REPORT



An insect pheromone primes tolerance of herbivory in goldenrod plants

Eric C. Yip¹ | Mark C. Mescher² | Consuelo M. De Moraes² | John F. Tooker¹

¹Department of Entomology, The Pennsylvania State University, University Park, Pennsylvania, USA

²Department of Environmental Systems Science, ETH Zürich, Zürich, Switzerland

Correspondence Eric C. Yip Email: ecy5039@psu.edu

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Abstract

Environmental cues that predict increased risk of herbivory can prime plant defenses; however, few studies have explored how such cues elicit broader plant responses, including potential effects on plant growth and other resource allocations that may affect tolerance to herbivore damage. We exposed goldenrod plants (Solidago altissima) to varying concentrations of the putative sex pheromone of a gall-inducing herbivore, which has previously been implicated in defense priming. In experiments with two plant genotypes and three herbivore populations, any level of exposure to the pheromone enhanced tolerance of galling, rescuing flower production to levels observed for ungalled plants. Exposure to low doses of the pheromone elicited greater resistance to galling than exposure to high doses, with unexposed plants exhibiting intermediate resistance, suggesting a nonlinear relationship between exposure and defense priming. These findings suggest plant responses to environmental cues associated with biotic stressors are broader and more complex than previously appreciated.

KEYWORDS

defense, Eurosta, gall, growth, herbivory, kairomone, resistance, Solidago, Tephritidae, tolerance

INTRODUCTION

Numerous studies have documented plant defense priming by environmental cues that predict herbivore or pathogen attack (Brosset & Blande, 2022; Frost et al., 2008a, 2008b; Kim & Felton, 2013). For herbivory, priming has been documented in response to cues associated with the physical presence of insect herbivores or their eggs (Kim & Felton, 2013; Pashalidou et al., 2020), volatile emissions from damaged leaves (Brosset & Blande, 2022; Frost et al., 2008a, 2008b; Kim & Felton, 2013), and insect pheromones (Bittner et al., 2019; Helms et al., 2013; Magalhães et al., 2019). In addition to defense priming, plants might be expected to respond to such cues in other ways; for example, oviposition-induced volatiles can mediate shifts in timing of resource allocation to growth versus flower production (Pashalidou et al., 2020). Furthermore, while work on priming by cues that predict herbivory has focused almost exclusively on defense responses that enhance resistance to subsequent attackthat is, reduce the amount of damage incurred (Frost et al., 2008a, 2008b; Kim & Felton, 2013)-plants might also respond to such cues via changes in patterns of growth or other resource allocations that enhance tolerance and help to maintain fitness despite tissue loss to herbivory (Fornoni, 2011). Such broader effects on plant phenotypes and plant-herbivore interactions could potentially have far-reaching ecological implications, yet little

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work to date has explored this possibility. Indeed, only a few, mostly recent, studies have reported the effects of any volatile cues on plant traits related to growth, phenology, and primary metabolism, and little is currently known about the ecological function of such responses (Brosset & Blande, 2022).

In a series of previous studies, we explored the responses of tall goldenrod (Solidago altissima) plants to volatile cues produced by a specialist herbivore, the goldenrod gall fly (Eurosta solidaginis). This system was the first documented example of a plant responding to an animal-derived odor (Helms et al., 2013), but cotton and pine trees have now been documented to respond to herbivore odors as well (Bittner et al., 2019; Magalhães et al., 2019), indicating this interaction has evolved multiple times in plants. In the goldenrod system, Eurosta males perch on goldenrod tips (Uhler, 1951) and emit copious amounts of a putative sex pheromone that attracts females (Helms et al., 2013). While still close to emitting males, mated females oviposit into nearby goldenrod stems, where larvae subsequently induce gall formation. Our previous work showed that exposure to the primary component of the fly pheromone, E-conophthorin, primes goldenrod defenses mediated by the jasmonic acid (JA) pathway, reduces overall levels of herbivory in the field and laboratory (Helms et al., 2013, 2017; Yip et al., 2017), and lowers rates of gall formation (Yip et al., 2021). We also found evidence that the intensity of pheromone exposure predicted the strength of JA induction following herbivory (Helms et al., 2017); however, exposing plants to male flies of different ages (age correlates with pheromone emission rate) revealed the nonlinear effects of exposure level on gall resistance, as well as interactions between pheromone exposure and plant genotype (Yip et al., 2021). Finally, we reported intriguing effects of exposure to the fly pheromone on goldenrod traits other than defense priming. In particular, we found that exposure accelerates plant growth prior to galling, which we speculated might compensate for subsequent tissue loss (Yip et al., 2017). Given that specialist herbivores like E. solidaginis frequently evolve countermeasures to host-plant defenses (Karban & Agrawal, 2002), such compensatory growth might represent an adaptive strategy favoring plant tolerance (i.e., maintaining flower or rhizome production following gall induction) rather than resistance (i.e., killing the larva and preventing gall induction).

Building on our previous findings, the current study explores both primed resistance and broader implications, specifically for growth and herbivore tolerance, of pheromone exposure for interactions between goldenrod plants and *E. solidaginis*. To accomplish this, we manipulated pheromone exposure levels under controlled greenhouse conditions and measured plant growth in terms of height (growth per day prior to gall formation and final height at the end of the growing season), root and rhizome mass, rates of gall formation (proportion of stems forming galls), and flower production (mass of flower heads) in galled and ungalled plants. Our primary hypothesis was that pheromone exposure, in addition to affecting plant-defense phenotypes, triggers adaptive changes in resource allocation (e.g., aboveground growth) that enhance tolerance of herbivory. To explore the complexity of plant responses to volatile cues and their ecological functions, we further tested whether variation in cue intensity (i.e., the level of pheromone exposure-which plausibly correlates with increased galling risk) would have linear effects on plant responses, as observed for priming of JA induction (Helms et al., 2017), or nonlinear effects, as observed for galling rates in a previous study (Yip et al., 2021). We also varied plant genotypes and fly genotypes (at the level of fly populations) to test whether plant genotypes might vary in their defense or growth responses to the priming cue and whether plants or flies might be locally adapted for defense or attack, respectively. We hypothesized not only that local flies would be better able to gall host plants than flies from more distant populations, but also that primed defenses may be more effective at reducing galling by local versus nonlocal flies.

METHODS

Experimental design

We selected two plant genotypes (S110 and Bell0) that, based on previous research, appear to have different primed responses (Yip et al., 2021). These genotypes were collected from the same field near Bellefonte, PA, USA (40.878278, -77.778888; see Appendix S1: Section S1 for additional details on collection and propagation). Because plant growth affects plant fitness, likelihood of gall formation, and attractiveness to ovipositing females, we measured initial plant height to record and control for variation in growth among our replicates. After recording initial plant height, we exposed plants to varying concentrations of the priming cue before allowing E. solidaginis females to oviposit. We varied priming cue intensity using crude extracts of male volatile emissions (see Helms et al., 2013 for headspace collection methods) and exposed plants to the average release rate of male flies ("full concentration" treatment; 75 μ g/24 h; n = 36), one-tenth the average release rate ("tenth concentration" treatment; 7.5 μ g/24 h; n = 36), or no emission components ("control" treatment; n = 72). We diluted pheromone components in 1.5 mL dichloromethane (CH_2Cl_2) , which we delivered to plants in gas chromatography vials

(Agilent Technologies) with 0.1 mm diameter cotton wicks passing through rubber septa. We placed these vials on bamboo skewers at the height of the apical bud and allowed the pheromone to evaporate off the wick for three days, the duration of exposure used previously (Helms et al., 2013; Yip et al., 2017, 2021).

We also included a separate treatment exposing plants to male flies ("fly" treatment; n = 36) rather than crude extract to test whether the presence of the fly itself influenced galling and plant fitness. Plants exposed to the full concentration of the crude pheromone extract were similar to plants exposed to male flies in terms of the proportion of stems galled, growth per day prior to gall formation, final height, or flower mass (see Appendix S1: Figure S1), suggesting that the presence of the male fly had no additional influence on plants over the volatile cue. We therefore combined full concentration and fly treatments for our analyses.

After three days of exposure to the priming cue, we removed flies and vials and individually placed at least three mated females on every plant over the course of three days. Each plant was assigned to one of three fly populations that differed in distance from the host-plant collection site: one population where the host-plant genotypes were collected ("Bellefonte"), one population 7.4 km from Bellefonte (40.848820, -77.859011; "State College"), and two combined populations (because neither site alone had sufficient galls) 80 and 88 km from Bellefonte (40.906302, -76.887638 and 41.02186, -76.74786, respectively; "Lewisburg"). To measure female oviposition preference, we recorded latency to ovipuncture the apical bud, duration of ovipuncture, and number of ovipunctures by each female over 10-min trials (see Appendix S1: Section S1 for additional details). Ovipunctures are wounds created by ovipositors inserted into bud tissues, and although not every ovipuncture results in oviposition (egg deposition), most plants with ovipunctures have at least one egg (Yip et al., 2021). Because previous oviposition can influence the choice of subsequent females in other tephritid fly species (Prokopy et al., 1978), we present only the behavior of the first female placed on each plant. For analyses on females across all three days of oviposition, see Appendix S1: Section S2.

The full factorial design comprised 24 treatment combinations (2 plant genotypes \times 3 fly populations \times 4 priming cue intensities). Each had six replicates, except control treatments, which had 12 replicates to increase the power to detect differences between primed and unprimed plants, for a total of 180 plants. As it was not feasible to run the experiment on all 180 plants simultaneously, we tested 30 plants at once, repeated over six rounds of the experiment, each round separated by 1–3 weeks (starting 24 April 2020 and 3 of 8

ending 21 July 2020). All treatment combinations were divided equally among rounds, with plants assigned randomly to priming and fly population treatments within weeks.

Fly and plant performance

We measured plant height about one week after oviposition when *E. solidaginis* eggs hatch and monitored gall formation daily starting at two weeks (Uhler, 1951). We used this height measurement and the initial height of the plant (measured before pheromone exposure) to calculate growth/day prior to the start of gall formation. We only measured gall formation as a measure of fly fitness, as previous results found that priming had no further effect on fly fitness after gall induction (Yip et al., 2021). At the end of the season, we recorded the final height of the plants and clipped flower heads (total capitulescence and supporting stems). To obtain flower, rhizome, and root mass, we rinsed soil from roots and rhizomes and dried all plant parts prior to weighing.

Statistical analyses

To examine the effects of our three manipulated variables (priming cue intensity, plant genotype, and fly population) on fly fitness (i.e., proportion of stems galled) and plant fitness (growth per day, final height, flower mass, and rhizome mass), we used generalized linear models (GLMs) with our three manipulations as explanatory variables, and we included any significant interactions to test whether different plant genotypes responded to priming cues differently or were locally adapted to fly populations. We modeled gall formation (yes/no) with a binomial distribution and logit link function. We tested for significance of parameters by comparing the full model to a model without each parameter and used likelihood ratio χ^2 tests. For continuous response variables, we used Gaussian distributions, and, to satisfy assumptions of normal residuals and homoscedasticity, flower mass was log transformed, while root mass, ovipuncture duration, and number of ovipunctures were square root transformed. We tested for significance in these models using ANOVA with type III sum of squares due to the unbalanced design. Initial height did not differ among any treatments (see Appendix S1: Section S1), but initial plant height and week of the experiment were included as covariates in our models to control for their effects (see Appendix S1: Tables S1–S9).

To examine female oviposition preference, we used mixed linear models with priming cue intensity, plant

genotype, and fly population (and any significant interactions) as fixed effects. To account for circadian variation in oviposition behavior, we also added time of day of the trial as a fixed effect if it significantly affected female behavior (see Appendix S1: Section S2). Although each plant was exposed to at least three different mated females, the number of mated females was limited, so individual females were placed on multiple plants. To account for this nonindependence among oviposition trials, we included ovipositing female identity as a random effect (Hedeker et al., 1994).

RESULTS

Plant growth and tolerance to galling

While different levels of priming cue intensity had variable effects on growth per day prior to gall formation (ANOVA: $F_{2,171} = 4.0$, p = 0.02, Figure 1A), at the end of the season only unexposed (control) plants suffered any cost of galling in terms of final height (Linear model: priming × gall $F_{2,154} = 7.3$, p = 0.0009; Figure 1B) or flower mass (Linear model: priming × gall $F_{2,154} = 6.3$, p = 0.002; Figure 1C). Overall (including galled and ungalled), plants exposed to the full concentration of

the pheromone produced greater flower mass than controls (Linear model: $F_{2,156} = 4.4$, p = 0.014).

Plant genotype also interacted with galling to influence flower mass, with Bell0 plants more tolerant of galling than S110 (Linear model: plant genotype × gall $F_{1,153} = 5.9$, p = 0.02) However, there was no three-way interaction among priming, galling, and plant genotype (Linear model: priming × plant genotype × gall $F_{2,149} = 0.71$, p = 0.49), suggesting that priming increased tolerance in both plant genotypes equally. The two plant genotypes differed in growth per day prior to gall formation, final height, and flower mass, but did not interact with priming cue intensity or fly population to influence plant growth or reproduction. Fly population had no effect on plant growth or flowering, and neither priming cue intensity nor fly population had any effect on belowground biomass (see Appendix S1: Section S2).

Gall formation

Sixty-seven plants (38%) formed galls, and, of these, 52 (78%) formed only one gall (see Appendix S1: Table S10 for data on plants with multiple galls). Priming cue intensity, fly population, and plant genotype all influenced the proportion of stems galled (Binomial GLM: priming



FIGURE 1 The effect of priming cue intensity on growth per day prior to gall formation (A) and the interaction between priming cue intensity and galling on final height (B) and flower mass (C). Plant genotype type did not interact with priming cue intensity, so differences by genotype are omitted for clarity. Note that in (B) and (C) the effects of galling and cue strength are taken from the residuals of a model examining the effect of fly population, plant genotype, experimental week, and initial height (B only) or final height (C only) on either height or flower mass to control for these factors and more accurately reflect effect sizes (see Appendix S1: Section S1). *Indicate that galled and not galled plants differed within a priming cue treatment or that all plants in the full treatment had greater flower mass than control plants in brackets in (C). Bars (A) that do not share a letter were significantly different based on a Tukey-Kramer comparison ($\alpha = 0.05$). Error bars are one SE.



FIGURE 2 The proportion of *Solidago altissima* plants forming galls by (A) plant genotype, (B) ovipositing fly population, and (C) cue exposure. There were no interactions between the three manipulated variables, so they are each presented in separate panels. Treatments that do not share a letter were significantly different based on a Tukey–Kramer comparison ($\alpha = 0.05$).

 $\chi^2 = 7.5$, df = 2, p = 0.02; clone $\chi^2 = 4.7$, df = 1, p = 0.03; fly population $\chi^2 = 14.7$, df = 2, p = 0.0006; Figure 2). However, there were no significant interactions between these three factors (Binomial GLM: anv of priming × plant genotype $\chi^2 = 0.94$, df = 2, p = 0.63; priming × fly population $\chi^2 = 4.9$, df = 4, p = 0.30; plant genotype × fly population $\chi^2 = 3.6$, df = 2, p = 0.16), suggesting that the strength of defense priming in this experiment did not vary with plant genotype or the genotype of the attacking fly. Plants with full exposure to the fly emission had over twice the rate of gall formation (34/71; 48%) of plants exposed to a 10% dose (8/35;23%), with control plants intermediate (25/70; 36%; Figure 2C).

Female oviposition preference

Two interactions (between fly population and plant genotype and between fly population and priming cue intensity) influenced latency to ovipuncture (Linear mixed model: fly population × plant genotype $\chi^2 = 15.4$, df = 2, p = 0.0004; fly population × priming $\chi^2 = 13.1$, df = 6, p = 0.04; Figure 3). Flies from State College more readily ovipunctured Bell0 clones, while Lewisburg flies were more hesitant to ovipuncture Bell0 clones, and Bellefonte flies showed no preference for plant genotype (Figure 3A). For priming cue intensity, flies from Lewisburg ovipunctured control plants more quickly than other treatments, while flies from Bellefonte or State College showed little preference for different priming cue intensities (Figure 3B). See Appendix S1: Figure S3 for analyses on number of ovipunctures and ovipuncture duration.

DISCUSSION

Our results support the hypothesis that environmental cues associated with increased risk of herbivore attack can alter resource allocation and thereby enhance tolerance of herbivory. Notably, primed resistance to galling showed little benefit to reproductive output (flower mass) because primed tolerance obviated any cost of galling (Figure 1C). Thus, while defense priming to enhance resistance to herbivory has been the near-exclusive focus of previous work in this area, the current findings suggest it is only one—and not always the most important—aspect of plant responses to environmental cues indicating increased risk of herbivore attack.

A likely reason that primed tolerance, in particular, has received limited attention arises from the practical difficulty of disentangling tolerance from resistance, as resistance necessarily influences the amount of damage that plants suffer. However, previous work in our study system suggested that primed resistance influences rates of successful attack (i.e., gall induction) by E. solidaginis, but has no effect on gall size or fly fitness once galling occurs (see Yip et al., 2021; Appendix S1: Section S2). This suggests that galled S. altissima plants lose similar amounts of resources to galling regardless of prior pheromone exposure or defense-priming state, and thus that the observed effects of pheromone exposure on flower production by galled plants (Figure 1C) are explained primarily by tolerance rather than resistance. Moreover, plants exposed to the full intensity of the priming cue had both the most galls (Figure 2C) and the highest flower mass (Figure 1C), which can only be explained by increased tolerance.

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FIGURE 3 Latency (in seconds) to ovipuncture *Solidago altissima* buds, showing interactions by female fly population and plant genotype (A) or priming cue strength (B). *Indicates a significant difference between Bell0 and S110 genotypes. Bars of the same shade that do not share a letter are significantly different based on a Tukey–Kramer comparison ($\alpha = 0.05$). S110 plants did not vary by fly population (A), and Bellefonte and State College females did not vary by priming cue strength (B); thus, letters for these bars are omitted. Error bars are one SE.

Unlike tolerance, which did not differ between plants exposed to high or low priming cue concentrations, plants exposed to 100% of the fly emission had over twice the rate of gall formation (48%) of plants exposed to a 10% concentration (23%), while neither treatment group differed from controls (Figure 2C). Thus, it is possible that galling rate increased with cue intensity, indicating primed vulnerability rather than resistance, or that resistance is nonlinear with respect to cue intensity. The latter interpretation fits with our previous observation of nonlinear effects for one goldenrod genotype, even as pheromone exposure increased overall resistance (Yip et al., 2021). In this previous study, cue intensity was inferred from fly age, as male pheromone emission declines in older flies (Yip et al., 2021), while the current study confirms that resistance varies with the degree of exposure to the pheromone (Figure 2C).

While cue intensity may have important effects on herbivore resistance, few studies have manipulated the intensity of cues that might predict future herbivory (Baldwin & Schultz, 1983; Choh & Takabayashi, 2006; Heil & Kost, 2006; Heil & Silva Bueno, 2007; Li et al., 2012; Marmolejo et al., 2021; Peng et al., 2011; van Doan et al., 2021), which limits our understanding of the relationship between cue intensity and plant responses. Cue intensity has most often been manipulated indirectly by varying distances between the source of the cue and receiver plants, resulting in a general decline in defense levels with distance from the cue source. Loss of plant responses with distance is often attributed to thresholds of detection (Frost et al., 2008a, 2008b), as the strength of airborne cues can attenuate rapidly with distance (Baldwin et al., 2006; Douma et al., 2019). If plant responses to olfactory cues are limited either by physical properties of the cue or by physiological mechanisms in the plant, then the dosage response should be a monotonic decline. However, the few studies that have manipulated cue intensity directly indicate that the relationship between cue intensity and defense response may not be linear (see our results; Hirao et al., 2012; Kikuta et al., 2011), which suggests that selection can tune the responses of plants to environmental cue intensity, rather than plant responses simply being limited by thresholds of detection.

Resistance to galling was unexpectedly highest for plants exposed to lower doses of the priming cue (Figure 2C). This conflicts with our hypothesis that stronger cues indicate greater risk of galling, against which plants should allocate greater defenses. One potential explanation for this pattern is that female flies appear to detect the primed state and prefer plants that are more susceptible to galling (Helms et al., 2013; Yip et al., 2021). If females avoid plants exposed to high doses of the pheromone, intermediate exposure might indicate the greatest risk of attack. Such a state would seem unstable, however, and instead frequency-dependent strategies might cycle, as plants adjust their defensive responses to the risk of fly attack and flies adjust their oviposition preferences to plant defenses. Notably, only flies from the more distant Lewisburg site showed preferences by primed states (preferring control plants, despite higher proportion of stems galled on plants with high cue exposure), while more local populations did not distinguish among the priming treatments (Figure 3B), suggesting that flies may locally adapt their oviposition preferences to defense priming.

We had predicted that flies might be locally adapted to their host plants, and indeed we found that flies from the same collection location as plant genotypes performed better than other populations (Figure 2B), although reciprocal experiments using both plants and flies from multiple populations are necessary to confirm local adaptation. Interestingly, flies originating only 7.4 km from host-plant populations performed no better than flies from over 80 km distant (Figure 2B), suggesting a "small tile mosaic" of coevolution, where ecological differences in even nearby habitats result in local adaptation (Craig et al., 2020). We had also predicted that the primed response might be more effective against local flies, but we found no interaction between priming cue intensity and fly population on proportion of stems galled (see Appendix S1: Table S6).

Finally, this study complements other recent work documenting diverse cues that plants use to construct ecologically relevant information about their environments, as well as the complex and sophisticated ways in which they respond to such information, including via changes in growth, phenology, and reproductive traits, in addition to traits relevant for defense (Gianoli & Carrasco-Urra, 2014; Johnson et al., 2016; Lucas-Barbosa et al., 2013; Pashalidou et al., 2020). Previous studies have shown that herbivore feeding itself can induce tolerance, in some cases including cross-tolerance of subsequent feeding by other herbivore species (Kafle et al., 2017). To our knowledge, however, the current findings provide the first report of enhanced plant tolerance elicited by a cue indicating future herbivore attack (Brosset & Blande, 2022). This work thus provides an important link between previous research on priming, which has focused almost exclusively on resistance (Frost et al., 2008a, 2008b; Kim & Felton, 2013), and work on tolerance, which to date has not considered the potential role of cues detected prior to attack (Fornoni, 2011). Further work in this emerging field will deepen our understanding of the functional diversity of plant behavior and the role of information in mediating adaptive phenotypic plasticity.

AUTHOR CONTRIBUTIONS

Eric C. Yip and John F. Tooker conceived and designed the project, and all authors helped secure funding for the project. Eric C. Yip performed the experiment, collected and analyzed the data, and wrote the first draft of the manuscript. All authors contributed substantially to revising the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Yip et al., 2024) are available in Zenodo at https://doi.org/10.5281/zenodo.11552040.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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