

Plant sex and induced responses independently influence herbivore performance, natural enemies and aphid-tending ants

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Abstract Sex is an ecologically important form of genetic variation in dioecious plants, with males and females generally differing in constitutive resistance to herbivores. Yet little is known about sexual dimorphism with respect to induced or indirect defense, or whether sex-based differences are underlain by trade-offs among modes of defense. We compared male and female *Valeriana edulis* plants for constitutive and induced direct resistance to two herbivores, an early-season caterpillar and a late-season aphid, and for constitutive and induced indirect resistance in terms of abundance of natural enemies and aphid-tending ants. No sexual dimorphism was found in constitutive direct plant resistance, yet the sexes differed for constitutive indirect resistance, with 78 % more natural enemies and 117 % more ants present on females than males. Past feeding damage by caterpillars induced direct and indirect resistance in both males and females, increasing caterpillar development time by 26 % and the abundance of natural enemies by 147 %. Caterpillar feeding did not induce direct resistance with respect to caterpillar final mass or aphid performance. In all cases, there were no interactions between the effects of caterpillar damage and plant sex. In summary, plant sexual dimorphism and induced responses to herbivore damage independently influenced herbivore

performance and the composition of arthropod communities at higher trophic levels.

Keywords Ant–aphid interactions · Dioecy · Indirect defense · Induced defense · Natural enemies · Parasitoids · Slow-growth/high-mortality hypothesis · Sexual dimorphism · *Valeriana edulis*

Introduction

Genetic variation in plant species can affect the structure of associated arthropod communities (Johnson and Stinchcombe 2007; Whitham et al. 2006; Whitham et al. 2003). Such effects can occur through genetic variation in both constitutive direct resistance to herbivores (reviewed by Marquis 1992; Linhart 1991) and induced direct resistance (reviewed by Karban and Baldwin 1997). In addition, plants may vary genetically in terms of protection by natural enemies, and this indirect defense can also be constitutive or induced (Hare 2011; Dicke and Baldwin 2010; Rico-Gray and Oliveira 2007; Rudgers 2004). The arthropod community associated with a plant is thus determined, in part, by plant genetic variation in resistance that can be constitutive and inducible, as well as direct and indirect.

One form of genetic variation in plants with large ecological effects is that of plant sex in dioecious species (Ågren et al. 1999; Cornelissen and Stiling 2005), a sexual system that occurs in 37 of 51 plant orders and 10 % of all angiosperm species (Geber et al. 1999; Cornelissen and Stiling 2005). Female plants invest more in reproduction than males (Lloyd and Webb 1977; Delph 1999) and probably grow more slowly as a consequence (Cornelissen and Stiling 2005). Because slow plant growth is associated with greater investment in herbivore resistance (Coley

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et al. 1985; Fine et al. 2004; Mooney et al. 2010), females most often have higher levels of constitutive direct resistance against herbivores, support lower herbivore densities and receive less herbivore damage (Ågren et al. 1999; Cornelissen and Stiling 2005).

In contrast to the well-documented sexual dimorphism in constitutive direct resistance (reviewed by Ågren et al. 1999; Cornelissen and Stiling 2005), there are far fewer studies with respect to induced direct resistance (including tolerance and compensation) and constitutive or induced indirect resistance. Sexual dimorphism in induced direct defenses has been found in most of the dioecious and gynodioecious plants studied (Table 1), but there are relatively few studies and these results are evenly divided

between females showing higher and lower investment relative to males or hermaphrodites. With respect to constitutive indirect resistance, sexual dimorphism has been found in all five dioecious and gynodioecious plants studied for differential abundance of predatory ants that also consume floral resources, but these studies are divided between higher and lower ant visitation to females relative to males or hermaphrodites (reviewed by Ashman and King 2005). While floral resources are known to attract natural enemies (reviewed by Heimpel and Jervis 2005), the importance of plant sexual dimorphism in such effects is unknown. Finally, to our knowledge, there are no studies testing for plant sexual dimorphism in induced indirect defense.

Table 1 Results of studies testing for sexual dimorphism in induced plant defenses

Plants	Breeding system	Damage	Variable(s) measured	Outcome	Citation
<i>Fragaria virginiana</i>	Gynodioecious	Experimentally imposed artificial damage	Tolerance (fruit number, seed number)	Female < hermaphrodite	(Ashman et al. 2004)
		Experimentally imposed artificial damage	Tolerance (flower number)	Female = hermaphrodite	
		Natural variation in spittlebug herbivory	Tolerance (vegetative and reproductive biomass)	Female = hermaphrodite	(Cole and Ashman 2005)
		Natural variation in spittlebug herbivory	Resistance to herbivory	Female < hermaphrodite	
		Natural variation in spittlebug herbivory	Susceptibility to fungal infection	Female > hermaphrodite	
<i>Geranium sylvaticum</i>	Gynodioecious	Experimentally imposed artificial damage	Reduction in phosphorous content	Female > hermaphrodite	(Varga et al. 2009)
		Experimentally imposed artificial damage	Root inoculation by mycorrhizae	Female = hermaphrodite	
		Experimentally imposed artificial damage	Tolerance (fruit set, seed set, seed number)	Female = hermaphrodite	
<i>Rhamnus alpinus</i>	Dioecious	Natural variation in leaf damage	Increase in anthraquinone content	Female = male	(Banuelos et al. 2004)
<i>Salix discolor</i>	Dioecious	Experimentally imposed artificial damage	Reduction in leaf length and leaf fold gaps with insect gall	Female > male	(Fritz et al. 2003)
		Experimentally imposed artificial damage	Tolerance (shot length, leaf length)	Female = male	
<i>Salix planifolia</i>	Dioecious	Experimentally imposed artificial damage	Tolerance (vegetative biomass)	Female = male	(Houle 1999)
<i>Urtica dioica</i>	Dioecious	Experimentally imposed parasitic plant infection	Tolerance (vegetative biomass)	Female = male	(Koskela et al. 2002)
		Experimentally imposed parasitic plant infection	Tolerance (reproductive biomass)	Female < male	
<i>Valeriana edulis</i>	Dioecious	Natural and experimentally imposed caterpillar herbivory	Indirect defense (ants, other natural enemies)	Female > male	This study
		Natural and experimentally imposed caterpillar herbivory	Resistance to herbivory	Female = male	

For sexual dimorphism in constitutive direct defense, females are most often better defended than males (reviewed by Ågren et al. 1999; Cornelissen and Stiling 2005). For sexual dimorphism in constitutive indirect defense, recruitment of ants to flowers is most often sexually dimorphic, with results evenly divided between higher and lower ant visitation to females relative to males or hermaphrodites (reviewed by Ashman and King 2005), and the present study found constitutively higher visitation of ants and other natural enemies to females than males



Fig. 1 Female *Valeriana edulis* (left, photo credit WKP) and *Aphis valerianae* being tended by the ant *Camponotus vicinus* (right, photo credit KAM) at a field site near Gothic, Colorado

In this study, we compared male and female individuals of a dioecious plant for constitutive and induced resistance to herbivory, as well as the indirect effects of plant sex and feeding damage on the attraction of natural enemies and aphid-tending ants. Working in a subalpine meadow, we measured the performance of two herbivores, an early-season caterpillar and a late-season ant-tended aphid, on male and female *Valeriana edulis* plants with and without previous caterpillar feeding damage (Fig. 1). For aphids, we also monitored the indirect effects of plant sex and induced plant responses for abundance of natural enemies and tending ants. In so doing, we provide tests for sexual dimorphism in plant resistance in terms of constitutive direct resistance, as has been studied previously (Ågren et al. 1999; Cornelissen and Stiling 2005), as well as novel tests with respect to variation in induced and indirect resistance. More generally, this study addresses the interactive consequences of plant sex and induced plant resistance on arthropod community composition across multiple trophic levels.

Methods

Study site and organisms

The study was conducted in Gunnison County, Colorado, at 2,900 m elevation in a 1.0-ha montane meadow 38.967°N, 106.995°W. The vegetation is described by Langenheim (1962). The host plant, *Valeriana edulis* var. *edulis* Nutt. ex Torr. & A. Gray, is a dioecious perennial herb distributed

throughout the western North America (Meyer 1951). Plants in the genus *Valeriana* have previously been shown to have high concentrations of iridoids in root tissues (Wang et al. 2010), and preliminary analyses of plants from our field site show these compounds to be at similarly high concentrations in *V. edulis* inflorescences (Petry et al. unpublished data). While it is unknown whether iridoids are encountered by *Valeriana*'s sap-feeding herbivores, aphids have been observed to sequester these compounds from other plant species (Nishida and Fukami 1989).

Valeriana edulis grows for several years as a basal rosette of leaves before flowering via one to many inflorescences of small (3–5 mm diameter) white flowers (Soule 1981). Inflorescences bolt during the second half of June and consist of a stalk supporting one to several compound cymes. Based on a 2009 survey of 97 plants (Petry et al. unpublished data), this population has a skewed sex ratio, with only 31 % of plants being male. Males and females do not differ in most vegetative morphological traits including diameter of basal rosette, longest leaf length and width, leaf number, and number of inflorescence stalks and inflorescence height ($P > 0.15$ in all cases), but the volume of individual compound cymes is significantly smaller for females than males (5.1 ± 0.3 and 8.4 ± 1.0 cm³, respectively; $P < 0.001$) (Petry et al. unpublished data).

Beginning in early June, *Valeriana edulis* is fed upon by a lepidopteran larvae provisionally identified as *Eana* spp. (Tortricidae). Caterpillars initially feed on leaves in the basal rosette, but move up the stalk to feed within compound cymes after bolting. Once within compound cymes, the caterpillars surround their feeding area with silk, but do

not otherwise modify the inflorescence structure. The 2009 survey documented that caterpillars were found on 48 % of the plants, with their frequency being similar between males and females (51 and 43 %, respectively; $P = 0.50$) (Petry et al. unpublished data).

The ant-tended aphid *Aphis valerianae* Cowen first appears in late June, after plants have bolted, and then persists at least through mid-August (Petry et al. 2012). It feeds upon the upper portions of the main inflorescence stalk and within compound cymes on the stalks supporting individual cymes where it is frequently tended by ants. The ant most frequently associated with *A. valerianae* in our study was *Tapinoma sessile* Say. The 2009 survey documented that aphids were found feeding on 22 % of the plants, with the frequency of their occurrence being significantly greater on females than males (28 and 7 %, respectively) (Petry et al. unpublished data).

Selection of experimental plants

In late June 2010, male and female plants were selected that either had no naturally visible feeding damage by any herbivores (male and female undamaged plants) or that had caterpillar damage to leaves and at least one inflorescence (male and female damaged plants). These four types of plant were randomly assigned to subsequent treatments of caterpillar and aphid addition (see below). At this time, aphids were largely absent at this site. Plant traits such as basal diameter, length of longest leaf, width of widest leaf, total number of leaves and plant height were measured on experimental plants, but did not differ between treatment groups and were not significant as covariates for any measured response (all $P > 0.15$).

Experiment 1: effects on caterpillars

This experiment assessed the individual and combined effects of plant sex and naturally occurring caterpillar damage on caterpillar performance. For some plants in all treatments, multiple focal inflorescences were studied, and data were pooled to make the plant the unit of replication. The number of plants in each treatment was 16 damaged males (23 inflorescences studied), 20 damaged females (28 inflorescences studied), 11 undamaged males (15 inflorescences studied) and 13 undamaged females (19 inflorescences studied). Between 21 and 23 June, all focal inflorescences were cleared of naturally occurring caterpillars and inoculated with a single experimental caterpillar collected from *V. edulis* in an adjacent field. These caterpillars were preweighed and placed within a sealed mesh bag on experimental plants of the same sex from which they were collected. Caterpillars were monitored daily for survival and pupation. Pupae and prepupae were collected

and weighed, and kept in the laboratory in Petri dishes with moist filter paper.

All analyses tested for the individual and interactive effects of plant sex and caterpillar damage on various aspects of caterpillar performance. Caterpillar survival (pupation vs. death as caterpillar or prepupae) was analyzed by log-linear contingency table analysis based on plant sex and caterpillar damage. Subsequent analyses used general linear models. Data on caterpillar final mass (mg) and development time (days) included both pupae and prepupae, which differed in mass. Accordingly, the difference between these two groups was accounted for by including stage at final weighing (prepupa vs. pupa) as a term in each analysis. The analysis of development time also included initial mass to account for ontogenetic variation among caterpillars at the start of the experiment. All residuals were normally distributed, and analyses were performed on untransformed variables by general linear model using the GLM procedure in SAS 9.2 (SAS Institute 2010). All covariates and interaction terms with $P > 0.15$ were removed, and the results from reduced models are presented.

Experiment 2: effects on aphids and higher trophic levels

This experiment assessed the effects of plant sex and caterpillar damage on aphid performance and the abundance of ants and natural enemies associated with those aphids. For some plants in all treatments, multiple focal inflorescences were studied, and data were pooled to make the plant the unit of replication. The number of plants in each treatment was 40 damaged males (65 inflorescences studied), 38 damaged females (60 inflorescences studied), 9 undamaged males (17 inflorescences studied) and 13 undamaged females (41 inflorescences studied). Aphids were collected from a single colony in an adjacent field and added to each plant at a density of 15 aphids per inflorescence (approximately 10 nymphs and 5 adults) between 14 and 21 July, approximately 10 days after the completion of caterpillar damage in Experiment 1. Aphid populations were monitored for an 8- to 12-day period until 26–30 July when an aphid count was made and bags were removed. At this time, aphid fecundity was used to calculate the per capita daily growth (r), according to the formula:

$$r = \frac{(e^{\ln(N_{t1}) - \ln(N_{t0})})}{(t_1 - t_0)}, \quad (1)$$

where t_0 and t_1 are the initial and final dates (Julian day) for aphid counts, and N_{t0} and N_{t1} are the aphid population sizes on those dates. After mesh bag removal, ants rapidly discovered and began tending aphids, and counts were made of ants and natural enemies present at each aphid colony on

4 August and 10 August, between 09:00 and 17:00 when weather conditions were clear and calm. For each count, the plant was visited once and inspected systematically for 1–2 min to count and record the taxonomic (family level) identity of all arthropods. Ants and natural enemies were only counted if they were within 10 cm of the aphid colony. Finally, on 13 August, a sample of adult aphids ($N = 5$) was collected and weighed from all experimental plants with surviving aphid colonies ($N = 20$).

Analyses tested for the effects of plant sex and caterpillar damage on aphid performance (per capita daily growth, adult mass) and the abundance of natural enemies and ants associated with those aphids. Because natural enemy abundance was low and evenly distributed among several taxonomic groups, analyses were only conducted on total natural enemy abundance pooled across both sampling dates. The residuals of aphid mass were normally distributed, and analyses were performed on the untransformed variable by general linear model using the GLM procedure in SAS 9.2 (SAS Institute 2010). Aphid mass was analyzed in two separate analyses for its dependence upon plant sex and caterpillar damage because only a single undamaged male was measured, precluding a test for interactive effects. The residuals of all other variables were not normally distributed, and Poisson regression was used with the GENMOD procedure in SAS 9.2 (SAS Institute 2010). Aphid fecundity and the abundance of natural enemies and ants were analyzed as dependent upon plant sex and caterpillar damage and their interaction. Analyses of effects on natural enemies and ants were based upon the sum of counts from the two sampling dates and included aphid abundance at the time of bag removal as a covariate. All covariates and interaction terms with $P > 0.15$ were removed, and the results from reduced models are presented.

Results

Experiment 1: effects on caterpillars

The 85 caterpillars collected from the field did not vary in initial mass based upon whether they were collected from male or female plants (male, 37.6 ± 2 mg; female, 38.9 ± 3 mg; $F_{1,83} = 0.01$, $P = 0.92$). Across all treatments, the mean (\pm SE) caterpillar development time on experimental plants for caterpillars that survived to the prepupal or pupal stage and were not parasitized was 16 ± 0.9 days. Of the 85 caterpillars placed on experimental plants, 15 escaped or were killed by infiltrating ants, leaving 70 for analysis. Of these, 3 died as caterpillars, 45 died as prepupae, and 27 successfully pupated. Two parasitoid wasps eclosed from pupae from female plants with previous feeding damage, and data from these caterpillars were excluded from the analysis.

Based upon a 3-way log-linear contingency table analysis, the number of caterpillars successfully reaching the pupal stage was not affected by plant sex ($G_{df=1} = 2.7$, $P = 0.10$), plant damage ($G_{df=1} = 0.02$, $P = 0.89$) or their interaction ($G_{df=4} = 2.78$, $P = 0.60$). Overall, survival to pupation was 32 % (27 of 70 caterpillars; 18 of 56 plants). Caterpillar final mass (mg) was not affected by plant sex ($F_{1,51} = 0.28$, $P = 0.60$), caterpillar damage ($F_{1,51} = 0.03$, $P = 0.85$) or their interaction ($F_{1,50} = 0.27$, $P = 0.61$) when accounting for differences in mass between pupae and prepupae ($F_{1,51} = 40.70$, $P < 0.0001$) (Fig. 2a). Caterpillar development time (days) was not affected by plant sex ($F_{1,51} = 0.01$, $P = 0.92$) and was increased 26 % by previous feeding damage ($F_{1,52} = 5.93$, $P = 0.0184$), and there was no interaction between plant sex and caterpillar damage ($F_{1,50} = 0.31$, $P = 0.58$) when accounting for differences in mass between pupae and prepupae ($F_{1,52} = 7.96$, $P = 0.0068$) and initial mass ($F_{1,52} = 16.16$, $P = 0.0002$) (Fig. 2b).

Experiment 2: effects on aphids and higher trophic levels

Aphid performance (per capita daily growth rate), measured within mesh bags with both ants and natural enemies excluded, was not affected by plant sex ($F_{1,86} = 0.21$, $P = 0.65$), caterpillar damage ($F_{1,86} = 0.59$, $P = 0.44$) or their interaction (Fig. 2c). Similarly, adult aphid mass was not affected by caterpillar damage ($F_{1,19} = 0.14$, $P = 0.71$) or plant sex ($F_{1,17} = 2.11$, $P = 0.16$) (Fig. 2d).

Once mesh bags were removed, a diversity of natural enemies was observed in close association with aphids, including predatory hemipterans (Miridae), parasitic wasps (Hymenoptera) and adult ladybird beetles (Coccinellidae). Natural enemy abundance was not influenced by aphid density ($F_{1,95} = 0.28$, $P = 0.60$). Natural enemy abundance was 78 % higher on females than males ($F_{1,97} = 5.40$, $P = 0.0223$), and 147 % higher on plants with previous feeding damage than undamaged plants ($F_{1,97} = 6.02$, $P = 0.0160$), but there was no significant interaction between plant sex and caterpillar damage ($F_{1,95} = 0.06$, $P = 0.81$) (Fig. 2e). Ant abundance was 117 % higher on female plants ($F_{1,96} = 8.91$, $P = 0.0036$) and was not affected by caterpillar damage ($F_{1,96} = 0.08$, $P = 0.78$) or the interaction between these two effects ($F_{1,95} = 0.81$, $P = 0.37$) when controlling for aphid density ($F_{1,96} = 26.31$, $P < 0.0001$) (Fig. 2f).

Discussion

This study documents sexual dimorphism in constitutive indirect resistance but not direct resistance, and induced direct and indirect resistance that were consistent between

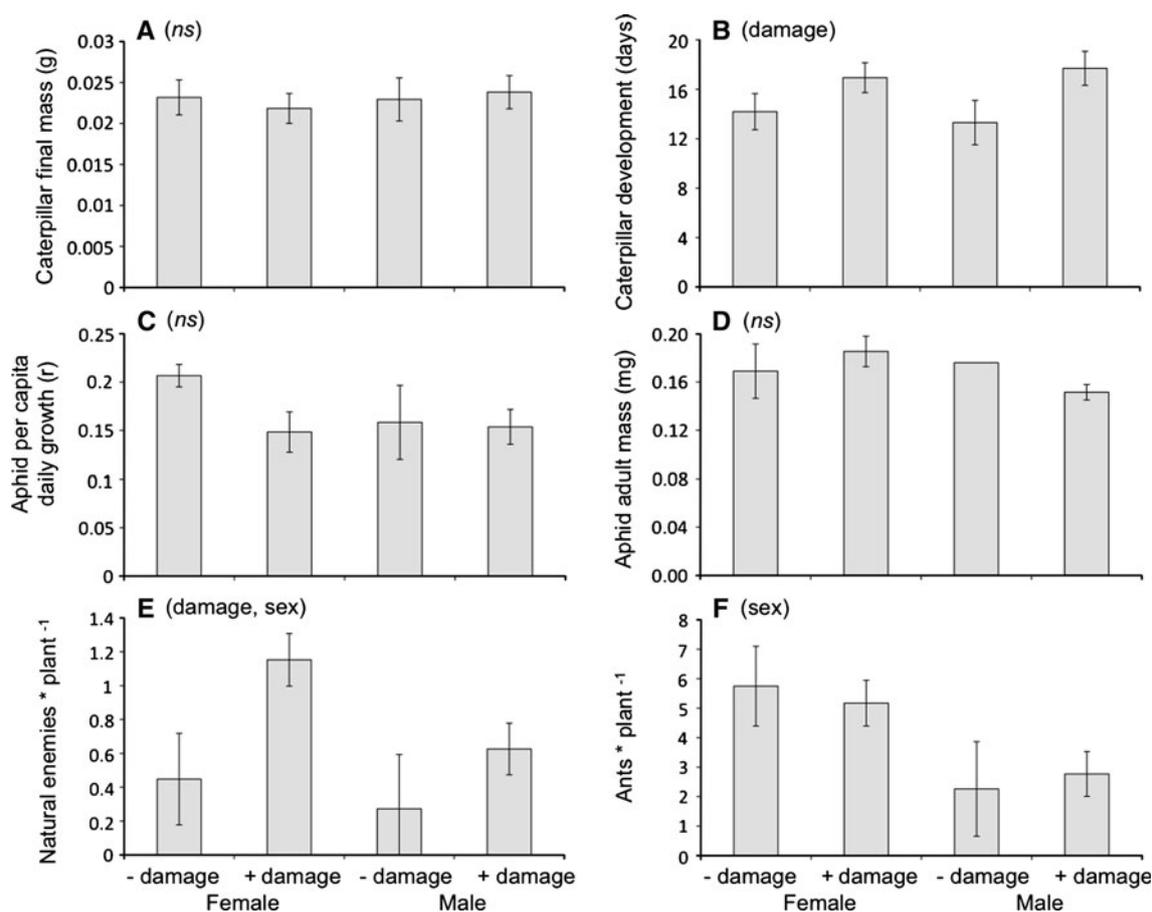


Fig. 2 Mean \pm SE **a** caterpillar final mass, **b** caterpillar development time, **c** aphid fecundity, **d** aphid adult mass, **e** natural enemy abundance and **f** aphid-tending ant abundance on male and female *V. edulis* plants either with (“+”) or without (“-”) previous caterpillar feeding damage. Least-square means for caterpillar development time and final mass are depicted from analyses controlling for caterpillar

stage at final weighing (pupa or prepupae), and for development time also control for caterpillar initial mass. Least-square means for natural enemy and ant abundance are depicted from analyses controlling for aphid abundance. For each panel, significant effects ($P < 0.05$) are shown parenthetically

the sexes (Fig. 2). While there was no sexual dimorphism in constitutive direct resistance to either caterpillars or aphids, constitutive indirect resistance differed between the sexes, with 78 % more natural enemies and 117 % more aphid-tending ants observed on females than males. With respect to induced direct resistance, there were no effects of feeding damage on caterpillar final mass or aphid performance, but caterpillar development time was lengthened by 26 % on both males and females. For induced indirect resistance, feeding damage by caterpillars increased natural enemy abundance by 147 % on both males and females, but did not affect aphid-tending ants. In all cases, there were no significant interactions between the effects of plant sex and caterpillar damage.

Plant sexual dimorphism was observed for indirect but not direct defense. The equivalent performance of caterpillars and aphids on males and females runs counter to the general pattern of male-biased herbivory and higher resistance in females for both foliage-chewing herbivores

(Cornelissen and Stiling 2005; Ågren et al. 1999) and sap-feeding herbivores (e.g. Ma et al. 2009; Wheeler 2009; Feller 2001; Polhemus 1988). Yet relatively few studies have investigated floral herbivores, and plant resource allocation to reproductive tissues might lead to different patterns from those observed in vegetative tissues. Nevertheless, consistent with patterns of greater female resistance, females had higher levels of constitutive indirect defense in terms of the densities of both natural enemies and aphid-tending ants. While the higher density of ants on female plants might be expected to increase herbivory by facilitating aphid population growth, aphid-tending ants simultaneously prey upon untended herbivores, with the net effect typically being an overall reduction in herbivore density and positive effects on plant performance (Styrsky and Eubanks 2007).

While the mechanism of sexual dimorphism in natural enemies abundance is currently unknown, such effects might occur both directly and indirectly. Both ants and the

most commonly observed natural enemies—mirids and parasitic hymenopterans—are known to feed regularly on plant nectar (Wäckers et al. 2005; Heimpel and Jervis 2005), and past studies have documented plant sexual dimorphism in the attractiveness of floral nectar (Ashman and King 2005) and in the composition of floral volatiles (Raguso 2009; Ashman et al. 2005; Galen et al. 2011). Alternatively, sexually dimorphic plants may affect aphid traits such as honeydew quality that are relevant to the attraction of both ants (Stadler et al. 2002; Mooney 2011) and natural enemies (Hatano et al. 2008). It is also possible that plant sex influences ant abundance (as above, either directly or indirectly), and natural enemies in turn use ants as a cue to locate aphid prey.

Induced responses to herbivory are believed to evolve as cost-saving strategies, where investment in anti-herbivore traits is only made in the presence of herbivore damage (Karban and Baldwin 1997; Mooney and Agrawal 2008). As a consequence, a trade-off is predicted between potentially redundant constitutive and induced defenses (Koricheva et al. 2004; Zangerl and Bazzaz 1992). We observed no such trade-off; females constitutively supported higher densities of both natural enemies and aphid-tending ants than males, and the only two instances of caterpillar parasitism were observed on females. Yet damaged female plants showed increases in both direct and indirect resistance equivalent to that of males. There was also no detectable difference between females and males in terms of plant size at this field site (Petry et al. unpublished data), suggesting that the greater abundance of natural enemies and aphid-tending ants was not driven by differences in plant apparency. Overall, our results are suggestive of superior female performance at this field site, a conclusion that is consistent with the observed female-biased sex ratio.

Our findings are also suggestive of potential synergism between the induction of direct and indirect resistance. Feeding damage had no detectable influence on caterpillar mortality, but instead delayed development time. The fitness value of such sub-lethal plant defenses is unclear, as they do not necessarily reduce herbivore feeding (Feeny 1976). The slow-growth/high-mortality hypothesis resolves this paradox by proposing that slow-developing herbivores are at a greater risk of attack by natural enemies (Moran and Hamilton 1980; Clancy and Price 1987; Mooney et al. 2012). Our finding of increased natural enemy abundance in conjunction with a lengthening of herbivore development suggests some degree of coordination between direct and indirect induced plant defenses. Consistent with this, the two instances of caterpillar parasitism occurred on previously damaged female plants.

Plant sex is well recognized to be an ecologically important form of genetic variation with respect to direct resistance to herbivores (Cornelissen and Stiling 2005;

Ågren et al. 1999). While dioecy is found in only a fraction of species in any given community (Geber et al. 1999), it occurs in many ecologically dominant species and may thus have important consequences for both community structure and ecosystem processes. Our findings add to a small but growing literature, showing plant sexual dimorphism in arthropod community composition at higher trophic levels, and how such effects depend on the history of past feeding damage. More broadly, there is a growing appreciation for the consequences of intra-specific variation in plant traits for the abundance and composition of arthropod communities (Whitham et al. 2006), and sexual dimorphism may be an especially important trait in this regard.

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