Chapter 24
Mexican Gall-Inducing Insects: Importance of Biotic and Abiotic Factors on Species Richness in Tropical Dry Forest

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Abstract In this chapter we provide a brief overview of the major abiotic and biotic factors that influence the diversity of gall-inducing insects in a Mexican tropical dry forest. We tested some current hypotheses (plant species richness, plant structural complexity, plant age, resource concentration and soil fertility) that seek to explain the variation in gall-inducing insect species richness in plant communities of deciduous and riparian habitats. Gall-inducing insect species maintain a great specificity on their host plant species; each gall-inducing insect species is associated with a different plant species. A significant positive correlation was found between gall-inducing insect species richness and plant species richness in both habitats. This suggests that radiation of gall-inducing insect species may be associated with plant species richness. Most of the galling species occurred on trees and shrubs but not on herbs and climbers. The structural complexity of these life forms may provide more potential sites to be colonized by gall insects. The frequency of gall-inducing insects was greater on saplings of most host plants, suggesting that early ontogenetic stages hold more sites with undifferentiated tissues or meristems susceptible to gall induction. In addition, we analyze the spatial distribution of gall-inducing insect species under different geomorphologic units of soils in a Mexican tropical dry forest. Gall-inducing insect species richness was negatively correlated with phosphorous and nitrogen availability.

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We found low frequency and abundance of galls in fertile soils suggesting that soil fertility affect the spatial distribution of gall-inducing insect favoring incidence, abundance and species richness.

Keywords Gall-inducing insects • Biotic factors • Abiotic factors • Tropical dry forest

24.1 Introduction

Biogeographical patterns in species richness for plants and animals have contributed substantially to the identification of ecological mechanisms underlying these patterns (Ricklefs 1987; Cornell and Lawton 1992; Huston 1999). Phytophagous insects are a major component of the world biodiversity and are represented in the main trophic interactions of tropical communities (Novotny and Missa 2000). Gall-inducing insects play an important role in developing these tropical trophic interactions but little is known about their abundance and distribution (Price and Clancy 1986; Cuevas-Reyes et al. 2003).

Gall-inducing insects represent endophagous herbivores that feed on mesophyll tissue of their host plants. The interaction between gall-inducing insects with their host plants is one of the most conspicuous components in natural communities (Weis et al. 1988; Cuevas-Reyes et al. 2003; Oyama et al. 2003) that assume a high degree of specificity between gall-inducing insects and their host plants (Cornell 1990; Floate et al. 1996; Rossi and Stiling 1998; Cuevas-Reyes et al. 2006; Pascual-Alvarado et al. 2008).

Gall induction on plants represents a specific and complex phenomenon that is initiated by insect chemical stimulus by secreting substances analogous to auxins in the oviposition on their host plants (Williams and Benson 1966; Ananthakrishan 1984; Jauffret and Shorthouse 1998). As a result of this interaction, metabolic changes occur mainly in the processes of development and growth of plant tissues, ending with the formation of abnormal structures called galls (Ananthakrishan 1984; Hartley 1998, 1999). The manipulation of the host plant by gall-inducing insects alters the chemical composition of the gall tissue (Larson and Whitham 1991; Hartley 1998; Pascual-Alvarado et al. 2008), resulting in a high content of nitrogen compounds, water and sugars (Hartley and Lawton 1992) and high levels of secondary compounds (e.g. phenols, terpenes). Therefore, has been proposed that the formation of gall allows certain benefits such as the kidnapping of these compounds associated with defensive functions against natural enemies (Askew 1984; Hartley and Lawton 1992; Hartley 1998).

Global patterns of gall-inducing insect species richness are not random in natural habitats (Fernandes and Price 1988). Comparisons at the ecosystems level indicate that gall-inducing insect species richness increases as decreases latitude and altitude for several localities in the world (Fernandes and Price 1988, 1991; Price 1991; Fernandes and Lara 1993; Price et al. 1998; Cuevas-Reyes et al. 2004a). Tropical regions include the highest gall-inducing insect species richness whereas temperate ecosystems register intermediate gall-inducing insect diversity and the lowest are in cold temperate regions (Fernandes and Price 1988; Price et al. 1998; Cuevas-Reyes et al. 2004a). The main of gall-inducing insects in the Neotropical region are dipterans (Cecidomyiidae) with nearly 500 described species classified into 170 genera (Gagné 2004) and induce galls on all plant organs, but predominantly on leaves (Mani 1964).

Because galling insects are usually host-specific, the generation and maintenance of gall-inducing insect species richness have been related to plant species richness (Wright and Samways 1996, 1998; Fernandes and Price 1991; Fernandes and Lara 1993; Lara and Fernandes 1996; Ribeiro et al. 1998; Cuevas-Reyes et al. 2003; Oyama et al. 2003). Therefore, population dynamics and species richness of gall-inducing insects seem to be influenced by both biotic (e.g., natural enemies, host plant composition, plant structural complexity, host density, host ontogenetic stage, host plant phenology and host resistance) and abiotic factors (e.g. hygrothermal stress, scleromorphic environments, and soil fertility) (Cuevas-Reyes et al. 2004a, b; Fernandes and Price 1988, 1991, 1992; Goncalves-Alvim et al. 2006; Lara and Fernandes 1996; Oyama et al. 2003; Cuevas-Reyes et al. 2011). These factors are not mutually exclusive and might be directly or indirectly affecting the incidence of gall-inducing insect in natural communities. Therefore, to explain the patterns of gall-inducing insect species richness, it is necessary to understand the way in which biotic and abiotic factors are related to galler insects at different scales. In this chapter, we provide a brief overview of the major biotic and abiotic factors that influence the abundance and species richness of gall-inducing insects in a Mexican tropical dry forest. Particularly, we documented the diversity of gall-inducing insect species within and between communities at a regional scale in a tropical dry forest and the specificity of gall-inducing insects with their host plants using extensive sampling. We tested five hypotheses that operate in different spatial scales comparing the species richness and local abundance of gall-inducing insects in plants distributed in two adjacent habitats with different conditions of humidity, vegetation and leaf phenology.

24.2 Exploring the Hypotheses of Galling Diversity in a Mexican Tropical Dry Forest

24.2.1 Importance of Biotic Factors

The main hypothesis explaining the variation in gall-inducing species richness is the "Plant species richness" (Fernandes and Price 1988). This hypothesis has been proposed to explain differences in species richness of gall-inducing insects between plant communities. This hypothesis states that the floristic diversity of habitats may be responsible for differences in local patterns of gall-inducing insect species richness because more plant species represent more potential sites to colonize. Therefore, gall-inducing insect species richness increases with more potential host plant species are available in the community (Fernandes and Price 1988; Wright and Samways 1996, 1998; Goncalves-Alvim and Fernandes 2001). A positive relationship between gall-inducing insect species richness and plant species richness has been found in some studies (Wright and Samways 1996, 1998; Goncalves-Alvim and Fernandes 2001; Cuevas-Reyes et al. 2004a). However, in some cases, this relationship could be more complex due to the presence of host plants that harbor a great diversity of gall-inducing insects in comparison with others (Blanche and Westoby 1995; Mendonça 2007).

The structural complexity hypothesis (i.e. a combination of life form, plant height, number of shoots, branches and leaves in relation to crown volume) has been proposed to explain the effects of life form of plants on phytophagous insect species richness (Lawton 1983; Leather 1986) and gall-inducing insect species (Fernandes and Price 1988; Goncalves-Alvim and Fernandes 2001; Cuevas-Reyes et al. 2004a) among species within plant communities. This hypothesis predicts that the abundance and species richness of gall-inducing insects will increase, as life forms of host plants are more structurally complex. Trees appear to 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). Both arguments have been used to explain the folivores species richness, but the pattern is not very clear when applied to specific guilds such as sucking and galling insects (Leather 1986). For example, some studies indicated that that gall-inducing insect species richness is higher in trees than both shrubs and herbs (Goncalves-Alvim and Fernandes 2001; Cuevas-Reyes et al. 2004a) but Fernandes and Price (1988) did not find differences between trees and shrubs.

Plant age hypothesis states that gall-inducing insect diversity is related to the ontogenetic stage of the host plants. The scale on which operates this hypothesis occur within single plant species. Differences in herbivory through the ontogenetic stages of host plants are poorly documented (Cuevas-Reyes et al. 2006; Castellanos et al. 2006; Fonseca et al. 2006). It has been assumed that the foliage of saplings must be extremely well-defended compared to mature plants (Coley et al. 1985). However, evidence shows that rates of damage by folivores are higher in younger stages mainly due to greater nutritional quality of the leaves rather than the concentration of secondary compounds (Coley and Barone 1996; Basset 2001). There is a lack of information relating to the richness and abundance of galling insects to the age of their host plants. However, Cuevas-Reyes et al. (2004a) show that saplings are more susceptible to the attack of gall-inducing insects than mature plants because these younger plants have greater defensive chemical compounds and gall-inducing insects are adapted to sequester secondary metabolites in gall tissue as a mechanism of protection against natural enemies (Hartley 1988).

The resource concentration hypothesis states that the abundance of gall-inducing insects on a particular host species will increase with increasing plant density. This hypothesis integrates the degree 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 and Denno 1979; Goncalves-Alvim and Fernandes 2001).

24.2.2 Importance of Abiotic Factors

Abiotic factors such as soil fertility also affect the abundance and distribution of gall-inducing insect species generating patterns in some communities (Blanche 1994; Cuevas-Reyes et al. 2003, 2004b, 2011). For example, water and nutrients availability in the soil are important factors influencing both growth and chemical quality of plants (White 1984), because in stressed environments (i.e. lower availability of water and nutrients), plants show low growth rates and high concentrations of secondary metabolites (Blanche 1994; Blanche and Westoby 1995; Coley and Barone 1996), that in turns, indirectly affects the incidence of gall-inducing insects increasing their abundance and richness on host plants since gall-inducing insects have the ability to sequester secondary compounds and nutrients in the gall tissue as protection against natural enemies (Hartley 1998; Pascual-Alvarado et al. 2008). This has been corroborated in different studies that indicated greater survival, abundance and species richness of gall-inducing insects on hosts that growth under harsher conditions (Waring and Price 1990; Fernandes and Price 1988, 1991; Fernandes et al. 1994; Cuevas-Reyes et al. 2004b, 2011).

Fertile soils at latitudinal scale represent a gradient of different conditions of nutrient status where several factors such as temperature and seasonal rain patterns determine availability of nutrients to plants (Clinebell et al. 1995). In contrast, at a regional scale it is possible to delimit land units with different soil types to evaluate directly the effects of soil fertility on gall-inducing insect species richness. Tropical dry forests develop on very different kinds of soil in terms of their fertility (Mooney et al. 1995). Therefore, tropical dry forest results ideal to evaluate the spatial patterns of herbivory and gall-inducing insect species richness.

Finally, these hypotheses have been tested independently in different localities and several authors have attempted to establish patterns at a global scale comparing results from tropical and temperate communities (Fernandes and Price 1988, 1991, 1992; Price et al. 1998). However, very few studies have tested the hypotheses of gall-inducing insect species richness in the same community with comparable methodologies (Wright and Samways 1996, 1998).

In this chapter, we show the variation in species richness of gall-inducing insects in the Chamela-Cuixmala Biosphere Reserve on the Pacific coast of Jalisco, Mexico, which covers an area of 13,200 ha. The predominant vegetation is tropical deciduous forest, with some patches of tropical riparian forest (Rzedowski 1978). Deciduous habitats are seasonal and xeric, while riparian habitats are aseasonal and mesic (Lott et al. 1987). Plants that occur in these habitats differ in their phenology soil fertility and moisture availability (Lott et al. 1987). Deciduous and riparian habitats have differences in foliar phenological patterns as a response to temporal availability of rainfall and hydrological processes (Bullock 1985; Frankie et al. 1974; Opler et al. 1980). In these habitats, plant species produce leaves before the initiation of the wet season and lose all leaves in the dry season. Contrary, plants that occur in riparian habitats retain a full canopy all year round and only lose 10 % of leaves in the dry season (Frankie et al. 1974). However, some species are common and ubiquitous in both habitats (Lott et al. 1987). In addition, each habitat have geomorphologic units of soil with differences among them in soil depth, pH, available phosphorus and total nitrogen contents, exchangeable base cations, particle size distribution, total organic carbon contents and the available water holding capacity (Cotler et al. 2003; Cuevas-Reyes et al. 2004b).

Geomorphologic units of soil were classified as follows: hill top over granite, hill top with conglomerate cover over tuffs, upland hills over granite, hill top over tuffs, irregular hillsides over granite, convex hills over tuffs, recent and old alluvium terraces (see Cuevas-Reyes et al. 2004b). Six geomorphologic units are located in deciduous habitats (i.e. hill top over granite, hill top with conglomerate cover over tuffs, upland hills over granite, hill top over tuffs, irregular hillsides over granite and convex hills over tuffs) and two units in riparian habitats (i.e. recent and old alluvium terraces). In both habitats, water stress during the wet season is low and sclerophyllous vegetation is not present (Reich and Borchert 1984; Holbrook et al. 1995).

24.3 Gall-Inducing Insect Diversity: Sampling Design in a Mexican Tropical Dry Forest

24.3.1 Biotic Factors

We sampled 30 transects of 50×5 m in each of two independent deciduous and riparian habitats at Chamela and Cuixmala (i.e. 60 transects in deciduous and 60 transects in riparian habitats) to determine gall-inducing insect diversity. Transects were randomly selected from points obtained from a grid system developed within each habitat using random numbers. Plant species were identified and the presence and identity of gall-inducing insect species on trees, shrubs, herbs and climbers were recorded within each transect. Gall-inducing insect were identified and counted on the basis of plant species and gall morphology.

Three branches were collected from the top, intermediate and bottom strata of the canopy of each individual for all plant life forms and, we recorded all gall-inducing insect species. Because many studies have considered that each gall morphology represent a different gall-inducing insect species on a particular host plant, we verify this specificity of each galling insect collected in the field by their taxonomic identification, rearing galls to adults in the laboratory.

We recorded the frequency of gall-inducing insects on trees, shrubs, herbs and climbers of host plants in each transect to test the structural complexity hypothesis. To control for plant age, the stem diameter at breast height (DBH) was measured for each tree and shrub. We estimated the frequency of gall-inducing insects on trees and shrubs to test their susceptibility to galls in different ontogenetic stages. Plant species density was estimated in each transect and the frequency and mean number of galls on each host plant were recorded. After a preliminary analysis of presence of gall-inducing insect species and their host plants in deciduous and riparian habitats at Chamela-Cuixmala Biosphere reserve, we found that only six gall-inducing species occur in both habitats. Therefore, to compare the susceptibility to galls on the same plant species located in different habitat conditions, mean number of galls per plant in each host species was estimated to each transect.

To compare the floristic similarity among deciduous and riparian habitats, we 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 most diverse flora, and N2 = species number of the less diverse flora (Cuevas-Reyes et al. 2004b). In addition, a *t* test was performed to compare the plant species richness between deciduous and riparian habitats. We performed a logistic regression analysis using GENMOD procedure (SAS 2000), to test if the frequency of gall-inducing insect families (dependent variable) is different between life forms of plants (independent variable).

We used a two-way ANOVA to determine the effect of life forms of plants (trees, shrubs and climbers) and habitat type (as independent variables) on the number of gall-inducing insect species (response variable). A LSMeans test was used for *a posteriori* comparisons. The number of gall-inducing insect 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 plants with galls, using a logistic regression analysis CATMOD procedure (SAS 2000), a general procedure for modelling categorical data).

To test if gall-inducing insect species richness is related with plant species richness, in each habitat we applied a linear regression analysis. To determinate in which habitats host plants supported more gall-inducing insect species, we applied a *t* paired test for each of the six plant species that occur in both habitats. Box-cox transformation data was applied on each plant species.

To test if the frequency of gall-inducing insects is influenced by host plant age, we applied a logistic regression analysis GENMOD (SAS 2000), which is a general procedure for modeling a binary logit for each plant species separately. Plant age was considered as the independent variable and frequency of gall-inducing insects was used as the response variable. A *t* test was conducted to evaluate the differences in plant density between deciduous and riparian habitats. Similar analyses were applied to determine the differences in gall-inducing insect species richness and abundance among habitats respectively.

To determinate the effect of plant density on the frequency of galls per plant for each plant species, we conducted a linear regression analysis using PROC CATMOD procedures.

24.3.2 Abiotic Factors

We selected eight different geomorphologic units of soil, which differ in soil types, topography, nutrient concentration and type of vegetation. Six geomorphologic units are localized in deciduous habitats (i.e. upland hills over granite, hill top over tuffs, convex hills over tuffs, irregular hillsides over granite, hill top over granite and hill top with conglomerate cover over tuffs) and two geomorphologic in riparian habitats (i.e. recent and old alluvium terraces). In each geomorphologic unit, we randomly sampled five transects of 50×5 m (i.e. 40 transects). In order to estimate gall-inducing insect species richness, we identified and collected all gall-inducing insect species and their respective host plants in all geomorphologic units. We verified the degree of specificity of each gall-inducing insect, identifying taxonomically each insect specimen collected in the field and rearing galls in the laboratory until the emergence of adult insects.

We considered three levels of soil fertility to evaluate the effects of phosphorous and nitrogen availability on gall-inducing species richness. The level of low fertility includes the following geomorphologic units: hill top over granite, hill top with conglomeritic cover over tuffs and hills top over tuffs; moderate fertility (upland hills over granite and irregular hillsides over granite) and high fertility (recent alluvium terrace, convex hills over tuffs and old alluvium terrace) (see Table 24.5).

We found that only 11 gall-inducing insect species were always present in all the selected geomorphologic units. Therefore, to compare the susceptibility to galls on the same plant species located under different soil nutrient availability, frequency of plants with galls and the mean gall number per plant were estimated only in these plant species. Fifty leaves were randomly collected in plants of 11 specific host species in all geomorphologic units and the gall abundance was estimated in order to test if soil fertility reduces the damage by gall-inducing insects.

To determinate the differences of content in soil properties between different geomorphologic units, we applied an ANOVA to compare each soil property at the eight geomorphologic units (box-cox transformation data) and Tukey's test (Stokes et al. 2000). Geomorphologic units were used as independent variables, and each soil property as the response variable.

A linear regression analysis was used to evaluate the relationship between gall-inducing insect species richness and soil fertility in all geomorphologic units of soil. We included the total number of gall-inducing insect species that occur in all geomorphologic units.

The effect of soil fertility on the number of gall-inducing insect species was tested with one-way ANOVA to nitrogen and phosphorous availability independently. We considered fertility levels (low, moderate and high) as independent variable and galling richness as response variable.

In the 11 gall-inducing insect species that occur in all geomorphologic units, we used a generalized linear model analysis to evaluate if the frequency of plants with galls and de mean number of gall per plant depend upon soil fertility.

24.4 Diversity Patterns of Gall-Inducing Insects

24.4.1 Importance of Biotic Factors

We found 39 gall-inducing insect species represented in the following orders: Diptera (Cecidomyiidae) induced the majority of galls in both habitats with 27 species (69.2 %); Homoptera (Psyllidae) (5.2 %) and Kermidae (7.7 %),

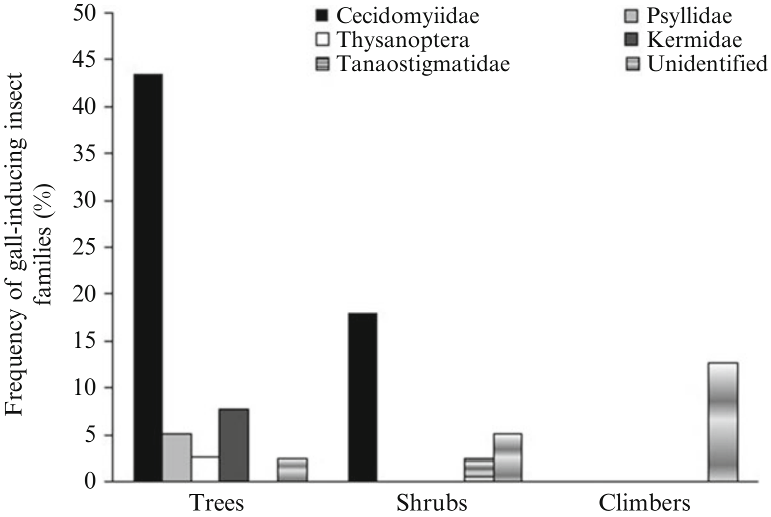

Fig. 24.1 Differences in the incidence of gall-inducing insect families on trees, shrubs and climbers

Table 24.1 Number of galled and ungalled plant species recorded in a Mexican tropical dry forest

Plant species	Deciduous habitats (%)	Riparian habitats (%)	Total (%)
Exclusive plant species	73 (42.3)	65 (37.8)	140 (80.2)
Shared plant species	34 (19.8)	34 (19.8)	34 (19.8)
Galled plant species	26 (24.3)	19 (19.2)	39 (22.4)
Exclusive galled plant species	20 (76.9)	13 (68.2)	33 (84.6)
Shared galled plant species	6 (23.1)	6 (31.6)	6 (15.4)
Sampled area	15,000 m^2	15,000 m^2	30,000 m^2

Hymenoptera (Tanaostigmatidae (2.6 %)) and Thysanoptera (2.6 %) galls being rare, and 15.4 % were unidentified. In all cases, the gall-inducing insect species maintain a great specificity on their host plant species; each gall-inducing insect species is associated with a different plant species. Only six galling species occurred in both habitats. In addition, we found that the frequency of gall-inducing insect family was different on trees, shrubs and climbers ($\chi^2 = 34.6$, d.f. = 5, $P < 0.001$, Fig. 24.1).

We observed a total of 174 plant species grouped in 37 families, of which 39 (22.7 %) were associated to specific gall-inducing species. From this, 73 plant species (42.3 %) were restricted to deciduous habitats and 65 (37.8 %) to riparian habitats. Only 34 plant species (19.8 %) occurred in both habitats types (Table 24.1). The plant species composition of Chamela-Cuixmala is very heterogeneous between habitats. The deciduous and riparian comparison shows low similarity in plant species composition (20 %), and gall-inducing species composition (15.3 %).

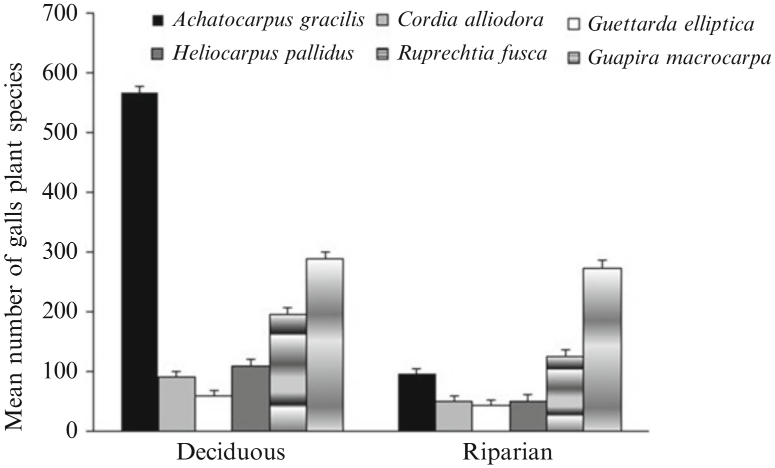

Fig. 24.2 Comparison of gall abundance in six host plant species that occurred in deciduous and riparian habitats. *t* paired test (box-cox transformation data) was applied on each plant species

No significance differences were found between deciduous and riparian habitats in the number of plant species ($t=0.4$; d.f. = 1; $P>0.05$). Deciduous habitats have similar number of tree species ($n=41$), shrubs ($n=37$) than riparian habitats in trees ($n=37$) and shrubs ($n=32$).

Six galling species occurred in both habitats, of these, five species supported more number of galls in deciduous than in riparian habitats: *A. gracilis* ($t=15.9$, d.f. = 1, $P<0.0001$), *C. alliodora* ($t=7.9$, d.f. = 1, $P<0.001$); *G. elliptica* ($t=10.1$, d.f. = 1, $P<0.01$); *R. fusca* ($t=13.6.1$, d.f. = 1, $P<0.001$, Fig. 24.2).

Gall-inducing insect species richness and plant species richness was positively correlated with plant species richness in deciduous ($y=0.3979x-2.93$, $r^2=0.89$); and riparian habitats ($y=0.3772\text{x}-2.04$, $r^2=78.6$ %, $F=198.3$, $P<0.0001$) corroborating the pattern predicted by plant species richness hypothesis (Fig. 24.3).

The gall-inducing insect species richness was associated with certain life forms of host plants. Galling richness was higher as structural complexity increases in both habitats being greater in deciduous than riparian habitats for both trees and shrubs ($F=130.4$; $P<0.001$) (Fig. 24.4a).

We found a total of 2,046 plants with galls on trees, shrubs and climbers, of which 58.8 % were presents in deciduous and 41.2 % in riparian habitats. The frequency of plants with galls was higher in deciduous than in riparian habitats (habitat $\chi^2=18.8$, d.f. = 2, $P<0.0001$) Particularly, in deciduous habitat, the frequency of plants with galls was greater in shrubs than trees and climbers (life form $\chi^2=8.0$, d.f. = 2, $P<0.004$), whereas riparian habitats, the frequency of plant with galls was greater in trees than shrubs and climbers (life form $\chi^2=10.5$, d.f. = 2, $P<0.001$).

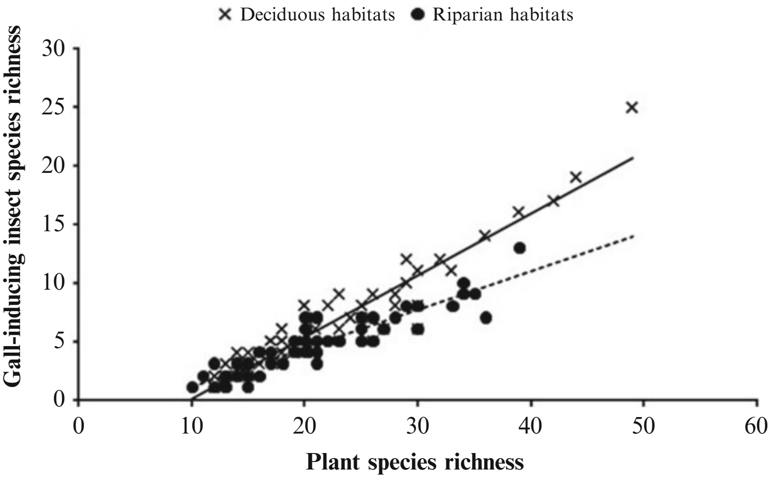

Fig. 24.3 Relationships between gall-inducing insect species richness and plant species richness in Chamela-Cuixmala Biosphere reserve in Jalisco, Mexico. Regression models were utilized in each habitat. Each *point* represents a sampling unit in different habitats

These results corroborate partially the plant structural complexity hypothesis (Fig. 24.4b).

The frequency of gall-inducing insects on host plants was greater in saplings than mature trees and shrubs. Of the total of plant species, 74.2 % had higher frequency of galls on saplings. Euphorbiaceae and Leguminosae families experienced the greatest galling richness (Table 24.2).

Plant density was significantly greater in deciduous than riparian habitats ($t = 63.7$, d.f. = 1, $P < 0.001$, Fig. 24.5a). There were no significant differences in plant density among trees and shrubs within deciduous and riparian habitats according to the Tukey-Kramer test ($P > 0.05$). Gall-inducing insect species ($t = 51.1$, d.f. = 1, $P < 0.001$, Fig. 24.5b) and gall abundance ($t = 77.3$, d.f. = 1, $P < 0.0001$, Fig. 24.5c) were higher in deciduous than in riparian habitats. In addition, the gall frequency increased with plant density in 18 host plants (50 % of total galled plant species (Table 24.3).

24.4.2 *Importance of Abiotic Factors*

In total for all geomorphologic units of soil, we found 38 gall-inducing insect species, of which, 11 occur in all geomorphologic units (Table 24.4). Geomorphologic units differed significantly in soil properties (Table 24.5). Phosphorous and nitrogen concentrations were chosen as indicators of soil fertility as in other studies (i.e. Blanche 1994). Phosphorous content was greater in alluvial soils and convex

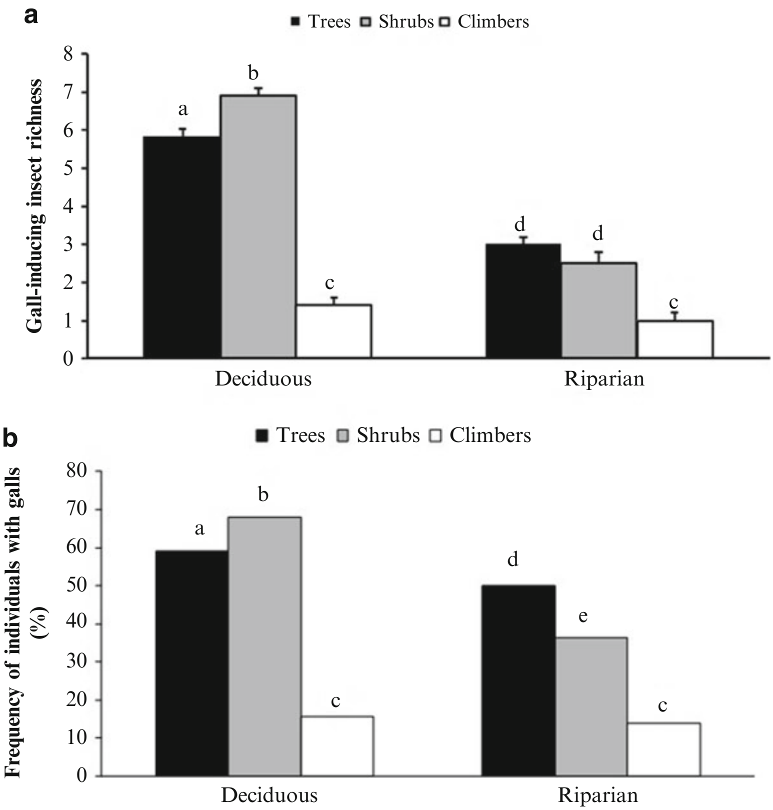

Fig. 24.4 Gall-inducing insect species richness on different life forms in deciduous and riparian habitats in a Mexican tropical dry forest (**a**). Two-way ANOVA analysis was applied between habitats and life forms of plants. Non-transformed data are shown. Means with the same letter did not differ significantly after a LSMeans test ($P<0.05$) by all life forms. Frequency of galling-inducing insect species on different life forms of host plants in deciduous and riparian habitats. PROC CATMOD procedure was applied for determine effects of habitat and life form of host plants on the frequency of plants with galls (**b**)

hills over tuffs than other geomorphologic units ($F=57.4$, $P<0.0001$). A similar pattern was found with nitrogen availability, which was greater in alluvial soils and irregular hillsides over granite than other geomorphologic units ($F=17.4$, $P<0.0001$, Table 24.5).

We found that the number of gall-inducing insect species was negatively correlated with nitrogen ($y=7.3x+24.9$, $r^2=0.46$, $P<0.01$, Fig. 24.6a) and phosphorous content ($y=1.2x+25.6$, $r^2=0.76$, $P<0.001$, Fig. 24.6b).

The effects of soil fertility on gall-inducing species richness were statistically significance (Nitrogen availability: $F=19.4$, d.f. $=2$, $P<0.001$, Fig. 24.7a) (Phosphorous availability: ($F=24.8$, d.f. $=2$, $P<0.0001$, Fig. 24.7b).

Table 24.2 Frequency of gall-inducing insect species on sampling of trees and shrubs in some plant species at Chamela-Cuixmala Biosphere reserve, Jalisco, México. PROC GENMODE procedure (SAS 2000) was applied for modeling binary logit to each plant species

Family	Host plant taxa	Gall taxa	Host plant age maximum likelihood estimates	χ^2	$P <$
Achatocarpaceae	*Achatocarpus gracialis*	Unidentified	–0.24	10.3	0.001
Apocynaceae	*Thevetia ovata*	*Aspondylia sp2.*	–0.62	16.6	0.0001
Bignoniaceae	*Bignoniaceae*	*Cecidomyiidae*: *Diptera*	–1.36	11.3	0.0008
Bombacaceae	*Ceiba aesculifolia*	*Coccoidea*: *Homoptera*	–0.16	3.2	**n.s.**
	Ceiba grandiflora	*Coccoidea*: *Homoptera*	–0.12	1.9	**n.s.**
Boraginaceae	*Cordia alliodora*	*Neolasioptera sp.*	–0.79	46.6	0.0001
Burseraceae	*Bursera excelsa*	*Cecidomyiidae*: *Diptera*	–1.13	11.9	0.0005
	Bursera instabilis	*Cecidomyiidae*: *Diptera*	–0.38	7.3	0.006
Convulvalaceae	*Ipomoea wolcottiana*	*Aspondylia convolvuli*	–0.46	24.6	0.0001
Erythroxylacaceae	*Erythroxylum mexicanum*	*Neolasioptera erythroxyli*	–0.62	2.3	**n.s**.
Euphorbiaceae	*Croton alamosanus*	*Cecidomyiidae*: *Diptera*	–0.46	19.5	0.0001
	Croton pseudoniveus	*Cecidomyiidae*: *Diptera*	–0.37	13.6	0.0002
	Croton suberosus	*Cecidomyiidae*: *Diptera*	–0.6	36.8	0.0001
	Jatropha malacophylla	*Aspondylia sp.*	–0.04	0.46	**n.s.**
	Jatropha standleyi	*Cecidomyiidae*: *Diptera*	–0.29	16.9	0.0001
Flacourtiaceae	*Flacourtiaceae*	*Cecidomyiidae*: *Diptera*	–0.99	10.6	0.001
Hernandiaceae	*Gyrocarpus jatrophifolius*	*Thysanoptera*	–0.76	17.5	0.0001
Leguminosae	*Caesalpinia caladenia*	*Cecidomyiidae*: *Diptera*	–0.06	0.53	**n.s.**
	Cynometra oaxacana	*Cecidomyiidae*: *Diptera*	–0.15	26.6	0.0001
	Lonchocarpus eriocarinalis	*Euphalerus sp.*	–0.55	20.6	0.0001
	Lonchocarpus sp.	*Euphalerus sp1.*	–0.7	11.7	0.0006
	Prosopis sp.	*Tanaostigma sp.*	–0.58	15.6	0.0001
Moraceae	*Brosimum alicastrum*	*Trioza rusellae*	–0.23	24.2	0.0001
	Chlorophora tinctoria	*Clinodiplosis chlorophora*	–0.19	5.6	0.01
	Ficus cotinifolia	*Cecidomyiidae*: *Diptera*	–0.02	0.95	**n.s.**

(continued)

Table 24.2 (continued)

Family	Host plant taxa	Gall taxa	Host plant age maximum likelihood estimates	χ^2	$P <$
Nictagynaceae	*Guapira macrocarpa*	Unidentified	–0.32	17.4	0.0001
Polygonaceae	*Coccoloba barbadensis*	*Ctenodactylomyia sp.*	–1.31	2.2	**n.s.**
	Ruprechtia fusca	Unidentified	–1.4	31.9	0.0001
Rubiaceae	*Guettarda elliptica*	*Cecidomyiidae*: *Diptera*	–0.61	21.6	0.0001
	Randia spinosa	Unidentified	–0.06	1.1	**n.s.**
Sapindaceae	*Thounidium decandrum*	Unidentified	0.011	0.01	**n.s.**
Simaroubaceae	*Recchia mexicana*	Unidentified	–0.31	12.7	0.004
Tiliaceae	*Heliocarpus pallidus*	*Neolasioptera heliocarpi*	–0.18	12.0	0.0005
Urticaceae	*Urera caracasana*	*Cecidomyiidae*: *Diptera*	–0.14	11.2	0.0008
Verbenaceae	*Vitex hemsleyi*	*Cecidomyiidae*: *Diptera*	–0.86	9.6	0.001

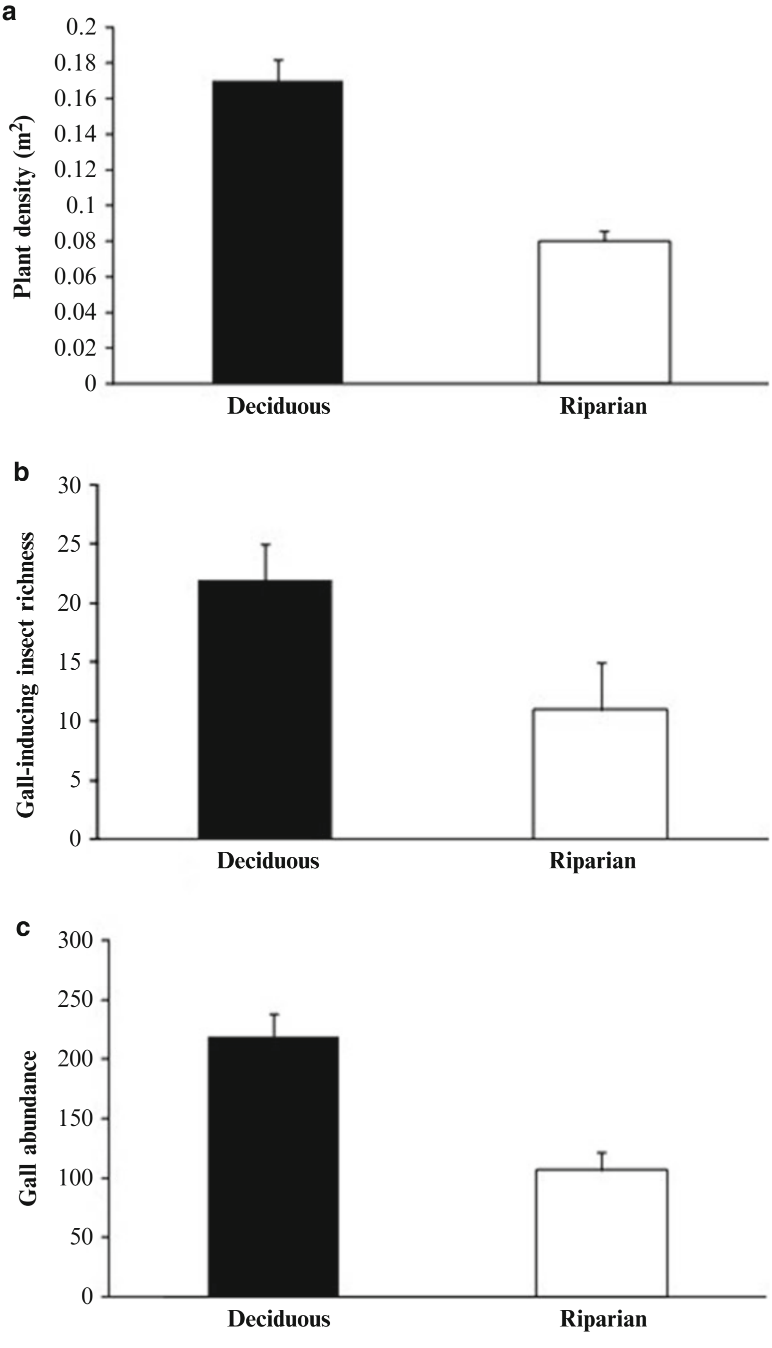

Fig. 24.5 Effects of plant density on gall-inducing insect species. Differences in plant density among deciduous and riparian habitats (**a**); Comparison of gall-inducing insect species between deciduous and riparian habitats (**b**); Patterns of gall abundance in deciduous and riparian habitats (**c**)

Table 24.3 Relationship between frequency of galls and plant density host in Chamela-Cuixmala Biosphere reserve, Jalisco, México. PROC CATMOD procedure (SAS 2000) was applied for modeling binary logit to each plant species

Family	Host plant species	Gall taxa	Host plant density	χ^2	$P<$
Achatocarpaceae	*Achatocarpus gracialis*	Unidentified	20.71	4.29	0.0381
Boraginaceae	*Cordia alliodora*	*Neolasioptera sp.*	39.63	4.95	0.0261
Burseraceae	*Bursera instabilis*	*Cecidomyiidae*: *Diptera*	95.41	3.96	0.0464
Convulvalaceae	*Ipomoea wolcottiana*	*Aspondylia convolvuli*	48.77	15.06	0.0001
Euphorbiaceae	*Croton alamosanus*	*Cecidomyiidae*: *Diptera*	10.46	9.14	0.0025
	Croton pseudoniveus	*Cecidomyiidae*: *Diptera*	136.0	10.05	0.0015
	Croton suberosus	*Cecidomyiidae* : *Diptera*	30.16	13.38	0.0003
Hernandiaceae	*Gyrocarpus jatrophifolius*	*Thysanoptera*	29.86	10.42	0.0012
Leguminosae	*Caesalpinia caladenia*	*Cecidomyiidae*: *Diptera*	29.53	18.1	0.0001
	Cynometra oaxacana	*Cecidomyiidae*: *Diptera*	22.48	31.2	0.0001
Moraceae	*Brosimum alicastrum*	*Trioza rusellae*	28.15	20.12	0.0001
Nyctaginaceae	*Guapira macrocarpa*	Unidentified	24.6	14.06	0.0002
Polygonaceae	*Coccoloba barbadensis*	*Ctenodactylomyia sp.*	59.26	12.92	0.0003
	Ruprechtia fusca	Unidentified	43.76	10.64	0.0011
Simaroubaceae	*Recchia mexicana*	*Unidentified*	112.4	8.17	0.0042
Tiliaceae	*Heliocarpus pallidus*	*Neolasioptera heliocarpi*	45.09	7.53	0.0061
Urticaceae	*Urera caracasana*	*Cecidomyiidae*: *Diptera*	132.0	14.22	0.0002
Verbenaceae	*Vitex hemsleyi*	*Cecidomyiidae*: *Diptera*	46.17	6.13	0.0133
Apocynaceae	*Thevetia ovata*	*Aspondylia sp2*	8.36	0.2432	**n.s.**
Bignoniaceae	*Bignoniaceae*	*Cecidomyiidae*: *Diptera*	6.42	0.0171	**n.s.**
Bombacaceae	*Ceiba aesculifolia*	*Coccoidea*: *Homoptera*	2.93	0.484	**n.s.**
	Ceiba grandiflora	*Coccoidea* : *Homoptera*	58.51	1.94	**n.s.**
Burseraceae	*Bursera excelsa*	*Cecidomyiidae* : *Diptera*	77.48	3.47	**n.s.**

Erythroxylacaceae	*Erythroxylum mexicanum*	*Neolasioptera erythroxyli*	21.18	0.9444	**n.s.**
Euphorbiaceae	*Jatropha malacophylla*	*Aspondylia sp.*	35.9	2.64	**n.s.**
	Jatropha standleyi	*Cecidomyiidae*: *Diptera*	6.09	0.053	**n.s.**
Flacourtiaceae	*Flacourtiaceae*	*Cecidomyiidae*: *Diptera*	6.67	0.0077	**n.s.**
Leguminosae	*Lonchocarpus eriocarinalis*	*Euphalerus sp.*	21.23	0.445	**n.s.**
	Lonchocarpus sp.	*Euphalerus sp.*	16.37	0.4093	**n.s.**
	Prosopis sp.	*Tanaostigma sp.*	55.88	1.48	**n.s.**
Moracea	*Ficus cotinifolia*	*Cecidomyiidae*: *Diptera*	25.24	1.49	**n.s.**
	Chlorophora tinctoria	*Clinodiplosis chlorophora*	20.41	17.44	**n.s.**
Rubiaceae	*Guettarda elliptica*	*Cecidomyiidae*: *Diptera*	4.02	0.36	**n.s.**
	Randia spinosa	*Bruggmannia randiae*	46.45	1.71	**n.s.**
Sapindaceae	*Paullinia cururu*	*Cecidomyiidae*: *Diptera*	58.63	0.4897	**n.s.**
	Paullinia sessiliflora	*Cecidomyiidae*: *Diptera*	15.79	0.1358	**n.s.**
Verbenaceae	*Lippia graveolens*	*Pseudomikola lippia*	25.05	0.247	**n.s.**

Table 24.4 Orders and families of gall-inducing insect species present in tropical dry forest at Chamela-Cuixmala Biosphere reserve in Jalisco, Mexico

Family	Host plant taxa	Order	Family	Gall taxa
Achatocarpaceae	***Achatocarpus gracilis***	**Unidentified**	**Unidentified**	**Unidentified**
Apocynaceae	*Thevetia ovata*	Diptera	Cecidomyiidae	*Aspondylia sp2*
Bignoniaceae	*Bignoniaceae*	Diptera	Cecidomyiidae	Cecidomyiidae
Bombacaceae	*Ceiba aesculifolia*	Homoptera	Psyllidae	Psyllidae
	Ceiba grandiflora	Homoptera	Psyllidae	Psyllidae
Boraginaceae	***Cordia alliodora***	**Diptera**	**Cecidomyiidae**	***Neolasioptera sp***
Burseraceae	*Bursera excelsa*	Diptera	Cecidomyiidae	Cecidomyiidae
	Bursera instabilis	Diptera	Cecidomyiidae	Cecidomyiidae
Convulvalaceae	***Ipomoea wolcottiana***	**Diptera**	**Cecidomyiidae**	***Aspondylia convolvuli***
Erythroxylacaceae	*Erythroxylum mexicanum*	Diptera	Cecidomyiidae	*Neolasioptera erythroxyli*
Euphorbiaceae	*Croton alamosanus*	Diptera	Cecidomyiidae	*sp1*
	Croton pseudoniveus	**Diptera**	**Cecidomyiidae**	***sp2***
	Croton suberosus	Diptera	Cecidomyiidae	*sp3*
	Jatropha malacophylla	**Diptera**	**Cecidomyiidae**	***Aspondylia sp***
	Jatropha standleyi	Diptera	Cecidomyiidae	Cecidomyiidae
Flacourtiaceae	*Flacourtiaceae*	Diptera	Cecidomyiidae	Cecidomyiidae
Hernandiaceae	*Gyrocarpus jatrophifolius*	Thysanoptera		Thysanoptera
Leguminosae	*Caesalpinia caladenia*	Diptera	Cecidomyiidae	Cecidomyiidae
	Cynometra oaxacana	Diptera	Cecidomyiidae	Cecidomyiidae
	Lonchocarpus eriocarinalis	**Homoptera**	**Kermidae**	***Euphalerus sp1***
	Lonchocarpus sp	**Homoptera**	**Kermidae**	***Euphalerus sp2***
	Prosopis sp	Hymenoptera	Tanaostigmatidae	*Tanaostigma sp*
Moraceae	*Brosimum alicastrum*	Homoptera	Kermidae	*Trioza rusellae*
	Chlorophora tinctoria	Diptera	Cecidomyiidae	*Clinodiplosis chlorophora*
	Ficus cotinifolia	Diptera	Cecidomyiidae	Cecidomyiidae

Nictagynaceae	***Guapira macrocarpa***	**Unidentified**	**Unidentified**	**Unidentified**
Polygonaceae	*Coccoloba barbadensis*	Diptera	Cecidomyiidae	*Ctenodactylomyia sp*
	Ruprechtia fusca	**Diptera**	**Cecidomyiidae**	**Cecidomyiidae**
Rubiaceae	***Guettarda elliptica***	**Diptera**	**Cecidomyiidae**	**Cecidomyiidae**
	Randia spinosa	Diptera	Cecidomyiidae	*Bruggmannia randiae*
Sapindaceae	*Paullinia cururu*	Diptera	Cecidomyiidae	*sp1*
	Paullinia sessiliflora	Diptera	Cecidomyiidae	*sp2*
	Thounidium decandrum	Unidentified	Unidentified	Unidentified
Simaroubaceae	*Recchia mexicana*	Unidentified	Unidentified	Unidentified
Tiliaceae	***Heliocarpus pallidus***	**Diptera**	**Cecidomyiidae**	***Neolasioptera heliocarpi***
Urticaceae	*Urera caracasana*	Diptera	Cecidomyiidae	Cecidomyiidae
Verbenaceae	*Lippia graveolens*	Diptera	Cecidomyiidae	*Pseudomikola lippia*
	Vitex hemsleyi	Diptera	Cecidomyiidae	*Cecidomyiidae*

Table 24.5 Comparison of soil properties among different geomorphological units in Chamela-Cuixmala Biosphere Reserve in Jalisco (Data from Cotler et al. 2003). Different letters indicate statistically significant differences among geomorphological units after a Tukey test ($P<0.05$)

Soil properties	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	*F*	*P* <
Phosphorous (mg kg^{-1})	0.19 (± 0.04)^{f}	0.36 (± 0.09)^{a}	0.64 (± 0.09)^{a}	0.47 (± 0.09)^{a}	1.7 (± 0.23)^{e}	3.8 (± 0.25)^{d}	7.4 (± 0.4)^{c}	11.7 (± 0.4)^{b}	57.4	0.0001
Nitrogen (Kg m^{-2})	0.1 (± 0.06)^{d}	0.2 (± 0.09)^{d}	0.57 (± 0.1)^{a}	0.37 (± 0.08)^{a}	1.1 (± 0.1)^{c}	0.84 (± 0.1)^{c}	0.54 (± 0.1)^{a}	1.9 (± 0.18)^{b}	17.4	0.0001
Calcium (cmol$_{c}$ kg^{-1})	5.1 (± 0.4)^{c}	17.3 (± 0.7)^{a}	32.8 (± 0.4)^{a}	19.8 (± 0.4)^{a}	7.0 (± 0.4)^{c}	5.6 (± 0.4)^{c}	18.5 (± 0.6)^{a}	15.0 (± 0.2)^{b}	12.6	0.0001
Magnesium (cmol$_{c}$ kg^{-1})	2.6 (± 0.2)^{a}	8.4 (± 0.3)^{b}	3.3 (± 0.2)^{a}	7.7 (± 0.3)^{b}	2.2 (± 0.2)^{a}	2.5 (± 0.2)^{a}	8.9 (± 0.2)^{b}	3.3 (± 0.2)^{a}	21.2	0.0001
Sodium (cmol$_{c}$ kg^{-1})	0.07 (± 0.01)^{b}	0.17 (± 0.07)^{a}	0.21 (± 0.02)^{a}	0.07 (± 0.04)^{b}	0.15 (± 0.04)^{a}	0.18 (± 0.06)^{a}	0.1 (± 0.02)^{b}	0.2 (± 0.03)^{a}	6.0	0.0002
Humus (Kg m^{-2})	9.2 (± 0.25)^{b}	7.1 (± 0.1)^{b}	7.1 (± 0.3)^{a}	0.4 (± 0.08)^{b}	8.5 (± 0.23)^{b}	0.8 (± 0.1)^{b}	0.5 (± 0.09)^{b}	15.0 (± 0.15)^{c}	113.2	0.0001

Hill top over granite (1)
Hill top with conglomeritic cover over tuffs (2)
Upland hills over granite (3)
Hills top over tuffs (4)
Irregular hillsides over granite (5)
Recent alluvium terrace (6)
Convex hills over tuffs (7)
Old alluvium terrace (8)

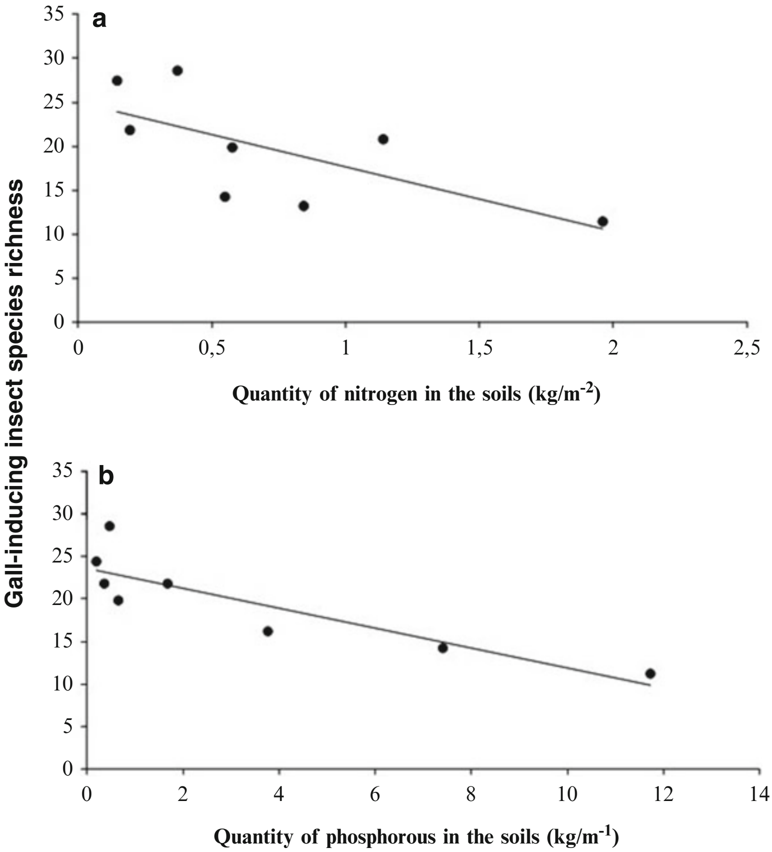

Fig. 24.6 Relationships between gall-inducing insect species richness and total nitrogen amount in soil (**a**); and available phosphorous at the Chamela-Cuixmala Biosphere reserve in Jalisco, Mexico (**b**) Regression models were utilized in each nutrient of soil. Each *point* represents a sampling unit in different land units

We registered only 11 gall-inducing insect species associated with specific host plants that occur in all geomorphologic units, the rest of galling species were present in one or another geomorphologic unit. In this 11 plant species, we recorded a total of 834 plants with galls. The frequency of plant with galls was significantly greater in soils with low fertility such as hill top over granite, hill top with conglomeritic cover over tuffs and hills top over tuffs than other geomorphologic units with higher soil fertility (soils: $\chi^2 = 34.2$, d.f. = 7, $P < 0.0001$, Fig. 24.8a). Finally, mean number of galls per plant was higher in geomorphologic units with low fertility in comparison with sites of higher fertility (soils: $\chi^2 = 47.8$, d.f. = 7, $P < 0.0001$, Fig. 24.8b).

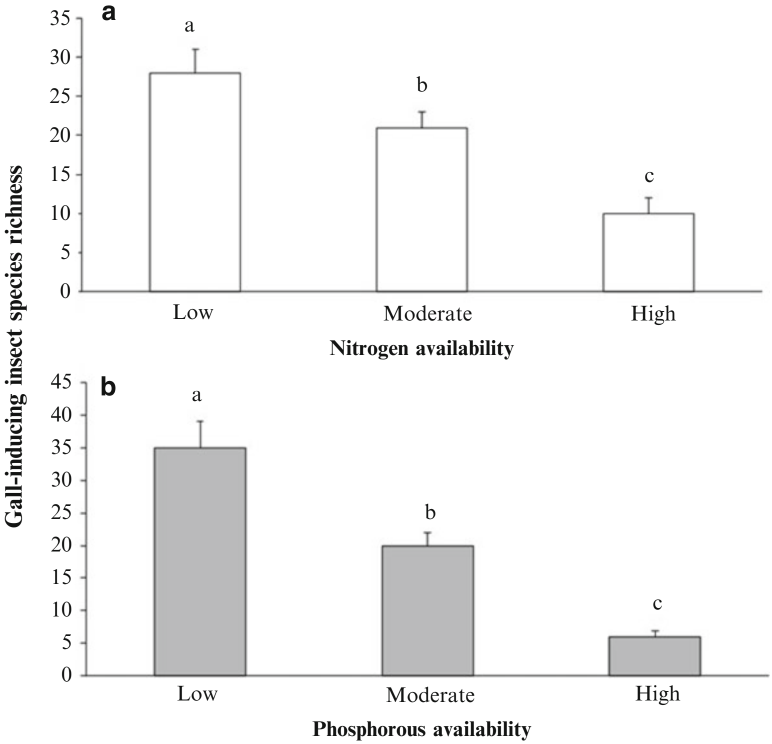

Fig. 24.7 Effects of soil fertility on gall-inducing insect species. Comparison of galling richness between low, moderate and high availability of nitrogen in the soils (**a**); Differences in galling richness between different available phosphorous (**b**). One-way ANOVA test was conducted for each soil nutrient. Means with the same letter did not differ significantly after a LSMeans test ($P < 0.05$)

24.5 Explanation of Gall-Inducing Insects Species Diversity

24.5.1 Importance of Biotic Factors

The taxonomy of groups such as gall-inducing insects are little studied. Several studies assumed that gall morphology is unique to each gall-inducing insect species and that each gall species is specific to a single plant species (Floate et al. 1996; Hartley 1998; Price et al. 1998; Nyman et al. 2000; Cuevas-Reyes et al. 2003; Oyama et al. 2003). However, none of these studies assess the specificity of galling insect species with their respective host plants. In some cases a single plant species hosted numerous gall-inducing insect species such as species of *Pontania* on *Salix* (willows), species of *Asphondylia* on *Larrea tridentate* and different galling species on *Baccharis* species (Fernandes and Price 1988; Waring and Price 1989).

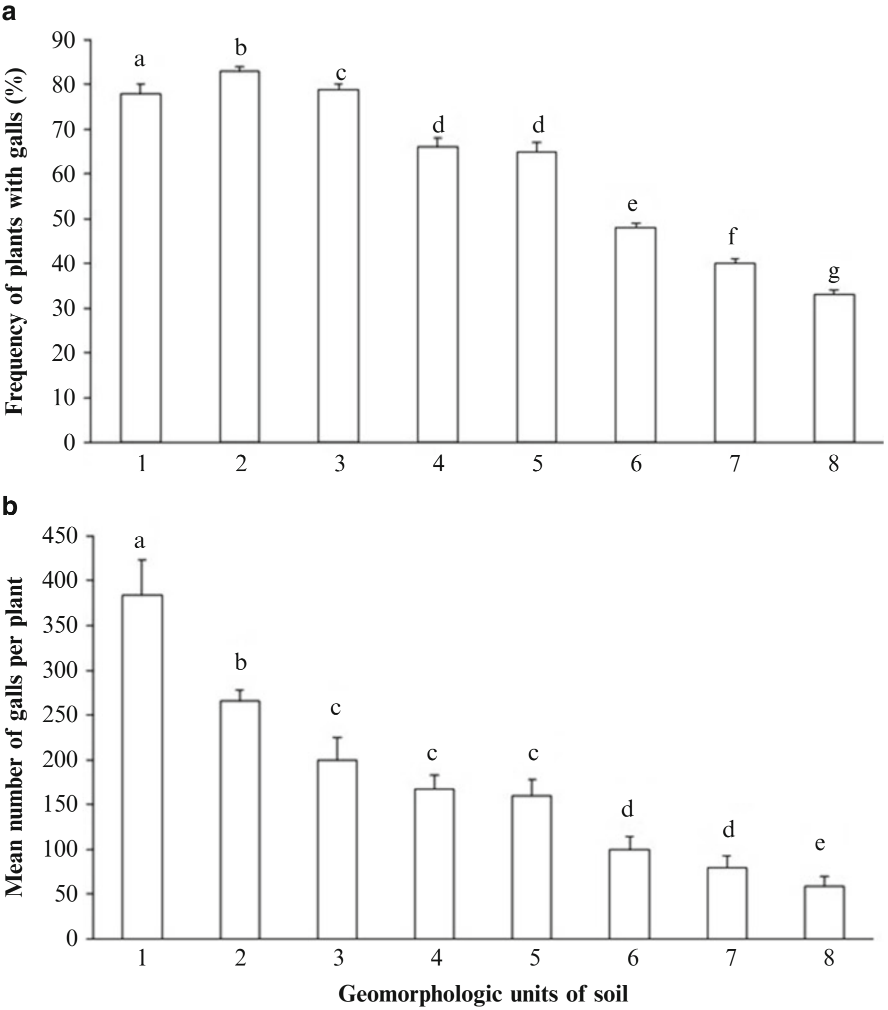

Fig. 24.8 Frequency of plants with galls on host plants that occur in all geomorphologic units of soils (**a**). Mean number of galls per plant on host plants that occur in all sites (**b**) GENMOD procedure (SAS 2000) were applied for generalized linear model in both analyses. Different letters indicate statistically significant differences after a least squares means test ($P < 0.05$). The sites are ordered from low to high soil fertility (*1*) hill top over granite, (*2*) hill top with conglomerate cover over tuffs, (*3*) upland hills over granite, (*4*) hills top over tuffs, (*5*) irregular hillsides over granite, (*6*) recent alluvium terrace, (*7*) convex hills over tuffs, (*8*) old alluvium terrace

In these cases, the gall- plant interactions were not specific and indicated extensive host plant shifts. Therefore, we argued that it is necessary to corroborate the specificity of galling species on host plant species in all studies of diversity. In our case, the galling species maintain a great specificity on their host plant species; each galling species is associated with a different plant species. These results corroborate assumed by some authors on high galling species specificity on their host plants (Koach and Wool 1977; Bearsley 1982; Ananthakrishan 1984; Dodson and George 1986; Weis et al. 1988).

In this study, we detected that groups such as Cecidomyiids induced the majority of galls in tropical dry forest. It is known that the gall midges are associated to a great range of host plant taxa in tropical regions (Gagné 1994; Fernandes et al. 1997; Price et al. 1998; Wright and Samways 1998). These gall midges appear to be excellent colonizing species and the induction of galls is common in isolated patches locally (Price et al. 1998). Five galling families were found in our study. The gall midges of Cecidomyiidae family (60 %) were those with the highest abundance and diversity; they were largely responsible for the patterns detected in both deciduous and riparian habitats. These gall midges species are associated with 20 different families of plants. Euphorbiaceae and Leguminosae families are very common in these habitats and support higher number of gall cecidomyiids species. This pattern may be due to historic factors and phylogenetic affinities between gall midges and plant families as result to gall-plant interaction and processes of radiation and high rates of speciation in both groups in this tropical region (Gagné 1994; Fernandes et al. 1997; Price et al. 1998; Wright and Samways 1998). Our results indicated that Cecidomyiids galls are the most diverse family of galling in the Mexican tropical dry forest. This is accord with studies that reports that Cecidomyiids are the most diversity family in Neotropical forests (Gagné 1994; Fernandes et al. 1997).

Our results showed that tropical dry forest harbor a higher galling-inducing insect species richness in comparison with others temperate and tropical regions (Wright and Samways 1996, 1998; Cuevas-Reyes et al. 2003; Oyama et al. 2003). The plant species richness may produce differences in local patterns of galling species richness because more plant species represent more potential niches to colonize (Goncalves-Alvim and Fernandes 2001). A positively relationship between galling species richness and plant species richness has been found in tropical sites (Wright and Samways 1996, 1998; Goncalves-Alvim and Fernandes 2001; Oyama et al. 2003). In our study, the galling species richness was positive correlated with plant species richness in deciduous and riparian habitats at the tropical dry forest and support the hypothesis that in tropical regions the radiation of galling species is associated with plant species richness. This correlation, suggests that at a regional scale, an increment in plant species richness at the community level results in an increase of the number of galling species (Oyama et al. 2003). In addition, we did not find differences between deciduous and riparian habitats in the incidence of galling species richness. Our results confirm that galling species richness will increase as host plant species increases and corroborating the plant species richness hypothesis.

Another factor that determines gall-inducing insect species richness is host plant architecture; plants with more ramifications, number of shoots, branches, leaves and crown volume (i.e. trees than shrubs and herbs) have more microhabitats which favoring the colonization for a wide variety of insects (Leather 1986). The plant structural complexity hypothesis has been partially supported from studies on galling species richness. Fernandes and Price (1988) found that galling species richness is higher on shrubs than trees and herbs. In this case, life forms with greater structural complexity as trees not support higher number of galling species than shrubs and herbs. In contrast, Goncalves-Alvim and Fernandes (2001) report higher galling species richness on trees followed by shrubs and herbs corroborating this hypothesis. In our study, trees and shrubs supported more galling species richness than herbs and climbers in deciduous and riparian habitats corroborating the plant structural complexity hypothesis. However although patterns in riparian habitats (trees > shrubs) were similar to Goncalves-Alvim and Fernandes (2001) and those in deciduous (shrubs > trees) were more like Fernandes and Price (1988). This pattern may be due to associated with the evolution of galling species on trees and shrubs of particular plant taxa than microhabitats availability that offered different plant architectures. The radiation and evolution of galling species involved physiological traits that affected offspring growth and reproductive success on a host plant, selective pressures exerted for predators and pathogens in different environments and female behaviors that affected the choice of host plants (Fernandes and Price 1991). Another 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 and Barone 1996), allowing trees and shrubs to provide more potential colonization sites.

In our case, the gall-inducing insect species richness on trees and shrubs was higher in deciduous than riparian habitats and the frequency of plants with damage by galls was greater in deciduous than riparian habitats. These results suggest the highest preferences of galling species by deciduous habitats (xeric habitats). The explanations of these pattern may be associated to greater predation and parasites rates on galling in riparian (mesic) than deciduous habitats (xeric), supporting the hygrothermal stress hypothesis and high level of synchrony between host and galling phenologies in deciduous habitats. De Souza (2001) suggests that seasonal vegetation such as deciduous habitats have synchronous leaf flushing with life history of galling species. Therefore, deciduous habitats are more likely to harbor higher galling species richness than others tropical systems because most insects induced galls on young plant tissues and mainly on leaves. The dynamics of leaf flushing can be important to determine possible host-shifts for dispersing insect females in this group. In our case, in deciduous habitats galling and host plants phenologies are higher synchronous, while riparian habitats we observed different galling species with galls development over the long-time reflected asynchrony phenologies (De Souza 2001).

Few studies have documented the richness and frequency of insect herbivorous on different ontogenetic stages of host plants. The patterns are not consistent, some insects guilds are more diverse on sapling plants, while others guilds are more abundant on mature plants (Basset 2001; Cuevas-Reyes et al. 2006). Differences in plant chemistry, leaf palatability, local microclimate, enemy free-space have been suggested as possible causes for these differences (Coley and Barone 1996; Castellanos et al. 2006). Microclimate effects must be consequence and may represent a behavioral barrier of many insects dispersing in the sunny upper canopy to shady understory. In our study, gall frequency was higher on saplings in 74.2 % of the total plant species. Considering host specialization of galling species, this pattern may be can be explained by two reasons, for the preference of females for sapling of host plants because them offer leaves with rapid expansion, higher nutritional quality and secondary metabolites and by the ability of galling to adapt and manipulate their host plant and secondary metabolites sequester to protection against natural enemies (Cornell 1983; Waring and Price 1990; Hartley 1998). In addition, saplings plants offer a great undifferentiated meristems that represented sites to galls induction in the majority of galling species and the physiology of gall morphogenesis requires that the insects stimulate undifferentiated plant tissues (Weis et al. 1988) which may be present some times in saplings than mature plants.

The resource concentration hypothesis proposes that gall-inducing insect species richness increase as host plant density increase. This hypothesis incorporated the roll of specificity and specialization of insects on host plants, female behaviors foraged that affected the choice of plants and different natural enemies pressures between isolated and aggregated hosts (Raupp and Denno 1979; Goncalves-Alvim and Fernandes 2001). In this study, we found that only 18 galling species (46.2 %) responded significantly to host plant density when averaged across deciduous and riparian habitats. A similar pattern was also observed by Goncalves-Alvim and Fernandes (2001) with galling species of Neotropical savannas. These results reflected that galling species richness increasing with increasing plant density. One explanation is that natural enemy's pressures are different between isolated and aggregated hosts and host plant density may act as an indicator of abundance or nutritional quality of the host plant (Janzen 1970).

24.5.2 Importance of Abiotic Factors

In Chamela-Cuixmala Biosphere Reserve, soil types combined with different conditions in temperature, humidity, soil pH and resources as nutrients and water availability, determine a patchy landscape with a mixed arrange of geomorphologic units supporting different vegetation types (Lott et al. 1987; Cotler et al. 2003). Availability of water and nutrients are also heterogeneous; seasonal rainy patterns are responsible of water stress and with respect to balance of nutrients, the limited factor in all geomorphologic units is phosphorous availability (Jaramillo and Sanford 1995). However, phosphorous concentration is high on alluvial sites, intermediate on tuffs and conglomerate sites, and low on granite sites. We used phosphorous and nitrogen availability as indicators of soil fertility. Blanche and Westoby (1995) found in Australia that galling species richness is not directly linked to soil fertility but via host plant taxon in a community dominated by *Eucalyptus spp*. The mechanism that explains this result is that eucalypts are adapted to infertile soils and always associated with galling species. In our study, galling species richness was negatively correlated with soil nitrogen and phosphorous availability across geomorphologic units of soils and corroborates the soil fertility hypothesis proposed by Fernandes and Price (1991) that suggest that plants mediated the effects of abiotic stress such as deficiency of nutriments in the soil. In addition, we categorize three levels of soil fertility (i.e. low, moderate and high) to evaluate the effects of phosphorous and nitrogen availability on gall-inducing species richness and found greater galling insect richness in soils of low fertility. The limiting macronutrients in the soils such as phosphorous and nitrogen affect the incidence of galling species on specific host plants across communities in this tropical region. The explanation of this pattern may be associated with differences in secondary metabolites and foliar nitrogen availability in host plants between different soil fertilities in all geomorphologic units (Coley and Barone 1996). Plant species respond to infertile soil by having long-lived parts defended by digestion-inhibiting secondary metabolites (Coley et al. 1985) which make them less palatable to herbivores in general. However, many galling species have the ability to manipulate the chemistry of their host plants and sequester defensive chemicals in the gall wall to protect them from external feeders that might eat the gall and natural enemies such as fungi and other pathogens (Cornell 1983). In addition, nitrogen and phosphorous deficiencies may block protein synthesis and reduce the production of starch formation in plants (White 1984). Therefore, plants growing on infertile soils may provide more potential sites to be colonized by gall insects (Cuevas-Reyes et al. 2003). Two possible explanations that are not mutually exclusive have been presented in the literature to explain the relationship between soil fertility and galling species richness. Blanche and Westoby (1995) found in Australia that galling species richness is not directly linked to soil fertility but, instead, via host plant taxon in a community dominated by *Eucalyptus spp*. The mechanism that explained this result is that eucalypts are adapted to infertile soils and may indirectly affect the incidence of galling that were already in association with the *Eucalyptus* community. In contrast, Fernandes and Price (1991) suggest that soil fertility directly affects plant traits via natural selection and that the colonization of galling species is favored by these plant traits.

Geomorphologic units with low levels of soil phosphorous and nitrogen had great incidence of individual plants with galls and great number of galls per plant. In contrast, fertility soils such as alluvial sites had low incidence of individual plants with decreased galls per plant. In some cases, plant species respond to infertile soil by having long-lived parts defended by digestion-inhibiting secondary metabolites (Coley et al. 1985), which make more difficult for external herbivores to obtain nutrients. However, many galling species have the ability to manipulate the chemistry of their host plants and sequestered defensive chemicals in gall wall close to the insect to protect them from external feeders that might eat the gall and natural enemies such as fungi and others pathogens (Cornell 1983). In addition, nitrogen and phosphorous deficiencies may block protein synthesis result in the accumulation of amino acid, as well as reducing starch formation in plants (White 1984, 1993). The mechanism above mentioned can explain this spatial pattern of galling species richness and the incidence and intensity of herbivory by galling species in Chamela-Cuixmala tropical dry forest.

Fernandes and Price (1988) suggest that galls are evolved as result to selective pressures of hot dry environments, where galls function primarily to protect insects from drying out. Our results support an alternative hypothesis proposed by Blanche and Ludwig (2001) that suggest that gall formation is primarily an adaptation to gain a better food supply from low nutrient well-defended plant tissue and not by main function of a gall. In our study, the galling species richness, the incidence and intensity of damage by these insects was higher in sites with infertile soils than fertile soils independent of specific host plant taxa, then, it is possible that this pattern may be explained by abiotic factors such as phosphorous and soil nitrogen availability rather than by adaptation of host plants to hot dry environment.

24.6 Conclusions

The species richness of galling in a tropical dry forest such as Chamela-Cuixmala, depend on the plant species richness, the life forms of host plants, the host plant age and plant density. We argued that it is necessary to corroborate the specificity of galling species on host plant species in all studies of diversity. In our case, the galling species maintain a great specificity on their host plant species; each galling species is associated with a different plant species. These results corroborate the assumed higher specificity of galling species and host plant species interaction in tropical plants. We consider for comparative purpose, similar methods must be used to test hypothesis of effects of potential factors on galling species diversity as Wright and Samways (1996, 1998) proposed.

Specialist folivores insect species show similar patterns that galling species, a positively relationships among plant species richness and insect richness at local and regional scales (Gilbert and Smiley 1978; Cornell 1983; Marquis and Braker 1994). Therefore, the role of plant species richness to radiation of many groups of specialized herbivores, including galling species is essential in tropical communities.

In addition, soil fertility is one of the factors that affect the patterns of spatial distribution of galling and favor the incidence, abundance and galling species richness at community level. In this chapter, we provided the first evidence of galling diversity for a tropical dry forest in the world.

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