ARTICLE

# Occurrence of gall complexes along a topographic gradient in an undisturbed lowland forest of central Amazonia

Paulo Sávio Damásio Silva[1], Bráulio Almeida-Santos[2],
Marcelo Tabarelli[2] and Jarcilene Silva Almeida-Cortez[2]*

**ABSTRACT:** (Occurrence of gall complexes along a topographic gradient in an undisturbed lowland forest of central Amazonia). The species richness of gall-inducing insects and their host plants, in an undisturbed lowland forest in central Amazonia, was analyzed to test whether there is a higher occurrence of galls in mesic *campinarana* habitats when compared to plateaus, slopes and valleys. In October 2005, 300 plants, which were 1 to 2 meters tall, were sampled along ten transects (5 meters wide) per habitat. Gall-inducing insects were found in only 35 (3%) of the 1200 plants studied. Thirteen families, eight genera and 27 morphospecies of plants were identified. The families Burseraceae and Rubiaceae had the highest number of host plant species. There was no significant difference in species richness between habitat types. However, the gall-inducing insects and host plant species were exclusive to each habitat. Furthermore, the frequency of host plants in *campinarana* was not higher when compared to the other habitats. Probably, tree canopies present more structural complexity, light availability and incidence of leaves with scleromorphic characteristics than understory plants, resulting in vertical stratification with a higher amount of gall-inducing insects in canopies when compared with individuals of the same species in the understory. The higher plant diversity and variation of physical characteristics of the forests in central Amazonia can help explain why specific interactions and the frequency of gall--inducing insects were found in each habitat. The results of this study indicate that central Amazonian forests have a high diversity of gall-inducing insects with an exclusive fauna related to each habitat, which is potentially due to the greater environmental heterogeneity, and suggests the importance of conducting additional studies about galling insects, principally in forest canopies.
**Key words:** host plants, *campinarana*, plateaus, hill slopes, bottom valleys**.**

**RESUMO:** (Ocorrência de galhas ao longo de um gradiente topográfico em uma floresta de terra firma na Amazônia Central). A riqueza de insetos galhadores e plantas hospedeiras foram investigadas em uma floresta de terra firme, na Amazônia Central, para testar se haveria uma maior ocorrência de galhas em habitats mais secos, como campinarana, comparados aos platôs, vertentes e baixios. Em outubro de 2005, foram amostradas 300 plantas em 10 transecções (com 5 m de largura cada) por habitat, totalizando 1.200 plantas. As galhas induzidas por insetos foram encontradas em apenas 35 (3%) das 1.200 plantas estudadas. Treze famílias, oito gêneros e 27 morfoespécies de plantas foram identificados, sendo que as famílias Burseraceae e Rubiaceae apresentaram maior número de espécies de plantas hospedeiras. Não foi observada nenhuma diferença significativa na riqueza de espécie de galhas induzidas por insetos entre os habitats, porém as interações foram exclusivas de cada habitat. Além disso, campinarana não apresentou maior frequência de plantas hospedeiras, em comparação aos outros habitats. Provavelmente, as copas das árvores apresentam maior complexidade estrutural, disponibilidade de luz e ocorrência de plantas com características escleromórficas do que o sob-bosque, resultando em uma estratificação vertical e maior frequência de galhas nas copas quando comparada com indivíduos da mesma espécie no sub-bosque. A alta diversidade vegetal e a variação abiótica podem explicar a especificidade e frequência de interações em cada habitat. Nossos resultados indicam que a vegetação da Amazônia Central apresenta uma alta riqueza de galhas entomógenas, além de um grande potencial para uma exclusiva fauna associada a cada habitat, devido a grande heterogeneidade ambiental, e recomenda o desenvolvimento de estudos com insetos galhadores, principalmente nas copas das árvores.
**Palavras-chave**: Galhas, plantas hospedeiras, Campinarana, platô, vertente, baixio.

## INTRODUCTION

Factors affecting the richness pattern of galling insects have been reported in many studies (Fernandes & Martins 1985, Fay *et al.* 1996, Downie *et al.* 2000, Gonçalves--Alvim & Fernandes 2001, Gonçalves-Alvim *et al.* 2001). According to the harsh environment hypothesis, for example, species richness of galling insects is strongly affected by physical conditions, such as temperature and increasing moisture relative to hygrothermal stress (*e.g.*, Price *et al.* 1987, Fernandes & Price 1988, Price *et al.*

1998, Lara & Fernandes 1996). In other words, more xeric habitats should have a higher number of galling species compared to mesic habitats (*i.e.*, sites near water), as observed by Fernandes *et al.* (1995) and Fernandes and Price (1992), respectively. In addition, galling insects are probably more susceptible to parasitoid, predator and pathogen attacks in mesic habitats than in hotter and drier habitats (Fernandes & Price 1992).

The diversity of galling species can also be related to soil fertility (Fernandes & Price 1991). Less fertile soils tend to have more gall-inducing insects and host

1. Laboratório de Biossistemática Animal, Universidade Estadual do Sudoeste da Bahia (UESB). BR 415, Km 03, s/nº, CEP 45700-000, Itapetinga, BA, Brazil.
2. Departamento de Botânica, Universidade Federal de Pernambuco.CEP 50670-901, Recife, PE, , Brazil.
*Author for correspondence. E-mail: jacortez@ufpe.br

plants than fertile soils (Blanche & Westoby 1995). Gonçalves-Alvim & Fernandes (2001) verified that the richness of insect-galling species had a negative correlation with magnesium, potassium, and zinc in the soils of a neotropical savanna, in the state of Minas Gerais, in southeastern Brazil. Indeed, less fertile and dry soils are likely to present a high number of sclerophyllous plants (Small 1973, Grime *et al.* 1997, Price *et al.* 1998). These plants usually have long-lived organs (Coley *et al.* 1985, Turner 1994) and high amounts of chemicals in their tissues for defense (Fernandes & Price 1991), which can be used by the gall-inducing insect as protection against chewing herbivores and fungi (Cornell 1983).

The lowland forests of the central Amazon are composed of a topographical gradient that can be divided into four habitats: plateaus, hill slopes, valleys and *campinarana* forests (Ribeiro *et al.* 1999). These habitats present different soil types, physical conditions and plant community compositions (Camargo & Kapos 1995). Therefore, it is reasonable to expect that the distribution of host plants and gall-inducing insects also changes along this gradient, especially when transitioning into *campinarana* forest. This type of forest presents drier, less fertile soils and higher degrees of sclerophylly than the other habitats (Ribeiro *et al.* 1999). Based on the harsh environment and soil fertility hypothesis, the present study describes the galls sampled in plateaus, hill slopes, valleys and *campinarana* habitat and tests the following predictions: species richness number (a) gall-inducing insects and (b) host-plants are higher in *campinarana* habitat than in plateaus, hill slopes and valleys. Further, we also investigated the number of host plant individuals in all of these habitats.

## MATERIALS AND METHODS

This study was performed in an undisturbed *terra firme* forest (1501 reserve; km 41), which is not seasonally inundated (Nascimento & Laurance 2004) and is located approximately 80 km north of Manaus, Brazil (2°34'S; 59°44'W). This reserve is controlled by the Biological Dynamics of Forest Fragments Project (BDFFP/INPA) and has a high diversity of trees that can reach 300 species of more than 10 cm of diameter at breast height (DBH) per hectare (De Oliveira & Mori 1999). The forest canopy is between 30-37 m tall with emergents reaching 55 m (de Oliveira & Mori 1999). According to Ribeiro *et al.* (1999), in central Amazonia, Leguminosae, Lauraceae, Rubiaceae, Sapotaceae, Myrtaceae, Melastomataceae, Annonaceae, Bignoniaceae, Araceae, Chrysobalanaceae, Clusiaceae, Burseraceae, Arecaceae, Euphorbiaceae, Moraceae and Lecythidaceae are the most species-rich families (≥ 45 species and 10 cm DBH).

Furthermore, in this reserve four habitat types can be found: *campinarana* and the tropical moist forests on plateaus, hill slopes and the bottoms of valleys. The vegetation in *campinarana* forest is adapted to extremely poor soil types and high amounts of light when compared to the other habitats. This habitat develops in a matrix of lowland tropical moist forest (e.g., between valleys and hill slopes), has white-sandy soils and high litter accumulation. Furthermore, *campinarana* habitats generally have low biomass and plant diversity. However, a high number of endemic species can be found in these forests. The plateau habitat represents the areas at the highest elevation, with large amounts of biomass and generally well-drained, nutrient-poor, clay soils. Palm species like *Attalea attaleoides* (palha-branca) and *Astrocaryum sciophilum* are common in this habitat. The hill slopes corresponds to transition zones that vary in length according to the level of relief inclination. In the higher areas, this habitat has vegetation and soil trends similar to the plateaus, and, in the lower areas, to the *campinarana* vegetation (when present) or valleys. Valleys are found in the lowest areas, along streams, and have sandy, wet soils, which become even wetter during the rainy season. The valley vegetation, contrary to plateau vegetation, has few emergent trees and is dominated by arboreal palms such as *Oenocarpus pataua* (see Ribeiro *et al.* 1999 for more information).

In October 2005, the presence of gall complexes and the diversity of their host plants were investigated in different areas of *campinarana*, plateaus, hill slopes and valleys in order to collect a representative sample of species that form galls. Ten transects were established in each habitat, which were 5 meters wide each (see Julião *et al.* 2005). Transects were more than 5 m from each other. In each transect, the first 30 individuals between 1 and 2 meters tall were randomly sampled for galls, totaling 300 plants per habitat. The census methodology used a fixed number of plants per transect that allowed the comparison of transects of different lengths. Further, the use of a fixed number of host plants in gall surveys has been utilized in various studies (*e.g.*, Santos-Mendonça *et al.* 2007, Araújo & Santos 2009). Only plants infested by galling insects were collected. The host plants were identified, and leaves harboring galls were collected and placed in numbered plastic bags. In the laboratory, the external morphology of galls was analyzed according to the methodology of Scareli-Santos (2001). Each gall was classified according to: (1) color, (2) shape (e.g., discoid, cylindrical, conical, spherical, oval, elliptical, triangular and non-regular), (3) location on the leaf (basal, medial, apical, adadaxial, abadaxial, petiole, limbo, margin, midvein, secondary veins), (4) distribution on the leaves (group or solitary) and (5) pubescence (pilose or glabrous).

Analysis of variance (ANOVA) was used to evaluate the relationships between species number of galling insects, host-plants species number, host-plant number and habitat type (Zar 1999). The analyses were developed using the software PAST (Hammer *et al.* 2001).

## RESULTS AND DISCUSSION

On average, galling species number and host-plant species number were not significantly different across habitat types (F = 1.008; g.l. = 3 p= 0.4004; Figs. 1A and 1B). Further, because gall insects are well adapted to living in stressful environments (Fernandes & Price 1988, Blanche & Westoby 1995), we expected a higher species number of gall-inducing insects and host plants in *campinarana* habitats, which had a higher number of plants with sclerophyllous vegetation compared to the plateaus, slopes and valleys. Sclerophyllous plants may have hard and long-lived leaves, require low amounts of nutrients, and have high concentrations of toxic and indigestible compounds, such as tannins, lignin and phenolic compounds (Fernandes & Price 1991, see also Chapin III *et al*. 1986), resulting in fewer attacks from parasites, predators and pathogens (Fernandes *et al*. 1995, Fernandes & Price 1988). Taper & Case (1987), for example, demonstrated that the levels of tannins in oak leaves positively influenced the richness and abundance of cynipid galling insects (see also Fernandes & Price 1992). Another study, which investigated the chemical composition of plant tissue with and without galls, showed that tissue with galls contained higher levels of phenolic compounds (Hartley 1998). Hartley (1998) argued that the high concentration of phenolic compounds in galled tissue might deter competitive folivores and/or gall predators and parasites.

In addition, we did not detect significant differences in the average number of host plants between habitats (F = 1.11; g.l. = 3 and p = 0.3566). However, with the exception of the *campinarana* habitat, we observed a tendency for the average host plant number to decrease from plateaus to hill slopes and valleys, as "mesic conditions" increased (Fig. 1A). Further, the average number of galling morphospecies tended to be lower in valleys compared to plateaus and hill slopes (Fig. 1B). This suggests that although we did not find a strong and significant pattern, the effects of the physical environmental (topographic factor) on galling insect species, and their host plant distribution, should not be discarded.

On the other hand, we also cannot ignore the effect of higher plant diversity in the lowland forests of the central Amazonia as a possible factor that influences both the availability of host plants and galling insects (Espírito--Santo & Fernandes 2007). Species richness of galling insects can be predominantly linked to plant community composition (Julião *et al*. 2005, Fernandes & Price 1988) where, for example, increased species richness is expected as the species diversity of plants increases (Fernandes & Prince 1988, Wright & Samways 1996). Besides this, plateaus have been shown, for example, to be a habitat that is more diverse in large liana species compared with the other habitats (Oliveira *et al*. 2008). If plateaus really are more diverse with regard to other species of plant groups, then this would help explain the tendency towards high galling species richness in relation to topographical gradient. Furthermore, according to Ribeiro *et al*. (1999), many plant species have a limited distribution and occur only in one type of habitat (e.g. on plateaus or in *campinarana*). This factor is probably associated with edaphic and environmental conditions and explains the species-specific exclusivity in each habitat with regard to the occurrence of galling morphospecies and host plant species (Table 1).

In summary, we expected to find a higher frequency and richness of host plants and gall-inducing insects because of the diversity of plant species and habitats (considering the variation in physical conditions) found in lowland foreststhe central Amazonia (Wright & Samways 1996, Ribeiro *et al*. 1999, Blanche & Ludwig 2001, Julião *et al*. 2005). However, galling insects were observed in only 35 (3%) of the 1200 plants analyzed. Thirteen families, eight genera and 27 morphospecies of plants were identified (Table 1). It is possible that in lowland forests of central Amazonia the insect herbivore communities are more common in the canopy and upper canopy than in the understory (Basset *et al*. 2001a, Medianero *et al*. 2003, Julião *et al*. 2005), and in larger plants than smaller plants (Castellanos *et al*. 2006). Medianero *et al*.
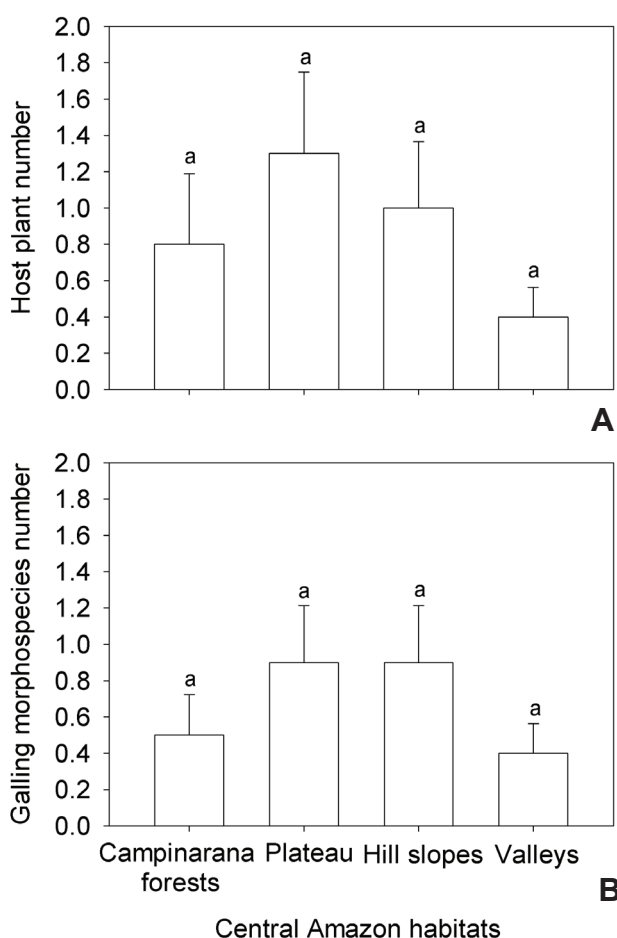


**Figure 1.** Host plant number (A) and gall morphospecies number (B) along a topographical gradient divided into four habitats (plateau, hill slopes, valleys and *campinarana* forests) in an undisturbed lowland forest of central Amazonia.

**Table 1 .** Host plant species and external morphology of galls observed in an undisturbed lowland forest of central Amazonia.

| Family | Species | Habitat | Abund. | Situation | Color | Shape | Pubescence | Group. | Solit. | Location | Distrib. |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Burseraceae | *Protium* sp.1 | Hill slopes | 1 | open | brown | cylindrical | glabrous | | X | adaxial-limbo | central |
| Burseraceae | *Protium* sp.2 | Hill slopes | 1 | open | brown | cylindrical | glabrous | | X | adaxial-limbo | basal |
| Burseraceae | *Protium* sp.3 | Valleys | 1 | open | brown | spherical | glabrous | | X | adaxial-midvein | central |
| Celastraceae | *Goupia glabra* | Campinarana | 1 | closed | green | pointed | glabrous | | X | adaxial-limbo | central |
| Crysobalanaceae | *Lycania irtusa* | Campinarana | 3 | closed | green | pointed | glabrous | X | | adaxial-limbo | leaf lamina |
| Euphorbiaceae | *Eschweilera* sp.1 | Hill slopes | 1 | closed | brown | spherical | glabrous | | X | midvein | base |
| Euphorbiaceae | *Mabea caudatus* | Valleys | 1 | open | brown | non-regular | glabrous | | X | adaxial-limbo | leaf lamina |
| Euphorbiaceae | *Mabea subsessilis* | Valleys | 1 | open | brown | cylindrical | glabrous | | X | adaxial-limbo | basal/central |
| Melastomataceae | *Miconia argyrophylla* | Plateau | 2 | closed | green | spherical | glabrous | X | | abadaxial-limbo | central |
| Mimosaceae | *Inga* sp.1 | Plateau | 1 | closed | brown | cylindrical | glabrous | X | | adaxial-limbo | basal/central |
| Mimosaceae | *Inga* sp.2 | Hill slopes | 1 | closed | green | non-regular | glabrous | X | | abadaxial-limbo | central |
| Myrtaceae | sp.1 | Plateau | 1 | closed | brown | conical | glabrous | X | | adaxial-limbo | central |
| Myrtaceae | sp.2 | Plateau | 1 | closed | brown | conical | glabrous | X | | adaxial-limbo | central |
| Ochnaceae | sp 1 | Hill slopes | 1 | closed | brown | non-regular | glabrous | | X | adaxial-limbo | central |
| Rubiaceae | *Palicouria* sp.1 | Campinarana | 2 | closed | green | cylindrical | glabrous | X | | adaxial-limbo | central |
| Rubiaceae | *Psychotria* sp.1 | Hill slopes | 1 | closed | green | non-regular | glabrous | | X | adaxial-limbo | leaf edge |
| Rubiaceae | *Psychotria* sp.2 | Plateau | 1 | closed | brown | spherical | glabrous | X | | adaxial-limbo | central |
| Sapindaceae | *Cupania hispida* | Plateau | 1 | closed | brown | cylindrical | glabrous | X | | secondary veins | central |
| Sapotaceae | *Microfila* sp.1 | Plateau | 1 | closed | brown | spherical | glabrous | | X | midvein | basal |
| Simaroubaceae | *Siparuna* sp.1 | Hill slopes | 2 | closed | green | spherical | pubescent | X | | abadaxial-limbo | central |
| | sp.1 | Plateau | 1 | closed | brown | non-regular | glabrous | X | | abadaxial-ljmbo | basal/central |
| | sp.2 | Hill slopes | 1 | closed | brown | conical | glabrous | X | | adaxial-midvein | leaf lamina |
| | sp.3 | Hill slopes | 1 | closed | green | pointed | glabrous | | X | adaxial-limbo | basal |
| | sp.4 | Plateau | 4 | open | brown | spherical | glabrous | X | | adaxial-limbo | central |
| | sp.6 | Valleys | 1 | closed | brown | conical | glabrous | | X | adaxial-mjdvein | central |
| | sp.7 | Campinarana | 1 | closed | brown | non-regular | glabrous | X | | adaxial-midvein | basal |
| | sp.8 | Campinarana | 1 | closed | green | pointed | glabrous | X | | adaxial-limbo | central |

Abbreviatures: Abund., Abundance; Group., Grouped; Solit., Solitary; Distrib., Distribution.

(2003) observed that the canopy of a tropical forest in the Republic of Panama supports a higher species richness of galling insects and leaf miners than the understory.

In addition, other resources, such as local light, environmental and humidity variations (Bach 1993, to see Basset *et al.* 2001b and Castellanos *et al.* 2006), enemy-free space and higher architectural complexity (Araújo *et al.* 2006), could favor the vertical stratification of insect herbivores. Canopy trees frequently have more leaves with scleromorphic characteristics than understory plants, due to higher exposure to solar radiation and wind (Wright & Colley 1996). According to Espírito-Santo & Fernandes (2007), a higher number of gall producing insects will be found as additional studies are conducted that sample canopies of rain forests, especially in the Neotropics.

In our study, Burseraceae and Rubiaceae had the highest numbers of host plant species (Table 1). Fernandes (1992) observed that plant family size was the factor that best correlated with galling species richness in the Indonesian Islands. Really, in lowland forests of central Amazonia, the families Burseraceae and Rubiaceae are two of the more important families, with 41 species within 5 genera and 90 species within 35 genera, respectively (Ribeiro *et al.* 1999). Additionally, in this region, species of Burseraceae are known to interact with specific gall-inducing insects, which can aid in the identification of these plants (Ribeiro *et al.* 1999).

In fact, the questions formed during in this study are fundamental to understanding the distribution patterns of gall-inducing insects in *campinarana*, plateaus, hill slopes and valleys of central Amazonia, and should stimulate the development of additional studies in this region because these insects are exceptionally important to tropical forest ecology. Therefore, we suggest that the next studies consider the regional scale of the host plant and gall-inducing communities and include the canopy and upper canopy of the forest. In addition, it would be important to investigate whether the distribution patterns of gall complexes between *campinarana* forests, for example, are a function of species-area and distance--area relationships because gall-inducing insects can be more vulnerable to predators in inter-*campinarana* areas. Finally, the recognition of historical events during forest formation is fundamental to explaining the coexistence of species.

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