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Evidence For Plant-mediated Competition Between Defoliating and Gall-forming Specialists Attacking Solidago altissima

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ABSTRACT.—Phytophagous insects from different feeding guilds may compete indirectly via altering the chemical defenses or nutritional quality of their shared host plants. Gall-formers are understudied in this context but may be susceptible to this mode of competition early in their life history, when they may be particularly sensitive to changes to the specific reactive tissue needed for gall development. Here, we conducted a natural experiment to investigate the effect of folivory of Canada goldenrod, *Solidago altissima,* by *Trirhabda* beetles on gall induction success for the goldenrod gall fly, *Eurosta solidaginis.* We monitored oviposition events and gall development on individual *Solidago* ramets at sites differing in their levels of *Trirhabda* folivory. We found a strong inverse relationship between *Trirhabda* leaf damage and successful gall induction rates. These results suggest *Trirhabda* beetles may negatively impact *Eurosta* demographics and highlight the need for further study on how factors affecting gall induction may influence the structure of insect communities.

INTRODUCTION

Interspecific interactions among phytophagous insects can have important effects on population abundances and community structure (Denno *et al.*, 1995). Although population densities frequently may be below levels that result in intense competition, (Lawton and Strong, 1981) occasional outbreaks by one phytophage can have negative impact on co- occuring species (*e.g.,* Work and McCullough, 2000). Instead of occurring through traditional modes of interference or simple exploitative competition, competition among phytophagous insects is largely thought to take place indirectly between spatially or temporally separated competitors and may be highly asymmetric (Stiling and Strong, 1983; Redman and Scriber, 2000; Kaplan and Denno, 2007). This results in the potential for strong antagonistic interactions between insects with apparently limited niche overlap, such as different feeding guilds each specialized on different plant tissues. Much about what traits may make some insects particularly strong or weak competitors remains to be understood. Both seasonality (Faeth, 1986; Wold and Marquist, 1997; Van Zandt and Agrawal, 2004) and feeding guild (Denno *et al.*, 2000; Kaplan *et al.*, 2011) have been invoked as being potentially important.

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Gall-formers have been largely understudied in this context but may be prime candidates for being both the victors and victims of plant-mediated competition. On one hand gall-formers canact as nutrient sinks (Price *et al.*, 1987; Stone and Schönrogge, 2003), and they may have particularly potent effects on the quality of plant tissue available to other herbivores. For example high abundances of the cynipid gall wasp *Neuoterus saltatorious* have been shown to result in decreased body weight and high overwinter mortality for a threatened lepidopteran, through a decrease in foliar nitrogen (Prior and Hellman, 2010). On the other hand, the very intimate nature of the relationship between gall-formers and their hosts, with insects manipulating plant gene expression, may make them highly vulnerable to host plant manipulations by other, earlier acting herbivores. Gall induction often requires the availability of very specific reactive tissue (Weis *et al.*, 1988; Stone *et al.*, 2002), and manipulation by other herbivores could render these tissues refractory to the gall-former's cues. The net result of interactions between gall formers and other herbivores may be complex and unexpected. The oak gall wasp *Belonocnema treatae* may benefit from defoliating herbivores through a phenological shift in resource availability and hence the timing of gall development that make them less prone to attack by parasitoids. (Hood and Ott, 2010).

Here we investigate the effect of interspecific herbivory on gall induction by *Eurosta solidaginis* (Diptera: Tephritidae), the goldenrod gall fly, a model system for insect-plant interactions (Abrahamson and Weis, 1997). *Solidago altissima* L. (Asteraceae), Canada goldenrod, is host to a diverse array of specialist and generalist herbivores as well their associated parasitoids and predators (Root and Cappuccino, 1992; Crawford *et al.*, 2007). Goldenrods and their insects have been intensively studied from community ecology and evolutionary ecology perspectives (*e.g.,* Messina, 1981; Kareiva, 1987; Brown and Weis, 1995; Carson and Root, 2000; Crutsinger *et al.*, 2006; Stireman *et al.*, 2006). However, we still have a limited understanding of the ecological interactions among the myriad phytophagous insects on goldenrod. Some of the most conspicuous of these insects are leaf beetles of the genus *Trirhabda* (Coleoptera: Chrysomelidae), which are specialist folivores of *S. altisssima* and other closely related *Solidago* species (Balduf, 1929; Messina and Root, 1980). Two species of *Trirhabda, T. virgata* LeConte and *T. borealis* Blake, co- occur in the region of this study and are indistinguishable as larvae. As *T. virgata* is typically more abundant (Messina and Root, 1980; Hufbauer and Root, 2002), the beetle communities in this study were likely to be dominated by *T. virgata.* However, either of these phylogenetically and functionally similar beetles (Messina, 1982a) may have contributed to defoliation, and we will refer to them collectively as simply *Trirhabda.* The population dynamics of *Trirhabda* are often characterized by asynchronous irruptive cycles that are restricted to a very small local spatial scale (Messina, 1982b; McBrien *et al.*, 1983; Brown, 1994; Brown and Weis, 1995). *Trirhabda* beetles are univoltine, with eggs oviposited in the litter beneath goldenrod ramets hatching in late spring (Balduf, 1929). The intense herbivory accompanying the larval stages of outbreaking *Trirhabda* populations occurs throughout the month of Jun., a critical time in the life cycle of the *E. solidaginis.*

The goldenrod gall fly ecloses from the previous season's galls and females oviposit into the terminal buds of young *S. altissima* ramets in late spring (Weis and Abrahamson, 1986). The larvae of *E. solidaginis* chew into the stem where they induce the growth of unilocular spheroid galls in the tissue just below the apical dome. The stimulation of *S. altissima* cells is thought to involve exogenous indole acetic acid and certain cytokinins produced by the larvae (Mapes and Davies, 2001a, b). However, experimental applications of these compounds fail to produce ball galls (Mapes and Davies, 2001b), suggesting the

TABLE 1.—Number of clones, area, ramet density, estimated number of ramets (area × density), number of recorded oviposition scars, and number of induced galls for each of six study plots. Area was calculated as an ellipse. Ramet density was based on 5 cm wide transect counts conducted during the following field season (summer 2014)

Plot	No. clones	Area (m^2)	Ramets/m^2	Est. no. ramets	No. oviposited	No. galls induced
1	4	12.1	116.1	1401	56	12
2	4	11.3	31.6	358	74	0
3	3	8.47	59.0	499	145	45
4	3	16.84	87.2	1467	173	84
5	4	23.6	92.8	2187	117	20
6	5	18.7	45.3	848	231	80

mechanisms of gall induction are complex in this system. The induction of goldenrod galls, like those of many insect galls, may require very precise interaction between the insect and the specific reactive tissue of the host plant. This complex interplay between gall-former and plant begins during the critical interval between oviposition and visible gall development, which in the case of *E. solidaginis*, coincides with periods of peak herbivory by *Trirhabda*. Intense host plant defoliation during this key interval could deny resources to sustain to *E. solidaginis* for gall initiation. But insect herbivory can have a multitude of possible effects on host plant physiology (Karban and Baldwin, 1997), and *Trirhabda* folivory has previously been shown to affect *Solidago* leaf quality (Brown and Weis, 1995). A recent study by Helms *et al.* (2013) also demonstrates a potentially strong role of induced defenses in *S. altissima*, with herbivore cues eliciting a strong up-regulation of jasmonic acid production. We hypothesize the effect of high levels of folivory by *Trirhabda* defoliation on the reactive tissue utilized by *E. solidaginis* may interfere with gall induction. To examine this we took advantage of the strong natural variation in localized *Trirhabda* densities and monitored *E. solidaginis* oviposition and gall induction on a daily basis over plots spanning a range of *Trirhabda* damage levels.

METHODS

The study was conducted at the Koffler Scientific Reserve (KSR) at Joker's Hill near Newmarket, Ontario, Canada (44°1′46″N, 79°31′54″W). Six plots of goldenrod, *S. altissima*, were selected at various locations on the reserve (Table 1). We chose plots based on the presence of between three and five discrete goldenrod clones to produce a defined and reasonably limited area for observations. All plots were within a 700 m radius, with a minimum distance between plots of 125 m. This distance is sufficient for these plots to be considered independent patches over the course of the experiment, as Cronin *et al.* (2001) estimated that 95% of *E. solidaginis* flies have a lifetime potential dispersal distance of <55 m. Analyses were conducted at the plot level, as this corresponds to the scale of the ''treatment'' in this natural experiment; *Trirhabda* outbreaks at our study site were locally patchy, on the scale of several square meters and occurred across all the clones in these small local areas.

To ensure sufficient numbers of gall formers, we supplemented the local galls that naturally occurred at each plot with galls collected elsewhere on the reserve. In Apr. and May, galls from the previous year (2012) were harvested from goldenrod stems. Galls collected from different areas of the reserve were mixed, and all six plots received a roughly equal portion of supplemented galls. Galls were held in planting trays and placed at the plots at the first sign of adult *E. solidaginis* eclosion. For the purposes of parallel experiment, we exposed some of the supplemented galls to warmer and cooler conditions in a greenhouse and incubator to decrease or increase adult eclosion time. These treatments were applied evenly across all six plots and therefore do not affect the results of this study.

After the first observed adult eclosion, we visually inspected the terminal bud of each goldenrod ramet in the plots for *E. solidaginis* oviposition scars each day. These scars are recognizable as a characteristic linear cluster of pinprick-like holes, typically numbering 3-5. They are readily distinguishable from other types of insect damage with little ambiguity. When an oviposition scar was detected, the stem was tagged and numbered and a small cardstock sleeve was placed over the bud to prevent subsequent oviposition attempts. This procedure was carried out daily from the first observed emergence of adult *E. solidaginis* until observed oviposition events ceased, at 21 d. We began inspecting ramets for signs of gall induction approximately 2 wk after the first recorded oviposition scar. Each day, the bud sleeves were removed and stems were examined for newly induced galls, marked by the presence of a small, symmetric, spherical bulge in the stem, located a few millimeters below the apical meristem. Daily monitoring took place until gall induction was no longer observed (25 d). Following recorded induction, galls were monitored twice weekly to ensure that galls of other insects, especially the Gelechiid moth, *Gnorimoschema gallaesolidaginis* and the Cecidomyiid fly *Rhopalomyia solidansis*, were not mistaken for early *E. solidaginis* galls. While the oviposition scars and mature galls of these three insects are easily distinguished, their newly-induced galls may appear similar. Gall induction rate was calculated for each plot as the number of *E. solidensis* gall inductions divided by the number of observed oviposition events.

To quantify *Trirhabda* damage, ungalled goldenrod ramets were randomly sampled from each plot at two dates, Jul. 10 and 17. During each sampling date, six ramets were selected from each plot. Ramets were chosen by counting stems to three randomly generated numbers along two transects, determined by randomly generated compass bearings. Stems were cut at the base and damage was assessed in the lab. Ten leaves from each stem, corresponding to random numbers counted from the first leaf, were placed in one of four *Trirhabda* damage categories: 0 = no visible damage, 1 = between 1% and 15% of leaf area removed, 2 = between 15% and 75% of leaf area removed, and 3 = >75% leaf area removed. The high level of damage observed for many of the leaves precluded the use of imaging software (*e.g.*, ImageJ) from being used to assess folivory. Mean damage scores were calculated for each stem and each plot. Ramets with all leaves chewed to the midrib were given scores of three for the entire stem. Use of these plots for a parallel experiment precluded our ability of accurately measure damage at the individual ramet level for our oviposited and galled stems.

Significance of the variation in stem level mean *Trirhabda* damage scores among plots was determined by a 2-way ANOVA with plot and date as factors. The relationship between *Trirhabda* herbivory and *E. solidaginis* gall induction rates (dates pooled, *see* below) was assessed by calculating the Pearson's product-moment correlation of gall induction rates at each plot against mean *Trirhabda* damage scores. All statistical analyses were implemented in R version 3.0.1 (R development core, Vienna, Austria).

RESULTS

Leaf damage index values, a proxy for *Trirhabda* folivory, varied considerably among the six plots ($F_{5,60} = 100.05$; $P < 0.0001$, Fig. 1), consistent with the described pattern of tightly

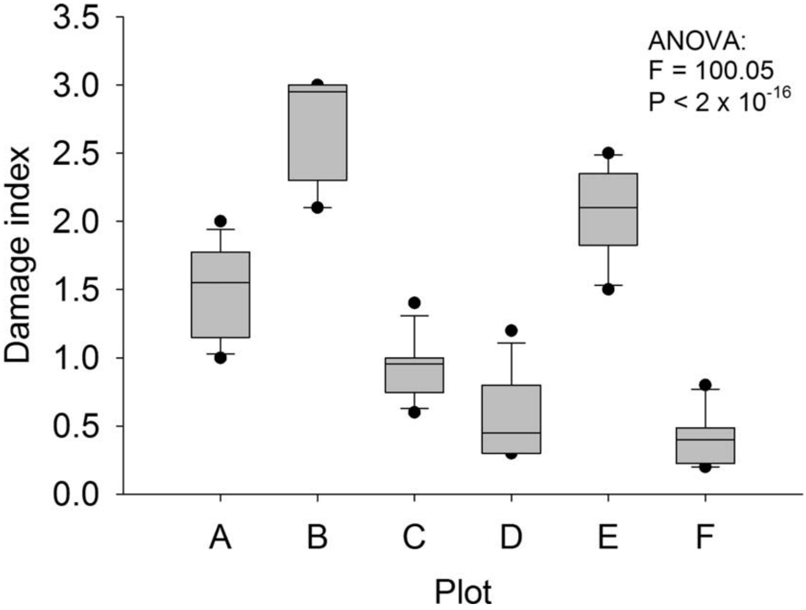

FIG. 1.—Box plots of damage indexes for 12 *S. altissima* ramets sampled from each of six plots (A–F). The top and bottom lines represent the 75th and 25th percentiles, the middle line represents the median. The circles represent the 95th and 5th percentiles

localized outbreaks of *Trirhabda*. Damage levels within each plot were consistent between dates ($F_{1,60} = 0.033$, $P = 0.5644$). The interaction term between plot and date was also not significant ($F_{5,60} = 0.591$, $P = 0.7072$). Therefore, damage values were pooled across dates within each plot to estimate mean damage level for each plot in the subsequent analysis. The greatest degree of herbivore damage was observed in plot B, in which we observed many ramets that were entirely defoliated (all leaf material removed to the midrib). Terminal buds and upper stems of some plants in this plot were dead by late Jun.

A total of 761 oviposition scars were recorded across the six sample plots, which resulted in 241 viable *E. solidaginis* galls. The rate of successful gall induction showed substantial heterogeneity among plots. The highest observed gall induction rate occurred at plot D, with 43% of oviposition events yielding galls. At the other end of the spectrum, plot B had zero galls induced, despite clones at this plot having borne galls the previous year. The rate of successful gall induction at each plot was inversely correlated with mean damage index [Fig. 2; $r = 0.924$; $P(r = 0) = 0.0086$, 4 df]. There was no relationship detected between gall induction rate and estimated oviposition rate (oviposition events / estimated number ramets) [$r = 0.0416$; $P(r = 0) = 0.9376$].

DISCUSSION

Our results suggest increasing levels of defoliation by *Trirhabda* beetles of *S. altissima* may negatively impact gall induction success by *E. solidaginis*. The strong inverse correlation between *Trirhabda* damage levels and rates of gall induction that we observed in the field is congruent with our hypothesis gall-formers may be prone to indirect competition from other insect feeding guilds by way of changes in plant reactive tissues. This study further

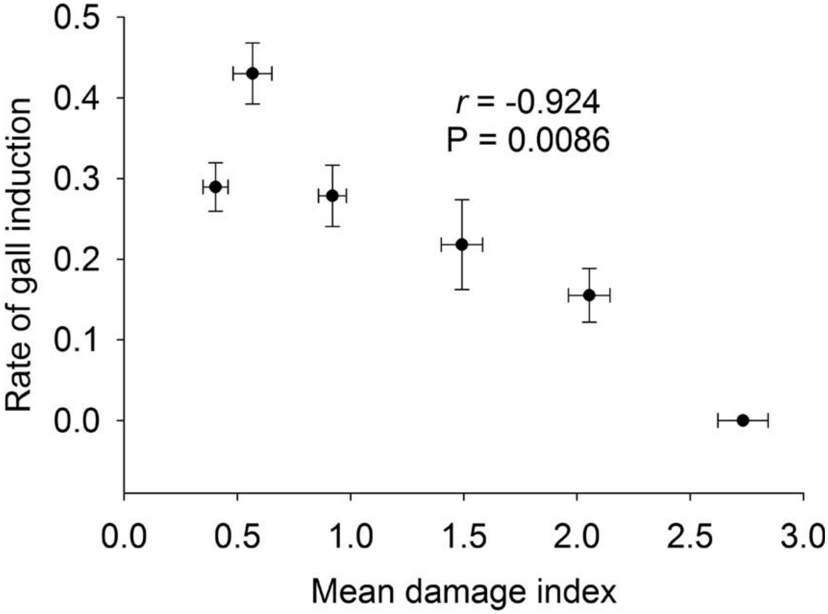

FIG. 2.—Scatter plot of the correlation between rate of *E. solidagensis* gall induction (±SE), calculate as the proportion of recorded oviposition events resulting in successful gall formation, at each plot and the mean damage index (±SE), a proxy for *Trirhabda* folivory, for 12 *S. altissima* ramets sampled across two dates from each plot

bolsters the growing support for the importance of indirect plant-mediated competition structuring factor in insect communities. This form of competition may play a strong but previously unnoticed role in the classic *Solidago/Eurosta* system.

Manipulative common garden experiments and/or multi-year studies of natural plots could verify a causal basis for the relationship between *Trirhabda* damage and gall induction we observed. While it is possible that the correlation was due to an inverse relationship between the preference and/or perfomance of *Trirhabda* performance of *E. solidaginis* on the *S. altissima* plants at each plot, independent of any herbivore induced effects, there are reasons to believe this is unlikely. First, each plot in this study represents multiple *S. altissima* clones, and *Trirhabda* damage was consistent within plots (Fig. 1). Second, the specific spatially and temporally sporadic nature of *Trirhabda* outbreaks (Brown, 1994) means these populations do not appear to be keyed in to particularly susceptible host plant individuals. Dense outbreaks resulting in complete defoliation lead to mass exodus of adult beetles which then go on to oviposit in the soil of other patches (Morrow *et al.*, 1989). Third, the preference of *E. solidganis* and the performance of *Trirhabda* on goldenrod clones differing in induced defenses both appear to respond in the same direction (Helms *et al.*, 2013).

The correlative, natural experiment nature of this study, necessarily limited the conclusions that can be drawn from our data on the relationship between beetle damage and gall induction. We are unable to discount other uncontrolled factors that may have differed among plots were responsible for a spurious correlation between our two focal variables. For instance a recent finding that *S. altissima* my up-regulate jasmonic acid (an important induced defensive compound in goldenrod) in the presence of *E. solidaginis* pheromones (Helms *et al.*, 2013) could mean lower gall induction success may also be caused by higher density of gall flies active within plots.

Gall induction rates for *E. solidaginis* were generally low at all sites in this study, with no plot having over 50%. Part of this low level of baseline success may be due to our observations being limited to recorded oviposition attempts, rather than actual egg deposition. The presence of an *E. solidaginis* egg can only be determined by dissecting the bud, and some females may choose to reject a bud after puncturing it with their aculeus (Abrahamson and Weis, 1997). However, a study by Hess *et al.* (1996) that involved dissection galls following oviposition in the laboratory found at least one egg for each bud with ovipuncture scars. Moreover, the period of *E. solidaginis* oviposition in our study occurred when *Trirhabda* damage was still low at all plots, which means females were unlikely to discriminate among buds at different plots based on damage. Therefore, differences among plots in induction correlated with damage levels were more likely to be driven by differences in the actual rate of successful gall initiation than differences in bud rejection by female flies.

Given failed gall induction acts so early in the gall-former's life history, it may be a significant cause of mortality for goldenrod gall flies. Parasitism and predation are known to have strong effects on *E. solidaginis* (Abrahamson and Weis, 1997), but these mortality factors act only on successfully induced galls. Based on the relationship presented in Figure 2, which would result in a slope of -0.147 in a regression framework, a shift in mean damage index from a low value of 0.5 to a moderate value of 1.5 would decrease the gall induction rate from 35.5% to 20.8%, translating to a 41% decrease in the number of surviving first instar larvae. If we assume parasitism, inquiline predation, and avian predation rates of 12%, 4%, and 32%, respectively (E. Cunan unpubl. data on 2012 galls from KSR, $n = 360$), a moderate *Trirhabda* outbreak could decrease overall *E. solidaginis* survivorship within a patch from 18.5% to 10.8%. This assumes the simple case of parasitoid and predation rates being independent of mature gall density; in scenarios with more complex functional responses, the net effect of *Trirhabda* outbreaks could be even stronger. Therefore, it is not unreasonable to hypothesize differences in gall induction rates may scale up to significant differences in population dynamics.

The effects of folivory by *Trirhabda* on *E. solidaginis* may extend beyond the decrease in gall induction rates reported here. Cronin and Abrahamson (2001) reported that the presence of *Trirhabda* was also a factor in the oviposition preference of gall flies. In their common garden study, gall flies were significantly less likely to lay eggs on ramets in the presence of *Trirhabda*. Our results suggest there may be strong fitness consequences for *E. solidaginis* flies ovipositing in highly defoliated patches; it is plausible that the avoidance reported by Cronin and Abrahamson may be an adaptive response to this. The zero percent successful gall induction observed here for the most highly *Trirhabda*-infested plot would certainly present strong, hard selection against flies that were unable to asses it as a suboptimal habitat.

Our results highlight an overlooked and potentially important facet of community structure in phytophagous insects. An estimated 13,000 insect species form galls (Stone and Schönrogge, 2003), and *S. altissima* alone is host to at least six other gall-formers (Root and Cappucino, 1992). This mode of indirect plant-mediated competition may have important consequences for gall abundance and insect community composition. Failed gall induction is a rather inconspicuous phenomenon in nature, as one has to be observing oviposition events to notice it. Little is known about the factors affecting failed gall development. However, studies of other gall-formers (*e.g.*, Egan and Ott, 2007; Prior and Hellmann, 2013) have noted failed gall development may be an important component of population demographics. Whether the gall induction success of other insects is also influenced by the action of interguild or intraguild competitors is a question that warrants further study.

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