

## Sources of Insect and Plant Volatiles Attractive to Cottonwood Leaf Beetles Feeding on Hybrid Poplar

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**Abstract** The cottonwood leaf beetle, *Chrysomela scripta*, is the most damaging insect affecting the production of *Populus*, an important source of sustainable forest products and biomass. Currently, there is no simple method for monitoring *C. scripta* populations, and nothing is known about potential chemical attractants for trapping. We conducted laboratory assays on sources of attraction to *C. scripta* adults. In olfactometer trials, beetles were attracted to volatiles released from conspecifics feeding on foliage. There was also significant, but lesser, attraction to odor from unwounded foliage, *C. scripta* alone, and frass. The latter two results indicate the presence of a pheromone. Wounding of foliage by *C. scripta*, but not by artificial means, enhanced its attractiveness compared to unwounded foliage, even when *C. scripta* by-products were removed. In direct comparisons, responses to odor from beetle-wounded foliage were not different from responses to odor from beetles feeding on foliage. We tested the attractiveness of volatiles emitted by adults feeding on foliage in the field using modified boll weevil traps. Results confirm that these volatiles are sufficient to increase trap catches in the field. Color is also important, with yellow baited traps catching more beetles than black baited. We propose that original landing by *C. scripta* is mediated by host odors and visual cues and that subsequent aggregation is enhanced by chemical cues associated with feeding by conspecifics. This may partially explain clustering in the field and likewise be incorporated into sampling schemes needed for integrated pest management.

**Keywords** Semiochemicals · *Chrysomela scripta* · *Populus* · Pheromone · Trapping

### Introduction

Many herbivores are known to exploit plant volatiles for host location (Visser 1986). Additionally, interactions between the herbivore and its host can alter the volatile emissions

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of both plants and insects, with the resulting induced plant volatiles and/or insect pheromones serving as important infochemicals (Turlings et al., 1990; Vet and Dicke, 1992; Landolt and Phillips, 1997; Reinecke et al., 2002). For example, some chrysomelid beetles are attracted to host plants that are infested or wounded by conspecifics (Bolter et al., 1997; Landolt et al., 1999; Kalberer et al., 2001; Tansey et al., 2005), and increase pheromone production when feeding on the host plant (Smyth and Hoffman, 2003). Once identified, semiochemicals can have useful pest management applications, such as improved monitoring and sampling of natural enemies (Burkholder and Ma, 1985; Howse 1998; Tinzaara et al., 2002).

The cottonwood leaf beetle, *Chrysomela scripta* (Fabricius) (Coleoptera: Chrysomelidae), is the most important arthropod pest affecting *Populus* plantations in North America (Coyle et al., 2005). Both larval and adult feeding can cause growth loss and destruction of leaders and shoots (Caldbeck et al., 1978; Bassman et al., 1982; Coyle et al., 2002). Current management strategies rely primarily on synthetic pesticides, largely because no simple and reliable sampling schemes are available. An ability to attract beetles to traps would greatly enhance development of sampling schemes for integrated pest management. To date, responses to volatiles have not been demonstrated for this insect. However, adult *C. scripta* have been observed to form feeding and mating aggregations on trees, suggesting the potential use of semiochemicals for location of conspecifics.

The first objective of this study was to identify the sources of attraction to *C. scripta*, with particular emphasis on whether these sources are likely to be a pheromone, host plant volatiles, induced plant volatiles, or a combination of herbivore and plant volatiles. The second objective was to evaluate the effectiveness of attractive odor sources in field trials.

## Materials and Methods

### Plants and Insects

Two-yr-old potted trees of clone DN34 (*Populus deltoides* × *nigra*) were obtained from KF Evergreens (Osseo, WI, USA). Clone NM6 (*P. nigra* × *maximowiczii*) was obtained as dormant cuttings from the USDA Forest Service in Rhinelander, WI, USA, and International Paper Company (Alexandria, MN, USA). Trees were maintained in a greenhouse (18L:6D photoperiod) with an average temperature of 20°C in the winter and 30°C in the summer, and were cultured for a period of 9 mo before being replaced by fresh material from the same sources. Plants were potted in commercial potting mix (Metro-Mix 300; Sungro, Bellvue, WA, USA), watered daily, and supplied with fertilizer via slow release pellets (Osmocote Plus; Scotts-Sierra Horticultural Products Company, Marysville, OH, USA). An additional aqueous fertilizer solution was delivered weekly at 300 ppm (Sunshine Technigro; Sungro, Bellvue, WA, USA). Foliage used for experiments and feeding was collected from actively growing branch terminals, washed in a mild dish-soap solution, rinsed with cold water, and placed in 22 -ml plastic water vials (#53–77; Syndicate Sales, Inc., Kokomo, IN, USA). Processed foliage was housed upright in an ice chest lined with a large plastic bag and stored in a walk-in cooler at 6°C.

A colony was established in the fall of 2004 from *C. scripta* collected in a hybrid poplar plantation near Carlos, MN, USA (45°N 59' 30"W, 95°W 06' 00"W). Beetles were housed in plastic boxes lined with a paper towel, and fed foliage from both DN34 and NM6 trees.

Foliage was supported above the box floor by metal screening. Beetle diet was occasionally supplemented with washed, field-collected foliage during the summer. Rearing boxes were housed in a growth chamber at 23°C and an 18L:6D photoperiod.

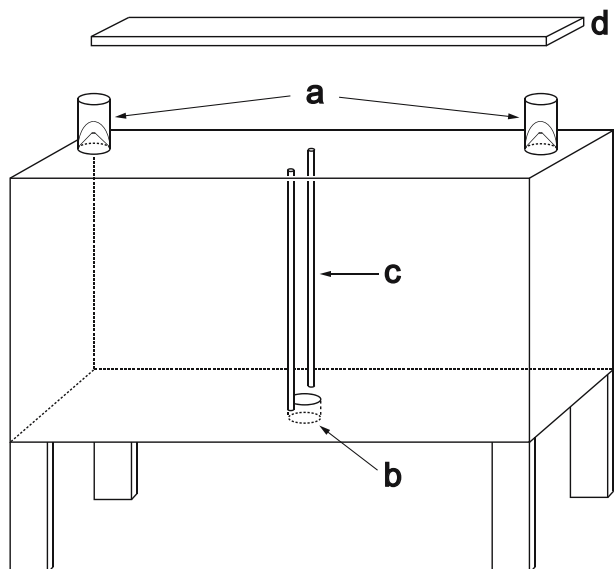
### Bioassays

Behavioral choice tests were conducted in an olfactometer (122×62×62 cm) housed in a climate controlled room at approximately 23°C with no outside light (Fig. 1). The frame was constructed with wood, the floor was made of fiberboard, and the walls and ceiling consisted of fiberglass window screening. A release port consisting of a hole (7.6 cm diam) fitted with a wide-mouth jar ring was located in the center of the floor, allowing attachment of a 0.24 -l glass jar (Ball Corporation, Bloomfield, CO, USA). Two lucite plates (each 12.7 cm<sup>2</sup>) were mounted at either end of the ceiling, each having a 7.6 -cm diam. hole fitted with a wide-mouth jar ring. These two plates served as external attachment points for the 0.95 -l glass odor source jars (Ball Corporation), which were inverted above the ceiling.

The plates were roughened with a 40 -grit electric sander to facilitate beetle traction. Each odor source jar was fitted with a cone of aluminum window screening with an entrance hole (1 cm diam.) at the apex that allowed movement into the jar. A second aluminum screen prevented access to the odor source, and the space between the two screens functioned as a trap. Two PVC tubes (1.3 cm inner diam) eter) mounted on lucite bases (15 cm<sup>2</sup>) on each side of the release chamber facilitated climbing from floor to ceiling. Lighting consisted of two 34-W fluorescent tubes suspended 40 cm above the olfactometer. The ceiling of the olfactometer was hinged to provide access for cleaning.

For each replicate, twenty 1- to -4-wk-old beetles of mixed sex were placed in the release jar. Release and odor source jars containing living specimens contained a folded

**Fig. 1** Olfactometer arena used for behavioral choice tests. The floor is solid; all other sides are screened. Insects are released from a central chamber in the floor and allowed to respond to odor sources in jars attached to the ceiling. Each odor source jar is fitted with a conical screen with a 1-cm hole serving as an insect entry. A second screen prevents access to the odor source and functions as a trap. Two vertically spanning posts focus insect activity in the center of the arena between the odor sources. (a) Odor source jars with trap screens, (b) release chamber, (c) beetle ladders, (d) light source



tissue (Kimwipe EX-L; Kimberly-Clark Corp., Roswell, GA, USA) to absorb extra moisture. Clone DN34 was used for all odor sources involving a plant, with sprigs trimmed as needed to standardize them to the meristematic tip through the first eight leaves, or through leaf plastochron index (LPI) 7 (Larson and Isebrands, 1971). Water-filled plastic vials preserved plants during experiments.

The location of odor sources was determined randomly. After 24 hr, non responding beetles were removed, and the response of trapped beetles was recorded. The arena was wiped down with ethanol and then hexane between trials. Odor source jars, release chamber jars, and screen traps were cleaned with a noninterfering cleansing solution (Powdered Precision Cleaner; Alconox, Inc., New York, NY, USA), air-dried, rinsed with ethanol, and then rinsed with hexane between trials. Each test consisted of 10 replicates unless otherwise noted. Insects and plants were used only once.

### Test of Odor Source Components

In the first series of experiments, the full complement of odors emanating from plants, beetles, and the plant–beetle interaction was tested against a blank. After this, several putatively attractive components were tested vs. a blank to identify active components. The odor sources were prepared as follows.

- 1) Plant–*C. scripta* complex (beetles feeding on foliage): one sprig of foliage with 20 beetles of mixed sex. The blank control consisted of a water vial and a tissue.
- 2) Unwounded foliage: one sprig of foliage. The blank control consisted of a water vial and a tissue.  $N=16$ .
- 3) Beetles: 20 beetles of mixed sex. The blank control consisted of a tissue. All responding beetles were dissected to determine sex.
- 4) Frass: frass from 20 beetles that had been feeding on one sprig of foliage for 24 hr. Frass was collected from the wax paper lining of a rearing chamber using a moistened tissue. The blank control consisted of a moistened tissue that had been rubbed across clean wax paper.
- 5) Visual stimulus (green or yellow paper): two colors of laminated paper rectangles ( $8 \times 14$  cm) were tested. The blank control consisted of laminate with no paper inside.

### Comparison of Attractiveness of Odor Source Components to the Full Complement of Odors

To determine if any single attractive component was as attractive as the full complement of odors from beetles feeding on foliage, we conducted direct comparisons between sources that proved attractive in the first series of assays. Each component was tested against the plant–*C. scripta* complex as described above and was prepared as follows.

- 1) Unwounded foliage: prepared as described above.
- 2) Beetles: prepared as described above with the addition of a water vial control.
- 3) Frass: prepared as described above with the addition of a water vial control and a tissue. A moistened tissue that had been rubbed over clean wax paper was added to the comparison odor source jar (plant–*C. scripta* complex) as a control.
- 4) Beetle-wounded foliage: one sprig of foliage was placed into a small plastic box and exposed to 20 beetles for 24 hr before being placed in the odor source jar.

## Effect of Plant Wounding

To determine whether wounding must be done specifically by feeding, or whether mechanical wounds alter attraction, two comparisons were made to unwounded foliage.

- 1) Beetle-wounded foliage: prepared as described above.  $N=11$ .
- 2) Artificially wounded foliage: immediately preceding the choice test, one sprig of foliage was treated with a 6 -mm diam hole-punch to simulate a level of defoliation comparable to 20 beetles feeding for 24 hr (100 punches).
- 3) Washed-beetle-wounded foliage: foliage was prepared as for “beetle-wounded,” then hand-washed, and rinsed  $\times 3$  in water. The unwounded comparison foliage was also hand-washed and rinsed  $\times 3$  in water.

## Comparison of Attractiveness of Volatiles Released from Starved vs. Fed Beetles

To discern whether frass plays a role in the attractiveness of volatiles from *C. scripta*, we made a direct comparison between the attractiveness of volatiles released from adults that had been starved for a period of 24 hr and volatiles from adults that had recently been fed.

## Field Trapping

We tested the effects of two odors and two colors on trap catches of adult beetles in the field. This study was located in a heavily infested 28.1 -ha plantation in the location reported above. The planting was 4 yrs old and composed of clone NM6. A 1 -ha plot was established and 120 standard boll weevil traps (Nebeker et al., 2002) were deployed on a  $10 \times 12$  grid with 10 m spacing. Traps were placed between rows on wooden posts at a height of 1 m from the ground.

There were two odor treatments: a blank control and three sprigs of NM6 foliage+20 beetles; and two color treatments: black and yellow. Bait treatments were prepared using washed greenhouse-grown NM6 foliage trimmed to include the meristematic tip through the first five leaves (LPI 4) and placed in plastic water vials as described above. The sprigs were then placed in a 12 -oz paper coffee cup with 20 beetles collected from a hybrid poplar nursery near Arlington, WI, USA ( $43^{\circ} 17' 30''\text{N}$ ,  $89^{\circ} 23' 00''\text{W}$ ) and then covered with mesh netting held in place with a rubber band. Controls consisted of a paper coffee cup containing three water vials covered with mesh netting. Bait cups were clipped to the inside of boll weevil traps using 0.95-cm metal binder clips.

Color treatments were prepared by spray painting traps with yellow or black plastic-bonding spray paint (Krylon Fusion Sunbeam and Black Gloss; Sherwin-Williams Co., Cleveland, OH, USA). The treatments were deployed in a completely randomized,  $2 \times 2$  two factorial design. Due to loss of data from the first four rows of traps, the final replication is as follows: black control,  $N=16$ ; black baited,  $N=26$ ; yellow control,  $N=18$ ; yellow baited,  $N=20$ . Trap catches were tallied and removed daily between 6 and 7 P.M. for the duration of the 4-d trial to prevent the build-up of potentially attractive adult *C. scripta* within traps.

## Statistics

Statistical analyses were performed using SAS for Unix (v.8, SAS Institute Inc., Cary, NC, USA). Beetle responses to the two different odor sources were subjected to an ANOVA

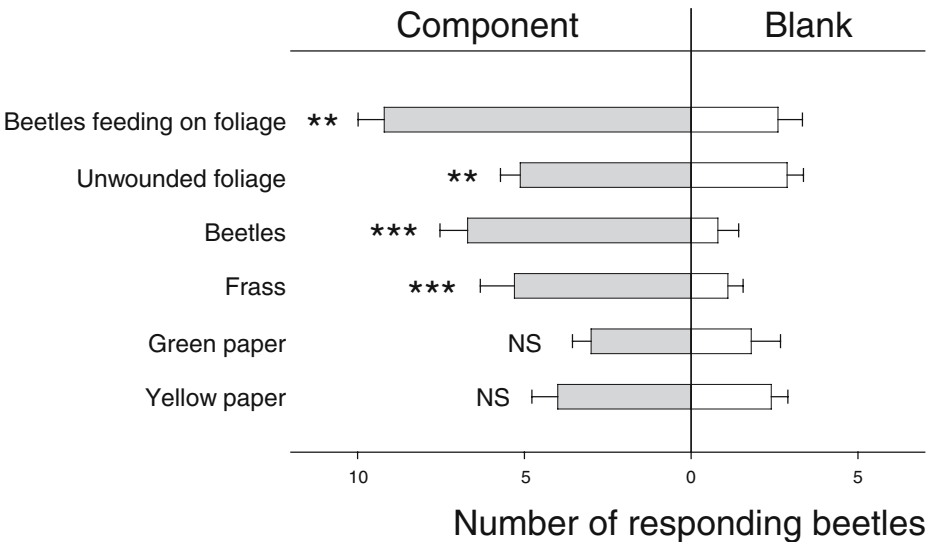
with beetle response in a given trial as the experimental unit. ANOVA was chosen for the analysis instead of chi square in order to allow for a more conservative approach that included blocking factors of odor source location, arena used, and trial period. The sex ratio of beetles responding to beetle volatiles was subjected to chi square analysis to determine if it deviated from the expected 1:1 ratio.

Statistical analysis of trap data was performed using SAS software as described above. Trap catch totals were  $\log(y+1)$  transformed and subjected to ANOVA for color, bait, and interaction effects. The least significant difference (LSD) method was used to determine mean separations between the four treatment combinations, with  $\alpha=0.01$  to insure a conservative interpretation.

## Results

### Laboratory Assays

None of the blocking factors of odor source location, arena used, or trial period were significant except in one instance noted below. Odors released from the plant–*C. scripta* complex ( $F_{1,8}=34.85$ ,  $P<0.001$ ) as well as those from unwounded foliage ( $F_{1,21}=10.59$ ,  $P=0.004$ ), beetles ( $F_{1,12}=47.15$ ,  $P<0.001$ ), and frass ( $F_{1,12}=9.91$ ,  $P=0.008$ ), were more attractive than a blank control (Fig. 2). Responses to green ( $F_{1,12}=2.69$ ,  $P=0.127$ ) or yellow ( $F_{1,12}=1.44$ ,  $P=0.253$ ) visual stimuli did not differ from those to a blank. The sex ratio of responders to volatiles from beetles alone was 32:35 (M/F) and was not statistically different from 1:1 ( $\chi^2_1, P=0.8$ ).



**Fig. 2** Number of adult *C. scripta* responding to potentially attractive odor sources and visual cues vs. blank controls in two-way behavioral choice tests. Beetles feeding on foliage = plant–*C. scripta* complex; Unwounded foliage = plant alone; Beetles = *C. scripta* alone; Frass = frass alone; Green paper = green visual cue; Yellow paper = yellow visual cue; NS = not significant. An asterisk indicates significant attraction to a given odor source (\* $P<0.05$ , \*\* $P<0.01$ , \*\*\* $P<0.001$ )

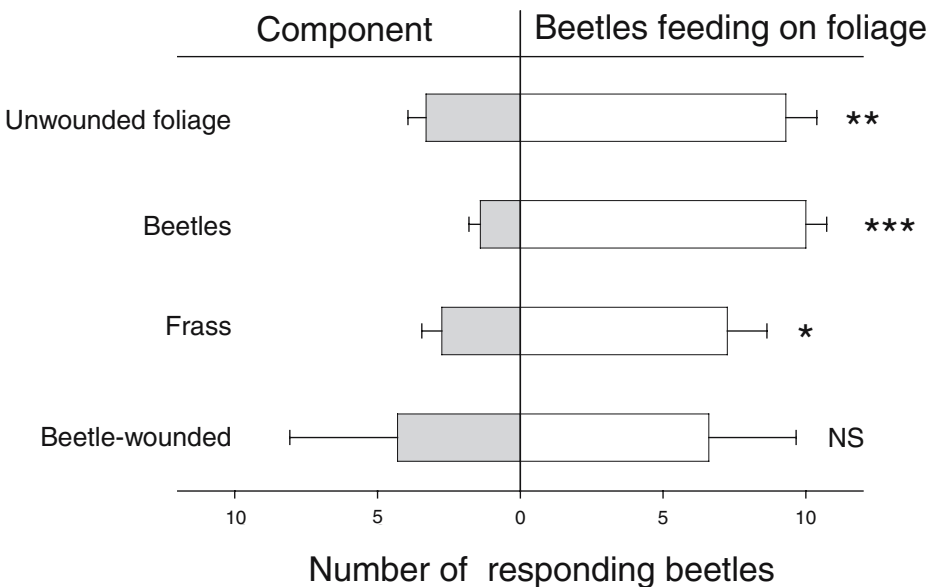
In direct comparisons, only volatiles from beetle-wounded foliage were as attractive as the full complement of odor from the plant–*C. scripta* complex ( $F_{1,12}=1.62, P=0.228$ ) (Fig. 3). Although attractive when compared to a blank, the odor sources of unwounded foliage ( $F_{1,11}=17.79, P=0.001$ ), beetles ( $F_{1,12}=122.93, P<0.001$ ), and frass ( $F_{1,12}=7.11, P=0.020$ ) were not as attractive as the plant–*C. scripta* complex in a direct comparison.

Beetle-wounded foliage was more attractive than unwounded foliage ( $F_{1,13}=13.97, P=0.002$ ) (Fig. 4). In contrast, attraction to artificially wounded foliage was not different from attraction to unwounded foliage ( $F_{1,12}=0.01, P=0.922$ ). Even with frass removed by washing, beetle-wounded foliage remained more attractive than unwounded foliage ( $F_{1,18}=8.17, P=0.010$ ). In this comparison only, the blocking factor of odor source location was also significant ( $F_{1,18}=6.44, P=0.021$ ).

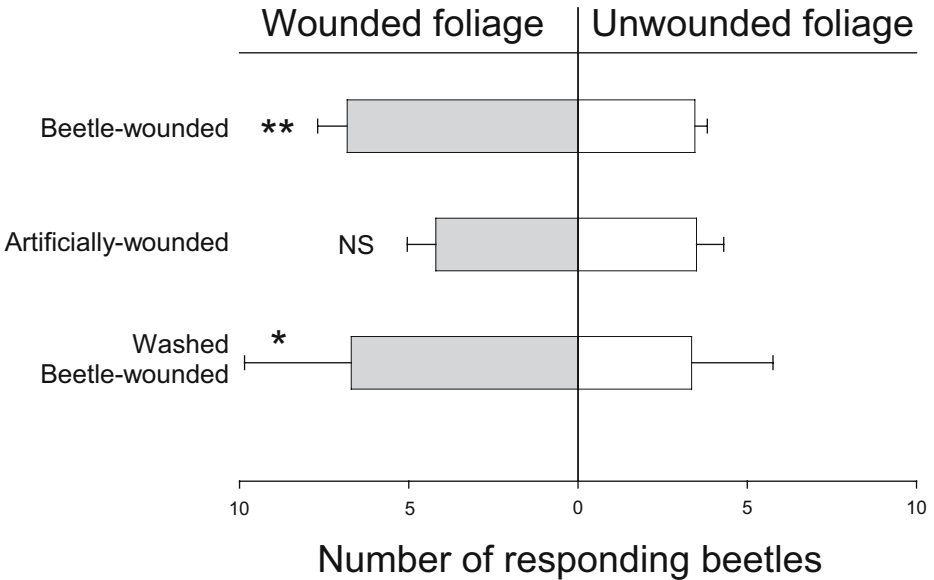
Attraction to adult beetles appears to exist independently of frass, with no difference in response to starved vs. fed beetles ( $F_{1,12}=0.02, P<0.891$ ).

### Field Trapping

Both color ( $F_{1,76}=9.00, P=0.004$ ) and bait ( $F_{1,76}=23.47, P<0.001$ ) affected trap catch (Fig. 5). There was no significant interaction between color and bait ( $F_{1,76}=0.63, P=0.429$ ). Baited yellow traps caught more than any other trap. Unbaited yellow trap catches did not differ from either of the black treatments, but among black traps, baited traps caught more beetles than unbaited ones (LSD,  $\alpha=0.01$ ).



**Fig. 3** Number of adult *C. scripta* responding to attractive odor source components when compared to the full complement of odors. Unwounded foliage = plant alone; Beetles = *C. scripta* alone; Frass = frass alone; Beetle-wounded = wounded plant with *C. scripta* by-products; Beetles feeding on foliage = plant–*C. scripta* complex; NS = not significant. An asterisk indicates significant attraction to a given odor source (\* $P<0.05$ , \*\* $P<0.01$ , \*\*\* $P<0.001$ )



**Fig. 4** Effect of wounding by beetle feeding and artificial means on attraction of *C. scripta* to foliage. Beetle-wounded = wounded plant with *C. scripta* by-products; artificially wounded = hole-punched plant; unwounded foliage = plant alone. Washed beetle-wounded = wounded plant with visible *C. scripta* by-products removed; NS = not significant. An asterisk indicates significant attraction to a given odor source (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ )

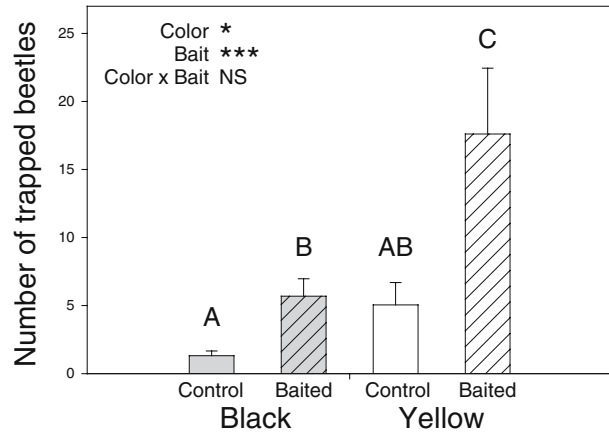
## Discussion

These results suggest that aggregation by *C. scripta* is mediated by the presence of beetles and their feeding on host plants. Similar results have been found for other chrysomelid beetles, such as the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), and two flea beetles, *Phyllotreta cruciferae* (Goeze) and *Aphthona nigricutis* (Foudras), each of which are attracted to volatiles from feeding conspecifics (Peng and Weiss, 1992; Landolt et al., 1999; Tansey et al., 2005). Moreover, attraction by other beetle species to wound-induced foliage has been demonstrated (Loughrin et al., 1995; Bolter et al., 1997; Kalberer et al., 2001).

The data indicate that both *C. scripta* and their host plants, especially wounded plants, emit attractive signals. The behavioral responses of *C. scripta* are consistent with the presence of a pheromone for two reasons: 1) beetles are attracted either to conspecifics that have recently fed or to conspecifics that had been starved for 24 hr; and 2) frass alone is attractive (Fig. 2). The release of pheromones through frass is common in other Coleoptera (Wood 1982). One or both sexes may produce a pheromone, and examples of each are known in the Coleoptera (Landolt and Phillips, 1997). In this study, the odor source beetles were of both sexes, so it is not yet known if the attractive compound functions primarily as a sex pheromone. However, both sexes respond equally to odors emitted by conspecifics.

Although beetle-produced volatiles are attractive by themselves, the host plant, particularly a wounded host plant, is critical in eliciting the strongest response by *C. scripta*. Because wounding of the plant by *C. scripta* but not by artificial means increases the attractiveness of the foliage, and beetle-wounded foliage remains more attractive than unwounded foliage even after removal of insect by-products (Fig. 4), our results suggest

**Fig. 5** Total number of adult *C. scripta* trapped in response to various odor and visual stimuli. Standard boll weevil traps were deployed for 4 d and assigned one of two color treatments: black or yellow; and one of two odor treatments: control or baited. Sampling was for 4 d. Letters A–C above the bars indicate significant differences in trap catches between treatments, with means sharing the same letter not significantly different (LSD,  $\alpha=0.01$ ). An asterisk indicates a significant treatment effect (\* $P<0.05$ , \*\* $P<0.01$ , \*\*\* $P<0.001$ ). NS = not significant



wound induction plays an important role in attraction. This is consistent with reports on the more widely-studied *L. decemlineata* (Landolt et al., 1999). Attraction to beetle-wounded foliage is not mutually exclusive with the presence of a pheromone, as pheromone production may be stimulated by feeding or require the co-occurrence of host volatiles to elicit a full response (Wood 1982; Landolt and Philips, 1997; Reinecke et al., 2002). Although we have demonstrated that beetle-wounded foliage from which frass has been removed retains its attractiveness when compared to unwounded foliage, we did not directly compare this treatment with beetles feeding on foliage. Thus, it remains to be determined whether the attractiveness of beetles feeding on plants is due solely to the emission of damage-induced volatiles, or also includes compounds of beetle origin.

Field evaluations confirmed attraction to volatiles from beetles feeding on foliage. Although laboratory assays did not provide evidence for attraction to color alone, visual cues influenced beetle responses to attractive volatiles in the field. Color-based differences in trap catches have been previously documented for other chrysomelid adults, such as *L. decemlineata* and two *Diabrotica* species (Zehnder and Speese, 1987; Hesler and Sutter, 1993). The order in which *C. scripta* responds to cues is not known, but based on these results, it seems likely that initial landings are based on visual (Fig. 5, A and AB) and olfactory (Fig. 2, Unwounded foliage) attraction to the host plant, with volatile cues from conspecifics subsequently increasing arrestment by *C. scripta* in a particular location (Figs. 3, 4, and 5).

With more knowledge of the chemical ecology of *C. scripta*, efficient sampling schemes could be developed for improved monitoring. A close correlation between trap catch and population density would aid plantation managers in making threshold-based pesticide applications, which are the cornerstone of integrated pest management. In summary, our results demonstrate orientation by *C. scripta* adults to volatile cues, and indicate that these interactions are of sufficient strength to function in commercial plantations.

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## References

- BASSMAN, J., MYERS, W., DICKMAN, D. and WILSON, L. 1982. Effects of simulated insect damage on early growth of nursery-grown hybrid poplars in northern Wisconsin. *Can. J. For. Res.* 12:1–9.
- BOLTER, C. J., DICKE, M., VAN LOON, J. J. A., VISSER, J. H., and POSTHUMUS, M. A. 1997. Attraction of Colorado potato beetle to herbivore-damaged plants during herbivory and after its termination. *J. Chem. Ecol.* 23:1003–1023.
- BURKHOLDER, W. E. and MA, M. 1985. Pheromones for monitoring and control of stored-product insects. *Annu. Rev. Entomol.* 30:257–272.
- CALDBECK, E. S., MCNABB, H. S. J., and HART, E. R. 1978. Poplar (*Populus*) clonal preferences of the cottonwood leaf beetle (*Chrysomela scripta*). *J. Econ. Entomol.* 71:518–520.
- COYLE, D. R., MCMILLIN, J. D., HALL, R. B., and HART, E. R. 2002. Cottonwood leaf beetle (Coleoptera: Chrysomelidae) defoliation impact on *Populus* growth and above-ground volume in a short-rotation crop plantation. *Agric. For. Entomol.* 4:293–300.
- COYLE, D. R., NEBEKER, T. E., HART, E. R., and MATTSON, W. J. 2005. Biology and management of insect pests in North American intensively managed hardwood forest systems. *Annu. Rev. Entomol.* 50:1–29.
- HESLER, L. S. and SUTTER, G. R. 1993. Effect of trap color, volatile attractants, and type of toxic bait dispenser on captures of adult corn rootworm beetles (Coleoptera: Chrysomelidae). *Environ. Entomol.* 22:743–750.
- HOWSE, P. E. 1998. *Insect Pheromones and Their Use in Pest Management*. Chapman and Hall, New York.
- KALBERER, N. M., TURLINGS, T. C. J., and RAHIER, M. 2001. Attraction of a leaf beetle (*Oreina cacaliae*) to damaged host plants. *J. Chem. Ecol.* 27:647–661.
- LANDOLT, P. J. and PHILLIPS, T. W. 1997. Host plant influences on sex pheromone behavior of phytophagous insects. *Annu. Rev. Entomol.* 42:371–391.
- LANDOLT, P. J., TUMLINSON, J. H., and ALBORN, D. H. 1999. Attraction of Colorado potato beetle (Coleoptera: Chrysomelidae) to damaged and chemically induced potato plants. *Environ. Entomol.* 28:973–978.
- LARSON, P. R. and ISEBRANDS, J. G. 1971. The plastochron index as applied to developmental studies of cottonwood. *Can J. For. Res.* 1:1–11.
- LOUGHRIN, J. H., POTTER, D. A., and HAMILTON-KEMP, T. R. 1995. Volatile compounds induced by herbivory act as aggregation kairomones for the Japanese beetle (*Popillia japonica* Newman). *J. Chem. Ecol.* 21:1457–1467.
- NEBEKER, T. E., WARINER, M. D., and HART, E. R. 2002. Cottonwood fiber farm pest management: Cottonwood leaf beetle, pp. 565–568, in Gen. Tech. Rep. SRS-48. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station, pp. 565–568.
- PENG, C. and WEISS, M. J. 1992. Evidence of an aggregation pheromone in the flea beetle *Phyllotreta cruciferae* (Goeze) (Coleoptera Chrysomelidae). *J. Chem. Ecol.* 18:875–884.
- REINECKE, A., RUTHER, J., and HILKER, M. 2002. The scent of food and defence: Green leaf volatiles and toluquinone as sex attractant mediate mate finding in the European cockchafer *Melolontha melolontha*. *Ecol. Lett.* 5:257–263.
- SMYTH, R. R. and HOFFMAN, M. P. 2003. A male-produced aggregation pheromone facilitating *Acalymma vittatum* (F.) (Coleoptera: Chrysomelidae) early-season host plant colonization. *J. Insect Behav.* 16:347–359.
- TANSEY, J. A., MCCLAY, A. S., COLE, D. E., and KEDDIE, B. A. 2005. Evidence for the influence of conspecific chemical cues on *Aphthona nigricutis* (Coleoptera: Chrysomelidae) behaviour and distribution. *BioControl* 50:343–358.
- TINZAARA, W., DICKE, M., VAN HUIS, A., and GOLD, C. S. 2002. Use of infochemicals in pest management with special reference to the banana weevil, *Cosmopolites sordidus* (Germar) (Coleoptera: Curculionidae). *Insect Sci. Appl.* 22:241–261.
- TURLINGS, T. C. J., TUMLINSON, J. H., and LEWIS, W. J. 1990. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science* 250:1251–1253.
- VET, L. E. M. and DICKE, M. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annu. Rev. Entomol.* 37:141–172.
- VISSER, J. H. 1986. Host odor perception in phytophagous insects. *Annu. Rev. Entomol.* 31:121–144.
- WOOD, D. L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. *Annu. Rev. Entomol.* 27:411–446.
- ZEHNDER, G. and SPEESE, J. I. 1987. Assessment of color response and flight activity of *Leptinotarsa decemlineata* (Say) (Coleoptera Chrysomelidae) using window flight traps. *Environ. Entomol.* 16: 1199–1202.