Sight unseen: Belowground feeding influences the distribution of an aboveground herbivore

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Abstract. Plants are under constant threat from insect herbivores that can consume all types of plant tissue, both aboveground and belowground. Because plants connect aboveground and belowground environments, they are uniquely positioned to mediate indirect herbivore interactions between the two ecosystems. The effects of this mediation may change over time with cascading consequences both aboveground and belowground. We used a system involving the larval belowground (BG) herbivore *Diabrotica speciosa* (Coleoptera: Chrysomelidae), corn, and the aphid aboveground (AG) herbivore *Rhopalosiphum maidis* to answer three questions: (1) What effects does belowground herbivory by *D. speciosa* have on feeding preferences and distributions of the aboveground *R. maidis*? (2) How do these preferences and distributions change over time? And (3) what are the longer term consequences for *R. maidis* populations? Adult alate aphids initially preferred corn seedlings with root feeding by *D. speciosa*, but preference declined over time driven by aphids leaving corn seedlings with root herbivory. Similarly, observations of aphid performance and colony growth indicated negative effects of root herbivory in contrast to previous studies. These results suggest that shifts in plant-mediated aboveground–belowground interactions can have important consequences for long-term distributions of aboveground herbivores.

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INTRODUCTION

Herbivory plays a prominent role in plant life histories. Herbivores shape plant evolution and diversity on multiple (Huntly 1991, Strauss and Agrawal 1999). Distributions of herbivores affect global plant communities that sustain and influence human life (Huntly 1991, Ohgushi 2005, Futuyma and Agrawal 2009, Asner et al. 2009, Poelman and Kessler 2016).

While many factors affect herbivore distributions, there is growing realization that indirect interactions with other herbivores can be extremely prevalent, influence feeding preferences of individual herbivores, and drive herbivore distributions (Ohgushi 2005, Kaplan and Denno 2007, Morrell and Kessler 2017, Poelman and Dicke 2018). Many of these indirect interactions are mediated by plants; herbivory by one species on one part of the plant can influence herbivory by another species on a different part of the plant, potentially across large spatial and temporal scales (Huntly 1991, Ohgushi 2005, Poelman and Kessler 2016). Understanding these indirect interactions is important, yet simultaneously difficult given the complex combinatorics inherent in systems with multiple interactions.

The means by which plants mediate indirect interactions between herbivores has become relatively well understood. Herbivory can alter

production of primary metabolites, thereby making a plant more or less desirable nutritionally for other herbivores (Van der Putten et al. 2001). For example, feeding by *Bikasha collaris* on the tree *Triadica sebifera* alters levels of nitrogen in a location-dependent manner with effects for conspecifics, while feeding by the planthopper *Prokelisia dolus* alters levels of amino acids with negative effects on congenerics (Denno et al. 2000, Huang et al. 2013). Herbivory can also alter levels of secondary metabolites, inducing plant defense pathways and effecting release of volatiles with potentially cascading consequences (Dicke and Baldwin 2010). In one particularly interesting example, volatile organic compounds released from *Solidago altissima* when fed upon by insect herbivores are used in plant–plant communication and result in altered movement patterns of mobile herbivores (Morrell and Kessler 2017).

The specific outcomes of plant-mediated indirect interactions for other herbivores are not always predictable or understood, however. A number of factors are recognized to influence these outcomes including the identity of the plant, the identity of the initial herbivore, the identity of the subsequent herbivore, the location of feeding, and the sequence of arrival (Wurst and van der Putten 2007, Xiao et al. 2012, Huang et al. 2013, 2014, 2017, Kafle et al. 2017). Aboveground (AG)–belowground (BG) interactions add another layer of complexity to understanding these plant-mediated indirect interactions because herbivores interact across the root–shoot continuum in two very distinct soil and atmosphere environments. There is growing evidence that aboveground herbivory can influence belowground herbivores and vice versa (Van der Putten et al. 2001, Bardgett and Wardle 2003, Wardle et al. 2004) with these interactions mediated by plant defenses (Bezemer and van Dam 2005). Measurement of these effects tends to be based on performance measures related to feeding and survival; in general, AG herbivores tend to have negative effects on BG herbivores on annual plants, whereas BG herbivores feeding by Coleoptera tend to have positive effects on AG Hemiptera (formerly Homoptera) such as aphids (Johnson et al. 2012).

Herbivore distributions are not temporally fixed; many herbivores can move, and their choices may have important consequences for their distributions and the plants upon which they feed. While work on larger scale field trials has demonstrated that plant-mediated indirect interactions can spur herbivore mobility, we were interested to investigate this phenomenon on a smaller scale (Morrell and Kessler 2017).

To explore temporal effects of belowground herbivory on aboveground herbivores, we used microcosms of a study system involving the larval belowground herbivore *Diabrotica speciosa* Germar (Coleoptera: Chrysomelidae), corn (*Zea mays* L.), and the aphid aboveground herbivore *Rhopalosiphum maidis* Fitch (Hemiptera: Aphididae) to answer three questions: (1) What effects does BG herbivory by *D. speciosa* have on feeding preferences and distributions of the aboveground *R. maidis*? (2) How do these preferences and distributions change over time? And (3) what are the longer term consequences for *R. maidis* populations?

Methods

To evaluate these questions, larvae of *D. speciosa*, corn seedlings, and *R. maidis* were collected, reared, and introduced to experimental microcosms.

Larvae of *D. speciosa* were reared from eggs laid by adults collected from experimental plots of corn, wheat, and bean around the Federal University of Lavras in Minas Gerais, Brazil. Adapting previous work (Ávila and Santana 2011, Ávila 2013), adults were maintained on a diet of bean (*Phaseolus vulgaris*) plants, chopped carrots, and 10% honey solution in a $40 \times 40 \times 60$ cm acrylic cage under controlled conditions ($25 \pm 1°C$, RH $70 \pm 10\%$, 12-h daylight) while laying eggs in black gauze strips placed on moist paper towels in petri dishes on the cage floor. *D. speciosa* larvae eclosing from eggs were used in experimental trials within 24 h.

Aphids (*R. maidis*) were collected from experimental corn plots on the Federal University of Lavras campus in Minas Gerais, Brazil. Following collection, aphids were placed on leaves of corn and allowed to feed following adapted protocols from previous work (Cabette 1992). In short, corn leaves were collected from the field, washed to remove unwanted residues, sliced into

15 cm long sections, and placed into 25-mL plastic cups filled with water. *R. maidis* aphids were then placed on these leaves and prevented from contacting the water with a polystyrene paper that also served to fix the corn leaves in the cup. Aphids were maintained under the same climate-controlled conditions used in rearing *D. speciosa* and were starved for 6 h prior to use in experiments.

Corn (*Zea mays* L.) plants were grown in 0.6-L polyethylene pots containing 0.5 kg of dark red latosol. A common conventionally grown hybrid variety popular in Brazil, P2530 (Pioneer), was chosen for these studies due to its widespread use in the region. Corn seedlings were grown under climate-controlled conditions (same as previously mentioned) in greenhouses maintained at the Federal University of Lavras. Monitoring and watering were done daily and uniformly across the plants used in the experiment. Corn seedlings were grown under these conditions until reaching phenological stage V4 (seedlings with the fourth leaf collar) when they were used in experiments (Abendroth et al. 2011).

To evaluate how belowground herbivory influenced distributions and preferences of aboveground herbivores over time, aphids were introduced to cages containing plants with and without root herbivory (two-choice trial) and monitored over the course of three days. Prior to the start of the experiment, corn seedlings were randomly assigned to either the root herbivory or no herbivory treatment. Ninety-six hours prior to the start of the experiment, plants were acclimated to experimental conditions by transferring them climate-controlled conditions in a laboratory setting (same settings as greenhouse, but different location) where an experimental unit consisted of two plants placed in 30 × 30 × 60 cm acrylic cages. Seventy-hours prior to the start of the experiment, the plant receiving the root herbivory treatment was infested by placing 20 recently eclosed *D. speciosa* larvae in the root zone of the potted plant, a density typically observed in the field on infested plants. At the start of the experiment (72 h post-*D. speciosa* infestation), a paper platform was introduced to the cages that fit around the corn seedlings and prevented aphids from interacting with the soil environment. Fifty adult *R. maidis* alates were then introduced to the

center of the platform in between the corn seedlings. At 0.5, 1, 3, 5, 24, 48, and 72 h post-introduction, the numbers of aphids on each seedling were counted. Five replications of this trial were conducted.

To analyze aphid distributions over time in this trial, raw counts of aphids per plant were converted to a preference score by subtracting the number of aphids on no herbivory treatment plants from the number of aphids on corn seedlings with root herbivory. Higher values of this score indicate an increased preference for corn seedlings with root herbivory. To facilitate comparisons across replications (which varied slightly in baseline levels of aphids responding to the plants), preference scores were normalized by subtracting the mean preference score for that replication. This allowed for comparison of preference trends over time between cages, even though starting points and baseline levels of response may have been different between cages. To further summarize preference trends over time, a locally estimated scatterplot smoothing (LOESS) model was fit to preference results to visually demonstrate changes over time.

To further model these preference changes, linear mixed-effects models were used to evaluate the effect of treatment, time, and their interaction on aphid preference with cage (replication) as a random effect. Best-fit models were selected based on considerations of likelihood-ratio tests, analysis of deviance, pseudo-R^2 values, information criteria, and examination of diagnostic plots to assure adherence to inherent modeling assumptions. Post hoc methods were conducted using Tukey's method for addressing the family-wise error rate.

To evaluate longer term consequences of belowground herbivory for aboveground herbivores, aphid colony size was monitored after seven days in no-choice trials as an indirect measure of performance. Ninety-six hours prior to the start of the experiment, corn seedlings were moved to climate-controlled conditions in a laboratory setting similar to the acclimatization procedure described above. In this case, though, an experimental unit consisted of an individual plant bagged with a fine mesh sealed against the base of the pot. As above, plants were randomly assigned to either the root herbivory or no herbivory treatment. Similarly, plants receiving the

root herbivory treatment were infested with *D. speciosa* larvae 72 h prior to the start of the experiment. At the beginning of the experiment, 30 apterous *R. maidis* adults were placed on each plant inside the mesh enclosure. After seven days, a total number of aphids (all life stages) on each plant were counted. Twelve replications of this trial were conducted.

To analyze longer term performance of *R. maidis* on corn seedlings with and without root herbivory, data were examined to ensure assumptions of normality and to investigate possible outliers prior to applying Student's *t*-test. In addition to visual inspection of quantile–quantile plots, applications of both Dixon's and Grubbs's tests identified one outlier ($P < 0.001$) that was removed. Estimates without the outlier are conservative; leaving the outlier in the analysis would have resulted in detection of even larger differences between treatments.

Raw data from these trials were entered into flat comma-separated value files, then read into the R computing language for further analysis. All analysis on the raw data was conducted in R version 3.5.2 using RStudio as an IDE (with Vim keybindings) (RStudio Team 2016, R Core Team 2018). The *tidyverse*, *car*, *lme*4, and *emmeans* packages were used to facilitate analysis (Fox and Weisberg 2011, Bates et al. 2015, Wickham 2017, Lenth 2018). All code, including manuscript documentation, is available upon request.

Results

Belowground herbivory by *D. speciosa* larvae influenced the preference and distribution of *R. maidis* adults aboveground. Models of treatment, time, and their interaction with cage as a random effect explained approximately 44% of observed variation in aphid preference. Marginal fixed effects accounted for approximately 16% of observed variation. There was a strong reversal of aphid preference and distribution over time; time alone ($\chi^2 = 0.42$, df = 1, $P = 0.52$) was not significant, but the presence of herbivory ($\chi^2 = 25.8$, df = 1, $P = 0.007$) and its interaction with time ($\chi^2 = 12.8$, df = 1, $P < 0.001$) significantly affected aphid preference and distribution.

Aphids initially preferred corn seedlings with belowground herbivory by *D. speciosa*, but this preference declined over time (Fig. 1A). While different replications had different numbers of aphids recruiting to plants, all replications demonstrated similar trends (LOESS fit in Fig. 1A). At one ($t = -2.6$, df = 62, $P = 0.01$) and three hours ($t = -2.5$, df = 62, $P = 0.02$), significantly more aphids were found on seedlings with belowground herbivory (Fig. 1B). By seventy-two hours, this preference had reversed; after three days, aphids significantly preferred corn seedlings without root herbivory ($t = 2.9$, df = 62, $P = 0.005$; Fig. 1B).

This change in preference was primarily driven by adult alate *R. maidis* leaving plants with belowground herbivory by *D. speciosa* (Fig. 1C). The number of aphids feeding on corn seedlings without herbivory remained more or less constant over time (Fig. 1C); the slope was not significantly different from zero ($t = 0.65$, df = 62, $P = 0.52$). The number of aphids feeding on corn seedlings with belowground herbivory declined over time, however. The slope was significantly different from the trend of aphids on corn seedlings without herbivory ($t = 3.6$, df = 62, $P = 0.001$) and significantly less than zero ($t = -4.4$, df = 62, $P < 0.001$) with approximately one aphid leaving every 10 h (slope = -0.08 ± 0.02).

Aphid recovery in these trials where *R. maidis* could choose between seedlings (Fig. 1D) declined over time. Recovery of introduced adults, 14 ± 3 individuals, approximately 28% of introduced adults, peaked at 1 h, then declined to 8 ± 2 individuals or approximately 16% of introduced adults by the end of the three-day observation period.

Over seven days, *R. maidis* performed better on corn seedlings without belowground herbivory. After seven days, there were significantly more aphids on seedlings without root herbivory as compared to those on seedlings with root herbivory ($t = 2.9$, df = 20.71, $P = 0.008$; Fig. 2A). The presence of root herbivory by *D. speciosa* reduced aphid numbers after long-term development by 50.3% [14.8%, 85.9%] (95% CI, Fig. 2A) in single-choice performance trials (Fig. 2B).

Discussion

Adult alate *R. maidis* distributions on corn seedlings with root herbivory change over time.
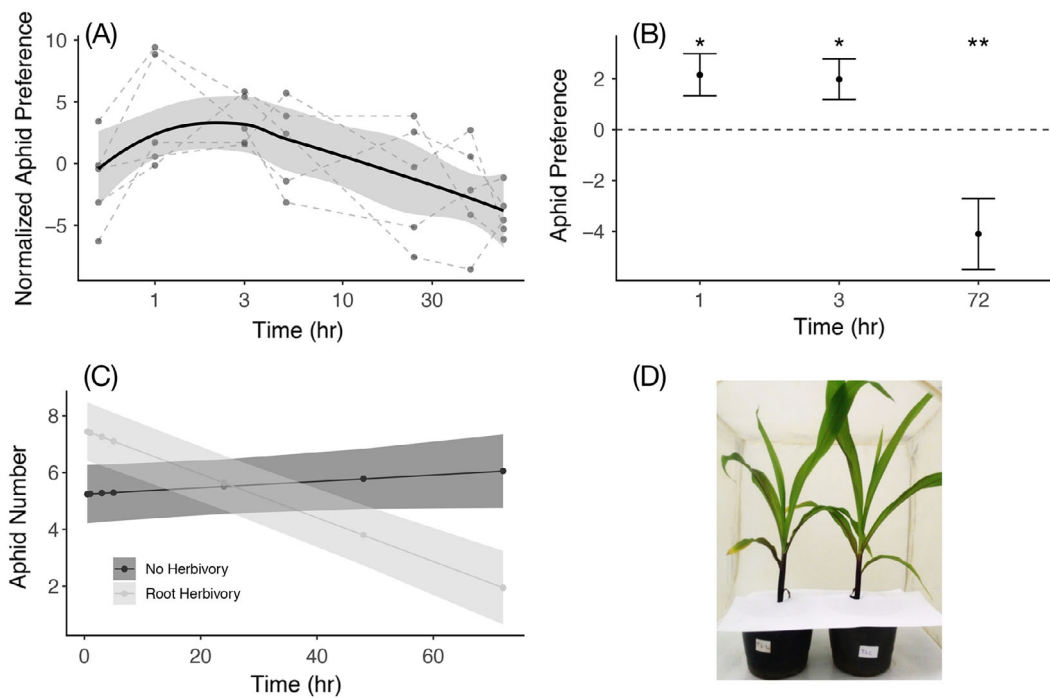
Fig. 1. Aphid preference for corn seedlings with and without belowground herbivory. Fifty adult alate *Rhopalosiphum maidis* were released into cages containing a corn seedling without belowground herbivory and a corn seedling the roots of which had been infested with 20 *Diabrotica speciosa* larvae. (A) Aphid preference for corn seedlings with belowground herbivory by *D. speciosa* larvae. Normalized preference for herbivory is calculated by subtracting the number of aphids observed on seedlings without root herbivory from the number of aphids observed on seedlings with root herbivory, then adjusted using the mean for comparison across replicates. Points and dotted lines indicate observed response. Black line and shaded area indicate LOESS fit and 95% confidence bands, respectively. (B) Modeled preference of adult *R. maidis* alates for plants with belowground herbivory over time. Higher preference indicates a greater number of individuals on corn seedlings with belowground herbivory by *D. speciosa*. Single asterisk denotes significance at $P < 0.05$; double asterisk denotes significance at $P < 0.01$. (C) Modeled trends of *R. maidis* aphid preference over time. Slopes are significantly different ($P = 0.07$) on seedlings with no herbivory and seedlings with belowground herbivory.

Initially, adult aphids are more prevalent on corn seedlings with belowground herbivory by *D. speciosa* larvae (Fig. 1). Volatile profiles from plants under attack from belowground herbivory are known to differ from those absent herbivory (Bezemer et al. 2003, Rasmann et al. 2005, Bezemer and van Dam 2005, Ali et al. 2010, Filgueiras et al. 2016). Aphids may initially prefer plants under attack belowground due to weakened defenses aboveground. By dedicating resources to defend from belowground attack, plants may be unable to mount an appropriate defense against the aphids. Our findings could suggest that adult aphids may be taking advantage of

this dynamic to avail themselves of poorly defended nutrients aboveground.

It seems, however, that this dynamic does not last. *R. maidis* presence on corn seedlings with root herbivory declines over time; after 72 h, adult aphids instead are more prevalent on corn seedlings absent root herbivory (Fig. 1). Interestingly, this change is driven primarily by aphids leaving the corn seedlings with root herbivory (Fig. 1C). More aphids do not significantly recruit to the corn seedlings without herbivory over time (Fig. 1C). These results are echoed in the performance trial where, after seven days, corn seedlings with herbivory had lower aphid
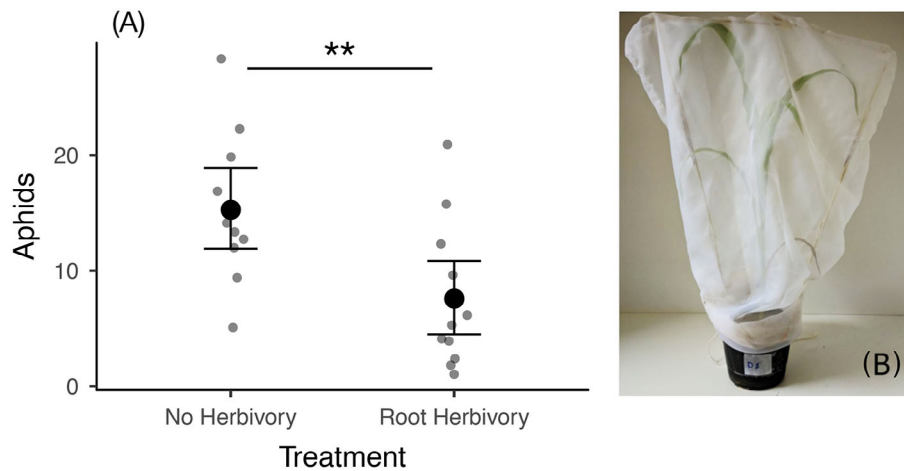
Fig. 2. (A) Aphid (*Rhopalosiphum maidis*) colony performance on corn seedlings. Thirty apterous adult aphids were placed on corn seedlings with either no belowground herbivory (no herbivory) or on corn seedlings the roots of which had been infested with 20 *Diabrotica speciosa* larvae (root herbivory). After seven days, the number of aphids on each seedling was counted. Gray points indicate aphid counts from individual replicates. Large black points and error bars denote mean and bootstrapped 95% confidence intervals, respectively. (B) Corn seedlings and experimental design. Individual seedlings in replicates were isolated from one another by mesh screening to prevent aphids moving from plant to plant.

populations. These results could be driven by two factors either independently or in combination. Aphid preference and movement could drive observed distributions or aphid mortality could be a factor. While parsing out mechanisms is the focus of ongoing work, the results suggest that belowground herbivory can drive distributions of aboveground aphid herbivores in this system.

The higher levels of aphids observed on the no belowground herbivory treatment in the performance trial stand in contrast to previous observations in the literature that belowground feeding by Coleoptera tends to have positive effects on aboveground Hemiptera (aphids) (Johnson et al. 2012). Indeed, this observation had one of the larger effect sizes in a meta-analysis with belowground feeding by wireworms and scarabeids promoting positive outcomes for aboveground aphid feeders (Gange and Brown 1989, Johnson et al. 2009, 2012). These observed effects were largely attributed to changes in nutritional quality in aboveground foliage as a result of belowground herbivory (Gange and Brown 1989, Johnson et al. 2009). Our observation of the opposite effect that belowground feeding by *D. speciosa* larvae suppresses colony growth of *R. maidis* over the period of seven days might be attributed to changes in secondary plant defenses given the rapid nature of the responses observed. A secondary metabolite that could be mediating these interactions is 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA). Root herbivory by *Diabrotica virgifera virgifera* induces greater concentrations of aboveground DIMBOA (Erb et al. 2009), which is toxic to *R. maidis* (Long et al. 1977, Beck et al. 1983). In contrast to previous trials that monitored changes in plant chemistry and herbivore effects on the scale of weeks to months, our results demonstrate a change in herbivore preference and distribution over the course of a few hours and performance consequences after seven days.

The change in distribution by *R. maidis* could reflect changes in plant defense strategy by the corn seedlings. While initially focusing on defending against belowground herbivory, the corn seedlings may re-prioritize and shift defense strategies after perceiving attack by the aboveground aphids. The response lags in time, but may be effective. After a few hours, the plants become less palatable and the aphids begin to leave in search of greener pasture.

This re-prioritization could be an explanation for the observed importance of sequence in aboveground–belowground effects (Erb et al. 2011, Johnson et al. 2012) and is an excellent example of plants influencing and being influenced by their environment. In these trials, the internal state of the corn seedlings (as influenced by their belowground herbivory) is dictating the initial effects on aphid distribution. Subsequently, though, the influence of aphid attack dictates the plant responses, which then, in turn, continues to influence aphid movement and preference.

This mediation occurs across a stark environmental divide. The belowground environment is directly influencing aboveground distributions of herbivores. The cascading consequences of this bidirectional forcing across the root–shoot continuum likely play a role in shaping ecosystem dynamics on a large scale. In examining these interactions, the temporal nature of the responses is an important consideration. This work suggests that plant responses to herbivory aboveground and belowground not only affect other herbivores, but also can change overtime. By mediating the connection between soil and shoot herbivores, plants link two disparate ecosystems with bidirectional consequences for members of both.

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