Does Herbivory Change the Relative Contributions of CL and CH Individuals to Population Growth?

To determine how sensitive the population dynamics of *I. capensis* are to cleistogamy and chasmogamy, we calculated the elasticities of \mathbf{A} for the L and W populations. Elasticities (e_{ij}),

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = \frac{\partial(\log \lambda)}{\partial(\log a_{ij})},$$

measure the proportional change in λ that would result from a proportional small change in each annual matrix element, a_{ij} (de Kroon et al. 1986; Caswell 2001). Because elasticities range from 0 to 1 and sum to 1, they provide

a measure of the relative importance of each matrix element (i.e., changes in matrix elements with large elasticities will cause larger changes in λ than will changes in matrix elements with smaller elasticities; de Kroon et al. 2000). We used randomization tests to determine whether populations and herbivory treatments differ in the elasticity of λ to cleistogamy and chasmogamy matrix elements (see “Confidence Intervals and Randomization Tests”).

What Is the Relative Contribution of Each Vital Rate to Changes in Population Growth Rate between Herbivory Levels?

Because herbivory occurs on both seedlings and adult plants, it could potentially affect six vital rates (i.e., CL and CH survival and all avenues for adult fecundity). We performed a periodic LTRE analysis to determine the contribution of each vital rate to the difference in λ between the ambient and reduced herbivory levels. A matrix element will have a large contribution to variation in λ if its magnitude varies greatly among treatments or if λ is highly sensitive to changes in that element. For the periodic matrix of *I. capensis*, the LTRE equation is

$$\lambda^{\text{RH}} - \lambda^{\text{AH}} \cong \sum_{hij} (b_{hij}^{\text{RH}} - b_{hij}^{\text{AH}}) \mathbf{S}_{\mathbf{B}(h)},$$

where the difference in λ between herbivory treatments is decomposed into contributions of each vital rate in the periodic matrix (Davis et al. 2003). Here, RH and AH designate the reduced and ambient herbivory treatments, and b_{hij} refers to individual matrix elements of the periodic projection matrices; $\mathbf{S}_{\mathbf{B}(h)}$ represents the sensitivity of λ to changes in the elements of periodic projection matrix $\mathbf{B}(h)$ and can be calculated using the formula

$$\mathbf{S}_{\mathbf{B}(h)} = \mathbf{D}^{\text{T}} \mathbf{S}_{\mathbf{A}(h)},$$

where \mathbf{D}^{T} represents the transpose of the product of the periodic projection matrices excluding $\mathbf{B}(h)$, and $\mathbf{S}_{\mathbf{A}(h)}$ represents the sensitivities of λ to changes in the elements of $\mathbf{A}(h)$ (the annual projection matrix for the interval beginning at time period h ; Caswell and Trevisan 1994). For example, in *I. capensis*, the sensitivity matrix for $\mathbf{B}(2)$ is $\mathbf{S}_{\mathbf{B}(2)} = [\mathbf{B}(1)\mathbf{B}(3)]^{\text{T}} \mathbf{S}_{\mathbf{A}(2)}$, where $\mathbf{A}(2) = \mathbf{B}(1) \times \mathbf{B}(3) \times \mathbf{B}(2)$. The sensitivities used in the periodic LTRE analysis were calculated from the mean annual matrices across the two herbivory levels.

Confidence Intervals and Randomization Tests

We calculated the 95% confidence intervals around all vital rates (g , p , f) and matrix projections (λ , \mathbf{w} , \mathbf{v} , e_{ij}) for each

demographic model by using bootstrapping (McPeck and Kalisz 1993; Caswell 2001). A bootstrap data set was calculated for a given herbivory level–population combination by resampling individuals with replacement at the level of the plot. The sample size of a bootstrap data set was identical to that of the original data set (i.e., 400 individuals per plot). This process of generating a bootstrap data set was repeated 1,000 times, to create 1,000 bootstrap data sets for each herbivory level–population combination. The mean vital rates for individuals in plots were calculated for each bootstrap data set, and then plots in the same population and herbivory level were averaged to generate mean vital rates for each population and treatment with the exception of germination rates (g_{CL} , g_{CH}). For these two vital rates, we averaged across all plots in a population because the herbivory treatment was imposed after germination and thus could not affect these vital rates. From these bootstrap data sets, we calculated the 95% confidence intervals for each vital rate. We used the bootstrap data sets to generate 1,000 values for each matrix projection (λ , \mathbf{w} , \mathbf{v} , e_{ij}), from which we calculated the mean matrix projection and 95% confidence intervals.

To determine whether populations (L vs. W) or herbivory treatments (RH vs. AH) significantly differed in their matrix projections, we performed randomization tests ($N = 1,000$ permutations; Caswell 2001). To test for differences in λ (and other matrix projections) between populations, we computed the observed difference in λ between the L and W populations and compared this value to 1,000 calculated differences in λ when population was randomly assigned to plots. The P value indicates the proportion of times the difference in λ from permutation was greater than the observed difference in λ . A similar method was used to test for a difference in λ (and other matrix projections) between herbivory treatments. We used the method described by Levin et al. (1996) to test for an interaction between our two main factors (i.e., population and herbivory treatment) on λ (and other matrix projections). The null hypothesis is that there is no interaction and that both populations respond to the herbivory treatment in parallel. If this is true, then differences in λ (and other matrix projections) between populations should be the same for each herbivory treatment. To get the observed value for our test statistic, θ_{int} , we first calculated the difference between populations in λ within each herbivory treatment and then computed the variance in these values. To generate the distribution of θ_{int} under the null hypothesis, we randomly assigned plots to herbivory treatments within populations and calculated θ_{int} for the permuted data set. We repeated this for 1,000 permutations. The significance of the interaction between population and herbivory is given by the proportion of values of θ_{int} generated by permutation that are greater than or equal to

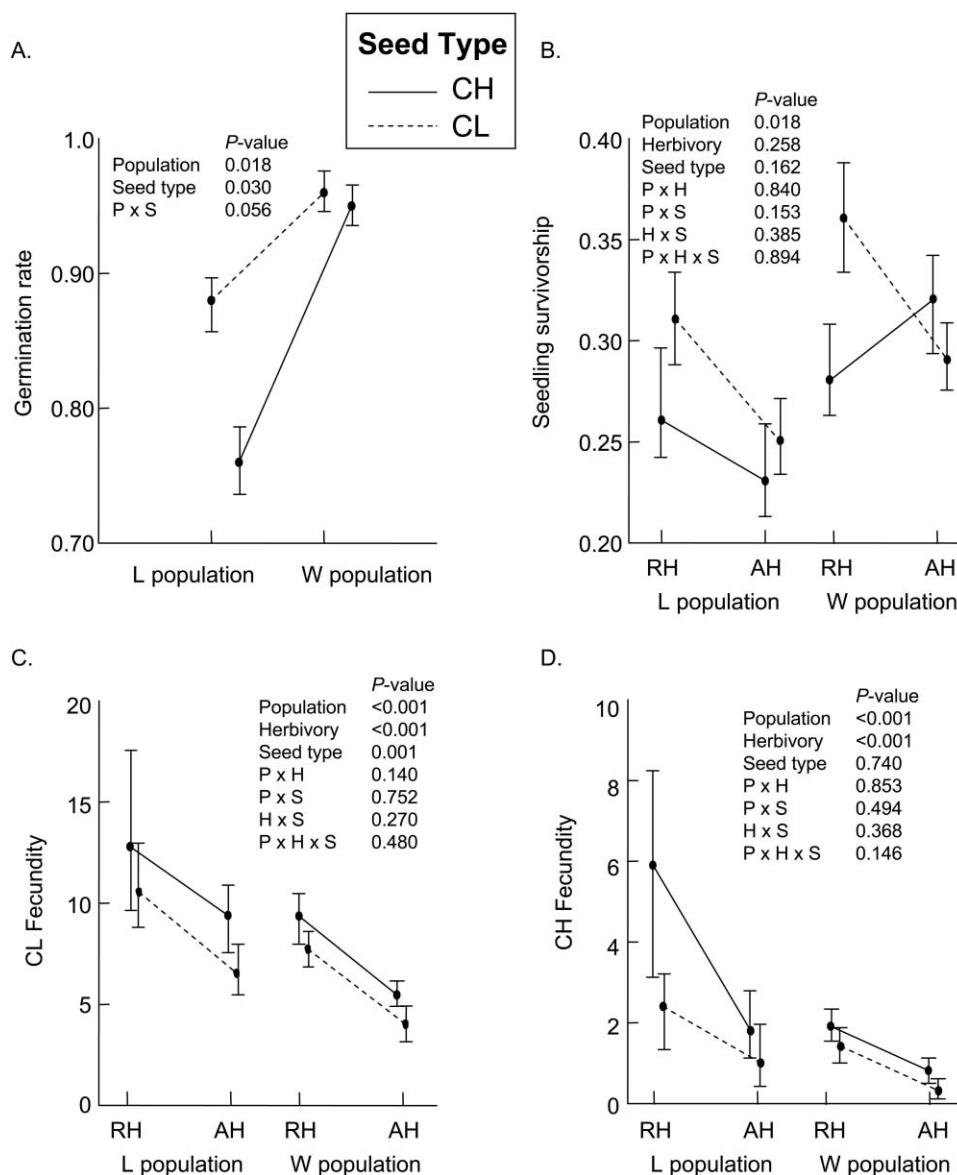


Figure 2: Germination rate (A), seedling survivorship to reproduction (B), cleistogamous (CL) fecundity (C), and chasmogamous (CH) fecundity (D) of two *Impatiens capensis* populations (L and W) under ambient (AH) and reduced (RH) herbivory treatments. Vital rates are shown separately for each seed type (CL and CH). Error bars represent 95% bootstrap confidence intervals. Significance levels of *F* statistics from ANOVAs are reported.

the observed value of θ_{int} . Because the vital rates of both seed types (CH and CL) are needed to project λ (and other matrix projections) for each population and herbivory treatment, seed type was not considered as a main factor for population projection. All confidence intervals and randomization tests were calculated using MATLAB (MathWorks 2000).

Results

How Do Herbivory and Mating System Affect Vital Rates?

Mating System Effects. We found significant differences in the vital rates of CL and CH individuals. At earlier stages of the life cycle, CL individuals had an advantage over CH individuals; CL seeds germinated at a higher rate than CH

seeds, particularly in the L population (fig. 2A). Seedlings of both seed types were equally likely to survive to reproduction (fig. 2B). However, later in the life cycle, CH individuals expressed a fecundity advantage over CL individuals, with CH adults producing 23% more CL seeds than CL adults (fig. 2C).

Herbivory Effects. The insecticide application reduced vegetative herbivory by 48% and 33% in the L and W populations, respectively (L population: 21% vs. 40% leaf damage, $d = 1.70$; W population: 33% vs. 49% leaf damage, $d = 3.27$; $F = 40.8$, $df = 1, 38$, $P < .0001$). The herbivory reduction treatment significantly increased fecundity vital rates; across populations, reducing herbivory increased CL seed production by 59% and CH seed production by 179% (fig. 2C, 2D).

Population and Interactive Effects. The L and W *Impatiens capensis* populations significantly differed in all vital rates. Plants in the W population were more likely to germinate and survive (fig. 2A, 2B), whereas plants in the L population had higher CL and CH fecundity (fig. 2C, 2D).

The interactive effects of herbivory, seed type, and population on all vital rates were nonsignificant (fig. 2). For germination rate, the population \times seed type interaction nearly reached significance ($P = .056$). For this vital rate, there tended to be a larger difference between CL and CH seed types in germination rate in the L population than in the W population (fig. 2A).

How Does Herbivory Affect Population Dynamics of I. capensis?

Population size was projected to increase under all herbivory level–population combinations (i.e., λ significantly greater than 1; fig. 3A). As predicted, the populations experiencing reduced herbivory were growing at a significantly faster rate than those subject to ambient levels of herbivory; reduced herbivory led to a 104% increase in λ in the L and a 132% increase in the W population (fig. 3A). Both populations had similar population growth rates and responded similarly to the herbivory treatment (fig. 3A). In addition, both populations displayed similar stable stage distributions with CL individuals constituting the majority of the population (77%–88%) at equilibrium (fig. 3B). Although we found that herbivory increased the proportion of CL individuals in the stable stage distribution, this trend was not statistically significant (fig. 3B). The L and W populations displayed similar reproductive values for CL and CH plants, and this was unchanged by herbivory (fig. 3C).

How Sensitive Are the Population Dynamics of I. capensis to Cleistogamy and Chasmogamy, and Does Herbivory Change the Relative Contributions of CL and CH Individuals to Population Growth?

For both populations, λ was most sensitive to the CL seed-to-CL seed transition, with the elasticities of this transition being more than four times larger than those for the other types of transitions (fig. 4), indicating that cleistogamy has a greater influence on λ than chasmogamy for both populations in the year studied. This pattern was not altered by herbivory (fig. 4; randomization tests all $P > .10$).

What Is the Relative Contribution of Each Vital Rate to Changes in Population Growth Rate between Herbivory Levels?

Many vital rates were altered by the herbivory manipulation; however, not all of these contributed equally to the difference in λ between herbivory levels (table 1). In both populations, the survival of CL seedlings (p_{CL}) and CL fecundity of CL adults (f_{CL-CL}) contributed the most to the difference in λ between herbivory levels (table 1, col. C). Although CL survival did not differ much with herbivory (table 1, col. B), it had a large contribution (0.42 and 0.37 in L and W populations, respectively) because λ was most sensitive to changes in this vital rate (table 1, col. A). On the other hand, CL fecundity of CL adults had a large contribution (0.77 and 0.96 in L and W populations, respectively) because this vital rate differed dramatically between herbivory levels (table 1, col. B). Despite the large differences in the other fecundity measures (f_{CL-CH} , f_{CH-CL} , f_{CH-CH}) between herbivory levels (table 1, col. B), they contributed less to the change in λ with herbivory (table 1, col. C) because λ is relatively insensitive to these vital rates (table 1, col. A). Finally, of the six vital rates contributing to the change in λ with herbivory, survival of CH seedlings had the lowest contribution (table 1, col. C) despite its high sensitivity (table 1, col. A) because herbivory had little effect on this vital rate (table 1, col. B).

Discussion

Our study adds a unique dimension to understanding the importance of mating system in plant ecology and evolution by demonstrating that mating system can have significant demographic consequences. In particular, we found that progeny of selfed flowers differ from progeny of outcrossed flowers in several important vital rates (fig. 2) and, as a consequence, differentially contribute to population growth of *Impatiens capensis* (fig. 4). In addition, we found that a prevalent ecological factor, vegetative herbivory, exerted differential effects on the two progeny types

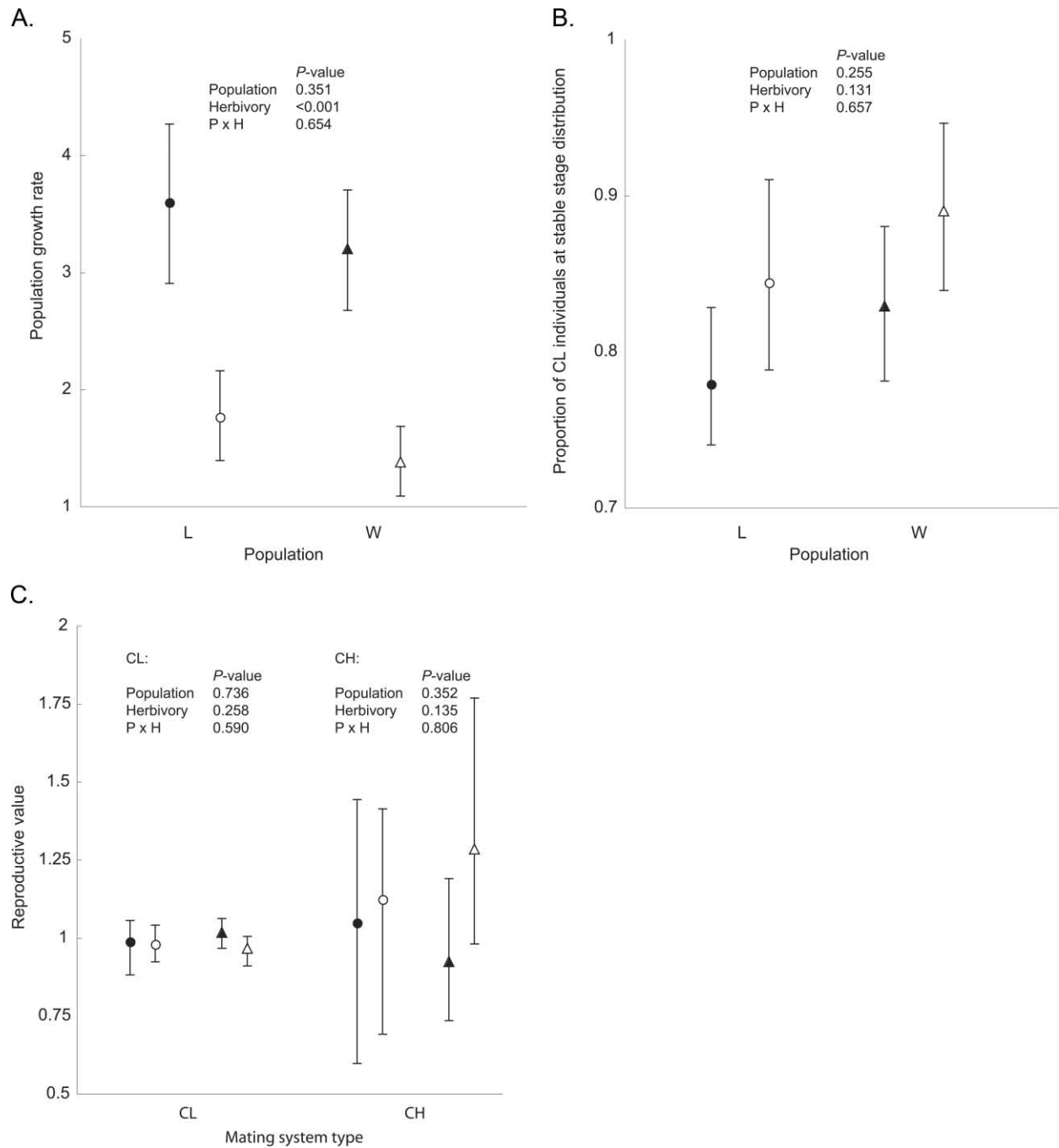


Figure 3: Effects of mating system and herbivory on population projections. Population growth rate (A), proportion of cleistogamous (CL) individuals at stable stage distribution (B), and reproductive value of CL and chasmogamous (CH) individuals (C) for two *Impatiens capensis* populations (L = circles; W = triangles) experiencing ambient (open symbols) or reduced (filled symbols) herbivory. The 95% bootstrap confidence intervals are displayed. Significance levels from randomization tests are reported.

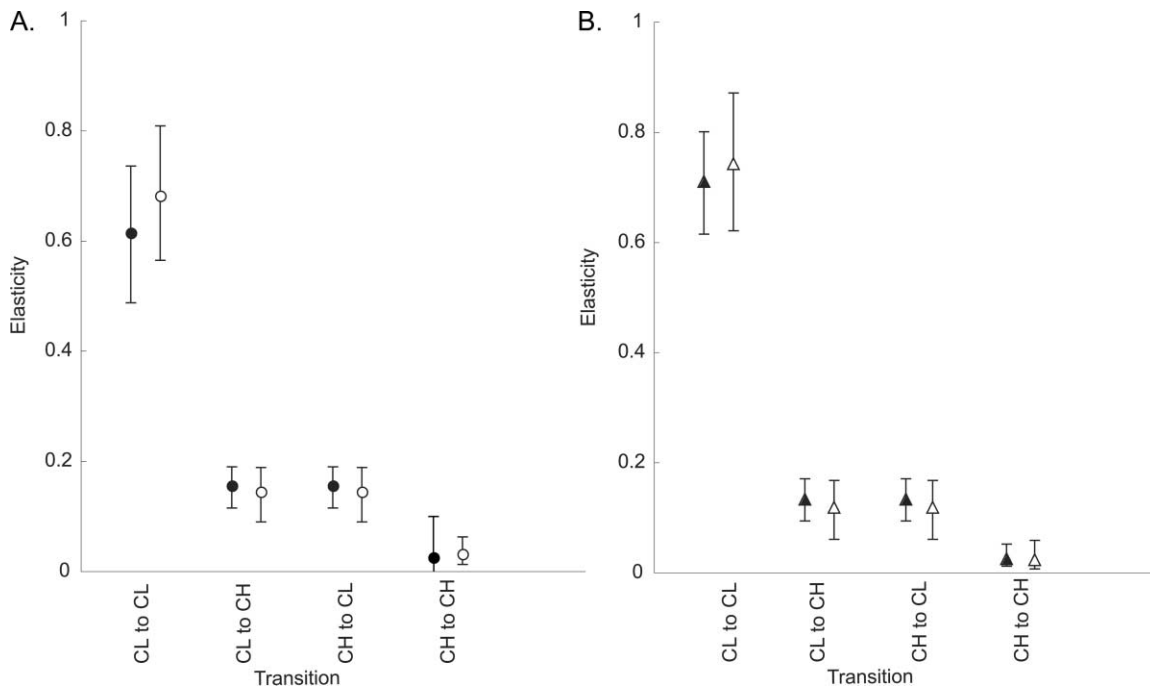


Figure 4: Elasticities of cleistogamous (CL) and chasmogamous (CH) transition rates for the annual matrix model of L (A) and W (B) *Impatiens capensis* populations experiencing ambient (open symbols) or reduced herbivory (filled symbols). Error bars represent 95% bootstrap confidence intervals. Refer to text and figure 1A for annual matrix model description.

that influenced projected population dynamics of *I. capensis* (table 1). We expand on each of these findings and discuss the implications of this work for the evolution of mixed mating.

Demographic Consequences of Mixed Mating

Mating system is an important factor structuring population genetic diversity (Hamrick and Godt 1990). Our study demonstrates that it also plays a central role in population dynamics of a species exhibiting a mixed strategy. Within the life cycle of *I. capensis*, we found evidence that mating system types differ in important vital rates and that these results are consistent with expectations based on inbreeding depression. However, because inbreeding depression was not explicitly measured in this experiment, our results cannot rule out the possibility that other differences, such as maternal effects, may have contributed to the differences seen in CL- and CH-derived individuals. Nevertheless, based on results from another experiment (see “Methods”), we think that maternal effects are an unlikely cause of our findings. In a primarily selfing species, such as *I. capensis*, inbreeding depression is expected to manifest at later stages of the life cycle, such as in growth and reproductive traits (reviewed in Husband and Schem-

ske 1996). In accordance with this prediction, we found that CH adults tended to have higher CL fecundity than CL adults (fig. 2C), despite having a disadvantage early in the life cycle (fig. 2A). Other researchers have demonstrated significant inbreeding depression in reproductive traits of *I. capensis* (Schmitt and Ehrhardt 1987; Schmitt and Gamble 1990; Lu 2002). For example, outcrossed CH individuals produced 22% more total flowers (Lu 2002) and up to 50% more CL flowers (Schmitt and Gamble 1990) than did selfed CL plants. In addition, Schmitt and Gamble (1990) found greater inbreeding depression in CL flowering than in seedling emergence, further supporting theoretical predictions of greater inbreeding depression in later stages of development of this mixed mating species.

Our finding of a CL advantage early in life may seem counterintuitive. However, another study on this species reports similar findings; CL seed germination was nearly 50% greater than CH seed germination (58% vs. 40%) in a natural population (Antlfinger 1986). The higher germination and survival of CL seeds could be due to several factors. First, maternal effects may differ between mating system types in a way that provides an advantage to the selfed seeds early in life. However, because CL seeds tend to be smaller in size than CH seeds (e.g., Schmitt and Gamble 1990), it seems unlikely that maternal effects on

Table 1: Periodic life table response experiment for two *Impatiens capensis* populations (L and W)

Vital rate	Sensitivity (A)		Difference (B)		Contribution (C)	
	L	W	L	W	L	W
g_{CL}	3.25	2.88
g_{CH}	.98	.47
p_{CL}	9.34	7.70	.06	.06	.42	.37
p_{CH}	2.84	1.59	.03	-.03	.07	-.04
f_{CL-CL}	.21	.29	4.04	3.64	.77	.96
f_{CL-CH}	.22	.27	1.32	1.11	.28	.32
f_{CH-CL}	.04	.05	3.43	3.96	.12	.16
f_{CH-CH}	.04	.04	4.14	1.13	.17	.05

Note: Sensitivity of population growth rate to changes in each vital rate (A), difference in vital rates between reduced and ambient herbivory levels (B), and total contribution of a vital rate to the observed difference in population growth between herbivory levels (C) are given. Vital rates include cleistogamous (CL) germination (g_{CL}), chasmogamous (CH) germination (g_{CH}), CL survival (p_{CL}), CH survival (p_{CH}), CL adult CL fecundity (f_{CL-CL}), CL adult CH fecundity (f_{CL-CH}), CH adult CL fecundity (f_{CH-CL}), and CH adult CH fecundity (f_{CH-CH}). Refer to figure 1B for periodic matrix model and text for description of periodic life table response experiment analysis. The herbivory treatments were applied after g_{CL} and g_{CH} were measured; thus, herbivory could not affect these vital rates.

seed types would explain the CL advantage. Alternatively, CL seeds may express a germination and survival advantage over CH individuals because of ecological factors, such as differential susceptibility to pathogens or attack by seed predators. While our study is not the first to demonstrate a CL advantage early in life (see also Antlfinger 1986), others have found inbreeding depression in germination and survival in natural *I. capensis* populations (i.e., Mitchell-Olds and Waller 1985). The conflicting results of these studies are likely due to population differences in mating system and environment.

Our sensitivity analyses demonstrate that the population dynamics of *I. capensis* would be affected disproportionately more by changes in the vital rates of the CL mating system type. For both populations, we found that CL individuals made up the greatest portion of the stable stage distribution, and thus population dynamics were most sensitive to changes in vital rates of CL plants (fig. 4). This finding is in contrast to that of the only other published study that considered plant mating system in a demographic context. Le Corff and Horvitz (2005) found that population growth rate of *Calathea micans* was more sensitive to changes in the production of CH seedlings than to changes in the production of CL seedlings. The differences between our findings and those of Le Corff and Horvitz (2005) are likely due to differences between study species in mating system expression; *I. capensis* derives a greater proportion of its fecundity from CL than from CH flowers (fig. 2C, 2D), whereas *C. micans* shows the opposite

pattern (Le Corff and Horvitz 2005). Given the importance of CL individuals for population growth of *I. capensis*, genetic factors, such as inbreeding depression, will dramatically reduce the growth rate of the population. Similarly, ecological factors, such as increases in plant density (i.e., intraspecific competition), that influence the mating system of this species (Waller 1985; Schmitt and Ehrhardt 1990; Lu 2000) are also expected to influence plant population dynamics.

Although our study indicates that selfing via CL flowers is key to maintaining population size in *I. capensis*, CH individuals may be contributing significantly to population dynamics in ways not considered. First, the demographic projections were based on a single year of data. Given that environmental conditions vary from year to year, it is possible that CH individuals will have greater demographic importance in other years. For example, in the year we performed the study, severe flooding late in the summer led to early mortality and curtailed continued CH flower production in both populations. In years with less late-summer flooding, it is likely that *I. capensis* plants will live longer and thus may extend CH reproduction until senescence in the fall. Under these growth conditions, CH reproduction may result in a greater proportion of the total reproductive effort of *I. capensis* and therefore may contribute more to population growth than our current estimates suggest. However, given that *I. capensis* occurs in moist, riparian habitat that is prone to flooding (J. A. Steets, personal observation), we think that our findings accurately reflect plant response to normal growth conditions. Second, the primarily outcrossed CH individuals (Steets et al. 2006a) may be favored over selfed CL individuals when they disperse to novel habitats. Work by Schmitt and Gamble (1990) provides support for this hypothesis; inbreeding depression in CL flower production nearly doubled when individuals were planted 12 m from their parental site relative to those planted in the parental site. If we are to gain a better understanding of the importance of outcrossing for population dynamics of *I. capensis*, the demographic differences between CL and CH individuals grown in novel and parental sites must be elucidated.

Application of Demographic Approach to Monomorphic Flowering Species

Given the prevalence of mixed mating among plant species (reviewed in Goodwillie et al. 2005) and the differential demographic importance selfing and outcrossing has for at least two species (Le Corff and Horvitz 2005; this study), it is crucial that researchers begin to examine the demographic consequences of mating system expression in other plants so that we can more generally understand how this

trait influences population persistence. In this study, we developed a demographic framework to determine the effect of mating system on population dynamics of a heteromorphic flowering species; however, this framework could easily be modified for monomorphic flowering, mixed mating species. In the demographic model of a monomorphic flowering species, seeds produced by reproductive individuals would be separated into two classes, selfed and outcrossed. The proportion of seeds entering each class can be estimated by quantifying the outcrossing rate of the population via genetic markers. As in our study, researchers would need to measure the stage-specific vital rates (e.g., germination rates, seedling survivorship, and adult fecundity) of the two seed types throughout their entire life cycle. With this empirical data, stage-structured demographic models could then be applied to estimate population growth rate and to determine the relative importance of selfed and outcrossed individuals for population dynamics. If the results of our study and those of Le Corff and Horvitz (2005) are representative of monomorphic flowering species, then selfing may contribute more to population growth rate in predominantly selfing species, whereas in predominantly outcrossing species population growth rate may be most sensitive to production of outcross progeny.

Demographic Consequences of Herbivory

Herbivory affected several components of *I. capensis* fitness. As has been demonstrated in other annual plants (e.g., Lee and Bazzaz 1980; Rand 2002), we found that herbivory significantly reduced reproduction (table 1). Furthermore, we found that the vital rates with the largest effect on population growth in terms of sensitivity (CL and CH survival) were the least affected by herbivory in terms of total change (table 1). Ehrlén (2003) reported similar findings; mollusk herbivory had the greatest effect on vital rates of *Lathyrus vernus* that were relatively unimportant for population growth. Thus, plants may evolve to preserve the functions most important for population fitness.

Our work joins that of others (e.g., Bastrenta et al. 1995; Ehrlén 1995, 2003; Rooney and Gross 2003; Knight 2004) in demonstrating major demographic consequences of herbivory. In both *I. capensis* populations studied, λ more than doubled when herbivory was reduced, but even under high herbivory, the populations were projected to grow significantly (fig. 3A). Our study adds a unique aspect to the large body of work investigating the effects of herbivory on population dynamics by demonstrating that the demographic consequences of herbivory are dependent on the mating system. We found that the vital rates of CL individuals were affected more by this antagonism than were those of CH individuals (table 1, col. C). Further, in

the W population, higher levels of herbivory tended to reduce CL survival but not CH survival (fig. 2B), a result consistent with the hypothesis that herbivory exacerbates inbreeding depression. Although this result was not statistically significant (herbivory \times seed type, $P = .38$), a power analysis indicates that our small sample size (i.e., 23 plots across two populations) limited our power to detect a significant interaction term (power analysis: power to detect interaction = 0.2). Increased expression of inbreeding depression with herbivory has been demonstrated by a few researchers (Carr and Eubanks 2002; Hayes et al. 2004; Ivey et al. 2004; but see Nunez-Farfan et al. 1996; Stephenson et al. 2004). For example, under field conditions, herbivory doubled inbreeding depression for biomass in *Mimulus guttatus* (Ivey et al. 2004) and for female fitness components in *Cucurbita pepo* ssp. *texana* (Hayes et al. 2004). Our study adds to this work by demonstrating that herbivory has differential demographic consequences for obligately selfed and primarily outcrossed progeny.

The LTRE analysis also demonstrated that λ of *I. capensis* is very sensitive to germination of CL seeds (table 1). This finding is very interesting when considered in light of potential transgenerational effects of herbivory. In a greenhouse experiment, Steets and Ashman (2004) found that herbivory more greatly reduced the quality (i.e., seedling size) of CL relative to CH progeny of *I. capensis*. If this differential effect of maternal herbivory on CL and CH offspring translates into reduced germination of CL relative to CH seeds from a high-herbivory environment, then mating system-dependent transgenerational effects of herbivory could have dramatic effects on population growth.

Consequences for the Evolution of Mixed Mating Systems

Understanding the evolution and maintenance of mixed mating systems is currently an area of intensive study by evolutionary biologists (reviewed in Goodwillie et al. 2005). Our study adds to this growing body of work by highlighting the role of herbivores in selecting for stable mixed mating. Specifically, our work indicates that herbivory may increase inbreeding depression in survivorship and that this has demographic consequences (see “Demographic Consequences of Herbivory”). Given that herbivore pressure often varies spatially and temporally in *I. capensis* (Steets and Ashman 2004; Steets et al. 2006a) and other species (Huntly 1991), this could lead to variation in inbreeding depression, which may select for stable intermediate rates of selfing (Cheptou and Mathias 2001). Overall, the work presented here, as well as that of others (e.g., Carr and Eubanks 2002; Hayes et al. 2004; Ivey et al. 2004; Stephenson et al. 2004), reinforces the need for

ecological context to be incorporated into models of mating system evolution.

Conclusions

Our results bring to light the importance of mating system for plant population dynamics in species with mixed mating systems. We have demonstrated that selfed and outcrossed individuals differ in important vital rates and differentially contribute to population growth. Furthermore, we found that vegetative herbivory significantly affects population dynamics primarily via its effects on obligately selfed individuals. These results, when considered with regard to a contemporary model of mating system evolution (Cheptou and Mathias 2001) that predicts that fluctuating environments (which influence the expression of inbreeding depression) can select for stable mixed mating, highlight the need for future study of the role of herbivores in maintaining mixed mating in plants.

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APPENDIX

Annual Matrix Transition Probabilities

Table A1: Mean transition probabilities (95% bootstrap confidence intervals) for annual matrix models for the L and W populations of *Impatiens capensis* experiencing reduced (RH) or ambient (AH) herbivory

Population and herbivory treatment	Transition probability			
	CL seed to CL seed (a_{11})	CH seed to CL seed (a_{12})	CL seed to CH seed (a_{21})	CH seed to CH seed (a_{22})
L:				
RH	2.87 (2.227–3.513)	2.56 (1.945–3.280)	.68 (.419–.885)	1.18 (.562–1.653)
AH	1.45 (1.158–1.783)	1.66 (1.297–2.053)	.27 (.120–.452)	.32 (.163–.507)
W:				
RH	2.70 (2.260–3.157)	2.44 (1.996–2.943)	.55 (.313–.845)	.51 (.276–.767)
AH	1.19 (.937–1.478)	1.53 (1.256–1.853)	.14 (.059–.251)	.23 (.077–.441)

Note: Refer to text and figure 1A for description of annual matrix model. CL = cleistogamous, CH = chasmogamous.

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