

# Shared semiochemicals in a tri-trophic system benefit crop plants

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## Research Article

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# Abstract

Prey commonly use volatile chemicals released from predators to infer the level of danger and can enact phenotypic changes to increase their chance of survival. Because some predators emit volatiles that are also used in plant defense signaling, there is the potential for plants to also respond to predator cues. In the Colorado potato beetle, *Leptinotarsa decemlineata*, predator spined soldier bug, *Podisus maculiventris*, potato, *Solanum tuberosum*, system, the beetle responds to the predator aggregation semiochemical, which is comprised of predator-specific compounds and compounds that are known to be used by plants as green leaf volatile signals to induce their own defenses. Given this shared sensory cue in the system we asked the question; is the effect of the predator semiochemical on prey driven by the full predator semiochemical, or are there bioactive compounds in the blend that are also shared with the plants that are responsible for the prey behavioral changes? By fractionating the semiochemical into three treatments (full blend, shared cues, and predator only) and dispensing it in a replicated potato field with free-ranging herbivores, we found that the cues shared with the plant reduced herbivore feeding by 37 percent and the full blend by 41 percent compared to the control or predator specific fraction. Potato plants also responded to the shared cues by growing larger over the season and initiating flowering earlier, indicating that prey responds to the semiochemical could be direct or mediated by the plant's response to the semiochemical. These findings highlight the potential utility of using shared cues for management purposes. Rather than using a semiochemical treatment that has a single target audience (i.e., the pest), we showed that a cue shared across multiple trophic levels decreased plant damage and increased growth, while eliciting anti-predation behavior in the prey.

## Introduction

The world is rife with sensory information and organisms are challenged with the task of sifting through all of these cues to make rapid judgements. The vast number of cue combinations possible across numerous modalities gives the impression that each signal is highly specific, and in many cases that is true, as in private channel communication (Raguso 2008). Conversely, there are certain cues with widespread distribution in the natural and managed systems that carry useful information for multiple trophic levels, setting up a situation where numerous organisms in a system detect and respond to the same cue, often for different purposes (Lee et al. 2015, Tomberlin et al. 2017).

There is the potential for information overlap in systems when numerous organisms make use of and produce the same cues. Although there are many differences in the perceptive abilities of plants and animals, chemoreception is an essential sensory modality in both. Many insects, including predatory Heteropterans, release a plethora of volatile compounds, many of which are the same compounds found in plant green leaf volatile (GLV) signals. For example, plant-produced GLV compounds like (*E*)-2-hexenal are also released and used by numerous animals (Aldrich 1985, Lockwood and Story 1987, Blatt et al. 1998, Gries et al. 2015) and at the time of writing this, (*E*)-2-hexenal is known to be a part of the communication systems of at least 209 insects, 62 of which are Pentatomid stink bugs (found in Pherobase, Dec. 2020).

In addition to other organisms releasing GLV-shared compounds, many organisms detect and make use of plant GLVs (Visser and Avé 1978, Turlings et al. 1995, Webster and Carde 2017). Since plants are sessile and cannot avoid attackers like motile organisms, one of their first lines of defense upon attack is the release of GLVs from damaged leaf tissue (Visser et al. 1979, Farag and Paré 2002, Szafranek and Szafranek 2008). The initial surge of GLVs after biotic stress consists of a single compound class, hexenals such as (*E*)-2-hexenal (Ameye et al. 2018). When plants receive an airborne GLV signal, secondary chemical defenses can be primed in preparation for an attack by an herbivore. Green leaf volatiles are also an important source of information for herbivores and predators for host identification purposes (Schütz et al. 1997, Kessler and Baldwin 2001).

In this study, we used a system involving a generalist Pentatomid predator (*Podisus maculiventris*, spined soldier bug), potatoes (*Solanum tuberosum*, cv Yukon Gold), and a common herbivorous insect (*Leptinotarsa decemlineata*, Colorado potato beetle). All three trophic levels under study are known to detect (*E*)-2-hexenal (De Jong and Visser 1988, Weißbecker et al. 1997, Dickens 1999, Farag and Paré 2002), and the predator (Aldrich, Kochansky, and Abrams 1984) and plant (Visser and Avé 1978) are both known to release large quantities of (*E*)-2-hexenal. Further, the extremely common plant terpenoid linalool is also released by potato plants and the predator as a semiochemical, albeit at much lower volume than (*E*)-2-hexenal (Aldrich, Kochansky, Lusby, et al. 1984). *L. decemlineata* has receptors that detect linalool (Weißbecker et al. 1997). In this system, it has been shown that the presence of the predator semiochemical cue causes the *L. decemlineata* to consume less leaf tissue and reduce the number of larvae found on treated plants (Hermann and Thaler 2014, Aflitto and Thaler 2020). Subsequent research has shown that plants that are pre-exposed to the predator semiochemical respond by becoming less palatable to *L. decemlineata*, illustrating a change in plant behavior (Aflitto et al., in prep).

Adult male *P. maculiventris*, releases sizeable amounts of an aggregation pheromone from a dorsal abdominal gland (DAG). At least two common GLVs are released from the DAG that plants also release when damaged. Although previous research has shown that the semiochemical elicits a response in the beetle prey, and changes in plant quality that negatively affect the prey, it is not clear if the plant is detecting and identifying the blend as information specifically from the predator. An alternative pathway for the change in plant behavior is that the semiochemical blend, which also shares greater than 60 percent of the same compounds as the potato GLV profile, is causing the plant to induce chemical defenses as if it were receiving a signal from a damaged plant, increasing defensive compounds, and reducing plant quality for the herbivore. For example, studies using *P. maculiventris* semiochemical treatments report using two compounds that overlap with potato plant GLVs that are also released from herbivore damaged potato leaf tissue: (*E*)-2-hexenal and linalool. Further, plant exposure to (*E*)-2-hexenal is known to prime trypsin protease inhibitors in a related plant species, *Nicotiana attenuata* (Kessler et al. 2006), which can be detrimental to feeding herbivores (Ryan 1990, Zavala et al. 2004).

To understand more about the convergent use of the same cues, we investigated the effects of dispensing the synthetic GLV-containing DAG semiochemical of *P. maculiventris* and measured the behavioral response of *L. decemlineata* and *S. tuberosum*. By fractionating the DAG blend into the

components that overlap with the prey's host plant and those exclusive to the predator, we were able to specifically ask two questions: 1) Does *L. decemlineata* reduce colonization, feeding, or oviposition in the full semiochemical blend and shared cues treated plots? 2) Is *S. tuberosum* responding to the GLV-containing shared cues treatment?

## Methods And Materials

On May 24 2019 *Solanum tuberosum* (cv Yukon Gold) seed potatoes were planted at the Cornell University's Homer C. Thompson Vegetable Research Farm in Freeville, NY using 0.3 meter interplant spacing, with 1 meter between rows. In total, two blocks of 13 rows were installed, separated by a 4-meter service road. The field was fertilized at the time of planting using triple 13 NPK at a rate of 733kg/ha.

Prior to the emergence of potatoes, experimental *L. decemlineata* were collected from wild populations in the surrounding farm by use of potted potato trap plants. The overwintering adults were collected from trap plants every 2-3 days and brought back to the lab until the study start. While waiting to be rereleased, *L. decemlineata* beetles were maintained on Yukon Gold potato plants under an 18:6 (L:D) light cycle.

The study was initiated on June 19, 2019. One hundred and eighty plots were installed consisting of a single plant marked by a pin flag. Three different treatments and a control plot were randomly installed throughout the site. The treatments included a full 5 compound blend mimicking *P. maculiventris* pheromone (full blend) (Aldrich, Kochansky, and Abrams 1984), a fractionated shared cues blend which contained 2 compounds shared with the potato plant (shared cues), and a fractionated 3 compound blend which included compounds not shared with potato (predator only) (Table 1). Each dispenser was made from 2mL opaque brown Eppendorf tubes with 3 0.55mm holes in the top, acting as open dispersion dispensers. Each dispenser was filled with 600uL of one of the blends or remained empty in the control plots. The plot pin flag was used to hang the dispenser at an approx. height of 15cm. Fresh dispensers were installed every 2 weeks throughout the study period. Once the treatments were installed, a total of 600 adult beetles were rereleased to initiate colonization of the field site by introducing 50 beetles at evenly spaced intervals down each of the rows.

For each plot, we measured plant size, flowering time, tuber yield (end of season), the number of adults, egg clutches and number of eggs, number of larvae, and the amount of new plant damage by *L. decemlineata*. New plant damage was measured by using a focal leaf on each plot plant. The focal leaf was marked by a small piece of flagging on the 2<sup>nd</sup> or 3<sup>rd</sup> fully expanded leaf from the top. The focal leaf was moved to an undamaged leaf each site visit. This prevented double counting damage, avoided

instances of missing herbivory where the leaf was fully consumed, and controlled for leaf age as the plants grew over the study. Damage was measured with a mm<sup>2</sup> grid printed on clear acetate on all site visits except for the last due to the high amount of damage. Instead, percent damage was estimated by 20% increments. In total, 5 site visits were completed between June 21 and July 19, 2019.

We tested the hypothesis that the treatment affected *L. decemlineata* behavior using mixed models. Hurdle models were used due to the large number of observed zero values in the response variables. A binomial generalized linear mixed model was used to model the probability of the presence or absence of each response variable (plant damage, adult colonization, oviposition, or larval abundance). In each model, treatment and plant size were included as fixed effects and plot and time of measurement were included as random effects. A linear mixed model was used to model the effect of the treatment on the non-zero amount of average plot damage and larval abundance. Plant trait measurements were analyzed using mixed effect models with plot as a random effect. Data points were transformed to meet the linear model assumptions of normality and homogeneous variance when appropriate. Note, the data presented in the figures are not transformed. Linear models were not fit to the oviposition and adult colonization data due to the low number of non-zero values. All analyses were completed using R statistical software (R Core Team 2014). Mixed models were analyzed using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015)

## Results

### Beetles

The shared cues treatment that contained the shared GLV compounds, and the full semiochemical blend treatment, which also contained the GLV compounds elicited the most consistent responses. Adult beetle presence was marginally reduced by the shared cues by 33 percent ( $Z = -1.81$ ,  $p = 0.071$ ) and by 37 percent in the full blend ( $Z = 2.02$ ,  $p = 0.044$ ). The presence of larvae was marginally reduced by the shared cues ( $Z = -1.87$ ,  $p = 0.062$ ). The average number of larvae per plot was reduced by the shared cues and predator only treatments, and marginally by the full blend (shared cues:  $T = -2.31$ ,  $p = 0.021$ , predator only:  $T = -2.20$ ,  $p = 0.028$ , full blend:  $T = -1.81$ ,  $p = 0.071$ ) (Fig. 1). Oviposition was not affected by any of the treatments.

### Plant Damage

There was a 37% reduction in average plant damage in shared cues plots ( $T = -2.48$ ,  $p = 0.014$ ) and a 41% reduction in the full blend ( $T = -2.03$ ,  $p = 0.044$ ) (Fig. 2). On July 17, the last measurement day, the percent damage was assessed for all of the study plants rather than the mm consumed due to the high amount of damage, providing a season-long damage estimate. Both the shared cues ( $T = -2.48$ ,  $p = 0.014$ ) and full blend ( $T = -2.03$ ,  $p = 0.044$ ) exhibited lower damage levels (Fig. 2). Plant damage was not affected by the predator only treatment ( $T = -0.85$ ,  $p = 0.398$ )

## Plant Measurements

By the second site visit (day 7 of the study) there was a clear difference in flowering in shared cues plots ( $Z = 2.35$ ,  $p = 0.019$ ) (Fig. 3). The shared cues plots also had larger plants for all measurement dates except for day 1 ( $d7 - T = 2.23$ ,  $p = 0.027$ ,  $d12 - T = 1.95$ ,  $p = 0.053$ ,  $d19 - T = 2.28$ ,  $p = 0.024$ ) (Fig. 3). At the end of the season, plant yield was not significantly different across the treatments ( $T = 1.33$ ,  $p = 0.184$ ) (Fig. 4).

## Discussion

We found that the shared cues reduced herbivore feeding by 37 percent and the full blend reduced feeding by 41 percent compared to the control blend. Adult beetle presence was also marginally reduced by the shared cues by 33 percent and by 37 percent in the full blend. The predator only compounds did not display biological activity except for the average number of larvae found on a plot. Plants were also found to change their behavior in the shared cues plots by increasing flower initiation by 51 percent and growing slightly larger over the season. Tuber yield trended higher in the shared cues plots, however was not significant. These results along with previous research show that predators, prey, and plants in this tri-trophic system all respond to shared components of the predator pheromone.

Interestingly, the synthetic aggregation semiochemical of *P. maculiventris* caused changes in their prey's host plant. Although the presence of the full pheromone and the shared cues blend appeared to negatively affect the prey's behavior, this result could be due to an interaction between the predator odors and prey or between the host plant and herbivore or both. A previous study supports both being involved, where it was found that plants pre-exposed to the full pheromone and the present exposure of the full pheromone, where the prey is directly interacting with the compounds, both elicited reduced feeding and weight gain in larvae (Aflitto et al. 2021, in prep). Thus, in the present field study, it is probable that the prey were affected directly (via the detection of compounds) and indirectly through changes in the plant. This illustrates the multi-trophic potential of using shared cues to modify the behavior of organisms under management, such as in agricultural systems. Traditionally, semiochemical pest management acts on a single trophic level such as mating disruption, attraction to traps, or repelling insects from an area under protection.

The current semiochemicals on the market that contain shared cues may be inadvertently acting on multiple trophic levels. For example, benzaldehyde is commonly dispensed in orchards to attract plum curculio (*Conotrachelus nenuphar*) to traps (Piñero et al. 2001, Prokopy et al. 2003). Benzaldehyde is also released by plants and is one of the most widely distributed floral VOCs (Farré-Armengol et al. 2020), with a known attractiveness to pollinators (Huber et al. 2005, Theis 2006). Further, new active semiochemical release devices being used such as aerosol 'puffers' are capable of releasing significantly larger volumes of compounds when compared to more traditional passive open dispersion devices. The vastly higher release-rates raises the potential for plant tissue to come into contact with active compounds, and there is growing evidence of the effect on crop plants. Phytotoxic effects have been documented near aerosol

release devices (Giroux and Miller 2001, Benelli et al. 2019), and although the mode of action has been tentatively attributed to nonspecific membrane disruption on the leaf surface, further research is needed to understand if, when shared cues are being dispensed, the plant is perceiving and responding to the treatment. In support of a more specific plant response to shared compounds are reports that semiochemical efficacy is increased when the surrounding plants are in regular contact with the compounds. Stelinski et al. reported that compounds released from aerosol devices can accumulate on nearby foliage and may result in higher concentrations of the semiochemical being present (Stelinski et al. 2007) and the exposure of apple foliage to dispenser compounds has been shown to enhance pest control in some cases (Suckling et al. 1996, 2007). The explicit applied use of shared cues has yet to be widely considered and may hold novel treatments for plant protection in the future. Our study provides a proof of concept, where shared cues that are used by several trophic levels in a system reduces plant damage and increases plant growth. Additionally, the full semiochemical blend is a known aggregation pheromone for the beneficial generalist predator *P. maculiventris* which may recruit wild predators to a field (Fig. 5).

The shared use of volatile chemical cues between plants and insects has long been a point of interest among chemical ecologists (Rodriguez and Levin 1976). Thomas Eisner in 1970, had a brief section in a book chapter dedicated to the remarkable overlap in secondary metabolites between plants and insects (Eisner 1970), where he points out that “Some of the substances in arthropods, such as (*E*)-2-hexenal,... are in fact widely distributed among plants.”. Whether we are artificially introducing sensory cues, such as with semiochemical treatments, or working to better understand ecological interactions, a greater knowledge of shared sensory cues will reveal the impact and interconnectedness of certain cues in systems.

## Declarations

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### Contributions

NCA and JST conceived and designed the experiment. NCA led the experiment and analysis. NCA and JST wrote the manuscript.

### Conflicts of Interest/Competing Interests

None.

Availability of data and material (data transparency)

Data will be available upon acceptance of the manuscript.

Code Availability

Not applicable.

Ethics Approval

Not applicable.

Consent to Participate

Not applicable.

Consent for Publication

Not applicable.

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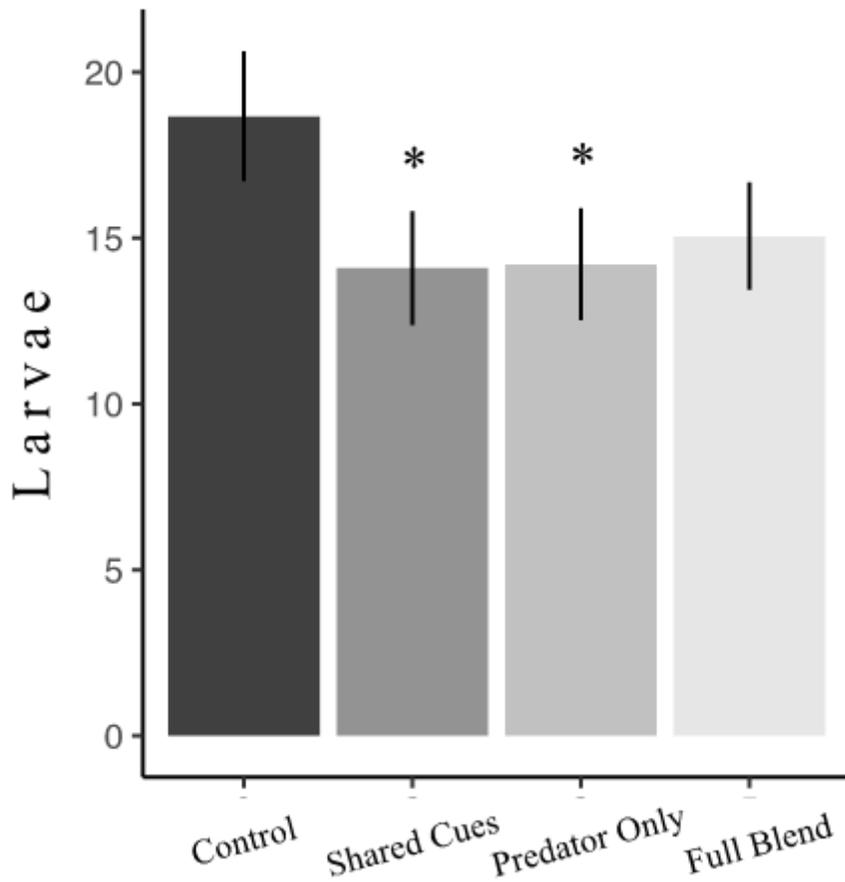
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## Tables

Table 1 Percent and volume of compounds contained in each volatile dispenser treatment blend. Control dispensers were empty and did not contain any compounds.

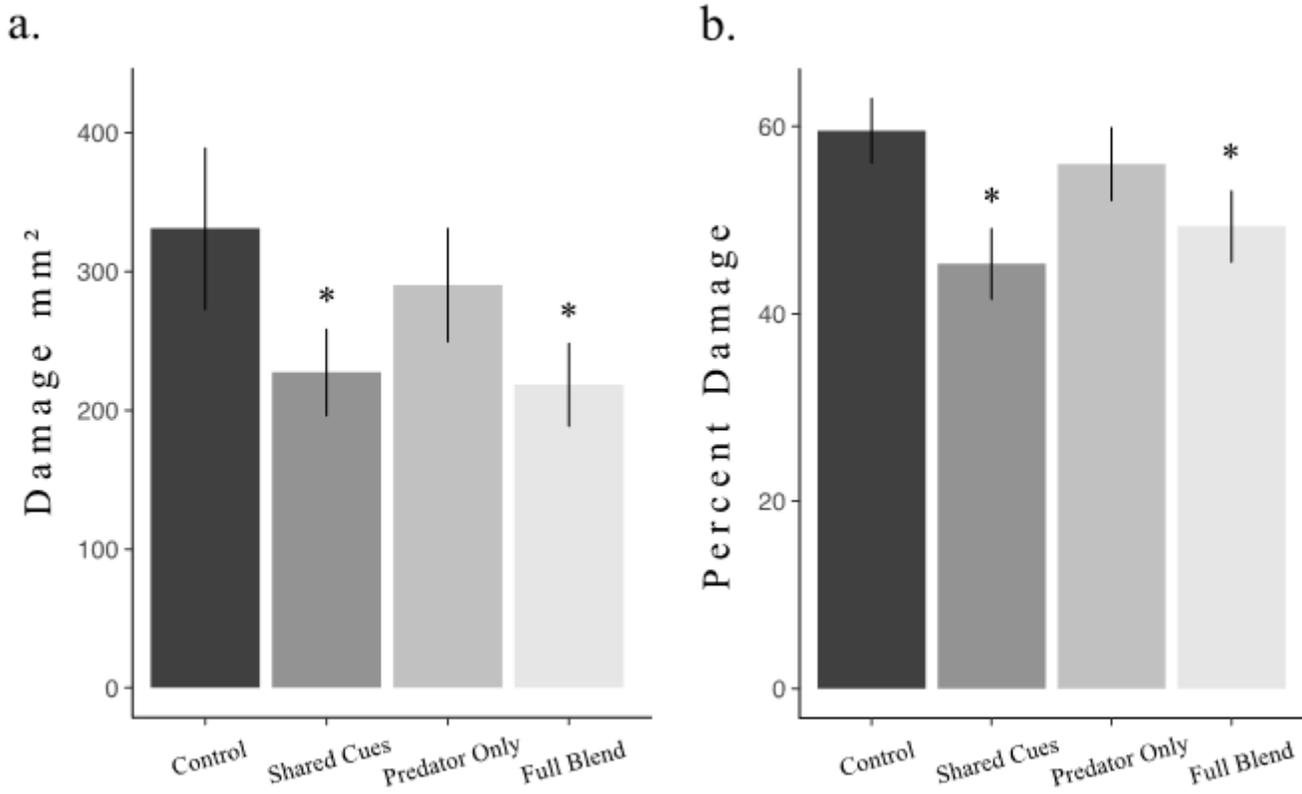
Blend	<i>(E)</i> -2-hexenal	<i>alpha</i> terpineol	<i>benzyl</i> alcohol	<i>linalool</i>	<i>terpinen-4-ol</i>
<i>Shared Cues</i>	99.33% (595.98uL)	-	-	0.67% (4.02uL)	-
<i>Pred. Only</i>	-	90.85% (545.1uL)	8.30% (49.8uL)	-	0.85% (5.1uL)
<i>Full Blend</i>	59.58% (357.48uL)	36.36% (218.16uL)	3.32% (19.92uL)	0.40% (2.4uL)	0.34% (2.04uL)
<i>Control</i>	-	-	-	-	-

## Figures



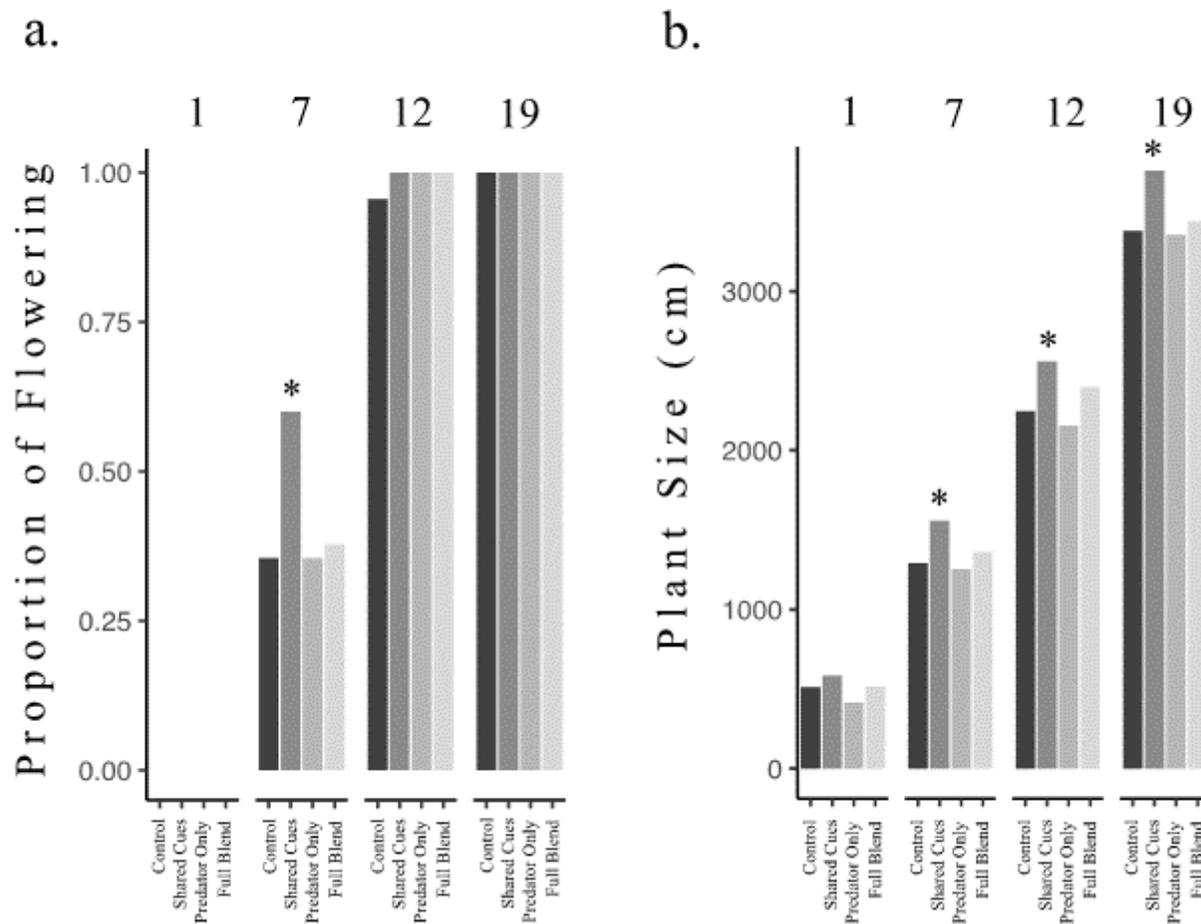
**Figure 1**

Mean number of *L. decemlineata* larvae found on *S. tuberosum* field plots over the study period. Shared Cues represent the compounds that are shared with potato plants, Predator Only represent the compounds only contained in the *P. maculiventris* aggregation pheromone, and the Full Blend represents the full *P. maculiventris* aggregation pheromone. Bars represent the standard error of the mean. Asterisks denote a p-value < 0.05.



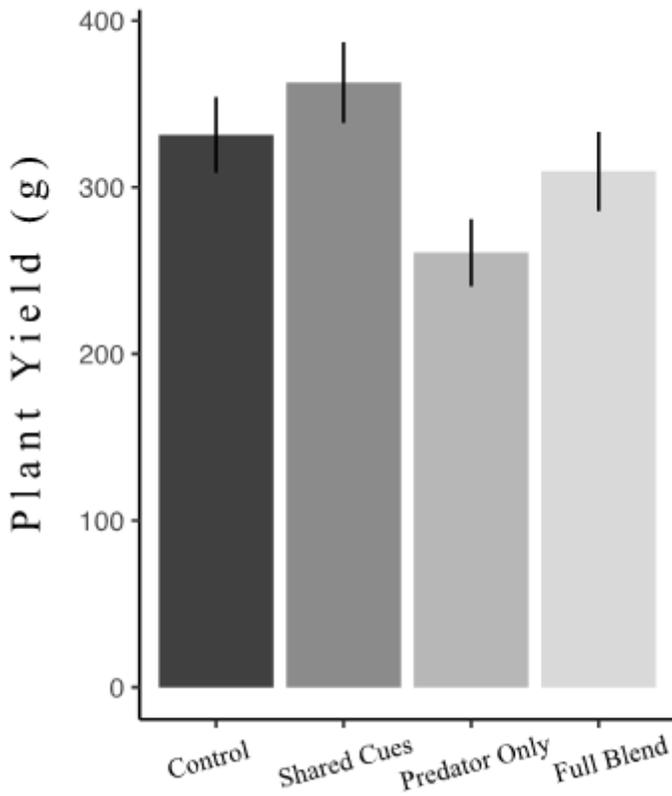
**Figure 2**

(a.) shows the average mm<sup>2</sup> over the measurement period in *S. tuberosum* field plots where the shared cues and full blend had lower damage. (b.) shows the end of season total percent damage estimate (estimates based on 20 percent increments), which followed the same damage trend as the average mm<sup>2</sup>. Shared Cues represent the compounds that are shared with potato plants, Predator Only represent the compounds only contained in the *P. maculiventris* aggregation pheromone, and the Full Blend represents the full *P. maculiventris* aggregation pheromone. Bars represent the standard error of the mean. Asterisks denote a p-value < 0.05.



**Figure 3**

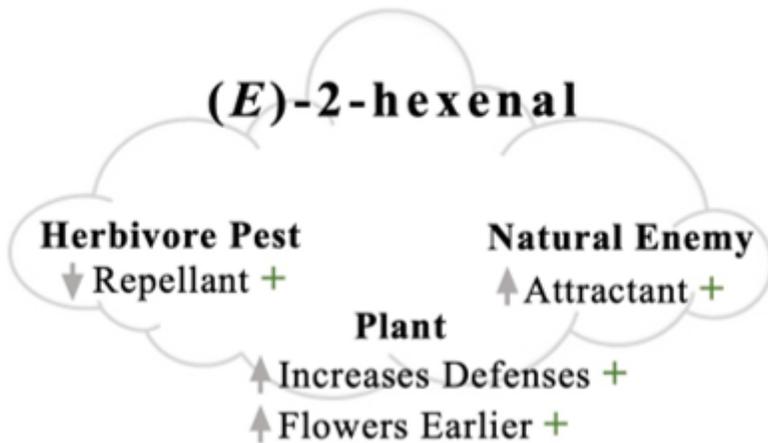
Each block represents the days since the field study start (i.e. 1, 7, 12, 19). (a.) shows a pulse of *S. tuberosum* flowering on day 7 in the shared cues treatment and a slight increase in the full blend. (b.) shows the shared cues consistently had larger plants over the study period. Plant size in the full blend trended non-significantly larger. Note volatile treatments were placed 3 days prior to the first measurement date. Shared Cues represent the compounds that are shared with potato plants, Predator Only represent the compounds only contained in the *P. maculiventris* aggregation pheromone, and the Full Blend represents the full *P. maculiventris* aggregation pheromone. Asterisks denote a p-value < 0.05.



**Figure 4**

Mean tuber yield per plant in grams. Shared Cues represent the compounds that are shared with potato plants, Predator Only represent the compounds only contained in the *P. maculiventris* aggregation pheromone, and the Full Blend represents the full *P. maculiventris* aggregation pheromone. Bars represent the standard error of the mean.

## Application of Shared Cues



**Figure 5**

Conceptualization of applying shared cues to meet insect management objectives. Positive signs indicate the net result to the plant. Since all levels in the tri-tropic system detect and use (E)-2-hexenal, there is the potential to modify the behavior of multiple organisms, resulting in the greatest benefit to the plant. This is contrasted by the current use of single, target organism-based semiochemical treatments. It is important to point out that the specific implications of a certain compound will vary from system to system and may not always yield a net positive benefit.