

Interactions between galling insects and leaf-feeding insects: the role of plant phenolic compounds and their possible interference with herbivores

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Abstract: The objective of this study was to determine the effects of gall induction on leaf phenolic compounds and their indirect effects on the subsequent attack of folivorous insects in *Achatocarpus gracilis*, *Cordia alliodora*, *Guapira macrocarpa*, *Guettarda elliptica* and *Ruprechtia fusca* that occur in both hillside and riparian sites at Chamela-Cuixmala tropical dry forest in western Mexico. There are differences in soil water content between riparian and hillside sites where trees in the first are mainly evergreen and deciduous in the second. A few tree species occur in both sites and their intraspecific phenological response is also different between sites. In this case, trees of a given species that occur in riparian sites will be evergreen whereas trees on hillsides of the same species will be deciduous. Four plant species had significantly greater total phenol concentrations in galled than ungalled leaves in both deciduous hillside and riparian sites. In three plant species associated with galls, host total phenol concentrations were significantly greater in short than in tall plants. The frequency and amount of folivore damage were greater in leaves without galls than leaves with galls in these four plant species. These results indicate that galling insect species may directly affect leaf phenolic concentrations and indirectly may affect the incidence and consumption of folivorous insects in tropical plant species. This may have important consequences on the preference of leaves by folivorous insects that might be excluded by galling insect species in this dry tropical system.

Key Words: folivorous insects, galling insects, herbivory, phenolic compounds, tropical dry forest

INTRODUCTION

Several studies of plant–insect interactions have evaluated the potential effects of plant chemical defences on herbivore performance and host-selection behaviour (Kolehmainen *et al.* 1994, Roininen *et al.* 1999). Studies of plant-mediated interactions between different types of insect feeding guilds are relatively rare, particularly in the tropics (Fisher *et al.* 2000, Taper & Case 1987). The best-documented case is the induction of plant defences (Tallamy & Raupp 1991). Plant secondary compounds may be induced by herbivore attack and these may vary with the herbivore species and the amount of leaf area removed in each plant species (Dicke 2000, Karban & Baldwin 1997). In some cases, changes induced by herbivory lead to the induction of plant resistance, but

in others, specialist herbivores are capable of inducing and sequestering the secondary compounds produced by the host plant (Dicke 2000).

Galling insects induce tumours on their host plants in response to chemical stimulus. This induction is either made by saliva injection or other fluid secretions produced by the adult insects while laying eggs; or by larvae inside of the plant tissue (Ananthakrishnan 1984, Dreger-Jauffret & Shorthouse 1992, Price *et al.* 1987). Each galling insect species has the ability to manipulate the growth and development of plant tissue (Cuevas-Reyes *et al.* 2003, 2004a; Weis *et al.* 1988) and may also be capable of modifying host nutritional quality and plant secondary metabolites for protection against natural enemies (Cornell 1983, Fernandes & Price 1992, Hartley & Lawton 1992, Langenheim & Stubblebine 1983, Waring & Price 1990).

The nutritional hypothesis states that galled plant tissues contain greater amounts of nutrients and lower

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concentrations of defensive compounds than other plant tissues not used by galls (Hartley 1998, Stone & Schönrogge 2003). However, the results in the literature are not consistent. In some cases, defensive chemical compounds are less abundant in galls than in normal tissues developed in the same plant (Nyman & Julkunen-Titto 2000), while other studies indicate that galls contain higher concentrations of chemical defences, such as host phenolic concentration (Hartley 1998), that in many plants constitute an important factor in the defence against herbivore attack (Bennet & Walls-Grove 1994, Harborne & Grayer 1993). Galling insect species can protect themselves with defence compounds of their host plants by sequestering secondary metabolites during the formation of gall tissues (Hartley 1998, Hartley & Lawton 1992); during this process, the host plant may induce defence compounds in leaves with galling insects that in turn may confer resistance against other herbivores that use the same leaf tissue.

In this paper, the effect of leaf-gall induction was examined on host phenolic concentration and its subsequent effects on herbivory caused by folivorous insects in several plant species that occur in both deciduous hillside and riparian sites at Chamela-Cuixmala tropical dry forest. This is the first observational study (but see Foss & Rieske 2004) that documents the interaction between galling insect species and folivorous insects and its relationship to host plant chemical defences. In particular, we addressed the following hypotheses: (1) In accordance with the nutritional hypothesis that proposed that galling insects are capable of controlling host nutritional quality and plant secondary metabolites (Hartley 1998, Hartley & Lawton 1992), we expected greater induction of phenolic compounds in leaves attacked by galls than in leaves free of herbivory in tropical plant species, (2) as a consequence of this, we expected that gall induction will decrease the frequency and leaf area damaged by folivores, and (3) because massive leaf-flushing occurs at the beginning of the wet season in deciduous forest and the vegetation of riparian sites remain evergreen throughout the year (Bullock & Solis-Magallanes 1990, Frankie *et al.* 1974, Opler *et al.* 1980, van Schaik *et al.* 1993), we expect greater levels of damage by galling insects in plants on hillsides than riparian sites.

MATERIALS AND METHODS

Study site

This study was conducted at the Chamela-Cuixmala Biosphere Reserve on the Pacific coast of Jalisco, Mexico that covers 13 200 ha. The elevation ranges between 0–500 m asl, with an average annual precipitation of 748 mm and the rainy season ranges from June to October (Bullock 1985). Vegetation is dominated by tropical deciduous forest, with patches of tropical riparian forest along the streams (Lott *et al.* 1987, Rzedowski 1978).

Sample collection

Surveys were conducted from July to October in 2004 during the rainy season. We chose two independent deciduous hillside and riparian sites at the Chamela-Cuixmala Biosphere Reserve. We sampled 30 transects of 50 × 5 m in each of two independent deciduous hillside and riparian sites at Chamela and Cuixmala (i.e. 120 transects in total, 60 deciduous hillside and 60 riparian sites). Transects were randomly selected from points obtained from a grid system developed within each site using random numbers to assure sampling independence. Individual transects were distributed in space within each site sampling across several uplands in deciduous forest, while in riparian forest transects were across different streams. Galling insect species were identified and counted on the basis of plant species and gall morphology. Because the induction by all galling insect species studied only affected leaves, we restrict our study to foliar galls.

After a preliminary analysis of presence of galling insect species and their host plants in deciduous hillside and riparian site at Chamela-Cuixmala Biosphere reserve, we found 39 galling insect species represented in several orders. Diptera (family Cecidomyiidae) induced the majority of galls in both sites with 27 species (69.2%), while Homoptera (Psyllidae (5.2%) and Kermidae (7.7%)), Hymenoptera (Tanaostigmatidae (2.6%)) and Thysanoptera (2.6%) were rare; five morphospecies (12.7%) were unidentified (Cuevas-Reyes *et al.* 2004a). Five out of a possible 39 species of galling insect were selected for study because these were the only species which were always present in both sites (Table 1).

Table 1. Galling insect species that occur in both deciduous hillside and riparian sites in the Chamela Cuixmala Biosphere Reserve in Jalisco, Mexico.

Gall taxa	Order: Family	Host plant species	Family
Cecidomyiidae sp. 1	Diptera: Cecidomyiidae	<i>Achatocarpus gracilis</i> H.Walter	Achatocarpaceae
<i>Neolasioptera</i> sp.	Diptera: Cecidomyiidae	<i>Cordia alliodora</i> (Ruiz & Pav.) Oken	Boraginaceae
Cecidomyiidae sp. 2	Diptera: Cecidomyiidae	<i>Guapira macrocarpa</i> Miranda	Nyctaginaceae
Cecidomyiidae sp. 3	Diptera: Cecidomyiidae	<i>Guettarda elliptica</i> Sw.	Rubiaceae
Unidentified	Unidentified: Unidentified	<i>Ruprechtia fusca</i> Fernald	Polygonaceae

We sampled 20 individuals of each of the study species to test if leaf-gall induction affected host phenolic concentration, frequency and amount of folivore damage in relation to the presence of galls on the same plant species that occur in different site conditions. We sampled the following plant species associated with galling-insect species: *Achatocarpus gracilis*, *Cordia alliodora*, *Guapira macrocarpa*, *Guettarda elliptica* and *Ruprechtia fusca* in all transects of each site. In all cases, the sampling extended from the canopy to the lower branches of each individual. In trees and shrubs associated with galls, we collected three galled branches and three ungalled branches at the top, intermediate and bottom of each stratum and collected in total 50 leaves in the same position along shoots, to ensure that phenological (i.e. leaf age) factors are controlled. All the leaves sampled from galled branches contained galls. The estimation of total phenol concentrations was made on a sample of leaf tissue obtained from galled and ungalled leaves, and for each leaf, determined the frequency of leaves with folivory and the leaf area removed by folivores. To estimate the leaf area removed by folivores we first obtained a digital image of each leaf and then estimated the total area of the leaf and the area removed using Sigma Scan Pro software. To control for plant size, the stem diameter at breast height (dbh) was measured for each tree and shrub sampled (Cuevas-Reyes *et al.* 2004b). We defined two categories of plant size: (1) short plants with dbh ≤ 1 cm and (2) tall plants with ≥ 2.5 (Gentry 1982, 1988).

Chemical analysis

In each individual of the five plant species of both sites, we sampled 25 leaves galled and 25 ungalled leaves without petioles. These are a subsample of the 50 leaves collected in the previous section. We only sampled surrounding leaf tissue from galled leaves and excluded the gall chamber. Fresh tissue samples of 125 mg were flash-frozen in liquid nitrogen. For each sample, 10 ml of ethanol (80%) was added and centrifuged (10 min, 3000 g). The supernatant samples (1 ml) were combined with deionized water (7 ml) and mixed with Folin-Ciocalteu reagent (0.5 ml, 2N). After 1 min, we added 1 ml of sodium carbonate to 20%. The tissue samples were analysed in the spectrophotometer (Cam spec M230) and the blank (deionized water: 7 ml; methanol: 1 ml; Folin-Ciocalteu reagent: 0.5 ml and sodium carbonate: 20%) was used to calibrate the spectrophotometer (Harborne 1988, Waterman & Mole 1994). We measured the absorbance at 760 nm for each leaf tissue sampled (i.e. four samples for each leaf) using tannic acid as standard.

Statistical analysis

To determine the effect of galling insects on leaf phenolic concentration, we used two-way ANOVA analysis (Littell

et al. 1991). The model used site (riparian vs. deciduous), presence of galling insects (leaves with galls vs. leaves without galls) as the independent variables and the concentration of leaf phenols as the response variable. To control the variation associated with plant size, we used dbh as a covariate in the model. To compare phenolic concentrations for leaves with and without galls we used LSMeans (Littell *et al.* 1991). This is an adjusted mean generated from least square estimate of the general linear model statistics (Littell *et al.* 1991).

We also compared the frequency of leaves with folivores and the area removed by folivory in leaves with and without galls for each of the five plant species. In the first case, we used a generalized linear model applying the GENMOD procedure (Stokes *et al.* 2000) to compare the frequency of leaves with folivores in leaves with and without galls for each of the five plant species that occurred in riparian and deciduous sites. The model used site (riparian vs. deciduous), presence of galling insects (leaves with galls vs. leaves without galls) and individual plant as the independent variables. The number of leaves with damage divided by the total number of leaves was used as the dependent variable. Because the scale and distribution of these variables did not follow a normal distribution, a binomial distribution and a logit link function were used in this analysis.

A similar analysis (i.e. generalized linear model applying the GENMOD procedure, Stokes *et al.* 2000) was used to compare the area removed by folivores in leaves with and without galls for each of the five plant species that occurred in riparian and deciduous sites. The model used site (riparian vs. deciduous), presence of galling insects (leaves with galls vs. leaves without galls) and individual plant as the independent variables. The area of leaf with folivore damage divided by the total leaf area (proportion of leaf area removed) was used as the dependent variable.

We also compared the frequency of leaves with folivores in each plant and the area removed by folivores in each leaf with and without galls between plants from riparian and deciduous sites. A generalized linear model applying the GENMOD procedure (Stokes *et al.* 2000) was used to analyse the frequency of folivores and leaf damage. The model used site (riparian vs. deciduous), presence of galling insects (leaves with galls vs. leaves without galls), plant species as the independent variables and all the two-way interactions. In the first analysis, the number of leaves with damage divided by the total number of leaves was used as the dependent variable and in the second analysis the area of leaf with damage divided by the total leaf area was used as the dependent variable. A binomial distribution and a logit link function were used in both analyses. To control the variation associated with plant size, we used dbh as a covariate in the model.

Table 2. Mean (\pm SE) total phenol concentration in galled and ungalled leaves of five host plant species that occur in both deciduous hillside and riparian sites.

Host plant species	Total phenols (mg g ⁻¹)		P
	Galled	Ungalled	
<i>Achatocarpus gracilis</i>	1.5 \pm 0.2	0.6 \pm 0.2	0.0001
<i>Cordia alliodora</i>	1.1 \pm 0.2	0.4 \pm 0.1	0.0001
<i>Guapira macrocarpa</i>	1.9 \pm 0.5	1.9 \pm 0.8	n.s.
<i>Guettarda elliptica</i>	5.8 \pm 0.5	2.5 \pm 0.5	0.0001
<i>Ruprechtia fusca</i>	10.8 \pm 1.2	6.2 \pm 0.9	0.0001

RESULTS

Galling insects and host total phenol concentration

In Chamela-Cuixmala Biosphere Reserve, we found only five galling insect species on their specific host plant species that occurred in both deciduous and riparian sites (Table 1). No significant differences in the plant total phenolic concentrations were found between host plants of deciduous and riparian sites ($F = 2.0$, $df = 1$, $P > 0.05$). However, the results of the *t*-test for each plant species indicate that four plant species had greater total phenolic concentrations in leaves with galls than in leaves without galls (Table 2).

In host tree species associated with galls, we found that host total phenolic concentration was significantly greater in smaller than larger plants (*Achatocarpus gracilis*: $\chi^2 = 4.1$, $df = 1$, $P < 0.04$; *Guettarda elliptica*: $\chi^2 = 13.0$, $df = 1$, $P < 0.0004$; *Ruprechtia fusca*: $\chi^2 = 25.9$, $df = 1$, $P < 0.0001$).

Frequency of folivorous insects

In four plant species associated with galls, the frequency of leaves with folivore damage was greater in leaves

without galls than in leaves with galls (Table 3). The frequency of folivores was affected by site type. The frequency of leaves with folivore damage was significantly greater in deciduous than in riparian sites ($\chi^2 = 24.4$, $df = 1$, $P < 0.0001$). The frequency of leaves with folivore damage was greater in leaves without galls than in leaves with galls ($\chi^2 = 92.5$, $df = 1$, $P < 0.0001$) (Table 4). We found significant differences between plant species in the frequency of folivory ($\chi^2 = 25.7$, $df = 4$, $P < 0.0001$), the interaction between plant species and site: ($\chi^2 = 24.6$, $df = 4$, $P < 0.0001$) and the interaction between plant species and presence of galling insects: ($\chi^2 = 24.9$, $df = 4$, $P < 0.0001$), but not for the interaction of site by presence of galling insects ($\chi^2 = 0.74$, $df = 1$, $P > 0.05$). In addition, we did not find significant differences in the frequency of leaves with folivore damage between shorter and taller plants ($\chi^2 = 0.57$, $df = 1$, $P > 0.05$).

Leaf area removed by folivores

Similarly, the proportion of leaf area removed by folivores was significantly greater in leaves without galls than in leaves with galls in four host-plant species (Table 3). The amount of folivore damage was affected by site type. The leaf area removed by folivore insects was greater in deciduous than in riparian sites and different between plant species ($\chi^2 = 164$, $df = 4$, $P < 0.0001$). The leaf area damaged by folivores was greater in leaves without galls than in leaves with galls (Table 4). There was a significant two-way interaction between plant species and presence of galling insects ($\chi^2 = 218$, $df = 4$, $P < 0.0001$) but not between plant species and site ($\chi^2 = 2.5$, $df = 4$, $P > 0.05$) nor between site and presence of galling insects ($\chi^2 = 0.28$, $df = 1$, $P > 0.05$). The leaf area removed by

Table 3. Mean (\pm SE) frequency of leaves with damage by folivores and proportion of leaf area removed by folivores on leaves with and without galls in host plant species that occur in deciduous hillside and riparian sites.

Host plant species	Frequency of leaves with damage by folivores (%)				Leaf area removed by folivores (%)			
	Galled	Ungalled	χ^2	P	Galled	Ungalled	χ^2	P
<i>Achatocarpus gracilis</i>	3.6 \pm 0.5	7.1 \pm 0.6	25.7	0.0001	2.5 \pm 0.6	9.8 \pm 0.6	81.2	0.0001
<i>Cordia alliodora</i>	2.3 \pm 0.5	5.9 \pm 0.59	20.2	0.0001	1.1 \pm 0.6	6.3 \pm 0.7	96.0	0.0001
<i>Guapira macrocarpa</i>	4.4 \pm 0.8	4.9 \pm 0.5	0.08	n.s.	8.4 \pm 0.5	8.7 \pm 0.6	0.1	n.s.
<i>Guettarda elliptica</i>	3.2 \pm 0.6	10.1 \pm 0.8	45.7	0.0001	3.0 \pm 0.5	12.5 \pm 0.8	241.1	0.0001
<i>Ruprechtia fusca</i>	3.9 \pm 0.5	7.8 \pm 0.6	21.1	0.0001	1.4 \pm 0.5	9.7 \pm 0.6	253.8	0.0001

Table 4. Comparison of the frequency of leaves with damage by folivores and proportion of leaf area removed by folivores on leaves with and without galls between deciduous hillside and riparian sites.

	Frequency of leaves with damage by folivores (%)			Leaf area removed by folivores (%)		
		χ^2	P		χ^2	P
Deciduous	60.5 \pm 4.6	6.1	0.001	15.3 \pm 0.6	4.6	0.03
Riparian	43.5 \pm 0.6			12.1 \pm 0.6		
Galled	36.4 \pm 1.8	92.5	0.0001	8.9 \pm 0.5	509.0	0.0001
Ungalled	67.0 \pm 4.5			19.1 \pm 1.6		

folivores was not significantly different between smaller and larger plants ($\chi^2 = 0.24$, $df = 1$, $P > 0.05$).

DISCUSSION

Galling insects and induction of phenolic compounds

Several studies have evaluated the mechanisms of manipulation and alteration of plant development involved in gall formation (Ananthakrishnan 1984, Birch *et al.* 1992, Dreger-Jauffret & Shorthouse 1992, Larson & Whitham 1991, Shorthouse 1986). However, little attention has been paid to the manipulation of galling insects on defensive secondary compounds of their host plants (Hartley 1998). Controversial results of this chemical manipulation have been reported. In some cases, chemical compounds such as host phenolics are less abundant in the galls than in normal plant tissues (Abrahamson & Weis 1986, Nyman & Julkunen-Titto 2000), while in other cases, galls contain higher concentrations of defence chemicals than in normal tissues (Hartley 1998, Hartley & Lawton 1992, Vereecke *et al.* 1997). It was originally suggested that phenolics were produced by plants as a defence mechanism against galling insects (Tjia & Houston 1975, Westphal *et al.* 1981, Zucker 1982). However, more recent studies show that host phenolic concentrations are not associated with plant resistance against galling insects (Abrahamson *et al.* 1991, Hartley 1999). In our study, we found that the concentration of phenols was greater in galled than ungalled leaves in four plant species that occur in both deciduous hillside and riparian sites at Chamela-Cuixmala Biosphere Reserve. These results support the nutritional hypothesis that galling insect species have the capacity to stimulate the production of host secondary compounds increasing phenolic concentrations in the surrounding leaf tissue of galled leaves. It has been proposed that gall-induction derives some benefits to their hosts because galling insects stimulate the induction of defence compounds in leaves that confer resistance against other herbivores (Abrahamson *et al.* 1991, Askew 1984, Hartley 1998, Hartley & Lawton 1992).

Galling insects, plant size and host phenolic concentration

Another result of our study shows that cecidomyiids induced the majority of galls in both deciduous hillside and riparian sites of the Chamela tropical dry forest. We found in three plant species associated with galling-insects greater concentration of leaf phenolic compounds in smaller than in larger plants in both sites. This pattern may be explained by two different reasons: (1) because the production of leaf phenolic compounds

is a response against galling insect attack (Hartley 1998) and (2) because shorter plants represent sites with higher nutritional tissue and undifferentiated meristems that favour the gall induction in the majority of galling insect species because the physiology of gall morphogenesis requires the stimulation by insects to undifferentiated plant tissues (Cuevas-Reyes *et al.* 2004b, Shorthouse 1986, Weis *et al.* 1988). In addition, theories of plant allocation to defence would predict that smaller plants which have grown less quickly would have higher levels of phenolics (Hartley & Jones 1997). Similarly a previous study showed that shorter plants had greater abundance of galls than larger plants (Cuevas-Reyes *et al.* 2004a, b, 2006).

Frequency and amount of leaf damage by folivorous insects

We also found that the frequency and amount of folivore damage on ungalled leaves were significantly greater in deciduous than in riparian sites. These results may be explained because in deciduous sites the presence of herbivore insects are synchronized with leaf flushing at the beginning of the wet season (Bullock & Solís-Magallanes 1990, Lieberman 1982, Opler *et al.* 1980, Reich & Borchert 1984) and some insect herbivores have adjusted their life history to synchronize their youngest larval stages to the appearance of host organs such as shoots and leaves (Taylor 1986, Weis *et al.* 1988, Yukawa 2000), whereas in riparian sites, plants are evergreen and produce new leaves through a more extended period during the wet season (Bullock & Solís-Magallanes 1990, Frankie *et al.* 1974, Opler *et al.* 1980, van Schaik *et al.* 1993). There are differences in soil water content between riparian and hillside sites where trees in the former are mainly evergreen and deciduous in the latter. A few tree species occur in both sites and their intraspecific phenological response is also different between sites. In this case, trees of a given species that occur in riparian sites will be evergreen whereas trees on hillsides of the same species will be deciduous (Bullock & Solís-Magallanes 1990, Frankie *et al.* 1974). Therefore, more availability of younger leaves, during a short period of time, occurs in the deciduous forest than in the riparian evergreen forest in the wet season.

Interactions between galling insects and folivorous insects

Few studies have evaluated the effects of gall induction on host defensive chemical compounds and the subsequent effects of these changes on the incidence of folivorous insects (Foss & Rieske 2004). Simultaneous herbivory by different insect guilds may result in higher selection pressures on host plants that may favour chemical

induction (Mooper & Simberloff 1995). In our study, we found that gall induction affects the chemical composition of their host plants by increasing phenolic concentration in the surrounding leaf tissue of galled leaves and affecting the subsequent incidence and herbivory levels of defoliators. The reduction of incidence and the leaf area removed in galled plant tissues by folivorous insects in four plant species of both deciduous and riparian sites is consistent with findings obtained in similar studies (Foss & Rieske 2004, Schultz 1992). Two possible ecological interactions may explain the incidence of galling insects and folivores on the same host leaves of the tropical dry deciduous forest. First, massive leaf flushing, at the beginning of the wet season, is a general phenological pattern of the tropical deciduous forests (Bullock & Solís-Magallanes 1990, Frankie *et al.* 1974, Opler *et al.* 1980) and synchronization of folivores and galling insects to their host phenology is particularly important in the first flush of new leaves of this deciduous forest (Filip *et al.* 1995, Weis *et al.* 1988, Yukawa 2000). Therefore, it is likely that both folivores and galling insects may directly compete for the same leaf resources but galling insects are better competitors and successfully colonize and displace folivores that would otherwise consume the same leaves. As a result galling insects will competitively exclude folivores. A second explanation is related to the sequestration and induction of host chemical compounds as a result of gall formation assigned to the surrounding host leaf tissue and the gall chamber (Hartley 1998, Hartley & Lawton 1992). This occurs when galling insects colonize new developing leaves and will indirectly deter folivores through an increase in secondary compounds mediated by galling insect–plant interactions more than the interaction of plants and folivores or folivores and galling insects.

Our results indicate that galling insects may directly affect host plant chemical traits, changing the concentration of foliar phenolics, and indirectly may affect the incidence and leaf-consumption of potential predators such as folivore insects. Schultz (1992) found that gall induction by several aphids reduce and deter the herbivory of some folivore insects. In this case, galling insects decrease the incidence of folivores. This may have important consequences on the preference of folivorous insects that interact with galling insects in these tropical plant species.

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