MATERNAL EFFECTS OF HERBIVORY IN *IMPATIENS CAPENSIS*

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Maternal effects of herbivory for fitness-related traits of offspring, especially those traits that are expressed later in a plant's life, have rarely been studied. To better understand how herbivory to the maternal plant influences traits of its progeny and whether this depends on the mating system that produced the seed or the growth environment of the seedling, we examined maternal effects of herbivory in *Impatiens capensis*. *Impatiens capensis* is well suited to this study because it exhibits a mixed mating system by producing obligately selfing cleistogamous flowers and facultatively outcrossing chasmogamous flowers on a single plant. In a natural *I. capensis* population, we manipulated maternal herbivory and collected seeds from cleistogamous and chasmogamous flowers and assessed their fitness in the presence or absence of intraspecific competitors in the greenhouse. We found that maternal herbivory had positive effects for many offspring traits but the magnitude of the maternal effect depended on the offspring competitive context. In addition, for offspring biomass and total flower production, the expression of maternal effects varied with seed source (i.e., chasmogamous or cleistogamous flower). Our results demonstrate that maternal herbivory has consequences for the next generation that persist throughout the offspring life cycle, indicating that there may be important demographic consequences of maternal effects.

Keywords: intraspecific competition, outcrossing, selfing, transgenerational effects, vegetative herbivory.

Introduction

Many studies have examined the contribution of the maternal abiotic environment (e.g., moisture, temperature, nutrients, light) to offspring phenotype and fitness (e.g., Lacey 1996; Sultan 1996; Huxman et al. 1998; Galloway 2001*a*, 2001*b*; Lundgren and Sultan 2005; Galloway and Etterson 2007). Less well studied are the consequences of the maternal biotic environment, such as herbivory and competition, to offspring trait expression. Herbivory is not only a ubiquitous biotic factor affecting plant populations, but it may also lead to significant maternal environmental effects because it reduces photosynthetic capacity and, thus, plant resources (Crawley 1983). Herbivory-mediated reduction in resource availability may have consequences for plant fitness via effects on both the number of progeny produced and the quality of those progeny (e.g., Marquis 1984, 1992; Crawley and Nachapong 1985; Crawley 1989; Mueller et al. 2005). For example, seeds produced on damaged mothers may be smaller and may develop into less vigorous seedlings than those produced in the absence of herbivory (e.g., Maun and Cavers 1971; Marquis 1984). In contrast, adaptive maternal effects of herbivory occur when maternal herbivory–induced changes in offspring trait expression, such as trichome production (Agrawal 2001; Holeski 2007), enhance the fitness of offspring growing under the same maternal herbivory conditions. To date, most studies examining the effect of herbiv-

ory for plant fitness quantify effects on seed number and, to a lesser extent, progeny traits expressed early in development, such as seed mass and seedling size. In the only studies to explore the effects of maternal herbivory for offspring traits expressed later in development, Agrawal (2001, 2002) found that maternal herbivory to *Raphanus raphanistrum* affected components of progeny fitness, including seed mass, plant growth, flower production, and fruit mass; however, these maternal effects depended on family membership. Given the limited research that has been conducted to date on maternal effects of herbivory for offspring fitness, the potential cross-generational consequences of maternal foliar damage largely remain unknown.

Herbivory may result in mating system–dependent maternal effects if maternal herbivory differentially affects the quality of selfed and outcrossed progeny. The only study to examine mating system–dependent maternal effects of herbivory found that maternal herbivory reduced seedling biomass of selfed progeny more than it reduced that of potentially outcrossed progeny (Steets and Ashman 2004). However, herbivory-mediated maternal effects on mating system may be even more complex because of interactions between progeny inbreeding level and resource allocation to progeny.

The expression of maternal effects may also depend on the growth environment offspring experience after dispersal (e.g., Stratton 1989; Wulff et al. 1994; Donohue and Schmitt 1998). For example, under competitive growth conditions, maternal effects in *Erigeron annuus* persist for a longer period in offspring ontogeny than they do under noncompetitive growth conditions (Stratton 1989). Furthermore, if environmental cues in the maternal generation are predictive

of the progeny growth environment, then maternal effects may be adaptive (Donohue and Schmitt 1998; Sultan et al. 2009). With respect to herbivory, leaf area loss can be quite similar across years for numerous plant species (Filip et al. 1995). Thus, maternal herbivore damage may predict offspring herbivore condition, creating the opportunity for maternal effects of herbivory to be adaptive.

We examined maternal effects of herbivory in *Impatiens capensis*, which exhibits a mixed mating system by producing obligately selfing (cleistogamous [CL]) and facultatively outcrossing (chasmogamous [CH]) flowers on an individual plant. Our previous work has shown that herbivory affects the mating system of *I. capensis* at two levels: (1) the proportion of reproduction that occurs through cleistogamy and (2) the CH outcrossing rate (Steets and Ashman 2004; Steets et al. 2006a). Overall, herbivory decreases whole-plant outcrossing, indicating that the effects of herbivory on proportional CL reproduction, which favors selfing, outweigh the effects of herbivory on the CH mating system, which favors outcrossing (Steets et al. 2006a). We have also found that maternal effects of artificial damage occur early in seedling development, with artificial defoliation of maternal plants causing a slight reduction in offspring cotyledon size and seedling biomass (Steets and Ashman 2004). However, whether maternal effects occur in response to natural herbivore damage and, if maternal effects occur, whether these effects persist throughout ontogeny or are influenced by offspring growth environment is unknown. Here we expand these earlier studies by asking the following questions: (1) Does natural herbivory to maternal plants affect offspring fitness–related traits in *I. capensis*? (2) Does herbivory to maternal plants differentially influence CL and CH offspring (i.e., are there mating system–dependent maternal effects of herbivory)? (3) Does the level of competition that offspring experience exacerbate or prolong the duration of maternal effects?

We hypothesized that maternal herbivory would differentially affect fitness-related traits of progeny derived from CL and from CH flowers (hereafter, CL and CH progeny). Mating system–dependent maternal effects may arise through at least two mechanisms. First, resource limitation due to leaf damage may lead to outcrossed seeds being provisioned with more resources than are selfed seeds (Stephenson 1981; Levri and Real 1998). For example, when 50% of leaf tissue of *I. capensis* maternal plants is artificially removed, the resulting CL offspring are significantly smaller in size than are CH progeny produced under the same maternal environmental conditions (Steets and Ashman 2004). In contrast, CL and CH offspring produced by undamaged maternal plants did not differ in seedling biomass (Steets and Ashman 2004). Second, mating system–dependent maternal effects of herbivory may manifest via differences in genetic quality of CH seeds produced under herbivory conditions. In wild *I. capensis* populations, herbivory causes an increase in the outcrossing rate of CH flowers (Steets et al. 2006a). Maternal plants that are subjected to greater herbivore pressure produce CH progeny that are more likely to be outcrossed, and thus these CH progeny may be more vigorous (e.g., larger in size, increased flower production) because of reduced inbreeding depression than those produced by maternal plants experiencing less herbivory. Thus, maternal effects might differ for CH and CL

progeny as a result of mating system and resource changes in the former and allocation changes in the latter. Regardless of the underlying mechanism, given that CH and CL seeds differ in their demographic values and contributions to population growth (Steets et al. 2007), it is worth considering the net effect of maternal herbivory on progeny fitness.

Material and Methods

Study System

Impatiens capensis Meerb. (Balsaminaceae) is a native annual that occurs throughout moist forests in eastern North America (Schemske 1978). Among natural populations in Pennsylvania, Steets et al. (2006a) found broad variation in the outcrossing rate of *I. capensis*; a significant portion of this variation was due to herbivory. Herbivory is common in *I. capensis* populations, and vegetative damage in Pennsylvanian populations is primarily caused by chrysomelid beetles, leaf miners, caterpillars, aphids, grasshoppers, and katydids (Steets 2005).

Experimental Design

This experiment was part of a larger study aimed at understanding the consequences of herbivory for the mating system of *I. capensis*. Here we briefly summarize the methods of this experiment (for details, see Steets et al. 2006a). In one wild *I. capensis* population located near the Pymatuning Laboratory of Ecology in Crawford County, Pennsylvania (W population; Steets et al. 2006a), we randomly selected 14 1-m^2 plots. Plots within the population were separated from one another by at least 5 m, and within each plot, seven focal maternal individuals were tagged. Plots were assigned to one of the following two treatments: (1) reduced or (2) ambient herbivory. Herbivory was reduced by applying two insecticides (Conserve [Dow AgroSciences, Indianapolis, IN] and Endeavor [Syngenta Crop Protection, Greensboro, NC]) biweekly to plants in the reduced-herbivory plots. These insecticides reduce herbivory by the primary herbivores observed in the population under study (J. A. Steets, personal observation). Conserve inhibits feeding by a variety of foliar-feeding insects, including lepidopteran larvae, chrysomelid beetles, thrips, leaf miners, and katydids. Endeavor targets sap-sucking aphids and whiteflies. These insecticides reduce herbivory without affecting pollinator visitation to or growth or reproduction of *I. capensis* (app. A in Steets 2005). Ambient herbivory plots were sprayed with water at the same frequency to serve as a control. Insecticide applications began prior to flowering and continued until 3 wk prior to a frost that killed the majority of plants. On average, plants in the ambient treatment experienced 2.5 times more leaf damage than did individuals in the reduced-herbivory treatment (leaves damaged, 33% ± 3.1% SE vs. 13% ± 1.7% SE; Steets et al. 2006a); the two treatments are hereafter referred to as ambient and reduced maternal herbivory environments (MHEs), respectively. No differences in the type of damage were observed between ambient and reduced MHEs (J. A. Steets, personal observation). We haphazardly collected CL and CH seeds from maternal plants in both MHEs. Seeds were kept separate by seed type but were pooled across ma-

ternal plants within a MHE; thus, the parentage of individual seeds in this experiment is unknown. Outcrossing rate differed among CH seeds from contrasting MHEs; on average, the outcrossing rate of CH seeds from the ambient and reduced MHEs was 0.56 ± 0.24 versus 0.33 ± 0.09, respectively (Steets et al. 2006a). Seeds were stored in distilled water in cell culture trays at 4°C for ~4 mo to break dormancy (Leck 1979). Once germinated, seeds were planted (treatments described below) in 10-cm^2 pots filled with Fafard #4 soil (Conrad Fafard, Agawam, MA) and transferred to a greenhouse, where supplemental heating and lighting were provided.

We employed a randomized complete block design consisting of 40 blocks. Equal numbers of CL and CH seeds from each MHE were assigned to one of the following offspring competitive environments (hereafter, OCEs):

1. Competitors present: The focal plant was grown in the presence of intraspecific competitors. Competitors were seeds derived from CH flowers that were collected from the same population as the focal plants. For seeds assigned to this treatment, one focal seed and two competitor seeds were planted in a single pot. This density (300 plants m^{-2}) is within the range of natural juvenile densities (88–340 plants m^{-2}; Steets et al. 2006b). Fifty-seven days after planting, the smaller of the two competitors was removed from the pot; this density (200 plants m^{-2}) is within the range for adult *I. capensis* in the wild (4–300 plants m^{-2}; Steets et al. 2006b).

2. Competitors absent: The focal plant was grown in the absence of competitors.

There were a total of 320 focal plants in the experiment (2 seed types $\times$ 2 MHEs $\times$ 2 OCEs $\times$ 40 replicates). As all of the focal seeds did not germinate, the final number of plants in the experiment was 309. We watered the plants daily throughout the duration of the experiment.

For each focal individual, we recorded the date of emergence as the date cotyledons emerged and completely reflexed. At 60 d of growth, we harvested, dried (at 60°C for 2 d), and weighed aboveground parts of focal plants from half of the blocks ($N = 156$ individuals across all treatments) to estimate aboveground dry biomass. Plants in the remaining 20 blocks ($N = 153$ individuals across all treatments) were followed through the reproductive phase (80 additional days of growth). At the end of the experiment, we quantified final plant height and total CL and CH flower production and estimated the mating system as the proportion of total flowers that were CL.

Statistical Analyses

We used mixed-model ANOVA or ANCOVA (PROC MIXED, SAS Institute, 1999) to test the fixed effect of MHE (ambient vs. reduced), OCE (competitors present vs. absent), offspring seed type (CL vs. CH), and their interactions on date of emergence, early plant biomass, final plant height, total flower production, and proportional production of CL flowers. Block was included in all models as a random factor. For all traits except emergence date, date of emergence was included as a covariate because the duration of growth can affect size and reproductive traits. To meet normality assumptions of ANOVA, proportional production of CL flowers was arcsine-square-root transformed before analysis (Zar 1999). With respect to our hypotheses, a significant main effect of MHE in the ANOVAs indicates that there are maternal effects of herbivory on offspring traits. A significant interaction between MHE and offspring seed type suggests that the expression of maternal effects depends on the seed type of the offspring. Finally, a significant interaction between MHE and OCE or among MHE, offspring seed type, and OCE indicates that expression of maternal effects or mating system–dependent maternal effects of herbivory depend on the competitive environment experienced by offspring. When we detected significant interaction terms, we investigated the interaction further by computing simple main effects (also known as interaction slices; Pedhazur 1982; Pedhazur and Pedhazur Schmelkin 1991) via the SLICE option in PROC MIXED (SAS Institute, 2007). Interaction slices assess the significance of a given factor (e.g., MHE) at specific levels of another factor (e.g., CL or CH seed type).

Results

Effects of Maternal Herbivory Environment

There was a significant main effect of MHE on emergence date, early plant biomass, final plant height, and total flower production (table 1; fig. 1). Across both seed types and both competition levels, progeny from the ambient MHE emerged 1.5 d later (ambient vs. reduced: 31.6 ± 0.55 d vs. 30.1 ± 0.53 d) than did progeny from the reduced MHE. Despite their later timing of emergence, progeny produced in the ambient MHE were 23% larger in aboveground biomass (0.64 ± 0.030 g vs. 0.52 ± 0.030 g), were 16% taller as reproductive individuals (69.5 ± 1.59 cm vs. 60.0 ± 1.54 cm), and produced 16% more flowers (62.3 ± 2.31 vs. 53.6 ± 2.24) than progeny from the reduced MHE. Although not statistically significant, maternal plants subjected to ambient herbivory tended to produce offspring that reproduced relatively more through chasmogamy than through cleistogamy relative to offspring from reduced-herbivory mothers (table 1; $P = 0.08$; proportion CL: 0.68 ± 0.0003 vs. 0.72 ± 0.0003).

Dependence of Maternal Effects on Offspring Seed Type

There was a significant interaction between maternal herbivory and progeny seed type for early plant biomass and total flower production (table 1; fig. 1b, 1d), indicating that for these traits, the expression of maternal effects depended on progeny seed type. CH offspring produced by maternal plants experiencing ambient levels of herbivory weighed 28% more before reproduction and produced 32% more flowers than did CL offspring produced in the same MHE (table 2; fig. 1b, 1d). CL and CH offspring produced in the reduced MHE did not differ in these traits (table 2; fig. 1b, 1d). In contrast, for timing of emergence, final plant height, and proportion of reproduction occurring through CL flowers, offspring seed type did not influence expression of maternal effects (table 1; fig. 1a, 1c, 1e).

Influence of Offspring Competitive Environment on Expression of Maternal Effects

The OCE affected the expression of maternal effects for emergence date, early plant biomass, plant height, and total

Table 1

Summary of *F* Statistics and *P* Values for Mixed-Model ANCOVA on Date of Seedling Emergence, Early Plant Biomass, Final Plant Height, Total Flower Production, and Proportion of Cleistogamous (CL) Flower Production

Source	Date of emergence		Early plant biomass		Final height		Total flower production		Proportion CL flowers	
	F	P	F	P	F	P	F	P	F	P
MHE	4.0	.05	8.5	.004	19.1	<.0001	8.8	.004	3.0	.08
OCE	3.7	.06	55.4	<.0001	110.7	<.0001	171.6	<.0001	54.0	<.0001
ST	.1	.8	3.1	.08	6.4	.01	6.6	.01	3.8	.05
MHE × ST	.01	.9	3.9	.05	.02	.9	11.2	.001	.2	.7
MHE × OCE	50.8	<.0001	11.1	.001	15.2	.0002	5.5	.02	1.2	.3
ST × OCE	.2	.7	4.2	.04	.09	.8	.3	.6	5.0	.03
MHE × ST × OCE	—	—	—	—	—	—	12.4	.0006	—	—

Note. MHE = maternal herbivory environment; OCE = offspring competitive environment; ST = seed type. Seedling emergence df = 1, 263; early plant biomass df = 1, 129; final plant height df = 1, 126; total flower production df = 1, 125; and proportion CL flower production df = 1, 126. For all traits, block was included in the model as a random factor ($P > 0.05$ for all traits). For early plant biomass, final plant height, total flower production, and proportion CL flower production, date of seedling emergence was included as a covariate ($P < 0.0001$ for all traits). For models in which the three-way interaction was not significant ($P > 0.1$), the interaction term was dropped from the model (denoted by a dash).

flower production (significant MHE × OCE interaction term; table 1; fig. 2). However, the effect of competitive conditions varied among traits. For one trait (total flower production), not only were maternal effects of herbivory dependent on the competitive environment of the offspring, but they also varied with seed type (table 1; fig. 3).

Maternal effects of herbivory for timing of emergence show contrasting patterns with offspring competitive context (table 3). In the absence of competition, offspring from the reduced MHE emerged 6.5 d earlier than did offspring from the ambient MHE (fig. 2*a*). In contrast, when offspring were grown in the presence of competitors, those derived from the reduced MHE emerged 4 d later than did offspring from the ambient MHE (fig. 2*a*).

For early plant biomass and final plant height, maternal effects on these traits were evident only when the progeny developed under competitive conditions (table 3; fig. 2*b*, 2*c*). Reducing maternal herbivory by 61% resulted in offspring that had 50% less aboveground biomass and were 30% shorter as reproductive adults than offspring produced in the ambient MHE when these offspring were grown in the presence of competitors (table 3; fig. 2*b*, 2*c*).

For total flower production, the interactive effects of MHE and OCE depended on seed type (table 1; fig. 3). In the absence of competition, CH offspring from the ambient MHE produced 45% more flowers than did CL offspring produced in the same MHE, whereas CH offspring from the reduced MHE produced 13% fewer flowers than did CL offspring produced in this MHE (fig. 3, open symbols). In contrast, in the presence of competition, both CL and CH offspring from the ambient MHE produced more flowers than did offspring from the reduced MHE (fig. 3, filled symbols).

Effects of Offspring Competitive Environment and Seed Type

Similar to previous findings with *I. capensis* (Waller 1984; Schmitt and Ehrhardt 1987; Steets et al. 2006*b*, 2007), we

found that both offspring growth environment and seed source affected offspring traits (table 1). Specifically, the presence of competitors reduced biomass before reproduction by 42% (competitors present vs. competitors absent: 0.42 ± 0.030 g vs. 0.73 ± 0.029 g), reduced height by 30% (53.3 ± 1.57 cm vs. 76.3 ± 1.56 cm), and reduced flower production by 50% (38.8 ± 2.29 vs. 77.2 ± 2.27), but it increased investment in CL flowers by 24% (0.77 ± 0.0003 vs. 0.62 ± 0.0003). Plants derived from CL seeds were 8% shorter (CL vs. CH: 62.04 ± 1.56 cm vs. 67.5 ± 1.54 cm), produced 12% fewer flowers (CL vs. CH: 54.3 ± 2.28 vs. 61.7 ± 2.26), and invested more in selfing CL flowers (0.72 ± 0.0003 vs. 0.68 ± 0.0003) than did those derived from CH seeds. Interestingly, and not previously demonstrated, there was a significant interaction between OCE and offspring seed type for early plant biomass and proportional production of CL flowers (table 1). In the absence of competitors, CL and CH individuals do not differ in biomass (table 4; CL vs. CH: 0.74 ± 0.042 g vs. 0.73 ± 0.043 g) or mating system (table 4; CL vs. CH: 0.62 ± 0.001 vs. 0.62 ± 0.001). In the presence of competitors, CH individuals are 47% heavier than CL individuals (table 4; CL vs. CH: 0.34 ± 0.043 vs. 0.50 ± 0.042 g), and a greater proportion of their reproduction is through chasmogamy than cleistogamy (table 4; CL vs. CH: 0.82 ± 0.001 vs. 0.73 ± 0.001).

Discussion

Our results demonstrate significant maternal effects of herbivory for offspring fitness–related traits. In general, although maternal herbivory reduces seed production in *Impatiens capensis* (Steets et al. 2006*a*), the results presented here show that it can also have positive effects for offspring traits. In addition, these maternal effects persisted well into offspring adulthood and affected reproductive traits. However, for many of the traits studied, the magnitude of maternal effect depended on offspring seed type and growth environment, suggesting that complex outcomes are possible for plant pop-
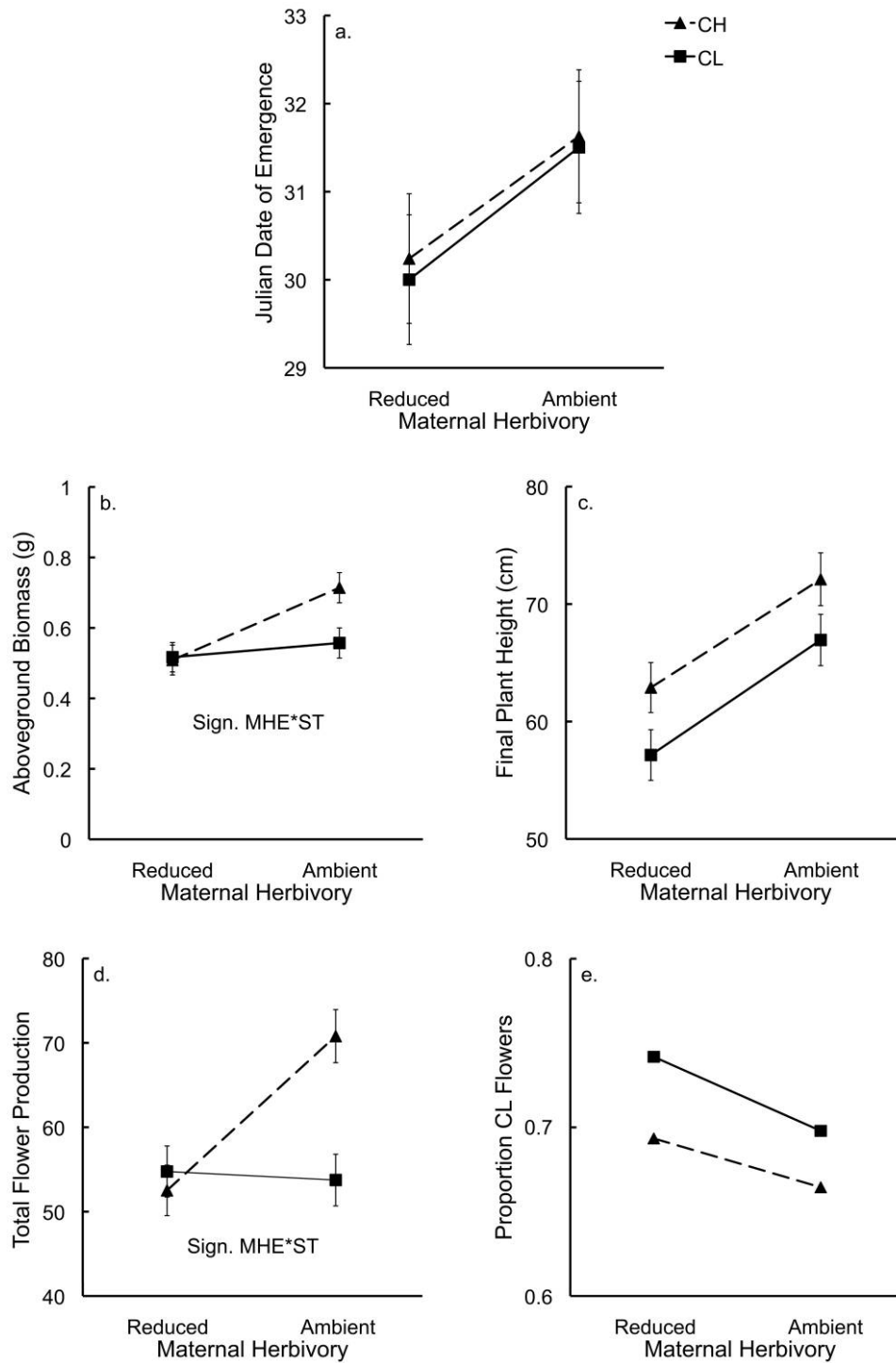
Fig. 1 Effect of maternal herbivory environment and offspring seed type for offspring traits. Least squares mean of *a*, Julian date of emergence, *b*, aboveground early plant biomass, *c*, final plant height, *d*, total flower production, and *e*, proportional production of cleistogamous (*CL*) flowers for individuals derived from CL (squares) and chasmogamous (*CH*; triangles) seeds produced by maternal plants experiencing ambient or reduced levels of herbivory. Traits with a significant interaction between maternal herbivory and progeny seed type (*Sign. MHE*ST*) are indicated. Error bars represent ±1 SE.

Table 2

F* and *P* Values of the Interaction Slices for the Effects of Maternal Herbivory and Progeny Seed Type on Early Plant Biomass and Total Flower Production of *Impatiens capensis

Source	Early plant biomass		Total flower production	
	F	*P*	*F*	*P*
Seed types, reduced herbivory	.02	.9	.3	.6
Seed types, ambient herbivory	6.9	.01	16.9	<.0001
Maternal herbivory, CH seed type	11.9	.0007	20.1	<.0001
Maternal herbivory, CL seed type	.5	.5	.06	.8

Note.   Degrees of freedom (df) for early plant biomass and total flower production are listed in the note of table 1.

ulation dynamics. Below we expand on these findings and discuss the implications of our results for plant population dynamics.

Maternal Effects of Herbivory

Maternal herbivory can have strong positive or negative effects on seed mass and progeny growth traits (Wulff 1986; Agrawal 2001, 2002). In this study, maternal effects of herbivory were primarily positive. In *I. capensis*, we found that plants experiencing higher rates of herbivory produced progeny that were larger in size. Given research findings that demonstrate a trade-off between seed mass and number (Smith and Fretwell 1974; Westoby et al. 1992) as well as increases in seed mass with herbivory (Wulff 1986), our finding of increased offspring size with higher rates of maternal herbivory may be the result of altered patterns of resource allocation in maternal plants experiencing damage. Specifically, it is possible that maternal plants subjected to higher rates of herbivory allocate their limited resources into rearing fewer, larger seeds that develop into larger, more vigorous seedlings and adults, because herbivore damage significantly reduces CH and CL seed production (Steets et al. 2006*a*). In addition, when considering the plant size differences we found between offspring from ambient MHEs and those from reduced MHEs in light of the fact that plant size is positively correlated with seed mass in *I. capensis* (Waller 1985), it is likely that seeds produced in the ambient MHE were larger than those produced in the reduced MHE. Given that plant size is an important determinant of survival in *I. capensis* populations (Schmitt et al. 1987), maternal plants may be able to compensate for herbivory-mediated losses in seed production by producing fewer but more vigorous progeny that are able to outcompete those produced under more benign conditions. If the maternal effects of herbivory for progeny size are caused by differential resource allocation, then maternal effects on progeny traits expressed early in development may mediate maternal effects on final plant size and reproductive traits. For example, in *Raphanus raphanistrum*, plants derived from larger seeds produce more flowers (Stanton 1984).

Few researchers have investigated maternal effects of herbivory for reproductive traits of offspring. Agrawal (2001, 2002) found that maternal herbivory to *R. raphanistrum* affected components of progeny fitness, including seed mass, plant growth, flower production, and fruit mass; however,

the strength and direction of maternal effects varied with family. Here we found significant positive maternal effects of herbivory for total flower production by offspring. Given that the maternal herbivore environment affects offspring traits related to life history (i.e., size, survival, reproduction), maternal effects of herbivory may have consequences for population dynamics, but this has yet to be quantified.

Competitive growth conditions have been shown to exacerbate expression of maternal effects in numerous species (e.g., Stratton 1989). Here we found that the OCE significantly affected the expression of maternal effects of herbivory for plant size and flower production (table 1; fig. 2). When *I. capensis* was grown in the presence of intraspecific competitors, offspring from the ambient MHE were significantly larger in size and produced more flowers than did those from the reduced MHE (table 1; fig. 2). In contrast, maternal effects of herbivory were not apparent among offspring grown in the absence of competitors (table 1; fig. 2). As *I. capensis* often grows in dense stands in which intraspecific competition is common (Schmitt et al. 1987; Steets et al. 2006*b*), and because the competitor-present treatment simulates intraspecific densities that are typical of those found in the wild (see "Material and Methods"), the results from this treatment are likely to be more relevant to natural populations than to those from the competitor-absent treatment. Our findings, as well as those of other researchers (e.g., Stratton 1989), highlight the importance of considering the offspring growth environment in the expression of maternal effects.

Mechanisms of Mating System–Dependent Maternal Effects of Herbivory

For progeny biomass and flower production, maternal effects of herbivory were evident only in CH offspring (fig. 2*b*, 2*d*). These mating system–dependent effects may be due to differential resource provisioning to CL and CH progeny (Steets and Ashman 2004) and/or herbivory-mediated alterations in maternal CH outcrossing rate (Steets et al. 2006*a*). First, it is possible that differential resource provisioning to CL and CH seeds, which develop at different positions on the plant and disperse different distances (Schmitt et al. 1985), underlies the response. For example, maternal effects are dependent on reproductive architecture in *Polygonum hydropiper*. Under optimal growth conditions, maternal plants produced terminal and axial offspring that did not differ in
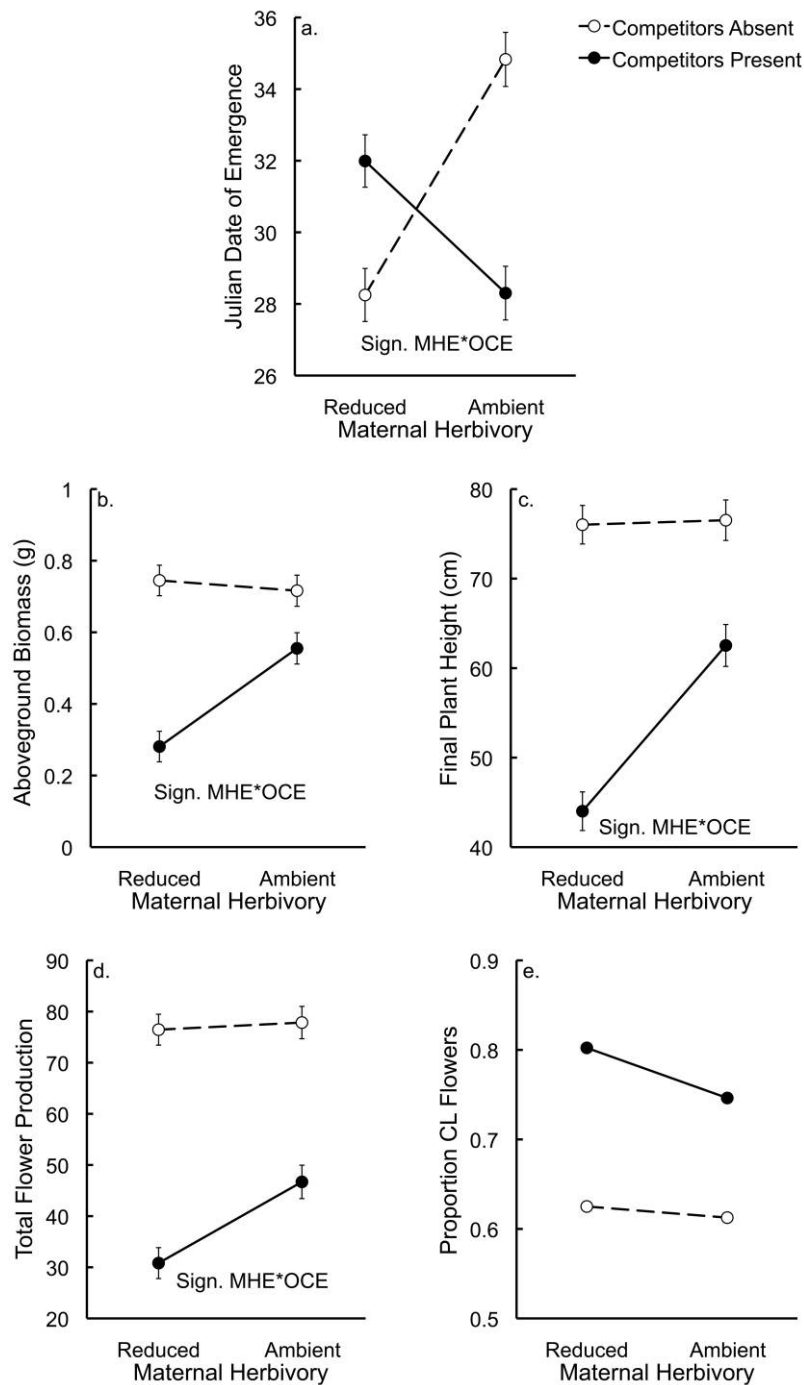
Fig. 2 Effect of maternal herbivory environment and offspring competitive environment for offspring traits. Least squares mean of *a*, Julian date of emergence, *b*, aboveground early plant biomass, *c*, final plant height, *d*, total flower production, and *e*, proportional production of cleistogamous (*CL*) flowers for offspring that were produced by maternal plants experiencing ambient or reduced levels of herbivory and that were grown in the absence (open circles) or presence (filled circles) of competitors. Traits with a significant interaction between maternal herbivory environment and offspring competitive environment (*Sign. MHE*OCE*) are indicated. Error bars represent ±1 SE.

seedling size traits but, under stressful conditions, produced terminal offspring that developed faster and had more biomass than the axial individuals (Lundgren and Sultan 2005). Lundgren and Sultan (2005) attribute this maternal effect to differences in resource allocation to terminal and axial

achenes; *P. hydropiper* prioritizes development of terminal offspring, which may disperse farther (given their position on the plant) than axial offspring. Similarly, in *I. capensis*, CH seeds disperse farther than CL seeds (Schmitt et al. 1985). Thus, maternal plants experiencing higher rates of herbivory
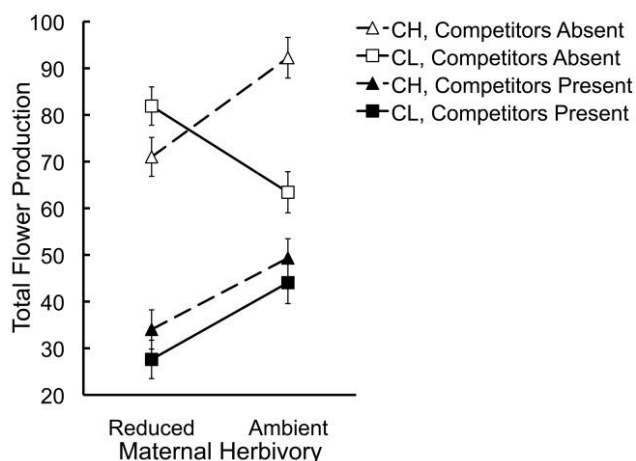
Fig. 3 Effect of maternal herbivory, seed type, and intraspecific competition for offspring total flower production. Open and filled circles represent competitor-absent and competitor-present treatments, respectively. Cleistogamous (*CL*) individuals are denoted with squares and chasmogamous (*CH*) individuals are denoted with triangles. Error bars represent ±1 SE.

may prioritize the development of the far-dispersing CH seeds over that of the CL seeds, as the CH seeds may experience less competition and thus have higher rates of establishment and survival than the CL plants. However, it is also plausible that mating system–dependent maternal effects were due to differences in inbreeding level between CH progeny produced under ambient and reduced herbivory conditions. A 60% reduction in herbivory led to a 41% decrease in the outcrossing rate of CH flowers in *I. capensis* (Steets et al. 2006a). In addition, because inbreeding depression has been documented in *I. capensis* (Schmitt and Gamble 1990; Lu 2002), the mating system–dependent maternal effects we document for biomass and flower production may be due to the higher outcrossing and concomitant lower inbreeding depression of CH seeds produced under ambient herbivory conditions. Unfortunately, the experimental design employed in this study does not allow us to identify the specific mechanism underlying the mating system–dependent maternal effects, and future experiments will be needed to address this topic.

In a previous study, we found that maternal plants subjected to simulated herbivory produced CL offspring that were smaller in size than their CH equivalents and all progeny types from undamaged maternal plants (Steets and Ashman 2004). The difference in the direction of mating system–dependent maternal effects between previous work and this study may be due to differences in several aspects of experimental context. First, simulated herbivory may not elicit the same cross-generational responses as natural herbivory. For example, removal of leaf tissue with scissors does not induce resistance or transgenerational resistance in *Raphanus raphanistrum*, whereas within- and between-generation resistance occurs when caterpillar feeding damages maternal plants (Agrawal 2002). In addition, the maternal competitive environment differed between the two studies (i.e., Steets and Ashman 2004 and this study), and this may have contributed to differences in mating system–dependent maternal effects. In the simulated herbivory experiment (Steets and Ashman 2004), maternal plants were grown individually in pots and thus were not subjected to intraspecific competitive interactions that are common in *I. capensis* populations (Schmitt et al. 1987; Steets et al. 2006b). The natural competitive dynamics among maternal plants in this study may have resulted in more stressful growth conditions and, thus, differences in maternal effects on CL and CH seeds relative to the simulated herbivory experiment (Steets and Ashman 2004). Given the more realistic conditions of this study, our current findings likely better reflect cross-generational responses of *I. capensis* to herbivory in nature.

Demographic Consequences of Maternal Effects

Researchers are just beginning to examine the demographic consequences of parental environment (Beckerman et al. 2002; Galloway and Etterson 2007; Donohue 2009). By considering our findings of mating system–dependent maternal effects of herbivory for offspring biomass and total flower production in light of the difference in demographic value between *I. capensis* CL and CH individuals (Steets et al. 2007), we can predict the potential population dynamic consequences of these maternal effects. Here we found that CH offspring produced by maternal plants experiencing ambient herbivory were significantly larger and had greater flower production than CL individuals from the same MHE and individuals of both seed types produced in the reduced MHE (table 2; fig. 1b, 1d). Because plant size is a significant predictor of survival in *I. capensis* populations (Schmitt et al. 1987), the greater size of CH individuals from ambient-

Table 3

F and P Values of the Interaction Slices for the Effects of Maternal Herbivory and Intraspecific Competition on Emergence Date, Early Plant Biomass, Final Plant Height, and Total Flower Production of *Impatiens capensis*

Source	Date of emergence		Early plant biomass		Final plant height		Total flower production	
	F	P	F	P	F	P	F	P
Competition, reduced herbivory	13.8	.0002	57.9	<.0001	112.0	<.0001	127.0	<.0001
Competition, ambient herbivory	40.1	<.0001	6.6	.01	17.7	<.0001	48.4	<.0001
Maternal herbivory, competitors absent	42.1	<.0001	.2	.6	.02	.9	.1	.7
Maternal herbivory, competitors present	13.0	.0004	20.1	<.0001	35.6	<.0001	14.6	.0002

Note.   Degrees of freedom (df) for date of emergence, early plant biomass, final plant height, and total flower production are listed in table 1.

Table 4

F and *P* Values of the Interaction Slices for the Effects of Intraspecific Competition and Progeny Seed Type on Early Plant Biomass and Proportional Production of Cleistogamous (CL) Flowers of *Impatiens capensis*

	Early plant biomass		Proportion CL flowers	
Source	*F*	*P*	*F*	*P*
Seed types, competitors absent	.04	.8	.04	.8
Seed types, competitors present	7.2	.008	8.7	.004
Competition, CH seed type	14.6	.002	13.3	.0004
Competition, CL seed type	45.1	<.0001	46.5	<.0001

Note. Degrees of freedom (df) for early plant biomass and proportion CL flowers are listed in table 1.

herbivory maternal plants will likely translate into higher survival rates among these individuals. The potential increase in CH survival and fecundity of offspring produced under higher rates of herbivory relative to those produced in more benign herbivory conditions may have only moderately beneficial effects on *I. capensis* population growth because vital rates of CH individuals contribute disproportionately less to *I. capensis* population dynamics than do those of CL individuals (Steets et al. 2007). This interesting link between maternal effects of herbivory and population growth warrants further investigation.

Conclusions

Our study demonstrates that the maternal herbivory environment can have consequences for offspring fitness-related traits, including traits expressed later in life. Furthermore, the magnitude of maternal effects varied for selfed (CL) and largely outcrossed (CH) offspring, and this difference was exacerbated by the offspring competitive environment. To better understand the ecological and evolutionary consequences of mating system–dependent maternal effects, demographic studies are needed that explicitly consider maternal effects on selfed and outcrossed individuals for population growth.

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