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Herbivory and Competition Interact to Affect Reproductive Traits and Mating System Expression in *Impatiens capensis*

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ABSTRACT: As a step toward understanding how community context shapes mating system evolution, we investigated the combined role of two plant antagonisms, vegetative herbivory and intraspecific competition, for reproduction and mating system expression (relative production of selfing, cleistogamous and facultatively outcrossing, chasmogamous flowers and fruits) of *Impatiens capensis*. In a survey of *I. capensis* populations, we found that vegetative herbivory and intraspecific competition were positively correlated. In a greenhouse experiment where leaf damage and plant density were manipulated, multispecies interactions had dramatic effects on reproductive and mating system traits. Despite having additive effects on growth, herbivory and competition had nonadditive effects for mating system expression, chasmogamous fruit production, flower number and size, and cleistogamous flower production. Our results demonstrate that competitive interactions influence the effect of herbivory (and vice versa) on fitness components and mating system, and thus antagonisms may have unforeseen consequences for mating system evolution, population genetic diversity, and persistence.

Keywords: antagonism, cleistogamy, floral traits, intraspecific competition, mixed mating system, vegetative herbivory.

In recent years, researchers have become aware that the outcome of pairwise interactions can be altered by the presence of other interacting species, and thus the net ecological and evolutionary effect of multispecies interactions cannot be predicted from their independent effects (e.g., Strauss 1991; Agrawal 2004). Two primary antago-

nistic interactions faced by plants are consumption by herbivores (Marquis 1992) and competition with other plants for above- and belowground resources (Harper 1977). In addition to affecting plant fitness (e.g., Harper 1977; Marquis 1992) and community composition (e.g., Hairston et al. 1960; Wardle and Barker 1997; Carson and Root 2000), these antagonisms may have consequences for population genetic diversity (reviewed in Linhart and Grant 1996); however, this is still largely unexplored. One mechanism by which these antagonisms might affect the genetic diversity and structure of plant populations is their joint effect on mating system expression.

There is mounting evidence that vegetative herbivory (hereafter herbivory) and competition independently influence mating system expression. For example, leaf damage can increase outcrossing rate by inducing selective abortion of selfed seeds (Levri and Real 1998), and leaf damage or intraspecific competition can reduce floral display size (Strauss et al. 1996; Lehtilä and Strauss 1997; Mothershead and Marquis 2000) and, consequently, geitonogamous selfing (Karron et al. 1995; Elle and Hare 2002). Alternatively, in species that produce dimorphic flowers on a single individual (i.e., large, facultatively outcrossing and small, obligately selfing flowers), both herbivory and competition can alter the relative production of flower types, shifting the mating system toward selfing (Schmitt et al. 1987a; Steets and Ashman 2004). Given that plants regularly experience both herbivory and competition, understanding how they jointly influence mating system will provide insight into their effect on population genetic diversity and the evolution of mating systems.

Mating system plasticity may be a generalized plant response to resource stress such that a plant subject to multiple antagonisms will exhibit altered mating system in a manner that is predictable from effects on plant growth. However, the largely additive effects of herbivory and competition seen for plant growth (e.g., Fowler and Rausher 1985; Mutikainen and Walls 1995; Reader and Bonser 1998; Erneberg 1999; but see Fowler 2002; Agrawal 2004; Haag et al. 2004) may not translate into additive effects on mating system for a few reasons. First, in species with dimorphic flowers, the demands of one antagonism may

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affect a plant's ability to maintain a certain level of allocation to expensive outcrossing flowers when a second antagonism is introduced, and thus the two antagonisms will have a nonadditive effect on mating system. Given that multiple antagonists can have nonadditive effects on plant reproduction (Friedli and Bacher 2001), a similar response might be expected for mating system. Second, nonadditive mating system effects may also occur if herbivory and competition differentially affect the architecture of dimorphic flowering species. For instance, competition for light can cause plants to decrease branch production (Schmitt et al. 1987b), whereas herbivory reduces plant height but has little effect on branching architecture (Steets and Ashman 2004). If selfing and outcrossing flowers are produced at different locations on a plant, then the differential effects of these antagonists on branching patterns could result in nonadditive effects on mating system. Third, because the realized mating system of the facultatively outcrossing flowers is a function of both intrinsic (i.e., flower morphology) and extrinsic (i.e., pollinator behavior, population genetic structure) factors, antagonistic interactions may also affect these and, ultimately, the mating system. As a first step at addressing the mechanisms by which multiple antagonisms may interact to affect plant mating system, we investigate the effects of two ubiquitous antagonisms, herbivory and intraspecific competition, on mating system expression of *Impatiens capensis* Meerb. (Balsaminaceae). First, we determined whether plants are likely to experience both antagonisms (i.e., whether they co-vary) in nature by conducting a survey of natural *I. capensis* populations. Second, we manipulated levels of herbivory and intraspecific competition in a greenhouse experiment to determine whether herbivory and competition interact to affect plant growth, reproduction, and mating system traits of *I. capensis*.

Methods

Study System

Impatiens capensis (jewelweed, touch-me-not) is a common native annual throughout moist forests in eastern North America (Schemske 1978) that is ideally suited to the objectives of this study because individuals exhibit a mixed mating system by producing both large, facultatively outcrossing (chasmogamous, CH) and small, obligately self-fertilizing (cleistogamous, CL) flowers (i.e., a dimorphic flowering system). The CH flowers are self-compatible, but strong protandry prevents autogamy. In populations in northwestern Pennsylvania, outcrossing rates for CH flowers range between 0.29 and 1.00 (mean: 0.57), decrease with increasing CH display and flower size, and vary with herbivory (J. A. Steets, J. L. Hamrick, and T.-L. Ashman,

unpublished manuscript). In wild populations in northwestern Pennsylvania, vegetative herbivores include chrysomelid beetles, leaf miners, grasshoppers, snails, and slugs, and average leaf damage is approximately 30% (Steets 2005). Intraspecific density varies widely among populations, with juvenile density ranging from 88 to 340 plants/m² and adult density from 4 to 300 *I. capensis*/m² (J. A. Steets and T.-L. Ashman, unpublished data).

Herbivory and Competition in Wild I. capensis Populations

To determine the levels of herbivory and competition and whether they co-vary, we surveyed three natural populations of *I. capensis* in Crawford County, Pennsylvania (W: 41°40.6'N, 80°25.6'W; L: 41°38.6'N, 80°25.7'W; T: 41°35.7'N, 80°21.2'W; see Steets 2005 for further details about populations). In each population, we set out five to 13 1-m² plots, for a total of 29 plots across populations. For all plots we quantified the level of intraspecific competition by enumerating adult *I. capensis* density at the middle of the growing season (mid-July to early August). In addition, for a subset of plants in each plot, we quantified herbivory as the proportion of total leaves damaged. To determine whether herbivory and competition co-vary, we performed a correlation (PROC CORR, SAS Institute 1999) between mean plot leaf damage and plot density across all populations.

The Effect of Herbivory and Competition on Growth, Reproduction, and Mating System Traits of I. capensis

Experimental design and data collection. We collected *I. capensis* seeds from the W population in Crawford County, Pennsylvania. Seeds were stored in distilled water in cell culture trays at 4°C for approximately 4 months to break dormancy (Leck 1979). Once germinated, seeds were planted (treatments below) in 10-cm-square pots filled with Fafard #4 soil (Conrad Fafard, Agawam, MA) and transferred to a greenhouse with supplemental heating and lighting.

We employed a randomized complete block design consisting of 50 blocks, with treatments factorially applied to plants as described below.

Competition treatment. Focal plants were grown in the absence (−C) or presence (+C) of another *I. capensis* plant. The +C treatment simulates a density of 200 plants/m², which is within the range of natural densities (see above and fig. 1).

Herbivory treatment. Focal plants were either undamaged (−H) or damaged (+H). We aimed for a level of leaf damage similar to the average experienced by *I. ca-*

cant, then the trait responded additively to the antagonisms. For traits where a significant herbivory \times competition interaction was present, we calculated interaction slices (SLICE option, SAS Institute 1999) to assess the significance of a given factor (e.g., competition) at different levels of the other factor (e.g., +H and -H; Littell et al. 2002). In addition to performing ANOVAs to test for non-additive plant response to the antagonism, we also generated log-response ratios for the effect of herbivory, competition, and the joint antagonism on each plant trait (sensu Haag et al. 2004). Because these results confirmed the ANOVA results, we present only those of the ANOVAs.

To determine whether herbivory and competition interact to affect CH floral traits, we performed a principal-components analysis (PROC FACTOR, SAS Institute 1999) on the correlation matrix of the eight floral dimensions. The first principal component explained 84% of the variance among plants in floral traits, and all traits loaded positively (all loadings >0.83), indicating that it reflects overall flower size. We explored the effect of herbivory and competition on flower size, using ANOVA (PROC GLM, SAS Institute 1999) with herbivory, competition, and their interaction as fixed effects. Block was not considered in this model because of the random sampling of individuals across blocks.

To determine whether herbivory and competition affected plant growth and mating system traits in similar ways, such that the mating system response is predictable from growth, we performed a mixed-model MANOVA (PROC MIXED, SAS Institute 1999) with trait type and its interactions with competition and herbivory as fixed effects and block designated as a random effect. We included two types of traits, a growth trait (aboveground dry biomass) and a mating system trait (proportional production of CL flowers). A significant herbivory \times competition \times trait type term indicates that the antagonisms have differential effects on growth and mating system, and thus one cannot accurately predict the mating system response from the growth response.

Results

Herbivory and Competition in Wild I. capensis Populations

We found a significant positive correlation between mean plot leaf damage and *Impatiens capensis* density (fig. 1; $r = 0.41$, $P = .03$, $n = 29$), indicating that intraspecific competition and herbivory often co-occur in natural *I. capensis* populations.

Effect of Herbivory and Competition on Plant Growth, Reproduction, and Mating System Traits of I. capensis

Herbivory and competition significantly reduced plant growth traits; however, the antagonisms did not interact to affect these traits, and thus the plant growth response to the combined antagonisms was additive (table 1, pt. A; fig. 2A). Competition had a larger effect on plant growth than did herbivory. When plants experienced no competition, 20% leaf damage reduced plant biomass by 13%, whereas in the absence of herbivory, the addition of a competitor reduced biomass by 57%. Overall, the combined antagonisms caused a 60% reduction in biomass relative to the control treatment (-C-H). This pattern of a stronger effect of competition than herbivory on *I. capensis* traits is seen for all reproduction and mating system traits.

Two of the six reproductive traits, CL fruit production and CH display size, responded to the antagonisms in a manner similar to the plant growth response (i.e., additive response; table 1, pt. B; fig. 2C, 2F). Both herbivory and competition decreased CL fruit production and CH display size; however, only competition reduced these traits significantly (table 1, pt. B; fig. 2C, 2F), with the competition-alone treatment reducing CL fruit production and CH display size by 29% and 42%, respectively.

Although we found that the combined effects of herbivory and competition were additive with respect to plant growth, we found that herbivory and competition interacted to affect CL flower production, CH flower and fruit production, CH flower size, and mating system at the level of proportional production of CL flowers (table 1, pts. B, C; fig. 2B, 2D, 2E, 2G, 2H). At the levels of competition and herbivory imposed in this experiment, competition had more dramatic effects on these plant traits than herbivory (fig. 2). For CL flower production, herbivory had a significant effect on this trait only when competitors were absent (table 2). Under these conditions, herbivory increased CL flower production by 10% compared to control plants (fig. 2B). In addition, competition had a more severe effect on the CL flower production when herbivores were present, in which case CL flower number was decreased by 14% relative to the control treatment (table 2; fig. 2B).

The antagonisms dramatically reduced CH flower and fruit production (fig. 2D, 2E) and interacted to affect both traits (table 1, pt. B). Herbivory and competition significantly reduced both CH reproductive traits in the absence of the other antagonism (table 2). Compared to controls, plants experiencing herbivory in the absence of competition and those subject to competition in the absence of herbivory reduced CH reproductive traits by approximately 65% and 90%, respectively (fig. 2D, 2E). In ad-

Table 1: Effect of intraspecific competition, vegetative herbivory, and their interaction on growth, reproduction, and mating system traits of *Impatiens capensis*, as determined by mixed-model ANOVAs

Trait	Herbivory		Competition		Competition × herbivory	
	df	F	df	F	df	F
A. Growth:						
Biomass	1, 143	6.8**	1, 143	293.3****	1, 143	2.7
Height	1, 143	12.4***	1, 143	174.5****	1, 143	0
Branch production	1, 143	.03	1, 143	122.0****	1, 143	.7
B. Reproduction:						
CL flowers	1, 143	.18	1, 143	52.1****	1, 143	7.41**
CL fruits	1, 27	.84	1, 27	5.45*	1, 27	2.4
CH flowers	1, 143	70.1****	1, 143	217.4****	1, 143	63.8****
CH fruits	1, 27	38.7****	1, 27	94.6****	1, 27	23.9****
CH display size	1, 24	1.36	1, 24	6.84*	1, 24	.01
CH flower size	1, 49	4.94*	1, 49	6.89**	1, 49	4.15*
C. Mating system:						
Proportion CL flowers	1, 143	29.3****	1, 143	167.4****	1, 143	30.73****
Proportion CL fruit	1, 27	11.3**	1, 27	45.5****	1, 27	1.79

Note. CL = cleistogamous; CH = chasmogamous; df = degrees of freedom (numerator, denominator).

Mating system metrics were arcsine transformed before analysis.

**** $P < .0001$.

*** $P < .001$.

** $P < .01$.

* $P < .05$.

dition, competition in the presence of herbivory enhanced the reduction in CH fruit production (table 2). The combined effect of herbivory and competition was to decrease CH flower and fruit production by 93% and 97%, respectively, compared to controls (fig. 2D, 2E).

In contrast to the nonadditive CH flower and fruit production responses, the nonadditive response in CH flower size was due to the fact that this trait declined only when plants were subject to both antagonisms (fig. 2G; table 1, pt. B, table 2). In particular, CH flower size was conserved when plants experienced only one antagonism; however, when plants experienced both antagonisms, CH flower size was reduced by more than 200% compared to the control treatment (fig. 2G).

We also found that herbivory and competition interacted to affect plant mating system. For proportional production of CL flowers, we detected significant nonadditivity in the plant response (table 1, pt. C). Here both herbivory and competition significantly increased proportional production of CL flowers when the second antagonism was absent but not when it was present (table 2). Relative to the control treatment, herbivory alone increased selfing (measured as proportion of CL flowers) by 21%, and competition increased selfing by 27% both with and without herbivory (fig. 2H). With respect to the second mating system metric, proportion of CL fruits, we did not find evidence that herbivory and competition in-

teracted to affect the trait. Given the similarity in pattern between the responses in proportions of CL flowers and fruits (fig. 2H, 2I), this discrepancy is due to the fact that subsampling fruit production reduced our sample size to the point where we were unable to detect a significant interaction term in the ANOVA (power analysis: power to detect interaction, $\beta < 0.35$).

The MANOVA conducted on growth and mating system confirms that plant responses to herbivory and competition differ between trait types (competition × trait type: $F = 150.6$, $df = 2, 335$, $P < .0001$; herbivory × trait type: $F = 25.5$, $df = 2, 335$, $P < .0001$; herbivory × competition × trait type: $F = 24.2$, $df = 2, 335$, $P < .0001$), indicating that mating system response cannot reliably be predicted from growth response.

Discussion

Combined Effects of Herbivory and Competition

The survey of natural *Impatiens capensis* populations showed that *I. capensis* must simultaneously respond to both herbivory and competition as these antagonisms covaried positively in nature (fig. 1). Our experimental manipulation of herbivory and competition revealed that plant responses to the antagonisms are often complex. Although the combined effects of herbivory and compe-

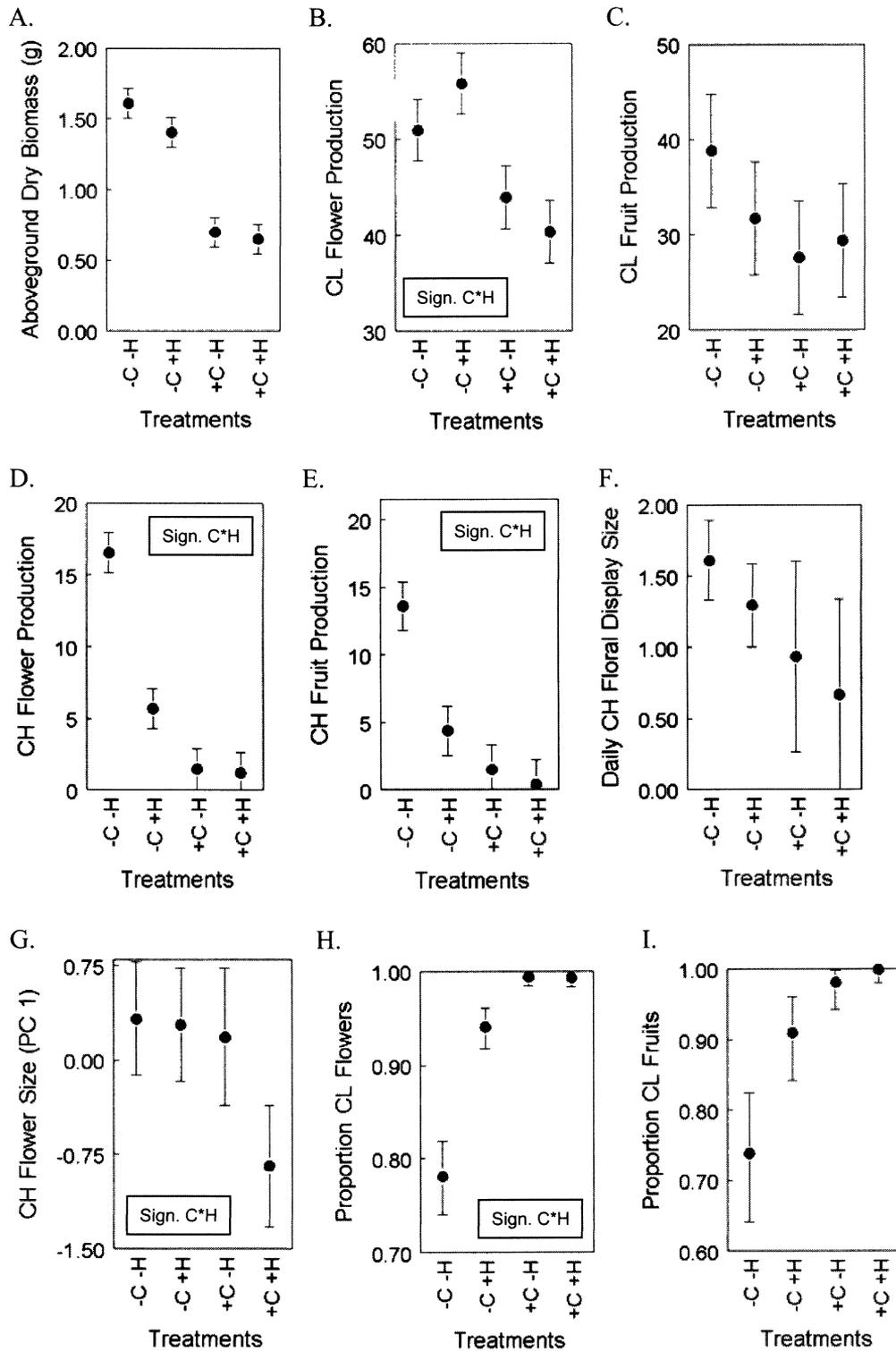


Figure 2: Mean aboveground dry biomass (A), cleistogamous (CL) flower production (B), CL fruit production (C), chasmogamous (CH) flower production (D), CH fruit production (E), CH daily floral display size (F), CH flower size (principal component 1; G), proportional CL flowers (H), and proportional CL fruits (I) for plants in the herbivore-damaged (+H), herbivore-undamaged (-H), competitor-present (+C), and competitor-absent (-C) treatments. Error bars represent 95% confidence intervals. Refer to the text and tables 1 and 2 for additional analyses.

Table 2: *F* values of the interaction slices for the effects of competitors and herbivores on cleistogamous (CL) flower production, chasmogamous (CH) flower and fruit production, CH flower size, and proportional production of CL flowers of *Impatiens capensis*

	CL flower production	CH flower production	CH fruit production	CH flower size	Proportion CL flowers
df	1, 143	1, 143	1, 27	1, 149	1, 143
Competitors, herbivores absent	1.5	73.3****	57.2****	.2	41.8****
Competitors, herbivores present	21.0****	.1	4.1*	11.7**	1.2
Herbivores, competitors absent	6.4*	124.4****	63.1****	.02	49.5****
Herbivores, competitors present	2.3	.0	.9	8.0**	.1

Note. Proportion CL flowers was arcsine transformed before analysis. Refer to table 1 for tests of main effects and their interaction.

**** $P < .0001$.

** $P < .01$.

* $P < .05$.

tion were additive with respect to plant biomass and other growth traits, we detected nonadditive effects of the joint antagonisms for CL and CH reproduction as well as mating system expression. Given the design of this experiment, nonadditive effects of competition and herbivory cannot be due to competition altering the magnitude of herbivory a plant experiences (but see Agrawal 2004). Rather, it is likely that the nonadditive responses reflect changes in plant resource allocation. Because CH flowers are more costly to produce than CL flowers (Schemske 1978), CH reproduction is often reduced when plants are grown in stressful environments (e.g., Schemske 1978; Waller 1980; Bell and Quinn 1987; Le Corff 1993; Lu 2000); thus, we expected a similar response in plants experiencing herbivory and competition. Indeed, we found that CL flower production was reduced only under the most stressful conditions, whereas small increases in antagonism (i.e., herbivory or competition alone) caused marked decreases in CH flower and fruit production. When total antagonism became more severe (i.e., herbivory and competition co-occur), CH flower and fruit production approached and reached their biological limits, respectively. Because CH flower and fruit production are components of the mating system metrics, it follows that both mating system estimates should also respond in a nonadditive manner to the antagonisms. Our results indicate that mating system estimated as the proportional production of CL flowers responded nonadditively to the antagonisms, whereas mating system measured as proportional production of CL fruits did not. The latter result, however, is more a consequence of statistical power rather than a biological difference. In fact, the nonadditive mating system response is corroborated by field data from Steets and Ashman (2004), who found a nonlinear response to increasing antagonism for proportional production of CL flowers along a natural herbivory gradient (i.e., in the context of a competitive background, modest increases in herbivory greatly

depressed outcrossing). Overall, these results indicate that antagonistic interactions have more severe consequences for reproductive traits and mating system than for plant growth.

We also found nonadditive effects of antagonists for CH flower size, with flower size reduction occurring only when plants were subject to both antagonisms. This result, in conjunction with our finding that CH flower production is greatly reduced when plants are subject to a single antagonism, suggests that there is a trade-off between allocation to CH flower size and number—flower size is more highly conserved than flower number with increasing antagonism. The conservation of flower size over number has also been demonstrated by other researchers (Cresswell et al. 2001) and could reflect the importance of maintaining flower size for pollinator attraction (J. A. Steets, J. L. Hamrick, and T.-L. Ashman, unpublished manuscript).

Our findings have interesting implications for the role plant antagonists have in mediating CH flower outcrossing, although these are not explored in this study. In particular, our finding that herbivory and competition synergistically reduced CH flower size of *I. capensis*, in conjunction with the findings of another experiment, which demonstrates that CH outcrossing rate decreases with increasing CH flower size (J. A. Steets, J. L. Hamrick, and T.-L. Ashman, unpublished manuscript), suggests that the joint antagonisms are likely to markedly increase CH outcrossing. What remains to be seen is whether the antagonist-mediated changes in CH floral size that favor increased outcrossing are strong enough to offset the effects of antagonists on relative dimorphic flower production. Data from another experiment (J. A. Steets, J. L. Hamrick, and T.-L. Ashman, unpublished manuscript) suggest that the increase in CH outcrossing can compensate for the reduction in outcrossing due to changes in relative heteromorphic flower production when plants are subject to increasing herbivory in the context of a constant

low-competition environment; however, data from this study also indicate that compensation is unlikely when plants are subject to higher levels of both antagonisms.

Consequences for Plant-Herbivore Dynamics

In *I. capensis*, the severe reduction in outcrossing with herbivory may influence expression of plant defensive traits. The work of Carr and Eubanks (2002) indicates that as levels of inbreeding increase in the plant population, resistance to herbivory may decline. These conditions may set up a positive feedback loop that may ultimately lead to plant population extinction because of reduced genetic diversity (Newman and Pilson 1997). For example, herbivory increases inbreeding, resulting in increased levels of herbivory in the following generation (because of reduced expression of resistance traits), which in turn will further reduce outcrossing in the plant population. Future studies should aim to explore whether this type of feedback loop occurs and ultimately influences plant population persistence.

Consequences of Plant Antagonists for Mating System Evolution

Understanding how multispecies interactions affect mating system is the first step in discerning how community context influences mating system evolution. The majority of studies exploring the effect of multispecies interactions on plant fitness or selection have investigated herbivore-herbivore and herbivore-pollinator interactions (reviewed in Strauss and Irwin 2004; but see Tiffin 2002), whereas those investigating the effect of ecological context on mating system have mainly studied plant-pollinator interactions (e.g., Kalisz et al. 2004). The current study adds significant breadth to these bodies of research by demonstrating that intraspecific competitive interactions interact with herbivory to affect components of fitness and mating system. Further, the antagonism-induced change in mating system that we report may be an adaptive plastic response to living in heterogeneous ecological conditions. Thus, plant antagonists may serve as selective agents on the mating system. To understand whether herbivory and competition exert selection on the mating system or its plasticity, we need to know how these antagonists affect the relationship between mating system and fitness and the degree to which these interactions vary in space and time. Theory predicts that mixed mating systems will evolve under variable environmental conditions (e.g., Schoen et al. 1996; Masuda et al. 2001). Although this environmental variation is primarily considered in terms of pollinator visitation, the large degree of spatial and temporal variation that exists in the intensity of herbivory and

competition (fig. 1; Louda 1989; Kadmon 1995; Rand 2002; Steets and Ashman 2004) is also likely to contribute to the stabilization of mixed mating systems. Future studies should aim to incorporate these prevalent ecological interactions into our view of mating system evolution. In addition, enhancing our understanding of the effects of multiple antagonisms will allow us to evaluate whether recent increases in the incidence of herbivory as a result of fragmentation (Lienert and Fischer 2003; Rand and Louda 2004) and competition as a result of greater presence of invasive species (Vilà and Weiner 2004) reflect novel selective pressures for native plants or whether they already possess mechanisms to deal with them.

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