

Diversity of gall-inducing insects in a Mexican tropical dry forest: the importance of plant species richness, life-forms, host plant age and plant density

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Summary

1 We tested four hypotheses concerning the variation in species richness of gall-inducing insects (GII) in plant communities. We sampled deciduous and riparian habitats in a tropical dry forest at Chamela-Cuixmala Biosphere Reserve in western Mexico, that differ in phenology and moisture availability.

2 GII species richness might be expected to increase with the richness of host plant species, with life-form complexity of host plants (trees to shrubs, herbs and climbers), with host age or with host plant density.

3 We found 172 plant species, of which more were present in deciduous than in riparian habitats, but 34 (19.8%) occurred in both. A different GII species colonized each of 39 host species. Most GII species (69.2%) were gall midges (Cecidomyiidae).

4 We found a significant positive correlation between GII species richness and plant species richness in both deciduous and riparian habitats, suggesting that radiation of GII species may be associated with plant species richness.

5 Most of the GII species occurred on trees or shrubs rather than herbs or climbers, consistent with structural complexity providing more colonization sites.

6 The frequency of GII was greater on saplings, which may have more undifferentiated meristems susceptible to gall induction.

7 Both the frequency and intensity of damage by galls were greater in deciduous than riparian habitats, indicating a preference of GII species for plants in the more xeric habitat.

8 The frequency of GII increased with host plant density in only 18 (46.2%) of GII species.

9 Richness of GII depends on all proposed factors, although density is often the least important. The effects of host richness and host age are similar to those seen in many specialist folivorous insects, although the unique association of a single insect with a single host is only seen for GII.

Key-words: gall species richness, herbivory, host plant age, life-forms, plant density, plant species richness, plant–animal interactions, tropical dry forest

Journal of Ecology (2004) **92**, 707–716

Introduction

Analyses of biogeographical patterns in species richness for plants and animals have contributed substantially

to the identification of ecological mechanisms underlying biodiversity (Ricklefs 1987; Cornell & Lawton 1992; Huston 1999). Phytophagous insects are a major component of the world biodiversity and are involved in the main trophic interactions of tropical communities (Novotny & Missa 2000). Despite the importance of tropical gall-inducing insects (GII) in such interactions,

little is known about their abundance and distribution (Price & Clancy 1986; Schönrogge *et al.* 2000; Cuevas-Reyes *et al.* 2003).

GII are found on specific host plants in natural communities across most biogeographical regions (Fernandes & Price 1991; Price 1991; Price *et al.* 1998). Their species richness is higher in tropical regions, intermediate in temperate and lowest in cold regions (Fernandes & Price 1988; Price *et al.* 1998; Gonçalves-Alvim & Fernandes 2001). Because galling insects are usually host-specific, generation and maintenance of GII species richness have been often related to plant species richness (Wright & Samways 1996, 1998; Oyama *et al.* 2003). However, abiotic factors, such as soil quality and water stress, and other biotic factors (life-form of host plant, plant age, plant density and natural enemies) may also affect tropical GII species richness at different scales (Fernandes & Price 1991; Lara & Fernandes 1996; Ribeiro *et al.* 1998). These factors are not mutually exclusive and their direct or indirect effects must be considered. These can be formalized in four alternative hypotheses.

The plant species richness hypothesis suggests that the floristic diversity of habitats may be responsible for differences in local patterns of GII species richness because more plant species represent more potential sites to colonize. Therefore, GII species richness increases as more potential host plant species are available (Fernandes & Price 1988; Wright & Samways 1998; Gonçalves-Alvim & Fernandes 2001).

The structural complexity hypothesis explains the effects of growth form of plants on phytophagous insect species richness in terms of host plant architecture (i.e. a combination of life-form, plant height and number of shoots, branches and leaves in relation to crown volume) (Lawton 1983; Leather 1986; Dansa & Rocha 1992) and its effects on GII (Fernandes & Price 1988; Gonçalves-Alvim & Fernandes 2001). Trees may be colonized by a wider variety of insect species than either shrubs or herbs because their complex architecture provides more microhabitats (Leather 1986). In addition, trees are also more 'apparent' to insects than either shrubs or herbs (*sensu* Feeny 1976). Although both arguments have been used to explain the frequency of folivorous species richness, the pattern is not very clear when applied to specific guilds such as sucking and galling insects (Leather 1986). Thus, Gonçalves-Alvim & Fernandes (2001) showed that GII richness is higher in trees than either shrubs and herbs, but Fernandes & Price (1988) did not find differences between trees and shrubs.

The plant age hypothesis proposes that the frequency of GII species on a particular host plant species is related to its ontogenic stage. Although it has been assumed that the foliage of saplings must be extremely well defended compared with mature plants, rates of damage by folivores are higher in younger stages, and this is mainly due to greater nutritional quality of the leaves rather than differences in concentration of secondary compounds (Coley & Barone 1996; Basset 2001). Some studies have shown frequency of galling insects

to be related to the age of their host plants (Price *et al.* 1987a, 1987b; Craig *et al.* 1989; Price 1989), and we predict that younger plants are more susceptible to attack because galls can sequester secondary metabolites as a mechanism to protect them against natural enemies (Cornell 1983; Langenheim & Stubblebine 1983; Waring & Price 1990).

The resource concentration hypothesis integrates the effects of insect specialization on host plants, the choice of host plants by female insects for oviposition and the incidence of natural enemies on isolated or aggregated hosts (Root 1973; Raupp & Denno 1979; Gonçalves-Alvim & Fernandes 2001) by proposing that frequency on a particular host will increase with plant density.

The four hypotheses have been tested independently in different localities. Although several authors have attempted to establish patterns at a global scale comparing results from tropical and temperate communities, very few studies have tested the same community with comparable methodologies ((Fernandes & Price 1988, 1991, 1992; Wright & Samways 1996, 1998; Price *et al.* 1998). We therefore compared GII species richness, and the specificity of GII plant interactions within and between communities at a regional scale in a tropical dry forest using extensive sampling over 3-ha plots. We tested the hypotheses by comparing two adjacent habitats that differed in humidity, vegetation and leaf phenology. In particular, we addressed the following questions. (i) What is the degree of specialization between GII species and their host plant species? (ii) What is the relationship between plant species richness and GII species richness in deciduous and riparian habitats in a tropical dry forest? (iii) Is GII species richness associated with the structural complexity of life-forms and host plant age? (iv) Does GII frequency increase with host plant density?

Materials and methods

STUDY SITE

This research was conducted at the Chamela-Cuixmala Biosphere Reserve on the Pacific coast of Jalisco, Mexico, which covers an area of 13 200 ha. The elevation of this site ranges between 50 and 500 m, the average annual precipitation is 748 mm and the rainy season ranges from June to October (Bullock 1985). The predominant vegetation is tropical deciduous forest, with some patches of tropical riparian forest in the 'arroyos' (Rzedowski 1978). Deciduous and riparian habitats have similar numbers of plant species, but the latter includes a greater number of species of climbers (Lott *et al.* 1987).

METHODS

Surveys were conducted from June to October 2001 during the rainy season. We sampled 30 transects of 50 × 5 m in each of two independent deciduous and

riparian habitats at Chamela and Cuixmala (i.e. 120 transects in total). Transects were randomly positioned on a grid system within each habitat. Within each transect, plant species were identified and GII species on trees, shrubs, herbs and climbers were recorded. GII were counted and identified on the basis of plant species and gall morphology. Sampling of GII extended from the canopy to the lower branches of each individual, collecting three branches at the top, intermediate and bottom of each stratum for all plant life-forms. All GII species recorded affected only leaves, so all belong to the same guild.

We checked that each different gall morphology on a particular host plant, was caused by a different GII by incubating galls in the laboratory and identifying the adult insect produced, thus also verifying their host specificity.

Frequency data for GII on trees, shrubs, herbs and climbers of host plants in each transect were used to test the structural complexity hypothesis, with stem diameter at breast height (d.b.h.) as a control for plant age in trees and shrubs. Susceptibility to galls in different ontogenetic stages was estimated for trees and shrubs. Plant species density was estimated in each transect and the frequency and mean number of galls on each host plant were recorded.

A preliminary analysis showed that only six GII species were present in both habitats. For comparative purposes therefore mean number of galls per plant was estimated only for these species. To compare the susceptibility to galls of the same plant species in different habitats, we registered the mean number of galls per plant for each host species in each transect.

STATISTICAL ANALYSES

The floristic similarity between deciduous and riparian habitats was compared using the Driver and Kroeber index calculated as $100 C / [(N1)(N2)]^{1/2}$, where C = number of shared species, $N1$ = species number of the more diverse flora, and $N2$ = species number of the less diverse flora (Sánchez & López 1988). We also conducted a t -test to determine if there are differences in species richness of plants between deciduous and riparian habitats.

A linear regression analysis was used to analyse the relationship between GII species richness and plant species richness among transects in deciduous and riparian habitats.

We applied a paired t -test to each of the six plant species that occurred at all sites to investigate differences between habitats in galling frequency.

We used a two-way ANOVA to determine the effect of host plant life-form and habitat type (both as independent variables) on the number of GII species on trees, shrubs and climbers (response variables). A LSMeans test was used for *a posteriori* comparisons. The number of GII species was pooled for each life-form for all dates and all transects at each habitat. Similar conditions were

applied to determine the effect of habitat and life-form of host plants on the frequency of GII, using a logistic regression analysis (CATMOD procedure, SAS 2000, general procedure for modelling categorical data).

We applied a logistic regression analysis using GENMOD (SAS 2000, general procedure for modelling a binary logit for each plant species separately) to test for effects of plant age on frequency of GII.

To determine the effect of plant density within and between habitats in different plant life-forms, we applied a two-way ANOVA and *a posteriori* LSMeans test for the comparison of means (SAS 2000).

We conducted a logistic regression analysis for each species separately, of host plant density on the frequency of GII using the CATMOD procedure (SAS 2000). To determine the effect of plant density on the number of GII per plant for each species, we conducted a linear regression analysis between host-plant density and the number of galls per plant for each plant species.

Results

The 39 GII species found represented several orders. Diptera (family Cecidomyiidae) induced the majority of galls in both habitats 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. All GII species were highly specific, occurring in only a single plant species (Table 1). The number of GII species did not differ significantly between deciduous and riparian habitats ($\chi^2 = 0.44$, d.f. = 1, $P > 0.05$) and only six GII species occurred in both habitats (see Table 1).

We sampled 172 plant species from 37 families, of which 39 (22.7%) were associated with specific GII species. Seventy-three plant species (42.4%) were restricted to deciduous forest and 65 (37.8%) to riparian habitats and only 34 species (19.8%) occurred in both habitats. The deciduous and riparian habitats showed low similarity in plant species (20%), and GII species composition (15.3%).

The number of plant species did not differ significantly between deciduous and riparian habitats (t -test: $t = 0.44$, d.f. = 1, $P > 0.05$). Deciduous habitats had a similar number of tree ($n = 41$) and shrub ($n = 37$) species as riparian habitats (37 and 32, respectively).

Only six GII–host plant associations occurred in both habitats and five of these host plants supported greater numbers of galls in deciduous than riparian habitats (Table 2).

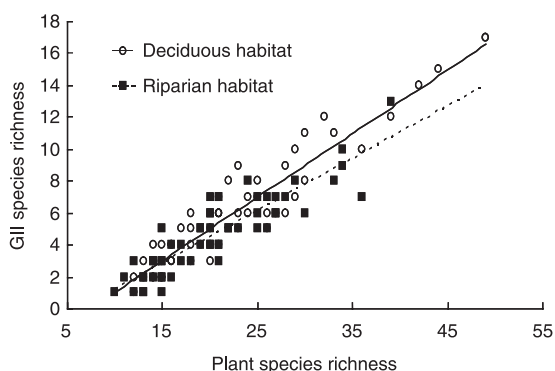
GII species richness was positively correlated with plant species richness in both habitats (deciduous, $y = 0.3979x - 2.93$, $r^2 = 89.2\%$, $P < 0.001$; riparian, $y = 0.3772x - 2.04$, $r^2 = 78.6\%$, $P < 0.0001$) (Fig. 1).

GII species richness was greater as structural complexity increased in both deciduous and riparian habitats and greater in deciduous forest than riparian habitats for trees, shrubs and climbers ($F_{2,292} = 42.48$,

Table 1 Orders and families of GII present in the Chamela-Cuixmala Biosphere reserve in Jalisco, Mexico

Family	Host plant taxa	Order	Family	Gall taxa
Achatocarpaceae	<i>Achatocarpus gracilis</i>	Unidentified	Unidentified	Unidentified*
Apocynaceae	<i>Thevetia ovata</i>	Diptera	Cecidomyiidae	<i>Aspondylia</i> sp2
Bignoniaceae	<i>Bignoniaceae</i>	Diptera	Cecidomyiidae	Cecidomyiidae
Bombacaceae	<i>Ceiba aesculifolia</i>	Homoptera	Psyllidae	Psyllidae
	<i>Ceiba grandiflora</i>	Homoptera	Psyllidae	Psyllidae
Boraginaceae	<i>Cordia alliodora</i>	Diptera	Cecidomyiidae	<i>Neolasioptera</i> sp.*
Burseraceae	<i>Bursera excelsa</i>	Diptera	Cecidomyiidae	Cecidomyiidae
	<i>Bursera instabilis</i>	Diptera	Cecidomyiidae	Cecidomyiidae
Convolvaceae	<i>Ipomoea wolcottiana</i>	Diptera	Cecidomyiidae	<i>Aspondylia convolvuli</i>
Erythroxylaceae	<i>Erythroxylum mexicanum</i>	Diptera	Cecidomyiidae	<i>Neolasioptera erythroxyl</i>
Euphorbiaceae	<i>Croton alamosanus</i>	Diptera	Cecidomyiidae	sp1
	<i>Croton pseudoniveus</i>	Diptera	Cecidomyiidae	sp2
	<i>Croton suberosus</i>	Diptera	Cecidomyiidae	sp3
	<i>Jatropha malacophylla</i>	Diptera	Cecidomyiidae	<i>Aspondylia</i> sp.
	<i>Jatropha standleyi</i>	Diptera	Cecidomyiidae	Cecidomyiidae
Flacourtiaceae	<i>Flacourtiaceae</i>	Diptera	Cecidomyiidae	Cecidomyiidae
Hernandiaceae	<i>Gyrocarpus jatrophifolius</i>	Thysanoptera		Thysanoptera
Leguminosae	<i>Caesalpinia caladenia</i>	Diptera	Cecidomyiidae	Cecidomyiidae
	<i>Cynometra oaxacana</i>	Diptera	Cecidomyiidae	Cecidomyiidae
	<i>Lonchocarpus eriocarinalis</i>	Homoptera	Kermidae	<i>Euphalerus</i> sp1
	<i>Lonchocarpus</i> sp.	Homoptera	Kermidae	<i>Euphalerus</i> sp2
	<i>Prosopis</i> sp.	Hymenoptera	Tanaostigmatidae	<i>Tanaostigma</i> sp.
Moraceae	<i>Brosimum alicastrum</i>	Homoptera	Kermidae	<i>Trioza rusellae</i>
	<i>Chlorophora tinctoria</i>	Diptera	Cecidomyiidae	<i>Clinodiplosis chlorophora</i>
	<i>Ficus cotinifolia</i>	Diptera	Cecidomyiidae	Cecidomyiidae
Nictagynaceae	<i>Guapira macrocarpa</i>	Unidentified	Unidentified	Unidentified*
Polygonaceae	<i>Coccoloba barbadensis</i>	Diptera	Cecidomyiidae	<i>Ctenodactylomyia</i> sp.
	<i>Ruprechtia fusca</i>	Unidentified	Unidentified	Unidentified*
Rubiaceae	<i>Guettarda elliptica</i>	Diptera	Cecidomyiidae	Cecidomyiidae*
	<i>Randia spinosa</i>	Diptera	Cecidomyiidae	<i>Bruggmannia randiae</i>
Sapindaceae	<i>Thoumadium decandrum</i>	Unidentified	Unidentified	Unidentified
Simaroubaceae	<i>Recchia mexicana</i>	Unidentified	Unidentified	Unidentified
Tiliaceae	<i>Heliocarpus pallidus</i>	Diptera	Cecidomyiidae	<i>Neolasioptera heliocarpi</i> *
Urticaceae	<i>Urera caracasana</i>	Diptera	Cecidomyiidae	Cecidomyiidae
Verbenaceae	<i>Vitex hemsleyi</i>	Diptera	Cecidomyiidae	Cecidomyiidae

*GII species present in both habitats.

**Fig. 1** Relationships between GII species richness and plant species richness in Chamela-Cuixmala Biosphere reserve in Jalisco, Mexico. Regression models were utilized in each habitat. Each point represents a sampling transect.

$r^2 = 68.2\%$, $P < 0.001$). LSMeans test indicates that trees have significantly more GII species than shrubs in riparian habitats (the inverse in deciduous), and both have more than climbers in both habitats ($P > 0.001$) (Fig. 2a). Herbs have few GII species (mean of two in deciduous forest, no GII on riparian herbs).

We recorded a total of 2046 plants with GII on trees, shrubs and climbers, of which 58.8% were present in deciduous and 41.2% in riparian habitats. The frequency of GII on each of the different life-forms was significantly greater in deciduous than riparian habitats (life-form, $\chi^2 = 18.8$, d.f. = 2, $P < 0.0001$). In both habitat types, the frequency of GII was greater in trees and shrubs than in climbers (habitat, $\chi^2 = 8.0$, d.f. = 1, $P < 0.0047$, Fig. 2b) but there was also a life-form by habitat interaction ($\chi^2 = 23.6$, d.f. = 2, $P < 0.0001$).

The results of the logistic regression analysis (Table 3) indicate that there is a negative relationship between plant age and the frequency of GII for each host species regardless of family. The frequency of GII was greater in saplings and young shrubs (which comprised 74.2% the galled host species) than mature plants.

Plant density was significantly greater in deciduous than riparian habitats for trees and shrubs ($F_{3,436} = 15.88$, $P < 0.001$), but density of trees did not differ from that of shrubs (Fig. 3) and both were significantly higher than the density of herbs and climbers in both habitats.

GII frequency increased with plant density in 18 species (c. 50% of total galled plant species) (Table 4). The

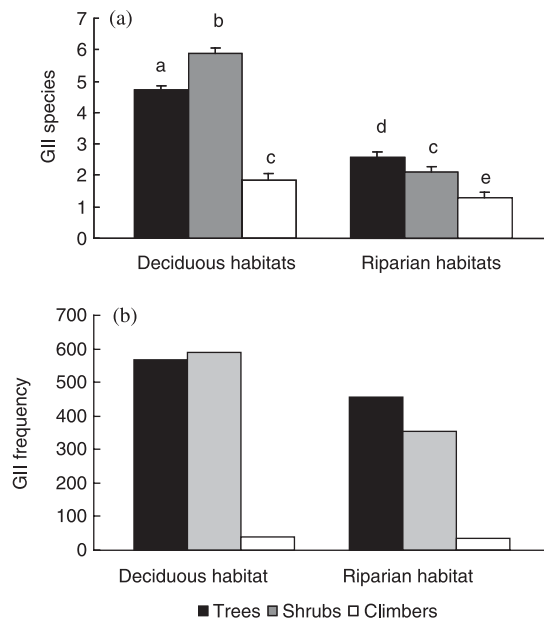


Fig. 2 (a) Effect on GII of different life-forms in deciduous and riparian habitats species richness. Non-transformed data are shown. Values with the same letter did not differ significantly after an LSMeans multiple comparison test ($P > 0.001$). (b) Frequency. PROC CATMOD procedure (SAS 2000) was applied for modelling categorical data: life-form ($\chi^2 = 18.8$, d.f. = 2, $P < 0.0001$), habitat ($\chi^2 = 8.0$, d.f. = 1, $P < 0.0047$), life-form \times habitat ($\chi^2 = 23.6$, d.f. = 2, $P < 0.0001$).

mean number of GII was also positively correlated with plant density in 15 plant species (Table 5).

Discussion

It is generally assumed that gall morphology is unique to a GII species and that each gall species is specific to a single plant species (Ananthakrishnan 1984; Dodson & George 1986; Weis *et al.* 1988; Dreger-Jauffret & Sorthouse 1992; Cuevas-Reyes *et al.* 2003). Some studies have, however, demonstrated that a single plant species is capable of hosting numerous GII species (Fernandes & Price 1988; Waring & Price 1989; Fernandes *et al.* 1996), suggesting that the specificity of gall–plant interactions might not be absolute. Our study represents a major advance in that we identified all taxa of GII on host plants, and confirmed that at this tropical site, each GII species is associated with one specific host plant species. Knowledge of the degree to which herbivorous

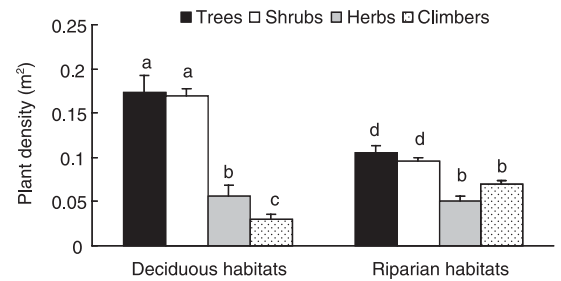


Fig. 3 Mean plant density within and between habitats in the different life-forms. Non-transformed data are shown. Common letters identify means that were not significantly different according to LSMeans test ($P > 0.001$) following ANOVA.

insects are specialized on their host plants is critical for understanding insects' life-history patterns as well as their impact on plant populations and their importance as selective agents for plant defences (Rhoades & Cates 1976; Thomas 1990).

We found that cecidomyiids induced the majority of galls in both deciduous and riparian habitats of the tropical dry forest, affecting 20 different families of plants, although Euphorbiaceae and Leguminosae supported the majority of galls. A greater specificity of GII is apparently associated with a greater diversity of host species in the tropics than in temperate regions. These associations may have occurred due to processes of radiation and high rates of speciation in both groups in tropical regions (Gagné 1994; Fernandes *et al.* 1997; Price *et al.* 1998; Wright & Samways 1998).

Our site showed greater GII species richness than another tropical study in Brazilian savanna where only four GII species were found on trees, five on shrubs and four on herbs in xeric and one on trees and one on shrubs and herbs (Price 1991). Plant species richness may produce differences in local patterns of GII richness because more plant species represent more diverse potential niches (Wright & Samways 1996, 1998; Gonçalves-Alvim & Fernandes 2001). The high plant species richness at Chamela-Cuixmala is similar to some tropical rain forests (Lott *et al.* 1987) and may be critical for GII species richness.

Another factor that determines species richness is host plant architecture; plants with more ramifications, greater numbers of shoots, branches and leaves and larger crown volume have more microhabitats, thus favouring the colonization of a wider variety of insects (Leather 1986). Trees and shrubs supported more GII

Table 2 Mean number (\pm SE) of galls per plant in six gall–host plant associations that occurred in deciduous and riparian habitats; t paired test (box-cox transformation data) was applied on each plant species

Plant species	Gall taxa	Deciduous habitats	Riparian habitats	t -value	d.f.	$P <$
<i>Achatocarpus gracilis</i>	Unidentified	(565.9 \pm 12.4)	(96.1 \pm 7.1)	12.9	37	0.0001
<i>Cordia alliodora</i>	<i>Neolasioptera</i> sp.	(90.7 \pm 7.5)	(50.1 \pm 5.3)	3.1	53	0.002
<i>Guettarda elliptica</i>	Cecidomyiidae	(59.6 \pm 5.3)	(43.4 \pm 3.6)	2.7	28	0.01
<i>Heliocarpus pallidus</i>	<i>Neolasioptera heliocarpi</i>	(109.8 \pm 6.3)	(50.4 \pm 3.9)	6.7	38	0.0001
<i>Ruprechtia fusca</i>	Unidentified	(196.4 \pm 4.7)	(126.7 \pm 5.8)	6.1	37	0.0001
<i>Guapira macrocarpa</i>	Unidentified	(288.9 \pm 11.9)	(274.0 \pm 13.4)	0.39	44	NS

Table 3 Logistic regression of frequency of GII on trees and shrubs of different ages. PROC GENMOD procedure (SAS 2000) was applied for each plant species

Host plant taxa	Host plant age maximum likelihood estimates	Chi-square	<i>P</i> <
<i>Achatocarpus gracilis</i>	−0.24	10.3	0.001
<i>Thevetia ovata</i>	−0.62	16.6	0.0001
<i>Bignoniaceae</i>	−1.36	11.3	0.0008
<i>Ceiba aesculifolia</i>	−0.16	3.2	NS
<i>Ceiba grandiflora</i>	−0.12	1.9	NS
<i>Cordia alliodora</i>	−0.79	46.6	0.0001
<i>Bursera excelsa</i>	−1.13	11.9	0.0005
<i>Bursera instabilis</i>	−0.38	7.3	0.006
<i>Ipomoea wolcottiana</i>	−0.46	24.6	0.0001
<i>Erythroxylum mexicanum</i>	−0.62	2.3	NS
<i>Croton alamosanus</i>	−0.46	19.5	0.0001
<i>Croton pseudoniveus</i>	−0.37	13.6	0.0002
<i>Croton suberosus</i>	−0.6	36.8	0.0001
<i>Jatropha malacophylla</i>	−0.04	0.46	NS
<i>Jatropha standleyi</i>	−0.29	16.9	0.0001
<i>Flacourtiaceae</i>	−0.99	10.6	0.001
<i>Gyrocarpus jatrophiifolius</i>	−0.76	17.5	0.0001
<i>Caesalpinia caladenia</i>	−0.06	0.53	NS
<i>Cynometra oaxacana</i>	−0.15	26.6	0.0001
<i>Lonchocarpus eriocarinalis</i>	−0.55	20.6	0.0001
<i>Lonchocarpus</i> sp.	−0.7	11.7	0.0006
<i>Prosopis</i> sp.	−0.58	15.6	0.0001
<i>Brosimum alicastrum</i>	−0.23	24.2	0.0001
<i>Chlorophora tinctoria</i>	−0.19	5.6	0.01
<i>Ficus cotinifolia</i>	−0.02	0.95	NS
<i>Guapira macrocarpa</i>	−0.32	17.4	0.0001
<i>Coccoloba barbadensis</i>	−1.31	2.2	NS
<i>Ruprechtia fusca</i>	−1.4	31.9	0.0001
<i>Guettarda elliptica</i>	−0.61	21.6	0.0001
<i>Randia spinosa</i>	−0.06	1.1	NS
<i>Thounidium decandrum</i>	0.011	0.01	NS
<i>Recchia mexicana</i>	−0.31	12.7	0.004
<i>Heliocarpus pallidus</i>	−0.18	12.0	0.0005
<i>Urera caracasana</i>	−0.14	11.2	0.0008
<i>Vitex hemsleyi</i>	−0.86	9.6	0.001

species richness than herbs and climbers in both deciduous and riparian habitats, thus, overall, supporting the plant structural complexity hypothesis. However, although patterns in riparian habitats (trees > shrubs) were similar to Gonçalves-Alvim & Fernandes (2001), those in deciduous (shrubs > trees) were more like Fernandes & Price (1988). One possibility is that this pattern may be associated with differences in secondary metabolites and nitrogen biomass between different life-forms (e.g. more in trees and shrubs than herbs and climbers) (Coley & Barone 1996), allowing trees and shrubs to provide more potential colonization sites.

The few studies that have documented the variation in diversity and frequency of insect herbivores with host plant age show that some insect guilds are more diverse on saplings and others on mature plants (Lowman 1992; Basset 2001). Differences in plant chemistry, leaf palatability, local microclimate and enemy-free space have been suggested as possible causes for these differences (Coley & Barone 1996). Microclimate effects, for instance, may prevent insects dispersing in the sunny upper canopy and the abundance of natural enemies

can be higher on mature plants than on saplings (Basset 2001). In our study, GII frequency was higher on juvenile stages of host plants in trees and shrubs in 74.2% of the plant species that were associated with GII, possibly because female insects favour juvenile stages of host plants whose leaves show rapid expansion, higher nutritional quality and more secondary metabolites. The association may also be related to the ability of GII to adapt and manipulate their host plants and to sequester secondary metabolites as a mechanism of protection against natural enemies (Cornell 1983; Waring & Price 1990; Hartley & Lawton 1992; Hartley 1998). Juvenile stages also offer the undifferentiated meristems that are stimulated by GII to initiate gall morphogenesis (Weis *et al.* 1988). From the point of view of GII, juvenile stages may therefore represent more vigorous plants with fast growth and greater temporal availability of resources (Price 1991).

The resource concentration hypothesis, which proposes that high host plant density increases GII frequency, had not previously been tested specifically for a set of GII species in a given community. We analysed

Table 4 Relationship between frequency of galls and plant density host. PROC CATMOD procedure (SAS 2000) was applied for modelling binary logit to each plant species

Host plant species	Host plant density	Chi-square	<i>P</i> <
<i>Achatocarpus gracilis</i>	20.71	4.29	0.0381
<i>Cordia alliodora</i>	39.63	4.95	0.0261
<i>Bursera instabilis</i>	95.41	3.96	0.0464
<i>Ipomoea wolcottiana</i>	48.77	15.06	0.0001
<i>Croton alamosanus</i>	10.46	9.14	0.0025
<i>Croton pseudoniveus</i>	136.0	10.05	0.0015
<i>Croton suberosus</i>	30.16	13.38	0.0003
<i>Gyrocarpus jatrophiifolius</i>	29.86	10.42	0.0012
<i>Caesalpinia caladenia</i>	29.53	18.1	0.0001
<i>Cynometra oaxacana</i>	22.48	31.2	0.0001
<i>Brosimum alicastrum</i>	28.15	20.12	0.0001
<i>Guapira macrocarpa</i>	24.6	14.06	0.0002
<i>Coccoloba barbadensis</i>	59.26	12.92	0.0003
<i>Ruprechtia fusca</i>	43.76	10.64	0.0011
<i>Recchia mexicana</i>	112.4	8.17	0.0042
<i>Heliocarpus pallidus</i>	45.09	7.53	0.0061
<i>Urera caracasana</i>	132.0	14.22	0.0002
<i>Vitex hemsleyi</i>	46.17	6.13	0.0133
<i>Thevetia ovata</i>	8.36	0.2432	NS
Bignoniaceae	6.42	0.0171	NS
<i>Ceiba aesculifolia</i>	2.93	0.484	NS
<i>Ceiba grandiflora</i>	58.51	1.94	NS
<i>Bursera excelsa</i>	77.48	3.47	NS
<i>Erythroxylum mexicanum</i>	21.18	0.9444	NS
<i>Jatropha malacophylla</i>	35.9	2.64	NS
<i>Jatropha standleyi</i>	6.09	0.053	NS
Flacourtiaceae	6.67	0.0077	NS
<i>Lonchocarpus eriocarinalis</i>	21.23	0.445	NS
<i>Lonchocarpus</i> sp.	16.37	0.4093	NS
<i>Prosopis</i> sp.	55.88	1.48	NS
<i>Ficus cotinifolia</i>	25.24	1.49	NS
<i>Chlorophora tinctoria</i>	20.41	17.44	NS
<i>Guettarda elliptica</i>	4.02	0.36	NS
<i>Randia spinosa</i>	46.45	1.71	NS
<i>Paullinia cururu</i>	58.63	0.4897	NS
<i>Paullinia sessiliflora</i>	15.79	0.1358	NS
<i>Lippia graveolens</i>	25.05	0.247	NS

Table 5 Relationship between mean number of galls per plant and host plant density

Family	Plant species	Equation	<i>r</i> ²	<i>F</i>	<i>P</i> <
Achatocarpaceae	<i>Achatocarpus gracialis</i>	$y = 3617x + 17.5$	79.9	212.5	0.0001
Bignoniaceae	Bignoniaceae	$y = 7573.4x + 25.6$	74.3	11.5	0.02
Boraginaceae	<i>Cordia alliodora</i>	$y = 2778.4x - 11.6$	89.4	102.9	0.0001
Convolvaceae	<i>Ipomoea wolcottiana</i>	$y = 7080.4x + 12.9$	58.1	8.4	0.02
Euphorbiaceae	<i>Croton alamosanus</i>	$y = 735.1x + 30.9$	74.4	17.4	0.005
	<i>Croton pseudoniveus</i>	$y = 8791.1x + 1.35$	60.9	17.2	0.0001
	<i>Croton suberosus</i>	$y = 939.9x + 18.1$	87.8	87.3	0.0001
Hernandiaceae	<i>Gyrocarpus jatrophiifolius</i>	$y = 20738x - 321.4$	62.0	8.2	0.03
Moraceae	<i>Brosimum alicastrum</i>	$y = 5949.3x - 19.9$	89.1	99.8	0.0001
	<i>Chlorophora tinctoria</i>	$y = 1267.1x + 27.6$	72.2	13.0	0.01
Nyctaginaceae	<i>Guapira macrocarpa</i>	$y = 2391.2x + 267.5$	72.8	35.8	0.0001
Polygonaceae	<i>Ruprechtia fusca</i>	$y = 917.6x + 154.5$	81.3	21.7	0.005
	<i>Coccoloba barbadensis</i>	$y = 4693.1x - 13.9$	81.2	30.3	0.0009
Rubiaceae	<i>Guettarda elliptica</i>	$y = 899.5x + 34.1$	89.9	35.8	0.0001
Verbenaceae	<i>Vitex hemsleyi</i>	$y = 9648.1x + 237.1$	45.5	10.2	0.008

the relationships between host-plant density per species and the number of galls per plant for each of the very specialized GII species and found that only 18 (46.2%) responded significantly to host plant density when

averaged across deciduous and riparian habitats. It is possible that the density and proximity within plant hosts regulate GII population sizes via density-dependent mechanisms (Janzen 1970; Connell 1971).

We compared two habitats with different moisture conditions. GII species richness on trees and shrubs was greater in deciduous than riparian habitats, as were the frequency and intensity of galling (i.e. mean number of galls by plant). Furthermore, all but one of the six host GII associations that occur in both habitats showed more galls in the deciduous habitats. Tree and shrub species richness does not differ between habitats, indicating a preference of GII species for plants in the more xeric deciduous habitat. Deciduous habitats show synchrony in leaf flushing, whereas riparian habitats maintain leaves in the dry season. Our results are therefore in accord with the idea proposed by De Souza (2001) that vegetation types with synchronous leaf flushing are more likely to harbour higher GII species richness than other tropical systems because most insect-induced galls occur on young plant tissues, particularly on leaves.

Although we did not evaluate the negative effects on growth and plant reproduction of herbivory by GII nor the costs to the plants of inducing galls, several studies have established that gall induction may damage plants. Negative physiological costs include altering the allocation patterns and vegetative growth (Askew 1984; Larson & Whitham 1991; Hartley & Lawton 1992, 1998; Wolfe 1997; Rossi & Stiling 1998), negatively affecting photosynthetic rates (Fay *et al.* 1996; Larson 1998) and reducing the plant fitness (Hartnett & Abrahamson 1979; Sacchi *et al.* 1988; Parra-Tabla & Bullock 1998).

We found that the species richness of GII in a tropical dry forest such as Chamela-Cuixmala, depends not only on plant species richness but also on life-forms of host plants, ontogenetic stage of host plant and plant density. Even though our study only analysed GII species that affected leaves, this taxonomically diverse group may have included different mechanisms of gall formation and this may have influenced the patterns of incidence of GII found in our study.

Specialist folivorous insect species behave similarly to GII in that species richness is positively correlated to plant species richness at local and regional scales (Gilbert & Smiley 1978; Cornell 1985; Marquis & Braker 1994). The importance of plant species richness for the radiation of many groups of specialized herbivores, including GII species, in tropical communities is beyond doubt (Marquis & Braker 1994). Specialist folivores also show greater levels of herbivory in saplings than adult trees in shade-tolerant and gap species (Waltz & Whitam 1997). However, unlike folivores such as *Heliconius* butterflies on *Passiflora* vines and geometrid moths on *Piper* species (Marquis & Braker 1994), specialization is apparently a general pattern associated with the GII guild in tropical dry forests: GII colonize young tissues of specific host species by modifying developmental cell differentiation. They become sessile insects that depend exclusively on their host, although their ability to sequester chemicals during gall formation (Hartley & Lawton 1992; Hartley 1998) confers protection to GII against natural enemies such as predators, parasitoids and pathogens (Cornell 1983; Waring & Price 1990;

Fernandes & Price 1992). These combinations of developmental and physiological adaptations have resulted in specialized interactions common to gall guilds but unusual for most folivorous insect species.

Acknowledgements

We thank Susan Hartley, Peter Price and Karsten Schönrogge for comments on previous versions of this manuscript. We thank Alfredo Pérez for plant species identification and Nidia Pérez Nasser for technical support. We thank the authorities of Chamela and Cuixmala Biosphere reserve for their permission to conduct this study. This study was partially supported by a scholarship granted by CONACYT and UNAM.

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Received 3 December 2003

revision accepted 17 March 2004

Handling Editor: Susan Hartley