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"PATRONES DE RIQUEZA DE ESPECIES DE INSECTOS FORMADORES DE AGALLAS EN UNA SELVA BAJA CADUCIFOLIA"

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"A mis padres: Pablo y María Elena por su incondicionalidad"

"A Yuri, el tesoro que descubrí en mi vida"

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RESUMEN GENERAL

En esta tesis se evaluaron diferentes hipótesis que consideran factores bióticos y abióticos para explicar la variación en la riqueza de especies de insectos formadores de agallas (IFA) en comunidades de plantas de hábitats deciduos y riparios del bosque tropical seco de la Reserva de la Biosfera Chamela-Cuixmala. Cuatro son las hipótesis que involucran factores bióticos. La primera predice que la riqueza de especies de IFA aumenta con una mayor riqueza de especies de plantas. La segunda hipótesis propone que la frecuencia de IFA se incrementa a mayor complejidad estructural en términos de la arquitectura de las formas de vida de las plantas hospederas. La tercera predice que la frecuencia de IFA es mayor en plantas juveniles que en plantas maduras y la cuarta hipótesis establece que la riqueza de especies de IFA se incrementa con la densidad de plantas hospederas. La hipótesis que incluye factores abióticos predice que la fertilidad del suelo reduce la incidencia de especies de IFA en comunidades de plantas. Además, se determinaron los patrones espacio-temporales de herbivoría por IFA y se cuantificaron los niveles de daño en hábitats deciduos y riparios. Finalmente, se determinó la diversidad y especificidad de especies de parasitoides asociados a IFA evaluando la hipótesis del hospedero "malo" ("nasty" host hipothesis) que involucra procesos ascendentes "bottom-up". Esta hipótesis establece que en los trópicos los parasitoides son especialistas y que la disponibilidad de potenciales hospederos es menor que en sitios no tropicales porque sus tejidos son químicamente más tóxicos. Los resultados de esta tesis muestran que existe una correlación positiva entre la riqueza de especies de IFA y la riqueza de especies de plantas en hábitats deciduos y riparios. La incidencia de especies de IFA fue mayor en formas de vida más complejas como árboles y arbustos que en hierbas y trepadoras. La frecuencia de IFA fue mayor en plantas juveniles que en maduras sugiriendo que los estados juveniles ofrecen sitios con meristemos indiferenciados susceptibles a la inducción de agallas. La frecuencia de IFA se incrementó a mayor densidad de plantas hospederas en 18 especies de IFA (42.2%). Utilizando el fósforo y nitrógeno como indicadores de la fertilidad del suelo, se encontró que la riqueza de IFA está relacionada negativamente con la fertilidad del suelo. Además, se registró una menor frecuencia y densidad de IFA sobre plantas que ocurren en suelos infértiles. Estos resultados indican que la fertilidad del suelo afecta la distribución espacial de IFA y favorece la riqueza, frecuencia y abundancia de especies de IFA en dos diferentes vías: (i) afectando indirectamente la riqueza de especies de IFA vía adaptaciones locales de algunas especies de plantas a diferentes condiciones de fertilidad y (ii) afectando directamente la incidencia de IFA por procesos de plasticidad fenotípica de las once especies de plantas que ocurren en el gradiente de fertilidad. Los niveles de herbivoría registrados por IFA (promedio de área foliar afectada 14.9% en la estación húmeda: rango 1.57-97.7) son considerablemente mayores que los reportados por insectos folívoros en bosques neotropicales, lo cual sugiere que este gremio de herbívoros puede tener un impacto importante sobre sus plantas hospederas en estas comunidades tropicales. Se encontraron mayores niveles de herbivoría en hábitats deciduos que en riparios durante la temporada húmeda. En hábitats riparios, la densidad de IFA fue mayor en la temporada seca que en la temporada húmeda para once especies de plantas (61.1 %). Similarmente, el área foliar afectada por IFA fue significativamente mayor en la época seca que en la húmeda en doce especies de plantas (66.7 %) lo cual sugiere que en los hábitats riparios las especies de plantas presentan dos temporadas de producción masiva de hojas; los IFA colonizan hojas en la primera temporada durante la estación húmeda y acumulan o recolonizan hojas producidas en la segunda temporada durante la estación seca. En todos los casos, se encontró una gran especificidad entre especies de IFA y sus especies de

plantas hospederas, cada especie de IFA está asociada con una especie particular de planta hospedera. Por el contrario, no existió especificidad entre especies de parasitoides y sus IFA hospederos, ya que en total 13 especies de parasitoides estuvieron asociados a 29 especies diferentes de IFA. Por lo tanto, la hipótesis del hospedero "malo" es rechazada, ya que los efectos en la variación química de las plantas no se extienden al tercer nivel trófico. Se sugiere que procesos descendentes "top-down" están regulando las interacciones tróficas de las especies de IFA en esta comunidad tropical.

INTRODUCCIÓN GENERAL

La biodiversidad comprende todos los niveles de variación natural que van desde el nivel molecular y genético hasta el de especies, comunidades y ecosistemas (Roughgarden y Diamond 1986). La búsqueda de patrones de diversidad ayuda a comprender el papel que juegan los eventos históricos y contemporáneos sobre la presente distribución, abundancia y riqueza de especies. También es fundamental la exploración de factores que estén relacionados con estos patrones y los potenciales mecanismos que los explican, puesto que, para prevenir la pérdida de biodiversidad es necesario entender los patrones de diversidad de los diferentes taxa en una variedad de escalas espacio-temporales (Vinson y Hawkins 1998).

Procesos regionales y locales inciden sobre las comunidades a distintas escalas espaciales afectando la composición y el número de especies. Se asume que en una escala regional existe un conjunto de especies y que cada miembro potencialmente puede colonizar una comunidad (Lawlor y Morin 1993). Por lo tanto, la diversidad regional de especies puede afectar la diversidad local de las comunidades debido a que el conjunto de especies está disponible para colonizar diferentes sitios (Ricklefs 1987; Caley y Schluter 1997; Ricklefs 2004). A una escala regional, el conjunto de especies dado en un área biogeográfica se incrementa por procesos de especiación de taxa existentes o por inmigración dentro del área por un nuevo taxa (Schluter y Ricklefs 1993; McPeek 1996). Por el contrario, la pérdida de especies de este conjunto regional se da por extinciones o por migraciones fuera de esta área. De esta manera, los patrones locales de diversidad son fuertemente influenciados por procesos regionales como la especiación, extinción, eventos históricos y biogeográficos (Ricklefs 1987; Eldredge 1989; Cornell y Karlson 1996; McPeek 1996). Mientras que en una escala local, existen procesos de depredación, herbivoría, exclusión competitiva (e.g. interacciones bióticas) y eventos demográficos estocásticos que pueden afectar los patrones de diversidad (Ricklefs 1987).

Existen algunas evidencias del efecto que tiene la herbivoría (Claughle y Lawton 1981; Ricklefs 1987), la depredación (Paine 1966) y la competencia (Connell 1961) sobre la composición y número de especies en las comunidades en una escala local. Sin embargo, la carencia de estudios sobre interacciones bióticas en comunidades naturales impone limitaciones serias para analizar cómo las interacciones afectan la diversidad en diferentes escalas espaciales. Por ejemplo, las comunidades de insectos son un sistema de estudio muy complejo debido a su gran riqueza y abundancia relativa, su pequeño tamaño corporal y la falta de conocimiento taxonómico. La importancia de los insectos radica en que constituyen un elemento fundamental en los ecosistemas terrestres como depredadores, herbívoros, parásitos, polinizadores, recicladores de nutrientes y de materia orgánica (Southwood 1972; Samways 1994).

El conocimiento de patrones de diversidad en insectos es muy limitado. Sin embargo, se ha determinado para algunos grupos de herbívoros que la riqueza de insectos se incrementa a menores latitudes y altitudes (MacArthur 1965; Price et al. 1991; Rosenzweig 1995), con el aumento del área de distribución, abundancia y riqueza de especies de plantas hospederas sobre un continuo de escalas geográficas hasta comunidades (Price 1984; Lawton et al. 1986; Southwood et al. 1988; Frenzel y Brandl 1998). Otros factores bióticos como la distribución, densidad y patrones fenológicos foliares de plantas hospederas potencialmente pueden afectar la diversidad y estructura de la comunidad de insectos (Cornell y Lawton 1992; Basset y Novotny 1999). Particularmente, este estudio se enfoca en determinar los patrones espacio-temporales de riqueza de especies y herbivoría de insectos formadores de agallas y en evaluar algunos factores bióticos y abióticos asociados a la riqueza y abundancia de este gremio de insectos herbívoros en el bosque tropical seco de Chamela-Cuixmala.

Sistema de estudio- Los insectos formadores de agallas (IFA) representan un gremio de herbívoros endófagos que se alimentan del tejido mesófilo de sus plantas hospederas. La interacción entre los IFA con sus plantas hospederas es uno de los componentes más conspicuos en las comunidades naturales (Weis et al. 1988; Cuevas-Reyes 2003; Oyama et al. 2003) que asume un alto grado de especificidad entre los IFA y sus plantas hospederas (Moran y Southwood 1982; Cornell 1990; Fritz y Price 1988, Floate et al. 1996; Rossi y Stiling 1998).

La inducción de agallas en plantas representa un fenómeno específico y complejo que se inicia por la interacción química entre el estímulo generado por el insecto al secretar sustancias análogas a las auxinas en el momento de ovipositar o alimentarse y la liberación de sustancias químicas por parte de la planta (Williams y Benson, 1966; Ananthakishan 1984; Jauffret y Shorthouse1992). Como resultado de esta interacción, se producen alteraciones metabólicas principalmente en los procesos de desarrollo y crecimiento de los tejidos vegetales, finalizando con la formación de estructuras anormales denominadas agallas (Ananthakishan 1984; Hartley 1998, 1999). La manipulación de la planta hospedera por parte del IFA altera la composición química del tejido de la agalla (Larson y Whitham 1991; Hartley 1998), ya que estos sitios contienen un alto contenido de compuestos nitrogenados, agua y azúcares (Hartley y Lawton1992) y niveles elevados de compuestos secundarios (e.g. fenoles, terpenos) por lo que se ha propuesto que la formación de la agalla permite ciertos beneficios como el secuestro de estos compuestos asociados a funciones defensivas contra enemigos naturales (Askew 1984; Hartley y Lawton 1992; Hartley 1998).

Debido a su hábito sedentario, la formación de agallas les proporciona a estos insectos beneficios tales como un microhábitat favorable que facilita los procesos de alimentación, desarrollo y reproducción, confiriéndoles protección ante cambios climáticos, depredación y parasitismo (Price y Pschorn 1980; Ananthakrishan 1984; Weis et al. 1988; Schultz 1992). Sin embargo, para las plantas, la formación de agallas representa costos fisiológicos en la asignación de recursos a la defensa química, cambios metabólicos en la dirección del crecimiento de los diferentes órganos ya que el crecimiento de la planta es afectado por el desarrollo de agallas (Askew 1984; Larson y Whitham 1991; Hartley y Lawton 1992; Wolfe 1997; Hartley1998; Rossi y Stiling 1998), efectos negativos al reducirse el área y la capacidad fotosintética por la cobertura de agallas (Fay et al. 1996) y efectos negativos sobre el éxito reproductivo de las plantas (e.g. producción de flores, inflorescencias, semillas) (Hartnett y Abrahamson 1979; Ananthakishan 1984; Sacchi et al. 1988; Fay et al. 1996; Parra-Tabla y Bullock 1998).

Price et al. (1986, 1987, 1988,) sugieren que la formación de agallas se encuentra asociada a variables ambientales como el estrés hídrico, en este caso la cámara de la agalla confiere un microhábitat favorable sin limitaciones de agua aún en ambientes áridos o xéricos. Sin embargo, la elevada incidencia y riqueza de especies de insectos formadores de agallas encontrada en ambientes de gran humedad como bosques tropicales húmedos sugieren que la función principal de las agallas no es la de ofrecer un microclima que proteja a los insectos de la desecación (Cuevas-Reyes et al. 2003; Oyama et al. 2000). Por ello se propone una hipótesis alternativa que sugiere que la formación de agallas es considerada una adaptación a la explotación de los tejidos nutricionales de las plantas debido a la formación de una zona celular nutritiva bien determinada en la agalla que presenta un alto contenido de nitrógeno soluble, azúcares y aminoácidos. Además, cada zona forma parches aislados de células organizadas alrededor de las agallas que contienen una gran cantidad de metabolitos secundarios asociados a defensa contra enemigos naturales (Ananthakrishan 1984; Abrahamson y Weis 1987). Por lo tanto, la hipótesis nutricional sugiere que la formación de agallas es una adaptación a obtener alimento de alta calidad nutricional químicamente bien defendido (Price et al. 1986, 1987; Hartley y Lawton 1992; Hartley 1998).

Los IFA tienen la capacidad de inducir agallas con características muy particulares en su anatomía y desarrollo morfológico (Ananthakrishnan 1984; Meyer 1987). Estudios filogenéticos en IFA sugieren que éstos pueden manipular el desarrollo de la planta para modificar la morfología, esencialmente por la extensión del fenotipo de la planta (Weis et al. 1988; Stern 1995). La mayoría de los estudios que han evaluado la interacción planta-IFA han asumido que la morfología de la agalla es única para cada especie de IFA y que cada especie de insecto es específico a cada especie de planta (Ananthakrishnan 1984; Weis et al. 1988; Dreger-Jauffret y Sorthouse 1992; Floate et al. 1996; Nyman et al. 1998; Price et al. 1998; Nyman et al. 2000; Cuevas-Reyes et al. 2003; Oyama et al. 2003; Veldtman y McGeoch 2003). Sin embargo, ninguno de estos estudios ha identificado taxonómicamente la especificidad de esta interacción. Por lo tanto, resulta crucial el reconocimiento taxonómico de IFA puesto que se ha encontrado que una especie de planta puede estar asociada a diferentes especies de IFA (Fernandes y Price 1988; Waring y Price 1989; Fernandes et al. 1996). En este estudio se establece una relación taxonómica directa entre los IFA y sus plantas hospederas como base fundamental del análisis de la diversidad y de las interacciones ecológicas asociadas a este gremio.

Estructura y objetivos del estudio- Esta tesis está formada por cuatro capítulos. El primero evalúa diferentes hipótesis que han sido propuestas para explicar la variación en la riqueza y abundancia de insectos formadores de agallas (IFA). Estas hipótesis: (i) "riqueza de especies de plantas"; (ii) "complejidad estructural de plantas"; (iii) "edad de la planta hospedera" y (iv) "concentración de recursos" fueron probadas en comunidades de plantas de hábitats deciduos y riparios del bosque tropical seco de Chamela-Cuixmala, Jalisco utilizando un muestreo intensivo (3 ha) y la misma metodología para ambos hábitats. Uno de los objetivos primordiales fue determinar el grado de especificidad de los IFA sobre sus plantas hospederas debido a que la mayoría de estudios sobre diversidad de IFA asumen que cada especie de IFA induce un tipo particular de morfología de agalla. Además, en este capítulo hacemos una comparación de la riqueza de IFA dentro y entre hábitats deciduos y riparios determinando la relación que existe entre factores bióticos como la riqueza de especies de plantas, formas de vida, edad y densidad de plantas hospederas con los patrones de abundancia y riqueza de especies de IFA.

En el segundo capítulo evaluamos algunos factores abióticos asociados a la fertilidad del suelo que establecen como hipótesis que la fertilidad del suelo está relacionada negativamente con la incidencia de especies de IFA en comunidades de plantas. Determinamos la riqueza de especies de IFA en hábitats deciduos y riparios, así como la relación entre la fertilidad del suelo y la riqueza de especies de IFA y el efecto de la fertilidad del suelo sobre la frecuencia y abundancia de IFA en plantas distribuidas en dos hábitats adyacentes con diferentes condiciones de humedad, tipo de vegetación y fertilidad de suelo.

En el tercer capítulo de esta tesis determinamos los patrones espacio-temporales de herbivoría por IFA. Además, cuantificamos los niveles de daño durante la estación húmeda y seca en comunidades de plantas de hábitats deciduos y riparios. Determinamos la variación en los niveles de herbivoría por IFA dentro y entre hábitats deciduos y riparios durante la estación húmeda, el efecto de la estacionalidad sobre la herbivoría por IFA en hábitats riparios y los niveles de área foliar afectada por IFA en ambos tipos de hábitats durante la estación húmeda y seca.

En el cuarto capítulo evaluamos la hipótesis del hospedero "malo" ("nasty"host hipótesis) que fue propuesta para explicar la variación en la riqueza de parasitoides en comunidades de plantas y el grado de especialización entre especies de parasitoides y sus hospederos. El objetivo de este capítulo fue determinar la especificidad de los parasitoides tropicales utilizando la interacción tri-trófica planta-IFA-parasitoide en el bosque tropical seco de Chamela-Cuixmala.

CAPÍTULO I.

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 could increase with the richness of host plant species, with life form complexity of host plants (trees to shrubs, herbs and climbers), with host ages 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 only18 (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, host plant age, life forms, plant density, plant species richness, herbivory, plant-animal interactions, tropical dry forest

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; Goncalves-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; Goncalves-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 (e.g. 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 GII (Fernandes & Price 1988; Goncalves-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, Goncalves-Alvim & Fernandes (2001) showed that GII richness is higher in trees than either shrubs and herbs but Fernandes and 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 to 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 reduced 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, 1987; 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 & Denno1979; Goncalves-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 which 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 that covers an area of 13,200 ha. The elevation of this site ranges between 50-500 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 thirty transects of 50 x 5 m in each of two independent deciduous and riparian habitats at Chamela and Cuixmala (e.g. 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 (DBH) 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 determinate if there are differences in species richness of plants between deciduous and riparian habitats.

A linear regression analysis was used to analyze 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 (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 a general procedure for modelling categorical data).

We applied a logistic regression analysis using GENMOD (SAS 2000 a general procedure for modeling 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 in 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 present in deciduous forest and 65 (37.8%) in 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 trees (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 number 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 increases in both deciduous and riparian habitats and greater in deciduous forest than riparian habitats for trees, shrubs and climbers ($F_{2,292} = 42.48$; $r^2 = 68.2\%$; $P < 0.001$). 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 2 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 eighteen species (ca. 50% of total galled plant species) (Table 4). The mean number of GII was also positively correlated with plant density in fifteen 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 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 defenses (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 twenty 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 *et al.* 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; Goncalves-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 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 Goncalves-Alvim & Fernandes (2001) and 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 mechanism of protection against natural enemies (Cornell 1983; Waring & Price 1990;

Hartley & Lawton1992; Hartley 1998). Juvenile stages also offer the undifferentiated meristems which are stimulated by GII to initiate gall morphogenesis (Weis *et al.* 1988). From the point of view of GII, 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, has not been tested specifically for a set of GII species in a given community. We analyzed 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 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 analyzed 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 1984). 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.

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References

Ananthakrishnan, T.N. (1984) Adaptative strategies in cecidogenous insects. *The biology of gall insects* (ed T.N. Ananthakrishnan), pp. 1-9. Oxford and IBH, New Delhi.

Askew, R.R. (1984) The biology of gall-wasps. *The biology of gall-insects (*ed T.N. Anathakrishnan), pp. 223-271. Edward Arnold, London.

Basset, Y. (2001) Communities of insect herbivores foraging on saplings versus mature trees of *Pourouma bicolor* (Cecropiaceae) in Panama. *Oecologia*, **129**, 253-260.

Bullock, S.H. (1985) Breeding systems in the flora of tropical deciduous forest in Mexico. *Biotropica*, **4**, 287-301.

Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, **27**, 305-335.

Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of populations* (eds P.J. Der Boer & G.R. Gradwell), pp. 298-312. Proceedings of the advanced study institute of numbers of populations, Oosterbeek. The Netherlands. Centre for Agricultural Publishing and Documentation, Wageningen.

Cornell, H.V. (1985) Local and regional richness of cynipine gall wasps on California oaks. *Ecology*, **66**, 1247-1260.

Cornell, H.C. (1983) The secondary chemistry and complex morphology of galls formed by Cynipinae (Hymenoptera): why and how? *American Midland Naturalist*, **110**, 225-234.

Cornell, H.V. & Lawton, J.H. (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: A theoretical perspective. *Journal of Animal Ecology*, **61**, 1-12.

Craig, T.P., Itami, J.K. & Price, P.W. (1989) A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. *Ecology*, **70**, 1691-1699.

Cuevas-Reyes P., Siebe, C., Martínez-Ramos M. & Oyama K. (2003) Species richness of gall-forming insects in a tropical rain forest: correlations with plant diversity and soil fertility. *Biodiversity and Conservation*, **3**, 411-422.

Dansa, C.V. & Rocha, C.F.D. (1992) An ant-membracid plant interactions in a cerrado area of Brazil. *Journal of Tropical Ecology*, **8**, 339-348.

Dreger-Jauffret, J.D. & Sorthouse, J.D. (1992) Diversity of gall-inducing insects and their galls. *Biology of insect-induced galls* (eds J.D. Sorthouse & O. Rohfritsch), pp 8-34. Oxford University Press, New York.

De Souza, M.M. (2001) Galling insect diversity patterns: the resource synchronization hypothesis. *Oikos*, **95**, 171-176.

Dodson, G. & George, S.B. (1986) Examination of two morphs of gall-forming *Aciurina* (Diptera: Tephritidae): ecological and genetic evidence for species. *Biological Journal of the Linnean Society*, **29**, 63-79.

Fay, P.A., Preszler, R.W. & Whitham, T.G. (1996) The functional resource of a gall-forming adelgid. *Oecologia*, **105**, 199-204.

Feeny, P. (1976) Plant apparency and chemical defense. *Recent Advances of Phytochemistry*, **10**, 1-40.

Fernandes, G.W. & Price, P.W. (1988) Biogeographical gradients in galling species richness: test of hypotheses. *Oecologia*, **76**, 161-167.

Fernandes, G.W. & Price, P.W. (1991) Comparison of tropical and temperate galling species richness: the roles of environmental harshness and plant nutrient status. *Plant-animal interactions: evolutionary ecology in tropical and temperate regions* (ed P.W. Price, T.M. Levinson, G.W. Fernandes & W.W. Benson), pp. 91-115. John Wiley and Sons Corporations, New York.

Fernandes, G.W. & Price, P.W. (1992) The adaptative significance of insect gall distributions: survivorship of species in xeric and mesic habitats. *Oecologia,* **90**, 14-20.

Fernandes, G.W., Carneiro, M.A.A., Lara, A.C.F., Allain, G.I., Andrade, G.R., Reis, T.R. & Silva I.M. (1996) Galling insects on neotropical species of *Baccharis* (Asteraceae). *Tropical Zoology*, **9**, 315-332.

Fernandes, G.W., Araujo, R.C., Araujo, S.C., Lombardi, J.A., Paula, A.S., Loyola, J.R. & Cornelissen, T.G. (1997) Insects galls from savanna and rocky fields of the Jequitinhonha valley, Minas Gerais, Brazil. *Naturalia* (Sao Paulo), **22**, 221-244.

Gagné, R.J. (1994) *The gall midges of the Neotropical region*. Cornell University Press, Ithaca, New York.

Gilbert, L.E. & Smiley, J.T. (1978) Determinants of local diversity in phytophagous insects: hosts specialists in tropical environments. *Diversity of insect faunas* (eds L.A. Mound & N. Waloff), pp. 89-105. Symposium of the Royal Entomological Society of London.

Goncalves-Alvim, S. & Fernandes, G.W. (2001) Biodiversity of galling insects: historical, community and habitat effects in four Neotropical savannas. *Biodiversity and Conservation*, **10**, 79-98.

Hartnett, D.C. & Abrahamson, W.G. (1979) The effects of stem gall insects on life history patterns in *Solidago canadiensis*. *Ecology*, **60**, 910-917.

Hartley, S.E. & Lawton, J.H. (1992) Host-plant manipulation by gall-insects: a test of the nutrition hypothesis. *Journal of Animal Ecology*, **61**, 113-119.

Hartley, S.E. (1998) The chemical composition of plant galls: are levels of nutrients and secondary compounds controlled by the gall-former. *Oecologia,* **113**, 492-501.

Huston, M.A. (1999) Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos,* **86**, 393-401.

Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist*, **940**, 501-528.

Langenheim, J.H. & Stubblebine, W.H. (1983) Variation in leaf resin between parent tree and progeny in *Hymenaea*: implications for herbivory in the humid tropics. *Biochemical Systematic and Ecology*, **11**, 97-106.

Lara, A.C.F. & Fernandes, G.W. (1996) The highest diversity of galling insects: Serra do Cipó, Brazil. *Biodiversity Letters*, **3**, 111-114.

Larson, K. 1998. The impact of two gall-forming arthropods on the photosynthetic rates of their hosts. *Oecologia*, **115**,161-166.

Larson, K. & Whitham, T. (1991) Manipulation of food resources by a gall-forming aphid: the physiology of sink-source interactions. *Oecologia*, **88**, 15-21.

Lawton, J.H. (1983) Plant architecture and diversity of phytophagous insects. *Annual Review of Entomology*, **28**, 23-29.

Leather, S.R. (1986) Insects species richness of the British Rosaceae: the importance of host range, plant architecture, age of establishment, taxonomic isolation and species-area relationships. *Journal of Animal Ecology*, **55**, 841-860.

Lott, E.J., Bullock, S.H. & Solis-Magallanes J.A. (1987) Floristic diversity and structure of upland and arroyo forests of Coastal Jalisco. *Biotropica*, **3**, 228-235.

Lowman, M.D. (1992) Herbivory in Australian rain forests, with particular reference to the canopies of *Doryphora sassafras* (Monimiaceae). *Biotropica*, **24**, 263-272.

Marquis, R.J. & Braker, H.E. (1994) Plant-herbivore interactions: diversity, specificity, and impact. *La Selva: ecology and natural history of a neotropical rain forest* (eds L.A. McDade, K.S. Bawa, A. Hespenheide & G.S. Hartshorn), pp. 261-294. University of Chicago, Chicago.

Novotny, V. & Missa, O. (2000) Local versus regional species richness in tropical insects: one lowland site compared with the island of New Guinea. *Ecological Entomology*, **25**, 445-451.

Oyama, K., Pérez-Pérez, M., Cuevas-Reyes, P. & Luna-Reyes R. (2003) Regional and local species richness of gall-forming insects in two tropical rain forest in México. *Journal of Tropical Ecology*, **19**, 595-598.

Parra-Tabla, V. & Bullock, S.H. (1998) Factors limiting fecundity of the tropical tree *Ipomoea wolcottiana* (Convolvulaceae) in a Mexican tropical dry forest. *Journal of Tropical Ecology*, **14**, 615-627.

Price, P.W. & Clancy, K.M. (1986) Interaction among three trophic levels: gall size and parasitoid attack. *Ecology*, **67**, 1593-1600.

Price, P.W., Roininen, H. & Tahvanainen, J. (1987a) Plant age and attack by the bud galler, *Euura mucronata*. *Oecologia*, **73**, 334-337.

Price, P.W., Roininen, H. & Tahvanainen, J. (1987b) Why does the bud-galling sawfly, *Euura mucronata*, attack long shoots? *Oecologia*, **74**, 1-6.

Price, P.W. (1989) Clonal development of coyote willow, *Salix exigua* (Salicaceae), and attack by the shoot galling sawfly *Euura exiguae* (Hymenoptera: Tenthredinidae). *Environmental Entomology*, **18**; 61-68.

Price, P.W. (1991) Patterns in communities along latitudinal gradients. *Plant animal interactions: evolutionary ecology of tropical and temperate region* (eds P.W. Price, T.M. Lewinson, G.W. Fernandes & W.W. Benson), pp. 51-68. John Wiley and Sons, New York.

Price, P.W., Fernandes, G.W., Lara, A.C., Brawn, J., Barrios, H., Wright, M.G., Ribeiro, S.P. & Rothcliff, N. (1998) Global patterns in local number of insect galling species. *Journal of Biogeography*, **25**, 581-591.

Raupp, M.J. & Denno, R.F. (1979) The influence of patch size on a guild of sap-feeding insects that inhabit the salt marsh grass *Spartina patens*. *Environmental Entomology*, **8**, 412-417.

Rhoades, D.F. & Cates, R.G. (1976) Toward a general theory of plant antiherbivore chemistry. *Recent Advances of Phytochemistry*, **10**, 168-213.

Ribeiro, K.T., Madeira, J.A. & Monteiro, R.F. (1998) Does flooding favour galling insects? *Ecological Entomology*, **23**, 491-494.

Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**, 167-171.

Root R.B. (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleraceae*). *Ecological Monographs*, **43**, 95-124.

Rossi, A.M. & Stiling P. (1998) The interactions of plant clone and abiotic factors on gall-making midge. *Oecologia*, **116**, 170-176.

Rzedowski, J. (1978) *Vegetación de México*. Editorial Limusa, México.

Sacchi, C., Price, P.W., Tomothy, P., Craig, P. & Itami, J.K. (1988) Impact of shoot galler attack on sexual reproduction in the arroyo willow. *Ecology*, **69**, 2021-2030.

Sánchez, O. & López, G. (1988) A theoretical analysis of some index of similarity as applied to biogeography. *Folia Entomologica Mexicana*, **75**, 119-145.

SAS (2000) *Categorical data analysis using the SAS system*. SAS Institute, Cary, North Carolina, USA.

Schönrogge, K. Walker, P. & Crawley, M.J. (2000) Parasitoid and inquiline attack in the galls of four alien, cynipid gall wasps: host switches and the effect on parasitoid sex ratios. *Ecological Entomology*, **25**, 208-219.

Thomas, C.D. (1990) Herbivore diets, herbivore colonization, and the escape hypothesis. *Ecology*, **71**, 610-615.

Waring, G.L. & Price, P.W. (1989) Parasitism pressure and radiation of gall forming group (Cecidomyiidae: *Aspondylia spp.*) on creosote bush (*Larrea tridentata*). *Oecologia*, **79**, 293-299.

Waring G.L. & Price, P.W. (1990) Plant water stress and gall formation (Cecidomyiidae: *Asphondylia spp.*) on creosote bush. *Ecological Entomology*, **15**, 87-95

Weis, A.E., Walton, R. & Crego, C.L. (1988) Reactive plant tissue sites and the population biology of gall makers. *Annual Review of Entomology*, **33**, 467-486.

Wolfe, M.L. (1997) Differential flower herbivory and gall formation on males and females of *Neea psychotriodes* a dioecious tree. *Biotropica*, **29**, 169-174.

Wright, M.G. & Samways, M.J. (1996) Gall-insect species richness in African Fynbos and Karoo vegetation: the importance of plant species richness. *Biodiversity Letters*, **3**, 151-155.

Wright, M.G. & Samways, M.J. (1998) Insect species richness tracking plant species richness in a diverse flora: gall-insects in the Cape floristic region, South Africa. *Oecologia*, **115**, 427-433.

Legends to figures

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.

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 a LSMeans multiple comparison test ($P > 0.001$). **b)** Frequency. PROC CATMOD procedure (SAS 2000) was applied for modeling 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 X Habitat ($\chi^2 = 23.6$; d.f. = 2; $P < 0.0001$).

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

Fig. 1

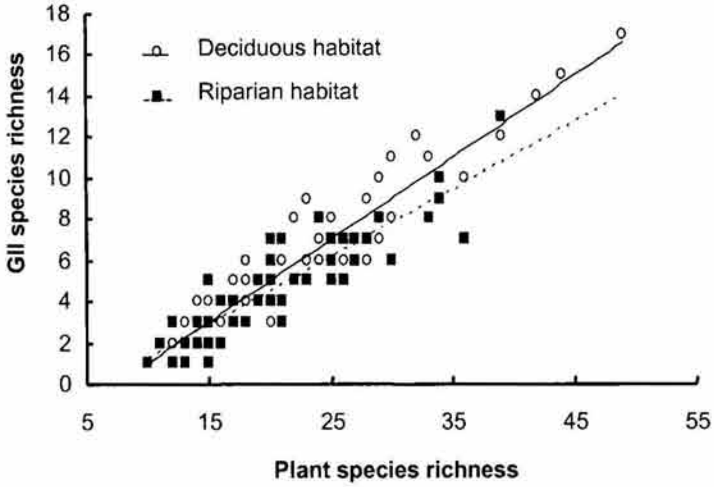
Deciduous habitat
Riparian habitat
GII species richness
Plant species richness
0
2
4
6
8
10
12
14
16
18
5
15
25
35
45
55

Fig. 2

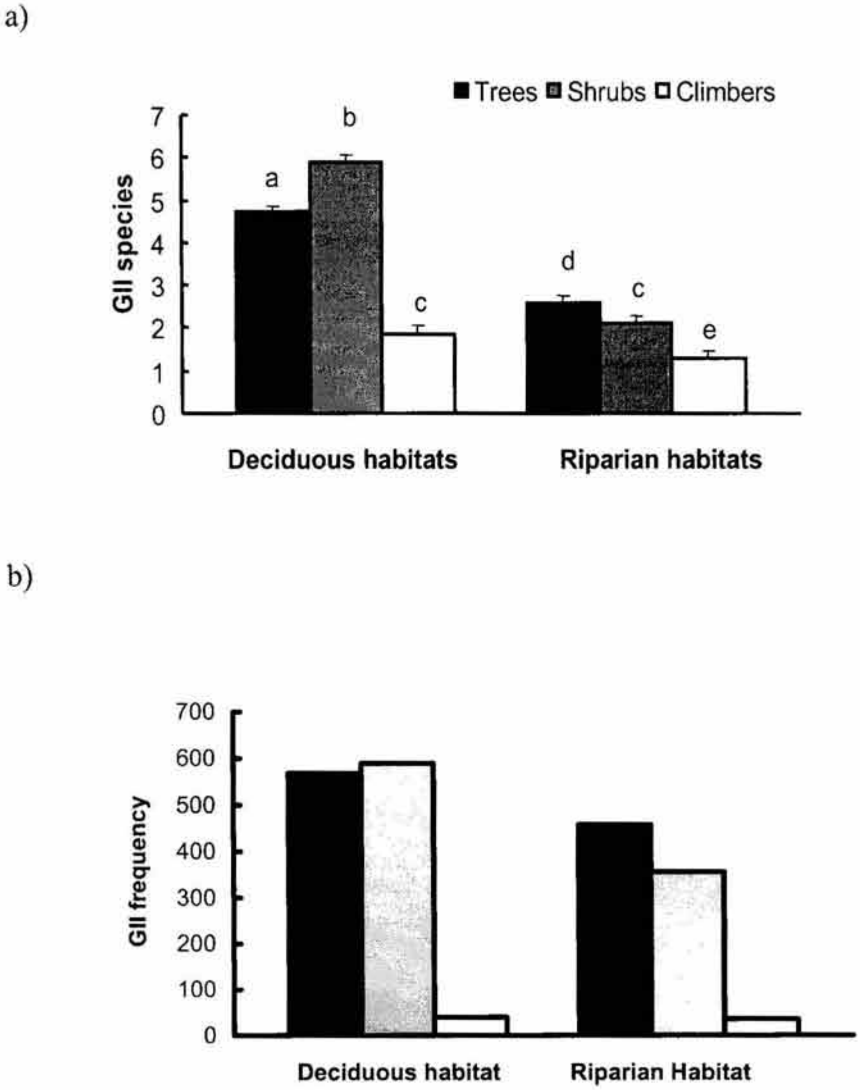
a)
■ Trees ▨ Shrubs ☐ Climbers
GII species
0
1
2
3
4
5
6
7
a
b
c
d
c
e
Deciduous habitats
Riparian habitats
b)
GII frequency
0
100
200
300
400
500
600
700
Deciduous habitat
Riparian Habitat

Fig. 3

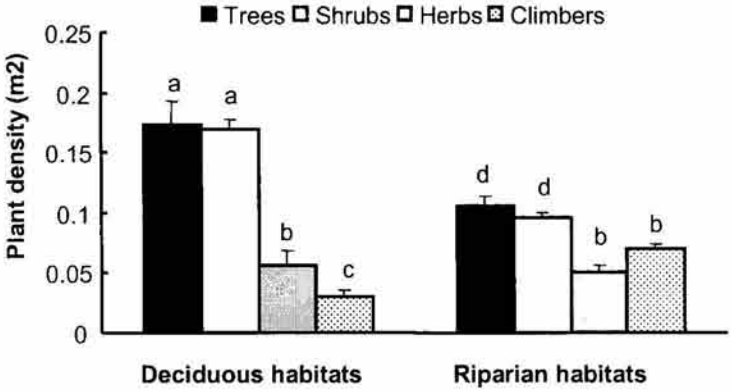
Trees
Shrubs
Herbs
Climbers
Plant density (m2)
0.25
0.2
0.15
0.1
0.05
0
a
a
b
c
d
d
b
b
Deciduous habitats
Riparian habitats

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	*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	Unidentified	Unidentified	Unidentified*
Rubiaceae	*Guettarda elliptica*	Diptera	Cecidomyiidae	Cecidomyiidae*
	Randia spinosa	Diptera	Cecidomyiidae	*Bruggmannia randiae*
Sapindaceae	*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	*Vitex hemsleyi*	Diptera	Cecidomyiidae	Cecidomyiidae

* GII species present in both habitats

Table 2 Mean number (± 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* <
Achatocarpus gracilis	Unidentified	(565.9 ± 12.4)	(96.1 ± 7.1)	12.9	37	0.0001
Cordia alliodora	*Neolasioptera sp*	(90.7 ± 7.5)	(50.1 ± 5.3)	3.1	53	0.002
Guettarda elliptica	Cecidomyiidae	(59.6 ± 5.3)	(43.4 ± 3.6)	2.7	28	0.01
Heliocarpus pallidus	*Neolasioptera heliocarpi*	(109.8 ± 6.3)	(50.4 ± 3.9)	6.7	38	0.0001
Ruprechtia fusca	Unidentified	(196.4 ± 4.7)	(126.7 ± 5.8)	6.1	37	0.0001
Guapira macrocarpa	Unidentified	(288.9 ± 11.9)	(274 ± 13.4)	0.39	44	**n.s.**

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

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

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

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

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

CAPÍTULO II.

Spatial patterns of herbivory by gall-forming insects: A test of the soil fertility hypothesis in a Mexican tropical dry forest

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Abstract. It has been proposed that fertile soils reduce the incidence of gall-forming insect (GFI) species in plant communities. This is known as the soil fertility hypothesis. The main objective of this study is to analyze the spatial distribution of GFI species under different habitats in a tropical dry forest at the Chamela-Cuixmala Biosphere Reserve, Mexico. Eight habitats which differ in soil type, topography, nutrient availability and vegetation were chosen. We found that 38 GFI species specialize on their host plant species. GFI species richness was negatively correlated with phosphorous and nitrogen availability. Using phosphorous as an indicator of soil fertility, we found low frequency and density of GFI on fertile soils. Our study indicates that soil fertility is one of the factors that negatively affects the patterns of spatial distribution of species richness, incidence and abundance of GFI at the community level in two different ways: i) indirectly affecting GFI species richness in plants adapted to infertile soils and ii) directly affecting GFI responses to plant traits of hosts found in a fertility gradient.

Keywords Gall species richness, Soil fertility, Tropical dry forest, Herbivory by GFI

Introduction

General patterns of gall-forming insect (GFI) species richness are not random in tropical and temperate communities. GFI species richness increases as latitude and altitude decrease for several regions in the world (Fernandes and Price 1988, 1991, Price 1991, Fernandes and Lara 1993, Price et al.1998). These patterns have indicated that GFI species richness tends to be highest in subtropical latitudes (25-38° N or S) and on scleromorphic vegetation (Price et al. 1998). Both biotic (e.g., natural enemies, host richness, plant structural complexity, host density) and abiotic factors (e.g. hygrothermal stress, scleromorphic environments and soil fertility) have been invoked to explain GFI species richness (Wright and Samways 1996, 1998, Fernandes and Price 1991, Lara and Fernandes 1996, Ribeiro et al. 1998, Oyama et al. 2003).

Several different hypotheses have been proposed to explain the observed patterns of GFI species richness. The hygrothermal hypothesis proposed by Fernandes and Price (1988) states that GFI species richness increases with an increase in hygrothermal stress. This hypothesis was based on two different sources of evidence: comparative studies looking for global patterns and local studies on the adaptive significance of GFI in plants located in xeric and mesic habitats. The first source of evidence found that GFI are more common in scleromorphic than mesophytic vegetations, because sclerophyllous plants present lower rates of leaf abscission, thereby reducing hygrothermal stress and increasing resistance against natural enemies. These plant traits provide favorable sites for GFI colonization (Price et al. 1998). The second evidence shows that GFI have lower rates of mortality in xeric than in mesic environments because pathogens and parasites are less abundant in this habitat (Fernandes and Price 1992).

In addition to the hygrothermal hypothesis, Fernandes and Price (1991) also argued that soil fertility is an important factor that affects GFI species richness in relation to latitudinal gradients. This hypothesis states that lower GFI species richness should occur in fertile soils. Evidence indicates that low contents of phosphorous are associated with a greater number of GFI species (Fernandes and Price 1991, Goncalves-Alvim and Fernandes 2001). Plant species that grow under conditions of infertile soils tend to have lower rates of growth and to accumulate higher concentrations of secondary metabolites such as oils, phenols, alkaloids and terpenoids (McKey et al. 1978, Medina et al. 1990, Fernandes and Price 1991, Fernandes et al. 1994). GFI species can use defense compounds of their host plants by sequestering secondary metabolites during the formation of gall tissues (Hartley 1992; 1998). The accumulation of these chemicals confer protection to GFI against natural enemies such as chewing herbivores, fungi and others pathogens (Cornell 1983, Hartman 1985, Waring and Price 1990, Fernandes and Price 1992). In contrast, Blanche and Westoby (1995) showed that GFI species richness was not linked directly to soil fertility but via host plants that have adapted to infertile soils, such as some eucalypt trees in Australia.

Only few empirical studies have evaluated the effect of soil properties on the abundance, survivorship and species richness of GFI at a local or regional scale (Blanche 1994, Blanche and Westoby 1995, Orians and Fritz 1996, Blanche and Ludwig 2001, Goncalves-Alvim and Fernandes 2001, Cuevas-Reyes et al. 2003). Because the patterns of GFI species richness are not always consistent in tropical regions, particularly the effect of soil fertility, the objective of our study is to evaluate the effects of soil fertility on GFI species richness in a tropical dry forest. It is known that this ecosystem contains soils with contrasting fertility (Mooney et al. 1995). Therefore, the tropical dry forest is ideal to evaluate the spatial patterns of herbivory and GFI species richness with regard to contrasting soil types.

The hygrothermal hypothesis and the soil fertility hypotheses are not mutually exclusive and both indicate that high GFI species richness is associated to sclerophyllous plants (Fernandes and Price 1988, 1992; Price et al. 1998). However, the patterns of GFI species on scleromorphic plants are inconsistent and in some cases do not support the hygrothermal stress or soil fertility hypotheses because these variables are confounded in habitats with scleromorphic vegetation (Veldtman and McGeoch 2003). In our study, in deciduous and riparian communities, hygrothermal stress during the wet season is not present and the occurrence of sclerophyllous vegetation is limited.

This is the first study that documents the specificity of GFI plant interactions in a tropical dry forest community. This study evaluates in detail the soil fertility hypothesis by examining how differences among plant species and differences within a plant species affect GFI species richness and abundance. We test the soil fertility hypothesis in eight distinct habitats with different soil types, topography, nutrient availability and vegetation. In particular, we address the following questions: (1) What is the degree of specialization between GFI and their host plant species? (2) What is the relationship between GFI species richness and soil fertility? (3) Does soil fertility reduce the incidence and intensity of damage by GFI?

Materials and methods

Study site

The study was conducted at the Chamela-Cuixmala Biosphere Reserve on the Pacific coast of Jalisco, Mexico that covers an extension of 13,200 ha. The elevation of this site ranges between 50-500 m, the average annual precipitation is 748 mm and the rainy season occurs 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). For more details on the site, see García-Oliva et al. (2003).

Soil fertility

In a previous study, Cotler et al. (2002) published a morphopedological map of the study site. This map is accompanied by a description of the main geomorphologic habitats and the soils associated with them. It was produced by interpretation of aerial photographs (scale 1/5 000). The soil data comprised the following: soil depth, pH, available phosphorous and total nitrogen contents, exchangeable base cations, particle size distribution, total organic carbon contents and the available water holding capacity. The soil survey was done on 21 representative soil profiles in the different geomorphological habitats. The chemical and physical analysis of the soil properties of each habitat were conducted by Cotler et al. (2002) and included the following: i) available phosphorous – phosphorus extraction with ammonium fluoride solution (Bray I) and colorimetric determination of blue complexes formed with ammonium molibdate using ascorbic acid-like reducer (ISRIC 1992); ii) total nitrogen – digestion with H_2SO_4 and colorimetry to 660 nm determination of the green complex formed with sodium nitro-ferricianure and sodium hypochlorite, iii) exchangeable cations (calcium, magnesium and sodium) – determination by ammonium acetate extraction 1 N to pH 7, ration 1:10 and determinate by atomic absorption (ISRIC 1992) and iv) humus – calculated from organic carbon multiplied by 1.724 factor.

Soil habitats 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. Hill top over granite habitats are located between 140 and 150 m in elevation, in haplic lixisol with sandy-clay texture at the surface with very low water holding capacity. Hill top with conglomerate cover over tuffs are found between 110 and 115 m in elevation, in eutric regosol soils with sandy-clay texture at the surface that allow moderate drainage and limited aeration. Upland hills over granite are found between 280 and 540 m in elevation in haplic lixisol soils with sandy-clay texture at the surface but with high drainage capacity and very well aerated. Hill top over tuffs are found between 110 and 130 m in elevation, in eutric cambisol soils with clay texture at the surface with low water holding capacity. Irregular hillsides over granite were located between 130 and 170 m in elevation, in luvi-eutric regosols soils with clay and sandy texture and with well drainage and aeration. Convex hills over tuffs are between 90 and 110 m in elevation, in eutric regosol soils with sandy and clay texture at the surface with low water holding capacity. Recent alluvium terraces are between 80 and 85 m in elevation, in eutric regosol soils in alluvial accumulations well drained and aerated. Recent alluvium terraces are between 80 and 95 m in elevation, in eutric fluvisol soils in alluvial accumulations well drained and aerated. Six habitats are located in deciduous communities (e.g. 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 habitats in riparian communities (recent and old alluvium terraces). In both communities, water stress during the wet season is low and sclerophyllous vegetation is not present (Reich and Borchert 1984; Holbrook et al. 1995). In each habitat, five transects of 50 x 5 m were randomly selected from a grid system developed within each habitat using random numbers to assure sampling independence. To corroborate sampling adequacy of GFI species, we used a GFI species accumulation curve across all habitats.

GFI Census: Species richness and abundance

In order to estimate GFI species richness, we identified and collected all GFI species and their respective host plants in all habitats. We verified the degree of specificity of each GFI, identifying taxonomically each insect specimen collected in the field and rearing galls in the laboratory until the emergence of adult insects. Because the induction by all GFI species studied only affected leaves, we restrict our study to GFI of the same guild.

After a preliminary analysis of presence of GFI species and their host plants in the Chamela-Cuixmala Biosphere reserve, we found that only eleven GFI species were always present in all the selected habitats. Therefore, for comparative purposes, GFI frequency and density were estimated only in these species. To compare the susceptibility to galls on the same plant species located in different conditions of soil fertility, we registered the frequency of GFI on specific host plants in each transect in all habitats. Fifty leaves were randomly collected in plants of eleven specific host species in all habitats, and the number of galls per square centimeter of vegetal tissue was estimated in order to test if soil fertility reduces the damage caused by GFI.

Statistical analyses

To determine the relationships between GFI species richness and nutrient availability, we included the total number of GFI species registered in all habitats. A regression analysis was used to analyze the relationship between GFI species richness and soil fertility across all habitats.

To determine if differences of content in soil properties occur between different habitats, we applied an ANOVA to compare each soil property at the eight habitats (box-cox transformation data) and a posteriori Tukey tests (Stokes et al. 2000). Habitats were used as independent variables, and each soil property as the response variable.

A generalized linear model analysis was used to determine if the frequency and density of GFI depended upon soil fertility (Stokes et al. 2000). Total frequency of galls and gall density of each GFI species were used as the dependent variables. Because the distribution of these variables does not follow a normal distribution, we used a Poisson distribution for the dependent variables, with a logarithmic link function using the GENMOD procedure from SAS (Stokes et al. 2000). The model used has two conditions as categorical independent variables (soil fertility and species). We analyzed the frequency and density of GFI on 11 species of host plants that occurred in 8 different soil habitats. A type III statistic is calculated for each effect (Stokes et al. 2000).

RESULTS

Soil fertility

Habitats differed significantly in soil properties (Table 1). Available phosphorous and total nitrogen concentrations were chosen as indicators of soil fertility as in other studies (e.g. Blanche and Westoby 1994). Phosphorous content was greater in alluvial soils and convex hills over tuffs than in other habitats ($F = 57.4$; d.f. = 7; $P < 0.0001$). A similar pattern was encountered with nitrogen content which was greater in alluvial terraces and irregular hillsides over granite than other habitats ($F = 17.4$; d.f. = 7; $P < 0.0001$) (Table 1).

General GFI diversity and GFI specialization

In total for all habitats, we found 38 GFI species represented in four orders: Diptera (Cecidomyiidae family) which induced the majority of galls on plants with 26 species (68.4 %); Homoptera [Kermidae (7.9%) and Psyllidae (5.3%) families], Hymenoptera [Tanaostigmatidae, (2.6%)] and Thysanoptera (2.6%) galls being rare, and five morphospecies (13.2%) were unidentified. In all cases, each GFI species was associated with one specific plant species (Table 2). Figure 1 shows adequacy of our sampling assessment, as the number of GFI species reach an asymptotic curve in relation to the number of habitats.

Our results indicate that there was not a significant relationship between the altitude of different habitats and GFI species richness ($y = 0.026x+ 15.58$; $r^2 = 0.09$; $P = 0.46$) and GFI density ($y = 0.002x + 0.3414$; $r^2 = 0.22$; $P = 0.23$).

GFI species richness and abundance

The number of GFI species was negatively correlated with availability of phosphorous ($y = 19.5\ x^{-0.2}$; $r^2 = 78.3\%$; $P < 0.02$) and total nitrogen content ($y = 15.6\ x^{-0.25}$; $r^2 = 44.7\%$; $P < 0.03$) in the tropical dry forest at Chamela-Cuixmala Biosphere Reserve (Fig. 2).

We registered only eleven GFI species associated with specific host plants that were always present in all habitats, the rest of the GFI species were present on host plant species in one or another habitat (Table 2). In these eleven plant species, we recorded a total of 834 plants with GFI. The frequency of GFI was significantly greater in habitats with low fertility such as hill top over granite, hill top with conglomerate cover over tuffs and hills tops over tuffs than other habitats with greater soil fertility (soils: $\chi^2 = 34.2$; d.f. = 7; $P <$

0.0001) (Fig 3a). The frequency of GFI did not differ significantly among eleven plant species that occurred in all habitats (species: $\chi^2 = 0.8$; d.f. = 10; $P > 0.05$) (Fig. 3a).

GFI density on specific host plants was associated with soil fertility and plant species. GFI density in plants was significantly greater in habitats with low available phosphorous and total nitrogen. Plants found in sites with low soil fertility such as hill top over granite and hill top with conglomerate cover over tuffs harbored greater GFI density than plants distributed in habitats with greater soil fertility such as alluvial soils (soils: $\chi^2 = 51.4$; d.f. = 7; $P < 0.0001$). In addition, GFI density was significantly different between host plant species (species: $\chi^2 = 98.8$ d.f. = 10; $P < 0.0001$) (Fig. 3b).

Discussion

In the Chamela-Cuixmala Biosphere Reserve, soil type combined with different conditions in temperature, humidity, soil pH, nutrients and water availability, establish a patchy landscape that supports different vegetation types (Lott et al 1987; Cotler et al. 2002). Availability of water and nutrients are also heterogeneous; seasonal rainfall patterns are responsible for changes in the water and nutrient balance, where the limiting factor in all habitats seems to be 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 availability and total nitrogen as indicators of soil fertility. Our study directly identified the specificity of GFI species with their respective host plants. This recognition of taxa demonstrated that there is a one to one relationship between plants and GFI, and that this relationship is maintained across different habitats. Our results showed that in a tropical dry forest soil fertility negatively affects GFI species richness. GFI species richness was negatively correlated with soil phosphorous and nitrogen availability in deciduous and riparian communities. Limiting macronutrients in the soils such as phosphorous and nitrogen, affects the frequency and density of GFI species on specific host plants across communities in this tropical region. Two possible explanations that are not mutually exclusive have been presented in the literature to explain the relationship between soil fertility and GFI species richness. Blanche and Westoby (1995) found in Australia that GFI 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 GFI 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 GFI species is favored by these plant traits.

Our first result indicates that the number of GFI species is negatively correlated with soil fertility for all the host plant species that occur in different habitats. As suggested by Blanche and Westoby (1995), this result may be explained by indirect effects associated with local adaptations of specific host plant taxa to soil fertility. Plants that have adapted to infertile soils tend to have a greater concentration of secondary metabolites and foliar nitrogen availability than plants in fertile soils (Coley et al. 1985; Coley and Barone 1996). Therefore, plants growing on infertile soils may provide more potential sites to be colonized by gall insects (Cuevas-Reyes et al. 2003). 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 GFI 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, 1993).

Our second result indicates that soil fertility negatively affects the frequency and density of GFI within individuals of 11 host plant species that are present in 8 soil habitats with contrasting fertility. A given host species that occurred in several habitats with low levels of soil phosphorous and nitrogen had greater GFI than the same host species that grew in fertile sites. Therefore, direct effects of soil fertility may also explain the reduction in the frequency and density of GFI on host plants species that are present across a soil fertility gradient. Adaptive phenotypic plasticity within each host species may explain differences in the incidence of GFI for the 11 host plant species analyzed in our study (Herms and Mattson, 1992, Schlichting and Pigliucci 1998). Host plants of the same species adapt to variable soil environments and GFI negatively respond to the quality of the environment experienced by their hosts. Because it has been shown that host plants produced more defensive compounds under low soil fertility and GFI sequestered these chemicals in the gall wall for protection, we expect GFI to select individuals of a given host species with greater chemical defenses under low nutrient availability.

Most studies have assumed that the morphology of gall chambers is unique to each GFI species and that gall species are specific to a single plant species (Koach and Wool 1977, Bearsley 1982; Ananthakrishnan 1984, Dodson and George 1986, Weis et al. 1988, Floate et al. 1996, Hartley 1998, Nyman et al. 1998, Nyman et al. 2000, Cuevas-Reyes et al. 2003; Oyama et al. 2003). However, none of these studies assessed the specificity of GFI species with their respective host plants. This assessment is important because various hypotheses on GFI species richness are based on this assumption and, in some cases, a single plant species hosted numerous GFI species that induced a particular gall morphology (Fernandes and Price 1988, Waring and Price 1989, Fernandes et al. 1996). Therefore, it is necessary to establish the specific relationship of GFI species with their host plant species. Our study is the first that shows directly the specificity of GFI with their host plants at the community level, and corroborates the assumed greater specificity of GFI species with their host plant species; one GFI species is associated with one specific plant species. We conclude that soil fertility is one of the factors that affects the patterns of spatial distribution of GFI and favor the GFI species richness, incidence and GFI abundance at the community level in two different ways: i) indirectly affecting the GFI species richness in plants adapted to infertile soils and ii) directly affecting GFI responses to plant traits of hosts found in a fertility gradient. We provide the first evidence of GFI diversity for a tropical dry forest in the world. These results show the ecological importance of abiotic factors in structuring plant-insect interactions in the tropics. We also show that it is necessary to corroborate the specificity of GFI species on host plant species in all studies of GFI diversity because all the hypotheses are based on this assumption. In our case, each GFI species maintained a great specificity to their host plant species.

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References

Ananthakrishan, T. N. 1984. Adaptative strategies in cecidogenous insects. In: Ananthakrishan, T. N. (ed.), The biology of gall insects. Oxford and IBH, New Delhi, pp. 1-9.

Blanche, K. R. 1994. Insect induced galls on Australian vegetation. In: Price, P. W., Mattson, W. J. and Baranchikov, Y. (eds), The ecology and evolution of gall-forming insects. Forest service US department of agriculture, St. Paul, pp. 49-55.

Blanche, K. R. and Westoby, M. 1995. Gall-forming insect diversity is linked to soil fertility via host plant taxon. - Ecology 76: 2334-2337.

Blanche, K. R. and Ludwig, A. J. 2001. Species richness of gall-inducing insects and host plants along and altitudinal gradient in Big Bend National Park, Texas. - Am. Midl. Nat. 145: 219-232.

Bearsley, W. J. 1982. On taxonomy of the genus *Pseudopsylla* Froggatt, with a redescription of the type species (Homoptera: Coccoidea). - Proc. Hawaiian Entomol. Soc. 24: 31-35.

Bullock, S. H. 1985. Breeding systems in the flora of tropical deciduous forest in Mexico. - Biotropica 4: 287-301.

Coley, P. D., Bryant, J. P. and Chapin, F. S. 1985. Resource availability and plant antiherbivore defense. - Science 230: 895-899.

Coley, P. D. and Barone, J. A. 1996. Herbivory and plant defenses in tropical forests. - Annu. Rev. Ecol. Syst. 27: 305-335.

Cornell, H. C. 1983. The secondary chemistry and complex morphology of galls formed by Cynipinae (Hymenoptera): why and how? - Am. Midl. Nat. 110: 225-23.

Cotler, E., Durán, E. and Siebe, C. (2002). Caracterización morfo-edafológica y calidad de sitio de un bosque tropical caducifolio. In: Noguera, F. A., Vega, R. H. J., García, A. N. A. and Quesada, M. (eds), Historia natural de Chamela. Universidad Nacional Autónoma de México, Instituto de Biología, México, pp. 17-47.

Cuevas-Reyes P., Siebe, C., Martínez-Ramos, M. and Oyama, K. (2003). Species richness of gall-forming insects in a tropical rain forest: correlations with plant diversity and soil fertility. - Biodiv. Conserv. 3: 411-422.

Dodson, G. and George, S. B. 1986. Examination of two morphs of gall-forming *Aciurina* (Diptera: Tephritidae): ecological and genetic evidence for species. - Biol. J. Linn. Soc. 29: 63-79.

Fernandes, G. W. and Price, P. W. 1988. Biogeographical gradients in galling species richness: test of hypotheses. - Oecologia 76: 161-167.

Fernandes, G. W. and Price, P. W. 1991. Comparison of tropical and temperate galling species richness: the roles of environmental harshness and plant nutrient status. In: Price, P. W., Levinson, T. M., Fernandes, G. W. and Benson, W. W. (eds), Plant-animal interactions: evolutionary ecology in tropical and temperate regions. John Wiley and Sons Corporations, New York, pp. 91-115.

Fernandes, G. W. and Price, P. W. 1992. The adaptative significance of insect gall distributions: survivorship of species in xeric and mesic habitats. - Oecologia 90: 14-20.

Fernandes, G. W. and Lara, A. C. F. 1993. Diversity of Indonesian gall-forming herbivores along altitudinal gradients. - Biodiv. Lett. 1: 186-192.

Fernandes, G. W., Lara, A. C. F. and Price, P. W. 1994. The geography of galling insects and the mechanisms that result in patterns. In: Price, P. W., Mattson, W. J. and Baranchikov, Y. N. (eds), The ecology and evolution of gall forming insects. USDA Forest Service Tech. Report NC-174, Minnesota, pp. 49-55.

Fernandes, G. W., Carneiro, M. A. A., Lara, A. C. F., Allain, G. I., Andrade, G. R., Reis, T. R. and Silva, I. M. 1996. Galling insects on neotropical species of *Baccharis* (Asteraceae). - Trop. Zool. 9: 315-332.

Floate, K. Fernandes, G. W. and Price, P. W. 1996. On the use of galls as bioassays to identification of plant genotypes. - Oecologia 105: 221-229.

García-Oliva, F., Camou, A. and Maass, J. M. 2003. El clima de la región central de la costa del pacífico mexicano. In: Noguera, F. A., Vega, R. H. J., García, A. N. A. and Quesada, M.) (eds), Historia natural de Chamela. Universidad Nacional Autónoma de México, Instituto de Biología, México, pp. 1-3.

Goncalves-Alvim, S. and Fernandes, G. W. 2001. Biodiversity of galling insects: historical, community and habitat effects in four Neotropical savannas. - Biodiv. Conserv. 10: 79-98.

Hartley, S. E. and Lawton, J. H. 1992. Host-plant manipulation by gall-insects: a test of the nutrition hypothesis. - J. Anim. Ecol. 61: 113-119.

Hartley, S. E. 1998. The chemical composition of plant galls: are levels of nutrients and secondary compounds controlled by the gall-former. - Oecologia 113: 492-501.

Hartman, H. 1985. Differential intensities of gall insect infectation among host plant size classes: outbreak frequency estimation model. - Zool. Ange. Entomol. 99: 329-332.

Herms, D. A. and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. - Q. Rev. Biol. 67:283-335

Holbrook, N. M., J. L. Whitebeck, and H. A. Mooney. 1995. Drought responses of neotropical dry forest tress. *In* S. H. Bullock, H. A. Mooney and E. Medina [eds.], Seasonally dry tropical forests, 243–276. Cambridge University Press, Cambridge, UK.

International Soil Reference and Information Centre (ISRIC) 1992. Procedures for soil analysis. Technical paper 9, Editado por L.P. van Reeuwijk, Wageninen.

Jaramillo, V. J. and Sanford, R. L. 1995. Nutrient cycling in tropical deciduous forests. In: Bullock, S. H., Money, H. A. and Medina, E. (eds), Seasonally dry tropical forests. Cambridge University Press, Cambridge, pp. 346-361.

Koach, J. and Wool, D. 1977. Geographic distribution and host specificity of gall-forming aphids (Homoptera, Fordinae) on *Pistacia* trees in Israel. - Marcellia 40: 207-216.

Lara, A. C. F. and Fernandes, G. W. 1996. The highest diversity of galling insects: Serra do Cipó, Brazil. - Biodiv. Lett. 3: 111-114.

Lott, E. J. Bullock, B. H. and Solis-Magallanes J. A. 1987. Floristic Diversity and Structure of Upland and Arroyo Forest of Coastal Jalisco. – Biotropica, 19: 228-235.

Mckey, D. Waterman, P. G., Mbi, C. N., Gartlan, J. S. and Struhsaker, T. T. 1978. Phenolic content of vegetation in two African rain forests: ecological implications: - Science, 202: 61-64.

Medina, E., García, V. and Cuervas, E. 1990. Sclerophylly and oligotrophic environments: relationship between leaf structure, mineral nutrient content, and drought resistance in tropical rain forest of the upper Rio Negro region. - Biotropica 22: 51-64.

Mooney, H. A., Bullock, S. H. and Medina, E. 1995. Introduction. In: Bullock, S. H., Money, H. A. and Medina, E. (eds), Seasonally dry tropical forests. Cambridge University Press, Cambridge, pp. 1-8.

Nyman, T., Roininen, H. and Vuorinen, J. A. 1998. Evolution of different gall types in willow-feeding sawflies (Hymenoptera: Tenthredinidae). - Evolution 52: 465-474.

Nyman, T., Widmer, A. and Roininen, H. 2000. Evolution of gall morphology and host-plant relationships in willow feeding sawflies (Hymenoptera:Tenthredinidae). - Evolution 54: 526-533.

Orians, C. M. and Fritz, R. S. 1996. Genetic and soil-nutrient effects on the abundance of herbivores on willow. - Oecologia 105: 388-396.

Oyama, K., Pérez-Pérez, M., Cuevas-Reyes, P. and Luna-Reyes, R. 2003. Regional and local species richness of gall-forming insects in two tropical rain forest in México. - J. Trop. Ecol. 19, 595-598.

Price, P. W. (1991). Patterns in communities along latitudinal gradients. In: Price, P. W., Lewinson, T. M., Fernandes, G. W. and Benson W. W. (eds), Plant animal interactions: evolutionary ecology of tropical and temperate regions. John Wiley and Sons, New York, pp. 51-68.

Price, P. W., Fernandes, G. W., Lara A. C., Brawn, J., Barrios, H., Wright, M. G., Ribeiro, S. P. and Rothcliff, N. 1998. Global patterns in local number of insect galling species. - J. Biogeogr. 25: 581-591.

Ribeiro, K. T., Madeira, J. A., Monteiro, R. F. 1998. Does flooding favour galling insects? - Ecol. Entomol. 23: 491-494.

Reich, P. B., and R. Borchert. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology* 72: 61-74.

Rzedowski, J. 1978. Vegetación de México. - Editorial Limusa, México.

Schlichting, C. D., and Pigliucci, M. 1998. Phenotypic evolution: A reaction norm perspective. Sinauer Press, MA, pp 54-56.

Stokes M. E., Davis, C. S. and Koch, G. G. 2000. Categorical data analysis using the SAS system, 2nd ed. SAS, Cary, N.C.

Veldman, R. and McGeoch M. A. 2003. Gall-forming insect species richness along a non-scleromorphic vegetation rainfall gradient in South Africa: The importance of plant community composition. Aust. Ecol. 28: 1-13.

Waring, G. L. and Price, P. W. 1989. Parasitism pressure and radiation of gall forming group (Cecidomyiidae: *Aspondylia spp.*) on creosote bush (*Larrea tridentata*). - Oecologia 79: 293-299.

Waring, G. L. and Price, P. W. 1990. Plant water stress and gall formation (Cecidomyiidae: *Asphondylia spp.*) on creosote bush. - Ecol. Entomol. 15: 87-95.

Weis, A. E., Walton, R. and Crego, C. L. 1988. Reactive plant tissue sites and the population biology of gall makers. - Annu. Rev. Entomol. 33: 467-486.

White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. - Oecologia 63: 90-105.

White, T. C. R. 1993. The inadequate environment: nitrogen and abundance of animals. - Springer-Verlag, Berlin.

Wright, M. G. and Samways, M. J. 1996. Gall-insect species richness in African Fynbos and Karoo vegetation: the importance of plant species richness. - Biodiv. Lett. 3: 151-155.

Wright, M. G. and Samways, M. J. 1998. Insect species richness tracking plant species richness in a diverse flora: gall-insects in the Cape floristic region, South Africa. - Oecologia 115: 427-433.

Table 1 Mean (± SE) values of selected soil properties in different habitats in Chamela-Cuixmala Biosphere Reserve in Jalisco (data from Cotler *et al.* 2002). ANOVA test were applied in each soil property (box-cox transformation data). Different letters indicate statistically significant differences among habitats after a Tukey test.

Soil properties	**(1)**	**(2)**	**(3)**	**(4)**	**(5)**	**(6)**	**(7)**	**(8)**	***F***	***P*** <
Available 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
Total Nitrogen (Kg m $^{-2}$)	0.1 (± 0.06)^{d}	0.2 (± 0.09)^{d}	0.57 (± 0.1)^{a}	0.37 (± 0.08)^{a}	0.84 (± 0.1)^{c}	1.2 (± 0.1)^{c}	0.54 (± 0.1)^{a}	1.9 (± 0.18)^{b}	17.4	0.0001
Exchangeable 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
Exchangeable 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
Exchangeable 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 conglomerate 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)

Table 2 Orders and families of GFI present in tropical dry forest at Chamela-Cuixmala Biosphere reserve in Jalisco, Mexico. The asterisk indicate GII species present in all habitats

Family	Host plant taxa	Order	Family	Gall taxa	Habitats							
					1	2	3	4	5	6	7	8
Achatocarpaceae	*Achatocarpus gracilis*	Unidentified	Unidentified	Unidentified *	x	x	x	x	x	x	x	x
Apocynaceae	*Thevetia ovata*	Diptera	Cecidomyiidae	*Aspondylia sp2*	x		x	x	x	x		
Bignoniaceae	*Bignoniaceae*	Diptera	Cecidomyiidae	Cecidomyiidae	x	x		x	x	x		
Bombacaceae	*Ceiba aesculifolia*	Homoptera	Psyllidae	Psyllidae	x	x	x	x	x	x		
	Ceiba grandiflora	Homoptera	Psyllidae	Psyllidae	x	x	x	x	x		x	
Boraginaceae	*Cordia alliodora*	Diptera	Cecidomyiidae	*Neolasioptera sp* *	x	x	x	x	x	x	x	x
Burseraceae	*Bursera excelsa*	Diptera	Cecidomyiidae	Cecidomyiidae	x	x	x	x	x		x	
	Bursera instabilis	Diptera	Cecidomyiidae	Cecidomyiidae	x	x	x	x	x			
Convulvalaceae	*Ipomoea wolcottiana*	Diptera	Cecidomyiidae	*Aspondylia convolvuli* *	x	x	x	x	x	x	x	x
Erythroxylacaceae	*Erythroxylum mexicanum*	Diptera	Cecidomyiidae	*Neolasioptera erythroxyli*	x	x	x	x	x			
Euphorbiaceae	*Croton alamosanus*	Diptera	Cecidomyiidae	*sp1*	x	x	x	x	x		x	
	Croton pseudoniveus	Diptera	Cecidomyiidae	*sp2* *	x	x	x	x	x	x	x	x
	Croton suberosus	Diptera	Cecidomyiidae	*sp3*	x	x	x	x	x		x	
	Jatropha malacophylla	Diptera	Cecidomyiidae	*Aspondylia sp* *	x	x	x	x	x	x	x	x
	Jatropha standleyi	Diptera	Cecidomyiidae	Cecidomyiidae	x	x	x	x	x		x	
Flacourtiaceae	*Flacourtiaceae*	Diptera	Cecidomyiidae	Cecidomyiidae	x	x		x	x			
Hernandiaceae	*Gyrocarpus jatrophifolius*	Thysanoptera		Thysanoptera	x	x	x	x	x		x	
Leguminosae	*Caesalpinia caladenia*	Diptera	Cecidomyiidae	Cecidomyiidae	x	x	x	x	x	x		
	Cynometra oaxacana	Diptera	Cecidomyiidae	Cecidomyiidae	x	x		x	x			
	Lonchocarpus eriocarinalis	Homoptera	Kermidae	*Euphalerus sp1* *	x	x	x	x	x	x	x	x
	Lonchocarpus sp	Homoptera	Kermidae	*Euphalerus sp2* *	x	x	x	x	x	x	x	x
	Prosopis sp	Hymenoptera	Tanaostigmatidae	*Tanaostigma sp*	x	x	x	x	x			
Moraceae	*Brosimum alicastrum*	Homoptera	Kermidae	*Trioza rusellae*	x	x		x	x	x		
	Chlorophora tinctoria	Diptera	Cecidomyiidae	*Clinodiplosis chlorophora*	x	x	x	x	x		x	
	Ficus cotinifolia	Diptera	Cecidomyiidae	Cecidomyiidae	x	x	x	x	x		x	
Nictagynaceae	*Guapira macrocarpa*	Unidentified	Unidentified	Unidentified *	x	x	x	x	x	x	x	x
Polygonaceae	*Coccoloba barbadensis*	Diptera	Cecidomyiidae	*Ctenodactylomyia sp*	x	x		x	x			
	Ruprechtia fusca	Diptera	Cecidomyiidae	Cecidomyiidae *	x	x	x	x	x	x	x	x
Rubiaceae	*Guettarda elliptica*	Diptera	Cecidomyiidae	Cecidomyiidae *	x	x	x	x	x	x	x	x
	Randia spinosa	Diptera	Cecidomyiidae	*Bruggmannia randiae*	x	x	x	x	x		x	
Sapindaceae	*Paullinia cururu*	Diptera	Cecidomyiidae	*sp1*	x	x	x	x	x			x
	Paullinia sessiliflora	Diptera	Cecidomyiidae	*sp2*	x	x	x	x	x		x	
	Thounidium decandrum	Unidentified	Unidentified	Unidentified	x	x		x	x			
Simaroubaceae	*Recchia mexicana*	Unidentified	Unidentified	Unidentified	x	x	x	x	x		x	
Tiliaceae	*Heliocarpus pallidus*	Diptera	Cecidomyiidae	*Neolasioptera heliocarpi* *	x	x	x	x	x	x	x	x
Urticaceae	*Urera caracasana*	Diptera	Cecidomyiidae	Cecidomyiidae	x	x		x	x			
Verbenaceae	*Lippia graveolens*	Diptera	Cecidomyiidae	*Pseudomikola lippia*	x	x	x	x	x		x	
	Vitex hemsleyi	Diptera	Cecidomyiidae	*Cecidomyiidae*	x	x		x	x	x		x

Hill top over granite (1)
Hill top with conglomerate 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)

Legends to figures

Figure 1 Species accumulation curve for GFI on different habitats

Figure 2 Relationships between GFI species richness and available phosphorous contents in soil **(a)**, total nitrogen amount in soil **(b)** at the Chamela-Cuixmala Biosphere reserve in Jalisco, Mexico. Regression models were utilized in each nutrient of soil.

Figure 3 **(a)** Mean frequency of GFI on host plants in different habitats in Chamela-Cuixmala Biosphere reserve in Jalisco. GENMOD procedure (SAS 2000) was applied for generalized linear model (soils $\chi^2 = 34.2$; d.f. = 7; $P < 0.0001$; species $\chi^2 = 0.8$; d.f.= 10 $P > 0.05$) **(b)** Mean GFI density per leaf on different host plants. GENMOD procedure (SAS 2000) was applied for generalized linear model (soils $\chi^2 = 52.4$; d.f. = 7; $P < 0.0001$; species $\chi^2 = 98.8$; d.f. = 10; $P < 0.0001$). Different letters indicate statistically significant differences after a least squares means test ($P < 0.05$). The habitats are ordered from low to great soil fertility (Phosphorous) (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

Figure 1

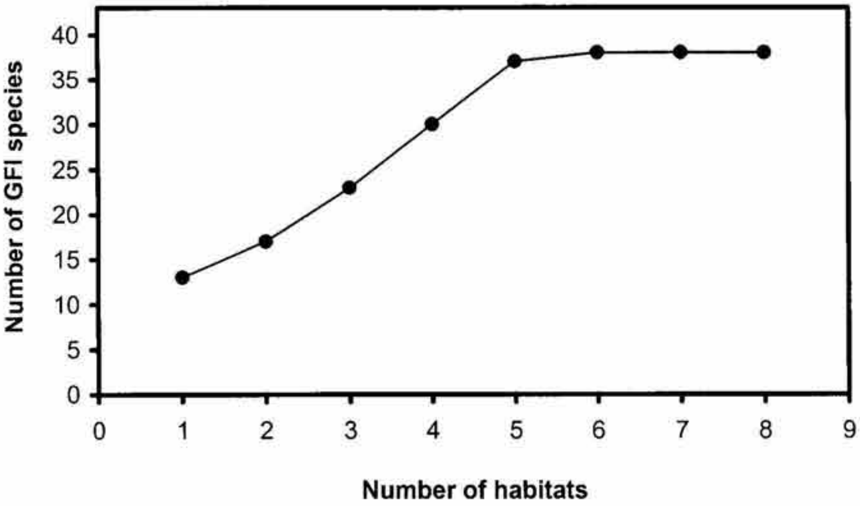

Number of GFI species
0
5
10
15
20
25
30
35
40
0
1
2
3
4
5
6
7
8
9
Number of habitats

Figure 2

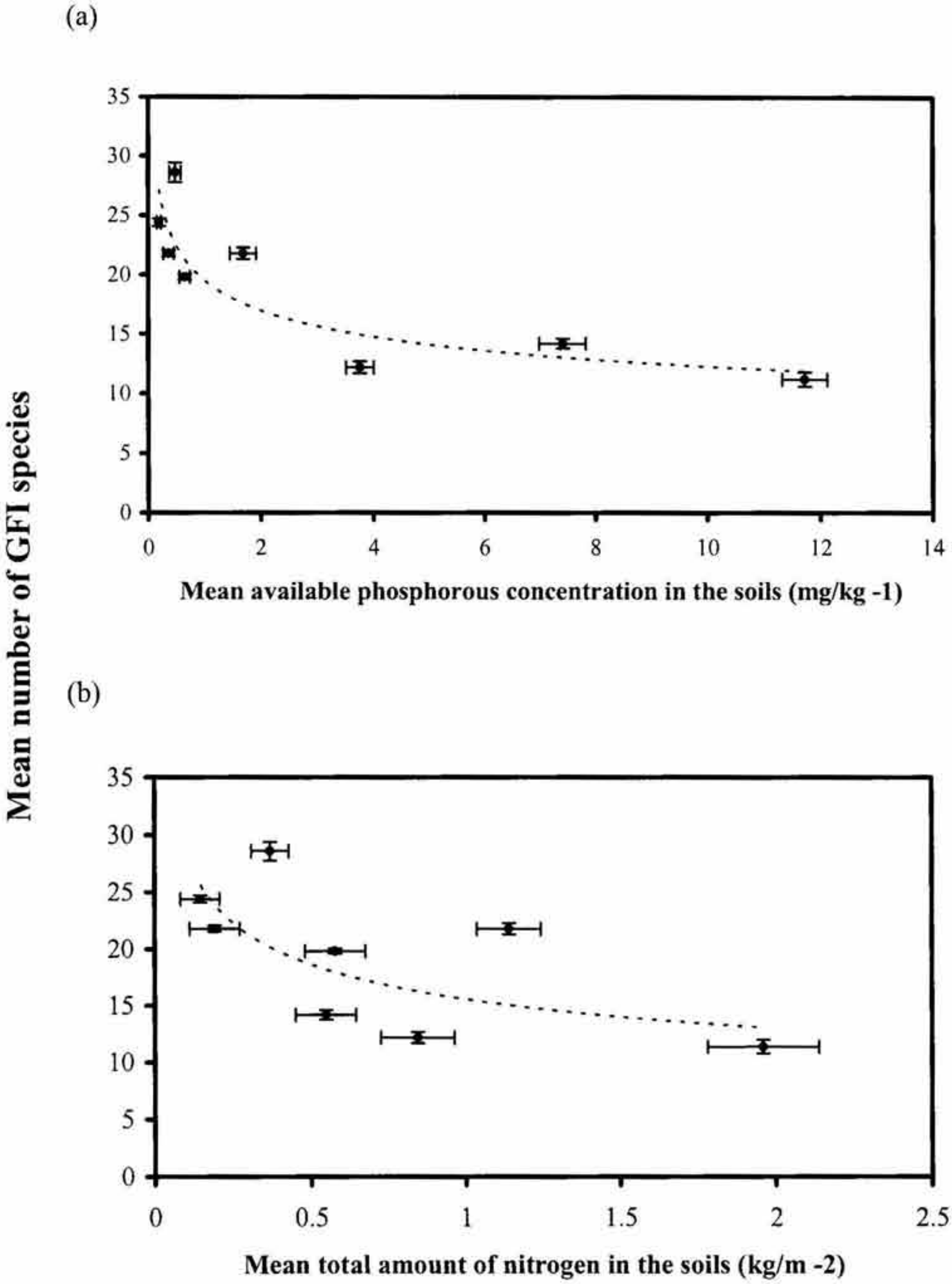
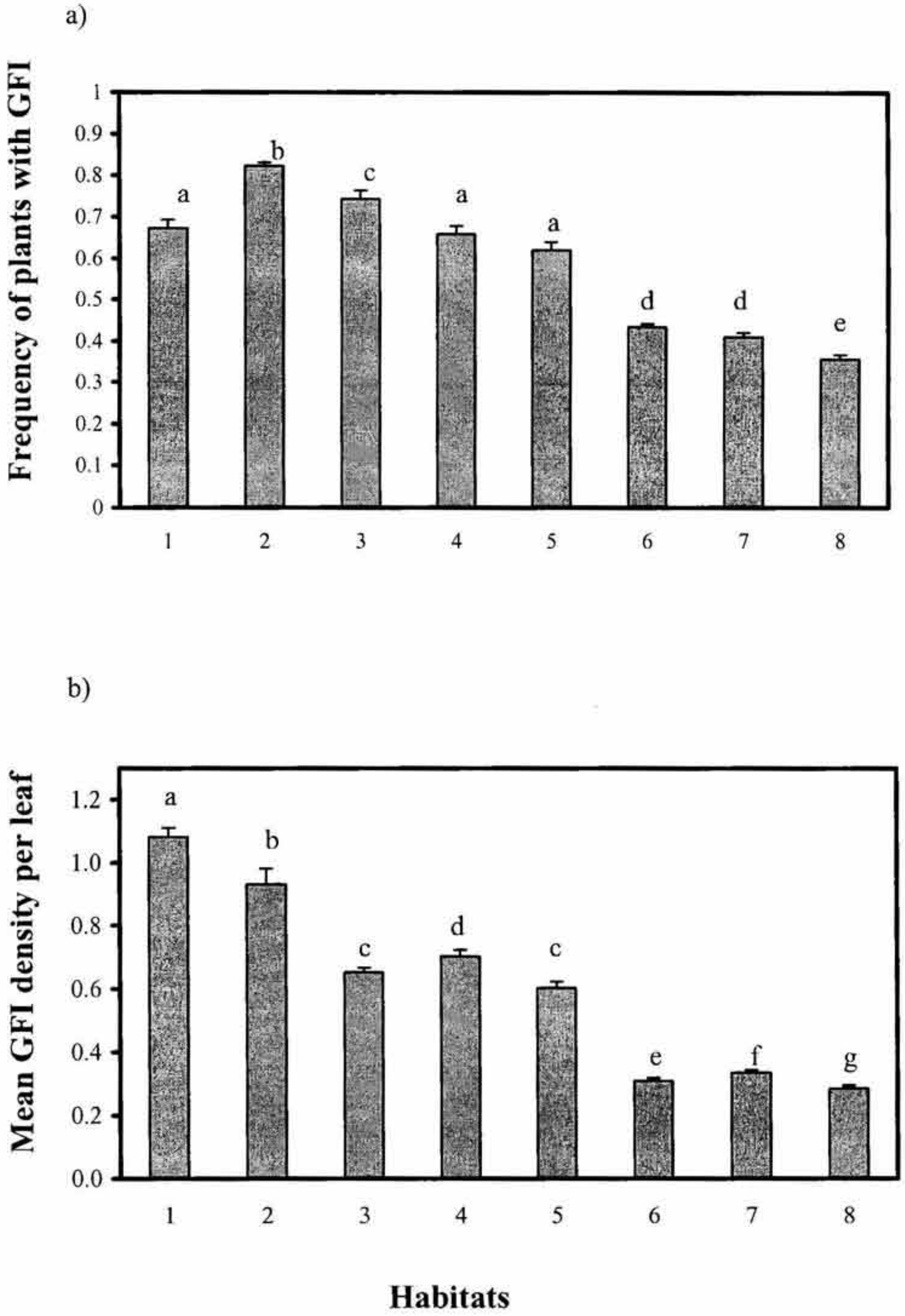

(a)
Mean number of GFI species
35
30
25
20
15
10
5
0
0
2
4
6
8
10
12
14
Mean available phosphorous concentration in the soils (mg/kg -1)
(b)
35
30
25
20
15
10
5
0
0
0.5
1
1.5
2
2.5
Mean total amount of nitrogen in the soils (kg/m -2)

Figure 3


a)
Frequency of plants with GFI
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
a
b
c
a
a
d
d
e
1
2
3
4
5
6
7
8
b)
Mean GFI density per leaf
1.2
1.0
0.8
0.6
0.4
0.2
0.0
a
b
c
d
c
e
f
g
1
2
3
4
5
6
7
8
Habitats

CAPÍTULO III.

Temporal and spatial herbivory patterns of gall-inducing insects in a Mexican tropical dry forest[1]

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Abstract

We evaluate the temporal and spatial patterns of herbivory and the amount of herbivory caused by gall-inducing insects (GII) in deciduous and riparian habitats in a seasonal tropical dry forest in Mexico. Plants occurring in these habitats differ in their phenology and moisture availability. Deciduous habitats are seasonal and xeric, while riparian habitats are aseasonal and mesic. We found 37 GII species associated with specific plant species, of which 19 (51.3%) were present in deciduous, 13 (35.2%) in riparian and only 5 (13.5%) occurred in both habitats. Herbivory by GII was greater in deciduous than riparian habitats during the wet season. In GII species that occurred in both habitats, we found that host plant species supported greater herbivory by GII in deciduous than in riparian habitats. These results indicate a greater preference of GII species for host plants in deciduous than riparian habitats during the wet season. In riparian habitats, 11 plant species (61.1%) had greater density of GII in the dry than the wet season. Similarly, leaf area affected by GII was significantly greater in dry than wet season in riparian habitats for 12 plant species (66.7%). These results indicate that dry forest plants of riparian habitats present two peaks of leaf-flushing, GII colonize leaves produced in the first peak at the beginning of the wet season and accumulate or re-colonize leaves in the second peak at the beginning of the dry season. The levels of herbivory by GII detected in this study (mean 14.9% in the rainy season: range 1.57-97.7) are considerably higher than those obtained for folivorous insects in other neotropical forests suggesting that this GII guild may have an important impact on their host plant species in this tropical community.

Keywords: Deciduous and riparian habitats; gall-inducing insects; herbivory; plant-insect interactions; seasonality; tropical dry forest.

TO UNDERSTAND THE IMPACT OF HERBIVORES ON THEIR HOST PLANT SPECIES it is necessary to quantify the variation in the amount of leaf area affected by herbivores and the composition of insect herbivores that affect the foliage of these plants (Marquis 1991). Several studies have shown that folivorous insects have negative effects on plant growth, reproduction and photosynthetic capacity in temperate and tropical forests (Bazzaz *et al.* 1987; Milewski *et al.* 1991; Karban & Strauss 1993; Morrison & Reekie 1995; Quesada *et al.* 1995; Parra-Tabla & Bullock 1998; Kaetaniemi *et al.* 1999; Mothershead & Marquis 2000) but see (Avila *et al.* 2003). In seasonal communities such as tropical dry forests, the impact of insect generalists on host plant has been much less documented (Janzen 1981; Filip *et al.* 1995) and herbivory patterns and abundance of insect specialists are unknown.

In tropical dry forests the timing of insect herbivore damage is particularly important given the strong seasonality between wet and dry season within a year. In this forest, the abundance of most herbivore insects in the dry season is relatively low and increases during the wet season (Wolda 1978, 1980; Lowman 1985; Murali & Sukumar 1993; Filip *et al.* 1995). The composition of the herbivore fauna is not temporally or spatially stable in these forests. Therefore, it is important to know the patterns of damage produced within plants, timing of damage relative to plant phenology and the degree of host specificity of the herbivore community in this habitat (Marquis 1991). It is likely that the seasonal presence of herbivore insects is synchronized with leaf flushing at the beginning of the wet season (Opler *et al.* 1980; Lieberman 1982; Reich & Borcher 1984; Bullock & Solís-Magallanes 1990) and that some insect herbivores have adjusted their life history to synchronize their youngest larval stages to the appearance of host organs such as shoots and leaves (Taylor 1986; Weis *et al.* 1988;Yukawa 2000).

Patterns of herbivory of folivorous insects in natural communities have been documented in few tropical localities (Coley 1980; Janzen 1981; Cruz & Dirzo 1987; Coley & Barone 1996). Even more poorly understood are the patterns of herbivory and abundance of specialist insect guilds such as gall-inducing insects (GII) in tropical communities. This insect guild has the ability to stimulate plant growth inducing the formation of amorphous masses of parenchyma cells denominated galls (Ananthakrishan 1984). The gall chamber induced in the host provides a stable microhabitat, protection against natural enemies and resources to feed to the larval stage of the life of GII (Cornell 1983; Ananthakrishan 1984; Waring & Price 1990; Hartley & Lawton 1992; Hartley 1998). In contrast to the majority of phytophagous insects that feed externally, GII may affect the inner organs of their hosts by removing some quantities of plant tissue or by directly obtaining nutrients from the mesophyll of leaves, stems, flowers or roots (Ananthakrishan 1984; Dreger-Jauffret & Sorthouse 1992). In the tropics, the studies on GII have not quantified the patterns and levels of herbivory on their host plants. Because GII are insect specialists, we should expect greater levels of leaf area affected by GII than by generalist folivorous insects. This is the first study that determines the spatial and temporal patterns and the amount of herbivory caused by GII in a tropical dry forest. In particular, we addressed the following questions: (i) What is the level of leaf area affected by each GII species on their host plants in a tropical forest (ii) Is GII abundance affected by habitat preferences in the wet season? (iii) Is GII abundance affected by seasonal variation in availability food in a tropical dry forest? (iv) Is there within variation in the levels of GII herbivory in deciduous and riparian habitats?

METHODS

STUDY SITE.–This study was conducted at the Chamela-Cuixmala Biosphere Reserve on the Pacific coast of Jalisco, Mexico that covers an extension of 13,200 ha. The elevation of this site ranges between 0-500 m, the average annual precipitation is 748 mm and the rainy season ranges from June to October (Bullock 1985). The mean monthly temperature is 24. 9° C (range 14.8-32.0° C). Vegetation is dominated by 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).

GII CENSUS: SPECIES RICHNESS AND SPECIFICITY.–Surveys were conducted from February to April 2001 during the dry season and from June to September 2001 during the rainy season. In order to estimate the spatial and temporal patterns of herbivory caused by GII, we sampled thirty transects of 50 x 5 m in riparian habitats during the dry season. In the wet season, we sampled thirty transects of 50 x 5 m in each of two independent deciduous and riparian habitats. Transects were randomly selected from points obtained from a grid system developed within each habitat using random numbers to assure sampling independence. In each transect, we identified and collected all GII species and their respective host plant species. We verified the degree of specificity of each GII by taxonomically identifying each insect specimen collected in the field. Collected galls were reared in the laboratory until the emergence of adult insects and later identified. Because the induction by all GFI species studied only affected leaves, we restrict our study to GII of the same guild.

ABUNDANCE AND AMOUNT OF HERBIVORY CAUSED BY GII.–During the dry season, in each plant species associated with GII, we sampled 20 individuals in riparian habitats and during the wet season, we sampled 20 individuals in each deciduous and riparian habitat. In all cases, the sampling of GII extended from the canopy to the lower branches of each individual, we collected three branches at the top, intermediate and bottom of each stratum for all plant species and randomly collected 50 leaves. For each leaf, we estimated the number of galls per square centimeter and the proportion of leaf area affected. To control for plant age, the stem diameter at breast height (DBH) was measured for each tree and shrub sampled.

After a preliminary analysis of presence of GII species and their host plants in deciduous and riparian habitats at Chamela-Cuixmala Biosphere reserve, we found that five GII species were always present in both habitats. Therefore, to compare the susceptibility to galls on the same plant species located in different habitat conditions and different temporal seasons, we registered the mean of GII density and the amount of leaf area affected to each plant in deciduous and riparian habitats during rainy season and only in riparian habitats during the dry season.

ANALYSIS.–We conducted a logistic regression analysis GENMOD (SAS 2000) to determine the effect of habitat (i.e. riparian vs. deciduous) on the density of GII and leaf area affected by GII during the wet season. Habitat and host plant age were considered as the independent variables and GII density and the proportion of leaf area affected by GII were used as the response variables. The proportion of leaf area affected by GII was estimated for each leaf as the area affected by GII divided by the total leaf area. Similar analyses were used to compare each of the five plant species that occurred in riparian and deciduous habitats during the wet season.

We used a logistic regression analysis GENMOD (SAS 2000) to determine the effect of seasonality on riparian habitats on the GII density and leaf area affected by GII. Season (wet vs. dry) and host plant age were considered as the independent variables and GII density and the proportion of leaf area affected by GII were used as the response variables. A similar analysis was conducted for each plant species to determine the effect on specific hosts.

We conducted a logistic regression analysis GENMOD (SAS 2000) within each habitat to test if herbivory caused by GII is different between all plant species in deciduous and riparian habitats during the wet season. Habitat and host plant age were considered as the independent variables and GII density and the proportion of leaf area affected by GII were used as the response variables. A LS Means test was used for a posteriori comparisons between plant species ($P < 0.05$).

RESULTS

GII SPECIES RICHNESS AND SPECIFICITY.–We found 37 GII species represented in the following orders: Diptera (Cecidomyiidae family) which induced the majority of galls in both habitats with 27 species (80.0 %); Homoptera [Psyllidae (5.4%) and Kermidae (8.1%) families], Hymenoptera [Tanaostigmatidae, (2.7%)] and Thysanoptera (2.7%) were rare and three morphospecies unidentified (8.1%). Of total of GII species, 19 (51.3%) were present in deciduous habitats (Figure 1), 13 (35.2%) in riparian habitats (Figure 2) and only 5 (13.5%) occurred in both habitats (Figures 2 and 3). No significant differences in the number of GII species were found between deciduous and riparian habitats ($\chi^2 = 0.48$; d.f. = 1; $P > 0.05$). In all cases, there was a great specificity between GII species and their host plant species, each GII species was associated with one different plant species.

ABUNDANCE AND AMOUNT OF HERBIVORY CAUSED BY GII.–The mean leaf area affected by GII in Chamela tropical dry forest was 14.9% in the wet season (range 1.57-97.7). Particularly, during the wet season, the mean leaf area affected by GII in deciduous habitats was 18.9% and in riparian habitats 10.0%. In the dry season, the mean leaf area affected by GII in riparian habitats was 15.7%.

GII density was significantly greater in deciduous than in riparian habitats during the wet season (habitat: $\chi^2 = 30.94$; d.f. = 1; $P < 0.0001$).(Table 1). GII density was greater on saplings (0.7 ± 0.08) than in mature plants (0.5 ± 0.06) (host plant age: $\chi^2 = 25.45$; d.f. = 1; $P < 0.0001$). The proportion of leaf area affected by GII was greater in deciduous than in riparian habitats (habitat: $\chi^2 = 402.96$; d.f. = 1; $P < 0.0001$) (Table 1). Proportion of leaf area affected by GII was significantly greater in saplings (18.9 ± 6.5) than in mature plants (11.8 ± 3.8) (host plant age: $\chi^2 = 143.57$; d.f. = 1; $P < 0.0001$).

In the five cases of GII species that occurred in both habitats, host plant species supported greater GII density and proportion of leaf area affected by GII species in deciduous than riparian habitats during the wet season (Table 2). In addition, we did not find significant differences in herbivory by GII between the same host plant species that occur during the wet season in deciduous habitats and those that occur during the dry season in riparian habitats ($P > 0.05$).

In riparian habitats, GII density was significantly greater in the dry season than during the wet season (habitat: $\chi^2 = 9.11$; d.f. = 1; $P < 0.002$ (Table 1). In addition, density of GII was greater on saplings (0.55 ± 0.05) than in mature plants (0.37 ± 0.06) (host plant age: $\chi^2 = 9.12$; d.f. = 1; $P < 0.002$). Proportion of leaf area affected by GII was greater in the dry than in the wet season (habitat: $\chi^2 = 105.06$; d.f. = 1; $P < 0.0001$)

(Table 1) and significantly greater in sapling (18.8 ± 2.3) than in mature plants (11.2 ± 1.8) (host plant age: χ^2= 18.5; d.f. = 1; $P < 0.002$).

In riparian habitats we found that 11 plant species (61.1%) had greater GII density (Table 3) and 12 plant species (66.7%) had higher leaf area affected by GII in the dry season than in the wet season (Table 4).

We found a statistically significant variation in GII density (species: χ^2= 135.66; d.f. = 23; $P < 0.0001$; host plant age: χ^2= 16.82; d.f. = 1; $P < 0.0001$) (Figure 1a) and leaf area affected by GII (species: χ^2= 1801.17; d.f. = 23; $P < 0.0001$; host plant age: χ^2= 193.34; d.f. = 1; $P < 0.0001$) within deciduous habitats (Figure 1b). Similarly, within riparian habitats, we found a statistically significant variation in GII density (species: χ^2= 140.18; d.f. = 17; $P < 0.0001$; host plant age: χ^2= 13.73; d.f. = 1; $P < 0.0001$) (Figure 2a) and the leaf area affected by GII (species: χ^2= 172.17; d.f. = 17; $P < 0.0001$; host plant age: χ^2= 26.26; d.f. = 1; $P < 0.0001$) (Figure 2b).

DISCUSSION

Our study is the first to measure the amount of herbivory caused by GII in a tropical forest. In general, the mean leaf area affected by GII in the Chamela tropical dry forest was 14.9% in the rainy season (range 1.57-97.7), 18.9% in the deciduous forest and 10 % in the riparian habitat, whereas in the dry season, the riparian habitat experienced 15.7%. Filip *et al.* (1995) reported similar levels of herbivory caused by folivorous insects in the Chamela tropical dry forest (17% range1.2-72.7). In contrast, these levels of herbivory are considerably greater than those reported for other tropical forests (Marquis & Braker 1994; Coley & Barone 1996). Coley and Barone (1996) suggested that specialist herbivores cause more leaf damage than generalists. Although the levels herbivory damage caused by specialist insects are not well documented, our study shows that a specialized guild such as GII affects a similar or greater leaf area to that of other generalist insects in tropical forests (Marquis 1994; Coley & Barone 1996, Cuevas-Reyes *et al.* 2004a, b).

The second objective of our study analyzed the relation of the abundance of GII in the wet season to particular habitats within a tropical dry forest. Leaf area and density of GII were greater in deciduous than riparian habitats during the wet season. In addition, in the five GII species that occurred in both habitats, their host plant species were more affected by GII in deciduous than riparian habitats. In tropical dry forests, temporal variation in food resources is critical for GII because they require undifferentiated tissue to induce a gall in their hosts (Weis *et al.* 1988; Dreger-Jauffret & Sorthouse 1992; De Souza 2001). Therefore, synchronization of GII to their host phenology is particularly important in the first flush of leaves of this deciduous forest (Weis *et al.* 1988; Yukawa 2000). Massive leaf flushing, at the beginning of the wet season, is a general phenological pattern of the tropical deciduous forests whereas in riparian habitats, plants are evergreen and produce new leaves throughout a more extended period during the wet season and a short period in the dry season (Frankie *et al.* 1974; Opler 1980; Bullock & Solís-Magallanes 1990; van Schaik *et al.* 1993). Therefore, more availability of younger leaves, during a short period of time, occurs in the deciduous forest than in the riparian evergreen forest in the wet season. Yukawa (2000) suggests that univoltine GII have adapted to synchronize with the appearance and development of host organs such as shoots and leaves in tropical regions. Similarly, host plant phenology affects the distribution and abundance of folivorous insects because of temporal variation in host quality and quantity (Basset & Burckhardt 1992; Floate *et al.* 1993; Rossi *et al.* 1999). Folivores often respond to seasonal variation of food resources by synchronizing their lifes cycles with the phenological stage of their hosts (Raffa *et al.* 1992, Mopper & Simberloff 1995).

The third objective of our study compared the intensity of GII between seasons in the riparian habitat because this is the only habitat of this forest that maintains the leaves during the dry season. Leaf area and density of GII were greater in the dry than in the wet season. Evidence from the literature provided two possible explanations for this pattern. First, dry forest plants of riparian habitats express two peaks of leaf flushing (Frankie *et al.* 1974, Bullock & Solís-Magallanes 1990; Wright 1996), GII colonize leaves produced in the first peak at the beginning of the wet season and accumulate or re-colonize leaves in the second peak at the beginning of the dry season. Second, some GII species that occur in both habitats will migrate from the deciduous leafless habitat to the riparian evergreen forest in the dry season. Therefore, riparian habitats in the dry season apparently accumulate the next generation of GII produced from the previous generation of the wet season from both habitats. This increment of GII during the dry season within riparian habitats suggests the existence of bivoltine GII species because GII can colonize in the first peak of leaf-flushing and the next generation during the second peak produced within the same year.

Finally, only some studies have documented the herbivory and abundance of folivorous insects on host plant age. The patterns are not consistent, various insect guilds are more abundant on saplings, while others on mature plants (Lowman 1992; Basset 2001). Differences in plant chemistry, leaf palatability, local microclimate, enemy free-space have been suggested as possible causes for these differences (Coley & Barone 1996). In our study, we found for all cases that GII density and leaf area affected by GII was greater in saplings than mature plants. Considering the host specialization of GII, these results may be due to the association with the preference of female insects for saplings because they offer leaves with rapid expansion, higher nutritional quality and secondary metabolites (Coley 1987; Basset 2001) and undifferentiated meristems that represent sites for gall induction because the physiology of gall morphogenesis requires the stimulation by insects to undifferentiated plant tissues (Weis *et al.* 1988). The association with saplings may also be related to the ability of GII to sequester secondary metabolites of their host plants as mechanism of protection against natural enemies (Cornell 1983; Waring & Price 1990; Hartley & Lawton 1992; Hartley 1998).

Because the foliar area occupied by each mature gall is eventually loss in each plant, this tissue losses its photosynthetic capacity prematurely with possible negative consequences to the performance of the plant. In our study, we did not evaluate the possible negative consequences of herbivory caused by GII on growth and plant reproduction nor the costs to the plants of inducing galls. However, several studies have established that gall induction on host plants negatively affect the allocation patterns and vegetative growth (Askew 1984; Larson & Whitham 1991; Hartley & Lawton 1992; Wolfe 1997; Hartley 1998; Rossi & Stiling 1998; Preus & Morrow 1999), photosynthetic rates (Fay *et al.* 1996; Larson 1998), and plant fitness (Hartnett and Abrahamson 1979; Ananthakishan 1984; Sacchi *et al.* 1988; Parra-Tabla & Bullock 1998). Therefore, the levels of herbivory by GII found in our study may have an impact on their host plants. Future studies need to evaluate the effects of GII on the fitness of plants.

In conclusion, our study is the first that document the patterns of herbivory by GII in a tropical plant community. Herbivory patterns by GII in a tropical dry forest are affected by seasonal and spatial availability of food resources. Our results show that for most species, GII herbivory was greater in deciduous habitats during the wet season. In riparian habitats, GII apparently colonize leaves produced in two different seasonal peaks of leaf-flushing within the same year. Herbivory by GII is related to the ontogeny of plants, density and leaf area affected by GII was greater in saplings than mature plants. The study of GII herbivory patterns is important to understand the potential impact of GII on their host plants in tropical systems.

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LITERATURE CITED

ANANTHAKRISHAN, T. N. 1984. Adaptative strategies in cecidogenous insects. In: T. N. Ananthakrishan (Ed.). The biology of gall insects, pp. 1–9. Oxford and IBH, New Delhi.

ASKEW, R. R. 1984. The biology of gall-wasps. In: T. N. Ananthakrishan (Ed.). The biology of gall insects, pp. 223–271. Edward Arnold, London.

AVILA-SAKAR, G., L. L. LEIST AND A. G. STEPHENSON. 2003. Effects of the spatial pattern of leaf damage on growth and reproduction I: nodes and branches. J. Ecol. 91: 867–879.

BASSET, Y., AND D. BURCKHARDT. 1992. Abundance, species richness, host utilization and host specificity of insect folivores from a woodland site, with particular reference to host architecture. Rev. S. Zool. 99: 771–791.

BASSET, Y. 2001. Communities of insect herbivores foraging on saplings versus mature trees of Pourouma bicolor (Cecropiaceae) in Panama. Oecologia 129: 253–260.

BAZZAZ, F. A., N. R. CHIARIELLO, P. D. COLEY, AND L. F. PITELKA. 1987. Allocating resources to reproduction and defense. Bioscience 37: 58–67.

BULLOCK, S.H. 1985. Breeding systems in the flora of tropical deciduous forest in Mexico. Biotropica 4: 287–301.

BULLOCK, S.H., AND J. A. SOLÍS-MAGALLANES. 1990 Phenology of canopy trees of a tropical deciduous forest in Mexico. Biotropica 22: 22–35.

COLEY, P. D. 1980. Effects of leaf age and plant life-history patterns on herbivory. Nature 284: 545–546.

COLEY, P. D. 1987. Patrones en las defenses de las plantas: ¿porqué los herbívoros prefieren ciertas especies? Rev. Biol. Trop. 1: 151–164.

COLEY, P. D., AND J. A. BARONE. 1996. Herbivory and plant defenses in tropical forests. Annu. Rev. Ecol. Syst. 27: 305–335.

CORNELL, H. C. 1983. The secondary chemistry and complex morphology of galls formed by Cynipinae (Hymenoptera): Why and how? Am. Midl. Nat. 110: 225–234.

CUEVAS-REYES, P., M. QUESADA, P. HANSON, R. DIRZO, AND K. OYAMA. 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. J. Ecol. (In press).

CUEVAS-REYES P., M. QUESADA, C SIEBE, AND K. OYAMA. Spatial patterns of herbivory by gall-forming insects: A test of the soil fertility hypothesis in a Mexican tropical dry forest. Oikos (In press).

CRUZ, M., AND R. DIRZO. 1987. A survey of the standing levels of herbivory in seedlings from a Mexican rain forest. Biotropica 19: 98–106.

DE SOUZA, M. M. 2001. Galling insect diversity patterns: the resource synchronization hypothesis. Oikos 95: 171–176.

DREGER-JAUFFRET, F., AND J. D. SORTHOUSE. 1992. Diversity of gall-inducing insects and their galls. In: J. D. Sorthouse and O. Rohfritsch (Eds.). Biology of insect-induced galls, pp.8–33. Oxford University Press, New York.

FAY, P. A., R. W. PRESZLER, AND T. G. WHITHAM. 1996. The functional resource of a gall-forming adelgid. Oecologia 105: 199–204.

FILIP, V., R. DIRZO, J. M. MASS, AND J. SARUKHÁN. 1995. Within-and among-year variation in the levels of herbivory on the foliage of tress from a Mexican tropica deciduous forest. Biotropica 27: 78-86

FLOATE, K. D., M. J. C. KEARSLEY, T. G., AND WITHAM. 1993. Elevated herbivory in plant hybrid zones: *Chrysomela confluens*, *Populus* and phenological sinks. Ecology 74: 2056–2065.

FRANKIE, G. W., H. G. BAKER, AND P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. J. Ecol. 62: 881–899.

HARTLEY, S. E., AND J. H. LAWTON. 1992. Host-plant manipulation by gall-insects: a test of the nutrition hypothesis. J. Anim. Ecol. 61: 113–119.

HARTLEY, S. E. 1998. The chemical composition of plant galls: are levels of nutrients and secondary compounds controlled by the gall-former. Oecologia 113: 492–501.

HARTNETT, D. C., AND W. G. ABRAHAMSON. 1979. The effects of stem gall insects on life history patterns in *Solidago canadiensis*. Ecology 60: 910–917.

JANZEN, D. H. 1981. Patterns of herbivory in a tropical deciduous forest. Biotropica 15: 108–111.

KAITANIEMI, P., S. NEUVONEM, AND T. NYYSSONEN. 1999. Effects of accumulative defoliations on growth, reproduction, and insect resistance in Mountain Birch. Ecology 80: 524–532.

KARBAN, R., AND S.Y. STRAUSS 1993. Effects of herbivores on growth and reproduction of their perennial host, *Erigeron glaucus*. Ecology 74: 39–46.

LARSON, K.C., AND T. C. WHITHAM. 1991. Manipulation of food resources by a gall-forming aphid: The physiology of sink-source interactions. Oecologia 88: 15–21.

LARSON, K. C. 1998. The impact of two gall-forming arthropods on the photosynthetic rates of their hosts. Oecologia 115:161–166.

LIEBERMAN, D. 1982. Seasonality and phenology in dry tropical forest in Ghana. J. Ecol. 791–806.

LOTT, E. J., S. H. BULLOCK, AND J. A. SOLIS-MAGALLANES. 1987. Floristic diversity and structure of upland and arroyo forests of Coastal Jalisco. Biotropica 3: 228–235.

LOWMAN, M. D. 1985. Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. Aust. J. Ecol. 10: 7–24.

LOWMAN, M. D. 1992. Herbivory in Australian rain forests, with particular reference to the canopies of *Doryphora sassafras* (Monimiaceae). Biotropica 24: 263–272.

MARQUIS, R. J. 1991. Herbivore fauna of Piper (Piperaceae) in Costa Rican wet forest: diversity, specificity, and impact. In: P. W. Price, T. M. Lewinsohn, G. W. Fernandes and W. W. Benson (Eds.), pp. 179–202. Plant-animal interactions: evolutionary ecology in tropical and temperate regions. John Wiley and Sons Corporations, New York.

MARQUIS R. J., AND BRAKER H. E. 1994. Plant herbivore interactions: diversity, specificity, and impact. In L. A. Mcdade, K. S. kawa, H. A. Hespenheide and . S. hartshorn (Eds.). La Selva: ecology and natural history of a Neotropical rainforest, pp. 261-281. Chicago/London: University of Chicago Press.

MILEWSKI, A. V., T. P. YOUNG, AND D. MADDEN. 1991. Thorns as induced defenses: experimental evidence. Oecologia 86: 70–75.

MOPPER, S., AND D. SIMBERLOFF. 1995. Differential herbivory in an oak population: the role of plant phenology and insect performance. Ecology 76:1233–1241.

MOTHERSHEAD, K., AND R. J. MARQUIS. 2000. Fitness impacts of herbivory through indirects effects on plant-pollinator interactions in *Oenothera macrocarpa*. Ecology 81: 30–40.

MORRISON, K. D., AND E. G. REEKIE. 1995. Pattern of defoliation and its effect on photosynthetic capacity in *Oenothera biennis*. J. Ecol. 83: 759–767.

MURALI, K. S., AND R. SUKUMAR. 1993. Leaf flushing phenology and herbivory in a tropical dry deciduous forest, southern India. Oecologia 94: 114–119.

OPLER, P. A., G. H. FRANKIE, H. G. BAKER. 1980. Comparative phenological studies of treelet and shrubs species in tropical wet and dry forests in the lowlands of Costa Rica. J. Anim. Ecol. 68: 167–188.

PARRA-TABLA, V., AND S. H. BULLOCK. 1998. Factors limiting fecundity of the tropical tree *Ipomoea wolcottiana* (Convulvalaceae) in a Mexican tropical dry forest. J. Trop. Ecol. 14: 615–628.

PREUS, L. A., AND P. A. MORROW. 1999. Direct and indirect effects of two herbivore species on resource allocation in their shared host plant: the rizoma galler *Eurosta comma*, the folivore *Trirhabda canadensis* and *Solidago missouriensis*. Oecologia 119: 219–226.

PRICE, P. W. 1991. Patterns in communities along latitudinal gradients. In: P. W. Price, T. M. Lewinson, G. W. Fernandes and W. W. Benson (Eds.). Plant animal interactions: evolutionary ecology of tropical and temperate regions, pp. 51–68. John Wiley and Sons, New York.

QUESADA, M., K. BOLLMAN, AND A. G. STEPHENSON. 1995. Leaf damage decreases pollen production and hinders pollen performance in *Cucurbita texana*. Ecology 76: 437–443.

RAFFA, K. F., HALL, D. J., KEARBY, W., AND S. KATOVICH. 1992. Seasonal life history of introduced basswood thrips (Thysanoptera:Thripidae) in Wisconsin, with observations on associated thrips species. Env. Entomol. 21:771–779.

REICH, P. B., AND R. BORCHERT. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. J. Ecol. 72: 61–74.

ROSSI, A. M., AND P. STILING. 1998. The interactions of plant clone and abiotic factors on gall-making midge. Oecologia 116: 170–176.

ROSSI, A. M., P. STILING, M. V. CATTELL, AND T. I. BOWDISH. 1999. Evidence of host-associated races in a gall-forming midge: trade-offs in potential fecundity. Ecol. Entomol. 24: 95–102.

RZEDOWSKI, J. 1978. Vegetación de México. Editorial Limusa, México.

SACCHI, C., P. W. PRICE, P. TOMOTHY, P. CRAIG, AND J. K. ITAMI. 1988. Impact of shoot galler attack on sexual reproduction in the arroyo willow. Ecology 69: 2021–2030.

SAS. 2000. Categorical data analysis using the SAS system. SAS Institute, Cary, North Carolina, USA.

TAYLOR, L. R. 1986. Synoptic dynamics, migration and the rothamsted insect survey. J. Anim. Ecol. 55:1–38.

VAN SCHAIK, C. P., J. W. TERBORGH, AND J. WRIGHT. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. Ann. Rev. Ecol. Syst 24: 353–377.

WARING, G. L., AND P. W. PRICE. 1990. Plant water stress and gall formation (Cecidomyiidae: *Asphondylia spp.*) on creosote bush. Ecol Entomol 15: 87–95.

WEIS, A.E., R. WALTON, AND C. L. CREGO. 1988. Reactive plant tissue sites and the population biology of gall makers. Annu Rev Entomol 33: 467–486.

WOLDA, H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. J. Anim. Ecol. 47: 269–381.

WOLDA, H. 1980. Seasonality of tropical insects. J. Anim. Ecol. 49: 277–290.

WOLFE, M. L. 1997. Differential flower herbivory and gall formation on males and females of *Neea psychotriodes* a dioecious tree. Biotropica 29: 169–174.

WRIGHT, J. 1996. Phenological responses to seasonality in tropical forest plants. In: S. S. Mulkey (Ed.). Tropical forest plant ecophysiology, pp. 440–460. Chapman and Hall.

YUKAWA, J. 2000. Synchronization of gallers with host plant phenology. Popul. Ecol. 42: 105–113

TABLE 1. Comparison of herbivory by GII within the wet season and between seasons in deciduous and riparian habitats in tropical dry forest at Chamela, Mexico.

	Wet season				Dry season		
	Deciduous	Riparian	Chi-square	*P* =	Riparian	Chi-square	*P* =
GII density	0.63 (± 0.06)	0.34 (± 0.08)	30.94	0.0001			
Leaf area affected by GII	24.5 (± 2.1)	10.9 (± 2.8)	402.9	0.0001			
GII density		0.34 (± 0.08)			0.53 (± 0.06)	6.41	0.01
Leaf area affected by GII		10.9 (± 2.8)			16.1 (± 1.5)	119.3	0.01

TABLE 2. Differences in density and leaf area affected by GII in plant species that occur in both habitats during the wet season. GENMOD procedure (SAS 2000) was applied for modeling log function to each plant species.

Plant species	Density of GII				Leaf area affected by GII			
	Deciduous	Riparian	Chi-square	*P* =	Deciduous	Riparian	Chi-square	*P* =
Achatocarpus gracilis	1.15 (± 0.12)	0.62 (± 0.07)	6.44	0.001	17.1 (± 1.7)	8.1 (± 0.6)	7.77	0.005
Cordia alliodora	0.4 (± 0.07)	0.19 (± 0.05)	10.61	0.0001	9.4 (± 1.1)	3.7 (± 1.5)	18.31	0.0001
Guettarda elliptica	0.41 (± 0.04)	0.28 (± 0.05)	4.4	0.01	12.6 (± 1.7)	8.7 (± 0.9)	4.71	0.03
Heliocarpus pallidus	0.27(± 0.05)	0.18 (± 0.06)	7.28	0.006	9.0(± 0.9)	5.1 (± 0.3)	6.95	0.008
Ruprechtia fusca	0.77 (± 0.09)	0.47 (± 0.06)	10.77	0.002	21.8(± 3.0)	11.3 (± 2.5)	13.48	0.0002

TABLE 3. Seasonal variation of GII density in plant species that occur in riparian habitats in Chamela tropical dry forest.

Plant species	GII taxa	Wet season	Dry season	Chi-Square	*P* =
Achatocarpus gracilis	Unidentified	0.55 (± 0.06)	1.23 (± 0.09)	5.26	0.002
Bignoniaceae	Cecidomyiidae	0.21 (± 0.1)	0.19 (± 0.16)	0.02	**n.s.**
Brosimum alicastrum	*Trioza rusellae*	0.49 (± 08)	0.66 (± 0.9)	5.73	0.003
Bursera instabilis	Cecidomyiidae	0.2 (± 0.07)	0.38 (± 0.04)	11.08	0.0002
Coccoloba barbadensis	*Ctenodactylomyiia sp*	0.38 (± 0.2)	0.55 (± 0.27)	0.32	**n.s.**
Cordia alliodora	Neolasioptera sp	0.2 (± 0.03)	0.41 (± 0.04)	5.53	0.002
Cynometra oaxacana	Cecidomyiidae	0.65 (± 0.1)	1.13 (± 0.09)	4.48	0.01
Ficus cotinifolia	Cecidomyiidae	0.2 (± 0.06)	0.44 (± 0.08)	5.32	0.007
Flacourtiaceae	Cecidomyiidae	0.2 (± 0.07)	0.4 (± 0.07)	10.39	0.002
Guettarda elliptica	Cecidomyiidae	0.3 (± 0.06)	0.42 (± 0.07)	3.24	0.03
Heliocarpus pallidus	*Neolasioptera heliocarpi*	0.19 (± 0.15)	0.2 (± 0.18)	0.9	**n.s.**
Paullinia cururu	Cecidomyiidae	0.56 (± 0.1)	0.55 (± 0.17)	0.41	**n.s.**
Paullinia sessiliflora	Cecidomyiidae	0.38 (± 0.14)	0.36 (± 0.19)	0.92	**n.s.**
Prosopis sp	*Tanaostigma sp*	0.41 (± 0.18)	0.58 (± 0.15)	0.73	**n.s.**
Recchia mexicana	Unidentified	0.19 (± 0.04)	0.35 (± 0.03)	3.51	0.03
Ruprechtia fusca	Cecidomyiidae	0.46 (± 0.03)	0.63 (± 0.08)	3.57	0.03
Urera caracasana	Cecidomyiidae	0.21 (± 0.05)	0.41 (± 0.03)	4.24	0.01
Vitex hemsleyi	Cecidomyiidae	0.39 (± 0.09)	0.46 (± 0. 16)	0.12	**n.s.**

TABLE 4. Comparison of leaf area affected by GII between the wet and the dry season in plant species that occur in riparian habitats.

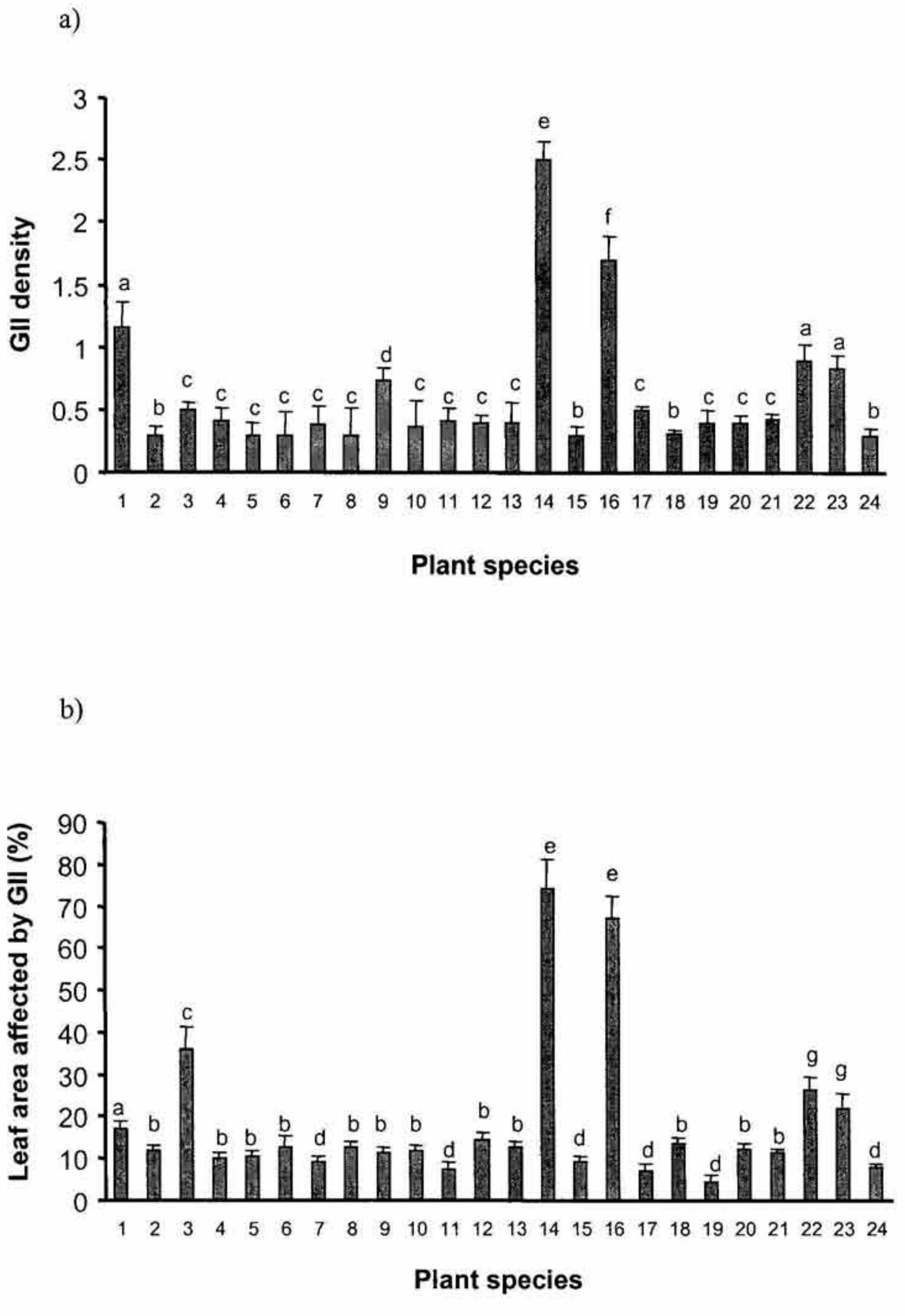
Plant species	GII taxa	Wet season	Dry season	Chi-Square	*P* =
Achatocarpus gracilis	Unidentified	8.1 (± 0.1.2)	19.5(± 1.8)	15.93	0.0001
Bignoniaceae	Cecidomyiidae	7.3 (± 1.1)	11.8 (± 0.8)	4.64	0.03.
Brosimum alicastrum	*Trioza rusellae*	9.7 (± 1.2)	15.8 (± 1.1)	12.86	0.0003
Bursera instabilis	Cecidomyiidae	8.8 (± 1.5)	16.1(± 1.1)	11.35	0.0008
Coccoloba barbadensis	*Ctenodactylomyiia sp*	13.4 (± 2.2)	21.9 (± 1.5)	0.18	**n.s.**
Cordia alliodora	Neolasioptera sp	3.7 (± 0.5)	12.7 (± 0.8)	29.6	0.0001
Cynometra oaxacana	Cecidomyiidae	16.0 (± 0.9)	22.4 (± 1.8)	6.66	0.009
Ficus cotinifolia	Cecidomyiidae	9.4(± 1.5)	15.6 (± 1.2)	5.08	0.02
Flacourtiaceae	Cecidomyiidae	8.4 (± 1.0)	14.6 (± 1.6)	10.85	0.001
Guettarda elliptica	Cecidomyiidae	8.7 (± 1.2)	13.9 (± 0.8)	6.16	0.01
Heliocarpus pallidus	*Neolasioptera heliocarpi*	8.4 (± 1.3)	6.0 (± 0.4)	0.4	**n.s.**
Paullinia cururu	Cecidomyiidae	15.7 (± 1.6)	14.9 (± 2.9)	0.87	**n.s.**
Paullinia sessiliflora	Cecidomyiidae	12.5 (± 2.1)	12.5 (± 1.7)	0.1	**n.s.**
Prosopis sp	*Tanaostigma sp*	12.8 (± 1.7)	15.0 (± 0.8)	1.68	**n.s.**
Recchia mexicana	Unidentified	3.9(± 0.59)	15.3 (± 0.2.1)	18.71	0.0001
Ruprechtia fusca	Cecidomyiidae	11.3 (± 1.2)	22.4 (± 2.4)	18.64	0.0001
Urera caracasana	Cecidomyiidae	6.3 (± 0.9)	16.1 (± 2.3)	39.84	0.0001
Vitex hemsleyi	Cecidomyiidae	15.9 (± 2.8)	16.3 (± 1.5)	0.11	**n.s.**

LEGENDS TO FIGURES

FIGURE 1 a) Variation of GII density on host plant species that occur in deciduous habitats during the wet season (species: χ^2= 135.66; d.f. = 23; $P < 0.0001$). Different letters indicate statistically significant differences after a least squares means test ($P < 0.05$); b) Variation of leaf area affected by GII on host plant species that occur in deciduous habitats during the wet season (species: χ^2= 1801.17; d.f. = 23; $P < 0.0001$). Different letters indicate statistically significant differences after a least squares means test ($P < 0.05$). The asterisk indicate GII species present in both habitats.

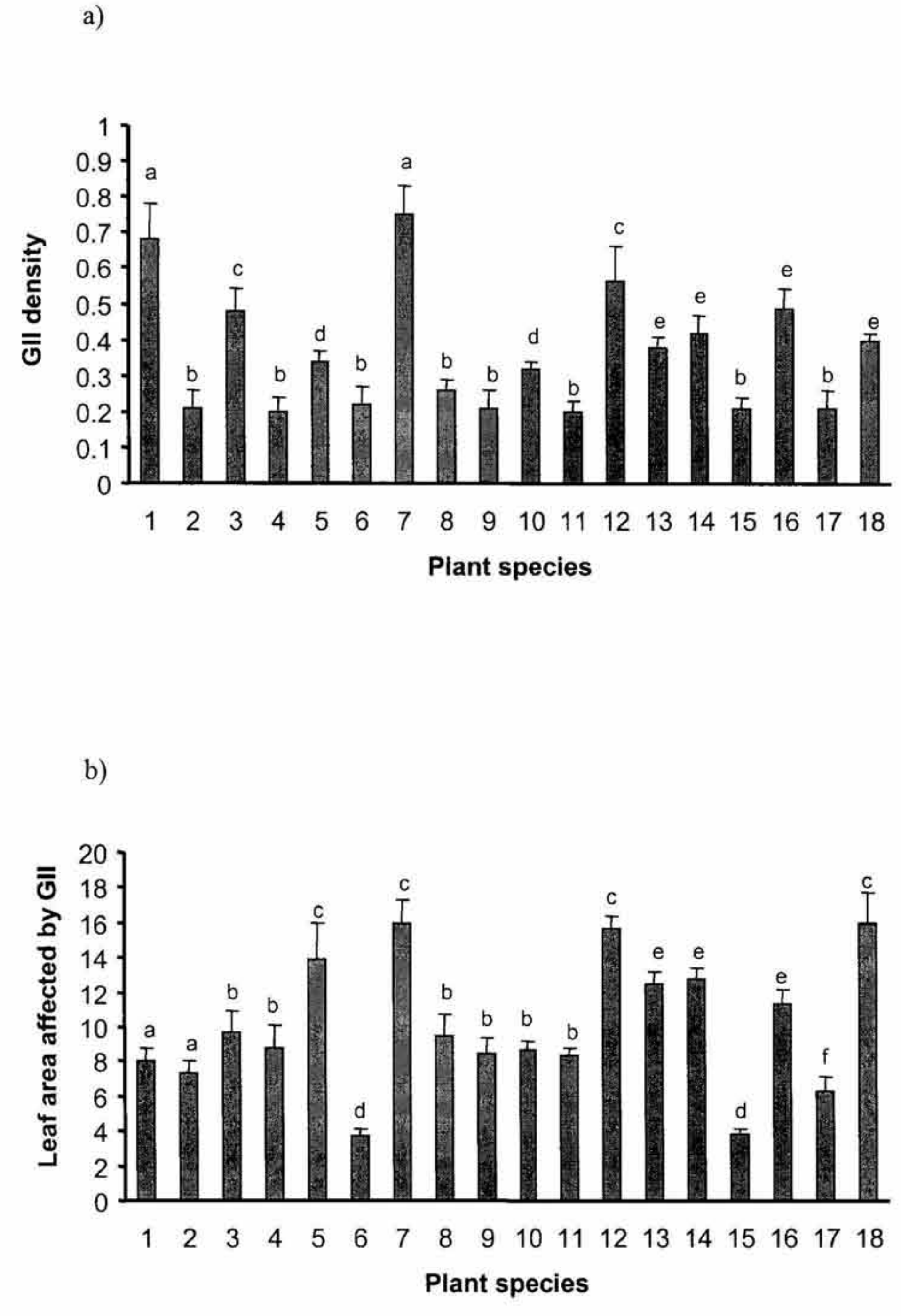
FIGURE 2 a) Variation of GII density on host plant species that occur in riparian habitats during the wet season (species: χ^2= 140.18; d.f= 17; $P < 0.0001$. Values with the same letter did not differ significantly after a LSMeans multiple comparison test ($P < 0.05$); b) Variation of leaf area affected by GII on host plant species that occur in riparian habitats during the wet season (species: χ^2= 172.17; d.f. = 17; $P < 0.0001$). Commons letters identify means that were not significantly different according to LSMeans test ($P < 0.05$). The asterisk indicate GII species present in both habitats

FIGURE 1



1 *Achatocarpus gracilis**
2 *Bursera excelsa*
3 *Caesalpinia caladenia*
4 *Ceiba aesculifolia*
5 *Ceiba grandiflora*
6 *Chlorophora tinctoria*
7 *Cordia alliodora**
8 *Croton alamosanus*
9 *Croton pseudoniveus*
10 *Croton suberosus*
11 *Erythroxylum mexicanum*
12 *Guapira macrocarpa*
13 *Guettarda elliptica**
14 *Gyrocarpus jatrophifolius*
15 *Heliocarpus pallidus**
16 *Ipomoea wolcottiana*
17 *Jatropha malacophylla*
18 *Jatropha standleyi*
19 *Lippia graveolens*
20 *Lonchocarpus eriocarinalis*
21 *Lonchocarpus sp.*
22 *Randia spinosa*
23 *Ruprechtia fusca**
24 *Thevetia ovata*

FIGURE 2



1 *Achatocarpus gracilis**
2 *Bignoniaceae*
3 *Brosimum alicastrum*
4 *Bursera instabilis*
5 *Coccoloba barbadensis*
6 *Cordia alliodora**
7 *Cynometra oaxacana*
8 *Ficus cotinifolia*
9 *Flacourtiaceae*
10 *Guettarda elliptica**
11 *Heliocarpus pallidus**
12 *Paullinia cururu*
13 *Paullinia sessiliflora*
14 *Prosopis sp.*
15 *Recchia mexicana*
16 *Ruprechtia fusca**
17 *Urera caracasana*
18 *Vitex hemsleyi*

CAPÍTULO IV

Interactions among three trophic levels and diversity of parasitoids in a Mexican tropical dry forest: an evaluation of "nasty" host hypothesis in tropical communities

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Abstract:

We tested the "nasty" host hypothesis that was proposed to explain the variation in species richness of parasitoids in plant communities and the degree of specialization between parasitoid species and their hosts. This hypothesis predicts that potential hosts in the tropics are also less available to parasitoids than extra-tropical hosts because their tissues are more chemically toxic and that tropical parasitoid species specialize on their host insect species. The objective of this study is to analyze the relationship between plant hosts, gall-inducing insects (GII) and their hymenopteran parasitoids in a tropical dry forest at Chamela-Cuixmala Biosphere Reserve, Mexico. We found 29 GII species in several orders: Diptera:Cecidomyiidae, which induced the majority of galls with 22 species (77 %), while Homoptera [Kermidae (10%) and Psyllidae (7%)], Hymenoptera: Tanaostigmatidae (3%)] were rare, one morphospecies (3%) was unidentified. In all cases, there is a great specificity between GII species and their host plant species, one GII species is associated with one specific plant species. In contrast, there is no specificity between parasitoid species and their host GII species. We found only 13 species of parasitoids associated with 29 GII species in several families: Torymidae (23%), Eurytomidae (23%), Eulophidae (14%), Pteromalidae (8%), Braconidae (8%), Eupelmidae (8%), Platygastridae (8%) and one (8%) was unidentified. Our results rejected the "nasty" host hypothesis in a tropical community, the effects of variation in plant defenses do not extend to the third trophic level and instead top-down processes seem to be regulating trophic interactions of GII species in tropical communities.

INTRODUCTION

Most studies of plant-insect interactions have examined the effects of plant chemical defenses on herbivore performance and host-selection behavior, with less attention to the study of the potential influence of these plant chemical compounds on higher trophic levels such as parasitoid wasps (Bernays & Bright 1993, Bernays & Chapmann 1994, Coley & Barone 1996, Rosenthal & Berenbaum 1992).

It has been suggested that global patterns of species richness of hymenopteran parasitoids do not increase with decreasing latitude (Gauld 1986, Janzen 1981). This is known as the "nasty" host hypothesis (Gauld & Gaston 1992). This hypothesis proposes that potential hosts in the tropics are also less available to hymenopteran parasitoids than in extra-tropical regions because their tissues are more chemically toxic. Some evidence indicates that tropical woody plants are, in general, richer in toxic secondary compounds that are used, in turn, by insects as a defensive mechanism to deter predators and parasitoids (Coley & Barone 1996, Levin 1976, Price *et al.* 1991). Therefore, a greater specialization of parasitoids on their host insect species is expected in the tropics (Gauld & Gaston 1992).

Many plant species may exert several effects on the plant-herbivore-parasitoid interactions (e.g. bottom-up forces, Lill *et al.* 2002). Host plants resistance, based on secondary metabolites mediate a set of behavior (e.g. localization of microhabitats where hosts may be present), physiological and chemical trophic interactions in different ways: (i) plant constitutive defenses emit novel compounds such as blends of volatiles that can attract natural enemies in response to feeding damage of insects (Dicke 1994, Masters *et al.* 2001, van Dam & Hare 1998); (ii) digestibility reducing compounds negatively affect the physiology and development of herbivorous insects (Karban & Baldwin 1997, Tollrian & Harvell 1999, van Dam *et al.* 2000); (iii) specialist insect herbivores can sequester and accumulate in their haemolymph or body tissues plant secondary chemicals that protect them against natural enemies such as parasitoids (Cornell 1983, Fernandes & Price 1992, Hartman 1985, Hartmann 1999, Muller *et al.* 2001, Sime 2002, Waring & Price 1990, Wink *et al.* 2000). Some studies have reported that differences in secondary metabolites in host plants or herbivores diet negatively affect the growth, development, survival of their parasitoids (Gunasena *et al.* 1990, Harvey *et al.* 2003, Havill & Raffa 2000). In generalist parasitoids, these effects are more prominent, whereas specialist parasitoids are adapted to plant toxins (Barbosa *et al.* 1991, Vinson 1999). Therefore, the effects of variation in plant defenses may extend to the third trophic level (Clancy & Price 1986, Singer & Stireman 2003).

The "nasty" host hypothesis has not been tested in natural communities. Here, we report the first study that tests this hypothesis with empirical data in a tropical dry forest using extensive sampling at a spatial scale. We use a tri-trophic approach to test the "nasty" host hypothesis in a tropical community that includes plants, gall inducing insects and hymenopteran parasitoids in a seasonal tropical dry forest in Mexico.

In this study we addressed the following questions (i) What is the degree of specialization between gall inducing insects and their host plant species? (ii) Is there specialization between tropical hymenopteran parasitoid species and their host gall-inducing insect species?

MATERIALS AND METHODS

Study site

This study was conducted at the Chamela-Cuixmala Biosphere Reserve on the Pacific coast of Jalisco, Mexico that covers an extension of 13,200 ha. The elevation of this site ranges between 0-500 m, the average annual precipitation is 748 mm and the rainy season ranges from June to October (Bullock 1985). Vegetation is dominated by tropical deciduous forest, with some patches of tropical riparian forest in the "arroyos" (Rzedowski 1978).

Surveys were carried from June to October in 2001 during the rainy season. We chose two independent deciduous and riparian habitats at the Chamela-Cuixmala Biosphere Reserve. In each habitat we sampled thirty transects of 30 x 5 m (i.e. 60 transects in deciduous forest and 60 transects in riparian habitats). All gall-inducing species were collected and their host plant species identified. GII were identified and counted on the basis of plant species and gall morphology. A total of 4059 galls of twenty nine GII species were reared and identified in the laboratory as well as the parasitoids associated to each GII species. All galls were kept in vials and plastic containers covered by fine cheesecloth and checked five times a week. Each hymenopteran parasitoid wasp that emerged was identified.

RESULTS

We found 29 GII species represented in the following orders: Diptera: Cecidomyiidae which induced the greatest number part of galls with 22 species (77 %); Homoptera [Kermidae (10%) and Psyllidae (7%) families], Hymenoptera: Tanaostigmatidae (3%)] galls being rare, and one morphospecie (3%) was unidentified (Table 1). In all cases, there is a great specificity between GII species and their host plant species, one GII species is associated with one specific plant species. With respect to hymenopteran parasitoids, we found only 13 species associated with these 29 GII species represented in the following families: Torymidae (23%), Eurytomidae (23%), Eulophidae (14%), Pteromalidae (8%), Braconidae (8%), Eupelmidae (8%), Platygastridae (8%) and one

(8%) was unidentified (see Table 1). Of the 4059 galls analyzed, 2034 had parasitoids associated to them and *Torymus sp* alone affected 34 % of the galls.

Twenty one species of GII (72%) were associated with only one parasitoid species, 6 GII species (21%) with two parasitoid species and only 2 GII species (7%) with three parasitoid species. Most GII species were associated with only one parasitoid species (Table 2), whereas the majority of parasitoids species were associated to more than one GII species (69%) (Table 3). Finally, a chi-square test indicates that the number of GII species ($\chi^2 = 0.27$; d.f. = 1; $P > 0.05$) and parasitoids species ($\chi^2 = 0.11$; d.f. = 1; $P > 0.05$) did not differ significantly between deciduous and riparian habitats.

DISCUSSION

Most studies of three-trophic level interactions address the importance of natural enemies in regulating insect herbivore species richness and abundance (Feder 1995, Sumerford *et al.* 2000, Washburn *et al.* 1991), and competition for resources (Abrahamson *et al.* 1989, Sisterson & Averill 2003). Our study is the first to evaluate the degree of specialization in tropical tri-trophic interactions in a seasonal dry forest. We showed that one GII species is associated with one specific plant species but such specificity is not maintained between GII and their parasitoid interactions. Fifty percent of GII have parasitoids and 34 % of these have a single species of parasitoid.

The "nasty" host hypothesis proposes that tropical hosts are less available to parasitoids than temperate hosts because their tissues are more chemically toxic. Therefore, tropical host insects should be more heavily protected against the parasitoid communities than temperate hosts and there should be more specialization of parasitoids to their host insect species in the tropics (Gauld & Gaston 1992). Our study does not support this hypothesis. Sixty nine percent (9 species) of parasitoid species were not specialized to their GII hosts, whereas 31% (4 species) were associated with only one GII species. These results are in accord with other studies that show that in natural communities one parasitoid species is able to attack different herbivore species that feed on one or more than one host plant species (Godfray 1994, Memmott & Godfray 1994). Host plants can affect herbivores directly by influencing their performance and survival, and indirectly by mediating the effects of natural enemies (Gratton & Denno 2003, Masters *et al.* 2001, Rosenthal & Berenbaum 1992). However, these bottom-up forces do not explain our results because of the following: (i) plant taxa that hosted GII species are represented in plant families with different phylogenetic groups and contain a wide variety of secondary compounds. For example, the Boraginaceae family is characterized by triterpens and pyrrolizidine alkaloids (Pasteels *et al.* 2001, 2003), Polygonaceae by flavonoid glycosides (Kim *et al.* 2000, Sartor *et al.* 1999), Leguminosae by flavonoids, isoflavonoids, alkaloids and terpens (García-Mateos *et al.* 1998, Giachi *et al.* 2002, Mitrocotsa *et al.* 1999, Susag *et al.* 2003), *Ficus* by flavonoid glycosides, triterpenoids and sterols (Pistelli *et al.* 2000, Sharaf *et a.l* 2000), *Jatropha* by phorbolesters (Winck *et al.* 2000) and *Lippia* by monoterpenes and sesquiterpenes (Juliani *et al.* 2002). (ii) Secondary chemicals may defend plants against generalist herbivores but specialists break this defence by sequestering or using these compounds for their own benefit (Stadler 1986, Dicke 2000). GII specialize on their host plant species by modifying cell differentiation on young tissues and by inducing or altering the chemical response of their hosts, sequestering plant secondary metabolites in their gall chamber for protection against natural enemies (Cornell 1983; Fernandes & Price 1992, Hartley & Lawton 1992; Hartley 1998, Hartman 1985, Langenheim &

Stubblebine 1983, Waring & Price 1990). (iii) As a result of (ii) the chemical protection given by the host plants is not specific to deter specific parasitoids but instead the same species of parasitoid is capable of attacking many species of galls that hosted several species of plants from different families. Therefore, the effects of variation in plant defenses do not extend to the third trophic level and instead we propose that top-down processes seem to be regulating these tropic interactions.

Our study shows that one parasitoid species attacks several species of GII and may reduce the damage of GII on their host plants. In seasonally dry forests leaf flushing is highly synchronized among plant species because rainfall triggers growth and the production of leaves (Bullock & Solis-Magallanes 1990, Lobo *et al.* 2003, Reich & Borchert 1984). Host plant phenology affects the distribution and abundance of several herbivore insects (Rossi *et al.* 1999). This is the case of GII species because they have specialized to colonize leaves in synchrony to the production of the new leaves of their host plants (Yukawa 2000). However, parasitoids have developed a more generalist strategy to parasitize different species of GII hosts. Therefore, few species of parasitoids can determine the community structure and composition of GII species in tropical plants.

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LITERATURE CITED

ABRAHAMSON, W. G., SATTLER, J. F., McCREA, K. D. & WEIS, A. E. 1989. Variation in selection pressures on the goldenrod gall fly and the competitive interactions of its natural enemies. *Oecologia* 79: 15-22.

BARBOSA, P., GROSS, P. & KEMPER, J. 1991. Influence of plant allelochemicals on the performance or the tobacco horn-worm and its parasitoid, *Cotesia congregate*. *Ecology* 72: 1567-1575.

BERNAYS, E. A. & BRIGHT, K. L. 1993. Dietary mixing in grasshoppers: a review. *Comparative Biochemistry and Physiology A: Physiology* 104: 125-131.

BERNAYS, E. A. & CHAPMANN, R. F.1994. *Host-plant selection by phytophagous insects*. Chapman and Hall.

BULLOCK, S. H. 1985. Breeding systems in the flora of tropical deciduous forest in Mexico. *Biotropica* 4: 287-301.

BULLOCK, S. H. & SOLÍS-MAGALLANES, J. A. 1990. Phenology of canopy trees of a tropical deciduous forest in México. *Biotropica* 22: 22-35.

CLANCY, K. M. & PRICE, P.W. 1986. Temporal variation in three trophic-level interactions among willows, sawflies, and parasites. *Ecology* 67: 1601-1607.

CORNELL, H. C. 1983. The secondary chemistry and complex morphology of galls formed by Cynipinae (Hymenoptera): why and how? *American Midland Naturalist* 110: 225-23.

COLEY, P. D. & BARONE, J. A. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* 27: 305-335.

VAN DAM, N. M. & HARE, J. D. 1998. Biological activity of *Datura wrightii* glandular trichome exudate against *Manduca sexta* larvae. *Journal of Chemical Ecology* 24: 1529-1549.

VAN DAM, N. M., HADWICH, K. & BALDWIN, I. T. 2000. Induces responses in *Nicotiana attenuate* affect behavior and growth of the specialist herbivore *Manduca sexta*. *Oecologia* 122: 371-379.

DICKE, M. 1994. Local and systemic production of volatile herbivore-induced terpenoids: their role in plant-carnivore mutualism. *Journal of Plant Physiology* 143: 465-472.

DICKE, M (2000) Chemical ecology of host-plant selection by herbivorous arthropods: a multitrophic perpective. *Biochemical Systematics and Ecology* 28: 601-617.

FEDER, J. L. 1995. The effects of parasitoids on sympatric host races of *Rhagoletis pomonella*. *Ecology* 76: 801-813.

FERNANDES, G. W. and PRICE, P. W. 1992. The adaptative significance of insect gall distributions: survivorship of species in xeric and mesic habitats. *Oecologia* 90: 14-20.

FERNANDES, G. W., ARAUJO, R. C., ARAUJO, S. C., LOMBARDI, J. A., PAULA, A. S., LOYOLA, J. R. & CORNELISSEN, T. G. 1997. Insects galls from savanna and rocky fields of the Jequitinhonha valley, Minas Gerais, Brazil. *Naturalia* (Sao Paulo) 22: 221-244.

GARCÍA-MATEOS, R., SOTO-HERNÁNDEZ,M. & NELLY, D. 1998. Alkaloids from six species endemic to Mexico. *Biochemical Systematics and Ecology* 26: 545-551.

GAULD, I. D. 1986. Latitudinal gradients in ichneumonid species richness in Australia. *Ecological Entomology* 11: 155-161.

GAULD, I. D. & GASTON, K. I. 1992. Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the "nasty" host hypothesis. *Oikos* 65: 353-359.

GIACHI, I., MANUNTA, A., MORELLI, I. & PISTELLI, L. 2002. Flavonoids and isoflavonoids from *Genista morissi*. *Biochemical Systematics and Ecology* 30: 801-803.

GODFRAY, H. C. J. 1994. *Parasitoids, behavioral and evolutionary ecology*. Princeton University Press, Princeton, New Jersey.

GRATTON, C. & DENNO, R. F. 2003. Seasonal shift from bottom-up to top-down impact in phytophagous insect populations. *Oecologia* 134: 487-495.

GUNASENA, G. H., VINSON, S. B. & WILLIAMS, H. J. 1990. Effects of nicotine on growth, development and survival of the tobacco budworm (Lepidoptera: Noctuidae) and the parasitoid *Campoletis sonorensis* (Hymenoptera: Ichneumonidae). *Journal of Economic Entomology* 83: 1777-1782.

HARTMAN, H. 1985. Differential intensities of gall insect infectation among host plant size classes: outbreak frequency estimation model. *Zoology Ange. Entomology.* 99: 329-332.

HARTMANN, T. 1999. Chemical ecology of pyrrolizidine alkaloids. *Planta* 207: 483-495.

HARTLEY, S. E. & LAWTON, J. H. 1992. Host-plant manipulation by gall-insects: a test of the nutrition hypothesis. *Journal of Animal Ecology* 61: 113-119.

HARTLEY, S. E. 1998. The chemical composition of plant galls: are levels of nutrients and secondary compounds controlled by the gall-former. *Oecologia* 113: 492-501.

HARVEY, J. A., VAN DAM, N. M. & GOLS, R. 2003. Interactions over four trophic levels: food plant quality affects development of a hyperparasitoid as mediated through a herbivore and its primary parasitoid. *Journal of Animal Ecology* 72: 520-531.

HAVILL, N. P. & RAFFA, K. F. 2000. Compound effects of induced plant responses on insect herbivores and parasitoids: implications for tritrophic interactions. Ecological Entomology 25: 171-179.

JANZEN, D. H. 1981. The peak in North American ichneumonid species richness lies between 38° and 42° N. *Ecology* 62: 532-537.

JULIANI, Jr. H. R., KOROCH, A. R., JULIANI, H. R., TRIPPI, V. S. & ZYGADLO, J. A. 2002. Intraespecific variation in leaf oils of *Lippia junelliana*. *Biochemical Systematics and Ecology* 30: 163-170.

KARBAN, R. & BALDWIN, I. T. 1997. Induced responses to herbivory. University of Chicago Press, Chicago.

KIM, M., PARK, J. H. & PARK, C. W. 2000. Flavonoid chemistry of Fallopia section (Polygonaceae). *Biochemical Systematics and Ecology* 28: 433-441.

LANGENHEIM, J. H. & Stubblebine, W. H. 1983. Variation in leaf resin between parent tree and progeny in *Hymenaea*: implications for herbivory in the humid tropics. *Biochemical Systematics and Ecology* 11: 97-106.

LEVIN, D. A. 1972. Alkaloid-bearing plants; an ecogeographical perspective. *American Naturalist* 110: 261-284.

LILL, J.T., MARQUIS, R. J. & RICKLEFS, R. E. 2002. Host plants influence parasitism of forest caterpillars. Nature 417: 170-173.

LOBO, J. A., QUESADA, M., STONER, K. E., FUCHS, E. J., HERRERIAS-DIEGO, Y., ROJAS-SANDOVAL, J. & SABORIO-RODRIGUEZ, G. 2003. Factors affecting phenological patterns of Bombacaceous trees in seasonal forests in Costa Rica and Mexico. *American Journal of Botany* 90:1054-1063.

MASTERS, G. J., JONES, T. H. & ROGERS, M. 2001. Host-plant mediated effects of root herbivory on insect seed predators and their parasitoids. *Oecologia* 127: 246-250.

MEMMOTT, J. & GODFRAY, H. C. J. 1994. The use and construction of parasitoid webs. Pp. 300-318 in Hawkins, B. A. & Sheehan, W. (eds.). *Parasitoid community ecology*. Oxford University Press, New York.

MITROCOTSA, D., SKALTSOUNIS, A., MITAKU, S., ARVALA, C. & TILLEQUIN, F. 1999. Flavonoid and terpene glycosides from European *Ebenus* species. *Biochemical Systematics and Ecology* 27: 305-307.

MULLER, C., AGERBIRK, N., OLSEN, C. E., BOEVE, J. L., SCHAFFNER, U. & BRAKEFIELD, P. M. 2001. Glucosinolates and differential herbivory in wild populations of *Brassica oleraceae*. *Journal of Chemical Ecology* 26: 2625-2641.

PASTEELS, J. M., TERMONIA, A., WINDSOR, D. M., WITTE, L., THEURING, C. & HARTMANN, T. 2001. Pyrrolizidine alkaloids and pentacyclic triterpene saponins in the defensive secretions of *Platyphora* leaf beetles. *Chemoecology* 11: 113-120.

PASTEELS, J. M., THEURING, C., WINDSOR, C. M. & HARTMANN, T. 2003. Uptake and metabolism of [^{14} C] rinderine and [^{14} C] retronecine in leaf-beetles of the genus *Platyphora* and alkaloid accumulation in the exocrine defensive secretions. *Chemoecology* 13: 55-62.

PISTELLI, L., CHIELLINI, E. E. & MORELLI, I. 2000. Flavonoids from *Ficus pumila*. *Biochemical Systematics and Ecology* 28: 287-289.

PRICE, P. W. 1991. Patterns in communities along latitudinal gradients. Pp. 51-68 in Price, P. W., Lewinson, T. M., Fernandes, G. W. & Benson, W. W. (eds.). *Plant animal interactions: evolutionary ecology of tropical and temperate regions*. John Wiley and Sons, New York.

REICH, P. B. & BORCHERT, R. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology* 72: 61–74.

ROSENTHAL, G. A. & BERENBAUM, M. R. 1992. *Herbivores: their interaction with secondary plant metabolites*. Academic press, New York.

ROSSI, A. M., STILING, P., CATTEL, M. V. & BOWDISH, T. I. 1999. Evidence for host associated races in a gall-inducing midge: trade-offs in potential fecundity. *Ecological Entomology* 24: 95-102.

RZEDOWSKI, J. 1978. *Vegetación de México*. Editorial Limusa, México.

SARTOR, C. F. P., DA SILVA, C. C. & DE SOUZA, M. C. 1999. Flavonoids glycosides of *Polygonium stelligerum* Cham. *Biochemical Systematics and Ecology* 27: 303-304.

SHARAF, M., ABU-GABAL, N. S. & EL-ANSARI, M. A. 2000. Exudate flavonoids from *Ficus altissima*. *Biochemical Systematics and Ecology* 28: 291-293.

SIME, K. 2002. Chemical defense of *Battus philenor* larvae again attack by parasitoid *Trogus pennator*. *Ecological Entomology* 27: 337-345.

SINGER, M. S. & STIREMAN, J. O. 2003. Does anti-parasitoid defense explain host-plant selection by a polyphagous caterpillar? *Oikos* 100: 554-562.

SISTERSON, M. S. & AVERILL, A. L. 2003. Interactions between parasitized and unparasitized conspecifics: parasitoids modulate competitive dynamics. *Oecologia* 135: 362-371.

STANDLER, E. 1986. Oviposition and feeding stimuli in leaf surface waxes. Pp. 105-121 in Juniper, B. E. & Southwood, T. R. E. (eds.). *Insects and the plant surface*. Edward Arnold, London.

SUMERFORD, D. V., ABRAHAMSON, W. G. & WEIS, A. E. 2000. The effects of drought on the *Solidago altissima-Eurosta solidaginis*-natural enemy complex: population dynamics, local extirpations, and measures of selection intensity on gall size. *Oecologia* 122: 240-248.

SUSAG, L., MATHENGE, S. & BENN, M. 2003. The alkaloids in two species of *Afrogalega*. *Biochemical Systematics and Ecology* 31: 645-647.

TOLLRIAN, R. & HARVELL, C. D. 1999. *The ecology and evolution of inducible defenses*. Princeton University Press, Princeton NJ.

VINSON, S. B. 1999. Parasitoid manipulation as a plant defense strategy. *Annals of the Entomological Society of America* 92: 812-828.

WARING, G. L. & PRICE, P. W. 1989. Parasitism pressure and radiation of gall inducing group (Cecidomyiidae: *Aspondylia spp.*) on creosote bush (*Larrea tridentata*). *Oecologia* 79: 293-299.

WARING, G. L. & PRICE, P. W. 1990. Plant water stress and gall formation (Cecidomyiidae: *Asphondylia spp.*) on creosote bush. *Ecological Entomology* 15: 87-95.

WASHBURN, J. O., MERCER, D. R. & ANDERSON, J. R. 1991. Regulatory role of parasites: impact on host population shifts with resource availability. *Science* 253: 185-188.

WINK, M., GRIMM, C., KOSCHMIEDER, C., SPORER, F. & BERGEOT, O. 2000. Sequestration of phorbolesters by the aposematically coloured bug *Pachycoris* *klugii* (Heteroptera: Scutelleridae) feeding on *Jatropha curcas* (Euphorbiaceae). *Chemoecology* 10:179-184.

YUKAWA, J. 2000. Synchronization of gallers with host plant phenology. *Population Ecology* 42: 105-113.

Table 1. Plant-GII-Parasitoid interactions in tropical dry forest at Chamela-Cuixmala Biosphere Reserve, Mexico.

Family	Host plant	Order	Family	Gall Taxa	Orden	Family	Parasotoid Taxa
Bignoniaceae	*Bignoniaceae*	Diptera	Cecidomyiidae	*Cecidomyiidae sp1*	Hymenoptera	Torymidae	*Torymus sp*
Bombacaceae	*Ceiba aesculifolia*	Homoptera	Psyllidae	*Psyllidae*	Hymenoptera	Eurytomidae	*Eurytoma sp1*
	Ceiba grandiflora	Homoptera	Psyllidae	*Psyllidae*	Hymenoptera	Eurytomidae	*Eurytoma sp1*
Boraginaceae	*Cordia alliodora*	Diptera	Cecidomyiidae	*Neolasioptera sp*	Hymenoptera	Torymidae	*Torymoides sp1*
Burseraceae	*Bursera excelsa*	Diptera	Cecidomyiidae	*Cecidomyiidae sp2*	Hymenoptera	Unidentified	*sp1*
	Bursera instabilis	Diptera	Cecidomyiidae	*Cecidomyiidae sp3*	Hymenoptera	Unidentified	*sp1*
Euphorbiaceae	*Croton alamosanus*	Diptera	Cecidomyiidae	*sp4*	Hymenoptera	Torymidae	*Torymus sp*
	Croton pseudoniveus	Diptera	Cecidomyiidae	*sp5*	Hymenoptera	Torymidae	*Torymus sp*
	Croton suberosus	Diptera	Cecidomyiidae	*sp6*	Hymenoptera	Torymidae	*Torymus sp*
					Hymenoptera	Eurytomidae	*Rileya sp*
	Jatropha malacophylla	Diptera	Cecidomyiidae	*Aspondylia sp*	Hymenoptera	Torymidae	*Torymoides sp2*
					Hymenopter	Pteromalidae	*Pteromalidae sp1*
	Jatropha standleyi	Diptera	Cecidomyiidae	*Cecidomyiidae sp7*	Hymenoptera	Torymidae	*Torymoides sp2*
Flacourtiaceae	*Flacourtiaceae*	Diptera	Cecidomyiidae	*Cecidomyiidae sp8*	Hymenoptera	Eupelmidae	*Eupelmus sp*
					Hymenoptera	Eulophidae	*Tetrastichinae*
					Hymenoptera	Platygastridae	*Platygastridae sp1*
Leguminosae	*Caesalpinia caladenia*	Diptera	Cecidomyiidae	*Cecidomyiidae sp9*	Hymenoptera	Braconidae	*Bracon sp*
	Cynometra oaxacana	Diptera	Cecidomyiidae	*Cecidomyiidae sp10*	Hymenoptera	Eurytomidae	*Eurytoma sp1*
	Lonchocarpus eriocarinalis	Homoptera	Kermidae	*Euphalerus sp1*	Hymenoptera	Torymidae	*Torymus sp*
					Hymenoptera	Eulophidae	*Tetrastichinae*
	Lonchocarpus sp	Homoptera	Kermidae	*Euphalerus sp2*	Hymenoptera	Torymidae	*Torymus sp*
					Hymenoptera	Pteromalidae	*Pteromalidae sp1*
	Prosopis sp	Hymenoptera	Tanaostigmatidae	*Tanaostigma sp*	Hymenoptera	Eulophidae	*Tetrastichinae*
Moraceae	*Brosimum alicastrum*	Homoptera	Kermidae	*Trioza rusellae*	Hymenoptera	Eulophidae	*Tetrastichinae*
					Hymenoptera	Platygastridae	*Platygastridae sp1*
	Ficus cotinifolia	Diptera	Cecidomyiidae	*Cecidomyiidae sp11*	Hymenoptera	Torymidae	*Torymus sp*
Nictagynaceae	*Guapira macrocarpa*	Unidentified	Unidentified	*Unidentified*	Hymenoptera	Eulophidae	*Tetrastichinae*
Polygonaceae	*Coccoloba barbadensis*	Diptera	Cecidomyiidae	*Ctenodactylomyia sp*	Hymenoptera	Eulophidae	*Eulophinae*
Rubiaceae	*Guettarda elliptica*	Diptera	Cecidomyiidae	*Cecidomyiidae sp12*	Hymenoptera	Eupelmidae	*Eupelmus sp*
	Randia spinosa	Diptera	Cecidomyiidae	*Bruggmannia randiae*	Hymenoptera	Torymidae	*Torymus sp*
Sapindaceae	*Paullinia cururu*	Diptera	Cecidomyiidae	*Cecidomyiidae sp13*	Hymenoptera	Torymidae	*Torymus sp*
	Paullinia sessiliflora	Diptera	Cecidomyiidae	*Cecidomyiidae sp14*	Hymenoptera	Torymidae	*Torymus sp*
Tiliaceae	*Heliocarpus pallidus*	Diptera	Cecidomyiidae	*Neolasioptera heliocarpi*	Hymenoptera	Eurytomidae	*Eurytoma sp2*
					Hymenoptera	Eurytomidae	*Rileya sp*
Urticaceae	*Urera caracasana*	Diptera	Cecidomyiidae	*Cecidomyiidae sp15*	Hymenoptera	Platygastridae	*Platygastridae sp1*
Verbenaceae	*Lippia graveolens*	Diptera	Cecidomyiidae	*Pseudomikola lippia*	Hymenoptera	Torymidae	*Torymoides sp2*
	Vitex hemsleyi	Diptera	Cecidomyiidae	*Cecidomyiidae sp16*	Hymenoptera	Pteromalidae	*Pteromalidae sp1*
					Hymenoptera	Eulophidae	*Tetrastichinae*
					Hymenoptera	Platygastridae	*Platygastridae sp1*

Table 2. Number of hymenopteran parasitoid species for each GII species in Chamela-Cuixmala tropical dry forest.

GII taxa	**Number of parasitoid species**
Cecidomyiidae *sp8*	3
Cecidomyiidae *sp16*	3
Cecidomiiydae *sp6*	2
Aspondylia sp	2
Euphalerus sp1	2
Euphalerus sp2	2
Trioza rusellae	2
Neolasioptera heliocarpi	2
Cecidomyiidae *sp1*	1
Psyllidae sp1	1
Psyllidae sp2	1
Neolasioptera sp	1
Cecidomyiidae *sp2*	1
Cecidomyiidae *sp3*	1
Cecidomiiydae *sp4*	1
Cecidomiiydae *sp5*	1
Cecidomyiidae *sp7*	1
Cecidomyiidae *sp9*	1
Cecidomyiidae *sp10*	1
Tanaostigma sp	1
Cecidomyiidae *sp11*	1
Unidentified	1
Ctenodactylomyia sp	1
Cecidomyiidae sp12	1
Bruggmannia randiae	1
Cecidomyiidae *sp13*	1
Cecidomyiidae *sp14*	1
Cecidomyiidae *sp15*	1
Pseudomikola lippia	1

Table 3. Number of host GII species for each parasitoid species in Chamela-Cuixmala tropical dry forest.

Parasitoid taxa	**Number of GII species**	**Percent of galls with parasitoids**
Torymus sp	10	34.5
Tetrastichinae	6	15.5
Platygastridae sp1	4	6.5
Torymoides sp2	3	4.9
Eurytoma sp1	3	14.9
Pteromalidae sp1	3	4.7
Rileya sp	2	2.0
Eupelmus sp	2	2.8
sp1	2	2.0
Bracon sp	1	1.5
Eulophinae	1	2.0
Eurytoma sp2	1	1.8
Torymoides sp1	1	6.9

DISCUSIÓN GENERAL.

La diversidad de especies de insectos formadores de agallas (IFA) ha sido estimada en algunas regiones tropicales considerando que la morfología de la agalla es única en cada especie de IFA y que cada especie es específica a una especie particular de planta hospedera (Ananthakrishnan 1984; Dreger-Jauffret y Sorthouse 1992; Price et al. 1998; Cuevas-Reyes et al. 2003; Oyama et al. 2003; Veldtman y McGeoch 2003). Sin embargo, no se ha identificado taxonómicamente la especificidad entre las especies de IFA y sus respectivas plantas hospederas. El reconocimiento de cada taxa de IFA es fundamental para entender estas interacciones ecológicas porque se ha demostrado que una sola especie de planta es capaz de hospedar diferentes especies de IFA (Fernandes y Price 1988; Waring y Price 1989; Fernandes et al. 1996), indicando que la especificidad no es absoluta. Este trabajo es el primero en identificar directamente la identidad de los diferentes taxa de IFA sobre sus plantas hospederas en un bosque tropical seco. Nuestros resultados corroboran la especificidad de los IFA a sus plantas hospederas en los trópicos, ya que cada especie de IFA estuvo asociada a una especie particular de planta.

La riqueza de especies de IFA encontrada en el bosque tropical seco de Chamela-Cuixmala fue mayor que la reportada en otras regiones tropicales (e.g. sabanas) (Price et al. 1991). La riqueza de especies de plantas puede producir diferencias en los patrones locales porque más especies de plantas representan mayor diversidad en nichos potenciales para ser colonizados por IFA (Wright y Samways 1996, 1998). En Chamela-Cuixmala, la riqueza de especies de plantas presente es equivalente a la de algunos bosques tropicales húmedos del mundo (Lott *et al.* 1987) y representa un factor importante asociado a la riqueza de especies de IFA.

La arquitectura de la planta hospedera es otro factor que determina la riqueza de especies de IFA. Plantas más complejas estructuralmente (e.g. con mayor número de ramificaciones, ramas y hojas) representan más microhábitats que favorecen la colonización de una gran variedad de insectos (Leather 1986). Fernándes y Price (1988) reportan una mayor riqueza de especies de IFA sobre arbustos y árboles que en hierbas. Similarmente, Goncalves-Alvim y Fernandes (2001) reportan un mayor número de especies de IFA sobre árboles seguido por arbustos y hierbas. En nuestro estudio, los árboles y arbustos presentan un mayor número de especies de IFA asociadas que hierbas y trepadoras en hábitats deciduos y riparios corroborando la hipótesis de la complejidad estructural de plantas. Este patrón puede estar asociado a posibles diferencias en compuestos secundarios entre las diferentes formas de vida (e.g. más en árboles y arbustos que en hierbas y trepadoras) (Coley y Barone 1996). Cabe mencionar que los estudios que han probado la hipótesis de la complejidad estructural no han incluido formas de vida como las trepadoras, las cuales pueden tener una arquitectura compleja debido a que su forma de crecimiento se desarrolla tanto en el sotobosque como en el estrato arbóreo. En nuestro estudio, la incidencia de IFA sobre trepadoras fue menor que en otras formas de vida como árboles y arbustos. Por lo tanto, es posible que la complejidad estructural pueda ser relativa cuando se incluyen formas de vida como las trepadoras y su posible explicación puede estar asociada a factores históricos y evolutivos de la interacción entre los IFA y las trepadoras.

Los patrones de riqueza y abundancia de gremios de insectos sobre diferentes estados ontogenéticos de las plantas hospederas son inconsistentes, algunos son más abundantes sobre plantas juveniles, mientras que otros sobre plantas maduras (Lowman

1992; Basset 2001). Variaciones en la palatabilidad de hojas, microclima local y la presencia de enemigos naturales han sido propuestas como posibles causas de estas diferencias. En nuestro estudio, la frecuencia de los IFA fue mayor sobre plantas juveniles en árboles y arbustos en 26 (74.2%) de las especies de plantas que estuvieron asociadas con IFA. Posiblemente la oviposición y el desarrollo de larvas es favorecido por los estados juveniles de las plantas hospederas porque ofrecen hojas de rápida expansión y meristemos indiferenciados que representan sitios potenciales para la inducción de agallas debido a que la fisiología de la formación de agallas requiere necesariamente de tejidos indiferenciados (Weis et al. 1988). Además, estados juveniles representan hojas de alta calidad nutricional y mayor cantidad de compuestos secundarios, lo cual puede favorecer a los IFA porque tienen la habilidad de manipular y secuestrar metabolitos secundarios como mecanismo de defensa contra enemigos naturales (Cornell 1983; Hartley y Lawton 1992; Hartley 1998). Por lo tanto, los estados juveniles de las plantas representan para los IFA, plantas de más rápido crecimiento y mayor disponibilidad temporal de recursos (Price 1991).

En este estudio analizamos la relación entre la densidad de hospederos por cada especie de planta y el número de agallas por planta para cada especie de IFA. Encontramos que solo 18 especies de los IFA (46.2%) responden significativamente al incremento en la densidad de hospederos. Es posible que la densidad y la proximidad dentro de plantas hospederas regule los tamaños poblacionales de los IFA vía mecanismos denso-dependientes (Janzen 1970).

La disponibilidad de agua y nutrientes en el bosque tropical seco de Chamela es heterogénea debido a los patrones estacionales de lluvia que producen cambios en el balance nutrientes-agua, el factor limitante en todos los hábitats es la disponibilidad de fósforo (Jaramillo y Sanford 1995). Por esta razón, la disponibilidad de fósforo y nitrógeno fueron utilizados como indicadores de la fertilidad del suelo en ocho diferentes hábitats. Nuestro primer resultado indica que el número de especies de IFA está correlacionado negativamente con la fertilidad del suelo para todas las especies de plantas que ocurren en diferentes hábitats. Este resultado puede ser explicado por efectos indirectos asociados con adaptaciones locales de taxa de plantas específicos a diferentes condiciones de fertilidad de suelo (Blanche y Westoby 1995). Plantas adaptadas a suelos infértiles tienden a tener una mayor concentración de compuestos secundarios y disponibilidad de nitrógeno foliar (Coley et al. 1985; Coley y Barone 1996). Los IFA pueden manipular la química de sus plantas hospederas secuestrando compuestos secundarios defensivos en las paredes de la agalla para protegerse de enemigos naturales como hongos y otros patógenos (Cornell 1983). Por lo tanto, plantas que crecen en suelos infértiles pueden proveer más sitios potenciales para ser colonizados por IFA (Cuevas-Reyes et al. 2003).

La fertilidad del suelo también afecta la frecuencia y la densidad de los IFA entre individuos de las once especies de plantas que están presentes en los ocho hábitats con diferente fertilidad de suelos. Para estas especies de plantas, individuos que ocurren en hábitats con baja disponibilidad de fósforo y nitrógeno presentaron una mayor frecuencia y densidad de IFA que cuando ocurren en hábitats con suelos fértiles. Por lo tanto, efectos directos de la fertilidad del suelo vía plasticidad fenotípica dentro de cada hospedero pueden explicar las diferencias en la incidencia de los IFA sobre las once especies de plantas hospederas que están presentes a lo largo del gradiente de fertilidad del suelo (Herms y Mattson 1992; Schlichting y Pigliucci 1998).

Este trabajo representa también el primer estudio que estima la cantidad de daño causada por IFA en bosques tropicales. Los niveles de herbivoría encontrados [(promedio 14.9% en la estación húmeda (rango 1.57-97.7), 18.9% en el hábitat deciduo y 10 % en el ripario)] son similares a los causados por insectos folívoros en el bosque tropical seco de Chamela (Filip et al. 1995) y considerablemente mayores a los reportados en otros bosques tropicales (Marquis y Braker 1994; Coley y Barone 1996).

El área foliar afectada y la densidad de IFA fueron mayores en hábitats deciduos que riparios en la estación húmeda. Además, en cinco especies de plantas que ocurren en ambos hábitats, la herbivoría por IFA fue mayor cuando están presentes en los hábitats deciduos indicando una mayor preferencia por plantas de estos hábitats. En este tipo de bosques tropicales, la variación estacional en la disponibilidad de alimento para los IFA es crucial porque requieren tejidos indiferenciados para inducir la formación de agallas (Weis et al. 1988; Dreger-Jauffret y Sorthouse 1992). Por lo tanto, resulta muy importante la sincronización entre los IFA y la producción masiva de hojas en los hábitats deciduos (Weis et al. 1988; Yukawa 2000) ya que la producción masiva de hojas en estos hábitats es al inicio de la temporada húmeda, mientras que en los hábitats riparios, las plantas son siempre-verdes y producen hojas en un periodo de tiempo más prolongado durante la estación húmeda (Frankie et al. 1974; Opler 1980). Por lo tanto, mayores niveles de herbivoría por IFA en hábitats deciduos pueden ser explicados por que estos hábitats ofrecen hojas jóvenes durante un periodo de tiempo corto a diferencia de las especies siempre verdes de hábitats riparios. De tal modo, es posible que en hábitats deciduos algunas especies de IFA presenten historias de vida univoltinas con una alta sincronización de sus ciclos de vida con la aparición y desarrollo de hojas.

En hábitats riparios durante la estación seca encontramos que el área foliar afectada por los IFA y la densidad de agallas fueron mayores que en la temporada húmeda para este hábitat. Dos posibles explicaciones pueden estar asociadas a este resultado: (i) que las especies de plantas de hábitats riparios tienen dos temporadas de producción de hojas (Frankie et al. 1974, Bullock y Solís-Magallanes 1990; Wright 1996) y que los IFA colonizan hojas producidas en la primera temporada durante la estación húmeda y se acumulan o recolonizan hojas producidas en la segunda temporada durante la estación seca, o (ii) que en algunas especies de plantas que ocurren en ambos hábitats, los IFA pueden migrar del hábitat deciduo al ripario en la estación seca. Por lo tanto, los hábitats riparios en la estación seca aparentemente acumulan la siguiente generación de IFA producida de la generación previa de la estación húmeda de ambos hábitats. Este incremento durante la estación seca dentro de hábitats riparios sugiere la existencia de especies de IFA bivoltinas por que pueden colonizar dos temporadas de producción de hojas en el mismo año.

Finalmente, esta tesis es la primera que evalúa el grado de especialización en interacciones tri-tróficas en un bosque tropical seco. Encontramos especificidad de los IFA sobre sus respectivas plantas hospederas, una especie de IFA está asociada a una especie particular de planta. Sin embargo, esta especificidad no es mantenida entre las especies de parasitoides y sus IFA hospederos. La hipótesis del hospedero "malo" ("nasty" host hipothesis) que involucra procesos ascendentes "bottom-up" establece que en los trópicos los parasitoides son especialistas y que la disponibilidad de potenciales hospederos es menor que en sitios no tropicales por que sus tejidos son químicamente más tóxicos (Gauld y Gaston 1992). Nuestros resultados no apoyan esta hipótesis ya que nueve (69%) de las especies de parasitoides desarrollan estrategias relativamente generalistas.

Muchas plantas pueden afectar directamente el desempeño de los herbívoros e indirectamente regular los efectos de los enemigos naturales (Rosenthal y Berenbaum 1992). Sin embargo, procesos ascendentes “bottom-up” no explican nuestros resultados porque los diferentes taxa de plantas hospederas de IFA representan familias de diferentes grupos filogenéticos que contienen una gran variedad de compuestos secundarios (Sartor et al. 1999; Kim et al. 2000; Pasteels et al. 2001, 2003; Giachi et al. 2002; Susag et al. 2003). Estos compuestos secundarios pueden ser efectivos contra insectos generalistas. Sin embargo, contra insectos especialistas como los IFA rompen estas defensas porque secuestran estos compuestos en las paredes de la agalla y los utilizan como mecanismo de defensa contra enemigos naturales (Cornell 1983; Fernandes y Price 1992, Hartley y Lawton 1992; Hartley 1998). Como resultado de esto, la protección química dada por las plantas no es específica para afectar a los parasitoides debido a que la misma especie de parasitoide es capaz de atacar muchas agallas inducidas en diferentes especies de plantas de diferentes familias. Por lo tanto, los efectos de la variación química de las plantas no se extienden al tercer nivel trófico y proponemos que procesos descendentes “top-down” están regulando estas interacciones porque una sola especie de parasitoide es capaz de atacar varias especies de IFA reduciendo el daño por agallas sobre sus plantas hospederas.

En resumen, la conclusión general de este trabajo indica que la riqueza de especies de IFA en el bosque tropical seco de Chamela-Cuixmala no solo depende de factores bióticos como la riqueza de especies de plantas, las formas de vida de plantas hospederas, la edad y la densidad de hospederos, sino también de factores abióticos como la fertilidad del suelo que afecta la distribución espacial de los IFA y que favorece la riqueza, incidencia y abundancia de especies de los IFA en dos diferentes vías: (i) afectando indirectamente la riqueza de especies de los IFA vía adaptaciones locales de algunas especies de plantas a diferentes condiciones de fertilidad y (ii) afectando directamente la incidencia de IFA por procesos de plasticidad fenotípica de las once especies de plantas que ocurren en el gradiente de fertilidad. Los patrones de herbivoría por IFA en el bosque tropical seco de Chamela son afectados por la disponibilidad espacial y temporal de alimento (e.g. hojas) y muestran que en muchas especies de plantas, la herbivoría por IFA fue mayor en hábitats deciduos durante la estación húmeda. Mientras que en los hábitats riparios, los IFA colonizan hojas producidas en dos diferentes picos estacionales de producción foliar dentro del mismo año. Nuestros resultados rechazan la hipótesis del hospedero "malo" ("nasty" host hipothesis) debido a que la mayoría de las especies de parasitoides muestran estrategias generalistas parasitando diferentes especies de IFA hospederos. Pocas especies de parasitoides pueden determinar la estructura y composición de la comunidad de especies de IFA en plantas tropicales. Por lo tanto, proponemos que procesos descendentes "top-down" están regulando esta interacción tri-trófica.

REFERENCIAS GENERALES

Abrahamson WG & Weis AE (1987) Nutritional ecology of arthropod gall maker. In: Slansky F & Rodriguez JG (Eds). Nutritional ecology of insects, mites, spiders and related invertebrates. John Wiley & Sons Publishers. New York, pp. 235-258.

Ananthakrishan TN (1984) Adaptative strategies in cecidogenous insects. In: Ananthakrishan TN (Ed). The biology of gall insects. Oxford and IBH, New Delhi, pp. 1-9.

Askew RR (1984) The biology of gall-wasps. In: Anathakrishnan TN (Ed). The biology of gall-insects. Oxford and IBH, New Delhi, pp. 223-271.

Basset Y & Novotny V (1999) Species richness of insect herbivore communities on *Ficus* in Papua New Guinea. *Biological Journal of Linnean Society* 67: 477-99.

Basset Y (2001) Communities of insect herbivores foraging on saplings versus mature trees of *Pourouma bicolor* (Cecropiaceae) in Panama. *Oecologia* 129: 253-260.

Blanche KR & Westoby M (1995) Gall-forming insect diversity is linked to soil fertility via host plant taxon. *Ecology* 76: 2334-2337.

Bullock SH & Solís-Magallanes JA (1990) Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* 22: 22-35.

Caley M.J & Schluter D (1997) The relationship between local and regional diversity: *Ecology* 78 70–80.

Claughle G & Lawton JH (1981) Plant-herbivore systems. In: May RM (Ed). Theoretical ecology: principles and applications. Blackwell Scientific Publications. Oxford, pp.132-166.

Coley PD, Bryant JP & Chapin FS (1985) Resource availability and plant antiherbivore defense. *Science* 230: 895-899.

Coley PD & Barone JA 1996. Herbivory and plant defenses in tropical forests. *Annual Review Ecology and Systematics* 27: 305-335.

Connell E (1961) The influence of interspecific competition and other factors on the distribution of barnacle *Chthamalus stellatus*. *Ecology* 42: 710-723.

Cornell HC (1983) The secondary chemistry and complex morphology of galls formed by Cynipinae (Hymenoptera): Why and how? *American Midland Naturalist* 110: 225-234.

Cornell HV & Karlson RH (1996) Species richness of reef-building corals determined by local and regional processes. *Journal of Animal Ecology* 65: 233-241.

Cornell HV (1990) Survivorship, life history, and concealment: a comparison of leaf miners and gall formers. *American Naturalist* 136: 581-597.

Cornell HV & Lawton JH (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* 61: 1-12.

Cuevas-Reyes P, Siebe C, Martínez-Ramos M & Oyama K (2003). Species richness of gall-forming insects in a tropical rain forest: correlations with plant diversity and soil fertility. *Biodiversity and Conservation* 3: 411-422.

Eldredge N (1989) Macroevolutionary dynamics: species, niches and adaptative peaks. McGraw-Hill, New York.

Fay PA, David FA & Knapp AK (1996) Plant tolerance of gall-insect attack and gall-insect performance. *Ecology* 77: 521-534.

Fernandes GW & Price PW (1988) Biogeographical gradients in galling species richness: test of hypotheses. *Oecologia* 76: 161-167.

Fernandes GW, Carneiro MAA, Lara ACF, Allain GI, Andrade GR, Reis TR & Silva IM (1996) Galling insects on neotropical species of *Baccharis* (Asteraceae). *Tropical Zoology* 9: 315-332.

Filip V, Dirzo R, Mass JM & Sarukhán J (1995) Within-and among-year variation in the levels of herbivory on the foliage of tress from a Mexican tropical deciduous forest. *Biotropica* 27: 78-86.

Floate KD, Fernandes WG & Nilsson JA (1996) Distinguishing intrapopulation categories of plant by their insect faunas: galls on rabbitbrush. *Oecologia* 105: 221-229.

Frankie GW, Baker HG & Opler PA (1974) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 62: 881–899.

Frenzel M, Brandl R (1998) Diversity and composition of phytophagous insect guilds on Brassicaceae. *Oecologia* 113: 391-399.

Fritz RR & Price PW (1988) Genetic variation among plant and insect community structure: willow and sawflies. *Ecology* 69: 845-856.

Gauld ID & Gaston KI (1992) Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the "nasty" host hypothesis. *Oikos* 65: 353-359.

Giachi I, Manunta A, Morelli I & Pistelli L (2002) Flavonoids and isoflavonoids from *Genista morissi*. *Biochemical Systematics and Ecology* 30: 801-803.

Goncalves-Alvim S & Fernandes GW (2001) Biodiversity of galling insects: historical, community and habitat effects in four Neotropical savannas. *Biodiversity and Conservation* 10: 79-98.

Hartnett DC & Abrahamson WG (1979) The effects of stem gall insects on life history patterns in *Solidago canadiensis*. *Ecology* 60: 910-917.

Hartley SE & Lawton JH (1992) Host-plant manipulation by gall-insects: a test of the nutrition hypothesis. *Journal of Animal Ecology* 61: 113-119.

Hartley SE (1998) The chemical composition of plant galls: are levels of nutrients and secondary compound controlled by the gall-former? *Oecologia* 113: 492-501.

Hartley SE (1999) Are gall insects large rhizobia? *Oikos* 84: 333-339.

Herms D.A. & Mattson WJ (1992) The dilemma of plants: to grow or defend. *Quarterly Review of Biology* 67:283-335.

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist* 940: 501-528.

Jauffret FD & Shorthouse JD (1998) Diversity of gall-inducing insects and their galls. In: Shorthouse JD & Roshftritsch O (Eds). Biology of gall insects-induced galls. Oxford University Press, pp. 8-33.

Kim M, Park JH. & Park CW (2000) Flavonoid chemistry of Fallopia section (Polygonaceae). *Biochemical Systematics and Ecology* 28: 433-441.

Larson KC & Whitham TC (1991) Manipulation of food resources by a gall-forming aphid: The physiology of sink-source interactions. *Oecologia* 88: 15-21.

Lowman MD (1992) Herbivory in Australian rain forests, with particular reference to the canopies of *Doryphora sassafras* (Monimiaceae). *Biotropica* 24: 263-272.

Lawlor SP & Morin PJ (1993) Food web architecture and population dynamics in laboratory microcosms of protist. *American Naturalist* 141: 675-686.

Lawton JH, MacGarvin M & Heads PA (1987) Effects of altitude on the abundance and species richness of insect herbivores on bracken. *Journal of Animal Ecology* 56: 147-160.

Lott EJ, Bullock SH & Solis-Magallanes JA (1987) Floristic diversity and structure of upland and arroyo forests of Coastal Jalisco. *Biotropica* 3: 228-235.

Marquis RJ & Braker HE (1994) Plant herbivore interactions: diversity, specificity, and impact. In Mcdade LA, Kawa KS, Hespenheide HA & Hartshorn S (Eds). La Selva: ecology and natural history of a Neotropical rainforest. University of Chicago Press, pp. 261-281.

McArthur RH (1965) Patterns of species diversity. *Biological Reviews* 40: 510-533.

McPeek MA (1996) Linking local species interactions to rates of speciation in communities. *Ecology* 77: 1355-1366.

Meyer J (1987) Plant galls and galls-inducers. Grebuder Borntraeger, Berlin.

Moran VC & Southwood TER (1982) The guild composition of arthropod communities in trees. *Journal of Animal Ecology* 51: 289-306.

Nyman T, Roininen H. & Vuorinen JA (1998) Evolution of different gall types in willow-feeding sawflies (Hymenoptera: Tenthredinidae). *Evolution*: 52: 465-474.

Nyman T, Widmer A. & Roininen H (2000) Evolution of gall morphology and host-plant relationships in willow feeding sawflies (Hymenoptera:Tenthredinidae). *Evolution* 54: 526-533.

Opler PA, Frankie GH & Baker HG (1980) Comparative phenological studies of treelet and shrubs species in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Animal Ecology* 68: 167–188.

Oyama K, Pérez-Pérez M, Cuevas-Reyes P & Luna-Reyes R (2003) Regional and local species richness of gall-forming insects in two tropical rain forest in México. *Journal of Tropical Ecology* 19: 595-598.

Paine RT (1966) Food web complexity and species diversity. *American Naturalist* 100: 65-75.

Parra-Tabla V & Bullock SH (1998) Factors limiting fecundity of the tropical tree *Ipomoea wolcottiana* (Convulvalaceae) in a Mexican tropical dry forest. *Journal of Tropical Ecology* 14: 615-627.

Pasteels JM, Theuring C, Windsor CM & Hartmann T (2003) Uptake and metabolism of [^{14} C] rinderine and [^{14} C] retronecine in leaf-beetles of the genus *Platyphora* and alkaloid accumulation in the exocrine defensive secretions. *Chemoecology* 13: 55-62.

Price PW (1984) Insect Ecology. John Wiley & Sons, New York.

Price PW, Waring GL & Fernandes GW (1986) Hypothesis on the adaptative nature of gall. *Proceedings of the Entomology Society of Washington* 88: 88 361-363.

Price PW, Fernandes GW & Waring GL (1987) Adaptative nature of insects galls. *Environment Entomology* 16: 15-24.

Price PW & Pschorn HW (1988) Are galling insects protected against parasitoids than exposed feeders? A test using tenthredinid sawflies. *Ecological Entomology* 13: 195-205.

Price PW & Fernandes WG (1991) Patterns in communities along latitudinal gradients. In: Price PW, Lewinson TM, Fernandes GW & Benson WW (Eds). Plant animal interactions: evolutionary ecology of tropical and temperate regions. Wiley. New York, pp. 51-68.

Price PW, Fernandes GW, Lara AC, Brawn J, Barrios H, Wright MG, Ribeiro S. & Rothcliff N (1998) Global patterns in local number of insect galling species. *Journal of Biogeography* 25: 581-591.

Ricklefs RE (1987) Community diversity: relative roles of local and regional processes. *Science* 235: 167-171.

Ricklefs RE (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters* 7: 1-15

Rosenzweig ML (1995) Patterns in space. In: Rosenzweig ML (Ed). Species diversity in space and time, Great Britain at the University Press, Cambridge, pp. 8-49.

Rossi AM & Stiling P (1998) The interactions of plant clone and abiotic factors on gall-making midge. *Oecologia* 116: 170-176.

Rosenthal GA & Berenbaum MR (1992) Herbivores: their interaction with secondary plant metabolites. Academic Press, New York.

Rougharden J & Diamond J (1986) Overview: The role of species interactions. In: Diamond R & Case (Eds). Community Ecology. Harper & Row. New York, pp. 333-343.

Sacchi C, Price PW, Tomothy P, Craig P & Itami JK (1988) Impact of shoot galler attack on sexual reproduction in the arroyo willow. *Ecology* 69: 2021-2030.

Samways MJ (1994) Insect conservation biology. Chapman & Hall. London, pp.358.

Sartor CFP, Da Silva CC & De Souza, MC (1999) Flavonoids glycosides of *Polygonium stelligerum* Cham. *Biochemical Systematics and Ecology* 27: 303-304.

Schlichting CD & Pigliucci M (1998) Phenotypic evolution: A reaction norm perspective. Sinauer Press, MA, pp. 54-56.

Schluter D & Ricklefs E (1993) Species diversity. In: Ricklefs E & Schluter D (Eds). Species diversity in ecological communities. University of Chicago. Chicago, pp. 1-12.

Schultz BB (1992) Insect herbivores as potential causes of mortality and adaptation in gall-forming insects. *Oecologia* 90: 297-299.

Southwood TRE (1972) The insect-plant relationship: an evolutionary perspective: *Symposium of Royal Entomology Society of London*. 6: 3-30.

Southwood TRE, Moran VC & Kennedy CEJ (1988) The richness, abundance and biomass of the arthropod communities on trees. *Journal of Animal Ecology* 51: 635-649.

Stern DL (1995) Phylogenetic evidence that aphids, rather than plants, determine gall morphology. *Proceedings of the Royal Society of London Series B* 260: 85-89.

Susag L, Mathenge S. & Benn M (2003) The alkaloids in two species of *Afrogalega*. *Biochemical Systematics and Ecology* 31: 645-647.

Veldtman R. & McGeoch MAM (2003) Gall-forming insect species richness along a non-scleromorphic vegetation rainfall gradient in South Africa: the importance of plant community composition. *Austral Ecology* 28: 1-13.

Vinson MR y Hawkins CP (1998) Biodiversity of stream insects: variation at local, basin, and regional scales. *Annuals Review of Entomology* 43: 271-293.

Waring GL & Price PW (1989) Parasitism pressure and radiation of gall forming group (Cecidomyiidae: *Aspondylia spp.*) on creosote bush (*Larrea tridentata*). *Oecologia* 79: 293-299.

Weis AE, Walton R & Crego CL (1988) Reactive plant tissue sites and the population biology of gall makers. *Annual Review of Entomology* 33: 467-486.

Williams WM & Benson RN (1966) Transfer of C14 component from *Psylla pyricola* for to pear seedlings. *Journal Institute of Physiology* 12: 251-254.

Wolfe ML (1997) Differential flower herbivory and gall formation on males and females of *Neea psychotriodes*, a dioecious tree. *Biotropica* 29: 169-174.

Wright J (1996) Phenological responses to seasonality in tropical forest plants. In: Mulkey SS, Chazdon RL & Smith AP (Eds). Tropical forest plant ecophysiology. Chapman & Hall. New York, pp. 440–460.

Wright MG & Samways MJ (1996) Gall-insect species richness in African Fynbos and Karoo vegetation: the importance of plant species richness. *Biodiversity Letters* 3 151-155.

Wright MG & Samways MJ (1998) Insect species richness tracking plant species richness in a diverse flora: gall-insects in the Cape floristic region, South Africa. *Oecologia* 115 427-433.

Yukawa J (2000) Synchronization of gallers with host plant phenology. *Population Ecology* 42: 105–113.