Geraldo Wilson Fernandes
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Neotropical Insect Galls

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Preface

This book is about the most fascinating group of insects; those who are able to trespass the defensive lines of their host plants and induce galls. The gall is often regarded as an extended phenotype of the inducing insect, from where their offspring are protected from environmental harshness and nourished with food of great quality. In this book the reader will find the most updated information on host induction, ecology, botany, entomology, evolution, and geography of galling insects in the New World Tropics and sub-Tropics. The book is rich in new information that addresses all sorts of subjects all the way from the first reactions of the host cells to the gall inducing larvae to biodiversity to species distribution and interactions.

The study of galling insects and their host plants in the Neotropics bloomed in the mid-1980s and became widespread in recent years. These studies were capable of unveiling many new phenomena, interaction forces, and of challenging many accepted paradigms in the science of insect ecology. These studies helped to bring this forgotten insect taxa to the main stream of modern ecology, botany and entomology. The reason to bring all these studies into a single book is an attempt to summarize the work done so far, to promote syntheses and open new perspectives for deeper understanding of galling insect evolutionary ecology and biogeography, and foster new collaboration among Neotropical students.

We hope that the reader will benefit from the information provided by the book. Many sources of studies related to galling insects in the Neotropics are difficult to be located, are in Portuguese or in Spanish. Hence, the book may represent a unique source where one can find a syntheses done by the authors themselves. The book was written to a broad audience interested in botany, zoology, and entomology. Otherwise, anyone interested in general biology will not find any difficulty in following it. Hence, a major goal of the contribution is to attempt to provide new insights and new tinkering, to foster and provide the space to galvanize communication among those interested in the Neotropical galling insects.

The sources of inspiration for writing the book were many, but perhaps the most important was the wish to provide a deep look into what Neotropical students had done in the field of galling insect ecology up to date and sieve the information in order to signal new pathways to lead to further understanding of the ecology of galling insects and their host plants. Also we aimed at start bridging the enormous gap existing in the studies of temperate and tropical galling studies.

The work was not an easy one and we hope we have succeeded. We thank the collaborators for the responsiveness to our pledge. The book is structured in three parts: a botanical one, an ecological/evolutionary one, and finally a more biogeographical one. Finally, we would like to express our most sincere gratitude to many colleagues, students, and sponsors that trusted in this endeavor.

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Contents

Chapter 1
Neotropical Insect Galls: Status of Knowledge and Perspectives

Geraldo Wilson Fernandes, Marcel S. Coelho, and Jean Carlos Santos

Abstract This book seeks to expose the reader to those studies which have made the greatest contribution to the body of knowledge surrounding the insect galls in the Neotropical region. There seems to be countless groups of researchers working both in Brazil and in other tropical regions of the Americas. The chapters presented here report the diversity of studies conducted to date as well as indicate the quality of the studies in progress.

Keywords Biogeography • Insect galls • Richness hypothesis • Neotropical region

1.1 Introduction

Galling insects make up a sophisticated guild, characterized by inducing some meristematic tissues of their host plants to provide their offspring with food of better nutritional quality and free of defense compounds (e.g., Mani 1964; Price et al. 1987; Rohfritsch and Shorthouse 1982; Ferreira et al. 1990; Shorthouse et al. 2005). Galling insects are considered parasites as they benefit from this ecological relationship, negatively impacting their host plants (Price et al. 1986, 1987; Andrade et al. 1995; Larson 1998; Florentine et al. 2005). Furthermore, they are species-specific,

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meaning that each insect species occurs in only one host-plant species, with extremely rare exceptions (Fernandes and Price 1992; Floate et al. 1996; Price et al. 1998; Carneiro et al. 2009a).

Galling insects probably evolved from selective pressures which favored the manipulation and induction of tissues with better nutritional qualities, protection against environmental stresses and natural enemies (Price et al. 1987). As the pressures imposed by the numerous abiotic and biotic variables vary widely in space and time, the geography of this group may be best represented by a mosaic determined by the interplay of environment and hosts stresses. Price et al. (1998) summarize the knowledge regarding these patterns on a local, regional and global scale, focusing on their mechanisms, as well as their generative and sustaining processes.

1.2 Early Studies on Galling Insects in the Neotropics

Studies between galling insects and their host plants in the Neotropical region are not recent. In the review of Mani (1964), many studies carried out in the Neotropical region were listed and briefly described whenever possible. Most of these studies are related to descriptions of the galls and whenever possible with records of the galling organisms and their host plants. More recently, Gagné (1994), in addition summarize the Cecidomyiidae (Diptera) fauna of tropical America, brought to the reader precious information on the work of those former researchers that first studied the galling cecidomyiids in the Neotropics. These include the pioneer work of J.J. Kieffer, E.H. Rübsaamen, J.S. Tavares, E. Möhn, P. Jörgensen, J. Brètes, C.A.V. Houard, A. Wünsh, and E. Felt, among others. The morphological diagnoses of galls in Brazil began with the classic studies of the Jesuit priest J.S. Tavares (1906, 1915, 1916a, b, 1917a, b, 1918a, b, 1920a, b, 1921, 1922, 1925) which resulted in the description of 26 genera and 56 cecidomyiid species. More modest studies, but of great contribution, were also conducted by others, including E. Felt and Rübsaamen (Felt 1908, 1915a, b). The excellent book of R.J. Gagné (1994) is the sole one devoted to the most diverse galling taxa in the Neotropical region, the cecidomyiids (see also Houard 1933).

Studies on the ecology of galling insects began to increase in the early 1980s when research was initiated on their distribution and natural history. Since then, research studies have been carried out in the most diverse ecosystems, principally in Brazil. These studies present schematic gall drawings, host plant identification, often by family level or genus, and galling that were not commonly identified. Certainly, a full listing of these studies is impracticable for reasons of space. However, consulting the listed studies and references in this book can provide the reader with more detailed information. With only this country as an example, the fauna of galling insects was studied in various and different vegetation types, e.g.: Pantanal wetlands (Julião et al. 2002), Amazonian rain forest (Julião et al. 2005; Almada and Fernandes 2011; Maia 2012), coastal sand dunes (Maia 2001, 2005; Oliveira and Maia 2005; Maia et al. 2002; Mendonça 2007), Cerrado (savanna) (Fernandes and Price 1988; Maia and Fernandes 2004; Gonçalves-Alvim and Fernandes 2001), rupestrian mountain ecosystems (Carneiro et al. 2009b), tropical dry forest on limestone outcrops (Coelho et al. 2009), Caatinga (Santos et al. 2011), and Atlantic rain forest (Santos et al. 2012a), among others. In this book the reader will find abundant material on the galling fauna in these vegetation types.

It is interesting to note that, despite the elevated richness of gall morphotypes recorded in these studies so far, approximately only 159 cecidomyiid species were in fact described from Brazil (Maia 2005). This illustrates the pressing need for taxonomic studies of galling insects and reports the need of more researchers focused on the taxonomy of the major galling taxa in the Neotropical region. Considering the high diversity of galling insects in the many ecosystems that comprise the Neotropics, it is unfortunate that the natural history, ecology and dynamics of these species continue to be overlooked. Sampling accompanied by descriptions of the gall morphotypes associated with their host plants throughout the Neotropical region must continue to be conducted, as the gaps in such knowledge are enormous. In many countries we failed to find any study on gall inducing insects. This kind of information is urgently needed so that we can carry out more detailed comparative summaries and refine our present knowledge on the geography and evolution of galling insects in the region (Carneiro et al. 2009a; Fernandes et al. 2011; Santos et al. 2012b).

Anatomical studies of Neotropical galls gained momentum only in the last quarter of century with the consolidation of some research groups (e.g., Formiga et al. 2009; Oliveira and Isaias 2009; Sá et al. 2009). These studies have sought not only to describe the anatomical, morphological and classic ontogenetic aspects of galls, but are also concerned with understanding the processes involved in their formation, patterns of growth and cell division on different plant tissue, degree of complexity, specific responses of each gall maker and host plants, as well as the restrictive morphogenesis limits imposed by the host plant (e.g., Oliveira and Isaias 2009, 2010; Campos et al. 2010; Castro et al. 2012; Formiga et al. 2012; Dias et al. 2013a, b). Again, in this book some of these key issues underlying the heart of the interactions of host and galling insects are brought to light.

1.3 Barometers of Insect Adaption to the Environment and Resulting Geographical Distribution

Distribution patterns of galling insect species and their host plants have been tested extensively across various continents, especially in temperate countries where these organisms have been identified as models in the analysis of species distribution (Fernandes and Price 1988; Price et al. 1998; Fernandes et al. 2005; see also Price et al. 2011). The use of gall insects as a “model organism” reflects its methodological abilities: they are frequently composed of many species of different insect orders; the galls are conspicuous structures, persistent on the plant, easily observed and collected, and the interactions between the inducing insect and other organisms are relatively simple to manipulate (Fernandes and Price 1988; Stone and Schönrogge 2003; Julião et al. 2005).

The understanding of species distribution and the forces that drive it continues to be a major goal of ecological studies (see Cornell 1985; Strong et al. 1984; Lawton 1990; Hawkins and Compton 1992; Cornell 1993; Lawton et al. 1993). Few studies have addressed the relationship between local and regional galling species richness in the Neotropics (e.g., Almeida et al. 2004; see also Price 1991; Medianero et al. 2010; Mendonça 2011). As more studies on the distribution of hosts and gallers are brought to light in the dozens of vegetation types across the Neotropics, we will be able to better understand the community structure of the galling insects in the region. There is a great chance for testing and generating new hypotheses on the structure of insect communities in this region where new interactions of galling insects and their environments have been often revealed.

The global distribution pattern of galling insects was argued not to fit the generalization regarding the decline of species richness with latitude (Fernandes and Price 1991; Willig et al. 2003). Gall inducing insects are richer in species at intermediate subtropical latitudes (25–38°N or S), in hot habitats and with tropical and temperate sclerophyllous vegetation (Cerrado, Chaparral and Mediterranean-type vegetation) (Fernandes and Price 1991; Price et al. 1998). In the different biogeographic regions, including the Neotropical, several studies showed that species richness of gall insects was negatively related to altitude (Fernandes and Price 1988; Fernandes and Lara 1993; Fernandes et al. 1994; Price et al. 1998; Lara et al. 2002; but see Waring and Price 1990; Carneiro et al. 2005). In this book, new information challenges the most accepted hypothesis on the geography of galling insects, therefore providing the fuel for more discussions on the driving forces that shape insect distribution.

Work conducted in the Neotropical region has demonstrated that, independent of altitude, species richness of gall-inducing insects varies between habitats. Gall-inducing insects are richer in species and abundance in xeric habitats (high temperatures, low humidity and nutrient-poor soils) than in mesic habitats (low temperatures, high humidity and soil rich in nutrients) (Fernandes and Price 1991, 1992; Cuevas-Reyes et al. 2004a, b). Previous studies affirm that the relationship between galling insect species richness and latitude/altitude would be due to increased hygrothermal and nutritional stress in habitats of intermediate latitudes and low altitudes, respectively (e.g., Price et al. 1998). The mechanisms responsible for the occurrence of more species in xeric habitats would be the survival and mortality differentials mediated by the habitat (Fernandes and Price 1992; Ribeiro-Mendes et al. 2002). Otherwise, we are left with only these two studies so far. The search for the mechanisms that shape insect communities is of major importance and hence many more studies are called for, be it in the Neotropics or elsewhere.

Besides hygrothermal and nutritional stresses, species richness and the taxonomic composition of vegetation exert an important role in galling insect species richness. While Wright and Samways (1996, 1998) showed that host plant species richness in

Fynbos vegetation (South Africa) is the main determinant of gall insect species richness, earlier studies carried out in the Neotropical region considered total host plant species richness a weak indicator of the variation of gall insect species richness in the rupestrain grassland vegetation (Fernandes and Price 1988; Lara et al. 2002). These discrepant results could be explained by the fact that in *Fynbos* vegetation gall insect species richness by plant species is low and varies very little between different host plant species. On the other hand, in the rupestrian grasslands a single plant species [e.g., *Baccharis concinna* (Asteraceae)] can present up to 32 % of the species found in a single habitat (Lara and Fernandes 1996). In the Australian savannas, *Eucalyptus* species would play the same aggregation role (Blanche 2000). On the other hand, recent review study by Araújo (2013) and that of Santos et al. (2013) showed strong effects of plant species richness on galling species richness, therefore opening the question for further debate and development.

In habitats where the number of galling insect species associated to the host plant species is quite variable, an important determining factor of galling insect species richness is the taxonomic composition. The high variability in the number of gall insect species has often being explained by the presence of "super-hosts". These hosts can greatly increase the number of gall insect species wherever they occur (Fernandes and Price 1988; Veldtman and McGeoch 2003; Espírito-Santo et al. 2007), see also (Hawkins and Compton 1992). For the Neotropical region the genus *Baccharis* was highlighted as an important one (Fernandes et al. 1996), but many other genera and species have recently entered the list, as reported in this book.

The size of the taxon is another factor that potentially influences gall insect richness (Fernandes 1992). Many studies in the Cerrado (Gonçalves-Alvim and Fernandes 2001), rupestrian grasslands (Maia and Fernandes 2004), Atlantic Forest (Fernandes et al. 2001), dry deciduous Forests (Coelho et al. 2009) and seasonal sub-tropical Forest (Mendonça 2007) corroborate this hypothesis (see also Araújo 2013). Intuitively, errors in the choice of host during oviposition could lead to a higher rate of speciation. In other words, the higher the number of representatives of a host in a given area and moment would result in higher rates of error and consequent speciation. In spite of it, the role of host taxa composition, size and evolutionary history on the richness of gallers are a matter still awaiting further investigation, be it in the Neotropics or elsewhere.

A well known variable that influence the distribution of insect herbivores is the distribution area of their host plants. Otherwise, Fernandes and Price (1988) failed to find a positive relationship between the distribution area of host plant species and gall insect species richness. Unfortunately, in the Neotropical region, the main difficulty for testing this hypothesis is the lack of basic information about distribution areas of plant species.

Mendonça (2001) observed that fire is a common phenomenon in habitats with sclerophyllous vegetation and that it could be an important selective force in the distribution of galling insects. In these environments, insects would benefit from fire because it promotes the synchronization and production of new vigorous branches for insect colonization. Price (2005) argued that fire could be included within the initial hygrothermal hypothesis of Fernandes and Price (1991).

The soils represent another important source of variation that is related to the geography of gall insects. Plants under nutritional stress have slow growth and, in this scenario, amino acid availability should be greater in their tissues (White 1969). While some studies corroborate this hypothesis (e.g., Blanche and Ludwig 2001; Gonçalves-Alvim and Fernandes 2001; Cuevas-Reyes et al. 2004a), others have not found a positive correlation between the indicating variables of soil stress and greater galling insect richness (e.g., Blanche and Westoby 1995; Fernandes et al. 2000; Cuevas-Reyes et al. 2003; Veldtman and Mcgeoch 2003). Although many studies are now providing information on the soil nutritional status, the lack of an experimental approach to it is evident. Experimental studies, such as the one conducted by Cuevas-Reyes et al. (2011), should be encouraged.

Although numerous studies have been conducted in the Neotropical region about the distribution and possible causes shaping the differential diversity of galling insects among habitats and ecosystems, there is a lack of experimental, large spatial and temporal scale studies. It is likely that significant breakthroughs would result from a more mechanistic approach around factors that influence the geography and diversity of galling insects. On the other hand, it is necessary to recognize the difficulties inherent in these experiments at a community level. However, in the Neotropical region, widespread experiments exist in which hypotheses testing of this nature could be carried out. In this regard, studies on water stress induction, fertilization, fire and even budding, in addition to the selective behavior and survival of gallers would be welcome.

1.4 Mechanisms and Processes at the Host Level

Galling insects can be profoundly influenced by the nutritional quality of their host plants, which can be distributed differentially in the mosaic of environments and/or habitats. The vigor hypothesis proposed by Price (1991, 1992) predicts that herbivores would be more abundant in plants and/or plant modules with rapid growth and reach a larger size when compared to the average. The galling insects would be the archetypes of these herbivores, according to Price et al. (1990). In a recent meta-analysis, Cornelissen et al. (2008) showed that herbivore insects are generally more abundant in more vigorous plants and that the effect of the vigor is stronger in the guild of suckers, leafminers and gall insects.

For six consecutive years, the plant vigor hypothesis (PVH) proposed by Price (1991) was tested by observing the attack and survival of a leaf gall species induced by *Schizomyia macrocapillata* (Diptera: Cecidomyiidae) on *Bauhinia brevipes* (Fabaceae) leaves (Santos et al. 2007). *Bauhinia brevipes* is a common shrub in the semi-arid of Brazil and which supports vast and varied herbivore insect fauna, especially galling insects (Cornelissen et al. 1997; Cornelissen and Fernandes 2001). Due to these characteristics, this system was used as a model for various studies on galling insect preference and performance. Santos et al. (2007) showed that, although short branches are always more abundant than long branches, the percentage of branches galled by *S. macrocapillata* was up to ten times greater in the long branches of *B. brevipes*, corroborating the predictions of the PVH. Furthermore, the survival of *S. macrocapillata* was positively related to the size of the branches (but see Cornelissen et al. 1997; Cornelissen and Fernandes 2001). For *Asphondylia microcapillata* (Diptera: Cecidomyiidae), another galling insect species that attacks the leaves of *B. brevipes*, and for a free-feeding geometridae species, there was no preferential pattern for the larger branches of *B. brevipes* (Cornelissen et al. 1997). Studies focusing on the dynamics, differential performance, species competition and community organization of galling insects on their hosts lies in the main stream insect ecology. The large numbers of galling insects, many times of different and distant taxa, on single Neotropical hosts may provide a perfect scenario for new developments and insights into insect community organization and ecology.

Plant architecture is another important factor that influences the richness and abundance of herbivorous insects (Lawton and Schröder 1977). Although Fernandes and Price (1988) and Lara et al. (2002) have not observed any architectural influence on gall insect richness among herbs, shrubs and trees, other studies corroborate the hypothesis of host plant architecture. For example, Cuevas-Reyes et al. (2004b) recorded greater galling insect richness on trees than on shrubs in mesic environments, but the reverse in xeric environments in Mexico; while Gonçalves Alvim and Fernandes (2001) recorded greater galling insect richness on trees than on shrubs and herbs in a savanna. In working with the species *Baccharis pseudomyriocephala* (Asteraceae), Araújo et al. (2006) found a positive influence of the architectonic complexity and the richness, abundance, and survival of the associated galling insect species. Working with 17 species from the genus *Baccharis* (Asteraceae), Espírito-Santo et al. (2007, 2012) found a positive correlation between some plant architecture variables and galling insect richness. They proposed that the difference in galling richness among the species of *Baccharis* may be related to interspecific factors, such as the availability of young indifferentiated tissues. The authors also postulate that plant architecture must have an important function in the evolutionary process of galling insect speciation. Congeneric plants with similar architecture could have enabled sympatric speciation processes through errors in the choice of host, at least in the case of the genus studied.

Aspects related to the ontogeny of the host plants have also been cause for studies using galling insects in the Neotropical region. Fonseca and Benson (2003) proposed the hypothesis that herbivore insects are associated with the different ontogenetic development phases of their host plants. Since trees have more ontogenetic development phases compared to shrubs, herbs and lianas, they would host a greater richness of galling insects (see Medianero and Barrios 2001; Medianero et al. 2003). Fonseca et al. (2006) tested this hypothesis for the first time, confirming the preference of two galling insect species in different stages of ontogenetic development of the species *Cryptocarya aschersoniana* (Lauraceae). In a simple walk in the understory of the main forest formations in South America, rain forests and dry forests or even in the second largest South American biome, the Cerrado, one will easily notice many saplings heavily attacked by galling insects. Plant ontogeny and development effects of galling insects are clearly important aspects yet to be studied in detail in the Neotropics.

The hypersensitivity reaction (HR) is an important defense induced against pathogens and has recently been studied against gall insects (Fernandes 1990, 1998; Cornelissen and Fernandes 1999; Fernandes and Negreiros 2001; Fernandes et al. 2003). HR is a resistance located immediately adjacent to the site of penetration attempted by the invader. The HR included morphological and histological changes, which causes the death of attacked tissue. Initially, Fernandes et al. (2000) proposed a description of the morphological and anatomical changes associated with the HR phenomenon in the leaves of the neotropical tree *Bauhinia brevipes*, in response to the attack of *Schizomya brevipes* Maia (Diptera: Cecidomyiidae). The HR begins as a rounded halo around the gall induction site. Subsequently, black-colored polyphenolic substances of unknown origin begin to accumulate around the attacked cells after larva penetration. Then, the area surrounding the invasive larva becomes dark brown. The cells become obliterated and necrotic, thus resulting in the narrowing of the tissue. Simultaneously, a reaction of the same characteristics begins near the midrib where cells divide, giving way to a similar tissue in the exchange, forming a protective layer around the conductive tissues. As a result, a blockage occurs in the flow of nutrients, and thus the plant slows the development process of the larva (Fernandes et al. 2000). In *B. brevipes,* HR proved to be the most important factor in the dynamics of galling insect population (Fernandes 1998; Fernandes et al. 2000; Santos et al. 2007). In spite of it, the studies on hypersensitive reactions of wild hosts against galling insects are scarse at best. The study of this important mechanism of host defense in which the galling larvae is located and eliminated early on without inducing large damage on the host, represents a potential source of knowledge that would bridge the gap in our knowledge on the very fist moment of induction of galls all the way to gall spatial distribution and evolutionary success.

1.5 Current Trends and Future Neotropical Gall Insect Studies

Recent studies using Neotropical gall insects indicate that the hypotheses which attempt to explain the significant richness of this guild (see Espírito-Santo and Fernandes 2007) and its differential distribution among habitats are not mutually exclusive. Each one of them can be part of the explanation of the patterns and have greater or lesser significance when considering local, regional and global distribution. Hence, once again scale is important to consider in future studies. Some of the hypotheses or described variables may even be the explanatory mechanisms for others. For instance, the altitude hypothesis may be explained by the hygrothermal stress hypothesis and be highly influenced by the soil quality mosaic. Thus, the degree of interaction between them, their explanatory force, indicate the need for more detailed studies in which there is greater control of the variables and interactions among them. While we assume that there is still a need to continue describing local patterns in the different biomes and Neotropical forest formations, the need to invest in experimental studies is clear. In this sense, the quest for species models could represent a viable alternative. Furthermore, the increase in sample strength by means of standardized methodologies is fundamental and can lead to alterations in existing distribution patterns of galling insects. Hence, we call the attention for the need to dedicate more attention to this dimension. The evidence clearly indicates that gall insect studies in the Neotropics represent a large portion of what has been produced worldwide, but otherwise we must advance in those studies that search for the mechanisms and processes that have shaped this important guild of insect herbivores.

Perhaps the first approach to conquer such goal is to construct the base ground information so that syntheses can be reached for the moment. We hope that this book may represent such opportunity. In the following chapters we focus on past and current advances, and provide the perspective of research studies involving galling insects in the Neotropical region. Throughout the book, aspects of natural history are thoroughly discussed. Richness patterns and mechanisms of galling insect occurrence, whether *bottom-up* or *top-down*, as well as their potential use as a bioindicator, are discussed under the conditions of various ecosystems. These include the rainforests of Brazil, Panama and Costa Rica, the Neotropical savannas, coastal environments, mountainous and tropical dry forests, as well as galling studies in Argentina, Panama, Costa Rica, and Mexico. Besides natural history, morphological and methodological aspects are also debated and new insights brought to the main stream studies in galling insects. With the already observed galling insect richness in the Neotropical region, the use of gall morphotypes as a tool to measure abundance and species richness in vegetal communities is justified with a convenient and innovative proposal for standardizing the nomenclature of the various gall morphotypes induced by these insects. In addition, the state of the art cytochemical alterations associated with the development of the galls is discussed with an emphasis on the most recent advances in this sphere of knowledge.

This book seeks to expose the reader to those studies which have made the greatest contribution to the body of knowledge surrounding the galls of Neotropical insects. There seems to be large and growing groups of researchers working in other regions of the tropical Americas not covered here, but we believe that these book chapters presented the diversity of questions addressed to date, an indication of the quality of the studies in progress as well as the fuel and opportunity for more to come.

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Chapter 2
Developmental Anatomy of Galls in the Neotropics: Arthropods Stimuli Versus Host Plant Constraints

**Rosy Mary dos Santos Isaias, Denis Coelho de Oliveira,
Renê Gonçalves da Silva Carneiro, and Jane Elizabeth Kraus**

Abstract As natural microlaboratories, galls are elegant models to study plant cell fates. Each gall morphotype is the product of repetitive patterns in cell division and differentiation, which culminate in a neoformed multicellular organ. Gall morphogenesis ruptures the patterns of cell polarization and expansion in relation to their host organs through cell redifferentiation, which results in changes in their functionality. As so, gall tissues guarantee nutrition, protection and a favorable microenvironment to the gall inducer. Sites of hyperplasia and hypertrophy are commonly reported for arthropod galls, and are commonly related to the feeding habits of each taxon. Nevertheless, there are some morphotypes in which the shapes are so peculiar that some other mechanisms must be involved, such as biochemical interactions, for instance. We revisit some Neotropical gall systems to check if the accumulation of phenolics is kept as one of the first cell responses to the presence of the inducer and if it is related to the changes in cell polarity and axiality. The final gall morphotypes require new spatial and developmental control of the host plant cells division and expansion, together with cell redifferentiation, but under the constraints imposed by the host plant organs.

Keywords Cell wall remodeling • Metabolites accumulation • Morphogenesis • Neoformations • Redifferentiation

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2.1 Morphogenesis: From Host Organ to Gall

Plant cells are early determined to develop specific structural characteristics to perform their roles in plant physiology. Their development generates tissues and organs whose specific organization guarantees the plant functionality (Taiz and Zeiger 2010). The morphogenesis of the host plant cells from their meristematic origin through their expansion and differentiation has been evaluated to define the alterations in their original fates, and the acquisition of new identities as part of the newly formed organs – the galls (*cf.* Moura et al. 2009; Oliveira and Isaias 2010a; Isaias et al. 2011). These studies have revealed a common pattern for the morphogenesis of the host leaves similar to that described by Foster (1936). The protoderm early differentiates into epidermis and their appendages. The adaxial and abaxial layers of the ground meristem differentiate into the palisade and spongy parenchymas in dorsiventral laminas, while the median layers may lately differentiate into specialized parenchyma. The procambium strands differentiate interspersed to the median ground meristem (Fahn 1990) (Fig. 2.1).

Insect-induced plant galls are the product of a deviation on the standard morphogenetic pattern of their host organs. During gall morphogenesis, the protoderm may either differentiate into a uniseriate or multiseriate gall epidermis with different degrees of alterations. In some leaf folding galls, the epidermis may specialize in a nutritive layer, altering both its structure and physiology towards a completely distinct role (Oliveira and Isaias 2009). The multilayered ground meristem undergoes major changes, sometimes differentiating into a homogeneous parenchyma, sometimes with functionally different layers, and as so being responsible for the great variety of gall shapes found in nature (Fig. 2.1). The procambium gives rise to the primary vascular system which alters its fate from the normal network of vascularization to a more complex net, commonly enhanced to nurture the gall tissues (Moura et al. 2009; Oliveira and Isaias 2010a; Isaias et al. 2011) with higher water and nutrients intake. During plant morphogenesis, cells are genetically programmed (Lee and Schiefelbein 2002), and should be reprogrammed towards a new and different path, during gall morphogenesis, for instance.

According to Meyer and Maresquelle (1983), the galls, like other regular plant organs, have their own characteristic morphology and histology. Although widely diverse when it comes to developmental processes which determine peculiar shapes, individual gall morphotypes appear in nature as repetitive and symmetrical structures (Raman 2007). By accompanying the ontogenesis of the host-organ and that of the gall through anatomical analyses, it is possible to accurately elucidate how plant cell fates change (Fig. 2.1). Also, as cells are recognized as units responsible for the determination of the final shape of the plant organs, the alterations during gall development targets new shapes and functions. As there is a high degree of specificity between host-plant and gall-inducing insects (Mani 1964; Dreger-Jauffret and Shorthouse 1992; Redfern and Askew 1992; Carneiro et al. 2009) the morphogenesis of these structures is very conservative, and thus reliable for studies of cell lineages and cell fate.

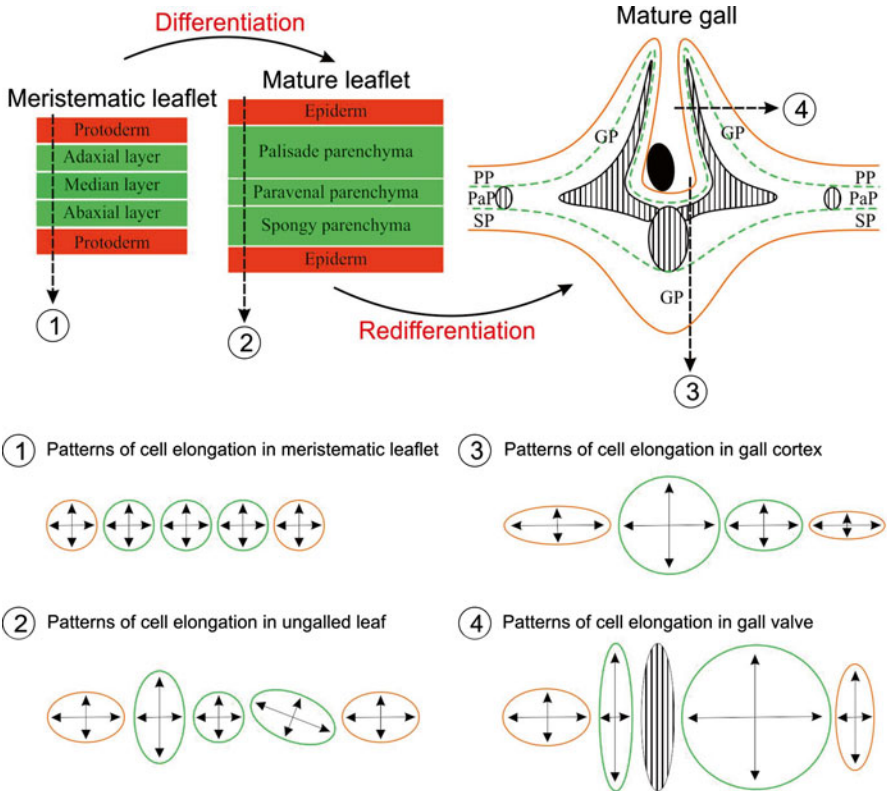

Fig. 2.1 Development of the galls induced by *Euphalerus ostreoides* (Hemiptera: Psylloidea) in *Lonchocarpus muehlbergianus* (Fabaceae). Non chlorophyllian tissues (*orange lines*) and chlorophyllian tissues (*green lines*) differentiate from leaf meristem until gall maturation, with distinct axis of cell expansion (*arrows*). Crosshatching indicates the development of vascular tissues. *PP* palisade parenchyma, *SP* spongy parenchyma, *PaP* paravenal parenchyma

2.2 Cell Responses to the Feeding Stimuli of Galling Herbivores

The nature of the first stimuli of gall induction has not been elucidated yet. Hori (1992) discussed the influence of the phenolics in the control of auxin levels and the generation of the sites of cell division and growth. Some other authors have investigated the levels of hormones, such as cytokinins and IAA in gall development and the evidences have pointed out that the sites of phenolics accumulation (Fig. 2.2) and the planes of cell divisions may indicate a distinct hormonal status in gall structure. Inside the phenol-rich cells located in gall sites, the activity of IAA oxidases is blocked (Hori 1992), consequently the local concentration of auxin increases, leading to cell hypertrophy. Furthermore, auxins are well known to drive very specific growth patterns in plant cells through the so called “acid

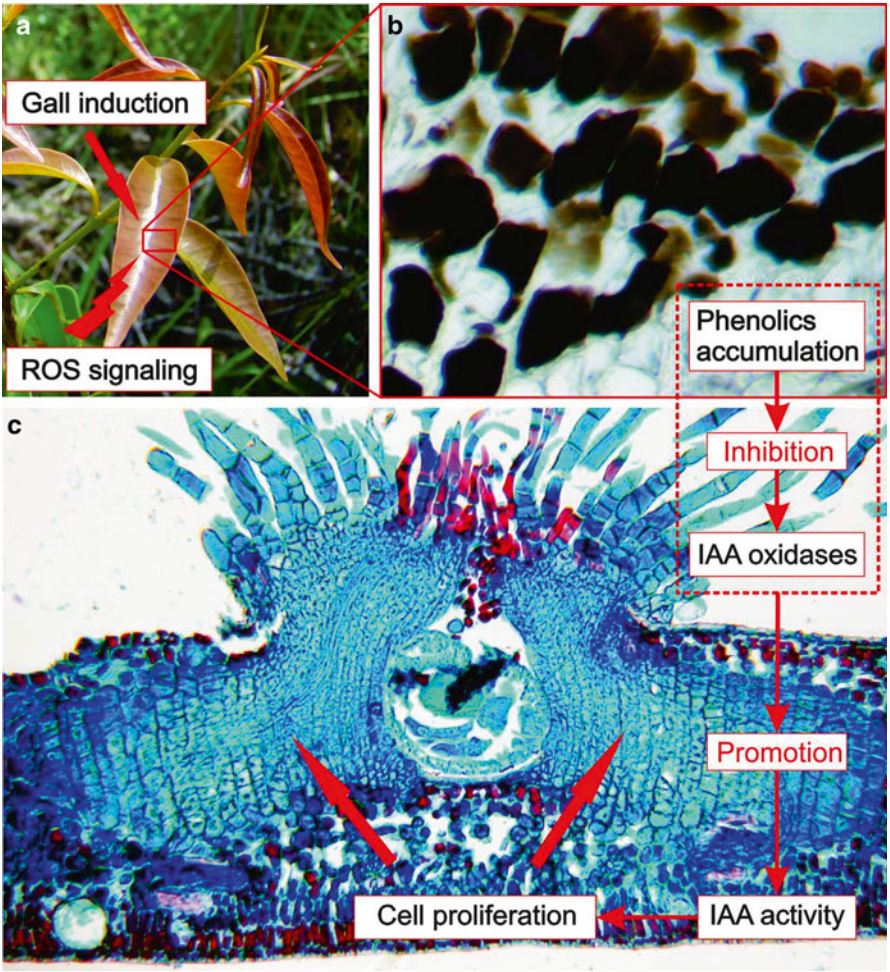

Fig. 2.2 Schematic representation of the cascade of events that leads to gall formation. (**a**) During gall induction, ROS production enhances, which is believed to be the first signaling step for gall development. (**b**) At the sites of gall induction, phenolic compounds quickly accumulate (Note the cell layers stained with ferrous sulfate forming a black precipitate), inhibiting the action of IAA oxidases locally. (**c**) Due to the inhibition of IAA oxidases, IAA activity is promoted, which leads to cell proliferation and cell expansion, as commonly observed in galls development

growth" (Rayle and Cleland 1992; Taiz and Zeiger 2010; Heldt and Piechulla 2011), which seems to be present in the sites of gall development. This mechanism works together with expansins that break the hydrogen bonds between cellulose microfibrils and xyloglucans allowing cell wall to expand (Smith et al. 2010). The auxin concentrations have been associated to intense cell division in gall developmental studies (*cf*. Abrahamson et al. 1991).

After the first steps of recognition between each galling herbivore and its specific host plant, there seems to be a cascade of events initiated by reactive oxygen species (ROS) (Oliveira and Isaias 2010b; Oliveira et al. 2010, 2011a; Isaias and Oliveira 2012). ROS signaling leads to phenolics accumulation and sequential molecular events (Del Río and Puppo 2009) which are believed to continue towards the process of gall morphogenesis. In plant pathogen recognition before these cascade of events, there is an increase of cytosolic Ca^{2+} and depolarization of membrane inducing the NADPH oxidase complex that generates ROS (Maffei et al. 2007). According to Baluska et al. (2006), some molecules, such as acetylcholin stearases, receptors of glutamate, of gamma-aminobutyric acid (GABA), and components of endocanabinoids are crucial for the synthesis of adenosine triphosphate (ATP), nitric oxide (NO), and ROS, which are involved in the stress signals between galling insects and their host plants. This cascade of molecular signals may be important for gall development as well as for specific cell responses. In fact, the current focus in plant developmental biology has shifted from the organization of the plant or organ to the single cell (Hülskamp 2004). The formation of tissues atypical to the host organs, such as the nutritive and mechanical tissues in galls, may be used to investigate the secondary cellular responses that galls may present.

The secondary cellular responses take place as gall morphogenesis proceeds to maturity through a finely regulated process of redifferentiation. Peculiarities such as the way the inducer feeds and its position inside the chamber are believed to be crucial for the determination of gall shape (Rohfritsch 1992). In fact, galls induced by different *taxa* of arthropods tend to present different shapes and degrees of tissue alteration and complexity, and consequently distinct cell responses. Classically, the simplest among the galls are those induced by mites that do not have highly specialized tissues, ranging from the formation of nourishing hairs, pocket-shaped galls or marginal rolls of the leaf lamina (Meyer 1987). Indeed, Moura et al. (2009) studied the galls induced by *Aceria lantanae* (Acarina: Eryophyidae) on the leaves of *Lantana camara* (Verbenaceae), and reported structural alterations similar to those described for other Eryophyidae-host plant systems.

Some inducers, such as the Hemiptera and Thysanoptera, are sucking and rasping feeding insects, with an impact on host cells similar to that of the Eryophyidae. They induce a greater diversity of gall forms, but with low tissue specialization. These insects suck cell contents and/or sap from the phloem, exerting low impact on plant tissues (Dreger-Jauffret and Shorthouse 1992), as evidenced by the simpler structures of their galls. The cortices of these galls are composed mostly by hyperplasic and hypertrophic parenchyma, with interspersed vascular bundles and sclerified tissues at maturity (Meyer 1987). Oliveira and Isaias (2010b) studied galls induced by a Hemiptera: Psylloidea on leaves of *Aspidosperma australe* (Apocynacaeae). These galls fit the described pattern and they are eminently parenchymatic and poorly vascularized, as well as the galls induced by *Gynaikothrips ficorum* (Thysanoptera) on *Ficus microcarpa* (Moraceae) (Souza et al. 2000). Nevertheless, for the *Euphalerus ostreoides* (Hemiptera: Psyllidae)–*Lonchocarpus muehlbergianus* (Fabaceae) system, tissue zonation was described (Isaias et al. 2011) denoting that not only the feeding habit of the galling agent is determinant for

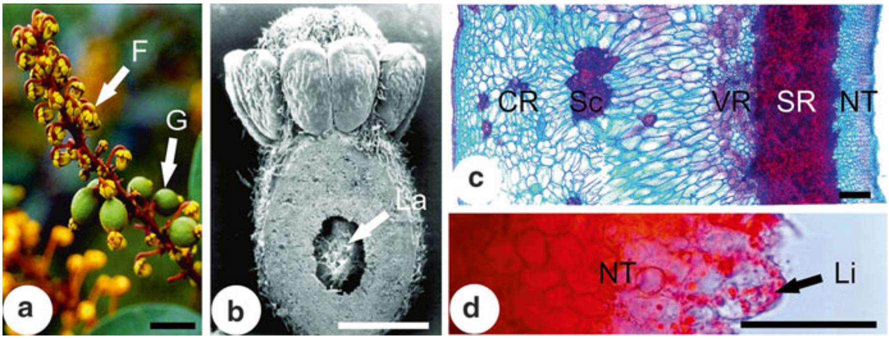

Fig. 2.3 Galls induced by an unidentified Lepidoptera on pedicels of *Byrsonima sericea* (Malpighiaceae). (**a**) Inflorescence with ungalled flowers and pedicel galls. (**b**) A scanning electron micrograph of a galled pedicel evidencing a larva inside the larval chamber. (**c**) Transverse section of an intermediate gall development showing the ground system alterations into the cortical region, vascular region, sclerenchyma region and nutritive tissue surrounding the larval chamber. Sclereids may appear in the cortical region. (**d**) Detail of the lipid-rich nutritive tissue. *CR* cortical region, *F* flowers, *G* galls, *La* larva, *Li* lipids, *NT* nutritive tissue, *Sc* sclereids, *SR* sclerenchyma region, *VR* vascular region. Bars: (**a**) = 1 cm, (**b**) = 1 mm, (**c**) 100 μm, (**d**) = 50 μm

the establishment of cell responses, but so are the potentialities and constraints of the host plant morphogenesis.

Gall inducing Coleoptera and Lepidoptera usually attack stems, generating galls that are poorly distinct in functional terms from their host organs. In this case, hypertrophy and hyperplasia of the pith and cambium occur, forming the tissues from which the larva feeds (Mani 1964; Dreger-Jauffret and Shorthouse 1992). Jayaraman (1989) compared 50 insect galls on stem axis and concluded that their developmental pattern seems to be correlated to the site of induction. When it is external on the stem, the epidermis or the outer cortex proliferate to form a "covering gall"; but when the oviposition occurs inside the stem tissues, the phloem, cambium, xylem and pith proliferate to form an internal gall, fusiform or spherical shaped. The galls induced by the fern-feeding *Tortrimosaica polypodivora* (Tortricidae) (Brown et al. 2004) on the stems of *Microgramma squamulosa* (Polypodiaceae) (Kraus et al. 1993), show alterations in the distribution of the vascular bundles, which present lateral expansions, forming bridges between neighboring meristeles. The medullary region is consumed by the larva, up to the immediate area of the vascular cylinder. The galls induced by an unidentified Lepidoptera on pedicels of *Byrsonima sericea* (Malpighiaceae) form a large larval chamber and alters basically the ground system with the differentiation of a lipid rich nutritive tissue (Vieira and Kraus 2007) (Fig. 2.3). The knowledge on the anatomical development of coleopteran and lepidopteran galls in the Neotropics deserves more studies.

Finally, the galls induced by Hymenoptera and Diptera are amongst the most complex structures, with largest tissue specialization. They generally have different concentric zones around the larval chamber. These zones are formed by true nutritive tissues which nourish the insects, surrounded by sclerified layers that confer mechanical protection, parenchymatic cortices which storage water and nutrients,

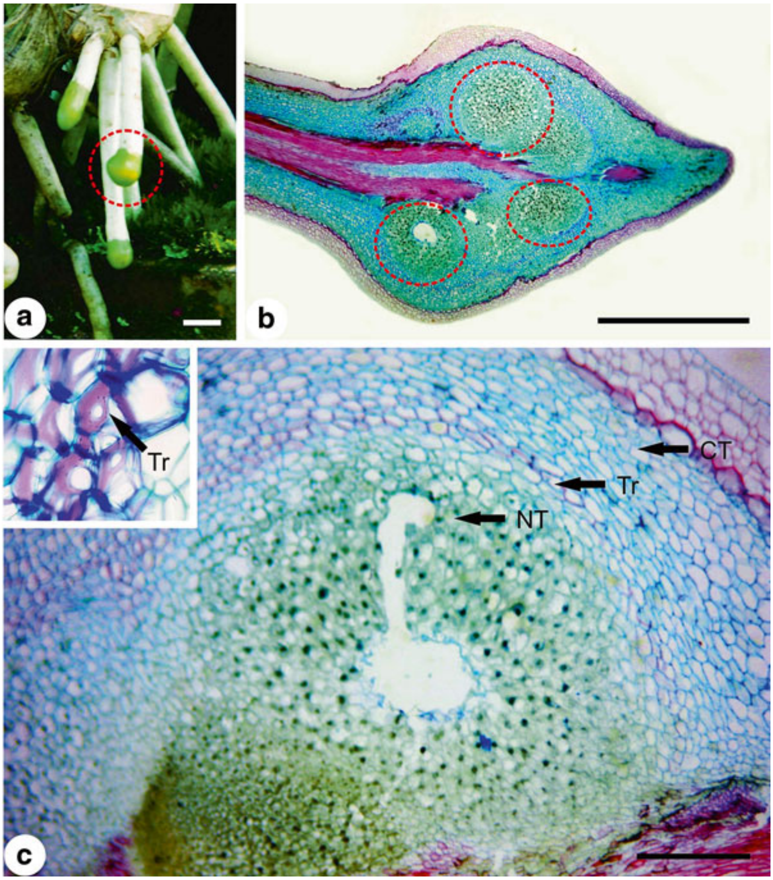

Fig. 2.4 Galls induced by *Calorileya nigra* (Hymenoptera: Chalcidoidea) on the roots of *Cattleya guttata* (Orchidaceae). (**a**) Macroscopic aspect of the attacked root apex (*dotted circle*). (**b**) General view of a longitudinally sectioned root apex with many inducers (*dotted circles*). Concentric tissue zones develop around the numerous larval chambers, each one with a single insect. (**c**) Detail of the concentric zones formed around the larval chamber, namely nutritive tissue, tracheoidal cells (in detail, *upper box*) and cortical tissue. *CT* cortical tissue, *NT* nutritive tissue, *Tr* tracheoidal cells. Bars: (**a**) = 1 cm, (**b**) = 0.5 cm, (**c**) = 500 µm

and an epidermal layer with different degrees of alterations (Mani 1964). Kraus and Tanoe (1999) presented one of the rare studies on the development of a hymenopteran gall from the Neotropics. This model deals with galls induced by *Calorileya nigra* (Hymenoptera: Chalcidoidea) on roots of *Cattleya guttata* (Orchidaceae). The galling insects attack the root apex, which swells due to prominent cell hypertrophy, and also tissue hyperplasia. Concentric tissue zones develop around the numerous larval chambers, each one with a single insect larva. All the other cortical layers are similar to those of the non-galled host organ, and the development of tracheoidal cells (Fig. 2.4), typical of Orchidaceae, is maximized. This is a good example of the manipulation of plant potentialities by the inducing agent. According to the authors, the tracheoidal cells may provide mechanical support, water intake and storage, which certainly improve the quality of the gall to its inducing agent. Kraus et al. (2002) studied a leaf gall on *Struthanthus vulgaris* (Loranthaceae) induced by an unidentified species of Hymenoptera with profound structural alterations. This gall hosts several inducing larva, each one in a chamber, and all three tissue systems are altered. The complexity of these two gall systems fit the proposal of Rohfritsch (1992) for the complex Hymenoptera (Cynipidae) gall models.

As galls represent species-specific relationships, and the large estimated number of galling herbivores around the world reaching 130,000 species (Espírito Santo and Fernandes 2007), a lot is yet to be revealed. The variability of gall structures, in color, shape and indumentum are strictly dependent on the morphogenetic capabilities of the host plant organs. It means that the probable number of different gall morphotypes can be as large as or even larger than the diversity of the gall-bearing plants around the world. The development of each morphotype is unique, occurring under the influence of the herbivore, but constrained by the morphogenetic forces imposed by the host plant.

2.3 The Morphogenetical Forces That Define Gall Morphotypes

The diversity of gall structures found in nature is the result of specific events occurred due to the interference imposed by the gall inducing agent on the standard cell differentiation pattern of its host organ. Through anatomical analysis of each gall morphotype it is possible to check the ways the insects change cell polarity, growth and divisions in different tissue layers, from the meristematic non-galled tissues to the mature phase of the gall (Kraus et al. 2002; Moura et al. 2009; Oliveira and Isaias 2010a; Isaias et al. 2011). The resulting structure forms a *continuum* from the non-galled tissues to the gall, which presents optimized new functions determined by cell redifferentiation (*sensu* Lev-Yadun 2003). If galls are analyzed as multicellular organs whose morphogenesis is under the control of the inducing organism, gall development must be finely regulated and lead to new functions related to the adaptive value of the gall structure to its inducing agent (Price et al. 1987; Stone and Schönrogge 2003). The control over cell lineages significantly alters the patterns of cell division and expansion (Baskin 2005) in different tissue layers of the galls. In addition to the functional perspective, the subversion of conservative developmental patterns such as cell differentiation must involve differential morphogenetic forces that lead to the formation of the new organs, the galls.

It is considered that by the time the plant cells come into contact with the gall inducing organism, a set of cell responses is triggered. The plants initiate a highly dynamic chemical battle with the recognition of the insect secretions and the consequent metabolic responses of the injured plant cells. These responses can lead either to hypersensitive responses (HR) or to gall formation (Isaias and Oliveira 2012).

In the first case, the cells are isolated by a halo of phenolics (Fernandes et al. 2000), and in the latter, the process can give rise to a whole new organ. The machinery of the cell responsible for its structure and functionality undergoes deep alterations which affect cell elongation, the key-point for the establishment of a plant organ morphogenesis (Obroucheva 2008).

Cell elongation is controlled by the physical properties of cell walls. The patterns in which cell wall polysaccharides are deposited are directly related to the final shape of each cell type (Carpita and Gibeaut 1993; Taiz and Zeiger 2010). In other words, cellulose microfibrils disposition is essential for the determination of the direction and extent of cell expansion. The deposition of this polysaccharide, in turn, depends on the internal distribution of microtubules and actin filaments which orient the protein complexes that catalyze the polymerization of cellulose. So, for the cell shape to change on the course of its development there must be a reorientation of the subcellular components that define cell wall architecture (Baskin 2001). From the host leaves to the galls of *Lonchocarpus muhelbergianus* (Fabaceae), the palisade cells turned into isodiametric parenchymatic cells (Isaias et al. 2011), which certainly demanded a reorientation of the microtubules. Other polysaccharides are also important: cross-linking glycans (hemicellulose) bind the cellulose microfibrils and maintain the distance between neighboring microfibrils. The pectins are related to several biological processes during the plant cell wall growth and differentiation such as the increase of elasticity, rigidity and porosity (Albersheim et al. 2011). These processes were firstly analyzed in galls of *Baccharis reticularia* (Asteraceae) and the variation on pectin methyl-esterification indicated the maintenance of the potential for flexibility and elongation during gall development (Formiga et al. 2013). However, other gall systems need to be investigated to corroborate the proposed results.

In order to expand its size, plant cells secrete proteins called expansins, which unlock the network of wall polysaccharides, leading to turgor-driven cell enlargement (Cosgrove 2000). This type of growth is precise and allows specific cell parts and cell types to grow differentially, which was measured in the midrib gall on *Copaifera langsdorffii* (Fabaceae) for the non-galled and the nutritive and storage tissues (Oliveira and Isaias 2010a). This is believed to be crucial for the development of the special shape of the gall, i.e., the morphotypes, and its functionality. Even though microtubules and actin filaments are critical for all modes of cell expansion, their precise roles remain poorly understood. The insect-induced galls may represent models for the study of the cytoskeleton arrangement during cell changes, once the shapes of plant cells are defined by their surrounding walls and are important for their function (*cf*. Smith 2003). Another variable related to cell size is the degree of polyploidy (Kondorosi et al. 2000), which is commonly observed in plants as the result of endoreplication. The association of such physiological and genetic approaches were proposed by Mani (1964) and Meyer and Maresquelle (1983), but remains to be explored during gall development.

More than just altering the cell size, the influence of the galling herbivores alters cell shapes, which can be a response to the mechanical stimuli such as tension and compression of cell walls (Boudaoud 2010). These forces are known to be the triggers that modulate cell division and elongation so as to express different cell shapes in specific cell lineages. During the induction phase of many gall morphotypes, cell hypertrophy is commonly the first visible response on the cells of the host plant organ (Mani 1964; Rohfritsch 1992). The swelling of a small group of cells exerts tension and compression in different cell layers in the mesophyll, leading them to respond differently to this stimulus. This kind of force induces a mismatch in the neighboring cells (Boudaoud 2010) which is translated into fast growing tissues, as it is commonly observed in galls. Also, the differential forces applied to the cells surrounding the site of induction could influence the determination of tissue zonation in galls as well as the redifferentiation of vascular tissues.

Plant primary vascular cells originate from procambium, which according to Fukuda (2004) are vascular stem cells. The maintenance and differentiation of procambial cells are regulated by signaling molecules such as peptide TDIF (tracheary element differentiation inhibitory factor) and hormones as auxin, cytokinin, brassinosteroids and xylogen (Fukuda 2004). The overstimulation of procambial activity, as observed in the valves of the galls induced on *Lonchocarpus muhelbergianus* (Isaias et al. 2011), requires an intercellular and intracellular signaling followed by changes in cell shape which is controlled by a fundamental and continuous interaction between cell wall and the microtubules (Lloyd et al. 2000). The developmental studies of some Neotropical gall systems proceed so as to document such morphogenetical processes as key elements of each species-specific system and the generated morphotypes.

2.4 Revisiting the Neotropical Gall Morphotypes

Gall morphogenesis follows an integrative system of host plant-galling organism genotypes, modulated by the environment, and culminating in a whole new plant phenotype (Abrahamson and Weiss 1997). As a general pattern, galls are integrative parts of their host organs, as the intralaminar leaf galls (Fig. 2.5a), which may photosynthesize and contribute to the development of the gall structure itself (Oliveira et al. 2011a). Others, as the extralaminar ones (Fig. 2.5b) behave as new structures, adjacent to the non-galled host tissues and may differentiate through specific patterns.

An interesting example of an intralaminar gall which has been the focus of studies in the Neotropics is the one induced by a Pseudophacopteronidae on the leaves of *Aspidosperma australe* (Apocynaceae) (Oliveira and Isaias 2010b; Oliveira et al. 2011a). This gall is predominantly parenchymatic, with the vascular tissues concentrated at the top of the nymphal chamber. It also has two distinct tissue zones, inner and outer cortices distinguishable by cell size, shape and metabolic activity (Oliveira and Isaias 2010b). The anatomical sections of this gall revealed that the chlorophyllian tissues were limited to the outer cortex, away from the larval chamber. As extralaminar examples, the horn-shaped (Oliveira et al. 2011b) and the

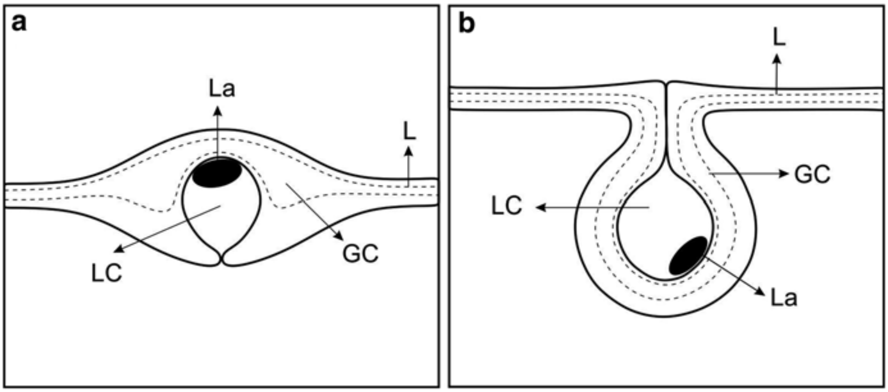

Fig. 2.5 Schematic representation of the cross section of intralaminar leaf gall of *Aspidosperma australe* (Apocynaceae) (**a**) and extralaminar leaf gall of *Psidium myrtoides* (Myrtaceae) (**b**). *Dotted lines* represent different cell lineages in a continuum between non-galled leaf tissues and gall tissues. *GC* gall cortex, *L* leaf tissues (non-galled), *La* larva, *LC* larval chamber

cup-shaped galls (Oliveira et al. 2008) are good models for developmental studies. They are induced on the leaflets of *Copaifera langsdorffii* (Fabaceae) by two distinct unidentified species of Diptera: Cecidomyiidae. Both of these galls initiate in intralaminar position and assume the final extralaminar position by distinct degrees of cell redifferentiation. These galls have a site of contact with their host lamina maintained by a narrow vascularized peduncle. This peduncle sustains parenchymatic structures developed by cell hypertrophy and tissue hyperplasia. In plant galls, hypertrophy and hyperplasia are constant phenomena and seem to occur mainly in response to the feeding activity of the galling herbivores (Arduin et al. 1991; Kraus et al. 1996, 2002; Oliveira and Isaias 2009, 2010a; Moura et al. 2009; Sá et al. 2009; Isaias et al. 2011). The topographical relationship of the gall with its host leaves may be similar for host stems and roots, forming a *continuum* between non-galled and galled tissues. The host plant–galling herbivore systems studied in the Neotropics have some peculiar features other than gall position in relation to the host organ. In the dermal system, while functional stomata are rare, the over-differentiation of trichoblasts is a common effect (Moura et al. 2008; Sá et al. 2009). According to Glover (2000), the default genetic program does not seem to be the epidermal pavement cells and the reducing or increasing in number of specialized cells may be consequence of gene inactivation or even different states of the same genetic possibilities.

The alterations in the epidermal cells due to gall formation are the evidence of the influence of the herbivore over cell capabilities. For instance, regular pavement cells may be replaced by suberized cells forming an atypical periderm such as in the spherical gall on *Struthanthus vulgaris* (Loranthaceae) (Kraus et al. 2002) and *Copaifera langsdorfii* (Fabaceae) (Oliveira et al. 2008). In the stem galls formed during the diapause period on *Rollinia laurifolia* (Annonaceae), periderm differentiation is inhibited just below the insect's body as a strategy to the maintenance of its feeding site (Gonçalves et al. 2009). Metacutinization may occur conferring protection against desiccation as observed in galls on *Aspidosperma spruceanum* (Apocynaceae) (Formiga et al. 2011), and in the midrib galls on *Copaifera langsdorffii* (Oliveira and Isaias 2010a). Also the nutritive tissue, which varies in number of cell layers, shape and content, may differentiate from the epidermal cells and the adjacent layers lining the larval chamber. In *Lantana camara–Schismatodiplosis lantanae* (Moura et al. 2009) and in *Lonchocarpus muhelbergianus–Euphalerus ostreoides* systems (Isaias et al. 2011), the larval chamber is unique and shelters one larvae, but some systems may have multiple chambers bearing one or several larva per chamber. The hymenopteran galls on *Cattleya guttata* (Kraus and Tanoe 1999) and on *Struthanthus vulgaris* (Kraus et al. 2002) have many chambers with one inducer per chamber. The fruit galls on *Eugenia uniflora* (Myrtaceae) are multi-chambered, but also with a single insect per chamber, which seems to be a conservative but not exclusive pattern (Fernandes et al. 2012).

The major alterations leading to the variety of gall morphotypes are related to the ground system. The most common of these alterations is observed in leaf galls where the early determined photosynthetic cells are transformed into reserve ones, and consequently the chloroplasts differentiation may be blocked. This blockage may occur by the time that the plastids are proplastids and not yet fully differentiated, but can also occur in mature cells, where the transformation is more drastic. During cell development, proplastids differentiate into particular plastid types according to the cell in which they reside (Pyke 1999). The well-established and constant relationship between chloroplast number and mesophyll cell during its expansion (Lamppa et al. 1980; Ellis and Leech 1985; Pyke and Leech 1992) is broken during gall cortex differentiation. So, the new functional design of these cells seems to be determined by the vacuole expansion and the new sort of accumulation denotes the triggering of molecular mechanisms not active in normal host leaf morphogenesis. Some authors (e.g., Leech and Pyke 1988; Cookson et al. 2003) have also proved that the controlled relationship between cell expansion, and the replication and expansion of plastids can be perturbed and that they initiate division in cells undergoing rapid expansion.

In galls, instead of differentiating into chloroplasts, these newly formed plastids turn into amiloplasts, for instance. In the *Lantana camara–Schismatodiplosis lantanae* system, the gall parenchyma is divided into three zones: (1) hypertrophied cells surrounding the nutritive tissue, (2) hypertrophied spongy parenchyma cells with few chloroplasts and conspicuous intercellular spaces occupying the majority of gall cortex, and (3) a one-layered palisade parenchyma just below the adaxial epidermis (Moura et al. 2008). In *Aspidosperma spruceanum* gall, the differentiation of spongy parenchyma is potentialized, forming the cortex external to the mechanical and nutritive layers (Oliveira et al. 2010; Formiga et al. 2011). In the *Lonchocarpus muhelbergianus–Euphalerus ostreoides* system, the parenchymatic cells of the outer layers accumulate a great amount of amiloplasts (Oliveira et al. 2006), and expanding in all directions, whereas those of the inner layer

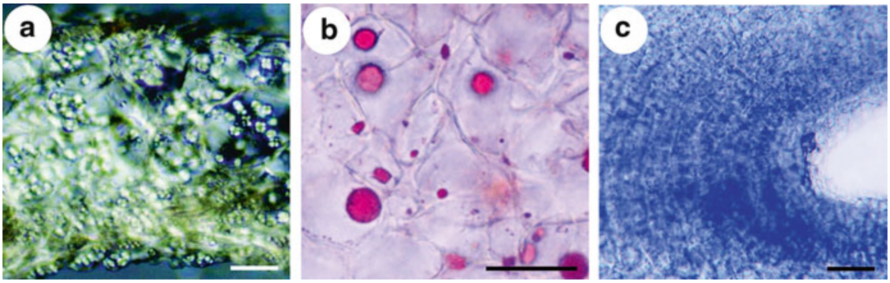

Fig. 2.6 Detection of (**a**) starch (Polarized Light – *bright spots*) in the globoid leaf gall on *Machaerium nyctitans* (Fabaceae); (**b**) histochemical detection of lipids (Sudan III – *red droplets*) in globoid leaf gall on *Psidium myrtoides* (Myrtaceae) and (**c**) proteins (Coomassie blue – *blue precipitate*) in lenticular leaf galls on *Aspidosperma australe* (Apocynaceae). Bars = 25 μm

expand minimally (Isaias et al. 2011). The pattern observed here is cell hypertrophy, even though the direction of cell elongation is distinct, which determines the final shape of the gall.

Either hypertropic or hyperplasic tissues may accumulate primary and secondary plant metabolites that may be identified and topographically observed through phytochemical and histochemical methods (Fig. 2.6). The contents of soluble phenols, tannins, lignins, fiber, carbohydrates and lipids, for instance, were significantly higher in the leaf gall on *Tibouchina pulchra* (Melastomataceae) than in non-galled tissues (Motta et al. 2005). The roles of such substances in gall structure are either related to plant defenses against herbivore attack or to the allocations of nutritive metabolites that ensure the nutrition of the gall inducer and the gall structure itself.

The vascular system is considered to be of major importance for gall development and its adaptive value for the galling herbivore. However, it is the most difficult of the three plant systems to be analyzed. In galls, it generally consists of small collateral bundles systematically positioned, as in the *Lantana camara*–*Schismatodiplosis lantanae* (Moura et al. 2009), *Bauhinia brevipes*–*Schizomyia macrocapillata* (Sá et al. 2009), and *Lonchocarpus muehlbergianus*–*Euphalerus ostreoides* systems (Isaias et al. 2011), and may be redifferentiated from parenchyma cells. The hyperplasia of vascular parenchyma is common either on hymenopteran (Kraus et al. 2002) or on dipteran galls (Arduin et al. 1991) on *Struthanthus vulgaris* (Loranthaceae). The new formation and distribution of vascular tissues in galls are crucial for the intake of water and nutrients which directly affects gall development and herbivore maintenance.

The ontogenetical and anatomical examination of the distinct gall morphotypes in the Neotropics have revealed that the final gall shape requires a new spatial and developmental control over the host plant cells planes of division and expansion. Also, cell redifferentiation must occur redirecting the host plant potentialities and constraints, which occur under the influence of the galling herbivore. Within this approach resides the key for the understanding of the generation of cell shapes and functions which prompt the galls as excellent models for developmental studies.

2.5 Chemical Bases of the Interaction

The knowledge on the structure of Neotropical galls has been complemented with some chemical evaluations. It is assumed that the galling insect manipulates the metabolism of the host plant to promote nutritional quality and the accumulation of defensive compounds (Hartley and Lawton 1992; Motta et al. 2005). Around the larval chamber, nutrients are increased but chemical defenses are normally decreased. The concentrations of secondary metabolites are generally lower in the galled tissues when compared with non-galled ones (Larew 1992; Cornell 1983; Formiga et al. 2009; Detoni et al. 2010). Price et al. (1987) have proposed that the gall serves as a shelter from plant defenses and a rich food source for the gall inducing agent.

The chemical content of the host plants may be crucial for the choice of the sites of oviposition. Susceptible plants may develop galls while resistant ones should present hypersensitive (HR) responses, for instance. Plants of *Bauhinia brevipes* (Fabaceae) were used to evaluate this premise through their nutritional quality and the potential responses to the galling herbivore *Schizomya macrocapilata* (Diptera). The protein fractioning by SDS–PAGE and silver-staining showed common and/or specific polypeptides between the resistant and susceptible plants. The results suggest that the galling larva are able to overcome the resistance barriers of their host plant, and induce the formation of a gall both on the susceptible and resistant host plants, but these galls are distinct regarding the protein metabolism. The higher protein concentrations in susceptible plants are possibly associated with the higher susceptibility to gall formation (Detoni et al. 2011a).

The decrease of plant defenses in gall sites is consequence of the balance between the investment in defense and growth (Herms and Mattson 1992). Defensive compounds, such as the phenolics, have been evaluated either histochemically or phytochemically (Bronner 1992; Cornell 1983; Hartley 1998; Motta et al. 2005) in gall tissues. The results have shown that their role may not be constant along the gall cycle, because the contents vary along the year, depending on environmental conditions such as water stress and light radiation (Formiga et al. 2009; Detoni et al. 2011b). Consequently, the phenolics based chemical defensiveness of gall structure may be absent or even reduced during part of the cycle. Histochemical analyses have shown the presence of phenolic substances, and also alkaloids, tannins, and flavonoids, mainly in the gall outer cortex (Carvalho et al. 2005; Oliveira et al. 2006; Moura et al. 2008). While alkaloids and tannins may be related to chemical defenses, flavonoids are believed to be signalers for host plant selection, or even protective substances against UV radiation as proposed by Oliveira et al. (2006) for the *Euphalerus ostreoides* (Hemiptera)–*Lonchocarpus muelhbergianus* (Fabaceae) system. The role of these secondary metabolites as preventing oxidative stress was discussed by Detoni et al. (2010) on *Calliandra brevipes*–*Tanaostigmoides ringueleti* and *T. mecanga* (Hymenoptera) systems, which suggests that the chemical interactions surpass the taxonomical level and may be similar in systems involving distinct *taxa* of galling herbivores.

The cytological and biochemical features of the nutritive tissues are peculiar and the determination of these characteristics is essentially dependent on the *taxon* of the galling herbivores (Bronner 1992). According to this author, the Diptera induce the accumulation of carbohydrates, while the Hymenoptera induce the accumulation of lipids on the nutritive tissues of their galls. These taxonomic based relationships have been extended to other sucking and chewing insects with similar results, i.e., carbohydrates accumulated in galls induced by Hemiptera (Oliveira and Isaias 2010b) and lipids accumulated in galls induced by Lepidoptera (Motta et al. 2005; Vieira and Kraus 2007). In general, the nutritional quality of gall tissues is improved, as reported by Detoni et al. (2010) for the accumulation of carbohydrates in the galls induced by two species of *Tanaostigmodes* (Hymenoptera) on *Calliandra brevipes* (Fabaceae). In these systems, the fructose content of the galled tissues is two-fold higher than that of the non-galled ones, either for *C. brevipes–Tanaostigmodes ringueleti* or *C. brevipes–T. mecanga*. These results show that even though the nutritive tissues accumulate lipids, the general nutritional content of the galls may involve other metabolites.

The contents of carbohydrates were evaluated in other Neotropical gall systems, and the best nutritive quality of gall tissues was reinforced. The nutrient contents in gall tissues were also higher than those of the respective non-galled ones in two species of *Aspidosperma* (Apocynaceae) (Campos 2011). The metabolism of carbohydrates is important either for the galling herbivore establishment or for gall development, once sugars are regulators of plant gene expression (Koch 1996), cell division and maturation. These aspects depend on the enzyme activities in the cecidogenetic field, as proved by Oliveira et al. (2010), and Oliveira and Isaias (2010b) by the evaluation of the enzymatic activity involved in sucrose, glucose and fructose metabolism in galls on *Aspidosperma australe* and *A. spruceanum*. When sucrose is cleaved by sucrose synthase, the products are involved in tissue maturation and starch storage (Koch and Zeng 2002), i.e., nutritional quality of the gall tissues, while when the process is mediated by invertase, the products are involved in cell respiration and division (Oliveira and Isaias 2010b), i.e., gall metabolism.

Another chemical based aspect of the carbohydrates metabolism is the establishment of a source-sink relationship between gall and the host plant tissues. This aspect was investigated in the horn-shaped gall induced by Cecidomyiidae on the leaflets of *Copaifera langsdorffii* (Fabaceae), which accumulate reducing sugars, histochemically detected in the nutritive tissue (Oliveira et al. 2011b). This gall was believed to photosynthesize in such a level that should compensate its large increment in mass. Nevertheless, Castro et al. (2012) has proved that water soluble polysaccharides and total soluble sugars are stored in gall tissues as a consequence of the sink strength rather than gall photosynthetic rates.

Sugars as well as proteins accumulate in gall tissues mainly around the larval chamber, a site of high cell metabolism (Schonrögge et al. 2000; Oliveira and Isaias 2010b; Oliveira et al. 2010). Some specificity of these two classes of metabolites has indicated other levels of chemical interactions in such special gall tissues. The nutritive tissue of the galls induced by Hymenoptera: Cynipidae on *Quercus* accumulates a specific protein, the formate dehydrogenase (FDH). The presence of this protein indicates high respiratory stress, and reinforces the observations for the galls on *Aspidosperma australe* (Oliveira and Isaias 2010b), on *A. spruceanum* (Oliveira et al. 2010), and on *Lonchocarpus muhelbergianus* (Isaias et al. 2011), where ROS accumulation was histochemically detected.

Histochemical, chromatographic and spectroscopic analyses may elucidate several aspects of the chemical interactions necessary for the establishment of the galling herbivore as well as the development of their galls. The qualification and quantification of primary and secondary metabolites in gall tissues are excellent tools for the understanding of gall-inducing feeding behavior and the whole metabolism of gall tissues.

2.6 Conclusions and Remarks

Galling insects are capable of altering the structure and chemistry of their host tissues for the establishment and development of their galls through mechanical and chemical stimuli. In addition to these stimuli, the physical forces generated by turgor pressure, cell wall resistance, patterns of cell division and elongation are important for the determination of the variety of gall morphotypes. Also molecule signaling is crucial for gall development, even though the process that triggers the alterations is yet to be elucidated. Efforts have been done to trace the cascade of events, probably starting with the generation of ROS, passing through the accumulation of phenolic derivatives and their influence on the indol-acetic acid metabolism. It should remain clear that cellular and subcellular alterations observed in plant galls are strictly dependent on the gall inducing agents and their host plants. So, much is yet to be done in the field of anatomy and biochemistry of plant galls to set reliable patterns of cell dynamics towards the determination of gall morphotypes. Such variety of shapes constitute elegant models to address these questions and will generate relevant knowledge on the morphogenesis of plants under the influence of the biotic agent – the galling herbivore.

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Chapter 3
Functional Gradients in Insect Gall Tissues: Studies on Neotropical Host Plants

Denis Coelho de Oliveira, Ana Silvia Franco Pinheiro Moreira, and Rosy Mary dos Santos Isaias

Abstract The first mechanism by which the insect recognizes its host plant was not elucidated yet. Once the induction occurs, the plant, in general, responds by the redifferentiation of tissues with typical features and functions of a new organ. These tissues may guarantee adaptive advantages to the galling insect against natural enemies, microenvironmental stresses, and also provide adequate nutrition. Moreover, the formation of the final gall body, i.e., its morphological design, is directly related to the formation of the tissues of the gall. This is especially true for the reserve tissue or the outer cortex, and the nutritive tissue or inner cortex. Interesting questions to be addressed are how these tissues differentiate, and whether cytological and histochemical gradients are developed in galls. In fact, these gradients seem to occur in the majority of the galls, and their formation may be related to the formation of reactive oxygen species (ROS) since the onset of the interaction.

Keywords Morphological evidences • Cellular responses • Photosynthesis in galls • Adaptive hypothesis • Plastoglobuli • Oxidative stress

3.1 Introduction

Plant tissues can react promptly to external abiotic and biotic stimuli by changing its morphogenesis. One of the major biotic factors that alter the morphogenesis of plants is the galling stimuli, which acts on plant tissues in which the inducers may feed and seek for shelter (Mani 1964; Shorthouse and Rohfritsch 1992). The development of

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the galls involves active redifferentiation of the host plant cells leading to the formation of new cells and tissues whose characteristics and functions are typical of a new organ, the gall (Mani 1964; Lev-Yadun 2003; Oliveira and Isaias 2010a, b). The molecular mechanisms that lead to the formation of galls have not been elucidated yet. However, proposals dating back to more than 40 years suggest that secretions injected during oviposition or during the feeding habit of the larva can trigger the development of the abnormal tissues (Shorthouse and Rohfritsch 1992; Higton and Mabberly 1994). However, the exact mode of action of these secretions remains unknown (Stone and Schönrogge 2003; Maffei et al. 2007). On the other hand, host plants signaling molecules such as auxins, cytokinins, amino acids and proteins have been proposed to be responsible for the formation of the galls (Shorthouse and Rohfritsch 1992). In general, the galling herbivore can use molecular signals similar to those normally used in plant metabolism (Shorthouse and Rohfritsch 1992; Abrahamson and Weiss 1997; Detoni et al. 2011). The lack of knowledge on the exact origin of the molecules involved in gall development makes it difficult to design experiments to follow the biochemical pathways during gall formation not only in the quantitative but also in the qualitative basis. Once the morphogenetical patterns of the host organs have been currently elucidated, comparative studies on the ontogeny of the galls and their host organs, with the documentation of the stimuli and response mechanisms, may provide relevant clues about the role of the galling herbivores on the formation of the new organ. The direction of cell divisions and elongation is indicative of the direction of the cecidogenetic field (Mani 1964; Oliveira and Isaias 2010a), and therefore may indicate metabolic and functional gradients in the galls. Histochemical analysis can also configure excellent tools for studies of functional gradients, especially in the detection of primary metabolites, and reactive oxygen species (Bronner 1992; Nyman 2000; Isaias et al. 2011; Oliveira et al. 2011a).

In this chapter, we present some Neotropical gall systems and discuss the signaling mechanisms which may lead to gall development, and the formation of cytological and histochemical gradients in their tissues; it also proposes the reactive oxygen species (ROS) as the main signaling molecules for gall induction and development. These molecules take part in the determination of the final body of the gall, i.e., they are responsible for the diversity of gall morphotypes found in nature. Finally, this study discusses the photosynthesis role in gall tissue.

3.2 Hypotheses for the Adaptive Value of the Gall for the Galling Herbivore: Morphological Evidences

Three main hypotheses have been discussed on the adaptive value of the gall to the galling herbivore: the microenvironment, the natural enemy, and the nutritional one. The first one establishes that gall tissues protect the herbivore against unfavorable environmental conditions such as desiccation and increasing in temperature (Price et al. 1987; Crespi and Worobey 1998; Whithan 1992; Danks 2002; Fernandes and Price 1992; Stone and Schönrogge 2003), which has been associated with various

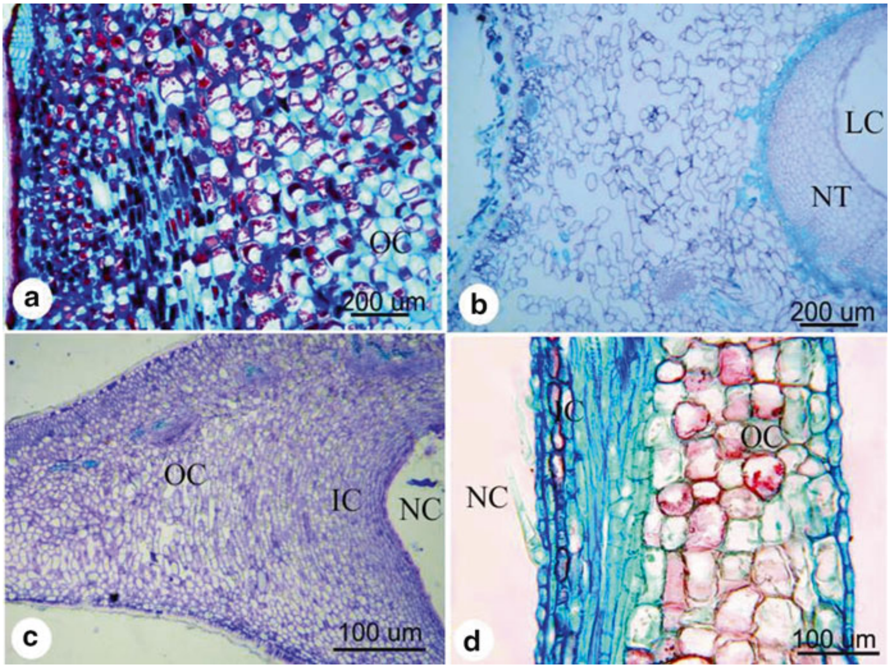

Fig. 3.1 Anatomy of galls. (**a**) *Copaifera langsdorffii* (Fabaceae) – horn-shaped gall induced by Cecidomyiidae; (**b**) *Aspidosperma spruceanum* (Apocynaceae) – Cecidomyiidae systems, detail of cellular spaces in the gall parenchyma and the formation of nutritive tissue (*NT*) near the larval chamber (*LC*); (**c**) *Aspidosperma australe– Pseudophacopteron* system, a sucking gall, there are a histological gradients from outer cortex (*OC*) to inner cortex (*IC*) near to nymphal chamber (*NC*); (**d**) *Lonchocarpus muelhbergianus* (Fabaceae) – *Euphalerus ostreoides* (Psyllidae), the cells of outer cortex are higher than inner cortex

anatomical and morphological characteristics of the galls. In general, the redifferentiation of trichomes on the edge of the galls opening, and the deposition of cuticle may prevent excessive loss of moisture in the chamber, and therefore help to maintain the internal temperature (Kraus et al. 2002; Stone and Schönrogge 2003; Oliveira et al. 2006; Moura et al. 2008, 2009; Oliveira and Isaias 2010a). The presence of papillose epidermal cells covered with thick cuticle, and periderm formation are also features commonly reported as mechanisms for controlling humidity and temperature in leaves (Fahn 1990; Woodman and Fernandes 1991; Gutschick 1999; Press 1999). Similarly, these characters can control the humidity and the temperature inside the gall chamber. Another important gall anatomical feature is the homogenization of the parenchymatic cells in addition to their hypertrophy (Fig. 3.1), the presence of numerous vacuoles with accumulation of water, and few intercellular spaces (Kraus 2009; Oliveira and Isaias 2010b), which are also interpreted as mechanisms to prevent excessive loss of water (Sack and Holbrook 2006; Kraus 2009). However many intercellular spaces can occur in gall tissue (Fig. 3.1). Generally, the tissues which maintain a favorable microenvironment inside the galls line the outer cortex, externally.

According to Price et al. (1987), Fernandes and Price (1992) and Stone and Schonrögge (2003), the main force that modulates gall diversity is the selective pressure imposed by natural enemies. This hypothesis postulates that the tissues of the galls may protect the inducer against its natural enemies, and are in addition, advantageous when the galling herbivores are compared to their free living ancestors. Moreover, morphological and anatomical features, such as the increasing in lignified tissues (Fig. 3.1) (Rohfritsch 1992; Kraus et al. 2002; Stone and Schönrogge 2003; Oliveira et al. 2006, 2008; Oliveira and Isaias 2009, 2010b), and in gall thickness due to cell divisions, as well as the development of trichomes (Rohfritsch 1992; Stone and Schonrögge 2003; Kraus 2009; Oliveira and Isaias 2010a) are considered protective mechanisms against natural enemies (Price 1987).

The nutritional hypothesis postulates that the galling herbivore manipulates host plant tissues in order to guarantee feeding resources, which is sustained by cell redifferentiation and the development of a tissue rich in nutrients when compared to non galled ones, the nutritive tissue. According to Bronner (1992), the nutritive tissue generally occurs around the larval chamber of galls induced by Cecidomyiidae (Fig. 3.1) and Cynipidae, but a storage tissue has been detected in galls induced by sucking insects (Oliveira et al. 2006; Álvarez et al. 2009; Oliveira and Isaias 2010b). The differentiation of such a specialized tissue is evidence of a strong alteration in host plant morphogenesis, with consequent impact on the diversity of gall morphotypes. This diversity has been explained by Stone and Schönrogge (2003) as mainly influenced by the enemy hypothesis, which is also plausible. Even though, phloem feeders do not feed directly in the tissues around the nymphal chamber, the galling insect injuries plant cells. Due to these injuries, cytological and physiological gradients are established, generating the cecidogenetic field (Mani 1964; Shorthouse and Rohfritsch 1992; Oliveira and Isaias 2010b; Oliveira et al. 2010, 2011a, b), and consequently the formation of the gall final body. The functional gradient towards the nymphal chamber was proved by cytological and histochemical analyses performed in a sucking insect induced gall (Oliveira and Isaias 2010b). These analyses may configure appropriate tools for the comprehension of the relationships between the feeding habit of the galling herbivore and the final gall shape related to all taxa of gall inducers. The final gall shape was related to the feeding pattern of the galling herbivore (Rohfritsch 1992). Nevertheless, this assumption does not explain, per se, the great diversity of shapes found in nature, once galling herbivores with similar feeding habit induce completely distinct gall morphotypes. Supposedly the physiology of host plant cells plays a fundamental role in the definition of the morphology of the galls.

3.3 Cytological and Histochemical Features of the Nutritive Tissue

In general, the nutritive cells of galls induced by Cecidomyiidae and Cynipidae are characterized by abundant cytoplasm, vacuole, hypertrophied nucleus and nucleolus, numerous cytoplasmic organelles, high enzymatic activity, RNA richness, and the accumulation of carbohydrates (Bronner 1992). This author also proposed that in galls induced by Cecidomyiidae, there is no formation of a cytological gradient, but an accumulation of starch in the outer cell layers, and of sugars in the inner cell layers. In galls induced by Cynipidae, a cytological gradient and accumulation of lipids occur.

Together with the cytological features, biochemical and histochemical alterations are conditioned to the cecidogenetic field imposed by the gall inducer (Mani 1964; Bronner 1992). Independently of their feeding habit, a histochemical gradient can be established during all the phases of gall development (Bronner 1992; Moura et al. 2008; Oliveira et al. 2010, 2011b; Oliveira and Isaias 2010a, b). Such a gradient related to the oxidative stress generated by the galling herbivore can be either centripetous or centrifugous, because of the influence of the insect's and host plant's cell respiration (Fig. 3.2).

3.3.1 Cecidomyiidae Systems

As long as the researches evolve in the Neotropics, some systems which do not follow the pattern proposed by Bronner (1992) have been revealed. Galls induced by *Schismatodiplosis lantana* (Cecidomyiidae) on *Lantana camara* (Verbenaceae) accumulate lipids in the nutritive tissues (Moura et al. 2008), while the ones induced by an unidentified species of Cecidomyiidae on *Aspidosperma spruceanum* (Apocynaceae) accumulate starch in the outer layers of the proper nutritive tissue (Fig. 3.2b). In this gall and in the horn-shaped galls on *C. langsdorffii*, the more internal cells of the nutritive tissue are protoplast free in the initial phases of gall development, which denotes a process of cell death previously reported for galls induced by *Mayetiola destructor* (Diptera: Cecidomyiidae) on *Triticum aestivum* (Poaceae) (Harris et al. 2006). The horn-shaped and the midrib galls induced by unidentified species of Cecidomyiidae on *Copaifera langsdorffii* (Fabaceae) accumulated starch in the reserve tissue, and reduced sugars in the nutritive one (Oliveira et al. 2011a).

There are some common metabolic features between the nutritive tissues of insect galls which have been currently investigated. High amylase activity, invertase, glucose-6-phosphatase, phosphorilase, acid phosphatases, and a decreasing gradient of starch establishes towards the larval chamber. Another enzyme, the sucrose synthase together with the invertases, may help in comprehending the metabolism of the galls. The sucrose synthase catalyzes the reversible breakdown of sucrose in fructose and UDP-glucose, taking part in the main processes which involve the maturation of organs, accumulation of starch, and synthesis of callose (Koch 2004; Asano et al. 2002; Salnikov et al. 2003; Subbaiah and Sachs 2001), and diverse polysaccharides of the cell wall (Doblin et al. 2002). The invertases catalyze the irreversible reaction of sucrose to glucose and fructose, and its activity is associated to strong physiological sinks (Koch 1996; Koch and Zeng 2002). The formation of sites of cell division, expansion, and respiration is associated to the high activity of

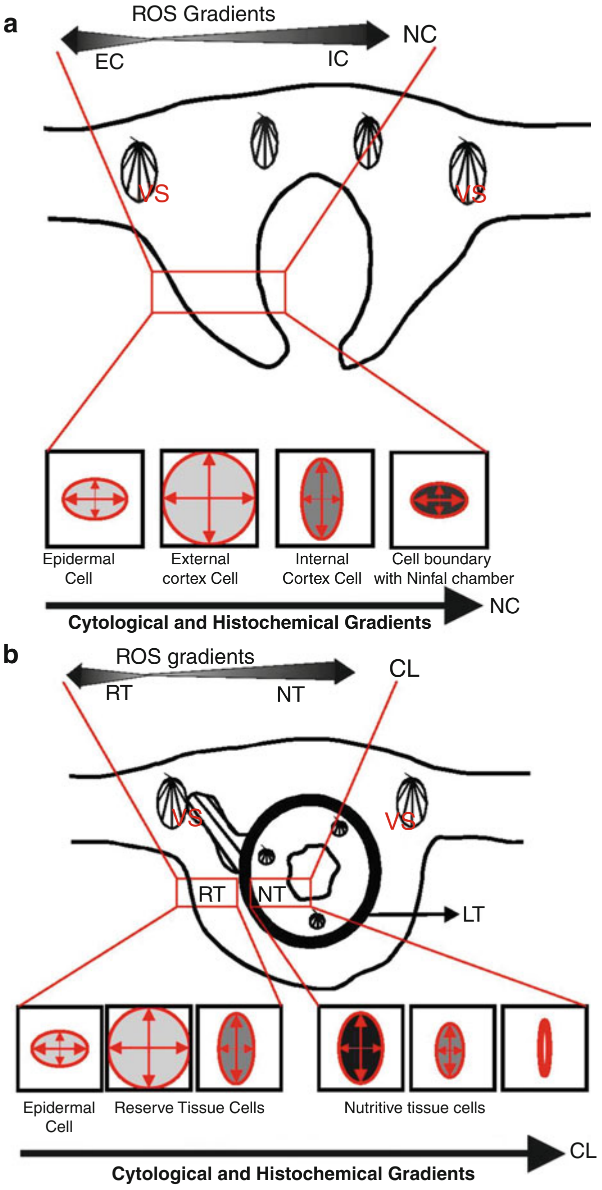

Fig. 3.2 Schematic representation of the cytological and histochemical gradients, and of the reactive oxygen species (*ROS*) established in galls of *Aspidosperma australe* (Apocynaceae) (**a**) and *Aspidosperma spruceanum* (**b**). The cytological and histochemical gradients occur towards the larval chamber, and are indicated by the differences in size and direction of cell growth (represented by the *red circles* inside the *squares*), the intensity of color indicate de accumulation of nutrients, i.e., the more intense the color, the higher the metabolism and the accumulation of nutrients are. The distinct degrees of cell hypertrophy are represented by *circles* inside the *squares*, the thickness of the *arrows* indicate the main axis of cell elongation. The gradient of ROS occurs along the tissues of the gall, being more intense in the cell layers next to the larval chamber and to the outer cortex. *LC* larval chamber, *ROS* reactive oxygen species, *VS* vascular bundles, *NT* nutritive tissue, *RT* reserve tissue

invertases (Koch 2004). The breakdown of sucrose by the invertases take part in the biosynthesis and signalizing of hormones, such as ABA, IAA and cytokinins (Koch 2004; Wachter et al. 2003). Bronner (1992) demonstrated the importance of the activity of these enzymes for the accumulation of nutrients in the nutritive tissue of galls induced by Cynipidae and Cecidomyiidae.

In *A. spruceanum*-Cecidomyiidae system, the activity of sucrose synthase may be related to the deposition of callose in the walls of the nutritive tissue cells, facilitating the passage of macromolecules to the cells next to the larval chamber (Oliveira et al. 2010). This function helps the maintenance of the nutritive cells and consequently the development of the gall inducer. The activity of invertases was detected in the tissues next to the larval chamber of this gall, being associated to the high oxidative stress generated by the galling herbivore (Oliveira et al. 2010).

3.3.2 Sucking Insect Systems

Sucking insects, in general, insert their feeding apparatus in phloem cells, with no accumulation of substances and development of reserve tissues (Bronner 1992). In the Neotropical region, the accumulation of reserve substances and the formation of a cytological gradient have been reported for galls induced by sucking insects. Galls induced by *Euphalerus ostreoides* (Psyllidae) on *Lonchocarpus muelhbergianus* (Fabaceae) (Ferreira et al. 1990) present a zonation of tissues similar to that of galls induced by Cecidomyiidae (Mani 1964; Shorthouse and Rohfritsch 1992; Oliveira and Isaias 2010b) but do not differentiate a true nutritive tissue. This gall accumulates starch and lipids in tissues around the nymphal chamber (Oliveira et al. 2006; Isaias et al. 2011). Oliveira and Isaias (2010b) detected cytological and histochemical gradients, as well as starch accumulation in galls induced by *Pseudophacopteron* sp. on *Aspidosperma australe* (Fig. 3.2a). Álvarez et al. (2009) reported the presence of starch grains in galls induced by an aphid on *Pistacia terebinthus*. Thus, the formation of a histochemical gradient and accumulation of starch seems to be a pattern for galls induced by sucking insects. In general, the role of this polysaccharide is related to gall maintenance and not to the feeding habit of the galling insect (Oliveira et al. 2006, 2011a; Oliveira and Isaias 2010b).

In galls on *A. australe* induced by *Pseudophacopteron*, the activity of invertases was related to sites of high respiratory stress and cell division (Oliveira and Isaias 2010b). By the histochemical gradients detected in this gall, either the activity of invertases or sucrose synthase were related to the oxidative stress imposed by the galling herbivore. Maffei et al. (2007) showed the consecutiveness of the events in plant tissues initiated by feeding insects. Immediately after the changes in the V_m at the plasma membrane, and in the $[Ca^{2+}]_{cyt}$, the first detectable molecules are the ROS. Thus, the study of these molecules may set lights on the processes of gall formation. Independently of the focused system, two groups of molecules have been currently addressed in gall tissues, the sugars and the reactive species of oxygen (ROS) (Oliveira et al. 2010, 2011b). Further, a fundamental question is proposed: what are

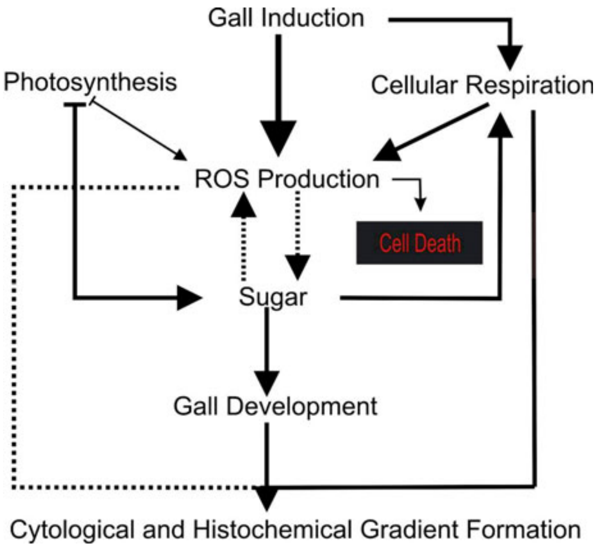

Fig. 3.3 Central position of sugars and ROS in relation to the establishment of the cytological and histochemical gradients in galls. The *black arrows* indicate processes already proposed in literature, and the *dotted arrows* indicate the hypothesis here proposed. The *arrows* indicate positive relationship, *bars* in "T" indicate negative relation

the molecules that initiates and maintains the functionality of the gall? It may be hypothesized that the answer lay on the relation between the production of ROS and that of the sugars (Fig. 3.3) involved in the respiratory metabolism in the inner cortex of the galls.

3.4 The Probable Role of ROS in the Formation of a Cytological Gradient

Due to the presence of a great amount of molecular oxygen in atmosphere, all the living cells are subjected to the reactiveness and toxicity of reduced oxygen species. These ROS, such as the superoxide anion (O_2^-), the peroxide of hydrogen (H_2O_2), the hydroxyl radical (HO.•), and the singlet oxygen ($^1O_2$), are produced either during the fundamental metabolism of the cell or due to abiotic and biotic stimuli (Möller et al. 2007; Couée et al. 2006; Rossel et al. 2002; Pham and Desikan 2009). In the cytological environment, the main producers of ROS are the chloroplasts, peroxisomes, and mitochondria. The chloroplasts produce $^1O_2$ e O_2^- in their photosystems, the mitochondria produce O_2^-, and the peroxisomes produce H_2O_2, which can be converted to HO• (Möller et al. 2007).

The production of ROS by the fundamental metabolism of the cells may trigger important steps during plant development, for instance, the increase in the elasticity of cell walls during cell growth (Bell et al. 2009). However, the ROS can also be capable of oxidizing all the cell components, leading to cell death (Moller et al. 2007), as consequence of an oxidative cascade as part of the immune response of the plant during the first steps of the interaction (Doke et al. 1996; Möller et al. 2007). Nevertheless, the production of ROS is not just related to the defense against the action of another organism, but it may also occur for gene regulation leading to hypersensitive responses, programmed cell death, and the signaling for local cell development (Doke et al. 1996; Möller 2007; Couée et al. 2006; Pham and Desikan 2009; Del Río and Puppo 2009). In this perspective, the action of galling insects can provoke an increase in the production of ROS in plant tissues (Oliveira and Isaias 2010b; Oliveira et al. 2010), which can be directed related to the formation of cytological and histochemical gradients in galls.

Even though Bronner (1992) had cited the formation of a cytological gradient just in Cynipidae galls, anatomical and cytological analyses in galls induced by Hemiptera and Diptera in the Neotropics have shown significant differences in the cell layers proximal and distal to the larval chamber (Souza et al. 2000; Kraus et al. 2002; Arduin et al. 2005; Oliveira et al. 2006; Moura et al. 2008, 2009; Oliveira and Isaias 2009, 2010a). Thus, the tissues of the inner cortex, next to the larval chamber, are subjected to a greater oxidative stress, and the galls, as a product of cell redifferentiation, may develop cytological and histological gradients, independently of the inducing taxa. The distinctiveness in the levels of ROS from the inner to the outer cortex should be the main generative force of the final gall shape. These forces are consequence of changes in the patterns of cell elongation (Oliveira and Isaias 2010b; Oliveira et al. 2010). The ROS provoke changes in the structure of the cell wall making it more elastic, favoring cell expansion and elongation (Barceló and Laura 2009; Del Río and Puppo 2009), and also causing changes in the organization of the microtubules and microfibriles of cellulose (Barceló and Laura 2009). As a consequence, the direction of cell divisions and their shapes are altered in function of the gradient formed by the accumulation of ROS in gall cortex.

In fact, the direction of cell elongation exerts a crucial role in the formation and determination of the morphology of plant organs (Steeves and Sussex 1989; Obroucheva 2008). In galls, distinct sites of cell hypertrophy and hyperplasia have been detected (Meyer and Maresquelle 1983; Bronner 1992; Rohfritsch 1992; Souza et al. 2000; Arduin et al. 2005; Oliveira et al. 2006; Moura et al. 2008; Álvarez et al. 2009), but rarely, the causes of such determination have been proposed (Oliveira and Isaias 2010b). During gall development, the hypertrophy of the cells of the outer cortex, as well as the hyperplasia of the cells of the inner cortex are constant for each morphotype in each particular system, being determinant for the final shape of the gall morphotype. These differences are generated by the cecidogenetic field imposed by the galling herbivore (Mani 1964), but it also seems to exist a strong relationship with the production of the ROS.

3.5 Synthesis and Scavenging of Reactive Oxygen Species (ROS) in Galls

The levels of ROS in plant tissues may act as signalizing molecules and directly influence the growth, development, responses to stress and biotic interactions (Ryter and Tyrrell 1998; Mittler et al. 2004; Couée et al. 2006; Oliveira et al. 2010; Oliveira and Isaias 2010a). In galls, the production of ROS in the tissues next to the larval chamber occurs mainly due to the high activity of the mitochondria. The high quantity of proteins on these cell layers and the high enzymatic activity denote an intense metabolism already detected in several host plant-galling herbivore systems (Bronner 1992; Schönrogge et al. 2000; Oliveira and Isaias 2010a; Oliveira et al. 2010). Once the production of ROS in excess may cause cell death (Möller et al. 2007), mechanisms to eliminated these radicals are essential for plant tissues. The activity of enzymes such as the invertases may be important in the scavenging of ROS in galls through the production of soluble sugars in the inner cell layers, the sites of high oxidative stress.

The soluble sugars may play an important role either in the elimination of ROS or in its production (Couée et al. 2006). The metabolism of sugars and the skeletons of carbon are essential for the synthesis of compounds involved in anti-oxidant protection. Within the sugars, the glucose acts as a precursor for the synthesis of carotenoids, ascorbate, as well as other amino acids such as Cys, Glu e Gly, which are involved in the defense mechanisms and elimination of ROS (Smirnoff et al. 2001; Couée et al. 2006). It is plausible to relate the accumulation of soluble sugars in plant tissues as defense mechanisms against the negative action of ROS (Couée et al. 2006). As the accumulation of sugars is a common feature of many galls (e.g., Bronner 1992), and it takes part in mechanisms of elimination of ROS, the storage of sugars in the cell layers around the larval chamber may be considered a local response to the production of ROS in galls.

3.6 Photosynthesis in Leaf Galls: Comparative Analysis of Two *Aspidosperma* Systems

The maintenance of photosynthesis in gall sites has not been evaluated in many systems. This evaluation together with the anatomical and cytological documentation of the distribution of photosynthesizing cells may detect peculiarities of gall metabolism. Differently from the inner gall cortex which is colorless, in many galls, the outer cortex has chloroplasts submitted to light stress which may be the main source of ROS (Asada 1999; Möller et al. 2007; Oliveira et al. 2010). The intralaminar shape of *Aspidosperma australe* and *A. spruceanum* galls guarantees a chlorophyllian tissue at the outer cortex, mainly next to the adaxial surface of host leaves. This structure forms a continuum with the palisade parenchyma. However, differently from the normal thylakoids organization of the chloroplasts of non-galled leaves, the chloroplasts in galls had disaggregation of the membrane system and loss of the integrity of the grana, with the formation of many peripheral plastoglobules (Oliveira et al. 2011b).

Alterations in thylakoid organization, high ROS concentration, and low concentration of photosynthetic pigments cause low photosynthetic quantum yield. However, galls and non-galled tissues of *A. australe* and *A. spruceanum* had similar apparent electron transport rates (Oliveira et al. 2011b) (see Fig. 3.4). Under abiotic and biotic

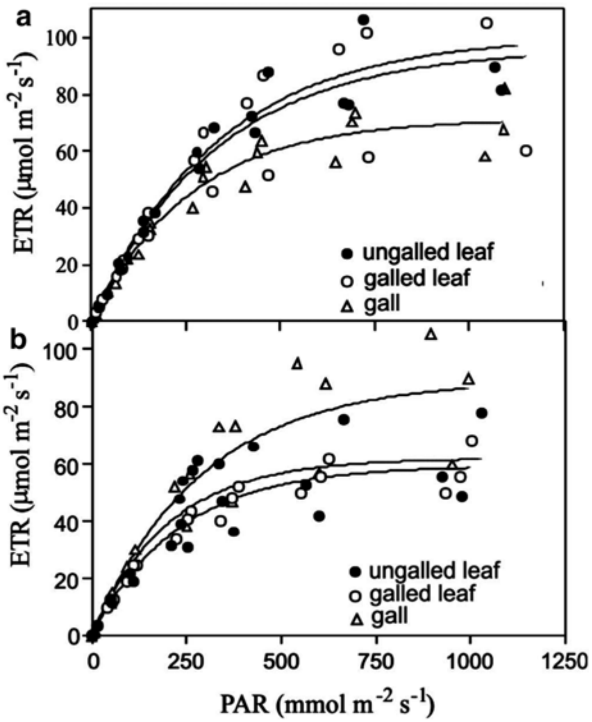

Fig. 3.4 Apparent electron transport rates (*ETR*) in ungalled leaf, galled leaf and gall tissue of *Aspidosperma australe* (**a**) and *Aspidosperma spruceanum* (**b**)

stresses, the chloroplasts may present numerous plastoglobules, corpuscles of mixed nature which generate a mechanism to reduce the damages provoked by the reactive oxygen species (Austin et al. 2006). The ROS are produced in response to light stress, but in these two *Aspidosperma*-galling herbivore systems, an increase of ROS concentration was observed in gall tissues as a consequence of the feeding habit of the gall inducers (Oliveira and Isaias 2010a, b). Oxidative stress induces plastoglobules production (Oliveira et al. 2011b), and consequently increases plastoglobuline synthesis, and tocopherol cyclase activity; molecules which protects the thylakoids membranes from photooxidation, and photosystem II from photoinactivation (Havaux et al. 2005; Bréhelin et al. 2007).

The maintenance of photosynthetic rates in *A. australe* and *A. spruceanum* galls is similar to the observation on Cecidomyiidae galls induced on *Clusia arrudae* (Clusiaceae) (Fernandes et al. 2010). Even though Larson (1998) and Florentine et al. (2005) observed that photosynthesis was reduced in gall tissues and sometimes in neighboring leaves, Other host plant–galling herbivore systems seems to present physiological and cytological strategies to photosynthetic maintenance. In *Aspidoperma* studied species, the plastoglobules are an alternative strategy for recovering of the membrane system of the thylakoids.

3.7 Conclusions and Remarks

Regardless the taxa of the inducing insect, galls have cytological and histological gradients. In general, the layers of cells nearest to the larval chamber have many mitochondria, large nucleus and conspicuous nucleolus, among other characteristics, presenting a high metabolism. In some mature galls, these cells may also be dead. A histochemical gradient follows the cytological one, particularly in relation to reserve substances directed to the gall inducer nutrition or to the maintenance of the cellular machinery within gall tissues. Also, the detection of enzyme activities in gall sites has reinforced the role of these histochemical gradients for gall development. We hypothesized that the main trigger for the formation of these cytological and histochemical gradients is the formation of reactive oxygen species (ROS). The ROS act as signaling molecules for various stages of gall development, including the accumulation of reserve substances. Some galls can perform photosynthetic activity, even if they are submitted to a high oxidative stress. In chloroplasts, the site of photosynthesis, the ROS produced during the interaction are eliminated by plastoglobules ensuring the integrity of PSII (photosystems II). Greater attention should be given to photosynthesis in galls for they interfere in the real rates of photosynthesis of their host plants.

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Chapter 4
Gall Morphotypes in the Neotropics and the Need to Standardize Them

**Rosy Mary dos Santos Isaias, Renê Gonçalves da Silva Carneiro,
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Abstract A morphotype can be defined as a specimen that illustrates a morphological variation within a species or, in the case of galls, a characteristic neo-formed plant organ generated by the interaction between a gall-inducing organism and a host plant. Once each gall morphotype is unique and derived from a species-specific interaction, there is a great confidence in using them to identify the different galling systems. In the Neotropics, where the biodiversity is high but somewhat unknown from the taxonomical point of view, the use of morphotypes helps assessing the abundance and richness of galling herbivores. This kind of knowledge would remain inaccessible if its report depended strictly on the taxonomic identification of the involved taxa. An effort on the standardization of the nomenclature used for inventories in the Neotropics revealed that some tridimensional shapes such as the globoid, ellipsoid, and lenticular are quite common, and may be the result of a series of similar events of cell division and expansion. When these morphotypes concomitantly occur on super-hosts of galling herbivores, special attention should be given to the possibility of overestimations, because variables such as the developmental stage of the gall, the age of the host organ by the time of oviposition, as well as morphological variations related to the sex of the inducer may be difficult to be visualized. In specific cases, the phenological and anatomical analyses are crucial to avoid misinterpretations.

Keywords Gall shapes • Inventories • Richness • Super-hosts • Terminology

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4.1 Why Standardizing the Gall Morphotypes

A morphotype can be defined as a specimen that illustrates a morphological variation within a species (Allaby 1999) or, in the case of galls, a characteristic neo-formed plant organ generated by the species-specific interaction between an inducing organism and a host plant (Isaias et al. 2013). Given that each gall-inducing insect is able to alter the morphogenesis of an organ of definite growth in very conservative patterns (Rohfritsch 1992), the morphotypes may be a confident mode of referring to several types of plant galls. The specificity between the involved taxa is strongly linked to the choice of the site of oviposition, which requires an efficient mode of attachment to plant surfaces (Eigenbrode and Jetter 2002). In fact, this event may be preceded by a series of contacts between the gall inducing organism and the plant surface leading to the recognition of the adequate host plant, beginning with host cell, host tissue and consequently host organ. In the temperate region, due to its relatively low biodiversity in comparison to the tropics (Fernandes and Price 1988; Price et al. 1998; Espírito-Santo and Fernandes 2007), the gall inducer – host plant systems are already well explored on the taxonomical basis (*cf. Quercus* spp. – Hymenoptera, *Salix* spp. – Diptera, *Fagus* spp. – Diptera systems). Therefore, studies in this region have advanced to the evaluation of global contexts (Kamata et al. 2002, 2006; Irwin and Lee 2003), trophic relationships among the gall inducer and the associated guild (Abrahamson and Weis 1997; Craig et al. 2007), and the search for experimental evidence of various gall traits (Inbar et al. 1998; Gish and Inbar 2006). On the other hand, the Neotropical region still presents a great unexplored biodiversity (see Espírito-Santo and Fernandes 2007), where new gall systems are frequently discovered and studied, generally bringing up a series of undescribed species of gall-inducing insects (*cf.* Arduin et al. 1991; Kraus et al. 1996, 2002; Motta et al. 2005). The lack of knowledge on the taxonomy of galling herbivores in Neotropical fauna could constitute a barrier for the correct identification and reference of the systems in further publication. This barrier can be somewhat surpassed by the use of morphotypes in the inventories of abundance and richness of galls and galling herbivores, as proposed by many authors (*cf.* Carneiro et al. 2009). Nevertheless, a brief view on the inventories reveals a large and sometimes confusing terminology, which is used to refer to similar shapes or morphotypes (Table 4.1).

An effort to standardize this terminology seems to be useful and is here presented based on the list of the most common morphotypes reported in the Neotropical literature (Maia and Fernandes 2004; Oliveira and Maia 2005; Maia et al. 2008; Carneiro et al. 2009; Santos et al. 2011, 2012) (Table 4.1).

The patterns extracted from this list are generated considering the most common and recurrent forms found in literature concerning Neotropical galls. Also, some possible causes of overestimations when super-hosts are included in the inventories are discussed. As it can be seen, nomenclature standardization of the approximate forms of the galls, i.e. their morphotypes, is necessary in order to avoid confusing and redundant terminology. Also, special attention is called to practical and methodological ways of avoiding overestimations by using phenological and developmental approaches.

Table 4.1 Morphotypes of neotropical gall systems as reported by Maia and Fernandes (2004), Oliveira and Maia (2005), Maia et al. (2008), Carneiro et al. (2009), and Santos et al. (2011, 2012)

Morphotypes (n = 613 galls)	Galls per morphotype (n)	(%)
Amorphous	16	2.61
Bivalve-shaped	1	0.16
Blister-shaped	1	0.16
Circular	19	3.10
Clavate	3	0.49
Conical	40	6.53
Cylindrical	8	1.31
Discoid	59	9.62
Elliptical	156	25.45
Fusiform	9	1.47
Globoid	169	27.57
Horn-shaped	1	0.16
Leaf fold	2	0.33
Legume	7	1.14
Lenticular	16	2.61
Mamiliform	1	0.16
Marginal roll	7	1.14
Ovoid	5	0.82
Pine-shaped	1	0.16
Pocket-shaped	1	0.16
Rosette	2	0.33
Spheroid	35	5.71
Spot	1	0.16
Star	1	0.16
Succulent	1	0.16
Swelling	42	6.85
Triangular	3	0.49
Tubular	3	0.49
Not described	3	0.49
Total	613	100

4.2 Patterns for Gall Morphotypes in the Neotropics

The description of gall morphotypes usually follows some common and naturally established procedures. In order to standardize the description of gall morphotypes, some procedures and terminologies are recommended: (1) identification of the host plant, (2) identification of the galling herbivore to the lowest possible taxonomical level, (3) description of the host organ, which should precise which organ is attacked and where in this organ the galls are located (*sensu* Bell 2008), (4) description of the neo-formed organ (i.e., the gall), classifying it into sessile (when it is inserted in the host organ) or pedunculated (with a narrow stalk which connects it to the host organ, making the gall easily detachable), (5) precise color description using a standardized color chart (http://www.immigration-usa.com/html_colors.html), (6) geometrical form approximation made by comparison to standard spatial forms (*sensu* Radford et al.

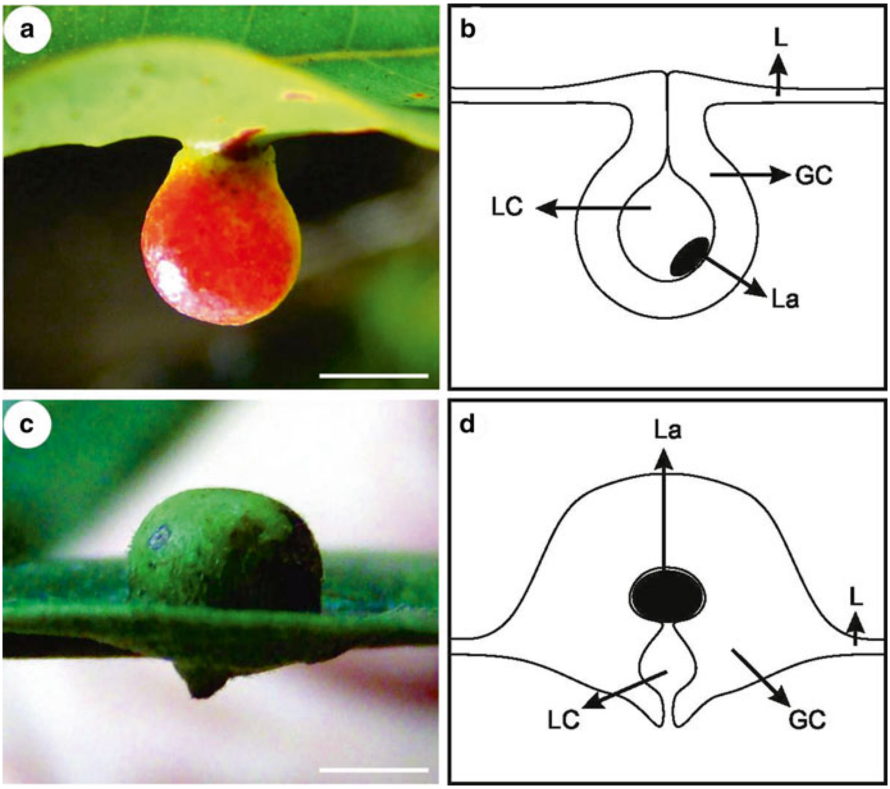

Fig. 4.1 Mature galls on *Psidium myrtoides* O. Berg (Myrtaceae) (**a–b**) and *Rollinia laurifolia* Schltdl. (Annonaceae) (**c–d**). (**a**) Extralaminar leaf gall. The peduncle is formed by a small contact area between the gall base and the leaf lamina. (**b**) Schematic diagram of the extralaminar leaf gall on *P. myrtoides* in cross section evidencing the *continuum* between the gall and the non-galled leaf tissues. This gall protrudes from the abaxial leaf surface. (**c**) Intralaminar leaf gall. There is a relatively large contact area between the leaf lamina and the base of the gall. (**d**) Schematic diagram of the intralaminar leaf gall on *R. laurifolia* in cross section evidencing the *continuum* between the gall and the non-galled leaf tissues. *GC* gall cortex, *L* non-galled leaf tissues, *La* larva, *LC* larval chamber. Bars = 0.5 cm

1974). For instance, conical galls have the format of a true cone, ellipsoid galls with axes in the proportion of 2:1 and 3:2, globoid galls with the axes in the proportion of 5:6, lenticular galls with the axes in the proportion of 1:3 – 1:6, and amorphous galls as those with no standard morphological pattern or approximated geometrical format.

For host leaves, the galls may occur just on one surface or protrude to both sides of the lamina, being considered extralaminar or intralaminar (Fig. 4.1). Even the precise topographical position may be adequately referred as apical (distal end), medium or basal (proximal end), in veins or in the regions between the veins (out of the veins) (Fig. 4.2).

The most common morphotypes listed in Neotropical inventories are the conical, ellipsoid, globoid and lenticular galls (Table 4.1). Some of the morphotypes are not

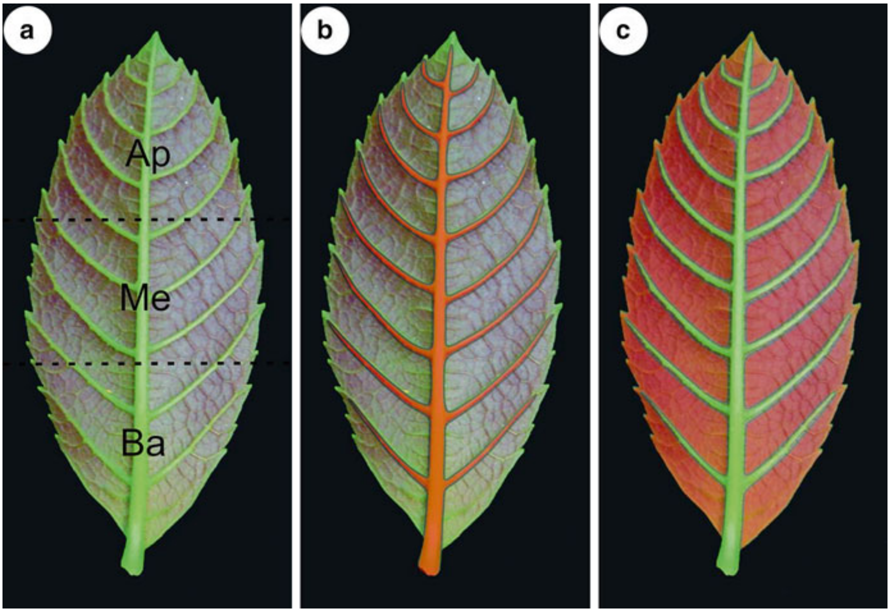

Fig. 4.2 (**a–c**) Leaves evidencing the possible sites for gall induction. (**a**) Division of leaf lamina in apical (*Ap*), medium (*Me*) and basal (*Ba*) region. (**b**) The leaf veins are indicated by *reddish lines*. (**c**) The leaf region between the veins are indicated by *reddish areas*

strictly geometrical, because they are constituted by grouped galls, or present an object-like shape. In these cases, the terminology may indicate the similarity to a resembling object as exemplified by the horn-shaped, cup-shaped or crown-shaped galls (Fig. 4.3).

Gall size, ornamentation and color generally confer conspicuousness to arthropod galls (Inbar et al. 2010). In the Neotropical region, galls tend to be as not as large as in some systems of the temperate region (*cf.* galls associated to *Pistacia* species that reach 25 cm) (Inbar et al. 2010). Nevertheless, insects with long life cycles should tend to induce larger galls when compared to those with short life cycles. It occurs because of the longer interaction with host cell genotype which imposes a long lasting chemical battle between the associated species (Price et al. 1987). The variation in size may be also a response to the number of developing larvae (Arduin et al. 1989), i.e., the maximum gall size attained reflects the interaction of insect and plant genome and the environment (Weis and Abrahamson 1985, 1986; Weis and Gorman 1990; Egan et al. 2011). As proposed by Rohfritsch (1971), Stone et al. (2002) and Egan et al. (2011), in many species of gall inducers, gall growth is maintained by active larval feeding. Thus, gall maximum size is attained at the completion of the larvae active feeding prior to pupation or it may be interrupted in case the larvae succumbs to the effects of natural enemies, host plant defenses, or pathogens (Mani 1964).

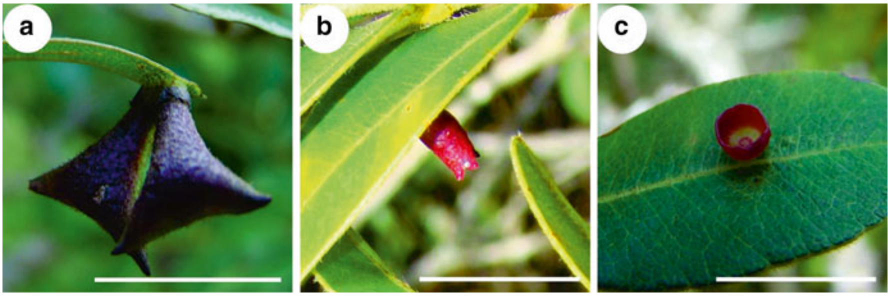

Fig. 4.3 Object-like gall morphotypes induced on *Copaifera langsdorffii*. These shapes do not fit any common geometrical shape. (**a**) Horn-shaped galls. (**b**) Crown-shaped gall. (**c**) Cup-shaped gall. Bars = 1 cm

Even though it is an easy trait to be recorded, the color of 37.7 % of the gall morphotypes is unreported in the inventories. The great majority are referred as greenish (37.7 %), 15.8 % are brownish, 5.3 % are yellowish, 2.3 % are reddish, 0.8 % whitish and just 0.4 % are black (Maia and Fernandes 2004; Oliveira and Maia 2005; Maia et al. 2008; Carneiro et al. 2009; Santos et al. 2011, 2012). This variation in color is due to changes in the accumulation of plant pigments (Fig. 4.4). According to Inbar et al. (2010), the color of galls may change during development, especially from green to red. Dias et al. (2013) measured the levels of pigments of the leaf galls on *Schinus polygamus* (Cav.) Cabrera. (Anacardiaceae), and demonstrated that the color change occurred due to gall senescence when the carotenoids and anthocianins are not masked by chlorophyll content anymore. This phenomenon is also common in other gall morphotypes (Fig. 4.4a, b). Chlorophyll concentration may also increase with gall age, which turns from red to green (Fig. 4.4c, d). Sometimes, the color of the same gall morphotype may vary from dark to yellowish green, reaching the red and even the brown tones, depending on the stimuli of the gall inducing insect and environmental conditions (Fig. 4.4e, f), such as the exposure to sun light (Carneiro et al. 2013; Dias et al. 2013).

Gall covering may vary considerably. In fact, it can be constituted of an unaltered *continuum* with the host organ epidermis or may be transformed in several ways. In Neotropical galls, 72.8 % of the galls do not cause macroscopic alterations in their host plant epidermis, and consequently has no differentiation of a singular indumentum. For 16 % of the morphotypes, no report on gall covering is presented, and just 11.2 % has conspicuous alterations. A cork (phellem) covering may develop either in stem or leaf galls, which may confer brown color, as is common in some *Copaifera langsdorffii* Desf. (Leguminosae Caesalpinioideae) galls (Oliveira et al. 2008) and was also observed in leaf galls on *Struthanthus vulgaris* Mart. (Loranthaceae) (Kraus et al. 2002). Also, gall surface may be either completely glabrous or densely hairy. Other common traits are a great variety of projections, such as emergences and even small leaves. All these structures may confer some protection against natural enemies and alter the final color of the gall morphotypes (Stone et al. 2002). To avoid some kind of overestimation or misleading with gall morphological variation during field evaluations of gall morphotypes, only mature galls with larvae next to pupation

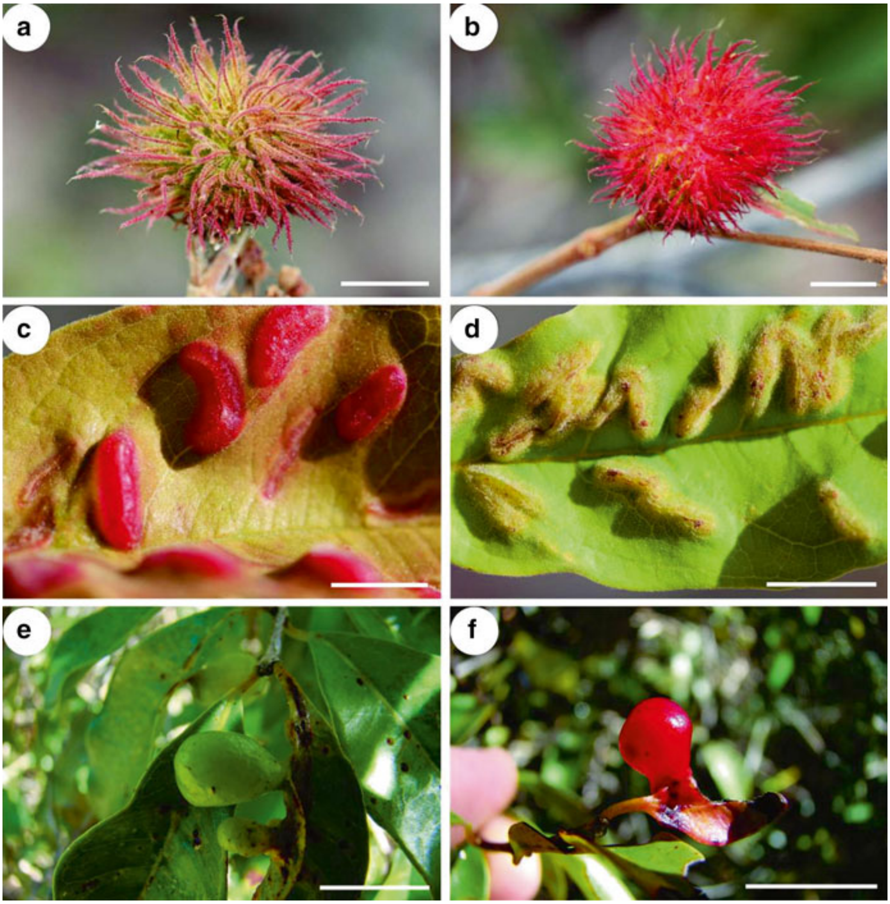

Fig. 4.4 Color variation in gall morphotypes. (**a–b**) Gall induced by a Lepidoptera on an unidentified host plant evidencing color change from *light greenish* to *dark reddish* due to gall senescence. (**c**–**d**) Galls induced by a Cecidomyiidae on *Andira humilis* evidencing color change from *deep red* to *greenish brown* due to tissue maturation. (**e–f**) Gall induced by a Triozid on *Psidium myrtoides* evidencing color variation as an evidence of the presence (*green gall*) or absence (*red gall*) of parasitoids. Bars = 1 cm

or in its last instar should be taken into account. The documentation of such morphological aspects should help identifying and accounting precisely the number of gall morphotypes of a given area.

4.3 The Most Common Morphotypes in Neotropical Inventories

In the Neotropical inventories of galling herbivores and their related galls, only a few reports identify the systems at the species level. The classification of the morphotypes is generally based on their geometric shapes, color, indumentum, and

Table 4.2 Distribution of gall morphotypes on neotropical plant host organs

	Host organs				
	Leaf	Stem	Buds	Reproductive organs	Roots
Morphotypes	N° (%)	N° (%)	N° (%)	N° (%)	N° (%)
Amorphous	10 (3.1)	–	5 (7.69)	1 (10)	–
Bivalve-shaped	–	–	1 (1.54)	–	–
Blister-shaped	1 (0.31)	–	–	–	–
Circular	19 (5.90)	–	–	–	–
Clavate	–	3 (1.40)	–	–	–
Conical	34 (10.56)	2 (0.93)	4 (6.15)	–	–
Cylindrical	7 (2.17)	–	1 (1.54)	–	–
Discoid	57 (17.70)	–	2 (3.08)	–	–
					–
Elliptical	38 (11.80)	104 (48.37)	13 (20)	–	1 (100)
Fusiform	3 (0.93)	4 (1.86)	1 (1.54)	1 (10)	–
Globoid	70 (21.74)	73 (33.95)	23 (35.38)	3 (30)	–
Horn-shaped	1 (0.31)	–	–	–	–
Leaf fold	2 (0.62)	–	–	–	–
Legume	7 (2.17)	–	–	–	–
Lenticular	16 (4.97)	–	–	–	–
Mamiliform	1 (0.31)	–	–	–	–
Marginal roll	7 (2.17)	–	–	–	–
Ovoid	1 (0.31)	–	2 (3.08)	2 (20)	–
Pine-shaped	–	–	1 (1.54)	–	–
Pocket-shaped	1 (0.31)	–	–	–	–
Rosette	–	–	2 (3.08)	–	–
Spheroid	30 (9.32)	2 (0.93)	3 (4.62)	–	–
Spot	1 (0.31)	–	–	–	–
Star	1 (0.31)	–	–	–	–
Succulent	–	1 (0.47)	–	–	–
Swelling	10 (3.11)	25 (11.63)	6 (9.23)	1 (10)	–
Triangular	2 (0.62)	–	–	1 (10)	–
Tubular	2 (0.62)	–	1 (1.54)	–	–
Not described	1 (0.31)	1 (0.47)	–	1 (10)	–
Total	322 (100)	215 (100)	65 (100)	10 (100)	1 (100)

position on the host plant (Maia and Fernandes 2004; Oliveira and Maia 2005; Maia et al. 2008; Carneiro et al. 2009; Santos et al. 2011, 2012). In these inventories, 52.6 % of the galls occurred on leaves, 35.2 % on stems, 5.2 % on apical meristems, 4.9 % on buds, 2 % on reproductive organs, and just 0.1 % on roots (Table 4.2). This may be partly due to the greater availability of some plant organs all over the year, which allow more interactions to be established or even the lack of field observations on some sites of oviposition which are difficult to check.

Considering the available inventories on the diversity and richness of galling herbivores, it can be noticed that some tridimensional shapes are recurrent while others are rare. Also, some shapes may be grouped to avoid inconsistencies and

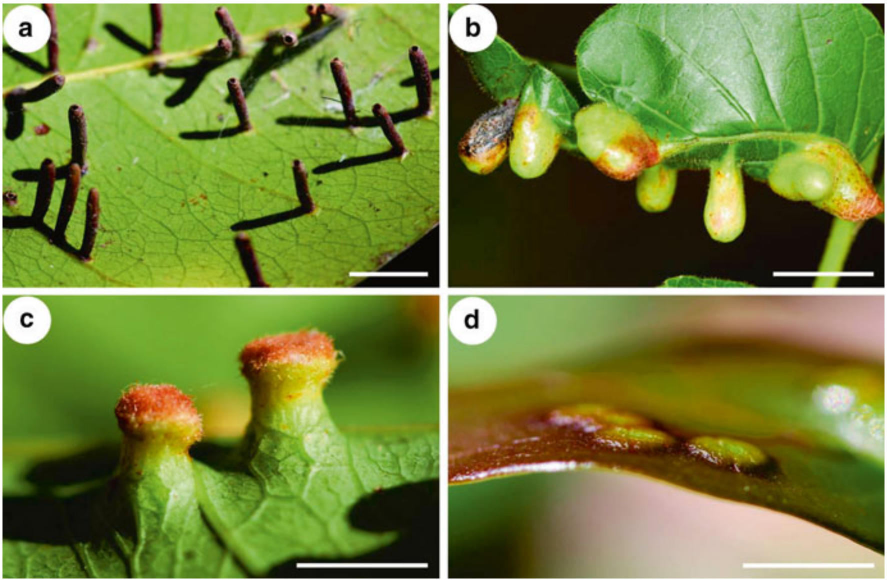

Fig. 4.5 Common shapes of Neotropical gall morphotypes. (**a**) Cylindrical galls induced by a Cecidomyiidae on *Eschweilera ovata* (Cambess.) Miers (Lecythidaceae). (**b**) Globoid galls induced by a Cecidomyiidae on *Apeiba tibourbou* Aubl. (Tiliaceae). (**c**) Cylindrical galls on *Matayba guianensis* Aubl. (Sapindaceae). (**d**) Lenticular galls on an unidentified host plant. Bars = 1 cm

facilitate the standardization of terminologies to be used in future inventories. The most common morphotypes referred in the literature for the Neotropics are the cylindrical, the globoid, and the lenticular galls (Fig. 4.5). In fact, globoid morphotypes are similar to the globose and spheroid, while ellipsoid, elliptical and ovoid means the same tridimensional shapes, and the lenticular morphotypes have been commonly referred as circular or discoid.

A closer look at the descriptions of gall morphotypes reveals that the lack of standardization may provide confusing data, although it reveals some peculiar aspects of the relationship between the occurrence of galls and their form in specific host organs. As it is seen in Table 4.2, leaves are the most affected host organs referred in the Neotropical inventories, accounting 321 gall systems with several shapes, hence being the most plastic organ. On the other hand, stems host a considerable number of galls (215 galls), but with few variations in shape. This is believed to be due to the constraints imposed by the host organ over the morphogenesis of the gall, since stems are considered to be less plastic organs when compared to leaves (Valladares et al. 2006). Galls in buds and reproductive organs are more difficult to be accounted since these organs are not always present or active in the plant body. Even though they are poorly reported as host organs, they still present a considerable amount of morphotypes, which is probably due to the great morphogenetical potentialities conferred by the meristematic tissues. Roots seem to be the most difficult host organs to be reported, probably due to their common underground position, which constitutes a barrier to the majority of galling insects, or even difficult the observation.

Despite the great variability in structures, no relationship could be established between the most common gall shapes and groups of host plants or insect *taxa*. What they are and why these repetitive processes lead to these convergent patterns is still unknown.

4.4 Super-hosts for Galling Herbivores: The Same House for Several Inducers

The development of gall structures requires a continued physical contact and tuned relationship between the host plant and the galling insect. Some of the important parameters that may define the possibility of gall formation are the co-occurrence of both taxa, the feeding habit of the galling herbivore, plant local abundance (Crawley 1989; Fernandes and Price 1991; Fernandes 1992; Gonçalves-Alvim and Fernandes 2001), and the systems of recognition established by plant surface traits (Eigenbrode and Spellie 1995; Eigenbrode and Jetter 2002). The diversity of shapes, sizes and colors makes the gall-inducing insects some of the most bizarre and interesting living organisms (Espírito-Santo and Fernandes 2007).

Even though the majority of the host plants, 64.5 % in the Neotropical inventories (Maia and Fernandes 2004; Oliveira and Maia 2005; Maia et al. 2008; Carneiro et al. 2009; Santos et al. 2011, 2012), are associated to just one *taxon*, some may support two or more galling herbivores and will be herein referred as super-hosts. This diversity of associated insects is intriguing for host plant-galling herbivore systems are, largely, species-specific (Dreger-Jauffret and Shorthouse 1992; Carneiro et al. 2009). According to Hardy and Cook (2010), gall-inducing insects are more host-specific than their non-galling relatives, even though there is no general significant increase in the diversification rate in galling herbivores. Gall induction on plants has evolved multiple times among insects, with over 13,000 species currently described (Hardy and Cook 2010). However, the perspective is of over 132,000 species in a global perspective including the undescribed taxa (Espírito-Santo and Fernandes 2007). More than taxa specific, gall-inducing herbivores seem to be exceptionally tissue specific, which make the super-hosts excellent models for the study of plant morphogenetical potentialities (Oliveira et al. 2008). The same specific host organ tissues respond distinctly to the stimuli of several and different biotic signalers. The galling herbivores are certainly very successful because the gall represents new tissues, at least initially, enemy-free (Price et al. 1987; Stone and Schönrogge 2003; Hardy and Cook 2010).

The alterations observed among four gall morphotypes co-occurring on *Copaifera langsdorffii* (Fabaceae) revealed that the distinct responses are consequence of the wide morphogenetical potentialities of the host plant (Oliveira et al. 2008). Each of the galling associated herbivores manipulated its host tissues in a peculiar mode, and generated particular qualitative responses in divergent patterns, resulting in the variety of morphotypes. More than denoting the specificity of the relationship, this peculiarity makes the insect galls important taxonomical tools (Floate et al. 1996), either in the botanical or entomological level (Fernandes et al. 1997). Curiously, the insects associated to *C. langsdorffii* are Cecidomyiidae, which represent such a diverse group of very specialized galling insects (Gagnè 1994). The number of Cecidomyiidae associated to this host plant species may range from 5 to 23 (Oliveira et al. 2008; Costa et al. 2010), and the generated morphotypes may occur either on leaves or stems.

The analyses of some inventories in Brazil (Maia and Fernandes 2004; Oliveira and Maia 2005; Maia et al. 2008; Carneiro et al. 2009; Santos et al. 2011, 2012) have accounted for 128 systems on super-hosts but it seems like there are no relationships between these plant *taxa* and their higher susceptibility to the attack by galling arthropods. A common host plant in the Neotropics, *Lantana camara* L. (Verbenaceae), hosts three *taxa* of galling arthropods (Moura et al. 2009). All these taxa explore the leaves and flowers of *L. camara* and induce very distinct galls. The diversification of the morphotypes does not permit misidentification of each system. *Asphondylia camarae* (Diptera: Cecidomyiidae) explores a very special niche, the flowers and consequently must have a peculiar life cycle adjusted to that of its host plant. *Schismatodiplosis lantanae* (Diptera: Cecidomyiidae) and *Aceria lantanae* (Acarina: Eriophyiidae) explore the leaves and may occur concomitantly on the same lamina, but are easily distinguishable (Moura et al. 2008).

When the super-host plants are found in nature, special attention should be given to the possibility of overestimations, because variables such as developmental stage of the gall, the age of the host organ by the time of oviposition, as well as morphological variations related to the sex and alternation of generations of the gall inducers may be difficult to be visualized. In specific cases, the phenological and anatomical analyses are crucial to avoid misinterpretations.

4.5 Phenological and Anatomical Analysis: Special Care to Avoid Overestimations

The relationships between host plants and gall inducing insects are subjected, most times, to a highly complex net of ecological relationships. Besides the parasitic relationship established upon gall induction, the host plant – gall inducer systems can be the base for many other associated trophic levels, such as predators and parasitoids (*cf.* Sanver and Hawkins 2000; Espírito-Santo et al. 2004; Santos et al. 2010). Parasitoids are known to disturb and/or stop the feeding activity of the gall inducers, since they can cause their premature death. Since gall development and structure directly depend on the action of the gall inducer, interferences such as those imposed by parasitoids should significantly affect the structure of the gall (Fernandes et al. 1987; Wiebes-Rijks and Shorthouse 1992). Yet, it should be taken into account that gall development can be either fast or slow, depending on the rate of cell division, growth and differentiation in each

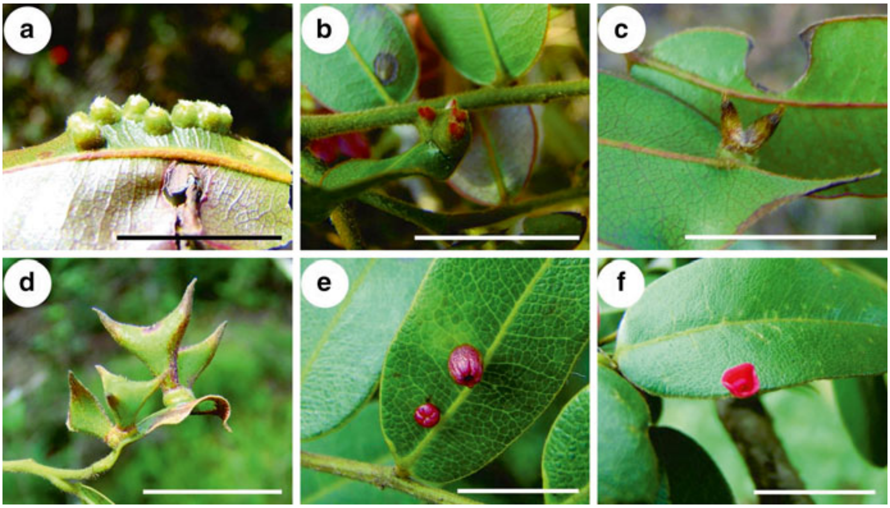

Fig. 4.6 Variation in shapes in two gall morphotypes induced by Cecidomyiidae on *Copaifera langsdorffii*. (**a–b**) Horn-shaped gall, passing through four distinct developmental stages. (**a**) Young dome-shaped gall. (**b**) Protrusion of two horns at the early growth and developmental stage. (**c**) Developed horns at the late growth and developmental stage. (**d**) Mature horn-shaped galls. (**e–f**) Development of the cup-shaped gall, passing through two distinct stages. (**e**) Ellipsoid galls at the growth and developmental stage. (**f**) Mature cup-shaped gall. Bars = 1 cm

specific gall system. During this process, gall shape may present great variance, which without phenological and developmental analyses, could be understood as different gall morphotypes, unrelated whatsoever. For instance, the cup-shaped gall on *C. langsdorffii* is red when mature, and may occur either on the abaxial or adaxial leaflet surface, with a membranous texture. The larval chamber is located at the basal portion of the gall which is monotalamous (Oliveira et al. 2008). This gall is structurally very simple and its development lasts 2–3 days, when it changes from light green to red. At the beginning of its development, the gall is globoid and closed, but it elongates axially and opens in its apical portion along linear preexisting scars. The alteration in shape is so drastic that these morphotypes could be easily misinterpreted as two distinct ones if the temporal variable is not evaluated. Another *C. langsdorffii* gall morphotype that may lead to this kind of overestimation in field studies is the horn-shaped gall, which can be either green or red when mature. It may occur in the abaxial or adaxial leaflet surface, and is pedunculated. The development of this gall morphotype lasts about 1 year. At the very beginning of its development, the gall assumes a volcano shape, from whose inner portion firstly emerges a large amount of trichomes. Secondarily, two hairy projections develop and form the gall body. Towards maturity, the basal portion develops originating the peduncle (Fig. 4.6). These two morphotypes indicate the importance of periodic field observation to follow the phenotypical changes along gall development.

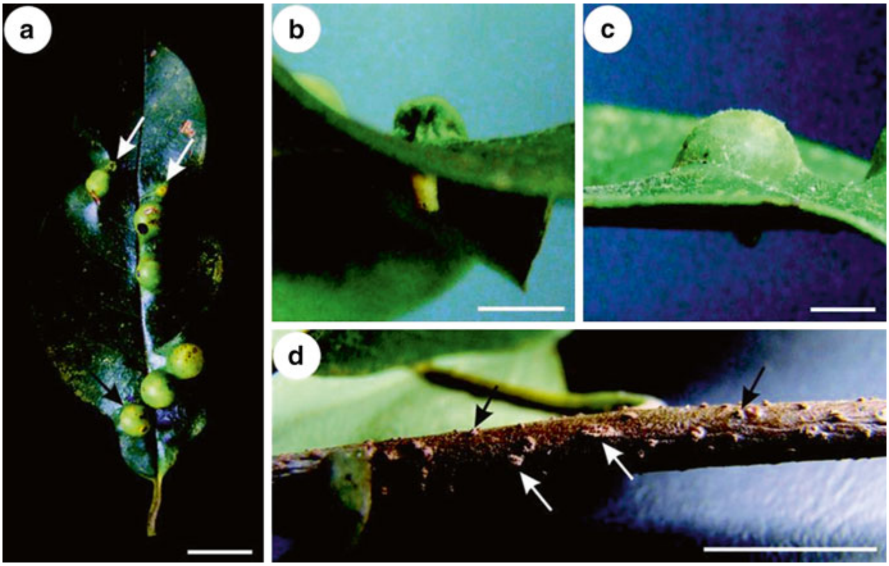

Fig. 4.7 Gall morphotypes induced by *Pseudotectococcus rolliniae* on *Rollinia laurifolia*. (**a**) Host leaf with female induced (*white arrows*) and male induced galls (*black arrows*). (**b**) Detail of a male induced gall. (**c**) Detail of a female induced gall. (**d**) Stem galls for dormancy induced by first instar nymphs resembling enlarged lenticels (*white arrows*) compared to the true regular sized lenticels (*black arrows*). Bars = 1 cm in a, d; 0.25 cm in b, c

Another peculiar case concerns the relationship between *Rollinia laurifolia* (Annonaceae) and the gall inducer *Pseudotectococcus rolliniae* (Erioccocidae) (Gonçalves et al. 2005, 2009). In this system, a reckless observer is subjected to committing several mistakes on the description of the galls. At the first sight, two different gall morphotypes can be accounted, being one of them larger and round and the other, smaller and conical. These two morphotypes could also be understood as two different developmental stages of the same gall, due to their relative size. However, anatomical, phenological and entomological analyses helped elucidating the occurrence of sexual dimorphism on these galls. In this specific case, females are sessile and spend their whole lives inside the gall chamber, while males are ephemeral and spend little time inside their galls, before leaving them to fertilize the females. The time spent by each gender of *P. rolliniae* inside their galls is believed to be the main determining factor of the distinct gall phenotypes (Gonçalves et al. 2005). Still, the phenological studies performed for this system indicated a lag-time between the adult forms and the nymphs that induce the galls of the following year. The nymphs could not host themselves on the leaves of their host plant, which is deciduous, shedding all its leaves during the winter. A third gall morphotype, resembling a lenticel, was found on the shoots of the host plant, in which the first instar nymphs induce a gall for dormancy (Gonçalves et al. 2009) (Fig. 4.7). This case illustrates an especially complex insect life cycle and evidences the importance of phenological and anatomical analyses for the reliability of gall morphotyping.

4.6 Conclusions and Remarks

The standardization of the nomenclature used in the inventories of the diversity of galls in the Neotropics should facilitate future comparative analyses of galling herbivores distribution, and patterns of gall development in Brazilian biomes. By properly accounting the gall morphotypes from the Neotropics, ecological parameters such as richness and abundance of galling herbivores should be accessed, and increase the knowledge on the biodiversity in such areas. The most common tridimensional morphotypes reported, the globoid, ellipsoid, and lenticular ones, are repetitive on several distinct systems which reinforces the necessity of taxonomical identification of the organisms to the lowest possible level, whenever it is possible. As well, the repetitiveness of these shapes elects such host plants-gall inducers systems for developmental studies in cytological level so as to explain how plant cell morphogenesis is manipulated in such convergent patterns.

It is particularly evident that the alterations in host plant organs, and the development of the morphotypes should be studied taking into consideration the developmental stage of the gall, the age of the host organ by the time of oviposition, as well as morphological variations related to sex and alternation of generations of the inducers. These characteristics may be difficult to be visualized in field conditions but may be key elements which allied to phenological and anatomical analyses would help avoiding misinterpretations or overestimations of gall diversity in nature.

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Chapter 5
Population Ecology of Galling Arthropods in the Neotropics

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Abstract The available information on the population ecology of galling arthropods (mainly insects) in the Neotropics is reviewed. Patterns of gall abundance in time and space are considered, with a discussion of seasonality and host synchronization. The contribution of various mortality factors to abundance is also compared, considering both top-down (parasitoids, predators) and bottom-up (host plant). Competition is also considered, but sources appear scarce. The methodological appropriateness of distinguishing galls and gallers is mentioned, since it is easier to only take galls and gallers within galls into consideration, not exploring other galler life stages as adults and eggs. Finally, plant biological control programs using gallers from the Neotropics are addressed in a more practical view of galling arthropod population ecology.

Keywords Galling insects • Life history • Model system • Mortality factors • Population dynamics

5.1 Introduction: How Galls Contribute to Population Ecology

In regions such as the Neotropics, species diversity is so large that there is a sensation that much more remains to be discovered, and thus inventories should come first. Many of the chapters in this book present the wonderful results of such inventories. But as we intend to show in this chapter, this sensation has not suppressed the urge to study the population ecology of gallers in this region. However, considering the

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possibility of relatively simple logistics when working with gallers and the amount of data on populations galls can provide, studies on galler populations could be expected to be more common than they are in the Neotropics. The proposition that host plant-galler systems ("gall system" from now on) can be viewed as model systems for ecological studies, and specifically population studies, can still progress much more in the Americas south of the USA.

We reinforce the use of gall systems as models, like suggested by Crespi et al. (2004) for thrips (Thysanoptera) species in Australia, calling them "model clades". The use of model systems is a widespread trend in the biological sciences, mostly based on model species (e.g. Metcalf and Mitchell-Olds 2009), which offer insights that can lead to extrapolation for other species or groups of species. Model clades, however, could give more robust information based on groups of related species by gathering information on the relationships between them as well as modelling each species and extrapolating to another (Crespi et al. 2004). Further than that, we propose that galls themselves offer a distinct situation: even more than model interactions, they represent model phenomena. Although galls are viewed as particular, they actually belong to a class of phenomena we can call engineered structures: an ecosystem engineer (the gall inducer, sensu Jones et al. 1994) alters its environment, usually adaptively in its favour, but ultimately benefiting other species as well (Maruyama et al. 2012). In this particular case, the structure is alive, derived from changes induced in the tissues of an organism. A Neotropical example of such situation is a gall induced by a weevil (Coleoptera: Curculionidae) on the host *Xylopia aromatica* (Annonaceae) used by 18 ant species of 9 genera (Craig et al. 1991; see also Araújo et al. 1995b; Fernandes et al. 1988; Ferraz and Monteiro 2003; Maruyama et al. 2012).

Galling arthropods can be useful model systems for population ecology studies for a gamut of reasons (see Yukawa 2000 for a review). Although not all these features are listed among those suggested for model systems (e.g. ease of rearing and handling, an audience of interested people), we consider that they are applicable to ecological studies. The ease of sampling is fundamental to field experiments, and arthropod galls are easily detectable due to their host specificity, immobility and conspicuousness, and can be separated into reliable morphotypes in the field (Carneiro et al. 2009). These features provide interesting work opportunities such as censusing whole populations, resampling the same individual (or same gall) repeatedly across time and observing other trophic interactions for galler and/or host plant directly or through identifiable evidences – e.g. markings on galls, resulting usually from attack by parasitoids or inquilines.

The most studied system in the Neotropics so far is the one formed by the shrub *Baccharis dracunculifolia* (Asteraceae) and its gallers, but mainly *Baccharopelma dracunculifoliae* (formerly *Neopelma baccharidis*, Homoptera, Burckhardt et al. 2004), in southeastern Brazil. Many aspects of the system were investigated in the last two decades, such as the influence of host spatial distribution on gall abundance (Collevatti and Sperber 1997; Fagundes et al. 2001; Ribeiro-Mendes et al. 2002), female preference for more vigorous shoots – the plant vigour hypothesis proposed by Price (1991) (Gonçalves-Alvim et al. 1999a; Faria and Fernandes 2001), sex-mediated herbivory, since *B. dracunculifolia* is a dioecious plant (Araújo et al. 1995a; Espírito-Santo and Fernandes 1998; Espírito-Santo et al. 2012; Faria and Fernandes 2001; Ribeiro-Mendes et al. 2002), plant phenology and population fluctuation (Espírito-Santo et al. 2012), bottom-up (Espírito-Santo and Fernandes 2002) and top-down effects (Espírito-Santo et al. 2004; Fagundes et al. 2005; Sperber and Collevatti 1996), effects of galls on the host plant (Lara and Fernandes 1994), and the description of gall morphogenesis (Arduin et al. 2005). Along with *B. dracunculifolia*, many other congeneric species are reported as gall hosts, depicting *Baccharis* as a super-host genus in the Neotropics (Fernandes et al. 1996), and some had their systems further evaluated (Carneiro et al. 2006; Espírito-Santo et al. 2012).

It is also important to understand ecological aspects of the galling arthropods in order to interpret studies of their populations. First, whether we consider gallers from the point of view of parasites or herbivores makes a difference because populations of these kind of organisms are usually considered differently – unique ecological aspects characterise each of these so called life strategies. The challenge lies in combining knowledge on both strategies to help study gallers, since most of them are both parasites and herbivores. Second, galls can represent a basal species interaction system, upon which many other interactions are built, such as inquilinism, parasitism, mutualism, etc. These can impact the population ecology of galler and/or host plant in ways that might be idiosyncratic among gall systems. Third, some aspects of galler host specificity are important, as the fact that specificity is toward young plant tissues (Weis et al. 1988), and plant tissue production patterns in time might lead to gallers having univoltine, bivoltine or multivoltine life cycles through host synchronisation (Yukawa 2000). Thus, different seasonal environments and differing host plant responses to environmental seasonality can strongly influence galler population biology.

We divided this chapter in topics attempting to approach a variety of population aspects important to galling arthropods: spatial distribution (at different scales), abundance in time (seasonality and host synchronization), mortality factors (leading to top-down and/or bottom-up processes), competition, life stages sampling, life history, gallers as biological control agents, and finally some perceived perspectives for the future of population studies on gallers in the Neotropics.

A first generalisation is the relatively limited amount of studies regarding investigations on the population ecology of specific study systems. This could be attributed to factors such as the small number of research groups investigating galls, an apparent lack of joint efforts between such groups to focus on specific host plant-galler systems for a broader view of the systems, and finally the enormous diversity of a poorly known fauna. As previously stated, efforts on biodiversity inventories sometimes override studies restrained to only one system, despite the opportunity of developing population ecology studies being in some cases taken due to the ease of working with populations of galls. There is an apparent trade-off between cataloguing biodiversity and studying specific species populations – but we would like to insist that such trade-off is only apparent.

5.2 Abundance in Space at Distinct Scales: Host Organ, Host Individual and Geographic Populations

Gall abundance patterns in space are probably the first step to population ecology studies, providing invaluable information about factors influencing gall occurrence. These patterns can be evaluated at different levels, from host organs to geographic scales, and can be approached depending on the aim of the research as we show with examples throughout the chapter. The geographic distribution of gall populations with respect to that of their hosts represent an important aspect which allows evolutionary and conservation insights, but was not yet investigated for any species in the Neotropics that we know of. Most studies are restricted to local analysis of gall abundance per host individual or organ, studying differences between vegetation types, host plant density or evaluation of hypotheses on the adaptive nature of gall induction.

5.2.1 Broad Scales

Studies on a same gall system in different regions or ecosystems are not common. We found such studies only for the *B. dracunculifolia*/*B. dracunculifoliae* gall system, performed in Cerrado and Atlantic Forest. The same system was also the only one to be evaluated in more than one spatial scale, in a semideciduous seasonal forest belonging to the Brazilian Atlantic forest (Collevatti and Sperber 1997). These were (1) host plant individual, with plant height and crown diameter and volume as descriptors; (2) local scale, represented by host plant patch; and (3) regional scale, between two spatially separated localities. The authors found that gallers were only affected by host plant size, which varies locally. Gall load increased with plant size, with small plants "escaping" galler attack, probably an indication of a minimum plant size to be gall-prone. Ribeiro-Mendes et al. (2002) performed a study on ten populations in four different Brazilian states, focusing on sex-mediated herbivory and differences between habitats, which we further analyse bellow.

5.2.2 Local Scale

Gall abundance in space at a local scale was evaluated at the host level attempting to detect environmental differences. For instance, galling insect populations were larger at xeric sites compared to mesic ones in a study with samples in United States (Arizona and Utah) and Brazil (Minas Gerais) (Fernandes and Price 1992). The influence of forest edges on gall abundance was also investigated, since these forest portions are expected to be more xeric than forest interiors and are expected to present more galls, matching the predictions for gall adaptive nature and diversity patterns.

At the Brazilian Cerrado, Araújo et al. (2011a) found that gall abundance was larger at forest edges in *Styrax pohlii* (Styracaceae). The system was based on just one host species but the authors analysed all gall morphotypes present and made additional considerations about galling insect diversity and their use as bioindicators (more details about galls as bioindicators in chapter 9). Another environmental influence on gall abundance at a local scale was investigated by Gonçalves-Alvim et al. (2001), who found that *Cecidomyia avicenniae* (Diptera: Cecidomyiidae) gall density in *Avicennia germinans* (Avicenniaceae) is affected not only by host plant habitat salinity but also by leaf sclerophylly along an interstitial salinity gradient in Amazonian mangrove stands and a varzea (seasonally flooded river margin) in northeastern Brazil. Leaf sclerophylly and interstitial salinity were positively correlated. At the same time, gall density (per unit of leaf area) showed positive relationships with both salinity and leaf sclerophylly, which explained 22 % of the variation in gall density. Density was negatively related to shoot length, which means longer shoots had lower gall density.

At a local scale, host plant density effects on gall abundance were also evaluated in four populations of the host *B. dracunculifolia*, but only gall density per plant was influential, suggesting that both host plant and galler dynamics of colonization/extinction could affect density regulation of the galler (Fagundes et al. 2001). Host distribution in space was probably influential on gall abundance for *Lopesia brasiliensis* (Diptera: Cecidomyiidae) galling *Ossaea confertiflora* (Melastomataceae), which harboured more galls when there were close conspecifics (Vrcibradic et al. 2000).

Host individual scale is often used to test the hypothesis of sex-mediated herbivory in dioecious plants (Cornelissen and Stiling 2005). For example, the hypothesis was not corroborated in the study from Faria and Fernandes (2001) in the Brazilian Cerrado, as in some other studies (Araújo et al. 1995a; Espírito-Santo and Fernandes 1998; Faria and Fernandes 2001; Ribeiro-Mendes et al. 2002; Araújo et al. 2003; Carneiro et al. 2006; Espírito-Santo et al. 2012). The plant vigour hypothesis (see Cornelissen et al. 2008), taken at the host organ level, on the other hand, was accepted in this case meaning that longer shoots presented higher gall frequency, as well as more oviposition sites (leaf buds). Galler performance, however, was not related to shoot length. The authors concluded that *B. dracunculifoliae* did not select shoots based on length only. Ribeiro-Mendes et al. (2002) evaluated the hypothesis of sex-mediated herbivory along with the influence habitat could exert on several populations of the *B. dracunculifolia/B. dracunculifoliae* gall system, finding a stronger influence of habitat on gall abundance. Espírito-Santo et al. (2012), studying the same system together with two other congeneric host plant species found that resource availability – through plant phenology (see also Araújo et al. 1995a; Espírito-Santo and Fernandes 1998) – was more influential than host plant sex. Host individual scale is also present in studies on effects of plant architecture (e.g. Araújo et al. 2006; Lara et al. 2008; Araújo and Santos 2009a) and size (e.g. Araújo et al. 2003; Araújo and Santos 2009b) on galls, essentially variants of resource availability.

5.2.3 Host Organ Scale

Few studies considered gall distribution at the host organ level. Leite et al. (2009, 2011), studied the host plant *Caryocar brasiliense* (Caryocaraceae) in the Brazilian Cerrado, with two gall-inducing species involved: an *Eurytoma* (Hymenoptera: Eurytomidae) (Leite et al. 2009) and the other an unknown galler. The studies analysed gall distribution within leaves finding more galls on the median portion. Additional analysis was performed for slope orientation influence on gall distribution within trees, with most galls occurring at the eastern tree slope due to the exposure to strong winds and sunlight, according to the authors. Galls induced by the eryophyid *Brachendus* on leaves of *Laguncularia racemosa* (Combretaceae) have a tendency to be more concentrated on the leaf tip than the leaf base, but differences are small (Mendonça and Almeida-Cortez 2007). Curiously, none of the three gallers has the expected trend for more galls toward the leaf base – which would lead to a closer access to photosynthates coming from the plant (e.g. Whitham 1979).

5.3 Abundance in Time: Gall and Galler Seasonality, Population Trajectories

In the Neotropics, studies of gallers taking time explicitly into consideration are not common. The influence time and seasonality have in the demography of gall-inducers is not frequently addressed, perhaps due to logistic questions. Following galls along time has been proposed as a positive aspect of gallers as model organisms for population studies, but that requires control over a series of ecological aspects affecting hosts and gallers. Thus, studies focusing on host plant (mainly) and spatial effects are perhaps deemed easier to develop. Moreover, repeated samples of galls on a given plant are not statistically independent points, thus for a true comparison we need anyway a series of spatial units, such as plants/populations.

We consider three separate questions regarding gallers over time: gall seasonality and synchrony between plant organ production and galls; the number of yearly generations of gallers (voltinism) and finally pure abundance patterns in time in terms of demography. There is quite a lot of information on development time and yearly occurrence for varied galls, but we only take into consideration systems or areas which have been explicitly explored for population seasonality across at least 1 year.

5.3.1 Gall Seasonality and Host Synchrony

Phenology is an important aspect of any organism, since Nature works in seasons – or does it not? A strong seasonal signal in the environment is sometimes held as the norm in ecological thinking, and organisms are expected to follow seasonal trends.

Clearly this is more a question of the geography of science than the geography of the organisms, because science is still developed mainly in temperate countries. This is not to say that many environments are not seasonal (and not only due to changes in temperature), just that not all need to be and this has important ecological consequences.

On the other hand, the widely held view that the tropics have no true seasons has been relativised, especially for insects. Wolda (1988) already proposed that apparently aseasonal habitats, such as tropical rainforests, may be home to highly variable populations (Wolda 1992) or strongly seasonal ones (Wolda and Denlinger 1984). Because gallers are so host- and site-specific, their population dynamics should be strongly linked to plant phenology. Host synchronisation should thus be a crucial issue for gallers as it has been stressed in the literature (Yukawa 2000) – that is, unless the plant is truly aseasonal or shows no clear phenological pattern the arthropod could follow. Anyway, crucial or not, seasonal or not, gallers are expected to mirror their host plant phenology, whatever organ is being galled. Thus, gallers should be a preferred system to ascertain the seasonality or not for tropical environments such as tropical rainforest. That is not what is found, unfortunately, with no single source on gall seasonality in the vast Amazon or any other equatorial tropical rainforest in the Neotropics that we know of.

Bi- or multivoltine gallers are systems for which seasonality and synchrony can be more easily tested, or at least would provide results in a shorter time. Table 5.1 lists 16 species of non-univoltine Neotropical galling arthropods for which there is relatively complete information on seasonality. Most galls in Table 5.1 are on leaves, and most induced by Cecidomyiidae, as is the norm for Neotropical literature. For some information, only an interpretation of the original source can be given. A few examples of apparently aseasonal resources (galled plant organ production) can be found, along with those present all year round but with differences in the amount of resource produced. For host organs reported to be produced on a given period of the year, (e.g., *Cordia verbenacea* (Boraginaceae) giving forth new leaves in autumn, Maia and Tavares 2000) but gallers having more generations (e.g., *Cordiamyia globosa*, Diptera: Cecidomyiidae, op.cit.) it is assumed that the resource is probably produced during a longer time, but perhaps in smaller quantities. In this case, a specific yearly population dynamics can emerge as a response, as peaks and troughs in numbers (autumn-winter peak and summer trough for *C. globosa*).

Univoltine gallers may have their single generation because the resource they need for gall induction is restricted in time, as in very seasonal environments, and there is not enough time for more than a generation a year to develop. That is usually considered an obvious situation, and is almost never pursued as a quantitative question (not whether, but how much synchronized a galler is with host phenology). For example, *Anadiplosis* sp. (Diptera: Cecidomyiidae) on *Machaerium aculeatum* (Fabaceae) has galls developing on plants from August to July in a single generation (Fernandes et al. 1987). New galls seem to appear mainly in August, and new leaf production by the plant happens from August to November, only. It seems this latter period is rather too short for this species to complete development, and thus a second generation in the same year would be impossible – but in evolutionary time

Table 5.1 Population ecology of bi/multivoltine Neotropical arthropod gall-inducers in time. Resource is the plant organ/part galled, resource phenology is information on its production across a year

Galler	Plant	Resource	Resource phenology	New gall occurrence	Gall phenology	Voltinism	Source
Asphondylia boerhaviae	*Boerhavia diffusa*	Flower buds	?	Year round	?	17	Freeman and Geoghagen (1989)
Brachendus enodis (Eriophyidae)	*Laguncularia racemosa*	Leaf	Increase in wet season	?	Wave pattern (more galls dry season, Sep–Apr)	?	Mendonça and Almeida-Cortez (2007)
Bruggmania acaudata	*Guapira opposita*	Leaf	?	Year round	?	Multivoltine	Maia and Monteiro (1999)
Bruggmania acaudata	*Guapira opposita*	Leaf	Year round, spring peak	Not in winter	High spring and summer, low winter	Multivoltine	Rodrigues et al. (2007) and Silva et al. (unpublished)
Bruggmania elongata	*Guapira opposita*	Leaf	?	Year round	Peak in May, low in Jan	Multivoltine	Maia and Monteiro (1999)
Bruggmania elongata	*Guapira opposita*	Leaf	Year round, spring peak	Year round	Year round, spring peak	Multivoltine	Rodrigues et al. (2007) and Silva et al. (unpublished)
Bruggmania robusta	*Guapira opposita*	Leaf	?	Year round	Peak in Aug, low in May	Multivoltine	Maia and Monteiro (1999)
Bruggmania robusta	*Guapira opposita*	Leaf	Year round, spring peak	Not in winter	Spring peak	Multivoltine	Rodrigues et al. (2007) and Silva et al. (unpublished)
Cecidomyiidae sp.	*Piper arboreum*	Leaf	New leaves in rainy season		Peak in Dec (rainy season)	Multivoltine?	Araújo and Santos (2009b)
Cecidomyiidae sp.	*Aspidosperma spruceanum*	New leaf	Nearly aseasonal	Year round	Most new galls Oct	Multivoltine	Campos et al. (2010) and Formiga et al. (2009)
Cordiamyia globosa	*Cordia verbenacea*	Leaf	New leaves in autumn		Peak autumn-winter (May–Jul), low summer	Multivoltine?	Maia and Tavares (2000)

Dasineura gigantea	*Psidium cattleianum*	Buds	?	Mar and Sep	?	2	Angelo (2008)
Eugeniamyia dispar	*Eugenia uniflora*	Leaf/shoot	Spring peak, cycles year round, except winter	Not in winter	Wave pattern (more galls summer)	10–19 cohorts/year	Mendonça and Romanowski (2012)
Myrciamyia maricaensis	*Myrcia lundiana*	Leaf	Year round (higher Sep-Apr)	Year round	Two wave pattern (Apr–May + Jul–Aug)	Multivoltine?	Ferraz and Monteiro (2003)
Neopelma baccharidis	*Baccharis dracunculifolia*	Leaf	Year round	Year round?	Year round	Multivoltine	Lara and Fernandes (1994)
Pisphondylia brasiliensis	*Guapira opposita*	Bud	?	Year round	Two peaks, spring and autumn	Bivoltine?	Rodrigues et al. (2007) and Silva et al. (unpublished)
Pseudophacopteron sp.	*Aspidosperma australe*	Mature leaf	Sep/Oct, nearly aseasonal	Year round	Two-wave pattern (more galls Dec/Jul)	Multivoltine	Campos et al. (2010)
Tanaostigmoses mecanga	*Calliandra brevipes*	Leaf	?	?	Two peaks (Nov–May)	Bivoltine?	Carvalho et al. (2005)
Tanaostigmoses ringueleti	*Calliandra brevipes*	Leaf	?	?	Annual increase (Feb–Dec)?	??	Carvalho et al. (2005)

New gall occurrence reports the period of the year galls are found being induced (early stages). Gall phenology means the period galls are found in any stage and/or the abundance pattern across a year. Voltinism reports whether the number of generations/cohorts per year is known (numbers) or at least supposed (only bi/multivoltinism reported). Question marks are shown when the information is unknown or not clearly deductible from the literature source this second generation could be expected to occur. A distinct situation occurs when plant phenology does not appear too restrictive. *Eugenia uniflora* (Myrtaceae) in Rio Grande do Sul State, southern Brazil, produces new leaves almost throughout the year, except for a brief period during winter (Mendonça and Romanowski 2012). However there is a clear peak of leaf production at the end of winter (a "physiological spring"), common to almost all plants irrespective of size and condition. *Clinodiplosis profusa* (Diptera: Cecidomyiidae) galls new leaves of *E. uniflora* in a single generation during this peak in Rio Grande do Sul (Mendonça, pers. obs.), although *Eugeniamyia dispar* (Diptera: Cecidomyiidae) continues to develop reaching at least ten overlapping cohorts, using new leaves produced along the year (Mendonça and Romanowski 2012). Why two similar species develop such different population dynamics is an interesting research question, requiring perhaps a deeper study on phenological and evolutionary aspects of this system.

It is important to mention an important paper in this discussion of identifying temporal patterns in plant and galler: Espírito-Santo et al. (2012) researched plant phenology of three *Baccharis* shrubs along with gall abundance every 3 weeks for a whole year. Although a longer period would be desirable for phenological studies (at least 2 years to lessen the effects of year-to-year changes), the detail and number of plant variables obtained (shoot number, shoot growth and inflorescences) makes this paper stand out. However, data for the gallers were pooled, so all galling species were considered together – thus, we could not include these species here in a population point of view. We strongly emphasize that this kind of in-depth view of the effect distinct plant characteristics can have on galler dynamics is the way forward for a better understanding of gall phenology.

Finally, studies on so-called super-hosts (plant species host to many galling species) can generate interesting phenological comparisons. Gallers being species-specific, community ecology studies on gallers usually have little to do with competition – almost each gall on a given site has its own host plant and would not compete with other gallers (but would compete against other herbivores). However, gallers on a same host plant would be competing, and thus distribution in space (see below) and time could be affected. We would thus expect phenological patterns to differ among species so as to avoid competition with other gallers. That is, unless of course there is no competition in the system, for example given no shortage of resources, or even if different organs of the plant are being galled (leaf gallers could be expected to compete more or less indirectly with flower gallers, for example). Finding differences in phenology however requires not only a proper super-host system on which to test these differences but a proper method. Oliveira et al. (2012) have developed a detailed study of a system around the super-host *Copaifera langsdorfii* (Fabaceae), recording phenophases and water stress for the plants while keeping track of gall abundance along the year for nine galling Cecidomyiidae. The result is that a general pattern of three distinct strategies in time can be found for the galler populations (details in Oliveira et al. 2012). Because these strategies (seasonal syndromes) are not clear cut, the ordination used to plot gall phenological patterns against time and against the plant phenophases (Fig. 5.1) is a way of synthetizing this complex information on a single plot. In an alternative stand to the usual classification frenzy

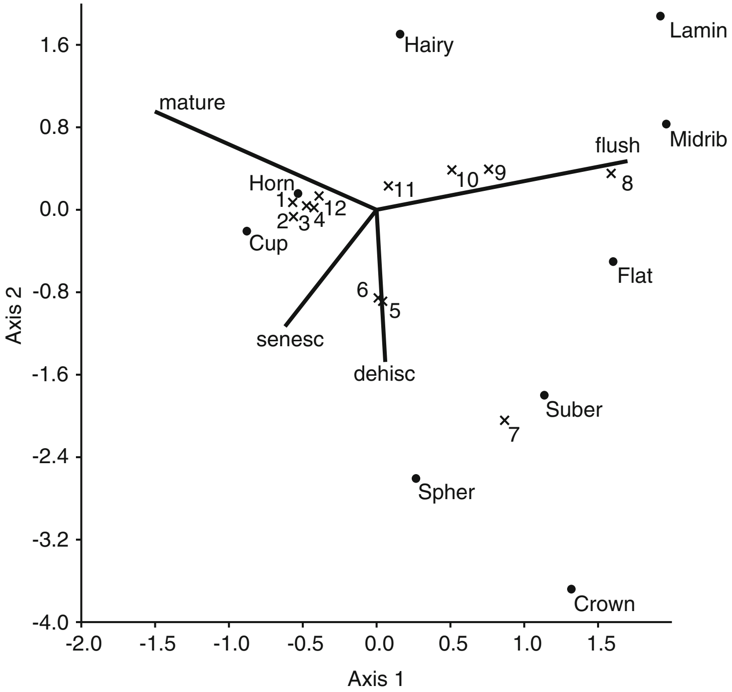

Fig. 5.1 Ordination (Canonical Correspondence Analysis) of seasonal patterns for Cecidomyiidae gall-inducers on *Copaifera langsdorfii* (Fabaceae) associated with plant leaf phenophases (vectors: mature, flushing, dehiscence and senescence) across a year. *Dots* are galling species (morphotypes, first capital letter: Horn-shaped gall, Cup-shaped, Hairy spherical, Midrib, Crown, Intralaminar, Spherical, Suberized, Flat); Xs and numbers are months (1 for January, 2 for February, etc). The closer galling species are in ordination space, the more similar their phenological abundance pattern (Adapted from Oliveira et al. 2012)

ecology sometimes still reveals in scientists, Fig. 5.1 shows that gall phenological patterns are actually rather scattered in ordination space, which could be considered a result of temporal niche differentiation. This form of analysis has potential not only for these super-host systems but also to help compare different environments, revealing the influence environmental factors can have in galler populations across time.

5.3.2 *Number of Yearly Generations of Gallers*

One of the main aspects in host-parasite ecology and evolution is the difference in generation time usually found for the species involved – the host is longer lived than the parasite (Gemmill and Read 1998). For gallers, this varies from system to system, given annual life cycles of both plant and arthropod could occur as well as trees that could host perhaps hundreds of galler generations over a lifetime.

The seasonal phenology of the galled plant organ could thus allow multiple yearly generations for the galler. Further, these generations could overlap or not, depending on the developmental time of the gallers in relation to plant organ production. In strongly seasonal environments, there are a few optimal ways to guarantee survival and reproduction in a short favorable period during the year. That has inspired researchers to even construct classifications for the known life cycles (Yukawa and Rohfritsch 2005). We will not attempt that in this chapter, because we believe we still do not know enough of the Neotropical gallers to be able to properly describe and classify their strategies.

We lack a proper knowledge on multivoltine gallers and the number of generations or cohorts they present from year to year. Table 5.1 reveals that for the 19 sources on 16 species of multivoltine gallers, we only have counts on generations for two apparently bivoltine and two truly multivoltine species (in these cases more than ten generations a year for each). It seems again that this question has not been deemed interesting enough to value a proper assessment in most work on population ecology of gallers in the Neotropics. We should pursue at least to understand whether most galls are actually univoltine or multivoltine in the tropical and temperate Neotropics – perhaps even striving to detect an expected latitudinal gradient in this proportion of multivoltinism towards the tropics.

Mopper (2005) states that deme formation and resulting fine-scale (local) adaptation to individual plants is expected for endophagous herbivores and also for host-specific herbivores. The former author argues that plant phenology is one of the aspects that herbivores should adapt to, but we would rather state that plant phenological pattern could either reinforce such evolutionary process (in seasonally produced plant organs) or disrupt it. The latter case would occur for aseasonal plant organ production, when any plant on a given population is producing the galled organs at any time, thus facilitating gene flow among plant individuals. Further, fine-scale adaptation is more probable when the number of generations of the galler *per generation of the host* is higher. This question has been explored superficially for a few (non-gall) systems (see Morgan and Buckling 2006 and references therein), and perhaps gallers and plants could be useful targets given the abovementioned range of relative generation times for either component of this coevolutionary arms race. Thus, we reinforce the need for more detailed population dynamics studies on host plant/galling arthropod systems.

5.3.3 Population Patterns in Time

Understanding population trajectories has been a crucial aim of population ecology, in order to find whether population regulation is at play or not (e.g. Sibly et al. 2007). It is supposed that longer trajectories would allow a higher statistical power to distinguish the presence of density dependence (or not). However, we have yet to see long-term following of any galler population in the Neotropics as has been done elsewhere (e.g., Redfern and Hunter 2005; Wool 1990). For most of the multivoltine species mentioned in Table 5.1, we can distinguish within-year trajectories that resemble a wave pattern: during some part of the year there is an increase in gall abundance, followed by a period (or periods) in which galls are still being produced, new generations develop, but numbers fall. Again, this could be a way of testing the effect seasonality has on galling organisms, and this wave pattern certainly stems from seasonal changes in host organ or other environmental variables. The relative importance of these variables is another question that has not been pursued. Certainly there is room for much more effort in trying to understand what are basic questions on population ecology of gallers in time. Considering the ease which galls provide in studying plant-herbivore relationships in time, this dynamics should not be relegated as an apparently low interest topic.

5.4 Mortality Factors Affecting Galling Arthropods: Relative Impacts of Bottom-Up and Top-Down Effects

Population regulation factors represent mechanisms that could theoretically explain patterns of abundance in time and space, thus being considered fundamental for the study of any population. For gallers, and for other herbivores, these forces are also directly related to the process of coevolution between insects and the other organisms with which they interact: the plants they feed on, but also importantly their natural enemies. A point of view usually taken is that of considering the coevolution between gallers and their hosts from the perspective of parasitism.

For gallers, mortality factors can be separated into top-down, such as predators and parasitoids, and bottom-up forces, mainly plant responses to gall induction. Some top-down forces on galling insects are somewhat easy to access due to the detection of parasitoids inside galls or other possible mortality factors that are noticeable, as we describe below. Bottom-up effects, on the other hand, are not that easy to detect and confirm (Ferreira et al. 1990), requiring further information on galler biology and development (for more information see Chap. 7) or on host genotypes (in the case of galler response to different plant genotypes). Mortality factors in general are frequently mentioned in biology and life history studies of some galler species, presently allowing good sources even for a little studied fauna such as Neotropical gallers.

5.4.1 Top-Down Effects

Both parasitoids and predators are common in the gall literature, with the latter including both the usual “carnivore” groups as well as herbivores eating the gall. Some studies approach a gamut of mortality factors of a given gall system, for example *Eugenia uniflora* (Myrtaceae)/*Eugeniamyia dispar* (Diptera: Cecidomyiidae), which were studied in terms of the natural enemies of the latter, represented by predatory ants and parasitoids (Mendonça and Romanowski 2002b) and recently again for their associated parasitoids and other aspects (Bierhals et al. 2012). Mortality factors in general were also compared for a few galling species between habitats differing in moisture (xeric and mesic) (Fernandes and Price 1992). The result was higher mortality rates in mesic sites due to predation (sensu *lato*), which these authors related to the adaptive significance of the galling habit to xeric conditions. On the other hand, flooding can also represent a mortality factor, yet also affecting host plants and thus possibly favouring galls (Ribeiro et al. 1998). As ecological systems are almost never simple, although most galls survive host plant flooding, they can even be eaten by fish (Cogni et al. 2003), introducing another predation source for gallers, in a different environment.

5.4.1.1 Parasitoids

Top-down effects represented by parasitoids are commonly found in the literature, and a full review is beyond the scope of this chapter. However, quantitative treatments of their prominence as mortality factors are still uncommon and of a varied quality. Information can range from indications to specific identification of parasitoid species and their impact. Indications can come for example from data on holes found in galls: 39.7 % of *Trichochermes magma* (Hemiptera: Psyllidae) galls were open by predators or parasitoids; three species of parasitoids were identified from gall rearing but no crossing of these two kinds of information was available (Briceño Lobo 1998). Contrastingly, Espírito-Santo et al. (2004) could ascertain a parasitism rate of 45.2 % on *B. dracunculifoliae* (Hemiptera: Psyllidae), with *Psyllaephagus baccharidis* (Hymenoptera: Encyrtidae) responsible for 93 % of this rate.

A variety of ecological situations can follow from parasitoid relationships with gallers. Parasitoid attack can affect the development of a gall system, such as *Baccharis dracunculifolia* (Asteraceae)/*Baccharopelma dracunculifoliae* (Hemiptera: Psyllidae) in which galls and parasitised gallers growth were unexpectedly favoured in detriment of the plant (Espírito-Santo et al. 2004). A negative relationship between gall mortality due to parasitoidism and gall wall thickness can also occur, as demonstrated for the *Quercus turbinella* (Fagaceae)/*Atrusca caprone* (Hymenoptera: Cynipidae) gall system (Fernandes et al. 1999) and for the *Nothofagus dombeyi* (Nothofagaceae)/*Aditrochus coihuensis* (Hymenoptera: Pteromalidae) system, the latter with an additional classification of gall success based on emergence-hole diameter and insect remains (Nilsson et al. 2011). In some cases, fluctuations in parasitoid and galler populations are expected to be synchronic, such as found for the *Lantana camara* (Verbenaceae)/*Schismatodiplosis lantanae* (Diptera: Cecidomyiidae) system (Dell'Aglio 2012). Parasitoids and their hosts, especially gallers, have been historically used to demonstrate density dependence (e.g. Washburn and Cornell 1979), a staple for population regulation. Parasitoids tend to be gall density dependent, for example on the above cited *B. dracunculifolia*/*B. dracunculifoliae* system (Fagundes et al. 2001). However, we believe this topic is clearly underexplored in the Neotropical gall ecology literature.

Sumoski et al. (2009) listed the parasitoids associated to the *Palafoxia feayi* (Asteraceae)/*Asphondylia* sp. (Diptera: Cecidomyiidae) system and tested the influence of urbanization on this tri-trophic interaction. Apparently, galler abundance and parasitoid diversity suffered minor impacts from this landscape change, allowing this food web to remain rather intact. This whole avenue of gallers being used in ecological applications is still not a prominent feature (see gallers as biological control agents below). Urban ecology is one of the cases where gallers could be used with profit – for the reasons mentioned in the beginning of this chapter. Although this has resulted in interesting scientific work, certainly many more systems in urban settings remain to be explored.

5.4.1.2 Predation

As for parasitoids, apart from many reports of predators attacking galls and gallers, very few quantitative treatments of predators are available for galling arthropods in the Neotropics. Reports of predation are relatively common, but less so than parasitoidism. Even predator larval cecidomyiids have been reported attacking galling cecidomyiids (*Lestodiplosis* sp. on *Lopesia aldinae*, Fernandes et al. 2010). Fernandes et al. (1987) reported a complex food web around *Anadiplosis* sp. (Diptera: Cecidomyiidae) galls on *Machaerium aculeatum* (Fabaceae), with one Vespidae species as a true, direct predator of the galler (and/or one of the parasitoids) on the gall. Similarly, a social Vespidae (yellowjacket) was seen attacking larval *Clinodiplosis profusa* (Diptera: Cecidomyiidae) inside the galls on *Eugenia uniflora* (Myrtaceae) leaves, after chewing a hole on the gall wall to access the single larva, proceeding to devour it on the spot (Mendonça 1996).

Sometimes complex predatory interactions may arise around galls and gallers. The same *Anadiplosis* sp. on *M. aculeatum* has three species of Berytidae hemipterans that suck on gall tissues whilst another herbivore, a larval Geometridae, chews through gall tissues. All these interactions lead to galling larval death and thus act as mortality sources. Should we classify these as top-down effects – but predation on the gall, not the galler – or interspecific competition, thus at the same trophic level? Almeida et al. (2006) even reported that most mortality (22.9 %) on *Anadiplosis waltheria* was caused by a lepidopteran caterpillar consuming gall tissue. There are further examples: the globular gall of an eulophid modifying *Myrciamyia maricaensis* gall (Ferraz and Monteiro 2003) is eaten by three herbivores, each from a different insect order (Coleoptera, Lepidoptera and Diptera); the first two species lead to death of the galler (the eulophid, which already had killed the original cecidomyiid galler). On the other hand, caterpillars of *Phocides polybius* (Hesperiidae) actively avoid eating galls of *E. dispar* (Mendonça 1996), chewing around the galls. It seems this phenomenon of close interaction between gallers and other herbivores, eating (or not) the galls, is quite prevalent. We should thus be looking at them more closely, both from the perspective of the ecological and evolutionary consequences for all sides involved.

A study evaluated the relationship between phenolic contents and a Cecidomyiidae gall cycle in *Aspidosperma spruceanum* (Apocynaceae) and found that the galler suppresses the chemical barrier imposed by plant phenolics, possibly being favoured by the resulting chemical protection against predators (Formiga et al. 2009). Although some aspects of the usefulness of gall chemical composition are usually considered relative to predation (from other herbivores as well as true predators) and parasitism (Hartley 1998), a proper assessment of this link is still missing from the literature. Reports on gall chemical composition are on the rise in the Neotropics in the last decade or so (e.g., Soares et al. 2000; Damasceno et al. 2010), and thus we could hopefully expect this link to be made in the near future.

5.4.1.3 Inquilinism

Inquilines present a distinct relationship to gallers: because they do not consume gallers directly, they are not predators nor parasitoids. They can cause mortality, though, and again the question is whether they can be considered very specialised herbivores, thus at the same trophic level as gallers, or actually top-down effects. Although inquilines were mentioned previously, and a few examples can be found in the literature, we would like to point out two systems in which inquilines modify galls and represent more than mortality sources. *Hylaeogena thoracica* is a buprestid beetle inducing ovoid leaf galls on *Amphilophium paniculatum* (Bignoniaceae) (Medianero et al. 2007). Galls are covered in hair-like projections, and occur on leaf veins. The attack of a curculionid beetle, *Philides anthonomoides*, kills the galler and renders the galls smaller and with less, longer projections much like thorns. Conversely, *M. maricaensis* galls can be modified by two species of eulophid microhymenopterans (Ferraz and Monteiro 2003), both leading to larger galls. One species modify galls so they remain mostly like the original one, apart from size. The other inquiline, however, leads to a much engorged gall with many chambers, completely distinct in structure. More than exceptions, the first eulophid alters more than 13 % of the galls Ferraz and Monteiro (2003) found, and the second eulophid attacks more than 44 % – thus more than half the galls produced by this galler result "inquilinised". Apart from representing a very important source of mortality, the danger here is that the gall altered by the inquiline may not be recognised as such. In a population study, this could result in a serious miscounting of mortality impacts, and in community studies these could be considered multiple galls on a given plant species, elevating galling species richness. Again, complex interaction webs around gallers justify the interest deposited in them and the need to open one's eyes to the possibilities this ecosystem engineered systems provide.

5.4.2 Bottom-Up Effects

Ferreira et al. (1990) studying the *Lonchocarpus guilleminiaus* (Fabaceae)/ *Euphaleurus ostreoides* (Hemiptera: Psyllidae) system in terms of mortality factors during gall development were the first to report the possibility of plant responses to gall induction. This came from the observation of very young galls vanishing from the leaf blade and being accounted as other mortality factors. Since then, many studies have considered that plants can respond to gall induction and directly affect gall survival (Fernandes 1990, 1998), ultimately resulting in an adaptive response of gallers to this selective pressure as further detailed in Chap. 7 for gall distribution. The most studied bottom-up effect is the hypersensitive reaction, which seems to be widespread across plant taxa (Fernandes and Negreiros 2001). A less commonly reported bottom-up effect, plant organ abscission, is known for a few cases of gallers in the Neotropics. Here we focus on the influence that considering bottom-up effects can exert on gall abundance for gall systems studies on the Neotropics.

5.4.2.1 Hypersensitivity

Study cases from the Neotropics are along the first to detect plant hypersensitivity reactions (HR) against gallers as important to their population ecology (Fernandes 1990). Quite a few systems from the Neotropics and elsewhere (Cornelissen et al. 2002) made clear this was a rather common phenomenon – and thus the idea that mortality for arthropod gallers was mainly due to natural enemies from trophic levels above had to be revisited. One of the main examples was *Bauhinia brevipes* (Fabaceae) using HR against *Schizomyia macrocapillata* (Cecidomyiidae), leading to a gall-inducing failure rate of more than 90 % (Cornelissen and Fernandes 1998). Another example is *Eugenia uniflora*, which reacts to galling by *E. dispar* by surrounding early galls with engorged cells which die and lead to galling larval death as well, which is perceived as a small reddish spot on the leaves (Mendonça 1996).

HR can interact with a series of ecological factors, both from the side of the plant and the galler. Araújo et al. (2011b), for example, found that smaller and less vigorous branches presented more hypersensitivity reaction to galls. The authors suggest that galler preference for more vigorous branches could be an attempt to escape hypersensitivity reaction and not directly a response to plant vigour. Clearly, much more remain to be uncovered on HR and the impact this reaction has on galler population ecology and ultimately evolution.

5.4.2.2 Plant Organ Abscission

The early abscission of galled plant organs can be regarded as a form of plant defence (Faeth et al. 1981). The direct advantage for the plant would be a reduction in future losses to a nutrient sink, and an indirect advantage would be the potential increase in mortality risk imposed on the galler. Any lost organ also means a loss in investment for the plant, but that is dependent on plant size in terms of number of organs. Gallers recorded suffering mortality from plant organ abscission in the Neotropics appear to be few, and it is difficult to evaluate whether this represents an overlooked phenomenon or actually an uncommon mechanism for host plants. One source reports directly on the issue and evaluates the population consequences of organ abscission for the galler, in the system *Neea madeirana* (Nyctaginaceae)/*Bruggmannia* spp. (Cecidomyiidae) (Fernandes et al. 2008). Galled leaves are abscised more frequently than healthy ones, but when on the ground galls decay more slowly than healthy leaves or surrounding healthy leaf tissue, forming "green islands". Nevertheless, mortality due to pathogens is five times higher on the ground, and thus abscission may be considered an effective defence against gallers.

Another study on leaf abscission as a response to gallers is that of Constantino et al. (2009) on *Clusia lanceolata* (Clusiaceae)/*Clusiamyia nitida* (Cecidomyiidae). A high number of galls on a leaf or galls formed close together coalescing on a leaf lead to deformed leaves, and these suffer abscission. No further information is there on the mortality impact this has on gallers. There are three other systems for which leaf abscission in response to galling has been reported. On *Caryocar brasiliense* (Caryocaraceae) a gall induced by an undescribed *Eurytoma* (Hymenoptera: Eurytomidae) is reported as very abundant in northern Minas Gerais State, in Brazil (Leite et al. 2009). When in large numbers on a leaf, galls cause premature abscission (Oliveira 1997); again, no reports on mortality for the galler are available. The other two systems are not in the peer-reviewed literature. Mendonça (1996) observed premature leaf abscission (with abscission lines forming in petioles) in *Eugenia uniflora* (Myrtaceae) associated with the presence of galls of *Eugeniamyia dispar* (Diptera: Cecidomyiidae). Higher gall densities on a leaf lead to higher chances of leaf fall. Fallen galled leaves mostly born mature galls, from which the galler had already left, and thus this may not represent a mortality factor. Miranda et al. (2009) mention the "green island" effect in the lab for a gall on *Miconia* cf. *cinnamomifolia* (Melastomataceae) (without providing information on the galler), arguing that this may be a counter-response of gallers to leaf abscission as plant defence.

Overall, it appears there is not enough information on plant organ abscission resulting from galls in the Neotropics to consider it clearly as a plant response and a mortality factor important there. Perhaps it may be a relatively difficult phenomenon to record, and thus the most likely possibility is that it is simply overlooked.

5.4.2.3 Host Quality

Abundance is one of the variables that can be used to test for the effects of various plant characteristics on gallers. The nutrition hypothesis, which states that gallers manipulate plant quality locally (inside galls) and gain from that in relation to free-feeding arthropods, was tested and did not apply for two gall inducer-host plant systems (Scareli-Santos and Varanda 2009). However, galling insects on *Qualea parviflora* (Vochysiaceae) were more affected by leaf quality than did free-feeding insects (Gonçalves-Alvim et al. 2004).

Another still nearly unexplored aspect of the galler-host plant relationship in the Neotropics is genetics. A few studies evaluated differences in gall abundance due to distinct host plant genotypes. In terms of suitability to gall induction by a gall midge, Moura et al. (2010) found differences of infestation levels among genotypes. Similarly, Thomazini et al. (2003) evaluated 22 sorghum (*Sorghum bicolor*, Poaceae) genotypes and found that only one genotype accounted for approximately 36 % of the adults emerged whilst some did not present any emerged adult; and no parasitoid was found on the sampled galls. It can be expected, as genetic studies become cheaper and thus more common, that in the near future we would learn much more on the response galler populations give to the genetic structure of their host populations.

5.5 Intraspecific Competition in Galling Arthropods: Evidence from the Neotropics?

Since some gallers are restricted to the use of plant meristems to induce their galls, this could lead to situations where gallers would be resource limited and that can result in competition. The use of different host plant organs by distinct galling species can in some cases be an indirect evidence of interspecific competition avoidance. However, in cases of resource limitation for a given species, intraspecific competition can be expected to remain.

Intraspecific competition in gall-inducing insects can basically occur in two situations: (1) when females are searching for oviposition sites or (2) when larvae are feeding. Additionally, for galling thrips another situation for competition was registered, as addressed by Crespi (1992), based on the fighting behaviour some males present. In such case, male thrips have access to developing galls and fight for the female foundress, even presenting specialized morphology to fight. Besides this fighting behaviour, the other situations of competition are not so conspicuous and are indirectly inferred, as performed in some studies other than the Neotropics (Whitham 1978; Craig et al. 1990, 2000; Hess et al. 1996; Larson and Whitham 1997) and a Neotropical one (Souza et al. 2001).

The Neotropical evidence of intraspecific competition in galling arthropods was inferred by phenotypic plasticity of a galler forming multilocular galls (Souza et al. 2001). Thereby, competition would arise between developing larvae and, in such case, an analysis of each stage size was performed in order to verify whether galls with more larvae had smaller occupants, which was the result found. Additionally, an evidence of competition avoidance coupled with an enhancement of resource use was found, since growing in low quality sites was not an obstacle to reach maturity, even if this resulted in smaller adults. Another study found no evidence of intraspecific competition along a host ontogeny for two galling insect species, but interspecific competition was inferred by population shifts of these species besides apparently having enough oviposition sites (Fonseca et al. 2006). Competition between different species was evaluated for three insect species that induce galls on *Bauhinia brevipes* (Fabaceae), but no evidence of interspecific competition was found (Santos and Fernandes 2010); the authors highlighted the difficulty in detecting interspecific competition and its effects, as previously pointed out by Fritz et al. (1987) for both intra-and interspecific competition for gall-forming sawflies.

5.6 Galls Are Not Gallers: What of the Other Life Stages?

Galls are literally a plant formation involving the insect offspring, not an insect itself (Isaias and Oliveira 2012). However, most studies consider galls as whole individuals which theoretically play the role of an organism. In some cases, this could be close to the truth, but some galls embrace two or more larvae that may not all become adults and can lead to a misinterpretation of population dynamics.

The difficulty in rearing adults of some gall midge species, especially tropical ones, represents an obstacle to our understanding of these systems. Some species pupate in the soil, others stop their development once the host organ is removed from the plant, and we must also consider problems with fungi. Adult insects reared from galls, in turn, are not guaranteed to be the gall inducer, since the obtained insect could be a parasitoid or an inquiline, as may be the case for *Dolichophaonia gallicola* (Diptera: Muscidae) on *Pteridium aquilinum* (Pteridophyta) (Monteiro and Oda 1999). Eggs, on the other hand, are difficult to detect due to their small size, and only a few studies presented egg counting (Angelo 2008; Mendonça and Romanowski 2012; Souza et al. 1998), which would be crucial information to include in any life tables as we present in the following topic.

Considering galls only morphologically can also lead to some mistakes. Despite gall morphotypes being reliable surrogates of galler species when associated with host plant species, some species are oligophagous and can even induce galls on hosts belonging to more than one plant genus (Carneiro et al. 2009). Additionally, sexual dimorphism influencing gall morphology was recorded for *Pseudotectococcus rolliniae* (Hemiptera: Eriococcidae) galls on *Rollinia laurifolia* (Annonaceae), with differences in galler development between sexes (Gonçalves et al. 2005). One way out of this problem may hide in the intensive use of molecular tools. This would not be an answer to all the problems above, but identification, and for example ascertaining a given adult arthropod is a galler, inquiline or parasite would be easier. Nevertheless, dealing with the behaviour and responses of adult gallers is paramount to solve questions related to sex and mate choice, oviposition and gall formation site choice, dispersal and so on.

5.7 A Call for Life Table Analysis Work with Neotropical Galling Arthropods

Galling arthropods can present from one to many generations throughout a year, as we addressed above. The distinct life histories recorded in such a few studies from the Neotropics represent an opportunity for developing more studies on this largely unexplored issue. Additionally, it is relatively easy to access life table data for gallers (Redfern and Cameron 1978; Yukawa 2000). However, there are few studies on all aspects regarding life table analysis for Neotropical gallers and none presenting a structured life table. Most studies only present data on one aspect of a species population dynamics, such as the ones presented in previous topics (e.g. mortality), or more specifically the lack of some life stages like eggs (Espírito-Santo and Fernandes 2002). Studies present life cycle duration (Andrade et al. 1995; Angelo 2008; Ferreira et al. 1990; Souza et al. 1998); even in taxonomic notes (De Santis and Fernandes 1989; Gagné et al. 1998; Madeira et al. 2002), sometimes divided in generations (Angelo 2008; Mendonça and Romanowski 2002a); some present information on gall survivorship (Espírito-Santo and Fernandes 2002; Espírito-Santo et al. 2004; Ferreira et al. 1990; Souza et al. 1998) or even information similar to life tables (Espírito-Santo and Fernandes 2002; Espírito-Santo et al. 2004; Mendonça and Romanowski 2012; Souza et al. 2001). Some of these quantitative information come along with a description of developmental phases (Angelo 2008; Ferreira et al. 1990; Mendonça and Romanowski 2002a; Souza et al. 1998) or are presented only descriptively (Arduin et al. 2005; Formiga et al. 2009; Gonçalves et al. 2005; Sá et al. 2009). Additionally, it is interesting to point out the sexual dimorphism on gall morphology recorded for *Pseudotectococcus rolliniae* (Hemiptera: Eriococcidae) (Gonçalves et al. 2005), which would allow or facilitate the construction of a life table with information on sexes.

There are two examples of Neotropical species that were identified and then had their life cycles described, and could thus be the first targets for life table studies. The gall midge *Dasineura gigantea* (Cecidomyiidae) galling *Psidium cattleianum* (Myrtaceae) (Angelo and Maia 1999; Angelo 2008), and another gall midge *Eugeniamyia dispar* (Diptera: Cecidomyiidae) galling *Eugenia uniflora*, another Myrtaceae host species (Maia et al. 1996; Mendonça and Romanowski 2002a), the latter being also studied in respect to its natural enemies (Mendonça and Romanowski 2002b) and population ecology (Mendonça and Romanowski 2012). The gall midge *Prodiplosis longifila* had some aspects of its biology studied (Peña et al. 1989), probably because of the economic importance it represents as a pest, as we describe in the next topic.

5.8 Galls Are Mortality Factors Too: Plant Biological Control Using Neotropical Gallers

Throughout this chapter we based our view on influences upon gallers but not galler influence on their hosts. On the one hand, galler ecological specialization can be considered a speciation driver instead of an evolutionary dead-end (Hardy and Cook 2010), and it is also an important attribute for weed biological control, despite being underestimated (Muniappan and McFadyen 2005). On the other hand gallers can be subjected to parasitism by generalist parasitoids that limit their effectiveness, but parasitism unpredictability and significant damage to the host sustains gallers as good candidates for biological control agents (see Muniappan and McFadyen 2005).

Some gall midges are reported as agronomic pests worldwide, such as *Mayetiola destructor* (Say 1817) on cereal crops including barley, wheat and rye, and *Orseolia oryzae* on rice (Riley 1881). A Neotropical example is the gall midge *Prodiplosis longifila*, widely reported as a pest for many plants, such as alfalfa, castorbean, green beans, potato, tomato, wild cotton, wormseed (Gagné 1994) and citrus (Peña et al. 1987, 1989). Examples in Brazil, all cecidomyiids, are *Iatrophobia brasiliensis* on manioc (*Manihot esculenta*, Euphorbiaceae) (Rübsaamen 1916), *Clinodiplosis profusa* on pitanga (*Eugenia uniflora,* Myrtaceae) (Maia 2001), *Dasineura gigantea* on guava (Angelo and Maia 1999), *Stenodiplosis sorghicola* on sorghum and *Clinodiplosis* sp. on hog plum (*Spondias mombin*, Anacardiaceae). The last two examples were further evaluated for infestation differences among host plants genotypes as mentioned above (Thomazini et al. 2003; Moura et al. 2010).

One invasive Neotropical plant merited a search for a suitable biological control agent among various gallers: *Psidium cattleianum* (Myrtaceae). This plant is a conservation problem in Hawaii where it grows in large numbers and covers large areas (Wikler et al. 2000). Apart from a stem and a leaf gall, a seed gall induced by a hymenopteran later described by DalMolin et al. (2004) as *Prodecatoma carpophaga*, was considered suitable since it kills seeds inside the fruits (Wikler et al. 2000). It thus actually acts like a parasitoid of the plant, not a parasite. Another example is the neotropical species *Clinodiplosis alternantherae* (Diptera: Cecidomyiidae) as a good candidate for the control of the alligator weed *Alternanthera philoxeroides* (Amaranthaceae) in Australia and North America (Gagné et al. 2004). Another study evaluated how mortality factors act upon the galler *Anisodiplosis waltheriae* (Diptera: Cecidomyiidae) on the invasive plant *Waltheria indica* (Sterculiaceae) in the Brazilian Atlantic forest and concluded that due to the low parasitism rate the galler could be employed for its host biological control (Almeida et al. 2006).

Most studies focus on the effects gallers exert on their host plants, either on plant growth or plant reproduction. For instance, Silva et al. (1996) showed the influence *Tomoplagia rudolphi* (Diptera: Tephritidae) galls exerts on the architecture and seed viability of its host plant *Vernonia polyanthes* (Asteraceae), which corroborates the hypothesis that galls are plant parasites (Price et al. 1986, 1987). Galled stems produced more shoots, on average, than ungalled ones. Seeds on galled stems were lighter and had smaller total percentage germination of seeds than those on ungalled stems. Similarly, Fernandes et al. (1993) reported the effects of *Neolasioptera* sp. (Diptera: Cecidomyiidae) stem galler on its host *Mirabilis linearis* (Nyctaginaceae) lifetime fitness and number of viable fruits, both of which are reduced. Other studies report gallers affecting host reproductive effort (Barrancos et al. 2008; Fernandes and Ribeiro 1990) or individual leaf fitness (Constantino et al. 2009; Gonçalves et al. 2005; Souza et al. 2006) or shoot fitness (Fernandes and Ribeiro 1990; Gonçalves-Alvim et al. 1999b; Lara and Fernandes 1994; Souza et al. 1998) or even the whole plant (Fernandes et al. 2007), or are restricted to describing gallers and report their damage on their hosts (Cano et al. 2009).

5.9 Remarks and Conclusions

Research on population ecology of galling arthropods in the Neotropics has shown substantial progress in the last decades. Different and sometimes innovative aspects regarding important questions on galler biology and ecology were addressed and constitute important evidences from highly diverse regions characterized by communities with complex interactions. However, it is clear that we are yet far from a reasonable knowledge on galling arthropod populations.

The opportunity offered by galls and their gallers, especially arthropods, have been explored previously, using galls as useful tools for studies in population ecology. We in this chapter summarize some of the work done in the Neotropics, but there are excellent examples from elsewhere: Europe (e.g. Stone et al. 2002), United States (e.g. McGeoch and Price 2004), Japan (e.g. Yukawa 2000), and Australia, the latter represented by studies of thrips galling *Acacia* (Fabaceae) (e.g. Crespi et al. 2004).

Some limitations are easily pointed out throughout the text, but that does not mean they are easy to overcome or stem necessarily from a lack of interest. The main question may be the lack of taxonomic knowledge on the extraordinary Neotropical diversity. Primarily to the study of a given population, the species concerned is expected to be properly identified. In some situations we face quite interesting gall systems but with no verifiable record or identification, no available specialised personnel, and thus we end up storing away information until we are able to have proper identifications (*pers. obs.*). The lack of available information on the natural history of gallers is also substantial. Most studies in the Neotropics deal with broader levels such as community and ecosystems, since morphotyping galls is considered an easy and trustable method to employ in the field, for example. However, we need to build a bridge between these higher level studies and the population ecology that remains theoretically and practically the base upon which they are built.

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Chapter 6
Bottom-Up Effects on Gall Distribution

Milton Barbosa and Geraldo Wilson Fernandes

Abstract The global pattern of insect gall distribution predicts that the highest richness of such insect guild is found in hot, dry and nutritionally poor environments. In search for a mechanism for this pattern, most studies have focused on top-down effects, such as predation and parasitism, which could potentially be weakened in those stressful environments and favour gall survivorship. In this chapter, however, we examine bottom-up effects that could also be suppressed under environmental stress and, therefore, create suitable hosts for galling insects. We discuss how plants can defend against galling insects and the role of such defences in shaping the pattern of gall distribution.

Keywords Hypersensitive reaction • Damage induced leaf abscission • Leaf turnover

6.1 Introduction

The global pattern on the distribution of galling insects predicts that the highest richness of such insect guild is found in hot and dry environments, situated between 25° and 45° of latitude, or equivalent altitudes in the tropics (Fernandes and Price 1988; Price et al. 1998). The mechanism proposed to explain how hygrothermal stress could lead to a higher richness of galling insects was the differential gall mortality rate between mesic and xeric habitats (Fernandes and Price 1991, 1992;

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Ribeiro-Mendes et al. 2002). Top-down effects would be weakened in harsh environments, where natural enemies such as parasitoids, pathogens and endophytic fungi would present lower incidence (Fernandes and Price 1991, 1992; Lara et al. 2002; Ribeiro-Mendes et al. 2002; Ribeiro and Basset 2007). This would have contributed to the speciation and radiation of galling insects in such *enemy-free spaces* (Fernandes and Price 1991, 1992).

In fact, recent works have also revealed high richness of galling insects in lowland tropical rainforests in Panama (Medianero and Barrios 2001) and in the Brazilian Amazonia (Julião et al. 2005; Julião et al. Unpublished). These rainforest surveys were conducted at the forest canopies, in contrast to most previous tropical surveys, which were carried out at the understorey (Fernandes and Price 1991; Price et al. 1998). The upper canopy present harsh conditions due to hydraulic stress at the upper branches and exposure to wind and high solar radiation (Parker 1995; Bell et al. 1999; Basset 2001), consequently the outer layer of a tropical forest is much similar to the Mediterranean vegetation than to the understorey vegetation (Bell et al. 1999). As a result, the forest canopy is also thought to be an *enemy-free space* and show lower gall mortality rates (Ribeiro and Basset 2007). Therefore, the latitudinal pattern of gall distribution proposed by Fernandes and Price (1988) and Price et al. (1998) need to incorporate the high diverse rainforest canopies of lower latitudes as a gall speciose habitat.

Other studies have found a high richness of galls in mesic sites, where hygrothermal stress is absent but other kinds of stresses can be identified, such as low nutritional content of soils, mainly phosphorus (Sobrado and Medina 1980; Blanche and Westoby 1995, 1996; Wright and Samways 1996, 1998; Blanche 2000; Blanche and Ludwig 2001), or seasonal flooding (Julião et al. 2005; Julião et al. Unpublished; see also De Simone et al. 2003). Ribeiro et al. (1998a) report a greater incidence of galls in flooded than non-flooded individuals of the Neotropical tree *Calophyllum brasiliense* (Clusiaceae) in an area of the Brazilian Atlantic rainforest. These studies imply that differential gall mortality by natural enemies in xeric habitats (Fernandes and Price 1991, 1992; Ribeiro-Mendes et al. 2002) may not be a sufficient explanation for the global distribution of galling insects since that some mesic sites can still show high diversity of galls. Furthermore, they indicate that environmental stress of several kinds, and not only hygrothermal, seems to be the key factor behind gall distribution, since it is the common factor shared by habitats with highest richness of galling insects.

It would be imperative to uncover the processes through which environmental harshness translates into selecting forces for higher incidence of galling insects in harsh habitats. In previous studies, most attention has been drawn to the consequence of environmental stress for top-down control on gall populations (Fernandes and Price 1991, 1992; Lara et al. 2002; Ribeiro-Mendes et al. 2002; Ribeiro and Basset 2007; for more information see the chapter by Toma and Mendonça in this book). The extents to which the bottom-up effects (plant driven pressures) on galling insect populations are compromised by adverse conditions remain largely unexplored.

The usual plant defences against free-living herbivores are generally ineffective against gall formation. Actually, galling insects can even use those habitual plant defences to improve their own protection, by concentrating plant chemical compounds at the external layers of the galls (Janzen 1977; Taper and Case 1987; Cornell 1983; Fernandes and Price 1991; Schultz 1992; Fernandes 1998). Galling insects can substantially reduce host plant fitness by reducing productivity, compromising the establishment of saplings, inducing premature leaf abscission (Oliveira 1997; Fernandes et al. 2008) and redirecting photoassimilates (Kirst 1974; Kirst and Rapp 1974; Rapp and Kirst 1974; Larson and Whitham 1991; Leite et al. 2007). Therefore, specific mechanisms of plant defence against galls must have evolved from such extremely specialized interaction.

If the effectiveness of the defences against galls is mediated by environmental conditions, they could clearly play a significant role in determining the regional and global distribution of galls. The suppression of bottom-up forces on galls due to environmental stress could increase host plant security to larval development. Bellow, we describe three of these mechanisms that are though to act as plant defences against galling insects, and, not surprisingly, they all have the potential to be suppressed under harsh environmental conditions: (i) hypersensitive reaction; (ii) damage induced leaf abscission; and (iii) fast leaf turnover.

6.2 Hypersensitive Reaction

The hypersensitive reaction (HR) has been recognized as an important mechanism whereby plants defend against endophagous herbivores such as mining and galling insects (reviewed by Fernandes 1990, see also Fernandes et al. 2000, 2003; Fernandes and Negreiros 2001; Ollerstam et al. 2002; Höglund et al. 2005; Santos et al. 2008). HR is a localized induced defence that can be detected as a rounded dark brown halo of necrotic tissue around the gall induction site (Fernandes and Negreiros 2001; Fig. 6.1). It results from a series of plant morphological, biochemical and physiological processes leading to the localization, confinement and death of the attacked tissue, and thus of the intruder (reviewed by Fernandes 1990, see also Fernandes et al. 2000).

Previous studies suggest that HR have evolved very early, probably against pathogens and nematodes at first (Maclean et al. 1974; Fernandes 1990), and represents by far the major mortality factor against galling insects across a wide array of plant taxa (Fernandes and Negreiros 2001). For instance, Fernandes (1998) report a 90–95 % mortality of galls of a Cecidomyiidae (Diptera) by HR on the host plant *Bauhinia brevipes* Vog. (Fabaceae) in Brazil. Therefore, only a few galling insects were available to be attacked by natural enemies such as parasites, predators, and pathogens. Similarly, Fernandes and Negreiros (2001) recognize HR as the most significant mortality factor against gall formation in seven out of eight plant species studied in three different vegetation types of south-eastern Brazil. In four species, HR killed more than two-thirds of the galling insects. Fernandes et al. (2003) also found that HR was the cause of mortality for more than 77 % of galling cecidomyiids (Diptera: Cecidomyiidae) on

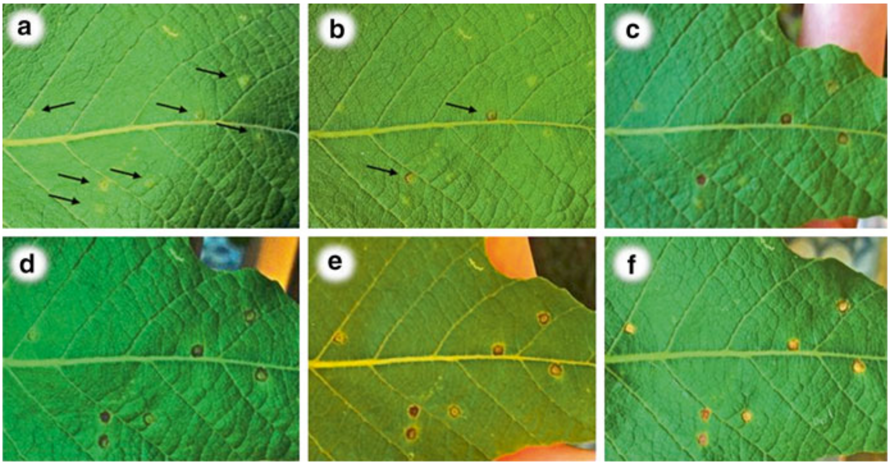
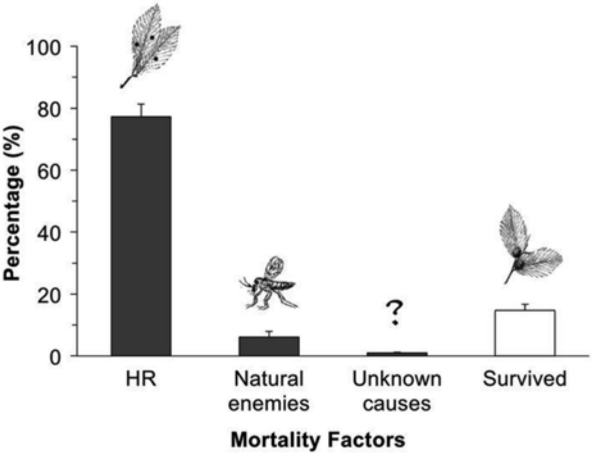


Fig. 6.1 Progression of hypersensitive reactions (*HR*) against galls of *Eurytoma* sp. (Hymenoptera: Eurytomidae) on a single leaf of *Caryocar brasiliense* Camb. (Caryocaraceae) over a 15 days period; (**a**) day 1: galls in initial stage (*arrows*) can be seen as clear spots; (**b**) day 2: the first signs of HR can be identified as a dark halo around two of the galls (*arrows*); (**c**–**e**) days 4–6: necrosis of the circled tissues and more HRs appear; (**f**) day 15: necrotic tissues resulted from HR remain as brown spots on the leaf

Fig. 6.2 Percent Mortality caused by hypersensitivity reaction and by natural enemies (parasitism, predators, pathogens, and unknown factors) on the populations of two cecidomyiid galling insects (*Mikiola fagi* and *Hartigiola annulipes*) on *Fagus Sylvatica* (Modified after Fernandes et al. 2003)



Fagus sylvatica L. (Fagaceae), in central Germany, which is several times greater than the mortality caused by natural enemies (Fig. 6.2).

HR can potentially be inhibited by high temperature (37 °C; Deverall 1977; Király 1980; Fernandes 1990) and is less effective under other hard conditions, such as water limitation (Puritch and Mullick 1975; Christiansen et al. 1987). The triggering of HR is also dependent on availability of energy (Berryman 1988;

Madden 1988; reviewed by Fernandes 1990). Therefore HR has the potential to be suppressed under stressful conditions and would then favour higher gall occurrence in harsh environments.

6.3 Damage Induced Leaf Abscission

Premature leaf abscission induced by attack have been recorded in several plant species as a defence against herbivorous insects, including endophagous insects such as galling and leaf-miners (Clarke 1962, 1963; Faeth et al. 1981; Williams and Whitham 1986; Risley and Crossley 1988; Fernandes and Whitham 1989; Stiling et al. 1991; Preszler and Price 1993; Yamazaki and Sugiura 2008; Fernandes et al. 2008; Bairstow et al. 2010). The premature abscission of damaged organs can be seen as an adaptive defence to reduce the loss of investing on an attacked tissue. The plant may have higher carbon gain by launching a new leaf than by maintaining the attacked one (Harper 1989), especially if the leaf is still immature (Kikuzawa 1991, 1995), and require further investment in carbohydrates and nitrogen, and if there is reabsorption of nutrients from the leaf through senescence (Woolhouse 1978; Grime 1979; Chapin 1980; Aerts 1990; Killingbeck 1996).

Induced leaf abscission may also be advantageous by reducing the insect herbivore population in future attacks (Yamazaki and Sugiura 2008). In order to be effective though, it is necessary that the abscission prevents the insect development or at least reduces its larval performance (Stiling and Simberloff 1989; Fernandes et al. 2008). However, at least some species of galling insects were able to evolve a strategy in which the larva maintain a tight control over the cells adjacent to the galls on the abscised leaves allowing the adults to emerge, a mechanism named *green island effect* (Fernandes et al. 2008). Fernandes et al. (2008) report a higher proportion of galled leaves on the forest floor than in the crown of the Amazonian tree *Neea madeirana* (Nyctaginaceae), which hosts two galling species of *Bruggmannia* (Diptera: Cecidomyiidae). For both galling species there were evidences of continued activity and health of the gall tissue after leaf abscission, while the rest of the leaf senesced and decayed. In spite of that, for both gall types, mortality by natural enemies, mainly pathogens, was at least five-fold greater on abscised leaves than on galls retained in the tree crown (Fig. 6.3).

The drawback of the induced leaf abscission is that it can reduce plant growth and fitness (Lowman 1982; Becker 1983; Crawley 1983; Wright et al. 1989). Thus, under stressful conditions, this type of induced defence would be constrained in detriment of the cost of leaf construction (Faeth et al. 1981; Coley et al. 1985; Williams and Whitham 1986; Preszler and Price 1993). Especially if there is no reabsorption of nutrients, leaf loss would have a substantial impact on the nutritional status of the plant and is restricted to plants not subject to nutrient limitation (Grime 1979; Chapin 1980; Aerts 1990). Indeed, more favourable habitats, such as rainforests, generally have higher rates of leaf abscission (Coley et al. 1985). Thus, plants in adverse environments, with a higher cost of leafing, would be compelled to conserve their leaves (Chapin 1980; Mooney and Gulmon 1982; Coley 1988;

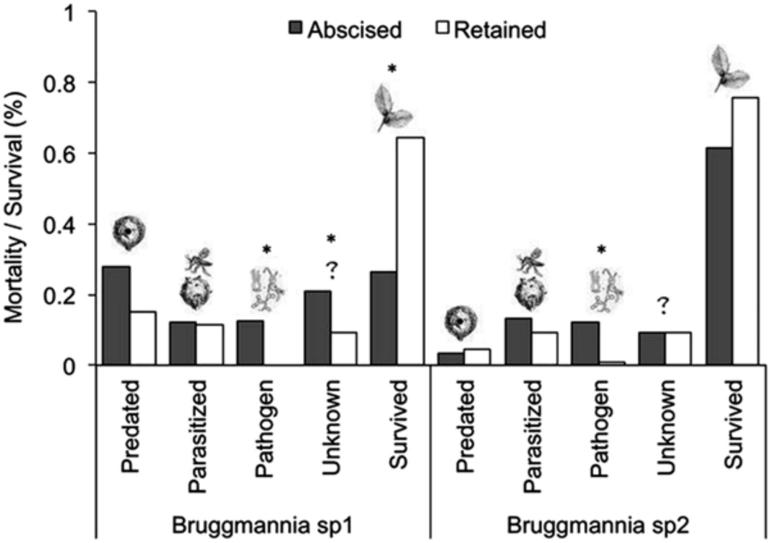


Fig. 6.3 Percent survival and mortality by predators, parasites, pathogens, and unknown factors on galls induced by *Bruggmannia* sp.1 and *Bruggmannia* sp.2 on retained and abscised leaves of *Neea madeirana.* (*) Indicates significant differences at $p < 0.05$ (Data from Fernandes et al. 2008)

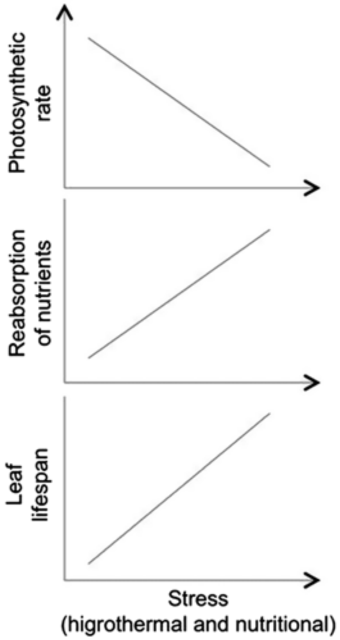
Fernandes and Price 1991; Herms and Mattson 1992) at the expense of tolerating endophagous insects, such as the gall inducing ones.

6.4 Fast Leaf Turnover

Plants growing in nutrient rich environments can adopt a strategy of carbon gain involving rapid leaf turnover as a way to escape herbivores (Coley et al. 1985; Wright and Cannon 2001). A short leaf lifespan can limit the time available for the development of endophagous insects. Fernandes and Price (1991, 1992) argue that long-lived leaves represent a more stable and predictable resource in space and time, increasing the chances of colonization and survival by galling insects.

In stressful environments longer leaf lifespans may be necessary to compensate for the low rates of return on investment in leaf construction (Givnish 1979; Chabot and Hicks 1982; Mooney and Gulmon 1982; Turner 1994). Thus, plants with increased leaf longevity allow light capture to outweigh the cost of leafing (Monk 1966; Chapin 1980; Coley et al. 1985; Gulmon and Mooney 1986; Wright et al. 2002). Furthermore, the reabsorption of nutrients in the process of leaf senescence represents a significant saving for plants under low nutrient availability (Grime 1979; Chapin 1980; Aerts 1990; Killingbeck 1996). Consequently, defending and maintaining the leaves to ensure the reabsorption of nutrients before leaf death should be more important in nutrient-poor habitats (Wright and Cannon 2001; Fig. 6.4).

Fig. 6.4 Common variation in plant photosynthetic rate, reabsorption of nutrients through senescence, and leaf lifespan, in response to environmental stresses caused by temperature, water and nutrients



Indeed, Reich et al. (1991), assessing 21 Amazonian trees, observed an inverse relationship between leaf lifespan and both photosynthesis and leaf nitrogen content (Fig. 6.5). Therefore, the selective pressure for long-lived leaves, appropriate for galling insects, would be higher in nutrient-poor environments (Wright and Cannon 2001).

6.5 Galls on Stressed Plants

Host-specific species tend to use host plant resources that are abundant and predictable in space and time (Bernays and Chapman 1994). Galling insects are not only highly specialized but also sessile and therefore particularly dependent on the stability and predictability of their hosts for safe larval development. Plants under environmental stress seem to be the most secure hosts for galling insects not only because they have weaker defences against gall formation, but also because they are better protected against free-feeding herbivores that could accidentally or intentionally prey on the galls, as discussed bellow (Cornell 1983; Schultz 1992; Price et al. 1998; Lara et al. 2002).

Previous studies have associated the global pattern of galling insect species distribution with leaf sclerophylly (Price et al. 1998; Ribeiro et al. 1998b; Ribeiro 2003; Lara et al. 2002; Ribeiro and Basset 2007) because the most gall speciose

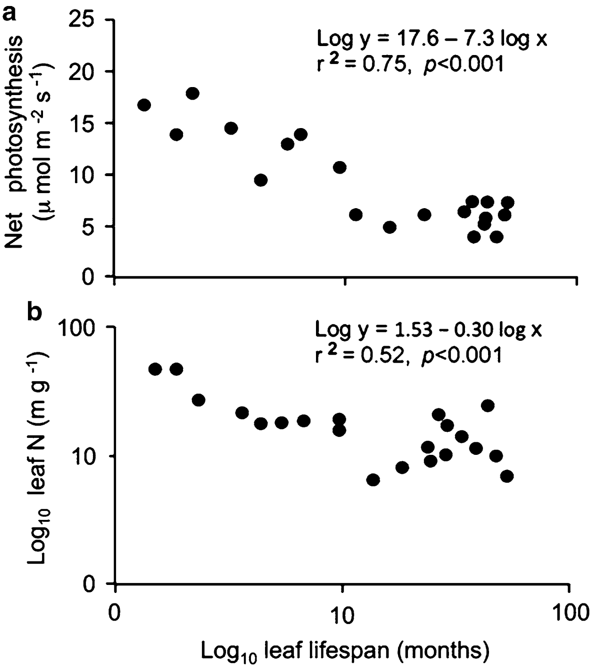


Fig. 6.5 Leaf lifespan relationship to: (**a**) area-based net photosynthetic rate (**a**; mol m^{-2} s^{-1}) and (**b**) weight-based leaf nitrogen concentration (mg g^{-1}) for sun leaves of 21 Amazonian tree species. Leaf lifespan and nitrogen concentration data were log (base 10)-transformed to linearize the regression functions (Modified after Reich et al. 1991)

habitats in the world are sclerophyllous Mediterranean types of vegetation (Fernandes and Price 1988; Price et al. 1998) or Mediterranean-like vegetation, such as the upper canopy of mesic tropical forests (Medianero and Barrios 2001; Julião et al. 2005; Julião et al. Unpublished), which are also highly sclerophyllous (Ribeiro and Basset 2007; Ribeiro et al. 2011). The “sclerophylly hypothesis” (Ribeiro et al. 1998b; Ribeiro 2003; Ribeiro and Basset 2007), proposed to explain such association, predicts that sclerophyllous leaves are less attractive to herbivorous insects (Turner 1994) and therefore galls on such leaves suffer lower predation by herbivores.

Indeed, many studies have found opposite patterns of distribution for galling insects and free-feeding herbivores (Fernandes and Price 1988, 1991; Ribeiro et al. 1998b; Ribeiro and Basset 2007; Neves et al. 2010). On the other hand, we are not aware, up to this moment, of any clear demonstration that leaf sclerophylly can effectively reduce gall mortality. Besides, there is the confounding effect that sclerophylly strongly correlates with plant defence compounds (Turner 1994; Coley et al. 1985; Fernandes and Price 1991), which can by themselves reduce folivory by free-living herbivores and mislead the conclusion that leaf sclerophylly prevents folivory.

Plants under conditions of limited resources (water, nutrients or light) tend to become more sclerophyllous (hard, rigid and resistant) at the same time that they have a higher content of defence compounds (McKey et al. 1978; Coley et al. 1985). In order to increase leaf longevity and offset the investment in leaf construction (Givnish 1979; Chabot and Hicks 1982; Mooney and Gulmon 1982; Turner 1994)

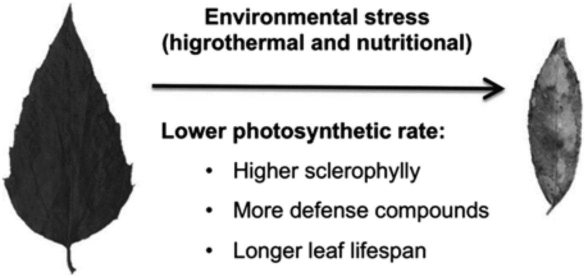


Fig. 6.6 Leaf traits variations in response to environmental stresses. Plants under limited resources usually present higher leaf sclerophylly and greater concentration of defence compounds in order to increase leaf longevity and allow enough time for the low photosynthetic rate to offset the investment in leaf construction

plants ought to protect their leaves against both physical (wind, sun and rain) and biotic (pathogens and herbivores) adversities. Therefore, they exhibit a higher fraction of sclerenchyma, which increases hardness, stiffness and resistance of the leaf tissues (Lucas et al. 1991; Vincent 1991; Choong et al. 1992; Niklas 1992; Turner 1994; Read et al. 2006). In addition, plants concentrate digestion-inhibiting compounds (McKey et al. 1978; Coley et al. 1985; Gutschick 1999; Fig. 6.6). This way, although sclerophylly and high concentration of defence compounds have a common cause (hydric and nutritional stresses; Turner 1994; Coley et al. 1985), they are independent leaf traits, and sclerophyllous leaves may or may not be rich in defence compounds.

There are evidences that sclerophylly itself (leaf hardness, toughness and stiffness; Schimper 1898, 1903; Warming 1909; Beadle 1966; Seddon 1974), which is only a morphological and textural leaf property, could act as a mechanical defence. Sclerophylly could certainly impose a physical barrier for chewing insect herbivores (Coley 1983; Choong 1996; Gutschick 1999; Read et al. 2006) by increasing resistance to tearing, bending and fracturing (Turner 1994). However, sclerophylly is a bit of an abstract concept in the sense that a wide range of leaf traits can determine leaf morphology and texture. As a result, some leaves considered sclerophyllous for its morphology or texture may not be resistant to tearing and fracturing and, therefore, be heavily attacked by chewing insect herbivores (Cowling and Campbell 1983; Turner 1994; Onoda et al. 2008). Mangroves, for instance, have though leaves, but with low sclerenchyma content (Choong et al. 1992). Moreover, some authors have not found relationship between sclerophylly and folivory studying plant species in the Brazilian cerrado (*Chamaecrista linearifolia* Barneby, Fabaceae, Madeira et al. 1998; *Qualea parviflora* Mart., Vochysiaceae, Gonçalves-Alvim et al. 2006). Conversely, some non-sclerophyllous leaves can be highly resistant to folivory because of a more efficient structural design (Onoda et al. 2008; Kitajima and Poorter 2010). Consequently, using leaf sclerophylly to explain the link between environmental harshness and gall richness could be quite troublesome. The relationship between gall richness and leaf sclerophylly remains an open avenue for more detailed studies.

6.6 The Ideal Host and Scenario

While the association between galls and some kind of environmental stress is evident in many surveys, the discovery of mechanisms whereby stressful conditions create selective forces that favour gall occurrence remains a challenge. Based on what has been depicted in this chapter, it is clear that the overlooked plant driven effects on galling insects have great potential to help solving the puzzle.

It is possible to portrait a unified mechanism for the global distribution of galling insects considering the bottom-up and top-down effects (Fig. 6.7). Galls appear to occur where these forces are "weakened" by adverse environmental conditions, which are not solely due to hygrothermal or nutritional stresses. These conditions can be represented, for example, by periodic flooding (Julião et al. 2005; Julião et al. Unpublished) or solar radiation. Such stressful conditions can lead to the creation of *enemy-free spaces* (Fernandes and Price 1992) and to increased concentration of defence compounds in the leaves (McKey et al. 1978; Coley et al. 1985). This way, it would promote the survival of galling insects, protecting them from attack by natural enemies, including free-living herbivores (Janzen 1977; Taper and Case 1987; Cornell 1983; Fernandes 1998). At the same time, environmental stress would suppress hypersensitivity reactions and damage induced leaf abscission, and

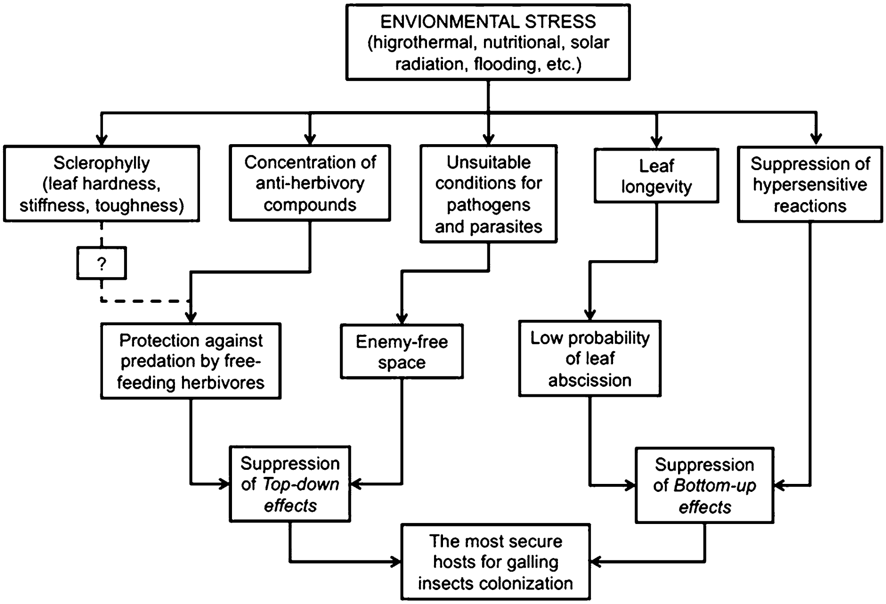


Fig. 6.7 Proposed unified mechanism for the pattern of higher incidence of galling insects in plants under environmental stress. Stressful conditions can potentially suppress top-down and bottom-up effects on galling insects through various processes, creating the most appropriate conditions for galling insect colonization

increase leaf longevity (Givnish 1979; Chabot and Hicks 1982; Mooney and Gulmon 1982; Turner 1994), favouring the colonization by galling insects.

As long as the insect larva is within the gall, where it usually has access to improved nutrition (Cornell 1983; Price et al. 1987; Isaev et al. 1988; Hartley and Lawton 1992; Stone et al. 2002), having an adverse external environment is an advantage against natural enemies. Additionally, stressed hosts would be less defended against galling insects than the ones under favourable conditions. Therefore, the profile of the most appropriate host plant for galls would be a plant under some kind of environmental stress, with long lasting leaves and low frequencies of hypersensitivity reaction, leaf abscission and herbivory.

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Chapter 7
Natural Selection on a Tropical System: Gall-Size Distribution on *Waltheria indica* (Malvaceae)

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Abstract The optimal foraging theory has provided a successful explanation of the complex aspects involved in resource utilization and selection by interacting species. Gall-inducing insects and their natural enemies have played an important role in generating testable evolutionary hypotheses. One scenario is provided by the galling insect *Anisodiplosis waltheriae* (Diptera: Cecidomyiidae), its natural enemies and host plant, *Waltheria indica* (Malvaceae). Here, we present our results of field studies concerning gall size and propose a foraging model that incorporates optimization of attack by natural enemies on size-dependent galls as the principal force driving natural selection. From our analysis we can conclude that unidentified enemies attacked the smallest size classes of the galls of *A. waltheriae*, while predators preferentially attacked medium diameter galls and parasitoids preferentially attacked the largest galls. The preference of different types of enemies results in an

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unexpected selection effect detected in post-selection gall-size distribution. Further, our model was able to characterize resource partitioning among the interacting natural enemies of the galling insect. This study may provide the fuel to stimulate more studies on the dynamic nature of how natural enemies select hosts based on gall size.

Keywords Foraging model • Foraging • Gall defense • Gall size • Galls • Insect galls • Insect plant interactions • Mortality factors • Natural enemies • Optimal foraging theory • Parasitoids • Predators

7.1 Introduction

Natural selection is defined as a primary process that affects the distribution of species populations through fitness pressure that differs dependent upon an individual's phenotype (Brodie III et al. 1995). Directional selection has been usually detected in the field to a sort of organisms (Endler 1986). Less common has been the detection of stabilizing and disruptive selection. The size of samples necessary to detect these forms of selection is in the order of several hundreds of measurements (Brodie III 1992). Recent evolutionary studies have focused on the determination of how natural selection acts on phenotypic traits of species populations. The optimal foraging theory (OFT), originally proposed by MacArthur and Pianka (1966), explains adaptation via natural selection through quantitative models, assuming that foraging behavior has been optimized by natural selection to feed in a way that maximizes their net rate of energy intake per unit time. This involves costs and benefits for searching, harvesting, and eating food. Natural selection will act to optimize foraging because of the increased reproductive success (see Begon et al. 2006) associated with increased efficiency of foraging.

Gall-inducing insects and their natural enemies have played an important role in the development of evolutionary theory (see Price and Clancy 1986). The system composed of gall-inducing insects and their natural enemies represents an ideal model to study the factors influencing mortality and survival because the gall structure conserves evidence of the whole life history (Fernandes et al. 1987; Fernandes and Price 1992). Gall size has been shown to play a strong role in the performance of gall inducing insects (see Sopow and Quiring 2001; Egan et al. 2012). For instance, the number and average size of emerging adults was positively related to gall volume of the spruce galling adelgid *Adelges abietis* (Phylloxeridae) (McKinnon et al. 1999). For the gall midge *Asphondylia borrichiae* (Cecidomyiidae), the diameter was related with midge size, and also larger midges had a higher potential fecundity (Rossi and Stiling 1998). Furthermore, gall size has been implicated in differential survivorship of immature stages of many galling species (e.g., Weis and Abrahamson 1985; Souza et al. 1998, 2001; van Hezewijk and Roland 2003). Parasitism is generally restricted to smaller galls, such as in *Eurosta solidagini*s (Tephritidae) (Weis et al. 1985), tenthredinid sawflies (Price and Clancy 1986), and in cynipid gall systems (Plantard and Hochberg 1998). Furthermore, gall size strongly influenced the variation in fundatrix fecundity of the aphid *Hormaphis hamamelidis* (Fitch) (Aphididae) (Rehill and Schultz 2001). On the other hand, while some models were proposed to describe the variation in natural selection of gall size in response to parasitism or predation (van Hezewijk and Roland 2003), other studies did not find consistent evidence for evolutionary change in gall size over the generations studied (Weis 1996).

Predators and parasites account for a large proportion of larval mortality in many galling insect species (Askew 1961, 1965, 1975; Weis and Abrahamson 1985; van Hezewijk and Roland 2003; but see Fernandes 1998; Santos et al. 2008; Cooper and Rieske 2010). Birds and parasitic wasps can differentially affect larval survivorship based in the size of the galls and exert both directional and stabilizing selection (see Weis and Abrahamson 1985; van Hezewijk and Roland 2003). For instance, in the relationship between gall size and mortality of the willow pinecone gall midge *Rabdophaga strobiloides* (Cecidomyiidae), birds attacked the smallest gall size classes, while the parasitoid *Torymus cecidomyiae* (Torymidae) consistently attacked medium diameter galls. Hence, *R. strobiloides* larvae avoided predation by birds in smaller galls. Otherwise, another parasitoid *Gastrancistrus* sp. (Pteromalidae) preferentially attacked the largest galls and consequently suffered lower rates of predation by both *T. cecidomyiae* and birds (van Hezewijk and Roland 2003). Weis and Abrahamson (1985) showed that small gall size increases the likelihood of successful attack by the *Eurytoma gigantea* wasp (Eurtyomidae), causing a selective pressure towards larger gall-size of *Eurosta solidaginis* (Tephritidae). A parasitoid wasp, for instance, search for a host gall in which to oviposit, and the ability to parasitize hosts successfully depends, in part, on the wasp's host preference behavior. Because galls may differ in size that leads to successful parasitism, parasitoids in different gall-sizes may evolve differences in response to natural selection.

In this chapter we evaluate the selective forces influencing the survival of the gall inducing midge *Anisodiplosis waltheriae* (Diptera: Cecidomyiidae) that induces galls on *Waltheria indica* L. (Malvaceae) (Maia and Fernandes 2005). We hypothesized that gall size could influence larval survival or determine larval susceptibility to natural enemies. We also hypothesized that natural enemies of *A. waltheriae* galls may maximize their energy intake or minimize the time spent foraging, since the energy content of galls may vary significantly. Natural enemies would then show a preference for galls of a certain circumference. The optimal foraging theory (OFT) lead us to predict that natural enemies of *A. waltheriae* galls, like parasitoids, will maximize their net rate of energy intake per unit gall-size probably on the basis of nutritional value. Therefore, we addressed two fundamental questions: (1) does gall size affect *A. waltheriae* larval survival?; and (2) is attack on *A. waltheriae* galls by its natural enemies mediated by gall-size?

7.2 The System: Host Plant and Galling Insect

The study was conducted in Fazenda Bulcão, located in Aimorés, Minas Gerais, southeast Brazil (19° 26′ 42″S, 41° 3′51′′W) which has an area of 676 ha and is recognized as a Natural Patrimony Reserve, where a large land reclamation program initiated in 2001. The Aimorés mountain ridge was originally covered by Atlantic Forest vegetation, but experienced an accelerated degradation stage due to the colonization process, wood logging, generalized deforestation and the Vitória – Belo Horizonte railroad construction. Further degradation and forest fragmentation were promoted by intensive agriculture and cattle farming activities.

The host plant *Waltheria indica* L. (Malvaceae) is a short-lived shrub species that grows throughout the tropics and warmer subtropics in India, Taiwan, Southeast Asia, South America, Mesoamerica and North America (Francis 2007). The species is apparently naturalized in Hawaii and in the Americas it occurs from Florida and Texas to Brazil. In Brazil it is easily found in the Cerrado (savanna) vegetation and grasslands (Lorenzi and Matos 2002). This shrub usually has a single, strong stem emerging from the ground and sometimes reaching 2 m in height. *Waltheria indica* is also known as sleepy morning, boater bush, buff coat, leather coat, monkey bush, velvet leaf, waltheria, among other popular names (Francis 2007). This species also has several synonyms: *Riedleia berteriana* DC., *W. africana* Schum. Thom, *W. americana* L., *W. angustifolia* L., *W. arborescens* Cav., *W. detonsa* Gray, *W. elliptica* Cav., *W. erioclada* DC., *W. guineensis* Schum. et Thon., *W. laevis* Schrank, *W. microphylla* Cav., *W. obtusa* Cav., *W. ovata* Willd., *W. paniculata* Miq., *W. pauciflora* Hochst., *W. pedunculata* Willd., *W. debilis* Bojer and *W. makinoi* Hayata (Francis 2007). Sleepy morning is an autochorous species that grows spontaneously in perennial agriculture forest plantations, old fields, along roadsides, construction sites, abandoned pastures, limestone mining quarries, unused plot of land and grasslands in Brazil (Rodrigues and Carvalho 2001), therefore being considered a weed of high economic importance in early-established communities (Frenedozo-Soave 2003). *Waltheria indica* represents a rich food source to wasps which predate upon crop insect plagues (Macedo and Martins 1998, 1999).

Waltheria indica is host of the recently described species, *Anisodiplosis waltheriae* (Diptera: Cecidomyiidae) (Maia and Fernandes 2005). Galls are induced on leaves, leaf buds and even inflorescences. They are spherical, covered with short light yellow to light brown trichomes and have one chamber where a single larva can be found (Fig. 7.1). Almeida et al. (2006) reported that nearly 90 % of all plants and 25 % of all leaves were attacked by the gall midge in Aimorés, MG, Brazil. They also recorded an average of 27.8 galls per individual plant while leaves supported an average of 0.67 galls. Natural enemies (top-down effects) killed one third of galls: predation by lepidopteran catterpillars that consumed the gall tissue (22.9 % of gall mortality), unknown factors (7.6 %), microhymenopteran parasites (2.5 %) and pathogens (unidentified fungi, around 1 %). In the system, mortality factors is not influenced by leaf area or gall density. Nearly 66 % of *A. waltheriae* survived after successfully inducing galls (Almeida et al. 2006).

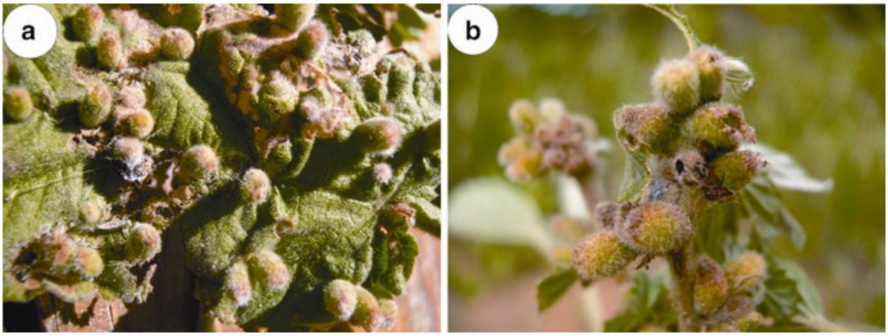

Fig. 7.1 (**a**) Distribution of *Anisodiplosis waltheriae* (Diptera: Cecidomyiidae) gall on a leaf *Waltheria indica* L. (Malvaceae). (**b**) A group of galls in detail

7.3 Sampling: Gall Collections and Measurements

We randomly sampled 2,244 galls on 70 *W. indica* plants in a roadside area that contour the various native restoration plots in Fazenda Bulcão, Aimorés, MG, Brazil. Sampled individuals were cut at the soil level, stored in plastic bags and immediately taken to the laboratory, where gall size (length) was recorded with the aid of a caliper (0.01 mm). Galls were later dissected to determine larva mortality factors according to Fernandes and Price (1992): death caused by parasitoids of the galling larvae, predation of the gall tissue and/or galling larvae, fungus-caused diseases and other factors such as plant resistance.

Since sampled galls come from a large spatial field (ca. 10 km long road) with arbitrary age it would be expected to observe a stationary population. The sample population was classified into the following groups: G_0 (before selection; it contains the hole sampled data), G_1 (survivors), and three extra groups related to mortality factors: G_2 (parasitoidism), G_3 (predation), and G_4 (other factors). Two additional groups, representing the occurrence of more than one mortality factors, were statistically uninformative and therefore discarded in the present analysis. A histogram for each group discriminating the set of gall sizes was then calculated. From these a set (one for each group) of frequency density, defined as bin frequency divided by bin size (here equal to 0.5 mm) were obtained. Sampled probability density distributions can readily be obtained as normalized versions of these histograms but give no additional information and are not presented here. The obtained density histograms data were fitted to an appropriate distribution function using standard minimum square error routines. These data and the associated adjusted profiles are displayed on Fig. 7.2.

Fitness profile for this system coincides with data for the survivor group G_1. Since this property has particular importance on determining the kind of selection process acting over the galls it deserves a more specific analysis. Thus we present its profile, the absolute survivor (fitness) data separately in Fig. 7.3.

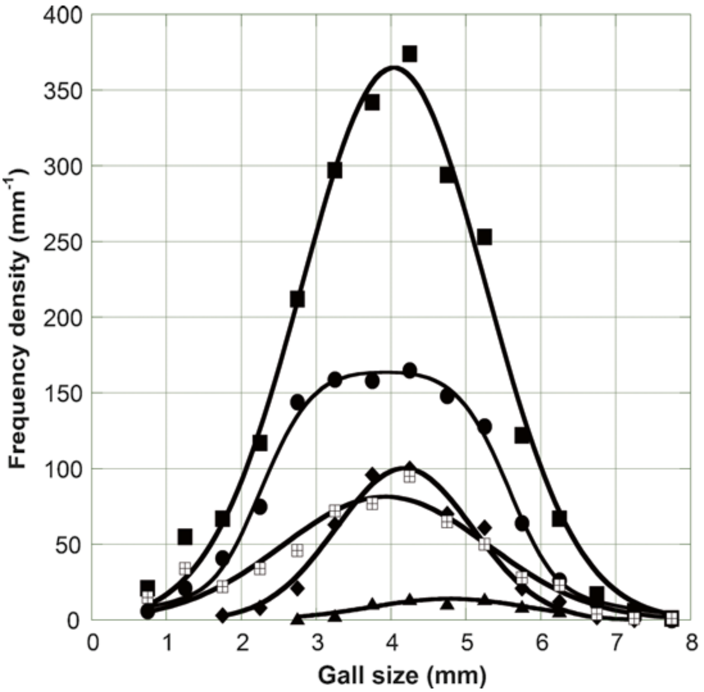

Fig. 7.2 Frequency density before selection (G_0, *squares* ■), survivors (G_1, *circles* ●), parasitoidism (G_2, *triangles* ▲), predation (G_3, *diamonds* ◆), and others mortality factors (G_4, *squares* ⊞) as function of gall-size of *Anisodiplosis waltheriae* (Diptera: Cecidomyiidae). *Lines* are the adjusted profiles

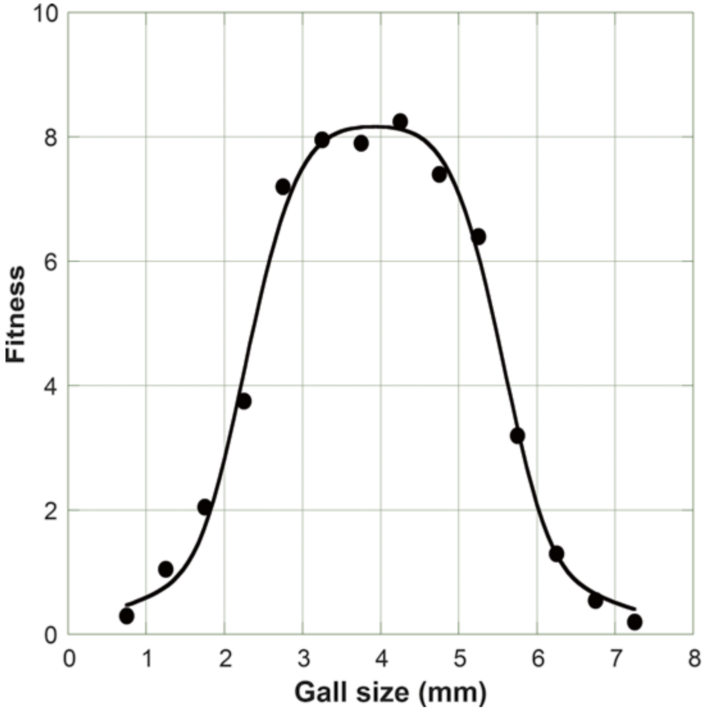

Fig. 7.3 The fitness profile for this system, a relationship between fitness and gall-size of *Anisodiplosis waltheriae* (Diptera: Cecidomyiidae)

7.4 Selection Process Derived from the Observed Histograms

We assumed that the collected samples faithfully described a stationary distribution representing the natural occurrence of galls on *W. indica*. In fact, as shown in Fig. 7.2, all the histograms fit to a Gaussian type:

$n(x)=a\ \exp(b*(x-c)^2)$, except the survivors group (G_1) which fits to a combination of a Gaussian and a fourth order exponential:

$$n(x)=a_1\ \exp\left(b_1*(x-c)^2\right)+a_2\ \exp\left(b_2*(x-c)^4\right) \tag{7.1}$$

Fitting parameter values for the groups are shown in Table 7.1. The G_0 histogram permits an excellent Gaussian fitting indicating that collected data are statistically independent. In all fits parameter “c” describes the center of the distribution and was calculated within 1 % precision. Thus, it indicates that the calculated variations on this parameter between groups have statistical significance implying that a natural selection process on average size galls larger than the natural occurrence defined by the G_0 is present.

Natural selection effects were more evident when represented by density histograms of the attacked groups by explicit biological cause (predatory or parasitism) than the whole population. In order to show this quantitatively we presented values of the standard error (δ) for each population and the ratio $R=\delta/\text{mean}$ (Table 7.2). Two population classes may be defined from this parameter. One class has values of R belonging to the interval 0.30–0.35 and the other class has R close to 0.22. Clearly

Table 7.1 Fitting parameter values for the groups G_0 (before selection), G_1 (survivors), G_2 (parasitoidism), G_3 (predation), and G_4 others mortality factors to gall-size of *Anisodiplosis waltheriae* (Diptera: Cecidomyiidae)

Groups	a (mm^{-1})	b (mm^{-2})	C (mm)	a_1(mm^{-1})	b_1 (mm^{-4})
All (G_0)	729.81	0.332	4.04		
Survivor (G_1)	90.86	0.160	3.92	236.46	0.096
Parasitoidism (G_2)	28.14	0.444	4.79		
Predator (G_3)	200.54	0.602	4.18		
Other (G_4)	163.00	0.266	3.93		

Table 7.2 Values of the mean ($\overline{\chi}$), standard error (δ) and the ratio $R=\delta/\text{mean}$ for each population groups G_0 (before selection), G_1 (survivors), G_2 (parasitoidism), G_3 (predation), and G_4 others mortality factors to gall-size of *Anisodiplosis waltheriae* (Diptera: Cecidomyiidae)

Groups	$\overline{\chi}$ (mm)	δ (mm)	R
All (G_0)	4.04	1.23	0.30
Survivor (G_1)	3.92	1.33	0.34
Parasitoidism (G_2)	4.79	1.06	0.22
Predator (G_3)	4.18	0.91	0.22
Other (G_4)	3.93	1.37	0.35

the attacked groups, by an explicit biological cause, had a smaller ratio R indicating a more selective profile. This means that attacked populations were selected by the attacking agent more precisely than its natural occurrence.

Although the survivor group falls into the class with larger *R* values, its profile does not present a pure Gaussian form, common to all other groups. This is an immediate consequence of a strong selection process involved in this system that results in a broader maxima region, shown in Fig. 7.2. Assuming the observed stationary distribution it appears that the typical size of surviving galls belongs to a moderately uniform distribution around a mean value that presumably would be responsible for generating the initial Gaussian profile observed in the group G_0.

7.5 Fitting Values and the Associated Selection Trend

The survival data values shown in Fig. 7.3 is a measure of the fitness for this system. Unlike the other data groups they were not adjusted to a simple Gaussian function of the gall size. Instead its distribution demands for a more complex function, displayed in Eq. (7.1). Since the whole gall data are Gaussian, a strong selection mechanism must be responsible for deviating the survivor group from its original natural occurrence in Nature. In fact, Eq. (7.1) presents a Gaussian component plus a "flat" exponential, described by a fourth order polynomial in the exponent. This additional term broads the Gaussian profile and reflects gall ability to survive against different predators, all presenting different strategies in gall attack.

This variety of predatory strategies leads to mortality curves of slightly different mean target sizes, but presenting relatively large dispersion. In order to respond to such a complex mortality scenario, gall natural occurrence presents a strong central peak, as compared to the various pos-selection occurrence data. The high occurrence of gall size at its mean value allows a survivor curve having a broad fitness distribution, with no specific natural selection gradient. This way, gall fitness reflects the complexity of its biological selection scenario which deviates from usual selection models.

7.6 Foraging Model

As we have already stressed, data displayed on Fig. 7.2 concerns frequency density distributions across various groups of collected data. Each bin score of the histograms (obtained from these data) was divided by bin interval length (here equal to 5 mm). Resultant histograms are thus proportional to the probability density for a specific group. Furthermore, the probability of a group event is obtained as the ratio of event frequency for a given gall size, to event frequency in the G_0 group (the "all" group), calculated for the same gall size:

$$pr_j(x) = \frac{p_j(x)}{p_0(x)} \qquad j = 1,2,3 \tag{7.2}$$

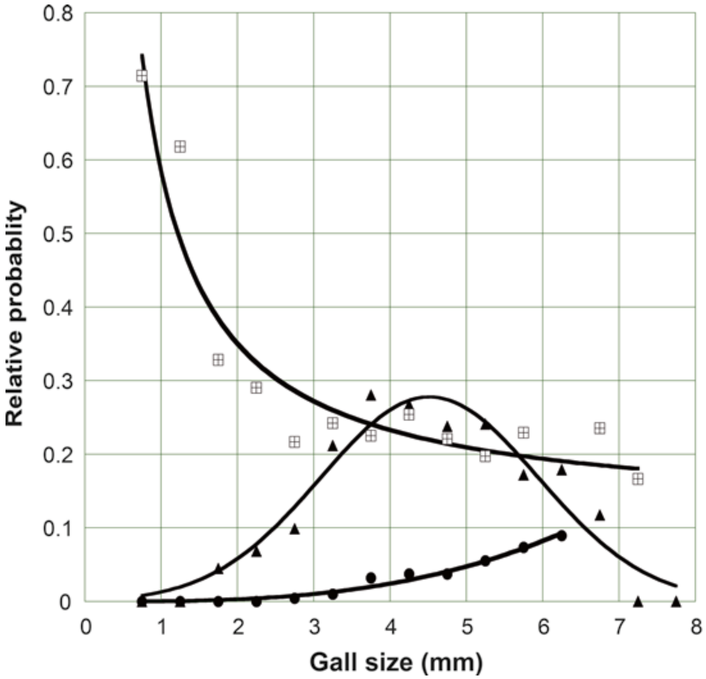

Fig. 7.4 Relative probability of mortality factors parasitoidism (G_2, *circles* ●), predation (G_3, *triangles* ▲), and other factors (G_4, *squares* ⊞) as function of gall-size of *Anisodiplosis waltheriae* (Diptera: Cecidomyiidae). *Lines* are the adjusted profiles

These set of values are displayed as symbols in Fig. 7.4 and may be considered as a stationary probability for the foraging process j, at each gall size *x*. The OFT proposed by MacArthur and Pianka (1966) and its further developments, are tractable by using both the prey and path models. The OFT tries to explain this kind of information by focusing on specific process that may occur when a forager encounters a prey of size (or type) *x*. These models describe decisions of attack in terms of gain and risk variables for each prey type.

In this work we focus on the gall-size of *A. waltheriae* using a different approach. It is assumed that many prey types (or prey size) are available. The forager must compare them and decide to attack one type based on a gain and risk decision algorithm. Differing from OFT, but consistent with our observations, we assume stationary probabilities, so no rates are involved. Let two preys *A* and *B*, of sizes x_a and x_b, both available at the same patch. A forager must decide among them. It is reasonable to assume that this decision process is governed by the ratio:

$$T = \frac{pr\left(x_a\right)}{pr\left(x_b\right)} \tag{7.3}$$

Let g(x) the energetic gain that a prey of size x supplies to forager, once it is caught, and r(x) the risk the forager is subject at the searching/attacking/manipulating time. We may describe the function g as an increasing monotonic function of prey size *x*, of the form:

$$g = g\left(x^{\alpha}\right) \tag{7.4}$$

For example $\alpha = 3$ means that the energetic gain scales approximately with prey mass. On other side the risk function r must have a minimum at some prey size $x = \mu$. This means that close to this point the Taylor expansion for the risk function may be approximated by a parabola:

$$r\left(x\right) \approx b\left(x-\mu\right)^{2} \tag{7.5}$$

At this point we describe the ratio function *T* as a balance of gain minus risk of the form:

$$T = 1 + \left[g\left(x_a\right) - g\left(x_b\right)\right] - \left[r\left(x_a\right) - r\left(x_b\right)\right] \tag{7.6}$$

This form intuitively describes where *T* is equal to one for two preys of same size and $T > 1$ if prey A has a net balance $g(x_a)$–$r(x_b)$ more favorable to the forager than prey *B*. If the balance displayed in Eq. (7.5) favors attack to prey B then $T < 1$. Since by definition the ratio T is always positive and Eq. (7.5) may assume, in principle, negative values for different values of x_a e x_b, it is tacitly assumed that this equation is valid only for sufficiently close values of prey lengths. This way we may write $x_a = x_b + \delta x$ and drop out the subscripts to obtain $p(x + \delta x) = \mathrm{p}(x) + \delta p$. Putting in this form Eqs. (7.3) and (7.6) becomes:

$$\frac{pr + \delta pr}{pr} = 1 + \frac{\delta pr}{pr} = 1 + \left[g\left(x+\delta x\right) - g\left(x\right)\right] - \left[r\left(x+\delta x\right) - r\left(x\right)\right] \tag{7.7}$$

Using expression (7.5) for the risk function we get, to first order in δ*x* and close to the optimal risk μ:

$$r\left(x+\delta x\right) - r\left(x\right) \approx b\left[\left(x+\delta x-\mu\right)^{2} - \left(x-\mu\right)^{2}\right] \approx 2b\delta x\left(x-\mu\right)$$

The difference in the gain function may also be written as a first order in δ*x*:

$$\left[g\left(x+\delta x\right) - g\left(x\right)\right] \approx \delta x\left(\frac{dg}{dx}\right)$$

The differential equation for the relative probability defined by Eq. (7.2) was then obtained. It accounts for the effects displayed in Eq. (7.6) viewed here as a balance between an energy-based feeding process and a risky handling process. Thus, from the above considerations and performing the limit of $\delta x \rightarrow 0$, Eq. (7.7) can be rewritten as:

$$\frac{dpr\left(x\right)}{dx} = \left[\left(\frac{dg\left(x\right)}{dx}\right) - 2b\left(x-\mu\right)\right] pr\left(x\right)$$

Introducing the dependence of g on the power of x, it has the following general solution

$$pr(x) = pr_0\left[\exp\left(g\left(x^{\alpha}\right) - b\left(x-\mu\right)^2\right)\right] \tag{7.8}$$

This function may describe two limiting processes. One, where $b=0$, describes a situation presenting small (or no) risk at all. In this case foraging is fully determined by energetic gains alone and will be named here as "easy foraging". In the other limiting case foraging is controlled by risk. The forager accepts any energetic gain at the expenses of minimum risk. For this case the gain function must have no effect on the foraging probability and $g=0$. It will be named here as "hard foraging". Thus, for these two cases Eq. (7.8) predicts different regimes described by the following foraging probabilities:

$$(\text{easy foraging}) \quad pr(x) \approx pr_0\left[\exp\left(g\left(x^{\alpha}\right)\right)\right]$$

$$(\text{hard foraging}) \quad pr(x) \approx pr_0\left[\exp\left(-b\left(x-\mu\right)^2\right)\right]$$

It seems that both regimes occur in the data collected.

As shown in Fig. 7.4, the predator case (G_3) presents relative mortality probability well described by a Gaussian, characteristic of the hard foraging regime. On *W. indica*, *Anisodiplosis waltheriae* galls are eaten by lepidopteran larvae that feed on the external gall walls (see Almeida et al. 2006). The attack on specific sized galls (larger than the average sized galls) represents an interesting phenomenon ought to be studied in more detail in the field, although it indicates a risk associate by attacking larger galls. Larger galls could present harder or even older tissues that could diminish their performance and/or represent larger risks such as competition with other natural enemies of the gall that would attack the larger ones. Relative probabilities for the other two mortality factors were fitted to power law functions.

The parasitoidism group (G_2) admits a fit proportional to x^3 (a volume energetic gain) thus implying that $g=ln(ax^3)$. The pattern of attack by the parasitoid species of *A. waltheriae* galls corroborates the OFT and provide support for the optimal oviposition theory, also called the oviposition preference–offspring performance hypothesis. This hypothesis was inspired in many studies on host selection by arthropods (e.g., Scheirs et al. 2000, 2004; Scheirs and De Bruyn 2002). According to the oviposition preference-offspring-performance hypothesis, oviposition preference patterns of insects are supposed to correspond to host suitability for offspring development because females are assumed to maximize their fitness by ovipositing on high-quality hosts (Jaenike 1978), although some exceptions have been reported (e.g., Price and Clancy 1986; Zurovchak and Shealer 1996; Marchosky and Craig 2004; Cornelissen et al. 2008).

Data for the other group (G_4) is consistent with an exponent equal to minus one and leads to $g=ln(ax^{-1})$, which may be viewed as area/volume effect (a surface energetic gain) an may indicate that this mortality factor could be assigned to physical/chemical factors like UV irradiation, external chemical agents, or even plant resistance mechanisms. These (and other) external mortality factors are passive and their actions depend on the availability of a reacting surface associated to sufficiently small mass. Both groups can be classified as easy foraging processes inside the model proposed here.

Obviously our foraging model is phenomenological. It cannot predict values of model parameters but may be useful to define mortality classes for different groups by comparison of the adjusted parameters. Those foraging processes that fall in the same functional dependence or in the same characteristic exponent may be understood as having common probabilistic nature.

Obtained density histograms reveal that a stationary sample population was collected and the pos-selection analysis showed an unusual unfitted selection pattern to the basic natural selection models. The relationship between gall size and the basic elements of the OFT, represented by attack and gain probabilities, was consistently obtained by the model we proposed here. However, in this study these elements were treated in a different context, because the observation of a stationary sample distribution needs no reference to rate variables.

Finally, niche partitioning is an important concept, yet seldom studied in more complex systems. The community of organisms associated with gall inducing insects may represent an important system where such concepts could be addressed due to several properties of the system (such as the sessile nature of the gall), and ease of evaluating mortality factors and survival in the field (see Fernandes and Price 1992). Otherwise, we expect spatial and temporal variation in the strength of the multitrophic interactions involving host plants, galling insects, and their mosaic of natural enemies. But as such, it provides the fuel to stimulate more studies on the dynamic nature of how natural enemies select hosts based on gall size and its connection to performance and fitness of both parasites and hosts.

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Chapter 8
Density of Insect Galls in the Forest Understorey and Canopy: Neotropical, Gondwana or Global Patterns?

Sérvio Pontes Ribeiro, Yves Basset, and Roger Kitching

Abstract Gall-forming insects reach highest diversity, abundance and survivorship on sclerophyllous vegetation. This pattern was recently reviewed and shown as a habitat rather than ecosystem effect. We tested the hypothesis that upper forest canopies are probably the best suitable habitat for gall-forming insects in any tropical vegetation, comparing the wet rainforest of Panama (Neotropical), and the subtropical forest of Australia (Australian). We further tested whether foliage/plant community traits could influence this gall distribution pattern, and we investigated the effect of host family size and evolutionary age. Foliage traits, leaf chewing herbivory, and gall abundance and survivorship were measured using vertical cylindric transects from the understorey to the canopy. In both Panama and Australia, leaf sclerophylly increased significantly with sampling height, while free-feeding herbivory decreased inversely. Gall distribution and survivorship responded significantly to sclerophylly, but distribution between understorey and canopy varied between study sites. The probability of gall survivorship increased with increasing leaf sclerophylly as death by fungi, parasitoids or accidental chewing were greater in the non-sclerophyllous vegetation in the understorey of both study sites. However, number of galls, proportion of infected sampled plants, and proportion of host species against total sampled species were all greater in Panamá than in Australia.

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On the other hand, the Australian forest had a fauna much more concentrated on fewer hosts, with 80 % of galls infesting six host species. The present study supports the existence of a global positive effect of sclerophylly on gall establishment and survivorship in the upper canopy of tropical and subtropical forests.

Keywords Canopy • Gall density • Leaf herbivory • Sclerophyllous habitats • Forest vertical distribution

8.1 Introduction: Galls in Forests

Galls are well known endoparasitic specialist herbivores related to highly sclerophyllous plants, thus a typical sun-love interaction. Seminal work of Fernandes and Price (1988, 1992) demonstrated that differential death by fungi and parasites, greater in shadowed and mesic compared to sunny and xeric sclerophyllous vegetations, is a likely mechanism driving the gall species distribution pattern. More recently, Mendonça (2001) added an evolutionary layer to this debate, proposing an ingenious evolutionary mechanism to explain the diversification of gall species based on the ecosystem-level synchrony of leaf flush. He predicted increasing speciation rates due to insect survival after mistaken oviposition, a likely event if all plants produce young leaves at the same time and insects have early oviposition to avoid hard tissues and thus facilitate the development of the gall tumour. Mendonça's hypothesis complements the harsh environment (Fernandes and Price 1988) and sclerophylly hypotheses (Fernandes and Price 1992). The former explains a mechanism of speciation and the latter of survivorship in sclerophyllous synchronous ecosystems. When considered together, these hypotheses help to explain why the highest gall diversity occurs in the Mediterranean-type vegetations, like the Brazilian cerrado (Price et al. 1998).

However, recent studies on gall diversity in Panama have shown a substantially larger number of galls in the canopy of tropical forests than in any other ecosystem, bringing to evidence a previously unexpected relation of this unique interaction with a very wet ecosystem. Furthermore, a significant amount of this diversity was detected by a yearly sampling protocol which measured the variation in gall species richness and abundance following each host-plant's leaf-flush (Medianero and Barrios 2001; Medianero et al. 2003). In Panama, no synchrony of leaf flush was observed at all, but gall diversity was among the highest ever found, thus contradicting the predictions of Mendonça (2001).

On the other hand, comparative analyses of the distribution of galls between xeric (upper canopy) and mesic (understorey) habitats within the forest seem to corroborate Fernandes and Price's (1992) prediction: a positive gradient between gall diversity and vegetation sclerophylly may exist. Nevertheless, even though the accepted mechanism to explain greater gall mortality in mesic over xeric habitats is apparently correct at the branch/leaf scale (Ribeiro and Basset 2007), it was first developed based on of a comparison between forest understorey and cerrado canopies, thus lack a proper vegetation-habitat control (reviewed in Ribeiro 2003). Indeed, Medianero et al. (2003, 2010) found that a humid closed rainforest on the Caribbean coast of Panama (San Lorenzo Protected Area) was richer in gall species than the dry semi-deciduous forest on the Panamanian Pacific coast (Parque Metropolitano). Mostly important, both forests were richer in galls in the canopy than in the understorey. Hence, the actual eco-physiology of the habitat (forest understorey vs. cerrado canopy) within which the galls live is more relevant to the pattern than the existence of a mesic or xeric state of the plant community as a whole. Hence, the present global estimate of 130,000 gall species from Espírito-Santo and Fernandes (2007), although accounting for previous bias in the literature, such as lesser studies in the canopies than in easier accessible vegetation in temperate or tropical latitudes, may have missed within-ecosystem habitats comparisons.

Despite the positive response to sclerophyllous habitats, wherever galls occur, they are restricted to very few host species (Espírito-Santo and Fernandes 2007; Ribeiro and Basset 2007). Why so few plant taxa across biomes are suitable hosts for gall species is so far an unanswered question. For instance, Ribeiro and Basset (2007) observed galls on few tree species (22 % out of 73 tree/liana sampled species), from which 50 % had congenerics or were also found (31 %) in the Brazilian cerrado. Both Price (1977) and Fernandes (1992) have proposed that gall diversity follows plant family size, but neither of these authors actually discussed evolutionary constraints to gall species distribution related to the life history of the host. Likewise, little have been done in order to understand what are the actual constraints to gall invasion success into most of host taxonomic groups, neither if this is a recent or old evolutionarily phenomena:

- how much of the Neotropical gall diversity resulted from local adaptive radiation in association with continuous sclerophyllous habitats, thus with wide and abundant host species distribution? Conversely,
- how much of such biodiversity was caused by an older Gondwana evolutionary history, which may influences gall species distribution in Neotropical, Cape Africa or Australasian regions?

This chapter revisited previous data obtained by the canopy-understorey cylinder transects protocol (Ribeiro and Basset 2007; Ribeiro et al. 2012), and add a new analytical approach in comparing the gall abundance distribution and survivorship between understorey and canopy of (a) a Neotropical wet rainforest, in Panama; and (b) an Australian subtropical rainforest (part of the Gondwana Rainforests of Australia), in Queensland. We explore the hypothesis that sclerophylly effect on gall distribution, previously demonstrated in the Neotropical region, is a general phenomenon, likely to be found in other regions, and is more important than other ecologic or evolutionary causes of gall abundance and distribution. Hence, besides testing the effect of leaf height and sclerophylly on gall distribution, we compared the forests foliage density and vertical distribution. In addition, we investigated whether gall diversity is restricted to few host species that belong to large pantropical or pre-Gondwana plant families.

8.2 Methodology

The IBISCA Project and global comparisons in insect diversity – IBISCA (Investigating Biodiversity of Insects in Soil and Canopy) is an international project with the goal of performing simultaneously several arthropod sampling protocols, targeting particular speciose taxonomic groups, and yielding adequate data to compare the fauna from the soil to the canopy (details in Basset et al. 2007, 2012; Kitching et al. 2012). So far, expeditions were conducted in San Lorenzo Protected Area, Panama, Lamington Park, Australia, Santo Island, Vanuatu, and Auvergne County, France.

This Chapter focus on San Lorenzo and Lamington Park. Details on each study site and methodology are found in Basset et al. (2007), Ribeiro and Basset (2007), Kitching et al. (2012) and Ribeiro et al. (2012). To study galls, parasites and herbivory, a new methodology was developed, which generates a comparable number of searched leaves in same space volume from top canopy to understorey. Such procedure, the canopy-understorey pin-cylinder transect (hereafter cylinder; Ribeiro and Basset 2007), allows a direct comparison of different forests by using a same volumetric sample unit. A different amount of understorey-canopy cylinders were set in each study site to adjust to the general sampling design of each IBISCA project. In San Lorenzo, five sites were sampled with one understorey and three canopy cylinders in each, and in Lamington Park four altitudes were each surveyed with one understorey and four canopy transect. Both study sites were sampled during two distinct seasons: August 2003 (rainy season) and May 2004 (end of the short dry season), in Panama; in October 2006 (early wet season) and March-April 2007 (early dry season), in Australia. A short description of the method, which is detailed in Ribeiro and Basset (2007) and Ribeiro et al. (2012), is presented below.

8.2.1 Sampling Protocol: The Pin-Cylinder Transect

The canopy cylinder transect is a cylindrical transect which started at the upper canopy and finished at 3 m above the ground. For the understorey cylinder transect, it followed along an equivalent horizontal transect of 20 m in Lamington and 30 in San Lorenzo (the average height of these forests, respectively) parallel to and 10 cm above the soil, thus preventing sampling seedlings. In each transect, a 'sample' consisted of a branch or continuous groups of leaves within the cylinder. From each sample, the total number of leaves, the number of young leaves, the number of buds and active meristems and the number of damaged leaves were counted. Leaf herbivory was taken from counting all leaves with more than 10 % of leaf area lost, estimated visually. Since this figure represents global average leaf area loss in tropical wet forests, leaves scored above this average may be considered "substantially damaged" (Coley and Aide 1991) and the proportion of damaged/total leaves per strata resulted in our estimate of free-feeding herbivory. Healthy leaves were collected for an analysis of specific leaf mass, an indirect measure of sclerophylly.

Specific mass per leaf area unit (Cooke et al. 1984) was obtained by dividing leaf dry weight by area, using mature leaves collected in 2006. To estimate gall densities, all leaves in a sample with galls, or any gall-like imperfections, were collected and frozen. Galls were opened in the laboratory to evaluate if they were alive or dead and if dead, the cause of death. We analysed the following gall categories: (a) all galls (including galls with live and dead insects; hereafter 'live' and 'dead' galls for sake of brevity); (b) only galls with live larvae; (c) recently hatched galls; and (d) galls with larvae that had died recently by fungal attack (recognized by rotten larvae or the presence of mould) or parasitoid attack (identified by the presence of the parasitoid ecdysis or several small asymmetric apertures in the gall, along with wastes inside).

8.3 Contrasting Foliage and Gall Distribution in the Panamanian San Lorenzo Forest and in the Australian Lamington Park

The Panamanian forest had substantially more plants in the understorey than in the canopy, but similarly more foliage in the opposite direction (8.5 times more, Table 8.1). Contrastingly, Lamington subtropical forest had only 50 % more plants in the understorey compared with the canopy, and only 2.5 more leaves in the canopy (Table 8.1). These figures reflect a much denser and entangled forest in Lamington than in San Lorenzo, which had 2.5 plant species per cylinder against 1.3 species in the latter. Hence, it is as if the tropical Panamanian forest was shaped by the top, with the upper canopy species shadowing down the rest of the forest, thus resulting in empty spaces within the forest.

8.4 San Lorenzo Forest Gall Distribution

8.4.1 Gall Distribution Among Tree Species

Galls were present only in 47 samples and 16 (out of 73) identified host species (Ribeiro and Basset 2007). Overall, 32 gall species were collected, including 59 % of which occurred exclusively in the canopy, 28 % only in the understorey, and 12.5 % found in both habitats. We noted that 81 % of our gall host plants at San Lorenzo have either congenerics (50 %) or are present (31 %) in the Brazilian cerrado (Table 8.1), where gall diversity is one of the highest in the world (Price et al. 1998).

Scaling down to leaf level, Ribeiro and Basset (2007) surveyed in average 21,997 leaves per year, of which 2.4 % bore galls in the wet season 2003 and 5.5 % by the end of the dry season, although restricted to fewer trees. However, a similar number of galls were sampled in the two seasons (average 2,507 galls), with 15.6 % of galls

Table 8.1 Canopy and understorey plant parameters, and gall versus chewing herbivory infestation obtained by understorey-canopy cylinder protocol, in San Lorenzo National Park, Panama, and Lamington National Park, Australia

Forest/gall parameter	San Lorenzo	Lamington park
Plant diversity	73 plant species	72 plant species
	50 genera	61 genera
	31 families	33 families
	231 sampled plants	329 sampled plants
Plant/foliage distribution	7.3 more plants in the understorey than canopy	1.5 more plants in the understorey than canopy
	8.5 more leaves in the canopy than in the understorey	2.5 more leaves in the canopy than the understorey
Total sampled leaves	22,155 sampled leaves	43,980 sampled leaves
Mean chewing herbivory	20 % damaged	35 % damaged
Numbers of host species	16 species	29 species
	22 % of total plant species	40.2 % of total plant species
Mean proportion of infected leaves per galls per year	2.4 % infected by galls	42 % infected by galls
Mean sampled galls per year	2,540 galls	7,447 galls
Gall distribution and host species specifics	31 % of galled host species are present in the cerrado	2006 – 80 % of these galls were concentrated in six host species: *Argyrodendron actinophyllum*, *Argyrodendron trifoliolatum*, *Arytera divaricata*, *Caldcluvia paniculosa*, *Melodinus australis*, *Orites excelsa*
	50 % of galled species have congeneric cerrado species	2007 – 65 % of galls on *Ficus watkinsiana*
		18 % on *Argyrodendron trifolialatum*
		10 % on *Arytera divaricata*
		Arytera divaricata – young saplings inflated the number of galls in the understorey

with live larvae in wet season against 5.4 % by the end of the dry season. Leaves substantially damaged by free-feeding herbivory were 20 and 17 % of leaves surveyed in the wet and dry seasons, respectively.

8.4.2 Gall Density, Sclerophylly and Leaf Chewing Distribution

Regardless of plant taxonomy, leaf sclerophylly increased significantly with sampling height (Fig. 8.1a). The regression supporting such pattern was not affected by sites, or by the distribution of foliage at different canopy strata (Ribeiro and Basset 2007).

Although there was a high variation in sclerophylly (some understorey leaves being as tough as canopy leaves), canopy leaves were nearly twice more sclerophyllous than understorey leaves. Leaf sclerophylly affected insect herbivory more significantly than foliage density, but in contrasting directions for gall-forming and free-feeding chewing insects. Although the absolute number of chewed leaves was proportional to the total number of leaves available, thus increasing with height, the proportion of chewed leaves decreased significantly with height. This pattern was similar in both sampling seasons (Fig. 8.1b). On the other hand, sclerophylly affected gall density positively, an effect more important than sample height, and more relevant to gall survivorship than oviposition patterns. The average number of live galls collected in the canopy was 13 times greater than in the understorey, a pattern consistent across sites and sampling years (Ribeiro and Basset 2007, Fig. 8.1c). Further, there was a negative relationship between leaf sclerophylly and the proportion of dead galls.

8.5 Lamington Forest Gall Distribution

8.5.1 Gall Distribution Among Tree Species

In the early wet season, we sampled 59 species of trees and shrubs, from among which 25 species had galls (42 % of total). Thirty-five percent of individual sampled plants had galls, reflecting a great concentration of galls on a relatively few hosts. A total of 4,089 galls were sampled in the year out of 61,107 sampled leaves (Table 8.1). From the total of sampled gall in the wet season, 80 % were concentrated in six host species: *Argyrodendron actinophyllum* Bailey (Edlin), *Argyrodendron trifoliolatum* F. Muell. (Malvaceae), *Arytera divaricata* F. Muell. (Sapindaceae), *Ackama paniculosa* (F. Muell.) Engl. (Cunoniaceae), *Melodinus australis* (F. Muell.) Pierre (Apocynaceae) and *Orites excelsa* R. Br. (Proteacae). For the dry season, 65 % of those were collected in only three individual branches of a single *Ficus watkinsiana* F. M. Bailey (Moraceae) (an average of 16.6 galls per leaf were sampled). *Argyrodendron trifoliolatum* had 18 % of the remaining galls and *A. divaricata* accumulated 10 %. A gall morphospecies never occurred in different host species and, mostly, hosts held one to two gall morphospecies. In summary, only seven species, or 9.7 % of the total number of identified plants (and 24 % of galled plant species), accumulated the majority of galls observed.

8.5.2 Gall Density, Sclerophylly and Leaf Chewing Distribution

A strong positive correlation between leaf height in the canopy and sclerophylly existed in the Lamington forest (Fig. 8.1d), consistent across all altitudes. In the wet season, both total and live galls showed the same distribution pattern, that is, a

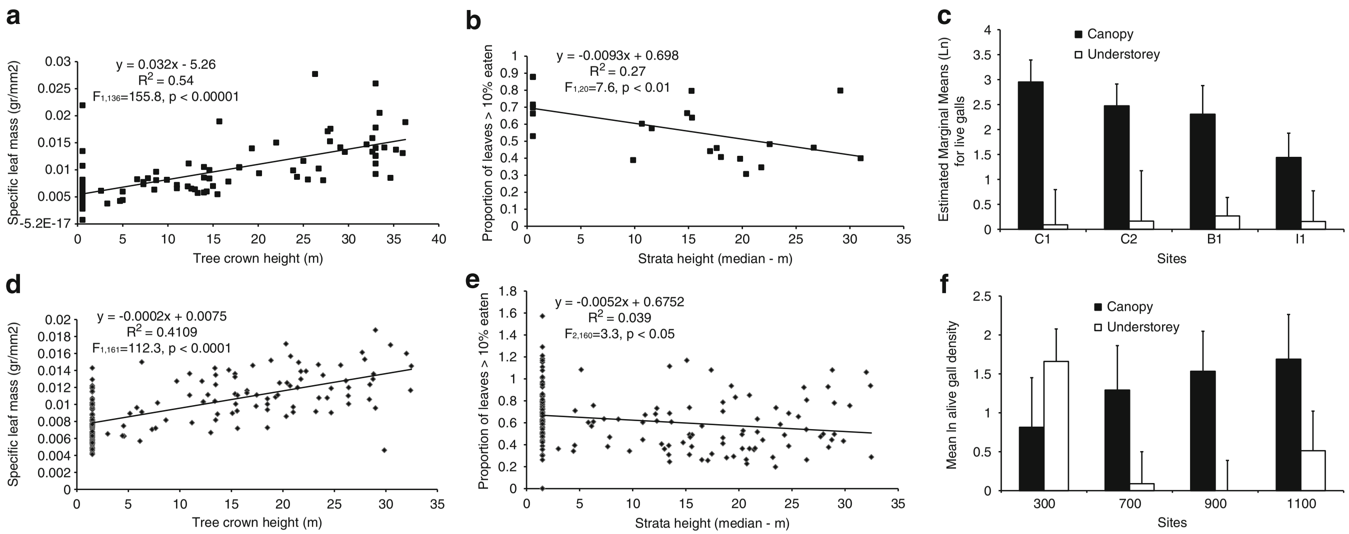

Fig. 8.1 Changes in sclerophylly (specific leaf mass), chewing herbivory (proportion of leaves with leaf area lost >10 %) and gall survivorship (ln alive galls) in the understorey and canopy of San Lorenzo, Panama (A) and Lamington, Australia (B) Parks

higher density in the canopy than in the understorey. For both total and live galls, altitude and "canopy x understorey" habitats interacted significantly (mixed ANOVA model: Total; $F_{1;63}=3.57$, p, 0.01; Live galls; $F_{1;47.3}=3.18$, $p<0.03$, Table 8.1, Fig. 8.1f), due to a similar density of galls in the two habitats at 300 m, in contrast to all other altitudes, where galls predominated in the canopy. However, it is important to note that the high understorey gall density at 300 m was caused by a specific infestation of three sampled saplings of the canopy tree *Arytera divaricata* and that 19 % of galls found on these hosts were dead. Hence, a clear confounding with a super-host species effect. Although no statistical difference was found when comparing the total galls in the canopy and the understorey at any site, above 300 m no live galls were found in the understorey (S.P. Ribeiro and R.L. Kitching, unpublished data).

There was a significant response in leaf chewing herbivory with altitude (Type III mixed ANOVA, $F_{1;160}=3.98$, $p<0.001$). As expected, lower, warmer altitudes had more leaf-chewing herbivory activity, with 300 and 700 m recording the highest rates, 900 m an intermediate level of herbivory and a significantly lower mean herbivory rate at the 1,100 m sites (Least Significant Difference post-hoc test, $p<0.0001$). However, no direct sclerophylly effect was found (Multiple regression, t-test on Beta $t=0.73$, $p>0.05$). Nevertheless, chewing decreased significantly with forest height, reflecting somehow a pattern indirectly related to habitat sclerophylly, and inverse from that found for gall (Fig. 8.1e). Regardless a low coefficient of determination, the robustness of the sample size allowed the detection of this trend, even though further explanations are needed for the huge overdispersion of chewing in the forest. An obvious factor affecting the pattern was the mountain altitude, as described before. Still, when comparing all leaf herbivory from understorey and canopy, a significantly higher leaf area lost rate was found for the former (t-test $t_{172;\,0.05}=3.27$, $p<0.001$).

8.6 Global Pattern Versus Biographic Idiosyncrasies: The Role of Gall Host Taxonomy and Phytogeographic Evolution

Few studies have explored patterns of herbivory distribution based on large samples actually randomized at the scale of the leaf. The use of the canopy-understorey cylinder allowed a proper comparative study on gall distribution between different forests and habitats. Before, a pioneer study from Price et al. (1998) produced a reliable global comparison in gall diversity among ecological communities, showing a strong positive response to sclerophyllous ecosystems. However, fine scale gall ecological responses that may have produced the global pattern were not properly explored, especially in comparisons between habitats within a forest community. Access to high canopies using really comparative sample protocol was needed to provide proper hypotheses test (Ribeiro 2003; Fleck and Fonseca 2007).

The Panamanian San Lorenzo and the Australian Lamington IBISCA sites presented a very similar number of plant species within the cylinders (72 in Australia compared with 73 in Panama). Such similarity suggests that the number of branches and species found in the same forest volume may differ little between these two ecosystems, despite a much greater leaf density and seasonal variation in Australia (mean values: 43,980 in Australia against 21,997 in Panama). The number of galled plant species in Australia, however, was nearly twice than found in Panama, even though 80–93 % of the gall density was concentrated in just seven host species and caused by an estimated number of only eight species of gall insects, found on those particular hosts.

The fact that Lamington forest was in average a more sclerophyllous vegetation than San Lorenzo and had the double number of galled tree species, suggest the importance of overall plant community sclerophylly in gall establishment and evolution. Such sclerophyllous trait may well relate to the widespread number of gall species in other ecosystems such as the Brazilian cerrado (Fernandes and Price 1992; Ribeiro et al. 1999).

Finally, the prediction from Fernandes (1992) that most frequently attacked and densely infested host species belong to large pantropical families was supported only for Lamington forest, where galls were found in Malvaceae (*Argyrodendron*), Moraceae (*Ficus*), Sapindaceae, Apocynaceae and Proteaceae. All these families have more than 60 genera and some (Moraceae) have more than 1,000 species. *Ackama paniculata* was the only exception to this pattern, belonging to the small, however primitive (pre-Gondwana) Cunoniaceae family which contains only 25 genera. Another interesting case to note is the galled Proteaceae *Orites excelsa*. This genus has a gall fossil register from the early Cenozoic and is also found in all south continents. Therefore, gall species distribution may have responded to its early radiation, from 115 to 100 million years ago, just before the split of Gondwana (Larew 1986; Tahvanainen and Niemela 1987).

Nevertheless, this pattern was not supported by the Panamanian data (Medianero et al. 2003; Ribeiro and Basset 2007), where most of galls where on species belonging to small families, and thus appears not to be a fundamental mechanism driving gall distributions worldwide. A strongly constrained evolutionary history of the gall-forming guild, related to a restricted number of host species (see Veldtman and McGeoch 2003), may better define a global pattern. Through analysis of the fossil record, Larew (1986) has shown a significant constancy in the gall fauna associated with a number of host species from the late Miocene-Pliocene, 20–13 million years ago. In addition, when analysed at the community level, following random sampling in the vegetation, we found that galls infected only 22 % of sampled tree species in San Lorenzo National Park, and 40.2 % in Lamington Park.

8.7 Conclusions

Unknown evolutionary constraints appear to restrict gall-inducing insects from spreading to the whole of the local flora. Although gall taxa diversification seem to respond to host range in an evolutionarily long time (Hardy and Cook 2010), radiation after host invasion may be more related to host species life history and ecology rather than to any taxonomic or biochemical traits. For instance, the greater expectation of finding galls in a plant from a large family could be just a neutral consequence of the sheer size of the family. One may suppose that in a large plant family at least some species will have a life history that matches gall adaptation and developmental demands, and thus increases the chance that indeed those plants will be surveyed by most of sampling methods (examples in Santos et al. 2011). Even authors that have been finding a strong relationship between family size and gall diversity in cerrado, such as Araújo (2011), have clearly posed that the event is host specific within a large family, and that has actually little echo at the genera level, for instance.

These life history components favourable to gall invasion are likely to be related to leaf quality/sclerophylly and the subsequent effects on risk of mortality, caused by fungi, parasitoids, or accidental chewing by herbivores. The latter effect was first proposed by Ribeiro and Basset (2007) and is also partially supported by Lamington data, which showed a substantially higher leaf area lost in the understorey compared with the canopy, where most of the galls were found.

Our work filled up a few gaps in cross-ecosystems/continents data, at a scale that allowed us to support or reject some unanswered hypotheses on galls species distribution patterns. Fleck and Fonseca (2007) listed flaws and deficiencies of 13 classic hypotheses on insect diversity distribution when applied to gall species. We may suggest that "taxonomic isolation", "soil fertility", "plant species richness" or "resource concentration" are unlikely to explain gall distribution. In addition, the lack of data on tall tropical forest galls jeopardizes previous negative conclusions on the "architecture complexity" hypothesis. In fact, the latter may be a complementary explanation to the "higrothermal/sclerophylly stress", the one our data corroborate most, along with the Price's (1994) "phylogenetic constraint" hypothesis, not explored by Fleck and Fonseca (2007).

In conclusion, micro-habitat harshness and leaf sclerophylly determine gall insects' oviposition preferences and/or survivorship (Fernandes and Price 1988, 1992; Ribeiro and Basset 2007), although in Lamington National Park these mechanisms were partially masked by a strong host specific association that constrained gall distribution, as well as the strong altitudinal factor. Comparison with San Lorenzo humid closed rainforest suggests the likely existence of a sclerophylly rate threshold above which galls tend to succeed better and spread in the plant community.

Nevertheless, specific evolutionary histories play an equally important role in the global patterns of local gall species richness and abundance. Idiosyncrasies ought to be related to biogeographic regions, and an isolated continent as Australia was indeed expected to reflect Gondwana events. On the contrary, the Neotropical region seems to be mostly influenced by a high number of widely distributed host species, which have a biogeographic range across biomes and sufficiently connected by xeric/canopy habitats.

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Chapter 9
Galling Insects as Indicators of Habitat Quality

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Abstract Galling insects present many interesting features that make them good candidates for bioindication, such as their sessile habit, host specificity, conspicuousness and abundance. In this chapter we summarize some of the studies performed in the Neotropics that have used galling insects as indicators of habitat quality. These studies have mostly investigated forest fragmentation and the edge effect on the gall community, while few use galling insects as indicators to evaluate restoration success, and lesser the effects of urbanization. There is a tendency for the increased use of galling insects and their galls as indicators of habitat health and environmental impact as they seem to be highly tuned with habitat properties and are easily sampled. Thereby, it is urgently needed to detail such studies by the inclusion of information on the effects of disturbance on the galling insect population performance and fitness.

Keywords Biodincators • Community structure • Edge effect • Forest fragmentation • Galls • Habitat health • Habitat indication • Insect galls • Restoration success • Richness

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9.1 Introduction

The assessment of habitat quality has been intensely studied in the last decades, and an intense debate on which indicators to apply is in progress (Jørgensen et al. 2005). Invertebrates are good candidates for ecological indicators, since they are diverse, susceptible to habitat change, respond rapidly to disturbance, and can be easily and cost-effectively sampled (e.g., McGeoch 1998, 2007; Uehara-Prado et al. 2009). For nearly two decades, researchers have utilized galling insects as indicators of environmental quality, since these organisms are highly sensitive to changes in their host plants and the environment in which they occur (Fernandes and Price 1988; Fernandes 1990; Fernandes et al. 1995; Shorthouse et al. 2005). For instance, in Canada, galls on *Vaccinium angustifolium* (Ericaceae) were innovatively used to evaluate copper and nickel concentration around an ore smelter, presenting the highest concentrations of these metals compared to other plant organs, but only for one of the sampled sites (Bagatto and Shorthouse 1991). In this chapter we summarize some studies on the use of galling insects as indicators of habitat quality conducted in the Neotropics.

The studies performed on such subject in the Neotropical region are restricted to the attempt in establishing relationships that may form the basis of bioindication. Therefore, it may not be different from the studies performed elsewhere, where three-quarters of the recent publications on insects as bioindicators are of same nature (McGeoch 2007). The studies that attempted to use galling insects as habitat health indicators were performed in different Brazilian biomes, excepting one in the northerly limit of the Neotropical region. In spite of their importance, this chapter may represent the first revision in which the studies of galling insects as bioindicators are reviewed.

9.2 The Use of Insect Galls as Indicators of Forest Fragmentation and Restoration

The Brazilian Amazon region is currently under strong development pressure and about 18 % of its forest area has been removed by anthropogenic activities, such as agriculture and livestock (Kirby et al. 2006; Nazareno et al. 2012). The use of insects as tools to monitor the environment is augmenting in this region (Klein 1989; Fowler et al. 1993; Vasconcelos 1999; Vasconcelos et al. 2006; Santos et al. 2008a; Coelho et al. 2009; Leidner et al. 2010). Given the high abundance and richness of galling insects in the Amazonian region, their use has been increasing and provided unique information on habitat quality and health.

9.2.1 Galling Insects in Fragmented and Continuous Forests

Fragment size and isolation determine colonization and extinction rates, and thus the survival and maintenance of animal and plant populations. Small fragments are usually dominated by edge processes, with an increase in air temperature and a decrease in soil and air moisture which affect the local flora and fauna (Gascon et al. 2001; Laurance et al. 2002). These factors are known to deeply influence the population dynamics of galling insects (e.g., Fernandes and Price 1988, 1992).

In central Amazon, the reserves of the Biological Dynamics of Forest Fragments Project encompass different sized fragments (1, 10 and 100 ha) and adjacent areas of preserved *terra firme* upland forest (hereafter, continuous forest). Samplings of galling insects were taken from upper canopy (sunny leaves, branches, fruits and flowers located at uppermost layer). A sound sample of 91,006 galls classified into 703 galling species on 503 tree individuals indicated no significant differences in the galling abundance and galling richness between fragments and continuous forests (Julião et al. 2014, in prep.). However, absolute values indicated that 1 ha fragments had higher richness and abundance of galling insects than do 10 and 100 ha fragments, although statistical differences among different fragment sizes were not significant (Julião et al. 2014, in prep.). The authors argued that the galling community was influenced by the spatial and biological configuration of the studied system: (i) the distance between fragments and the colonization source (continuous forest), (ii) the similar number of tree species in fragment and continuous forest samples, and (iii) the matrix of secondary vegetation around the fragments which may not constitute a barrier to galling insect dispersion.

9.2.2 Galling Richness as an Indicator of Restoration Success

Many abiotic and biotic factors are changed during the process of biological succession, and alterations in plant species composition (Capers et al. 2005) consequently affect resource availability for the herbivore community. Usually, regeneration ability of Neotropical forests depends on the proximity to propagule sources, use intensity before land abandonment and on soil initial properties (Guariguata and Ostertag 2001). In the Brazilian Atlantic rain forest, galling insect species richness was used to compare three succession stages, including areas enriched with native species (Moreira et al. 2007). This study indicated a positive influence of host plant composition on galling insect community, which was affected by an allelopathic species, *Myracrodruon urundeuva* (Anacardiaceae).

Galling insect richness was assessed in 36 reforestation plots in a bauxite mining area and in native primary forests in the region of Porto Trombetas, state of Pará, in northern Brazil (Fernandes et al. 2010; Almada and Fernandes 2011). About 80–100 species of native forest species were used in the restoration programme. Forest regeneration time ranged from 0 to 21 years. The survey resulted in the record of 309 galling insect species on 255 host plant species, hence with an average of 1.2 galling insect species per host plant. Galling insect richness increased with stand age. Otherwise, an increased richness of galling insects was observed at stands of intermediate age. The authors argued that such trend was affected by increased plant species richness, thus supporting the contention that plant composition affects the galling community (Fernandes et al. 2010).

9.3 Galling Insects as Indicators of Edge Effects

9.3.1 Edge Effects on Galling Insect Richness in Natural Forest Patches

Two studies evaluated the edge effect on galling insects in natural patches of forest, one in Pantanal (Julião et al. 2004) and the other in the Atlantic Forest (Toma and Mendonça 2014, in prep.). These studies presented an interesting approach since they considered natural edges instead of created edges in fragments originated from a preexisting continuous forest. Julião et al. (2004) in their study in the Pantanal floodplain investigated differences in galling insect species richness between forest patch edges and interiors and the species-area relationship. The authors found no evidence that galling insect assemblages are richer in larger forest patches and no differences in galling insect species richness between edges and interiors.

Disturbances on the vegetation can affect galling insects by changes in their hosts occurrence and/or performance. These predictions were tested in the Araucaria Forest (Toma and Mendonça 2014, in prep.), an ecoregion of the Atlantic Forest in south Brazil, where forest-grassland boundaries naturally occur over thousands of years commonly maintained by cattle grazing and anthropogenic fire. Twenty sites were sampled by two 60 min transects searching for galls, one at the edge and the other at the interior for each site; half of the sites were under disturbance while the other half were regenerating for nearly 17 years without cattle or fire disturbances. Disturbed forest interiors were richer in galling insects than corresponding edges while there was no difference between edges and interiors for sites under recovery. Galling species composition, on the other hand, differed between edge and interior and between sites under recovery and under disturbance. The authors argued that species composition is probably a better indicator of disturbance effects on the galling fauna. In addition, disturbance resulted in species evenly distributed in space but lower total richness; thus areas without disturbance seem to allow suitable hosts to persist determining the occurrence of herbivores such as galling insects.

9.3.2 Edge Effects on Galling Insect Richness in Forest Fragments

In a study performed in the Atlantic rain forest of northeastern Brazil, Souza (2013) reported that habitat influenced host plant and galling insect assemblages. An emerging pattern demonstrated that host plant assemblages and galling insect richness of forest fragment core areas and edge habitats differed in nearly half, with 43 galling insect species found in core areas and 19 galling insect morphospecies at edges. Souza (2013) argued that impoverishment in sapling wood plants taxonomic composition (see Tabarelli et al. 2008), with large dominance of pioneer species at edges (majority of host plants were pioneer with 78 % and for shade tolerant were found 19 % of host plants) (Oliveira et al. 2004; Laurance et al. 2006; Michalski et al. 2007) and a group of shade tolerant in forest interior (71 % of host plants were shade tolerant tree species and 17 % were pioneer plants) (Santos et al. 2008b; Oliveira et al. 2004; Tabarelli et al. 2010), could lead to trophic cascade effects across galling insect species which require resource exclusively of their host plants, resulting in impoverishment of galling insect assemblages in several spatial portions of Atlantic rain forest. Recently, a revision by Wirth et al. (2008) highlighted that in edge habitats there are events which support increased herbivore activities, which are mediated by the altered microclimatic conditions, increased abundance of pioneer species, and consequently qualitative changes in host plant chemistry, and ultimately altered tri-trophic interactions among organisms. Thereby, Araújo and Espírito-Santo (2012) reported a positive response of galling insects to forest edges in forest fragments in the Brazilian Amazon. The authors also considered differences between disturbed and undisturbed areas, and found that disturbed areas were richer in galling insects. The results were attributed to increased stress for host plants and the disruption of top-down forces.

The effect of forest edge on insect population was evaluated for the galling insects associated with *Styrax pohlii* (Styracaceae) in the Brazilian Cerrado (Araújo et al. 2011). Branches from 15 host plant individuals were sampled at a forest fragment edge and another 15 at the interior. In total, 8,208 galls were sampled and separated into eight galling species, six on leaves and two on stems. Richness and abundance of galls differed significantly between edge and interior of the forest fragment, supporting the prediction of greater gall richness at forest edges compared to the interior. Two galling species were considered great candidates as bioindicators since they had quite different abundances between forest edge and interior; one was more abundant at the edge and the other at the interior.

9.4 Impact of Urbanization on Galler Populations and Tri-trophic Interactions

In urban and peri-urban areas, galling insects proved to be an efficient tool for assessing habitat quality; availability of resources, biotope structure, and the frequency and intensity of habitat management (reserves, parks, squares, and vacant lots) were suggested as main determinants in galling presence (Julião et al. 2005). Similarly, Carvalho-Fernandes et al. (2012) compared gall richness in peri-urban areas they classified as preserved, intermediate and anthropogenic in northeastern Brazil, and found higher richness in preserved areas. Urbanization impact was tested on a tri-trophic interaction among the endemic Florida scrub plant *Palafoxia feayi* (Asteraceae), a gall midge (*Asphondylia* sp.) and its associated parasitoid wasps in Florida, USA (Sumoski et al. 2009). The authors analyzed changes in plant architecture, gall abundance and parasitoid diversity by sampling 1,473 host plants in sites differing in degree of urbanization (urban and pristine sites), and taking galls to the laboratory for parasitoid rearing. Plant architecture differed between degrees of urbanization, but gall abundance was only slightly greater in urban sites. Parasitoid abundance was greater in galls collected in disturbed sites, which also had a higher proportion of parasitized galls, but the average parasitism success per gall and parasitoid diversity were similar. It seems that the impacts of urbanization on plant architecture do not strongly influence utilization by the insects galling this host plant or its parasitoids. Although only plant architecture responded to urban impact, the approach of this study is very interesting since it considers more than one trophic level in the evaluation of disturbances.

9.5 Remarks and Conclusions

Most studies addressed the effects of forest fragmentation and forest edges on galling insects, while only two focused on the effects of succession in restored areas on galling insect community and three on the effects of urbanization on galling community and success. Although galling insects are finely tuned with their host plants and habitats, the applicability of galls as indicators of habitat quality and environmental impacts needs further studies and clear evaluation in the field. The contribution of these studies performed in the Neotropical region may have paved the way for the use of galling insects as reliable indicators of habitat quality and ecosystem functioning.

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Chapter 10
Host Specificity of Gall Midges (Diptera: Cecidomyiidae) on Ten Species of *Inga* (Fabaceae)

Amandine Bourg and Paul Hanson

Abstract Studies of host specificity in gall-inducing Cecidomyiidae are hindered by the difficulties encountered in obtaining adult stages, which are essential for species identifications, and even when adults are reared from galls, the vast majority of species are undescribed. For this reason gall morphotypes (morphospecies based on the extended phenotype) are commonly used as a surrogate for species. We used this methodology to examine the host-specificity of gall-inducing Cecidomyiidae associated with ten species of *Inga*, one of the most species-rich genera of trees in the Neotropics. A total of 5,756 galls were collected, which were conservatively classified into 30 gall morphotypes. Species richness of gall-inducers was highest on *I. oerstediana*, with 14 morphospecies. Thirteen cecidomyiid morphospecies were restricted to just one species of *Inga*. Of the 17 morphospecies found on more than one species of *Inga*, only three were restricted to a single section of the genus. We discuss possible reasons for these results, as well as the complications involved in using gall morphotypes as a surrogate for species.

Keywords Gall morphotypes • Extended phenotype • Cecidomyiidae

10.1 Introduction

The induction of plant galls by insects involves a complex physiological and biochemical interaction between the insect and the plant, a process that is still poorly understood. There is a general consensus that gall-inducing insects generally show a greater degree of host specificity than do most other phytophagous insects (Carneiro et al. 2009), which probably stems from the intimate nature of the

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interaction between insect and plant. When a particular species of gall-inducing insect occurs on more than one species of plant it is generally restricted to a set of closely related plant species. For example, among gall-inducing Cynipidae (Hymenoptera) on oaks (Fagaceae), individual gall wasp species are nearly always restricted to members of a single section of *Quercus* (Abrahamson et al. 1998).

A wide diversity of insects are known to induce plant galls (Raman et al. 2005), but there is little question that the most species-rich group is Cecidomyiidae (Diptera). The majority of species in this family induce galls, and as of 2010, a total of 6,131 species and 783 genera had been described worldwide (Gagné 2010), but the real number of species lies in the realm of speculation (Espírito-Santo and Fernandes 2007). Based on the assumption that each species of flowering plant has at least two species of gall midge of the subfamily Cecidomyiinae, it has been suggested that there could be 18,000 species of Cecidomyiinae in Costa Rica, but this enormous number obviously needs to be verified (Brown et al. 2009). Whatever the actual number, it is highly probable that less than 1 % of gall midges have scientific names, which makes Cecidomyiidae one of the most extreme examples of the "taxonomic impediment" (Flowers 2007) facing researchers.

In poorly studied groups of organisms, such as many families of insects, morphospecies are sometimes used as a surrogate for named species. However, this procedure entails the risk of improperly distinguishing species and poses problems in terms of replicability. Nonetheless, gall researchers frequently use morphospecies (e.g., Carneiro et al. 2009; Cuevas-Reyes et al. 2003; Dalbem and Mendonça 2006; Nieves-Aldrey et al. 2008), not merely due to sheer necessity, but also because gall morphology provides an additional and easily accessible character for distinguishing species. The size, shape and complexity of plant galls vary considerably between species of gall-inducers, but is generally constant within a particular species. Gall morphotype can therefore be considered as part of the extended phenotype of the gall inducer (Stone and Cook 1998). While there is probably some validity to the use of gall morphotypes as a surrogate for species, caution is required in distinguishing differences in gall morphology that are due to the identity of the gall inducer versus differences due to the developmental stage of the gall or alterations in gall morphology caused by an inquiline (Brooks and Shorthouse 1998). On the other hand, when identical gall morphotypes occur on two closely related plant species, the decision to lump them in one species or split them in two depends upon one's assumptions about host specificity.

In this study we used gall morphotypes to examine host specificity of gall-inducing Cecidomyiidae on ten sympatric species of *Inga* (Mimosaceae). Our specific goal was to test the hypothesis that closely related species of *Inga* (i.e., members of the same section) would share more species of gall-inducers than more distantly related species of *Inga* (members of different sections). We chose *Inga* not only because species in this genus harbor a large diversity of galls, but also because they are common trees throughout the Neotropics, comprising about 300 species that occur from central Mexico and the Caribbean to northern Argentina (Richardson et al. 2001). Although a complete phylogeny of the genus is lacking, *Inga* has been the subject of a relatively recent taxonomic monograph (Pennington 1997), which provided the basis for our selection of plant species representing different sections within the genus.

10.2 The Study

Galls and hosts were studied in three main sites located on the Caribbean side of Costa Rica. La Selva Biological Station, in Puerto Viejo de Sarapiquí (10°26′N, 83°59′W, 50–150 m altitude), has 1,600 ha of forest, a mean annual temperature of 25.8 °C and an annual precipitation of 4,000 mm (Palow and Oberbauer 2009). La Tirimbina Biological Reserve is located 7 km from La Selva, in La Virgen de Sarapiquí (10°23′N, 84°08′W, 175 m altitude), has a mean annual temperature of 25.3 °C and an annual rainfall rate of 3,800 mm (Segura and Kanninen 2005). The Alberto Manuel Brenes Reserve, located in San Ramón, Alajuela province (10°13′12″N, 84°36’6″W, 850 m altitude), includes 7,800 ha of montane cloud forest and has an annual precipitation of 4,500 mm (Gómez-Laurito and Ortiz 2004). Three other sites, all of them in the metropolitan area (Central Valley) of San José, were included in order to obtain samples from *Inga vera*: Parque de la Paz (9°54′N, 84°4′W), San Pedro de Montes de Oca (9°56′N, 84°2′9″W) and Santo Domingo de Heredia (9°58′ N, 84°5′W). The species of *Inga* used in each location are summarized in Table 10.1.

In order to facilitate the standardization of sample collections, only leaf galls were included in this study. Another reason for using only leaf galls was that prior observations suggested that most of the galls found on other plant organs (e.g., stems and fruits) were induced by insects other than Cecidomyiidae (Pujade-Villar et al. 2012). The sampling was conducted every 2 months on mature trees of the ten *Inga* species listed in Table 10.1. On each tree, ten galled leaves were collected from a single branch. The same trees were used on every sampling date. Dissections of galls were carried out in the laboratory in order to classify them into morphospecies. Characteristics used to define gall morphospecies included: size, shape, number of chambers, color, insects found inside, and whether or not the gall was readily detachable from the leaf.

Several chi squares were done to compare richness and abundance of gall morphospecies between *Inga* species. To minimize the sample effect, a rarefaction

Table 10.1 *Inga* species, study sites from which gall samples were collected, and number of trees sampled

Section	Species	Tirimbina	La Selva	Alberto Manuel Brenes Reserve	Santo Domingo, San Pedro y and Parque Paz	Number of trees
Bourgonia	*I. alba*		X	X		2
Bourgonia	*I. samanensis*	X				7
Pseudinga	*I. barbourii*			X		9
Pseudinga	*I. mortoniana*			X		3
Pseudinga	*I. punctata*			X		3
Pseudinga	*I. ruiziana*	X	X			8
Tetragonae	*I. sapindoides*	X	X	X		22
Vulpinae	*I. leonis*			X		6
Inga	*I. oerstediana*	X	X			22
Inga	*I. vera*				X	9

analysis was conducted to determine the potential richness of every *Inga* species if a resampling of galls was done. Correlations were done to see if the distance between trees of the same species of *Inga* had an effect on abundance and richness of gall morphospecies. For the two species of *Inga* that had the most galls (*I. oerstediana* and *I. sapindoides*) the number of trees harboring galls was graphed with respect to sampling dates to observe possible changes with respect to phenology.

10.3 Comparison of Species Richness of Gall-Inducers Between *Inga* Species

We found 5,756 galls, which were separated into 30 morphospecies (Fig. 10.1). Two additional galls were found, but were not included in the analysis because it was not possible to determine the identity of the gall inducer. Even within single *Inga* species, we often observed what we interpret to be intraspecific variation in gall morphospecies (Fig. 10.2): different degrees of pubescence, colors and sizes.

Fig. 10.1 Morphospecies found in this study. The gall size varies from 1 to 9 mm

Fig. 10.2 Gradient in morphospecies 21. The gall size varies from 1 to 4 mm

We adopted conservative criteria in grouping of galls into morphospecies; in other words, when two morphotypes showed intermediate forms we counted it as just one morphospecies.

Distance between trees did not seem to have an effect on gall abundance and richness in *I. oerstediana* (for San Ramón: $r_{rich} = -0.144$, $p_{rich} = 0{,}173$, $r_{abund} = -0{,}108$, $p_{abund} = 0{,}307$; for La Selva: $r_{rich} = -0{,}403$, $p_{rich} = 0{,}428$, $r_{abund} = -0{,}317$, $p_{abund} = 0{,}540$; for La Tirimbina $r_{rich} = 0.487$, $p_{rich} = 0{,}327$, $r_{abund} = 0{,}046$, $p_{abund} = 0{,}930$), or in *I. sapindoides* (for San Ramon: $r_{rich} = 0.160$, $p_{rich} = 0.350$, $r_{abund} = 0{,}860$, $p_{abund} < 0.0001$; for La Selva: $r_{rich} = 0{,}175$, $p_{rich} = 0{,}308$, $r_{abund} = 0{,}121$, $p_{abund} = 0{,}479$; for La Tirimbina $r_{rich} = -0.367$, $p_{rich} = 0.474$, $r_{abund} = -0.129$, $p_{rich} = 0.807$).

There was some temporal fluctuation in the number of trees harboring galls in *Inga oerstediana*, *I. ruiziana* and *I. sapindoides* (Fig. 10.3). Dry months, such as June 2009 and December 2009, tended to have fewer trees with galls, and very rainy months, such as October 2009 and May 2010, tended to have more trees with galls.

The species richness of galls was similar between the tree species studied ($X^2 = 14.469$, $p = 0.075$, gl = 8) but gall abundance was higher on *Inga oerstediana* ($X^2 = 10{,}128$, $p < 0.00001$, gl = 8). The tree species that had the highest richness of galls

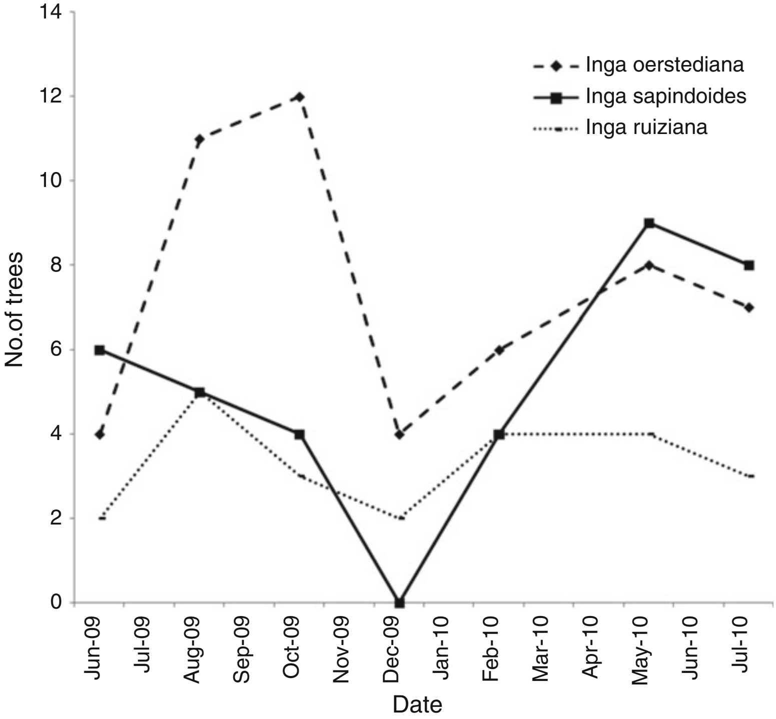

Fig. 10.3 Timeline of number of *Inga oerstediana*, *I. sapindoides* and *I. ruiziana* trees harbouring galls

were *I. oerstediana* and *I. sapindoides*, with 14 and 13 morphospecies, respectively; while the ones that had the lowest richness were *I. alba* and *I. punctata*, each of which had four morphospecies (Table 10.2). The rarefaction analysis showed that if random samples of between three and six galls were collected, *I. alba* would have the greatest richness of galls (Fig. 10.4).

It is not uncommon to find that within a genus of plants, certain species harbor a greater species richness of gall-inducers than do others. For example, in north temperate regions some species of oaks have a greater species richness of cynipid gall wasps than do other oak species (Cornell and Washburn 1979). The results of the present study indicate that the same pattern might occur in the genus *Inga*: *Inga oerstediana* and *I. sapindoides* had the greatest number of gall morphotypes whereas *I. alba* and *I. punctata* had the least number. While this difference may in part reflect different sampling efforts (Table 10.1), long-term observations of *I. oerstediana* and *I. punctata* at several other sites (P.H., *unpublished*) suggest that, at least in these two species, the difference is real.

In the case of oaks two hypotheses, both with some supporting evidence, have been proposed to explain inter-specific differences in numbers of gall-inducers. First, oak species with larger geographic distributions tend to harbor a greater number of gall wasps (Cornell and Washburn 1979). It is difficult to evaluate this hypothesis

Table 10.2 Gall morphospecies found on ten species of Inga, representing five section of the genus (for abbreviated names of Inga see Table 10.1 for complete names)

Morpho-	Bourgonia		Pseudinga				Tetragonae	Vulpinae	Inga	
species	*I. alba*	*I. sam.*	*I. barb.*	*I. mort.*	*I. punct.*	*I. ruiz.*	*I. sap.*	*I. leon.*	*I. oer.*	*I. vera*
1			x	x			x	x		x
2							x		x	
3		x					x		x	x
4									x	
5		x		x		x				x
6								x		
7								x		
8				x	x	x				
9								x		
10	x									
11									x	
12				x			x			
13							x		x	
14			x			x	x	x	x	
15			x		x					
16					x					
17							x			
18	x									
19	x						x	x		
20								x	x	x
21									x	x
22							x	x	x	x
23			x		x	x	x	x	x	
24									x	
25			x	x			x		x	x
26		x				x			x	
27		x	x				x		x	
28	x									
29		x								
30							x			
Total	4	5	6	5	4	5	13	9	14	7

in the case of the *Inga* species studied here. For example, both *I. oerstediana* and *I. punctata* occur from central Mexico to Bolivia, although the latter also extends into Brazilian Amazonia; however, *I. oerstediana* has a wider altitudinal range (from sea level to 3,000 m) than *I. punctata* (sea level to 2,000 m), and the latter is usually associated with disturbed vegetation and forest gaps (Pennington 1997).

The second hypothesis that has been suggested for oaks is that species with a higher tannin content tend to have a greater number of gall wasp species, presumably because higher tannin levels result in decreased larval mortality due to fungal infestation (Taper and Case 1987). Like oaks, most (about 65 %) *Inga* species contain condensed tannins (proanthocyanidins) in their leaves (Harborne *in* Pennington 1997). While both *I. oerstediana* and *I. punctatata* are reported to have these tannins, we

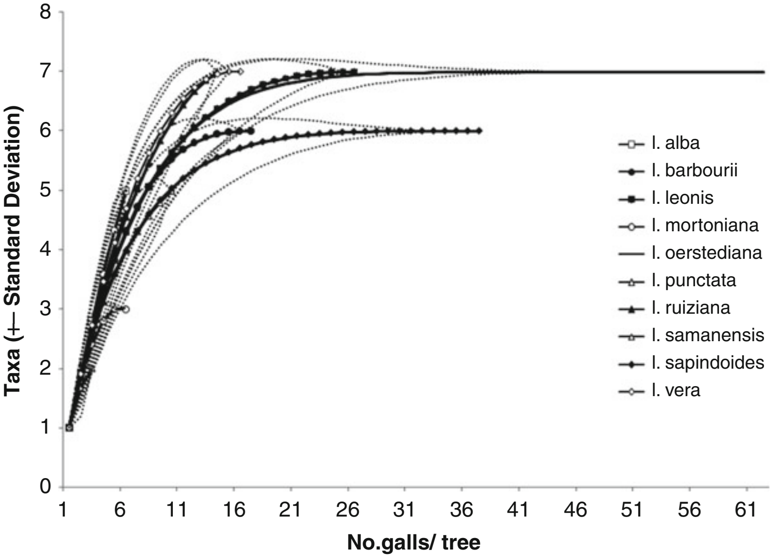

Fig. 10.4 Rarefaction of gall morphospecies compared to Inga species

have been unable to find data comparing the concentrations in these two species. In future studies of gall inducers of *Inga* it would be interesting to include species that are reported to lack condensed tannins, for example *I. capitata*.

10.4 Gall-Inducing Species and Taxonomic Affinity of Host Plants

Thirteen cecidomyiid morphospecies were restricted to just one species of *Inga*. Of the 17 morphospecies found on more than one species of *Inga*, only three (morphospecies 8, 15, and 21) were restricted to a single section of the genus. In other words, nearly half of the species (14 of 30 morphospecies) were shared between sections of *Inga*. Four species occurred on trees in two sections, six species in three sections, four species in four sections, but none were found on trees in of all five sections of *Inga* (Table 10.2).

Our finding that roughly half of the cecidomyiid morphospecies were present on *Inga* species belonging to distinct sections of the genus is surprising given that gall-inducers are expected to be quite host specific (Carneiro et al. 2009). There are at least two potential explanations for this result. First, we were too conservative in our recognition of gall morphotypes; in other words, at least in some cases, what we categorized as a single morphospecies, is in fact more than one species. Second, there is evidence suggesting that speciation in *Inga* has been concentrated in the past ten million years, with many species having arisen as recently as two million years ago (Richardson et al. 2001), which results not only in a poorly resolved phylogeny of the genus, but perhaps also in less host specificity by gall inducers.

While there is currently insufficient evidence to evaluate the second hypothesis, we can provide some comments regarding the first explanation. Using gall morphotypes to distinguish cecidomyiid species undoubtedly entails a certain degree of imprecision. The solution of course is to rear the adult stages, but this involves intensive rearing throughout the year. Moreover, sufficient quantities need to be reared since it is quite common to obtain more parasitoids and inquilines than gall inducers. For example, we made some preliminary attempts to rear the adult gall-inducers from morphospecies number 21 on *Inga vera* but the only cecidomyiid we obtained was an undetermined species of *Meunieriella*, and most members of this genus are inquilines (Gagné and Jaschhof *in* Brown et al. 2009). By far the most abundant adult insects emerging from this gall were six hymenopteran parasitoids: *Astichomyiia hansoni*, *A. latiscapus* (Eulophidae), *Chrysonotomyia conostegiae* (Eulophidae), *Galeopsomyia* sp. (Eulophidae), *Eurytoma* sp., (Eurytomidae), and *Allorhogas ingavera* (Braconidae). We have indirect evidence that at least a couple species of Tanaostigmatidae (*Tanaoneura hirticoxa* and a species of *Tanaostigmodes* in the *gracilis* group) feed as inquilines in various leaf galls on *Inga* (including morphospecies 21) and modify gall morphology (Fig. 10.2), as has been reported in another tanaostigmatid species (Fernandes et al. 1987) and cynipid gall wasps (Brooks and Shorthouse 1998). We attempted to take this into account in our methodology and hence our conservative approach to delimiting morphospecies based on gall morphology.

The difficulties involved in obtaining adult stages are probably less serious in the case of certain other groups of gall-inducers. For example, it is generally easier to obtain adults from galls induced by Psylloidea (Hemiptera), and when this was done with psyllid galls on *Baccharis* (Asteraceae) it was found that morphologically similar galls on different plant species were in fact distinct species of gall inducers (Burckhardt et al. 2004). Thus, it is certainly possible that by not rearing adult cecidomyiids we underestimated both the species richness and host specificity of gall inducers on the ten species of *Inga*.

10.5 Conclusion

We suggest that the genus *Inga* provides a Neotropical system comparable to that of *Quercus* in north temperate regions. Both are common, widely distributed, species-rich genera that harbor large numbers of gall-inducers. With further study, *Inga* could potentially provide independent data to test the two hypotheses (geographic area and tannins) that have been proposed to explain differences in numbers of gall-inducing species associated with different species of oaks. Unlike oaks, *Inga* species also possess extra-floral nectaries that attract ants (e.g., Brenes-Arguedas et al. 2008; Kursar et al. 2009), whose effects on ovipositing cecidomyiids are unknown.

Despite the obvious differences between the two genera of trees, we would like to conclude by suggesting that if more research is dedicated to the gall midges associated with *Inga*, we might someday find that *Inga* species are the oak equivalents of the Neotropics.

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Chapter 11
Galling Insect Community Associated with *Copaifera langsdorffii* (Fabaceae): The Role of Inter- and Intra-annual Host Plant Phenology

Marcilio Fagundes

Abstract Super-host plants of galling insects are important systems for hypotheses testing. Plant phenology directly affects the gall community through the synchronism between the target organs development and insect attack, or indirectly by promoting changes in plant resource quality and/or quantity. This study focus on the effects of inter- and intra-annual variations in plant phenology on the galling insect community associated with the host plant *Copaifera langsdorffii*. The species *C. langsdorffii* is a super-host of galling insect that have supra-annual fruiting and broadly intra-annual variation in phenology. Supra-annual fruiting affected the resource allocation among vegetative growth, reproduction and production of chemical defenses. The galling insect community changed between reproductive and non-reproductive years of *C. langsdorffii.* Moreover, leaf biomass and gall richness and abundance were also affected by intra-annual variation in plant phenology. Finally, the possible roles of plant phenology on gall community associated with *C. langsdorffi* are discussed.

Keywords Cerrado • Gall dynamics • Gall seasonality • Host phenology • Host specificity • Insect galls • Plant phenology • Plant-animal interactions • Richness • Seasonality • Super-host • Tropical savanna

11.1 Introduction

The discovery of patterns in nature stimulate the generation of factually based hypotheses and further experimental test of these hypotheses (Price et al. 1998). One of the concerns among ecologists has been the search for patterns and the

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mechanisms that shape them (e.g., Huston 1979; Fernandes and Price 1988; Novotny and Basset 2005; Kozak and Wiens 2010). In this sense, while population ecology theory has reached relative advance in recent decades, community ecology still deserves more attention. Probably, the inherent complexity of the natural system is the main obstacle to community ecology development (Morin 2011).

The fact that in tropical systems the most species alive are arthropods associated with plants (Price et al. 1995) could elect these organisms as model for studies on community ecology. However, some other characteristics of the tropical insect assemblage (the majority of these arthropods still is poorly identifiable, the species occur in low density, the composition of local assemblage is highly variably and the species present low specificity with their host plant) difficult the replicates attainment optimal and constrain hypotheses test at community level (Basset et al. 1996; Novotny and Basset 2005; Lewinsohn and Roslin 2008; Novotny et al. 2006).

Herbivorous insects are composed of several feeding guilds (e.g. sap-sucking, chewing, mining, seed predators and galling insects), with different specialization levels on their host plant and habitat (Koricheva et al. 1998; Novotny and Basset 2005). For example, comparatively to free-feeding insects, galling insects generally are considered more specialized herbivores (Carneiro et al. 2009; Fagundes and Fernandes 2011). Moreover, the structure (gall) resulted of the galling insect plant interaction are sessile, and easily sampled. The galls generally occur in high density on their host plant (e.g. Costa et al. 2010) and gall form and size is dependent on plant tissue quality (Fagundes et al. 2005). These characteristics make this guild very suitable for studies at different levels of ecological organization.

In this scenario, super host plants of galling insects (*sensu* Veldtman and McGeoch 2003) emerge as interesting systems for the community ecologist. Several studies developed in tropical areas relate the occurrence of super host plant of galling insects across different phytofisionomies (e.g. Amazonian Forest: Almada and Fernandes 2011, Atlantic Forest: Santos et al. 2012, Dry Tropical Forest: Luz et al. 2012, Neotropical Savanna: Araújo 2011, Rupestrian Fields: Espírito-Santo et al. 2007, restinga: Maia and Oliveira 2010). Thus, the existence of super host plants of galling insects allows the test of hypotheses at the community level; within (e.g. Fagundes et al. 2005; Espírito-Santo et al. 2007; Costa et al. 2010) and across different habitats (e.g. Cuevas-Reyes et al. 2006; Silva et al. 2009; Fagundes and Fernandes 2011). However, the mechanisms that have driven the existence of super host plants remain unknown. In this study the focus is on the effects of intra and inter-annual variations in phenology of *Copaifera langsdorffii* (Fabaceae), a super host of galling insects with supra-annual mass fruiting and complete deciduousness, on their galling insect community structure.

Phenology describes the timing of transitions between stages in organisms' life cycles. Plant phenology vary among and within years and can affect the insect herbivores directly by synchronism between specific phenological stages and population dynamics of insects (How et al. 1993; Fox et al. 1997; Vitou et al. 2008) or indirectly, by determining the quality of plant tissues for herbivores (Jarzomski et al. 2000; Russel and Louda 2004; Coyle et al. 2010). Moreover, the supra annual phenology also produces variation in resource for herbivores between years of high and low plant reproduction (Obeso 2002; Forister 2005; Fagundes et al. 2013).

Thereby, plant phenology can dictate resource availability and quality to herbivores both within a growing season and throughout the life of trees with broad effect on plant-herbivores interactions.

Plant tissues are more adequate for insect development at a specific time in plant's phenology, generating a window of suitability in which plants are most adequate for insect herbivores development (Yukawa 2000; Mopper 2005; Yukawa and Akimoto 2006). Thus, insects using these resources during unfavorable phenological stages may suffer reduction on their performance (Forister 2005). For instance, galling insect emerging after leaf maturation, and even those using late-produced foliage, may have insufficient resource to ideal development before leaf abscission (Egan and Ott 2007; Hood and Ott 2010). Thereby, synchronization of consumers with the resources upon which they depend is of fundamental importance to consumer fitness.

Given the specific feeding habit of galling insects, one expects a distribution pattern synchronized with their host plants phenology (Fernandes 1990; Coyle et al. 2010). However, the nature of this phenological window, being it predictable or variable, broad or narrow, has a large impact on the evolutionary history of plant-herbivore interactions (Yukawa 2000; Egan and Ott 2007). In fact, the selection would favor galling insects that attack early bud-breaking plants if plants present high bud-breaking synchronism (e.g. Yukawa and Akimoto 2006). Alternatively, asynchronic bud-breaking within a plant population results in temporal isolation between herbivore allowing the formation of demes and sympatric gall speciation (see Mopper 2005; Egan and Ott 2007).

Supra-annual mass fruiting is another plant phenological behaviour that affect herbivorous insects by changes in plant tissue quality. In reproductive years, plants show reduction or suspension of other physiological processes as a result of the internal reallocation of resources for production of fruits (Isagi et al. 1997; Obeso 2002). This differential allocation of resources produces changes in the characteristics of plants (e.g., architecture, growth, and chemical compounds), which may extend their effects to higher trophic levels (Bazzaz et al. 1987; Obeso 2002; Stamp 2003).

Trade-offs between reproduction and growth seem to be a common phenomenon in higher order plants. During the development of fruits, plants may reduce or even stop their growth because the fruits are strong nutrient drains (Abrahamson and Caswell 1982; Larcher 1995). Additionally, the differential allocation of resources for reproduction or growth may affect the phenolic content in leaf tissues, as those physiological activities interfere in the carbon/nutrient balance of plants (Bryant et al. 1983; Herms and Mattson 1992). Consequently, the synthesis of carbon-based defence compounds will be affected with broad effects on herbivore insects (Bryant et al. 1983; Herms and Mattson 1992; Stamp 2003).

Copaifera langsdorffii Desf. (Fabaceae: Caesalpinioideae) is a tropical tree species that reaches heights of up to ten meters in the Brazilian Cerrado (savanna). Fruiting is supra-annual, i.e. years of intense fruit production are followed by years of little or no fructification (Souza and Fagundes 2014). The plant shows complete deciduousness in the dry season of the year (July to September) and emission of new leaves immediately after the fall of leaves that were produced in the

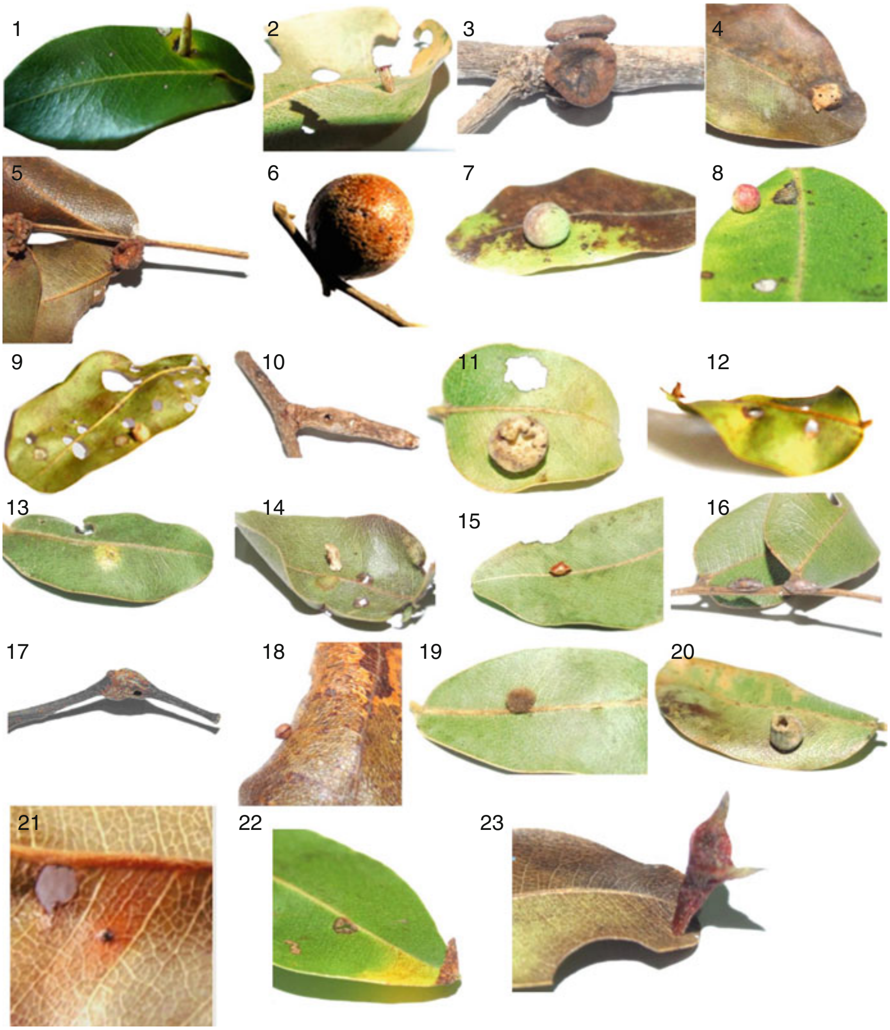

Fig. 11.1 Gall morphospecies collected from *Copaifera langsdorffii* in a cerrado (Brazilian Savanna) fragment, Minas Gerais, Brazil (After Costa et al. 2010)

previous year (Carvalho 2003). A total of 23 morphospecies of galls were found on *C. langsdorffii*, characterising the plant a super-host of galling insects (Costa et al. 2010, Fig. 11.1). Recent studies showed that plant ontogeny (see Costa et al. 2011) and plant tissue quality (Costa et al. 2011) may affect the gall community associated with *C. langsdorffii*. The leaves of *C. langsdorffii* grow slowly and leaflets have two extrafloral nectaries which are active only in the initial phase of leaf development (Costa et al. 2011). These extrafloral nectaries attract several ant species capable to inhibit herbivore attack on young leaves of *C. langsdorffi* (Queiroz et al. 2013).

This scenario lead us to expect that inter- and intra annual plant phenology (supra-annual fruiting and annual asynchronic leaf production after annual deciduousness, respectively) are important characteristics capable to shape the galling insect community associated with *C. langsdorffii*, both in ecological and evolutionary contexts. The study was conducted in a cerrado (Brazilian Savanna) fragment (16° 40′26″ S and 43° 48′44″ W) at the northern limit of the city of Montes Claros, Minas Gerais, Brazil. The region is inserted in the transition between the domains of Cerrado and Caatinga (Rizzini 1997). Usually, the Cerrado occurs in soils with low availability of nutrients that affect the characteristics of vegetation (Haridasan 1992) and its herbivore fauna (Neves et al. 2010). The local climate is of a semi-arid type, with well-defined dry and rainy seasons. The annual average temperature is of 23 °C, with rainfall of approximately 1.000 mm/year, concentrated rain mainly in the months of November to January (Santos et al. 2007). The soil of the study area is dystrophic with a developed herbaceous-subshrub layer, generally affected by fire (Costa et al. 2011; Fagundes et al. 2011).

11.1.1 Effects of Inter-annual Plant Phenology on Galling Insects

During the month of March 2008, 35 *C. langsdorffii* individuals were selected and marked in the study area. Those individuals were from five to seven meters high, with a well-formed crown and in a good phytosanitary state (e.g. without presence of lianas or parasitic plants). All selected plants were monitored monthly during two consecutive years to determine the presence of flowers or fruits, thereby characterising the occurrence of a reproductive stage. All the marked individuals produced fruits in the first year, while none of them produced flowers or fruits in following year.

In May 2008 (period before deciduousness of leaves and when the vegetative growth of the species is completely) of each year of study, ten terminal branches were collected from all the selected plant individuals. The branches were collected at different points of the three crown to minimize possible microclimatic effects on plant growth or herbivores attack. Collected branches were approximately 30 cm long, corresponding to the plant growth of last season. Then, the branches were taken to the laboratory, where the following parameters were determined: the number of fruits, biomass of fruits, leaf biomass, and richness and abundance of galls. In addition, a total of 30 leaves per tree were collected to determine the tannin concentration in leaf tissues.

The number of fruits produced by the plants was determined by counting the fruits that were present in the ten sampled branches of each individual. To determine the biomass, the material was previously dried in an oven at 70 ºC for 72 h. After that, all branch fruits were weighed on an electronic precision scale. Similarly, all the leaves present in those ten branches were taken and weighed to determine leaf biomass. The method of radial diffusion was used to determine the tannin

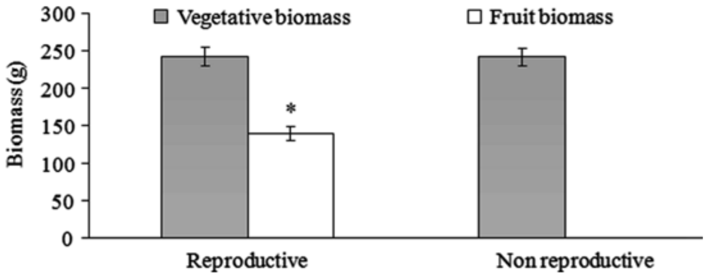

Fig. 11.2 Vegetative biomass (leaf and woody) and biomass of fruits produced by *C. langsdorffii* in the reproductive and non-reproductive year (n = 35; average ± SE; * represents significant differences between years)

concentration in *C. langsdorffii* leaves (Hagerman 1987). The richness and abundance of galls were determined by counting the number of galls present on the ten collected branches in each plant. The external morphology of galls was used to characterise and define each galling morphospecies (see Stone and Schönrogge 2003). Details of the characterisation and the determination of the galling insect morphospecies can be seen in Costa et al. (2010).

The population of *C. langsdorffii* studied presented intense fruit production in the first study year, followed by lack of fructification in the subsequent year (Fig. 11.2). In first year there was a production of 13.3 ± 5.8 (average ± EP) fruits and 139.5 ± 53.8 g (average ± EP) fruit biomass by collected branch. This fruit biomass corresponds to 57.6 % of the total vegetative biomass produced per individual of *C. langsdorffii* in 2008. Moreover, leaf biomass was 28.9 % higher in the non-reproductive year (Fig. 11.3a) while tannin concentration in the leaves of *C. langsdorffii* was approximately 157 % higher in the reproductive year (Fig. 11.3b).

There was a high inter-annual variation in the production of fruits by *C. langsdorffii*. This pattern of supra-annual fruiting seems to be common phenomenon in the *Copaifera* genus (Leite and Salomão 1992; Dias and Oliveira-Filho 1996; Pedroni et al. 2002). The study also showed that *C. langsdorffii* produced higher leaf biomass in non reproductive year and larger tannin production in reproductive years. Thus, based in the resource allocation theory (Herms and Mattson 1992) one would argument that higher investments in leaf biomass in non-reproductive year preclude tannin production because carbon is mainly allocated for vegetative growth.

In the reproductive year, 952 galls distributed into 18 galling morphospecies on *C. Langsdorffii* plants were found while in the non-reproductive year, 1,772 galls belonging to 19 morphospecies were collected. The total richness ($F = 4.08$, $P = 0.04$) and abundance ($F = 11.49$, $P < 0.01$) of galls associated with *C. langsdorffii* were 34.3 % and 85.7 % higher in the non-reproductive year, respectively (Fig. 11.4a, b). The increased galling species richness and abundance in the non-reproductive year can be associated to two factors: (1) in the non-reproductive year plants produced more leaves which resulted in more oviposition sites to galling females; and (2) in the reproductive year plants invested more resources in chemical defences, reducing the success of galling insect attack.

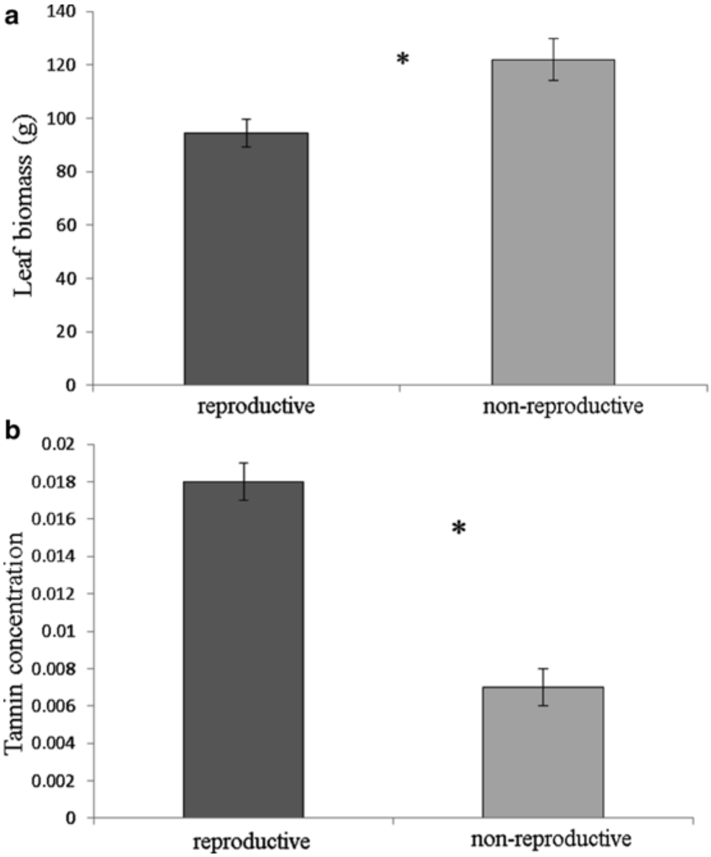

Fig. 11.3 Leaf biomass (**a**) and tannin concentration (**b**) produced by *Copaifera langsdorffii* in the reproductive year and in the non-reproductive year (n = 35; average ± SE; * represents significant differences between years)

Several studies were conducted with the objective of understanding the internal allocation of resources necessary to keep the costs of supra-annual reproductive cycles (e.g., Norton and Kelly 1988; Isagi et al. 1997; Satake and Iwasa 2000; Monks and Kelly 2006). However, no studies to date have attempted to characterise the ecological role of supra-annual fructification of tropical species and their effects in the allocation of resources inside the individual, what prevent us to extrapolate their effects in the different trophic levels. Some authors (e.g. Stamp 2003; Russel and Louda 2004; Kon et al. 2005; Tsvuura et al. 2011) suggest that supra-annual mass fruiting is an important plant strategy to reduce herbivore pressures. Although no experimental study was performed to date, it is reasonable to hypothesize that the supra-annual mass fruiting observed in *C. langsdorffii* affects gall community by changes in resource allocation.

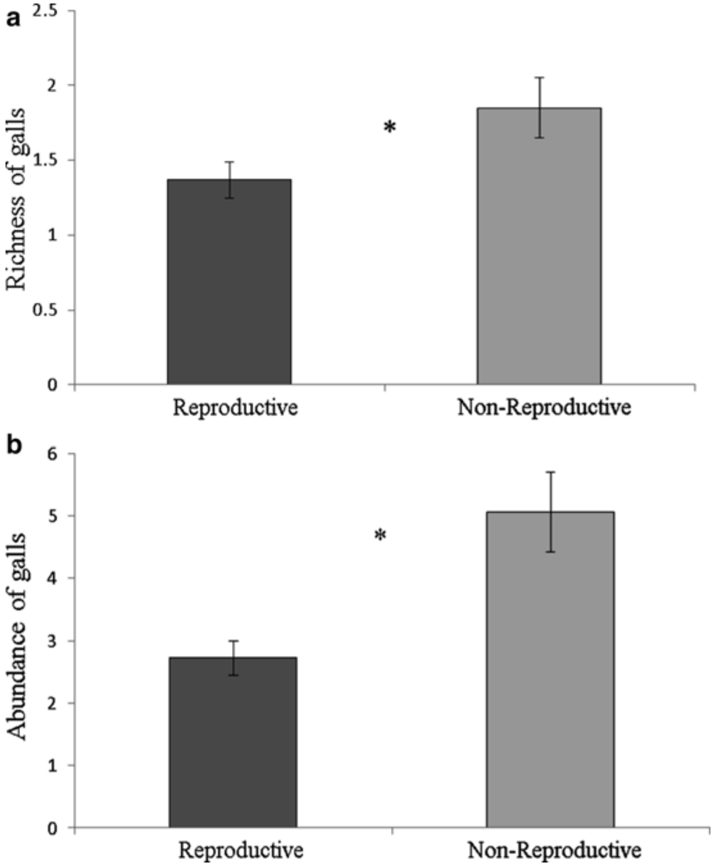

Fig. 11.4 Variation in gall insect richness (**a**) and abundance (**b**) collected from *Copaifera langsdorffii* branches between reproductive and non-reproductive years (n = 35; average ± SE; * represents significant differences between years)

11.1.2 Effects of Intra-annual Plant Phenology on Galling Insects

In order to characterize the effect of intra-annual variation in plant phenology on gall community associated with *C. langsdorffii* a total of 100 trees were selected and marked in the study area. All these plants were monitored weekly from July through October 2010 to access the period of leaf production. According the date of bud-breaking individual plants, trees were categorized into three phenological cohorts: *precocious plants* (tree that produced new leaves before September, n = 24); *intermediate plants* (trees that produced new leaves during September, n = 46) and *delayed plants* (trees that produced new leaves after October, n = 31).

During the May 2011, ten terminal branches were collected from all 100 marked plants (n = 1,000). These branches were individually conditioned in plastic bags and taken to laboratory to determine leaf biomass, leaf tannin concentration, and gall richness and abundance per tree, as previously described. Insect galls collected from all branches were then categorized into morphospecies.

All plants monitored during this study did not show evidence of flower or fruit production, indicating that 2010 was a non-reproductive year for the *C. langsdorffii* population. Moreover, leaf biomass did not change among plant phenological cohorts (F = 0.048, P = 0.640). The presence of tannin was detected only in few plant individuals and hence the comparisons of leaf tannin concentration among plant cohorts were not considered in this study.

A total of 5,115 insect galls belonging to 21 morphospecies were collected from the 100 *C. langsdorffii* individuals. All gall morphospecies were observed on precocious and intermediated plants cohorts while morphospecies 1, 14, and 19 were not found on the delayed cohort plants (see Fig. 11.1 for galling morphospecies identification).

Gall richness (*Wald Stat* = 10.05, $P<0.01$) and abundance (*Wald Stat* = 10.05, $P<0.01$) varied among plant phenological cohorts. In fact, gall richness decreased on the delayed cohort plants (Fig. 11.5a) and total gall abundance was higher on the precocious cohort plants (Fig. 11.5b). However, at the population viewpoint we can detect variation species idiosyncratic attack on specific plant cohort. For instance, galling morphospecies 2, 4, 8, 9, 11 and 20 were more abundant on the precocious plant cohort while galling morphospecies 3 reached greater density on the delayed plant cohort (Fig. 11.6).

The results provide greater support for the contention that the galling insect community associated with *C. langsdorffii* is also affected by intra-annual variation in plant phenology. Many herbivores have adjusted their life cycle to synchronize their larval stadium with the appearance of target host tissues and organs (Fernandes 1990; Yukawa 2000). Female adults of galling insects primarily oviposite on undifferentiated tissues of host plant because their progeny must stimulate plant cell hyperplasia and hypertrophy, inducing the formation of the gall (Fernandes 1990; Cuevas-Reyes et al. 2006). Galling insects emerging early or later budburst of the host plant experience reduction in their fitness because quality and quantity of available resource decay (Mopper 2005). Thus, adults of galling insects are restricted to a few days to find suitable sites to achieve their maximum fitness and larval characteristics are dictated by maternal host selection (Russel and Louda 2004; Cuevas-Reyes et al. 2006). This key issue on galling success/failure determine the population dynamics and the entire community organization (see Fernandes 1990); unfortunately it has been neglected in galling studies.

At the plants' perspective, the host species is able to reduce galling insect fitness escaping temporally the attack by the galling females. For example, adult

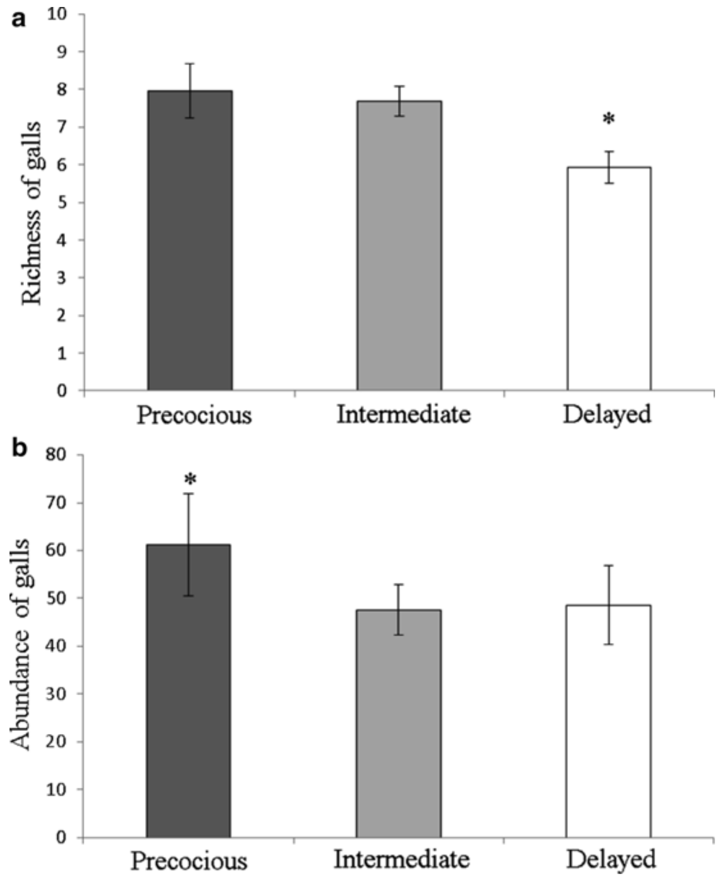

Fig. 11.5 Variation in gall richness (**a**) and abundance (**b**) collected from *Copaifera langsdorffii* branches among three plant phenological cohorts (average ± SE; * represents significant differences)

emergency from the gall is not always synchronized with plant budbreaking if the plant population present unsynchronized leaf production. In fact, recent studies report that early budbreaking plants are more attacked by galling insects (Yukawa and Akimoto 2006). As a result, temporal variation in plant phenology can generate islands of adequate resources for galling insects allowing deme formation and sympatric speciation (Egan and Ott 2007). The studied population of *C. langsdorffi* showed broadly temporal variation in leaf flushing. The galling species associated with *C. langsdorffii* may show strong preference by specific phenological cohort. Thus, one can argument that intra-annual plant phenology is a possible element responsible by the high gall richness associated with *C. langsdorffii*.

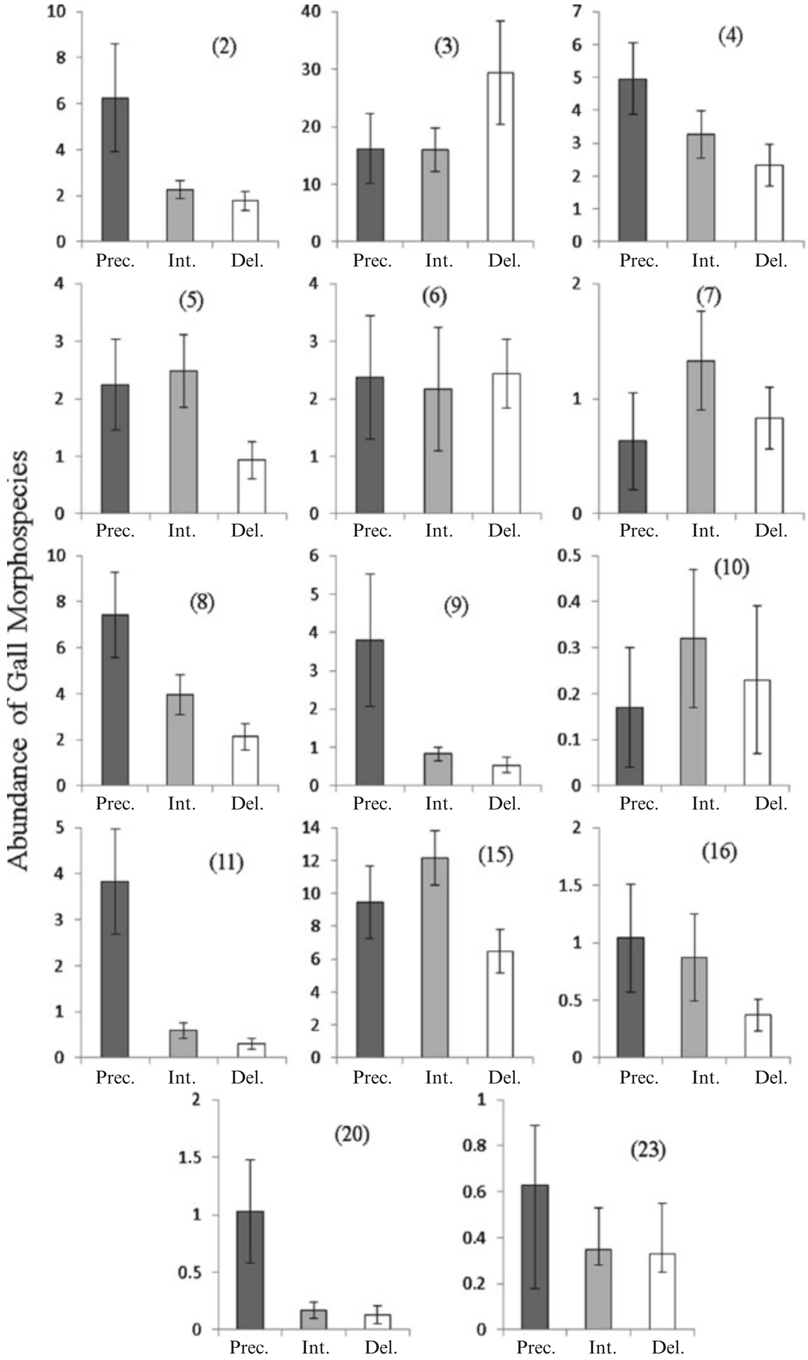

Fig. 11.6 Abundance (average ± SE) of more frequent galls collected from *Copaifera langdorffii* branches among three plant phenological cohorts (see Fig.11.1 for gall morphospecies identification)

11.2 Remarkable Conclusions

Copaifera langsdorffii is a super-host of galling insect that have supra-annual fruiting and broadly intra-annual variation in flushing leaves. Using this system, the present study calls attention for two relevant questions related to herbivore community organization. Firstly, the study suggests the possibility that inter- and intra-annual variation in plant phenology can be associated with herbivore community organization on *C. langsdorffii* both, in ecological and historical context. Second, the study also points out the possibly relationship between phenological asynchrony and the existent of super host plants. While some authors (see Egan and Ott 2007 and references therein) have stressed the importance of individual plant variation (e.g., phenology) on sympatric speciation of herbivores the debate about the factors that explain the existence of super host plants deserve more attention. In this study, these two questions are integrated and we suggest that variations inter- and intra-annual in plant phenology would determine high gall richness on *C. langsdorffii*.

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Chapter 12
Galling Insects on *Caryocar brasiliense* Camb. (Caryocaraceae)

Germano Leão Demolin Leite

Abstract *Caryocar brasiliense* is one of the most common and important plant species in the dry and harsh semi-arid vegetated areas of Brazil and is host to at least four galling species. In this chapter, I discuss the within-tree distribution of the four galling species. The gall inducers exhibit different distributions in the crown, and I discuss the influence of biotic and abiotic factors on these distributions. The distributions of the galls were also evaluated at the leaf and branch level. I present evidence of competition among galling insects on *C. brasiliense*.

Keywords Cerrado • Insect distribution • *Eurytoma* sp. • Ecological niche • Competition

12.1 The System *Caryocar brasiliense*

Caryocar brasiliense Camb. (Caryocaraceae) is widely distributed in the Brazilian savannah, called the Cerrado, occupying approximately 23 % of the Brazilian territory (2 million km^2) (Bridgewater et al. 2004; Leite et al. 2006a), and can reach over 10 m in height and 6 m in canopy width (Leite et al. 2006a, 2011a, 2012a). The leaves of *C. brasiliense* are alternate, trifoliate and have high trichome density; the flowers are hermaphrodite but are mostly cross-pollinated (Araújo 1995). Its fruits have an internal mesocarp that is rich in oil, vitamins, and proteins and contain many compounds of medicinal importance. This plant is known as the steak of man backlands due to be important protein source. Fruit production is annual, and *C. brasiliense* blooms between July and September (during the dry period) with fructification from October to January (during the rainy season) (Leite et al. 2006a).

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Table 12.1 The most abundant herbivore arthropods on *Caryocar brasiliense*

Order	Family	Species	Feeding
Acari	Tetranychidae	*Tetranychus* sp.1	Leaves
		Tetranychus sp. 2	Leaves
		Eutetranychus sp.	Leaves
Coleoptera	Curculionidae	*Naupactus* sp.	Fruits/leaves
	Elateridae	*Apoptus* sp.	Leaves
Lepidoptera	None identified	Leaf miner	Leaves
	Cossidae	Unidentified	Borer of trunks
	Nymphalidae	*Eunica bechina*	Leaves
	Sesiidae	*Carmenta* sp.	Borer of fruits
Hemiptera	Aleyrodidae	*Bemisia tabaci* (Genn.)	Leaves
	Aphididae	*Aphis gossypii* (Glover)	Leaves
	Cercopidae	*Mahanarva* sp.	Leaves
	Cicadellidae	*Dikrella* sp.	Leaves
		Frequenamia sp.	Leaves
	Membracidae	*Aconophora* sp.	Fruits/leaves
	Pentatomidae	*Edessa rufomarginata*	Fruits/leaves
	Pseudococcidae	*Pseudococcus* sp.	Leaves
Hymenoptera	Eulophidae	Unidentified	Leaves
	Eurytomidae	*Eurytoma* sp.	Leaves
Isoptera	Termididae	*Constrictormes cyphergaster*	Organic matter

The fruit is a drupe with 1–4 seeds, weighing 158.49 ± 8.14 g (wet weigh) and with a volume of 314.90 ± 20.93 cm^3 (Leite et al. 2006a). Moreover, the fruit is also used by humans for food, production of cosmetics and lubricants, and in the pharmaceutical industry (Segall et al. 2005; Ferreira and Junqueira 2007; Garcia et al. 2007; Khouri et al. 2007). *Caryocar brasiliense* represents the main source of income of many communities (Leite et al. 2006a).

Due to protection by federal law, *C. brasiliense* trees are left in deforested areas of the Cerrado, but the production and natural regeneration of *C. brasiliense* has been impaired due to the practice of only retaining the worst and most impoverished areas, in which the soil's physical structure does not allow for *C. brasiliense* survival or colonisation (sandy or rocky), as forest or Cerrado reserve areas. This is the scenario that is found in the northern region of the Minas Gerais State (Leite et al. 2006a, 2011a, 2012a). Isolated individuals in the agro-landscape suffer from increased leaf, flower, and fruit damage from insect herbivorous, which affects their natural enemies (i.e., parasitoids and predators) (Tables 12.1 and 12.2). Among these insects, there are four types of galling insects found on the *C. brasiliense* leaves (Table 12.3, Fig. 12.1). Among the insects that attack *C. brasiliense*, hymenopterans are the most abundant galling species in the Cerrado of northern Minas Gerais. These galls, principally galling *Eurytoma* (Eurytomidae), can cause premature leaf abscission when they are found at a high density on

Table 12.2 The most abundant natural enemies of herbivores on *Caryocar brasiliense*

Order	Family	Species	Feeding
Acari	Stigmeidae	*Agistemus* sp.	Predator
Aranae		Complex of spiders[a]	Predator
Coleoptera	Coccinelidae	*Neocalvia fulgurata*	Predator
Hemiptera	Geocoridae	*Epipolops* sp.	Predator
	Reduviidae	*Zelus armillatus*	Predator
Hymenoptera	Aphelinidae	*Ablerus magistretti*	Parasitoid
	Eulophidae	*Quadrastichus* sp.	Parasitoid
	Eurytomidae	*Sycophila* sp.	Parasitoid
	Formicidae	*Camponotus novograndensis*	Generalist
		Crematogaster sp.	Generalist
		Pseudomyrmex termitarius	Predator
Neuroptera	Chrysopidae	*Chrysoperla* sp.	Predator
Thysanoptera	Phlaeothripidae	*Holopothrips* sp.	Predator
		Trybonia intermedius	Predator
		Trybonia mendesi	Predator

[a] complex of spiders = *Cheiracanthium inclusum* (Miturgidae); *Peucetia rubrolineata* (Oxyopidae); *Anelosimus* sp., *Achaearanea hirta* (Theridiidae); *Gastromicans albopilosa*, *Chira bicirculigera*, *Rudra humilis*, *Thiodina melanogaster* and *Lyssomanes pauper* (Salticidae); *Dictyna* sp. (Dictynidae); *Tmarus* sp. (Thomisidae); and *Argiope argentata*, *Gasteracantha cancriformes*, *Argiope* sp., *Parawixia* sp. (Araneidae)

Table 12.3 Morphological characteristics of the galls found on *Caryocar brasiliense* leaves

	Kinds of galls			
Characteristics	Globoid gall	Spherical gall	Discoid gall	Vein gall
Species	*Eurytoma* sp.	Eulophidae	Hymenoptera	*Bruchophagus* sp.
Diameter (mm^2)	–	1.61	3.70	–
Height (mm)	2.53	1.84	0.57	1.91
Length (mm)	1.28	–	–	2.04
Width (mm)	0.90	–	–	5.56
Hairs	Yes	No	No	No
Color	Yellowish	Brown	Light green	Light green
Larval chamber	One	UN	UN	UN
Number of larval/chamber	One	UN	UN	UN

UN unstudied

C. brasiliense seedling and adult plants (Oliveira 1997; Leite et al. 2006b, 2009). Despite biological and social importance of *C. brasiliense*, its herbivores are still poorly known and the identification of many of them has been hampered due to the lack of specialists (Lopes et al. 2003; Boiça et al. 2004; Leite et al. 2011a, 2012a). Furthermore, to date, there are no long-term data on the herbivore dynamics on this species.

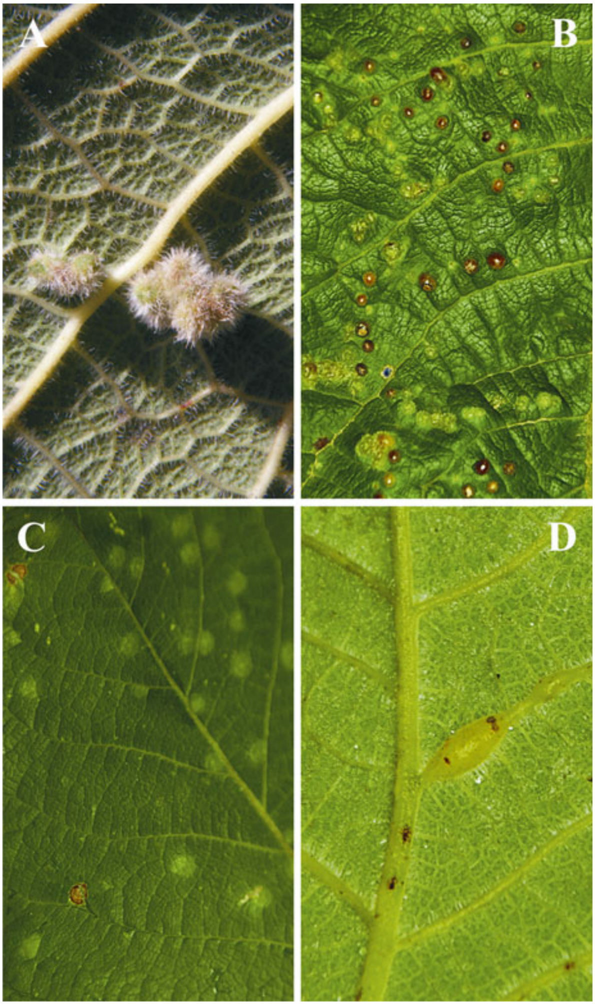

Fig. 12.1 Globoid gall (**a**), spherical gall (**b**), discoid gall (**c**), and vein gall (**d**) on *Caryocar brasiliense* leaf

12.2 Floristic Diversity and Complex Architecture of Canopy

The diversity and abundance of galling insects can vary among different environments. Several hypotheses can explain this trend, including: (1) more complex environments (higher floristic diversity) increase the number of galling insect species associated with a host plant (Auslander et al. 2003; Price et al. 2004a; Price 2005); (2) host plant attributes, such as a complex architecture, can increase the number of galling insects (Fritz et al. 2000; Hjältén et al. 2003; Ferrier and Price 2004; Price and Hunter 2005; Espírito Santo et al. 2007); (3) soil characteristics that are more favourable to trees can indirectly effect galling insects (e.g., nutritional quality) (Auslander et al. 2003; Price et al. 2004a; Ferrier and Price 2004; McGeoch and

Table 12.4 Number of galls on *Caryocar brasiliense* leaflets and floristic diversity under four different habitat conditions

Galls	Cerrado	Active pasture	Abandoned pasture	University campus
Globoid gall	1.25	3.56	5.19	14.81
Spherical gall	0.13	0.12	0.10	0.00
Discoid gall	0.73	0.61	0.54	0.00
Vein gall	0.18	0.07	0.00	0.00
Floristic diversity	4	3	2	1

Adapted by Leite et al. (2009, 2011a, b, c, d, e, 2012a)

Price 2005; Price and Hunter 2005; Espírito Santo et al. 2007); and (4) natural enemies can respond to a local increase in vegetation complexity and the presence of an alternative prey and effectively suppress herbivores as galling insects (Auslander et al. 2003; Ferrier and Price 2004; McGeoch and Price 2005).

With the increase in floristic diversity, the diversity of leaf gall species on *C. brasiliense* increased (Table 12.4). On the other hand, the density of *Eurytoma* sp. (globoid gall), the most abundant species, and consequently, its natural enemies (i.e. *Sycophila* sp., *Z. armillatus*, *Holopothrips* sp., and spiders) were highest in an environment with lowest floristic diversity (i.e. university campus). These natural predators were seen preying upon *Eurytoma* galls. This galling insect can colonise up to 70 % of the leaf area on *C. brasiliense* on the university campus (Leite et al. 2006b, 2007, 2009).

Fewer trees, groves, shrubs and herbs were found in the university campus than in the active pasture, abandoned pasture and the Cerrado (non-degraded area) (Leite et al. 2011a, b, 2012a). On the other hand, the Cerrado has less *C. brasiliense* per hectare than the pastures and the university campus, and these trees are bigger in active pasture than in the other areas (Leite et al. 2006a, 2011b). The complex architecture (i.e. greater width and height of crown) cannot explain the differences among the areas with regard to the attack by galling insects, but in each area, we observed higher number of galls in larger trees (*unpublished data*). In addition, the soils in active pasture and the Cerrado are more acidic; active pasture is richer in aluminium and sum of bases and less sandy than the abandoned pasture, Cerrado and university campus. On the other hand, the soil of the university campus has more silt and a more compressed texture compared to the other areas (Leite et al. 2006a, 2011b). Soils of the Cerrado are, in general, deep and loamy (with an excellent rainwater storage capacity) but are poor in nutrients, rich in aluminium and have a low pH (Sousa and Lobato 2004). The *C. brasiliense* (Oliveira 1997; Leite et al. 2006a, 2011a, 2012a) and its galling insects may have adapted to these conditions. Perhaps floristic diversity and the soil conditions can explain the differences in the densities of the galling insects among the areas (Fernandes and Price 1988, 1992; Gonçalves-Alvim and Fernandes 2001; Fernandes et al. 2005).

Some studies provide evidence supporting the preference prediction of the Plant Vigor Hypothesis (PVH). Sawfly galls were found on significantly longer shoots compared to shoots without galls, and shoots with 2, 3, 4, and 5 galls were successively longer than shoots with fewer galls (Fritz et al. 2000), and the similar results were observed by Ferrier and Price (2004) and Hjältén et al. (2003). Larger plant species support more insect herbivore species as well as higher nitrogen and lower digestibility reducers such as tannins to be more favourable for insect herbivore.

Therefore, including larger members of a flora in a conservation area may provide the resources for a larger number of insect species as well as fewer species in smaller areas (Price et al. 2004a; Price 2005). Price and Hunter (2005) concluded that precipitation and drought, by influencing the soil moisture available for willow growth, had the greatest impact on sawfly populations from the bottom up. Another important point is enemy-free space. Fritz et al. (2003a) suggest that selection for enemy-free space could be a major cause of the oviposition patterns of sawfly, refuting the PVH. The galls can support higher diversity of natural enemies, and they can cause much mortality – top down impact of natural enemies – (Price et al. 2004b; McGeoch and Price 2005; Price 2005).

12.3 Sunlight and Wind Direction Exposure

Caryocar brasiliense loses its leaves in Aug/Sep with new ones in the end of Sep, period with without rainfall, strong wind and high sunlight (Leite et al. 2006a). We observed higher numbers of *Eurytoma* sp. (globoid galls) and its parasitoid *Sycophila* sp., and discoid galls in Aug; and greater numbers of total galls in Sep, period that *C. brasiliense* trees have old leaves. On the other hand, in Oct when *C. brasiliense* trees have new leaves, higher abundance of vein and spherical galls were observed in this plant, but lower numbers of globoid and discoid galls (unpublished data).

The number of galls can vary with the arrangement of the branches on *C. brasiliense* trees in relation the cardinal points (i.e. north, south). Some hypotheses have been posed to explain this trend, for example, (1) the direction of wind may influence the dispersion of galling insects (Leite et al. 2009, 2011c, d, e), and it can desiccate the leaves and reduce fruit production by causing flowers and fruits to fall (Leite et al. 2006a); (2) the greater exposure of the sun-exposed foliage may influence the quality of host plant tissues (i.e. less tender leaf) (Unsicker and Mody 2005); (3) microclimate more appropriate for the development of these herbivores (i.e. high humidity); and (4) arrangement of the branches of a tree helps folivory insects to avoid natural enemies, thus providing an enemy-free space (Unsicker and Mody 2005).

The highest numbers of globoid and discoid galls on *C. brasiliense* leaves were found on the eastern slope, and spherical and vein galls are found on the northern slope (Leite et al. 2009, 2011c, d, e). The foliage on the eastern and northern slopes of the host trees were exposed to higher winds and strong sunlight, as prevalent winds in the region are north-eastern/eastern (Leite et al. 2006a). These findings corroborate the hypothesis that galling insects are most abundant on sunlight-exposed (Fernandes and Price 1991). Leite et al. (2006a) argued that the desiccant effect of wind, especially in regions with a low relative humidity and high temperature, which are typical of the Cerrado of the semi-arid northern area of the Minas

Gerais, can reduce fruit production and photosynthesis, causing bad formation of leaves or the dropping of flowers and fruits (Leite et al. 2006a). On the other words, the leaves exposure to winds and sunlight can negatively influence their resistance against galling insects.

Differential sun exposure may influence the quality of the host plant (i.e. less tender leaf) and gall tissue or even the plant's ability to find and elicit induced responses to the invading organism (Fernandes and Price 1991). As galling insects are generally small, there is a possibility that wind may play an important role in their distribution within trees. The dispersion (i.e. migration) of many insects can be influenced by wind direction (Feng et al. 2004, 2005; Leite et al. 2009). We observed a greater number of ants and predator bugs on the east and north sides of *C. brasiliense* trees, respectively. Ants positively affect galling insects, mainly due to the inhibition of the action of insect defoliators. We also noted the negative effect of ants on some galling insect parasitoids (*unpublished data*).

12.4 Gall Distribution at the Leaf and Branch Level

Insect galls are known to be distributed differentially within host organs (Fritz et al. 2000; Price et al. 2004b; Price 2005; Leite et al. 2009, 2011c, d, e; Compson et al. 2011). Many galling larva achieve higher densities, sizes, and even higher performances at the proximal portion of the leaf, compared to a more distal portion, due to the more rapid and efficient interception of plant photosynthates at the leaf base (Whitham 1978; Auslander et al. 2003). Similarly, galls can be also more abundant and larger at the basal portion of the stems of its host plants, where galls reach larger sizes perhaps due to stronger sinks in this region of the plant, as was shown by De Souza (1998, 2001).

Greater numbers of globoid, discoid, and vein galls were found in the interior than on the border of the tree crown (Leite et al. 2009, 2011c, e) while the spherical galls were more frequently found at the border of the tree crown (Leite et al. 2011d). Several mechanisms may influence this observed trend. First, differential mortality caused by parasitoids, predators, and even differential plant resistance could diminish the galling success on the more proximal region of the stems (Leite et al. 2009). Even if females prefer to attack leaves at the interior of the tree crown, stronger selective pressures would impair their success in such a habitat (Leite et al. 2009). An alternative hypothesis is that the most distal leaves – border of the tree crown – (leaves one and two) were too young to be found by the gallers, while leaves in the interior of the tree crown (leaves three and four) were exposed to galling insects for a longer period. (Leite et al. 2009). Finally, the concentration of plant hormones (i.e., indole butyric acid) can vary along the branches of the host plant, affecting the colonisation of galling insects (Leite et al. 2007). Positive relationships were found between indole butyric acid concentrations and successfully induced globoid galls and between the number of adults of the galling *Eurytoma* sp. and its major parasitoid, *Sycophila* sp., and higher concentrations of this hormone (Leite et al. 2007).

This galling insect may select plant modules or plants with higher hormone concentrations and indole butyric acid may play a role in gall induction (Leite et al. 2007). Otherwise, further studies are needed to address hormonal roles in gall formation for the other galling species in the system and their indirect effect on the community of associated parasitoids.

Globoid and spherical gall insects were mostly found at the leaf margin, while the vein and discoid galls were mostly frequently found on the central portion of the leaf (Leite et al. 2009, 2011c, d, e). Although the density of trichomes is higher on the leaf margin than on the other transversal leaf portions in *C. brasiliense* (Leite et al. 2009), extrafloral nectaries are also mostly frequent on the leaf margins (Rezende 1998). The role of extrafloral nectaries on the host plant's interactions with galling insects is not known. Otherwise, we postulate that they might influence the female galling insect's survival, as they may have an indirect positive role in protecting the galling insects against natural enemies by attracting ants. Fritz et al. (2000, 2003a) suggested that selection for enemy-free space could be a major cause the oviposition patterns of galling insects. Ants are reported to be associated with leaf extrafloral nectaries on *C. brasiliense* (Oliveira 1997). Although rarely studied, ants have an interesting and important role with respect to gall-inducing insects, which is worth detailed study in the future (Fernandes 1994; Price et al. 2004b; Izzo et al. 2006; Santos and Fernandes 2010).

More globoid and discoid galls were found on the median region, and vein galls are found on the distal and median regions rather than on the proximal longitudinal region on *C. brasiliense* leaflets (Leite et al. 2009, 2011c, e). The average number of spherical galls was not statistically different among the longitudinal regions of *C. brasiliense* leaflets (Leite et al. 2011d). The distal and median leaf portions exhibited lower trichome densities than the proximal portion (Leite et al. 2009) and the authors suggested that the higher abundance of these galling species on the leaf lamina could be influenced by trichome density. Females may prefer to oviposit on leaf regions where trichomes are less dense, as has been reported for the leaf miner *Liriomyza trifollii* (Burgess) (Diptera, Agromyzidae) (Hawthorme et al. 1992). Leaf miners are also negatively affected by latex and the density of trichomes in *Asclepias* spp. (Agrawal 2004). Leaf trichomes are known to have a strong influence on the behavior, selection, and performance of insect herbivorous (Woodman and Fernandes 1991; Fernandes 1994; Leite et al. 1999a, b, 2001). On the other hand, the galls can induce trichomes neoformation in their galls as well as the leaf trichomes does not interfere in gall induction insects (Oliveira et al. 2006; Moura et al. 2009).

12.5 Evidence of Competition Among Galling Insects

The study on the four galling species on *C. brasiliense* indicates the existence of competition in the system. We had two possible situations: (a) high number of *Eurytoma* sp. (globoid galls) and (b) low number of this galling insect on *C. brasiliense* leaves (Figs. 12.2 and 12.3).

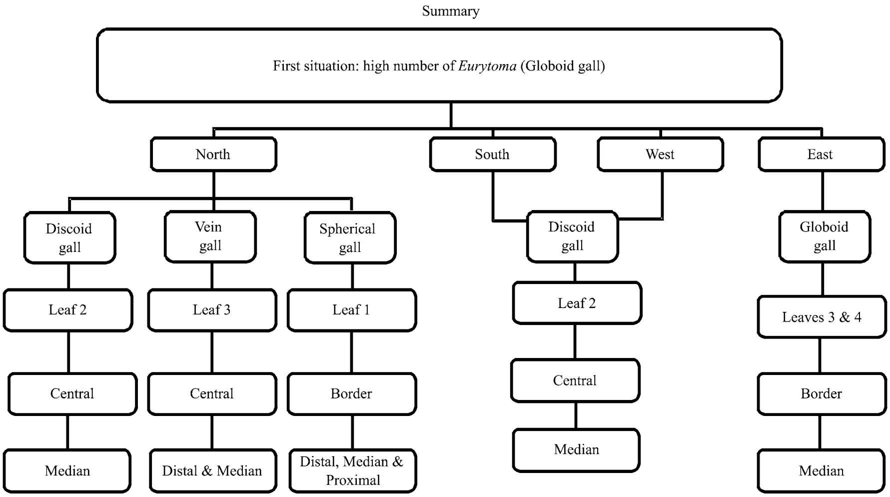

Fig. 12.2 The effect of high numbers of *Eurytoma* sp. on other galling insects on *Caryocar brasiliense* leaves. Leaves 1 and 2 are on the border of the crown, and leaves 3 and 4 are on the interior of the plant crown. Transversal regions on a leaflet: border, central and near the mid vein. Longitudinal regions on a leaflet: distal, median and proximal (near to petiole) (Adapted from Leite et al. 2009, 2011c, d, e)

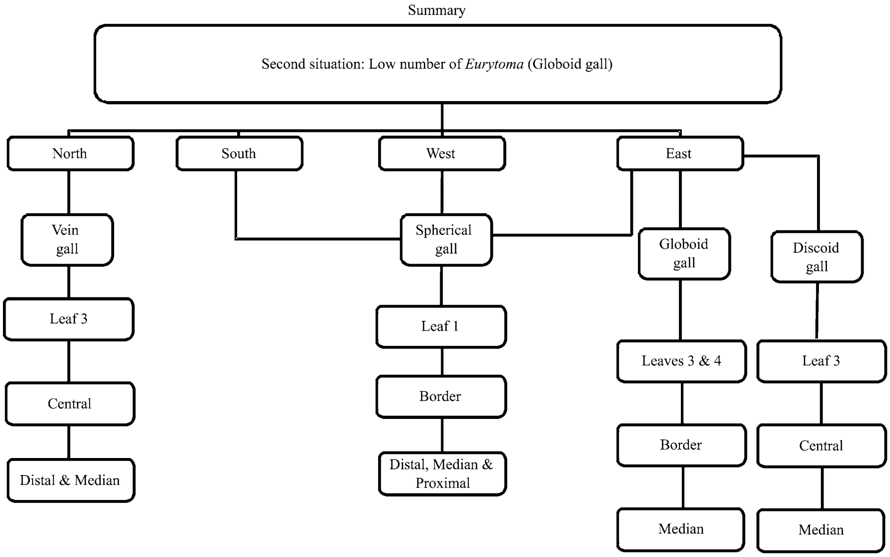

Fig. 12.3 The effect of low numbers of *Eurytoma* sp. on other galling insects on *Caryocar brasiliense* leaves. Leaves 1 and 2 are on the border of the crown, and leaves 3 and 4 are on the interior of the plant crown. Transversal regions on a leaflet: border, central and near the mid vein. Longitudinal regions on a leaflet: distal, median and proximal (near to petiole) (Adapted from Leite et al. 2009, 2011c, d, e)

In both situations, the globoid galls and vein did not change their attack patterns. The globoid galls, the most abundant gall *C. brasiliense*, had higher attack preferentially at median part of the margin of the leaves of the branches of the interior of the crown on the eastern slope of the host trees. On the other hand, the vein gall, the gall least abundant of the four galling insects in *C. brasiliense* and the one that attacks the leaf veins, found most abundantly in regions distal and median of leaves, leaf veins located in the central part of the leaf lamina (between the midrib and the leaf margin) of the branches of the interior of the crown on the northern slope (Figs. 12.2 and 12.3).

The discoid and spherical galls changed their attack patterns when there were a low number of globoid galls. The discoid galls preferentially colonized the interior of the branches facing east when the density of globoid galls was low. But in high density of the globoid galls, the gall discoid often most were found at the border of the tree crown facing north, south and west. On the other hand, the spherical galls, second most abundant galls on *C. brasiliense* leaves, in low density of globoid galls, it spread through the canopy of the tree, colonizing the faces south, east and west instead of north face of the crown of this tree (Figs. 12.2 and 12.3).

As discussed in this chapter, leaves exposure to winds and sunlight can negatively influence their resistance against galling insects on *C. brasiliense*. Higher number of galls in the leaves at the interior of the tree crown probably is due to more protection against natural enemies, concentration of plant hormones or for to be easier to find galls (exposed time to colonization). Compson et al. (2011) related competition between galling insect for the basal position of the leaf, better place to obtain ^{14}C assimilates.

Then these factors can explain the colonization pattern, with higher oviposition and larval survival. We observed a greater number of ants and predator bugs on the east and north sides of *C. brasiliense* trees, respectively. Ants positively affect galling insects, mainly due to the inhibition of the action of insect defoliators. We also noted the negative effect of ants on some galling insect parasitoids (*unpublished data*). Price et al. (2004b) related the larval performance in relation to establishment in safe feeding sites was very high, at 100 % across all shoot length classes in some cases as well as galling sites with stronger sinks for nutrients resulting larger galls, and many more individuals per gall (Price 2005). Fritz et al. (2000, 2003a) concluded that selection for enemy-free space could be a major case of the oviposition patterns of galling insects, and to choose the correct oviposition site is very important, i.e. shape and size of the leaf, position of the gall in the leaf lamina.

Perhaps there is a chemical or visual marker that indicates that a species of galling insect dominates a particular ecological niche (i.e., part of a leaf, branch or even a tree). Leite et al. (1995) suggested chemical marker oviposition for *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) in *Lycopersicon esculentum* Mill. leaves. Innovations in the substrates used for oviposition by sawflies have enable evolution for free-feeding ancestors into diverse gall types and galling sites, e.g. leaf edge to leaf lamina, leaf midrip, petiole, bud, and stem (Price 2005), resulting in absence of competitive interactions (McGeoch and Price 2004). Another possibility is that there are genetic differences among *C. brasiliense* plants that are responsible for this process or differences in the chemical or morphological composition in different parts of a leaf or in leaves at different positions on a branch, differences in exposure to the sun/wind, or differences in the relationship with other arthropods (i.e. defoliators). Hochwender et al. (2005) and Hochwender and Fritz (2004) demonstrated that genetic variation among plants can act as a direct effect modifying the structure of the arthropod community (i.e. galling insects). Epistatic interactions for host recognition traits, probably oviposition/feeding stimulants or attractants (i.e. phenolic glycosides), appeared to be important in determining herbivore abundance as galling insects (Fritz et al. 2003b). Finally the low numbers of coleopteran and lepidopteran defoliators on the campus may have been caused by competition for food and space with galling insects and aphids in this area (Leite et al. 2012b). Aphids were negatively affected for gall-forming nematode on tobacco plants (Kaplan et al. 2011).

12.6 Concluding Remarks

Galling insects were mostly found in leaves of *C. brasiliense* that are most exposed to the wind and sun and are on the interior of the branch and prefer the border and median of the leaves (Fig. 12.3). However, with larger populations of *Eurytoma* sp. (globoid galls) (Fig. 12.2), other galling insects attack other parts of *C. brasiliense* leaves, avoiding competition or free space for feeding. *Eurytoma* sp. seems to be the fastest to colonise plants and to have greater biotic potential. In other words, the owner of the tree was the first to arrive and will leave the greatest number of descendants, and in this respect, *Eurytoma* sp. seems to be very efficient. As for other galls, they colonize areas that are not populated by *Eurytoma* sp. (food abundance), and low number of parasitoids and predators.

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Chapter 13
Baccharis: A Neotropical Model System to Study Insect Plant Interactions

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Abstract The genus *Baccharis* is composed of ca. 500 species which are distributed primarily in tropical America. It is dioecious and highly diverse in chemistry, architecture, phenology and occupy many different niches across several gradients of light, temperature, humidity, altitude and succession. It is host to the most speciose galling fauna, with more than 121 galling species on 40 host plant. This system provides an ideal scenario to test several ecological hypotheses, including the long standing plant sexual differences on timing and intensity of energy allocation, vigor, architecture and herbivore attack. Moreover its wide distribution enables to test latitudinal and altitudinal gradients on gall attack. We review the studies performed on these Neotropical shrubs related to galling insects. These studies have been crucial for the establishment of generalities and testing of ecological and evolutionary theories across the Americas, as well as to generate new ideas and hypotheses. For these reasons and power of the field and experimental observations we suggest that the galling insects on their *Baccharis* hosts may represent a Neotropical model system for studies on insect plant interactions.

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13.1 Introduction

There are thousands of host plant genera and species of galling insects throughout the world, but only some of them offer unique opportunities for the study of galling insects. The inspiration they provide to the scientists may originate from a simple economic question to the bizarre shapes. Some plants attract the attention by the diversity of gallers that a single species or individuals present. Others are attracted by the complexity of the interactions between the gall and the host plant or even with the galler's natural enemies. But whatever the fascination is, some genera or species have been selected to bring to light the curiosities and peculiarities of this interaction throughout the world. For instance, in the Neartic and Paleartic regions an astonishing amount of work have been developed on the genera *Quercus* (Felt 1940), *Salix* (Price et al. 1995), *Populus* (Floate and Whitham 1995), *Rose* (Shorthouse and Rohfritsch 1992; Stone et al. 2002), and *Solidago* (Abrahamson and Weis 1997), to cite perhaps the most known ones. From the continued study of the interactions among the galling organisms and their host plants and associated fauna emerged many classical studies on the ecology of insect-plant interactions. Consequently, many hypotheses were tested, as well as raised, in modern ecology by the study of galling insects (e.g., Askew 1960; Cornell 1983; Price 1991; Fernandes and Price 1988, 1991, 1992; Fernandes 1990; Hartley and Lawton 1992; Hawkins and Compton 1992; Stone and Schönrogge 2003; Espírito-Santo et al. 2007, 2012; Inbar et al. 2010).

In the Neotropics no other single taxa of galling host plants has been studied in such detail as *Baccharis* De Candole (Asteraceae). Based on a web of Science search with the words insect galls, galls, cecidia, galling insects, galhas, gallmucken, and agallas we were able to record at least 47 studies on galling insects on eight species of *Baccharis* in the last 25 years (1985–2012). Clearly, many other studies were developed on the genus *Baccharis* owing to the interest generated by the study of their galling insects, but this escapes the purpose of this chapter.

Due to the accumulated knowledge and long term studies done so far, we show that the system *Baccharis*-galling insects serves as an excellent model where one could construct the basis for understanding patterns of adaptation, biodiversity and evolution in insect-plant relationships, as well as to test hypotheses on galling insects in the Neotropics at different scales.

13.1.1 Genus Baccharis

The genus *Baccharis* belongs to the Baccharidinae subtribe (Asteraceae), which is restricted to the American continent (Barroso 1976). The Baccharidinae probably appeared during the Middle Miocene when South America and Africa continents were totally separated by the Atlantic Ocean (Cox and Moore 1993), justifying its natural occurrence just in the New World. *Baccharis* is the largest genus of the Baccharidinae subtribe, with more than 500 species distributed from south United States to Argentina (Boldt 1989). Interestingly, this number of species does not consider the hybrids that may be widespread in the genus (GWF, pers. observ.). Of the hundreds of species, 90 % occur in South America and most species are found in the south and southeastern regions of Brazil, suggesting that this region is the center of the genus origin (Jarvis et al. 1991). More than 120 species are known to occur in southeastern Brazil alone (Barroso 1976). All *Baccharis* species are perennial and dioecious shrubs, excepting *Baccharis monoica*, a species found in Mexico (Nesom 1988). Besides, many species of *Baccharis* disperse their seeds over long distances, present optional demand of light for the germination, are seed shade tolerant with wide adaptability to soil nutrient concentration and has the ability to sprout after fire. All these traits favor their establishment and development in nutritionally poor and disturbed areas (Gomes and Fernandes 2002).

Baccharis species are known in traditional culture for treatment of diseases as female infertility and male impotence, gastrointestinal and liver disorders, anemia, diabetes, diarrhoea, infections, cancer, gout, rheumatism, ulcers, skin problems and others (Abad and Bermejo 2007). Currently, about 120 *Baccharis* species are being investigated for production of phytochemicals for pharmaceutical, cosmetic and other applications (Verdi et al. 2005). According to Abad and Bermejo (2007), over 150 compounds have been isolated and identified from this genus. Many substances isolated from *Baccharis* have been used as medicine (e.g. trichothecenes from *B. coridifolia*, used as antiviral), perfumes (essential oils of *B. dracunculifolia*, *B. uncinella*, *B. genistelloides*, *B. trimera*) and repellents (terpenoids and flavonoids found in many species), among other products (Jarvis et al. 1988; Argandoña and Faini 1993; Ferracini et al. 1995; Agostini et al. 2005; Verdi et al. 2005; Wollenweber et al. 2006). The *Baccharis* species more deeply studied chemically are *B. megapotamica*, *B. incarum*, *B. trimera*, *B. trinervis*, *B. salicifolia*, *B. crispa*, *B. coridifolia*, *B. dracunculifolia*, *B. grisebachii* and *B. tricuneata* (Verdi et al. 2005).

The species of the genus *Baccharis* also harbors many ecological associations. One of the most known interactions is the relationship between *B. dracunculifolia* and africanized honey bee *Apis mellifera* (Kumazawa et al. 2003). This bee collects resin from apical buds of *B. dracunculifolia* and uses it to produce a resinous layer inside the hive, known as green propolis (Teixeira et al. 2005). This resinous mass, due to the antiseptic, anti-inflammatory, anti-cancer and healing properties, is widely studied, commercialized and used primarily by pharmaceutical and cosmetics industry (Banskota et al. 2001; Chan et al. 2012). Among the chemicals isolated from propolis, it is worth noticing the presence of flavonoids, phenylpropanoids, phenolic acids and essential oils (Kumazawa et al. 2003; Teixeira et al. 2005).

A large number of galls induced by insects have been studied on many species of the genus *Baccharis*. The genus *Baccharis* likely support the highest galling insect fauna of the Neotropical region, with more than 121 galling species reported on 40 host plants more than a decade and half ago (Fernandes et al. 1996). Probably no other Neotropical galling community and host plant genus has been studied in such detail as this one. These studies vary from simple description of the gall morphotypes to anatomical descriptions of the galls to more detailed and/or long term ecological studies. Here we provide some ecological background information on the system *Baccharis-g*alling herbivores.

The largest majority of the studies on galling insects on *Baccharis* were done on Brazilian species. Likely, the system comprised by *Baccharis dracunculifolia* DC and *Baccharopelma dracunculifoliae* (Hemiptera: Psyllidae) was the best studied single system in the Neotropics, with more than 15 publications (Araújo et al. 1995; Collevatti and Sperber 1997; Espírito-Santo and Fernandes 1998, 2002; Faria and Fernandes 2001; Fagundes et al. 2001, 2005; Ribeiro-Mendes et al. 2002; Espírito-Santo et al. 1999, 2003, 2004, 2007, 2012; Fagundes and Fernandes 2011). Studies on other species of *Baccharis* also deserve to be mentioned due to their relatively high numbers, such as *B. concinna*, *B. pseudomyriocephala*, and *B. ramosissima* (Madeira et al. 1997; Araújo et al. 2003, 2006; Carneiro et al. 2005, 2006; Espírito-Santo et al. 2007, 2012; See Table 13.1 for more details). In this chapter we review the studies performed primarily on *B. dracunculifolia*, *B. concinna*, and *B. ramosissima*.

13.2 The Diversity of Galling Insects on *Baccharis*

The highest number of galling species in the Neotropics has been recorded on species of the genus *Baccharis*. We must recognize, however, the high galling species richness on other tropical systems, such as on the speciose genera *Quercus* (135–200 spp.) in Mexico and southeastern US (Manos et al. 1999), *Copaifera* (23 spp.) southeastern Brazil (Costa et al. 2010), *Protium* (17 spp.) in the Amazonian region (Maia 2011), *Eucalyptus* (12 spp.) in Australia (Blanche 2000), and *Chrysothamnus* (39 spp.) in southwestern North America (Fernandes et al. 2000). Fernandes et al. (1996) reviewed the galling insects on *B. dracunculifolia*, *B. ramosissima* and *B. concinna* during four consecutive years, and extracted data from literature from other 37 species of *Baccharis*. The review resulted in the discovery of 121 species of gall inducing insects on 40 different *Baccharis* species. Gallers were not evenly distributed across host plant species while only four species of *Baccharis* (10 % of the species studied) supported 46 % of the total galling fauna (56 galling species). The host plants that supported the highest numbers of gallers were *B. dracunculifolia* (17 spp.), *B. concinna* (15 spp.), *B. salicifolia* (13 spp.), and *Baccharis* sp. 1 (11 spp.).

In the southeastern mountains of Brazil, the Mantiqueira and Espinhaço mountains, we have recorded 106 galling species on 17 *Baccharis* species (Table 13.2; Figs. 13.1, 13.2, and 13.3). In this study, the highest richness of galling insects (13 galling species) was recorded on *B. dracunculifolia*. The study also recorded a large richness of galling insects on *B. minutiflora* (12 spp.), *B. cognate* (10 spp.), *B. reticularia* (9 spp.), *B. intermixta* (8 spp.), and *B. concinna* (7 spp.). Six galling species each was recorded on *B. ramosissima*, *B. helychrysoides*, and *B. truncata*, with

Table 13.1 Summary of studies that tested ecological hypotheses on galling insects on *Baccharis* species in Neotropical America

References	Ecosystem, country	Host	Tested hypotheses
Araújo et al. (1995)	Cerrado (savanna), Brazil	*B. dracunculifolia*	(1) Sex-mediated herbivory
Collevatti and Sperber (1997)		*B. dracunculifolia*	(1) Plant architecture (2) Host plant patch size
Madeira et al. (1997)	Cerrado (savanna), Brazil	*B. concinna*	(1) Vigor hypothesis
Espírito-Santo and Fernandes (1998)	Cerrado (savanna), Brazil	*B. dracunculifolia*	(1) Gall abundance seasonality (2) Sex-mediated differences in tannin gall abundance and mortality rates (3) Tannin concentration on gall abundance
Faria and Fernandes (2001)	Ecotone Atlantic rainforest and cerrado (savanna), Brazil	*B. dracunculifolia*	(1) Vigor hypothesis (2) Sex-mediated gall abundance
Fagundes et al. (2001)	Rupestrian fields	*B. dracunculifolia*	(1) Resource concentration
Espírito-Santo and Fernandes (2002)	Dry forest and cerrado (savanna), Brazil	*B. dracunculifolia*	(1) Sex-mediated gall survivorship
Ribeiro-Mendes et al. (2002)	Atlantic rainforest, cerrado and rupestrian field, Brazil	*B. dracunculifolia*	(1) Hygrothermal stress hypothesis (2) Sex-mediated gall survivorship
Araújo et al. (2003)	Semi-deciduous forest	*B. pseudomyriocephala*	(1) Vigor hypothesis (2) Meristems availability (3) Sex-mediated gall abundance
Espírito-Santo et al. (2004)	Cerrado (savanna), Brazil	*B. dracunculifolia*	(1) Parasitoid attack on gall growth dynamics
Fagundes et al. (2005)	Semi-deciduous forest, Brazil	*B. dracunculifolia*	(1) Ant effects on galling growth, Performance and parasitoidism
Carneiro et al. (2005)	Cerrado (savanna) and rupestrian field, Brazil	*B. concinna*	(1) Hygrothermal stress hypothesis (2) Atitudinal gradient (3) Sex-mediated herbivory
Carneiro et al. (2006)	Rupestrian filed, Brazil	*B. concinna*	(1) Intersexual differences (2) Sex-mediated herbivory
Araújo et al. (2006)	Semi-deciduous forest	*B. pseudomyriocephala*	(1) Plant architecture on gall abundance and performance

(continued)

Table 13.1 (continued)

References	Ecosystem, country	Host	Tested hypotheses
Espírito-Santo et al. (2007)	Canga, rupestrian field and Cerrado (savanna), Brazil	17 *Baccharis* species	(1) Plant architecture (2) Meristem availability
Fagundes and Fernandes (2011)	Canga, rupestrian field and Cerrado (savanna), Brazil	*B. dracunculifolia*	(1) Latitudinal gradient
Espírito-Santo et al. (2012)	Cerrado (savanna) and rupestrian field, Brazil	*B. dracunculifolia* *B. concinna* *B. ramosissima*	(1) Intersexual differences (2) Sex-mediated herbivory (3) Plant phenology and gall synchronism

three galling species each recorded on *B. serrulata*, *B. ligustrina*, and *B. medullosa*. Only one galling species was recorded on *B. oreophila*. These galls were all ascribed to insects after the analysis of internal remains. Among the 106 galling species, 47 species (44 %) were not previously reported, hence representing new species and records. Among the 59 identified ones, the majority (68 %) was induced by Cecidomyiidae, followed by Lepidoptera (17 %), Psyllidae (12 %), Tephritidae (1.7 %), and Curculionidae (1.7 %). The high number of galls induced by the Cecidomyiidae is a trend already reported on several other faunal studies in the tropics (see Mani 1992; Fernandes et al. 1996; Carneiro et al. 2009a; Coelho et al. 2009; Santos et al. 2011). Carneiro et al. (2009b) studying the galling insects in the Espinhaço mountain range supported the assertion that rupestrian fields present are one world hotspot for galling insects (Lara and Fernandes 1996) and that the *Baccharis* is the most speciose genus (see Fernandes et al. 1996). These mountains are extremely species rich and harbor one of the most spectacular flora of the world (see Safford 1999).

13.3 Super Host *Baccharis* Species

Some Neotropical families of plants are notably rich in galling insects including Leguminosae *sensu lato*, Asteraceae, Myrtaceae, Malpighiaceae, Rubiaceae, and Bignoniaceae (Fernandes 1992; Fernandes et al. 1988, 1997; Julião et al. 2002; Carneiro et al. 2009b). One of the main determinants of galling species richness is the taxonomic composition of the flora. This conclusion is supported by the fact that a few taxa of host plants concentrate a large number of insect species, regardless of the sample (Fernandes 1992; Hawkins and Compton 1992). Host plants with high gall diversity have been named super host (Fernandes and Price 1988; Veldtman and McGeoch 2003; Espírito-Santo et al. 2007; Costa et al. 2010, 2011). The presence of "super hosts" is common in some tropical regions; hence contributing to the increase of the local and regional gall richness in the communities. *Baccharis* is certainly a super host genus.

Table 13.2 Insect taxa and morphological characteristics of the galls found on 17 species of *Baccharis* (following the definitions from Fernandes et al. 1996)

Host plant	Insect taxa	Organ	Shape	Color	Pubescence	Chambers	Reference
B. ramosissima Gardner	Cecidomyiidae sp.1	Stem	Elliptical	Brown	Glabrous	One	Fig. 13.1a
	Cecidomyiidae sp.2	Lateral bud	Tubular	Green	Glabrous	One	Fig. 13.1b
	Geraldesia sp.2 (Cecidomyiidae)	Leaf	Discoid	Green	Glabrous	One	Fig. 13.1c
	Cecidomyiidae sp.3	Apical bud	Globulous	Green	Glabrous	One	Fig. 13.1d
	Cecidomyiidae sp.4	Stem	Elliptical	Brown	Glabrous	One	Fig. 13.1e
	Baccharopelma brasiliesis (Psyllidae)	Leaf	Elliptical	Green	Glabrous	One	Fig. 13.1f
B. cognata DC	Psyllidae	Leaf	Elliptical	Green	Glabrous	One	
	Cecidomyiidae	Leaf	Discoid	Green	Glabrous	One	
	Lepidoptera	Stem	Elliptical	Green	Glabrous	One	
	Unidentified	Stem	Globulous	Brown	Glabrous	Several	
	Unidentified	Apical bud	Globulous	Green	Glabrous	One	
	Unidentified	Apical bud	Rosette	Green	Glabrous	One	
	Unidentified	Apical bud	Tubular	Green	Glabrous	One	
	Unidentified	Stem	Elliptical	Brown	Glabrous	One	
	Unidentified	Lateral bud	Globulous	Brown	Glabrous	One	
	Unidentified	Stem	Globulous	Brown	Glabrous	One	
B. helychrysoides DC	Unidentified	Stem	Elliptical	Brown	Glabrous	One	
	Unidentified	Stem	Elliptical	Brown	Glabrous	One	
	Unidentified	Apical bud	Cylindrical	Brown	Glabrous	One	
	Unidentified	Apical bud	Tubular	Brown	Glabrous	One	
	Unidentified	Stem	Spherical	Brown	Glabrous	One	
	Unidentified	Stem	Elliptical	Brown	Glabrous	One	
B. serrulata	Cecidomyiidae	Stem	Spherical	Green	Glabrous	One	

(continued)

Table 13.2 (continued)

Host plant	Insect taxa	Organ	Shape	Color	Pubescence	Chambers	Reference
Person	Unidentified	Leaf/Petiole	Elliptical	Green	Glabrous	One	
	Unidentified	Stem	Elliptical	Brown	Glabrous	One	
B. platypoda DC	Cecidomyiidae	Leaf	Discoid	Green	Glabrous	One	
	Unidentified	Stem	Globulous	Brown	Glabrous	Several	
	Unidentified	Leaf	Tubular	Green	Glabrous	One	
	Unidentified	Petiole	Elliptical	Green	Glabrous	One	
	Unidentified	Stem	Spherical	Brown	Glabrous	One	
B. dracunculifolia DC	Cecidomyiidae sp.8	Leaf bud	Spherical	Green	Glabrous	One	
	Cecidomyiidae sp. 9	Apical bud	Rosette	Green	Hairy	One	Fig. 13.1g
	Asphondylia sp. 1 (Cecidomyiidae)	Apical bud	Rosette	Green	Glabrous	One	Fig. 13.1h
	Roasphondylia friburguensis (Cecidomyiidae)	Stem	Globulous	Brown	Glabrous	One	
	Cecidomyiidae sp. 10	Stem	Elliptical	Brown	Glabrous	Several	
	Cecidomyiidae sp. 11	Stem	Tubular	Green	Glabrous	One	
	Cecidomyiidae sp. 12	Leaf	Conical	Green	Glabrous	One	
	Cecidomyiidae sp. 13	Apical bud	Rosette	Green	Glabrous	One	Fig. 13.1i
	Geraldesia sp. 1 (Cecidomyiidae)	Leaf	Discoid	Green	Glabrous	One	Fig. 13.1j
	Cecidomyiidae sp. 14	Stem	Globulous	Green	Hairy	One	Fig. 13.1k
	Tephritidae sp. 2	Apical bud	Globulous	Green	Glabrous	One	
	Lepidoptera sp. 2	Stem	Spherical	Green	Hairy	One	Fig. 13.1l
	Baccharopelma dracunculifoliae (Psyllidae)	Leaf	Elliptical	Green	Glabrous	One	Fig. 13.1m

B. concinna Barroso	Cecidomyiidae sp. 16	Apical bud	Tubular	Yellow	Glabrous	One	Fig. 13.1n
	Cecidomyiidae sp. 17	Stem	Elliptical	Brown	Glabrous	One	Fig. 13.1o
	Cecidomyiidae sp. 18	Apical bud	Globulous	Purple	Glabrous	Several	Fig. 13.2a
	Geraldesia sp. 3 (Cecidomyiidae)	Leaf	Discoid	Green	Glabrous	One	Fig. 13.2b
	Curculionidae sp. 1	Stem	Elliptical	Brown	Glabrous	One	Fig. 13.2c
	Lepidoptera sp. 3	Stem	Elliptical	Red	Glabrous	One	Fig. 13.2d
	Baccharopelma concinnae (Psyllidae)	Leaf	Elliptical	Green	Glabrous	One	Fig. 13.2e
B. trimera DC	Cecidomyiidae	Stem	Elliptical	Green	Glabrous	Several	
	Unidentified	Stem	Elliptical	Brown	Glabrous	One	
	Unidentified	Stem	Cylindrical	Brown	Glabrous	Several	
	Unidentified	Lateral bud	Conical	Brown	Glabrous	One	
	Unidentified	Lateral bud	Tubular	Brown	Glabrous	One	
B. tarchonanthoides DC	Lepidoptera	Stem	Elliptical	Brown	Glabrous	One	Fig. 13.2f
	Unidentified	Stem	Elliptical	Brown	Glabrous	One	
	Unidentified	Stem	Cylindrical	Brown	Glabrous	One	
	Unidentified	Leaf	Spherical	Green	Glabrous	One	
	Unidentified	Stem	Globulous	Brown	Glabrous	One	
B. trinervis Person	Lepidoptera	Stem	Elliptical	Green	Glabrous	One	
	Cecidomyiidae	Leaf	Blister	Green	Glabrous	One	Fig. 13.2g
	Unidentified	Apical bud	Tubular	Green	Glabrous	One	
	Unidentified	Stem	Cylindrical	Brown	Glabrous	One	Fig. 13.2h
B. ligustrina DC	Lepidoptera	Stem	Elliptical	Brown	Glabrous	One	Fig. 13.2i
	Cecidomyiidae	Stem	Elliptical	Brown	Glabrous	One	Fig. 13.2j
	Unidentified	Stem	Tubular	Brown	Glabrous	Several	Fig. 13.2k
B. reticularia DC	Lepidoptera	Stem	Elliptical	Brown	Glabrous	One	Fig. 13.2l
	Psyllidae	Leaf	Elliptical	Green	Glabrous	One	Fig. 13.2m
	Cecidomyiidae	Apical bud	Tubular	Green	Glabrous	One	Fig. 13.2n
	Cecidomyiidae	Leaf	Discoid	Green	Glabrous	One	

(continued)

Table 13.2 (continued)

Host plant	Insect taxa	Organ	Shape	Color	Pubescence	Chambers	Reference
	Cecidomyiidae	Apical bud	Globulous	Brown	Glabrous	Several	
	Cecidomyiidae	Leaf	Discoid	Green	Glabrous	One	
	Unidentified	Stem	Spherical	Green	Glabrous	One	
	Unidentified	Inflorescence	Conical	Yellow	Glabrous	One	
	Unidentified	Apical bud	Conical	Brown	Glabrous	One	
B. truncata Gardner	Lepidoptera	Stem	Elliptical	Brown	Glabrous	One	Fig. 13.2o
	Cecidomyiidae	Apical bud	Tubular	Green	Glabrous	One	
	Unidentified	Lateral bud	Spherical	Green	Glabrous	One	Fig. 13.3a
	Unidentified	Stem	Elliptical	Brown	Glabrous	One	
	Unidentified	Apical bud	Conical	Brown	Glabrous	One	
	Unidentified	Stem	Elliptical	Brown	Glabrous	One	
B. intermixta DC	Psyllidae	Leaf	Elliptical	Green	Glabrous	One	Fig. 13.3b
	Cecidomyiidae	Leaf	Discoid	Green	Glabrous	One	
	Cecidomyiidae	Apical bud	Tubular	Green	Glabrous	One	
	Cecidomyiidae	Apical bud	Globulous	Purple	Glabrous	Several	
	Lepidoptera	Stem	Elliptical	Brown	Glabrous	One	Fig. 13.3c
	Cecidomyiidae	Stem	Globulous	Brown	Glabrous	Several	
	Unidentified	Apical bud	Conical	Brown	Glabrous	Several	
	Unidentified	Stem	Elliptical	Brown	Glabrous	One	Fig. 13.3d
B. minutiflora Martius	Psyllidae	Leaf	Elliptical	Green	Glabrous	One	Fig. 13.3e
	Cecidomyiidae	Leaf	Discoid	Green	Glabrous	One	
	Cecidomyiidae	Apical bud	Tubular	Green	Glabrous	One	Fig. 13.3f
	Cecidomyiidae	Apical bud	Globulous	Purple	Glabrous	Several	Fig. 13.3g
	Lepidoptera	Stem	Elliptical	Brown	Glabrous	Several	Fig. 13.3h
	Cecidomyiidae	Stem	Spherical	Brown	Glabrous	One	Fig. 13.3i
	Cecidomyiidae	Stem	Spherical	Green	Glabrous	One	
	Unidentified	Stem	Elliptical	Brown	Glabrous	Several	

	Unidentified	Stem	Cylindrical	Brown	Glabrous	One
	Unidentified	Stem	Elliptical	Brown	Glabrous	One
	Unidentified	Stem	Elliptical	Brown	Glabrous	Several
	Unidentified	Inflorescence	Conical	Yellow	Glabrous	One
B. medullosa DC	Cecidomyiidae	Leaf	Discoid	Green	Glabrous	One
	Unidentified	Stem	Spherical	Brown	Glabrous	One
	Unidentified	Stem	Cylindrical	Brown	Glabrous	One
B. oreophila Malme	Unidentified	Apical bud	Tubular	Brown	Glabrous	One

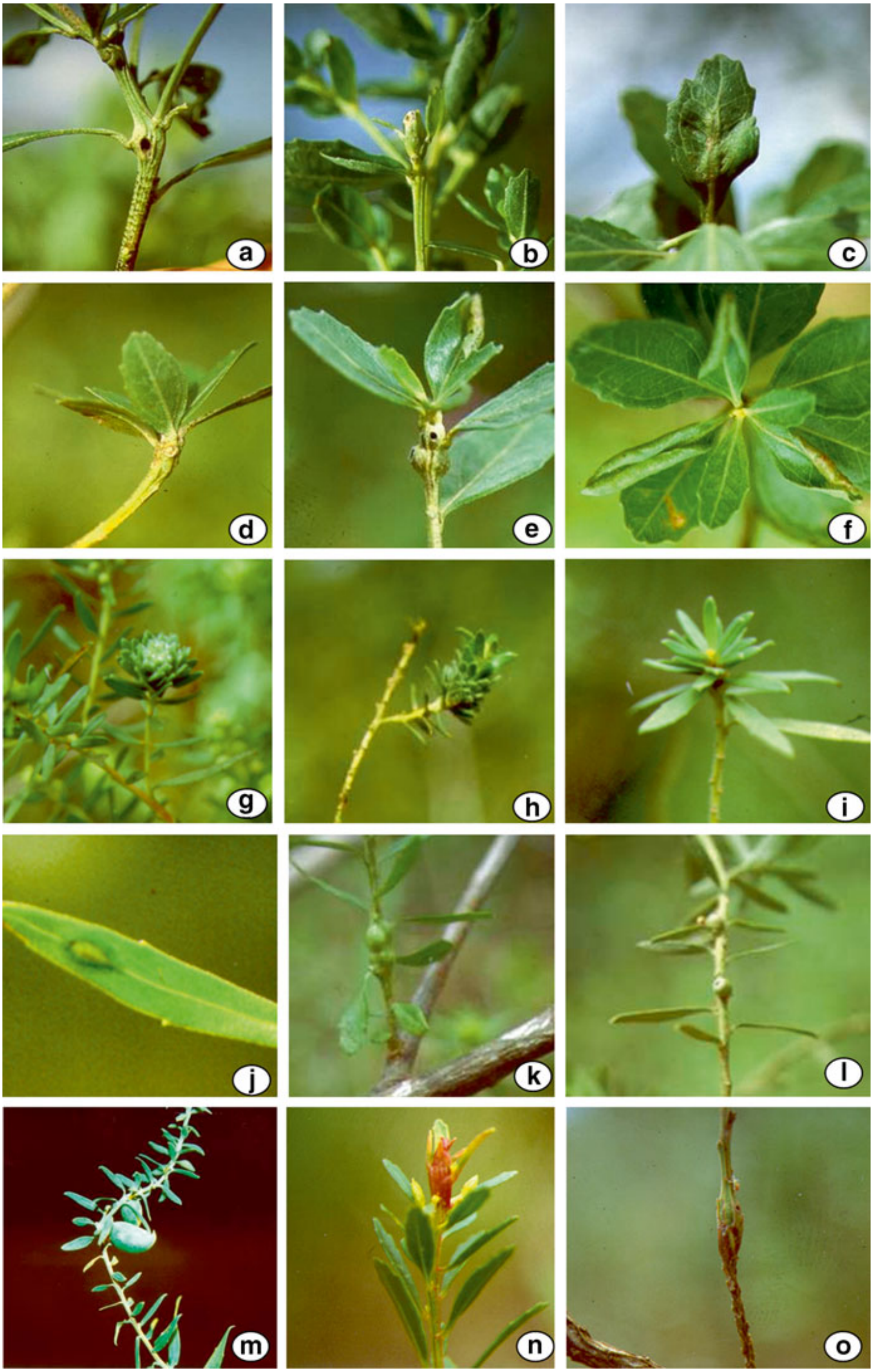


Fig. 13.1 Galling insect morphospecies found on *Baccharis* genus in Brazil. *Baccharis ramosissima* (**a**–**f**), *B. dracunculifolia* (**g**–**m**) and *B. concinna* (**n**–**o**)

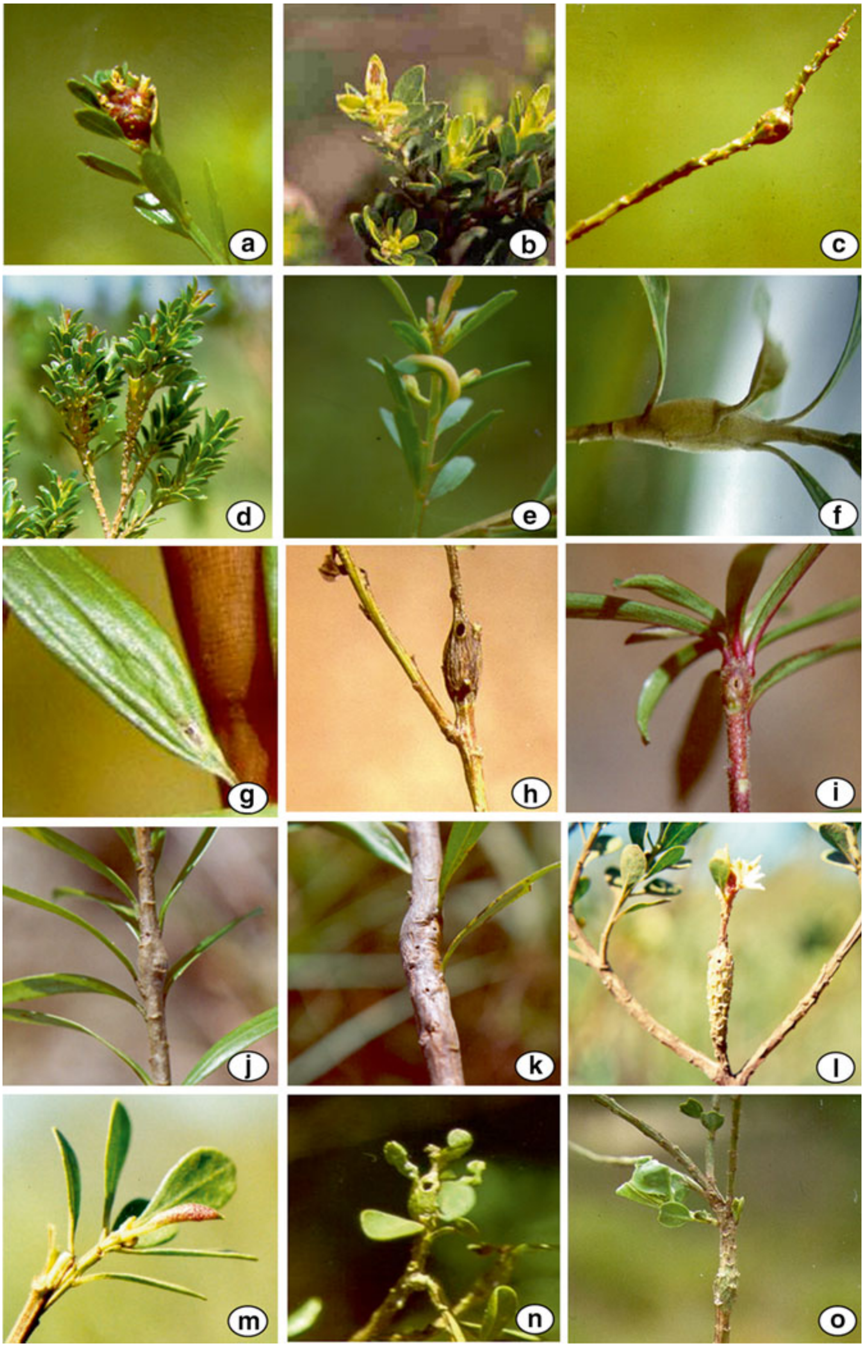


Fig. 13.2 Galling insect morphospecies found on *Baccharis* genus in Brazil. *Baccharis concinna* (**a**–**e**), *B. tarchonanthoides* (**f**), *B. trinervis* (**g**–**h**), *B. ligustrina* (**i**–**k**), *B. reticularia* (**l**–**n**) and *B. truncata* (**o**)

Fig. 13.3 Galling insect morphospecies found on *Baccharis* genus in Brazil. *Baccharis truncata* (**a**), *B. intermixta* (**b**–**d**), *B. minutiflora* (**e**–**i**)

Two galling insect genera are commonly found on the species of *Baccharis* throughout the Espinhaço mountains. The genus *Geraldesia* (Diptera: Cecidomyiidae) was recorded on nine species of *Baccharis*, while the genus *Baccharopelma* (Hemiptera: Psyllidae) was recorded on seven *Baccharis* species (Table 13.2). These genera may have experienced a large radiation inside this host genus, such as the genus *Asphondylia* (Cecidomyiidae) on *Larrea tridentata* (Waring and Price 1990). This similarity could lead to a convergence in community structure of galling insects. Host shift followed by subsequent reproductive isolation, adaptation, and ultimately speciation and radiation through sympatric speciation seems a plausible hypothesis (see also Craig et al. 1997). But while galling species radiations can be seen in some species of *Baccharis*, another interesting evolutionary aspect in this system is the distinct communities of galling insects attacking single host species. *Baccharis* tend to host gallers of different and unrelated taxa, such as dipterans, lepidopterans, hemipterans, coleopterans, thysanopterans, and even mites and mistletoes. Therefore, a peculiar or singular feature of the galling community on *Baccharis* spp. is the broad range of species composition. While in some galling speciose systems around the world we primarily see a diversification of a single taxon of gallers within the hosts, such as in *Quercus* (Cynipidae) (Shorthouse and Rohfritsch 1992; Stone et al. 2002), and *Larrea tridentata* (*Asphondylia*) (Waring and Price 1990), for instance, in *Baccharis* we observe many unrelated insect taxa attacking a single host species (see Fernandes et al. 1996; Espírito-Santo et al. 2007, 2012).

Curiously, we also observe each *Baccharis* host plant species having its own galling species of the genus *Baccharopelma* (Burckhardt et al. 2004). Based on gall abundance, *Baccharopelma* (Hemiptera: Psyllidae) (Burckhardt et al. 2004) has been shown to be the most abundant galling genus on *Baccharis* (Espírito-Santo et al. 2007, 2012). *Baccharopelma dracunculifoliae* represents 80 % of the galls found on *B. dracunculifolia*, whereas *Baccharopelma concinnae* represents 56 % of the galls on *B. concinna*, and *Baccharopelma brasiliensis*is responsible for 53.5 % of the galls on *B. ramosissima*. The reasons for the dominance of these galling hemipteran species on their hosts awaits further investigation.

While no evolutionary studies on the host relations with the galling fauna were developed so far in this genus, speciation through host shifting, species radiation within single hosts, plus colonization by different taxa are all taking place. The combination of these phenomena may account for such high and unprecedented diversity. In spite the fact that studies phylogenetic studies on the genus *Baccharis* are still underway, its species present similar architecture (see Table 13.3), and biology what could select for similar chemistry, physical and physiological traits (Espírito-Santo et al. 2007, 2012). The only system most similar to that found in *Baccharis* is perhaps that of *Chrysothamnus* spp. (Asteraceae) in southwestern United States, where at least dozens of still undescribed species of galling insects belonging to Tephritidae, Cecidomyiidae, and Lepidoptera are observed on hybrids and sub-species of *Chrysothamnus* (e.g. Floate et al. 1996; Fernandes et al. 2000).

13.4 Global and Regional Patterns of Gall Diversity on *Baccharis*

13.4.1 Latitudinal Gradient

Fagundes and Fernandes (2011) tested the spatial heterogeneity hypothesis in galling insects by evaluating the variation in richness of galling herbivores associated with 17 populations of a single species of host plant, *Baccharis dracunculifolia*. Habitats were maintained somehow homogeneous along the distributional limits of the host plant, near the Brazilian sea coast (for details see Fagundes and Fernandes 2011).

Table 13.3 Architectural traits and gall richness and abundance of the 17 species of *Baccharis*

Species	Number of ramifications	Level of ramification	Number of fourth-level shoots	Height (m)	Biomass (g)	Gall richness (total)	Gall abundance
B. ramosissima	21.9 ± 1.32	5.12 ± 0.15	138.7 ± 9.79	1.99 ± 0.05	273.8 ± 45.2	6	11.28 ± 1.29
B. cognata	17.4 ± 1.43	4.46 ± 0.09	87.4 ± 9.32	0.97 ± 0.02	56.5 ± 9.08	10	3.95 ± 1.09
B. helychrysoides	1.62 ± 0.13	2.96 ± 0.13	4.47 ± 0.84	1.46 ± 0.03	30.4 ± 4.33	6	0.98 ± 0.18
B. serrulata	3.34 ± 0.22	3.74 ± 0.16	8.72 ± 1.35	0.78 ± 0.04	37.7 ± 10.2	3	1.15 ± 0.37
B. platypoda	4.72 ± 0.37	3.06 ± 0.11	6.13 ± 1.57	1.22 ± 0.06	150.5 ± 28.3	5	3.15 ± 1.20
B. dracunculifolia	10.7 ± 0.59	5.18 ± 0.16	141.1 ± 13.0	1.84 ± 0.06	253.5 ± 23.1	13	54.1 ± 7.23
B. concinna	11.5 ± 0.66	5.25 ± 0.20	92.8 ± 9.98	1.05 ± 0.04	81.5 ± 12.7	7	15.63 ± 3.34
B. trimera	1.62 ± 0.13	4.01 ± 0.12	22.4 ± 2.29	0.85 ± 0.03	56.2 ± 11.9	5	3.02 ± 0.61
B. tarchonanthoides	2.13 ± 0.14	3.91 ± 0.14	12.5 ± 1.93	1.17 ± 0.04	150.4 ± 23.9	5	0.85 ± 0.20
B. trinervis	3.11 ± 0.24	3.88 ± 0.14	27.1 ± 8.15	0.97 ± 0.04	84.2 ± 23.7	4	1.83 ± 0.35
B. ligustrina	2.42 ± 0.18	3.13 ± 0.12	4.81 ± 0.77	0.54 ± 0.02	37.5 ± 7.97	3	2.11 ± 0.44
B. reticularia	17.4 ± 1.26	5.45 ± 0.17	86.9 ± 8.09	1.65 ± 0.04	305.0 ± 26.8	9	16.08 ± 1.87
B. truncata	4.82 ± 0.39	4.15 ± 0.15	26.5 ± 3.79	0.67 ± 0.03	37.8 ± 6.16	6	1.07 ± 0.26
B. minutiflora	25.2 ± 2.14	5.47 ± 0.15	119.3 ± 11.0	1.00 ± 0.03	68.7 ± 9.56	12	30.97 ± 4.82
B. intermixta	10.1 ± 0.49	5.09 ± 0.15	79.2 ± 8.27	1.34 ± 0.04	184.6 ± 24.7	8	36.32 ± 5.27
B. medullosa	3.05 ± 0.26	3.86 ± 0.11	27.1 ± 3.51	1.95 ± 0.06	201.0 ± 36.1	3	9.35 ± 1.57
B. oreophila	2.78 ± 0.38	2.88 ± 0.08	6.03 ± 1.39	1.89 ± 0.04	66.6 ± 8.26	1	0.08 ± 0.04

The authors did not find support for the spatial heterogeneity hypothesis; indicated by the lack of variation of galling insect richness associated with *B. dracunculifolia* along the latitudinal gradient studied. This result associated with the fact that the genus *Baccharis* is more species-rich in the southern region of Brazil (see Jarvis et al. 1991) and the narrow host plant requirements of gall-inducing insects (specialists) (see Carneiro et al. 2009a) support the hypothesis that galling insect associated with the genus *Baccharis* radiated into the southern region of Brazil (Fagundes and Fernandes 2011).

13.4.2 Altitudinal Gradient

Galling insect species diversity is generally negatively correlated with altitude (Fernandes and Price 1988, 1991; Fernandes and Lara 1993), whereas in some cases galling insect diversity peaks at intermediate altitudes (Waring and Price 1990). Fernandes and Price (1991) observed that the negative relationship between altitude at regional scale and galling species richness was heavily dependent on xeric habitat than mesic habitat, suggesting that altitude is a spurious correlate, and environmental harshness is the key factor determining galling species richness. Such a conclusion is supported by the latitudinal pattern.

Carneiro et al. (2005) verified the effects of the altitudinal gradient (800–1,400 m) on the galling insect community on *Baccharis concinna* within the same latitude. The total number of galling species and the richness of galling cecidomyiids showed a peak at intermediate altitudes (=1,100 m). The richness of all galling species and galling cecidomyiids were strongly influenced by habitat. A similar peak has been reported for *Asphondylia* spp. (Cecidomyiidae) on *Larrea tridentata* by Waring and Price (1990) in North America. Since Carneiro et al. (2005) used a system nearly void of confounding effects (effects of latitude, plant species richness, and plant architecture controlled as only a single host taxon was studied), the results indicate that local factors were more important than regional factors structuring the galling insect community on *B. concinna*.

13.5 Local Patterns of Gall Diversity on *Baccharis*

13.5.1 Architecture and Galling Insects

Among the plant traits known to affect herbivorous insects, architecture is probably the least studied (Marquis et al. 2002). According to Lawton (1983), plant architecture has five components: size, growth form (mainly herbs, shrubs, and trees), seasonal development, variety of above-ground parts, and the persistency of these parts. *Baccharis* represents an ideal system to verify architectural features effects on gall attack since interspecific variation in architecture is high, with species varying

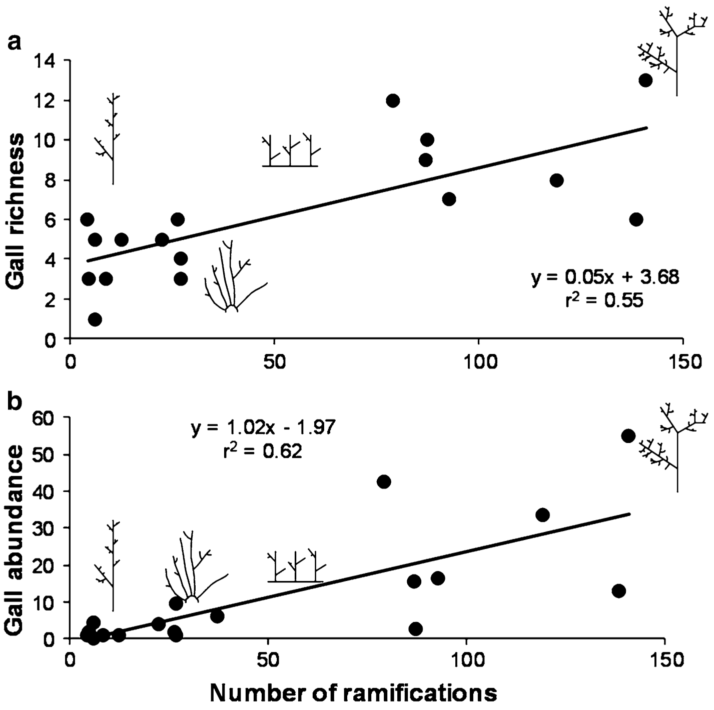


Fig. 13.4 Relationship between total (**a**) gall richness and (**b**) abundance and number of ramifications for 17 species of *Baccharis*

from 0.3 to 4 m in height, and with very distinct ramification patterns (see Barroso 1976); thus allowing comparisons between species with great discrepancy in architecture and gall richness.

Espírito-Santo et al. (2007) investigated the influence of plant architecture on the speciose fauna of gall-inducing insects associated with the 17 species of *Baccharis* previously cited (Table 13.3). Five architectural variables were evaluated: plant height, number of fourth-level shoots, biomass, average level, and number of ramifications (Table 13.3). Fourth-level shoots are usually young and possess many sprouting leaves, therefore being a natural indicator of the amount of active meristems in a given individual. Higher-level shoots (e.g., fifth and sixth level) are encountered only in few architecturally complex individuals of some *Baccharis* species and hence were not considered here for clarity (for details see Espírito-Santo et al. 2007).

The higher richness and abundance of galling insects was found on host species that presented the higher number of ramifications (architecturally complex) (Fig. 13.4). The most important architectural trait influencing gall richness at the species level was the number of fourth-level shoots, which is indicative of the availability of plant meristems, a fundamental tissue for gall induction and development (Fig. 13.5). This variable also showed a positive correlation with gall

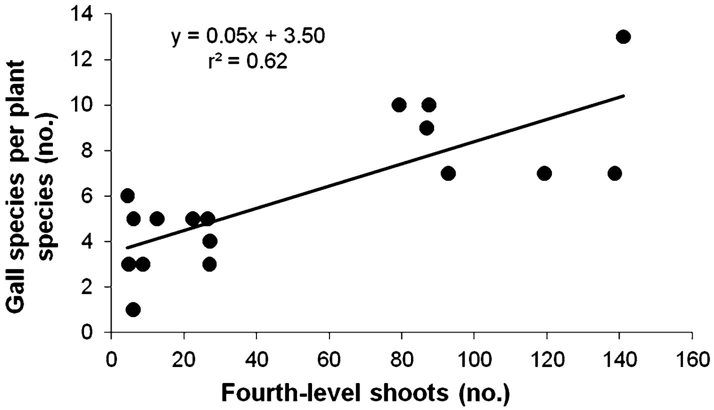


Fig. 13.5 Relationship between total gall richness and the average number of fourth-level shoots per species for 17 species of *Baccharis* ($y = 0.05x + 3.50$, $r^2 = 0.62$)

richness and abundance at the individual level on *B. concinna*, *B. dracunculifolia*, and *B. ramosissima* (see also Sect. 13.5.2). Hence, plant individuals and species with a higher average number of fourth-level shoots may support a higher richness of galling insects.

Galling insects require relatively undifferentiated tissues for the induction and development of galls (Mani 1964; Weis et al. 1988; Rohfritsch 1992). In general, apical dominance is reduced on shrubs (Steeves and Sussex 1989; Sussex and Kerk 2001) and the plants maintain a steady supply of young branches suitable for attack by galling female (Price et al. 1996). Variations in gall richness among host species may be driven by interspecific differences in plant architecture via availability of young, undifferentiated tissue, which is genetically controlled by the strength of the apical dominance. This is reinforced in our studies (see Espírito-Santo et al. 2007), in which *Baccharis* species with higher meristem availability supported higher gall richness and abundance. Corroborating this finding, Araújo et al. (2003) showed that galling insect richness on *Baccharis pseudomyriocephala* was positively related to host architectural complexity (height, biomass, and shoot size). Although many factors influence the evolutionary radiation of galling species (e.g., plant chemistry, physical defenses, phenology, gall competition and natural enemies), we must yet untangle the role of resource availability and meristem dynamics in the system (Espírito-Santo et al. 2007).

13.5.2 Dioecy and Gall Attack

Plants have limited resources for their physiological processes and there is a trade-off between the various processes. Dioecious plants present different adaptations related to each gender investing differentially their nutrients and energy into reproduction, growth rates and production of chemical compounds.

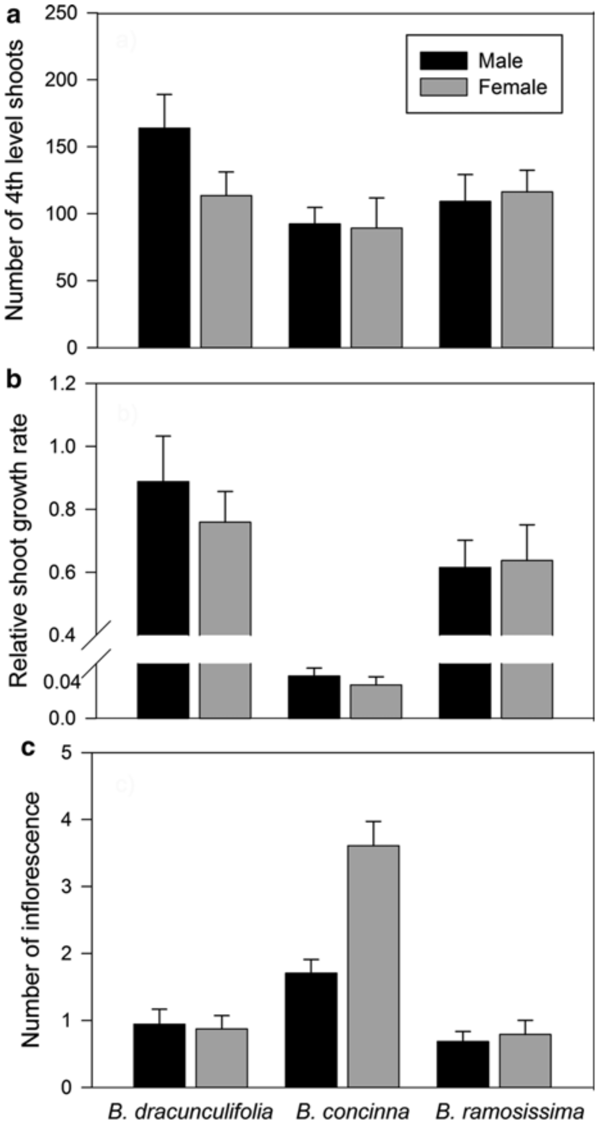
Female plants growth rates are lower than in male plants, while male plants may experience greater damage by herbivores than female plant conspecifics (Ågren 1987; Boecklen et al. 1990, 1994; Herms and Mattson 1992; Cornelissen and Stiling 2005). In dioecious species, where male and female plants have different growth rates, the resource availability hypothesis predicts that: (1) female plants (slow growth) invest more resources in the production of secondary compounds against herbivores than male plants (rapid growth); and that (2) female plants due to the high concentration of secondary compounds will be less attacked by herbivores than males. Several studies have indeed indicated that female plants are less attacked by different guilds of herbivores, including free-feeding and galling herbivores (Boecklen et al. 1990; Boecklen and Hoffman 1993), other invertebrate herbivores (Elmqvist et al. 1991), herbivorous mammals (Danell et al. 1985, 1991; Hjaltén 1992), and fungi (Varga and Kytöviita 2008), while some exceptions were found (e.g., parasites, Gehring and Whitham 1992; and pathogens, Lee 1981).

The system comprised of *Baccharis* species and their gall-inducing insects appears to provide an ideal scenario to test for plant sexual differences on timing and intensity of energy allocation and herbivory attack. The effects of vegetative (number of fourth-level shoots and relative shoot growth rate) and reproductive traits (inflorescence number) on gall attack on *Baccharis dracunculifolia*, *B. concinna*, and *B. ramosissima* was studied during a 1 year period. Intersexual differences were only observed in inflorescence number on *B. concinna*, in which was male biased (Fig. 13.6). On the other hand, gall abundance did not differ between sexes of the three *Baccharis* species studied (Fig. 13.7).

Females of *B. concinna* produced a significantly higher number of inflorescences than males. However, this species is wind-pollinated (Barroso 1976) and has the smallest inflorescences among the three species studied. Its low-cost flowers are produced throughout the year by both gender (see Espírito-Santo et al. 2012). Thus, due to the absence of differences in relative shoot growth rate between genders, a high female investment in flowering do not provoke a trade-off between reproduction and growth, ultimately resulting in the absence of difference of gall abundance between sexes. Furthermore, carbon-based defenses such as tannins do not vary between sexes in *B. dracunculifolia* (Espírito-Santo et al. 1999), although nothing is yet known for the chemistry of *B. concinna* and *B. ramosissima*. In general, plant sex does not seem to be an important variable that affects gall attack on *Baccharis*.

The findings in these three species corroborate the previous studies in this speciose genus (Espírito-Santo and Fernandes 1998; Faria and Fernandes 2001; Araújo et al. 2003; Carneiro et al. 2006; Espírito-Santo et al. 2012). On *B. dracunculifolia*, Faria and Fernandes (2001) did not find difference in relative growth rate and gall abundance between sexes, whereas Espírito-Santo and Fernandes (1998), and Ribeiro-Mendes et al. (2002) were not able to find any statistically significant difference on gall performance (e.g. gall parasitoidism and predation) between sexes. In *B. pseudomyriocephala*, Araújo et al. (2003) also failed to verify any effect of

Fig. 13.6 Average (**a**) number of fourth-level shoots, (**b**) relative shoot growth rate and (**c**) inflorescence number on male and female individuals *Baccharis dracunculifolia*, *B. concinna* and *B. ramosissima*. Data were measured every 3 weeks during 1 year and averaged per plant species (mean ± s.e.)



host plant gender on shoot size, meristem availability or gall attack. Although the abundance of galling insects showed a positive correlation with shoot size, larval survivorship was not influenced by shoot size. Finally, although *B. concinna* male plants presented longer shoots and a lower average number of inflorescences than female plants, no statistically significant difference was found in the number of galls between male and female plants (Carneiro et al. 2006).

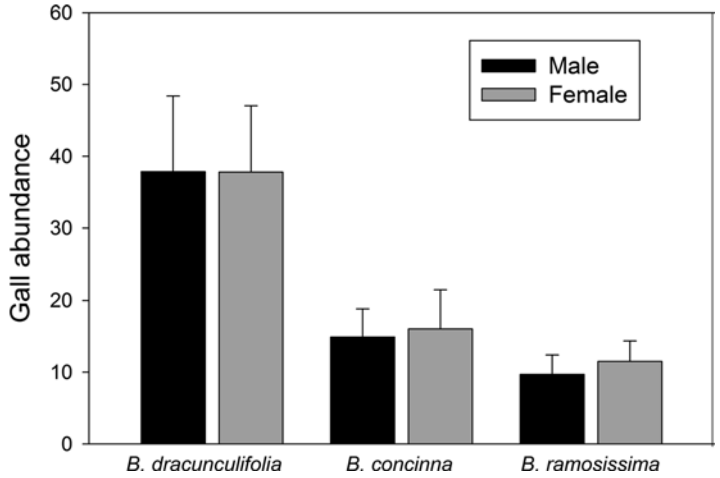


Fig. 13.7 Average number of galls (mean ± s.e.) on male and female individuals of *Baccharis dracunculifolia*, *B. concinna* and *B. ramosissima*. Galls were counted every 3 weeks during 1 year and averaged per plant species

In spite of the intersexual differences in *B. concinna* (e.g., number of inflorescence), the *Baccharis* species do not exhibit significant differences in growth rates, number of shoots, nutritional status, and chemical properties between male and female plants. At this moment, there is compelling evidence to the lack of differential gall attack between host plant sexes. Our long-term data support the hypothesis that shoot growth rate is an important variable influencing temporal variations in gall attack, whereas the number of fourth-level shoots is responsible for spatial and individual differences in plant susceptibility regardless of plant gender.

13.6 Concluding Remarks

Baccharis support the highest galling insect fauna in the Neotropics and is a super host genus for gall inducing insects. Within single species or within the genus, many insects belonging to different taxa succeeded, evolved and radiated to form one of the most spectacular communities of gallers in the world. Their study has been crucial for the establishment of generalities and testing of ecological and evolutionary theories across the Americas, as well as to generate new ideas and hypotheses. For these reasons and power of the field and experimental observations we suggest that the galling insects on their *Baccharis* hosts may represent a Neotropical model system for studies on insect plant interactions.

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Chapter 14
Galls and Galling Arthropods of Southern Brazil

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Abstract A review of the work on galls from southern Brazil is presented, including historical and contemporary sources. A database of gallers and host plants from Rio Grande do Sul (RS) state arising from an up to date inventory is presented. Galls from RS are discussed in terms of inducer taxa found, host plant taxa galled in the region and gall morphological aspects. Diversity patterns in space across environments are evaluated. Research gaps regarding issues such as environments and geographical areas are proposed.

Keywords Rio Grande do Sul • Subtropical • Atlantic forest • Pampa

14.1 Introduction: The South of Brazil

The southern region of Brazil is a 400 km wide north-south strip of land south of the Tropic of Cancer and adjoining the South Atlantic Ocean. This position and the presence of the Serra Geral highlands (about 1,000 m a.s.l.) occupying most of the western part determines the climate there as subtropical. To the south, the highlands tamper off and rolling plains appear, composing the grasslands and savannas of the Pampa region (Rambo 1956). The south is rich in the variety of ecosystems present, with three

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biomes (Pampa, Atlantic Forest and enclaves of Cerrado, IBGE 2004) and at least six ecoregions (according to the WWF scheme, Olson et al. 2001) represented.

Three States officially compose the South of Brazil: Paraná, Santa Catarina and Rio Grande do Sul (from north to south). Paraná has borders with São Paulo State to the north where Atlantic forest and Cerrado continues. On the west, all States have borders with Argentina, with the Chaco and Espinal ecoregions occurring nearby. Rio Grande do Sul has its southern borders with Uruguay, where the Pampas, or Uruguayan savannas ecoregion (Olson et al. 2001) also continue.

Because of the subtropical climate of the region, it is generally supposed to harbour a less diverse biota. South Brazilian grasslands, for example, are considered a neglected biome, because of its representativeness and overlooked high biodiversity levels (Overbeck et al. 2007). A lower plant species richness would be a first indicator that less galls would be found there (given the widely believed association between the two variables, Espírito-Santo and Fernandes 2007), although the relationship might be broken if preferred hosts (super-hosts) are more common there.

14.2 A Brief History of Gall Studies in Southern Brazil from Early European Researchers to the Present

Despite the rich diversity of environments, the south region lags behind at least the southeastern one in terms of our knowledge of the galls and gallers to be found there. Until now, research has been sporadic in time and space, although lately a few research groups have increased efforts. This has generated new data, either faunistically on the galls and host plants present, or on biological and ecological aspects of galls.

The history of gall studies in the south of Brazil begins with the founders of Brazilian cecidology: Tavares, Rübsaamen and Kieffer. Tavares was the only one to actually travel to the southern states (albeit a forced trip after being deported by the Portuguese dictatorship) and collect galls there, whilst the others received material from other collectors and did only taxonomy. Judging from the Cecidomyiidae World Catalog (Gagné 2010) the number of galling Cecidomyiidae described from the southern states is rather small (18 spp.), but still most species (15) were described in the early twentieth century by these three researchers. The State of Rio Grande do Sul has nine species (six described by Tavares, one by Kieffer), Santa Catarina also has nine species (one described by Tavares, four by Kieffer, three by Rübsaamen) while Paraná state has only one recorded galling species (also known for Santa Catarina), described in contemporary times. Clearly, a concerted effort is needed to allow the galling fauna of the southern region of Brazil to be known while we still have sufficiently good examples of the native vegetation available.

Since the beginning of the twentieth century, galls from the south of Brazil have been rarely studied, although the number of sources has increased considerably, especially in the last decade. Records from proper inventories are virtually lacking in the peer-reviewed literature. There are very recent sources revealing sampled galling faunas and galled floras in Rio Grande do Sul state, for example Toma and Mendonça (in press) for galls in *Araucaria* forests and forest-grassland edges.

Mendonça and Rodrigues (in press) will reveal galls and host plants from natural and planted *Araucaria* forests and Mendonça and Correa (in press) from the adjoining dense subtropical Atlantic forest. Also, in Santa Catarina state an inventory from coastal restinga shrublands is in preparation (Cividini and Harter-Marques 2012).

There are other sources available, but also unpublished, that can be revealing on the fauna and on the potential this region has for gall studies. Some of these sources are discussed below, along with a few published papers mainly on ecology and biology of south Brazilian galls.

Fleck (2005) worked in the National Forest of São Francisco de Paula (FLONA-SFP) evaluating among other things the response of abundance, richness and composition of galls to a mosaic of environments (native forest and planted forests – araucaria, eucalyptus and pine). Overall 81 gall morphotypes were found, and a list of host plants and galled host organs is provided, with no other detail included. Because of that, these galls were not included in the list provided below nor compared to the ones on the list – although probably half of the galls found by Fleck (2005) are absent from said list. Another result from this effort is the work on *Cryptocarya aschersoniana* galls (Fonseca et al. 2006), one induced by an unknown Hemiptera and another supposedly by a Hymenoptera. Although the Hemiptera gall was not found in later efforts by the authors of this chapter (it occurs high up in the tree crown), the other gall is erroneously attributed to Hymenoptera, being induced by a Lasiopteridi (Cecidomyiidae, see Table 14.2 below).

Apart from inventories, several studies report on galls and gallers on plants in south Brazil, however usually dealing with a single or a few inducers. The kind of information available on the galls on such publications is highly varied. A few only mention the existence of galls on a given plant, as Bianchini and dos Santos (2005) for leaf galls in *Chrysophyllum gonocarpum* (Sapotaceae) in Londrina, Paraná state – it should be pointed out that there is no actual mention of the gall being insect-induced. Another such case is the rosette gall on terminal buds of *Tibouchina reitzii* (Melastomataceae) found in herborised plant material from Paraná state, also without an identified inducer (Meyer et al. 2010) – although the structure is indicative of an insect. This same gall is mentioned for the states of São Paulo, Paraná and Santa Catarina by Guimarães and Oliveira (2009).

Few gall systems have been studied for economic reasons. In Paraná, gallers on native plants that are invasive elsewhere were considered for use as biological control agents. *Psidium cattleianum* is locally known in southern Brazil as araçá, and in English as strawberry guava. It is a common Myrtaceae native to Brazil and found in different environments, naturally and artificially distributed especially because the fruit is edible (Ellshoff et al. 1995). However, it has become invasive in several places, especially in the USA (Florida, Wessels 2005; Hawaii, Wikler et al. 2000). Several galls found on this plant were suggested as biological control agents of *P. cattleianum*, since no pathogens were found to that end: (1) *Prodecatoma carpophaga* (Hymenoptera, Eurytomidae) galls the fruits inducing fruit deformities (Wikler et al. 1996, DalMolin et al. 2004); (2) *Dasineura gigantea* (Diptera, Cecidomyiidae) galls the buds generating rosettes (Wikler et al. 2000); (3) *Tectococcus ovatus* (Hemiptera, Eriococcidae) galls the leaves producing a fusiform whitish gall (Wessels 2005); (4) *Neotrioza tavaresi* (Hemiptera, Psyllidae) also galls the leaves, producing a lenticular to spherical gall (Wikler et al. 2000); (5) *Eurytoma* sp. (Hymenoptera, Eurytomidae) galls the stems inducing fusiform structures (Wikler et al. 2000); and (6) *Sycophila* sp. (Hymenoptera, Eurytomidae) galls the seeds deforming them (Wikler et al. 2000). Even with all these possibilities, it appears that none of these species will be able to positively help in host control at least in Hawaii (Patel 2012).

There are a couple of cases of the inverse situation of that described above occurring in the south of Brazil: gallers which are introduced, attacking their native hosts which are planted here. The main example comes from infestations of *Eucalyptus* plantations. *Epichrysocharis burwelii* (Hymenoptera: Eulophidae) is a very small wasp inducing galls on leaves of *Corymbia citriodora* (Myrtaceae). It has been recorded from southern Brazil in Rio Grande do Sul (Cachoeira do Sul area) and Paraná States (Colombo area) (Queiroz 2009).

Finally, three systems have been explored for purely scientific reasons. First there are the Cecidosidae, represented especially by *Cecidosis eremita*, a distinct galler moth with a distinct gall. The seven species belonging to the Cecidosidae family, as its name imply, are all gallers mostly in Anacardiaceae hosts (Miller 2005). The family has a classical Gondwanan distribution (South America, South Africa, New Zealand) (Pellmyr and Leebens-Mack 1999). The gall is spherical on the stems of *Schinus polygamous* (Anacardiaceae), pupation is inside the gall and an operculum appears to let the adult out. This round operculum later gives the gall its characteristic “whistling” sound: when the cold *minuano* wind (a southern wind typical of the winter) blows through a galled plant, the whole plant seems to whistle and can be heard from a distance – thus the plant is locally called “whistler” (*assoviadeira*). *C. eremita* has been known from southern South America for a long time (Wille 1926), and nearly a century passed before more studies were developed in Rio Grande do Sul. An abstract in a local student event reported novelties, with updates in the description of the larvae and pupae, for example a structure in the pupal head (ruptor) with the function of pushing the operculum (Aymone et al. 2005). Further, an undescribed species of Cecidosidae galling *Schinus weinmanifolius* (Anacardiaceae) had its genetic variation and population structure evaluated (Eltz et al. 2009), again with only an abstract reporting high genetic population structure for this species.

Guapira opposita is a common Nyctaginaceae tree in many forest types of Brazil. It is considered a super-host, being attacked by a suite of Cecidomyiidae gallers initially reported for Rio de Janeiro state (see Maia 2005). In forests around Porto Alegre (Rio Grande do Sul state, RS), the plant hosts at least six species of galling Cecidomyiids, and there are studies being developed on the temporal pattern of gall occurrence, as yet unpublished (Rodrigues et al. 2007; Menzel et al. 2009; Silva et al. 2011). These preliminary reports demonstrate large variation in the abundance of the different galls, and little seasonality in terms of species richness – most species are present all year round, although more galls are found during springtime. There are also a couple of ongoing studies on the spatial distribution of galls on the plants and relationship with environmental variables, either related to the plant (size, new leaf production, vigour) or to abiotic factors (temperature, humidity, etc.).

Eugeniamyia dispar is a Cecidomyiidae galling leaves and stems of *Eugenia uniflora* (Myrtaceae). The insect has been described as a new genus (Maia et al.

1996) and is found from at least three States in the southern-southeastern region of Brazil (RS, Santa Catarina and São Paulo, pers. obs.). The system has been studied from an anatomical and ecological point of view (Mendonça et al. 1998). The life history of the galler involves oviposition on the new, red leaves of the host, followed by gall development, with the last instar larva using its prothoracic spatula to cut through gall tissue, leaving the gall to pupate in the soil (Mendonça and Romanowski 2002a). Mendonça (1996) described the gall as a spongy and whitish structure, due to hypertrophy of the mesophyll cells which elongate and lose chlorophyll, generating the spherical shape and absence of colour. Thus, instead of hard tissues, this gall relies on soft ones to somehow protect the galler, probably avoiding parasitoid attack given the thickness of the gall. Nevertheless the gall is highly attacked by an undescribed *Rileya* (Eurytomidae) wasp, which can be commonly found around galled leaves showing oviposition and protective behaviour towards the galls (Mendonça and Romanowski 2002b). The galler also has three ant species found as predators. The galls cannot be found during the winter in Rio Grande do Sul state, being absent from plants from 1 to 3 months. As development is fast, and becomes faster with increasing temperatures, more or less separate generations follow each other until they overlap in the summer, again becoming more distinct during autumn (Mendonça and Romanowski 2012).

These few studies highlight how much gall systems can contribute to varied questions, from pure ecology and genetics to applied forestry and agronomical problems. However, we have not even tapped the full potential of such systems. There is clearly more room for research in southern Brazil on galls and their gallers.

14.3 A Bestiary of Galls in the Temperate South: Rio Grande do Sul State

There are a few sources from Rio Grande do Sul State dealing with galling arthropods under an ecological perspective, with no individual records of galls provided (Dalbem and Mendonça 2006; Mendonça 2007, 2011; Mendonça et al. 2006, 2010). Unpublished sources also include records of galls from this southern most state of Brazil, representing the work of a single laboratory, which is increasing over the years (Mendonça 2003; Correa 2008; Rodrigues 2010; Gonçalves 2010). The galls accumulated from some of these sources, identified at least to host genus level and recorded in detail for morphology, are presented here. Approximately a third of the galls is also illustrated. The intention is to present a general view on which galls are there in Rio Grande do Sul, the plants they attack, their inducers and the most common types of gall structure that are to be found.

The study sites include the two biomes found in RS; some sites are entirely within a biome but at least two can be considered as transitionary (Table 14.1). Nine municipalities have been sampled (Fig. 14.1). Five ecoregions (as recognized by the WWF, Olson et al. 2001) in two types of climate (Cfa and Cfb, Köppen-Geiger classification, Kuinchtner and Buriol 2001) can be found, spanning altitudes from 10 to 907 m above sea level.

Table 14.1 Sampling areas in Rio Grande do Sul state, with geographical coordinates, climate (Köppen-Geiger classification), altitude (above sea level), area or conservation unit name, ecoregion (according to the WWF classification) and vegetation types sampled

Municipality	Coordinates	Climate	Altitude (a.s.l.)	Area/conservation unit	Biome	WWF ecoregion	Vegetation types
Derrubadas	27° 8′ S 53° 53′ W	Cfa	200 m	Turvo State Park	Atlantic forest	Alto Paraná Atlantic forests	Subtropical semideciduous forest, edge and interior
Torres	29° 20′ S, 49° 43′ W	Cfa	16 m	Itapeva State Park	Atlantic forest	Atlantic coast restingas	Restinga scrubland, subtropical moist forest
São Francisco de Paula	29° 26′ S, 50°23′ W	Cfb	907 m	National forest	Atlantic forest	*Araucaria* moist forests	Mixed *Araucaria* subtropical moist forest
Maquiné	29° 34′ S, 50° 16′ W	Cfa	12 m	Maquiné river basin	Atlantic forest	Serra do Mar coastal forests	Dense subtropical moist forest
Viamão	30° 04′ S, 51° 01′ W	Cfa	89 m	Itapuã State Park	Atlantic forest/ Pampa	Uruguayan savanna	Restinga scrubland, subtropical moist forest
Porto Alegre	30° 01′ S, 51° 13′ W	Cfa	10 m	Morro Santana wildlife reserve	Atlantic forest/ Pampa	Uruguayan savanna	Subtropical moist forest
Barra do Quarai	30° 12′ S, 57° 33′ W	Cfa	35 m	Espinilho State Park	Pampa	Uruguayan savanna	Subtropical gallery forest, espinilho parkland
Caçapava do Sul	30° 30′ S, 53° 29′ W	Cfb	444 m	Pedra do Segredo Municipal Park	Pampa	Uruguayan savanna	Subtropical gallery forest, edge and interior
Canguçu	31° 23′ S, 52° 40′ W	Cfb	386 m	Private rural properties	Pampa	Uruguayan savanna	Subtropical gallery forest, edge and interior

For more details see text

Fig. 14.1 Map of Rio Grande do Sul state divided in municipalities with the nine sampled sites indicated by *maroon circles*. In detail: Rio Grande do Sul (*red*) in Brazil

On each site, a number of transects was established through homogeneous vegetation, usually using available trails ranging from frequently used to abandoned ones. In all sites, transects cut through a single vegetation type with different levels of disturbance or through different but adjoining vegetation types. The transects were sampled by a maximum of two persons during 90 min, attentively scanning the vegetation for galls, walking at a slow pace. Thus, transects covered from 200 to 300 m at most. Transects were repeatedly visited from three to eight times at different seasons. Galls when found were inspected for inducers, collected separately in plastic bags when an insect or mite was found and were provisionally morphotyped (for organ, shape, colour and host plant). In the lab, half the galls collected of each morphotype was opened under a stereomicroscope to check for the galler and gall internal structure. The other half was left in plastic pots to allow galler/parasitoid emergence. Galls were photographed for future reference whenever possible.

We report 291 gall morphotypes for Rio Grande do Sul state (Table 14.2, Figs. 14.2, 14.3, 14.4, 14.5, 14.6 and 14.7). For 144 galls the galler is known at least down to order level, and for 123 galls down to family level, thus comprising at least seven

Table 14.2 Host plants, morphological characters and inducers for galls sampled in Rio Grande do Sul state from 2001 to 2010

Host species	Host family	Plant organ	Shape	Colour	Number of chambers	Pilosity	Inducer taxon	Inducer species
Acacia caven	Fabaceae	Stem	Spherical	Brown	m	g		
Acacia caven	Fabaceae	Stem	Fusiform	Brown	m	g		
Acacia caven	Fabaceae	Leaflet	Spherical	Green	m	h	Eriophyidae	
Allophylus edulis	Sapindaceae	Stem	Spherical	Green	m	g		
Allophylus edulis	Sapindaceae	Leaf	Lenticular	Light green	m	g	Cecidomyiidae	*
Allophylus edulis	Sapindaceae	Stem	Cylindrical	Light brown	m	g	Lepidoptera	
Allophylus edulis	Sapindaceae	Stem	Fusiform	Light brown	p	g		
Allophylus edulis	Sapindaceae	Leaf vein	Fusiform	Green	m	g	Diptera	
Aloysia gratissima	Verbenaceae	Leaf	Fusiform	Green	m	h	Hemiptera	
Aloysia gratissima	Verbenaceae	Stem	Fusiform	Light brown	m	g	Curculionidae	
Aloysia gratissima	Verbenaceae	Leaf	Discoidal	Black	m	g		
Annona rugulosa	Annonaceae	Leaf	Fusiform	Green	m	g	Cecidomyiidae	*
Annona salicifolia	Annonaceae	Leaf	Spherical	Green	m	h		
Asplenium sp.	Aspleniaceae	Leaf	Conical	Green	m	g		
Baccharis anomala	Asteraceae	Stem	Fusiform	Green	m	g	Cecidomyiidae	*Asphondylia* sp. 1
Baccharis anomala	Asteraceae	Stem	Rosette	Green	m	g		
Baccharis dentata	Asteraceae	Bud	Rosette	Green	m	g	Cecidomyiidae	*
Baccharis dentata	Asteraceae	Stem	Spherical	Light brown	m	g	Cecidomyiidae	*
Baccharis dentata	Asteraceae	Stem	Fusiform	Light brown	m	g	Cecidomyiidae	*
Baccharis dracunculifolia	Asteraceae	Stem	Fusiform	Light brown	m	g	Hemiptera	
Baccharis dracunculifolia	Asteraceae	Leaf	Hemispherical	Green	m	g	Eriophyidae	
Baccharis microdonta	Asteraceae	Stem	Fusiform	Light brown	m	g	Cecidomyiidae	*
Baccharis microdonta	Asteraceae	Stem	Rosette	Light brown	m	g	Lepidoptera	
Baccharis sp.	Asteraceae	Leaf	Spherical	Green	m	g		
Baccharis sp.	Asteraceae	Stem	Rosette	Green	m	g		
Baccharis sp.	Asteraceae	Stem	Rosette	Green	m	g		

Baccharis sp.	Asteraceae	Bud	Fusiform	Light green	m	g		
Baccharis sp.	Asteraceae	Stem	Amorphous	Light green	m	g		
Baccharis sp.	Asteraceae	Stem	Spherical	Light brown	m	g	Cecidomyiidae	
Baccharis trimera	Asteraceae	Stem	Fusiform	Green	m	g		
Berberis laurina	Berberidaceae	Stem	Fusiform	Brown	m	g		
Berberis laurina	Berberidaceae	Leaf	Spherical	Red/l. green	m	g	Psyllidae	
Calea pinnatifida	Asteraceae	Stem	Spherical	Green	m	g	Cecidomyiidae	*
Calea pinnatifida	Asteraceae	Stem	Fusiform	Green	m	g		
Calea serrata	Asteraceae	Stem	Spherical	Light brown	m	g		
Calea serrata	Asteraceae	Stem	Fusiform	Green	p	g	Cecidomyiidae	*
Calea serrata	Asteraceae	Stem	Spherical	Light brown	p	g	Cecidomyiidae	*
Calea serrata	Asteraceae	Stem	Drop-shaped	Green	m	g	Cecidomyiidae	*Asphondylia* sp. 2
Calea serrata	Asteraceae	Stem	Fusiform	Green	m	g	Cecidomyiidae	*Asphondylia* sp. 3
Calliandra brevipes	Mimosaceae	Stem	Fusiform	Light brown	m	g		
Calliandra brevipes	Mimosaceae	Stem	Fusiform	Light brown	m	g		
Calliandra tweediei	Fabaceae	Bud	Spherical	Brown	m	g		
Calyptranthes concinna	Myrtaceae	Leaf	Conical	Green	m	g	Cecidomyiidae	*
Calyptranthes concinna	Myrtaceae	Leaf	Spherical	Green	m	g	Cecidomyiidae	*
Calyptranthes concinna	Myrtaceae	Stem	Fusiform	Light brown	m	g		
Campomanesia xanthocarpa	Myrtaceae	Leaf	Spherical	Light green	m	g	Cecidomyiidae	*
Campomanesia xanthocarpa	Myrtaceae	Stem	Fusiform	Light brown	m	g		
Campomanesia xanthocarpa	Myrtaceae	Stem	Amorphous	Light brown	p	g	Cecidomyiidae	*
Casearia decandra	Salicaceae	Stem	Fusiform	Green	m	g		
Casearia sylvestris	Salicaceae	Leaf	Fusiform	Green	m	g	Cecidomyiidae	*
Casearia sylvestris	Salicaceae	Stem	Fusiform	Light brown	p	g	Cecidomyiidae	*
Casearia sylvestris	Salicaceae	Leaf	Lenticular	Green	m	g	Diptera	
Celtis ehrenbergiana	Cannabaceae	Stem	Fusiform	Light brown	m	g		
Celtis iguanaea	Cannabaceae	Leaf vein	Fusiform	Green	m	g		
Celtis iguanaea	Cannabaceae	Leaf/leaf vein	Fusiform	Green	m	g		

(continued)

Table 14.2 (continued)

Host species	Host family	Plant organ	Shape	Colour	Number of chambers	Pilosity	Inducer taxon	Inducer species
Celtis iguanaea	Cannabaceae	Stem	Spherical	Light brown	m	g	Cecidomyiidae	
Celtis sp.	Cannabaceae	Leaf	Amorphous	Green	m	g	Eriophyidae	
Cestrum strigillatum	Solanaceae	Bud	Fusiform	Green	m	g		
Cissampelos pareira	Menispermaceae	Stem	Fusiform	Light brown	m	g		
Cissus striata	Vitaceae	Leaf	Lenticular	White	m	g	Cecidomyiidae	*
Clematis dioica	Ranunculaceae	Leaf/stem	Fusiform	Light green	m	g		
Cordia americana	Boraginaceae	Leaf	Spherical	Green	m	g		
Cordia monosperma	Boraginaceae	Stem	Spherical	Light brown	m	g		
Cryptocarya aschersoniana	Lauraceae	Leaf	Spherical	Green	m	g	Cecidomyiidae	Lasiopteridi *
Cupania vernalis	Sapindaceae	Leaf	Lenticular	Light brown	m	g	Cecidomyiidae	*
Dalbergia frutescens	Fabaceae	Stem	Spherical	Green	m	g	Cecidomyiidae	*
Dalbergia frutescens	Fabaceae	Leaf	Amorphous	Green	m	g	Cecidomyiidae	*
Dalbergia frutescens	Fabaceae	Stem	Cylindrical	Green	m	g	Cecidomyiidae	*
Dasiphylum spinescens	Asteraceae	Stem	Spherical	Light brown	m	g	Cecidomyiidae	Lasiopteridi
Dioscorea sp.	Dioscoreaceae	Stem	Fusiform	Light brown	m	g	Cecidomyiidae	
Duranta vestita	Verbenaceae	Leaf	Fusiform	Light brown	m	g		
Erythroxylum argentinum	Erythroxylaceae	Stem	Amorphous	Light brown	p	g	Coleoptera	
Erythroxylum argentinum	Erythroxylaceae	Stem	Fusiform	Light brown	m	g	Cecidomyiidae	*
Escallonia bifida	Escalloniaceae	Stem	Rosette	Green	m	g	Cecidomyiidae	*
Eugenia florida	Myrtaceae	Leaf/stem	Discoidal	Red/l. green	m	g	Cecidomyiidae	
Eugenia pyriformis	Myrtaceae	Leaf	Fusiform	Light green	m	g		
Eugenia rotundicosta	Myrtaceae	Stem	Spherical	Light brown	m	g		
Eugenia scheuchiana	Myrtaceae	Leaf	Discoidal	Light brown	m	g		
Eugenia uniflora	Myrtaceae	Leaf	Spherical	White	m	g	Cecidomyiidae	*Eugeniamyia dispar*
Eugenia uniflora	Myrtaceae	Leaf	Fusiform	Red/green	m	g/h	Cecidomyiidae	*Clinodisplosis profusa*

Eugenia uniflora	Myrtaceae	Stem	Fusiform	Light brown	p	g		
Eugenia uniflora	Myrtaceae	Stem	Fusiform	Light brown	m	g	Lepidoptera	
Eugenia uniflora	Myrtaceae	Leaf	Cylindrical	Red	m	g		
Eugenia uruguayensis	Myrtaceae	Leaf	Fusiform	Green	m	g	Hemiptera	
Eugenia uruguayensis	Myrtaceae	Leaf	Spherical	Red/white	m	g	Cecidomyiidae	*
Eupatorium cruplenifolium	Asteraceae	Stem	Fusiform	Green	m	g		
Eupatorium inulifolium	Asteraceae	Stem	Spherical	Green	m	g	Tephritidae	
Eupatorium luplenifolium	Asteraceae	Stem	Rosette	Green	m	g		
Eupatorium luplenifolium	Asteraceae	Stem	Fusiform	Green	m	g		
Eupatorium sp.	Asteraceae	Stem	Fusiform	Light brown	p	g		
Ficus cestrifolia	Moraceae	Leaf	Lenticular	Green	m	g	Cecidomyiidae	*
Ficus eximia	Moraceae	Leaf	Discoidal	Green	m	g		
Ficus luschnatiana	Moraceae	Leaf	Spherical	Green	m	g	Cecidomyiidae	*
Gochnatia polymorpha	Asteraceae	Stem	Fusiform	Light brown	m	g	Cecidomyiidae	
Guapira opposita	Nyctaginaceae	Bud	Rosette	Green	p	g	Cecidomyiidae	*Pisphondylia brasiliensis*
Guapira opposita	Nyctaginaceae	Leaf	Spherical	Green	m	g	Cecidomyiidae	
Guapira opposita	Nyctaginaceae	Leaf	Conical	Green	m	g	Cecidomyiidae	*Bruggmania acaudata*
Guapira opposita	Nyctaginaceae	Leaf	Spherical	Rosy	m	h	Cecidomyiidae	*Bruggmania robusta*
Guapira opposita	Nyctaginaceae	Leaf	Lenticular	Green	m	g	Cecidomyiidae	*Bruggmania elongata*
Guapira opposita	Nyctaginaceae	Stem	Fusiform	Green	m	g	Cecidomyiidae	
Guarea macrophylla	Meliaceae	Leaf vein/stem	Lenticular	Light brown	m	g	Cecidomyiidae	
Guarea macrophylla	Meliaceae	Leaf	Spherical	Green	m	h	Cecidomyiidae	*Guarephila* sp.
Guarea macrophylla	Meliaceae	Stem	Fusiform	Green	m	g		
Guettarda uruguensis	Rubiaceae	Leaf	Cylindrical	Green	m	g		
Heimia myrtifolia	Lythraceae	Stem	Fusiform	Light brown	m	g		

(continued)

Table 14.2 (continued)

Host species	Host family	Plant organ	Shape	Colour	Number of chambers	Pilosity	Inducer taxon	Inducer species
Ilex brevicuspis	Aquifoliaceae	Stem	Spherical	Green	m	g		
Ilex brevicuspis	Aquifoliaceae	Stem	Fusiform	Green	m	g	Cecidomyiidae	*
Ilex microdonta	Aquifoliaceae	Stem	Fusiform	Brown	m	g		
Ilex microdonta	Aquifoliaceae	Stem	Spherical	Green	m	g		
Ilex theezans	Aquifoliaceae	Stem	Spherical	Green	m	g		
Ilex theezans	Aquifoliaceae	Stem	Fusiform	Light brown	m	g		
Inga marginata	Fabaceae	Stem	Amorphous	Light brown	p	g	Cecidomyiidae	*
Inga marginata	Fabaceae	Stem	Cylindrical	Light brown	m	g		
Inga marginata	Fabaceae	Leaf vein	Fusiform	Light green	m	g	Cecidomyiidae	*
Justicia brasiliana	Acanthaceae	Bud	Fusiform	Green	m	g	Cecidomyiidae	*
Justicia brasiliana	Acanthaceae	Stem	Fusiform	Brown	m	g		
Lantana camara	Verbenaceae	Leaf	Spherical	Green	m	g	Cecidomyiidae	*Schismatodiplosis lantanae*
Lantana montevidensis	Verbenaceae	Stem	Cylindrical	Green	m	h	Cecidomyiidae	
Leandra australis	Melastomataceae	Leaf	Spherical	Green	m	h	Cecidomyiidae	*
Leandra sublanata	Melastomataceae	Leaf	Spherical	Red/green	m	h	Cecidomyiidae	*
Lithraea brasiliensis	Anacardiaceae	Stem	Fusiform	Light brown	p	g	Cecidomyiidae	*
Lithraea brasiliensis	Anacardiaceae	Stem	Fusiform	Light brown	m	g		
Lithraea brasiliensis	Anacardiaceae	Leaf vein	Fusiform	Brown	m	g	Diptera	
Lithraea sp.	Anacardiaceae	Leaf	Lenticular	Green	m	g	Eriophyidae	
Lonchocarpus campestris	Fabaceae	Stem	Spherical	Green	m	g	Lepidoptera	
Lonchocarpus campestris	Fabaceae	Stem	Amorphous	Green/l. brown	m	g		
Lonchocarpus costatus	Fabaceae	Leaf	Oyster-shaped	Green	m	g	Psyllidae	
Lonchocarpus nitidus	Fabaceae	Stem	Fusiform	Light Brown	m	g		
Lonchocarpus sp.	Fabaceae	Leaf	Amorphous	Green	m	g		
Luehea divaricata	Malvaceae	Leaf	Hemispherical	Light brown	m	g	Cecidomyiidae	*
Luehea divaricata	Malvaceae	Leaf	Fusiform	Green/white	m	g		

Luehea divaricata	Malvaceae	Leaf	Conical	Green	m	g	Diptera	
Luehea divaricata	Malvaceae	Leaf vein	Fusiform	Green	m	g		
Luehea divaricata	Malvaceae	Stem	Fusiform	Light brown	m	g		
Macfadyena unguis-cati	Bignoniaceae	Stem	Spherical	Light brown	m	g	Cecidomyiidae	*
Machaerium stipitatum	Fabaceae	Leaflet	Spherical	Green	m	h		
Manetia sp.	Rubiaceae	Leaf/stem	Spherical	Green	m	g		
Matayba elaeagnoides	Sapindaceae	Leaf	Lenticular	Light green	m	g		
Matayba eleagnoides	Sapindaceae	Petiole	Fusiform	Brown	m	g		
Maytenus aquifolia	Celastraceae	Leaf	Fusiform	Green	m	g	Cecidomyiidae	*
Mendoncia puberula	Acanthaceae	Stem	Spherical	Light brown	m	h	Cecidomyiidae	*
Miconia cinerascens	Melastomataceae	Leaf	Spherical	Light brown	m	h		
Miconia hiemalis	Melastomataceae	Leaf	Spherical	Light brown	m	h		
Miconia sp.	Melastomataceae	Leaf	Spherical	Red	m	g		
Microgramma squamulosa	Polypodiaceae	Stem	Fusiform	Brown	m	g	Tortricidae	*Tortrimosaica polypodivora*
Mikania burchelli	Asteraceae	Stem	Spherical	Green	m	g	Curculionidae	
Mikania burchelli	Asteraceae	Stem	Fusiform	Green	m	g		
Mikania campanulata	Asteraceae	Leaf	Amorphous	Purple	m	g		
Mikania glomerata	Asteraceae	Leaf/stem	Spherical	Green	m	g	Cecidomyiidae	
Mikania involucrata	Asteraceae	Leaf	Amorphous	Green	m	g		
Mikania involucrata	Asteraceae	Stem	Fusiform	Purple	p	g	Cecidomyiidae	Alycaulini
Mikania involucrata	Asteraceae	Stem	Amorphous	Green/purple	m	g		
Mikania laevigata	Asteraceae	Leaf	Ellipsoidal	Light green	m	g	Cecidomyiidae	*
Mikania laevigata	Asteraceae	Stem	Spherical	Light brown	m	g		
Mikania laevigata	Asteraceae	Leaf	Cylindrical	Green	m	g	Cecidomyiidae	*
Mikania sp.	Asteraceae	Leaf	Spherical	Green	m	g	Cecidomyiidae	
Mikania sp.	Asteraceae	Leaf	Cylindrical	Green	m	g		
Mikania sp.	Asteraceae	Leaf/stem	Lenticular	Green	m	g		
Mikania sp.	Asteraceae	Leaf	Spherical	Light green	m	g	Cecidomyiidae	
Mikania sp.	Asteraceae	Stem	Fusiform	Green	m	g		

(continued)

Table 14.2 (continued)

Host species	Host family	Plant organ	Shape	Colour	Number of chambers	Pilosity	Inducer taxon	Inducer species
Mikania sp.	Asteraceae	Stem	Cylindrical	Green	m	g	Cecidomyiidae	
Mikania sp.	Asteraceae	Leaf	Fusiform	Green/purple	m	g		
Mikania sp.	Asteraceae	Stem	Spherical	Light brown	m	g		
Mikania sp.	Asteraceae	Stem	Cylindrical	Green	m	g		
Mikania sp.	Asteraceae	Leaf	Lenticular	Green	m	g	Cecidomyiidae	
Mikania sp.	Asteraceae	Leaf/stem	Spherical	Green	m	g		
Mikania sp.	Asteraceae	Leaf	Cylindrical	Green	m	g	Cecidomyiidae	
Mikania sp.	Asteraceae	Leaf	Lenticular	Yellow-green	m	g	Cecidomyiidae	
Mikania sp.	Asteraceae	Leaf	Lenticular	Green	m	g	Diptera	
Mimosa incana	Fabaceae	Stem	Fusiform	Light brown	m	g		
Mimosa incana	Fabaceae	Leaf	Spherical	Green	m	h		
Mimosa scabrella	Fabaceae	Stem	Fusiform	Light brown	m	g	Cecidomyiidae	*
Mollinedia schottiana	Monimiaceae	Stem	Fusiform	Dark brown	m	g		
Mollinedia schottiana	Monimiaceae	Stem	Fusiform	Light brown	m	g		
Mollinedia schottiana	Monimiaceae	Stem	Fusiform	Light brown	m	g	Cecidomyiidae	*
Mollinedia sp.	Monimiaceae	Stem	Fusiform	Light brown	m	g		
Myrceugenia mesomischa	Myrtaceae	Stem	Amorphous	Light brown	m	g		
Myrceugenia miersiana	Myrtaceae	Bud	Horn-shaped	Green	m	g		
Myrceugenia miersiana	Myrtaceae	Stem	Fusiform	Green	m	g		
Myrcia guianensis	Myrtaceae	Stem	Fusiform	Light brown	m	g		
Myrcia hartwegiana	Myrtaceae	Stem	Fusiform	Light brown	m	g		
Myrcia palustris	Myrtaceae	Stem	Fusiform	Green/l. brown	m	g		
Myrcia palustris	Myrtaceae	Stem	Spherical	Green	m	g	Lepidoptera	
Myrcia palustris	Myrtaceae	Stem	Fusiform	Green/brown	m	g	Cecidomyiidae	*
Myrcia pubipetala	Myrtaceae	Stem	Fusiform	Light brown	m	g		
Myrcia pubipetala	Myrtaceae	Leaf	Spherical	Green	m	g		

Myrcia retorta	Myrtaceae	Stem	Spherical	Green	m	g		
Myrciaria cuspidata	Myrtaceae	Stem	Fusiform	Ligth brown	p	g		
Myrciaria cuspidata	Myrtaceae	Leaf	Fusiform	Red	m	g		
Myrciaria cuspidata	Myrtaceae	Bud	Spherical	Green	m	h		
Myrciaria cuspidata	Myrtaceae	Leaf	Fusiform	Green	m	g		
Myrciaria delicatula	Myrtaceae	Stem	Spherical	Light brown	m	g		
Myrciaria delicatula	Myrtaceae	Leaf	Spherical	Light green	m	g	Cecidomyiidae	*
Myrsine coriacea	Myrsinaceae	Stem	Fusiform	Green/l. brown	m	g		
Myrsine coriacea	Myrsinaceae	Stem	Spherical	Green	m	g	Curculionidae	
Myrsine lorentziana	Myrsinaceae	Stem	Fusiform	Green	m	g	Coleoptera	
Myrsine lorentziana	Myrsinaceae	Leaf	Lenticular	Red	m	g	Cecidomyiidae	
Myrsine parvifolia	Myrsinaceae	Stem	Fusiform	Light brown	m	g	Coleoptera	
Myrsine parvifolia	Myrsinaceae	Stem	Fusiform	Light brown	m	g		
Myrsine umbellata	Myrsinaceae	Bud	Fusiform	Green	m	g	Coleoptera	
Myrsine umbellata	Myrsinaceae	Stem	Drop-shaped	Green	m	g		
Nectandra megapotamica	Lauraceae	Stem	Fusiform	Green	p	g	Cecidomyiidae	
Nectandra sp.	Lauraceae	Leaf	Lenticular	Red	m	g		
Nectandra sp.	Lauraceae	Leaf	Cylindrical	Dark brown	m	g		
Ocotea puberula	Lauraceae	Leaf	Spherical	White	m	h	Cecidomyiidae	*
Ocotea pulchella	Lauraceae	Stem	Amorphous	Green	m	g	Cecidomyiidae	*
Ocotea pulchella	Lauraceae	Stem	Fusiform	Green	p	g		
Ocotea pulchella	Lauraceae	Leaf	Spherical	Rosy	m	h		
Ocotea sp.	Lauraceae	Leaf	Fusiform	Green/l. brown	m	h		
Pavonia communis	Malvaceae	Stem	Fusiform	Green/white	p	g	Cecidomyiidae	*
Pavonia ramosissima	Malvaceae	Stem	Fusiform	Green	m	g	Cecidomyiidae	*
Peperomia sp.	Piperaceae	Leaf	Lenticular	Green	m	g		
Peperomia sp.	Piperaceae	Stem	Fusiform	Green	m	g	Cecidomyiidae	*
Piper aduncum	Piperaceae	Stem	Spherical	Green	m	g	Cecidomyiidae	*
Piper aduncum	Piperaceae	Leaf	Spherical	Green	m	h		

(continued)

Table 14.2 (continued)

Host species	Host family	Plant organ	Shape	Colour	Number of chambers	Pilosity	Inducer taxon	Inducer species
Piper aduncum	Piperaceae	Leaf	Spherical	Green	m	g	Cecidomyiidae	*
Piper aduncum	Piperaceae	Stem	Fusiform	Green	m	g		
Piper dilatatum	Piperaceae	Leaf/stem	Discoidal	Green	m	g	Cecidomyiidae	*
Piper mikanianum	Piperaceae	Bud	Fusiform	Green/l. brown	p	g	Cecidomyiidae	*
Piptocarpha tomentosa	Asteraceae	Leaf	Spherical	Green	m	g		
Podocarpus lambertii	Podocarpaceae	Stem	Fusiform	Brown	m	g	Coleoptera	
Polygonum sp.	Polygonaceae	Leaf	Fusiform	Light green	p	g	Cecidomyiidae	
Prosopis nigra	Mimosaceae	Stem	Fusiform	Green/brown	m	g		
Prosopis nigra	Mimosaceae	Stem	Spherical	Green/l. brown	p	g	Cynipidae	
Prosopis nigra	Mimosaceae	Bud	Fusiform	Brown	m	g	Cecidomyiidae	*
Prosopis nigra	Mimosaceae	Stem	Fusiform	Green	p	g		
Prunus sellowi	Rosaceae	Stem	Fusiform	Brown	p	g		
Psidium cattleyannum	Myrtaceae	Leaf	Fusiform	Green/white	m	g	Eriococcidae	*Tectococcus ovatus*
Psidium cattleyannum	Myrtaceae	Leaf	Lenticular	Green/l. brown	m	g	Psyllidae	*Neotrioza tavaresi*
Psychotria carthagenensis	Rubiaceae	Leaf vein	Spherical	Green	m	g	Cecidomyiidae	
Pthecoctenium sp.	Bignoniaceae	Stem	Fusiform	Green	m	g		
Pyrostegia verusta	Bignoniaceae	Stem	Fusiform	Green	m	g		
Rhypsalis sp.	Cactaceae	Stem	Spherical	Green	m	g		
Rubus erifloclades	Rosaceae	Stem	Fusiform	Green	p	g		
Rudgea parquioides	Rubiaceae	Leaf	Lenticular	Green	m	g	Cecidomyiidae	*
Ruellia sp.	Acanthaceae	Stem	Fusiform	Green	m	g		
Sapium glandulosum	Euphorbiaceae	Leaf	Hemispherical	Red/green	m	g	Psyllidae	
Sapium haematospermum	Euphorbiaceae	Stem	Spherical	Light brown	p	g	Psyllidae	
Schinus polygamus	Anacardiaceae	Leaf	Hemispherical	Red	m	g	Psyllidae	*Calophya* aff. *duvauae*

Schinus polygamus	Anacardiaceae	Stem	Fusiform	Light brown	m	g		
Schinus polygamus	Anacardiaceae	Stem	Spherical	Brown	m	g	Cecidosidae	*Cecidoses eremita*
Schinus polygamus	Anacardiaceae	Stem	Barrel-shaped	Brown	m	g	Cecidomyiidae	
Schinus polygamus	Anacardiaceae	Stem	Spherical	Brown	m	g	Diptera	
Scutia buxifolia	Rhamnaceae	Stem	Spherical	Light brown	p	g		
Scutia buxifolia	Rhamnaceae	Stem	Fusiform	Green	m	g	Cecidomyiidae	*
Sebastiania brasiliensis	Euphorbiaceae	Bud	Cylindrical	Green	m	g	Cecidomyiidae	*
Sebastiania commersoniana	Euphorbiaceae	Leaf	Spherical	Green	m	g	Cecidomyiidae	*
Sebastiania commersoniana	Euphorbiaceae	Stem	Spherical	Brown	m	g		
Sebastiania commersoniana	Euphorbiaceae	Bud	Fusiform	Light brown	m	g		
Sebastiania commersoniana	Euphorbiaceae	Leaf	Discoidal	Green	m	g	Cecidomyiidae	*
Sebastiania commersoniana	Euphorbiaceae	Stem	Fusiform	Light brown	p	g	Coleoptera	
Sebastiania commersoniana	Euphorbiaceae	Leaf vein	Fusiform	Light green	m	g		
Sebastiania commersoniana	Euphorbiaceae	Stem	Spherical	Brown	p	g		
Seguieria aculeata	Phytolaccaceae	Leaf/stem	Fusiform	Green	m	g		
Seguieria aculeata	Phytolaccaceae	Stem	Fusiform	Green	m	g		
Serjania meridionalis	Sapindaceae	Leaf	Spherical	Light brown	p	g		
Serjania meridionalis	Sapindaceae	Leaf vein	Fusiform	Green	m	g	Diptera	
Serjania meridionalis	Sapindaceae	Stem	Fusiform	Brown	m	g	Cecidomyiidae	
Sida rhombifolia	Malvaceae	Stem	Fusiform	Grey	m	g	Cecidomyiidae	
Smilax campestris	Smilacaceae	Stem	Spherical	Green	m	g		
Smilax campestris	Smilacaceae	Leaf	Discoidal	Green	m	g	Cecidomyiidae	*Smilasioptera* sp.
Smilax cognata	Smilacaceae	Stem	Spherical	Green	m	g		
Smilax cognata	Smilacaceae	Leaf	Discoidal	Green	m	g	Cecidomyiidae	
Smilax quinquenervia	Smilacaceae	Leaf	Lenticular	Light green	m	g		
Solanum pseudo-quina	Solanaceae	Leaf/stem	Fusiform	Green	m	g		
Solanum pseudo-quina	Solanaceae	Stem	Fusiform	Light brown	p	g		
Solanum ramulosum	Solanaceae	Stem	Spherical	Light brown	p	g	Cecidomyiidae	
Solanum ramulosum	Solanaceae	Leaf	Fusiform	Green	m	g		
Solanum ramulosum	Solanaceae	Stem	Spherical	Green	m	g		

(continued)

Table 14.2 (continued)

Host species	Host family	Plant organ	Shape	Colour	Number of chambers	Pilosity	Inducer taxon	Inducer species
Solanum ramulosum	Solanaceae	Leaf	Fusiform	Green	m	g		
Solanum ramulosum	Solanaceae	Stem	Fusiform	Light brown	m	g		
Solanum ramulosum	Solanaceae	Leaf	Amorphous	Light green	m	g	Eriophyidae	
Styrax leprosus	Styracaceae	Stem	Fusiform	Light brown	p	g	Cecidomyiidae	
Styrax leprosus	Styracaceae	Leaf	Hemispherical	Green	m	g	Eriophyidae	
Symphyopappus reticulatus	Asteraceae	Stem	Spherical	Light green	m	g	Cecidomyiidae	*
Symplocos uniflora	Symplocaceae	Leaf	Lenticular	Light green	m	g	Cecidomyiidae	*
Symplocos uniflora	Symplocaceae	Stem	Spherical	Green	p	g	Cecidomyiidae	*
Tabebuia sp.	Bignoniaceae	Leaf vein	Fusiform	Red	m	g		
Tibouchina sp.	Melastomataceae	Leaf/stem	Spherical	Green	m	h	Cecidomyiidae	
Tibouchina sp.	Melastomataceae	Bud	Rosette	Red/green	m	g		
Trichilia sp.	Meliaceae	Leaf	Discoidal	Green	m	g		
Trichilia sp.	Meliaceae	Leaf	Spherical	Yellow	m	g		
Trichilia sp.	Meliaceae	Stem/bud	Rosette	Green	m	g		
Triumfetta sp.	Malvaceae	Stem	Fusiform	Green	m	g		
Trixis praestans	Asteraceae	Leaf	Hemispherical	Green	m	g	Eriophyidae	
Urbanolophium sp.	Bignoniaceae	Stem	Spherical	Light brown	m	g		
Vernonia discolor	Asteraceae	Stem	Spherical	Light brown	m	g		
Vernonia discolor	Asteraceae	Stem	Drop-shaped	Light brown	m	g		
Vernonia puberula	Asteraceae	Stem	Spherical	Green	m	g		
Vitex megapotamica	Lamiaceae	Leaf	Amphor-shaped	Green	m	g	Cecidomyiidae	*
Zanthoxylum sp.	Rutaceae	Leaf	Discoidal	Light green	m	g		

ch.: number of chambers in the gall (*m* monothalamous, *p* polythalamous); **pil**.: gall pilosity (*g* glabrous, *h* hairy)
*indicate a Cecidomyiidae galler on a plant species never mentioned as galled by an insect of this family before

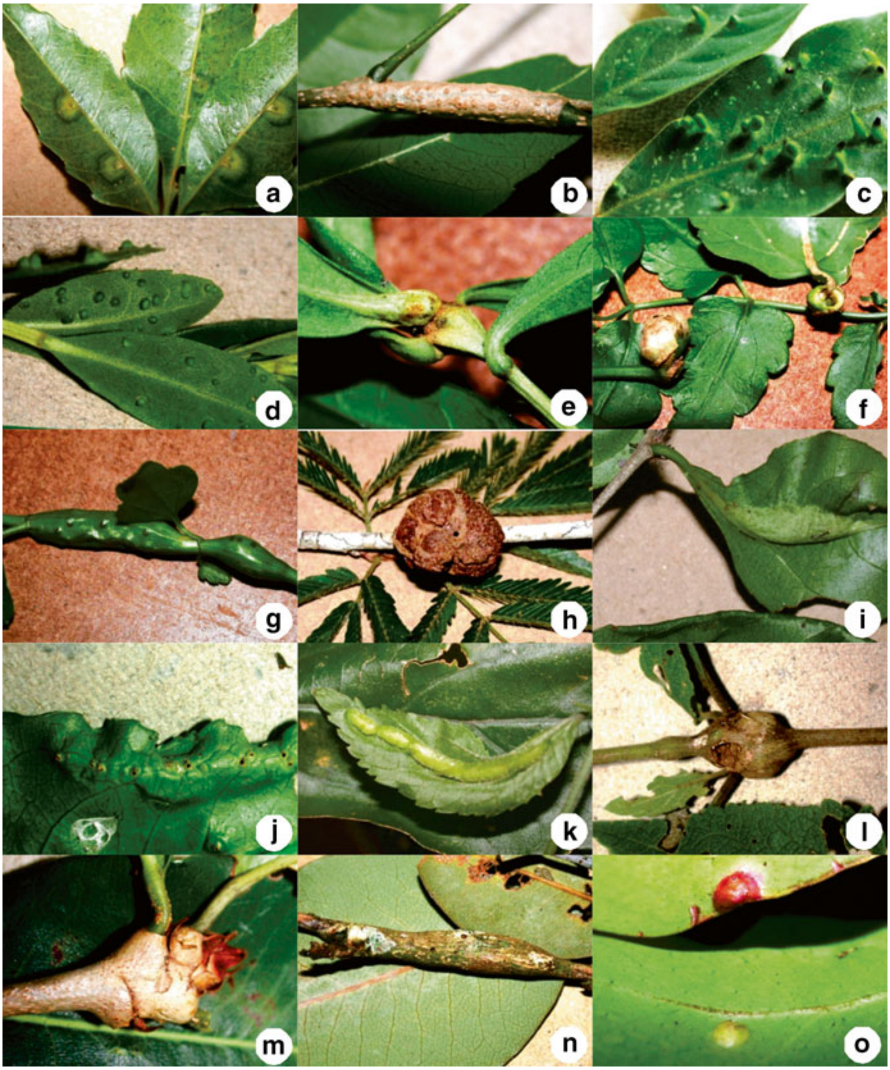

Fig. 14.2 Galls of Itapuã State Park, Viamão city, Rio Grande do Sul. (**a**) *Allophylus edulis* flat leaf gall; (**b**) *Allophylus edulis* cylindrical stem gall; (**c**) *Annona rugulosa* fusiform leaf gall; (**d**) *Baccharis dracunculifolia* blister leaf gall; (**e**) *Baccharis* sp. bud gall; (**f**) *Calea serrata* spherical stem gall; (**g**) *Calea serrata* fusiform stem gall; (**h**) *Calliandra tweedii* spherical bud gall; (**i**) *Casearia sylvestris* leaf vein gall; (**j**) *Casearia sylvestris* blister leaf gall; (**k**) *Celtis ehrenbergiana* leaf vein gall; (**l**) *Cordia monosperma* stem gall; (**m**) *Erythroxylum argentinum* flat bud gall; (**n**) *Erythroxylum argentinum* stem gall; (**o**) *Eugenia florida* conical leaf gall

insect and one mite family (Fig. 14.8a). Only 17 of the gallers are named, unfortunately, but 61 of the Cecidomyiidae are recorded on plant species that have not been mentioned as galled by this group before, according to the latest catalog available (Gagné 2010) – and are thus probably new species. Cecidomyiidae are also by far

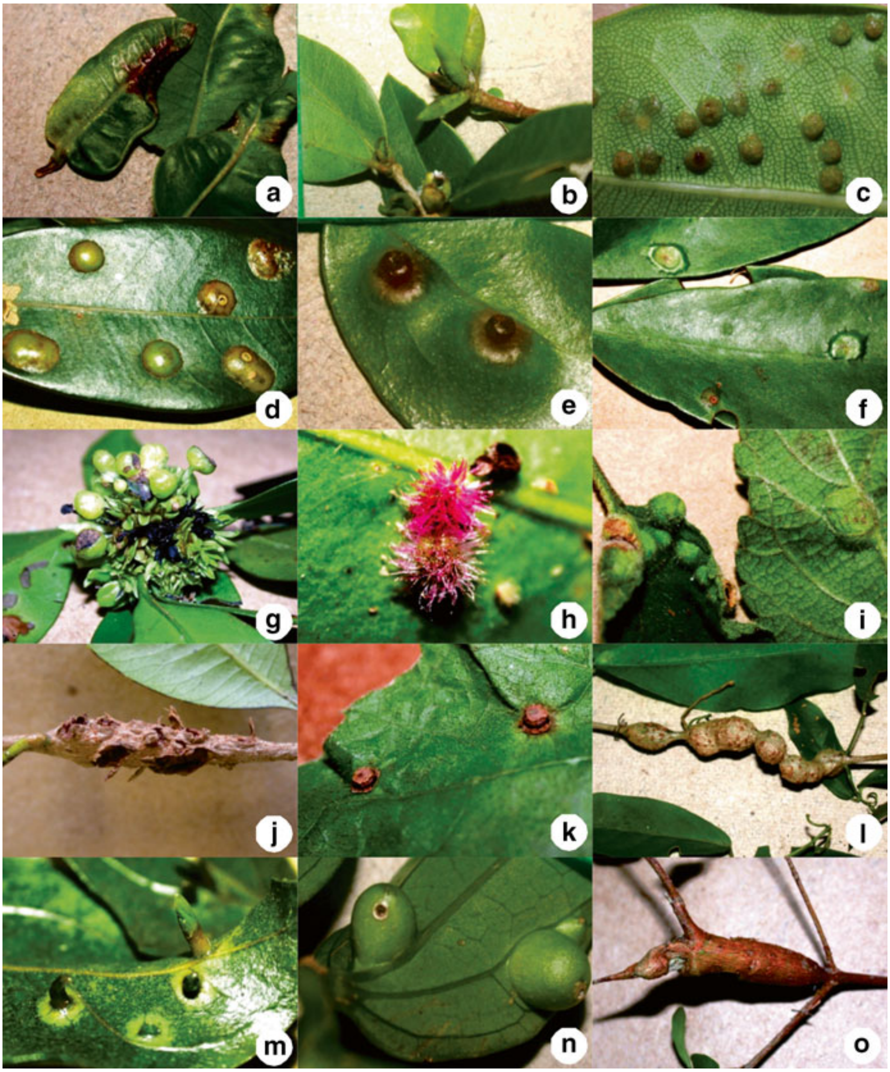

Fig. 14.3 Galls of Itapuã State Park, Viamão city, Rio Grande do Sul. (**a**) *Eugenia uniflora* leaf margin roll gall; (**b**) *Eugenia uruguayensis* whole leaf fold gall; (**c**) *Ficus cestrifolia* spherical leaf gall; (**d**) *Ficus cestrifolia* lenticular leaf gall; (**e**) *Guapira opposita* conical leaf gall (the underside is shown); (**f**) *Guapira opposita* flat leaf gall; (**g**) *Guapira opposita* spherical leaf gall on pseudoleaves of the rosette bud gall; (**h**) *Guapira opposita* spherical hairy leaf gall; (**i**) *Lantana camara* spherical leaf gall; (**j**) *Lithrea brasiliensis* fusiform stem gall; (**k**) *Luehea divaricata* barrel-shaped leaf gall; (**l**) *Macfaydienia unguis-catti* stem gall; (**m**) *Mikania laevigata* fusiform leaf gall; (**n**) *Mikania laevigata* spherical leaf gall; (**o**) *Myrciaria cuspidata* stem gall

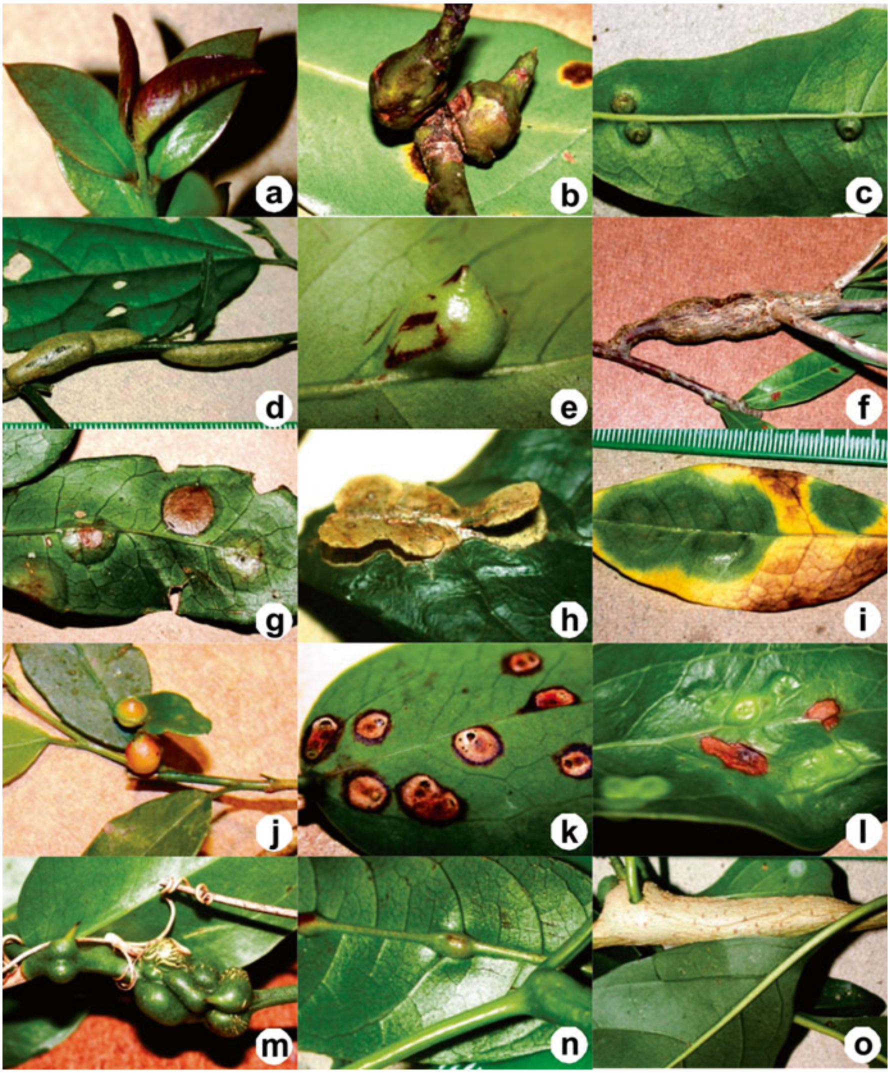

Fig. 14.4 Galls of Itapuã State Park, Viamão city, Rio Grande do Sul. (**a**) *Myrciaria cuspidata* whole leaf fold gall; (**b**) *Myrsine umbellata* stem gall; (**c**) *Patagonula americana* spherical leaf gall; (**d**) *Pavonia communis* fusiform stem gall; (**e**) *Psidium cattleyanum* spherical leaf gall; (**f**) *Schinus polygamus* fusiform stem gall; (**g**) *Sebastiana commersoniana* flat leaf gall; (**h**) *Sebastiana commersoniana* with flat leaf galls open; (**i**) *Sebastiana commersoniana* flat leaf gall with "green island effect"; (**j**) *Sebastiana commersoniana* spherical leaf gall; (**k**) *Smilax campestris* flat leaf gall; (**l**) *Smilax campestris* discoid leaf gall; (**m**) *Smilax campestris* fusiform stem gall; (**n**) *Solanum pseudo-quina* green leaf vein and stem gall; (**o**) *Solanum pseudo-quina* beige stem gall

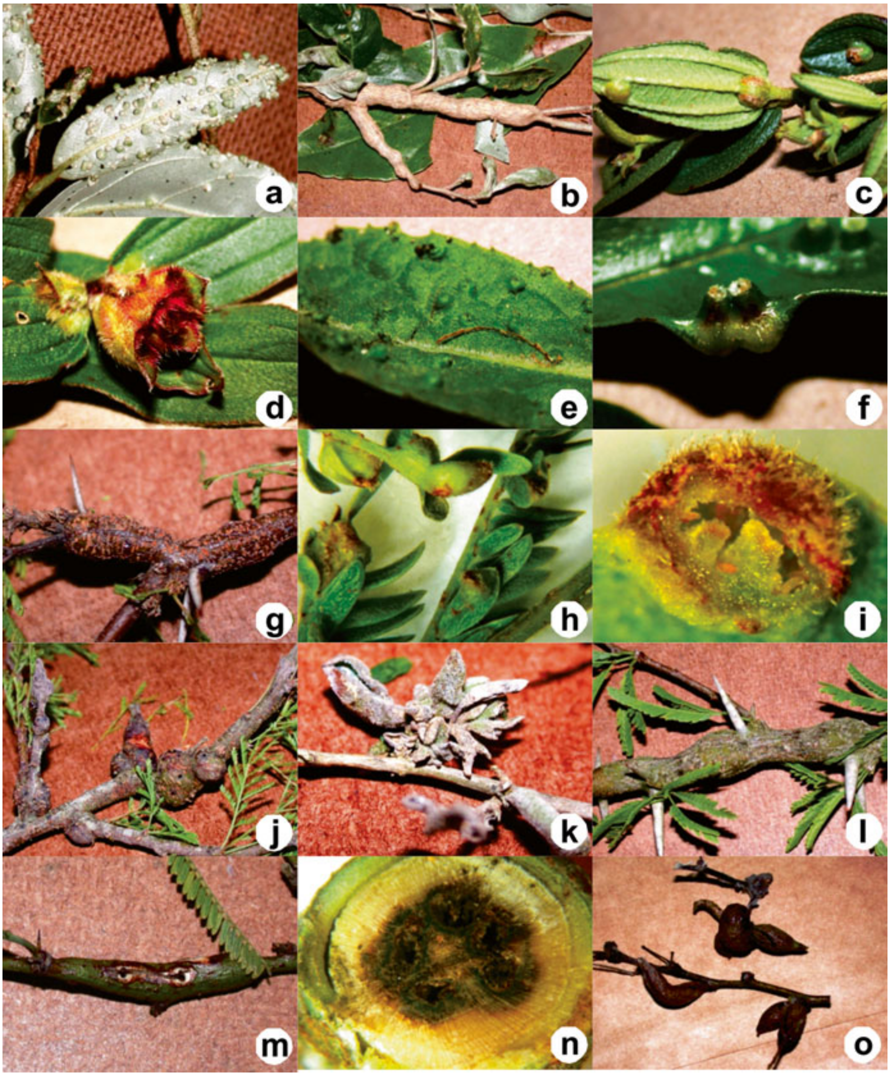

Fig. 14.5 Galls of Itapuã State Park, Viamão city, Rio Grande do Sul. (**a**) *Styrax leprosus* leaf gall; (**b**) *Styrax leprosus* stem gall; (**c**) *Tibouchina* sp. leaf and stem gall; (**d**) *Tibouchina* sp. rosette bud gall; (**e**) *Trixis praestans* leaf gall; (**f**) *Vitex megapotamica* amphora-shaped leaf gall; Galls of Espinilho State Park, Barra do Quaraí city, Rio Grande do Sul. (**g**) *Acacia caven* fusiform stem gall; (**h**) *Acacia caven* open spherical leaf gall; (**i**) *Acacia caven* spherical leaf gall in detail; (**j**) *Acacia caven* spherical stem gall; (**k**) *Aloysia gratissima* leaf roll gall; (**l**) *Prosopis nigra* fusiform stem gall; (**m**) *Prosopis nigra* fusiform stem gall – orifices; (**n**) *Prosopis nigra* fusiform stem gall – internal structure; (**o**) *Prosopis nigra* fusiform bud gall

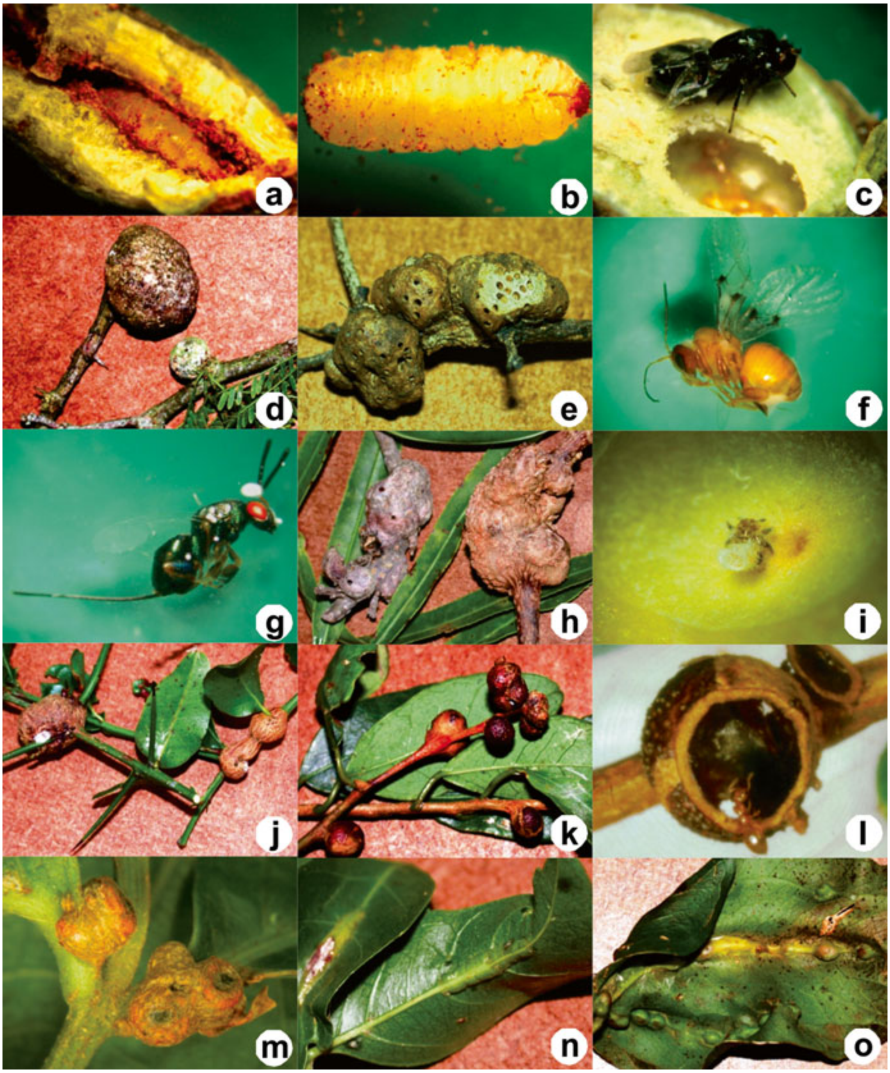

Fig. 14.6 Galls of Espinilho State Park, Barra do Quaraí city, Rio Grande do Sul. (**a**) *Prosopis nigra* fusiform bud gall open; (**b**) *Prosopis nigra* fusiform bud gall – inducer larva (*Cecidomyiidae*); (**c**) *Prosopis nigra* fusiform bud gall – adult parasitoid wasp from inside the gall; (**d** and **e**) *Prosopis nigra* spherical bud gall; (**f**) *Prosopis nigra* spherical bud gall – adult inducer (*Cynipidae*); (**g**) *Prosopis nigra* spherical bud gall – adult parasitoid wasp (*Torymidae*); (**h**) *Sapium haematospermum* spherical stem gall; (**i**) *Sapium haematospermum* spherical stem gall – inducer in the chamber (*Psyllidae*); (**j**) *Scutia buxifolia* spherical stem gall; (**k**) *Sebastiana commersoniana* spherical stem gall; (**l**) *Sebastiana commersoniana* spherical stem gall – with occupying ants (*Formicidae*); (**m**) *Serjania meridionalis* spherical petiole and stem gall; (**n**) *Serjania meridionalis* leaf vein gall; (**o**) *Smilax* sp. spherical leaf vein gall

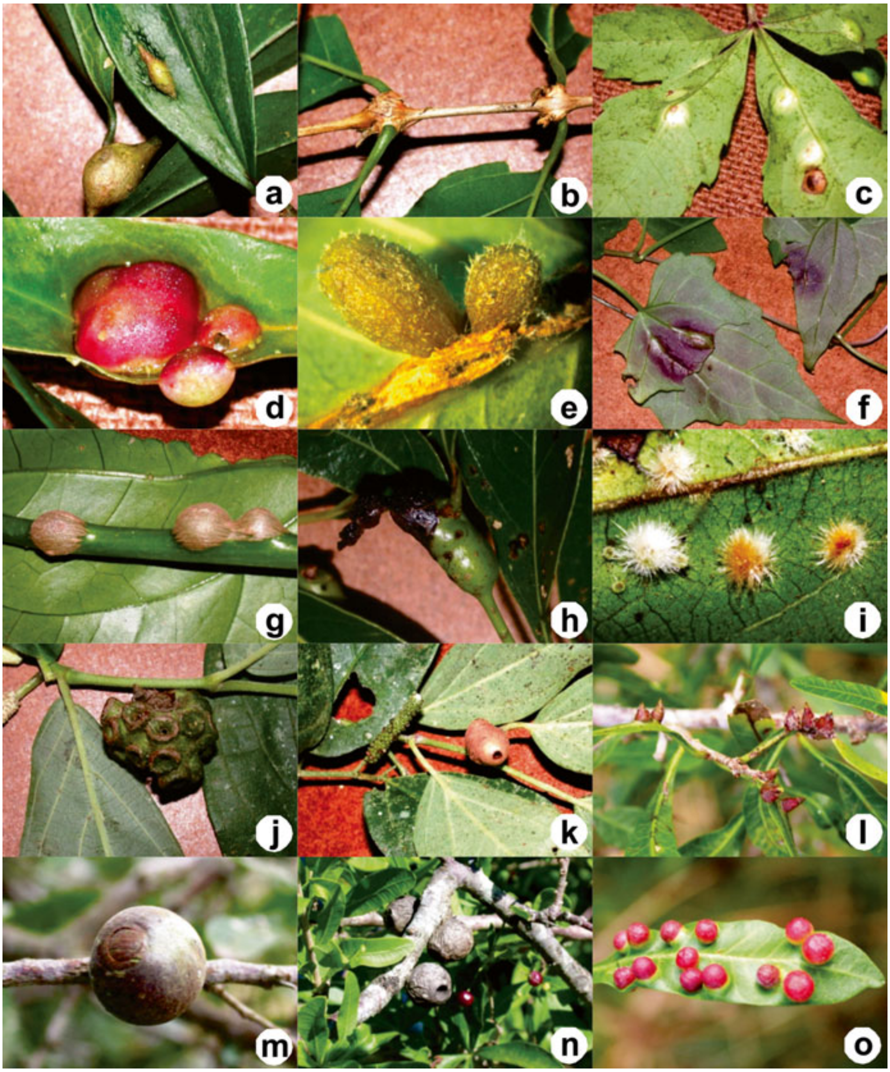

Fig. 14.7 Galls of Southeastern Hills region, Rio Grande do Sul. (**a**) *Berberis laurina* fusiform leaf vein and stem gall; (**b**) *Campomanesia xanthocarpa* stem internode gall; (**c**) *Cissus striata* flat leaf gall; (**d**) *Eugenia uruguayensis* spherical leaf gall; (**e**) *Lithraea brasiliensis* fusiform leaf vein gall; (**f**) *Mikania campanulata* flat leaf vein gall; (**g**) *Mikania glomerata* spherical stem gall; (**h**) *Nectandra megapotamica* fusiform stem gall; (**i**) *Ocotea puberula* hairy leaf gall; (**j**) *Piper aduncum* "multiple volcanoes" bud gall; (**k**) *Piper xylosteoides* fusiform bud gall; (**l**) *Schinus polygamus* conical leaf gall; (**m**) *Schinus polygamus* spherical stem gall – with opening scar visible; (**n**) *Schinus polygamus* spherical stem gall – "whistling" open galls; (**o**) *Schinus polygamus* spherical leaf gall

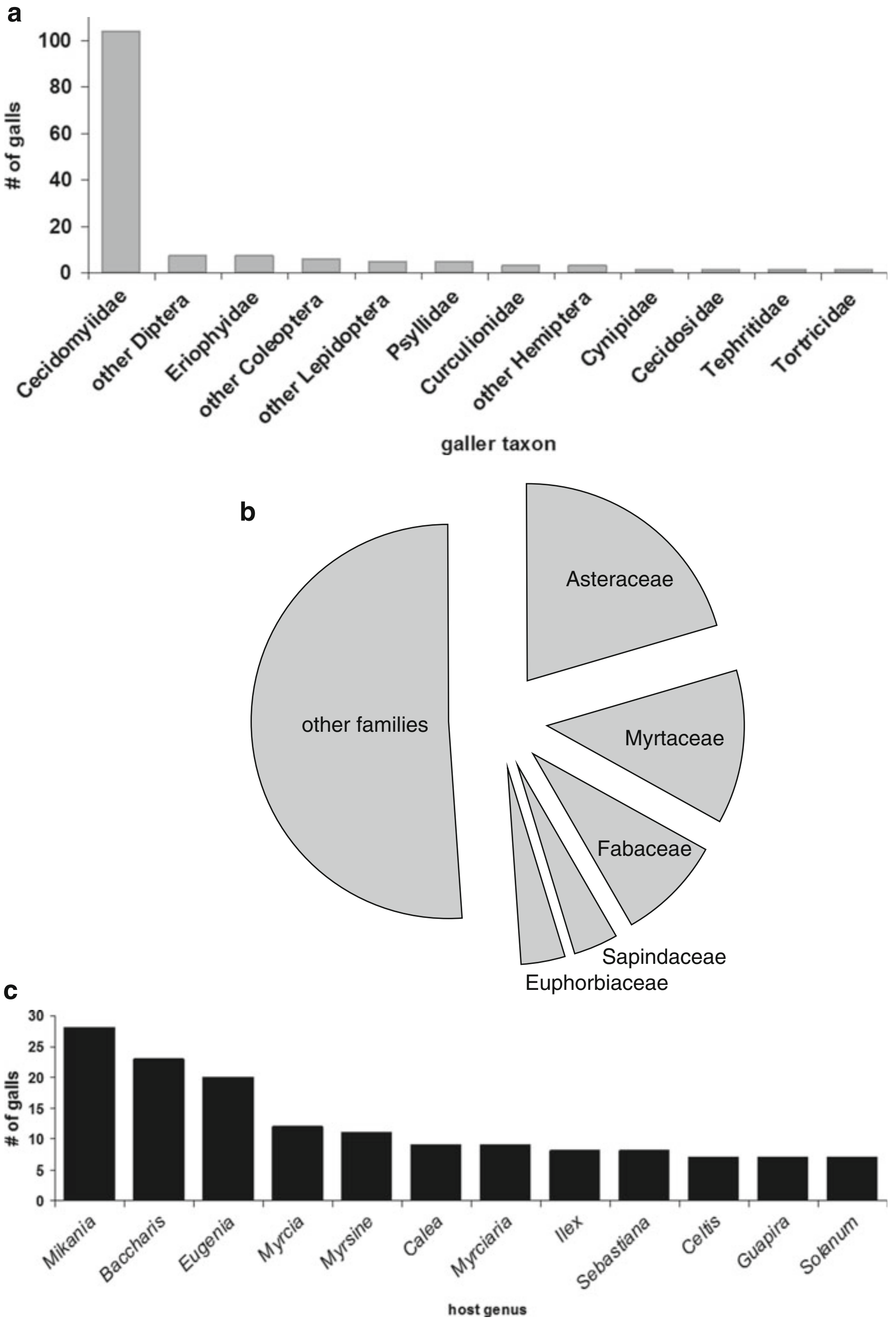

Fig. 14.8 Taxonomic data on gallers and host plants: (**a**) proportion of gallers in different taxons (arthropod orders and families); (**b**) proportion of plants in the five most common host plant families and (**c**) proportion of plants in the 12 most common host plant genera

the dominant galler taxon, with 104 galls representing 72 % of all known gallers. The second most important galler family, Eriophyidae, pales beside the cecidomyiids in species richness, having only seven morphospecies recognized. This very high proportion of galling cecidomyiids appears to be the norm in the Neotropics (Yukawa and Rohfritsch 2005; Hanson and Gómez-Laurito 2005; Maia 2011).

Host plants are also dominated by a few groups, although less strongly so as with gallers (Fig. 14.8b). Almost half (48.8 %) of all hosts belong to only five families: Asteraceae (60 spp.), Myrtaceae (36 spp.), Fabaceae (25 spp.), Sapindaceae (11 spp.) and Euphorbiaceae (10 spp.). These are some of the most common and speciose groups in Rio Grande do Sul State flora, and previous analyses have reveal positive relationships between gall occupancy of hosts and host diversity for this flora (Mendonça 2007). Compiling data from 16 localities in Brazil and Panama, Maia (2011) reported Asteraceae as highly galled by insects from only five places, whilst Fabaceae was cited as rich in galls from 11 places and Myrtaceae from ten places. Although this could be interpreted as a peculiarity of Rio Grande do Sul State, many Asteraceae genera are reported as hosting rich gall faunas elsewhere, as *Baccharis* (Fernandes et al. 1996) and *Mikania* (Maia et al. 2008). It seems that Asteraceae might be richer in galls on a continental perspective, not a regional or local one, with exceptions such as Rio Grande do Sul State.

The term “super-host” has been used in the literature to refer to plant species or even genera that harbour many different kinds of galls (Veldtman and McGeoch 2003) and would thus seem “preferred” by gallers. There are a few examples of this in the literature (*Baccharis*: Fernandes et al. 1996; *Eucalyptus*: Blanche and Westoby 1996; *Eugenia*: Mendonça 2001; *Copaifera*: Costa et al. 2010) and this specific, potentially competing community of gallers can be used as systems to test ecological ideas. These previous suggestions were done to stress the importance or variety of gall morphology in a single host or a few related hosts, but without proper quantitative comparisons – that is, how “super” were these hosts relative to other plant taxa. Mendonça (2007) used a previous version of the Rio Grande do Sul State gall database presented here, and identified “super-host” genera in *Mikania* and *Eugenia* because they hosted more than double the number of galls compared to other genera. With the additions presented here, this “super-host” condition is not so clear anymore (Fig. 14.8c): three genera have more than 20 galls each (*Mikania*, *Baccharis* and *Eugenia*), but two genera have more than ten galls each (*Myrcia* and *Myrsine*) and the decreasing ranking is rather smooth. When there are no steps formed by ranking taxa by number of galls, then the meaning of “super-host” is perhaps lost, although it is clear that some plant taxa show a disproportionate number of gallers associated to them.

Gall structure is sometimes seen either as only a form of identifying a specific galler (for some ecological studies) or a crucial question regarding nutrition of the galler (for some anatomical studies). It can be both, and can be more, since under phylogenetic and community ecology perspectives galler species might differ in gall structure from each other for reasons beyond optimization of plant nutrients (see Stone and Cook 1998). Structural gall traits deserve a better consideration and among the first steps to be taken we suggest a stricter definition of adaptive expectations and direct quantitative treatment of traits in gall communities from a variety of faunas and floras so as to generate basic patterns.

In Rio Grande do Sul State, more than half the galls are found on the stems of their hosts, with nearly 40 % on leaves and a few (5 %) strictly on buds (Fig. 14.9a). This is not what is considered usual, ever since Mani (1964) stated that most galls were on leaves. Recent Neotropical gall inventories also record higher proportions of galls on leaves, as Araújo et al. (2011) with 82.6 %; these authors also cite other references with similar results. Proportions for Rio Grande do Sul State gall database are so different from what the literature reports that an explanation is called for – sampling does not appear to be an issue, since it does not differ much from what is used by research groups found in other Brazilian states. One possible idea would be the deciduousness of the vegetation in the southern most state, which would mean lower probabilities of finding old galls on old leaves in terms of sampling, and perhaps less gallers on leaves because of this lower leaf availability in evolutionary terms. However, the cerrado vegetation is reported as very rich in galls (Lara and Fernandes 1996), foliar galls being very representative (Coelho et al. 2009), and also has most plants losing leaves seasonally. More galls on stems are reported from montane environments in the cerrado of southeastern Brazil (Carneiro et al. 2009) and from one study in South Africa (Veldtman and McGeoch 2003). The difference may then rely on temperature seasonality, with cold winters harsher in Rio Grande do Sul State than in any other part of Brazil. However, this would imply that temperate regions should have even more stem galls than Rio Grande do Sul State, a pattern never mentioned before as far as we are aware. It remains to be seen whether by increasing sampling intensity, a future extended database of Rio Grande do Sul State gallers would still show more stem gallers. If the matter persists, we may then need to look for a deeper explanation.

Most galls are fusiform in shape (41.5 %), with spherical also an important category (29 %) and each of the other shapes covering less than 5 % of all galls (actually lenticular galls are 6.9 % of the total). Gall shapes are rarely analysed in any detail in the literature. It is perhaps assumed that they reflect the growth pattern of the gall and would not be informative, especially because galls are induced on different plant organs. That is actually true for the Rio Grande do Sul State gall database: for example, most stem galls are fusiform or spherical (84 %), given the pattern of local plant tissue growth induced by the insect. Leaf galls have a wider range of shapes (11 shapes compared to 7 for stem galls, even with more galls in the latter category) and a lower proportion of simple shapes, with 54 % of fusiform and spherical. Bud galls have more or less the same proportions for shapes, but with less spherical and more rosettes.

As for colours, the same as above is true, as expected: colouration depends strongly on the organ the gall is induced on. Leaf galls are green on 60 % of the cases (plus 13 % light green), whilst stem galls are green 39.3 % and light brown 43.3 % of the time (a rare colour for leaf galls, making up 6.6 % of them). Leaf galls also assume more colours (14 hues, including red, rosy, white, yellow and black) than stem galls (ten, most greenish or brownish), again even though there are more stem galls. Even more important than gall colour on itself, the distinctiveness of gall

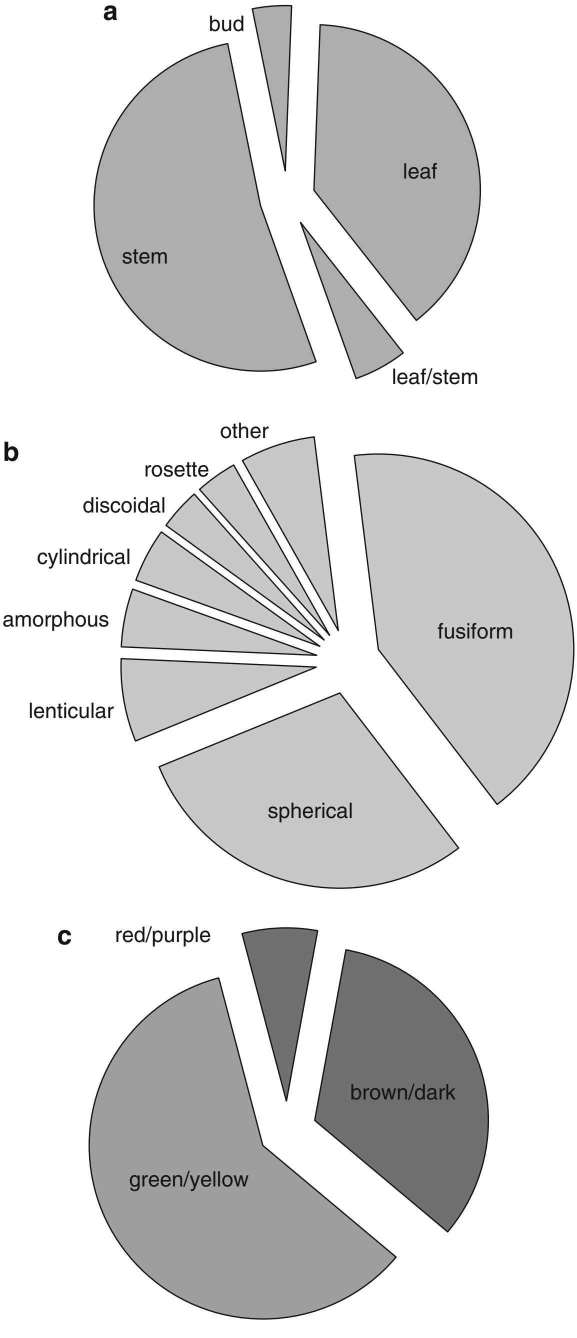

Fig. 14.9 Structural aspects of galls from Rio Grande do Sul: (**a**) proportion of galls on different plant organs (leaf, stem, bud, and both leaf and stem); (**b**) proportion of galls with basic shapes and (**c**) proportion of galls with basic colours. See text and Table 14.2 for more details on categories

colour in relation to normal and surrounding plant tissue might be an important aspect. A debate has arisen in the literature about gall conspicuousness, referring to gall colour in specific (Inbar et al. 2010; White 2010). Some galls develop colours quite different from the originating tissues, and this might occur as a side effect of galler control over plant tissue, or it might serve a function (a sort of signaling, Inbar et al. 2010). Each gall is a different case, potentially, and even galls induced by phylogenetically close species can differ not only in structure but in conspicuousness – a good example are the *Guapira opposita* galls induced by cospecific cecidomyiids (three *Bruggmania* spp., Table 14.2, Fig. 14.2e, f, h).

The other two gall traits reported here are again good examples that interdependence might prove a difficult task if we decide to disentangle the roles of multiple morphological characteristics galls display. Both are greatly dependent on the organ of induction. For pilosity, 13.4 % of leaf galls present trichomes, whilst 98.7 % of stem galls are glabrous. For the number of chambers a gall has, the reverse is true: 13.3 % of stem galls are polythalamous and 98.2 % of leaf galls are monothalamous.

Overall, we can conclude that galls can be more or less conspicuous depending on the attacked organ and its plasticity. Some gall traits are derived from normal plant traits (e.g. trichomes), but can be altered "to the insect's will" (Stone and Schönrogge 2003) We usually record gall traits to allow gall morphotype identification, as we did here. We may have to add a new perspective when recording gall traits, that of recording normal plant traits (a difficult and relative concept anyway) as well, or at least surrounding plant traits. Only then we may develop ways of assessing conspicuity of galls and then test the commonness of this phenomenon and its effect on gallers and other interacting organisms.

Summarising, galls from Rio Grande do Sul State do not break many rules in the world of galls, in terms of most aspects considered here, except for the number of stem galls found. As suggested above, gall traits are amenable to more detailed, quantitative analysis, but there are issues to be solved, as which traits are actually informative, the need for standardization of categories, and the explicit treatment of gall conspicuity.

14.4 Comparing Ecosystems for Galling Species Diversity

Because each one of the surveys used to generate the RS (= Rio Grande do Sul State) gall database followed specific needs and logistic peculiarities, we do not have a clear way of standardizing data among sampled sites, allowing direct quantitative comparisons. For example, sampling in Porto Alegre at Morro Santana was done twice per season, because proximity to the University allowed constant access to the sites. On the other hand, sites in Turvo State Park were visited a single time, given the distance to Porto Alegre (473 km). Thus, analyses such as sample-based rarefaction are not possible given that different sites had different efforts – space and time would be confused. However, sampling was standardised by time (90 min), and thus time can be used to calculate sampling effort and make comparisons.

In this case we included galls not listed in Table 14.2, but for which we had evidence they were distinct morphotypes (that is, identification did not go down to plant genus level, but morphology or inducer were distinct from other galls).

Our aim is to compare distinct vegetation types, under the expectations of the harsh environment hypothesis (HEH, see Price et al. 1998). This idea is interesting because it goes against the most conspicuous pattern in nature: the latitudinal diversity gradient, of more species occurring in the tropics (Ricklefs 2004). The expectations under the HEH are that xeric sites should bear more galls than mesic sites, irrespective of latitude. Most evidence conform to this (see sources in Price et al. 1998), but there are exceptions (e.g. Wright and Samways 1996, 1998; Blanche and Westoby 1995, 1996; Mendonça 2011). The latter exception is from Rio Grande do Sul State, but the comparison was local, between xeric espinilho savanna and mesic nearby riparian forests. Here we add more vegetation types and more sampling effort to see whether over a larger geographic area the pattern predicted by the HEH appears.

We grouped vegetation types by a measure of canopy openness and distance to water bodies (the latter a particularity mentioned by Price et al. (1998) in choosing mesic sites). Sampling did not include gathering of vegetation structure variables, or microclimatic variables (and the macroclimatic variables are nearly the same). Thus, environmental harshness was not assessed in an ideal way, but there was a clear degree of change in canopy openness (CO) depending on the vegetation that was irrespective of site, ecoregion or biome. We recognise seven vegetation types with six levels of CO: (1) moist forest, far from rivers and with closed canopies (CO level 1); (2) riparian forest, close or adjacent to a river or brook and with relatively closed canopy (CO level 1); (3) peat swamp forest, far from rivers but subjected to flooding during certain periods of the year (CO level 2); (4) forest edges, not properly vegetation types, but forest ecotones with open vegetation, far from rivers (CO level 3); (5) restinga scrubland, on well drained sandy soils (CO level 4); (6) espinilho savanna, with sparse trees of a few species (CO level 5); and (7) grassland (CO level 6). A multiple regression analysis was implemented in PASt software (Hammer et al. 2001) with hours of sampling and canopy openness as explanatory variables, and total gall richness as the response variable.

The regression was highly significant ($SS = 38{,}099.01$; $F_{2,6} = 31.53$; $p < 0.01$) and explained a large amount of the variation in the data ($r^2 = 0.94$). Gall richness for a given vegetation type was highly dependent on the sampling intensity in hours spent on that vegetation type ($p = 0.01$, Fig. 14.10a) but not on the canopy openness index used ($p = 0.22$, Fig. 14.10b).

The HEH predicts that xeric environment sites have more galls locally than mesic sites. This is not what is found for the samples developed so far for galls in Rio Grande do Sul State. The reasons for this can be varied. We classify vegetation types without actually measuring the degree of hygrothermal stress (HS) they face. However, neither Price et al. (1998) nor its predecessors established any clear cut protocol to define how HS should be measured, or had shown whether they measured it quantitatively. Climate, soil type and vegetation structure could all combine to create a complex spatial disposition of xeric and mesic environments. Environments

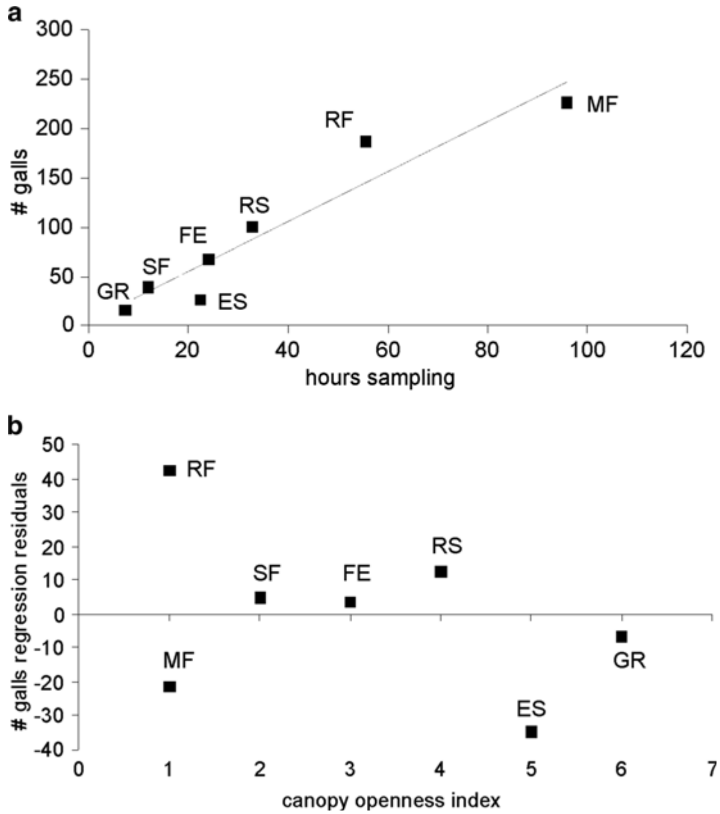

Fig. 14.10 Gall richness by vegetation type in Rio Grande do Sul: (**a**) number of galls per vegetation type against sampling time (hours) dedicated to each one; (**b**) regression residuals of sampling time for the number of galls against canopy openness index. Abbreviations: *MF* moist forest, *RF* riparian forest, *SF* peat swamp forest, *FE* forest edge, *RS* restinga scrubland, *ES* espinilho savanna, *GR* grassland

with intermediate hygrothermal stress (not too xeric or too mesic) may have perhaps been previously avoided to leave categories better defined, but at a cost. Perhaps for the Rio Grande do Sul State gall database, as all environments were evaluated, the pattern disappears – although again the measure of hygrothermal stress employed here was rather subjective. The scale at which the HEH predicts differences can also be discussed. It has been claimed that the results supporting the HEH can be valid both on a local scale and on larger, biogeographical ones (Mendonça 2001). However, this is disputed because almost certainly there are many unknown/unreported tropical species of gallers (Espírito-Santo and Fernandes 2007), far outnumbering the recorded local richness in Price et al. (1998) for tropical forests. Although we sampled from two distinct biomes in terms of biogeographical history (one tropical, the Atlantic forest, another temperate, the Pampas), and distinct in average higrothermal stress, it is not clear how this could imply different gall richness. For example, restinga scrubland is one of the most hygrothermally stressful environments in Rio Grande do Sul State: it has sandy soils that do not hold water, it is close to the sea and is subjected to salt and wind, and it has an open canopy with a predominance of shrubs. However, it is biogeographically related to the Atlantic forest biome, usually characterized as a continuous of humid forests – should we expect many galls to be found there? That is, can historical hypotheses have an impact on the HEH, or be combined with it? On Fig. 14.10a it is slightly above the regression line, with the number of galls found there more or less what we expected to find in any environment given the sampling effort employed. Clearly, a discussion over the geographical scale on which to sample and test the HEH is necessary and might bring about new ideas on this still interesting hypothesis.

14.5 Conclusions and Perspectives

There is much to know about galls, gallers and their hosts in the south of Brazil. We have barely scratched the surface of an untapped rich fauna affecting a rich flora on a rich tapestry of environments. Much more effort would be needed to develop our understanding of galls “down-south” in Brazil to answer at least some of the questions posed above. Certainly, more research, on a wider perspective, preferably a concerted research among different groups, is desirable. There are many potentials to be explored that are common to all research on galls, and the south of Brazil has the same opportunities to offer: (1) on the relationship between plant biochemistry, for example growth hormones and gall development, with implications for agriculture (galls are experiments by the insects that may help us understand plant development); (2) on the degree and nature of the modification induced by the insect on the plant tissues (the extended phenotype, Dawkins 1982), which have implications for the concept of gall conspicuousness mentioned above and thus for ecological interactions (natural enemies); (3) on the impact the gallers have on the individual host plant (an its implications for plant biological control); (4) on the phylogenetic pattern of attack by gallers on hosts, from both perspectives (arthropod and plant phylogenies), and their relationship to the biogeographical setting in which this pattern is analysed; and (5) on the environmental factors affecting gall diversity (species richness and composition), especially plant diversity (a sort of null model), but also abiotic conditions and ultimately evolutionary history (thus linking it to item 4, above).

It is hard to come by with more specific suggestions, since there is so much to do. Geographically, only the southern half of Rio Grande do Sul State has been given a cursory cover in terms of inventorying galls; most of south Brazil is an open question, and many environments are left with no coverage at all. It would be helpful to sample this region more evenly so as to be able to develop a mesoecological or even macroecological perspective on some of the patterns shown above. Macroecology deals with large geographical areas, so that could only happen if we could combine data from the southern, southeastern and other parts of Brazil, of which only the southeast is relatively well explored.

Also, at least some of the gall systems found in the south of Brazil deserve a deeper treatment – to help unveil and quantify species relationships, and their relationships with gall and plant structure. Some systems found in the south of Brazil, as the *G. opposita* gallers mentioned earlier, involve congeneric species inducing distinct galls on the same plant, some apparently with the help of fungi (ambrosia galls) and some without it – a situation allowing comparisons at various levels of understanding. The anatomical aspects of some of these galls have already been described (Araújo 2009), and more data on the ecology of plants, gallers, natural enemies and the fungi involved in the ambrosia galls would certainly add new elements to help clarify the particularities of the so-called "super-hosts" and even to begin to understand galler evolution within a single host plant species.

Another issue is what the south of Brazil could offer that would be intrinsically distinct from what we have in other regions. This answer can be given on a biogeographical basis: the south of Brazil is truly subtropical, being transitionary between tropical and temperate regions in terms of present climate and history of the biota. Thus, this area is expected to regionally harbour less galls than the tropical regions of Brazil, and to respond to climate in a different way (seasonality is due to temperature, and not to rainfall as in areas classically studied for galls as the Cerrado biome). These macro-level questions are interesting and open, but depend, again, on a much more solid base on which to build on. We can only hope that this could be achieved in the near future, to help as well in the conservation of the galling species, an issue only rarely mentioned, although of utmost importance.

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Chapter 15
Galling Insects in the Brazilian Cerrado: Ecological Patterns and Perspectives

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Abstract In recent decades, there has been growing research interest in insect galls. Most of the processes and mechanisms related to ecological richness of galling insect-plant interactions have been investigated in the Cerrado. Therefore, several ecological hypotheses and patterns have been described in Cerrado. In this chapter we discuss: (a) a historical overview of studies with focus on insect galls from the Cerrado highlighting key studies and ecological issues; (b) galling insect richness and host plants, emphasizing especially the most representative taxa; (c) studies that have investigated the differential gall distribution between mesic and xeric environments, one of the most established and tested ecological hypotheses in the Cerrado; and finally (d) the main challenges and perspectives for future studies investigating patterns of galling insect richness in the Cerrado. We showed some mechanisms that are responsible by the high galling diversity in the Cerrado and discuss the main ecological hypothesis that explain these mechanisms.

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15.1 The Brazilian Cerrado and Interest in Galling Studies

Studies of biological and ecological aspects of insect-plant interactions provide the grounds for research in areas of great social concern, such as agriculture, and the conservation and management of natural environments (Tylianakis et al. 2010). Historically, interest in galling insects has promoted major contributions to the ecological and evolutionary understanding of insect-plant interactions, and also in applied areas such as ethnobotany (Berlin and Prance 1978) and biological control (Fernandes 1987). Studies in galling insect ecology have clarified community structure throughout three trophic levels: host plants, herbivores as well as their natural enemies (Price et al. 1980; Fernandes et al. 1999; Tabuchi et al. 2011). Research advances have also provided basic information for applied ecology (Araújo and Espírito-Santo 2012), agriculture (Fernandes 1987) and the conservation of natural areas (Moreira et al. 2007; Fernandes et al. 2010; Araújo 2011a).

Although galls are known from ancient times, the first scientific studies concerning their anatomy and etiology date back to the late seventeenth century (Fernandes and Martins 1985). In the twentieth century, studies on ecological and evolutionary aspects of the interaction among gallers, host plants and parasitoids were prominent (Cook 1923; Felt 1940; Uhler 1951; Mani 1964). In Brazil, the first contributions to galling insect research were conducted by Tavares (1906). Since then, a series of articles has been published which focus on the occurrence and gall characterization in several plant families from different Brazilian ecosystems (e.g., Tavares 1917a, b, 1920).

The Cerrado is the second largest phytogeographical domain of Brazil, occupying an area of ca. 2 million km^2, which corresponds to 23 % of the national territory, covering states in all regions of the country (Oliveira and Ratter 2002). This biome consists of many different types of vegetation, making it one of the richest ecosystems of Brazil and in the world (Klink and Machado 2005). According to Ribeiro and Walter (2008), the Cerrado contains three major vegetation groups: grassland (e.g., clean field and rock field), savannas (e.g., buritizal and neotropical savanna) and forest (e.g., cerradão and forest). This ecosystem comprises between 20 and 50 % of Brazilian biodiversity, depending on the group of organisms evaluated, and is considered a priority area (hotspot) for conservation on the planet (Myers et al. 2000; Klink and Machado 2005). Fragmentation and loss of habitat have caused the extinction of many species and threatened the diversity of the biome (Klink and Machado 2005). From the floristic point of view, the Cerrado features more than 12,000 species of vascular plants (Mendonça et al. 2008), many of which have suffered major threat (Ratter et al. 1997).

Throughout the 1980s, a series of studies focusing on galling insects in the Brazilian Savanna (Cerrado) was conducted by Fernandes and colleagues (Fernandes and Martins 1985; Fernandes et al. 1987, 1988). Historically, these studies used two major approaches. The first one was exploratory, to increase knowledge about gall richness and their natural history. Examples of this approach include surveys of gall diversity, their host plants, anatomical and morphological characterizations, as well as descriptions of new species (e.g., Fernandes et al. 1988, 1997; Gonçalves-Alvim and Fernandes 2001a; Scareli-Santos and Varanda 2003; Maia and Fernandes 2004; Urso-Guimarães and Scareli-Santos 2006; Scareli-Santos et al. 2008; Santos et al. 2010). The second approach was related to the development of ecological-evolutionary hypotheses, with a focus on diversity patterns of galling insects (Fernandes and Price 1991, 1992). The most important contributions, considering the several hypotheses initially developed and designed for these Neotropical savannas, have been applied in different regions and ecosystems worldwide (e.g., Price et al. 1987; Fleck and Fonseca 2007).

Most advances in knowledge of insect galls in the Cerrado date back to the 1980s, with the development of floristic, physiological and chemical studies of its plants (e.g., Langenheim et al. 1986; Kaplan et al. 1994). These studies identified a cause-effect relationship between low soil nutrient concentration, large insolation levels and high photosynthesis rates in Cerrado species, contributing to the high carbon and nitrogen rates in plant tissues (Franco et al. 2008). Furthermore, sclerophyllous plants have high fiber content, lignified, and waxy tissues as well as many trichomes (Fernandes 1994; Turner 1994). Galling insects, unlike the other herbivore guilds, respond positively to these structural and physiological modifications and have attracted the attention of researchers especially from the 1990s (Fernandes and Price 1992; Fernandes et al. 1995, 2005; Fernandes and Gonçalves-Alvim 2006). According to Ribeiro and Fernandes (2000), extreme conditions can restrict the diversity of free-feeding herbivores in the Cerrado, a fact not observed for galling insects. These extreme conditions include microclimatic severity (Ribeiro and Fernandes 2000), soil nutrient deficiency (Haridasan 2008) and elevated investments in C-based defenses (Franco et al. 2008). This has direct effects on differential mortality in xeric vs. mesic sites (Fernandes et al. 2005), rates of speciation and resource synchrony in the Cerrado (Mendonça 2001), as will be discussed throughout the chapter.

At the end of the twentieth Century, a significant advance in galling insect studies was reached, represented by comparative studies of vegetation from temperate and tropical regions (see Fernandes and Price 1988; Price et al. 1998). Tropical ecosystems are highly complex because of their great diversity and heterogeneity (Fernandes and Price 1991). The Cerrado is represented by a complex of different vegetation types and represents an excellent ecosystem in which to evaluate the applicability of ecological hypotheses and therefore elucidate many aspects of insect-plant interactions (Fernandes and Gonçalves-Alvim 2006; Scareli-Santos and Varanda 2009).

15.2 Galling Insect Richness in the Cerrado

Galling insects are classified as a guild of phytophagous insects known for their unique ability to modify plant tissues before their consumption (Shorthouse et al. 2005). Changes in plant tissues are attributed to abnormal growth and development of plant cells induced by specific stimuli from galling insects (Hartley 1998;

Table 15.1 Number of galling species, host plant species, host plant families and mean number of galls per host plant species in different localities of the Cerrado

Locality	Number of gall morphospecies	Number of galled plant species	Number of galled plant families	Mean number of gall morphospecies per host plant species	Reference
Campus Pampulha	37	22	11	1.7	Fernandes et al. (1988)
Vale do Jequitinhonha	236	134	27	1.8	Fernandes et al. (1997)
Estação Ecológica de Pirapitinga	92	62	28	1.5	Gonçalves-Alvim and Fernandes (2001a)
Delfinópolis	22	19	19	1.2	Urso-Guimarães et al. (2003)
Serra de São José	137	73	30	1.9	Maia and Fernandes (2004)
Santa Rita do Passa Quatro	36	24	15	1.5	Urso-Guimarães and Scareli-Santos (2006)
Fazenda Bulcão	29	24	12	1.2	Fernandes and Negreiros (2006)
Serra do Espinhaço	241	142	29	1.7	Carneiro et al. (2009)
Serra do Cipó	90	50	19	1.8	Coelho et al. (2009)
Goiânia	34	20	12	1.7	Santos et al. (2010)
Serra dos Pireneus	62	51	28	1.2	Araújo et al. (2011)
Reserva Biológica Boqueirão	57	43	18	1.3	Malves and Friero-Costa (2012)
Caldas Novas	56	34	21	1.6	Santos et al. (2012)
Mean	86.8	53.6	20.6	1.5	–

Moura et al. 2008). This ability has been developed independently by many different insect taxa (Shorthouse et al. 2005; Price 2005). The most diverse taxa belong to the orders Hymenoptera (Tenthredinidae and Cynipidae) and Diptera (Cecidomyiidae) (Price 2005). Among these, Cecidomyiidae are prominent, representing approximately 6,131 known species (Gagné 2010) and accounting for the highest galling species diversity from Neotropical regions (Gagné 1994). In the Cerrado, the local (and regional) galling species richness varies greatly among locations (Table 15.1).

Table 15.2 Proportion of Diptera, Lepidoptera, Hemiptera and others insect galls from different locations in Cerrado

Locality	% of dipteran galls	% of lepidopteran galls	% of hemipteran galls	% of indeterminated/others galls
Campus Pampulha	59.0	0.0	13.0	28.0
Vale do Jequitinhonha	82.6	2.5	1.8	13.1
Estação Ecológica de Pirapitinga	64.1	5.4	2.1	28.4
Delfinópolis	54.5	0.0	13.6	31.9
Serra de São José	73.7	7.3	5.8	13.2
Santa Rita do Passa Quatro	88.0	0.0	4.0	8.0
Fazenda Bulcão	93.0	0.0	3.5	3.5
Serra do Espinhaço	85.0	4.0	3.0	8.0
Serra do Cipó	77.0	4.0	6.0	13.0
Goiânia	61.7	0.0	0.0	38.3
Serra dos Pireneus	50.9	9.8	5.8	33.5
Reserva Biológica Boqueirão	38.8	5.5	2.7	53.0
Caldas Novas	72.0	16.0	8.0	0.0
Mean	69.2	4.1	5.3	20.9

Taxonomic knowledge of galling species in the Cerrado is scarce, as it is for the rest of Brazilian ecosystems. Most surveys and studies in the Cerrado identify galling insects only at the order or family level, with Diptera (Cecidomyiidae), Lepidoptera and Hemiptera being the most speciose taxa (e.g., Gonçalves-Alvim and Fernandes 2001a; Maia and Fernandes 2004; Santos et al. 2010; Araújo et al. 2011). Cecidomyiidae is responsible for approximately 70 % of all gall morphospecies from the Cerrado (Table 15.2). In Serra do São José (MG), for example, gall-midges induced 73.7 % of gall morphotypes (see Maia and Fernandes 2004). In other areas of the Brazilian Cerrado, such as the Estação Ecológica de Pirapitinga (Gonçalves-Alvim and Fernandes 2001a) and Vale do Jequitinhonha (Fernandes et al. 1997), Cecidomyiidae accounted for 76.8 % and 82.6 % of galls, respectively. Some examples of galls induced by Cecidomyiidae are presented in the Fig. 15.1.

The high richness and dominance of the Cecidomyiidae family in the Cerrado indicate the evolutionary success that the group has attained throughout the Neotropics (Gonçalves-Alvim and Fernandes 2001a). The Cecidomyiidae, unlike other galling taxa, exhibits strongly opportunistic adaptive radiation (Price 2005). Cecidomyiidae species are generally specific to their host (Carneiro et al. 2009) and the genera are distributed among several plant taxa (Gagné 1994). Radiation patterns can be attributed to the "host shift process", characterized by errors of galling females throughout oviposition (Price 2005) that result in speciation events (Craig et al. 1994). According to Mendonça (2001), such errors are favored by phenomena that promote the synchrony of phenology of host plant species. In the Cerrado, vegetation resprouting is intensified at the onset of the rainy season after fire (Vieira et al. 1996; Mistry 1998) and is perhaps the main reason for the great gall richness in the Cerrado.

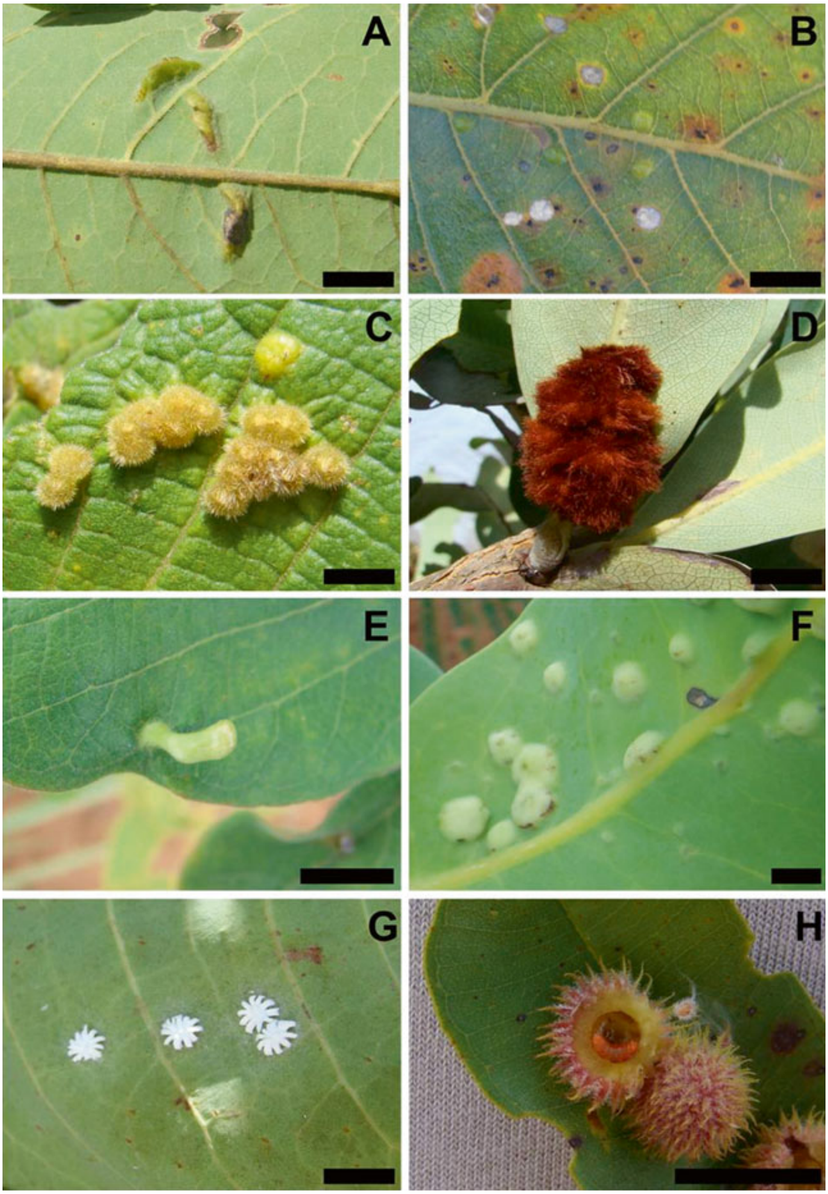

Fig. 15.1 Examples of gall morphotypes sampled in Cerrado. (**a**) laminar leaf gall induced by Cecidomyiidae in *Andira paniculata* (Fabaceae), (**b**) discoid leaf gall induced by Cecidomyiidae in *Aspidosperma tomentosa* (Apocynaceae), (**c**) globoid leaf gall induced by Cecidomyiidae in *Caryocar brasiliense* (Caryocaraceae), (**d**) globoid leaf gall induced by *Myrciariamyia admirabilis* (Cecidomyiidae) in *Erythroxylum suberosum* (Erythroxylaceae), (**e**) cylindrical leaf gall induced by *Iatrophobia brasiliensis* (Cecidomyiidae) in *Manihot* sp. (Euphorbiaceae), (**f**) discoid leaf gall induced by Cecidomyiidae in *Neea theifera* (Nyctaginaceae), (**g**) globoid leaf gall induced by Hemiptera in *Pouteria torta* (Sapotaceae), (**h**) globoid leaf gall in *Qualea parviflora* dissected in order to expose the larva of Cecidomyiidae (Diptera). Scale: 0.5 cm

Gall-midges of the genera *Asphondylia* and *Dasineura* are examples of taxa that have successfully radiated in the Cerrado. *Asphondylia* has been recorded in many host plant orders and families such as the Asteraceae, Dilleniaceae and Nyctaginaceae (Maia and Fernandes 2004). The genera *Dasineura* predominantly parasitizes members of the Anacardiaceae and Erythroxylaceae families (Maia and Fernandes 2004; Urso-Guimarães and Scareli-Santos 2006). This is an indication of the great ability of the host shift to act across genera and families, mainly in such a rich flora where more opportunities exist for adaptive radiation (Price 2005). Issues related to plant richness in the Cerrado and its importance to the diversity of galling is discussed in the next section.

Lepidoptera and Hemiptera occupy the second and third positions, respectively, in the ranking of galling diversity in the Cerrado. Species of Lepidoptera induce between 7.3 % (Maia and Fernandes 2004) and 9.8 % (Araújo et al. 2011) of known insect galls. Hemipteran galls induce about 5.8 % of galls in the Neotropical savannas (Maia and Fernandes 2004). The Lepidoptera and Hemiptera are the other taxa most frequently recorded in gall inventories in the Cerrado (Maia and Fernandes 2004; Araújo et al. 2011). Galling lepidopteran fauna in the Cerrado is not well-documented, but appears to be relatively diverse in Melastomataceae and xeric vegetation (Tavares 1917b; Maia and Fernandes 2004; Maia 2006; Lara et al. 2008). Hemipteran galling taxa are associated with many different hosts and are differentiated by presenting hole to the external environment (Maia and Fernandes 2004; Santos et al. 2010). Both lepidopteran and hemipteran galling insects are taxonomically poorly known and mostly remain undescribed.

15.3 Host Plants of the Galling Insect Fauna

The Cerrado is one of the phytogeographical domains with the highest plant diversity in the world, with over 12,000 species (Mendonça et al. 2008; Klink and Machado 2005) that are potential host plants for galling insects (Fernandes and Gonçalves-Alvim 2006). A consistent pattern observed in the Cerrado suggests that the Fabaceae is the most important host plant family (e.g., Fernandes et al. 1997; Gonçalves-Alvim and Fernandes 2001a, b; Maia and Fernandes 2004; Urso-Guimarães and Scareli-Santos 2006; Santos et al. 2010, 2012; Araújo et al. 2011). The main reason for the great gall richness hosted by the Fabaceae is its high species number (Araújo et al. 2012) of nearly 800 (Mendonça et al. 2008). The ranking of the major galling host families in different locations of the Cerrado is shown in Table 15.3.

Other host plant families often recorded in studies performed in the Cerrado are the Asteraceae and Myrtaceae (Maia and Fernandes 2004; Urso-Guimarães and Scareli-Santos 2006; Malves and Frieiro-Costa 2012). These families are also listed among those with the highest plant species richness in the Cerrado (Mendonça et al. 2008). Based on these observations, some studies conducted in the Cerrado that related plant family size and gall richness mostly found a positive relationship between these two variables (Gonçalves-Alvim and Fernandes 2001b; Araújo et al. 2012), as shown in Fig. 15.2a.

Table 15.3 Ranking of major galling host families from different localities in Cerrado

Plant family	Campus Pampulha	Vale do Jequitinhonha	Estação Ecológica de Pirapitinga	Delfinópolis	Serra de São José	Santa Rita do Passa Quatro	Fazenda Bulcão	Serra do Espinhaço	Serra do Cipó	Goiânia	Serra dos Pireneus	Reserva Biológica Boqueirão	Caldas Novas
Asteraceae	3rd	3rd	–	–	3rd	–	–	1st	3rd	–	–	2nd	–
Bignoniaceae	–	–	–	–	–	–	3rd	–	–	–	–	–	–
Boraginaceae	2nd	–	–	–	–	–	–	–	–	–	–	–	–
Euphorbiaceae	–	–	–	–	–	–	2nd	–	–	–	–	3rd	–
Fabaceae	1st	1st	1st	1st	1st	1st	1st	–	1st	1st	1st	–	1st
Malpighiaceae	–	2nd	3rd	–	–	3rd	–	3rd	–	–	3rd	–	3rd
Melastomataceae	–	–	–	–	–	–	–	2nd	–	–	–	–	–
Myrtaceae	–	–	2nd	–	2nd	2nd	–	–	2nd	–	–	1st	–
Rubiaceae	–	–	–	2nd	–	–	–	–	–	–	–	–	–
Styracaceae	–	–	–	–	–	–	–	–	–	2nd	2nd	–	–
Ulmaceae	–	–	–	–	–	–	–	–	–	3rd	–	–	–
Vochysiaceae	–	–	–	3rd	–	–	–	–	–	–	–	–	2rd

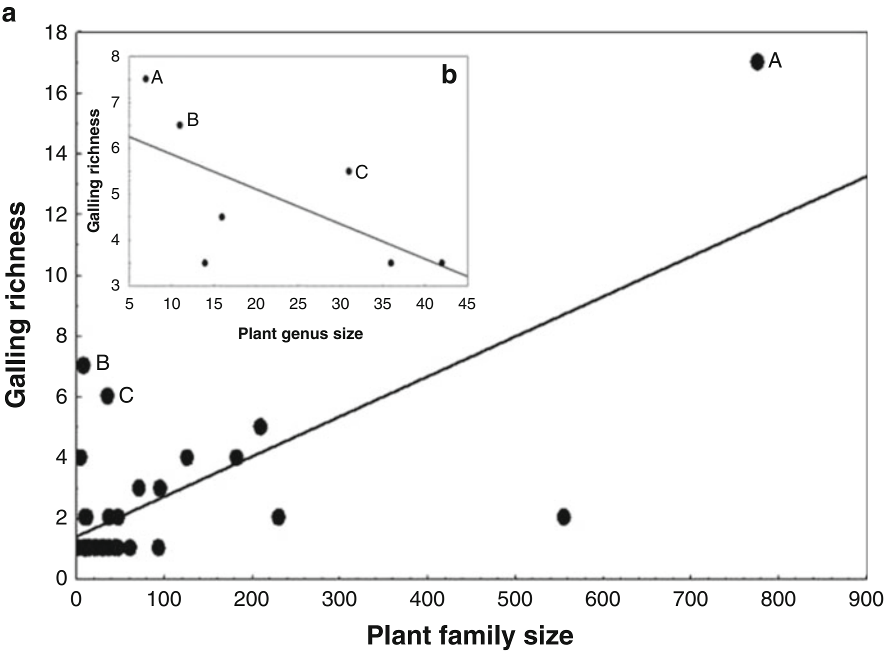

Fig. 15.2 Relationship between gall richness and plant taxa size in Cerrado, Goiás, Midwestern, Brazil: (**a**) Positive relationship to plant family size ($y = 1.39 + 0.01x$, $r^2 = 0.49$, $N = 30$, $p < 0.001$). *A*, *B*, and *C* represent the families Fabaceae, Styracaceae and Vochysiaceae, respectively. Families with highest galling insect richness; (**b**) Negative relationship to plant genus size and gall specie richness ($y = 1.09 – 0.36x$; $r^2 = 0.47$; $N = 7$; $p = 0.08$). Letters *A*, *B*, and *C* in both graphics represent the genera *Styrax*, *Qualea*, and *Bauhinia*, respectively. Genera with highest galling insect richness from different locations in Cerrado, Goiás, Midwestern, Brazil (Adapted from Araújo et al. 2012)

Other taxonomic levels of host plants have shown great gall diversity in the Cerrado. For example, Fernandes et al. (1996) recorded 121 gall morphotypes on *Baccharis* (Asteraceae) and 17 for a single species, *B. dracunculifolia*, mostly occurring in the Cerrado. The plant species *Copaifera langsdorffii* (Fabaceae) also hosts a great diversity of galls, with 23 species (Costa et al. 2010), whereas Araújo (2011a) recorded 18 galling species on *Qualea* (Vochysiaceae) and eight on *Q. parviflora*. Recent reports have also shown a great galling diversity associated with plant genera, that is not related to the number of plant species, in contrast to results related to the taxa size hypothesis (Araújo et al. 2012). According to these results, those genera displaying the highest host species richness were not the richest in terms of gall morphotypes (Fig. 15.2b). These genera and species are examples of super-hosts (Veldtman and McGeoch 2003), that exhibit a high intrinsic diversity of galling insects due to phenology and synchronous development and to the sympatric occurrence of phylogenetically close species (Araújo 2011b).

The diverse flora of the Cerrado influences the richness of galling insects in different ways. Taxa size (Gonçalves-Alvim and Fernandes 2001b), local plant richness

(Araújo 2011a), vegetation structure (Gonçalves-Alvim and Fernandes 2001b) and community composition (Araújo et al. 2012) are some plant features of the Cerrado that have been linked to the diversity of galling insects. Moreover, as mentioned above, galling insect radiation in the Cerrado might also be a product of systemic processes related to the synchronous development of the plant community (Mendonça 2001; Yukawa 2000). This phenomenon is produced by a strong climate seasonality that causes new shoots to resprout from the whole community within the same short period (Oliveira 1998). Thus, all these factors related to the heterogeneity and synchrony of the Cerrado, associated with sclerophylly (discussed in detail below), play a relevant role in determining the high diversity of galling species in the Cerrado.

15.4 Differential Distribution of Insect Galls Between Xeric and Mesic Habitats

The Cerrado contains a wide variety of vegetation types, ranging from forests to typical grassland formations (Ribeiro and Walter 2008). According to Oliveira-Filho and Ratter (2002), variations in fire, climate, water availability and soil fertility are the most important factors affecting the distribution of vegetation in the Cerrado. In this context, the Cerrado constitutes a mosaic of phytophysiognomies, with many mesic and xeric vegetation types. These differences between habitat types can directly affect the distribution of galling species (Fernandes and Price 1992).

Comparisons between mesic (non-sclerophyllic) and xeric (sclerophyllic) vegetation have pointed to a higher galling insect richness in the latter type, both along latitudinal and altitudinal gradients (Price et al. 1998; Lara et al. 2002; Fernandes et al. 2005). Indeed, several gall surveys illustrate this differential distribution of galling insects in sclerophyllous vegetation as well as a higher galling insect richness in savannas than in other ecosystems (e.g., Fernandes et al. 1995; Gonçalves-Alvim and Fernandes 2001a; Araújo et al. 2011). The hygrothermal stress hypothesis is proposed as an explanation for this pattern, suggesting higher gall richness in stressed environments (xeric) (Fernandes and Price 1988). Evidence for this hypothesis has been observed by several studies in the Cerrado (e.g., Fernandes and Price 1988; Lara and Fernandes 1996; Price et al. 1998; Gonçalves-Alvim and Fernandes 2001b; Lara et al. 2002; Araújo et al. 2011) and in other ecosystems worldwide (Fernandes and Price 1988; Fernandes and Lara 1993; Wright and Samways 1998; Cuevas-Reyes et al. 2004). The main mechanisms responsible for the high gall richness in stressed environments are their nutritional robustness and relationships with natural enemies (Fernandes and Price 1988; Fleck and Fonseca 2007).

Galling insects have developed the ability to circumvent the toxic and nutritional restrictions of sclerophyllous plants under stressed conditions (Cornell 1989; Wright and Samways 1998). Sclerophyllous plants have a large investment in lipid storage and carbohydrates and are also characterized by a low protein production (Allain et al. 1998). These characteristics, together with the presence of hair and trichomes affect plant palatability, restricting herbivorous consumption (Fernandes and Price 1988; Ribeiro et al. 1998). Thus, host plants from xeric habitats, under parasitization by other herbivorous guilds represent a better nutritive reserve for several galling species (Gonçalves-Alvim and Fernandes 2001b).

Another important factor favoring higher gall richness in xeric environments is the low diversity and frequency of natural predators (Fleck and Fonseca 2007). Fernandes and Price (1992) attributed higher survival rates of galling species in xeric environments to the lower mortality caused by parasitoids and pathogens. Furthermore, the high concentration of tannins as well as other compounds in sclerophyllous plants decreases the frequency of other herbivores, predators and fungi (Fernandes and Price 1988; Fleck and Fonseca 2007). Evidence for this are studies showing that parasitism rates in xeric vegetation are generally lower than in other environments. Maia and Fernandes (2004), for example, recorded 35 % of gall mortality caused by natural predators in the Cerrado. This value is much lower than those reported in Brazilian Atlantic Rain Forest ecosystems, which ranged from 48 % (Maia et al. 2008) to 60 % (Maia 2001). Although xeric environments are not predator-free, these results indicate that attack intensity in these environments is much lower than in mesic habitats. This has important implications for galling success because parasitoids are the leading cause of mortality in populations of galling insects (Espírito-Santo et al. 2004).

Studies that contradict the hygrothermal stress hypothesis are scarce (e.g., Blanche 2000; Blanche and Ludwig 2001; Veldtman and McGeoch 2003; Araújo and Santos 2008; Mendonça 2011), compared to the large number that corroborate it. Nevertheless, we cannot rule out the effects of inappropriate or different methods or sub-sampling carried out by studies conducted in mesic environments (Fleck and Fonseca 2007). Mesic vegetation tends to have greater structural complexity, including a higher canopy strata, which complicates sampling in these environments. Studies that focus on the Amazon Rainforest canopy also point to mesic vegetation hosting a galling insect richness equivalent, or superior to, that in xeric habitats (Medianero and Barrios 2001; Julião et al. 2005; Ribeiro and Basset 2007). High gall diversity in canopies of tropical forests might also be due to physiological constraints (Julião et al. 2005). Current research is not sufficient to resolve whether the canopy of mesic forests from the Cerrado also hosts a high gall species richness. Thus, further comparative studies between xeric and mesic habitats (with appropriate and standardized sampling effort and methods) are needed to strengthen the observed richness patterns of gall-inducing insects in the Cerrado.

15.5 Future Challenges for Gall Study in the Cerrado

An overview of gall studies in the Cerrado indicates areas where knowledge is lacking. For example, the vast majority of studies have been performed in southeastern Brazil, whereas other regions which host the largest Cerrado area are still poorly studied (such as the center-west, north and northeast). These transition zones can provide valuable information, due to the great floristic diversity of congruent ecosystems and also because the flora of these regions is constantly undergoing compositional changes (Castro et al. 2007). Thus, a greater research effort is needed to further understanding of gall richness in the Cerrado. Associated with this, the gall inventories in ecotone zones (e.g., Cerrado-Amazon, Cerrado-Caatinga, Cerrado-Atlantic Rain Forest), could reveal unique information and more and better-distributed inventories might contribute significantly to furthering knowledge.

The number of publications and studies that focus on galling insects in the Cerrado has increased dramatically in recent decades (Moreira 2006). The great diversity and relevance of galling insects, both in Neotropical savannas as well as in other regions of the world, was highlighted by Espírito-Santo and Fernandes (2007). Nevertheless, research with a focus on the biology and taxonomy of galling species is still lacking. We used a similar approach to that of Espírito-Santo and Fernandes (2007) to estimate gall richness in the Cerrado. We multiplied the mean gall richness per host plant found by the main studies carried out in the Cerrado (1.5 galls/plant species, see Table 15.1) by the number of 12,356 vascular plant species recorded by Mendonça et al. (2008) for the Cerrado. To make the results more realistic, we corrected the estimates using the proportion of galled plant species within a community (0.48), calculated by Araújo and Guilherme (2012) for several areas of Neotropical savannas along the Brazilian Cerrado and obtained an estimate of 9,282 species of galling insects. It is known that creating an insect inventory is a difficult task to be accomplished in a short period, due to the shortage of taxonomists, and the great species richness found in Neotropics (Espírito-Santo and Fernandes 2007).

Empirical and experimental studies with ecological and evolutionary approaches are necessary to better understand the distribution of galling insect richness in the Cerrado. These types of studies, where variables that influence gall richness are experimentally controlled, are lacking in Brazil. Moreover, the large number of explanatory hypotheses and contrasting results found in the literature focusing on gall richness (e.g., Fernandes and Price 1988; Gonçalves-Alvim and Fernandes 2001b; Mendonça 2001; Araújo et al. 2012), point to the use of standardized approaches and methods in order to compile patterns as the most reasonable route to dissect the mechanisms of gall diversity. Meta-analytical approaches are important to implement future research avenues (Borenstein et al. 2009). A further approach is the use of network analyses as valuable tools to explore plant-galling interactions. These analyses can evaluate structural properties related to galling insect-plant interactions, phylogenetic links, and also co-evolutionary dynamics between galling insects and their host plants (Riede et al. 2010; Thébaut and Fontaine 2010).

Many of the hypotheses to explain the diversity of galling insects in the Cerrado are not mutually exclusive (Fleck and Fonseca 2007). However, the structure and diversity of the flora as well as climatic and physical environment conditions are critical to the patterns so far identified. Associated with this, investigations on phytophysionogmic gradients, anatomical hypothesis and tri-trophic interactions can also considerably contribute to more specific issues. The growing interest by researchers and the advancement of novel techniques and methods is expected to further the understanding of these patterns and mechanisms in the near future.

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Chapter 16
Galls in Brazilian Mountains: New Reports and Perspectives

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and Geraldo Wilson Fernandes

Abstract In the last decade, a significant project was undertaken with the objective of studying the patterns of distribution of gall-forming insects across different individual mountains in the Espinhaço mountain range and *Serra da Mantiqueira*. Three hypotheses were tested that seek to describe the patterns of gall-inducing insects in order to test their "generality". (1) hypothesis of altitudinal gradient, which predicts that the richness of gall-forming insects diminishes with altitude, (2) hypothesis of plant richness, which predicts that richness of gall-forming insects increases with plant richness, and (3) hypothesis of plant density, which predicts that the richness of gall-forming insects increases with plant density. We have found that the richness of gall-forming insects does not vary linearly with altitude. Gall-inducing insects respond significantly to the number and composition of host plants. The majority of regional richness of gall-forming insects is explained by their beta richness component, suggesting that the composition of the community of gall-forming insects reflects the patterns of distribution of their host plants in the tropics.

Keywords Biogeography • Altitudinal gradients • Richness hypothesis • β diversity

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16.1 Elevation Gradient: Past and Current Studies

One of the most intriguing issues that fascinate ecologists and biogeographers is understanding the spatial and temporal patterns in the variation of species richness (MacArthur 1972; Lomolino et al. 2006). In order to conserve and manage biodiversity, it is imperative that these patterns, as well as the factors that create and maintain them, be understood (Rosenzweig 1995).

One of the key biogeographical patterns is the variation in species richness related to altitude (Lomolino et al. 2006). Altitudinal variation remains as one of the greatest biogeographical frontiers to be understood and represents a laboratory or "natural experiment" (*sensu* Whitcomb et al. 1994) that can contribute to the understanding of the responses of organisms to environmental changes, such as temperature, humidity and radiation (Fernandes and Price 1988; Lomolino 2001). Today, amid global climate changes, specifically caused by the release of gases into the atmosphere by anthropic activity, significant changes are expected over the medium and long term with respect to species distribution and the structure of their communities. Since altitudinal variations in mountainous environments have a thermal and hydric gradient (Hodkinson 2005), it is expected that global climatic changes will directly affect these ecosystems.

In the tropics, there are few studies in mountain ranges, despite their importance and potential for generating new patterns, as well as in aiding in the understanding of the processes and mechanisms that influence biodiversity. In Brazil, gall-inducing insects are extremely diverse in rupestrian fields (Lara and Fernandes 1996). Patterns of species distribution of gall-inducing insects and their host plants have been widely tested on various continents and used as models of analysis for species distribution (Table 16.1). Gall-inducing insects are directly affected by variations in humidity, temperature, altitude, and latitude (e.g. Fernandes and Price 1988, 1991, 1992; Fernandes and Lara 1993; Lara et al. 2002; Price et al. 1998). The pioneering work of Fernandes and Price (1988, 1991) sparked an intense debate about the patterns and mechanisms that influence biodiversity in this group of herbivores (e.g. Wright and Samways 1998; Price et al. 1998; Blanche and Ludwig 2001; Mendonça 2001; Yukawa et al. 2001; Veldtman and McGeoch 2003; Cuevas-Reyes et al. 2003, 2004a, b; Julião et al. 2004, 2005; Carneiro et al. 2005, 2006 and cited references). Despite this intense debate, unification seems far from reach. In this chapter, we revisit the original hypothesis proposed by Fernandes and Price (1988, 1991, 1992), comparing it with competing hypotheses and other studies conducted in different areas of the world. We also provide a summary and the perspectives of new studies.

Table 16.1 Altitudinal variation of the richness of gall-inducing insects

Gall-forming insects	Host plants	Biome	Pattern	Explanation	Reference
Entire community	Entire community	Savannah/rocky field (Neotropical) desert (Arizona)	Straight line	Hygrothermal stress	Fernandes and Price (1988)
Entire community, taxa-specific	Entire community	(Oriental)	Straight line	Hygrothermal stress	Fernandes and Lara (1993)
Entire community	Entire community	Savannah/rocky field (Neotropical)	Straight line	Hygrothermal stress	Lara et al. (2002)
Entire community	Entire community		Straight line		Blanche and Ludwig (2001)
Asphondylia spp. (Cecidomyiidae)	Salix tridentata		Quadratic	Oviposition sites	Waring and Price (1989)
Entire community	*Baccharis concinna*	Savannah/rocky field (Neotropical)	Quadratic	Hygrothermal stress	Carneiro et al. (2005)

16.2 Mountain Vegetation in Southeastern Brazil

Brazilian grassland located in high altitudes were named by Barreto (1949) as “alpine fields”, while Rizzini (1963) named them as “Upper Montane Fields.” However, these classifications cover ecosystems that, despite being physiognomically similar, differ with respect to their lithological characteristics, geological origins, surrounding matrix, as well as biological features such as forest composition (Rizzini 1979). Due to these differences, grasslands located in high elevations were subdivided into “quartzic fields” and “Upper Montane Fields” by Rizzini (1979) and later “rupestrian fields” and “altitude fields” by Ferri (1980).

While physiognomically similar, the ‘rupestrian fields’ and ‘altitude fields’ differ with respect to forest composition, associations with other adjacent vegetal formations, and primarily, predominant lithology (Ferri 1980; Benites et al. 2003). The expression ‘Upper Montane Fields’ is frequently used to refer to a grouping of plant formations that are predominantly herbaceous and restricted to the high elevation regions of southeastern and southern Brazil, where the climate is cold and humid, with granite formations and quaternary orogeny, within the four key forest regions: Mata Atlântica (Rainforest), Cerrado (Savannah), Florestas de Araucária (Araucária Forests) and Pampas (Pampas) (Safford 1999). The term rocky field is more often applied to plant formations in highland areas associated to the degradation of quartzite and sandstone, which produce rocky and sandy soils with a Paleozoic origin, found in the Cadeia do Espinhaço (Espinhaço Range) (Minas Gerais and Bahia) and in the Chapada dos Veadeiros (Goiás), both located in the Cerrado (Savannah) (Giulietti et al. 1987; Filgueiras 2002; Oliveira-Filho and Ratter 2002).

Rupestrian fields or quartzite rock complexes (*sensu* Semir 1991) in the Cadeia do Espinhaço can be divided into two large groups according to Pereira (1994). The Fig. 16.1 shows the fields where herbaceous species are observed growing out of sandy, rocky soil with numeric predominance of individuals in the following families: Poaceae, Cyperaceae, Eriocaulaceae, Xyridaceae and Velloziaceae. These fields occupy extensive areas, primarily in ranges of highest elevation (above 1,300 m altitude), and many times are restricted to rocky outcrops, which in turn predominate in middle altitude ranges (between 1,100 and 1,300 m altitude). In rocky outcrops, the predominant shrubs and subshrubs are from the Asteraceae, Melastomataceae, Velloziaceae families and some Poaceae species, herbaceous plants that are about one meter in height (Pereira 1994; Benites 2003). An ecotone, with species from the Cerrado and rupestrian field, is found in the lowest altitudes (between 900 and 1,100 m altitude), and Cerrado vegetation, with its different physiognomies, is found below 900 or 1,000 m altitude (Fig. 16.1).

Rupestrian fields are predominantly formed by rocks, such as quartzite and sandstone and are primarily associated to the Cerrado biome, while also being found in the matrices of other biomes (Caiafa and Silva 2005). Upper Montane Fields are predominantly located on granite rock, within a rainforest matrix, and primarily associated with the Serra da Mantiqueira (Mantiqueira Mountain) (Moreira and Camelier 1977). The province of Mantiqueira is the largest (700,000 km) and

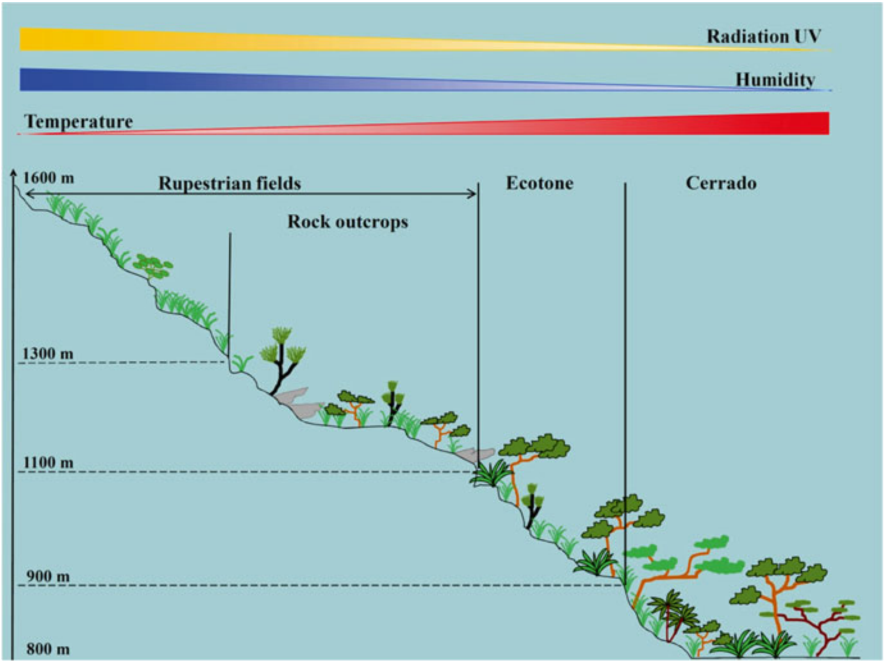


Fig. 16.1 Abiotic and biotic variations along the hypothetical altitudinal gradient in the Cadeia do Espinhaço

highest province in South America formed by the Brasiliano "orogenetic cycle" during the Neoproterozoic cycle/start of the Paleozoic cycle (900/480 Ma). It extends from 35°S in Uruguay to the southeastern border of the state of Bahia, Brazil (15°S). With a length of about 3,000 km and a width of 200 km, it stretches along the Atlantic coast. In southeastern Brazil, the mountains related to the *Mantiqueira* have a mesothermal humid climate (classification by Koppen) (Silva et al. 2006). The vegetation of both physiognomies is predominated by herbs and shrubs, with the most common families in Upper Montane Fields being Asteraceae, Melastomataceae, Orchidaceae and Bromeliaceae, and the most common in rupestrian fields being Asteraceae, Xyridaceae, Velloziaceae, Cyperaceae and Melastomataceae (Martinelli 1996).

In addition to their biological and geological importance, the mountainous areas of southeastern Brazil are regions of river headwaters. For example, the Upper Montane Fields linked to the "Serra do Mar" (Mountain of the Sea) and Serra da Mantiqueira are responsible for supplying water to 25 % of the Brazilian population, which thus justifies its conservation (Safford 1999). Both the Upper Montane Fields of "Serra da Mantiqueira" and the Rupestrian fields connected to the Espinhaço range, as well as their junctures, are associated to the Cerrado and the Rainforest biome, two biodiversity *hotspots* (Myers et al. 2000).

The number of endemic species of flora and fauna in the rupestrian fields associated with the Espinhaço range is surprisingly high (Giulietti et al. 1987), and according to data published to date, between 17 and 31 % of the species in the Upper Montane Fields are endemic (Safford 1999). Due to this extremely high diversity, endemism and geographic mosaic, part of the Serra do Espinhaço was declared as a Biosphere Reserve by UNESCO in 2005.

16.3 Biotic and Abiotic Pressures Determining Diversity in Gall-Inducing Insects Along Altitudinal Gradients

Changes in abiotic factors occur along altitudinal gradients. In general, it is assumed that an increase in altitude results in a decrease in temperature and an increase in humidity, as well as radiation (Hodkinson 2005). Of course, local conditions, such as topographical and meteorological variations, can cause significant changes that are difficult to predict, but we can more or less estimate the behavior of these variables along altitudinal gradients (see Hodkinson 2005 and references therein). In mountainous regions, the lapse rate (drop in temperature related to increase in altitude) in "free atmosphere" is between 5.5 and 6.5 °C for every 100 m of altitude (Anslow and Shawn 2002). The orographic precipitation in the form of rain or snow often increases significantly with altitude. For example, the eastern slope of the Serra do Cipó National Park has constant humidity condensation. This is due to the influence of the Atlantic Tropical Air Mass, which varies throughout the year but that exists even in the dry period, hosting significantly greater humidity than that found on the western slope, characterizing an orographic climate (Ribeiro et al. 2009). Short wave radiation, such as UV, increase with altitude and the degree of increase depends on the length of the wave. Comparisons conducted in alpine regions at 3,576 m (Jungfraujoch) and 577 m (Innsbruck) suggest an increase of about 8–9, 9–11, and 18–19 % 1,000 m^{-1} in the total annual UV, UV-B and UV-A radiation, respectively. The total amount of UV radiation can be changed by different factors, such as angle of incidence of solar rays, cloud cover and aerosol pollution (Alados-Arboledas et al. 2003).

16.3.1 Diversity of Gall-Forming Insects Along a Topographical Gradient

The hygrothermal stress hypothesis, initially proposed by Fernandes and Price (1988), argues that species richness and the abundance of gall-inducing insects are greater in hygrothermically-stressed habitat, that is, in dry, sunny habitats generally covered by sclerophyll vegetation. The hygrothermal stress hypothesis combines the arguments and evidence of the predictions of the three hypotheses about adaptative nature to the habit of inducing galls in order to explain the distribution patterns of gall-inducing insects in ecological time.

The studies of Fernandes and his collaborates show that, along altitude gradients, the species richness of gall-forming insects reduces with altitude (Fernandes and Price 1988, 1991, 1992; Fernandes and Lara 1993; Lara et al. 2002). The majority of their studies indicate a negative relationship (Fernandes and Price 1988, 1991; Fernandes and Lara 1993; Lara et al. 2002), but the quadratic function is also apparent in few studies (Waring and Price 1990; Blanche and Ludwig 2001; Carneiro et al. 2005) (see Table 16.1).

This variation in species richness spurred the authors to speculate about the mechanisms that determine this pattern. Fernandes and Price (1991) observed that the negative relationship between altitude and species richness of gall-inducing insects was dependent on the type of habitat. The richness of insect species is related to altitude in xeric habitats, but not in mesic habitats of the same altitude, suggesting that the relationship between altitude and species richness is questionable, and that hygrothermal stress is the key determinant of species richness for gall-forming insects. This conclusion is corroborated by the latitudinal pattern: the species richness of gall-forming insects is greater in middle latitudes (25–40° North or South), coinciding with habitats under hydric and nutritional stress with sclerophyll vegetation (e.g., Savannah, Chaparral, and Mediterranean-type vegetation (Fernandes and Price 1988, 1991; Blanche and Westoby 1995; Lara and Fernandes 1996; Wright and Samways 1996, 1998; Price et al. 1998).

A few mechanisms were proposed: (1) the gall could be an effective form of protection from climatic variations (Price et al. 1987), (2) considering that the nutrients of the plants become toxic at high levels (Nyman and Kulkunen-Titto 2000) and that the gall acts as a drain, mobilizing nutrients from other parts of the plant (Nyman and Julkunen-Titto 2000), inducing insects could be more successful in stressed habits where plants tend to have a lower nutritional state (Fernandes and Price 1991), with low concentrations of nutrients and excess of secondary compounds (Müller et al. 1987). Furthermore, gall-inducing insects are able to circumvent these defensive compounds, inducing a fiber free of phenolic compounds and rich in nutrients (Larew 1982; Nyman and Julkunen-Titto 2000). The third factor that could shape the pattern of species richness is the differential selection pressure imposed by natural enemies and by the plant's resistance to gall-forming herbivores between xeric and mesic habitats (see Fernandes 1990; Fernandes and Price 1988, 1992).

16.3.2 Effects of Taxonomic Composition and Forest Richness

Some plant families are prominently rich in galling insects, including Leguminosae *sensu lato*, Asteraceae, Myrtaceae, Malpighiaceae, Rubiaceae and Bignoniaceae (Carneiro et al. 2009b; Fernandes and Price 1988; Gonçalves-Alvim and Fernandes 2001a, b; Julião et al. 2002). The Neotropical region seems to present a higher number of species of gall-inducing insects; particularly Cerrado regions and rupestrian fields are noted as having the most speciose galling fauna in the world (Lara and Fernandes 1996). Nevertheless, to date there have been few local studies conducted over a short period of time. Most studies about species richness of gall-forming insects have been conducted in Serra do Cipó (Fernandes and Price 1988; Lara et al. 2002). Few studies were done in other rupestrian fields and Upper Montane Fields, forest formations known for their rich vegetal and animal species, primarily insects (Lara and Fernandes 1996).

In addition to hygrothermal stress, species richness and taxonomic composition of vegetation play an important role in the species richness of gall-forming insects. At the same time, Wright and Samways (1996, 1998) demonstrated that species richness for host plants in the South African *Fynbos* vegetation is the key determinant of species richness for gall-forming insects; while other studies considered that the total species richness of host plants in rupestrian fields (Fernandes and Price 1988; Lara et al. 2002) and in the Australian savannah (Blanche 2000) is a weak indicator of species richness variation for gall-forming insects. These conflicting results can be explained by the fact that, in *Fynbos* vegetation (South Africa), species richness of gall-forming insects by plant species is low and varies very little (plant species have one, two or rarely three species of gall-forming insects). On the other hand, in rupestrian fields, one single plant (*Baccharis concinna* Barroso) exhibited 15 species of gall-forming insects of the 46 species found in one habitat (Lara and Fernandes 1996); and in the Australian savannah, *Eucalyptus* species have from 1 to 12 species of gall-forming insects while other species are only associated with one to three species of gall-forming insects.

Within habitats, where the number of species of gall-forming insects associated to species of host plants is quite variable, the key determining factor of species richness for gall-forming insects is the taxonomic composition of the plants, rather than species richness. This high variability in the number of species of gall-forming insects is explained by the presence of these “super-hosts” which can greatly increase the number of species of gall-forming insects when present (Veldtman and McGeoch 2003). This conclusion is supported by the fact that few taxa of host plants amalgamate a large number of insect species, independent of the sample (Hawkins and Compton 1992). Different plant taxa exhibit greater species richness for gall-forming insects in different biogeographical regions. For example, *Baccharis* (Neotropical Region, Fernandes et al. 1996) and *Solidago* (Nearctic Region, Gagné 1994) are rich in Cecidomyiidae species; *Quercus* (Nearctic Region) and *Acacia* (Ethiopian Region) are rich in Cynipidae species (Stone et al. 2002); and *Eucalyptus* (Australian Region) are rich in Chalcidoidea and Coccoidea species (Blanche 1994).

It is difficult to separate the effects of hygrothermal stress, species richness and taxonomic composition of vegetation. Insect communities are richer in species with specific host taxa, which primarily occur in xeric habitats. For example, there are more gall-forming insects on *Eucalyptus* and more species of *Eucalyptus* in xeric habitats (Blanche and Westoby 1995).

The majority of studies conducted to date failed to find a positive relationship between the species distribution area of host plants and the species richness of gall-forming insects (Fernandes and Price 1988; Blanche and Westoby 1996; Cuevas-Reyes et al. 2003). However, more widely distributed *Eucalyptus* species exhibited greater regional storage of gall-forming insect species than those with less distribution (Blanche and Westoby 1996). Finally, one study showed a positive relationship between species richness of gall-forming insects and the density of host plants in a similar way as that described for other insect groups (Gonçalves-Alvim and Fernandes 2001a).

16.3.3 Architecture of Host Plants

Contrary to expectations for other herbivore insects, the number of species of gall-inducing insects does not increase for herbs, shrubs and trees (Fernandes and Price 1988; Price et al. 1997). In Serra do Cipó, shrubs exhibit more gall-forming insect species than do trees (Fernandes and Price 1988). The same argument was used by Blanche and Ludwig (2001) to explain the higher number of species found in middle altitudes across the altitudinal gradient in Texas. According to these authors, species richness for gall-forming insects was greater in middle altitudes because these altitudes present greater species richness for host plants, primarily shrubs. The same results were reported for other areas of the Brazilian Cerrado (savannah). On the other hand, Gonçalves-Alvim and Fernandes (2001a) found a greater number of gall-forming insect species in trees in a Cerrado area in southeastern Brazil. The difference between the number of species of gall-forming insects among different architectonic types of host plants can be explained by the dynamics of oviposition sites.

Gall-inducing insects are defined as a feeding group of herbivorous insects which, in order to complete their life cycle, develop a pathological modification in the tissue of a host plant (gall). The gall is produced as a result of hypertrophy and/or hyperplasia of the vegetal tissue (Mani 1964), caused by the interaction between the insect and the host plant (Weis et al. 1988). In general, each insect species induces a gall on one organ of a specific host plant species (Dreger-Jauffret and Shorthouse 1992; Floate et al. 1996; Carneiro et al. 2009b). The great majority of gall-forming insects induce galls in meristematic tissues with undifferentiated cells that are reactive to gall-inducing insects; few species can induce the re-differentiation of the tissue of the host plant in a healthy tissue (Raman et al. 2005; Price 2005).

If, in fact, this high specificity occurs, gall-forming insects probably respond to the quantity and/or quality of meristematic tissues in host plants. Waring and Price (1990) showed that *Asphondylia* species responded positively to an increase in the number of meristems. Creosote bushes populations with a higher number of meristems exhibited a higher number of galls induced by *Asphondylia* than populations with a lower number of meristems. Similarly, Fernandes and Price (1991) discerned that the higher number of gall-forming insect species in xeric habitats in Serra do Cipó could be explained by the fact that plants in xeric environments that are hygrothermically-stressed showed a more diffused growth with production of lateral meristems, thus creating more oviposition sites for gall-forming insects (see Price et al. 1987).

The same argument could explain the difference in species richness of gall-forming insects in architectonic types of host plants (Fernandes and Price 1988; Price et al. 1997). For example, independent of the distribution area of host plants of the genus *Salix*, shrub species of this genus support more gall-forming insect species compared with tree species. This result was explained by the authors in terms of the appearance of plants; that is, reduced appearance of trees for gall-forming insects is the result of the apical dominance of their form of growth, as well as of onthogenetic and physiological characteristics, making trees difficult to be colonized by gall-forming insects. Trees have poor production of meristems and new vigorous branches for colonization by gall-forming insects; that is, production occurs in a low number and in an unpredictable manner (Price et al. 1997; Price 2005).

A fundamental critique of the hypothesis of Fernandes and Price (1988) was made by Mendonça (2001) regarding these authors not indicating which mechanism was responsible for the increase in the number of species of gall-inducing insects in branches in xeric habitats.

16.3.4 Synchronization of Gall-Inducing Insects and Their Host Plants

Considering that the predictability (Fernandes and Price 1988; Price et al. 1997) and the quantity (Waring and Price 1989) of meristems in shrub plants could be critical factors for colonization of gall-forming insects, Mendonça (2001) suggested that the increase in the number and predictability of these resources (oviposition sites) over time could explain the global patterns of richness of gall-forming insects. Habitats with sclerophyll vegetation are characteristic of environments with strong seasonality, primarily in temperature and water availability, both of which are limiting factors for the growth and production of new aerial parts of host plants (Edwards et al. 2000). In these environments, fire is a common phenomenon and could be an important selective force regarding the distribution of gall-forming insects. The insects benefit from fire because it promotes synchronized budding, with the production of new vigorous branches for the colonization of insects. Synchronized production of new buds would increase the chances of “oviposition errors” and the occurrence of “host substitution”, the primary mechanism for sympatric speciation proposed for herbivore insects (Bush 1994). Price (2005) argues that the approach taken by Mendonça (2001) is not compatible with the model of Fernandes and Price (1988, 1991) and that fire could be included within their initial hypothesis.

The three key geographical gradients were considered separately; however, as they represent similar abiotic (temperature, humidity) and biotic (species richness of host plants, architectonic types, or production of oviposition sites) variations, these get confused and the interpretation of the mechanisms responsible for species richness of gall-forming insects becomes difficult.

For example, the species richness of gall-forming insects diminishes with altitude due to the increase in humidity and a concurring reduction in temperature (= hypothesis of hygrothermal stress), or due to the fact that in high altitudes fewer species of host plants are found (= hypothesis of richness of host plants), or even because, on the top of mountains, there are fewer species and/or shrub or tree individuals than herbs (= hypothesis of plant architecture). Consequently, herbs exhibit a meristem dynamic that is unfavorable to the habit of gall induction which, over time, results in a lower incidence of fire with a reduced rate of species substitution.

16.3.5 *Most Recent Results in the Neotropical Region*

In the last decade, a significant project was undertaken (data not published) with the objective of studying the patterns of distribution of gall-forming insects across different individual mountains in the Espinhaço mountain range and *Serra da Mantiqueira*, using the same approach as the pioneering studies of Fernandes and Price (1988). We tested three hypotheses that seek to describe the patterns of gall-inducing insects in order to test their "generality"; that is, does altitude play a decisive role in the distribution of gall-forming insects? Thus, the following hypotheses were tested: (1) hypothesis of altitudinal gradient (Fernandes and Price 1988), which predicts that the richness of gall-forming insects diminishes with altitude, (2) hypothesis of plant richness (Wright and Samways 1996, 1998; Gonçalves-Alvim and Fernandes 2001a; Oyama et al. 2003; Cuevas-Reyes et al. 2004b), which predicts that richness of gall-forming insects increases with plant richness, and (3) hypothesis of plant density (Gonçalves-Alvim and Fernandes 2001a; Cuevas-Reyes et al. 2004b), which predicts that the richness of gall-forming insects increases with plant density.

In the two key mountain regions of Brazil, the Espinhaço range and the "Serra da Mantiqueira", seven and four mountainous regions were selected, respectively (Fig. 16.2). The gall-forming insects and their host plants were sampled according to the methodology proposed by Fernandes and Price (1988) in each of the 11 mountain regions studied. In each region, 10 points were selected along the altitudinal gradient and with herbaceous-shrub vegetation, totalling 110 collection points ($n = 110$). Excluded from the samples were wooded areas, areas near trails, and areas with any visible anthropic interference. In order to obtain standardization, at each point the richness of the branches of the first 100 shrub-like woody plants (up to 2 m in height) were sampled, by directly counting the crowns, totalling 1,000 plants per region and 11,000 plants for the entire project. Earlier studies show differences in the richness of branch morphotypes in vegetation with different types of architecture, suggesting that plant architecture is one of the factors that explains richness concentration in gall-forming insects, with shrubs being the type of vegetation that has the greatest branch richness (Fernandes et al. 1996; Price et al. 1997;

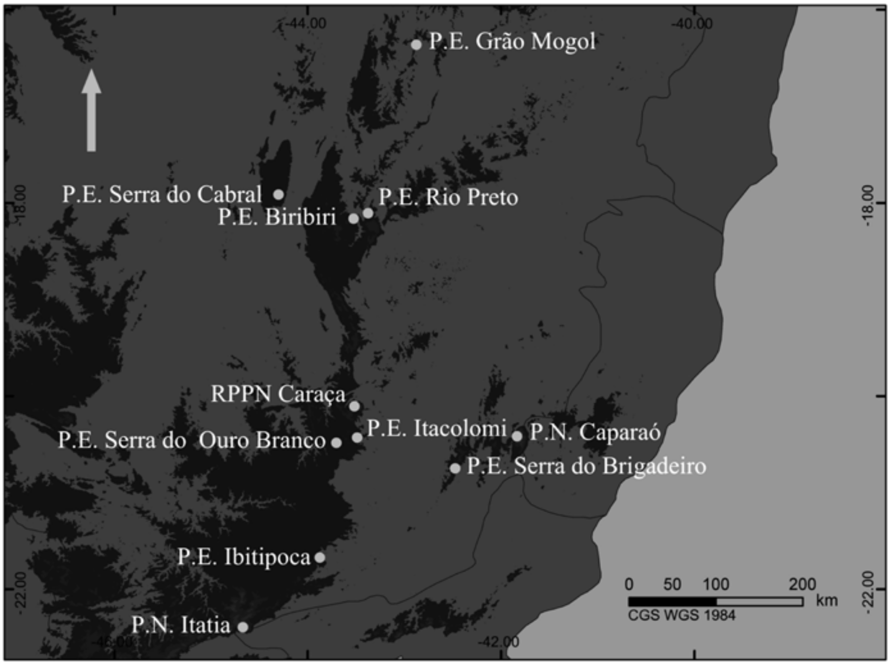


Fig. 16.2 The two key mountain regions of Brazil, the Espinhaço range and the "Serra da Mantiqueira", with seven (P.E. Biribiri, P.E. Caraça, P.E. Grão Mogol, P.E. Itacolomi, P.E. Serra do Cabral, P.E. Serra do Ouro Branco, P.E. Rio Preto) and four (P.E. Serra do Brigadeiro, P.N. Caparaó, P.E. Ibitipoca, P.N. Itatiaia) mountainous regions, respectively

Carneiro et al. 2009b). According to Carneiro et al. (2009a), the description of branch morphotype associated to species identification of host plants is a reliable indicator of the richness of gall-forming insects. Close to 95 % of Cecidomyiidae species described in Brazil can be identified based on their external form that is associated to the host plant in which it occurs, reinforcing the reliable use of this methodology in studies of gall-forming insects (Price et al. 1998; Blanche 2000; Cuevas-Reyes et al. 2003, 2004a, b; Oyama et al. 2003).

In total, 284 morphologically distinct types of insect galls (species) were found in 394 species of studied plants. The galls occurred in 171 species of host plants in 32 families and 89 genera (Carneiro et al. 2009b; Coelho et al. 2013b). Fewer galls were found in Serra da Mantiqueira than in the Espinhaço range. In total, 93 morphotypes of insect galls were found in 13 families, 30 genera and 50 species of host plants in a universe of 51 families, 118 genera and 22 species of host plants (Coelho et al. 2013a). Figure 16.3 represents the total number of galls found in each region. Since we are concerned with finding patterns and not differences, statistics between the mountains analyzed have not been explored.

Contrary to expectations, the richness of gall-forming insects did not vary with altitude (Fig. 16.4). The distribution of sites shows that, rather than a gradual

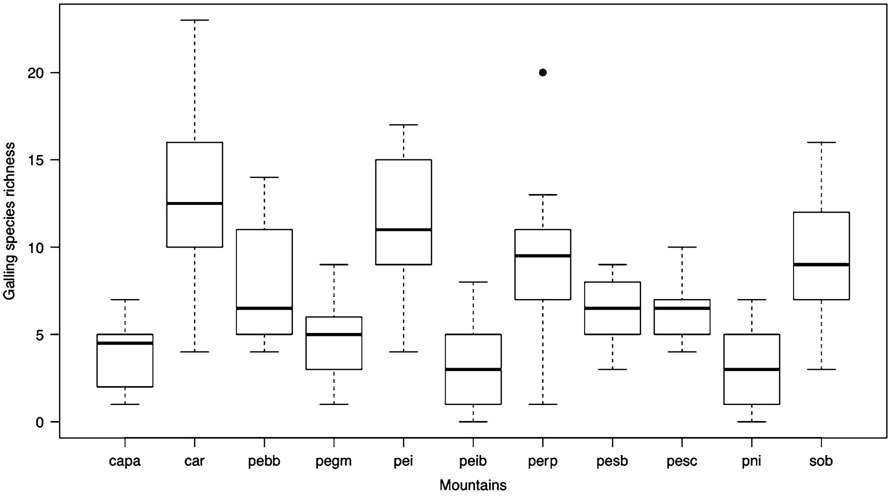


Fig. 16.3 Variation in richness of gall-forming insects among the studied regions in the Cadeia do Espinhaço (*car* Caraça, *pebb* P. E. Biribiri, *pegm* P. E. Grão Mogol, *pei* P. E. Itacolomi, *perp* P. E. Rio Preto, *pesc* P. E. Serra do Cabral, *sob* Serra do Ouro Branco) and in the Serra da Mantiqueira (*capa* Caparaó, *peib* P. E. Ibitipoca, *pesb* P. E. Serra do Brigadeiro, *pni* P. N. Itatiaia)

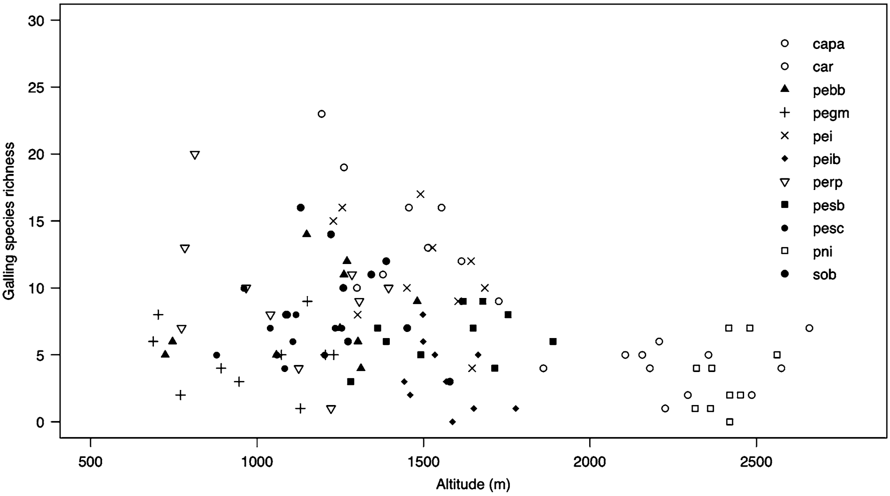


Fig. 16.4 Variation in richness of gall-forming insects and altitude. The species richness of gall-inducing insects did not diminish linearly with altitude ($y = \exp^{2.6420279 - 0.0004579*alt}$; $F_{1,108} = 14{,}177$; $P = 0{,}0002$) (*car* Caraça, *pebb* P. E. Biribiri, *pegm* P. E. Grão Mogol, *pei* P. E. Itacolomi, *perp* P. E. Rio Preto, *pesc* P. E. Serra do Cabral, *sob* Serra do Ouro Branco) and in the Serra da Mantiqueira (*capa* Caparaó, *peib* P. E. Ibitipoca, *pesb* P. E. Serra do Brigadeiro, *pni* P. N. Itatiaia)

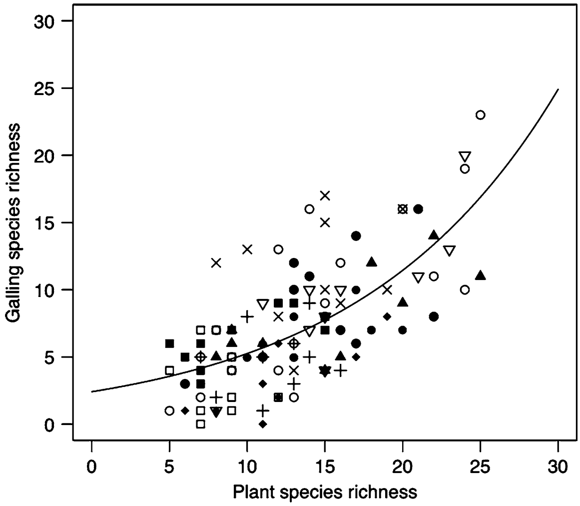


Fig. 16.5 Variation between species richness of gall-inducing insects and species richness of host plants. The species richness of gall-inducing insects increased with the species richness of host plants ($y = \exp^{0.881562 + 0.077786*\mathrm{rph}}$; $F_{1,108} = 82{,}166$; $P < 0{,}001$) (*car* Caraça, *pebb* P. E. Biribiri, *pegm* P. E. Grão Mogol, *pei* P. E. Itacolomi, *perp* P. E. Rio Preto, *pesc* P. E. Serra do Cabral, *sob* Serra do Ouro Branco) and in the Serra da Mantiqueira (*capa* Caparaó, *peib* P. E. Ibitipoca, *pesb* P. E. Serra do Brigadeiro, *pni* P. N. Itatiaia)

reduction in richness of gall-forming insects with an increase in altitude, what can be seen is a marked difference between extremes. In other words, the richness of gall-forming insects is less at the top than at the bottom of the mountains. Between the superior and inferior extremes of a gradient, there is a large variation in the number of species of gall-forming insects between habitats. These local variations in richness of gall-forming insects was interpreted by Carneiro et al. (2009b) with a reflection of the higher number of species of super-hosts (*sensu* Veldtman and McGeoch 2003) in the vegetation of rupestrian fields. The existence of host plants that concentrate a large number of gall-forming species along the altitudinal gradient establishes values of richness for gall-forming insects that vary little between altitudinal limits, independent of altitudinal variation or even the number of host plants, and consequently reduce the significance of the pattern. In rocky field areas in Serra do Cipó, a unique plant species *Baccharis concinna* Barroso exhibited 15 species of gall-forming species of the 46 species found in a single habitat (Lara and Fernandes 1996).

On the other hand, the richness of gall-forming insects increased with the richness of host plants (Fig. 16.5). Gall-inducing insects are host-specific, and therefore, it is expected that an increase in the number of plants in a local habitat represents an increase in the number of niches available for colonization, increasing the number of insect species (Mendonça 2007). Earlier studies showed the existence of this correlation in different vegetal formations (Wright and Samways 1996, 1998;

Blanche and Ludwig 2001; Dalbem and Mendonça 2006; Mendonça 2007). Other authors disregarded the fundamental role played by species richness of host plants in the structuring of a community of gall-inducing insects (e.g., rupestrian fields: Fernandes and Price 1988; Lara et al. 2002; Australian savannah: Blanche 2000).

Few studies have tested the influence of altitude on the richness of gall-forming insects. Using data in old-world (Indonesia) literature, Fernandes and Lara (1993) established a model where altitude has a very high influence over the richness of gall-forming insects. In this study, there was altitudinal variation of 3,400 m. Altitude represented 76 % ($r^2 = 0.76$) of the variation in richness of gall-forming insects. Then in studies that tested the variation of richness of gall-forming insects at the same altitudes, while using paired samples in mesic and xeric environments, altitude was the explanatory factor of richness variation in gall-forming insects only in xeric environments (Fernandes and Price 1988; Lara et al. 2002). Fernandes and Price (1988) worked with an altitudinal variation of 3,538 m, while Lara et al. (2002) worked with an altitudinal variation of 700 m. The authors argued that greater richness in gall-forming insects is more associated with sclerophyll vegetation, characteristic of xeric environments, rather than altitude, per se. Sclerophyll vegetation is common in stressed environments and, in addition to having long-lasting leaves, is rich in defense compounds, providing protection to the group of gall-forming insects against predators (Fernandes and Price 1988). Various studies have corroborated this hypothesis (Fernandes and Price 1988; Price et al. 1998; Fernandes and Lara 1993; Cuevas-Reyes et al. 2004b; Lara et al. 2002; Ribeiro and Basset 2007). However, studies conducted by Blanche (2000), Blanche and Ludwig (2001) and Veldtman and McGeoch (2003) had opposite results, that is, greater richness in gall-forming insects in mesic environments.

16.4 Beta Diversity Versus Altitudinal Gradient

Variations with altitude in the number of species received greater attention from the researchers than the changes in species composition. Only a few studies have called attention to changes in species composition between habitats (richness β). Changes in species composition in mountain ranges were found in few taxonomic groups. In tropical regions, trees (Lieberman et al. 1996), vascular plants (Vásquez and Givnish 1998) and insects (Brehm et al. 2003) showed a gradual change in species composition along altitudinal gradients, suggesting that species distribution occurs independently from each other. In this case, species distribution would reflect environmental conditions for each species, creating a separate pattern of gradual substitution. Thus, high β diversity values along the altitudinal gradient reflect habitat heterogeneity and species specialization to the particular conditions of the habitat (Jankowski et al. 2009).

Recently a study published by Medianero et al. (2010) showed changes in local and regional richness of gall-forming insects. Medianero and his team demonstrated that regional richness of gall-forming insects has a strong β component, reflecting

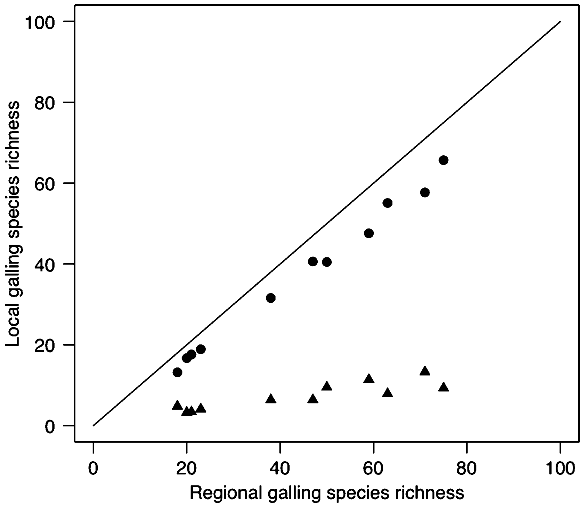


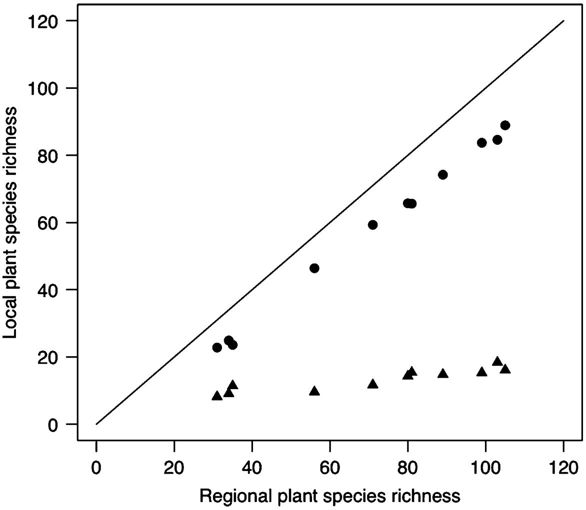
Fig. 16.6 Relationship between regional richness and local richness of gall-forming insects in the Cadeia do Espinhaço and in the Serra da Mantiqueira. Local richness or α (•) in gall-forming insect species is low related to regional richness, and it is β richness (▲) that comprises the majority of regional richness. The *diagonal line* represents the theoretical limit (local richness = regional richness)

their distribution tied to the aggregate distribution (space and in time) of their host plants. According to the authors, gall-forming insects, which are specialists in their host plants, distribute themselves in local (patches) according to the phenological patterns of the host plant and the presence of super-hosts.

Our data collected in the last two decades reinforce the patterns described above (Carneiro 2009). We consider regional diversity (or richness) Dγ as the total number of species in the region (e.g., P. E. Itacolomi), and diversity was obtained using the average number of species of the 10 collection sites within each region. Additive separation of these levels of diversity was used, according to the proposal of Lande (1996). Thus, Dβ diversity is obtained by subtracting from Dγ, instead of by using division. The use of additive separation of the diversity of their α and β components expresses the α and β richness in the same unit and allows for a direct evaluation of the relative contribution of each toward regional richness (Loreau 2000; Veech et al. 2002; Crist et al. 2003).

The separation of regional richness (γ) into α richness and β richness in both mountain ranges showed that local richness in gall-forming insect species is low in relation to regional richness, and that it is beta richness that comprises the majority of regional richness (Figs. 16.6 and 16.7). In the Espinhaço range, the separation of the α and β components showed that local richness is low in relation to regional richness, for gall-forming insects and the host plants (Fig. 16.5). Thus, β richness comprised the majority of regional richness of gall-inducing insects (> 73 %) and their host plants (> 80 %), indicating that, in general, the insects and plants were restricted to local habitats. The same pattern was found for *Serra da Mantiqueira*; that is, local richness is low in relation to regional richness, for gall-forming insects and the host plants (Figs. 16.6 and 16.7). Therefore, β richness comprised the majority of regional richness of gall-inducing insects (> 82 %) and their host plants (> 67 %), indicating that, in general, the insects and plants were restricted to local habitats. Therefore, species composition changes along the altitudinal gradient, and

Fig. 16.7 Relationship between regional richness and local richness of plants in the Cadeia do Espinhaço and in the Serra da Mantiqueira. Local richness or α (•) in species of host plants is low in relation to regional richness, and β richness (▲) is what comprises the majority of regional richness. The *diagonal line* represents the theoretical limit (local richness = regional richness)



local richness remains relatively low in comparison with regional richness (Fig. 16.5) and does not change significantly (see discussion below).

Changes in the taxonomic composition of vegetation occur along the altitudinal gradient (Smith and Young 1987; Lieberman et al. 1996). Our data show that, for rupestrian fields, abrupt changes in forest composition occur between habitats along the altitudinal gradient. These abrupt changes can reflect geographic isolation, due to barriers imposed by raised ground. In rupestrian fields, populations are generally disjointed and frequently restricted to small geographically-isolated mountains (Giulietti et al. 1997). As a result, there is a high number of species and high plant endemism. Consequently, there is significant discontinuity in species composition of plants and their associated gall-forming insects. The more important, and extremely relevant, result presented here is that, while species composition of gall-forming insects changes along the altitudinal gradient, local richness remains relatively low and does not change significantly with altitude or with forest composition. Therefore, the addition of local habitats with different landscapes can greatly affect regional richness of gall-forming insects.

16.5 Conclusions

The latest data on changes in richness of gall-inducing insects in the two key mountain ranges of southeastern Brazil show that the richness of gall-forming insects does not vary linearly with altitude. Gall-inducing insects respond significantly to the number and composition of host plants. The majority of regional richness of gall-forming insects is explained by their beta richness component, suggesting that the composition of the community of gall-forming insects reflects the patterns of distribution of their host plants in the tropics.

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Chapter 17
Galls in the Brazilian Coastal Vegetation

Valéria Cid Maia, Sheila Patrícia Carvalho-Fernandes, Alene Ramos Rodrigues, and Sharlene Ascendino

Abstract Brazilian coastal vegetation comprises 480 insect gall morphotypes on 61 plant families and 243 plant species. Myrtaceae, Fabaceae, Asteraceae, and Melastomataceae show the greatest number of galled species and the greatest richness of insect gall morphotypes. The super host plant species are *Mikania* cf. *biformis*, *Mikania* cf. *glomerata* and *Guapira opposita*. These plant taxa are among the best represented in restinga ecosystem, suggesting the influence of the plant composition on gall diversity. The galls are induced by Diptera, Hemiptera, Lepidoptera, Coleoptera, Thysanoptera and Hymenoptera, being the first responsible for the majority of the galls. The galls were found on leaf, bud, stem, flower, fruit, tendril, and aerial root. Leaves were the most attacked plant organ, followed by stems, and buds. A rich arthropods fauna has been associated with insect galls. Parasitoids are the most frequent and diversified. They are represented by 15 families of Hymenoptera, being Eulophidae, Eupelmidae, and Platygastridae the most frequent. The predators comprise gall midges (Diptera: Cecidomyiidae), ants (Hymenoptera: Formicidae) and pseudoscorpions (Olpiidae). Inquilines are represented by six insect orders: Diptera, Lepidoptera, Coleoptera, Hemiptera, Hymenoptera, and Thysanoptera. They cause the galler's death, probably due to competition and modifications in the microenvironment provided by the gall. Diptera are the most frequent inquilines. Successors are represented by mites, springtails, booklices and ants. The majority of the insect records are presented at suprageneric categories, showing that the taxonomic of galling insects is still poorly studied.

Keywords Brazilian coastal vegetation • Gall richness • Host plant • Gallers • Parasitoids

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17.1 Restinga: The Brazilian Coastal Vegetation

Restinga or coastal shrub zone is a very complex environment whose diversity is exceeded only by rain forests. It is part of the Atlantic Forest biome, being defined as long strip of marine deposits dated from Quaternary (Araújo 1992; Araújo et al. 1998; Scarano 2002). Until the nineteenth century, the Atlantic Forest spread over 80 % of the Brazilian coast (Lacerda et al. 1993) and its original area was about 1,315,460 km^2, but this biome has been suffering a great loss of the original area due to human influence (urbanization, industrialization, population growth, hydroelectric dam constructions, property speculation, agricultural and pasture expansion). Nowadays, about 70 % of the Brazilian population lives along the coast, what reflects in the high deforestation of the Atlantic Forest. The current cover is only about 8 % (102,012 km^2 of area). In the last 10 years, 11 % of this biome was deforested. Nevertheless, the Atlantic Forest comprises a high biodiversity (about 20,000 plant species) and endemism.

According to Rocha et al. (2004), the restingas also comprise a considerable biological diversity and a great variety of plant communities, due to diversified topography and environmental conditions, including marine and continental influences. This diversity provides many different habitats, and consequently a rich (Araújo and Henriques 1984) and characteristic flora (Lacerda et al. 1982; Rizzini 1992), which is highly adapted to the harsh conditions imposed by the extreme conditions, such as high salinity, low water availability and intense solar radiation (Scarano et al. 2001).

The physiognomy of restingas is varied, including tall forests that can reach 12 m high, fields with predominance of grasses and marshes with weeds (Neiman 1989) (Fig. 17.1). The best represented plant families are Fabaceae, Rubiaceae, Orchidaceae,

Fig. 17.1 Restinga vegetation in Arraial do Cabo City, Rio de Janeiro, Brazil

Myrtaceae, Poaceae, Bromeliaceae and Compositae (Rizzini 1979). Among them, Myrtaceae contribute significantly to the flora characterization, being *Eugenia* the largest genus in number of species (Rizzini 1979). Many plant communities are recognized in the restinga ecosystem. According to Araújo and Henrique (1984), the following plant communities are recognized in the restingas of the State of Rio de Janeiro: sclerophyllous, halophillous, swamp forests, and hydrophillous.

The richness of the restinga flora is highly variable; for example, the Restinga of Barra de Maricá, RJ (with about 1.0 ha of extension) comprises 204 plant species; the Parque Nacional da Restinga de Jurubatiba, RJ (with about 14.7 ha) presents 588 species, while Bertioga, SP (with about 9,000 ha) has 611 species.

The coastal regions of the States of Rio de Janeiro and Espírito Santo are one of the most diversified of the Brazilian coast. The flora reflects a high diversity of habitats and comprises more than 1,400 recorded plant species.

17.2 Review of the Literature

Insect galls in the Brazilian coastal areas (restingas) begun to be investigated in the 1980s. Ricardo Ferreira Monteiro at the Universidade Federal do Rio de Janeiro and collaborators were the first researchers to study insect galls in this ecosystem. They collected material in two municipalities of the State of Rio de Janeiro: Maricá and Arraial do Cabo. The main focus of their investigation was the ecology of the galls, but part of the collected material was used in the first taxonomic publications on Diptera galls inhabiting this coastal vegetation. These first articles were published by Couri and Maia (1992) and Maia et al. (1992), where one and five new species of cecidomyiid gallers (Diptera, Cecidomyiidae) were, respectively, described. In the following year, Maia (1993a, b, c, d) described 09 galling species, revealing a great number of unknown gall midges in these environments (Maia and Barros 2009).

Latter, Monteiro et al. (1994) published a survey of insect galls of Maricá and Arraial do Cabo, including a list of galled plant species, a brief characterization of gall morphotypes (galled organ and galling insect) and some data on parasitoids. In this article, the gallers and parasitoids were treated above supra-generic level. From 1994 until 2011, Maia and collaborators described ca. 50 new species and 13 new genera of gall midges (Maia and Barros 2009; Maia 2010; Maia and Santos 2011), mainly from Maricá.

In an effort to increase the knowledge of the insect galls of State of Rio de Janeiro, Brazil, other restinga areas were surveyed by Maia and collaborators, namely Carapebus, Grumari, and Praia do Sul, as well as by Monteiro and collaborators (Jurubatiba), resulting in several publications focusing on the diversity of galls (Maia 2001a; Maia and Oliveira 2010; Maia et al. 2002a, b; Monteiro et al. 2004; Oliveira and Maia 2005). In addition, some records of insect galls from restinga areas of Paraty and Cabo Frio were mentioned in the studies by Fernandes and Maia (2011) and Silva and Rodrigues (2011), respectively.

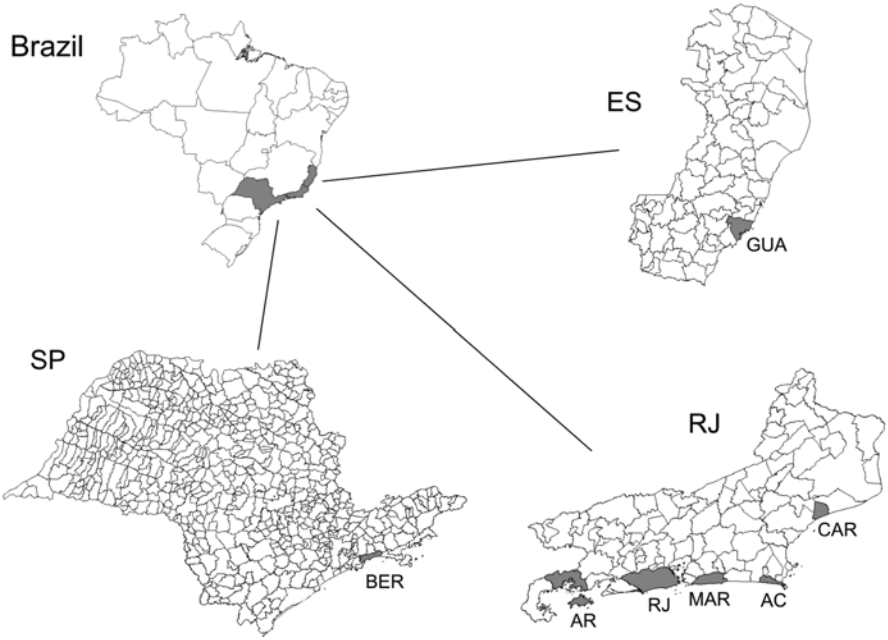

Fig. 17.2 Maps of Brazil, Espírito Santo, São Paulo and Rio de Janeiro States. *ES* Espírito Santo, *RJ* Rio de Janeiro, *SP* São Paulo, *AC* Arraial do Cabo, *AR* Angra dos Reis, *BER* Bertioga, *CAR* Carapebus, *GUA* Guarapari, *MAR* Maricá

Although we have now a large amount of published data on the galling cecidomyiids of Rio de Janeiro restingas, a very different scenario can be observed in other Brazilian states, where the current knowledge is still incipient at best. This is, for example, the case of São Paulo (SP) and Espírito Santo (ES) states, where few surveys were developed. Lima et al. (2000) and Maia et al. (2008) investigated the municipality of Bertioga in São Paulo, whereas Bregonci et al. (2010) focused on the galls in the Parque Estadual Paulo César Vinha, in Guarapari in the state of Espírito Santo. For the other restinga areas along the long stretch of the coast of Brazil, there are no published surveys or information on galling insects (Fig. 17.2).

Besides the galling species, other arthropods are frequently associated with insect galls, mainly as parasitoids, but also as predators, and inquilines. Data on these guilds in the restinga vegetation can be found in 11 articles, some of them focusing gall diversity, but also providing records of parasitoids (e.g., Monteiro et al. 1994; Maia 2001a; Maia et al. 2008; Bregonci et al. 2010).

Maia and Monteiro (1999), Maia (1999) and Maia and Tavares (2000) published data exclusively on tri-trophic systems (host plant versus galling species versus parasitoids), being *Guapira opposita* (Vell.) Reitz. (Nyctaginaceae), *Clusia lanceolata* Camb. (Clusiaceae) and *Eugenia rotundifolia* Casar (Myrtaceae), and *Cordia verbenacea* DC. (Boraginaceae) the studied plants.

Table 17.1 Most common Hymenoptera families per gall morphotypes, plant species and botanic families in Brazilian restingas

Hymenoptera family	Galls morphotypes	Plant family	Plant species
Eulophidae	56	22	38
Eurytomidae	48	19	33
Platygastridae	42	18	34
Eupelmidae	41	18	29
Torymidae	35	17	26
Pteromalidae	27	17	20

Maia and Azevedo (2009), Maia et al. (2008), Bregonci et al. (2010)

Other approaches can be found in Maia and Azevedo (2001a, b), that addressed the interactions of two large families of parasitoids of galls in the restinga, the Eurytomidae and Platygastridae (Hymenoptera) while Ferraz and Monteiro (2003) studied the influence of inquilines on gall morphology. A recent review article on parasitoids of gallers was written by Maia and Azevedo (2009), based on 16 years of collecting in the restingas of Rio de Janeiro. The authors recorded 14 families of parasitoids (identified at family, genera and/or species level) associated with 45 plant species (35 genera and 25 families) and 26 Cecidomyiidae genera (Table 17.1).

Additional records from restingas can be found in Maia and Oliveira (2004) and Maia (2006). The former compiles data of coleopterous galls from South America, and the latter those of Lepidoptera, Hemiptera and Thysanoptera from Central and South Americas. Twenty-seven coleopterous gall morphotypes were recorded on 24 host plant species (Fabaceae and Asteraceae mainly), with occurrence of about 70 % in stems or buds (Maia and Oliveira 2004). Lepidoptera, Hemiptera and Thysanoptera gallers were found in 108, 134, and 14 galls, respectively, associated with 74, 102, and 12 plant species. Lepidopteran galls occurred mainly in stems or buds (81.5 %) and on Melastomataceae, while Hemiptera and Thysanoptera galls primarily attacked leaves (about 85 % per each) and Myrtaceae (Maia 2006).

17.3 Insect Galls from Restingas

17.3.1 Richness of Insect Galls

The richness of gall inducing insects in restingas is very high (Fig. 17.3a–n), as reported by Monteiro et al. (1994, 2004), Maia (2001a), and Maia et al. (2008). Although the surveys were not done with the aim to test any hypotheses, it seems that the high richness is probably due to the increased hygrothermal stress (caused by daily temperature contrasts, humidity, wind gusts, strong radiation and sandy soil) in such vegetation, as suggested by Fernandes and Price (1988, 1992).

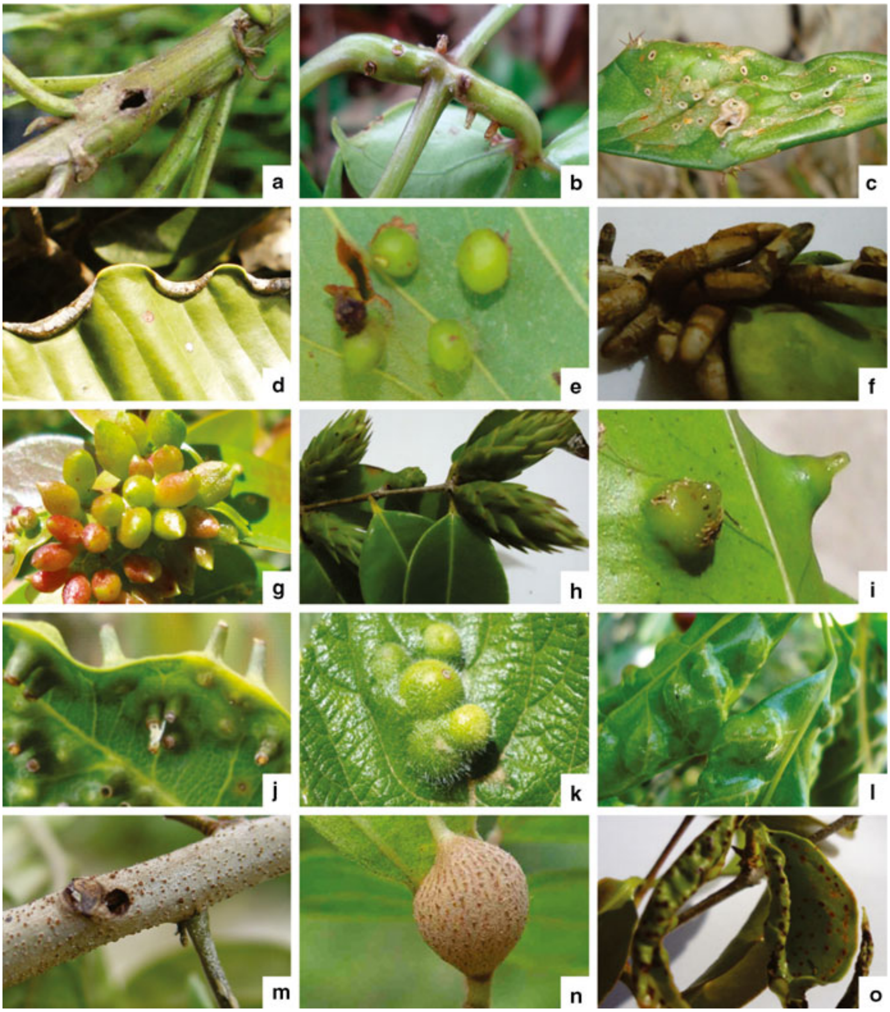

Fig. 17.3 Insect galls from restinga vegetation. (**a**) Tephritidae gall on *Vernonia beyrichii*; Cecidomyiidae galls: (**b**) *Alycaulus trilobatus* on *Mikania micrantha*, (**c**) *Neolasioptera cerei* on *Selenicereus setaceus*, (**d**) *Lopesia marginalis* on *Couepia ovalifolia*, (**e**) *Lopesia grandis* on *Dalbergia ecaslophylla*, (**f**) *Stephomyia rotundifoliorum* on *Eugenia rotundifolia*, (**g**) *Clinodiplosis profusa* on *Eugenia uniflora*, (**h**) *Neomitranthella robusta* on *Neomitranthes obscura*, (**i**) *Bruggmannia acaudata* on *Guapira opposita*, (**j**) *Youngomyia pouteriae* on *Pouteria caimito*, (**k**) *Schismatodiplosis lantanae* on *Lantana camara*; (**l**) Psyllidae (Hemiptera) gall on *Protium icicariba*; (**m**) Lepidoptera gall on *Schinnus terebinthifolium*; (**n**) Curculionidae (Coleoptera) gall on *Tibouchina pulchra*; (**o**) Thysanoptera gall on *Neomitranthes obscura*

Surveys of insect galls in the Brazilian restingas were developed mainly in the State of Rio de Janeiro, in Maricá (Barra de Maricá and Itaipuaçu) (Monteiro et al. 1994; Maia 2001a), Arraial do Cabo (Monteiro et al. 1994), Carapebus (Maia 2001a), Rio de Janeiro (Grumari) (Oliveira and Maia 2005), Reserva Biológica

Estadual da Praia do Sul (Ilha Grande, Angra dos Reis) (Maia and Oliveira 2010), and Parque Nacional da Restinga de Jurubatiba (Monteiro et al. 2004), totaling about 140 morphotypes. Additionally, some records are known from Cabo Frio (Parque da Boca da Barra) and Paraty (Vila de Trindade) (Silva and Rodrigues 2011; Fernandes and Maia 2011, respectively) (Table 17.2, Fig. 17.1).

In the State of São Paulo, two surveys were developed in the same locality, Bertioga (Lima et al. 2000; Maia et al. 2008); the former was a preliminary study, where 73 gall morphotypes were recorded; while the latter was the most extensive, resulting in the record of 233 morphotypes (Table 17.2).

In the State of Espírito Santo, the Parque Estadual Paulo César Vinha was the only investigated restinga area, with 38 gall morphotypes (Bregonci et al. 2010) (Table 17.2).

The current knowledge totalizes about 480 insect gall morphotypes on 61 plant families and 243 plant species in the Brazilian restinga. The average number of galled species per plant family is about 4.0 (20 botanic families overpass this number), and the average number of gall morphotypes per plant species is about 1.97. In cerrado areas of Minas Gerais, the average number of gall morphotypes per plant species varies from 1.15 (Urso-Guimarães et al. 2003) to 1.87 (Maia and Fernandes 2004), in cerrado areas of São Paulo and Goiás, the recorded media were 1.44 (Urso-Guimarães and Scareli-Santos 2006) and 1.50 (Araújo et al. 2007), respectively. In areas of Atlantic forest of Pernambuco, and Rio Grande do Sul, 2.0 (Fernandes et al. 2009), 1.63 (Santos et al. 2011a) and 1.54 (Dalbem and Mendonça-Júnior 2006) were the recorded values. In caatinga areas the average was 1.3 (Santos et al. 2011b) and 1.4 (Carvalho-Fernandes et al. 2012). In the Amazon forest, where the number of insect galls is high, the average is 2.33 (Julião et al. 2005). In spite of referring to different biomes, the average of gall richness does not vary much, although gall richness is highly variable (from 21 to 233) (Table 17.3). As a more complete data set from the Brazilian cerrado and ombrophyllous forest (Atlantic Forest) is still incipient, a comparison may be premature at the moment.

17.3.2 Host Plants

The restinga vegetation comprises 61 galled plant families. Among them, Myrtaceae, Fabaceae, Asteraceae, and Melastomataceae show the greatest number of galled species and the greatest richness of insect gall morphotypes (Table 17.4). As Myrtaceae, Fabaceae, and Asteraceae are the best represented plant families in this ecosystem, the most important plant families are also the most galled ones, suggesting plant composition as an important factor to influence gall diversity (Table 17.5).

Other well represented families are Rubiaceae, Orchidaceae, Poaceae, Bromeliaceae, but they comprise few or no insect galls. Excepting for Rubiaceae, the low diversity of galls on these families is already known, probably due to their simple architecture and chemical characteristics.

Table 17.2 Surveys of insect galls in Brazilian restingas

State	Municipality	Galls richness	Plant species richness	Plant family richness	References
Rio de Janeiro	Maricá	76	40	28	Maia (2001a)
	Maricá	87	44	27	Monteiro et al. (1994)
	Arraial do Cabo	40	27	19	Monteiro et al. (1994)
	Carapebus	64	31	23	Maia (2001a)
	Reserva Biológica Estadual da Praia do Sul, Ilha Grande, Angra dos Reis	36	22	16	Maia and Oliveira (2010)
	Grumari, Rio de Janeiro	43	25	19	Oliveira and Maia (2005)
	Parque Nacional da Restinga de Jurubatiba	99	40	25	Monteiro et al. (2004)
São Paulo	Bertioga	233	123	48	Maia et al. (2008)
	Bertioga	73	51	26	Lima et al. (2000)
Espírito Santo	Parque Estadual Paulo César Vinha, Guarapari	38	21	17	Bregonci et al. (2010)

The plant species with the greatest richness of galls are *Mikania* cf. *biformis*, *Mikania* cf. *glomerata* and *Guapira opposita*, with eight morphotypes each, followed by *Eugenia adstringens* and *Myrcia fallax* with seven morphotypes each, and *E. multiflora*, *Myrciaria floribunda*, *Neomitranthes obscura*, *Erythroxylum ovalifolium*, and *Manilkara subsericea*, with six morphotypes. They are the super host plant species in restingas. We can notice that the majority of them belong to Myrtaceae, and two species belong to *Eugenia*. According to Rizzini (1979), Myrtaceae contribute significantly to the flora characterization. This appears to be true to the insect galls characterization. And *Eugenia*, the largest genus in number of species in restingas (Rizzini 1979), also presents the highest richness of insect galls, suggesting, once again, the influence of the plant composition on gall diversity.

17.3.3 Insect Galls Groups

The galls are induced by Diptera, Hemiptera, Lepidoptera, Coleoptera, Thysanoptera and Hymenoptera. Diptera were responsible for the majority of the galls. Diptera, Lepidoptera, Hemiptera, Coleoptera, Hymenoptera and Thysanoptera are associated with 48 (80 %), 09 (15 %), 08 (13 %), 06 (10 %), 02 (3 %) and 02 (3 %) plant families, respectively. Inducers on 11 plant families were not determined.

The galls were found on leaf, bud, stem, flower, fruit, tendril and aerial root. Leaves were the most attacked plant organ, followed by stems, and buds. The only

Table 17.3 Comparison among richness of galls, plant species and plant families recorded in Brazilian ecosystems

Ecosystem	Galls richness	Plant species richness	Plant family richness	Galls morphotype per plant species	References
Restinga	94	47	28	1.2	Maia (2001a)
	233	123	48	1.8	Maia et al. (2008)
	43	25	19	1.7	Oliveira and Maia (2005)
Amazon Forest	84	–	–	–	Yukawa et al. (2001)
	236	–	–	–	Julião et al. (2005)
	54	25	18	2	Oda (2006)
	1,150	493	53	2.3	Julião (2007)
Atlantic Forest	273	139	40	2	Fernandes et al. (2001)
	130	84	34	1.5	Dalbem and Mendonça Jr. (2006)
	32	16	14	2	Fernandes et al. (2009)
Seasonally dry tropical forest	92	51	19	1.8	Coelho et al. (2009)
Rupestrian fields	236	134	27	1.7	Fernandes et al. (1997)
Cerrado	37	22	11	1.6	Fernandes et al. (1988)
	125	80	31	1.5	Gonçalves-Alvim and Fernandes (2001)
	22	19	16	1.1	Urso-Guimarães et al. (2003)
	137	73	30	1.8	Maia and Fernandes (2004)
	36	26	15	1.3	Urso-Guimarães and Scarelli-Santos (2006)
	57	43	18	1.3	Malves and Frieiro-Costa (2012)
Pantanal	133	75	37	1.7	Julião et al. (2002)
Caatinga	64	48	17	1.3	Santos et al. (2011b)
	25	18	8	1.4	Carvalho-Fernandes et al. (2012)

(_): No data available

insect group that induced galls on all plant organs was Cecidomyiidae. The majority of the Diptera (53 %), all Hemiptera and Thysanoptera induced leaf galls. Most part of Lepidopteran galls (69 %) were found on stems. Coleopteran galls occurred on two plant organs: leaf and stem (50 % on each), and Hymenoptera on three organs: leaf, stem, and bud (33.3 % on each) (Table 17.6). As few gall morphotypes were induced by these two last insect orders, plant organ preference cannot be discussed.

Table 17.4 Distribution of the number of plant species with insect galls and Cecidomyiidae (Diptera) galls per plant family in Brazilian restingas

Plant family	Number of host plant species with insect galls	Number of insect gall morphotypes	Number of host plant species with Cecidomyiidae galls	Number of Cecidomyiidae gall morphotypes
Anacardiaceae	03 (1.2 %)	04 (0.8 %)	01 (0.6 %)	01 (0.3 %)
Annonaceae	03 (1.2 %)	07 (1.5 %)	01 (0.6 %)	01 (0.3 %)
Apocynaceae	05 (2.0 %)	08 (1.7 %)	03 (1.9 %)	03 (1.0 %)
Aquifoliaceae	04 (1.6 %)	08 (1.7 %)	03 (1.3 %)	06 (2.0 %)
Araceae	02 (0.8 %)	03 (0.6 %)	01 (0.6 %)	01 (0.3 %)
Asclepiadaceae	02 (0.8 %)	03 (0.6 %)	02 (1.3 %)	03 (1.0 %)
Asteraceae	**18 (7.4 %)**	**43 (8.9 %)**	**14 (8.9 %)**	**33 (11.2 %)**
Avicenniaceae	01 (0.4 %)	01 (0.2 %)	01 (0.6 %)	01 (0.3 %)
Bignoniaceae	05 (2.0 %)	09 (1.9 %)	05 (3.2 %)	07 (2.4 %)
Boraginaceae	02 (0.8 %)	07 (1.5 %)	02 (1.3 %)	05 (1.7 %)
Burseraceea	03 (1.2 %)	10 (2.1 %)	03 (1.3 %)	08 (2.7 %)
Cactaceae	01 (0.4 %)	01 (0.2 %)	01 (0.6 %)	01 (0.3 %)
Cecropiaceae	01 (0.4 %)	01 (0.2 %)	0 (0.0 %)	0 (0.0 %)
Celastraceae	03 (1.2 %)	04 (0.8 %)	02 (1.3 %)	04 (1.3 %)
Chrysobalanaceae	02 (0.8 %)	05 (1.0 %)	02 (1.3 %)	03 (1.0 %)
Clethraceae	01 (0.4 %)	02 (0.4 %)	01 (0.6 %)	02 (0.7 %)
Clusiaceae	06 (2.5 %)	11 (2.3 %)	04 (2.5 %)	08 (2.7 %)
Commelinaceae	01 (0.4 %)	01 (0.2 %)	01 (0.6 %)	01 (0.3 %)
Connaraceae	01 (0.4 %)	01 (0.2 %)	0 (0.0 %)	0 (0.0 %)
Convolvulaceae	01 (0.4 %)	01 (0.2 %)	01 (0.6 %)	01 (0.3 %)
Cyatheaceae	01 (0.4 %)	01 (0.2 %)	0 (0.0 %)	0 (0.0 %)
Dilleniaceae	01 (0.4 %)	01 (0.2 %)	0 (0.0 %)	0 (0.0 %)
Dioscoreaceae	01 (0.4 %)	01 (0.2 %)	0 (0.0 %)	0 (0.0 %)
Ebenaceae	01 (0.4 %)	01 (0.2 %)	0 (0.0 %)	0 (0.0 %)
Eleaocarpaceae	01 (0.4 %)	03 (0.6 %)	01 (0.6 %)	02 (0.7 %)
Erythrtoxylaceae	02 (0.8 %)	07 (1.5 %)	02 (1.3 %)	07 (2.4 %)
Euphorbiaceae	08 (3.3 %)	16 (3.3 %)	05 (3.2 %)	08 (2.7 %)
Fabaceae	**21 (8.6 %)**	**31 (6.5 %)**	**17 (10.8 %)**	**23 (7.85)**
Gesneriaceae	03 (1.2 %)	08 (1.7 %)	01 (0.6 %)	03 (1.0 %)
Hippocrateaceae	01 (0.4 %)	01 (0.2 %)	0 (0.0 %)	0 (0.0 %)
Lamiaceae	04 (1.6 %)	04 (0.8 %)	02 (1.3 %)	02 (0.7 %)
Lauraceae	08 (3.3 %)	20 (4.2 %)	03 (1.3 %)	05 (1.7 %)
Loranthaceae	04 (1.6 %)	05 (1.0 %)	04 (2.5 %)	04 (1.3 %)
Malpighiaceae	05 (2.0 %)	10 (2.1 %)	03 (1.3 %)	05 (1.7 %)
Melastomataceae	**18 (7.4 %)**	**28 (5.8 %)**	**07 (4.4 %)**	**09 (3.0 %)**
Meliaceae	01 (0.4 %)	04 (0.8 %)	01 (0.6 %)	04 (1.3 %)
Moraceae	02 (0.8 %)	02 (0.4 %)	02 (1.3 %)	02 (0.7 %)
Myrsinaceae	03 (1.2 %)	05 (1.0 %)	02 (1.3 %)	02 (0.7 %)
Myrtaceae	**28 (11.5 %)**	**92 (19.2 %)**	**17 (10.8 %)**	**57 (19.5 %)**
Nyctaginaceae	04 (1.6 %)	15 (3.1 %)	03 (1.3 %)	12 (4.1 %)
Ochnaceae	01 (0.4 %)	03 (0.6 %)	01 (0.6 %)	02 (0.7 %)
Olacaceae	01 (0.4 %)	01 (0.2 %)	01 (0.6 %)	01 (0.3 %)

(continued)

Table 17.4 (continued)

Plant family	Number of host plant species with insect galls	Number of insect gall morphotypes	Number of host plant species with Cecidomyiidae galls	Number of Cecidomyiidae gall morphotypes
Onagraceae	01 (0.4 %)	01 (0.2 %)	01 (0.6 %)	01 (0.3 %)
Orchidaceae	01 (0.4 %)	01 (0.2 %)	0 (0.0 %)	0 (0.0 %)
Passifloraceae	01 (0.4 %)	01 (0.2 %)	01 (0.6 %)	01 (0.3 %)
Phytolacaceae	01 (0.4 %)	01 (0.2 %)	01 (0.6 %)	01 (0.3 %)
Picramniaceae	01 (0.4 %)	02 (0.4 %)	0 (0.0 %)	0 (0.0 %)
Piperaceae	04 (1.6 %)	06 (1.2 %)	03 (1.3 %)	03 (1.0 %)
Poaceae	01 (0.4 %)	01 (0.2 %)	0 (0.0 %)	0 (0.0 %)
Polygonaceae	04 (1.6 %)	05 (1.0 %)	02 (1.3 %)	02 (0.7 %)
Polypodiaceae	01 (0.4 %)	01 (0.2 %)	01 (0.6 %)	01 (0.3 %)
Rubiaceae	12 (4.9 %)	13 (2.7 %)	07 (4.4 %)	07 (2.4 %)
Sapindaceae	07 (2.9 %)	19 (4.0 %)	05 (3.2 %)	13 (4.4 %)
Sapotaceae	06 (2.5 %)	11 (2.3 %)	05 (3.2 %)	08 (2.7 %)
Smilacaceae	02 (0.8 %)	08 (1.7 %)	02 (1.3 %)	06 (2.0 %)
Solanaceae	09 (3.7 %)	13 (2.7 %)	06 (3.8 %)	08 (2.7 %)
Styracaceae	01 (0.4 %)	01 (0.2 %)	0 (0.0 %)	0 (0.0 %)
Theaceae	02 (0.8 %)	02 (0.4 %)	01 (0.6 %)	02 (0.7 %)
Thymelaeaceae	01 (0.4 %)	01 (0.2 %)	0 (0.0 %)	0 (0.0 %)
Urticaceae	01 (0.4 %)	01 (0.2 %)	0 (0.0 %)	0 (0.0 %)
Verbenaceae	03 (1.2 %)	03 (0.6 %)	02 (1.3 %)	02 (0.7 %)
Total: **61**	**243**	**480**	**157 (= 64.61 %)**	**295**

Monteiro et al. (1994, 2004), Lima et al. (2000), Maia (2001a, 2006), Maia et al. (2002a, b, 2008), Maia and Oliveira (2004, 2010), Oliveira and Maia (2005), Bregonci et al. (2010), Fernandes and Maia (2011), Silva and Rodrigues (2011)

Table 17.5 Richness of insect galls and main plant families in Brazilian ecosystems

Ecosystem	Galls richness	Plant families
Amazon forest	1,800	Fabaceae, Burseraceae
Restinga	480	Myrtaceae
Pampas	405	Asteraceae, Myrtaceae e Fabaceae
Rupestrian fields	241	Asteraceae, Melastomataceae, Malpighiaceae
Pantanal	133	Bignoniaceae, Fabaceae, Sapindaceae
Caatinga	64	Fabaceae, Euphorbiaceae

Carvalho-Fernandes, Carneiro, Julião and Almeida-Cortez, personal communication

17.3.4 Associated Arthropods Fauna

A rich arthropods fauna has been associated with insect galls and comprises parasitoids, inquilines, predators, and successors, revealing that galls represent a true microhabitat, where several trophic relations are established (Maia 2001a). Among them, the parasitoids represent the most frequent and diversified, occurring on ca.

Table 17.6 Distribution of insect galls per plant organ in Brazilian restingas

	Number of gall morphotypes per plant organ					
Galling insect	Diptera	Lepidoptera	Coleoptera	Hemiptera	Thysanoptera	Hymenoptera
Leaf	147	02	04	15	04	01
Bud	48	02	0	0	0	01
Stem	48	11	04	0	0	01
Flower	20	01	0	0	0	0
Fruit	07	0	0	0	0	0
Tendril	03	0	0	0	0	0
Aerial root	02	0	0	0	0	0

Monteiro et al. (1994, 2004), Lima et al. (2000), Maia (2001a, 2006), Maia et al. (2002a, b, 2008), Maia and Oliveira (2004, 2010), Oliveira and Maia (2005), Bregonci et al. (2010), Fernandes and Maia (2011)

30, 50 and 60 % of the gall morphotypes from Parque Estadual Paulo César Vinha (ES) (Bregonci et al. 2010), Bertioga (SP) (Maia et al. 2008), and Maricá and Carapebus (Maia 2001a), respectively. They are represented by 15 families of Hymenoptera (Maia and Azevedo 2009), being Eulophidae, Eupelmidae, and Platygastridae the most frequent (Table 17.1).

The predators comprise gall midges (Diptera: Cecidomyiidae), ants (Hymenoptera: Formicidae) and pseudoscorpions (Olpiidae) (Table 17.7). They were obtained from 15 gall morphotypes on 15 plant species distributed in 8 families, occurring more frequently (ca. 50 %) on Myrtaceae. The majority of these galls are induced by gall midges (80 %), excepting by three morphotypes (one is induced by Thysanoptera and two whose gallers are unknown). The predaceous Cecidomyiidae are associated with eight gall morphotypes on eight host plants species and five families: Myrtaceae, Fabaceae, Malpighiaceae, Sapindaceae, Solanaceae (the first with four gall morphotypes and the others with one). They are represented by a single genus, *Lestodiplosis* Kieffer, 1894, with occurrence mainly on leaf galls (five morphotypes), but also on bud, flower bud, and fruit galls.

Ants were obtained from six gall morphotypes on six plant species of five families (Nyctaginaceae, Asteraceae, Myrtaceae, Fabaceae and Smilacaceae), occurring on leaf and stem galls, induced by Cecidomyiidae, excepting by one morphotype whose galling species was not identified.

The pseudoscorpion, represented by *Novohorus* sp., was found in cylindrical galls of *Stephomyia rotundifoliorum* (Cecidomyiidae) on two species of Myrtaceae: *Eugenia multiflora* and *Eugenia adstringens*.

Inquilines are found in galls still inhabited by the galler. They are represented by phytophagous insects of six orders: Diptera, Lepidoptera, Coleoptera, Hemiptera, Hymenoptera, and Thysanoptera. In spite of feeding on galled tissue, they cause the galler's death, probably due to competition and modifications in the microenvironment provided by the gall. They were reared from 52 gall morphotypes on 39 plant species and 19 families (Table 17.8).

Table 17.7 Predators, host plant and gallers found at Brazilian restinga

Associated fauna predator	Host plant	Galler	Plant organ	Locality	References
Diptera Cecidomyiidae					
Lestodiplosis sp.	*Aureliana fasciculata* Solanaceae	*Clinodiplosis* sp. Cecidomyiidae	Leaf	BER	Maia et al. (2008)
	Eugenia adstringens Myrtaceae	*Dasineura marginalis* Cecidomyiidae	Leaf	MAR, MAC	Maia et al. (2002a, b)
	Heteropteris nitida Malpighiaceae	*Clinodiplosis floricola* Cecidomyiidae	Flower bud	MAR	Maia et al. (2002a, b)
	Inga laurina Fabaceae	*Neolasioptera* sp. Cecidomyiidae	Fruit	MAR	Maia et al. (2002a, b)
	Myrcia fallax Myrtaceae	Not det.	Bud	BER	Maia et al. (2008)
	Myrcia multiflora Myrtaceae	Thysanoptera	Leaf	BER	Maia et al. (2008)
	Myrciaria floribunda Myrtaceae	*Dasineura myrciariae* Cecidomyiidae	Leaf	MAR	Maia (2001a)
	Paullinia weinmanniaefolia Sapindaceae	*Clinodiplosis costai* Cecidomyiidae	Leaf	MAR	Maia (2001a)
Hymenoptera: Formicidae	*Dalbergia sampaioana* Fabaceae	Not det.	Stem	BER	Maia et al. (2008)
	Guapira opposita Nyctaginaceae	Cecidomyiidae	Leaf	BER	Maia et al. (2008)
	Guapira pernambuscensis Nyctaginaceae	Cecidomyiidae	Leaf	PEPCV	Bregonci et al. (2010)
	Mikania cf. *biformis* Asteraceae	*Liodiplosis spherica* Cecidomyiidae	Leaf and stem	BER	Maia et al. (2008)
	Myrciaria floribunda Myrtaceae	Cecidomyiidae	Leaf	GUA	Bregonci et al. (2010)
	Smilax rufescens Smilacaceae	Cecidomyiidae	Leaf	GUA	Bregonci et al. (2010)
Pseudoscorpion Olpiidae	*Eugenia adstringens* Myrtaceae	*Stephomyia rotundifoliorum* Cecidomyiidae	Stem	MAR	Maia (2001a)
Novohorus sp.	*Eugenia multiflora* Myrtaceae	*Stephomyia rotundifoliorum* Cecidomyiidae	Stem	CAR	Maia (2001a)

Locality: *BER* Bertioga (SP), *CAR* Carapebus (RJ), *GUA* Guarapari (ES), *MAC* Macaé (RJ), *MAR* Maricá (RJ), *PEPCV* Parque Estadual Paulo César Vinha (ES)

Table 17.8 Inquilinous, host plant and gallers found in Brazilian restinga

Inquilines	Host plant	Galler	Plant organ	Locality	References
Diptera Cecidomyiidae					
Clinodiplosis sp.	*Atronium* sp. Anacardiaceae	Coccoidea	Leaf	MAR	Maia (2001a)
Contarinia ubiquita	*Mikania* cf. *biformis* Asteraceae	*Mikaniadiplosis annulipes* Cecidomyiidae	Stem, petiole or vein	BER	Maia et al. (2008)
Contarinia sp.	*Manilkara subsericea* Sapotaceae	Cecidomyiidae	Leaf	MAR	Maia (2001a)
Resseliella sp.	*Miconia cinnamomifolia* Melastomataceae	*Epihormomyia miconiae* Cecidomyiidae	Bud	MAR	Maia (2001a)
	Parabignonia unguiculata Bignoniaceae	Cecidomyiidae	Leaf	BER	Maia et al. (2008)
Trotteria quadridentata	*Pouteria caimito* var. *laurifolia* Sapotaceae	*Youngomyia pouteriae* Cecidomyiidae	Leaf	MAR	Maia (2001b)
Trotteria sp.	*Mikania* cf. *biformis* Asteraceae	*Liodiplosis conica* Cecidomyiidae	Leaf or stem	BER	Maia et al. (2008)
	Myrcia fallax Myrtaceae	Lasiopteridi Cecidomyiidae	Leaf or stem	BER	Maia et al. (2008)
	Ocotea lobbii Lauraceae	Not det.	Stem	BER	Maia et al. (2008)
	Ocotea pulchella Lauraceae	Not det.	Stem	BER	Maia et al. (2008)
Diptera Sciaridae	*Aureliana fasciculata* Solanaceae	*Clinodiplosis* sp. Cecidomyiidae	Midvein	BER	Maia et al. (2008)
	Eugenia speciosa Myrtaceae	Schizomyiina Cecidomyiidae	Leaf	BER	Maia et al. (2008)
	Mikania cf. *biformis* Asteraceae	*Perasphondylia mikaniae* Cecidomyiidae	Bud	BER	Maia et al. (2008)
	Mikania hoehnei Asteraceae	*Clinodiplosis* sp. Cecidomyiidae	Leaf	MAR	Maia (2001a)
	Serjania communis Sapindaceae	*Clinodiplosis* sp. Cecidomyiidae	Bud	BER	Maia et al. (2008)
	Vernonia beyrichii Asteraceae	Tephritidae Diptera	Stem or bud	BER	Maia et al. (2008)

Coleoptera Curculionidae	*Andira fraxinifolia* Fabaceae	Cecidomyiidae	Leaf	BER	Maia et al. (2008)
	Andira fraxinifolia Fabaceae	Asphondyliina (Cecidomyiidae)	Leaf	BER	Maia et al. (2008)
	Aureliana fasciculata Solanaceae	*Clinodiplosis* sp. Cecidomyiidae	Midvein	BER	Maia et al. (2008)
	Cordia curassavica Boraginaceae	Lopesiini Cecidomyiidae	Leaf	BER	Maia et al. (2008)
	Hyptis fasciculata Benth. subsp. *fasciculata* Lamiaceae	Cecidomyiidae	Petiole, stem or vein	BER	Maia et al. (2008)
	Mikania cf. *biformis* Asteraceae	*Perasphondylia mikaniae* Cecidomyiidae	Bud	BER	Maia et al. (2008)
	Mikania cf *biformis* Asteraceae	*Asphondylia glomeratae* Cecidomyiidae	Petiole or vein	BER	Maia et al. (2008)
	Mikania cf. *biformis* Asteraceae	*Liodiplosis spherica* Cecidomyiidae	Leaf or stem	BER	Maia et al. (2008)
	Piptocarpha cf. *cinerea* Asteraceae	*Asphondylia* sp. Cecidomyiidae	Petiole, Stem or bud	BER	Maia et al. (2008)
	Tibouchina trichopoda Melastomataceae	Cecidomyiidae	Stem	BER	Maia et al. (2008)
Coleoptera	*Calophyllum brasiliense* Clusiaceae	*Lopesia elliptica* Cecidomyiidae	Leaf	BER	Maia et al. (2008)
	Andira nitida Fabaceae	Cecidomyiidae	Leaf	GUA	Bregonci et al. (2010)
	Ouratea cuspidata Ochnaceae	*Contarinia* sp. Cecidomyiidae	Leaf	GUA	Bregonci et al. (2010)
Hemiptera Coccidae	*Myrcia fallax* Myrtaceae	Lasiopteridi Cecidomyiidae	Leaf or stem	BER	Maia et al. (2008)
Coccidae and Membracidae	*Mikania* cf. *biformis* Asteraceae	*Liodiplosis spherica* Cecidomyiidae	Leaf or stem	BER	Maia et al. (2008)
Membracidae	*Campomanesia guaviroba* Myrtaceae	*Clinodiplosis* sp. Cecidomyiidae	Leaf	BER	Maia et al. (2008)
Hemiptera	*Peperomia glabella* Piperaceae	Cecidomyiidae	Leaf	BER	Maia et al. (2008)
Tingidae *Acanthocheilla* sp.	*Mikania* cf. *biformis* Asteraceae	*Liodiplosis spherica* Cecidomyiidae	Leaf or stem	BER	Maia et al. (2008)

(continued)

Table 17.8 (continued)

Inquilines	Host plant	Galler	Plant organ	Locality	References
Lepidoptera	*Andira fraxinifolia* Fabaceae	Cecidomyiidae	Leaf	BER	Maia et al. (2008)
	Baccharis speciosa Asteraceae	Alycauliini Cecidomyiidae	Stem or bud	BER	Maia et al. (2008)
	Elachyptera micrantha Celastraceae	Cecidomyiidae	Bud or leaf	BER	Maia et al. (2008)
	Gordonia fruticosa Theaceae	*Clinodiplosis* sp. Cecidomyiidae	Bud	BER	Maia et al. (2008)
	Guapira pernambucensis Nyctaginaceae	Cecidomyiidae	Leaf	GUA	Bregonci et al. (2010)
	Guapira opposita Nyctaginaceae	*Bruggmannia elongata* Cecidomyiidae	Leaf	BER	Maia et al. (2008)
	Paullinia sp. Sapindaceae	*Neolasioptera* sp. Cecidomyiidae	Petiole, vein or tendril	BER	Maia et al. (2008)
	Piptocarpha cf. *cinerea* Asteraceae	*Asphondylia* sp. Cecidomyiidae	Petiole, stem or bud	BER	Maia et al. (2008)
	Piptocarpha cf. *cinerea* Asteraceae	Cecidomyiidae	Stem, bud or vein	BER	Maia et al. (2008)
	Pouteria venosa Sapotaceae	*Lopesia singularis* Cecidomyiidae	Leaf	BER	Maia et al. (2008)
	Psidium cattleyanum Myrtaceae	Not det.	Leaf	BER	Maia et al. (2008)
	Tibouchina trichopoda Melastomataceae	Lasiopteridi Cecidomyiidae	Leaf or stem	BER	Maia et al. (2008)
	Vernonia beyrichii Asteraceae	Tephritidae Diptera	Stem or bud	BER	Maia et al. (2008)
Stenoma annosa Oecophoridae	*Neomitranthes obscura* Myrtaceae	*Clinodiplosis* sp. Cecidomyiidae	Leaf	MAR	Maia (2001a)

Hymenoptera Eulophidae	*Eugenia adstringens* Myrtaceae	*Stephomyia rotundifoliorum* Cecidomyiidae	Stem	MAR	Maia (2001a)
	Paullinia weinmanniaefolia Sapindaceae	*Paulliniamyia ampla* Cecidomyiidae	Leaf	MAR	Maia (2001a)
Eulophidae Tetrastichinae	*Erythroxylum ovalifolium* Erythroxylaceae	*Lopesia erythroxyli* Cecidomyiidae	Bud	MAR	Maia (2001a)
	Myrcia ovata Myrtaceae	*Dasineura* sp. Cecidomyiidae	Leaf	MAR	Maia (2001a)
Aprostocetus sp.	*Myrcia ovata* Myrtaceae	*Myrciamyia maricaensis* Cecidomyiidae	Bud	MAR	Maia (2001a)
Thysanoptera	*Baccharis singularis* Asteraceae	Not det.	Stem or vein	BER	Maia et al. (2008)
	Myrciaria floribunda Myrtaceae	Cecidomyiidae	Leaf	GUA	Bregonci et al. (2010)

Locality: *BER* Bertioga (SP), *GUA* Guarapari (ES), *MAR* Maricá (RJ)

Diptera are the most frequent inquilines. They are associated with 20 gall morphotypes on 17 plant species distributed in eight families. They occurred in galls induced by Diptera (17 morphotypes, being 16 of Cecidomyiidae and one of Tephritidae) and Hemiptera (one morphotype). The gallers of two morphotypes were not determined. These inquilines are represented by two families: Cecidomyiidae and Sciaridae. The former are associated with 14 gall morphotypes on 12 plant species and 7 families, occurring mainly in galls induced by other Cecidomyiidae (11 morphotypes), but also in Hemipteran galls. They are represented by four genera: *Clinodiplosis*, *Contarinia*, *Resseliella* Seitner, 1906 and *Trotteria* Kieffer, 1901, being the last the most common.

Sciaridae are less frequent than cecidomyiids. They were obtained from six gall morphotypes on six plant species and four families. They occurred only in galls induced by Diptera (Cecidomyiidae, five morphotypes and Tephritidae, one morphotype).

Lepidoptera were the second most frequent inquiline, occurring in 14 gall morphotypes on 13 plant species and nine families. The majority (about 85 %) was found in galls induced by Cecidomyiidae, excepting by two records (one in galls of Tephritidae and the other in galls of an undetermined insect). They occur in leaf, stem, bud and tendril galls, being more frequent in the first. Little is known about the taxonomy of these moths, as the records are at the order level. There is a single exception, represented by an inquiline identified at species level, *Stenoma annosa* (Oecophoridae) (Maia 2001a).

Coleoptera were the third most frequent inquiline, being associated with 13 gall morphotypes, all induced by Cecidomyiidae, on 10 plant species of eight families. They are represented mainly by Curculionidae (10 morphotypes) and occur in leaf, stem and bud galls, being more frequent in the first. Once again, the taxonomic information is deficient, as most records are at the family level.

Few Hemiptera, Hymenoptera and Thysanoptera were found as inquilines. Hemiptera were obtained from five gall morphotypes, all induced by gall midges, in leaves and stems. They are associated with four plant species distributed in three families. The inquiline records are also at the family or order level, excepting by *Acantocheilla* sp. (Tingidae) (Maia et al. 2008).

Hymenoptera were found in five gall morphotypes of Cecidomyiidae on four plant species and three families. They modify the original shape of the gall, causing an increase in size or more drastic morphological changes, such as the development of endogalls. They occur in stem, leaf and bud galls. The taxonomic knowledge of these modifiers is quite incipient, as the records are at family or order level, with a single exception, *Aprostocetus* sp. (Eulophidae).

Thysanoptera were the less frequent inquilines. They were found in two gall morphotypes on two plant species and two families.

Successors are inquilines that invade galls which were already abandoned by the galler. Generally, they feed on fungus. They are represented by mites, springtails, booklices and ants (Table 17.9). They are associated with ten gall morphotypes on nine plant species and seven families, occurring in leaf, stem or bud galls, which are induced mainly by Cecidomyiidae, but also by Tephritidae. Collembola are the most

Table 17.9 Successors, host plant and gallers found at Brazilian restinga

Successor	Host plant	Galler	Plant organ	Locality	References
Leptothorax sp. Formicidae	*Eugenia adstringens* Myrtaceae	*Stephomyia rotundifoliorum* Cecidomyiidae	Stem	MAR	Maia (2001a)
	Eugenia multiflora Myrtaceae	*Stephomyia* sp. Cecidomyiidae	Stem	CAR	Maia (2001a)
Collembola	*Baccharis speciosa* Asteraceae	Alycauliini Cecidomyiidae	Stem or bud	BER	Maia et al. (2008)
Collembola	*Vernonia beyrichii* Asteraceae	Tephritidae (Diptera)	Stem or bud	BER	Maia et al. (2008)
Collembola	*Tibouchina trichopoda* Melastomataceae	Lasiopteridi (Cecidomyiidae)	Leaf or stem	BER	Maia et al. (2008)
Collembola	*Peperomia glabella* Piperaceae	Cecidomyiidae	Leaf	BER	Maia et al. (2008)
Psocoptera	*Pouteria venosa* Sapotaceae	*Lopesia singularis* Cecidomyiidae	Leaf	BER	Maia et al. (2008)
	Chaetocarpus myrsinites Euphorbiaceae	Not det.	Leaf	GUA	Bregonci et al. (2010)
Acari	*Guapira pernambucensis* Nyctaginaceae	Cecidomyiidae	Leaf	GUA	Bregonci et al. (2010)
	Guapira pernambucensis Nyctaginaceae	Cecidomyiidae	Stem	GUA	Bregonci et al. (2010)

Locality: *BER* Bertioga (SP), *CAR* Carapebus (RJ), *GUA* Guarapari (ES), *MAR* Maricá (RJ) frequent successors, followed by Psocoptera, Acari and Formicidae. They were found in four, two, two, and one gall morphotypes, respectively. A colony of *Leptothorax* sp. (Formicidae) was found in stem galls of *Stephomyia rotundifoliorum* (Cecidomyiidae).

Data on associated arthropod fauna from other biomes is very scarce in literature. Some records from cerrado areas of Goiás, São Paulo and Minas Gerais are known. Araújo et al. (2011) found parasitoids of five Hymenoptera families (Chalcididae, Encyrtidae, Eulophidae, Eupelmidae and Trichogrammatidae) occurring in approximately 40 % of galls from Serra dos Pirineus (Goiás) and indicated Eulophidae as the most representative family. Urso-Guimarães et al. (2003) found parasitoids of the families Braconidae, Eulophidae, Eurytomidae, Pteromalidae and Torymidae, and occasional inquilines, Polyxenidae (Diplopoda) and Psocodea (Psocoptera) in Delfinópolis (Minas Gerais). Maia and Fernandes (2004) recorded the parasitoids of seven families (Eurytomidae, Braconidae, Platygastridae, Eulophidae, Pteromalidae, Ichneumonidae, and Encyrtidae) in about 35 % of the galls from Serra de São José, MG. They also found a predaceous fly, *Friebrigella* sp. (Chloropidae: Diptera), and gall midges larvae (Cecidomyiidae), Sciaridae, Muscomorpha larvae, Coleoptera, Lepidoptera, Psyllidae, and Hemiptera as inquilines.

Comparative data on restinga and cerrado indicate that the associated arthropods fauna from the former is more diversified than the latter, but it is important to emphasize that the fauna from restingas have been more investigated than that from cerrado.

17.3.5 Taxonomical Problems

The taxonomic of galling insects is still poorly studied. Many cecidomyiids (57 %), almost all Hemiptera (87 %), the majority of the Coleoptera (75 %), and all Lepidoptera, Thysanoptera and Hymenoptera records are presented at suprageneric categories. The same is true to associated arthropod fauna as already commented. Perhaps the explanation lies on the facts that the main objective of the studies is to provide data on diversity of insect galls and ecological issues; that most studies do not attempt to rear the inducers, and to the fact that the amount of taxonomists is not enough to identify them.

17.3.6 Dipterous Galls

At least, eight families of Diptera comprise galling species: Cecidomyiidae, Agromyzidae, Chloropidae, Fergusoninidae, Tephritidae, Lauxaniidae, Lonchaeidae, and Anthomyiidae, being the cecidomyiids the most common one in all biogeographic regions (Felt 1940). In restingas, two dipteran families have been recorded as gall-inducing: Tephritidae and Cecidomyiidae. Tephritidae (with 5,000 spp.) are best known as fruit pests (Foote and Steyskal 1987). There is only one record of Tephritidae gall, and about 295 records of Cecidomyiidae galls. The Tephritidae species induces stem or bud galls on *Vernonia beyrichii* (Asteraceae) (Fig. 17.3).

Cecidomyiidae, commonly known as gall midges, is the fourth family of Diptera in species richness (Brown 2009). It is cosmopolitan and diverse, with more than 6,000 described species (Gagné 2010). The great majority of them (about 90 %) are gall-inducing, but fungivorous, free-living phytophagous, predaceous and parasitic species are also found.

The gall midges are associated with 48 host plant families, what corresponds to 78 % of the total number of attacked plant (Table 17.10). Myrtaceae, Fabaceae, Asteraceae, and Melastomataceae were the plant families with the greatest richness of Cecidomyiidae galls (Fig. 17.3b–k). In spite of occurring on all plant organs, Cecidomyiidae galls are more common on leaves (with about 50 % of the records), followed by buds and stems (both with about 16 % of the records). This result probably reflects the high and frequent availability of leaves.

Eighty-seven Cecidomyiidae records are at species and 82 at genus level (Table 17.11). Forty-two genera of Cecidomyiidae were found in restingas, being *Clinodiplosis* Kieffer, 1895, *Neolasioptera* Felt, 1908, *Lopesia* Rübsaamen, 1908, *Asphondylia* Loew, 1850 and *Dasineura* Rondani, 1840 the best represented, with 30, 15, 16, 16, and 12 species, respectively. These genera, excepting *Lopesia*, are widespread and are the most diversified of the family with 102, 134, 18, 289 and 466 described species (Gagné 2010). All are represented by determined and not determined species. The last ones probably correspond to new species, considering the specificity of host plants and gall morphotypes, what shows that they are more diversified than the current knowledge indicates. *Contarinia* is also one of the most diversified genera of gall midges, being cosmopolitan, but it is poorly represented in restinga areas.

17.3.7 Hemipterous Galls

Hemiptera is a wide-spread group with 100,000 species distributed in 145 families and four suborders, namely: Auchenorrhyncha, Sternorryncha, Coleorrhyncha, and Heteroptera. There are about 42,500 species of Heteroptera in 2,600 genera (Gullan and Cranston 2010). Hemiptera mouthparts are adapted for sucking. Adults generally feed on plant sap while others are gall-inducing or predators. Many species have medical importance as plant pests or disease vectors (Triplehorn and Johnson 2005; Gullan et al. 2005).

About 135 hemipteran galls are known from Latin America, and the galling species belong to four families: Psyllidae, Aphididae, Brachyscelidae, and Coccidae. According to Maia (2006), 44 Psyllidae galls and 21 Coccidae galls have been recorded from Brazil.

In Brazilian restingas, 15 plant species host a total of 15 hemipteran galls. These hosts are distributed in eight plant families. The number of morphotypes per plant

Table 17.10 Host plants and description of cecidomyiids galls morphotypes found in Brazilian restinga

Host plant family	Host plant species	Galled organ	Gall shape	Color	Trichomes	Number of internal chambers	Galler	Locality	Figures and references
Anacardiaceae	*Tapirira guianensis* Aubl.	Leaf	Conical	Green	Absent	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)
Annonaceae	*Rollinia sericea* R. E. Fr.	Closed flower	Ovoid	?	Absent	?	*Clinodiplosis* sp. (Cecidomyiidae)	BER	No fig. Maia et al. (2008)
Apocynaceae	*Aspidosperma parvifolium* A. DC	Flower bud	Ovoid	Green	Absent	1	Cecidomyiidae	GRU	No fig. Oliveira and Maia (2005)
	Forsteronia leptocarpa (Hook. and Arn). A. DC.	Leaf	Conical	Green	Absent	1	Cecidomyiidae	BER	Fig. 4 Maia et al. (2008)
	Madevilla funiformis (Vell.) K. Schum.	Bud	?	?	?	?	Cecidomyiidae	MAR	No fig. Monteiro et al. (1994)
Aquifoliaceae	*Ilex pseudobuxus* Reissek	Bud	Flattened	Green	Absent	Various	Cecidomyiidae	BER	Fig. 5 in Maia et al. (2008)
		Stem	Globose	Brown	Absent	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)
	Ilex theezans Mart.	Leaf	Circular (parenchymatical)	Green	Absent	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)
		Stem	Globoid	Brown	Absent	1	Cecidomyiidae	BER	Fig. 7 in Maia et al. (2008)
	Ilex sp.	Bud	Spherical	Green	Absent	1	Cecidomyiidae	PS PEPCV	Fig. 4 in Maia and Oliveira (2010), Fig. 20 in Bregonci et al. (2010)

Araceae	*Philodendron appendiculatum* Nadruz and Mayo	Root	Ovoid	Brown	Absent	1	Cecidomyiidae (Diptera)	BER	Fig. 9 in Maia et al. (2008)
Asclepiadaceae	*Peplonia asteria* (Veil.) Font. and Schw	Closed flower	Ovoid	Green	Absent	1	*Asphondylia peploniae* Maia, 2001 (Cecidomyiidae)	MAR CAR	Fig. 5 in Maia (2001a, b)
		Leaf	Leaf roll	Red	Absent	1	*Clinodiplosis* sp. (Cecidomyiidae)	CAR	Fig. 4 in Maia (2001a)
	Oxypetalum banksii	Closed flower	Ovoid	Green	Absent	1	*Asphondylia* sp.	AR MAR JU	No fig. Monteiro et al. (1994, 2004)
Asteraceae	*Baccharis conyzoides* DC	Leaf	Globose	Black	Absent	1	*Asphondylia* sp. (Cecidomyiidae)	BER	Fig. 11 in Maia et al. (2008)
	Baccharis singularis (Vell.) G.M. Barroso	Bud	Ovoid	Green	Absent	1	*Neolasioptera* sp. (Cecidomyiidae)	BER	Fig. 14 in Maia et al. (2008)
	Baccharis speciosa DC	Stem or bud	Fusiform	Brown	Absent	1	Alycaulini (Cecidomyiidae)	BER	No fig. Maia et al. (2008)
	Mikania argyreiae DC	Stem	Fusiform	Brown	Absent	1	Cecidomyiidae	BER	Fig. 15 in Maia et al. (2008)
	Mikania cf. *biformis* DC	Leaf	Globose	Green	Absent	1	*Liodiplosis spherica* Gagné, 2001 (Cecidomyiidae)	BER	No fig. Maia et al. (2008)
		Stem	Fusiform	Green	Absent	1	*Mikaniadiplosis annulipes* Gagné, 2001 Cecidomyiidae	BER	No fig. Maia et al. (2008)
		Stem	Fusiform	Green	Absent	1	*Asphondylia moehni* Skuhravá, 1989 (Cecidomyiidae)	BER	No fig. Maia et al. (2008)

(continued)

Table 17.10 (continued)

Host plant family	Host plant species	Galled organ	Gall shape	Color	Trichomes	Number of internal chambers	Galler	Locality	Figures and references
		Leaf	Conical	Green	Absent	1	*Liodiplosis conica* Gagné, 2001	BER	Fig. 17 in Maia et al. (2008)
		Leaf	Circular	Green	Absent	1	*Alycaulus globulus* Gagné, 2001	BER	No fig. Maia et al. (2008)
		Leaf (vein or petiole)	Fusiform	Green	Absent	1	*Asphondylia glomeratae* Gagné, 2001 (Cecidomyiidae)	BER	No fig. Maia et al. (2008)
		Leaf	Cylindrical	Green	Absent	1	*Liodiplosis cylindrica* Gagné 2001 (Cecidomyiidae)	BER	Fig. 18 in Maia et al. (2008)
		Bud	Spherical	Green	Absent	Various	*Perasphondylia mikaniae* Gagné, 2001 (Cecidomyiidae)	BER	Fig. 19 in Maia et al. (2008)
	Mikania cf. *glomerata* Spreng.	Leaf	Circular	Green	Absent	1	*Alycaulus globulus* Gagné, 2001	GRU	No fig. Oliveira and Maia (2005)
		Stem	Globose	Green	Absent	1	*Asphondylia moehni* Skuhravá, 1989	GRU	No fig. Oliveira and Maia (2005)
		Leaf (vein or petiole)	Fusiform	Green	Absent	1	*Asphondylia glomeratae* Gagné, 2001 (Cecidomyiidae)	BER	No fig. Maia et al. (2008)
		Leaf	Conical	Green	Absent	1	*Liodiplosis conica* Gagné, 2001	GRU	No fig. Oliveira and Maia (2005)
		Bud	Spherical	Green	Absent	Multichambered	*Perasphondylia mikaniae* Gagné, 2001 (Cecidomyiidae)	PT	Fig. 8 in Gagné et al. (2001)
		Leaf	Globose	Green	Absent	1	*Liodiplosis spherica* Gagné, 2001 (Cecidomyiidae)	PT BER	Fig. 7 in Gagné et al. (2001), Maia et al. (2008)

	Leaf	Cylindrical	Green	Absent	1	*Liodiplosis cylindrica* Gagné 2001 (Cecidomyiidae)	PT	Fig. 5 in Gagné et al. (2001)
	Leaf (petiole)	Fusiform	Green	Absent	1	*Clinodiplosis* sp. (Cecidomyiidae)	BER	No fig. Maia et al. (2008)
Mikania hoehnei Robinson	Leaf	Leaf roll	Green	Absent	1	*Clinodiplosis* sp. (Cecidomyiidae)	MAR	Fig. 6 in Maia (2001a)
	Stem	Ovoid	Brown or green	Absent	1	*Alycaulus* sp. (Cecidomyiidae)	AC MAR	Fig. 7 in Maia (2001a), Monteiro et al. (1994)
Mikania involucrata Hook. and Arn.	Stem	Fusiform	Brown	Absent	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)
Mikania cf. *micrantha* Kunth.	Leaf (midvein or petiole)	Fusiform	Green	Absent	1	*Alycaulus trilobatus* Möhn, 1964 (Cecidomyiidae)	BER	No fig. Maia et al. (2008)
Mikania ternata (Vell.) B.L. Rob.	Bud	Spherical	Green	Absent	1	Lopesiini (Cecidomyiidae)	BER	Fig. 20 in Maia et al. (2008)
Mikania sp.	Stem	Fusiform	Green	Absent	1	*Mikaniadiplosis annulipes* Gagné, 2001 Cecidomyiidae	PS	Fig. 7 in Maia and Oliveira (2010)
	Leaf	Spheroid	Green	Absent	1	*Liodiplosis spherica* Gagné, 2001 Cecidomyiidae	PS	Fig. 8 in Maia and Oliveira (2010)
	Leaf	Cylindrical	Green	Absent	1	*Liodiplosis cylindrica* Gagné, 2001 Cecidomyiidae	PS	No fig. Maia and Oliveira (2010)
	Leaf/stem	Conical	Green	Absent	1	*Liodiplosis conica* Gagné, 2001 Cecidomyiidae	PS	Fig. 9 in Maia and Oliveira (2010)

(continued)

Table 17.10 (continued)

Host plant family	Host plant species	Galled organ	Gall shape	Color	Trichomes	Number of internal chambers	Galler	Locality	Figures and references
	Piptocarpha cf. *cinerea* Baker	Stem/bud/leaf (vein)	Ovoid	Brown	Absent	1	Cecidomyiidi (Cecidomyiidae)	BER	Fig. 22 in Maia et al. (2008)
		Bud/stem/leaf (petiole)	Globose	Brown	Absent	1	*Asphondylia* sp. (Cecidomyiidae)	BER	Fig. 23 in Maia et al. (2008)
	Vernonia rufogrisea	Bud	Spherical	Yellowish	Present	1	*Asphondylia* sp. (Cecidomyiidae)	CAR	Fig. 8 in Maia (2001a)
Avicenniaceae	*Avicennia schaueriana* Stapf and Leechm. ex Moldenke	Leaf	Spheroid	Yellowish	Absent	1	Cecidomyiidae	CF BER	No fig. Maia et al. (2008)
Bignoniaceae	*Anemopaegma chamberlaynii* (Sims) Bureau and K. Schum.	Stem/leaf (petiole or vein)	Fusiform	Green	Absent	1	*Neolasioptera*	BER	Fig. 25 in Maia et al. (2008)
	Fridericia conjugata (Vell.) Mart.	Leaf	Conical	Green	Absent	1	*Arrabidaeamyia serrata* Maia, 2001	GRU MAR CAR AC	Fig. 9 in Maia (2001a, b), Oliveira and Maia (2005), Monteiro et al. (1994)
		Stem, tendril or leaf (midvein)	Fusiform	Green	Absent	1	*Neolasioptera* sp. (Cecidomyiidae)	MAR, CAR, GRU, AC	Fig. 10 in Maia (2001a), Oliveira and Maia (2005), Monteiro et al. (1994)
		Flower (ovary)	Globose	Purple	Absent	1	Cecidomyiidae	MAR	No fig. Maia (2001a)
	Lundia virginalis DC. var. *nitidula*	Stem	–	–	–	–	*Clinodiplosis* sp. Cecidomyiidae	BER	Maia et al. (2008)
	Parabignonia unguiculata (Vell.) A.H. Gentry	Leaf	Circular	Green	Absent	1	Cecidomyiidae	BER	Fig. 26 in Maia et al. (2008)
	Tabebuia sp.	Leaf	Leaf roll	Green	Absent	1	*Clinodiplosis* sp. Cecidomyiidae	BER	Fig. 29 in Maia et al. (2008)

Boraginaceae	*Cordia curassavica* (Jacq.) Roem. and Schult.. (=*Cordia verbenaceae* D.C.)	Leaf	Globose	Green	Present	1	*Cordiamyia globosa* Maia, 1996 (Cecidomyiidae)	PEPCV BER JU MAR CAR AC	Fig. 11 in Maia (2001a), Bregonci et al. (2010), Monteiro et al. (1994)
		Closed flower	Ovoid	Green or yellow	Present	1	*Asphondylia cordiae* Möhn, 1975	MAR, CAR CF	Fig. 12 in Maia (2001a)
		Leaf (petiole or midvein)	Fusiform	Green	Present	1	Lopesiini (Cecidomyiidae)	MAR, CAR, CF	Fig. 13 in Maia (2001a)
	Cordia sellowiana Cham.	Leaf	Spherical	Brown	Present	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)
Burseraceae	*Protium brasiliense*	Leaf	Marginal leaf roll	Green	Absent	1	*Lopesia maricaensis* Rodrigues and Maia, 2010 (Cecidomyiidae)	MAR	Fig. 15 in Maia (2001a), Maia et al. (2002a, b), Rodrigues and Maia (2010)
		Leaf	Conical	Green	Absent	1	Cecidomyiidae	MAR	Fig. 14 in Maia (2001a)
	Protium heptaphyllum	Leaf	Ovoid	Green	Absent	1	*Dactylodiplosis heptaphylli* Maia, 2004 (Cecidomyiidae)	CAR AC MAR JU	Fig. 16 in Maia (2001a), Narahara et al. (2004)
		Leaf	Marginal roll	Green	Absent	1	*Lopesia similis* Maia, 2004 (Cecidomyiidae)	CAR	Fig. 17 in Maia (2001a), Narahara et al. (2004)
	Protium icicariba (DC.) Marchand	Leaf	Conical	Green	Absent	1	*Dactylodiplosis icicaribae* Maia, 2002 (Cecidomyiidae)	PEPCV CAR JU	Fig. 18 in Maia (2001), Maia et al. (2002a, b), Bregonci et al. (2010)
		Leaf	Marginal roll	Green	Absent	1	*Lopesia simplex* Maia, 2002 (Cecidomyiidae)	BER PEPCV	Fig. 19 in Maia (2001), Maia et al. (2002a, b), Bregonci et al. (2010)

(continued)

Table 17.10 (continued)

Host plant family	Host plant species	Galled organ	Gall shape	Color	Trichomes	Number of internal chambers	Galler	Locality	Figures and references
		Fruit	Kidney shaped (lateral view),	Green or red	Absent	1	Cecidomyiidae	CAR	Fig. 20 in Maia (2001a)
		Leaf	Ovoid	Green	Absent	1	Cecidomyiidae	CAR	Maia (2001a)
Cactaceae	*Selenicereus setaceus* (SD) Berg	Stem	Spheroid	Green	Absent	Various	*Neolasioptera cerei* Rübsaamen, 1905 Cecidomyiidae	PS JU MAR	Fig. 21 in Maia (2001a), Fig. 10 Maia and Oliveira (2010)
Celastraceae	*Elachyptera micrantha* (Cambess.) A.C. Sm.	Leaf/bud	Globose with apical conical projection	Green	Absent	1	Cecidomyiidae	BER	Fig. 35 in Maia et al. (2008)
	Maytenus obtusifolia Mart.	Leaf	Circular	Green or yellow	Absent	1	*Mayteniella distincta* Maia, 2001 (Cecidomyiidae)	GRU AC MAR	Fig. 22 in Maia (2001a, b), Monteiro et al. (1994)
		Fruit	Ovoid	Red	Absent	2–3	*Bruggmanniella maytenuse* (Maia et al. 1992) (Cecidomyiidae)	MAR	Maia et al. (1992), Fig. 23 in Maia (2001a,b)
Chrysobalanaceae	*Couepia ovalifolia* (Schott) Benth.	Leaf	Circular	Green	Absent	1	*Dasineura couepiae* Maia, 2001 (Cecidomyiidae)	PEPCV MAR AC	Fig. 24 in Maia (2001a, b), Bregonci et al. (2010), Monteiro et al. (1994)
		Leaf	Marginal roll	Green	Absent	1	*Lopesia marginalis* Maia, 2001 (Cecidomyiidae)	MAR AC	Fig. 25 in Maia (2001a,b), Monteiro et al. (1994)
	Licania nitida Hook. f.	Stem	Fusiform	Brown	Absent	1	*Lopesia* sp. (Cecidomyiidae)	BER	Fig. 38 in Maia et al. (2008)
Clethraceae	*Clethra scabra* Pers. var. *laevigata* (Meisn.) Sleumer	Stem	Fusiform	?	Absent	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)
		Bud	Globose	Green	Absent	1	*Clinodiplosis* sp. (Cecidomyiidae)	BER	No fig. Maia et al. (2008)

Clusiaceae	*Calophyllum brasiliense* Cambess.	Leaf	Spheroid	Green	Absent	1	*Lopesia conspicua* Maia, 2002 (Cecidomyiidae)	BER JU	Fig. 34a, b in Madeira et al. (2002), Monteiro et al. (2004), Lima et al. (2000)
		Leaf	Elliptical	Green	Absent	1	*Lopesia elliptica* Maia, 2002 (Cecidomyiidae)	CAR BER	Fig. 51a, b in Madeira et al. (2002), Monteiro et al. (2004), Lima et al. (2000)
		Leaf	Linear	Green	Absent	1	*Lopesia linearis* Maia, 2002 (Cecidomyiidae)	CAR BER	Fig. 67a, b in Madeira et al. (2002), Monteiro et al. (2004), Lima et al. (2000)
		Stem	Ovoid	Brown	Absent	1	*Lopesia caulinaris* Maia, 2002 (Cecidomyiidae)	CAR BER	Fig. 17a, b in Madeira et al. (2002), Monteiro et al. (2004), Lima et al. (2000)
		Bud	Spheroid	Brown	Absent	1–8	*Contarinia gemmae* Maia, 2003 (Cecidomyiidae)	CAR BER	Fig. 83 in Madeira et al. (2002), Monteiro et al. (2004)
	Clusia hilariana Schltdl.	Leaf	Circular	Green	Absent	1	*Clusiamyia granulosa* Maia, 2001 (Cecidomyiidae)	CAR PEPCV	Fig. 27 in Maia (2001a, b), Fig. 11 Bregonci et al. (2010)
	Clusia fluminensis Planch. and Trian	Leaf	Circular	Green	Absent	1	*Parazalepidota clusiae* Maia, 2001 (Cecidomyiidae)	GRU MAR AC	Fig. 26 in Maia (2001a, b), Oliveira and Maia (2005), Monteiro et al. (1994)

(continued)

Table 17.10 (continued)

Host plant family	Host plant species	Galled organ	Gall shape	Color	Trichomes	Number of internal chambers	Galler	Locality	Figures and references
	Clusia lanceolata	Leaf	Blister	Green or red	Absent	1	*Clusiamyia nitida* Maia, 1996 (Cecidomyiidae)	MAR AC	Maia (1996), Fig. 28 in Maia (2001a), Monteiro et al. (1994)
Commelinaceae	*Commelina diffusa* Burm. f.	Stem	Fusiform	?	Absent	1	*Clinodiplosis* sp. (Cecidomyiidae)	BER	No fig. Maia et al. (2008)
Convolvulaceae	*Jacquemontia holosericea* (Weinman) O'Donell	Closed flower	Ovoid	Green	Present	1	*Schizomyia santosi* Maia and Araújo, 2009 (Cecidomyiidae)	MAR	Fig. 29 in Maia (2001a), Maia and Araújo (2009)
Eleaocarpaceae	*Sloanea guianensis* (Aubl.) Benth.	Leaf	Circular				Cecidomyiidae	BER	No fig. Maia et al. (2008)
		Leaf	Marginal leaf roll foliar				*Clinodiplosis* sp. (Cecidomyiidae)	BER	No fig. Maia et al. (2008)
Erythroxylaceae	*Erythroxylum amplifolium* (Mart.) O.E. Schulz	Bud	Conical	Green with brown apex	Absent	1	*Lopesia* sp. (Cecidomyiidae)	BER	Fig. 46 in Maia et al. (2008)
	Erythroxylum ovalifolium Peyr	Bud	Conical	Green	Absent	1	*Lopesia eryhtroxyli* Rodrigues and Maia, 2010 (Cecidomyiidae)	PS GRU MAR CAR AC	Fig. 33 in Maia (2001a), Fig. 11 Maia and Oliveira (2010), Monteiro et al. (1994), Rodrigues and Maia (2010), Oliveira and Maia (2005)
		Leaf	Triangular	Green	Absent	1	*Dasineura ovalifoliae* Fernandes and Maia, 2011 Cecidomyiidae	MAR GRU AC	Fig. 30 in Maia (2001a), Fig. 15 em Fernandes and Maia (2011), Oliveira and Maia (2005), Monteiro et al. (1994)

		Leaf	Marginal leaf roll	Green	Absent	1	Cecidomyiidae	PS	Fig. 12 in Maia and Oliveira (2010)
		Closed flower	Ovoid	Greenish	Absent	1	*Asphondylia* sp. (Cecidomyiidae)	MAR, CAR GRU	Fig. 31 in Maia (2001a), Oliveira and Maia (2005)
		Young leaf	Leaf roll	Greenish	Absent	1	*Clinodiplosis* sp. Cecidomyiidae	MAR, CAR	Fig. 32 in Maia (2001a), Oliveira and Maia (2005)
		Fruit	Ovoid	Brownish	Absent	1	Cecidomyiidae	GRU	No fig. Oliveira and Maia (2005)
Euphorbiaceae	*Alchornea triplinervia* (Spreng.) Müll. Arg.	Stem	Fusiform	?	Absent	Multi-chambered	Cecidomyiidae	BER	No fig. Maia et al. (2008)
	Dalechampia leandrii Baill.	Bud	Cylindrical	Green	Present	1	Schizomyiina (Cecidomyiidae)	PS BER	Fig. 13 in Maia and Oliveira (2010), Fig. 47 in Maia et al. (2008)
	Manihot sp.	Leaf	Cylindrical	Green or red	Absent	1	*Iatrophobia brasiliensis* Rübsaamen, 1916 (Cecidomyiidae):	BER	Fig. 48 in Maia et al. (2008)
	Pera glabrata (Schott) Poepp. ex Baill.	Bud	Ovoid	Green	Absent	1	Cecidomyiidae	BER	Fig. 49 in Maia et al. (2008)
	Sebasliania glandulosa	Bud	Globose	?	Absent	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)
		Bud	Conical	Red	Absent	1x	*Clinodiplosis conica* Oliveira and Maia, 2008 (Cecidomyiidae)	MAR CAR	Fig. 35 in Maia (2001a), Oliveira and Maia (2008)

(continued)

Table 17.10 (continued)

Host plant family	Host plant species	Galled organ	Gall shape	Color	Trichomes	Number of internal chambers	Galler	Locality	Figures and references
		Bud	Spherical	Green or yellow	Absent	1	*Schizomyia spherica* Maia and Oliveira, 2007 (Cecidomyiidae)	MAR, CAR, AC	Fig. 36 in Maia (2001a), Monteiro et al. (1994)
		Leaf	Marginal leaf roll	Green	Absent	1	*Dasineura* sp. (Cecidomyiidae)	MAR, CAR	Fig. 37 in Maia (2001a), Maia and Oliveira (2010)
Fabaceae	*Abarema brachystachya* (DC.) Barneby and J.W. Grimes	Leaf	Marginal leaf roll	Green	Absent	1	Cecidomyiidae	BER	Fig. 51 in Maia et al. (2008)
	Andira fraxinifolia Benth.	Leaf	Vermiform	Green	Absent	1	Cecidomyiidae	BER	Fig. 52 in Maia et al. (2008)
		Leaf	Globose	Yellow	Absent	1	*Meunieriella* sp. (Cecidomyiidae)	MAR	Fig. 53 in Maia et al. (2002a, b)
	Andira nitida Mart. ex Benth	Leaf	Circular	Green	Absent	1–3	Cecidomyiidae	PEPCV	Fig. 6 in Bregonci et al. (2010)
		Leaf	Marginal leaf roll	Green	Absent	1	Cecidomyiidae	PEPCV	Fig. 7 Bregonci et al. (2010)
	Dalbergia ecaslophylla L. Taub	Leaf	Discoid	Green	Absent	1	*Lopesia grandis* Maia, 2001 Cecidomyiidae	MAR CAR PS JU	Fig. 39 in Maia 2001a, b, c, Fig. 14 in Maia and Oliveira (2010)
	Dalbergia frutescens (Vell.) Britton	Leaf	Discoid	Green	Absent	1	*Lopesia grandis* Maia, 2001 Cecidomyiidae	BER	Fig. 54 in Maia et al. (2008)
	Inga edulis Mart.	Leaf (vein)	Globoid	Brown	Absent	1	*Neolasioptera* sp. (Cecidomyiidae)	BER	Fig. 57 in Maia et al. (2008)

Inga laurina (Sw.) Willd	Leaf (nervura central)	Fusiform	Brown	Absent	1	*Neolasioptera* sp. (Cecidomyiidae)	MAR	Fig. 1 in Maia et al. (2002a, b)
	Leaf	Cylindrical	Green	Absent	1	*Meunieriella* sp. (Cecidomyiidae)	MAR	Fig. 2 in Maia et al. (2002a, b)
Inga maritima Benth.	Stem or leaf (petiole or midvein)	Fusiform	Green	Absent	1	*Neolasioptera* sp. (Cecidomyiidae)	MAR GRU	Fig. 40 in Maia (2001a), Oliveira and Maia (2005)
Inga sellowiana Benth.	Leaf (vein)	Fusiform	Brown	Absent	1	(Lasiopteridi) Cecidomyiidae	BER	Fig. 60 in Maia et al. (2008)
	Leaf	Marginal leaf roll	Green	Absent	1	*Clinodiplosis* (Cecidomyiidae)	BER	Fig. 61 in Maia et al. (2008)
Inga sp.	Leaf	Spherical	Green	Absent	1	Cecidomyiidae	PS	Fig. 15 in Maia and Oliveira (2010)
	Leaf	Marginal leaf roll	Green	Absent	1	Cecidomyiidae	PT	New record
Machaerium uncinatum (Vell.) Benth.	Leaf	Leaf fold	Green	Absent	1	*Clinodiplosis* (Cecidomyiidae)	BER	Fig. 62 in Maia et al. (2008)
	Leaf	Globose	Yellow	Absent	1	Cecidomyiidae	BER	Fig. 63 in Maia et al. (2008)
Mimosa bimucronata (DC) Kuntze	Bud	Fusiform	Brown	Absent	1	*Contarinia* sp. Cecidomyiidae	GRU	No fig. Oliveira and Maia (2005)
Ormosia arborea (Vell.) Harms	Leaf	Circular	Green	?	?	Cecidomyiidae	JU	No fig. Monteiro et al. (2004)
Senna bicapsularis (L.)	Flower (ovary)	Globose	Yellow	Absent	1	*Asphondylia sennae*	MAR	No fig. Monteiro et al. (1994), Maia et al. (1992)
Stylosanthes guianensis	Inflorescence	–	–	–	–	*Lestodiplosis maricaensis* Santos and maia, 2008	MAR CAR JU	Fig. 41 in Maia (2001a)
Swartzia langsdorffii Raddi	Leaf	Circular	Yellowish	Absent	1	*Burseramyia braziliensis* Maia and Fonseca, 2011 (Cecidomyiida)	BER	Fig. 63 in Maia et al. (2008), Maia and Fonseca (2011)

(continued)

Table 17.10 (continued)

Host plant family	Host plant species	Galled organ	Gall shape	Color	Trichomes	Number of internal chambers	Galler	Locality	Figures and references
	Not determined	Leaf	Linear	Green	Absent	1	Cecidomyiidae	PS	Fig. 16 in Maia and Oliveira (2010)
Gesneriaceae	*Codonanthe gracilis* (Mart.) Hanst.	Leaf	Globose	?	Absent	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)
		Inflorescence	Fusiform	?	Absent	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)
		Aerial root	Fusiform	Brown	Absent	1	*Neolasioptera* sp. Cecidomyiidae	BER	No fig. Maia et al. (2008)
Lamiaceae	*Hyptis fasciculata* Benth. subsp. *fasciculata*	Stem/leaf (petiole, vein)	Fusiform	Brown	Absent	1	Cecidomyiidae	BER	Fig. 65 in Maia et al. (2008)
	Melissa officinalis	Leaf	Globose	Green	Present	1	*Clinodiplosis melissae* Maia, 1993	MAR	Fig. 12 in Maia (1993)
Lauraceae	*Ocotea notata*	Bud	Ovoid and with an apical spine-like projection	Green	Absent	1	Cecidomyiidae	CAR MAR	Fig. 38 in Maia (2001a)
Loranthaceae	*Phoradendron piperoides*	Leaf	Circular	Green/ yellowish	Absent	1	Cecidomyiidae	MAR	Monteiro et al. (1994)
	Psittacanthus dichrous	Leaf	Circular	Green	Absent	1	*Costadiplosis maricaensis* Viceconte and Maia 2009	MAR	Fig. 42 in Maia (2001a), Viceconte and Maia (2009)
	Struthanthus concinnus Mart.	Bud	Ovoid with filiform projections	Green	Absent	2	*Schizomyia* sp. Cecidomyiidae	BER	No fig. Maia et al. (2008)
	Sthruthanthus maricensis	Leaf (midvein)	Ovoid	Green	Absent	1	*Asphondylia maricensis* Maia et al. 1992 (Cecidomyiidae)	MAR	No fig. Maia et al. (1992), Maia (2001a)

	Byrsonima sericea	Leaf	Circular	Brown	Absent	1	*Dasineura byrsonimae* Maia, 2011 (Cecidomyiidae)	MAR CAR GRU PS PEPCV	Fig. 44 in Maia (2001a), Maia and Oliveira (2010), Maia (2011), Oliveira and Maia (2005) Bregonci et al. (2010)
		Stem	Spheroid	Brown	Absent	Various	Cecidomyiidae?	PS GRU PEPCV AC	Fig. 45 in Maia (2001a), Fig. 17 in Maia and Oliveira (2010), Oliveira and Maia (2005), Bregonci et al. (2010), Monteiro et al. (1994)
		Closed flower	Ovoid	Green or brown	Absent	2–3	*Bruggmanniella byrsonimae* (Maia et al. 1992) (Cecidomyiidae)	CAR, MAR, AC	Maia et al. (1992), Fig. 43 in Maia (2001a, b), Monteiro et al. (1994)
	Heteropteris nitida	Closed flower	–	–	–	–	*Clinodiplosis floricola* Novo-Guedes *and* Maia, 2008 (Cecidomyiidae)	MAR JU	Fig. 46 in Maia (2001a), Novo-Guedes and Maia (2008)
	Tetrapteris phtomoides	Bud gall	Rosette with small cylinders at the bottom;	Green	Absent	1	*Schizomyia maicaensis* Sousa and Maia, 2007 (Cecidomyiidae)	MAR	Fig. 47 in Maia (2001a), Sousa and Maia (2007)
Melastomataceae	*Clidemia neglecta* D. Don	Leaf	Globose	Green	Present	1	Cecidomyiidae	BER	Fig. 76 in Maia et al. (2008)
	Clidemia sp.	Leaf	Globose	Green	Present	1	Cecidomyiidae	PT	New record

(continued)

Table 17.10 (continued)

Host plant family	Host plant species	Galled organ	Gall shape	Color	Trichomes	Number of internal chambers	Galler	Locality	Figures and references
	Huberia ovalifolia DC.	Bud	Cylindrical	?	?	1	*Clinodiplosis* sp. Cecidomyiidae	BER	No fig. Maia et al. (2008)
	Leandra cf. *ionopogon* (Mart.) Cogn.	Leaf	Globose	Red	Present	1	*Lopesia* sp. Cecidomyiidae	BER	Fig. 77 in Maia et al. (2008)
	Miconia cinnamomifolia	Bud	Ovoid	Green	Absent	1–3	*Epihormomyia miconiae* Maia, 2001 (Cecidomyiidae)	CAR JU	Fig. 48 in Maia (2001a, b)
	Miconia fasciculata Gardner	Leaf	Globose	Brown	Absent	1	Cecidomyiidae	BER	Fig. 78 in Maia et al. (2008)
	Tibouchina pulchra Cogn.	Leaf	Globose	Green	Present	1	*Lopesia* sp. (Cecidomyiidae)	BER	Fig. 83 in Maia et al. (2008)
	Tibouchina trichopoda (DC.) Baill.	Leaf/stem	Globoid	?	Present	1	Lasiopteridi (Cecidomyiidae)	BER	No fig. Maia et al. (2008)
		Leaf (vein)	Fusiform	Green	Absent	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)
		Stem	Fusiform	Green	Absent	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)
Meliaceae	*Guarea macrophylla* Vahl subsp. tuberculata (Vell.) T.D. Penn.	Leaf	Globose	Red	Absent	1	*Guareamyia purpura* Maia, 2007 (Cecidomyiidae)	BER	Fig. 85 in Maia et al. (2008)
		Leaf	Globose	Yellow	Absent	1	*Sphaeromyia flava* Maia, 2007 (Cecidomyiidae)	BER	Fig. 86 in Maia et al. (2008)
		Leaf (vein)	Fusiform	Brown	Absent	1	*Neolasioptera* sp. (Cecidomyiidae)	BER	Fig. 87 Maia et al. (2008)

Moraceae	*Ficus enormis* (Mart. ex. Miq.) Miq.	Leaf	Circular	Yellow	Absent	1	Cecidomyiidae	BER	Fig. 89 in Maia et al. (2008)
	Ficus guaranitica Chodat ex Chodat and Vischer	Leaf	Marginal leaf oll	Green	Absent	1	*Clinodiplosis* sp. (Cecidomyiidae)	BER	Fig. 90 in Maia et al. (2008)
Myrsinaceae	*Myrsine ferruginea* Spreng.	Leaf	Circular	Yellow	Absent	1	Cecidomyiidae	BER	Fig. 91 in Maia et al. (2008)
	Myrsine parvifolia DC.	Leaf	Circular	Green	Absent	1	Cecidomyiidae	MAR CAR	Fig. 49 in Maia (2001a)
Myrtaceae	*Campomanesia guaviroba* (DC.) Kiaersk.	Leaf (vein)	Globoid	Green	Absent	1	*Clinodiplosis* (Cecidomyiidae)	BER	No fig. Maia et al. (2008)
	Eugenia adstringens Camb.	Leaf	Marginal leaf roll	Green	Absent	1	*Dasineura marginalis* Maia, 2005	MAR GRU BER JU	Fig. 58 in Maia (2001a), Monteiro et al. (2004), Oliveira and Maia (2005), Maia et al. (2005)
		Leaf	Circular	Yellow	Absent	1	*Dasineura globosa* Maia, 1995 (Cecidomyiidae)	MAR GRU AC	Monteiro et al. (1994), Fig. 59 in Maia (2001a), Oliveira and Maia (2005)
		Stem/leaf	Cylindrical	Brown	Absent	1	*Stephomyia rotundifoliorum* Maia, 1993 (Cecidomyiidae).	MAR AC JU	Monteiro et al. (1994), (2004), Fig. 60 in Maia (2001a)
		Leaf	Conical	Yellow	Absent	1	Cecidomyiinae	JU	Monteiro et al. (2004)
		Leaf	Pyriform	Yellow	Absent	1	Cecidomyiinae	JU	Monteiro et al. (2004)
		Leaf	Circular	Green	Absent	1	Lasiopteridi (Cecidomyiinae)	JU	Monteiro et al. (2004)
		Leaf	Claviform	Green or red	Absent	1	*Stephomyia clavata* Tavares, 1920	JU	Fig. A in Monteiro et al. (2004)

(continued)

Table 17.10 (continued)

Host plant family	Host plant species	Galled organ	Gall shape	Color	Trichomes	Number of internal chambers	Galler	Locality	Figures and references
	Eugenia copacabanensis	Leaf	Spiral	Green or red	Absent	1	*Stephomyia espiralis* Maia, 1993 (Cecidomyiidae)	MAR AC	Maia (1993), Monteiro et al. (1994), Fig. 50 in Maia (2001a)
		Leaf	Fusiform	Green or red	Absent	1	*Stephomyia tetralobae* Maia, 1993 (Cecidomyiidae)	MAR AC	Fig. 51 in Maia (2001a), Monteiro et al. (1994)
		Bud	Ovoid	Green	Absent	1	*Dasineura copacabanensis* Maia, 1992	AC	Fig. 7 in Maia (1992), Monteiro et al. (1994)
		Young leaf	–	–	–	–	*Dasineura* sp. (Cecidomyiidae)	MAR	No fig. Maia et al. (2002a, b)
	Eugenia multiflora	Stem	Cylindrical	Brown	Absent	1	*Stephomyia* sp. (Cecidomyiidae)	CAR	Fig. 52 in Maia (2001a)
		Leaf	Circular	Green	Absent	1	Lasiopteridi	CAR	Fig. 53 in Maia (2001a)
		Leaf	Marginal leafroll	Green	Absent	1	Cecidomyiinae	CAR	Fig. 54 in Maia (2001a)
		Leaf	Pyriform	Yellow	Absent	1	Cecidomyiinae		Fig. 55 in Maia (2001a)
		Leaf	Claviform	Green or red	Absent	1	*Stephomyia cfr. clavata* (Tavares, 1920) (Cecidomyiidae).	CAR	Fig. 56 in Maia (2001a)
		Leaf	Conical	Yellow	Absent	1	Cecidomyiinae	CAR	Fig. 57 in Maia (2001a)
		Leaf	?	?	?	?	Cecidomyiidae	AC	No fig. Monteiro et al. (1994)
		Fruit	?	?	?	?	Cecidomyiidae	MAR	No fig. Monteiro et al. (1994)
	Eugenia speciosa Cambess.	Leaf	Ovoid	Yellow	Absent	1	Schizomyiina (Cecidomyiidae)	BER	Fig. 93 in Maia et al. (2008)
		Leaf	Claviform	Green/ yellow	Absent	1	Schizomyiina (Cecidomyiidae)	BER	Fig. 94 in Maia et al. (2008)

Eugenia uniflora	Leaf	Circular	Green	Absent	1	*Neolasioptera eugeniae* Maia, 1993 Cecidomyiidae	MAR PS GRU CAR CF PT AC	Monteiro et al. (1994), Fig. 23 in Maia and Oliveira (2010), Oliveira and Maia (2005)
	Leaf	Conical	Green or red	Absent	1	*Clinodiplosis profusa* Maia, 2001	MAR GRU CF AC JU	Monteiro et al. (1994, 2004), Fig. 62 in Maia (2001a, b), Oliveira and Maia (2005)
	Fruit	Conical	Red	Absent	1	Cecidomyiinae	MAR	Fig. 64 in Maia (2001a)
	Closed flower	Conical	Red	Absent	1	Cecidomyiinae	GRU	No fig. Oliveira and Maia (2005)
Eugenia sp.	Leaf	Circular	Green	Absent	1	Cecidomyiidae	PS	Fig. 25 em Maia and Oliveira (2010)
	Leaf	Discoid	Yellow	Absent	1	Cecidomyiidae	GRU	No fig. Oliveira and Maia (2005)
	Leaf	Leaf roll	Green	Absent	1	Cecidomyiidae	GRU	No fig. Oliveira and Maia (2005)
Myrcia fallax (Rich.) DC.	Stem	Globoid	Brown	Absent	1	Oligotrophini (Cecidomyiidae)	BER	Fig. 100 in Maia et al. (2008)
	Leaf (vein)	Fusiform	Green	Absent	1	Oligotrophini (Cecidomyiidae)	BER	Fig. 101 in Maia et al. (2008)
	Bud	Globoid	Green	Absent	1	Lasiopteridi (Cecidomyiidae)	BER	No fig. Maia et al. (2008)
	Stem	Fusiform	Brown	Absent	Various	Cecidomyiidae	BER	No fig. Maia et al. (2008)
	Leaf/stem	Fusiform	Brown	Absent	?	Lasiopteridi (Cecidomyiidae)	BER	No fig. Maia et al. (2008)

(continued)

Table 17.10 (continued)

Host plant family	Host plant species	Galled organ	Gall shape	Color	Trichomes	Number of internal chambers	Galler	Locality	Figures and references
	Myrcia lundiana	Bud	Ovoid with longitudinal ridges extending from base to apex				*Myrciamyia maricaensis* Maia, 1995 (Cecidomyiidae)	JU	No fig. Monteiro et al. (2004)
		Flower (peduncle)	Ovoid	Green	Absent	1	Cecidomyiinae	JU	No fig. Monteiro et al. (2004)
	Myrcia multiflora (Lam.) DC.	Leaf	Globose	Yellow	Absent	1	*Dasineura* sp. (Cecidomyiinae)	MAR CAR	Fig. 65 in Maia (2001a), Maia et al. (2002a, b)
	Myrcia ovata	Bud	Ovoid with longitudinal ridges extending from base to apex	Yellow	Absent	1	*Myrciamyia maricaensis* Maia, 1995 (Cecidomyiidae)	MAR CAR AC	Monteiro et al. (1994), Fig. 66 in Maia (2001a)
		Flower (peduncle)	Ovoid	Green	Absent	1	Cecidomyiinae	MAR, CAR	Fig. 68 in Maia (2001a)
		Leaf (midvein)	Fusiform	Green	Absent	1	*Dasineura* sp. (Cecidomyiinae)	MAR	No fig. Maia et al. (2002a, b)
	Myrciaria floribunda (H. West ex Willd.)	Leaf	Marginal leaf roll	Green	Absent	1	*Dasineura myrciariae* Maia, 1993 (Cecidomyiidae)	MAR CAR PEPCV	Fig. 69 in Maia (2001a), Fig. 25 in Bregonci et al. (2010)
		Bud	Bivalve	Green or yellow	Absent	1	*Myrciariamyia bivalva* Maia, 1994 (Cecidomyiidae)	MAR CAR	Fig. 70 in Maia (2001a)
		Leaf	Stellate with a small cylinder in the middle	Green or yellow	Absent	1	Cecidomyiinae	CAR MAR (pers. communication) PEPCV	Fig. 71 in Maia (2001a), Fig. 24 in Bregonci et al. (2010)

Myrciaria jaboticaba (Vell.) Berg	Leaf	Marginal leaf roll	Green	Absent	1	Cecidomyiidae	PS	Fig. 20 in Maia and Oliveira (2010)
	Bud	Cylindrical	Green	Absent	1	Cecidomyiidae		Fig. 21 in Maia and Oliveira (2010)
Neomitranthes obscura Sobral and Zambom	Leaf	Marginal leaf roll	Green	Absent	1	*Dasineura tavaresi* Maia, 1993 (Cecidomyiidae) and *Clinodiplosis* sp. (Cecidomyiidae)	MAR CAR PEPCV AC	Monteiro et al. (1994), Fig. In 72 Maia (2001a), Bregonci et al. (2010)
	Leaf	Conical	Green or red	Absent	1	Cecidomyiinae	MAR CAR	Fig. 72 in Maia (2001a)
	Bud	Pine-like	Green	Absent	Without internal chamber	*Neomitranthella robusta* Maia, 1995 (Cecidomyiidae)	MAR CAR	Fig. 73 in Maia (2001a)
	Leaf	Conical	Green or red	Absent	1	*Stephomyia mina* Maia, 1993 (Cecidomyiidae)	MAR CAR	Fig. 74 in Maia (2001a)
Psidium cattleyanum Sabine	Leaf/bud	Spheroid	Amarela	Absent	1	Cecidomyiidae	PS	Fig. 27 em Maia and Oliveira (2010)
	Leaf	Cylindrical	Green	Absent	1	Lasiopteridi (Cecidomyiidae)	BER	Fig. 104 in Maia et al. (2008)
	Bud	Rosette of leaves	Green	Absent	1	*Dasineura gigantea* Angelo and Maia, 1999 (Cecidomyiidae).	BER	Fig. 105 in Maia et al. (2008)
	Leaf	Conical	Green	Absent	1	Cecidomyiidae	BER	Fig. 106 in Maia et al. (2008)
	Leaf	Circular	Green	Absent	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)

(continued)

Table 17.10 (continued)

Host plant family	Host plant species	Galled organ	Gall shape	Color	Trichomes	Number of internal chambers	Galler	Locality	Figures and references
Nyctaginaceae	*Guapira nítida* (Mart. ex Schmidt) Lundell	Leaf	Circular	Green	Absent	1	*Bruggmannia* sp. (Cecidomyiidae)	BER	No fig. Maia et al. (2008)
	Guapira opposita (Vell.) Reitz	Leaf	Circular	Green	Absent	1	*Bruggmannia elongata* Maia and Couri, 1993 Cecidomyiidae	MAR CAR PS AC BER	Monteiro et al. (1994), Fig.in 75 Maia (2001a), Fig. 108 in Maia et al. (2008), Fig. 28 em Maia and Oliveira (2010)
		Leaf	Globose	Red	Present	1	*Bruggmannia robusta* Maia and Couri, 1993 Cecidomyiidae	MAR CAR PS AC BER	Monteiro et al. (1994), Fig. 79 Maia (2001a), Fig. 107 in Maia et al. (2008) Fig. 29 in Maia and Oliveira (2010)
		Leaf	Conical	Green	Absent	1	*Bruggmannia acaudata* Maia, 2004 Cecidomyiidae	MAR CAR PS AC	Monteiro et al. (1994) Fig. 78 Maia (2001a), Fig. 30 em Maia and Oliveira (2010)
		Stem	Fusiform	Brown	Absent	1	*Proasphondylia guapirae* Maia and Couri, 1993 Cecidomyiidae	MAR CAR PS BER	Fig. 77 Maia (2001a), Fig. 31 em Maia and Oliveira (2010)
		Leaf	Rosette with tubular galls in the base	Green	Absent	1	*Pisphondylia braziliensis* Maia et al. 1992 (Cecidomyiidae)	MAR, JU BER	Fig. 76 Maia (2001a), Monteiro et al. (2004), Maia et al. (2008)
		Leaf/stem	Spherical	Red	Present	1	*Bruggmannia monteiroi* Maia and Couri, 1993 Cecidomyiidae	MAR	Fig. 31 in Maia and Couri (1993)

		Stem	Fusiform	Brown	Absent	?	*Bruggmannia* sp.	BER	No fig. Maia et al. (2008)
		Leaf	Globose	Green	Absent	1	Cecidomyiidae	BER	Fig. 109 in Maia et al. (2008)
	Guapira pernambucensis (Casar.) Lundell	Leaf	Circular	Green	Absent	1	Cecidomyiidae	GRU PEPCV	Oliveira and Maia (2005), Fig. 17 in Bregonci et al. (2010)
		Leaf	Globose	Green	Absent	1–3	Cecidomyiidae	PEPCV	Fig. 16 in Bregonci et al. (2010)
		Leaf/stem	Globose	Pink	Present	1	*Bruggmannia* sp. (Cecidomyiidae)	PEPCV	Fig. 18 in Bregonci et al. (2010)
Ochnaceae	*Ouratea cuspidata* (A. St.-Hil) Engl	Leaf	Circular	Amarela	Absent	1	Cecidomyiidae	PS	Fig. 32 em Maia and Oliveira (2010)
		Leaf	Cylindrical com projeção apical	Brown	Absent	1	Cecidomyiidae	MAR PS GRU PEPCV JU	Fig. 80 in Maia (2001a), Monteiro et al. (2004), Fig.in 33 em Maia and Oliveira (2010), Fig. 29 in Bregonci et al. (2010), Oliveira and Maia (2005)
Olacaceae	*Ximenia americana* L. var. *americana*	Stem	Ovoid	Brown	Absent	1	*Asphondylia communis* Maia and Couri, 1993 (Cecidomyiidae)	MAR	Fig. 81 in Maia (2001a)
Onagraceae	*Ludwigia octovalvis* (Jacq.) P.H. Raven	Bud	Cylindrical	Green	Hairy	1	*Clinodiplosis* sp. Cecidomyiidae)	BER	Fig. 110 in Maia et al. (2008)
Passifloraceae	*Passiflora mucronata* Lam.	Young leaf;	Leaf roll	Green	Absent	1	*Clinodiplosis* sp. (Cecidomyiidae)	MAR	Fig. 82 Maia (2001a)

(continued)

Table 17.10 (continued)

Host plant family	Host plant species	Galled organ	Gall shape	Color	Trichomes	Number of internal chambers	Galler	Locality	Figures and references
Phytolaccaceae	*Phitolacca* cfr. *esculenta* Van Houtte	Bud	Rosette	Green	?	?	Asphondyliina (Cecidomyiidae).	MAR	Fig. 3 in Maia et al. (2002a, b)
Piperaceae	*Peperomia glabella* (Sw.) A. Dietr.	Leaf	Circular	Green	Absent	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)
	Piper amalago	Stem	Fusiform	Green	Absent	1	Cecidomyiidae	GRU	No fig. Oliveira and Maia (2005)
	Piper divaricatum Meyer	Inflorescence	–	–	–	–	Cecidomyiidae	CAR	No fig. Maia (2001a)
Polygonaceae	*Coccoloba mosenii* Lindl.	Stem	Fusiform	Red	Absent	1	Cecidomyiidae	BER	Fig. 112 in Maia et al. (2008)
	Coccoloba cf. *warmingii* Meisn.	Leaf	Circular	Green	Absent	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)
Polypodiaceae	*Microgramma vacciniifolia* (Langsd. and Fisch.) Copel.	Stem	Globoid	Green	Present	1	*Primadiplosis microgrammae* Maia, 2011	MAR	Fig. 17 in Maia and Santos (2011)
Rubiaceae	*Borreria* cf. *ocymifolia* (Willd. ex Roem. and Schult.) Bacigalupo and E.L. Cabral	Stem	Fusiform	Green	Present	1	*Neolasioptera* sp. (Cecidomyiidae)	BER	Fig. 114 in Maia et al. (2008)
	Borreria verticillata (L.) Meyer	Inflorescence	Fusiform	Green	Absent	1	*Asphondylia borreriae* Rtibsaamen, 1905 (Cecidomyiidae)	MAR CAR AC	Fig. 83 in Monteiro et al. (1994), Maia (2001a)
	Diodia gymnocephala (DC.) K. Schum	Inflorescence	Fusiform	Green	Absent	1	*Clinodiplosis diodiae* Maia, 2001 (Cecidomyiidae)	CAR JU	Fig. 84 in Maia (2001a, b)

	Diodia radula (Will and Hoffmanns) Cham. and Schltdl.	Inflorescence	Fusiform	Green	Absent	1	Cecidomyiidae	GRU	No fig. Oliveira and Maia (2005)
	Psychotria carthagenensis Jacq.	Bud	Globoid	Green and pink	Absent	Various	Cecidomyiidae	BER	No fig. Maia et al. (2008)
	Psychotria hoffmannseggiana (Willd. and Hoffg. ex Roem. and Schult.) Müll. Arg.	Leaf	Globoid	Green	Absent	1	*Neolasioptera* sp. Cecidomyiidae	BER	Fig. 115 in Maia et al. (2008)
	Psychotria leiocarpa Cham. and Schltdl.	Leaf	Globoid	Green	Absent	1	*Dasineura* sp. (Cecidomyiidae):	BER	Fig. 116 in Maia et al. (2008)
Sapindaceae	*Matayba guianensis* Aubl.	Leaf	Conical	Green	Absent	1	*Paulliniamyia ampla* Maia, 2001 (Cecidomyidae)	BER	Fig. 118 in Maia et al. (2008)
	Paullinia weinmanniaefolia Mart.	Young leaf	Leaf roll	Green or yellow	Absent	1	*Clinodiplosis costai* Maia, 2005 (Cecidomyiidae)	MAR CAR	Fig. 85 in Maia (2001a), Maia (2005)
		Leaf	Conical	Green or yellow	Absent	1	*Paulliniamyia ampla* Maia, 2001 (Cecidomyiidae)	MAR CAR AC	Monteiro et al. (1994), Fig. In 86 Maia (2001a, b)
		Tendril	Fusiform	Brown	Absent	1	Cecidomyiinae	CAR	Fig. 87 Maia (2001a)
	Paullinia sp.	Leaf (vein/ petiole)/ tendril	Fusiform	Brown	Absent	1	*Neolasioptera* sp. (Cecidomyiidae)	BER	No fig. Maia et al. (2008)

(continued)

Table 17.10 (continued)

Host plant family	Host plant species	Galled organ	Gall shape	Color	Trichomes	Number of internal chambers	Galler	Locality	Figures and references
		Leaf	Leaf fold	Green	Absent	1	*Clinodiplosis costai* Maia, 2005 (Cecidomyiidae):	BER	Fig. 120 in Maia et al. (2008)
		Leaf	Elliptical	Green	Absent	1	*Neolasioptera* sp. (Cecidomyiidae))	(Cecido-myiidae))	Fig. 121 in Maia et al. (2008)
		Leaf	Conical	Green	Absent	1	Cecidomyiidae	BER	No fig. Maia et al. (2008)
		Leaf	Globose	Yellow	Absent	1	Cecidomyiidae	BER	Fig. 122 in Maia et al. (2008)
	Serjania communis Cambess.	Bud	Ovoid	Brown	Absent	Various	*Clinodiplosis* sp. Cecidomyiidae	BER	Fig. 123 in Maia et al. (2008)
	Urvillea stipitata Raldlk.	Leaf	Fusiform	Green	Absent	1	Cecidomyiinae	GRU	No fig. Oliveira and Maia (2005)
		Leaf	Conical	Green	Absent	1	Cecidomyiinae	GRU	No fig. Oliveira and Maia (2005)
		Bud	Ovoid	Green	Absent	1	Cecidomyiinae	GRU	No fig. Oliveira and Maia (2005)
Sapotaceae	*Bumelia obtusifolia*	leaf	?	?	?	?	Cecidomyiidae	MAR	No fig. Monteiro et al. (1994)
	Manilkara subsericea (Mart.) Dubard.	Leaf	Circular or elliptical	Green	Absent	1	Cecidomyiidae	MAR CAR PS GRU PEPCV AC	Monteiro et al. (1994), Fig. 88 in Maia (2001a), Fig. 34 in Maia and Oliveira (2010), Oliveira and Maia (2005), Bregonci et al. (2010)
		Bud	Spherical	Green	Absent	1	(Cecidomyiidae)	PEPCV	Fig. 23 in Bregonci et al. (2010)

		Bud	Ovoid bud gall with a spine-like projection at the apex;	Green	Absent	1–2	*Manilkaramyia notabilis* Maia, 2001 (Cecidomyiidae)	CAR AC	Monteiro et al. (1994), Fig. 89 in Maia (2001a, b)
		Leaf	Tubular	Yellow	Absent	1	Asphondylini	CAR AC	Monteiro et al. (1994), Fig. 90 in Maia (2001a)
	Pouteria caimito (R. and P.) Radlk. var. *laurifolia* (Gomes) Baehni	Leaf	Tubular	Green	Absent	1	*Youngomyia pouteriae* Maia, 2001 (Cecidomyiidae)	MAR GRU AC	Monteiro et al. (1994), Fig. 91 in Maia (2001a), Oliveira and Maia (2005)
	Pouteria venosa (Mart.) Baehni (= *Pouteria marginata*)	Leaf	Circular	Green	Absent	1	*Lopesia singularis* Maia, 2001 (Cecidomyiidae	MAR AC	Monteiro et al. (1994), Fig. 92 in Maia (2001a)
	Pouteria psammophyla (Mart) Radlk	Leaf	Circular	Green	Absent	1	*Lopesia singularis* Maia, 2001 (Cecidomyiidae	MAR GRU	Fig. 92 in Maia (2001a), Oliveira and Maia (2005)
Smilacaceae	*Smilax quinquenervia* Vell.	Leaf (vein)	Fusiform	Green	Absent	1	Cecidomyiidae	BER	Fig. 124 in Maia (2001a)
		Leaf	Circular	Green	Absent	1	Cecidomyiidae	BER	Fig. 125 in Maia (2001a)
	Smilax rufescens Griseb	Leaf	Circular	Green or yellow	Absent	1	*Smilasioptera candelariae* Mohn, 1975 (Cecidomyiidae)	CAR MAR GRU	Fig. 93 in Maia (2001a), Oliveira and Maia (2005)
		Leaf	Blister	Green	Absent	1	Cecidomyiinae	PEPCV	Fig. 33 in Bregonci et al. (2010)
		Fruit	–	–	–	–	*Clinodiplosis* sp. (Cecidomyiidae)	MAR	Fig. 94 in Maia (2001a)
		Leaf (midvein)	Fusiform	Green	Absent	1	Cecidomyiinae	MAR CAR GRU	Fig. 95 in Maia (2001a), Oliveira and Maia (2005)

(continued)

Table 17.10 (continued)

Host plant family	Host plant species	Galled organ	Gall shape	Color	Trichomes	Number of internal chambers	Galler	Locality	Figures and references
Solanaceae	*Aureliana fasciculata* (Vel!.) Sendth.	Young leaf	Leaf roll	Brownish	Absent	1	Cecidomyiinae.	CAR	Fig. 96 in Maia (2001a)
		Leaf	Elliptical	Green	Absent	1	Cecidomyiinae.	CAR	Fig. 97 in Maia (2001a)
		Stem	Fusiform	Green	Absent	1	*Asphondylia* sp. (Cecidomyiidae)	BER	Fig. 127 in Maia et al. (2008)
		Leaf (midvein)	Fusiform	Green	Absent	1	*Clinodiplosis* sp. Cecidomyiidae	BER	No fig. Maia et al. (2008)
	Solanum affine Sendth	Leaf	Globose	Yellow	Absent	1	Cecidomyiinae	MAR	Fig. 98 in Maia (2001a)
	Solanum curvispinum Dun.	Leaf	Globose	Yellow	Present	1	Cecidomyiidae	GRU	No fig. Oliveira and Maia (2005)
	Solanum inaequale Vel!.	Leaf	Globose	Green	Absent	1	Cecidomyiinae	CAR	Fig. 99 in Maia (2001a)
	Solanum aff. subscandens	Leaf	?	?	?	?	Cecidomyiidae	AC	No fig. Monteiro et al. (1994)
Theaceae	*Gordonia fruticosa* (Schrad.) H. Keng.	Bud	Ovoid	?	Absent	1	*Clinodiplosis* sp. Cecidomyiidae	BER	No fig. Maia et al. (2008)
		Leaf (vein)	Fusiform	?	Absent	1	*Neolasioptera* sp. Cecidomyiidae	BER	No fig. Maia et al. (2008)
Verbenaceae	*Lantana camara* L.	Leaf	Globose	Green	Present	1	*Schismatodiplosis lantanae* Riibsaamen, 1907 (Cecidomyiidae)	MAR	Fig. 100 in Maia (2001a)
	Lantana undulata Schrank	Leaf	Globose	Green	Present	1	*Clinodiplosis* sp. Cecidomyiidae	BER	Fig. 130 in Maia et al. (2008)

Locality: *BER* Bertioga (SP), *CAR* Carapebus (RJ), *CF* Cabo Frio (RJ), *GUA* Guarapari (ES), *MAR* Maricá (RJ), *PT* Paraty (RJ)

Table 17.11 Cecidomyiidae (Diptera) genera in Brazilian restingas

Cecidomyiidae genera	Species in Brazilian restingas	Localities	Nr. spp. in Brazil	Nr. spp. in the world
Alycaulus Rübsaamen 1916	*A. globulus* Gagné, 2001	BER GRU		
	A. tribolatus Möhn 1964	GRU		
	Sp. 1 (in *Mikania hoehnei*)	AC MAR		
	Total: 02 det. + 01 not det. =03		03	03
Arrabidaeamyia Maia, 2001	*A. serrata* Maia, 2001	GRU MAR CAR AC		
	Total: 01 (det.)		01	01
	A. borreriae Rübsaamen 1905	MAR CAR AC		
	A. communis Maia et al. 1992	MAR		
	A. cordiae Möhn 1959	MAR CAR CF		
	A. glomerata Gagné 2001	BER		
	A. maricensis Maia et al. 1992	MAR		
	A. moehni Skuhravá 1989	BER		
	A. peploniae Maia 2001	MAR CAR		
	A. sennae Maia et al. 1992	MAR		
	Sp. 1 (in *Oxypetalum banksii*)	AC MAR JU		
	Sp. 2 (in *Baccharis conyzoides*)	BER		
	Sp. 3 (in *Piptocarpha* cf. *cinerea*)	BER		
	Sp. 4 (in *Vernonia rufogrisea*)	CAR		
	Sp. 5 (in *Erythroxylum ovalifolium*)	MAR CAR GRU		
	Sp. 6 (in *Aureliana fasciculata*)	CAR		
	Total: 08 det. + 06 not det. = 14		21	289

(continued)

Table 17.11 (continued)

Cecidomyiidae genera	Species in Brazilian restingas	Localities	Nr. spp. in Brazil	Nr. spp. in the world
Bruggmannia Tavares 1906	*B. acaudata* Maia 2004	MAR CAR PS AC		
	B. elongata Maia and Couri 1993	MAR CAR PS AC BER		
	B. monteiroi Maia and Couri 1993	MAR		
	B. robusta Maia and Couri 1993	MAR CAR PS AC		
	Sp. 1 (in *Guapira niítida*)	BER		
	Sp. 2 (in *Guapira nitida*)	BER		
	Sp. 3 (in *Guapira opposita*)	PEPCV		
	Total: 04 det. + 03 not det. = 07		14	19
Bruggmanniella Tavares 1909	*B. byrsonimae* (Maia et al. 1992)	CAR MAR AC		
	B. maytenuse (Maia et al. 1992)	MAR		
	Total: 02 (det.)		07	10
Clinodiplosis Kieffer 1894	*C. conica* Oliveira and Maia 2008	MAR CAR		
	C. costai Maia 2005	MAR CAR BER		
	C. diodiae Maia, 2001	CAR JU		
	C. floricola Novo-Guedes and Maia 2008	MAR JU		
	C. melissae Maia 1994	MAR		
	C. profusa Maia 2001	MAR GRU CF AC JU		
	Sp. 1 (in *Rollinia sericea*)	BER		
	Sp. 2 (in *Peplonia asteria*)	MAR CAR		
	Sp. 3 (in *Mikania* cf. *glomerata*)	GRU		
	Sp. 4 (in *Mikania hoehnei*)	MAR		

	Sp. 5 (in *Lundia virginalis* DC. var. *nitidula*)	BER		
	Sp. 6 (in *Tabebuia* sp.)	BER		
	Sp. 7 (in *Clethra scabra* Pers. var. *laevigata*)	BER		
	Sp. 8 (in *Commelina diffusa*)	BER		
	Sp. 9 (in *Sloanea guianensis*)	BER		
	Sp. 10 (in *Erythroxylum ovalifolium*)	MAR CAR		
	Sp. 11 (in *Inga sellowiana*)	BER		
	Sp. 12 (in *Machaerium uncinatum*)	BER		
	Sp. 13 (in *Huberia ovalifolia*)	BER		
	Sp. 14 (in *Ficus guaranitica*)	BER		
	Sp. 15 (in *Campomanesia guaviroba*)	BER		
	Sp. 16 (in *Neomitranthes obscura*)	MAR		
	Sp. 17 (in *Ludwigia octovalvis*)	BER		
	Sp. 18 (in *Passiflora mucronata*)	MAR		
	Sp. 19 (in *Serjania communis*)	BER		
	Sp. 20 (in *Smilax rufescens*)	MAR		
	Sp. 21 (in *Aureliana fasciculata*)	CAR		
	Sp. 22 (in *Gordonia fruticosa*)	BER		
	Sp. 23 (in *Lantana undulata*)	BER		
	Total: 06 det. + 23 not det. = 29		16	102
Clusiamyia Maia, 1996	*C. granulosa* Maia, 2001	CAR PEPCV		
	C. nitida Maia 1996	MAR AC		
	Total: 02 (det.)		02	02
Contarinia Rondani 1860	*C. gemmae* Maia 2003	CAR BER		
	Sp. 1 (in *Mimosa bimucronata*)	GRU		
	Sp. 2 (in *Ouratea cuspidate*)	MAR PS GRU PEPCV JU		
	Total: 01 det. + 02 not det. = 03		02	311
Cordiamyia Maia, 1995	*C. globosa* Maia 1996	PEPCV BER JU MAR CAR AC		
	Total: 01 (det.)		01	01

(continued)

Table 17.11 (continued)

Cecidomyiidae genera	Species in Brazilian restingas	Localities	Nr. spp. in Brazil	Nr. spp. in the world
Costadiplosis Viceconte and Maia, 2009	*C. maricaensis* Viceconte and Maia, 2009	MAR		
	Total: 01 (det.)		01	01
Dactylodiplosis Rübsaamen 1916	*D. heptaphylii* Maia 2004	CAR AC MAR JU		
	D. icicaribae Maia 2004	PEPCV CAR JU		
	Total: 02 (det.)		03	03
Dasineura Rondani 1840	*D. byrsonimae* Maia, 2010	MAR CAR GRU PS PV		
	D. copacabanensis Maia 1993	AC		
	D. couepiae Maia, 2001	PEPCV MAR AC		
	D. gigantea Angelo and Maia 1999	BER		
	D. globosa Maia, 1996	MAR GRU AC		
	D. marginalis Maia 2005	MAR GRU BER JU		
	D. myrciariae Maia 1996	MAR CAR PEPCV		
	D. ovalifoliae Maia and Fernandes, 2011	MAR GRU AC		
	D. tavaresi Maia, 1996	MAR CAR PEPCV AC		
	Sp. 1 (in *Psychotria leiocarpa*)	BER		
	Sp. 2 (in *Sebastiania glandulosa*)	MAR CAR		
	Sp. 3 (in *Eugenia copacabanensis*)	MAR AC		
	Total: 09 det. + 03 not det. = 12		08	466
Epihormomyia Maia, 2001	*E. miconiae* Maia, 2001			
	Total: 01 (det.)		01	02
Eugeniamyia Maia, Mendonça and Romanowski, 1997	*E. dispar* Maia, Mendonça and Romanowski, 1997			
	Total: 01 (det.)		02	02
Guareamyia Maia 2007	*G. purpura* Maia 2007			
	Total: 01 (det.)		01	01
Iatrophobia Rübsaamen, 1916	*I. brasiliensis* Rübsaamen, 1916			
	Total: 01		01	01

Jorgenseniella Maia, 2005	*J. eugeniae* Maia, 2005			
	Total: 01		01	01
Liodiplosis Gagné, 2001	*L. spherica* Gagné, 2001	BER PT PS		
	L. cylindrica Gagné, 2001	BER PT PS		
	L. conica Gagné, 2001	GRU PS BER		
	Total: 03 (det.)		03	03
Lopesia Rübsaamen 1908	*L. caulinaris* Maia, 2003	CAR BER		
	L. conspicua Maia, 2003	BER JU		
	L. elliptica Maia, 2003	CAR BER		
	L. erythroxyli Rodrigues and Maia, 2010	PS GRU MAR CAR AC		
	L. grandis Maia, 2001	MAR CAR PS JU		
	L. linearis Maia, 2003	CAR BER		
	L. marginalis Maia, 2001	MAR AC		
	L. maricaensis Rodrigues and Maia, 2010	MAR		
	L. similis Maia, 2004	CAR		
	L. simplex Maia, 2002	BER PEPCV		
	L. singularis Maia, 2001	MAR AC		
	Sp. 1 (in *Licania nitida*)	BER		
	Sp. 2 (in *Leandra* cf. *ionopogon*)	BER		
	Sp. 3 (in *Tibouchina pulchra*)	BER		
	Sp. 4 (in *Erythroxylum amplifolium*)	BER		
	Total: 11 det. + 04 not det. = 15		15	18
Manilkaramyia Maia, 2001	*M. notabilis* Maia, 2001			
	Total: 01 (det.)		01	01
Mayteniella Maia, 2001	*M. distincta* Maia, 2001			
	Total: 01 (det.)		01	01
Meunieriella Rübsaamen, 1905	*Meunieriella* sp.			
	Total: 01 (not det.)		02	21
Mikaniadiplosis Gagné, 2001	*M. annulipes* Gagné, 2001			
	Total: 01 (det.)		01	01

(continued)

Table 17.11 (continued)

Cecidomyiidae genera	Species in Brazilian restingas	Localities	Nr. spp. in Brazil	Nr. spp. in the world
Myrciamyia Maia, 1996	*M. maricaensis*			
	Total: 01 (det.)		01	01
Myrciariamyia Maia, 1995	*M. bivalva* Maia, 1995			
	Total: 01 (det.)		03	03
Neolasioptera Felt, 1908	*N. cerei* (Rübsaamen, 1905)	PS JU MAR	07	134
	N. eugeniae Maia, 1993	MAR PS GRU CAR CFPT AC		
	Sp. 1 (in *Baccharis singularis*)	BER		
	Sp. 2 (in *Anemopaegma chamberlaynii*)	BER		
	Sp. 3 (in *Fridericia conjugata*)	MAR CAR GRU AC		
	Sp. 4 (in *Inga edulis*)	BER		
	Sp. 5 (in *Inga laurina*)	MAR		
	Sp. 6 (in *Inga maritima*)	MAR		
	Sp. 7 (in *Codonanthe gracilis*)	BER		
	Sp. 8 (in *Guarea macrophylla* Vahl subsp. tuberculata)	BER		
	Sp. 9 (in *Borreria* cf. *ocymifolia*)	BER		
	Sp. 10 (in *Psychotria hoffmannseggiana*)	BER		
	Sp. 11 (in *Paullinia* sp.)	BER		
	Sp. 12 (in *Paullinia* sp.)	BER		
	Sp. 13 (in *Gordonia fruticosa*)	BER		
	Sp. 14 (in *Nectandra oppositifolia*)	BER		
	Sp. 15 (in *Ocotea pulchella*)	BER		
	Total: 02 det. + 15 not det. = 17			
Neomitranthella Maia, 1996	*N. robusta* Maia, 1996	MAR CAR		
	Total: 01 (det.)		01	01

Parazalepidota Maia, 2001	*P. clusiae* Maia, 2001	GRU MAR AC		
	Total: 01 (det.)		01	01
Paulliniamyia Maia, 2001	*P. ampla* Maia, 2001	MAR CAR AC		
	Total: 01 (det.)		01	01
Perasphondylia Möhn, 1960	*P. mikaniae* Gagné, 2001	BER PT		
	Total: 01 (det.)		01	02
Pisphondylia Möhn, 1960	*P. braziliensis* Couri et al. 1992	MAR JU BER		
	Total: 01 (det.)		01	02
Primadiplosis Maia, 2011	*P. microgrammae* Maia, 2011	MAR		
	Total: 01 (det.)		01	01
Proasphondylia Felt, 1915	*P. formosa* Maia, 1994	MAR		
	P. guapirae Maia, 1994	MAR CAR PS BER		
	Total: 02 (det.)		03	03
Schizomyia Kieffer, 1889	*S. maricaensis* Sousa and Maia, 2007	MAR		
	S. spherica Maia and Oliveira, 2007	MAR CAR AC		
	S. santosi Maia and Araújo, 2009	MAR		
	Sp. 1 (in *Struthanthus concinnus*)	BER		
	Sp. 2 (in *Stachytarpeta* sp.)	GRU		
	Total: 03 det. + 02 not det. = 05		06	53
Sphaeramyia Maia, 2007	*S. flava*			
	Total: 01 (det.)		01	01
Stephomyia Tavares, 1916	*S. espiralis* Maia, 1994		06	07
	S. mina Maia, 1994			
	S. rotundifoliorum Maia, 1994			
	S. tetralobae Maia, 1994			
	S. cfr. clavata (Tavares, 1920)			
	Sp. 1			
	Sp. 2			
	Total: 05 det. + 02 not det. = 07			

(continued)

Table 17.11 (continued)

Cecidomyiidae genera	Species in Brazilian restingas	Localities	Nr. spp. in Brazil	Nr. spp. in the world
Schismatodiplosis Rübsaamen, 1916	*S. lantanae* Rübsaamen, 1916			
	Total: 01 (det.)		01	01
Smilasioptera Möhn, 1975	*S. candelariae* Möhn, 1975			
	Total: 01 (det.)		01	01
Youngomyia Felt 1908	*Y. pouteriae* Maia, 2001			
	Total: 01 (det.)		01	06
Total: 41	Total: 89 det. + 63 not det. = 152		Total: 145	Total: 1,673

Gagné (2010), Maia (2001a, b), Maia et al. (2002a, b, 2008), Maia and Oliveira (2010), Oliveira and Maia (2005), Bregonci et al. (2010), Fernandes and Maia (2011), Silva and Rodrigues (2011)

Det determined, *undet* undetermined, *AC* Arraial do Cabo (RJ), *BER* Bertioga (SP), *CAR* Carapebus (RJ), *GRU* Grumari (RJ), *JU* Jurubatiba (RJ), *MAR* Maricá (RJ), *PEPCV* Parque Estadual Paulo César Vinha (ES), *PS* Angra (RJ)

Table 17.12 Characterization of Hemipterous galls in Brazilian restingas

Host plant family (n = 8)	Host plant species (n = 15)	Plant organ	Galler	Locality
Anacardiaceae	*Astronium* sp.	Leaf	Coccoidea (Hemiptera)	MAR
	Schinnus terebinthifolius Raddi	Leaf	*Calophya terebinthifolii* Burckhardt and Basset, 2000 (Psyllidae, Hemiptera)	MAR PS
Apocynaceae	*Aspidosperma parvifolium* A. DC	Leaf	Psyllidae (Hemiptera)	GRU
	Aspidosperma pyricollum Muell. Arg	Leaf	Psyllidae (Hemiptera)	MAR PS
Aquifoliaceae	*Ilex theezans* Mart.	Leaf	Psyllidae (Hemiptera)	BER
Burseraceae	*Protium heptaphyllum*	Leaf	Psyllidae (Hemiptera)	MAR AC JU
	Protium icicariba (DC.) Marchand	Leaf	Psyllidae (Hemiptera)	PECPV JU
Euphorbiaceae	*Chaetocarpus myrsinites* Baill.	Leaf	Hemiptera	PEPCV
	Sebasliania glandulosa	Leaf	Hemiptera	AC
Lauraceae	*Ocotea lobbii* (Meisn.) Rohwer	Leaf	Coccidae (Hemiptera)	BER
	Ocotea notate	Leaf	Hemiptera	MAR PEPCV AC
	Ocotea pulchella (Nees) Mez	Leaf	Coccidae (Hemiptera)	BER
Myrtaceae	*Psidium cattleyanum* Sabine	Leaf	Hemiptera	PS
Smilacaceae	*Smilax quinquenervia* Vell	Leaf	Sternorrhyncha (Hemiptera)	BER
	Smilax rufescens Griseb	Leaf	Hemiptera	PS PEPCV MAR AC

Monteiro et al. (1994, 2004), Maia (2001a), Oliveira and Maia (2005), Maia et al. (2008), Bregonci et al. (2010)

BER Bertioga (SP), *MAR* Maricá (RJ), *AC* Arraial do Cabo (RJ), *PS* Angra (RJ), *PEPCV* Guarapari (ES)

family varied from one to three. The galls were recorded in all surveyed states: Rio de Janeiro (n = 24), São Paulo and Espírito Santo, each with four records (Maia 2001a; Maia et al. 2008; Oliveira and Maia 2005; Bregonci et al. 2010) (Table 17.12).

All the galls occur on leaves and 93 % are glabrous and one-chambered. Regarding the taxonomic level of gallers 33 % are identified at the order level, 46 % at family (Psyllidae) (Fig. 17.31), and only one record for suborder, superfamily and species (7 % each).

17.3.8 Lepidopteran Galls

Lepidoptera is a much diversified insect order, with about 160,000 species organized in more than 120 families (Pogue 2009). There are about 7,900 described species from Neotropics (Heppner 1991), being approximately 3,300 from Brazil (Brown and Freitas 1999). The majority of Lepidoptera larvae are phytophagous, with varied way of feeding. Free-living, leaf-miners, gallers and wood-boring species are known (Triplehorn and Johnson 2005). Some species live as inquilines in Cecidomyiidae (Diptera) galls (Maia 2006). Few are predators of other insects (Triplehorn and Johnson 2005).

In Latin America, 108 lepidopteran gall morphotypes have been recorded in 11 countries (Argentina, Bolivia, Brazil, Chile, Colombia, Costa Rica, República Dominicana, French Guyana, Peru, Puerto Rico and Uruguay). The gallers belong at least to six families: Cecidosidae, Cosmopterigidae, Diaschinidae, Gelechiidae, Momphidae, and Tortricidae (Maia 2006).

About 70 % of lepidopteran galls were recorded from Brazil, where the following families include galling species: Cecidosidae, Cosmopterigidae, Gelechiidae, and Momphidae (Maia 2006).

Lepidopteran galls have been mainly observed on stem, and rarely on leaf, as in Cosmopterigidae and *Mompha* sp. (Momphidae) (Maia 2006).

Brazilian restingas comprise few lepidopteran galls: 14 morphotypes on nine plant families. It represents about 13 % of the Brazilian records. As the number of morphotypes is low, we cannot point out any plant family preference (Table 17.13).

In Brazilian restingas, lepidopteran galls have been recorded mainly on stem (69 %), but also on bud (13 %), leaf (12 %) and flower bud (6 %) (Table 17.13), what corroborates the Neotropical pattern pointed by Houard (1933) (Fig. 17.3m). Concerning gall morphology, the predominance of the fusiform (about 80 %), glabrous and one-chambered galls (93 % each) has been observed. The locality records are restricted to Rio de Janeiro and São Paulo states, revealing the lack of taxonomic studies in other restinga areas (Table 17.13).

17.3.9 Coleopteran Galls

Coleoptera is probably the largest order of insects, with 350,000 described species in about 170 families. Beetles are in every conceivable habitat, including fresh water, a few marine and intertidal habitats, and, above all, every vegetation microhabitat from external foliage, flowers, buds, stem, bark, and roots, to internal sites such as in galls in any living plant tissue or in any kind of dead material in various stages of decomposition (Gullan and Craston 2010).

In Orient and eastern Palearctic, about 150 species of Coleoptera are known to be associated with plant galls. Buprestidae, Cerambycidae, Chrysomelidae, and Curculionoidea are the major gall-inducing groups. The curculionids are the most diverse with about 70 galling species. Thirty-six species are gall inquilines, some of

Table 17.13 Distribution of lepidopterous galls per species and plant family in Brazilian restingas

Host plant family (n = 9)	Host plant species (n = 14)	Galler	Locality
Anacardiaceae	*Schinnus terebinthifolius* Raddi	Lepidoptera	BER GRU
Asteraceae	*Mikania ternata* (Vell.) B.L. Rob.	Lepidoptera	BER
Boraginaceae	*Cordia curassavica* (Jacq.) Roem. and Schult.. (=*Cordia verbenaceae* D.C.)	Lepidoptera	BER
Clusiaceae	*Clusia criuva* Cambess. subsp. *parviflora* Vesque	Lepidoptera	BER
Gesneriaceae	*Nematanthus fritschii* Hoehne	Lepidoptera	BER
Malpighiaceae	*Byrsonima sericea*	Lepidoptera	MAR AC JU
	Stigmaphyllon paralias A. Juss.	Lepidoptera	MAR AC
Melastomataceae	*Huberia ovalifolia* DC.	Lepidoptera	BER
	Tibouchina pulchra Cogn.	Lepidoptera	BER
	Tibouchina trichopoda (DC.) Baill.	Lepidoptera	BER
Myrsinaceae	*Rapanea ferruginea* (Ruiz and Pav.) Mez	Lepidoptera	BER
	Rapanea parvifolia	Lepidoptera	MAR AC
	Rapanea sp.	Lepidoptera	PS
Sapindaceae	*Paullinia* sp.	Lepidoptera	BER

Monteiro et al. (1994, 2004), Lima et al. (2000), Oliveria and Maia (2005), Maia et al. (2008), Maia and Oliveira (2010)

BER Bertioga (SP), *MAR* Maricá (RJ), *AC* Arraial do Cabo (RJ), *JU* Jurubatiba (RJ), *PS* Angra (RJ)

them feeding on gall tissues, some others being saprophagous on the decaying galls, or predators of gall-inducing arthropods (Ramamurthy 2007; Triplehorn and Johnson 2005). Few data are known from Central America, except by Costa Rica, where 13 species of gall-inducing weevils have been recorded on 9 plant families. The galls occur on stems and petioles (Hanson and Gomes-Laurito 2005), and the group that stands out most is Curculionidae, found on eight plant families. In South America, 27 morphotypes of coleopteran galls are known on 24 plant species in 14 host families. Most were recorded on Fabaceae and Asteraceae, being stem and bud the most attacked plant organs (Maia 2004).

In Brazilian restingas, eight coleopteran galls have been recorded on eight species of host plants, distributed in six families. Myrtaceae was the most galled family with three host species (*Calyptranthes brasiliensis*, *Gomidesia fenzliana* and *G. martiniana*), while the others present only one host species. The plant organs attacked were leaves and stems, with four records for each one. All the galls were glabrous and one-chambered (Table 17.14) (Fig. 17.3n). Among the inducing beetles, only two species were identified (*Pacholenus monteiroi* Vanin, 2008 and *P. pelliceus* Vanin, 2000), the other records were at family (n = 4) and order (n = 1) level. The galls were recorded for two Brazilian states: São Paulo (five morphotypes), and Rio de Janeiro (four morphotypes, two from Maricá, one from Carapebus and the other from Grumari).

Table 17.14 Characterization of Coleopterous galls in Brazilian restingas

Host plant family (n = 06)	Host plant species (n = 08)	Plant organ	Galler	Locality
Annonaceae	*Rollinia sericea* R.E. Fr.	Leaf (petiole)	Coleoptera Curculionidae	BER
Ebenaceae	*Diospyros brasiliensis* Mart. ex. Miq.	Leaf	Curculionidae (Coleoptera)	BER
Fabaceae	*Andira fraxinifolia* Benth.	Stem	Curculionidae (Coleoptera)	BER
Hippocrateaceae	*Hippocratea volubilis* L.	Leaf (petiole)	Coleoptera	GRU
Melastomataceae	*Tibouchina pulchra* Cogn.	Leaf (petiole or midvein)	Curculionidae (Coleoptera)	BER
Myrtaceae	*Calyptranthes brasiliensis Spreng*	Stem	*Pacholenus monteiroi* Vanin 2008 (Curculionidae)	CAR
	Gomidesia fenzliana O. Berg	Stem	*Pachonelus pelliceus* Vanin, 2000 (Curculionidae)	MAR BER
	Gomidesia martiniana O. Berg	Stem	*Pachonelus pelliceus* Vanin, 2000 (Curculionidae)	MAR

Lima et al. (2000), Maia et al. (2008), Monteiro et al. (1994), Oliveira and Maia (2005), Vanin (2008)

BER Bertioga (SP), *CAR* Carapebus (RJ), *GRU* Grumari (RJ), *MAR* Maricá (RJ)

17.3.10 Thysanopteran Galls

Thysanoptera is a worldwide order of minute to small insects, comprising nearly 6,000 species in 10 families (Gullan and Craston 2010). The primitive trips probably were fungal feeding, most others are primarily phytophagous, feeding on flowers or leaves, including some gall inducers, and there are also a few predators (Gullan and Craston 2010).

In the world, there are about 330 species recognized as gall-formers and inquilines, associated with Angiosperms. Trips galls occur mostly on leaves, and rarely on buds and flowers. Normally, these galls occur as simple curls, rolls and folds, but complex galls such as rosettes, pouches and horns are also found (Price 2005). In Latin America, 14 kinds of thysanopteran galls have been recorded on 7 plant families, 12 from Brazil and 2 from Cuba (Maia 2006).

In Brazilian restingas, there are four records of thysanopteran galls on four species of host plant distributed in two families: Annonaceae with one host species and Myrtaceae with three. All galls occur on leaves, are glabrous and one-chambered (Table 17.15) (Fig. 17.3o). Considering the taxonomy of the inducing insects, all are identified only at the level of order.

Table 17.15 Characterization of Thysanopterous galls in Brazilian restingas

Host plant family (n = 02)	Host plant species (n = 4)	Plant organ	Galler	Locality
Annonaceae	*Rollinia sericea* R.E. Fr.	Leaf	Thysanoptera	BER
Myrtaceae	*Myrcia multiflora* (Lam.) DC	Leaf	Thysanoptera	BER
	Myrciaria floribunda (H. West ex Willd.)	Young leaf	Thysanoptera	MAR
	Neomitranthes obscura Sobral and Zambom	Young leaf	Thysanoptera	MAR, AC

Maia et al. (2008), Monteiro et al. (1994)
BER Bertioga (SP), *MAR* Maricá (RJ), *AC* Arraial do Cabo (RJ)

The records are restricted to two Brazilian states: São Paulo (two morphotypes), and Rio de Janeiro (two morphotypes, one from Arraial do Cabo, and Maricá; and the other from Maricá) (Table 17.15).

17.3.11 Hymenopteran Galls

The Hymenoptera is one of the most diversified insect orders, with about 150,000 species, the majority known from the temperate areas (Huber 2009). They occur mainly in terrestrial and some in aquatic environments, and can be phytophagous (including gall-forming species), predators or parasitic (Huber 2009).

Gallers are found at least in seven families, namely: Agaonidae, Braconidae, Cynipidae, Eulophidae, Eurytomidae, Tanaostigmatidae, and Tenthredinidae. Hymenopteran galls are more common in Neartic and Paleartic regions than in the Neotropics (Mani 1964). They are not frequent in Brazilian coastal vegetation, where only three morphotypes have been recorded: two on Myrtaceae (*Eugenia copacabanensis* and *Eugenia ovalifolia*) and one on Erythroxylaceae (*Erythroxylum ovalifolium*). The first is a midvein gall, the second a stem one and the third a bud gall (Monteiro et al. 1994; Oliveira and Maia 2005).

In addition to the gall-forming species, there are many records of parasitoids and some others of inquiline species in Brazilian restingas. Among the inquilines, a Tanaostigmatidae species was found in cylindrical leaf cecidomyiid gall on *Inga laurina* (Fabaceae) (Maia et al. 2002a, b). This family is represented by gallers and inquilines and most species occurs in Neotropics (Rao and Hayat 1985).

There is a remarkable predominance of the parasitic species, which can be considered as an important mortality factor of the gallers (Maia and Azevedo 2009; Maia et al. 2008; Bregonci et al. 2010).

In Brazilian restingas, about 25 % of the insect galls are parasited by Hymenoptera (Maia and Azevedo 2009; Maia et al. 2008; Bregonci et al. 2010). The parasitoids belong to 14 families (Aphelinidae, Bethylidae, Braconidae, Encyrtidae, Eulophidae, Eupelmidae, Eurytomidae, Mymaridae, Platygasteridae, Pteromalidae, Signiphoridae, Torymidae, Elasmidae, and Scelionidae) and occur in about 120 gall morphotypes on 69 plant species distributed in 32 families (Maia and Azevedo 2009; Maia et al. 2008; Bregonci et al. 2010). The galls are induced by three insect orders: Hemiptera (n = 1), Lepidoptera (n = 1), Diptera (n = 111). The other gallers (n = 8) are still unknown. All parasitoid families are associated with cecidomyiid galls. Besides, an Encyrtidae species was recorded in galls induced by Psyllidae (Hemiptera) on *Ilex theezans* (Aquifoliaceae), and an Eurytomidae species in lepidopteran galls on *Cordia curassavica* (Boraginaceae). Among the Diptera, 29 genera of Cecidomyiidae were attacked by parasitoids, being *Lopesia*, *Asphondylia*, *Dasineura*, *Bruggmannia*, *Clinodiplosis*, and *Neolasioptera* the most parasitized.

The most common parasitoid family was Eulophidae, recorded in 46 % of the galls, followed by Eurytomidae (39 %), Platygasteridae (34 %), Eupelmidae (33 %), Torymidae (28 %), and Pteromalidae (22 %). The eight other families were together presented in 30 % of the galls (Maia and Azevedo 2009).

Some hymenopteran species modify the gall morphology. This issue is not so well investigated, although it is very interesting. In Brazilian restingas, three Cecidomyiidae bud galls are modified by wasps: (1) gall of *Lopesia erytroxyli* Rodrigues and Maia, 2010 on *Erythroxylum ovalifolium* (Erythroxylaceae) (Maia 2001a); (2) gall of *Stephomyia rotundifoliorum* Maia, 1993 on *Eugenia rotundifolia* Casar (Myrtaceae) (Maia 2001a), and (3) gall of *Myrciamyia maricaensis* Maia, 1995 on *Myrcia lundiana* (Myrtaceae) (Ferraz and Monteiro 2003).

17.4 Conclusions and Remarks

The results presented here illustrate the high richness of insect galls in the Brazilian restinga. The taxonomic composition of vegetation in restinga may have been driving the diversity of gall inducing insects in this ecosystem. Furthermore, restinga is among the Brazilian areas with a great richness of insect galls. The most important plant families and the most represented plant genus of restinga flora are also the most galled ones, suggesting the plant composition as an important factor to explain the gall diversity in this ecosystem (as predicted by the plant diversity hypothesis).

All the galler insect orders were found in the Brazilian restingas. Gall midges have been induced the majority of the galls, which corroborates with the world pattern. The same occurs with the attacked plant organs, being leaves the most galled organ. Few hymenopteran galls were found, contrasting with the Nearctic region, where cynipid galls are abundant.

Insect galls from restinga have a rich associated fauna of arthropods, which includes parasitoids, inquilines, predators, and successors. Among them, parasitoids are the most common and diversified, playing an important rule as natural enemies of the gallers.

More investigative studies are necessary to understand the complexity, distribution and ecological patterns of the galling fauna from restingas. There are many gaps in the current knowledge, specially related to taxonomy and geographic distribution. While the data are scarce, scattered, and incipient, endemism, ecological patterns, and other questions cannot be evaluated.

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Chapter 18
Galls from Brazilian Atlantic Forest: Status of Knowledge and Perspectives

Jean Carlos Santos, Marcel S. Coelho, Danielle G. Souza, and Geraldo Wilson Fernandes

Abstract The Atlantic Rain Forest is one of largest and most diversified forest on the planet, a hotspot of biodiversity with the occurrence of unique plant-animal interactions, especially insect herbivores. Galling insects are a highly specialized guild of herbivores that induce abnormal growth in tissues of their host plants, the galls. These provide better food for the galling larvae and protection against natural enemies. Despite the great biological importance of the Atlantic rain forests, there are few ecological studies on insects in this ecosystem. In this chapter, we review the literature and analyzed the inventories of nine studies on galling insect diversity in Atlantic rain forests and provide the most up to date knowledge of gall inducers diversity associated with host plant species. The number of galling morphotypes varied between 29 and 282 on 16–139 host plant species belonging to 12–40 plant families. When compared to the other different Brazilian ecosystems, the Atlantic rain forests showed one of the highest levels of gall richness. Given the extension of the Atlantic rain forests more studies on galling studies are needed.

Keywords Sclerophylly • Richness • Diversity • Galling insects • Host plant

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18.1 Introduction

Gall-inducing insects are a special guild of endophytic and specialist herbivores (Shorthouse et al. 2005) with most galling species confined to one specific host plant (see Carneiro et al. 2009). This species-specific relationship between galling insects and the host plants suggests the use of galling insects as a model to test broad ecological concepts (Price et al. 2004), such as species distribution patterns. Recently, a study on global richness of gall-inducing insects estimated the existence between 21,000 and 211,000 species, with an average of 132,930 species (see Espírito-Santo and Fernandes 2007). The huge inaccuracy of this global estimate is due the lack of more studies in the many different ecosystems of the globe.

The Atlantic rain forest and its associated ecosystems (e.g., Atlantic costal vegetation) involved originally an area of 1,360,000 km^2, which corresponded approximately to 16 % of the Brazilian territory, and was spread across 17 states: Rio Grande do Sul, Santa Catarina, Paraná, São Paulo, Goiás, Mato Grosso do Sul, Rio de Janeiro, Minas Gerais, Espírito Santo, Bahia, Alagoas, Sergipe, Paraíba, Pernambuco, Rio Grande do Norte, Ceará, and Piauí (MMA 1999). The Atlantic rain forest is immersed in heterogeneous environmental conditions and is in fact one of the largest forest in the Americas. Its longitudinal distribution in the Brazilian territory is important as we can easily observe through the extreme rainfall gradient from the dry inland called “sertão” to the coastal region, in which we find different forest composition (Câmara 2003). There are high levels of biological diversity in the Atlantic rain forests with more than 20,000 plant species, 261 mammal species, and 688 bird species (Mittermeier et al. 1999; Silva and Castelleti 2003) as well as high endemism levels which are attributed to the geographic features associated to the wide altitudinal extension (Ribeiro et al. 2009). According to Silva and Castelleti (2003), the Atlantic rain forest has five endemism centers: Bahia, Brejos nordestinos, Pernambuco, Diamantina, and Serra do Mar which were classified according to the distribution of butterflies, birds, and primates. The fauna and flora of the Atlantic rain forest comprise from 1 % to 8 % of the total world species (Silva and Castelleti 2003).

For centuries this biome has suffered a strong human impact and, consequently nowadays is one of the most threatened ecosystem worldwide (see Myers et al. 2000). Impacts have began since the sixteenth Century due to the colonial agriculture in which forest gave place to the agricultural cycles such as sugar cane, cocoa, coffee, banana, logging and pasture fields (Galindo-Leal and Câmara 2003). The Atlantic rain forest is now limited to an area of 11.4–16 % of its original territory, with 80 % of fragment remnants in all Brazilian biogeographic regions with less than 50 ha (Ribeiro et al. 2009). The Atlantic rain forest is classified as “hotspot” of biodiversity, in other words, a priority area to conservation in consequence of its high diversity levels, endemisms as well as for the advanced fragmentation standing (Myers et al. 2000).

18.1.1 Northern Atlantic Forests of Brazil: An Important Center of Species Endemism

The landscapes of the northern Atlantic forests were profoundly modified through the last 500 years resulting in vegetation patches of different sizes and quality. Only small and isolated Atlantic rain forest patches were left (Brown Jr. and Brown 1992; Lima and Capobianco 1997). The northern of the São Francisco River is the most threatened and extremely exploited region of the Atlantic rain forest. The "Pernambuco Endemism Center" (PEC) is found inside this region. This endemism center has a large contribution to the endemism of South America plants and animals, because one portion of its biota is influenced by the Amazonian region (Prance 1982) the other is influenced by the southeastern Brazil (see Silva and Castelleti 2003; Santos et al. 2007).

The Biosphere Reserve of the Atlantic rain forest in Pernambuco, with only 5 % of the original vegetation remaining (Galindo-Leal and Câmara 2003), covers a large part of the coastal counties, nearly reaching the limits with the states of Alagoas at the south, and Paraíba at the north (Goiana River estuary) (Lima and Capobianco 1997). In consequence of the high environmental degradation levels, there are reasons to expect a decrease in habitat quality to specialized herbivorous insects. Santos et al. (2008) and Santo-Silva et al. (2013) reported clear reorganization in the composition and richness of plant communities, while Oliveira et al. (2008) reported an impoverishment in the vertical structure of large-trees. These changes drive the biotic interactions at several scales (Wirth et al. 2007, 2008; Lopes et al. 2009; Tabarelli et al. 2012). Modifications in plant functional groups exert strong influences in the dynamics of interspecific interactions (Wirth et al. 2008; Lopes et al. 2009). In this scenario of deep changes in plant structure and composition we analyzed the galling insect inventories of nine studies in northeastern Atlantic rain forest to understand how galling insect communities were affected (Fig. 18.1).

18.2 Trends in Gall Richness in the Atlantic Rain Forest

Nine different inventories carried out at different forests associated to the Brazilian Atlantic rain forest reported gall descriptions as well as galling insect taxa (Fernandes et al. 2001, 2009; Dalbem and Mendonça 2006; Fernandes and Negreiros 2006; Mendonça 2007; Moreira et al. 2007; Santos et al. 2011a, 2012; Silva et al. 2011). These studies have been concentrated at the south and southeastern regions of Brazil (e.g., Fernandes et al. 2001; Maia 2005; Dalbem and Mendonça 2006; Fernandes and Negreiros 2006; Mendonça 2007; Moreira et al. 2007). These nine inventories accounted from 29 to 282 galling morphotypes occurring on 16–139 host plant species belonging from 12 to 40 plant families (Table 18.1). Fourteen plant families

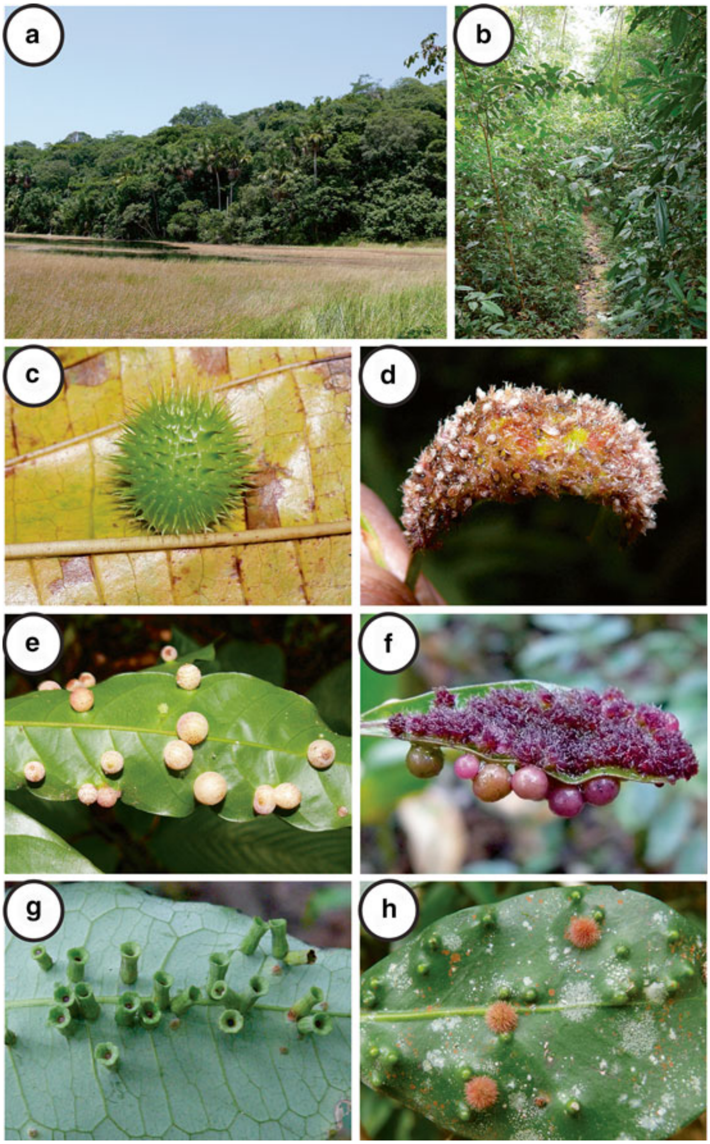

Fig. 18.1 Brazilian Atlantic rain forests and their galls: (**a**) and (**b**) forest fragment in Recife, Pernambuco State, Brazil; (**c**) gall on *Miconia prasina* (Sw.) DC. (Melastomataceae); (**d**) gall on *Guapira* sp. Aubl. (Nyctaginaceae); (**e**) gall on *Guarea* cf. *macrophylla* Vahl ssp. *tuberculata* (Vell) T.D. Penn (Meliaceae); (**f**) gall on *Guapira* sp. Aubl. (Nyctaginaceae); (**g**) gall on *Mabea occidentalis* Benth (Euphorbiaceae) and (**h**) gall on *Guapira* sp. Aubl. (Nyctaginaceae)

were the main hosts for galling insects: Annonaceae, Asteraceae, Bignoniaceae, Burseraceae, Euphorbiaceae, Fabaceae, Lecythidaceae, Melastomataceae, Meliaceae, Myrtaceae, Nyctaginaceae, Sapindaceae, Piperaceae, and Polygonaceae.

Table 18.1 Comparison among the studies on the diversity of galling insect species in different Brazilian Atlantic forests

Richness	Number of host plants/families	Main host families	Ecosystems	Region	Sampling method	References
282	–/39	Asteraceae, Myrtaceae and Sapindaceae	Atlantic forest and Pampas	Southern	Random walks	Mendonça (2007)
273	139/40	Asteraceae, Myrtaceae, Bignoniaceae and Melastomataceae	Atlantic forests	Southeastern	Random walks	Fernandes et al. (2001)
136	79/35	Myrtaceae, Polygonaceae and Melastomataceae	Atlantic forest	Northeastern	Random walks	Santos et al. (2012)
130	84/34	–	Subtropical forest	Southern	Random walks	Dalbem and Mendonça (2006)
80	49/28	Nyctaginaceae, Fabaceae and Meliaceae	Altitudinal wet forest	Northeastern	Random walks	Santos et al. (2011a)
50	37/19	Melastomataceae and Piperaceae	Secondary successional Atlantic forest	Northeastern	Random walks	Silva et al. (2011)
32	16/13	Burseraceae, Lecythidaceae, Annonaceae and Melastomataceae	Urban fragment of Atlantic forest	Northeastern	Random walks	Fernandes et al. (2009)
31	26/15	Fabaceae, Asteraceae and Bignoniaceae	Disturbed Atlantic forest	Southeastern	Random walks	Moreira et al. (2007)
29	24/12	Leguminosae and Euphorbiaceae	Disturbed Atlantic forest	Southeastern	Random walks	Fernandes and Negreiros (2006)

In spite of the fact that these studies were conducted on different types of Atlantic rain forest, generalizations are attempted here. Disturbed areas of Atlantic rain forests had lower galling diversity [35.5 ± 9.7 galls $(\bar{x} \pm \mathrm{SD})$, n = 4] compared to undisturbed areas [180.2 ± 91.4 galls $(\bar{x} \pm \mathrm{SD})$, n = 5, Table 18.1]. The highest diversity (282 morphospecies) was reported by Mendonça (2007) in the Atlantic rain forest and Pampas in southern Brazil and by Fernandes et al. (2001) that reported 273 galling species in several Atlantic rain forest fragments in southeast Brazil. Mendonça (2007) argues that the result of the high diversity of insect galls is due to the larger plant families which hosted more galls, such as Asteraceae (see also Fernandes 1992). The lowest diversity (29 galling morphospecies) was reported by Fernandes and Negreiros (2006) in a disturbed area of Atlantic rain forest in southeastern Brazil, who argued that the low diversity was due to environmental degradation of the area. In this study, galls were surveyed in different habitats such as: abandoned pasture, secondary succession vegetation, and secondary succession vegetation dominated by *Miracruodon urundeuva* (Anacardiaceae). Galling insects are highly specific with relation to their host plants (Carneiro et al. 2009) and the lack of potential hosts in disturbed vegetation could result in impoverished galling fauna (see Moreira et al. 2007).

The level of environmental conservation might has been the major factor influencing the diversity of galling insects in the Atlantic forest. Higher galling species richness will certainly be found in (a) areas with high conservation degree (e.g., MMA 2007), (b) high plant species richness, (c) better habitat quality (see Ries et al. 2004), and (d) areas with higher number of potential hosts (e.g., Guedes and Santos 1998). In comparison with other studies (Table 18.1) the richness of insect galls in the Atlantic forest of Pernambuco (136 morphospecies) was intermediary. One likely explanation for the low richness of galling insects found in the Atlantic forest fragments in Pernambuco state in comparison with other Atlantic forests in the southeastern is the fact that the Atlantic forests located up north to the São Francisco River have lower plant species richness (Tabarelli et al. 2006). Moreover, most of the remaining forests are small and suffer strong changes in floristic structure and composition due to abiotic edge effects and habitat fragmentation (see Tabarelli et al. 2005). Given the clear nonrandom loss of species and plants functional groups, we propose that shifts in plant community or its simplification drive the impoverishment of habitats hence resulting in the erosion of the galling community (e.g., Souza 2013).

Despite the importance of specialized insects to plant diversity and ecosystem process in tropical forests (Coley and Barone 1996), the mechanisms that have shaped these insect communities have been neglected and unclear in ecosystems such as Atlantic rain forest. While some studies have focused on communities patterns of galling insects, they have not properly investigated other ecological aspects such as local (fragment size and shape, habitat type), landscape (connectivity), spatial scales and attributes. More gall samplings at local and regional scales are needed in order to verify the existence of regional patterns or even to make broader generalizations about the differences between northern and southern Atlantic rain forest based on the galling insect patterns. An aspect of major importance still to be investigated in detail is that of the Atlantic rain forest fragmentation, edge effects, and even forest structure and composition.

18.3 Richness of Gall-Inducing Insects Along a Rainfall Gradient: A Case Study

A comparison of the richness of galling insects on their host plants from dry forest, altitudinal wet forest, and Atlantic forests of the state of Pernambuco, Brazil is attempted. A clear natural rainfall gradient characterizes the Pernambuco state ranging from the coast to inland (Fig. 18.2). The average annual rainfall of the Atlantic forests range from 1,000 to 4,000 mm (Tabarelli et al. 2005). The altitudinal-wet forests (called Brejos de Altitude) are disjunctions patches of Atlantic forests surrounded by the tropical dry forest (known as Caatinga). These areas are considered forest wetlands refuges that have penetrated the interior of the continent for thousands years by effects of interglacial climatic variations, resulting in islands of wet forests surrounded by dry forests. A typical altitudinal wet forests has a strong resemblance with coastal rainforest, sharing many plant and animal species. The existence of these forest islands in the dry forest region, where the precipitation average ranges from 240 to 900 mm, is only possible because they are located on plateaus with altitude ranging from 500 to 1,100 m which allows precipitation levels greater than 1,200 mm/year (see Porto et al. 2004). The tropical dry forest (caatinga)

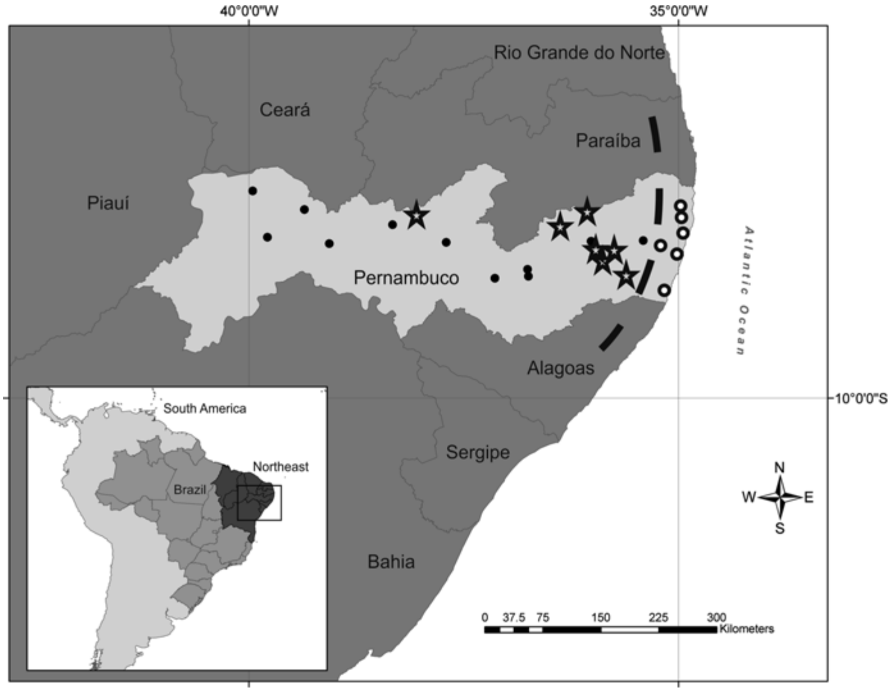

Fig. 18.2 Location of the research sites along a rainfall gradient, Pernambuco State, Brazil. Brazilian dry forest (*black circles*), Altitudinal wet forest (*stars*) and Atlantic rain forest (*white circles*)

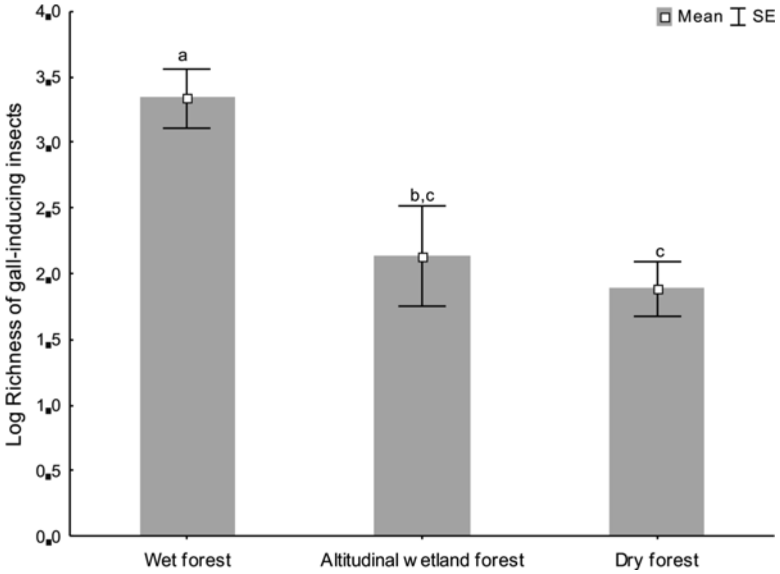

Fig. 18.3 Richness of gall-inducing insects along a rainfall gradient in the tropical forests [Data from studies conducted in six areas of wet forest (Atlantic rain forest) (Santos et al. 2012), seven areas of Altitudinal wet forests (Santos et al. 2011a), and in eleven areas of Dry forest (Caatinga) (Santos et al. 2011b)]

is the fourth largest Brazilian biome, characterized by a deciduous forest adapted to an extreme drought, in which plants undergo severe water shortage through a large portion of the year (March through October). The rains are irregular throughout the year. The low annual rainfall distribution (500–750 mm/year) occurs only through 3–5 months, with a water deficit through the rest of the year (see Castelletti et al. 2003; Prado 2003; Leal et al. 2005). The studies were conducted in 6 areas of Atlantic forests (Santos et al. 2012), 7 areas of altitudinal-wet forests (Santos et al. 2011a), and in 11 areas of dry forest (Santos et al. 2011b).

The greatest number of galling insects were found in the Atlantic rain forest, followed by Altitude Wetlands, and Caatinga, respectively. Along the rainfall gradient, the Atlantic Forest showed twice the number of galling insects compared to Caatinga ($F_{(2;22)} = 7{,}31$; $p = 0.0037$, Fig. 18.3). The rain forest also showed the greatest diversity of host plants (Tables 18.2 and 18.3). However, when we compared the average gall richness from Caatinga and Altitude Wetlands, no statistical difference was found (Fig. 18.3). The trends reported here argue against the hygrothermal stress hypothesis (Fernandes and Price 1992, see too Fernandes and Price 1988; Price et al. 1998), and even against the synchronous leaf production hypothesis (see Mendonça 2001). In spite of the high plant species richness, the tropical rain forest generally has asynchronous leaf production among species (Morellato et al. 2000), and hence one would expect a low gall richness in such vegetation. Contrarily, one would expect a high number of galling insects in the tropical dry forest due to its generalized

Table 18.2 Comparison among three studies on the diversity of galling insect species in different Brazilian ecosystems: dry forest, altitudinal wet forest and Atlantic forest

Ecosystems	Richness	Number of host richness	Number of host families	Main host families	Number of host genera	Main host genera	Main insect galls (%)
Brazilian dry forest	64	48	17	Fabaceae, Euphorbiaceae, Boraginaceae, Malpighiaceae and Myrtaceae	31	*Croton*, *Cnidoscolus*, *Bauhinia* and *Byrsonima*	Cecidomyiidae (89.00 %)
Altitudinal wet forest	80	49	28	Nyctaginaceae, Fabaceae, Meliaceae, Myrtaceae and Sapindaceae	35	*Guapira*, *Guarea*, *Myrcia* and *Paullinia*	Cecidomyiidae (81.25 %)
Atlantic forest	136	79	35	Lecythidaceae, Myrtaceae and Nyctaginaceae	53	*Guapira*, *Protium*, *Coccoloba*, *Miconia*, *Ocotea* and *Eschweilera*	Cecidomyiidae (94.85 %)

Table 18.3 Test of the hygrothermal stress hypothesis in different galling insect species studies. *Arrow* points to positive effect

Gradient	Ecosystems (region)	Hygrothermal stress hypothesis	References
Gall-inducing insect richness *versus* median annual rainfall	Tropical savannah (Australia)	Refuted (null effect)	Blanche (2000)
Gall-inducing insect richness *versus* habitat	Riparian and deciduous habitats in tropical dry forest (Mexico)	Refuted (null effect)	Cuevas-Reyes et al. (2004)
Galled plant richness *versus* median annual rainfall	Tropical savannah (Australia)	Refuted (↑ mesic)	Blanche (2000)
Gall-inducing insect richness *versus* altitude	Montane forest and desert shrubland (USA)	Refuted (↑ mesic)	Blanche and Ludwig (2001)
Gall-inducing insect richness *versus* habitat	Cerrado and rupestrian fields (savannah) (Brazil)	Confirmed (↑ xeric)	Fernandes et al. (1995)
Gall-inducing insect richness *versus* altitude	Cerrado and rupestrian fields (savannah) (Brazil)	Confirmed (↑ xeric)	Lara et al. (2002)
Gall-inducing insect richness *versus* structural complexity	Cerrado and rupestrian fields (savannah) (Brazil)	Confirmed (↑ xeric)	Lara et al. (2002)
Gall-inducing insect richness *versus* habitat	Cerrado and rupestrian fields (savannah) (Brazil)	Confirmed (↑ xeric)	Carneiro et al. (2005)
Gall-inducing insect richness *versus* altitude	Arizona (USA)	Confirmed (↑ xeric)	Fernandes and Price (1988)
Gall-inducing insect richness *versus* latitude	Global patterns	Confirmed (↑ xeric)	Price et al. (1998)

sclerophylly and habitat harshness. However, studies have reported significant galling richness in distinct tropical rain forests (Fernandes et al. 2001; Almada and Fernandes 2011; Maia 2012); especially at the forest canopies (Medianero and Barrios 2001; Medianero et al. 2003; Julião 2007; Ribeiro and Basset 2007). A possible explanation would be the harsh environment found at such forest stratum (see Ribeiro and Basset 2007). Otherwise, no attempt was made to observe the differential distribution of galling insects in the canopy versus the understory of the Atlantic rain forest so far. Our galling species data from the dry forest provide support for the harsh environment hypothesis. This vegetation is known for its strong leaf Symphenology (Murphy and Lugo 1986; Bullock and Solis-Magallanes 1990). Most of the galls found in the northeast dry forests are on leaves, what makes their development possible only in the rainy season.

Plant phenology, leaf sclerophylly, and the presence of natural enemies are not the sole variables influencing the gall richness in an ecosystem. As gall-inducing insects are the most specialized insects, plant richness has proved to be an important determinant of the gall richness level particularly at a local or regional scale (Wright and Sanways 1996, 1998; Gonçalves-Alvim and Fernandes 2001; Oyama et al. 2003; Cuevas-Reys et al. 2004). The plant richness is one of the most important determinants of gall richness in an ecosystem, despite the fact that some plant species known as super-host can host a high number of gall species making the plant composition more important than plant richness in some specific cases (Blanche 2000; Lara et al. 2002; Cuevas-Reyes et al. 2003). Many sampled areas of altitudinal wet forests have suffered strong degradation in their ecosystems; e.g., loss of habitat, hunting, wood extraction, agriculture and fragmentation (see Tabarelli and Santos 2004; Santos et al. 2011a). The historical use of those areas can be the main cause of plant diversity and structure impoverishment. Moreover, these ecosystems are true mountain top islands surrounded by the dry forest vegetation, and therefore, they had a smaller spatial area compared to areas of continuous Atlantic rain forest of the coast and dry forest. All these factors may contribute to a reduction in the richness of insect galls in this ecosystem.

Finally, tropical dry forests are little diverse and structurally simpler when compared to tropical rain forests and other ecosystems with lesser values in tree height, basal area, density as well as specie richness (Murphy and Lugo 1986). Whereas the number of tree species ranges from 35 to 90 in dry forests, in rain forests the number ranges from 50 to 200. Similar differences are found in other important vegetation structure traits such as complexity index, which ranges from 5 to 45 in dry forests and between 180 and 405 in rain forests; canopy height (ranging from 10 to 40 in dry forests; and between 20 and 84 in rain forests; number of canopy strata (Dry Forests: 1–3; Rain Forests: three or more); and basal area, that ranges from 17 to 40 in dry forests and between 180 and 405 in rain forests.

18.4 Concluding Remarks

Overall, the richness of gall inducing insects has just started to be revealed in the Atlantic rain forests; hence many questions still remain to be answered on the factors that shape their ecological interactions and evolution in this speciose biome. Some aspects related to the community ecology of galling insects are in need to be better understood in this forest formation, such the distribution of the diversity of galling insect fauna, the host relations of galling insects, and the mechanisms that drive their distribution and success.

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Chapter 19
Galling Insects in the Pantanal Wetland and Amazonian Rainforest

Genimar Rebouças Julião, Emmanuel Duarte Almada, and Geraldo Wilson Fernandes

Abstract It were collected 133 morphospecies of galling insects on 75 host plant species in the Pantanal forest patches while studies compilation pointed the interesting record of 1,549 galling morphospecies in 66 botanical families, 251 genera and 713 species of host plants in the Amazonian forests. No difference was observed in the number of galling species between Pantanal patch edge and interior. However, dissimilarity in galling species composition was verified in the patch habitats. To date, galling insect fauna of Pantanal region have not been properly sampled. In the Amazonian forests and Pantanal wetlands, galling species richness was strongly affected by hygrothermal and nutritional stress, even though mediated by soil fertility, topography, and flooding. Upper canopy of the Amazonian rainforests was the most speciose environment for galling fauna. Their microclimatic conditions, similar to scleromorphic/sclerophyllous vegetations, favor the attack by these herbivores. Besides, the Amazonian super-host and host/non-host plant diversity seems to play an important role on the richness and distribution patterns of galling insects.

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19.1 Introduction

The understanding of the eco-physiological as well as the evolutionary mechanisms and processes that regulate the interactions between galling insects and their host plants has increased dramatically in the last decade. In spite of it some gaps still persist, such as the low advance in the taxonomical and systematic work on galling species (primarily those in the tropical region), as well as the lack of deeper studies in some important ecoregions of the world, such as the South American wetlands and Amazonian equatorial rainforests. While Espírito-Santo and Fernandes (2007) estimated a world average of ca. 120,000 galling species, the number of known species for this guild is only ca. 15,000 species. The largest South American wetlands, the Pantanal, and the Amazonian rainforests represent important areas not sampled adequately. These regions are known for their high species richness of other organisms (e.g., Oliveira and Mori 1999; Laurance et al. 2002; Junk et al. 2010, 2011). In this chapter we provide pioneer information on the galling insects and summarize the studies in the Pantanal and in some areas of the Amazonian rainforests.

The main proposed hypotheses to explain local/regional patterns of galling insect diversity expected a low diversity of gallers in the tropical rainforests. Such hypotheses stated the premise that galling insect diversity is positively associated with the sclerophylly of host plants and xeric habitats (distant from any body of water); thereby, galler performance and success could be limited by microclimatic variables as humidity and temperature (Fernandes and Price 1992; Lara et al. 2002).

The sclerophyllous vegetations present several traits that favor the diversity of galling insects (Fernandes et al. 2005), such as low probability of leaf abscission, evergreen leaves, high concentration of phenols, low nutrient status in the soil, especially with respect to the primary nutrients, like phosphorus (Fernandes and Price 1991; Blanche and Westoby 1995). The xeric habitats represent niches relatively free of pathogens and natural enemies (parasitoids and herbivores) that feed on gall tissue due to their high concentration of nutrients as opposed to mesic habitats, where galling insects could face higher rates of parasitism and predation (Fernandes and Price 1992; Fernandes et al. 2005). The Amazon basin, which encompasses a large area of tropical moist forest, and the Pantanal, a seasonal floodplain, should not be strong candidates as regions with greater richness of this guild of herbivores. In spite of the high average temperatures, an extremely wet environment characterizes the Amazonian region: annual rainfall can range about 3,600 mm and relative humidity not uncommonly reaches 100 % saturation at night (Sioli 1983). The Amazonian floodplains occupy an area equivalent to 1.35 million km^2, about 30 % of the total area of the Amazon basin, considering only three frequencies of flooding regime (Piedade et al. 2001). The Pantanal has a clearly defined wet and dry season, annual rainfall varies from 800 to 1,400 mm, and floodplains receive the overflowing of river channels and natural impoundment of water, due to the small variation in the terrain inclination (Damasceno Jr. et al. 2009). As Pantanal and Amazonian forests do not present habitats clearly defined as xeric or dominant sclerophyllous vegetation (in terms of area), it would be plausible to argue that these regions would present a lower diversity of galling insects. Otherwise, flooding regime in these regions represents a stress condition for some terrestrial invertebrates (Junk and Piedade 2005; Adis et al. 2010), while other organisms can tolerate or couple up their survival to fluctuation in water level (Junk et al. 1989).

In this chapter we show, for the first time, solid and large data set that indicate that the Amazonian region supports a diverse fauna of galling insects, contrarily to what was hypothesized, but that the foundation or primordial mechanism behind these variables are still associated to hygrothermal and nutritional stress levels and to vegetation scleromorphy/sclerophylly. In addition, we present the data on the galling insects attacking plants in the Pantanal vegetation. Finally, we also present new information indicating that the hyperdiverse flora of Amazonian region also plays a major role in the distribution patterns of galling insect richness.

19.2 The Landscape Scenario Provided by the Amazonian Rainforest and South Pantanal for the Understanding of the Distribution Patterns of Galling Insects

The environmental heterogeneity that typifies the Amazonian and Pantanal ecosystems offer an interesting scenario for the investigation on the ecological factors that shape the spatial and temporal distribution of galling insects. In the Amazonian landscape there is a mosaic of vegetation physiognomies, such as savannas, mangroves, liana forests, restinga, estuarine *várzea*, short-period floodplains, marshes, meadows, *campinarana* forest, upland forest (never flooded), and permanent and seasonally flooded forests (*várzea* and *igapó*) (Prance 1979; Pires and Prance 1985). Semideciduous seasonal forests, savannas, pioneer formations and vegetation with fluvial or lacustrine influence can be found in the south Pantanal floodplains, at the Brazilian state of Mato Grosso do Sul (Silva et al. 2000).

The main studies presented in this chapter focused on the distribution patterns of galling insects in four vegetation types: patches of semideciduous forest (small and isolated stands of forests, regionally known as *capões*) in south Pantanal (see Silva et al. 2000), and three types of Amazonian rainforests (Fig. 19.1): *terra firme* (non-flooded forest), and *várzea* and *igapó* forests, both seasonally flooded areas in response to river-level rise (*sensu* Prance 1979).

The assortment of vegetation formations in the Pantanal results from their centered location in the American continent; hence, distinct phytogeographic domains involve this landscape. In the north, the Pantanal is influenced by the Amazonian rainforest, in the east by the Cerrado, in the south by Meridional forests, while in the west it is influenced by the Bolivian and Paraguayan Chaco vegetation (Pott et al. 2011). Pantanal forest patches (*capões*) in the region of Miranda-Abobral (where galling insects were sampled) are located in soils characterized by calcareous

Fig. 19.1 Brazilian wetland and Amazonian rain forest landscapes where galling insect richness were assessed. (**a**) Pantanal floodplain, in the sub-region Miranda-Abobral, state of Mato Grosso do Sul; (**b**) forest patch (*capão*) detail, in the South Pantanal floodplain; (**c**) upper canopy strata in *terra firme* forest, central Amazonia; (**d**) sampling with telescoping pole and climbing in *terra firme* forest; (**e**) sampling with telescoping pole inside a boat in the Amazonian flooded forest (*várzea* and *igapó*), state of Amazonas; (**f**) submerged trees in the várzea forest at Mamirauá Sustainable Development Reserve; (**g**) *terra firme* restoration stand in Porto Trombetas, state of Pará

concretions derived from the calcium carbonate of shells. The Abobral *capões* arose from palaeochannels fragmentation, since these forest patches accompany the river meanders (Damasceno Jr. et al. 2009).

The *terra firme* forest grows on poor and acid soils, strongly leached, with high concentrations of toxic aluminum (Laurance et al. 1999), representing more than 65 % of the Amazonian rainforest ecoregion (Silva et al. 2011). The *várzea* forest is flooded by white waters, which carry a great amount of nutrients (Ca, Mg, Al, K, Fe, Zn and Mn) and suspended sediments (Prance 1979; Haugaasen and Peres 2006). Black or clear waters, which are poor in nutrients, seasonally flood the *igapó* forests (Prance 1979). On the other hand, high levels of phosphorus are found in these environments (Haugaasen and Peres 2006). The black water presents this color due to high concentration of humic and fulvic acids (see Prance 1979).

Each component of the landscape mosaic in the Amazon region has been specifically linked to certain types of soils and vegetations (Sombroek 2000). Taking into account that differences in hydric conditions of the soil and in nutrient availability at the whole system (soil + water), a very appropriate environmental gradient allowed to test contrasting patterns in galling insect diversity and distribution. This chapter examines the role of intrinsic hydric, nutritional and thermal conditions in the Amazonian and Pantanal ecosystems on species richness and abundance of host plants and galling insects, in light of the Harsh Environment Hypothesis (Fernandes and Price 1988, 1991; Price et al. 1998).

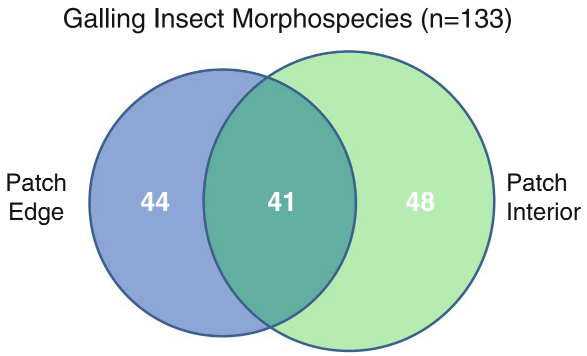
Several questions are addressed in such environments: (I) Do the edges of forest patches surrounded by an inhospitable matrix present greater diversity of galling insects?; (II) Is galling insect diversity influenced by topography and soil fertility in the Amazonian landscape?; (III) What are the effects of environmental disturbances due to flooding on galling insects?; (IV) What is the role of the diversity of Amazonian flora on the richness of galling herbivores?; (V) How many galling insect species have been recorded in the Amazonian forests?; and (VI) Why forest strata matter to galling insects?

19.3 Galling Insect Diversity in the Pantanal Forest Patches

The south Pantanal *capões* are important refuges for local fauna, constituting forest formations amid vast areas of seasonally floodplains (Julião et al. 2002; Corrêa et al. 2006). The first surveys of galling insects were done in the Miranda-Abobral subregion of south Pantanal, where 27 patches with area ranging from 0.13 to 4.97 ha were investigated. Most of them (25 forest patches) had less than 3.5 ha in area; samplings were carried out in the patch interior – corresponding to the higher elevation habitat – and in the edges, corresponding to the lower terrain (Julião et al. 2004).

Overall, 133 morphospecies of galling insects were found on 75 host plant species. There were no significant differences in galling insect richness between patch interior and edge. Plant species richness also did not differ between patch interior and edge. On the other hand, host plant and galling insect species composition varied according to the sampled habitat (Fig. 19.2). Many host plants families (46 % of the 37 families) were unique to the interior or to the edge of vegetation patches.

The ratio between galling insect richness and host plant richness (GIR/HPR) increased positively with patch size. However, neither host richness nor galling insect richness *per se* was affected by patch size, indicating that only the number of gall morphospecies *per* host plant was influenced by a weak area effect. Removal of the largest patch (4.97 ha) in the regression analysis between GIR/HPR and patch size reinforced the evidence of weak relationship between these variables ($r^2 = 0.35$, $p = 0.001$; analysis excluding the largest forest patch: $r^2 = 0.24$, $p = 0.01$, Fig. 19.3).



Commom Botanical Families

Annonaceae, Asteraceae, Bignoniaceae, Boraginaceae, Celastraceae, Ebenaceae, Erythroxylaceae, Euphorbiaceae, Fabaceae, Lamiaceae, Lythraceae, Malvaceae, Menispermaceae, Moraceae, Myrtaceae, Nyctaginaceae, Polygonaceae, Rhamnaceae, Sapindaceae, Smilacaceae.

Exclusive at Edges

Chrysobalanaceae, Malpighiaceae, Salicaceae, Verbenaceae, Vitaceae

Exclusive in the Interior

Acanthaceae, Apocynaceae, Cannabaceae, Capparaceae, Clusiaceae, Convolvulaceae, Lauraceae, Olacaceae, Phytolaccaceae, Rubiaceae, Rutaceae, Sapotaceae

Fig. 19.2 Number of galling morphospecies and botanical families exclusive and common to the edge and interior of Pantanal patches, state of Mato Grosso do Sul

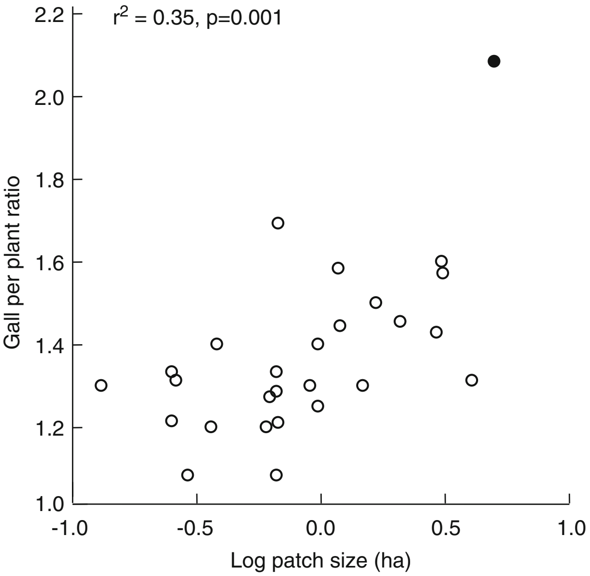


Fig. 19.3 Variation in the ratio between insect gall richness and host plant richness in patches of different sizes in the Pantanal wetland. A unique *filled circle* depicts the largest patch (4.97 ha) which was excluded in a posterior regression analyses (See text for details; Modified from Julião et al. 2004)

Such results can be explained by the size and nature of forest patches sampled in this Pantanal region, which would be dominated by edge vegetation or a highly unstable environment. *Capões*, natural forest formations, would not be subject to the same processes emerged from edge creation observed during the forest fragmentation process. Furthermore, the factors that regulate galling insect distribution in these patches may be operating at a different scale. For instance, individual host plants could represent "islands" to their associated galling insects, which depend on (i) the dispersal ability of each galling insect taxa, (ii) on the distance among patches and; (iii) on the permeability/hostility of the adjacent matrix. We reiterate that in spite the small size of the *capões*, characteristic of the Pantanal Miranda-Abobral, they harbor a high diversity of gallers and other insects (Julião et al. 2004; Corrêa et al. 2006). Few studies currently available in the literature preclude a critical and accurate conclusion about ecological interactions among galling insects and their host plants in the Pantanal region (Julião et al. 2002, 2004; Costa 2010). At the same Pantanal subregion, Costa (2010) recorded and described at the genus level, the galling insect fauna, parasitoids, inquilines, pollinators, and predators associated with three species of *Ficus* (*F. pertusa* and *F. obtusifolia luschnathiana*, Moraceae). Although this floodplain occupies an area about 140,000 km^2 (Junk et al. 2006), we assume that these punctual investigations recorded only a sub-sample of this herbivore guild, since the Pantanal has eight other sub-regions (Junk 1993) beyond the Miranda-Abobral and 16 vegetation classes with different phytophysiognomic aspects (Silva et al. 2000).

19.4 Fertility, Topography and Flooding as Explanatory Factors of Galling Insect Distribution in the Amazonian Rainforest

Galling insect diversity and distribution in the Amazonian rainforest also remains a major research gap. The few studies designed to understand the spatio-temporal mechanisms shaping interactions among these organisms have been done only in the last 10 years. In this sense, studies about possible biodiversity loss in these insect communities due to human intervention in undisturbed forests are also scarce. For instance, a survey in Manaus, in the Brazilian state of Amazonas, reared 84 species of gall-inducing arthropods; the majority (63.1 %) was represented by dipterans from the Cecidomyiidae family (Yukawa et al. 2001). Host plant richness was considered the main factor acting on the galling insect diversity of forest understory in these sites. Furthermore, Price et al. (1998) found a low richness of galling insects in a tropical rainforest. These authors verified that the Amazonian *campina* (known as "Amazonian caatinga") compose an exception among the moist tropical vegetation, with a richness peak of gall-inducing insects. Such fact was related to the scleromorphic features of Amazonian caatinga, characterized by high levels of endemism and a low diverse flora which grows on sandy and poor soils subjected to periodic hydric limitation (Anderson 1981; Pires and Prance 1985).

Among the recent research efforts, studies conducted by Julião et al. (2005, 2014a, b, c), Fernandes et al. (2010), Almada and Fernandes (2011) and Almada et al. (2014) represent the most detailed and extensive knowledge we have about the galling insect distribution in the Amazonian rainforest ecosystem. Sampling the upper forest canopy, Julião (2007) and Julião et al. (2014a, b, c) tested the role of hydric and nutritional stress, and tree richness on galling insect richness in different habitats and forest physiognomies while a pioneer research on the insect galls in restored forest stands of different ages was the theme explored by Fernandes et al. (2010). This study also supports the use of galling insects as a suitable tool to evaluate environmental health. In the forest stands, the majority (97 %) of the galls were induced by Cecidomyiidae (Diptera), while Fabaceae, Chrysobalanaceae, and Burseraceae were the main host plant families (Almada and Fernandes 2011).

In the following topics we summarize the main results found in these studies and their implications for the understanding of the determinant factors of gall inducing insect distribution. Finally, we describe the outcomes from compilation of surveys and ecological studies in the Amazon region, emphasizing the importance of host plants as one of the key components in galling insect diversity.

19.4.1 Soil Fertility at Local and Regional Scales

Studies in several biogeographical regions validate a positive relationship between the richness of galling insects and soil infertility. However, nutrients chosen as predictors of soil fertility vary from study to study, according to local and regional edaphic conditions. In Australia, more galling insects were found in infertile sites than in sites with higher concentration of total phosphorus. The proportion of plants attacked by gall-inducing insects did not differ between these sites, but there was greater richness of the Myrtaceae host family in places with less fertile soil, and a positive relationship between the number of species of galling insects and Myrtaceae species at each site (Blanche and Westoby 1995). In Mexico, host plant abundance and galling insect density per host plant was negatively correlated with total phosphorus concentration (Cuevas-Reyes et al. 2003).

About 40 % of the Brazilian Amazon basin has its soils dominated by ferralsols; these porous soils are generally strongly weathered and leached, have a low base saturation and varied clay content (Richter and Babbar 1991). In order to verify if galling insect diversity can be affected by nutritional status of the soil in a local scale, galling insects were sampled in the canopy of the reserves of the Biological Dynamics of Forest Fragments Project (BDFFP/INPA) and related to 25 edaphic parameters (Julião et al. 2014b). The chemical and physical properties of soils and details about sampling, field and laboratory procedures are provided by Nascimento and Laurance (2011). In some situations, analysis presented here employed averages of edaphic parameter value, since some reserves had 3–10 replicates of soil samples.

In these sites in the Central Amazon rainforest predominate very acid soils (pH between 3.4 and 4.5), infertile, with limited water retention and toxic levels of aluminum (Laurance et al. 1999). The richness and abundance of galling insects at

Table 19.1 Pearson correlation coefficients between the galling insect (GI) richness and abundance (Julião et al. 2014b) and some potential predictor variables on soil fertility at the reserves of the Biological Dynamics of Forest Fragments Project (BDFFP/INPA), Amazonia, Brazil. The number of plots used in the analysis varied depending on the data availability (Nascimento and Laurance 2011). Only strong and moderate correlations were presented and the correlations with weak and negligible values were excluded

Soil traits	GI richness	GI abundance	Sites (n)
Primary nutrients			
Total N (%)	0.544*	0.324	12
PO_4^{3-} (m.e./100 g dry soil)	−0.433	−0.309	12
K^+ (m.e./100 g dry soil)	0.556*	0.493	12
Secondary nutrients			
Mg^{2+} (m.e./100 g dry soil)	0.419	0.347	12
Micronutrients			
Fe (ppm)	0.522	0.227	10
Mn^{2+} (ppm)	0.480	0.037	10
Zn^+ (ppm)	−0.823**	−0.682**	10

* p values marginally significant ($0.05 < p < 0.07$), ** p values < 0.05

10–12 sampling points were correlated (Pearson correlations, with Bonferroni corrected probability) with the concentration of primary and secondary nutrients, micronutrients, C/N ratio, pH and soil texture, measurement of ions and cations (Julião et al. 2014b). A negative correlation between galling insect richness and abundance (GIR and GIA) and levels of zinc (ppm) were the only significant relationships observed (Table 19.1, Fig. 19.4). Furthermore, Zn and PO_4^{3-} concentration explained alone 70 % of the variation in GIR ($r^2 = 0.70$, $y = 56.68 + 437.82\ PO_4^{3-} - 15.68\ Zn$, $F_{2,7} = 8.10$, $p < 0.05$); thus corroborating the hypothesis that GIR is negatively affected by soil fertility (Julião et al. 2014b).

The PO_4^{3-} and Zn are recognized as essential nutrients to the basal plant metabolism. Organically bound phosphates are the form of phosphorus available to plants, and its deficiency can result in delayed flowering, stunting and steam and leaf discoloration. On the other hand, zinc participates in the enzyme activation, protein catabolism and formation of growth regulators and their insufficiency can lead to leaf discoloration, problems in plant development and fructification (Larcher 1973). In fact, it was also observed that GIR showed a negative correlation with the concentrations of zinc, magnesium, and potassium at the Brazilian savannas (Gonçalves-Alvim and Fernandes 2001).

Regardless the spatial scale, soil infertility seems to be an appropriate explanatory variable associated with the diversity patterns of galling insects and host plants in the Brazilian Amazonian rainforest. With different soil characteristics and vegetation, *terra firme*, *várzea* and *igapó* areas differ greatly in concentration of soil nutrients. The phosphorus content are lower in the soils of *terra firme* forest while in the *várzea*, fertile soils usually have higher concentrations of K, Fe, Mn, Ca, Mg, Al and Zn. Furthermore, *terra firme* and *igapó* soils do not differ in the concentration of the last four elements (Haugaasen and Peres 2006). A comparison of these three vegetations unveiled that the ratio between GIR and richness of sampled trees

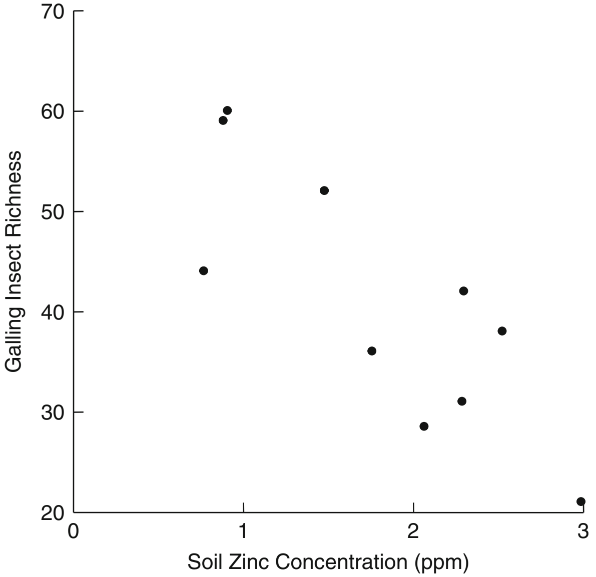


Fig. 19.4 Correlation scatterplot between soil zinc concentration in parts per million (ppm) and galling insect richness sampled in the canopy of terra firme forests in the BDFFP reserves (n = 10), Amazon

(hosts and non-hosts) was higher in areas located in poorer soils (ANOVA, $F_{2,53} = 5.041$; $p < 0.05$) (Julião et al. 2014a). Tree species in *terra firme* and *igapó* present a larger number of galling species in comparison with the *várzea* trees, consequently, few trees were not attacked by galling insects in *terra firme* (28 trees, 5.3 % of sampled individuals) and *igapó* forests (21 trees, 8.4 % of the total), compared to 20.6 % in the *várzea* forest (64 individuals) (Julião et al. 2014a). Concomitantly, *igapó* and *terra firme* forests present, on average, a greater number of galling insect morphospecies *per* sampled plant than *várzea* (*Igapó*: 2.48 ± 0.39; *Terra firme*: 2.39 ± 0.42; *Várzea*: 2.04 ± 0.37; Fig. 19.5).

19.4.2 Topography

Besides the physical and chemical features of Amazonian soils, topography represents another key variable influencing plant community structure and distribution, both in canopy and in understory (Costa et al. 2005, 2009; Bohlman et al. 2008; Laurance et al. 2010). Strong correlations between local topography and soil characteristics indicates that altitude and terrain inclination (topographic components) can be used as alternative measurement of soil texture and fertility in the central region of the Amazonian rainforest (Costa et al. 2005). Several studies have pointed out the importance of topography on the distribution of terrestrial vertebrates and invertebrates. Richness, abundance and fauna composition varied along a topographic gradient and many species were inferred as generalists or specialists regarding the occupation of

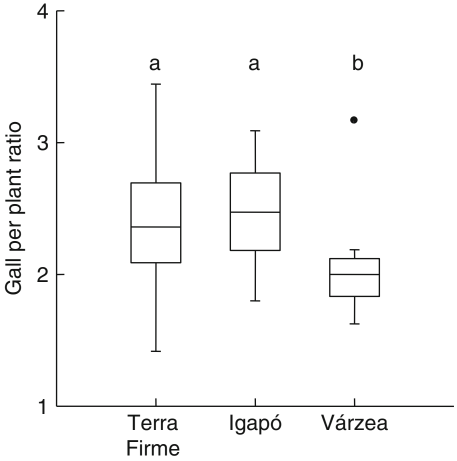


Fig. 19.5 Ratios between galling insect richness and number of plant species sampled from *terra firme* (N = 28), *igapó* (N = 14), and *várzea* (N = 14) forests, central Amazon. *Terra firme* and *igapó* presented a higher number of gall morphospecies per sampled tree than do *várzea* forest ($F_{2,53} = 5.041$; $p < 0.05$). Same letters did not differ significantly after an ANOVA followed by a Tukey's post hoc test

plateau, slope and valley habitats (Menin et al. 2007; Murphy et al. 2008; Oliveira et al. 2009; Cintra and Naka 2012). In the case of galling insects, the findings of a survey made by Almada et al. (2014) indicate the same trend. Galling insect richness differed significantly among plateaus, slopes, valleys and areas of transition between slope and plateau (H = 12,576, df = 3, p-value = 0.006). Multiple comparisons by the minimal significant differences test (dms) showed that stepper areas, less able to retain water in the soil (slope habitat), presented a higher number of galling insect species than valley habitats (dms 12.450 > 9.922, $p < 0.05$), with sandy soils usually near water bodies (rivers and groundwater) (Fig. 19.6). Terrain inclination has been related to characteristics of soil and vegetation in the central Amazon rainforest. Usually, flatter terrains have higher concentration of silt and clay, carbon, nitrogen, phosphorus, potassium, magnesium, iron and manganese and low aluminum saturation, providing fertile soils, while steeper areas have soils with higher sand content and high aluminum saturation (Laurance et al. 1999, 2010). Moreover, steeper and sandy terrains accumulate a high density of trees, but lower biomass, with a scarcity of large trees (Laurance et al. 2010). Some plant families and genera [*Licania* (Chrysobalanaceae), Myristicaceae] have their distribution strongly related to terrain inclination (Bohlman et al. 2008). In conclusion, the distribution of galling insects is also affected by topography (altitude and inclination), supporting both the hypothesis of water and nutrition stress. However, detailed studies are needed on the mechanisms behind this pattern, in which host and non-host plant composition and additional measures (at local scale) of nutritional and hydric status of the soils at plateau, slope, and valley habitats in the *terra firme* rainforest are addressed.

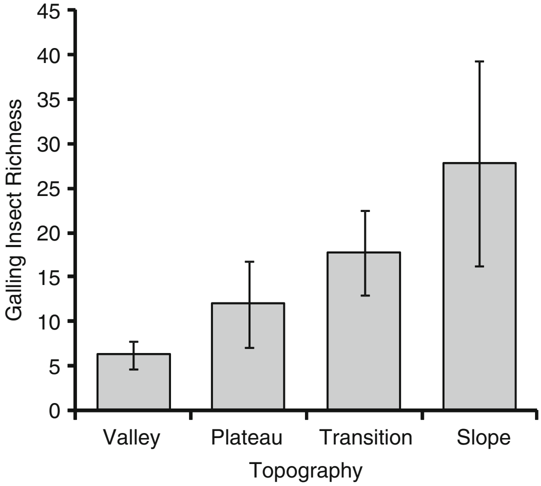


Fig. 19.6 Relationships between galling insect richness and topography in central Amazon, Brazil. Higher number of galling species was found in slope terrain compared to valley areas (Modified from Almada et al. 2014)

19.4.3 Flooding as Stress

Among the various mechanisms that influence the interactions between galling insects and their host plants, hygrothermal stress is constantly pointed out as one of the most important. Plants under these stress conditions could be more susceptible to galling attack, which results in an uneven distribution among habitats (Julião et al. 2005). To evaluate these mechanisms in the Amazonian ecosystem, Julião et al. (2014c) conducted a survey of canopy galling insects in habitats with different levels of hydric stress. Fourteen *várzea* plots and 14 *igapó* plots were sampled both in the Mamirauá and Amanã Sustainable Development Reserves (MSDR and ASDR). *Várzea* and *igapó* vegetation were classified according to flooding duration and level (Wittmann et al. 2002): low *várzea*/*igapó* (LV/LI: average height of flood on tree >3 m; inundation period >50 days/year) and high *várzea*/*igapó* (HV/HI: average height of flood on tree <3 m; inundation period <50 days/year). Julião et al. (2014c) also took into account the differential nutritional status of soils, since the *várzea* has the most fertile soils of the Amazonian region in contrast to the poor and sandy soils of the *igapó* areas (Haugaasen and Peres 2006). Considering hydrical and nutritional conditions in the forests, we hypothesized the existence of an ecological gradient of environmental stress determining galling species distribution. At one extremity the lowland *igapó* forest present high flood level and infertile soils, while at the opposite extreme the high *várzea* forest present low flood level and highly productive soils. Overall, 50,238 insect galls were collected, with 235 galling morphotypes recorded in the *igapó* and 297 galling morphotypes in the *várzea* forest (Julião et al. 2014c). Of the 250 tree individuals sampled in the *igapó*, 229 had insect galls. In *várzea* forest we recorded the higher number of non-host trees

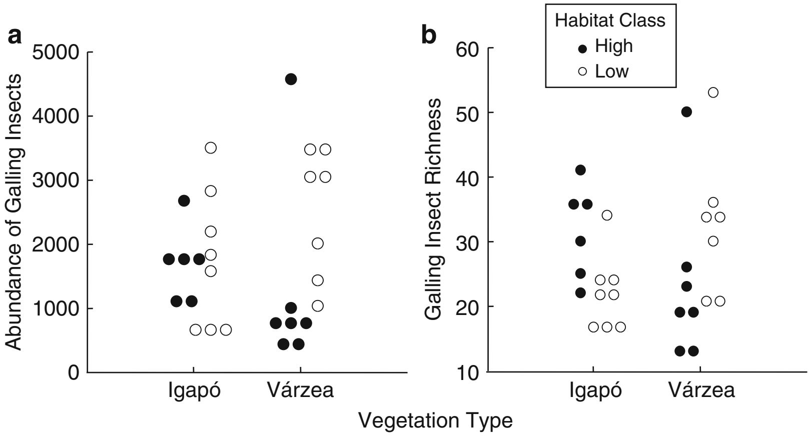


Fig. 19.7 Abundance (**a**) and richness (**b**) of galling insects in igapó and várzea forests with two categories of habitat based on flood heights and duration of flooding (see text for details) in the Mamirauá Sustainable Development Reserve and Amanã Sustainable Development Reserve, Amazon

(64 individuals out of 312 sampled trees). The abundance of galling insects did not differ between habitats [flooding level (low or high); $F_{1,24}=2.407$, $p=0.134$], forest types (*várzea* or *igapó*; $F_{1,24}=0.154$, $p=0.698$), and no interaction between the two factors ($F_{1,24}=2.132$, $p=0.157$; Fig. 19.7a) (Julião et al. 2014c).

In spite of no influence of flooding ($F_{1,24}=0.000$, $p=0.992$) and forest formation ($F_{1,24}=0.120$, $p=0.732$) on the number of galling insects, the interaction between the two variables significantly influenced the number of galling insect species ($F_{1,24}=6.868$, $p=0.015$; Fig. 19.7b). These results reinforce the hypothesis that a combination of hydrical and nutritional stresses directly affects the richness of galling insects in Amazonian forests, at least on a local scale. Furthermore, fewer tree species of *igapó* forest tends to accumulate, on average, a greater galling insect richness ($F_{3,24}=5.623$, $p=0.005$; Fig. 19.8) (Julião et al. 2014c).

19.4.4 Plant Species Number and Scleromorphic Features at the Upper Canopy Level

Given the continental extent of the Amazon region, plant richness and composition ought to play a prominent role in the distribution patterns of galling insects. The Amazonian ecosystem presents a wide range of variation in the hydric and edaphic/topographic traits, both in local and regional scale, which directly determines the flora composition.

We found that tree richness (host and non-host) varied greatly at each site and forest type (*terra firme*, *igapó*, *várzea*). In *terra firme*, 9–25 tree species per sampling point were sampled; in *igapó* 8–17 species were sampled, while in *várzea* samples ranged from 7 to 33 tree species (Julião et al. 2014a). Relationships between galling insects and sampled plant richness were significantly positive in the three landscapes.

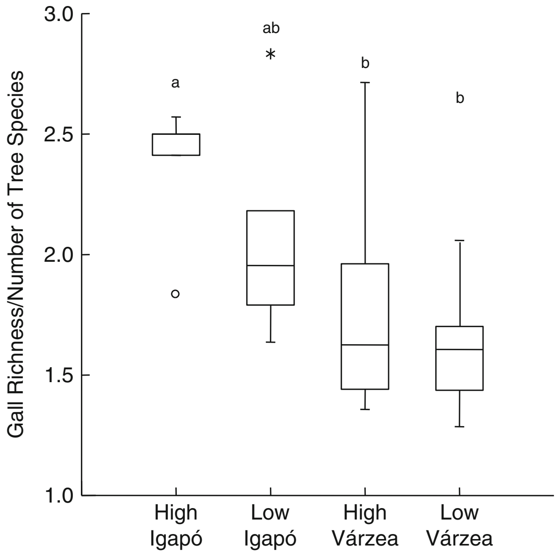
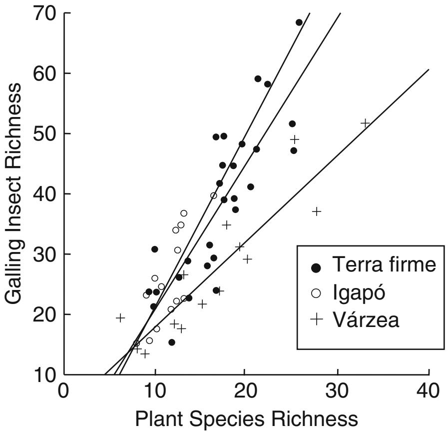


Fig. 19.8 Ratio between richness of galling insects and the number of tree species collected in high-igapó, low-igapó, high-várzea and low-várzea forests (see text for details) in the Mamirauá Sustainable Development Reserve and Amanã Sustainable Development Reserve, Brazilian Amazon. Same letters did not differ significantly after an ANOVA followed by a Tukey's post hoc test

Fig. 19.9 Relationship between galling insect richness and richness of plant species sampled in *terra firme* ($r^2=0.713$; $p<0.0001$; $N=28$), *igapó* ($r^2=0.721$; $p<0.0001$; $N=14$) and *várzea* ($r^2=0.834$; $p<0.0001$; $N=14$) forests from central Amazon



Variation in the number of plant species explained 83 % of variation in galling insect richness in *várzea* forest, in *igapó* this value was 72 %, and in the *terra firme* the value was 71 % (Fig. 19.9) (Julião et al. 2014a).

The Amazonian forests constitute one of the moistest and "non-scleromorphic vegetation" so far investigated to biogeographical patterns of galling insect diversity and distribution. These results contradict the "predictions on the gall richness peak", proposed by Price et al. (1998) based on the vegetation/landscape traits.

However, these results can be explained by two factors: tree diversity in the Amazon (Laurance 2001) and sampling in the upper forest canopy (Ribeiro 2003; Medianero et al. 2003; Ribeiro and Basset 2007; Ribeiro et al. 2011). The local richness of trees ranges from 280 to 285 species per hectare, including trees with diameters ≥10 cm at breast height (Oliveira and Mori 1999). Some authors have already noted the positive influence of plant species diversity on galling insect richness (Fernandes 1992; Gonçalves-Alvim and Fernandes 2001; Lara et al. 2002). In fact, the majority (89.6 %) of sampled trees in the *várzea*, *igapó* and *terra firme* forests were attacked by galling insects (978 individuals out of 1,091 trees), resulting in a high abundance and richness of galling insects. The second explanatory factor for the highest galling diversity on "non-scleromorphic rainforest" would be abiotic and biotic conditions found in the canopy, similar to those observed where galling species records are numerous (Ribeiro 2003), namely scleromorphic Mediterranean-type vegetation (savannas, fynbos, chaparral, Brazilian rupestrian fields, see Fernandes and Price 1991; Fernandes et al. 2005). Several studies pointed that canopy trees are subjected to hydrical stress, high temperatures, high levels of UV radiation and low humidity (Mulkey et al. 1996; Bell et al. 1999; Basset et al. 2003). Plants in the upper canopy are affected in their photosynthesis and respiration due to the intense light exposure and high temperatures. Some leaves on the upper canopy can have their temperatures very close to the lethal temperature (Tribuzy 2005). Consequently, upper canopy leaves generally are tougher and more sclerophyllous, with high concentrations of phenolic compounds (van der Meulen and Werger 1984; Dominy et al. 2003; Oishi et al. 2006). Such leaf characteristics have often been related to the distribution and diversity of galling insects (see Fernandes and Price 1991; Fernandes et al. 2005). In addition, large and emergent trees may also present hydrical stress (>35–50 m, depending on the vegetation type). Limitations can occur in water flux to the canopy due to a natural obstacle imposed by gravity; phenomena known as hydraulic limitation (Hydraulic Limitation Hypothesis; Ryan et al. 2006) and xylem dysfunction by cavitation (Goldstein et al. 1998). We then conclude that, despite the majority of Amazonian forest strata being characteristically humid, canopy habitat present differential microclimatic conditions, which are similar to Mediterranean-type ecosystems. The combination of Amazonian flora diversity and such abiotic conditions favor the occurrence of an unnoticed peak in the galling richness and abundance.

19.5 Galling Insect Diversity in Amazonian Rainforests

In this topic we present a compilation of the main studies done in the Brazilian Amazon region. To accomplish this task we considered the studies done by Schwartz et al. (2003), Izzo et al. (2006), Julião (2007), Carvalho-Fernandes (2010), Maia (2011), Almada and Fernandes (2011) and Almada et al. (2014) (Table 19.2).

The families, genera, and species of host plants listed in these studies were checked for changes in taxonomic nomenclature and synonymies. We used the web interfaces of The Plant List and Tropicos© to search for species names and

Table 19.2 Number of galling insect and host plant species sampled in the Amazonian studies, with localities and geographical coordinates

Locality	Coordinates	Galling species (n)	Host species (n)	References
BDFFP reserves	2°30′S; 60°W	1,150	491	Julião (2007)
Mamirauá SDR	3°3′S, 64°51′W			
Amanã SDR	2°38′S, 64°38′W			
Ducke reserve	3° 00′S, 59° 55′W	98	15	Carvalho-Fernandes (2010)
Platô Bacaba	1°20′S; 56°W	76	39	Maia (2011)
Porto Trombetas	1°40′S; 56° 27′W	309	255	Almada and Fernandes (2011)
BDFFP reserves	2°30′S; 60°W	231	213	Almada et al. (2014)
Ilha da Marchantaria	3°14′S; 59° 57′W	4	1	Schwartz et al. (2003)
BDFFP- ZF3road/km 41	2°30′S; 60°W	1	1	Izzo et al. (2006)

corresponding synonyms. In order to avoid overestimation of galling diversity and to produce a general list of gall insect morphospecies it was adopted the following criteria for inclusion and exclusion: (1) host plants identified at the genus level could be included only when there were no representatives of the botanical genus, or when the insect gall occurred on a vegetative organ not yet recorded, (2) species of host plants with nomenclature not registered in the sites have been excluded; (3) the standardization of gall morphology (very variable between studies) was based on the descriptions of shape, color, occurrence and pubescence as proposed by Julião et al. (2002); (4) photographic records and technical drawings provided by the authors were used to compare gall morphology, and a gall morphospecies was excluded when its description was similar to others already listed for a given host plant species. Since a small number of galling insect species has been identified and described, the information presented herein refer almost entirety to the galling insect morphospecies. Based on a rigorous and extensive taxonomic review, Carneiro et al. (2009) supported the strong correspondence between the morphology and specificity of gall-inducing species.

19.5.1 Host Plants: Main Families and Genera

In the survey compilation were recorded 66 botanical families, 251 genera and 713 species of host plants of galling insects. Overall, 1,549 galling morphospecies were considered. Half of them (52 %) occurred on only five families: Fabaceae, Sapotaceae, Burseraceae, Chrysobalanaceae and Lecythidaceae. The average number of galling morphospecies per host plant species ranged from one (Asclepiadaceae, Bixaceae, Calophyllaceae) to eight (Goupiaceae). Although having only one species, *Goupia glabra*, the family Goupiaceae is attacked by eight different galling insects. These results indicate the existence some super host families in the region (see Fernandes and Price 1988, 1991; Veldtman and McGeoch 2003) (Table 19.3).

Table 19.3 Family, number of host plant genera and species, number of galling insect species, and averaged galling species per host plant species (GS/HS) compiled from studies in the Brazilian Amazon region

Host plant			Galling insect species	
Family[a]	Genera	Species	Number	GS/HS
Fabaceae	45	132	259	1.96
Sapotaceae	6	63	164	2.60
Burseraceae	4	37	160	**4.32**
Chrysobalanaceae	4	44	117	2.66
Lecythidaceae	8	28	105	**3.75**
Lauraceae	10	37	95	2.57
Moraceae	10	27	51	1.89
Melastomataceae	4	25	50	2.00
Annonaceae	11	26	49	1.88
Euphorbiaceae	12	20	40	2.00
Myrtaceae	7	17	27	1.59
Anacardiaceae	5	10	26	2.60
Humiriaceae	5	9	24	2.67
Malvaceae	10	13	22	1.69
Malpighiaceae	4	13	21	1.62
Apocynaceae	7	13	20	1.54
Rubiaceae	9	15	20	1.33
Salicaceae	4	10	19	1.90
Vochysiaceae	3	10	18	1.80
Clusiaceae	7	11	17	1.55
Urticaceae	3	12	17	1.42
Combretaceae	3	6	16	2.67
Sapindaceae	6	11	14	1.27
Meliaceae	3	11	13	1.18
Elaeocarpaceae	1	6	11	1.83
Hypericaceae	1	5	11	2.20
Myristicaceae	3	9	11	1.22
Siparunaceae	1	9	11	1.22
Violaceae	3	5	11	2.20
Bignoniaceae	3	8	10	1.25
Caryocaraceae	1	3	8	2.67
Goupiaceae	1	1	8	8.00
Ochnaceae	2	5	8	1.60
Olacaceae	3	4	8	2.00
Polygonaceae	3	3	8	2.67
Celastraceae	2	2	6	3.00
Dilleniaceae	3	5	6	1.20
Ebenaceae	1	4	6	1.50
Aquifoliaceae	1	1	5	5.00
Dichapetalaceae	2	3	5	1.67
Boraginaceae	1	3	4	1.33
Connaraceae	2	4	4	1.00

(continued)

Table 19.3 (continued)

Host plant			Galling insect species	
Family[a]	Genera	Species	Number	GS/HS
Lacistemataceae	1	2	4	2.00
Peraceae	2	4	4	1.00
Passifloraceae	2	3	3	1.00
Phyllanthaceae	1	1	3	3.00
Picramniaceae	1	1	3	3.00
Picrodendraceae	1	1	3	3.00
Solanaceae	2	2	3	1.50
Achariaceae	1	2	2	1.00
Convolvulaceae	1	1	2	2.00
Erythroxylaceae	1	2	2	1.00
Nyctaginaceae	1	1	2	2.00

[a] Asclepiadaceae, Bixaceae, Calophyllaceae, Loranthaceae, Menispermaceae, Myrsinaceae, Polygalaceae, Proteaceae, Quiinaceae, Rutaceae, Simaroubaceae, Smilacaceae, Styracaceae families presented only one gall morphospecies in one host plant species

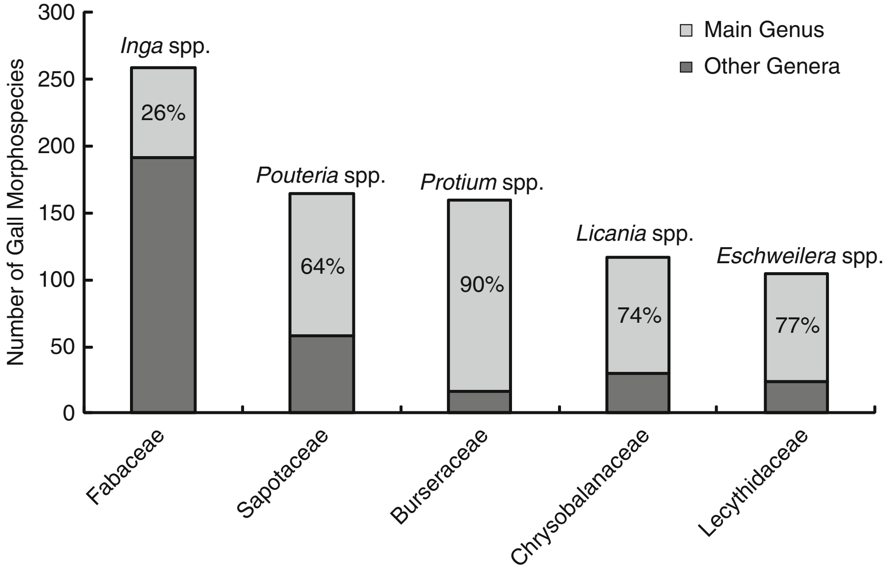


Fig. 19.10 Number of galling insect morphospecies on the main botanical families, and the contribution percentage of each main super-host genera of Amazonian forests

Among the botanical families with large numbers of galling insects, we emphasize the importance of the genera *Inga*, *Pouteria*, *Protium*, *Licania* and *Eschweilera*. However, the contribution of these genera as super hosts is quite variable. On the one hand, *Inga* spp. contributes with 26 % to the total Fabaceae morphospecies, while *Protium* spp. comprises 90 % of galling insect morphospecies sampled in the Burseraceae family (Fig. 19.10).

These data reinforce the importance of community composition (not just richness) of host plants in a given ecosystem or habitat. As *Baccharis* spp. in South America (Fernandes et al. 1996) and *Eucalyptus* spp. in Australian forests (Blanche 2000), super-host genera in the Amazon rainforest dramatically shape the diversity and the community of galling insects. Carvalho-Fernandes (2010) sampled 98 galling insect morphospecies on 15 species of *Protium* spp. in only one collecting site: the Adolpho Ducke Forest Reserve, located near the city of Manaus, Amazonas. Among the host species, *P. divaricatum* had the most speciose group of associated galling insects, with 17 morphospecies. Other authors report Neotropical super-host species elsewhere, such as *Copaifera langsdorffii* with 23 galling insect morphotypes (Costa et al. 2010), and *Baccharis concinna* (Asteraceae), attacked by 15 species of galling insects (Lara and Fernandes 1996).

In the Neotropics, the Burseraceae family is represented by seven genera and approximately 228 species. *Protium* spp. is the main genus of the Burseraceae in South America, and includes about 130 known species. Since species distinction by vegetative organs is usually difficult, insect galls have been suggested as tools in taxonomic identification in this genus (Ribeiro et al. 1999).

19.5.2 Galling Fauna in the Brazilian Amazon

The enormous and fascinating variety of epidermal traits, colors and shapes of insect galls associated with the Amazonian vegetations are shown in Fig. 19.11.

Except for the studies done by Julião (2007) and Almada et al. (2014), the other studies in the region have identified galling insects only at family or order level. Of the 1,549 morphospecies surveyed here, only 386 morphotypes of galls were tentatively identified, while 24 % of the gall inducing insects could not be identified to any possible level. As also observed in other Neotropical regions, the Cecidomyiidae family (Diptera) is the main group attacking host plants sampled in Amazonian forests (see Carneiro et al. 2009). On the other hand, there are many galls induced by Hemiptera, Coleoptera, Lepidoptera, Homoptera, and Hymenoptera (Table 19.4).

19.6 Canopy × Understory Forest

In preserved forests at the Biological Dynamics Forest Fragmentation Project (BDFFP/INPA), simultaneous surveys of galling insect diversity were done by Almada et al. (2014) and Julião et al. (2014b). Although sampling overlapped in some reserves in the *terra firme* forest, they employed different methods in their investigations. The former collected in 19 plots (5×250 m^2, each plot), totaling a sampling area of 14,250 m^2, and found 229 morphospecies of galling insects on 173 species of understory host plants (Almada et al. 2014). The later study sampled insect galls in 14 plots (8×100 m^2, each plot) which were visually

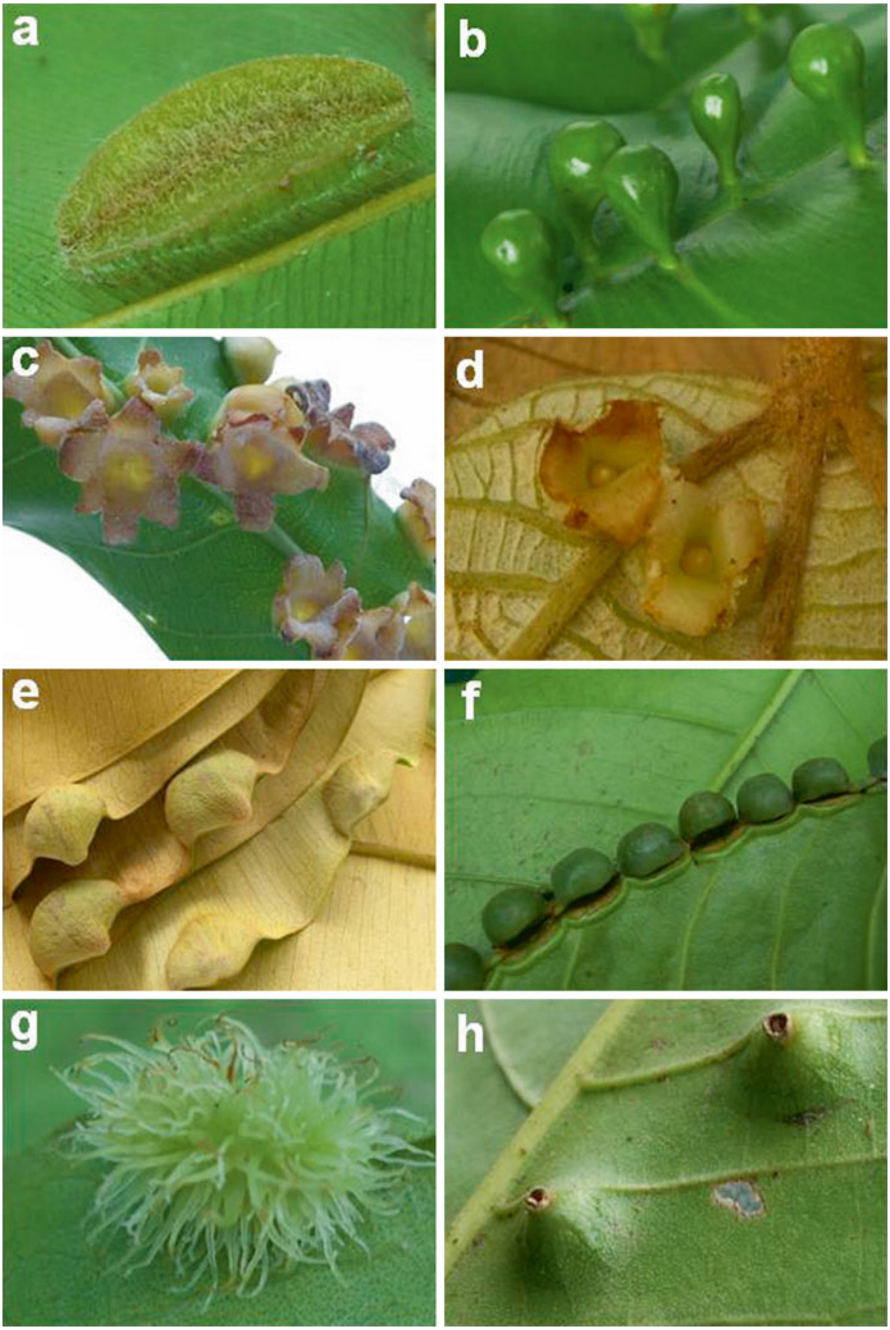


Fig. 19.11 Some insect galls found in the Amazonian rainforest, Brazil. On *Calophyllum brasiliense*: (**a**) leaf gall induced by *Lopesia linearis* (See Madeira and Monteiro 2004), and (**b**) pedunculate leaf gall induced by Cecidomyiidae; on *Naucleopsis* sp.: (**c**) spherical leaf gall induced by Psyllidae (Hemiptera); on *Luehea cymulosa*: (**d**) spherical leaf gall induced by Cecidomyiidae; on *Manilkara huberi*: (**e**) leaf gall induced by Cecidomyiidae; on *Symmeria paniculata*: (**f**) spherical leaf gall induced by Cecidomyiidae, and (**g**) spherical and pubescent leaf gall induced by Cecidomyiidae; on *Tabebuia barbata*: (**h**) conical leaf gall induced by

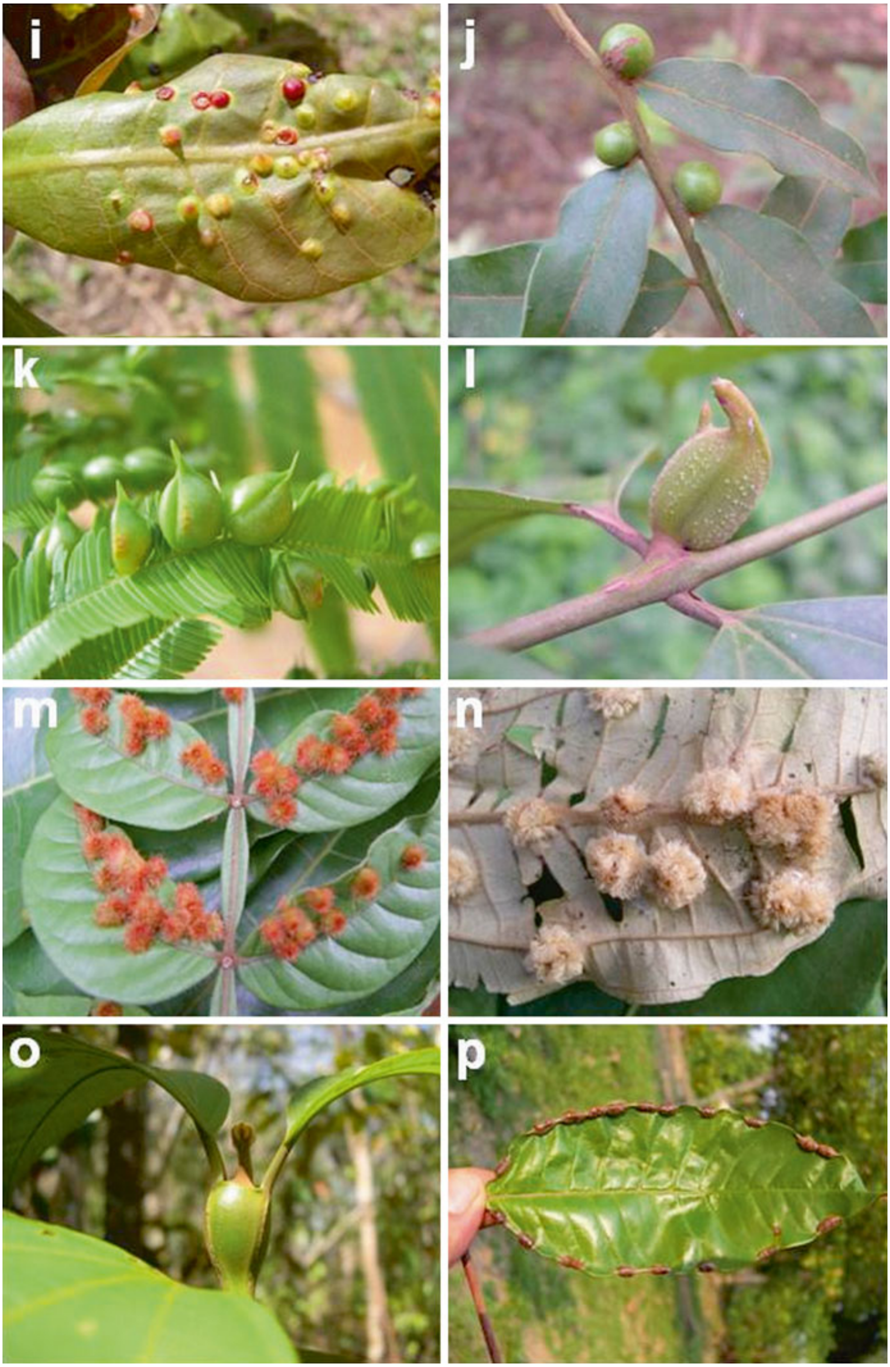


Fig. 19.11 (continued) Cecidomyiidae; on *Anacardium occidentale*: (**i**) spherical leaf gall induced by Cecidomyiidae; on *Diospyros praetermissa*: (**j**) stem gall induced by Coleoptera; on *Parkia pendula*: (**k**) spherical leaf gall induced by Cecidomyiidae; on *Miconia* sp.: (**l**) leaf bud gall induced by Cecidomyiidae; on *Inga* sp. (**m**) and *Miconia gratissima* (**n**): spherical and pubescent leaf galls induced by Cecidomyiidae; on *Bellucia* sp.: (**o**) stem gall induced by Coleoptera; on *Vismia latifolia*: (**p**) elliptical leaf gall induced by Cecidomyiidae

Table 19.4 Number and relative frequency of galling insect taxa in the Amazon forests, Brazil

Galling insect taxa	Number	(%)
Cecidomyiidae – Diptera	276	71.5
Hemiptera	9	2.3
Coleoptera	5	1.3
Lepidoptera	2	0.5
Homoptera	1	0.3
Hymenoptera	1	0.3
Not identified	92	23.8
Total	386	100.0

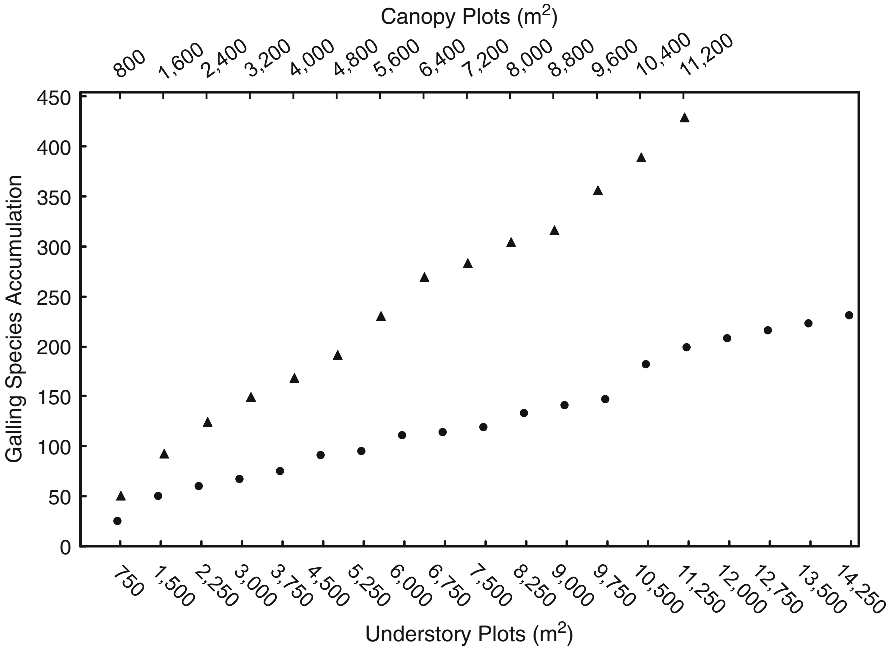


Fig. 19.12 Species accumulation curves of galling insects collected in understory (Almada et al. 2014) and upper canopy (Julião et al. 2014b) of continuous and preserved forest in the BDFFP reserves, central Amazon. *Full circles* depict the number of new galling species sampled to each 750 m^2 sampling area rising. *Full triangles* show augmentation in the galling species number in function of 800 m^2 sampling area increasing

projected in the upper canopy of the continuous and intact forest. In this later study the authors recorded 428 galling morphospecies associated with 165 tree species, in a total sampled area of 11,200 m^2 (Julião et al. 2014b). Species accumulation curves highlighted the clear difference in the gall diversity between these habitats (Fig. 19.12).

On average, the upper canopy strata harbored about twice more galling morphospecies compared to understory plants (1.3 galling morphospecies *per* plant species in understory *versus* 2.6 galling morphospecies *per* tree species). Although, we recorded a lower number of plant species collected in the canopy, trees usually offer more resources (leaves and stems) to galling herbivores. As previously discussed, microclimatic conditions at the canopy of Amazonian rainforests seem to play major role in the spatial distribution of galling insects. However, it remains to investigate whether the patterns observed here vary over time, season, and phenology of the host plants. For instance, further studies shall be designed to compare the galling fauna in the canopy versus understory, to evaluate not only host plant and galling richness but also host and non-host composition (see Julião et al. 2014a), as well as to measures diversity and dominance of certain galling taxa throughout the differential ontogeny of the hosts (Fonseca et al. 2006).

19.7 Conclusions

Our review focused on galling insects found in several landscapes in the Brazilian Amazonian and Pantanal forests. The data indicate the critical importance of habitat heterogeneity for the patterns in the spatial-temporal distribution for this guild of insects. The following remarks summarize these studies: (i) The knowledge on edge and insularization effect is incipient (only one study) and indicates no effect on galling herbivores; (iii) In the Amazon and Pantanal region, the primordial mechanism influencing galling species richness is hygrothermal and nutritional stress, even though mediated by soil fertility, topography, and flooding; (iii) Similar microclimatic conditions found by other studies in scleromorphic/sclerophyllous vegetations are also present in the upper canopy of the Amazonian rainforests. Such variables modulate the susceptibility/resistance of plant species to the attack by galling herbivores, and ultimately result in a differential distribution in the forest strata (understory and canopy); (iv) Super-host plants (genera or species) are also present in the Amazonian rain forests, and more studies to evaluate their diversity and distribution patterns are needed. Finally, the data presented here reaffirm and support the importance of Amazonian tropical rainforests as a cradle of insect diversity.

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Chapter 20
Galls from Brazilian Tropical Dry Forests: Status of Knowledge and Perspectives

Marcel S. Coelho, Geraldo Wilson Fernandes, Frederico Siqueira Neves, and Jean Carlos Santos

Abstract In this chapter we review the available information of the distribution of galling insects on Brazilian Tropical Dry Forests and discuss the possible mechanisms and processes leading to the trends reported. The number of studies conducted in TDFs so far are extremely limited. Only four studies were conducted on Tropical Dry Forests from South America. In spite of the fact that these studies were conducted on different types of Tropical Dry Forests, generalizations were attempted. A trend can be observed indicating low gall inducing insect species richness. The low level of secondary chemistry in low diverse vegetation seems the most plausible explanation for the results unveiled. The regional colonizers from adjacent vegetation types may influence gall-inducing insects richness in the Brazilian Tropical Dry Forests.

Keywords Biogeography • Insect galls • Richness hypothesis • Vegetation structure • Phytogeographic domains

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20.1 Introduction

Recent estimates of the global number of gall-inducing insects range from 21,000 to 211,000 species, with an average of 132,930 species (Espírito-Santo and Fernandes 2007). In spite of the increasing number of studies on galling insects in Brazil the diversity of such herbivores and the association with their host-plants are poorly known in some vegetation types, such as the seasonally dry tropical forests. The studies of gall-inducing insects and their host plants in several Brazilian vegetation types indicate a high richness (e.g., Pantanal) (Julião et al. 2002), Amazonian rain forests (Julião et al. 2005), coastal dune vegetation (restinga) (Maia 2001, 2005; Maia et al. 2002; Oliveira and Maia 2005; Mendonça 2007), savanna (Cerrado) (Fernandes and Price 1988; Maia and Fernandes 2004; Gonçalves-Alvim and Fernandes 2001), rupestrian grasslands (Lara and Fernandes 1996; Lara et al. 2002; Carneiro et al. 2009), and tropical dry forests (Coelho et al. 2009; Santos et al. 2011a).

Tropical dry forests (TDFs) are widely distributed (Mesoamerica and South America, Africa, Asia, and Oceania) and originally representing ca. 42 % of the tropical forests in the world (Miles et al. 2006). Despite the strong dissimilarities, in consequence of different environmental variables, surrounding vegetations and their distinct biogeographic history (see Santos et al. 2012) some generalizations can be made. TDFs occur in frost-free areas where the mean annual biotemperature is higher than 17 °C, annual mean rainfall is between 250 and 2,000 mm, and the differences between evapotranspiration to precipitation exceeds a unity (Murphy and Lugo 1986). In terms of composition, although there is a great variation among sites, TDFs have a local tree species average ranging from 35 to 90, complex index 5–45, canopy height 10–45 and number of canopy strata 1–3, whereas these same variables applied for Tropical Rain Forests are (TWFs), 50–200, 180–405, 20–84, three or even more, respectively (Murphy and Lugo 1986). In Brazil, the TDF can be easily separated into three categories: (i) Caatinga; (ii) Tropical Dry Forests on flat soils; and (iii) Tropical Dry Forests of basalt and limestone outcrops (Nascimento et al. 2004; Coelho et al. 2012).

Caatinga extends for 750,000 km^2 and is located on a flattened depression (300–500 < a.s.l.) on a Pre-Cambrian crystalline rock (Leal et al. 2005). Caatinga is composed by woody vegetation ranging in height from 3 to 9 m with a conspicuous presence of deciduous and semiarid thorny vegetation with succulent and non-succulent shrubs and trees. The Caatinga is surrounded by the Amazon forest on the west, Atlantic Rain Forest on the east and by the Cerrado on the south. Consequently, mixed with endemic elements, contrasting climates and vegetation types are found.

The TDFs on flat soils or arboreal caatinga is predominantly found in northeast Brazil and comprise the largest areas of continuous dry forests. The average of the canopy is high (ca. 12 m), with fertile soils and not associated with watercourses (Madeira et al. 2009). Many studies developed on Brazilian TDFs were carried out on such forests (e.g., Pezzini 2008; Madeira et al. 2009; Arruda et al. 2011).

The TDFs on limestone outcrops are generally comprised of small fragments associated with the Cerrado biome, in central of Brazil. Small fragments of this dry forest can be found, however, all over Brazil (see Meguro et al. 2007). The floristic composition of these dry forests strongly related to the Amazon Rain Forest, Atlantic Rain Forest, Caatinga, Cerrado, and Pantanal (Chaco) vegetation, but with a low similarity among them (Pérez-García et al. 2009). The average of the canopy height is 8 m (Meguro et al. 2007; Coelho et al. 2012). Almost extinct due to human activities and still found in southeastern Brazil, TDFs on basalt outcrops have similar topography, plant phenology, and in spite of soils rich in P, K, Ca and Mg, these forests have strong similarity with the TDFs on limestone outcrops (Rodrigues and Araújo 1997; Oliveira-Filho et al. 1998; Werneck et al. 2000; Coelho et al. 2012).

Although some studies points to a high association of the galling habit with sclerophyllous hosts, a generally low galling richness was reported for the Seasonally Dry Forest formations (Neves 2009). In this chapter we review the available information of the distribution of galling insects on SDTFs and discuss the possible mechanisms and processes leading to the trends reported (Fernandes et al. 2002; Coelho et al. 2009; Santos et al. 2011a; Neves 2009).

20.2 Trends in Gall Richness

Only four studies were conducted on Tropical Dry Forests from South America so far (Fernandes et al. 2002; Coelho et al. 2009; Santos et al. 2011a; Neves 2009). They were conducted using the methodology proposed by Fernandes and Price (1988, 1992). In spite of the fact that these studies were conducted on different types of TDFs, generalizations will be attempted. Fernandes et al. (2002) working in a semi-arid chaco forest reported 29 galling species occurring on 17-host plant belonging to 10 host families. The most attacked family was Fabaceae (8 species), which supported 15 species, representing 52 % of the studied Chaco galling fauna. Sampling TDFs on limestone outcrops in southeastern Brazil, Coelho et al. (2009) recorded 92 galling species on 19 host families (37 genera and 51 host plant species). The family with the highest occurrence of galling species in this study was Fabaceae (24 %, Figs. 20.2 and 20.3), followed by Myrtaceae (12 %, Fig. 20.1), and Asteraceae (9 %). Santos et al. (2011a) sampling 10 different sites in the Caatinga, recorded 64 galling species on 48 host plant species from 17 families and 31 genera. Neves (2009) sampling 185 tree individuals in a tropical dry forest on flat soils recorded an extremely low value of leaf galling insects. Galls were found in only (0.5 %) of the trees sampled and only on 1.01 ± 0.287 % of the leaves sampled, falling the same pattern. Important to mention that the samplings conducted by Neves (2009) were at the canopy.

Overall, 108 host plant species from 29 families hosted a total of 187 gall-inducing insect species in the TDFs of Argentina and Brazil. The main gall-inducing taxa was the Cecidomyiidae (Diptera) representing 84 % (152) of the total galls recorded followed by Hymenoptera 5 % (9), Homoptera 4 % (7), Lepidoptera 2 % (5), Coleoptera 2 % (5), Acarina 1 % (2) and Heteroptera >1 % (1). The galls occurred primarily on leaves 63 % (118), followed by stems 34 % (64), flowers 16 % (3), thorns >1 % (1), and fruits >1 % (1) (see Table 20.1). The families of host plants with the highest gall richness were Fabaceae 28 % (52), Myrtaceae 8 % (15) and

Table 20.1 Host plant species, origin, endemism, geographic distribution in Brazil, phytogeographic domains, tissue, shape, color, pubescense, chambers and gall recorded on three studies carried out on tropical dry forests

Host plant species	Galls	Origin	Endemism	Phytogeographic domains	Tissue	Shape	Color	Pubescense	Chambers	Gall maker	Reference
Anacardiaceae											
Anacardium microcarpum Ducke	1	Native	No	AM, CA CE MA, PP, PT	Leaf	Globular	Red	Glabrous	One	Cecidomyiidae	3
Annonaceae											
Rollinia laurifolia Schltdl.	1	Native	Yes	MA	Leaf	Spherical	Green	Glabrous	One	Homoptera	2
Rollinia sylvatica (A.St.Hil.)	1	Native	Yes	MA	Stem	Globular	Brown	Glabrous	One	Homoptera	2
Apocynaceae											
Aspidosperma cylindrocarpon Müll.Arg.	1	Native	No	AM, CE, MA	Leaf	Cylindrical	Green	Glabrous	One	Homoptera	2
Aspidosperma pyrifolium Mart	1	Native	No	MA, CE, CA	Stem	Conical	Green	Glabrous	One	Cecidomyiidae	2
	2				Leaf	Discoidal	Pale Green	–	One	Cecidomyiidae	1
	3				Stem	Globular	Brown	–	One	Cecidomyiidae	1
Asteraceae											
Baccharis dracunculifolia DC.	1	Native	No	CE, MA, PP	Leaf	Legume	Green	Glabrous	One	*Neopelma baccharidis* Buckhardt	2
	2				Stem	Elliptical	Green	Glabrous	Various	Cecidomyiidae	2
	3				Leaf	Conical	Green	Glabrous	One	Cecidomyiidae	2
	4				Stem	Spherical	Green	Glabrous	One	Cecidomyiidae	2
	5				Stem	Elliptical	Green	Glabrous	One	Lepidoptera	2
Baccharis salicifolia (Ruiz & Pav.) Pers.	1	Native	No	AM, CE	Leaf	Elliptical	Green	Glabrous	One	Neopelma sp.	1
Baccharis sp. 1	1			–	Leaf	Conical	Green	Glabrous	One	Acarina	2

Vernonanthura phosphorica (Vell.) H.Rob.	1	–	–	AM, CE, MA	Leaf	Spherical	Green	Glabrous	One	Cecidomyiidae	2
	2				Stem	Globular	Brown/ Green	Glabrous	One	Cecidomyiidae	2
Bignoniaceae											
Arrabidae elata	1	–	–	–	Flower	Elliptical	Green	–	Various	Cecidomyiidae	1
Tabebuia impetiginosa (Mart. Ex DC.) Standl	1	Native	No	CE, CA	Leaf	Spherical	Green	Glabrous	One	Coleoptera	3
Boraginaceae											
Cordia leucocephala Moric.	1	Native	Yes	CA	Leaf	Spherical	Green	Glabrous	One	Cecidomyiidae	3
	2				Leaf	Elliptical	Green	Glabrous	One	Cecidomyiidae	3
	3				Stem	Elliptical	Green	Glabrous	Various	Cecidomyiidae	3
Cordia trichotoma (Vell.) Arráb. Ex Steud	1	Native	No	AM, CA, CE	Leaf	Spherical	Brown	Glabrous	One	Cecidomyiidae	2
	2				Leaf	Discoidal	Brown	Glabrous	One	Cecidomyiidae	2
	3				Stem	Globular	Brown	Glabrous	Various	Cecidomyiidae	2
	4				Leaf	Spherical	Brown	Hairy	One	Cecidomyiidae	2
	5				Stem	Elliptical	Green	Glabrous	Various	Lepidoptera	2
Tournefortia rubicunda Salzm. Ex DC.	1	Native	Yes	CA, CE, MA	Fruit	Globular	Green	Hairy	Various	Cecidomyiidae	3
Cannabaceae											
Celtis brasiliensis (Gardner)Planch.	1	Native	Yes	MA	Stem	Elliptical	Brown	Glabrous	One	Lepidoptera	2
	2				Thorn	Conical	Green	Glabrous	One	Cecidomyiidae	2
	3				Stem	Globular	Brown	Glabrous	One	Cecidomyiidae	1.2
	4				Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	2
	5				Leaf	Spherical	Yellow	Hairy	One	Cecidomyiidae	2
Celtis iguanaea (Jacq.) Sarg.	1	Native	No	AM, CA, CE, MA, PP, PT	Leaf	Conical	Green	Glabrous	One	Cecidomyiidae	2

(continued)

Table 20.1 (continued)

Host plant species	Galls	Origin	Endemism	Phytogeographic domains	Tissue	Shape	Color	Pubescense	Chambers	Gall maker	Reference
Celtis pallida Torr.	1	Native	No	CE, MA, PT	Stem	Elliptical	Green	–	One	Cecidomyiidae	1
	2				Stem	Globular	Green	–	One	Cecidomyiidae	1
Capparidaceae											
Capparis salicifolia. Griseb.	1	Non-native	No	CH	Leaf	Ellipsoid	Green	–	One	Cecidomyiidae	1
	2				Stem	Globular	Pale green	–	–	Cecidomyiidae	1
Combretaceae											
Buchenavia tomentosa Eichler	1	Native	No	AM, CE	Leaf	Spherical	Green	Glabrous	One	Cecidomyiidae	2
Terminalia argentea Mart.	1	Native	No	CA, CE	Leaf	Discoidal	Brown	Glabrous	One	Cecidomyiidae	2
	2				Leaf	Spherical	Brown	Hairy	One	Cecidomyiidae	2
Convolvulaceae											
Convolvulaceae sp. 1	1	–	–	–	Stem	Elliptical	Green	Glabrous	One	Cecidomyiidae	3
	2				Flora bud	Globular	Green	Glabrous	–	Cecidomyiidae	3
	3				Leaf	Amorphous	Green	Glabrous	–	Cecidomyiidae	3
Erythroxylaceae											
Erythroxylum citrifolium A.St.-Hil.	1	Native	No	AM, CE, MA	Stem	Globular	Green/ Brown	Glabrous	Various	Cecidomyiidae	2
	2				Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	2
Erythroxylum pungens O.E. Schulz	1	Native	Yes	CA	Leaf	Spherical	Green	Glabrous	One	Cecidomyiidae	3
Erythroxylum vacciniifolium Mart.	1	Native	No	CA, CE, MA	Stem	Spherical	Green	Glabrous	One	Hymenoptera	2
	2				Leaf	Spherical	Green	Glabrous	One	Cecidomyiidae	2

Euphorbiaceae										
Cnidoscolus loefgrenii (Pax & K. Hoffm.) Pax & K. Hoffm.	1	Native	Yes	CA	Leaf	Globular	Green	Glabrous	One	Cecidomyiidae	3
Cnidoscolus phyllacanthus (Müll. Arg.) Pax & L. Hoffm.	1	Native	Yes	CA	Leaf	Spherical	Green	Glabrous	One	Cecidomyiidae	3
Cnidoscolus urens (L.) Arthur	1	Native	Yes	AM, CA, CE, MA	Leaf	Discoidal	Yellow	Glabrous	One	Cecidomyiidae	3
Croton adamantinus Müll.Arg.	1	Native	Yes	CA	Stem	Spherical	Brown	Glabrous	–	Not identified	3
Croton blanchetianus Baill.	1	Native	Yes	CA	Leaf	Spherical	Green/ Brown	Glabrous	One	Cecidomyiidae	3
	2				Stem	Elliptical	Green	Glabrous	Various	Cecidomyiidae	3
Croton echioides Baill.	1	Native	Yes	CA	Leaf	Spherical	Green	Hairy	One	Cecidomyiidae	3
Croton rhamnifolioides Pax & K. Hoffm.	1	Native	No	CA	Leaf	Spherical	Green	Hairy	One	Cecidomyiidae	3
Croton sarcopetalus Müll. Arg.	1	Non-native	No	CH	Leaf	Elliptical	Brown	–	One	Cecidomyiidae	1
Manihot dichotoma Ule	1	Native	Yes	CA	Leaf	Cylindrical	Green/Red	Glabrous	One	Cecidomyiidae	3
Fabaceae											
Acacia aroma var.	1	Non-native	No	CH	Stem	Elliptical	Green	–	Various	Cecidomyydae	1
Acacia curvifructa Burkart	1	Non-native	No	CH	Stem	Elliptical	Brown	–	Various	Hymenoptera	1
Acacia macrantha Willd.	1	Non-native	No	CH	Stem	Elliptial	Brown	–	One	Cecidomyiidae	1

(continued)

Table 20.1 (continued)

Host plant species	Galls	Origin	Endemism	Phytogeographic domains	Tissue	Shape	Color	Pubescense	Chambers	Gall maker	Reference
Acacia martii Benth.	1	Non-native	No	CH	Leaf	Conical	Brown	Glabrous	One	Cecidomyiidae	2
	2				Leaf	Spherical	Yellow	Glabrous	One	Cecidomyiidae	2
Acacia praecox Gris.	1	Non-native	No	CH	Leaf	Globular	Green	–	One	Cecidomyiidae	1
	2				Stem	Globular	Brown	–	–	Hymenoptera	1
Acacia sp. Mill	1	–	–	–	Meristem	Globular	Green	Glabrous	Various	Cecidomyiidae	3
Acacia sp. 2	1	–	–	–	Leaf	Spherical	Green/ Brown	Glabrous	One	Cecidomyiidae	2
	2				Leaf	Cylindric	Brown	Glabrous	One	Cecidomyiidae	2
Anadenanthera colubrina (Vell.) Brenan	1	Native	No	CA, CE, MA	Stem	Spherical	Brown	Glabrous	One	Cecidomyiidae	2
	2				Leaf	Conical	Brown	Glabrous	One	Cecidomyiidae	2
	3				Leaf	Spherical	Brown	Glabrous	One	Cecidomyiidae	2
Bauhinia acuruana Moric.	1	Native	Yes	CA	Leaf	Globular	Green	Hairy	One	Cecidomyiidae	3
	2				Leaf	Discoidal	Green/ Brown	Glabrous	One	Cecidomyiidae	3
	3				Stem	Elliptical	Brown	Glabrous	Varrious	Cecidomyiidae	3
Bauhinia brevipes Vogel	1	Native	No	AM, CA, CE	Stem	Elliptical	Brown	Glabrous	Various	Lepidoptera	2
	2				Leaf	Elliptical	Green	Glabrous	One	Cecidomyiidae	2
	3				Stem	Globular	Brown	Glabrous	Various	Cecidomyiidae	2
	4				Leaf	Spherical	Red	Hairy	One	Cecidomyiidae	2
Bauhinia cheilantha (Bong.) Steud.	1	Native	No	CA, CE	Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	3
	2				Leaf	Spherical	Green	Glabrous	One	Cecidomyiidae	3
	3				Stem	Globular	Brown	Glabrous	Various	Cecidomyiidae	3
	4				Leaf	Discoidal	Green	Glabrous	One	Coleoptera	3
Bauhinia longifolia (Bong.) Steud.	1	Native	Yes	AM, CE, MA	Leaf	Discoidal	Green	Glabrous	One	Homoptera	2
	2				Leaf	Spherical	Red	Glabrous	One	Cecidomyiidae	2
	3				Stem	Elliptical	Brown	Glabrous	One	Cecidomyiidae	2

Bauhinia rufa (Bong.) Steud.	1	Native	No	CE	Stem	Irregular	Brown	Glabrous	Various	Cecidomyiidae	2
Bauhinia sp.	1	–	–	–	Stem	Irregular	Brown	Glabrous	Various	Cecidomyiidae	2
	2				Leaf	Spherical	Red	Hairy	One	Cecidomyiidae	2
Caesalpinia bracteosa Tul.	1	Native	Yes	CA	Leaf	Elliptical	Red	Hairy	One	Cecidomyiidae	3
	2				Stem	Globular	Brown	Glabrous	Various	Cecidomyiidae	3
Copaifera langsdorffii (Vogel)	1	Native	No	CE, MA	Leaf	Legume	Green	Glabrous	Various	Cecidomyiidae	2
Geoffroea decorticans (Gillies ex Hook. & Arn.) Burkart	1	Non-native	No	CH	Leaf	Conical	Green	–	One	Cecidomyiidae	1
Hymenaea eriogyne Benth.	1	Native	Yes	CA, CE	Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	3
Mimosa tenuiflora (Wild.) Poir.	1	Native	No	CA, CE	Leaf	Discoidal	Green	Hairy	One	*Bivalvaemyia pernambucensis* Maia (Cecidomyiidae)	3
	2				Leaf	Discoidal	Green	Glabrous	One	*Bivalvaemyia mimosae* Maia (Cecidomyiida)	3
Piptadenia gonoacantha (Mart.) J.F. Macbr.	1	Native	No	CE, MA	Leaf	Spherical	Green	Hairy	One	Cecidomyiidae	2
	2				Leaf	Spherical	Green/ Brown	Glabrous	One	Cecidomyiidae	2
	3				Leaf	Globular	Yellow	Glabrous	Various	Cecidomyiidae	2
Piptadenia moniliformis Benth.	1	Native	No	CA, MA	Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	3
Prosopis elata (Burkart) Burkart.	1	Non-native	No	CH	Stem	Elliptical	Green	–	One	Coleoptera	1
	2				Stem	Elliptical	Green	–	One	Cecidomyiidae	1
	3				Leaf	Elliptical	Green	–	Various	Hymenoptera	1

(continued)

Table 20.1 (continued)

Host plant species	Galls	Origin	Endemism	Phytogeographic domains	Tissue	Shape	Color	Pubescense	Chambers	Gall maker	Reference
Prosopis nigra (Grisebach)	1	Non-native	No	CH	Stem	Globular	Brown	–	Various	Cecidomyiidae	1
	2				Stem	Globular	Brown	–	Various	Hymenoptera	1
	3				Stem	Elliptical	Brown	–	Various	Hymenoptera	1
Prosopis ruscifolia Griseb.	1	Native	No	CA, CE, CH	Stem	Elliptical	Green	–	One	Coleoptera	1
	2				Stem	Globular	Brown	–	Various	Hymenoptera	1
	3				Stem	Cylindrical	Green	–	One	Cecidomyiidae	1
Stylosanthes sp.	1			–	Stem	Elliptical	Green	Hairy	Various	Cecidomyiidae	2
sp. 6	1	–	–	–	Leaf	Conical	Red	Glabrous	One	Cecidomyiidae	3
Lamiaceae											
Hyptis sp. 1. Jacq.	1			–	Leaf	Amorphous	Green	Hairy	Various	Cecidomyiidae	3
	2				Leaf	Spherical	Green	Glabrous	One	Cecidomyiidae	3
	3				Leaf	Conical	Green	Glabrous	One	Cecidomyiidae	3
Hyptis sp. 2	1	–	–	–	Stem	Elliptical	Green	Glabrous	One	Cecidomyiidae	2
sp. 1	1	–	–	–	Stem	Elliptical	Green	Hairy	One	Cecidomyiidae	2
Loranthaceae											
Phthirusa pyrifolia (Kunth) Eichler	1	Native	No	AM, CA, CE	Leaf/Stem	Conical	Green	Glabrous	One	Cecidomyiidae	3
Malpighiaceae											
Banisteriopsis sp.	1	–	–	–	Leaf	Irregular	Green	Glabrous	Various	Acarina	2
	2				Leaf	Discoidal	Green	Glabrous	Various	Cecidomyiidae	2
Byrsonima gardnerana A. Juss.	1	Native	Yes	CA, CE	Leaf	Discoidal	Green/Red	Glabrous	One	Cecidomyiidae	3
Byrsonima intermedia A. Juss.	1	Native	Yes	AM, CE, MA	Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	3
Byrsonima sp. 1	1	–	–	–	Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	3

Heteropterys anoptera A. Juss.	1	Native	Yes	AM, CE	Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	3
Heteropterys sp.	1	–	–	–	Stem	Spherical	Whitish	Hairy	One	Cecidomyiidae	2
	2				Leaf	Conical	Green	Glabrous	One	Cecidomyiidae	2
Malvaceae											
Guazuma ulmifolia K. Schum.	1	Native	No	AM, CA, CE, MA	Leaf	Conical	Green	Glabrous	One	Cecidomyiidae	2
Sida rhombifolia L.	1	Native	No	AM, CA, CE, MA, PP, PT	Stem	Ellipsoid	Green	Glabrous	One	Cecidomyiidae	1
Sida sp. 1	1	–	–	–	Leaf	Spherical	Green	Hairy	One	Cecidomyiidae	2
sp. 1	1	–	–	–	Stem	Elliptical	Green	Hairy	One	Cecidomyiidae	2
Myrtaceae											
Blepharocalyx salicifolius (Kunth) O. Berg	1	Native	No	CA, CE, MA, PP	Stem	Elliptical	Brown	Glabrous	Various	Hymenoptera	2
	2				Flower	Globular	Green	Glabrous	One	Hymenoptera	2
Eugenia punicifolia (Kunth) DC.	1	Native	Yes	AM, CA, CE, MA	Leaf	Spherical	Green	Glabrous	One	Cecidomyiidae	3
Eugenia sonderiana O. Berg	1	Native	Yes	CA, CE, MA	Stem	Elliptical	Brown	Glabrous	Various	Cecidomyiidae	2
	5				Stem	Elliptical	Brown	Glabrous	Various	Cecidomyiidae	2
	6				Leaf	Elliptical	Green	Glabrous	Various	Cecidomyiidae	2
	7				Leaf	Conical	Green	Glabrous	One	Cecidomyiidae	2
	8				Leaf	Globular	Green	Glabrous	Various	Cecidomyiidae	2
Myrcia tomentosa (Aubl.)DC.	1	Native	No	AM, CA, CE, MA	Leaf	Conical	Brown	Glabrous	One	Cecidomyiidae	2
	2				Leaf	Elliptical	Green	Hairy	One	Cecidomyiidae	2
	3				Leaf	Spherical	Brown	Hairy	One	Cecidomyiidae	2
Myrtaceae sp. 1	1	–	–	–	Stem	Globular	Brown	Hairy	Various	Not identified	3
Myrtaceae sp. 2	1	–	–	–	Leaf	Discoidal	Green/Red	Glabrous	One	Cecidomyiidae	3

(continued)

Table 20.1 (continued)

Host plant species	Galls	Origin	Endemism	Phytogeographic domains	Tissue	Shape	Color	Pubescense	Chambers	Gall maker	Reference
Psidium guineense Sw.	1	Native	No	AM, CA, CE, MA	Leaf	Discoidal	Green	Glabrous	–	Cecidomyiidae	3
Psidium sp.	1			–	Leaf	Spherical	Brown	Glabrous	One	Cecidomyiidae	2
Nyctaginaceae											
Guapira laxa (Netto) Furlan	1	Native	Yes	CA, MA	Stem	Globoid	Brown	Glabrous	–	Cecidomyiidae	3
Phytolaccaceae											
Phytolacca thyrsiflora Fenzl ex J.A. Schmidt	1	Native	No	AM, CA, CE, MA, PP	Leaf	Spherical	Green	Hairy	One	Cecidomyiidae	3
Rubiaceae											
Guettarda viburnoides Charm. & Schltdl.	1	Native	Yes	AM, CA, CE, MA	Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	2
	2				Leaf	Elliptical	Green	Glabrous	One	Cecidomyiidae	2
sp. 1	1	–	–	–	Stem	Elliptical	Brown	Glabrous	Various	Not identified	2
Salicaceae											
Casearia rupestris Eichler	1	Native	No	CE	Leaf	Conical	Green	Glabrous	One	Cecidomyiidae	2
Prockia crucis P. Browne ex L.	1	Native	No	AM, CA, CE, MA	Stem	Elliptical	Brown	Hairy	One	Cecidomyiidae	2
Sapindaceae											
Cupania vernalis Cambess.	1	Native	No	AM, CE, MA	Stem	Irregular	Brown	Glabrous	Various	Not identified	2
Serjania glabrata Kuhth	1	Native	No	AM, CA, CE, MA, PT	Leaf	Spherical	Green	Glabrous	One	Cecidomyiidae	3

Serjania sp. 1	1	–	–	–	Leaf	Spherical	Green	Glabrous	One	Cecidomyiidae	2
	2				Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	2
Serjania sp. 2	1	–	–	–	Leaf	Elliptical	Green	Glabrous	One	Cecidomyiidae	2
	2				Stem	Elliptical	Green	Glabrous	Various	Cecidomyiidae	2
	3				Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	2
Serjania sp. 3	1	–	–	–	Leaf	Conical	Green	Hairy	One	Cecidomyiidae	2
Talisia esculenta (A. St. -Hil.) Radlk.	1	Native	No	AM, CA, CE, MA	Leaf	Spherical	Brown	Hairy	One	Cecidomyiidae	3
Sapotaceae											
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.)	1	Native	No	AM, CE, MA	Leaf	Amorphous	Green	Glabrous	One	Heteroptera	3
Manilkara dardanoi Ducke	1	Native	Yes	MA	Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	3
	2				Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	2
Smilacaceae											
Smilax sp. 1	1	–	–	–	Leaf	Spherical	Whitish	Glabrous	One	Cecidomyiidae	2
Smilax sp. 2	1	–	–	–	Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	2
Smilax sp. 3	1	–	–	–	Stem	Globular	Brown	Glabrous	Various	Cecidomyiidae	2
Solanaceae											
Capsicum parvifolium Sendtn.	1	Native	Yes	CA, MA	Stem	Elliptical	Brown	Glabrous	Various	Cecidomyiidae	2
Capsicum chacoense A.T. Hunz.	1	–	–	CH	Leaf	Discoidal	Green	–	One	Cecidomyiidae	1
	2				Stem	Ellipsoid	Green	–	One	Cecidomyiidae	1
Solanaceae sp. 1	1	–	–	–	Leaf	Spherical	Green	Hairy	One	Cecidomyiidae	3
	2				Stem	Globular	Brown	Glabrous	Various	Coleoptera	3

(continued)

Table 20.1 (continued)

Host plant species	Galls	Origin	Endemism	Phytogeographic domains	Tissue	Shape	Color	Pubescense	Chambers	Gall maker	Reference
Solanum argenteum Dunal	1	Native	Yes	CE, MA	Stem	Elliptical	Green	–	Various	Cecidomyiidae	1
Solanum paludosum Moric.	1	Native	No	AM, MA	Leaf	Spherical	Green	Hairy	One	Cecidomyiidae	3
Malvaceae											
Helicteres velutina K. Schum.	1	Native	Yes	CA, CE, MA	Leaf	Discoidal	Green	Glabrous	One	Cecidomyiidae	3
Waltheria indica L.	1	Native	No	AM, CA, CE, MA, PT	Leaf	Spherical	Green	Hairy	One	Cecidomyiidae	3
Verbenaceae											
Aloysia scorodonoides var.	1	Native	No	CH	Stem	Elliptical	Brown	–	One	Lepidoptera	1
Lantana camara L.	1	Native	No	AM, CA, CE, MA	Leaf	Spherical	Green	Hairy	One	Cecidomyiidae	3
	2				Stem	Elliptical	Green	Hairy	–	Not identified	3
Lantana fucata Lindl.	1	Native	No	CA, CE, MA	Leaf	Spherical	Green	Hairy	One	Cecidomyiidae	2
Lippia gracilis Schauer	1	Native	Yes	CA, CE	Leaf	Spherical	Green	Glabrous	One	Cecidomyiidae	3
Lippia sp.	1			–	Leaf	Cylindrical	Green	Hairy	One	Cecidomyiidae	2
	2				Leaf	Spherical	Green	Hairy	One	Cecidomyiidae	2
Not identified											
Not identified sp. 1	1	–	–	–	Leaf	Globular	Green	Glabrous	One	Cecidomyiidae	3

Not identified											
Not identified sp. 2	2	–	–	–	Leaf	Spherical	Brown	Glabrous	One	Cecidomyiidae	3
Not identified											
Not identified sp. 3	1	–	–	–	Leaf	Spherical	Green	Hairy	One	Cecidomyiidae	3
Not identified											
Not identified sp. 4	1	–	–	–	Leaf	Amorphous	Brown	Glabrous	Various	Cecidomyiidae	3
Vochysiaceae											
Callisthene major Mart.	1	Native	Yes	CA, CE, MA, PT	Leaf	Spherical	Green	Glabrous	One	Homoptera	2

Acronyms of geographic distribution of host plants in Brazil: *N* North, *RR* Roraima, *AP* Amapá, *PA* Pará, *AM* Amazonas, *TO* Tocantins, *AC* Acre, *RO* Rondônia, *NE* Northeast, *MA* Maranhão, *PI* Piauí, *CE* Ceará, *RN* Rio Grande do Norte, *PB* Paraíba, *PE* Pernambuco, *BA* Bahia, *AL* Alagoas, *SE* Sergipe, *MW* Midwest, *MT* Mato Grosso, *GO* Goiás, *DF* Distrito Federal, *MS* Mato Grosso do Sul, *SE* Southeast, *MG* Minas Gerais, *ES* Espírito Santo, *SP* São Paulo, *RJ* Rio de Janeiro, *S* South, *PR* Paraná, *SC* Santa Catarina, *RS* Rio Grande do Sul. Acronyms of phytogeographic domains of hosta plants: *CE* Cerrado, *MA Mata Atlântica* (Atlantic Rain Forest), *CA* Caatinga, *AM Amazônia* (Amazon Rain Forest), *PT* Pantanal., *PP* Pampa., *CH* Chaco. Acronyms of references: (1) Fernandes et al. 2002, (2) Coelho et al. 2009, (3) Santos et al. 2011a

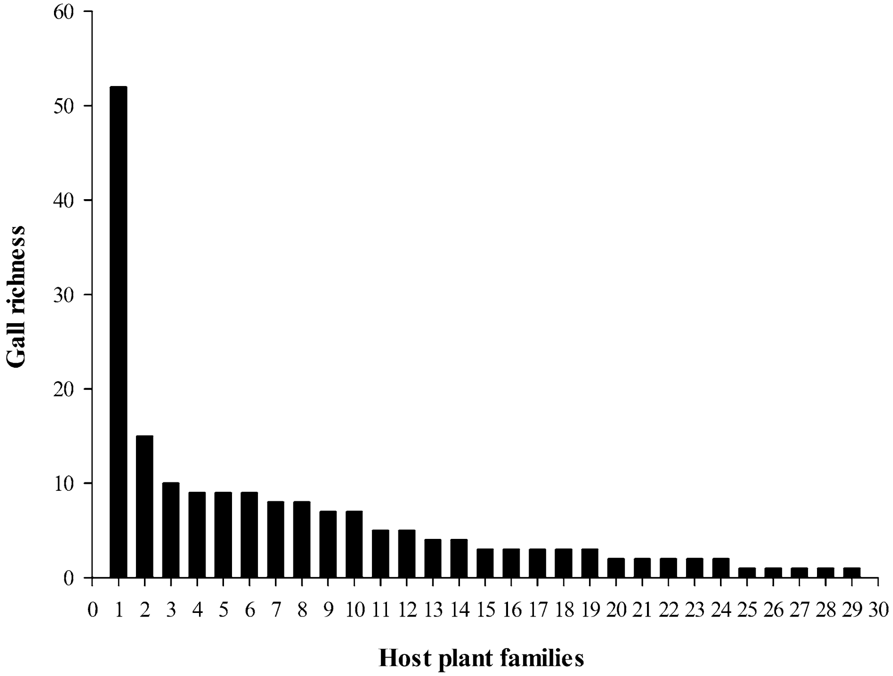

Fig. 20.1 Gall species richness of 29 gall host families recorded in three studies carried out on Brazilians tropical dry forests from Brazil. (1) Fabaceae, (2) Myrtaceae, (3) Euphorbiaceae, (4) Asteraceae, (5) Boraginaceae, (6) Sapindaceae, (7) Cannabaceae, (8) Malpighiaceae, (9) Solanaceae, (10) Verbenaceae, (11) Erythroxylaceae, (12) Lamiaceae, (13) Apocynaceae, (14) Malvaceae, (15) Combretaceae, (16) Convolvulaceae, (17) Rubiaceae, (18) Sapotaceae, (19) Smilacaceae, (20) Annonaceae, (21) Bignoniaceae, (22) Capparidaceae, (23) Malvaceae, (24) Salicaceae, (25) Anacardiaceae, (26) Loranthaceae, (27) Nyctaginaceae, (28) Phytolaccaceae, (29) Vochysiaceae

Euphorbiaceae 5 % (10) (Fig. 20.1). As expected, the most speciose host families were Fabaceae 23 % (26), followed by Euphorbiaceae 8 % (9), and Myrtaceae 7 % (8) (Fig. 20.2). Some species as *Bauhinia brevipes* (Fabaceae), *Bauhinia queilantha* (Fabaceae) and *Eugenia sondoriana* (Myrtaceae), which hosted 4, four and five galls, respectively, contributed significantly for the results found (Table 20.1).

Considering how the fragments of TDFs are scattered in the Brazilian territory, one can track the biogeographical distribution of the galling species to better understand their common traits as well as their differences. Few host plant species have their occurrence restricted to a single Brazilian phytogeographic domain. Under a general analysis, summing every single host species occurrence on the Brazilian domains, (1) Cerrado was the most abundant domain followed by, (2) Caatinga, (3) Atlantic Rain Forest, (3) Amazon Rain Forest, (4) Chaco, (5) Pantanal, and (6) Pampa (Table 20.1, Fig. 20.3). When the co-occurrence of the host species on Brazilian phytogeographic domains were considered, most of host species were

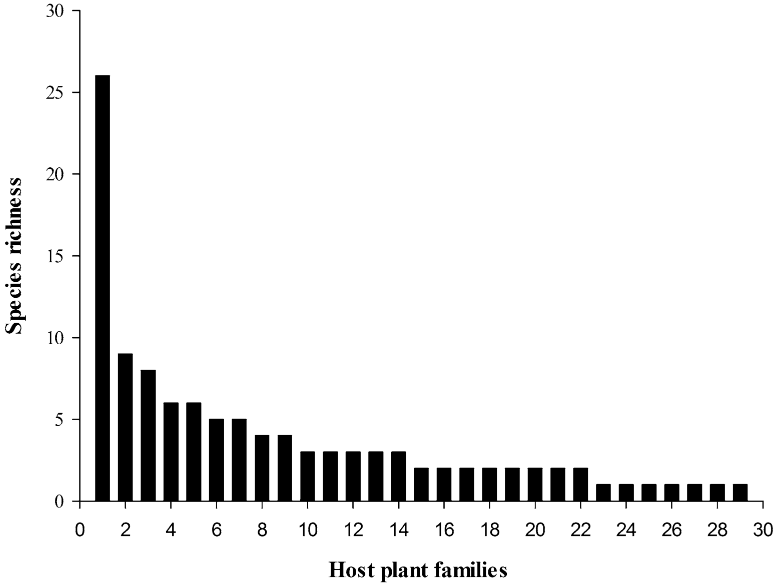

Fig. 20.2 Species richness of 29 gall host families recorded in three studies carried out on Brazilians tropical dry forests from Brazil. (1) Fabaceae, (2) Euphorbiaceae, (3) Myrtaceae, (4) Malpighiaceae, (5) Sapindaceae, (6) Solanaceae, (7) Verbenaceae, (8) Asteraceae, (9) Malvaceae, (10) Boraginaceae, (11) Cannabaceae, (12) Erythroxylaceae, (13) Lamiaceae, (14) Smilacaceae, (15) Annonaceae, (16) Apocynaceae, (17) Bignoniaceae, (18) Combretaceae, (19) Rubiaceae, (20) Salicaceae, (21) Sapotaceae, (22) Malvaceae, (23) Anacardiaceae, (24) Capparidaceae, (25) Convolvulaceae, (26) Loranthaceae, (27) Nyctaginaceae, (28) Phytolaccaceae, (29) Vochysiaceae (Forzza et al. 2010; Oliveira-Filho 2006)

present exclusively in (1) Chaco, (2) Caatinga, followed by simultaneously (3) Amazon Rain Forest, Caatinga, Cerrado, Atlantic Rain Forest, and (4) Amazon Rain Forest, Cerrado, Atlantic Rain Forest (Table 20.1, Fig. 20.4).

20.3 Mechanisms Driving the Low Gall Richness

TDFs present low gall richness in comparison to other Brazilian ecosystems. Larger number of galling insect species have been recorded in other vegetation types: Amazon rain forests: 309 species (Almada and Fernandes 2011), 236 species (Julião et al. 2005), 255 species (Julião 2007), and 76 species (Maia 2012); Atlantic Rain Forest: 130 species (Dalbem and Mendonça 2006), 80 species (Santos et al. 2011b), 34 species (Santos et al. 2010), 29 species (Fernandes and Negreiros 2006); Cerrado: 273 species (Fernandes et al. 2001), 241 species (Carneiro et al. 2009), 236 species (Fernandes et al. 1997), 92 species (Gonçalves-Alvim and Fernandes 2001), 62 species (Araújo et al. 2011); Pantanal: 133 species (Julião et al. 2002). Although the results

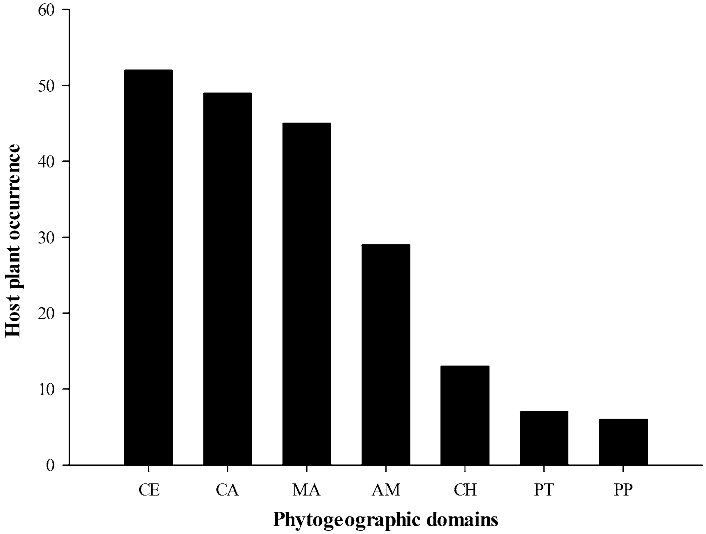

Fig. 20.3 Brazilian phytogeographic domains of the host plant species recorded on three studies carried out on Brazilians tropical dry forests. Acronyms: *CE* Cerrado, *MA Mata Atlântica* (Atlantic Rain Forest), *CA* Caatinga, *AM Amazônia* (Amazon Rain Forest), *PT* Pantanal., *PP* Pampa., *CH* Chaco (Forzza et al. 2010; Oliveira-Filho 2006)

found by Santos et al. (2011a) in TDFs, northeastern Brazil, are comparable to studies conducted in other ecosystems, the authors highlight that 51 % of the galls were collected in a region strongly influenced by the Cerrado vegetation (Table 20.1). The same pattern was found by Coelho et al. (2009) in TDFs, in southern Brazil, but again the islands of TDFs on limestone outcrops were surrounded by Cerrado vegetation. The influence of the Cerrado vegetation on the composition of TDFs on limestone outcrops in central and southern Brazil are strong (Pedralli 1997; Pennington et al. 2000; Silva and Scariot 2003; Scariot and Sevilha 2005; Oliveira-Filho et al. 2006; Pennington et al. 2006; Meguro et al. 2007; Arruda et al. 2011; Coelho et al. 2012, see also Pérez-Garcia et al. 2009) (Fig. 20.3). As Brazilian enclaves of TDFs are commonly surrounded by Cerrado is likely that some galls from Cerrado can also be found in TDFs as well as galls from other domains, even at lower proportions (Fig. 20.4).

Some studies have addressed how gall-inducing insects are distributed throughout the different ecosystems worldwide and reported a clear latitudinal pattern. The region with highest gall richness was located between the latitudes 25° and 45° associated mainly with scleromorphic vegetation (Price et al. 1998). According to the authors, these regions encompass warm regions with hot dry summers and warm wet winters, or warm wet summers and warm dry winters and are also associated with poor and dry soils. Scleromorphic vegetation is characterized by long-lived and tough leaves and present high concentration of chemical defenses (e.g., phenolics and tannins). However, Price et al. (1998) did not explain the evolutionary

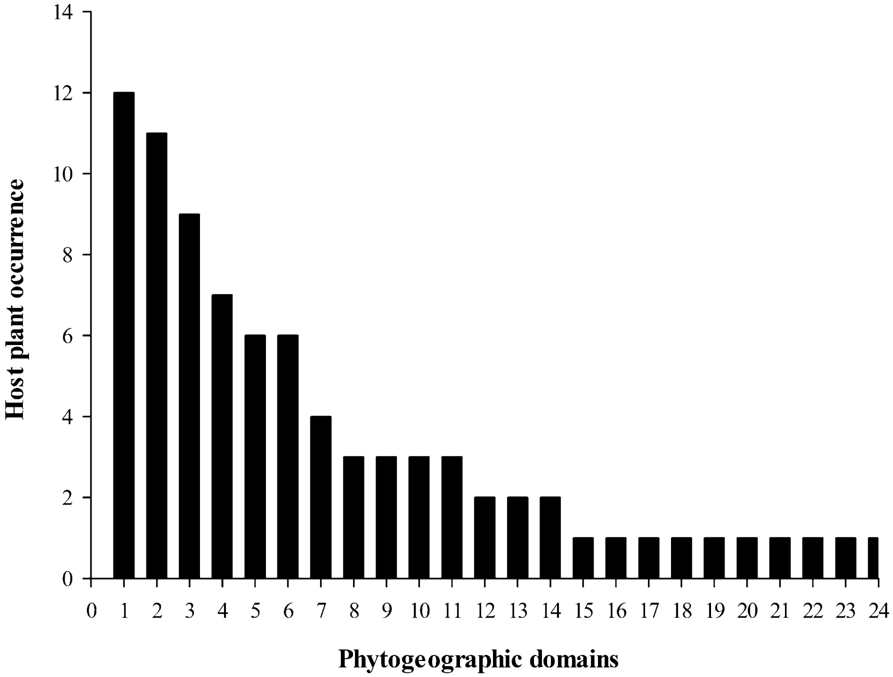

Fig. 20.4 Co-occurrence of the host plant species recorded on three studies carried out on tropical dry forests in Brazilians phytogeographic domains. Acronyms: *CE* Cerrado, *MA Mata Atlântica* (Atlantic Rain Forest), *CA* Caatinga, *AM Amazônia* (Amazon Rain Forest), *PT* Pantanal., *PP* Pampa., *CH* Chaco. (1) CH, (2) CA, (3) AM, CA, CE, MA, (4) AM, CE, MA, (5) CA, CE, MA, (6) CA, CE, (7) MA, (8) CE, MA, (9) CA, MA, (10) AM, CE, (11) AM, CA, CE, (12) CE, (13) AM, CA, CE, MA, PT, (14) AM, CA, CE, MA, PP, PT, (15) MA, CE, CA, (16) CE, MA, PT, (17) CE, MA, PP, (18) CE, CA, (19) CA, CE, MA, PT, (20) CA, CE, MA, PP, (21) CA, CE, CH, (22) AM, MA, (23) AM, CA, CE, MA, PP, (24) AM, CA, CE MA, PP, PT (Forzza et al. 2010; Oliveira-Filho 2006)

mechanism promoting such trends. Mendonça (2001) hypothesized that the speciation mechanism would be host-shifts associated to the leaf flush synchronization of plant communities. According the author, mistakes committed by the female insect in choosing its host could promote sympatric speciation, especially in ecosystems where the species produce leaves synchronously; e.g., Cerrado (resprouting after fire), Fynbus (resprouting after fire), and Tropical Dry Forests (leaf symphenology). Plant species richness would represent an important contributing variable to the trends. Thus, Tropical Rain Forests with an asynchronous leaf production among species would have low gall richness, despite their high plant richness, whereas Tropical Dry Forest would have a high galling richness when compared to the total plant richness. The data presented in this chapter corroborate the harsh environment hypothesis given that number of galling species in the Tropical Dry Forests is low despite the symphenoloy of their leaves in the dry season (Murphy and Lugo 1986; Bullock and Solis-Magallanes 1990).

Plant phenology, level of sclerophylly, and the natural enemies are not the only variables influencing the gall richness. Plant richness has proved to be an important determinant of the gall richness particularly at a local or regional scale (Wright and Sanways 1996, 1998; Gonçalves-Alvim and Fernandes 2001; Oyama et al. 2003; Cuevas-Reyes et al. 2004b). Plant composition is another important variable that must be evaluated (Blanche 2000; Lara et al. 2002; Cuevas-Reyes et al. 2003). Tropical Dry Forests present fewer plant species compared to other vegetation types and are structurally simpler with lower values in tree height, basal area, and density (Murphy and Lugo 1986). Whereas the number of tree species ranges from 35 to 90 on Dry Forests, on Rain Forests the number ranges from 50 to 200. The complexity index of dry forests ranges from 5 to 45 but between 180 and 405 on Rain Forests, and dry forest canopy height ranges from 10 to 40 and between 20 and 84 on Rain Forests. Furthermore, the number of canopy strata ranges from 1 to 3 in Dry Forests and 3 or more in Rain Forests, basal area ranges from 17 to 40 on Dry Forests and between 180 and 405 on Rain Forests.

The significant gall richness previously reported by the studies conducted in Mexican (Cuevas-Reyes et al. 2004a, b), and Brazilian (Coelho et al. 2009; Neves 2009) dry forests adjacent to evergreen habitats (e.g., riparian forests) or savannas (but see Santos et al. 2011a; Neves 2009) suggest the influence of potential colonizers coming from surrounding vegetations. Finally, historical constrains could be also a reason to explain the low gall richness at Tropical Dry Forests (see also Cuevas et al. 2003, 2004a, b).

20.4 Conclusions

The number of studies conducted in TDFs so far are extremely limited. However, a trend can be observed indicating low gall-inducing insect species richness. The low level of secondary chemistry in low diverse vegetation seems the most plausible explanations for the results unveiled. The regional colonizers from adjacent vegetation types may influence gall-inducing insects richness in the TDFs. However, considering that TDFs represent 42 % of the Tropical Forests, more studies are extremely recommended in order to strengthen the results here reported.

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Chapter 21
Galls of the Temperate Forest of Southern South America: Argentina and Chile

Carolina Quintero, Lucas A. Garibaldi, Audrey Grez, Carlo Polidori, and José Luis Nieves-Aldrey

Abstract South American temperate forests are of special conservation concern due to their highly endemic flora and fauna, and the occurrence of unique plant-animal interactions. Yet, knowledge regarding gall inducers diversity is limited although increasing rapidly in the last two decades. Here, we performed a review of the literature, supplemented with field collected data by the authors, in order to provide the most up to date knowledge of gall inducers' diversity associated with native woody species of the temperate forest of Chile and Argentina. We present data for 90 morphospecies of galls associated with 39 host-plant species (21 genera, 15 families), spanning insects and arachnids of at least 6 orders and nematodes. Most of this richness is associated to the best surveyed host-plant genus, *Nothofagus*, with up to 43 morphospecies of galls in just 8 dominant tree species. Moreover, we provide evidence that gall species richness across all woody host-plant species decreases with elevation, probably driven by decreased temperature and number of available host-plant species. However, this overall trend vary among host plant species and

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scales of observation. Overall, the study of gall diversity and the biotic and abiotic factors that shape their distribution in these austral forests offer an exciting and fertile field for future research. Besides emphasizing the need for more in depth taxonomic and diversity studies of the gall fauna of these forests, we propose several future lines of research that promise to further elucidate our understanding of the evolution of plant-gall interactions in these forests.

Keywords *Nothofagus* • *Aditrochus* • Temperate forest • Elevation gradient • Latitudinal gradient

21.1 Introduction

The temperate forest of South America stretches as a narrow belt, 100–250 km wide, along the Andes from 37° to 55°S, surrounded by the Pacific Ocean to the west and south and a series of arid and semi-arid ecosystems to the east and north (Fig. 21.1) (Cabrera and Willink 1973; Grau 1995). Its highly endemic biota evolved under a warmer climate than today during much of the Cenozoic, and thus, these forests are nowadays considered a biogeographically isolated biome (Villagrán and Hinojosa 1997). The particular biogeographic history, highly endemic flora, and past and current climate of these forests have shaped distinct gall communities compared to those found in the Neotropics and temperate forests in other regions (e.g., Fernandes and Price 1988; Price et al. 1998; Espírito-Santo and Fernandes 2007). Nonetheless, many general gall biodiversity and geographic distribution patterns reported elsewhere (Fernandes and Price 1988; Fernandes and Lara 1993; Price et al. 1998; Blanche 2000; Fagundes and Fernandes 2011), may also apply to this largely unexplored ecosystem.

Here, we review the literature documenting taxonomic diversity of gall inducers associated with native woody species, and supplement this review with recent field surveys assessing gall inducers diversity, higher-trophic interactions, and geographic distribution patterns. In particular, we focus our attention on the gall inducers' diversity associated with *Nothofagus* spp. (Nothofagaceae), the most widely distributed tree genus in the region, and identify a rich galling insect fauna (~40 spp.), of seemingly constrained taxonomic diversity. In particular, the evolutionary and ecological importance of the best known *Nothofagus*' galls, induced by *Aditrochus* (Hymenoptera, Chalcidoidea), which in turn hosts a rich inquiline and parasitoid community, is emphasized. Moreover, we provide evidence that gall species richness across all woody host-plant species decreases with elevation, probably driven by decreased temperature and number of available host-plant species. However, this overall trend may vary depending on the scale of observation. Finally, we discuss how systematic, phylogenetic, evolutionary and ecological studies on gall insect biodiversity in South America's temperate forest can improve our understanding of the evolution of plant-gall interactions worldwide and suggest future lines of research.

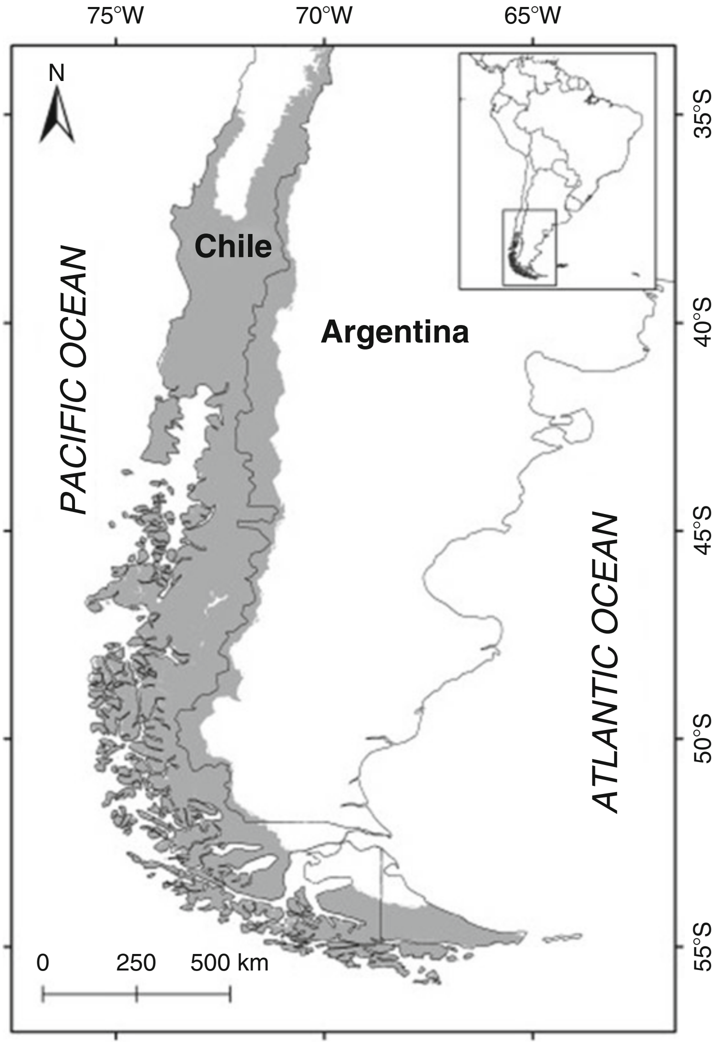

Fig. 21.1 The temperate forest of southern South America (TFSSA, in *grey*) is located along the Chilean and Argentinean Andes. Ice fields and other non-vegetated land cover types within the forest perimeter are omitted for simplicity

21.2 The Temperate Forests of Southern South America (TFSSA)

South American temperate forests encompass a flora rich in endemisms, with at least three endemic angiosperm families (Misodendraceae, Gomortegaceae, and Aextoxicaceae) and several endemic genera (34 % of the woody flora) and species

(90 % of the seed plant species) (Arroyo et al. 1996; Villagrán and Hinojosa 1997). This biome, currently isolated, was once connected with the Neotropics, during much of the Paleocene and early Eocene (65–40 Ma), when this land was covered by a continuous tropical-like forest extending north and south what is today southern South America (Arroyo et al. 1996; Markgraf et al. 1995; Hinojosa and Villagrán 1997). That warmer past can be revealed through its congeneric relationship with extant tropical taxa (Arroyo et al. 1996), the unexpectedly high incidence of epiphytism, unique plant-animal mutualisms (Armesto and Rozzi 1989; Aizen and Ezcurra 1998; Aizen et al. 2002), and anatomical characters such as leaf-margin of woody dicotyledoneous species (Aizen and Ezcurra 2008), among others.

The long-lasting geographical isolation of these forests resulted from the separation and drifting away of South America from Antarctica (~30 Ma) and by the rain shadow created by the uplift of the Andes (~15 Ma) (Villagrán and Hinojosa 1997; Aizen and Ezcurra 2008). Subsequently, the establishment of the Antarctic circumpolar current and the extensive glaciations during the last million years resulted in the cooling of southern South America, causing the extinction of many tropical plant taxa (~60 % of paleoforests' genera) and a strong north to south temperature gradient (Villagrán and Hinojosa 1997; Aizen and Ezcurra 2008). Hence, the current distribution of the biota of this "biogeographic island" depends on the dispersal ability of the surviving species to recolonize the land from multiple glacial refugia (Markgraf et al. 1995). Today, the biota of the TFSSA is composed by a high proportion of shared Neotropical genera (28 %), now separated by the so-called "Arid-Diagonal of South America", Australasian genera (20 %) currently 10,000 km away (Villagrán and Hinojosa 1997), and several taxa from the Holarctic region that migrated southwards across the cold corridor of the Andes from late Miocene (~11 Ma) onwards (Villagrán and Hinojosa 1997; Aizen and Ezcurra 2008).

The climate of this region is characterized by three key gradients. First, there is a poleward decrease in annual temperature, which originates a sequence of bioclimatic zones: Mediterranean, Temperate and Sub-Antarctic. Second, there is a poleward increase in annual precipitation with rainfall uniformly distributed throughout the year at the southern most latitudes. And third, there is a pronounced west-to-east gradient of decreasing precipitation (~4,000 to 400 mm), originated from air masses coming from the Pacific that encounter the orographic barrier of the Andes, which creates a rain shadow effect east of the mountains. This west-to-east precipitation gradient limits the occurrence of the TFSSA to just 10–45 km wide following the Andes into Argentinean territory (Fig. 21.1) (Amigo and Rodriguez-Guitian 2011). Finally, a common feature in all these bioclimatic zones is the strong influences of the Oceans (Pacific and Atlantic) that moderate temperature fluctuations (Amigo and Rodriguez-Guitian 2011). All these climatic characteristics lead to a marked north-to-south and west-to-east decrease in the richness of the flora and fauna of the TFSSA. For example, Kuschel (1960) reported that the insect fauna of the Magellanic forest is essentially a small subset of the richer Valdivian forest to the north.

Among its unique flora, Patagonian forest canopies are commonly dominated by *Nothofagus* species (Nothofagaceae), which include evergreen and deciduous trees known as southern beeches. This trans-Antarctic genus has 35 described species distributed among cold temperate South America, New Zeeland, Australia, New Guinea, and New Caledonia. In Chile and Argentina there are ten dominant or co-dominant canopy tree species extending from 35° to 56°S (ca. 2,500 km, see Fig. 21.1) in the southern cone of South America (Rodríguez and Quezada 2003). The most common and widespread of these species are: *N. pumilio* (Poepp and Endl.) Krasser (lenga), *N. dombeyi* (Mirb.) Blume (coihue), *N. betuloides* (Mirbel) (coigüe de Magallanes), and *N. antarctica* (G. Forster) Oerst. (ñirre or ñire) (Hoffmann 1978). Other species are *N. alpina* (raulí), *N. obliqua* (Mirb.) Oerst (roble), *N. alessandrii* Espinosa (ruil), *N. nitida* (Phil.) Krasser (roble de Chiloé), and *N. glauca* (Phil.) Krasser (hualo). One last recently described species, *N. rutila* Ravenna, closely allied to *N. obliqua*, is restricted to Valparaíso region in Chile (Ravenna 2000), while another described species, *N. leonii* Espinosa, is suggested to be a hybrid of *N. glauca* and *N. obliqua* (Hoffmann 1982).

Nothofagus forests are located in one of the 34 biodiversity hotspots for conservation priorities (Mittermeier et al. 2004; Arroyo et al. 2004); but are currently threatened by deforestation, fragmentation, forest fires and the introduction of exotic species (Armesto et al. 2009; Echeverría et al. 2006; Grez et al. 2006 and references therein). *Nothofagus* forests hold a special conservation concern given that, as compared to other worldwide temperate biomes, the TFSSA has one of the highest reported rates of animal pollinated and seed dispersed floras (Armesto et al. 2009). Approximately, 85 % of the woody genera in these forests have flowers visited by vertebrate or invertebrate pollinators and more than 50 % of the woody genera have fleshy fruits indicating a high dependence on vertebrate dispersers (Aizen et al. 2002). Yet, these interactions might be particularly fragile given that they are highly asymmetric (i.e. one bird pollinator for every 14 plant species and four seed dispersers for every 23 plant species; Aizen et al. 2002). Lastly, plant-animal interactions involving insects are one of the least explored aspects of the ecology of the TFSSA, but recent studies highlight their high diversity and ecological relevance (Aizen et al. 2002), emphasizing the need to protect these forest and the expectedly rich associated insect fauna. Hence, given its species richness, its biogeography and current geographic extent and its ecological role, this chapter focuses mostly on the biodiversity of gall inducers associated with the genus *Nothofagus* and, to a lesser extent, to the most common native understory woody species under *Nothofagus* canopies.

21.3 Gall Inducer Diversity of the TFSSA

Although considerable efforts to describe the diversity of gall inducers for Argentina and Chile were made before 1930 (e.g. Molina 1782; Philippi 1873; Neger 1900; Rübsaamen 1902; Trotter 1902; Kieffer 1904a, b; Kieffer and Herbst 1905, 1906, 1909, 1911; Kieffer and Jörgensen 1910; Manganaro 1914; Tavares 1915; Porter 1920a, b, 1930; and see the key reference Houard 1933 for a synthesis), up to the beginning of this century gall inducers were one of the least explored guilds of all phytophagus insects associated with the flora of these austral forests. Take for example the case of the genus *Nothofagus*. While there is an extensive database of the insect fauna associated with these species (Gentili and Gentili 1988; McQuillan 1993; Grandon 1996; Carrillo and Cerda 1987), adding up to at least 30 genera worldwide (McQuillan 1993), only two morphospecies of galls were cited in McQuillan (1993). This report, in fact, missed two other gall inducers previously described for *N. obliqua*, such as the gall midge *Rhopalomyia nothofagi* (Diptera, Cecidomyiidae) (Madrid 1974) and a Nematode, *Tylenchus arboricolus* (Tylenchidae) (Cobb 1922). Yet, most of the biodiversity of gall species associated to *Nothofagus* spp. were described in the last two decades (e.g. Moreno et al. 1999; Cerda and Angulo 2002; Nieves-Aldrey et al. 2009; Sandoval and Beeche 2010; Buffington and Nieves-Aldrey 2011). Finally, for other genera besides *Nothofagus*, our knowledge is even scarcer. Only gall faunas of *Colliguaja* spp. (Euphorbiaceae); *Schinus* spp. (Anacardiaceae), *Baccharis* spp. (Asteraceae) and *Prosopis* spp. (Fabaceae) have been more extensively studied (Stuardo 1930; Drathen 1958; Díaz and De Santis 1975; Díaz 1981; Martinez et al. 1992; Fernandes et al. 1996; Fuentes-Contreras et al. 1999; Gonzales et al. 2005; Barrancos et al. 2008), together with some invading gall wasps associated with the exotic host-plant *Hypochaeris glabra* (Asteraceae) (Hym., Cynipidae: *Phanacis hypochoeridis*, Pujade-Villar and Díaz 2001; Nieves-Aldrey and Grez 2007).

Therefore, to provide the most up to date knowledge of the gall inducers' biodiversity of the TFSSA, we perform a literature review and present new unpublished field data collected by the authors of this chapter. For the past 12 years, we performed sporadic and systematic surveys of gall inducers associated with *Nothofagus* species and other native Patagonian genera, ranging from 35° to 56°S, in both Chile and Argentina. In general, the surveys were conducted during the austral summers and encompassed all nine *Nothofagus* species (*N. obliqua, N. pumilio, N. dombeyi, N. antarctica, N. glauca, N. alessandrii, N. betuloides, N. nitida* and *N. alpina*) as well as other common native genera, sampled in national parks and reserves of Chile (Regions: VII Maule, IX Araucanía, X Los Lagos, XI Aisén and XII Magallanes) and Argentina (Andean regions located across five provinces: Neuquén , Río Negro, Chubut, Santa Cruz and Tierra del Fuego). Plants were sampled by walking linearly in transects during at least 1 h (see Price et al. 1998). The trees or shrubs were visually searched for galls, with plants and galls collected and photographed. If possible, branches of galled plants were dried and saved into a herbarium collection. In addition, if the galls were from the current season, they were dissected in the laboratory for adult and larval identification at family level. The gall species were identified by external morphological traits of the galls, the larvae and the host plant.

This work revealed a total of 90 morphospecies of gall inducers on 39 native host-plant species (21 genera, 15 families), of which approx. half of them are described in association with *Nothofagus* spp. (Tables 21.1 and 21.2). This rich gall fauna comprise all major gall inducers taxa, with records spanning at least five orders of insects (Diptera, Hymenoptera, Lepidoptera, Hemiptera, Homoptera), one of arachnids (Acari), and few species of nematodes (Tables 21.1 and 21.2).

Table 21.1 Summary records of 47 gall species associated with native woody species of the TFSSA, excluding *Nothofagus* spp. trees. Most of these records represent previously unpublished data (see Ref. abbreviations below), product of sporadic surveys performed by the authors in small trees and shrubs located from 35° to 56°S, in both Chile and Argentina. For each morphospecies, we summarize: taxonomic information of the host-plant, total number of gall species identified so far, the plant tissue attacked, available taxonomic information of the gall inducer, record locations, references, and pictures if available

Host-plant			Gall	Plant	Gall-maker					
Family	Genus	Species	spp.	tissue	Order	Family	Genus and species	Record	References	Figures
Aextoxicaceae	*Aextoxicon*	*punctatum*	1	Leaf	Acari	Eriophyoidea	–	Chile: VII (RN Los Queules)	(a)	21.2a
Anacardiaceae	*Schinus*	*patagonicus*	51	Leaf*	Hemiptera	Psylloidea	*Calophya clausa*	Chile V–VII, IX. Arg: RN (PN Nahuel Huapi)	(c, e)	21.2l
				Leaf	Hemiptera	Psylloidea	*Calophya hermicitae*	Chile: V, VII, IX	(e)	–
				Leaf*	Hemiptera	Psylloidea	*Calophya patagonica*	Chile: IX. Arg: RN (PN Nahuel Huapi), CH	(c, e)	–
				Leaf	Hemiptera	Psylloidea	*Tainarys acuticauda*	Chile: VII–IX	(e)	–
				Stem*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
Araliaceae	*Pseudopanax*	*laetevirens*	1	Leaf*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
Asteraceae	*Senecio*	*sp.*	1	Leaf	Acari	Eriophyoidea?	–	Chile: X (Huinay)	(b)	21.2f
	Chillotricum	*rosmarinifolium*	1	Bud*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
	Baccharis	*sacilifolia*	2	Leaf*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
				Stem*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
	Dasyphyllum	*diacanthoides*	1	Leaf*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–

(continued)

Table 21.1 (continued)

Host-plant			Gall spp.	Plant tissue	Gall-maker			Record	References	Figures
Family	Genus	Species			Order	Family	Genus and species			
Berberidaceae	*Berberis*	*buxifolia*	2	Bud*	Diptera	Cecidomyiidae?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
				Bud*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
	Berberis	*darwinii*	3	Bud*	Diptera	Cecidomyiidae?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
				Stem*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
				Leaf*	Acari	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
	Berberis	*serrato-dentata*	2	Bud*	Diptera	Cecidomyiidae?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
				Stem*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
Celastraceae	*Maythenus*	*sp.*	1	Leaf*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
	Maythenus	*chubutensis*	1	Stem*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
Cunionaceae	*Weinmania*	*trichosperma*	1	Leaf*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
Ericaceae	*Gaultheria*	*mucronata*	3	Bud*	Diptera	Cecidomyiidae	–	Chile: X (Huinay)- Arg: RN (PN Nahuel Huapi)	(b)	21.2d
				Leaf*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
				Stem*	?	?	–	Chile: X (Huinay) – Arg: RN (PN Nahuel Huapi)	(b)	21.2k

	Gaultheria	*phillyreifolia*	2	Leaf*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
				Stem*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
	Gaultheria	*insana*	1	Stem	Insect	?	–	Chile: VII (RN Los Queules)	(a)	21.2c
	Pernettya	*furens*	1	Bud	Insect	?	–	Chile:NA	(d)	–
Escalloniaceae	*Escallonia*	*rubra*	3	Leaf*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
				Stem*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
				Bud*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
	Escallonia	*sp.*	1	Bud	?	?	–	Chile: X (Huinay)	(b)	21.2i
Flacourtiaceae	*Azara*	*integrifolia*	1	Stem	?	?	–	Chile: VII (RN Los Queules)	(a)	21.2m
Hydrangeaceae	*Hydrangea*	*scandens*	1	Leaf	Diptera	Cecidomyiidae	*Angeiomyia spinulosa*	Chile: NA	(d)	–
	Hydrangea	*serratifolia*	1	Leaf	Diptera	Cecidomyiidae	–	Chile: VII (RN Los Queules), X (Huinay)	(a)	21.2e
Myrtaceae	*Blepharocalyx*	*crukshanskii*	1	Leaf	Acari	Eriophyoidea	–	Chile: NA	(d)	–
	Luma	*apiculata*	1	Leaf	Acari	Eriophyoidea	–	Chile: NA	(d)	–
	Myrceugenia	*exsucea*	2	Leaf*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
				Stem*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
	Myrceugenia	*lanceolata*	1	Bud	Diptera	Cecidomyiidae	*Oligotropus eugeniae*	Chile: VII (RN Los Ruiles)	(a, d)	21.2b
	Myrceugenia	*rufa*	1	Bud	Diptera	Cecidomyiidae	–	Chile: NA	(d)	–
	Myrceugenia	*sp.*	1	Fruit	Hymenoptera	Eurytomidae	–	Chile: X (Huinay)	(b)	21.2j
	Myrceugenia	*sp.*	1	Leaf	Homoptera	Psyllidae	–	Chile: X (Huinay)	(b)	21.2g

(continued)

Table 21.1 (continued)

Host-plant			Gall spp.	Plant tissue	Gall-maker			Record	References	Figures
Family	Genus	Species			Order	Family	Genus and species			
Rhamnaceae	*Discaria*	*chacaye*	2	Leaf*	Homoptera	Psyllidae	–	Arg: RN (PN Nahuel Huapi)	(c)	–
				Stem*	?	?	–	Arg: RN (PN Nahuel Huapi)	(c)	–
Winteraceae	*Drimys*	*winteri*	1	Leaf*	Diptera	Cecidomyiidae	–	Chile: X (Huinay), RN (PN Nahuel Huapi)	(b)	21.2h
Total			47							

Tissue: gall morphospecies marked with an *asterisk* are those that were included in the analyses described for northern Patagonia, Argentina
Records: Chile: Region VII Maule, IX Araucanía, X Los Lagos, XI Aisén and XII Magallanes. Argentina (Provinces: *N* Neuquén, *RN* Río Negro, *CH* Chubut, *SC* Santa Cruz, and *TF* Tierra del Fuego; and for both countries (*RN* National Reserve, *PN* National Park, *NA* Not available)
References: (a) Nieves-Aldrey and Grez, unpub.; (b) Nieves-Aldrey unpub.; (c) Quintero et al. unpub.; (d) Houard (1933); and (e) Burckhardt and Basset (2000)

Table 21.2 Summary records of 43 gall species associated with all nine *Nothofagus* spp. present in the TFSSA. These records summarize bibliographic data and systematic surveys performed mostly in protected areas from 35° to 56°S, in both Chile and Argentina. For each morphospecies, we summarize: scientific and common name of the host-plant, total number of gall species identified so far, the plant tissue attacked, available taxonomic information of the gall inducer, as well as known parasitoids and inquilines, record locations, references, and pictures if available

Host-plant	Gall spp.	Tissue	Morphospecies	Order	Family	Genus and species	Parasitoid	Inquilines	Records	References	Figures
N. alessandrii (Ruil)	0	–	–	–	–	–	–	–	–	–	–
N. alpina (Raulí)	1	Bud	Rosette	Hym.	Pteromalidae	*Espinosa nothofagi*	?	?	Chile: IX (PN Conguillío). Arg: N (PN Lanín)	De Santis et al. (1993), Klein Koch and Waterhouse (2000); (b)	21.4a
N. antartica (Ñirre o Ñire)	4	Bud*	Rounded gall w/spine surface	Hym.	Pteromalidae	*Adritrochus gnirensis*	*Lanthanomyia* sp., *Eulophidae* sp. and *Torymidae* sp.	*Noterapion meorrhynchum* (Coleopt., Brentidae)	Chile: XII (Punta Arenas, Torres del Paine). Arg: RN (PN Nahuel Huapi)	De Santis et al. (1993), Vergara and Jerez (2010); (b)	21.4f
		Bud*	Rosette	Dipt.	Cecidomyiidae	–	?	?	Chile: IX (PN Conguillío). Arg: RN (PN Nahuel Huapi)	(b)	21.3r
		Leaf	Blíster, irregular, large	Dipt.	Tephritidae?	–	?	?	Chile: IX (PN Conguillío)	(b)	21.3s
		Leaf*	Pit gall?	Acari	Eriophyoidea?	–	?	?	Chile: X (Osorno) Arg: RN (PN Nahuel Huapi)	(b)	21.3q
N. betuloides (Coigüe de Magallanes)	4	Bud	Spherical, covering	Hym.	Pteromalidae	*Aditrochus* sp.	?	?	Chile: X (Huinay)	(b)	–
		Bud	Rosette gall	Dipt.	Cecidomyiidae	–	?	?	Chile: X (Huinay)	(b)	–
		Bud	Conical, elongated gall	Dipt.	Cecidomyiidae	–	?	?	Chile: X (Huinay)	(b)	21.3h
		Seed	Covering gall	Acari	Eriophyoidea	–	?	?	Chile: X (Huinay)	(b)	–

(continued)

Table 21.2 (continued)

Host-plant	Gall spp.	Tissue	Morphospecies	Order	Family	Genus and species	Parasitoid	Inquilines	Records	References	Figures
N. dombeyi (Coihue)	14	Bud*	Globular, covering gall	Hym.	Pteromalidae	*Aditrochus coihuensis*	*Cecinothofagus gallaecoihue* and *C. ibarrai* *Plectocynips pilosus*	*Noterapion meorrhynchum* (Coleopt., Brentidae)	Chile: VII (RN Los Ruiles), IX (PN Conguillío, Temu -co), X (Osorno), XII (PN Torres del Paine, RF Magallanes). Arg: RN (PN Nahuel Huapi), CH (PN Los Alerces)	De Santis et al. (1993), Nieves-Aldrey et al. (2009), Buffington and Nieves-Aldrey (2011); (b)	21.4b
		Bud	Globular, covering gall	Hym.	Pteromalidae	*Aditrochus sp.*	*Plectocynips longicornis*	?	Arg: RN-N (PN Nahuel Huapi: Isla Victoria)	Díaz (1976), Buffington and Nieves-Aldrey (2011)	–
		Leaf	Blíster, large, solitary gall	Hym.	Pteromalidae	*Aditrochus* sp.	*Plectocynips* sp.	?	Chile: X (Huinay)	(b)	–
		Bud	Covering small red gall	Hym.	Pteromalidae	*Aditrochus* sp.	?	?	Chile: X (Huinay)	(b)	21.4d
		Leaf	Blíster, smaller gall - several	Dipt.?	Cecidomyiidae?	–	?	?	Chile: VII (RN Los Ruiles)	(a)	21.3d
		Bud*	Covering gall, cylindrical, apex with flower shaped prolongations, sticky	Dipt.	Cecidomyiidae	–	?	?	Chile: VII (RN Los Ruiles), X (Petrohué). Arg: RN (PN Nahuel Huapi)	(a)	21.3f
		Bud*	Conical, pointed gall	Dipt.	Cecidomyiidae	–	?	?	Chile: VII (RN Los Ruiles), X (Huinay). Arg: RN (PN Nahuel Huapi)	(a)	21.3b
		Bud	Small gall, translucid walls	Dipt.?	Cecidomyiidae	–	?	?	Chile: X (Huinay)	(b)	–

		Stem	Mark gall, slight hypertrophy	Dipt. o Lepid.	–	–	?	?	Chile: VII (RN Los Ruiles)	(a)	21.3e
		Bud and leaf*	Large rosette gall, open	Dipt.	Cecidomyiidae	–	?	?	Chile: VII (RN Los Ruiles), IX (Conguillío), X (Huinay). Arg: RN (PN Nahuel Huapi)	(b)	21.3a
		Bud and leaf	Smaller rosette gall, closed	Dipt.	Cecidomyiidae	–	?	?	Chile: X (Huinay)	(b)	21.3g
		Leaf*	Filtz gall	Acari	Eriophioidea	–	?	?	Chile: X (Huinay). Arg: RN (PN Nahuel Huapi)	(b)	–
		Fruit	Covering gall, spherical red	Acari	Eriophyoidea	–	?	?	Chile: X (Puerto Mont)	(b)	21.3c
		Bud*	Fusiform gall	Nemat.?	–	–	?	?	Arg: RN (PN Nahuel Huapi)	(c)	–
N. glauca (Hualo)	2	Leaf	Filz gall	Acari	Eriophyoidea	–	?	?	Chile: VII (RN Los Queules)	(a)	–
		Leaf	Pit gall	Acari	Eriophyoidea	–	?	?	Chile: VII (RN Los Queules)	(a)	21.3t
N. nitida (Roble de Chiloé)	5	Leaf	Blíster gall	Hym.	Pteromalidae	*Aditrochus* sp.	?	?	Chile: X (Huinay)	(b)	21.4c
		Leaf	Gregarious blíster gall	Dipt.	Cecidomyiidae	–	?	?	Chile: X (PN Alerce Andino, Huinay)	(b)	21.3j
		Leaf	Rosette closed gall	Dipt.?	–	–	?	?	Chile: X (PN Alerce Andino).	(b)	21.3i
		Leaf	Distorted rosette	Dipt.	–	–	?	?	Chile: X (PN Alerce Andino)	(b)	21.3l
		Leaf	Pit gall	Acari	Eriophyoidea	–	?	?	Chile: X (Huinay)	(b)	21.3k
N. obliqua (Roble)	7	Bud	Surface with fusiform pedunculate	Hym.	Pteromalidae	*Espinosa nothofagi*	?	*Noterapion* sp. (Coleopt. Brentidae)	Chile: VII (RN Los Queules, Parral), IX (Angol, Temuco), XI (Coyhaique). Arg: N (PN Lanín)	De Santis et al. (1993); (a, b)	21.4g

(continued)

Table 21.2 (continued)

Host-plant	Gall spp.	Tissue	Morphospecies	Order	Family	Genus and species	Parasitoid	Inquilines	Records	References	Figures
		Bud	Covering gall, irregular globose	Hym.	Pteromalidae	*Espinosa* sp.	?	?	Chile: VII (RN Los Queules). Arg: N (PN Lanín)	De Santis et al. (1993); (a)	21.4h
		Bud	Rosette gall	Dipt.	Cecidomyiidae	*Rhopalomyia nothofagi*	?	?	Chile: IX, X (NA)	Madrid (1974), Klein Koch and Waterhouse (2000)	–
		Bud	Ovoid gall	Dipt.?	Cecidomyiidae?	–	?	?	Chile: VII (RN Los Queules)	(a)	21.3m
		Leaf	Filz gall, erinosis	Acari	Eriophyoidea	–	?	?	Chile: VII (RN Los Queules)	(a)	21.3n
		Leaf	Blíster gall	Nemat.	Tylenchidae	*Tylenchus arboricolus*	?	?	Chile: NA	Cobb (1922)	–
		Leaf	Pit gall	Nemat.	Anguinidae	*Afrina* sp.	?	?	Chile: NA	Moreno et al. (1999)	–
N. pumilio (Lenga)	6	Leaf*	Covering gall	Hym.	Pteromalidae	*Aditrochus fagicolus*	*Cecinothofagus gallaelenga*, *Plectocynips pilosus*	*Noterapion* sp. (Coleopt., Brentidae)	Chile: IX (Conguillío), X (Volcán Osorno), XII (PN Torres del Paine), XII (RF Magallanes). Arg: RN (PN Nahuel Huapi)	De Santis et al. (1993), Nieves-Aldrey et al. (2009), Buffington and Nieves-Aldrey (2011); (b)	21.4e
		Leaf*	Pit gall	Dipt.	Cecidomyiidae	–	?	?	Chile: X (PN Alerce Andino, PN Vicente Pérez Rosales). Arg: RN (PN Nahuel Huapi), CH, TF	(b)	–
		Fruit	Seed covering gall	Homop./ Lepid./ Dipt.?	–	–	?	?	Arg: N (PN Lanín)	Díaz and Peris (2011)	–

		Leaf	Filz/pit gall	Acari	Eriophyoidea	–	?	?	Chile: XII (Punta Arenas, RF Maga-llanes)	(b)	–
		Leaf*	pit gall	Acari	Eriophyoidea	–	?	?	Chile: X (Huinay). Arg: RN (PN Nahuel Huapi)	(b)	21.3p
		Bud*	Fusiform gall	Nemat.	–	–	?	?	Chile: XII (Punta Arenas, RF Maga-llanes). Arg: RN (PN Nahuel Huapi)	(b, c)	21.3o
Total	43										

Tissue: gall morphospecies marked with an *asterisk* are those that were included in the analyses described for northern Patagonia, Argentina
Records: Chile: Region VII Maule, IX Araucanía, X Los Lagos, XI Aisén and XII Magallanes. Argentina (Provinces: *N* Neuquén, *RN* Río Negro, *CH* Chubut, *SC* Santa Cruz, and *TF* Tierra del Fuego; and for both countries (*RN* National Reserve, *PN* National Park, *RF* Forest Reserve, *NA* Not available)
References: (a) Nieves-Aldrey and Grez, unpub.; (b) Nieves-Aldrey unpub.; (c) Quintero et al. unpub

Yet, further taxonomic studies are required, given that a bit more than 20 % of the gall fauna has been identified to genera and/or species level, and 60 % to order and/or family level.

Outside of gall species associated to *Nothofagus* spp. (Table 21.1, Fig. 21.2), summary statistics of gall inducers' diversity are hard to interpret as no systematic or exhaustive surveys had been conducted for the entire region. However, few general trends emerge from Table 21.1. First, most host-plant species that presented galls had one or two gall morphospecies each, with only four plant species reaching 3–5 gall morphospecies, suggesting that systematic surveys of this flora may lead to higher gall diversity than that known today. Second, plant genera with higher number of gall inducers were the most specious genus surveyed so far (e.g., *Berberis, Escallonia*, and *Gaultheria*), potentially supporting the positive relationship seen between host-plant diversity and gall diversity in other ecosystems (e.g., Espírito-Santo and Fernandes 2007). Third, despite that species identity is only known in 6 out of the 47 described species, and around half are identified to order and/or family level, a potentially high taxonomic diversity of gall inducers is expected given the diversity of tissues attacked and the presence of most gall inducer orders. Fourth, except for one report on fruits, gall inducers attacked mostly leaf blades (~50 %), followed by stems (26 %), and buds (23 %). Finally, no ecological knowledge regarding diversity of parasitoids and/or inquilines had been described for any of these gall species.

For the genus *Nothofagus*, and in contrast to what we observed for all other native host-plant genera, extensive field surveys supplemented by our literature review has revealed a surprisingly rich gall fauna, adding up to 43 different gall species (Table 21.2, Figs. 21.3 and 21.4). The *Nothofagus* species with the higher number of galls was *N. dombeyi*, with 14 different galls, followed by *N. obliqua* with 7, *N. pumilio* with 6, and *N. nitida* with 5. Two species counted with four gall species each (*N. antarctica, N. betuloides*), while *N. glauca* and *N. alpina* reported two and one gall species, respectively, and no galls were reported for *N. alessandrii* (Table 21.2, Fig. 21.5). The most attacked tissues by gall inducers were buds and leaf blades (>45 % each), and to a lesser extent stems, fruits and seeds with one or two records each. Taxonomically, ca. 40 % of the galls are induced by midge galls (Diptera, Cecidomyiidae), 25 % by chalcidoid wasps (Hymenoptera, Pteromalidae), 23 % by mite galls (Acari, Eriophyoidea), around 10 % by Nematoda, and less than 5 % by Lepidoptera or unknown insect orders (Fig. 21.5). This diverse gall fauna seems to be, at the same time, taxonomically restricted to few genera (Table 21.2). For instance, for the best studied galling order on *Nothofagus* spp., Hymenoptera, the 11 gall species described are restricted to two genera (*Aditrochus* and *Espinosa*), suggesting a common ancestor and radiation within the *Nothofagus* genus.

The galls induced by species of *Aditrochus* (Hymenoptera, Pteromalidae) on South American *Nothofagus* are of particular interest (see Table 21.2 and Fig. 21.4), hosting some taxa of Chalcidoidea and Cynipoidea that are potentially crucial for the understanding of their early evolution (Nieves-Aldrey et al. 2009). These complex galls (Fig. 21.4) have been object of considerable debate concerning which are the gall inducer agents. Galls have been attributed to cynipids of the genus *Paraulax*

Fig. 21.2 Galls on plant species of the temperate forest of southern South America. (**a**) dipterocecidia on leaf of *Aextoxicon punctatum* (Aextoxicaceae); (**b**) galls of Cecidomyiidae en *Myrceugenia lanceolata* (Myrtaceae); (**c**) galls on stems of *Gaultheria insana* (Ericaceae); (**d**) galls on buds of *Gaultheria mucronata* (Ericaceae); (**e**) leaf galls on *Hydrangea* sp. (Hydrangeaceae); (**f**) acarocecidia on *Senecio* sp. (Asteraceae); (**g**) leaf gall of a psyllid on *Myrceugenia* sp. (Myrtaceae); (**h**) leaf galls on *Drymis winteri* (Winteraceae); (**i**) galls on *Escallonia* sp. (Escalloniaceae); (**j**) fruits of *Myrceugenia* sp. (Myrtaceae) with galls of Eurytomidae; (**k**) galls on twigs of *Gaultheria mucronata* (Ericaceae); (**l**) leaf gall of a psyllid on *Schinus patagonicus* (Anacardiaceae); (**m**) stem gall on *Azara integrifolia* (Flacourtiaceae) (Photos by J.L. Nieves-Aldrey, except for 2L by C. Quintero)

(Ronquist 1999; Ronquist and Nieves-Aldrey 2001; Csoka et al. 2005; Liu and Ronquist 2006), to an uncertain hymenoptera agent (De Santis et al. 1993) or even to a beetle of the Apionidae family (Kissinger 2005). Recently, Nieves-Aldrey et al. (2009) found strong evidence of the galls being induced by pteromalids of the genus

Fig. 21.3 Galls on *Nothofagus* species (Nothofagaceae) of the temperate forest of southern South America, excepting those induced by *Aditrochus* species (Pteromalidae): (**a**) dipterocecidia on *Nothofagus dombeyi*; (**b**) midge galls on *N. dombeyi*; (**c**) acarocecidia in seeds of *N. dombeyi*; (**d**) dipterocecidia on *N. dombeyi*; (**e**) galls of undetermined insects in stems of *N. dombeyi*; (**f**) galls of Cecidomyiidae on *N. dombeyi*; (**g**) dipterocecidia on *N. dombeyi*; (**h**) dipterocecidia on *N. betuloides*; (**i**) dipterocecidia on *N. nitida*; (**j**) dipterocecidia en leafs of *N. nitida*; (**k**) acarocecidia on *N. nitida*; (**l**) dipterocecidia on *N. nitida*; (**m**) dipterocecidia on *N. obliqua*: (**n**) acarocecidia on *N. obliqua*; (**o**) galls induced by nematode on *N. pumilio*; (**p**) acarocecidia on *N. pumilio*; (**q**) acarocecidia on *N. antarctica*; (**r**), (**s**) dipterocecidia on *N. antarctica*; (**t**) acarocecidia on *N. glauca* (Photos by J.L. Nieves-Aldrey)

Aditrochus (Pteromalidae, Ormocerinae), with the associated cynipid *Cecinothofagus* and the figitid *Plectocynips* being inquilines or parasitoid, as well as the apionids of the genus *Noterapion* Kissinger (Coleoptera, Brentidae, Apioninae) being inquilines (Table 21.2, see also Kissinger 2005; La Salle 2005; Buffington and Nieves-Aldrey 2011).

All in all, the diversity of gall species on *Nothofagus* is far above the richness observed for any other host-plant genus survey to date from the TFSSA. Until

Fig. 21.4 Galls on *Nothofagus* species (Nothofagaceae) of the temperate forest of southern South America induced by pteromalid species (Hym., Pteromalidae): (**a**) *Espinosa nothofagi* Gahan on *N. alpina*; (**b**) *Aditrochus coihuensis* Ovruski on *N. dombeyi*; (**c**) *Aditrochus* sp. indet. on *N. nitida*; (**d**) *Aditrochus* sp. indet. on *N. dombeyi*; (**e**) *Aditrochus fagicolus* Ruebsaamen on *N. pumilio*; (**f**) *Aditrochus gnirensis* Fidalgo on *N. antarctica*; (**g**) *Espinosa* sp. on *N. obliqua*; (**h**) *Espinosa* sp. on *N. obliqua* (Photos by J.L. Nieves-Aldrey)

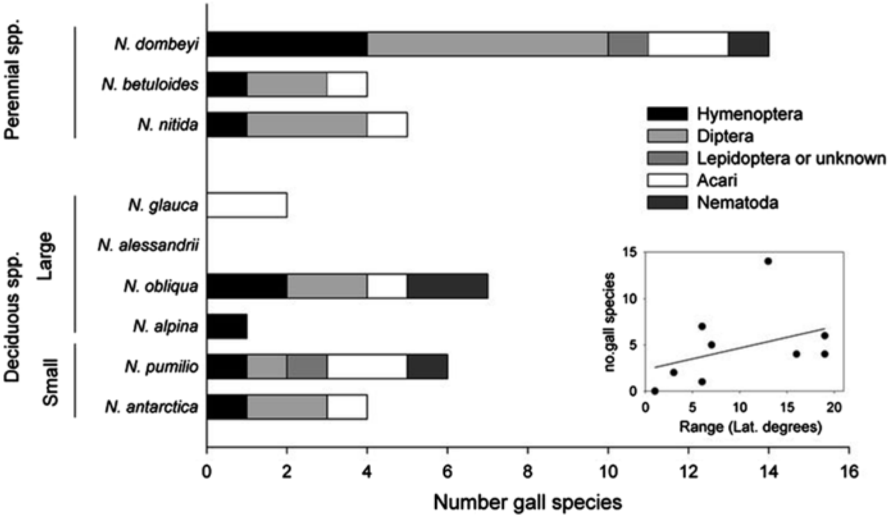

Fig. 21.5 Number of gall species and morphospecies per insect order for each *Nothofagus* (Nothofagaceae) host-plant species present in the TFSSA. *Nothofagus* species are arranged into three large ecological groups: perennial species associated to the "Valdivian Region", and deciduous species further separated into large-leaved trees restricted to "Mediterranean-like climates" and small-leaved trees typical of the "Subantarctic region". In addition, their top to bottom order within each of these three groups corresponds, more or less, to the species occurrence from north to south. The *small panel* to the *right* shows the relationship between number of gall morphospecies and host-plant distributional range [calculated in number of covered latitudinal degrees, from Amigo and Rodriguez-Guitian (2011)], for all nine *Nothofagus* species. See Table 21.1 for further taxonomic and ecological information of gall morphospecies

now, it is unknown whether this remarkable biodiversity of gall inducers associated to South American *Nothofagus* is rare or not, as compared to the fauna of gall inducers in Australasian *Nothofagus*, since this guild has not been widely study in other *Nothofagus* species outside of the TFSSA. Similarly, which biotic and/or abiotic conditions favor the disparity in gall inducers' diversity among *Nothofagus* spp. is also still unknown. In this respect, no mayor trends have emerged yet (Fig. 21.5). First, there is not a clear pattern in gall species richness or diversity between perennial and deciduous *Nothofagus* species, or between small- and large-leaved deciduous trees. Second, in contrast to expected (Ribeiro and Basset 2007), *Nothofagus* species located in mostly Mediterranean-like climates (i.e. large-leaved deciduous trees) did not have higher richness as compared to those adapted to mostly temperate and boreal climates. Finally, although there is a trend suggesting that species more widely distributed host richer gall faunas than those spatially restricted (Fig. 21.5), there is not a significant relationship between these variables ($r = 0.42$, $N = 9$, $p = 0.26$), as tested by a simple Pearson correlation coefficient between *Nothofagus* spp. galling richness and geographical range.

It is important to mention though, that discussions regarding causal factors explaining differences in *Nothofagus* gall species richness need to take into account that the differences in gall species richness reported this far may just reflect differences in sampling effort, and not true ecological differences. Nonetheless, in a more general study on richness of herbivorous insects on *Nothofagus* trees, Lavandero et al. (2009) found that phytochemical uniqueness of the host plants was an important factor to explain insect species richness. For example, they show that *N. alessandrii*, the species with the most unique chemistry, had very few and mostly specialized herbivores, whereas *N. dombeyi*, with the least unique chemistry, had the highest number of related insect species. These findings are consistent with our dataset of the guild of gall-inducing organisms on *Nothofagus* (Table 21.2, Fig. 21.5), suggesting that intrinsic biotic factors, such as plant defenses, may play a key role structuring the gall fauna associated to *Nothofagus* spp., as has been seen in other systems (Abrahamson et al. 2003).

Wherever basic taxonomic knowledge is scarce, as it is for the TFSSA, the description of distributional patterns of species richness and abundance can be more informative than the number of species itself. Hence, below we present two data sets aimed to describe general geographic patterns and mechanism driving gall species richness and abundance associated to common native host-plant species of the TFSSA.

21.4 Gall Species Richness Across an Elevation Gradient in Northern Patagonia, Argentina

Agreement in worldwide distributional patterns can help us elucidate the causes driving gall species diversification and assign a primary function to the adaptation of gall-inducing structures inside plant tissues. Several studies, along altitudinal gradients, have shown that galling species richness increases as temperature and dryness increases (e.g., Fernandes and Price 1988; Fernandes and Lara 1993; Lara and Fernandes 1996), probably driven by fewer enemies (e.g., fungal diseases and predators) in hot, dry environments (Fernandes and Price 1992). This trend, together with the known peak of gall diversity at intermediate latitudes (Price et al. 1998), has been used to hypothesize that galls may function primarily as a way of protecting insects from 'hygrothermal stress' in relatively enemy-free, hot and dry environments (Price et al. 1998; Fernandes and Price 1991). Yet, these trends do not apply to all ecosystems explored (e.g., Blanche 2000; Blanche and Ludwig 2001; Carneiro et al. 2005), implying that other factors might also play a relevant role.

In this section, we present data of gall species richness associated to native woody species surveyed across an elevation gradient, spanning from 760 to 1,760 m.a.s.l., in the Nahuel Huapi National Park region (41°S in northern Patagonia, Argentina). In this area, we sampled 30 sites around the Nahuel Huapi Lake (~780 m.a.s.l.) from the Chilean border to the steppe, and 35 higher sites belonging to three mountains sampled every 80 m, from 880 to 1,760 m.a.s.l. A total of 46 different native woody species and 44 gall morphospecies were recorded, using the methods previously described (see also Price et al. 1998). The forest surveyed were dominated by the tree species *Austrocedrus chilensis* (Cupressaceae), *Nothofagus dombeyi*, *N. pumilio* and *N. antartica*, and common encountered shrub genera were *Baccharis*, *Berberis*, *Escallonia*, *Gautheria*, *Maythenus*, and *Schinus*, among others. For a list of the 44 gall morphospecies included in this study, and their host-plants, see Tables 21.1 and 21.2 (species marked with asterisk under the tissue column).

This work revealed that ~40 % of the native woody flora (N = 18) hosted between one and six gall morphospecies each (described in Tables 21.1 and 21.2), and that the relationship between gall species richness and elevation varied among scales. Linear regressions showed that gall species richness decreased with elevation ($R^2 = 0.19$, $p < 0.0003$, Fig. 21.6a), at a rate of one gall species less every 220 m. This trend could be driven by a decrease in the number of available woody host-plant species as we increased in elevation, which showed a decline of one woody species less every 85 m ($R^2 = 0.55$, $p < 0.0001$, Fig. 21.6b); yet, many intrinsic and extrinsic variables that correlate with elevation remain to be tested to assess the causal factor/s of that relationship (see below). Nonetheless, this decreasing trend may not be supported by every one of the host-plants surveyed. For instance, for *N. pumilio*, a dominant canopy tree widely distributed across that elevation gradient, we observed the opposite trend with gall species richness increasing as its host-plant reaches higher altitudes ($R^2 = 0.35$, $p < 0.001$, Fig. 21.6c), with similar trends seen for each mountain (data not shown).

The overall decrease in gall species richness with elevation agrees with the consistent pattern previously observed in different parts of the globe (Waring and Price 1990; Fernandes and Price 1991; Fernandes and Lara 1993; Price et al. 1998); however, we have not tested yet what variables may be driving this pattern. While richness of host-plant species can be a potential factor (e.g. Santos de Araújo 2011), a negative relationship between altitude and gall species richness might be dependent on differential proportion of xeric versus mesic habitats, nutrient availability, variable top-down control of gall populations, and/or plant resistance traits among others (Fernandes and Price 1991, 1992; Blanche and Ludwig 2001; Cuevas-Reyes et al. 2004; Fernandes et al. 2004). In our study site, the increase in altitude is correlated with a decrease in temperature and plant species richness but not necessary by an increase in precipitation, implying that the TFSSA may not support the ‘hygrothermal stress’ hypothesis. In this regard, it was interesting to see that for a single host-plant, *N. pumilio*, the trend was actually opposite (Fig. 21.6c), suggesting that a combination of climatic and plant species traits may likely explain the observed patterns (e.g. Bairstow et al. 2010). Subsequent studies may benefit by the high diversity of gall species present in the TFSSA, in addition to the pronounced temperature and precipitation gradients, to test the potential environmental versus ecological causes driving distributional patterns in gall diversity in these austral forests.

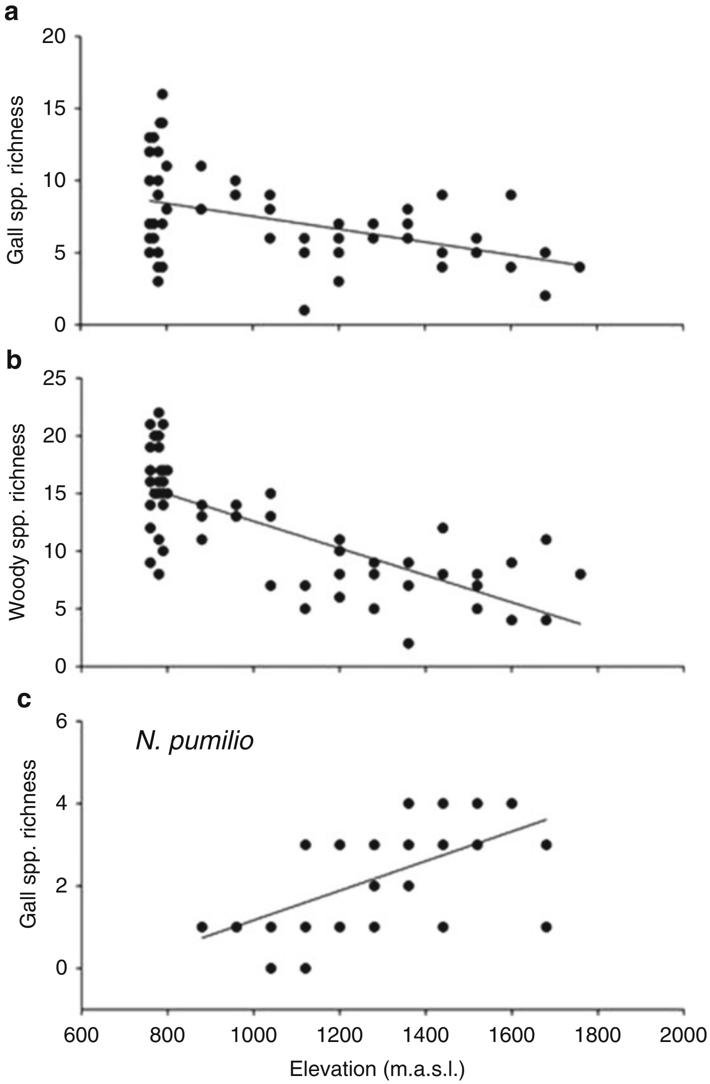

Fig. 21.6 Gall and host-plant species richness across an elevation gradient in the Nahuel Huapi National Park region (41°S, Río Negro, Argentina). Plots represent the change across elevation in (**a**) gall species richness found in all native woody species, (**b**) native woody plant species richness, and (**c**) gall species richness found only in *Nothofagus pumilio* trees (Nothofagaceae)

21.5 Geographical Variation in Gall Abundance Across Elevation and Latitudinal Gradients: The Case Study of *N. pumilio* and a Cecidomyiidae Gall Species

Following the above regional community study, here we will focus on the mechanisms driving gall abundance of a single gall species on *N. pumilio* forests in Argentina (38–55°S). In general, the studies evaluating geographical patterns of galling insects

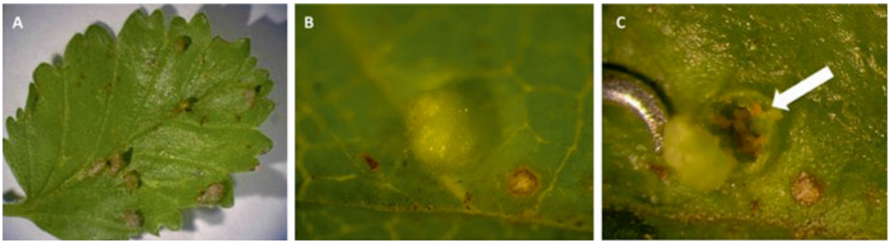

Fig. 21.7 Galls performed by a midge gall larvae (Diptera) in a leaf of *Nothofagus pumilio* (Nothofagaceae). (**a**) A dorsal leaf of *N. pumilio* with multiple midge galls (20×), (**b**) close up of a single midge gall close to a leaf vein (60×), and (**c**) midge gall open showing several orange Cecidomyiidae larvae (60×) (Photos by Lucas A. Garibaldi)

focus on species richness, whereas drivers of gall abundance have been less studied. Nevertheless, the effects of gall inducers on plant fitness (Marini-Filho and Fernandes 2011; Viana et al. 2013), and therefore on agriculture or forestry may be strongly regulated by gall abundance. Specifically, we will explore the role of temperature and precipitation shaping latitudinal and elevation gradients in the abundance of a gall midge species (Diptera, Cecidomyiidae) (Fig. 21.7) associated to *N. pumilio*, the geographically most extended species of *Nothofagus* in the region.

Temperature has been singled out as the dominant abiotic factor affecting insect abundance (Bale et al. 2002), since it affects insects directly through development and survival, and indirectly by affecting, for example, their host plants and parasitoids. In the lowland tropics, mean annual temperature is close to the physiological optimal of insects; therefore, increases or decreases in temperature should reduce insect abundance (Deutsch et al. 2008). Alternatively, at temperate latitudes (or high elevations), annual mean temperature is suboptimal for insects; and therefore, increases in temperature when moving towards lower latitudes or lower elevations should promote insect abundance ("temperature hypothesis", Deutsch et al. 2008). So far, evidence for galling insects is consistent with the temperature hypothesis, as higher species richness of galling insects was found at lower, warmer elevations (e.g. Fernandes and Lara 1993; Price et al. 1998). A similar trend was also found for the abundance of free living insects and herbivory rates in *N. pumilio* forests of Patagonia (Garibaldi et al. 2011a, b); and thus, it is possible that temperature would be a good predictor for galling insects.

Yet, given their concealed life form (Sinclair and Hughes 2010), gall inducers are supposed to be less susceptible to variation in abiotic factors during the galling phase than free living insects. Accordingly, it has been proposed that the gall forming habit is an adaptation to hygrothermal stressful conditions, namely low humidity and high temperature ("harsh environmental hypothesis"; Fernandes and Price 1988). Nonetheless, gall inducers may respond to hygrothermal stress in a similar way to free living insects during the non-galling phase, such as diapause. Patterns of species richness of galling insects across precipitation gradients provide controversial evidence for the harsh environmental hypothesis (e.g. Fernandes and Price 1988; Blanche 2000). Inconsistencies among studies may be a consequence of different prevalence of galling insects on diverse plant taxa, or intra-specific variation in plant traits (Blanche 2000) due to soil fertility among other factors. For example, it was found that hypersensitivity reaction of plants can kill more than 90 % of the galls, while natural enemies played a minor role (Fernandes 1998; Santos et al. 2008).

To explore these questions, we performed two independent observational studies. The first study focused on the latitudinal pattern of gall abundance across 48 sites between 38° and 55°S, whereas the second one focused on the elevation pattern of gall abundance in each of six mountains located across a precipitation gradient in northern Patagonia (see Garibaldi et al. 2011a, b). If temperature is suboptimal for insects in these forests (temperature hypothesis, Deutsch et al. 2008), gall abundance will increase with temperature at lower latitudes and lower elevations. In contrast, the harsh environmental hypothesis predicts that the positive effects of rising temperature would be evident in drier sites, as reflected by a negative statistical interaction between temperature and precipitation, and an overall higher galling abundance in drier sites (Fernandes and Price 1988). By comparing trends in the latitudinal and elevation studies, we reduce the possible influence of confounding factors in our conclusions. For example, along latitude, temperature varies concomitantly with photoperiod (an important driver of diapause); however, along elevation, temperature varies drastically but photoperiod does not change. In addition, the wide latitudinal range and the general monospecific nature of *N. pumilio* forests, provide a great opportunity to evaluate the above hypotheses because spatial co-variation in gall abundance, leaf traits, and abiotic factors are not confounded with spatial changes in tree community composition. For both studies, we present data sampled during 2007, as similar results were found for previous years (Garibaldi et al. 2011a, b).

In the latitudinal study, we fitted models including latitude, longitude, and their interaction as predictors of gall frequency (percentage of leaves with galls) or gall density (number of galls per leaf). These models adequately represented the spatial structure of gall abundance, as semivariogram analyses demonstrated no spatial correlation in the residuals, as well as isotropy (Zuur et al. 2009). We found that both gall frequency and gall density increased with latitude (Fig. 21.8; gall frequency: $F_{1.44}=5.9$, $p=0.019$; gall density: $F_{1.44}=5.5$, $p=0.023$). The effect of latitude was greater in the east than in the west, as reflected by a negative statistical interaction between the effects of latitude and longitude (gall frequency: $F_{1.44}=5.9$, $p=0.019$; gall density: $F_{1.44}=5.6$, $p=0.023$). Overall, both gall frequency and gall density increased to the west (gall frequency: $F_{1.44}=6.7$, $p=0.021$; gall density: $F_{1.44}=5.4$, $p=0.025$), and this effect was greater at northern sites. In agreement, although focussing on species richness rather than gall abundance, a study performed from 16° to 30°S near the Brazilian coast found an increase in species richness of galling insects with latitude on *Baccharis dracunculifolia*, probably because galling insects associated with *Baccharis* radiated in southern Brazil (Fagundes and Fernandes 2011).

In the elevation study, we fitted models including elevation, site (each of six mountains), and their interaction as predictors of gall frequency or gall density. As above, semivariogram analyses demonstrated no spatial correlation in the residuals,

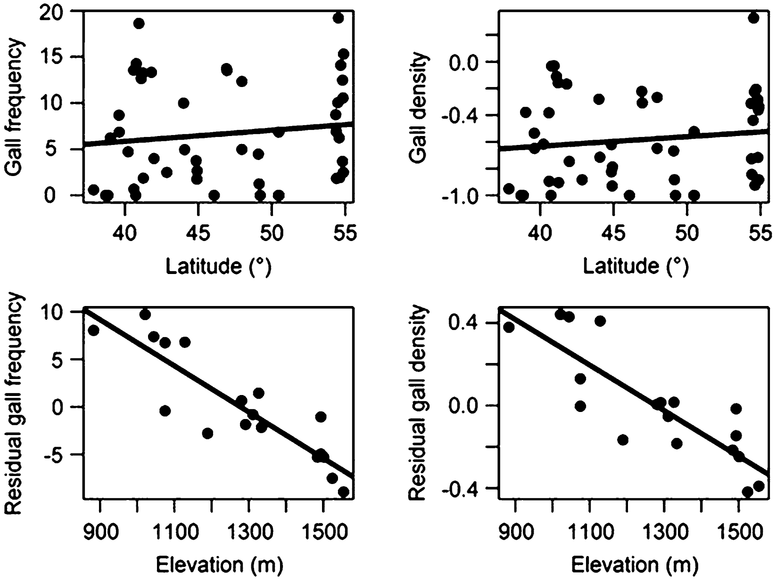

Fig. 21.8 Gall frequency (% of leaves with galls) and gall density (no. of galls per leaf) show a slight increase with latitude but a strong decrease with elevation on *Nothofagus pumilio* (Nothofagaceae) forests. Gall density was log10 transformed to achieve normality and homoscedascity assumptions in the latitudinal study. Residues from mountain (site) effects are plotted for gall frequency and gall density in the elevation study

as well as isotropy. We found that both gall frequency and gall density decreased strongly with elevation (Fig. 21.8; gall frequency: $F_{1,6}=120$, $p<0.001$; gall density: $F_{1,6}=73$, $p<0.001$). At 1,000 m, gall frequency and gall density were on average 19 % and 1.1 galls*leaf^{-1}, respectively, whereas these values decreased to 1 % and 0.028 galls*leaf^{-1} at 1,500 m, respectively (Fig. 21.8). We also found differences in gall frequency and gall density among the six mountains (gall frequency: $F_{5,6}=6.5$, $p=0.020$; gall density: $F_{5,6}=6.8$, $p=0.018$), and the effect of elevation varied in magnitude across mountains but it was always negative (gall frequency: $F_{5,6}=4.7$, $p=0.044$; gall density: $F_{5,6}=4.3$, $p=0.051$). These results are in agreement with the decrease in species richness of galling insects reported across elevation gradients (e.g., Price et al. 1998; Fernandes and Lara 1993), mostly in tropical ecosystems.

When looking at the mechanisms underlying these patterns, interesting results emerged. Gall frequency increased with temperature across the sites of the elevational study, whereas no association was found in the latitudinal study (Fig. 21.9). Precipitation did not co-vary with gall frequency in either study (Fig. 21.9). The same results were observed for gall density (data not shown for brevity). The absence of association between gall abundance and climate in the latitudinal study (Fig. 21.9) is in agreement with the weak association between gall abundance and latitude (Fig. 21.8), probably because of concomitant variation in other drivers of gall abundance, such as leaf traits or photoperiod. On the other hand, results for the

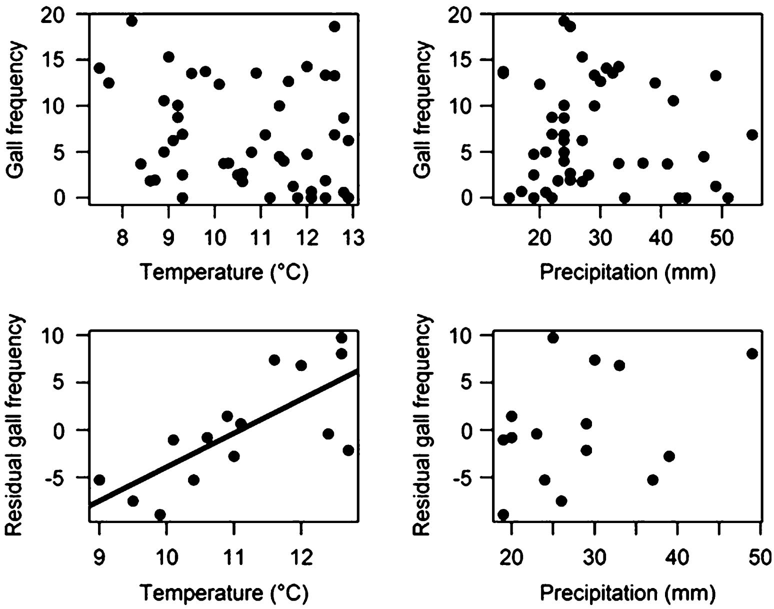

Fig. 21.9 Gall frequency (% of leaves with galls) as a function of mean temperature and precipitation on *Nothofagus pumilio* (Nothofagaceae) forests in the latitudinal study (*upper panels*) and the elevation study (*lower panels*). Both temperature and precipitation are for the warmest (and driest) quarter of the year (i.e. summer); the same results were found for annual mean temperature and annual precipitation. Residues from mountain (site) effects are plotted for gall frequency in the elevation study. The *solid line* is plotted after significant linear relationship between variables

elevational study are in agreement with the temperature hypothesis, suggesting that temperature limitation on gall abundance is reduced at lower elevations. In addition, the absence of association between gall abundance and precipitation in the elevation study does not support the harsh environmental hypothesis. The consistent decrease in species richness of galling insects with elevation in other studies (Fernandes and Lara 1993; Price et al. 1998), conjointly with the controversial results for species richness as a function of precipitation gradients (Blanche 2000; Fernandes and Price 1988), also give higher support for the temperature hypothesis over the harsh environmental hypothesis as a main driver of the spatial variation in richness and abundance of galling insects.

21.6 Conclusions

The study of gall diversity and the biotic and abiotic factors that shape their distribution in these austral forests offer an exciting and fertile field for future research. Here, we presented data for 90 morphospecies of gall inducers; associated to 39 native woody plant species (21 genera, 15 families; Tables 21.1 and 21.2), most of which have never been previously reported. Yet, because we have just started to perform systematic field surveys across taxa and geographic ranges, we believe this number probably underestimates the actual richness of this guild for the TFSSA.

To put our results into perspective, we took advantage of species diversity estimations. Applying Espírito-Santo and Fernandes (2007)'s formulas designed to estimate gall species diversity worldwide (ranging from 21,000 to 211,000), and assuming a positive relationship between plant richness and gall species diversity for these forests, species estimations for the TFSSA should range from ~8 to 84 gall species. This estimate originates from the 167 native woody species reported for this region (Aizen and Ezcurra 2008) and is conservative given that it excludes herbaceous plant species (~1,300 spp.), and that the formula only estimates galling insects and not other gall inducers such as Acari, Nematodes and Bacteria. Similarly, just for the genus *Nothofagus*, with nine species, the expected gall insect diversity should lead to a range of <1–5 estimated gall species. Based on these estimations, we conclude that the total number of species reported here for South American *Nothofagus* (43 spp.) is noticeably larger than expected; whereas the described biodiversity of galling insects associated to all other native woody species (47 spp.) fall within the estimates. Moreover, while it is uncertain if this high gall diversity in South American *Nothofagus* is expected or not based on other Australasian *Nothofagus*, it is at least high in comparison with other common temperate and tropical dominant tree genus worldwide (e.g., *Acacia* (Fabaceae) N = 84, Bairstow et al. 2010; *Eucalyptus* (Myrtaceae) N = 30+, Blanche and Westoby 1996; *Quercus* (Fagaceae) N = 1,000, Stone et al. 2009; *Salix* (Salicaeae) N = 200, Nyman 2000). From these observations two questions emerge: (i) Are we closer to a comprehensive list of gall inducers for the TFSSA?, and (ii) Why does *Nothofagus* spp. host such a rich community of galls?

Although we know that reaching a comprehensive inventory of gall inducer diversity is implausible for almost any ecosystem worldwide, we believe that a rich fauna of galling insects associated with the TFSSA still remains to be described. To date, less than 25 % of the native woody flora has been surveyed for gall inducers and herbaceous species are nearly unexplored, suggesting that the known diversity of gall inducers reported here might be at least a fourth of the actual diversity present in these forests. Moreover, the incipient trend of higher gall biodiversity in the most specious host-plant genus surveyed such us *Berberis* (Berberidaceae) and *Gaultheria* (Ericaceae) suggests that further field studies focused on other native specious genera [e.g., *Azara* (Flacourtiaceae), *Baccharis* (Asteraceae), *Drimys* (Winteraceae), *Escallonia* (Escalloniaceae), *Myrceugenia* (Myrtaceae), *Pernettya* (Ericaceae), and *Ribes* (Grossulariaceae) among others] may lead to the discovery of undescribed species. Lastly, geographically explicit studies are still scarce and thus, we lack knowledge regarding geographic variation in gall species richness across space. Hence, we highlight the need for expanding the ecological and taxonomic characterization of new as well as currently described species.

Exploring the causes responsible for the rich community of gall inducers associated to *Nothofagus* spp. may provide support for various proposed hypotheses explaining patterns of gall diversification worldwide. First, the plant taxon age hypothesis proposes that older host taxa should host richer gall faunas, since greater evolutionary time leads to an increase in number of speciation events (Fernandes 1992). Given that South America has been identified as the likely ancestral area of *Nothofagus* (Swenson et al. 2000), future comparisons of gall faunas associated to *Nothofagus* across continents or associated with other younger genera of the TFSSA warrant promising results. Second, the taxon size hypothesis predicts that the most diverse host taxa have greater galling richness, assuming that each host species is a potential niche for insects (Mendonça 2007). Our data, preliminary supports this trend for the TFSSA with the most diverse host-plant genera hosting richer gall faunas, but today the *Nothofagus* genus with nine host-plant species still rise as a super-host as compared to other specious genera of the TFSSA. Hence, other factors besides taxon size may explain this pattern. Lastly, the taxon geographical area hypothesis expect a positive relationship between host-plant range size and local or regional gall species richness, as seen in *Quercus* (Cornell 1985a, b) and *Eucalyptus* (Blanche and Westoby 1996). Although this relationship was not supported by our data so far (Fig. 21.5), studies designed just to test this pattern should be performed before discarding this hypothesis. Testing among these hypotheses would definitively enhance our knowledge of the biogeography of the TFSSA and the causes driving gall diversification worldwide.

Regarding gall geographic distribution patterns, our preliminary data on the TFSSA supported existent trends of decrease gall species richness and/or abundance with elevation and latitude (e.g., Waring and Price 1990; Fernandes and Price 1991; Fernandes and Lara 1993; Price et al. 1998). For the most part, although not fully tested yet, this trend is believed to be driven by decrease temperature and host-plant species richness and composition as we increase in altitude and latitude, but not by changes in precipitation. Yet, studies incorporating soil fertility and plant physical and chemical traits are expected to enhance our understanding of the drivers shaping the observed patterns (i.e. Ribeiro and Basset 2007; Lavandero et al. 2009; Bairstow et al. 2010). Furthermore, we have to be cautious with the implications of these preliminary trends since they are based on the response to elevation of a small fraction of the gall community of the TFSSA (those found in northern Patagonia, Argentina) and a single midge gall species across latitudinal and elevation gradients (i.e. last two sections, respectively).

Spatial distributions of gall species is expected to be the result of complex interactions between species-specific population demography, behavioral traits, phylogenetic and biogeographic history, and species interactions. Hence, we believe that each gall species and local gall assemblages, across the TFSSA, can show variable patterns. For instance, here we showed for *N. pumilio*, the geographically most extended species of *Nothofagus* in the region, that while gall richness increased with elevation at northern latitudes (N = 0 to 4 gall spp., Fig. 21.6c), gall abundance of a midge gall decreased with both increasing elevation and latitude (Fig. 21.8). This, seemingly contradictory pattern might be explained by host-plant traits and ecological interactions. Plant traits adaptive in higher elevations such as higher constitutive defenses, low tissue turnover, and resprouting ability may indirectly favor higher gall species richness, while gall abundance might be controlled by other plant traits such as leaf surface area and/or variable top-down forces. For instance, gall inducers in *N. pumilio* forests are exposed to other less common natural enemies, such as the case of the endemic Austral Parakeet (*Enicognathus ferrugineus*), which has been observed consuming hymenoptera larvae of *Aditrochus fagicolus* leaf galls and Homoptera, Lepidoptera, and Diptera larvae present in seed galls, mainly during its pre-reproductive period, when other resources are scarce (Díaz and Peris 2011). Thus, if at higher elevations gall inducers encounter more susceptible host species but higher predation rates, due to lack of other nutritious foods, that might explain the increased richness but lower gall abundance observed. Given the rich gall fauna hosted by the flora of the TFSSA, especially *Nothofagus* spp., and their exposure to extreme environmental gradients, these temperate forests represent a unique opportunity to test hypotheses focused on the relative contribution of biotic and abiotic factors driving gall species distribution patterns.

Finally, knowledge regarding galls taxonomy and higher trophic interactions is at this time extremely limited, but also guarantees a fruitful new area of research. In particular, higher trophic interactions among gall inducers, parasitoids, hyperparasitoids, and inquilines are of particular taxonomic and conservation interests given that the biodiversity of this group can be enormous (Price et al. 1987). Currently, given the high probability of endemism for this group and based on recent publications (Moreno et al. 1999; Burckhardt and Basset 2000; Nieves-Aldrey et al. 2009; Buffington and Nieves-Aldrey 2011), we expect that several species of gall inducers as well as their associated higher trophic communities might be new to science. Following a more in depth taxonomic characterization of this fauna, phylogenetic and biogeographic studies of key gall families (i.e. Pteromalidae) may contribute to reconstruct the evolutionary history of these forests, as has been done for example with other obligated parasites of *Nothofagus* spp. (i.e. *Cyttaria* spp., Peterson et al. 2010).

In sum, the richness and diversity of this gall community has just started to be revealed and many questions still remain to be answered about the ecological and evolutionary interactions of gall inducers in the TFSSA. We identify the following four areas to be of particular importance. First, it is clear from this chapter that we lack critical taxonomic knowledge of the gall fauna of the TFSSA; and thus, considerable efforts should be allocated to improve this basic knowledge. Second, assessment of the factors explaining *Nothofagus*' rich gall fauna as well as among species variation in gall diversity may shed light on the proximate and ultimate drivers of gall species diversification and adaptation. Third, the biodiversity of higher trophic levels (i.e. parasitoids, hyperparasitoids, and inquilines) associated to this unique gall fauna and their top-down control need to be further elucidated. Lastly, disentangling the biotic and abiotic components influencing geographical patterns in gall inducers' diversity may help us to understand how natural selection actually shapes the evolution of this herbivore guild. In particular, a fruitful area of research in the TFSSA is related to studies focused on key natural history traits of the gall inducers as well as of the host-plants to assess the relative contribution of these biotic variables over other relevant environmental factors shaping the latitudinal and elevation gradients observed here.

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Chapter 22
Gall-Inducing Insects and Their Associated Parasitoid Assemblages in the Forests of Panama

Enrique Medianero, Héctor Barrios, and José Luis Nieves-Aldrey

Abstract During the past 20 years several studies have documented gall-inducing insect species richness in Panama. Additionally, host plant and parasitoid assemblages associated to galls have been studied. The effects of habitat, altitude, vegetation, and climate on the richness of insect gall assemblages have been addressed in these studies. Similarly, the effects of temporal, spatial, and vertical variation on the local richness of gall-inducing species have also been discussed. The use of a crane in the rainforests of Panama has enabled us to study gall communities in the forest canopy. The taxonomic knowledge on oak gall wasps and their patterns in species richness and distribution in Panama have been the focus of attention in recent years. Here, we review the literature documenting the taxonomic diversity of the Cynipidae and oak gall wasps (tribe Cynipini) in the Neotropics, supplementing it with recent field surveys assessing oak gall wasp diversity in montane forests of Panama. In particular, we studied gall wasp diversity associated with *Quercus* spp. (Fagaceae), the dominant tree genus in montane forests of Panama, and identified a rich gall wasp insect fauna (~65 spp).

Keywords Gall maker • Oak gall wasps • Cynipidae • Panama • Neotropical region • Central America

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22.1 Introduction

Different to most phytophagous arthropods that actively feed on outer or inner parts of plants, many groups of insects and mites, estimated at 21,000-211,000 species (Espírito-Santo and Fernandes 2007), are capable of inducing galls on plants, which are structures that involve active differentiation and growth of plant tissues providing shelter, nutrition and protection for the gall-inducing organism (Meyer 1987; Nieves-Aldrey 1998; Stone and Schönrogge 2003). Galls and gall-inducing arthropods have been the object of research for the last three centuries by dozens of naturalists and scientists worldwide (Mani 1992, see Raman et al. 2005 for a recent synthesis).

The interest in ecological studies that attempt to explain the factors that determine local and global richness of gall-inducing insects has increased exponentially over the last 25 years, especially after the studies of Fernandes and Price (1988, 1991, 1992) and Price et al. (1986, 1987, 1998). However, taxonomic studies on gall-inducing insects are relatively scarce, especially in the Neotropical region. The most important ones are the classic study by Houard (1933) and the book by Gagné (1994) on gall midges (Cecidomyiidae), and the studies of Maia in Brazil (Maia 2001, 2005; Maia and Fernandes 2004; Costa De Oliveira and Maia 2005).

In Panama, interest in the study of gall-inducing arthropods began in the early 1990s. Since then various aspects of this insect guild have been investigated and the hypotheses (e.g., global pattern in local number of gall-inducing insects, hygrothermal stress or harsh environment hypothesis) that attempt to explain patterns of local species richness and distribution have been tested. Investigations have been developed in different Panamanian habitats such as islands, mainland lowland forests and montane forests, with altitudinal gradients ranging from sea level to 3,475 m (Barrios and Medianero 1999; Nieves-Aldrey et al. 2008; Medianero and Nieves-Aldrey 2011b). Different life zones and vegetation types have been sampled to test the hypotheses proposed in the literature (Barrios and Medianero 1999). In addition, temporal aspects of the species richness and community structure and vertical distribution (from the canopy to the understory) of arthropods that induce galls on the rainforest canopy have been investigated with the aid of a crane (Medianero and Barrios 2001; Medianero et al. 2003, 2010a; Ribeiro and Basset 2007).

Due to the limited taxonomic knowledge of all gall-inducing groups in the country, in recent years the emphasis of researches is aimed to describe the gall-inducing species of the family Cynipidae (Medianero and Nieves-Aldrey 2011b). The family Cynipidae, commonly called cynipids or “gall wasps” (Hymenoptera, Cynipoidea, Cynipidae), is one of the most successful arthropod lineages with the ability to induce galls. Gall wasps are the second most speciose gall-inducing group after gall midges (Diptera: Cecidomyiidae), and the most species-rich galling radiation associated with any single plant genus (Csóka et al. 2005; Stone et al. 2009). The galls induced by these insects are one of the most morphologically complex, diverse and specialized of all the zoocecidia (Nieves-Aldrey 2001; Csoka et al. 2005). The most diverse gall wasp lineage is the Cynipini, comprising around 1,000 species commonly called oak gall wasps, all inducing galls on plants of the Fagaceae family, mainly on *Quercus* but also *Castanea*, *Castanopsis*, *Chrysolepis*, and *Lithocarpus*.

The species richness and geographic distribution of oak gall wasps is linked to the distribution of their host plant species *Quercus* spp. There are 202 *Quercus* species in the Nearctic and Neotropical regions, all endemic (Kappelle 1996). The highest diversity of the genus *Quercus* in North America is found in Mexico, where 140 species have been recorded. The number of *Quercus* species per country then decreases rapidly towards southern Central and South America; nonetheless 14 species have been recorded in Costa Rica and nine in Panama. Colombia is the southern range of *Quercus* in the Neotropical region, where one species, *Quercus humboldtii* Bonpland, is still widely distributed in the highlands of the Andes Cordillera.

Following the distribution of their host plants, Neotropical oak gall wasps are distributed from southern Mexico across Guatemala, Costa Rica, and Panama, and reach its southern most distribution in Colombia, associated to *Quercus humboldtii*. Until recently it was assumed that only a few oak gall wasp species (tribes Cynipini and Synergini) extended into the northern hemisphere tropics (Askew 1984), but further studies estimated that the fauna may be potentially rich (Liu and Ronquist 2006; Pujade-Villar and Hanson 2006). Available data make reference to only six gall wasps and four inquiline species from Guatemala and one gall inducer from Panama (Cameron 1883; Ritchie and Shorthouse 1987).

The aim of this study is to compile the information on gall-inducing arthropods from Republic of Panama and the main results after 20 years of studying this group of arthropods. Here, we review the literature documenting the taxonomic diversity of the Cynipidae and oak gall wasps (tribe Cynipini) in the Neotropics, supplementing it with recent field surveys assessing oak gall wasp diversity in montane forests of Panama. In particular, we studied gall wasp diversity associated with *Quercus* spp. (Fagaceae), the dominant tree genus in montane forest of Panama.

22.2 Panamanian Study Sites

The Republic of Panama is located in the northern hemisphere tropics near the equator, between 7°12′08″–9°38′46″ N and 77°09′24″–83°03′07″ W. Panama is bounded by the Caribbean Sea to the north, the Pacific Ocean to the south, Republic of Colombia to the east, and Republic of Costa Rica to the west. The territory of Panama has an area of 75,845.072 Km^2 and connects North and South Americas, with altitudes ranging from 0 to 3,475 m a.s.l. Twenty four vegetation types and 12 life zones have been identified in Panama according to UNESCO (Atlas Ambiental de la Republica de Panama 2010).

Field data was obtained from several studies conducted between September 1994 and December 2009. Four localities in different provinces, with different vegetation, life zones and altitude, were more intensely sampled for at least 12 months: Parque Natural Metropolitano (PNM), Area Protegida de San Lorenzo (APSL), Parque Nacional Isla Coiba (PNIC), and Cordillera Central (CC). In addition, six localities were sampled only once for 10 h in different years (Table 22.1).

Table 22.1 Geographical data of sampling sites in Panama and number of different gall morphotypes sampled in each site. The *asterisks* indicate an average of 10 sampling hours in sites that were visited one time

		Coordinates				
Province	Localities	North	West	Altitude (m a.s.l)	Gall number	Life zones
Chiriquí	Cordillera Central (13 sites)	8°46′36.8″	82°31′39.9″	1,000–3,445	65	bh-MB, bp-MB, bh-PM
	Reserva Forestal Fortuna	8°43′01″	82°11′56″	1,200	7*	bp-PM
Panamá	Parque Natural Metropolitano	8°58′	79°35	30	57	bh-T, bs-T
	Cerro Azul	9°09′59″	79°24′57″	733	10*	bmh-PM
Colon	Área protegida de San Lorenzo	9°17′	79°58′	130	58	bmh-T
Veraguas	Parque Nacional Isla Coiba (17 sites)	7°39′	81°53′	420	59	bh-T, bmh-PM
Coclé	EL Valle	8°37′2″	80°07′13″	821	3*	bmh-PM
	Río Hato	8°23′55″	80°05′04″	25	6*	bs-T
Comarca Guna Yala	Reserva Natural Nusagandi	9°20′53″	78°57′10″	280	12*	bmh-T
Bocas del Toro	Cusapin	9°10′48″	81°53′23″	3,5	5*	bh-T

Tropical montane moist forest -bh-MB
Lower montane rain forest -bp-MB
Premontane rain forest -bh-PM
Premontane rain forest -bp-PM
Tropical wet forest -bh-T
Montane dry forest -bs-T
Premontane wet forest -bmh-PM
Tropical wet forest -bmh-T
Tropical dry forest -bs-T

22.3 Understory Sampling Protocol

At Parque Nacional Isla Coiba (PNIC) (Nieves-Aldrey et al. 2008) we used 60 min censuses to estimate the local number of insect galling species (see Price et al. 1998). At each site, at least 1 h, census was taken by carefully examining all plants while moving slowly through. Trails were commonly used as census routes because foliage was lower in the canopy at their edges, and they provided access through dense vegetation. Vegetation disturbance, including trimming, increases the chances of finding galls because many species attack rapidly growing shoots (Price et al. 1998). Therefore, using trails undoubtedly increased the rate of discovery of galling species, although the total species richness in a locale would be little affected because all species should be usually discovered well within the 1 h sample time (Price et al. 1998). According to Price et al. (1998), this method is similar to sampling a 10 m wide transect, wherein all plants are checked for the presence of galls until 1,000 herbs, 100 shrubs, and 45 trees have been examined.

At lowland forests of Parque Natural Metropolitano (PNM) and Area Protegida de San Lorenzo (APSL), 258 plant species and 546 individuals were marked and sampled every 15 days for 13 months (Medianero and Barrios 2001; Medianero et al. 2003, 2010a). Each plant was examined for 5 min in search of insect galls in each sampling campaign.

22.4 Canopy Sampling Protocol

To access the canopy we used two cranes installed by the Smithsonian Tropical Research Institute (STRI). Each crane allows the study of 1 ha of forest (Fig. 22.1). One crane is installed on the Pacific coast in the forest of Parque Natural Metropolitano, and the other on the Caribbean coast in the Area Protegida de San Lorenzo (Table 22.1). Sampling was conducted in circular fashion, moving the arm of the crane in clockwise direction. The plants were chosen at random from a point and marked as they were found. More than one individual of each plant species was marked with tape, except for mature trees with only a single individual within the area of the crane, in which case three branches were marked. All individuals were coded and sampled every 2 weeks during each study period.

22.5 Oak Gall Wasp Sampling Protocol in the Field and Laboratory Studies

For the past 6 years, we performed sampling surveys of gall wasps associated with *Quercus* species in Panama. Nine *Quercus* species occur in Panama representing the main component of montane forests in eastern regions such as Chiriquí (above 2,000 m).

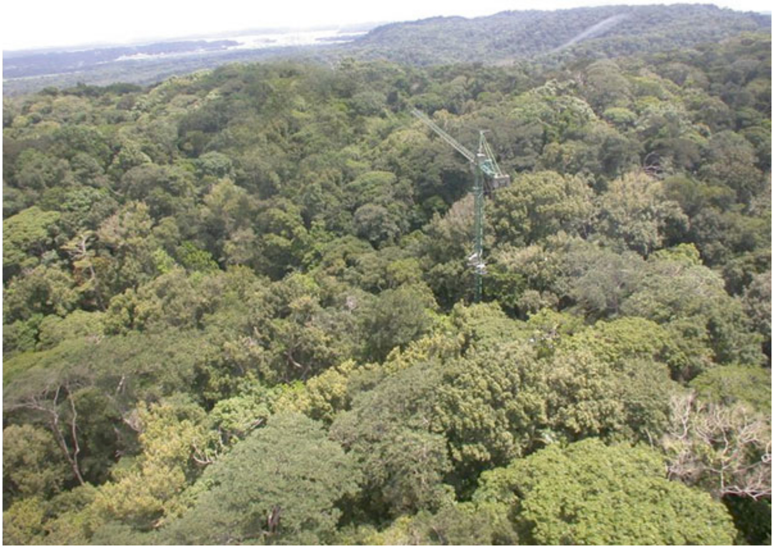

Fig. 22.1 Crane in Area Protegida de San Lorenzo, Colon, Caribbean cost. This crane has access to 0.9 ha. Canopy height is 35–45 m (Picture: IBISCA-PANAMA project)

Isolated *Quercus* populations remain at high elevations in center and south Panama (Coclé and Herrera regions), while *Q. humboldtii* populations are distributed in the Darien region, close to the northern border of Colombia. Field trips were conducted all year long in national parks and reserves for 3 years, mainly in the Chiriquí region (Cordillera Central). Eight of the nine *Quercus* species of Panama were sampled. Host plants were sampled by walking along transects for at least 1 h, when all trees or shrubs were visually inspected for the presence of galls.

In all sampled sites, plants with galls were collected and photographed. Specimens of galled plants were dried and deposited into a herbarium collection, where plants were identified at species level. Gall samples were also stored in 70 % ethanol to allow further dissection and identification. Altitude and geographic position were recorded in the field (Table 22.1).

In most cases galls were dissected in the laboratory for adult and larval identification to family level. Gall species were separated by the external morphology of galls, larvae and host plants. We assumed that gall morphotypes are unique for each gall species (Mani 1964; Ananthakrishnan 1984; Fernandes and Price 1988).

Oak gall wasps were observed under a scanning electron microscope (SEM), previously adult cynipids were dissected in 70 % ethanol, air dried, mounted on a stub and coated with gold. Micrographs from several standardized views were taken with a FEI QUANTA 200 microscope (high vacuum technique). Forewings were mounted in Euparal on slides and later examined under a Wild MZ8 stereo microscope. Images of adult habitus and gall dissections were taken with a NIKON Coolpix 4500 digital camera attached to a Wild MZ8 stereo microscope.

Measurements were made with a calibrated micrometer scale attached to an ocular lens of the light microscope.

Parasitoids associated to gall midges were sampled in the understory and canopy of Parque Natural Metropolitano (PNM) and understory of Area Protegida de San Lorenzo (APSL) (Paniagua et al. 2009).

22.6 Data Analysis

The Chi-square test for Goodness of fit was used to determine differences in the number of gall-inducing insect species between study sites and the distribution of each species. The expected frequencies were those that we would hope to find if the null hypothesis ($H_o=0$) were true, given the total number of observations (Zar 1999). In all cases Fisher's Alpha diversity index was estimated (Fisher et al. 1943). The level of similarity between sites was calculated using a multiple-site similarity (Diserud and Ødegaard 2007) and Jacard and Routledge coefficients (Koleff 2005). A Mantel test with data from PNIC was used to determine the correlation between the matrix of dissimilarity of the sites based on the presence of gall-inducing species and a matrix of geographic distance between the sites (10,000 permutations). The Mantel test can be considered a "distance approach" because the input data are in the form of distance matrices, based on the raw data, and it has been extensively used in ecological studies (Tuomisto and Ruokolainen 2006). We used the software XL-STAT for this test.

Non-parametric analyses (Mann-Whitney test) were used to test for differences in parasitoid assemblages between canopy and understory. Quantitative trophic webs were built to describe graphically the structure of host-parasitoid communities (Paniagua et al. 2009). Trophic webs show the summary of all the interactions found during the sampling period, summing up the absolute density of hosts, parasitoids and trophic links (Lewis et al. 2002).

22.7 Main Taxonomic Groups Inducing Galls in Panama

Five orders, 11 families and 235 species of gall-inducing arthropods were identified at least to family level in the four main study sites (PNM, APSL, PNIC, and CC). Most galls were induced by Cecidomyiidae (Diptera) species (60 %) (Fig. 22.2a–j and l–o), followed by Cynipidae (Hymenoptera) (28 %). The remaining 12 % of the galls were induced by insects of the families Buprestidae (Fig. 22.2u), Cerambycidae, Curculionidae (Coleoptera), Coccidae, Psyllidae (Hemiptera), Eurytomidae, Pteromalidae (Hymenoptera), Phlaeotripidae (Thysanoptera) and mites of the family Eriophyidae (Acari) (Table 22.2). Galls induced by species of the families Coccidae (Fig. 22.2s), Phlaeotripidae (Fig. 22.2r) and Eriophyidae (Fig. 22.2k) were recorded on plants of the families Asteraceae, Bignoniaceae, Myrtaceae,

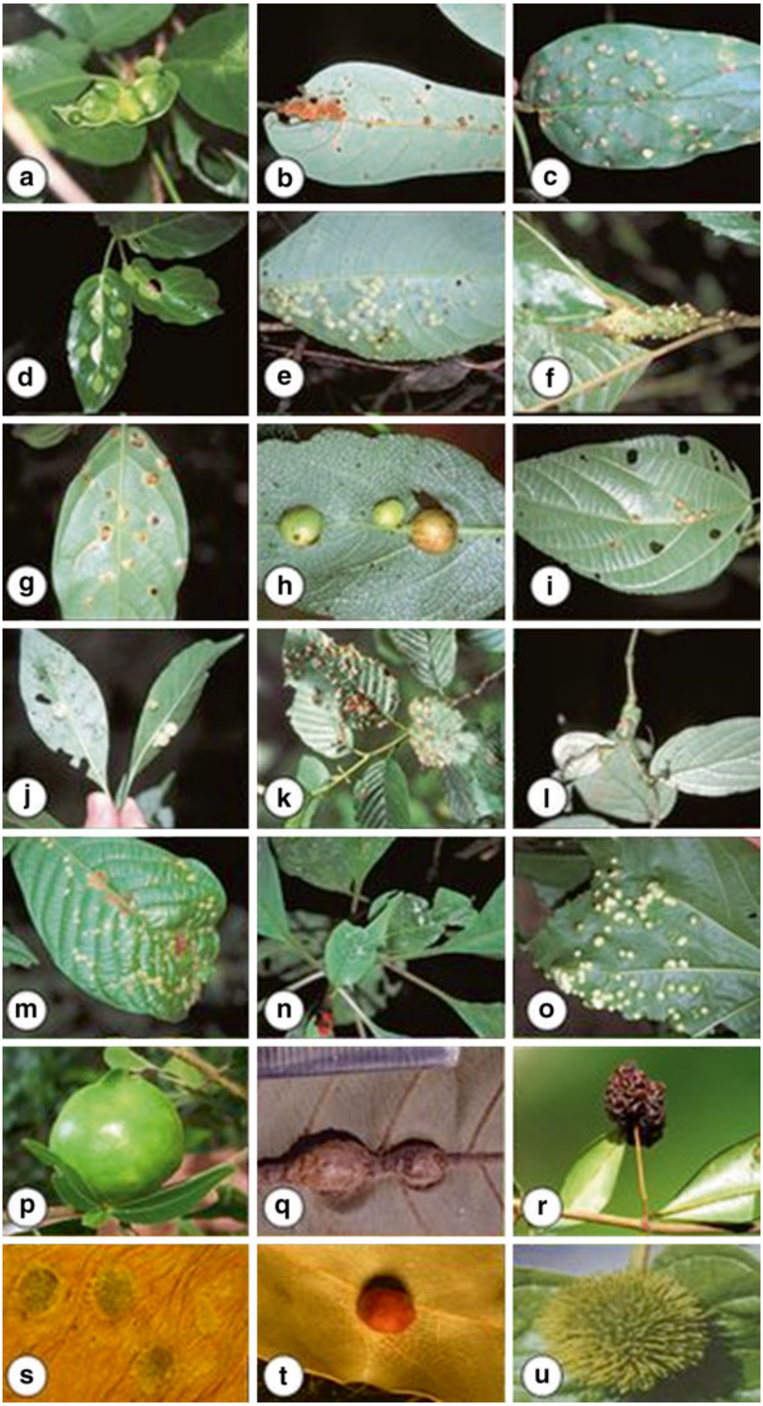

Fig. 22.2 Galls from Panama: (**a**–**j**) gall midge; (**k**) mite on *Lantana camara*; (**l**–**o**) gall midge; (**p**) Eurytomyiidae in Myrtaceae; (**q**) Pteromalidae in *Doliocarpus major*; (**r**) thrip gall on Myrtaceae; (**s**) coccoid gall on Myrtaceae; (**t**) psyllid on *Sorocea* sp.; (**u**) *Hylaeogena* sp. (Buprestidae) in *Amphilophium paniculatum*

Table 22.2 Number of gall-inducing species and arthropod families sampled in Panama. More species belong to Cecidomyiidae family

Orden	Family	Species number
Acari	Eriophyidae	9
Coleoptera	Buprestidae	1
Coleoptera	Cerambycidae	1
Coleoptera	Curculionidae	1
Diptera	Cecidomyiidae	138
Hemiptera	Coccidae	4
Hemiptera	Psyllidae	7
Hymenoptera	Cynipidae	65
Hymenoptera	Eurytomidae	4
Hymenoptera	Pteromalidae	2
Thysanoptera	Phlaeothripidae	3

Pellicieraceae, Rhizophoraceae, Clusiaceae, Euphorbiacae, Melastomataceae, and Verbenacae in Parque Nacional Isla Coiba, while galls induced by species of Psyllidae (Fig. 22.2t) were found on plants of the families Burseraceae, Fabacaeae, Lauraceae, and Moraceae in Parque Nacional Isla Coiba and Area Protegida de San Lorenzo. Galls induced by Coleoptera species were collected in the canopy of Parque Natural Metropolitano, as well as galls induced by chalcidoids of the Eurytomidae (Fig. 22.2p) and Pteromalidae (Fig. 22.2q) families (Hymenoptera). The Coleoptera galls were associated with plants of the families Bignoniacae and Lauraceae, while hymenopteran galls were found on plants of the families Dilleniaceae, Fabaceae, Moraceae, and Tiliaceae. All the galls induced by Cynipidae (Hymenoptera) were collected in the Cordillera Central of Panama on *Quercus* (Fagaceae) species.

22.8 Host Plant Families, Genera and Species of Gall-Inducing Species in Panama

One hundred forty nine species from 103 genera and 55 Angiosperm families are hosts to the fauna of gall-inducing arthropods in the studied area (Table 22.3). The families Fagaceae (65 gall species), Fabaceae (17), and Bignoniaceae (14 galls) supported the highest number of gall-inducing arthropod species, followed by the families Clusiaceae, Moraceae, Myrtaceae, Cecropiaceae, Melastomataceae, and Rubiaceae. Twenty one plant families have only one associated species of gall-inducing arthropods (Table 22.4). *Quercus* spp. (Fagaceae) was the host plant genus with the highest number of associated gall species (65 gall wasp species), followed by *Inga* (Fabaceae), *Amphilophium* (Bignoniaceae), *Miconia* (Melastomataceae), *Cordia* (Boraginaceae), *Calophilum* (Clusiaceae), and *Cecropia* (Cecropiaceae) (Table 22.3). In the lowland forests of PNM and APSL 35 % (N = 258 species; 546 specimens) of the sampled plants were hosts to gall inducing species.

Table 22.3 Host plant species of gall-inducing arthropods in Panamanian forests. The number of genera identified as hosts appears in *parentheses* next to each plant family

Host plant species	Gall-inducing number
ACANTACEAE (1)	
Aphelandra campanesis	1
ANACARDIACEAE (2)	
Spondias mombin	2
Tapirira guianensis	1
ANNONACEAE (3)	
Guateria demeterum	1
Unonopsis panamensis	1
Gen. Ind.	1
APOCYNACEAE (2)	
Aspidosperma cruenta	1
Tabernaemontana arborea	1
ARACEAE (1)	
Philodendron sp	1
ARALIACEAE (1)	
Dendropanax s.p	1
Dendropanax arboreus	1
ASTERACEAE (2)	
Mikania leiostachya	3
Gen. sp. Indet.	1
BETULACEAE (1)	
Alnus acuminata	1
BIGNONIACEAE (8)	

(continued)

Table 22.3 (continued)

Amphitecna latifolia	2
Cydista aequinoctialis	1
Mansoa sp.	2
Amphilophium paniculatum	4
Arrabidea patellifera	1
Paragonia pyramidata	1
Jacaranda sp	1
Phryganocydia corymbosa	1
Cydista sp.	1
BOMBACACEAE (1)	
Quararibea asterolepis	1
BORAGINACEAE (2)	
Cordia alliodora	2
Cordia bicolor	2
Tournefortia bicolor	1
BURSERACEAE (2)	
Tetragastris panamensis	1
Protium confusum	1
Protium panamense	1
CELASTRACEAE (1)	
Maytenus schippi	1
CHRYSOBALANACEAE (2)	
Licania hypoleuca	1
Licania platypus	1
Licania sp.	1
Hirtella racemosa	1

(continued)

Table 22.3 (continued)

CLUSIACEAE (3)	
Calophyllum longifolium	4
Clusia sp.	1
Clusia sp.	1
Tomovita longifolia	1
Tovomita sp.	1
Tovomita stylosa	1
COMBRETACEAE (2)	
Combretum fruticosum	2
Combretum decandrum	1
Terminalia amazonia	1
CONVOLVULACEAE (1)	
Odontodenia punticulosa	1
DILLENIACEAE (1)	
Doliocarpus major	1
ERICACEAE (1)	
Cavendishia atroviolaceae	1
EUPHORBIACEAE (4)	
Acalypha diversifolia	3
Croton schiedeanus	1
Manihot esculenta	1
Pera arborea	1
FABACEAE (7)	
Inga multijuga	1
Dussia munda	1
Dussia sp	1

(continued)

Table 22.3 (continued)

Enterolobium cyclocarpum	3
Inga cocloeensis	1
Inga pezizifera	2
Inga sp	1
Inga sp.	1
Lonchocarpus longifolium	2
Lonchocarpus sp.	1
Machaerium riparium	1
Prioria copaifera	1
Copaifera sp.	1
FAGACEAE (1)	
Quercus salicifolia	14
Quercus benthamii	2
Quercus cortesii	3
Quercus bumelioides	35
Quercus lancifolia	20
Quercus insignis	3
FLACOURTIACEAE (1)	
Casearia commersoniana	2
HIPPOCRATACEAE (1)	
Tontelea richardiil	1
LACISTEMATACEAE (1)	
Lacistema aggregatum	2
LAURACEAE (2)	
Cinnamomum triplinerve	2
Nectandra cuspidata	1

(continued)

Table 22.3 (continued)

LILIACEAE (1)	
Smilax panamensis	1
LORANTHACEAE (1)	
Psittcanthus chrismarri	1
MALPIGHIACEAE (1)	
Hiraea guapara	1
MELASTOMATACEAE (2)	
Clidemia discolor	1
Miconia nervosa	1
Miconia lacera	1
Miconia minutiflora	1
Miconia sp	1
Clidemia strigilosa	1
MELIACEAE (1)	
Carapa guianensis	1
MONIMIACEAE (2)	
Siparuna sp.	1
Mollidenia sp.	1
MORACEAE (6)	
Ficus popenoei	1
Sorocea sp.	1
Castilla elastica	1
Ficus insipida	1
Poulsenia armata	1
Perebea xanthochyma	1
Ficus nymphaeaefolia	1

(continued)

Table 22.3 (continued)

Brosimum utile	1
CECROPIACEAE (2)	
Cecropia longipes	1
Cecropia obtusifolia	2
Cecropia peltata	1
Pourouma bicolor	1
Cecropia sp.	1
MYRISTICACEAE (1)	
Virola sp.	1
Virola sp.	1
Virola serbifera	1
MYRSINACEAE (1)	
Ardisia sp.	1
MYRTACEAE (?)	
Gen. Ind.	7
Sttylogyne standleyi	1
NYCTAGINACEAE (1)	
Nea amplifolia	1
Neea sp.	1
OCHNACEAE (2)	
Ouratea lucens	1
Cespedezia macrophylla	1
OLACACEAE (1)	
Heisteria scandens	1
PELLICIERACEAE (1)	
Pelliciera rhizophorae	1

(continued)

Table 22.3 (continued)

PHYTOLACCACEAE (1)	
Trichostigma octandrum	1
PIPERACEAE (1)	
Piper aequale	1
Piper sp.	2
POLYGONACEAE (1)	
Coccoloba parimensis	1
RHAMNACEAE (1)	
Gouania lupuloides	2
RHIZOPHORACEAE (1)	
Cassipourea elliptica	3
ROSACEAE (2)	
Licania hypoleuca	1
Marantes panamensis	1
RUBIACEAE (3)	
Faramea occidentalis	1
Psychotria horizontalis	1
Psychotria chagrensis	1
Alseis blackiana	1
Psychotria pubescens	1
Psychotria sp.	1
SAPINDACEAE (4)	
Pseudima frutescens	1
Serjania mexicana	2
Cupania latifolia	1
Matayba apetala	1

(continued)

Table 22.3 (continued)

SAPOTACEAE (3)	
Pouteria cf. foveolata	2
Chrysophyllum cainito	1
Manialkara bidentata	1
SIMARUOBACEAE (1)	
Simaruoba amara	1
STERCULIACEAE (2)	
Sterculea recordiana	1
Theobroma angustifolium	1
Theobroma bernouli	1
TILIACEAE (1)	
Luehea speciosa	1
VERBENACEAE (2)	
Aegiphyla odontophylla	1
Lantana camara	1
VITACEAE (2)	
Cissus microcarpa	1
Vitis tiliifolia	3
VOCHYSIACEAE (1)	
Vochisia ferruginia	1

Table 22.4 Plant families, and number of genera and species that are host to gall-inducing arthropods in Panama

Family plant	No. of genus of host plant	No. of species of host plant	No. of gall makers
Fagaceae	1	6	65
Fabaceae	7	13	17
Bignoniaceae	8	9	14
Clusiaceae	3	6	9
Moraceae	6	8	8
Myrtaceae		8	8
Cecropiaceae	2	5	6
Euphorbiaceae	4	4	6
Melastomataceae	2	6	6
Rubiaceae	3	6	6
Boraginaceae	2	3	5
Sapindaceae	4	4	5
Asteraceae	2	2	4
Chrysobalanaceae	2	4	4
Combretaceae	2	3	4
Sapotaceae	3	3	4
Vitaceae	2	2	4
Anacardiaceae	2	2	3
Annonaceae	3	3	3
Burseraceae	2	3	3
Lauraceae	2	2	3
Myristicaceae	1	3	3
Piperaceae	1	2	3
Rhizophoraceae	1	1	3
Sterculiaceae	2	3	3
Apocynaceae	2	2	2
Araliaceae	1	2	2
Flacourtiaceae	1	1	2
Lacistemataceae	1	1	2
Monimiaceae	2	2	2
Nyctaginaceae	1	2	2
Ochnaceae	2	2	2
Rhamnaceae	1	1	2
Rosaceae	2	2	2
Verbenaceae	2	2	2
Acantaceae	1	1	1
Araceae	1	1	1
Betulaceae	1	1	1
Bombacaceae	1	1	1
Celastraceae	1	1	1
Convolvulaceae	1	1	1
Dilleniaceae	1	1	1
Ericaceae	1	1	1

(continued)

Table 22.4 (continued)

Family plant	No. of genus of host plant	No. of species of host plant	No. of gall makers
Hippocrataceae	1	1	1
Liliaceae	1	1	1
Loranthaceae	1	1	1
Malpighiaceae	1	1	1
Meliaceae	1	1	1
Myrsinaceae	1	1	1
Olacaceae	1	1	1
Pellicieraceae	1	1	1
Phytolaccaceae	1	1	1
Polygonaceae	1	1	1
Simaruobaceae	1	1	1
Tiliaceae	1	1	1
Vochysiaceae	1	1	1

22.9 Spatiotemporal Distribution Patterns of Gall Inducing Species in Panama

22.9.1 Spatial Patterns

Only two galling species were collected simultaneously in the three lowland forests (PNM, APSL and PNIC). The average number of galling species collected per sample in the canopy of PNM was 6 ± 3, and 4 ± 2 in the understory. In APSL the average per sample in the canopy was 17 ± 3, and 5 ± 3 in the understory.

The distribution of gall-inducing species was mostly aggregated in all studied sites. For instance, at Parque Nacional Isla Coiba gall species richness ranged between 1 and 19 species per site; 71 % of all species were found in only one site, 22 % in two, 5 % in three, 2 % in four, and no species were present in more than four sites. The multiple-similarity measures indicated that similarity in gall composition and community structure between sites at PNIC was generally low (0.292), even between close sites. The higher percent similarity between two sites was approximately 18 % (Jaccard's index). The gall inducing arthropod community studied exhibited high complementarity among sampling sites. The Mantel test indicated that there was no correlation between the matrix of community dissimilarity and geographic distance at PNIC (Pearson's product-moment correlation $r = -0.15$, $P > 0.05$) (Medianero et al. 2010b).

In the six sites surveyed for 10 h, the average number of gall species sampled per hour was 6 ± 4 galls/h. The maximum number of galls sampled in 1 h was 19 and the minimum 0 (Fig. 22.3).

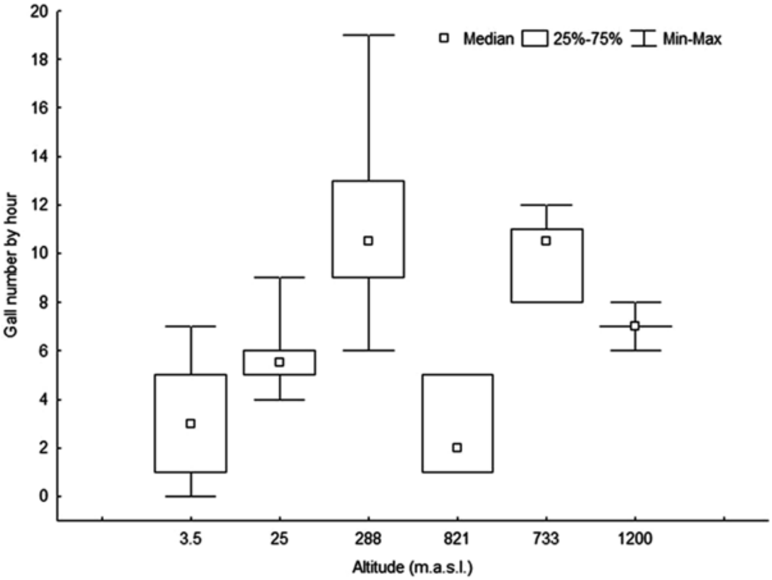

Fig. 22.3 Average number of gall species sampled in 10 h. The *x-axis* shows the altitude of the sites

22.9.2 Temporal Patterns

The number of gall inducing species increased with time in all study areas. Temporal variables had a significant effect on the estimated richness of gall inducing arthropods in the sampling sites. The number of gall-inducing insects in PNM differed significantly among different months of the year ($X^2=37.52$, df = 12, $P<0.01$), both in canopy and understory samples (Fig. 22.4). For instance, in lowland forests of PNM and APSL, 26 % of gall-inducing insects were sampled exclusively in the rainy season, 18 % in the dry season, and 56 % in both seasons (Table 22.5).

Temporal patterns in years also showed changes in community structure. Canopy communities of gall inducing species in PNM exhibited a similarity of 55 % (Jacard index) and 16.3 % of the species were replaced (Routledge index) after a 9 year period (Medianero et al. 2010a).

22.9.3 Vertical Pattern

There was a significant difference in the number of species found in the canopy and understory in all study sites ($X^2=5.667$, $P<0.05$ at PNM; $X^2=5.586$ $P<0.05$ at APSL, df = 1). Our results indicate that this ratio is 2:1, with more species in the

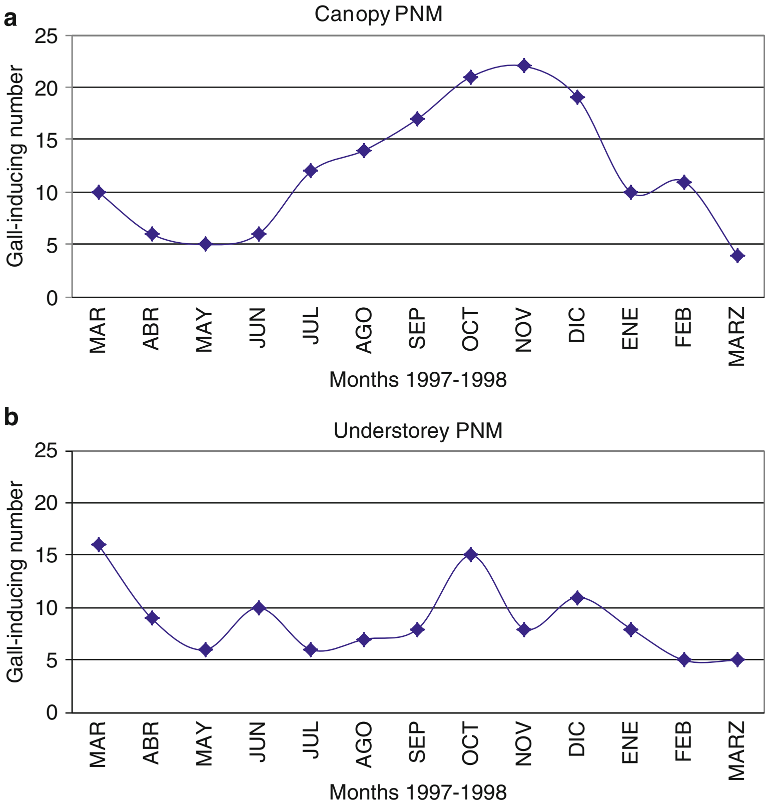

Fig. 22.4 Monthly variation in the number of gall species sampled in the (**a**) canopy and (**b**) understory of Parque Natural Metropolitano

Table 22.5 Number of gall-inducing species sampled over two seasons in Panama

Gall-inducing number					
Season	Canopy PNM	Understorey PNM	Canopy FTS	Understorey FTS	Total
Dry	7	6	5	1	19
Rain	14	1	4	9	28
Rain-dry	13	9	29	10	61
Total	34	16	38	20	108

canopy (Fig. 22.5). A strong stratification pattern was found in these studies, with an overlap of only two species in APSL and three in PNM (Fig. 22.6).

More plant species were hosts to gall inducing insects in the canopy than in the understory. In the canopy of PNM, 43 % of the plant species sampled were infested by one gall species (n = 53), while only 18 % (n = 85) were hosts in the understory. At APSL, 61 % (n = 57) of the plants in the canopy were hosts to galls, while only 30 % (n = 63) were hosts in the understory. Our results suggest that gall

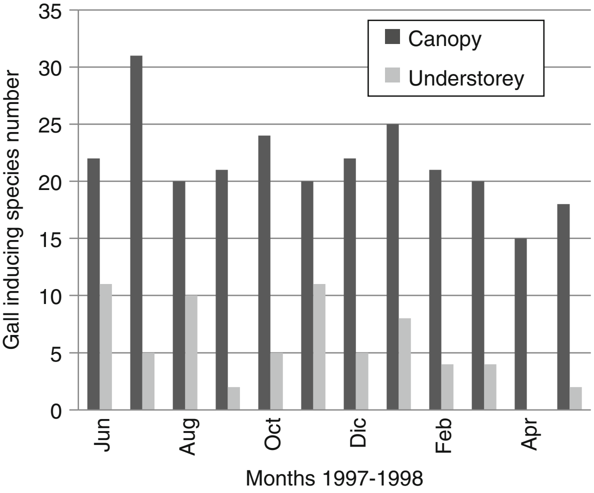

Fig. 22.5 Number of galls sampled in the canopy and understory in Area Protegida de San Lorenzo

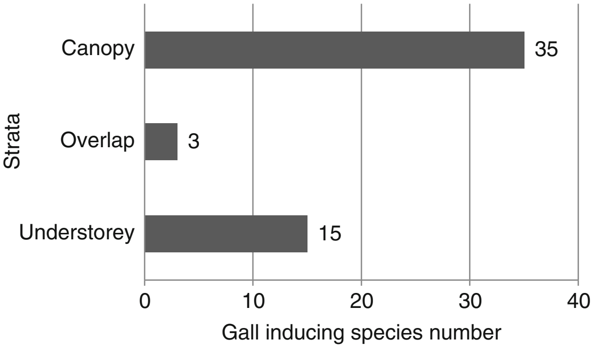

Fig. 22.6 Number of gall species sampled for 13 months in Parque Natural Metropolitano

species are associated to the presence of new leaves in their hosts. In lowland forest of PNM and APSL, 69 species out of 104 were associated to this phenological status of the plant ($X^2 = 8.32$, $P < 0.05$). Thus, this pattern is likely caused by the fact that more galling species are associated to new leaves in the canopy than in the understory.

Rainforests in Panama harbor a rich fauna of gall-inducing insects mainly composed of Cecidomyiidae and Cynipidae species. Depending on site, stratum and season, it is possible to sample up to 25 gall species per sample. In all study areas gall species richness increased with sample size in temporal and spatial scales. The results obtained in Panama do not support the "global pattern hypothesis" in local number of insect galling species described by Price et al. (1998), because species richness was higher than or similar to that reported in mesic sites. Our results support the hypothesis of Espírito-Santo and Fernandes (2007), who suggested that

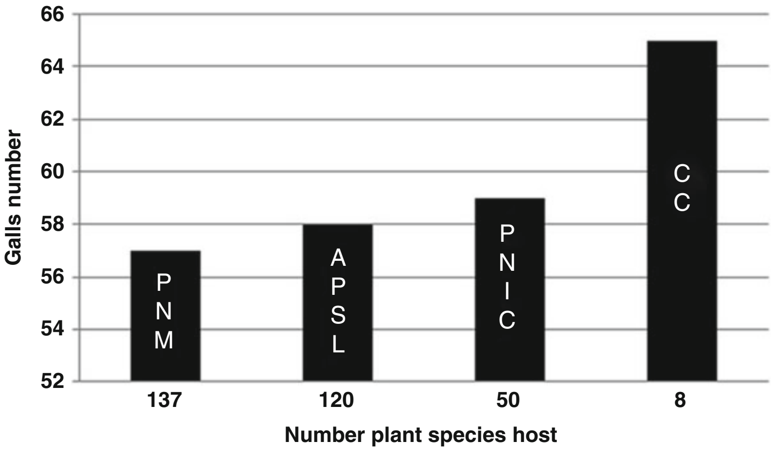

Fig. 22.7 Number of gall-inducing species per site, and number of plant species sampled for at least 1 month. *PNM* Parque Natural Metropolitano, *APSL* Area Protegida de San Lorenzo, *PNIC* Parque Nacional Isla Coiba, *CC* Cordillera Central

Price's results could be affected by an under-sampling of tropical rainforests, where gall species richness could be higher than predicted by Price et al. (1998). Therefore, it may also be premature to conclude that gall species richness declines near the equator (Hanson and Gómez-Laurito 2005).

Gall inducing arthropods had high alpha diversity in Panamanian forests. In fact, most insect galling species had aggregated distributions, and geographic distance was not correlated with percent similarity of gall species composition between study sites. This pattern is similar to the ones observed in other Neotropical areas. For instance, the highest similarity between communities of galling insect was 0.117 in four Neotropical savannas (12 sampling sites) of Brazil (Gonçalves-Alvin and Fernandes 2001). Moreover, Cuevas-Reyes et al. (2004) reported that 62 % of the gall-inducing species found at seven sites in a tropical rainforest of Mexico had restricted distributions. Our results suggest that galling species richness per site in Panamanian forest is the result of the complementarity in gall inducer communities between different habitats.

Plant species richness was not associated with galling species richness (Fig. 22.7). Conversely, the results suggest that plant species composition is more important to determine local species richness of galling insects. The occurrence of host plant species that are evolutionary linked to groups of gall inducing species is directly associated to the increase in galling species richness. In the absence of a particular plant species, plant species richness alone does not seem to directly affect galling species richness. Other important factor is the phenological status of host plants: according to our results, more gall-inducing insects are associated to the presence of new leaves in the host plant. According to Weis et al. (1988), because gall-inducing species are highly specialized (even at the plant organ level) their presence in a site is determined by the presence, abundance, physiological and phenological status of its host plant.

Two important patterns arise from our results: (i) galling species richness in the rainforest canopy is higher than in the understory; (ii) there is strong vertical stratification in the communities of galling insects inside a rainforest. The pattern of higher species richness in the canopy may be related to the greater production of new leaves in this forest stratum. Another possibility could be that the forest canopy is exposed to more solar radiation, resulting in higher temperatures in the canopy than in other forest strata. Additionally, evaporation processes are more intense in the canopy, resulting in lower relative humidity, which may be analogous to a harsh environment, and higher galling species richness as suggested by Fernandes and Price (1988, 1991). However, more studies are needed in the forest canopy to fully understand this pattern.

There was a replacement in the major groups that induce galls along the altitudinal gradients. Cecidomyiidae species were dominant in lowland forests, while Cynipidae species were dominant in montane forests of Panama. This pattern was caused by the presence of species of the genus *Quercus* in different montane forests.

22.10 Parasitoid Assemblages Associated to Galls in the Canopy and Understory in Dry Forests

Fifty-seven parasitoid morphospecies of the genera *Allorhogas* (Braconidae), *Ablerus* (Aphelinidae), *Ametallon*, *Chrysonotomya*, *Klyngon*, *Pentastichus*, *Tropicharis* (Eulophidae), *Eurytoma* (Eurytomidae), *Lyrcus*, *Cecidellis*, *Holcaeus* (Pteromalidae), and *Brasema* (Eupelmidae) were reared from sampled galls. Individuals of the families Torymidae and Platygastridae could be sorted to morphospecies only. Twenty five parasitoid morphospecies were reared from galls of the PNM understory, 17 from PNM canopy, and 22 from APSL understory. The chambers corresponded to 24 gall morphospecies associated with 28 host plants, six from PNM understory, 14 from PNM canopy, and 11 from APSL understory.

22.11 Vertical and Horizontal Stratification of Parasitoid Assemblages

There were no differences in the relative density of viable chambers reared between the understory at the PNM and APSL ($U=52.00$, $n=21$, $P=0.541$), but density was higher in the understory than in the canopy at PNM ($U=29.50$, $n=24$, $P<0.05$).

The APSL understory had higher gall and parasitoid diversity than the understory and canopy of PNM. In PNM, gall inducers were more diverse in the canopy than in the understory (H’t = 2.79, d.f. = 336, $P < 0.001$), but parasitoid diversity exhibited the opposite pattern (H’t = 3.927, d.f. = 326, $P < 0.001$) (Paniagua et al. 2009).

Similarity between gall-maker communities in the understory and canopy of PNM was $J_{\text{Chao}} = 0.0697$ (SE = 0.1087), but there was no overlap between understory assemblages at the two localities. However, parasitoid communities were less similar between the understory and canopy of PNM ($J_{\text{Chao}} = 0.0715$, SE = 0.0612) than between the understory at the two localities ($J_{\text{Chao}} = 0.1410$, SE = 0.0886). The quantitative trophic webs are shown in Fig. 22.8. The canopy trophic web is completely composed of sub-webs of species-specific parasitoids. In the understory, trophic webs were comprised of a small number of species-specific parasitoids and their hosts, and a larger group of gall-makers interconnected through polyphagous parasitoids. In both cases, sub-web size is homogeneous. The differences in compartmentalization patterns between strata were caused by the small contribution of polyphagous parasitoids. These species were the same for the understory of both localities, but were absent from the canopy web (Paniagua et al. 2009).

22.12 Gall Wasps (Hymenoptera, Cynipidae) of the Neotropical Region with Particular Reference to Oak Gall Wasps (Cynipini) in Montane Forests of Panama

The sampling programs in montane *Quercus* forests of Panama developed in recent years by the authors have revealed high oak gall wasp diversity. The first account of this fauna amounted a total of 65 gall morphospecies in six of the eight *Quercus* species sampled. The associated gall fauna was especially rich in *Q. bumelioides*, *Q. lancifolia*, and *Q. salicifolia* with 33, 20 and 14 galls, respectively. (Table 22.6; see also Fig. 22.9). First detailed taxonomic studies of this fauna have resulted in the first record of the genera *Amphibolips*, *Disholcaspis*, *Bassettia*, *Loxaulus*, and *Odontocynips* for Panama and the Neotropics, including eight species new to science (Medianero and Nieves-Aldrey 2010a, b, 2011a; Medianero et al. 2011a, b). Additionally, one genus of inquilines new to science (*Agastoroxenia*) and eight new species of *Synergus*, components of Panamanian fauna have also been described (Nieves-Aldrey and Medianero 2010, 2011). Other genera of oak gall wasps have also been identified in the samples, including some new to science, but they are still being taxonomically studied (Table 22.7) (Medianero and Nieves-Aldrey unp.).

A recent revision of the Cynipidae recorded in the Neotropical region listed 45 species, 4 introduced from Europe (Medianero and Nieves-Aldrey 2011b). The list has been updated and is shown in Table 22.8. Three genera and 24 species new to science of oak gall wasps associated to *Quercus*, including true gall species and inquilines from Costa Rica, Nicaragua, Panama, and Colombia have been described,

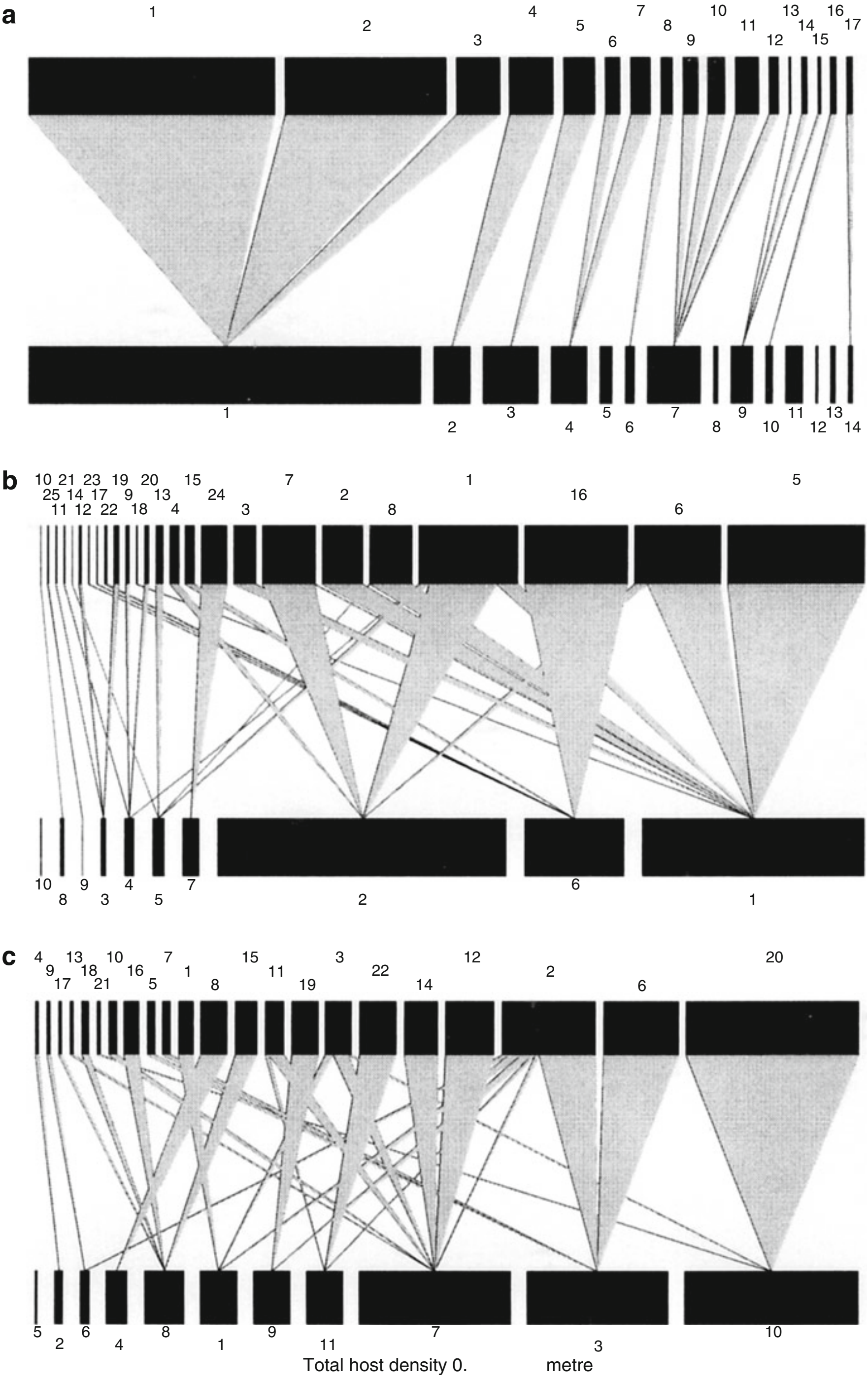

Fig. 22.8 Quantitative gall maker-parasitoid trophic webs for (**a**) PNM canopy, (**b**) PNM understory, and (**c**) SLPA understory. In each case, the *lower bar* shows the density of hosts and the *upper bar* the density of parasitoids (After Paniagua et al. 2009)

Table 22.6 List of species in the genus *Quercus* of Panama, indicating their taxonomic section within the genus *Quercus*, and the number of gall morphospecies found in each species sampled

Quercus species	Section	Number of galls
Q. salicifolia	Lobatae	14
Q. benthamii	Lobatae	2
Q. cortesii	Lobatae	3
Q. gulielmi-treleasei	Lobatae	
Q. humboldtii	Lobatae	
Q. bumelioides	Quercus	33
Q. lancifolia	Quercus	20
Q. insignis	Quercus	3
Total		65

totaling 3 genera and 35 species of oak gall wasps (tribes Cynipini and Synergini) currently recorded in the Neotropics.

Data are here presented demonstrating that the oak gall wasp fauna is far richer than previously reported for Panama and the entire Neotropical region. Available field data indicate that rich and diverse oak gall wasp faunas are established in montane forests of Panama and other regions of Central America. Ongoing phylogenetic studies on the origin and radiation of oak gall wasps attempt to find evidence that support two contrasting hypotheses: the old "out of America" hypothesis proposed by Kinsey (1920, 1936), who postulated Mexico as the center of origin and radiation of oak gall wasps, and the more recently published "out of Asia" hypothesis, which proposed that oak gall wasps originated and radiated in Asia (Stone et al. 2009). The recently found rich Neotropical fauna may give additional support to the Kinsey hypothesis.

Oak montane forests of Panama are fragile habitats whose extension is being reduced because of global warming, and current populations represent only reduced refuges of much more large areas occupied in times with colder climate. Moreover, these remaining areas are seriously threatened by deforestation and fragmentation caused by human activities. Thus, the oak gall wasp populations inseparably linked to these forests are threatened of extinction, and thus deserve our best conservation efforts.

22.13 Concluding Remarks

The results found in Panama show strong distribution patterns of gall-inducing insects. Local species richness was affected by temporal and spatial factors, but mostly by vegetation composition. Species richness was higher in the canopy, but further studies are needed to determine the causes of this pattern. Oak gall wasps have high species richness in the Neotropical region, and our results revealed several distribution patterns of this group of gall-inducing species. In addition, parasitoid complexes were more specific in the canopy and showed less compartmentalization. However, there was high parasitoid species richness affecting the galls in the understory.

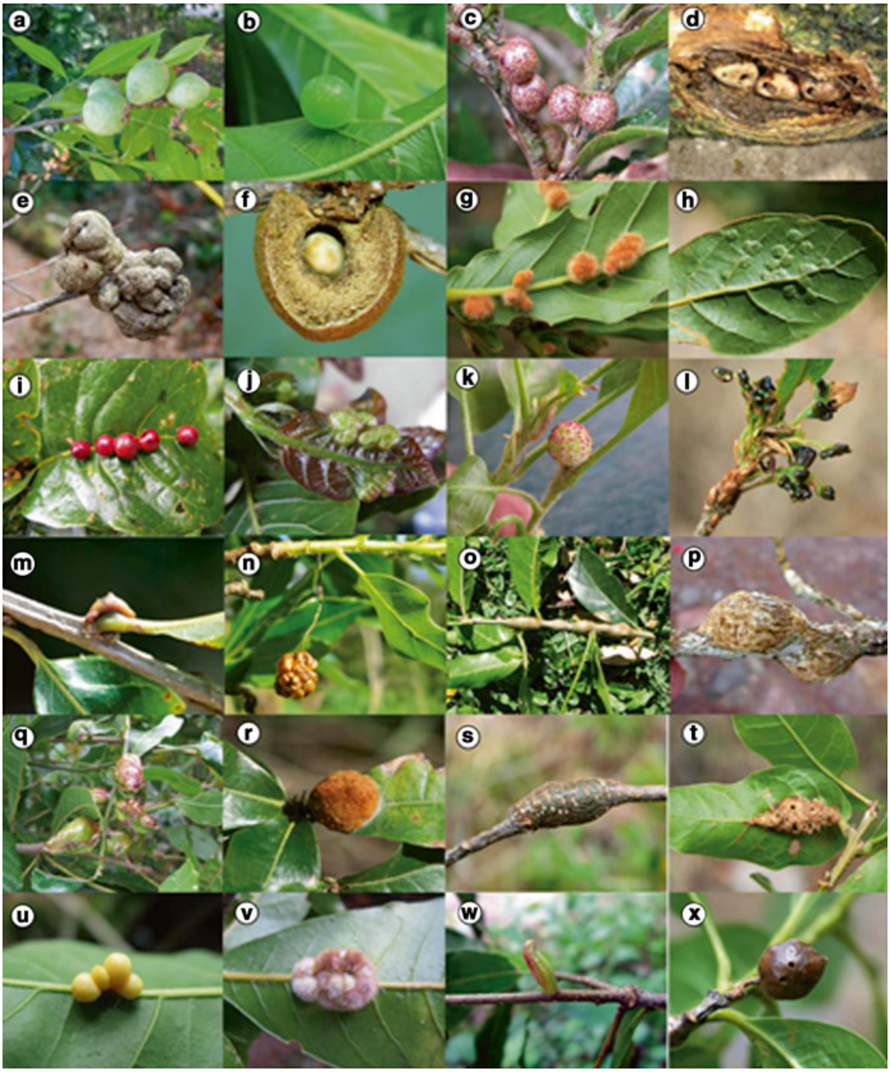

Fig. 22.9 A sample of oak gall wasp diversity in montane forests of Panama: (**a**–**b**) Galls of *Amphibolips castroviejoi* and *A. salicifoliae* on *Quercus salicifolia*. (**c**–**d**) Galls of two undescribed species of *Coffeikokkos* on *Quercus bumelioides* and *Q. insignis*. (**e**) Galls of *Odontocynips championi* on *Q. bumelioides*. (**f**) Gall of *Disholcaspis bettyannae* on *Q. bumelioides*. (**g**–**h**) Galls of unidentified species of *Neuroterus* on *Q. bumelioides*. (**i**–**m**) Galls of undetermined species of *Dryocosmus* on *Q. bumelioides* (**i**, **j**, **l**, **m**) and *Q. lancifolia* (**k**). (**n**–**p**) Galls of undetermined species of *Andricus* on *Q. salicifolia* (**n**, **o**) and *Q. lancifolia* (**p**). (**q**) Galls of an undescribed species of *Callirhytis* on *Q. salicifolia*. (**r**) Gall of *Andricus guatemalensis* on *Q. bumelioides*. (**s**–**x**) Galls of undetermined cynipid species on *Q. salicifolia*, *Q. bumelioides*, and *Q. lancifolia*

Table 22.7 List of genera of oak gall wasps (Cynipidae: Cynipini) recorded in the Neotropical region, and number of species described. The species with an *asterisk* under a given genus are only estimated according to the morphospecies identified in samples (Medianero and Nieves-Aldrey unp.)

Gall wasp genera	Number species/morphospecies
Amphibolips	3
Andricus	12*
Bassettia	1
Callirhytis	1*
Coffeikokkos	2
Disholcaspis	2
Loxaulus	2
Dryocosmus	7*
Neuroterus	8*
Odontocynips	2
Undescribed genus 1	1*
Undescribed genus 2	1*
Undescribed genus 3	1*

Table 22.8 List of Cynipidae species recorded in the Neotropical region

Tribes and species	Country	Tribes and species	Country
Aylacini		**Paraulacini**	
*Phanacis hypochoeridis**	Chi-Arg	*Cecinothofagus gallaecoihue*	Chi-Arg
*Timaspis cichorii**	Chi	*Cecinothofagus gallaelenga*	Chi-Arg
Cynipini		*Cecinothofagus ibarrai*	Chi-Arg
Acraspis fugiensi	Gua	*Paraulax perplexa*	Chi
Amphibolips aliciae	Pma	*Paraulax queulensis*	Chi
Amphibolips castroviejoi	Pma	*Paraulax ronquisti*	Chi
Amphibolips dampfi	Mex	**Pediaspidini**	
Amphibolips salicifoliae	Pma	*Pediaspis aceris**	Arg
Andricus costaricensis	CRi	**Synergini**	
Andricus guatemalensis	Gua	*Agastoroxenia panamensis*	Pma
Andricus imitator	Gua	*Synergus baruensis*	Pma
Atrusca luminata	Gua	*Synergus chiricanus*	Pma
Atrusca lucaris	Gua	*Synergus colombianus*	Col
Bassetia caulicola	Pma	*Synergus cultratus*	Gua
Coffeikokkos copeyensis	CRi	*Synergus elegans*	Pma
Disholcaspis bettyannae	Pma	*Synergus filicornis*	Gua
Disholcaspis bisethiae	Pma	*Synergus gabrieli*	Pma
Loxaulus championi	Pma	*Synergus kinseyi*	Gua
Loxaulus panamensis	Pma	*Synergus laticephalus*	Pma
Odontocynips championi	Pma-Gua	*Synergus luteus*	Pma
Odontocynips hansoni	CRi-Pma	*Synergus mesoamericanus*	Gua
*Plagiotrochus amenti**	Arg	*Synergus nicaraguensis*	Nic
Zapatella grahami	CRi	*Synergus ramoni*	Pma
Zapatella nievesaldreyi	Col	*Synergus rufinotaulis*	Pma
Eschatocerini			
Eschatocerus acaciae	Uru		
Eschatocerus myriadeus	Arg		
Eschatocerus niger	Arg		

An * indicates the species introduced from Europe, and thus nonnative to the Neotropics (After Medianero and Nieves-Aldrey 2011b)

Country abbreviations: *Arg* Argentina, *Col* Colombia, *Cri* Costa Rica, *Chi* Chile, *Gua* Guatemala, *Mex* Mexico, *Nic* Nicaragua, *Pma* Panama, *Uru* Uruguay

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Chapter 23
Insect Galls of Costa Rica and Their Parasitoids

Paul Hanson, Kenji Nishida, and Jorge Gómez-Laurito

Abstract Approximately 1,100 morphospecies of gall-inducing insects have been found thus far in Costa Rica. Seventy percent of these are Cecidomyiidae, a group whose true species richness is potentially huge; other prominent groups include Psylloidea, Hymenoptera (5 families), and Lepidoptera (14 families). About half of the lepidopteran galls are induced by Momphidae on Melastomataceae and these galls are more modified than most other lepidopteran galls. Some groups of gall-inducers are probably much more diverse than present numbers suggest because their galls are hidden, for example eulophid galls in fruits of Araceae and braconid galls in fruits of Fabaceae, Melastomataceae, and Rubiaceae. Eleven families of hymenopteran parasitoids have been reared from galls in Costa Rica. Platygastridae are restricted to cecidomyiid galls and Encyrtidae occur in either sternorrhynchan (Hemiptera) or lepidopteran galls, whereas Eupelmidae and *Torymus* (Torymidae) are associated with a diversity of gall-inducers. An independent inventory of Entedonini (Eulophidae) and the resulting taxonomic monographs allow for a more detailed analysis of this group, which shows that while the vast majority of *Chrysonotomyia* and *Omphale* species are probably associated with galls, very few have been reared: only 27 of 97 species, and 10 of 129 species, respectively. This and other evidence suggest that many, perhaps most, insect galls remain to be discovered.

Keywords Gall-inducing insects • Cecidomyiidae • Coleoptera • Diptera • Hemiptera • Hymenoptera • Lepidoptera • Thysanoptera • Natural enemies • Idiobiont • Koinobiont

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We dedicate this chapter to Jorge Gómez-Laurito, whose recent passing leaves us greatly saddened. His friendship, humor, and botanical knowledge shall be greatly missed.

Jorge Gómez-Laurito (deceased)

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23.1 Introduction

For the last 20 years we have been surveying the gall-inducing insects of Costa Rica, a country whose small size (approximately 51,000 km^2) facilitates sampling the diverse altitudes and habitats. Because the sampling has rarely been intensive, the purpose was not to make quantitative comparisons between habitats, but rather to obtain a broad, overall view of the potential diversity present within the country. A secondary objective was to test the hypothesis that the species richness of gall-inducing insects found in a region is approximately correlated with the number of plant species, and the preliminary data appear to support this hypothesis (Hanson and Gómez-Laurito 2005).

Each time a particular site was visited as many plant species as possible were searched for galls. Samples of galls were collected for later examination in the laboratory and samples of the host plant were taken when there was uncertainty about its identity. A subset of the galls was dissected under a microscope to determine the family-level identity of the gall-inducer, and if the results were uncertain (e.g., in very young or very old galls) further samples were collected when possible. Galls that were not dissected were reared in plastic bags in order to obtain adult stages of the gall-inducers and their parasitoids (specimens are deposited in the Zoology Museum at the University of Costa Rica).

There is usually a very low success rate in obtaining adult gall-inducers from a given sample and the most practical way of increasing the success rate is by recollecting the same galls throughout the year, which was often not possible. However, it was generally possible to identify the gall-inducer to family level on the basis of the larval stages encountered during the dissections of the galls (except for Lepidoptera and Hymenoptera). Even when adult stages were obtained, identification of most insects beyond the family level is severely limited by lack of taxonomic publications. The vast majority of gall-inducing insects in Costa Rica, like elsewhere in the Neotropics, are undescribed species. For this reason we separated morphospecies of gall-inducers on the basis of gall morphology. When similar galls were found on congeneric plant species they were generally considered to be the same species of gall-inducer and our estimates of numbers of gall-inducing insects are therefore conservative.

There are three objectives of the present chapter. First, we provide an update to the data provided in our earlier publication (Hanson and Gómez-Laurito 2005), adding new records of insect-induced galls that have been discovered subsequent to the previous publication; however, many details from this previous publication are not repeated here, but rather summarized (see the previous publication for more information). Second, we provide preliminary results on the parasitoids that have been obtained from Costa Rican galls, information that was not included in our previous publication. Third, we briefly discuss what would be entailed in undertaking a more complete inventory of the gall-inducing insects.

23.2 Gall-Inducing Insects

Thus far we have found 1,100 morphospecies of gall-inducers belonging to six orders of insects; these numbers exclude galls induced by mites, nematodes and fungi. Below, we provide more details on each of these six orders.

23.2.1 Thysanoptera

Seven species of thrips have been found inducing galls, all of them in the family Phlaeothripidae. Host plants include one fern (Lomariopsidaceae: *Elaphoglossum*; Retana-Salazar and Nishida 2007; Fig. 23.1a) and six families of dicotyledons: Araliaceae, Euphorbiaceae, Gesneriaceae, Lauraceae, Sapotaceae, and Winteraceae (Fig. 23.1b). Most of these cause just a wrinkling of the leaf surface or a rolling of the leaf margin, but the species on *Sarcaulus* (Sapotaceae) induces the leaf blade to thicken, fold along the midvein, and close very tightly, with the upper surface of the leaf forming the interior of the gall.

23.2.2 Hemiptera

In Costa Rica gall-inducers in the order Hemiptera are restricted to the suborder Sternorrhyncha: at least 70 species of Psylloidea, seven of Coccoidea and one of Aphidoidea (Phylloxeridae on Vitaceae, Fig. 23.2d; some Aphididae cause leaf wrinkling and are not included in this tabulation). Psylloidea ranks as one of the major groups of gall-inducers in the country although they are restricted to 20 families of dicotyledons. They are especially diverse on Fabaceae, Lauraceae, and Moraceae. Examples of gall-inducing genera include: *Euphalerus* on *Lonchocarpus* (Fabaceae; Fig. 23.1c, d); *Trioza* on Araliaceae and Lauraceae; *Trichochermes* and *Trioza* on Moraceae (Fig. 23.1e, f); *Callophya* on Anacardiaceae; *Gyropsylla* on Aquifoliaceae; *Leuronota* on Cunoniaceae and Juglandaceae; and *Tuthillia* on Myrtaceae. Psyllid galls vary from a simple rolling of the leaf edge or pits in the surface of the leaf, to the very large, completely enclosed galls caused by an undescribed species of *Neolithus* on *Sapium glandulosum* (L.) Morong (Euphorbiaceae; Fig. 23.2a). In the latter gall, individual chambers split open when the psyllids reach the adult stage.

Gall-inducing Coccoidea found in Costa Rica include: *Quadrigallicoccus lauracearum* Williams and Miller (Pseudococcidae) on *Aiouea* and *Nectandra* (Lauraceae); *Dromedaricoccus hansoni* Hodgson and Miller (Eriococcidae) on *Ceiba* (Malvaceae); an undetermined Eriococcidae on *Astronium* (Anacardiaceae; Fig. 23.2c); and undetermined Coccoidea on *Smilax* (Smilacaceae), *Justicia* (Acanthaceae; just a wrinkling of the leaf), *Lonchocarpus* (Fabaceae; Fig. 23.2b), and *Drimys* (Winteraceae; just a rolling of the leaf margin).

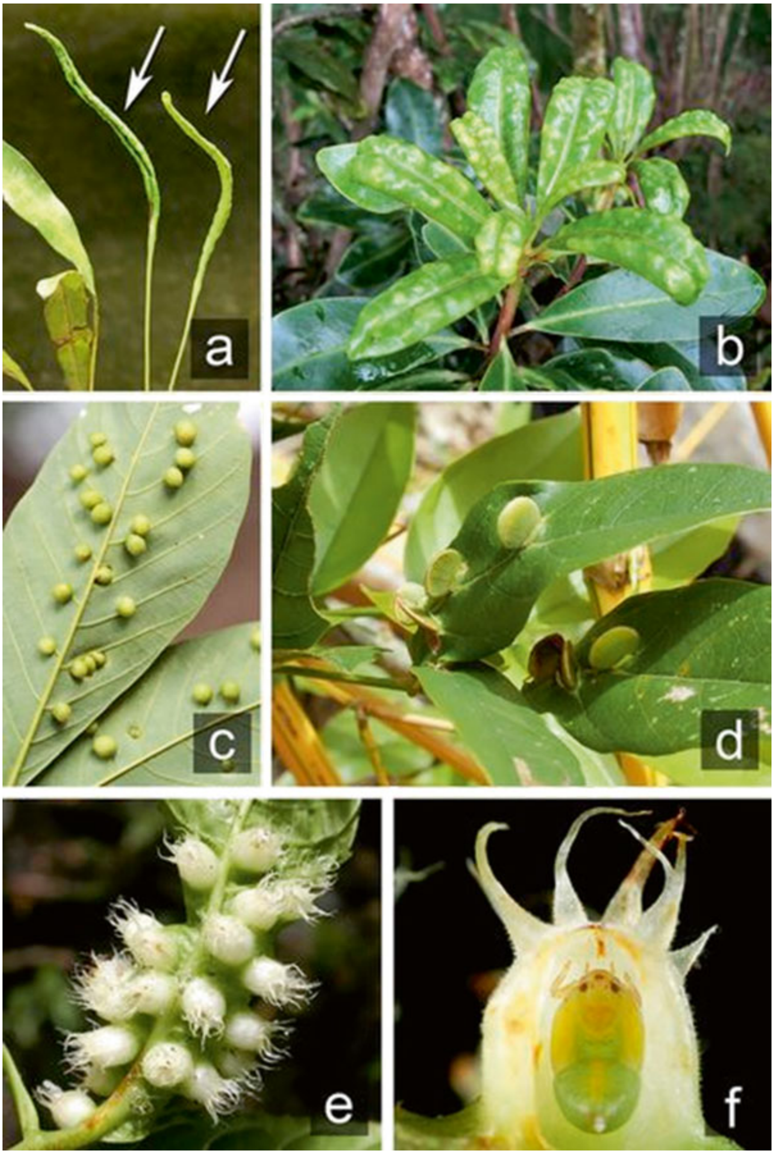

Fig. 23.1 Galls induced by Thysanoptera and Psylloidea: (**a**) "*Jersonithrips*" *galligenus* on the fern *Elaphoglossum moranii* (Lomariopsidaceae) (*arrows* indicate galls); (**b**) unknown Thysanoptera on *Drimys granadensis* (Winteraceae); (**c**) *Euphalerus* (Psyllidae) on *Lonchocarpus heptaphyllus* (Fabaceae); (**d**) *Euphalerus* on *Lonchocarpus salvadorensis*; (**e**) *Trichochermes magna* (Triozidae) on *Pseudolmedia mollis* (Moraceae); (**f**) same gall sectioned to show nymph

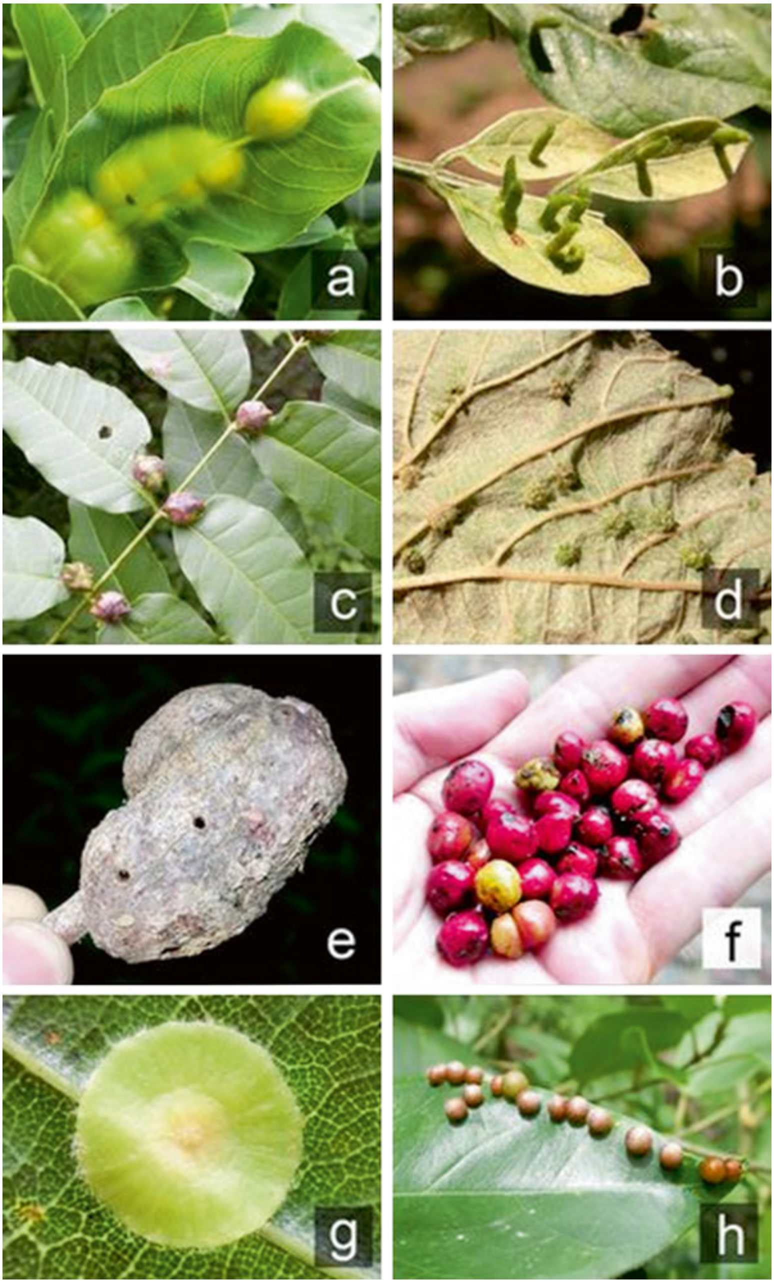

Fig. 23.2 Galls induced by Hemiptera and Hymenoptera: (**a**) *Neolithus* (Triozidae) on *Sapium glandulosum* (Euphorbiaceae); (**b**) undetermined Coccoidea on *Lonchocarpus minimiflorus* (Fabaceae); (**c**) Eriococcidae on *Astronium graveolens* (Anacardiaceae); (**d**) *Viteus* (Phylloxeridae) on *Vitis tilifolia* (Vitaceae); (**e**) *Andricus costaricensis* (Cynipidae) on *Quercus costaricensis* (Fagaceae); (**f**) *Coffeikokkous copeyensis* (Cynipidae) on *Q. bumelioides* (galls detach from twigs and fall to the ground); (**g**) undetermined Cynipidae on *Q. bumelioides*; (**h**) *Labania minuta* (Braconidae) on *Ficus colubrinae* (Moraceae)

23.2.3 Hymenoptera

Because virtually all parasitoids in galls are hymenopterans (Sect. 23.3), it is often very difficult to determine the identity of the gall-inducer when only hymenopteran larvae are present. Thus far, we have found nearly 100 species, in five families, of gall-inducing hymenopterans, but these numbers do not include those that induce galls in the syconia of figs (Moraceae: *Ficus*). Approximately half the hymenopteran records are of Cynipidae, which in Costa Rica are exclusively associated with oaks (Fagaceae: *Quercus*; Fig. 23.2e–g), unlike in north temperate regions where some species induce galls on other plant families (e.g. Rosaceae and Asteraceae). After years of neglect, the taxonomy of cynipids in Costa Rica and Panama is finally beginning to receive some attention (Medianero and Nieves-Aldrey 2010, 2011; Medianero et al. 2011a, b; Melika et al. 2009, 2011; Nieves-Aldrey and Medianero 2010, 2011; Pujade-Villar 2008; Pujade-Villar et al. 2012b, c).

Other families of hymenopteran gall-inducers include Eulophidae, Eurytomidae, Tanaostigmatidae, and Braconidae. Most eulophid gall-inducers in Costa Rica belong to the subfamily Tetrastichinae, which often induce galls in fruits/seeds, for example those of Araceae (Gibernau et al. 2002), and possibly those of *Blakea* (Melastomataceae) and *Eugenia* (Myrtaceae). It is possible that some members of the subfamily Entedoninae are also gall-inducers, for example in stems of *Andira inermis* (W. Wright) Kunth (Fabaceae). Eurytomid gall-inducers have been found primarily on Myrtaceae (stem, leaf, and fruit galls), but they also occur on plants in other families. Among eurytomids, species of *Prodecatoma* appear to be mostly associated with fruits/seeds and they often occur together with other gall-inducing hymenopterans (e.g. with tetrastichine eulophids in Araceae and with *Allorhogas* braconids in Rubiaceae). Both Eulophidae and Eurytomidae require much more taxonomic and biological research, especially since these families include both gall-inducers and parasitoids/inquilines. For example, the genus *Foutsia* (Eurytomidae) has been reared from root galls on *Philodendron* (Araceae), but it is still unclear whether it is a gall-inducer or a parasitoid/inquiline in cecidomyiid galls. Virtually all Tanaostigmatidae are associated with galls, primarily on Fabaceae, but some species are inquilines (Fernandes et al. 1987) while others are gall-inducers, for example in stems of *Inga* (Fabaceae) (Pujade-Villar et al. 2012a) and stems of *Eschweilera* (Lecythidaceae).

One of the most notable differences between gall-inducers of north temperate regions and those of the Neotropics is the potentially large number of braconid gall-inducers in the latter region (Wharton and Hanson 2005). Until relatively recently, members of this family were thought to be strictly parasitoids, but this misconception changed when *Allorhogas dyspistus* Marsh was shown to induce galls in the seed arils of *Pithecellobium tortum* Martius (Fabaceae) in Brazil (Macêdo and Monteiro 1989). Although some species of *Allorhogas* occur in cecidomyiid galls (whether as parasitoids or inquilines remains unknown), many are gall-inducers in fruits/seeds of Fabaceae, Melastomataceae (Centrella and Shaw

2010; Chavarría et al. 2009), and Rubiaceae. Given the species-richness of the host plants (e.g. *Conostegia*, *Miconia*, *Palicourea*, *Psychotria*) there are potentially large numbers of undiscovered species of *Allorhogas*. With respect to other braconid genera, preliminary observations suggest that all species of *Labania* are associated with galls on figs (Moraceae: *Ficus*), either on aerial roots or leaves; those in root galls and at least some in leaf galls (Fig. 23.2h) are gall-inducers, but more research is needed to determine whether all species are gall-inducers. Nearly 20 species of *Monitoriella* are known to occur in Costa Rica (S.R. Shaw, pers. comm.) and it is possible that most, if not all, of these species induce leaf galls on Araceae (Fig. 23.3a–c), although only a minority have been reared (Infante et al. 1995). A recent phylogenetic analysis places all of these braconid genera (plus *Psenobolus*, which occurs in fig syconia) in the same clade within the subfamily Doryctinae (Zaldivar-Riverón et al. 2007).

23.2.4 Coleoptera

Relative to the size of the order, beetles are poorly represented among gall-inducers. They include one Buprestidae, *Hylaeogena* on *Amphilophium paniculatum* (Bignoniaceae; Medianero et al. 2007; Fig. 23.3d) and about 20 weevil species (Curculionoidea), which were found on 12 families of angiosperms. Undetermined species of Apioninae were found inducing galls in stems of *Aiouea* (Lauraceae), in the stem apex of *Peperomia* (Piperaceae), in petioles of *Bauhinia* (Fabaceae), and in stems and petioles of *Nissolia* (Fabaceae). In the subfamily Dryophthorinae, a species of *Rhodobaenus* induces stem galls on *Clibadium* (Asteraceae). In the subfamily Baridinae, *Thanius biennis* Prena and Nishida produces stem galls on *Psychotria marginata* Swartz (Rubiaceae; Fig. 23.3f) and is noteworthy for its 2-year life cycle (Prena and Nishida 2005); five Costa Rican species of *Eurhinus* induce stem galls on Vitaceae (Ulmer et al. 2007; Vaurie 1982); *Peridinetus wyandoti* Prena induces stem galls on *Peperomia* (Piperaceae) (Prena 2010); and an undetermined species induces galls in petioles of *Hoffmannia* (Rubiaceae). In Conoderinae, a species of *Mnemynurus* induces galls on young leaves of *Philodendron* (Araceae), and two other undetermined species induce galls in stems of *Philodendron* and in petioles of *Beilschmiedia* (Lauraceae). In Curculioninae, an undescribed species of *Camptocheirus* induces galls in stems of *Cinnamomum* (Lauraceae; Fig. 23.3e) and a species of *Myrmex* induces galls on stems of *Struthanthus* (Loranthaceae). *Scolytodes ageratinae* Wood (Scoytinae) causes stem galls on *Ageratina* (Asteraceae). Undetermined weevils were found inducing galls in roots of *Clusia* (Clusiaceae), petioles and stems of *Blakea* and *Miconia* (Melastomataceae), petioles of *Piper* (Piperaceae), and stems of *Phoradendron* (Viscaceae). It is worth noting that additional species of weevils were frequently found in galls induced by other insects (presumably as inquilines), and thus when weevils emerge from a particular type of gall careful observations are required to determine whether or not the weevils are gall-inducers.

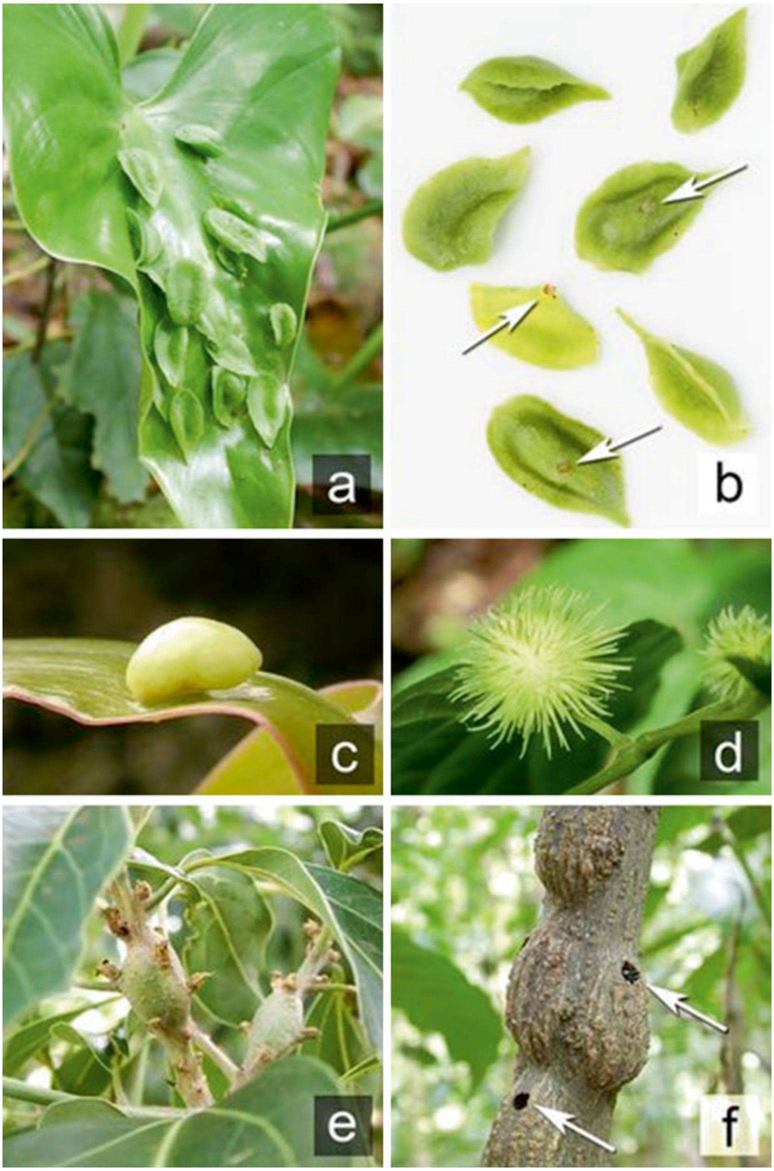

Fig. 23.3 Galls induced by Braconidae and Coleoptera: (**a**) *Monitoriella* (Braconidae) on *Philodendron wilburii* (Araceae); (**b**) same, but showing how galls naturally detach from the leaf and fall to the ground, where they remain green (*arrows* indicate attachment points to leaf); (**c**) *M. elongata* on *P. radiatum*; (**d**) *Hylaeogena* (Buprestidae) on *Amphilophium paniculatum* (Bignoniaceae); (**e**) *Camptocheirus* (Curculionidae) on *Cinnamomum* (Lauraceae); (**f**) *Thanius biennis* (Curculionidae) on *Psychotria marginata* (Rubiaceae) (*arrows* indicate exit holes)

23.2.5 Lepidoptera

More than 100 species of gall-inducing Lepidoptera belonging to at least 14 families and 10 superfamilies have been found in Costa Rica. The galls were found on 27 families of dicotyledons and one of monocotyledons. Approximately half of the galls were found on Melastomataceae, mostly on *Miconia* and *Conostegia*, and were induced by species of "*Mompha*" (Gelechioidea: Momphidae; Fig. 23.4c, d). Other momphid galls were found on *Cuphea* (Lythraceae) (Graham 1995; Fig. 23.4e) and *Hoffmannia* (Rubiaceae). The momphid galls occur on various plant organs – stems, petioles, veins, peduncles, flowers, fruits, and roots – and are highly modified compared to galls induced by most other Lepidoptera.

Galls induced by other groups of lepidopterans include: *Stigmella* (Nepticulidae) in leaf veins of *Hampea* (Malvaceae); Gracillariidae in leaf blades of *Clusia* (Clusiaceae; Fig. 23.4a) and *Aegiphila* (Verbenaceae); *Aetole* (Heliodinidae) in stems of *Iresine* (Amaranthaceae; Fig. 23.4b); *Glyphpterix* (Glyphipterigidae) in stems of *Hyptis* (Meliaceae) (Calvo and Suárez 1991; Calvo 1993); Agonoxenidae in petioles of *Conostegia*; *Ithome* (Cosmopterigidae) in stems of *Guazuma* (Sterculiaceae) and several other cosmopterigids in stems of *Myrsine* and *Ardisia* (Myrsinaceae; Fig. 23.4f); and *Tecia* (Gelechiidae) in stems of *Chusquea* (Poaceae). Among Sesiidae, *Carmenta* induces galls in stems of *Coussarea* (Rubiaceae), and another *Carmenta* and *Alcathoe* in stems of *Phaseolus* (Fabaceae). *Morpheis* (Cossidae) induces stem galls on *Senna* (Fabaceae). Among Tortricidae, *Lusterala* induces galls in stems of *Phaseolus* (Brown and Nishida 2007), *Saphenista* in stems of *Ageratina* (Asteraceae) and *Monnia* (Polygalaceae) (Nishida and Adamski 2004), and *Seticosta* in stems of *Rubus* (Brown and Nishida 2003). Two species of Alucitidae induce galls in stems of *Drymonia* and *Columnea* (Gesneriaceae), respectively. *Schacontia* (Crambidae) induces stem galls on *Podandrogyne* (Capparidaceae). *Meskea* (Thyrididae) induces stem galls on *Sida* (Malvaceae) and another thyridid induces stem galls on *Hampea*. There are many other gall-inducing Lepidoptera which cannot be identified until adult specimens are reared.

23.2.6 Diptera

By far the dominant group of gall-inducing insects, both in Costa Rica and most other parts of the world, are the gall midges (Cecidomyiidae). Larvae, at least the later stages, are readily identified by the presence of a sternal spatula. We presently have records for about 800 gall-inducing species, only a very small minority of which have scientific names. They account for at least 70 % of all insect galls in the country and they occur on virtually all groups of vascular plants: six families of ferns, one family of gymnosperms (Podocarpaceae), nine families of monocotyledons, and more than 100 families of dicotyledons. These galls include the full range of gall types and occur on all parts of the plant: roots (Fig. 23.5c, d), stems (Fig. 23.5f), buds (Fig. 23.5g), flowers/fruits (Fig. 23.5h), leaves (Fig. 23.5i–j), or a

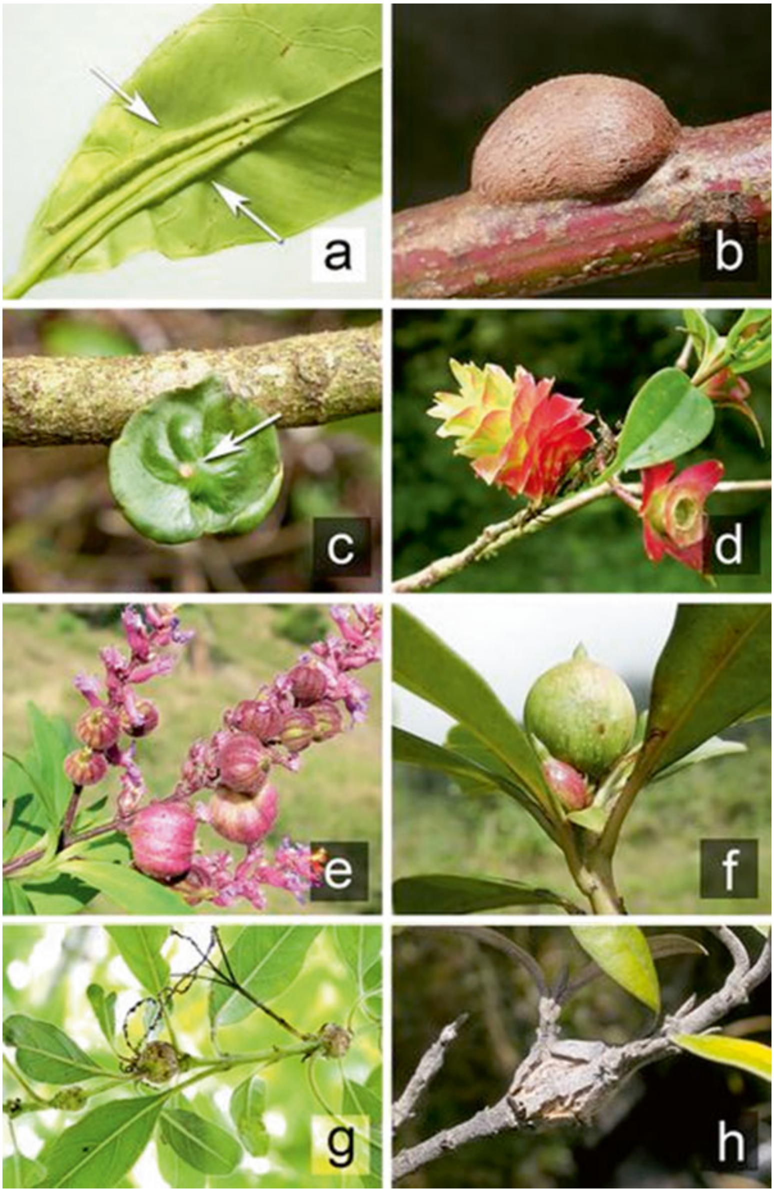

Fig. 23.4 Galls induced by Lepidoptera and Tephritidae: (**a**) "*Acrocercops*" (Gracillariidae) on *Clusia cooperi* (Clusiaceae); (**b**) *Aetole* (Heliodinidae) on *Iresine diffusa* (Amaranthaceae); (**c**) "*Mompha*" (Momphidae) on *Conostegia pittieri* (Melastomataceae) (*arrow* indicates exit window); (**d**) "*Mompha*" on *Blakea litoralis* (Melastomataceae) (gall on *left*, fruit on *right*); (**e**) "*Mompha*" on *Cuphea epilobiifolia* (Lythraceae); (**f**) Cosmopterigidae (possibly *Periploca*) on *Myrsine coriacea* (Myrsinaceae); (**g**) *Eutreta* (Tephritidae) on *Citharexylum donnell-smithii* (Verbenaceae); (**h**) Tephritidae on *Buddleja nitida* (Buddlejaceae)

Fig. 23.5 Galls induced by Agromyzidae and Cecidomyiidae. (**a**) *Ophiomyia* (Agromyzidae) on *Iresine diffusa* (Amaranthaceae); (**b**) *Japanagromyza lonchocarpi* (Agromyzidae) on *Lonchocarpus oliganthus* (Fabaceae); (**c**) Cecidomyiidae on root apex of *Asplundia brunneistigma* (Cyclanthaceae); (**d**) Cecidomyiidae on roots of *Vriesea* (Bromeliacae); (**e**) Cecidomyiidae on *Peperomia alpina* (Piperaceae); (**f**) two types of cecdiomyiid galls (*arrows* indicate smaller, "rolled" galls) on *Acalypha leptopoda* (Euphorbiaceae); (**g**) Cecidomyiidae on *Otopappus verbesinoides* (Asteraceae); (**h**) Cecidomyiidae on *Struthanthus marginatus* (Loranthaceae); (**i**) Cecidomyiidae on *Psychotria monteverdensis* (Rubiaceae); (**j**) closeup of same gall

combination of these (Fig. 23.5e). The only other nematoceran family found inducing galls in Costa Rica was Chironomidae; an undescribed species induces galls on *Marathrum schiedeanum* (Cham.) Tul. (Podostemaceae), a submerged aquatic dicotyledon. Galls on young leaf petioles of *Iresine diffusa* Humb. & Bonpl. ex Willd (Amaranthaceae) appear to be induced by chironomid larvae, but this unusual record requires further study.

We have encountered two families of gall-inducers in the suborder Brachycera, Tephritidae and Agromyzidae. The former includes at least 15 species, found mostly on Asteraceae, but also Verbenaceae (Fig. 23.4g) and Buddlejaceae (Fig. 23.4h). Tephritid galls on *Diplostephium costaricense* S.F. Blake and *Senecio andicola* Turcz. (Asteraceae) are among the very few insect galls found in the "páramo" vegetation above tree-line (above 3,000 m). Five species of gall-inducing Agromyzidae have been seen thus far: *Ophiomyia* in the stems of *Iresine* (Amaranthaceae; Fig. 23.5a), *Japanagromyza lonchocarpi* Boucher in the rachis of *Lonchocarpus* (Fabaceae; Fig. 23.5b; Boucher and Hanson 2006), and undetermined agromyzids in the leaf veins of *Acalypha* (Euphorbiaceae) and *Hasseltiopsis* (Salicaceae), and in the petioles of *Schultesianthus* (Solanaceae).

23.3 Parasitoids

Nearly all insect parasitoids associated with gall-inducers belong to the order Hymenoptera and in terms of biology they can be divided into two categories, idiobionts and koinobionts (Hanson and Gauld 2006). Preceding oviposition female idiobionts inject a venom that causes permanent paralysis in the host and the latter therefore discontinues feeding. In galls, idiobionts are mostly ectoparasitoids (the larva feeds from the surface of the host) and include many Eulophidae, Eurytomidae and Pteromalidae, and probably all Eupelmidae, Ormyridae, Torymidae and Pimplinae (Ichneumonidae).

On the other hand, koinobionts do not permanently paralyze the host but instead allow it to continue feeding and developing, at least for a while (often until the host reaches the pre-pupal stage). At least in galls, virtually all koinobionts are probably endoparasitic and the prediction is that endoparasitic koinobionts are more host specific than idiobionts since the former require specific adaptations to avoid or counteract the host's immune system. There is considerable evidence for this prediction in other parasitoids (summarized in Hanson and Gauld 2006) and there is no reason to believe that parasitoids of gall-inducers are any different in this regard. Koinobionts in galls include Ceraphronidae, Platygastridae, Encyrtidae, a few Eulophidae, and probably *Rileya* and *Sycophila* (Eurytomidae).

An aspect of gall biology that has not been well studied is the different effects these two groups of parasitoids could potentially have on gall formation. For example, in cases where gall development depends upon the continued presence of larval secretions, an idiobiont that permanently paralyzes the host larva would be expected to halt gall development. Koinobionts on the other hand would not be expected to

Table 23.1 Number of gall-inducing morphospecies (categorized by gall-inducing taxa) from which major parasitoid taxa have been reared in Costa Rica

	Gall-inducing taxa						
Parasitoids	Psylloidea	Coccoidea	Hymenop.	Coleop.	Lepidop.	Cecidom.	Tephrit.
Platygastridae						82	
Encyrtidae	11	1			4		
Eulophidae: *Chrysonotomyia*	1		2		2	27	
Eupelmidae	2	1	4	1	2	15	1
Eurytomidae: *Rileya*						22	
Eurytomidae: *Sycophila*			19			7	
Pteromalidae: *Cecidellis*			2			14	
Torymidae: *Torymus*	1		16		1	53	1
Ichneumonidae: Pimplinae				1	8		2

have this effect. At least some species in both categories can potentially feed on nutritive tissue in the gall after devouring the host. However, there are very few studies of such biological details for most parasitoid species, especially in the tropics. It should also be noted that for most parasitoids, the above categorization of parasitoid groups into idiobiont versus koinobiont is based on taxonomic trends. While groups such as Platygastridae probably do in fact consist entirely of endoparasitic koinobionts, groups such as Eulophidae appear to be much more variable with respect to their biology. In these cases detailed observations are required to determine which species are idiobionts and which are koinobionts.

23.3.1 Ceraphronidae

This family of parasitoids is very uncommon in galls, where it is represented by the genus *Aphanogmus*. Ceraphronids were found in only six gall types, all induced by Cecidomyiidae.

23.3.2 Platygastridae

While a few members of this family are parasitoids of beetle eggs or the immature stages of whiteflies and mealybugs, the vast majority are exclusively associated with the larvae of Cecidomyiidae. Thus it is not surprising that they have only been obtained from cecidomyiid galls (Table 23.1). Indeed, rearing Platygastridae from a particular type of gall is evidence for the gall-inducer being Cecidomyiidae, although caution is required since some cecidomyiids can be inquilines in galls formed by other groups of insects. All platygastrids (as far as known) are

Fig. 23.6 Parasitoids in galls: (**a**) Platygastridae in the larger cecidomyiid gall shown in Fig. 23.5f, on *Acalypha leptopoda*; (**b**) *Copidosoma* (Encyrtidae) in the *Aetole* gall shown in Fig. 23.4b, on *Iresine diffusa*

endoparasitic koinobionts and at least some have polyembrionic development (Leiby and Hill 1924), although it is not known how widespread this feature is in the family. Upon dissecting a cecidomyiid gall it is not uncommon to find a thin translucent sac containing several pupae (Fig. 23.6a). As far as known, all platygastrids, whether gregarious or solitary, produce a parchment-like cocoon formed from solidified anal secretions. Unfortunately, very little work has been done on the taxonomy of this family and so identification of genera is difficult and of species impossible.

23.3.3 Encyrtidae

Very few representatives of this large family parasitize gall-inducers, and those that do were found exclusively in two types of galls, those induced by Sternorrhyncha (primarily Psylloidea) and those induced by Lepidoptera (Table 23.1). These two groups of gall-inducers are parasitized by distinct taxa of Encyrtidae: Psylloidea by genera such as *Psyllaephagus*, and lepidopteran larvae by members of the tribe Copidosomatini (specifically, the genus *Copidosoma*), which are polyembrionic (Grbić 2003; Fig. 23.6b). While the second group has not yet been analyzed, species of *Psyllaephagus* have been reared from psylloid galls on *Sapium* (Euphorbiaceae), *Lonchocarpus* (Fabaceae), *Cinnamomum* (Lauraceae), *Pseudolmedia* (Moraceae), and *Avicennia* (Verbenaceae); species of *Caldencyrtus* have thus far only been reared from galls on *Cinnamomum* (Noyes and Hanson 1996).

23.3.4 Eulophidae

While we have reared occasional Eulophinae (Eulophini) and Entiinae from galls, the vast majority (>95 %) of eulophids obtained in our study belong to the subfamilies

Entedoninae and Tetrastichinae. The latter is the most frequent parasitoid taxon reared from Costa Rican galls, but unfortunately the lack of a good taxonomic foundation prevents us from discussing this important group in greater detail. There are no keys to the Neotropical genera of Tetrastichinae and the vast majority of species are undescribed. Moreover, some species are gall-inducers, so one cannot assume that a tetrastichine reared from a gall is a parasitoid. Parasitic tetrastichines can be found in virtually all categories of galls and are the only group of Hymenoptera that we are aware of that occur in galls induced by mites, although in this case the tetrastichine larva acts as a predator rather than as a parasitoid. We have found a species of *Aprostocetus* to be very common in mite galls on the leaves of *Acnistus arborescens* (L.) Schltdl. (Solanaceae). Nonetheless, tetrastichines appear to be absent from the vast majority of mite galls, probably because most are not enclosed (as are those on *Acnistus*).

The other eulophid subfamily occurring in galls is Entedoninae (specifically the tribe Entedonini) and fortunately the Costa Rican entedonines have been well studied (Hansson 2002, 2004, 2005; Hansson and LaSalle 2010). Because *Klyngon* is the basal genus in Entedonini, and is associated with galls, it has been suggested that association with galls is an ancestral trait in this tribe (Hansson and LaSalle 2010). Several genera consist primarily of species that are parasitoids in galls: *Ametallon*, *Astichomyiia*, *Chrysonotomyia*, *Driopteron*, *Eprhopalotus*, *Omphale*, and *Tropicharis*. Most of the species in these genera are associated with cecidomyiid galls, and the most frequently reared genus was *Chrysonotomyia* (Table 23.1). The data are not sufficient to allow a discussion of host ranges of individual species, but it is worth noting that at least a few have been recorded from gall-inducers belonging to different orders; for example *Chrysonotomyia conostegiae* has been reared from both cecidomyiid and lepidopteran galls. Relatively few entedonines were found in cynipid galls and those that we did obtain belong mostly to genera (*Eprhopalotus* and *Pediobius*) that were uncommon in cecidomyiid galls.

23.3.5 Eupelmidae

This family, primarily species in the genera *Brasema* and *Eupelmus*, was found in all types of insect galls (Table 23.1). In north temperate regions individual species are known to be quite polyphagous, but the lack of keys for Neotropical species prevents us from determining actual host ranges. In general eupelmids were less frequently reared than eulophids, eurytomids, pteromalids and torymids.

23.3.6 Eurytomidae

In terms of frequency of rearing records, this family was second to Eulophidae. The genera in this family are currently undergoing redefinition (Lotfalizadeh et al. 2007) and many Neotropical gall-associates that had previously been identified as *Eurytoma* are now placed in *Phylloxeroxenus* and *Tenuipetiolus* (M. Gates, pers. comm.). Here, we focus our attention on two other genera, *Rileya* and *Sycophila* (Table 23.1). The former has been the subject of a recent taxonomic revision (Gates 2008) and in our study the species were primarily associated with cecidomyiid galls. *Sycophila* is primarily associated with hymenopteran galls, mostly those of Cynipidae and Braconidae (this genus also occurs in fig syconia, but these are not included in the tabulation). The seven records from cecidomyiid galls require more detailed investigation to determine whether *Sycophila* species in these galls are parasitizing cecidomyiids or hymenopteran inquilines. For example, two of the cecidomyiid galls harbored Tanaostigmatidae and one had *Allorhogas* (Braconidae). Although the evidence is meager, it is possible that both *Rileya* and *Sycophila* are endoparasitic koinobionts. A North American species of *Rileya* has been observed to develop as an endoparasitoid in cecidomyiid larvae, but at some point the parasitoid larva exits the host to feed on it from the outside, and then finishes its development by feeding on gall tissue (Hawkins and Goeden 1984).

23.3.7 Ormyridae

This small family comprises just two known species in Costa Rica, *Ormyrus unifasciatipennis* Girault and *O. venustus* Hanson, which are exclusively associated with cynipid galls on oaks. Although some Old World species are associated with hymenopteran galls in fig syconia, and a few with dipteran galls, these host associations have not been documented in the New World. In the Americas nearly all records are from cynipid galls, except for one Nearctic species in a pteromalid gall. However, there are two anomalous observations that require further investigation: *O. thymus* Girault was once recorded from seeds of *Bucida* (Combretaceae) in Belize, and specimens of an undetermined genus (possibly belonging to Ormyridae) have been reared from "galls in twigs of *Moquinea polymorpha*, Pelotas Brazil", a plant belonging to the tribe Mutisieae in the family Asteraceae (Hanson 1992).

23.3.8 Pteromalidae

This is the most poorly defined family of Chalcidoidea, although many of the subfamilies are better circumscribed. One of the most commonly reared genera was *Lyrcus* (Pteromalinae), but we have not yet analyzed all the specimens and cannot provide a tabulation at this time. However, the genus *Cecidellis* (Coelocybinae) has been analyzed and occurs primarily in galls induced by cecidomyiids, but also those induced by braconids (Heydon and Hanson 2005; Table 23.1).

23.3.9 Torymidae

The principal torymid genus reared from galls is *Torymus*, which occurs primarily in cecidomyiid and hymenopteran galls, but also various other galls (Table 23.1). Many species have a long ovipositor and are therefore capable of ovipositing into more mature galls, a process that can take 10 min or more (Weis 1983). Like some other ectoparasitic idiobionts, some species of *Torymus* are thought to be facultatively hyperparasitic.

We have reared three other torymid genera from galls but these were very restricted in their occurrence. *Physothorax* is strictly associated galls in the outer part of fig syconia, which are probably induced by *Aepocerus* and/or *Nadelaia* (Pteromalidae). *Boucekinus* has only been reared from a cecidomyiid gall on *Anemopaegma chrysoleucum* (Kunth) Sandwith (Bignoniaceae) (Janšta et al. 2011). *Torymoides* has only been reared from a cecidomyiid gall in leaves of red mangrove (Rhizophoraceae: *Rhizophora*) and a hymenopteran gall in stems of *Psidium guineense* Sw. (Myrtaceae).

23.3.10 Ichneumonidae

Relative to the size of the family, very few ichneumonids were reared from galls, and the vast majority of these belong to the subfamily Pimplinae, which were associated mostly with lepidopteran galls (Table 23.1). Species that have been reared from galls include: *Calephialtes deyanrae* Gauld, *Clydonium cabrerai* Gauld, *Scambus basseyi* Gauld, *S. emeritae* Gauld, *S. yalileae* Gauld (these last two from tephritid galls), and *Zonopimpla hebeae* Gauld et al. (1998). One of the few non-pimplines found in galls was *Meniscomorpha xeresha* Ugalde & Gauld (Banchinae) in stem galls induced by *Alcathoe* (Sesiidae) on *Phaseolus lunatus* L. (Fabaceae). Other ichneumonids were occasionally reared from insects that facultatively invade old galls, for example Orthocentrinae from Sciaridae.

23.3.11 Braconidae

Like Ichneumonidae, braconids were infrequently reared from galls, but unlike Ichneumonidae, some braconids are gall-inducers. Among those that are parasitoids, several were associated with facultative invaders of old galls such as weevils. Parasitoids of gall-inducers were associated primarily with lepidopteran and weevil galls, for example Cheloninae with lepidopteran galls, and Brachistini (Helconinae) and Braconinae (Fortier and Nishida 2004) with weevil galls; the first two are endoparasitic koinobionts whereas Braconinae are ectoparasitic idiobionts. The braconid genus that has been most commonly reared from galls in Costa Rica is *Allorhogas* (Doryctinae), which includes both gall-inducers (primarily in fruits) as well as species that are parasitoids/inquilines in cecidomyiid galls (mostly on leaves). The biology of these latter species has not been studied.

23.4 Perspectives on Inventorying Tropical Galls

Despite our many years of collecting galls in a relatively small, accessible country, several lines of evidence suggest that we have barely scratched the surface, especially with regard to Cecidomyiidae. The parasitoid data alone suggest that the vast majority of galls remain to be discovered. For example, the taxonomic monographs of Entedonini (Hansson 2002, 2004) were based on both reared specimens and specimens collected by methods that do not yield biological information (e.g. Malaise traps and sweeping). All available information suggests that the vast majority of species of *Chrysonotomyia* and *Omphale* are associated with galls (especially those of Cecidomyiidae), yet there are host records for only 27 of 97 species, and 10 of 129 species, respectively. While some of the parasitoid species that have not yet been reared might eventually show up in galls that we have already recorded, it seems likely that the majority will come from galls that we have not yet seen. Moreover, while the monographs mentioned above were based on extensive sampling of the Costa Rican fauna, there are certainly many more gall-associated entedonines that have not yet been described.

The most convincing evidence that we are a long way from knowing the true diversity of gall-inducing insects comes from a consideration of the obstacles confronting a complete inventory, especially in tropical rainforests. Leaving aside the taxonomic limitations, the logistical challenges involved in merely finding the galls are potentially intimidating. First, many galls are difficult to access, for example root galls (Fig. 23.5c, d) and galls found in the canopy. Second, many galls that are accessible are not evident in the field. For example, *Allorhogas conostegia* (Braconidae) induces galls in the fruits of *Conostegia xalapensis* (Bonpl.) D. Don (Melastomataceae) (Chaverría et al. 2009), but these galls are not readily noticed until the fruits are dissected in the laboratory. The same is true of many bud and flower galls.

Thus, to do an “All Gall-Inducer Biodiversity Inventory” of a particular area would entail collecting roots, stems, leaves, flowers and fruits of all the vascular plant species, and some of these plant parts (e.g. flowers and fruits) would require dissection under a microscope. Moreover, because many galls are seasonal, and not all individuals of a particular plant species harbor galls, multiple samples would be needed from each plant species. While these prospects are certainly daunting, one can also see this in a more positive light – the pleasures of finding new galls are guaranteed for generations to come, assuming we can protect the forests where they occur.

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

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

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

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

24.1 Introduction

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

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

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

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

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

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

24.2.1 *Importance of Biotic Factors*

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

The structural complexity hypothesis (i.e. a combination of life form, plant height, number of shoots, branches and leaves in relation to crown volume) has been proposed to explain the effects of life form of plants on phytophagous insect species richness (Lawton 1983; Leather 1986) and gall-inducing insect species (Fernandes and Price 1988; Goncalves-Alvim and Fernandes 2001; Cuevas-Reyes et al. 2004a) among species within plant communities. This hypothesis predicts that the abundance and species richness of gall-inducing insects will increase, as life forms of host plants are more structurally complex. Trees appear to be colonized by a wider variety of insect species than either shrubs or herbs, because their complex architecture provides more microhabitats (Leather 1986). In addition, trees are also more “apparent” to insects than either shrubs or herbs (sensu Feeny 1976). Both arguments have been used to explain the folivores species richness, but the pattern is not very clear when applied to specific guilds such as sucking and galling insects (Leather 1986). For example, some studies indicated that that gall-inducing insect species richness is higher in trees than both shrubs and herbs (Goncalves-Alvim and Fernandes 2001; Cuevas-Reyes et al. 2004a) but Fernandes and Price (1988) did not find differences between trees and shrubs.

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

The resource concentration hypothesis states that the abundance of gall-inducing insects on a particular host species will increase with increasing plant density. This hypothesis integrates the degree of insect specialization on host plants, the choice of host plants by female insects for oviposition, and the incidence of natural enemies on isolated or aggregated hosts (Root 1973; Raupp and Denno 1979; Goncalves-Alvim and Fernandes 2001).

24.2.2 Importance of Abiotic Factors

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

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

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

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

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

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

24.3.1 Biotic Factors

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

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

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

To compare the floristic similarity among deciduous and riparian habitats, we using the Driver and Kroeber index calculated as 100 C/[(N1)(N2)]$^{1/2}$, where C = number of shared species, N1 = species number of the most diverse flora, and N2 = species number of the less diverse flora (Cuevas-Reyes et al. 2004b). In addition, a *t* test was performed to compare the plant species richness between deciduous and riparian habitats. We performed a logistic regression analysis using GENMOD procedure (SAS 2000), to test if the frequency of gall-inducing insect families (dependent variable) is different between life forms of plants (independent variable).

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

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

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

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

24.3.2 Abiotic Factors

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

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

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

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

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

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

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

24.4 Diversity Patterns of Gall-Inducing Insects

24.4.1 Importance of Biotic Factors

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

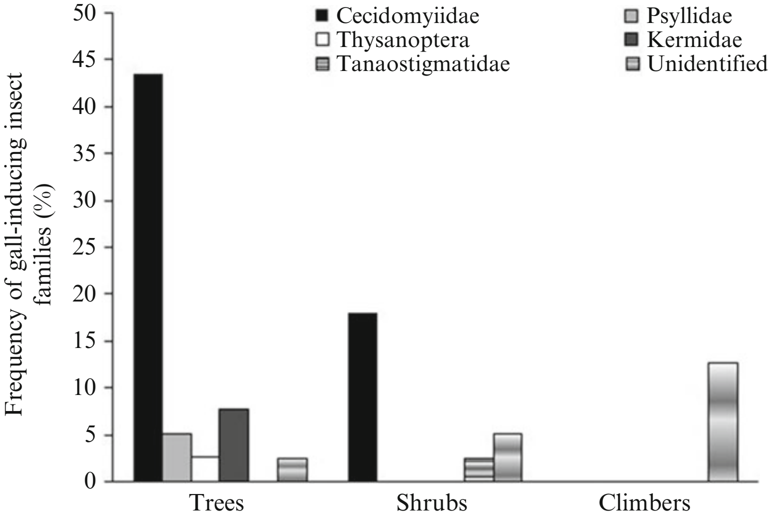

Fig. 24.1 Differences in the incidence of gall-inducing insect families on trees, shrubs and climbers

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

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

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

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

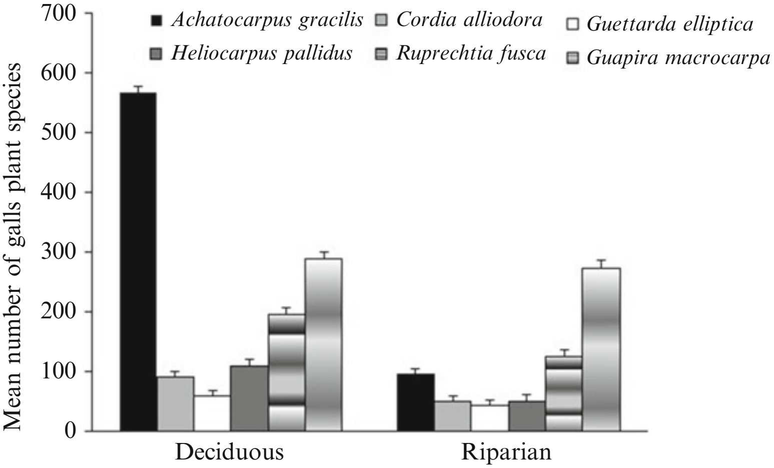

Fig. 24.2 Comparison of gall abundance in six host plant species that occurred in deciduous and riparian habitats. *t* paired test (box-cox transformation data) was applied on each plant species

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

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

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

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

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

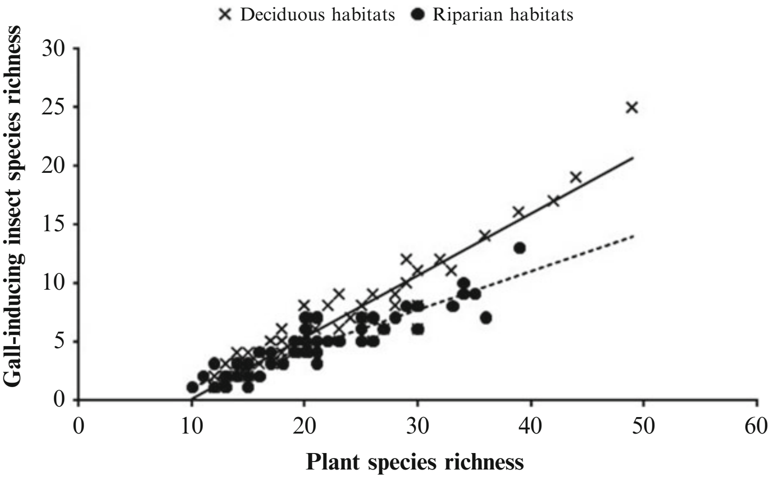

Fig. 24.3 Relationships between gall-inducing insect species richness and plant species richness in Chamela-Cuixmala Biosphere reserve in Jalisco, Mexico. Regression models were utilized in each habitat. Each *point* represents a sampling unit in different habitats

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

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

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

24.4.2 Importance of Abiotic Factors

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

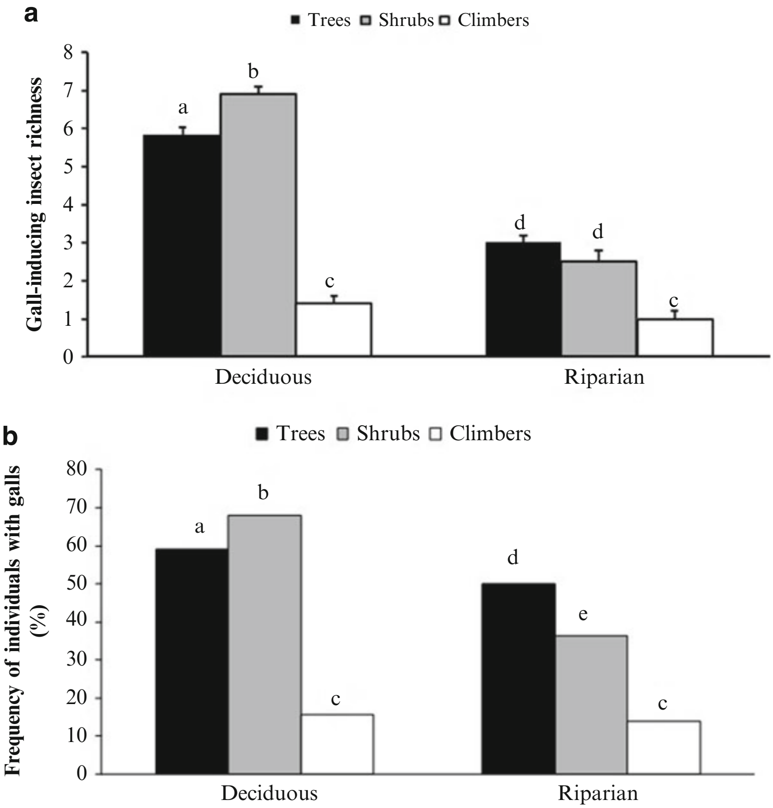

Fig. 24.4 Gall-inducing insect species richness on different life forms in deciduous and riparian habitats in a Mexican tropical dry forest (**a**). Two-way ANOVA analysis was applied between habitats and life forms of plants. Non-transformed data are shown. Means with the same letter did not differ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

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

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

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

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

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

(continued)

Table 24.2 (continued)

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

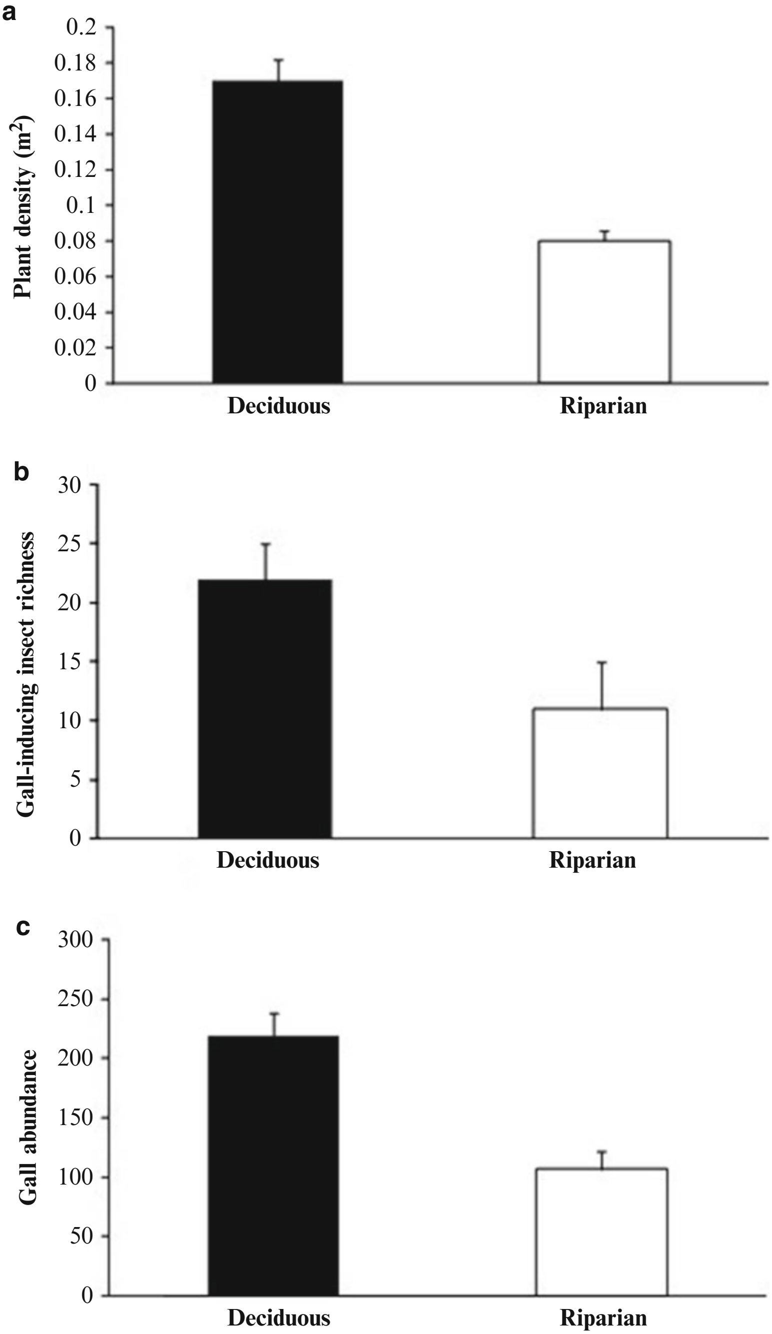

Fig. 24.5 Effects of plant density on gall-inducing insect species. Differences in plant density among deciduous and riparian habitats (**a**); Comparison of gall-inducing insect species between deciduous and riparian habitats (**b**); Patterns of gall abundance in deciduous and riparian habitats (**c**)

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

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

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

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

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

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

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

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

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

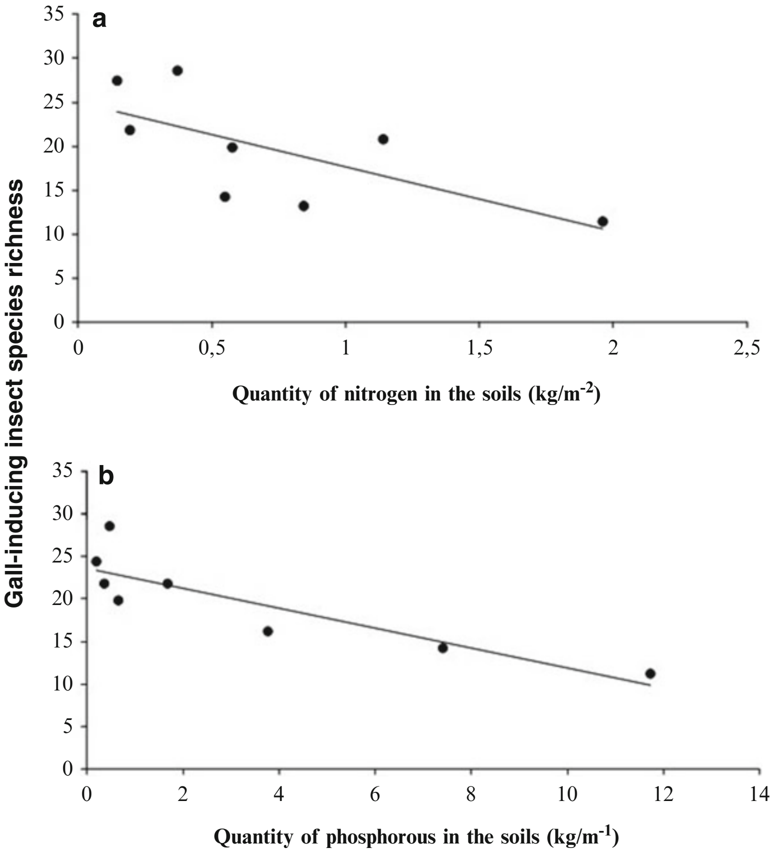

Fig. 24.6 Relationships between gall-inducing insect species richness and total nitrogen amount in soil (**a**); and available phosphorous at the Chamela-Cuixmala Biosphere reserve in Jalisco, Mexico (**b**) Regression models were utilized in each nutrient of soil. Each *point* represents a sampling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

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

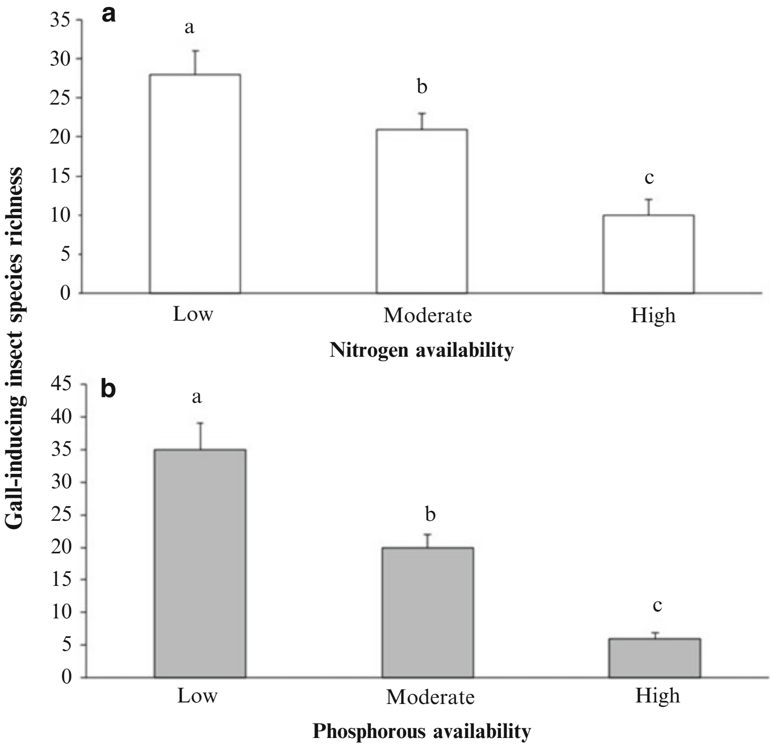

Fig. 24.7 Effects of soil fertility on gall-inducing insect species. Comparison of galling richness between low, moderate and high availability of nitrogen in the soils (**a**); Differences in galling richness between different available phosphorous (**b**). One-way ANOVA test was conducted for each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

24.5 Explanation of Gall-Inducing Insects Species Diversity

24.5.1 Importance of Biotic Factors

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

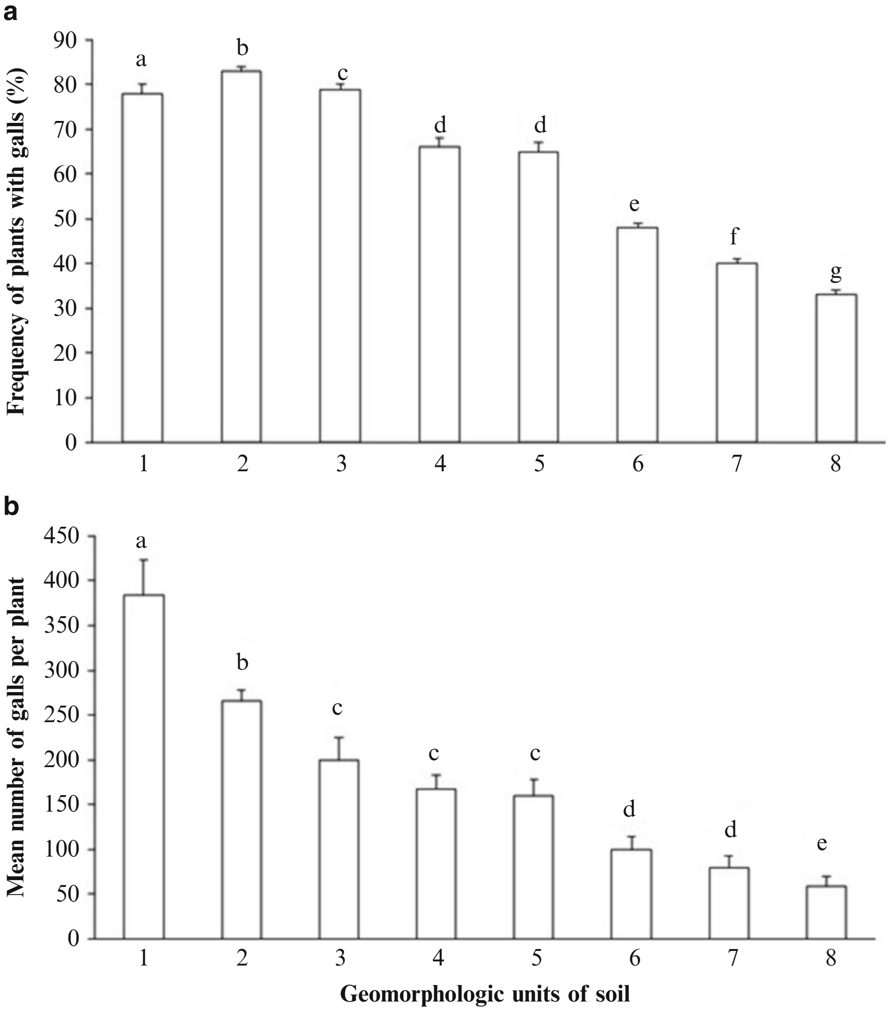

Fig. 24.8 Frequency of plants with galls on host plants that occur in all geomorphologic units of soils (**a**). Mean number of galls per plant on host plants that occur in all sites (**b**) GENMOD procedure (SAS 2000) were applied for generalized linear model in both analyses. Different letters indicate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

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

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

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

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

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

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

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

24.5.2 Importance of Abiotic Factors

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

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

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

24.6 Conclusions

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

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

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

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