16

Gall-Inducing Insects: From Anatomy to Biodiversity

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CONTENTS

16.1	Introduction	369	
16.2	Herbivore Insect Guilds	370	
16.3	Gall-Inducing Insect Taxa	372	
	16.3.1 Hemiptera	372	
	16.3.2 Thysanoptera	.374	
	16.3.3 Coleoptera	.374	
	16.3.4 Hymenoptera	.375	
	16.3.5 Lepidoptera	.375	
	16.3.6 Diptera	376	
16.4	Host Plant Taxa	377	
16.5	Location and Choice of the Host Plant	377	
16.6	Gall Morphology	379	
16.7	Gall Anatomy and Physiology	.381	
16.8	Gall Development	383	
16.9	Gall Classification	385	
16.10	Adaptive Significance	386	
16.11	Concluding Remarks	389	
Refer	References		

16.1 Introduction

The earliest records of galls date to the times of Hippocrates (460–377 BC), Theophrastus (371–286 BC), and Pliny the Elder (23–79 AD). In his *Historia Naturalis XXVI*, published in the first century, Plinius, known as "the Merciful," was the first to use the word "gall" to designate the structure induced in oak trees by wasps from the family Cynipidae (Meyer 1987). Although the emergence of insects from these structures has been described by these ancient authors, it was only in the 17th century, with the works of Marcello Malpighi (1628–1694), Anthony van Leeuwenhoek (1632–1723), and Jan Schwammerdam (1630–1680) that gall development was linked to the oviposition of an insect.

Galls, or vegetative tumors, are plant tissues or organs formed by hyperplasia (increased cell number) and/or hypertrophy (increased cell size) induced by parasitic or pathogenic organisms (Mani 1964; Dreger-Jauffret and Shorthouse 1992). Galls can be induced by a wide variety of organisms (Figure 16.1), including viruses, bacteria, fungi, algae, nematodes, rotifers, copepods, and plants from the family Loranthaceae (popularly known as mistletoes), but are mainly caused by insects (Mani 1964; Raman et al. 2005).

Among all herbivorous insects, gall-forming insects are the most sophisticated because they are able to control and redirect the host plant for their own benefit. Galls represent a fascinating natural phenomenon reflecting intimate interactions between organisms that have been shaped by organic evolution throughout millions of years (see Larew 1992; Labandeira et al. 1994; Labandeira and Phillips 2002;



FIGURE 16.1 Galls induced by distinct organisms. (a) Insect-induced gall. (b) Acari-induced gall. (c) Ambrosia gall (induced by an insect symbiont fungus). (d) Fungus-induced gall (Witch's broom). (e) Nematoid-induced gall. (f) Loranthaceae-induced gall (*Struthantus flexicaulis*).

Stone et al. 2008). Gall-forming insects are able to modify the host plant's growth pattern, altering the structure of the vegetative tissue and driving the host to produce a food source that is rich in nutrients and free from chemical defenses together with a protective structure that is isolated from the environment (Price et al. 1986; 1987).

Galls are also known and used for their pharmacological properties, which have been recognized since ancient times. Aleppo galls (spherical galls formed on the twigs of *Quercus infectoria* by gall-wasp larvae) contain 50% to 60% galactonic acid and significant levels of gallic and ellagic acids. These substances are used to treat diarrhea, oral swelling, and hemorrhoids. The commercial exploitation of galls dates to the 17th century, when pigments extracted from galls were used to dye hair and other tissues, and as writing ink (Fernandes and Martins 1985). In China, galls have been extensively used for more than 1000 years in medicine, industrially, and as human food. In South America, the indigenous Aguaruna-Jívaro people of the Peruvian Amazon use leaf galls from *Licania cecidiophora* (Chrysobalanaceae) to make necklaces (Berlin and Prance 1978).

Change from Moreira et al. 2007 to Moreira and Fernandes 2007 correct? Recently, interest in galls has increased because of their potential uses as biological control agents for invasive plants and as bioindicators of environmental quality and health (Fernandes 1987; Julião et al. 2005; Moreira and Fernandes 2006) ernandes et al. 2010). Additionally, several authors have suggested that the interaction between plants and gall-forming insects is ideal for testing hypotheses about ecological relationships (Fernandes and Price 1988; Price 2003). Gall-forming insects present certain methodological advantages as model organisms, primarily due to their sessile habit. Gall-forming insect communities frequently include many species from different orders; galls are conspicuous structures that are persistent on the plant and can be easily observed and collected. Further, the interactions between the inducing insects and other organisms can be easily manipulated (Fernandes and Price 1988; Stone and Schönrogge 2003).

16.2 Herbivore Insect Guilds

Herbivorous or phytophagous insects are those that consume living parts of plants. They make up the largest portion of all extant species diversity. Nearly 50% of all herbivorous organisms are insects

(Gullan and Cranston 2005). Herbivorous insects are found in the orders Phasmatodea, Orthoptera, Thysanoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera, and Hymenoptera (Triplehorn and Johnson 2005).

Considering the great diversity of species, different classifications can be used to differentiate the forms of use and distributions of insects and their host plants. In most cases, these classifications are useful only for didactic purposes because they do not encompass the full range of interactions among the organisms or because the different classes of interactions are not precisely delimited. Herbivorous insects can be grouped in terms of the variation in the number of host plants they utilize. Monophagous insects utilize a single plant taxon; oligophagous insects utilize a few plant taxa that are usually phylogenetically related (i.e., from the same genus or family); and polyphagous insects utilize a wide variety of host plant species that are not phylogenetically related (Price 1997).

Insects can also be separated into functional groups according to the type and form of utilization of a particular resource. These groups are called guilds (Root 1967); that is, they consist of species that exploit the same food class (or other type of resource) in a similar way. The species within a guild may or may not be phylogenetically related (generally, they are not). Herbivorous insects are divided into five principal guilds: chewers, suckers, miners, drillers, and gall makers (Price 1997). Chewers and suckers feed externally on the host plant and are therefore called free-living or exophytic herbivorous insects. Chewers possess mouthparts that are specialized for chewing and consume tissues from roots, stems, leaves, flowers, and fruits. They belong to the orders Orthoptera (grasshoppers, crickets), Coleoptera (beetles, weevils), Lepidoptera (butterflies and moths), and Hymenoptera (wasps). Sucking insects possess mouthparts that are modified to consume sap from plant vessels or the liquid contents of plant cells. These insects can feed on xylem sap, which is found in the xylem vessels (cells that carry nutrients and mineral salts from the soil to the plant); on phloem sap, which is found in phloem sieve tubes (cells that distribute carbohydrates and amino acids throughout the plant); or on the intracellular contents of vegetative cells in various organs of the host plant. Sucking insects are found in the order Hemiptera (true bugs, leafhoppers, and aphids; see Chapters 13 and 20). Many chewing and sucking insects are specialized feeders on seeds, which are nutrient-rich compared with other plant tissues. These insects are commonly referred to as seed predators. Seed-predating insects are found in the orders Hymenoptera, Coleoptera, Hemiptera, and Lepidoptera. Among coleopteran seed predators, members of the subfamily Bruchinae (Chrysomelidae), which mainly attack plant species from the family Fabaceae, are particularly important (see Chapter 14).

The three remaining guilds (miners, drillers, and gall makers) consist of insects whose larvae feed internally on plant tissues. Therefore, they are called endophytic insects. Mining insects are those whose larvae live in and feed on plant tissue between the epidermal layers (Dempewolf 2005). According to this definition, miners generally feed on parenchyma in leaves, fruits, and the cortex of branches but do not include insects that feed on pith or deep tissues. As a mining insect feeds, it forms a characteristic, externally visible tunnel called a mine, which often appears as a whitish track on the leaf. Mines are canals formed by insects feeding inside the parenchyma or epidermal tissue of a plant whose external walls remain intact. These canals can assume a variety of shapes depending on the species involved (DeClerck and Shorthouse 1985). The tissue that is most often consumed is the palisade parenchyma in the mesophyll, but many species preferentially consume other types of tissue (DeClerck and Shorthouse 1985). Mining insects are found in the orders Lepidoptera, Hymenoptera, Coleoptera, and Diptera (flies, midges) (Dempewolf 2005).

Drilling insects are differentiated from gall-making insects because they do not induce the formation of modified tissues, and from mining insects because they live and feed deeper within the plant tissue, forming cavities called galleries. Drilling insects can feed on living or dead tissue. Galleries are most often formed in stems but can also be formed in flower buds, roots, fruits, and seeds. Drilling insects are found in the orders Coleoptera, Lepidoptera, and Hymenoptera (Coulson and Witter 1984).

Gall makers are highly abundant, but their ecology and taxonomy remain poorly known; most gallforming species have been described relatively recently or remain undescribed (Espírito-Santo and Fernandes 2007). In general, gall-forming insects are defined as herbivorous insects that, to complete their life cycles, obligatorily induce pathological modifications in the tissue of their host plants (galls). The interaction between the insect and the host plant results in hypertrophy and/or hyperplasia of



FIGURE 16.2 Orders of insects with gall-inducing species. (a) Gall induced by a Diptera: Cecidomyiidae (*Paradasineura admirabilis* Maia) in the host plant *Erythroxylum suberosum* (Erythroxylaceae). (b) Gall induced by a Hemiptera: Psyllidae (*Baccharopelma dracunculifoliae* Burkhardt) in the host plant *Baccharis dracunculifolia* (Asteraceae). (c) Gall induced by a Lepidoptera (unknown species) in *Macairea radula* (Melastomataceae). (d) Gall induced by a Hymenoptera: Cynipidae (unknown species) in the host plant *Quercus turbinela* (Fagaceae). (e) Gall induced by a Thysanoptera (unknown species) in an unidentified the host plant. (f) Gall induced by a Coleoptera: Brentidae: Apioninae in the host plant *Diospyrus hispida* (Ebenaceae).

the plant tissue (Weis et al. 1988). Gall-forming insects are found in all orders of herbivorous insects (Hemiptera, Thysanoptera [thrips], Coleoptera, Hymenoptera, Lepidoptera, and Diptera), with the exception of Orthoptera (Figure 16.2).

16.3 Gall-Inducing Insect Taxa

Around 13,000 species of gall-inducing insects are known worldwide, representing about 2% of the total number of insect species (Dreger-Jauffret and Shorthouse 1992; Raman et al. 2005). However, recent estimates have extrapolated this value to nearly 120,000 species of gall-forming insects (Espírito-Santo and Fernandes 2007). The habit of inducing galls in plants has evolved independently several times among the phytophagous insects (Roskam 1992; Gullan et al. 2005), occurring in at least 51 families distributed in six different orders (Figure 16.3), and is found in all biogeographic regions. Still, some groups are more species-rich in some regions than in others. Because of the great diversity of gallforming insects and their host plants, and the great variability of the structures they form, we present some generalizations about the natural history, biology, and ecology of these organisms. More detailed information about each group can be found in a review by Raman et al. (2005).

16.3.1 Hemiptera

This citation is not listed in the References. Please check. The order Hemiptera contains a large number of gall-forming insects distributed in 11 families, principally in the suborder Sternorrhyncha (Schaefer 2005). Less than a dozen species of gall-inducing insects are found in the suborder Heteroptera, all of them in the family Tingidae (Schaefer 2005).

The superfamily Psylloidea includes around 3000 described species of gall-forming insects, which are found mainly in tropical and temperate regions of the southern hemisphere (especially in tropical Asia and the Australian region) (Gullan et al. 2005). This group remains poorly studied in tropical

1. Order Hemiptera 5. Order Lepidoptera Suborder Heteroptera Family Nepticulidae Family Tingidae Family Heliozelidae Suborder Sternorrhyncha Family Prodoxidae Family Psyllidae Family Cecidosidae Family Aleyrodidae Family Bucculatricidae Family Aphididae Family Gracillariidae Family Phylloxeridae Family Tponomeutidae Family Adeligidae Family Ypsolophidae Family Eriococcidae Family Glyphipterigidae Family Kermisidae Family Elachistidae Family Asterolecaniidae Family Oecophoridae Family Coccidae Family Coleophoridae Family Diapididae Family Cosmopterigidae 2. Order Thysanoptera Family Gelechiidae Suborder Tubulifera Family Sesiidae Family Phlaeotripidae Family Torticidae Suborder Terebrantia Family Alucitidae Family Thripidae Family Pterophoridae 3. Order Coleoptera Family Crambidae Suborder Polyphaga Family Thyrididae Family Cerambycidae 6. Order Diptera Family Chrysomelidae Suborder Nematocera Family Brentidae Family Cecidomyiidae Family Curculionidae Suborder Cyclorrhapha Family Buprestidae Family Tephritidae Family Mordellidae Family Chloropidae Family Nitidulidae Family Agromyzidae Family Scolytidae Family Anthomyzidae 4. Order Hymenoptera Family Clythiidae Suborder Symphyta Family Tenthredinidae Suborder Apocrita Family Agaonidae Family Pteromalidae Family Erytomidae Family Cynipidae

FIGURE 16.3 Families of gall-inducing insects are distributed into six different orders and found in all biogeographic regions.

areas, which probably contain the greatest species richness of gall-forming insects (Burckhardt 2005). Species in the superfamily Psylloidea induce galls of various shapes that are conspicuous in plant species from the families Asteraceae, Myrtaceae, Melastomataceae, Fabaceae, Lauraceae, Polygonaceae, Moraceae, and Salicaceae. For example, Ferreira et al. (1990) have described the biology and natural history of *Euphaleurus ostreoides* Crawford, which parasitizes a species of the family Fabaceae, while Lara and Fernandes (1994) and Espírito-Santo and Fernandes (2002) have described the natural history and ecology of *Baccharopelma dracunculifoliae* Burckhardt, which parasitizes *Baccharis dracunculifolia* (Asteraceae). Galls induced by species of the family Psylloidea are found in several plant genera, but they are particularly abundant in species of *Baccharis* (Burckhardt et al. 2004) and *Eucalyptus* (Burckhardt 2005).

The superfamily Coccoidea consists of plant parasites found in all biogeographic regions except the polar regions. They are classified into nearly 20 families, among which 230 gall-forming species (3% of known coccoidean species) are found in 10 families (Gullan et al. 2005). Coccoidean insects induce galls in 20 angiosperm families, principally in Myrtaceae (around 130 species), Fagaceae, Asteraceae, Ericaceae, and Verbenaceae. Records of galls formed by species of Coccoidea are rare in the Neotropics, although Gonçalves et al. (2005, 2009) have presented some biological and anatomical aspects of galls induced by Pseudotectococcus rolliniae Hodgson and Gonçalves (Eriococcidae) in Rollinia laurifolia (Annonaceae).

The superfamily Aphidoidea includes around 440 species of gall-forming aphids (Wool 2004). They exhibit complex life cycles, alternating between primary and secondary hosts and entering into sexual and parthenogenetic reproduction (holocycle). Each gall is induced by a single individual, the founder, which reproduces by parthenogenesis (Wool 2005). Thus, every individual within a gall is genetically identical. The individual insects within a gall obtain their food by sucking phloem contents from the vascular system of the plant inside the gall, but they are not capable of inducing gall formation. The number of nymphs per gall is highly variable but can reach thousands. For example, the host plant Rhus glabra (Anacardiaceae) can abscise its leaves in response to the galls induced by Melaphis rhois Ficht (Aphididae), which can contain more than 1700 nymphs in a single chamber (Fernandes et al. 1999).

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16.3.2 Thysanoptera

The order Thysanoptera includes about 5500 species distributed in nine families, but gall-forming species are found mainly in the subfamily Phlaeothripinae (Mound and Morris 2005). Gall-inducing This citation is not listed in the Thysanopteran species are found in all biogeographic regions, especially in tropical Asia and the References. Please check. Australian region (Mound and Morris 2005). These insects live in colonies formed by multiple individuals. It is common to find more than one species associated with a single gall, thus making it difficult to determine the species responsible for inducing the gall. The galls are formed mainly on leaves, in flowers, or in fruits. Records of galls formed by species in the order Thysanoptera are rare in the Neotropics (Souza et al. 2000), although they are common in some species of the Brazilian Cerrado biome (GWF, personal observation).

16.3.3 Coleoptera

There are few gall-forming coleopteran species relative to the high species richness of beetles associated with plants. Gall-forming beetles are found mainly in the family Curculionidae. The habit of inducing galls is found exclusively in the derived superfamilies Chrysomeloidea and Curculionoidea. In these groups, the larvae are more sedentary, with reduced sensory (ocelli and antennae) and locomotor (legs) This citation is abilities, and present a lack of pigmentation on the body (Korotyaev et al. 2005).

Beetle larvae possess chewing mouthparts and cause considerable structural damage within galls, References. Please check resulting in the rapid destruction of the tissues in contact with the larvae (Dreger-Jauffret and Shorthouse 1992). Galls induced by coleopterans can be recognized by the presence of large internal chambers. There may be one or multiple chambers within each gall, generally hosting only one larva per chamber. The pupal phase may occur inside the gall or in the soil; in the latter case, the larva pierces the wall of the gall and reaches the soil to initiate the pupal phase. The galls are primarily induced on branches and roots, but some insects from the superfamily Curculionoidea induce galls in leaves and flowers (Korotyaev et al. 2005). Galls induced by coleopterans vary from simple tumescences to structures that look like fruits, which are very different from the healthy organs of the plant (Souza et al. 1998; Korotyaev et al. 2005). There is no differentiation of nutritive tissue. Coleopterans induce galls in various plant families, including Asteraceae, Solanaceae, Brassicaceae, and Fabaceae. For example, Collabismus clitellae Boheman induces globular galls on the stems of Solanum lycocarpum (Solanaceae) in the cerrado (Souza et al. 1998, 2001), while Apion sp. (Brentidae) induces galls in sprouts of Diospyros hispida (Ebenaceae) (Araújo et al. 1995; Souza et al. 2006). In the Brazilian Cerrado biome, coleopteran galls are frequently used by large ant communities as shelter and for nest building (Craig et al. 1991; Araújo et al. 1995).

374

16.3.4 Hymenoptera

Along with the order Diptera, the order Hymenoptera presents the most complex entomogenous galls. Gall-inducing species of the order Hymenoptera are distributed into five families (Tenthredinidae, Cynipidae, Agaonidae, Tanaostigmatidae, and Eurytomidae) and are found in all biogeographic regions (Dreger-Jauffret and Shorthouse 1992; Stone et al. 2002).

The family Tenthredinidae (suborder Symphyta) consists of species that are primitively phytophagous. Their larvae are adapted to utilize a variety of resources, feeding externally or internally on plant tissues from branches, leaves, and fruits (Gauld and Bolton 1988). The distribution of gall-inducing species is restricted to the Northern Hemisphere, with records in the Palearctic, Nearctic, and Oriental regions (Roininen et al. 2005). Most wasps of the family Tenthredinidae are species specific; a few exceptions are known to induce galls in a few related host plant species. These wasps induce galls in leaves, branches, and flower buds in 11 genera in five angiosperm families (Salicaceae, Rosaceae, Caprifoliaceae, and Grossulariaceae) and one gymnosperm family (Pinaceae) (Price 2003).

There is an extensive literature concerning the biology and ecology of gall-inducing species that parasitize the genus *Salix* (Price 2003). Prominent among these insects are members of the family Cynipidae, which includes 1000 species in 41 genera that are mainly found in the Northern Hemisphere (Ronquist 1995; Liljeblad and Ronquist 1998). The largest number of known species occurs in the Nearctic region, particularly in Mexico, where 700 species of wasps in 29 genera are estimated to occur (Ronquist 1995; Liljeblad and Ronquist 1998). Species from the family Cynipidae are found on all continents except Australia. In terms of number of gall-forming species, this family is exceeded only by the family Cecidomyiidae; however, these families are equal in terms of their complexity and the great variety of families of host plants that they parasitize, especially Fagaceae, Fabaceae, Rosaceae, and Aceraceae (Csóka et al. 2005).

Chalcidoidea is a large superfamily of parasitoid wasps that attack numerous hosts. More than 20,000 species are known (Noyes 2002, 2003). Gall-inducing species in this superfamily are found in six families: Agaonidae, Eulophidae, Eurytomidae, Pteromalidae, Tanaostigmatidae, and Torymidae (La Salle 2005). Here, we comment on some aspects of the biology of the three largest families within the Neotropical region.

Wasps belonging to the family Agaonidae (Hymenoptera: Chalcidoidea) include many species that are intimately associated with the inflorescences of species of the genus *Ficus* (Moraceae) (Galil and Eisikowitch 1968; Wiebes 1979; Weiblen 2002). Species of the family Agaonidae can induce galls internally, penetrating figs as their pollinators, or externally (Kerdelhué et al. 2000; Kjellberg et al. 2005). This family contains more than 900 species and is found in tropical regions (Price 1997). The intimate and specific interactions between species of the family Agaonidae and their host plants may represent one of the clearest example of coevolution.

Tanaostigmatidae is a small family of wasps with a principally Neotropical distribution. Currently 92 species are known in nine genera worldwide (La Salle 2005). The great majority of species in this family induce galls or are to be in galls induced by other insects (Hardwick et al. 2005; La Salle 2005). These wasps induce galls in oushes and trees of the families Fabaceae, Polygonaceae, Lecythidaceae, and Rhamnaceae (La Salle 1987, 2005). Fernandes et al. (1987) have recorded the first occurrence of term behavior in a species of this family in galls induced by a species of *Anadiplosis* (Diptera: Cecidomyiidae) on the legume *Machaerium aculeatum*.

The family Eurytomidae includes 1420 described species in 87 genera (Noyes 2002). Species of this family include parasitoid species, phytophagous species, gall-inducing species and terms of galls. The gall-forming species are united in the subfamily Eurytominae. Galls are induced in species of the families Myrtaceae, Campanulaceae, Boraginaceae, Orchidaceae, and Pinaceae (2005). The number of galls induced by species in this family is likely to increase in tropical regions as more studies are conducted (Leite et al. 2007).

16.3.5 Lepidoptera

About 180 species of gall-forming lepidopterans have been identified. These insects parasitize members of 20 plant families. The lepidopteran families with the largest numbers of species are Gelechiidae and

Tortricidae (47 and 39 species, respectively). Gall-forming lepidopteran species occur in all biogeographic regions (Miller 2005).

Because of their feeding habits and chewing mouthparts, the larvae rapidly destroy tissues with which they come into contact. Lipid-rich nutritive tissues were detected in several lepidopteran galls by Vecchi (2004). Most galls formed by lepidopteran insects contain a single chamber hosting a single larva. The galls are induced by the larvae, except in the species *Heliozela staneella* Fischer Von Röslerstamm (Heliozelidae), in which the female injects a gall-inducing substance during oviposition (Miller 2005). In addition to the identification of immature individuals, galls from species of Lepidoptera can be recognized by the large quantity of feces left by the larva.

Galls formed by lepidopteran species present a great variety of shapes, from simple tumescences to more complex structures that appear similar to fruits, which are very different from the healthy organs of the plant (Dreger-Jauffret and Shorthouse 1992). Galls are predominantly induced in the branches, although they also commonly develop in leaves of Melastomataceae (Gonçalves-Alvim et al. 1999). Lepidopteran species induce galls in at least 41 families of host plants, especially Asteraceae, Salicaceae, and Fabaceae (Miller 2005).

16.3.6 Diptera

Gall-forming species in the order Diptera occur in seven families, but mainly in the families Cecidomyiidae and Tephritidae. Species of the family Cecidomyiidae are the most important gallforming insects and are widely distributed in all biogeographic regions, with 5451 described species in 598 genera (Gagné 2004). Their total number may exceed 100,000 species (Espírito-Santo and Fernandes 2007). Most of the species belonging to this family are associated with plants, inducing galls or living as termine therein, while a few species are predatory (Gagné 1994). Species of the subfamily Porrycondimine feed on fungi, a condition considered ancestral with respect to the habit of inducing galls (Gagné 1994). Some species can induce galls in related plant species of the same genus or family. The existence of polyphagous species (using host plants from different families) is rare in the family Cecidomyiidae. Members of this family are particularly species-rich in certain plant families and genera, depending on the biogeographic region. In the Neotropical and Nearctic regions, they are most diverse in host plants from the genera Baccharis and Solidago (Asteraceae), respectively (Gagné 1989; Fernandes et al. 1996). In the Neotropical region, they are less numerous, with 500 species and 170 genera recorded (Maia 2005). In Brazil, 159 species and 75 genera have been described (Maia 2005). Many species described from Brazil are found in the restinga vegetation (a community characterized by shrubs and low forests growing on sandy dunes) in the state of Rio de Janeiro (Maia 2001a,b), where 95 species and 47 genera have been recorded (Maia 2005). However, records of species from the family Cecidomyiidae have increased considerably in recent years (Maia and Fernandes 2004, 2006).

This citation is not listed in the References. Please check Approximately 5% of the 4300 described species in the family Tephritidae are gall inducers, the majority of which belong to the subfamily Tephritinae (Friend 1998; Korneyev et al. 2005). The galls are induced principally in branches, flowers, leaves, and roots. More than 90% of the galls known to be induced by members of this family occur in host plants of the family Asteraceae (Freiberg 1998). For example, *Tomoplagia rudolphi* (Lutz & Lima) forms galls in *Vernonia policipes* (Asteraceae), which is widely distributed in southeastern Brazil (Silva et al. 1996). The families melastomataceae, Aquifoliaceae, Acanthaceae, Fabaceae, and Onagraceae are also attacked by gall-forming species of this family.

Gall-forming insects of the family Chloropidae are apparently restricted to host plants of the family Poaceae, except for species of a genus that induce galls in species of the genus *Scirpus* (family Cyperaceae) (Dreger-Jauffret and Shorthouse 1992). As in other gall-forming cyclorrhaphan dipterans, the gall-forming process is not initiated at oviposition. The eggs are laid externally on branches or on the leaf surface. After hatching, the larva actively penetrates the branch, opening a hole with its mouthparts (Bruyn 2005). Once inside the branch, the larva begins to feed on the leaves that surround the meristem. Although the family is widely distributed, studies on gall-making species of Chloropidae are concentrated in the Palearctic and Nearctic regions.

16.4 Host Plant Taxa

Vascular plants, including gymnosperms (mainly conifers) and angiosperms, are the main hosts of gallforming arthropods. In general, flowering plants (angiosperms) host more species of gall-forming insects. For example, in Brazil, plant families that are associated with a large number of gall-forming insects include Asteraceae, Myrtaceae, Malpighiaceae, Fabaceae, Rubiaceae, and Bignoniaceae (Fernandes 1987, 1992; Fernandes et al. 1988, 1996, 1997; Julião et al. 2002; Maia 2001b; Maia and Fernandes 2004). In one area of the Brazilian Cerrado, in Minas Gerais, the families Fabaceae, Myrtaceae, Malpighiaceae, Bignoniaceae, and Malvaceae accounted for 65% of the host plant species and hosted 70% of the gallforming insect species (Gonçalves-Alvim and Fernandes 2001a,b). However, a brief analysis indicates substantial variation among biomes in the frequency of families attacked by gall-forming insects. This variation may be explained by the relative frequency of occurrence of the plant families. Broader studies across all Brazilian biomes are needed to better understand these patterns.

The species richness of gall-forming insects varies widely across biogeographic regions, and galls occur much more frequently in certain plant taxa. Species of the genus Baccharis (Fernandes et al. 1996), for example, have a large number of associated insect species (Table 16.1). In the region of Ouro Preto, Baccharis pseudomyriocephala (Figure 16.4) hosts 11 species of gall-forming organisms (Araújo et al. 2003). In addition to Baccharis, species of Copaifera (Neotropical region; GWF, personal observation; Oliveira et al. 2008), Solidago, and Chrysothamnus (Neartic region; GWF, personal observation; Gagné 1994, Fernandes 1992) are rich in species of Cecidomyiidae; species of Quercus and Rosa (Nearctic region) and Acacia (Ethiopic region) are rich in species of Cynipidae (Shorthouse and Rohfritsch 1992; Stone et al. 2002); and species of *Eucalyptus* (Australian region) are rich in species of Chalcidoidea and Coccoidea (Blanche 1994). In the Sonoran desert, Atriplex, Chrysothamnus, and Larrea host a high diversity of gall-forming insects (McArthur 1986; McArthur et al. 1979; Fernandes and Price 1988; Waring and Price 1990). These data indicate the existence of super-hosts, that is, host plant taxa that sustain a large number of associated gall-forming insects (Fernandes and Price 1988; Veldtman and McGeoch 2003; Espírito-Santo et al. 2007). This conclusion is supported by the fact that few host plant taxa support a large number of insect species, independently of the sampling method (Hawkins and Compton 1992). However, the ecological mechanisms and selective pressures that influence these patterns within certain taxa remain unexplained or have not been adequately studied.

16.5 Location and Choice of the Host Plant

The free-living stage (adult stage) of gall-inducing insects is very short compared with the time they spend immersed in host plant tissues. In some cases, the larval stage may take several months. However, the adult stage is of extreme importance as it is at this stage of their life cycle that the galling herbivores must find their appropriate host plants and organs within all the available options. This is not an easy task as all plants may present a mosaic of resistance mechanisms to defend themselves against unbidden guests. The most studied ones are the physical and chemical defenses. Physical defenses include several types of trichomes that impair movement or even trap the adults, and tissue sclerophylly, which confer resistance to oviposition and feeding (Woodman and Fernandes 1991; Fernandes 1994; Lucas et al. 2000; Chen 2008). Further, as pointed out by Rasmann and Agrawal (2009), plant defenses are dependent on its genetics, ontogenesis, and also on environmental factors. Together, these features shape the multivariate defensive phenotype and outcome of the interaction. Also, the chemical defenses include the synthesis and accumulation of secondary metabolites (Gottlieb et al. 1996; Cheng et al. 2007). By the time the host This citation is the plant and organ are found, a succession of recognizing systems between both organisms are required to References. Please check. permit gall development (Rohfritse P2). However, the elucidation of the plant's response to herbivore attack is much complex for it is difficult to establish the relevance of a particular trait for the interaction (Rasmann and Agrawal 2009).

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For galling herbivores, host selection is vital because it is the offspring that stays most of their lifetime inside the host plant tissues, and most defenses are against the larval stage. On the basis of the crucial

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Number of Galling Species on Species of the Genus Baccharis

Host Plants	Galling Richness
Baccharis aphylla	1
Baccharis artemisioides	1
Baccharis bogotensis	2
Baccharis boyacensis	1
Baccharis capitalensis	1
Baccharis cf. bacchridastrum cabr.	1
Baccharis concinna	15
Baccharis confertifolia	1
Baccharis coridifolia	2
Baccharis dracunculifolia	17
Baccharis effusaaphylla	1
Baccharis elaegnoides	1
Baccharis eupatorioides	3
Baccharis genistelloides	1
Baccharis glutinosa	1
Baccharis latifolia	5
Baccharis lineares	1
Baccharis macrantha	2
Baccharis microphylla	1
Baccharis myrsinites	1
Baccharis nitida	2
Baccharis paucidentata	2
Baccharis platypoda	3
Baccharis poeppigiana	1
Baccharis prunifolia	1
Baccharis pseudomyriocephala	11 ^a
Baccharis rosmarinifolia	7
Baccharis salicifolia	13
Baccharis schultzii	2
Baccharis serrulata	4
Baccharis spartioides	2
Baccharis subulata	2
Baccharis tricuneata	1
Baccharis trimera	1
Baccharis trinervis	2
Baccharis vulnerave	1
Total	125

^a Fernandes G. W., et al., Trop. Zool., 9, 315, 1996; Araújo, A. P. A., et al., Rev. Bras. Entomol., 47, 483, 2003.





events required to gall establishment, Moura et al. (2009) showed that the absence of *Aceria lantanae* (Acari) galls on sympatric varieties of *Lantana camara* (Verbenaceae) that present pink and white flowers could be related to their chemical contents and density of trichomes, which constitute part of the first line of resistance to herbivores, in general (Levin 1973, Woodman and Fernandes 1991, Lucas et al. 2000). Phytochemical profiles showed differences that could explain the selection of the group with red flowers as the host plants by the mite.

16.6 Gall Morphology

Galls can be formed on any organ of the host plant; nevertheless, the leaf is the most susceptible of the plant organs for the development of galls, and relatively few galls occur on branches, vegetative parts, or floral buds (Dreger-Jauffret and Shorthouse 1992). Although galls on fruits are not so numerous as

galls on vegetative organs, they are interesting models to study sink and source relationships and of phenological synchronism. As an example, there is an unidentified species of wasp that oviposits through the pericarp of immature fruits of *Eugenia uniflora*. The mature galls are multichambered and no seeds develop, which constitute a serious damage to the host plant reproduction (Figure 16.5). There must be a synchronism between the life cycles of the wasp and the reproductive phase of *E. uniflora*; otherwise, the gall-inducing organism life cycle should be interrupted. Dorchin et al. (2006) affirm that the phenology and position of the gall on its host plant influence its ability to compete with other sinks. By the size and number of insects inside the galls on the fruits of *E. uniflora*, this affirmation seems to fit this system. In a Cerrado (savanna) vegetation reserve in Minas Gerais (Brazil), about 60% of the insect galls are formed on the leaves (Gonçalves-Alvim and Fernandes 2001a,b). In vegetation of rupestrian fields, the percentage of galls on the leaves was also similar, while in another Cerrado formation in Serra of San José, 70% of the galls were induced on leaves (Maia and Fernandes 2004). However, ratios may change as scale changes. For instance, in *Baccharis concinna*, *B. pseudomyriocephala*, and *B. dracunculifolia* most galls develop on stems (Fernandes et al. 1996; Araújo et al. 2003).

This citation is not listed in the References. Please check. Morphological, biochemical, and phylogenetic studies on aphids (Stern 1995), cynipids (Stone and Cook 1998), sawflies (Nyman (1, 2000), and thrips (Crespi and Worobey 1998) support the idea that the morphology of the gall is defined by the inducing insect and not by the host plant. Thus, the gall may be understood as an extended phenotype (sensu Dawkins 1982) of the inducing insect (Weis et al. 1988; Bailey et al. 2009). Besides the morphology, the inducing insect is also capable of controlling



FIGURE 16.5 Galls induced by an unidentified species of Hymenoptera in fruits of *Eugenia uniflora* L. (Myrtaceae). (a) Immature non-galled fruit. (b) Immature fruit opened to show sites of oviposition through pericarp (arrow). (c) Detail of oviposition site (arrows). (d) Mature multichambered gall. (e) Detail of two larval chambers with insect's excrement. (Photos courtesy of R. M. S. Isaias.)

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the chemical properties of the galls (Nyman and Julkunen-Tiito 2000), which may be regulated by the feeding activity of the insect, indicating that gall development depends on the behavior of its inducing insect. Insects that feed moving in a circle should produce round galls; insects that feed at one end of the gall (usually at the base) produce conical galls; while in lenticular galls, insects feed in the lateral margins (Rohfritsch and Shorthouse 1982). Thus, it is reasonable to assume that the gall has a function or adaptive significance for the inducing insect (see Price et al. 1986, 1987). The shape of the gall seems to be independent of the host plant, but as it is completely formed of plant tissues, its development must obey some constraints imposed by the cycle of the host plant cells at the site of oviposition. The gall is a phenotypic entity that represents the interaction between the genotype of the insect, that of the host plant, and the environment (Weis et al. 1988). Since most aspects of gall morphology are controlled by the galling insects, it is clear that the size and shape of the gall is crucial for their survival. Thus, if gall morphology results in differential survivorship, and the insect population shows a heritable variation in the ability of setting this feature, then the selection can act on it.

One of the best-studied galling insects is *Eurosta solidaginis* Fitch (Tephritidae), which induces galls on Solidago altissima (Asteraceae) and a few related species (Abrahamson and Weis 1997). In this system, gall size is important for the survival of the insect, although the genotype of the host plant has an important role in determining the characteristics of the gall. The variation in this gall morphology is explained by the genotype of the inducing insect. Thus, this system has proved that gall morphology should be understood as the extended phenotype of the insect and adaptive explanations can be related to the fitness of the insect.

16.7 Gall Anatomy and Physiology

The complexity in the structure of galls may vary by several degrees. The galls may vary from simple and isolated cytological transformations to a new arrangement of plant tissues. In these cases, the galls may be defined as new multicellular organs generated by coordinated cell division and expansion. The variation in morphological complexity is also followed by a variety of physiological traits.

In general, the galls induced by Cecidomyiidae and Cynipidae are the best studied from the structural point of view. The Cynipidae galls have two cortical regions, the inner cortex formed by a multilayered nutritive tissue located around the larval chamber and the outer cortex with a reserve tissue externally delimited by the epidermis. In some galls, the outer cortex is limited from the inner one by a thin layer of sclerenchyma. In fact, the high diversity of the outer cortex is said to be responsible for the great variety of gall morphotypes (Stone et al. 2002). Also, the number of larvae or nymphs per chamber may vary from one to hundreds, and may also be responsible for variations in the final size and shape of galls. Therefore, galling insects do not only control the developmental patterns of the host plant, so as to define the gall phenotype, but also its physiology. Moura et al (2009) studied the ontogenesis of galls induced This citation is by an Acari and proposed that the cell divisions alter the leaf pattern first related to photosynthesis, and References. result in a new vertucous structure that guarantee an adequate microenvironment and nutrition source. This is also true for the majority of the gall morphotypes, from the simplest ones to the most complex.

That galls are sinks of photoassimilates is common sense (Larson and Whitham 1991; Larson 1998; Dorchin et al. 2006). Lemos Filho et al. (2007) presented data on the transpiration and photosynthetic performance in galls of two species on Aspidosperma (Apocynaceae) from southeast Brazil. These data showed that gall induction did not affect the photosystem II, and consequently there was no reduction of the relative electron transport rates. By establishing a relationship between the physiological and morphological features of the two gall systems, they concluded that the galls may produce photoassimilates, but in such low values that it seems improbable that they could guarantee gall maintenance without draining resources from their host organ. Another important feature are the physiological gradients inside and outside the gall tissues (Bronner 1992; Hartley 1998; Nyman and Julkunen-Tiito 2000). These gradients have revealed specific enzymatic activities and are also accompanied by cytological peculiarities (Rehill and Schultz 2003; Oliveira and Isaias 2010a,b; Oliveira et al. 2010). The galls function as sinks of nutrients mobilized from the other host plant parts (Kirst and Rapp 1974; Fay et al. 1993; Whitham 1992). A large set of evidences support that the galling insect is able to manipulate the host plant, inducing the formation

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This citation is not listed in the References. Please check. of nutritionally superior cells in comparison to the other healthy plant tissues, the nutritive tissue (Mani 1964; Shannon and Brewer 1980; Bronner 1992; Rohfritsch and Sharingh enzymatic activity, including phosphatases, proteases, and aminopeptidases rich in RNA and ribosomal RNA of the nucleolus (Bronner 1992). On the other hand, the parenchyma cells of the outer cortex form a reserve tissue characterized by a high concentration of starch, low concentration of lipids and glucose, and low enzyme activity. As the larva feeds on the cells of the nutritive tissue, there is a replacement of substances by the cells of the reserve tissue (Bronner 1992). The translocation of substances between the two tissue zones has been proven to need an intense enzymatic activity (Bronner 1992; Oliveira and Isaias 2010b; Oliveira et al. 2010). Also, the substances accumulated may be diverse, such as proteins, carbohydrates, and lipids (Figure 16.6).



FIGURE 16.6Histochemistry of galls. Flavonoid derivatives detected with 3,3'-diaminobenzidine in Calliandra brevipes
Benth: (a) non-galled stem; (b) stem gall. Machaerium uncinatum (Vell.) Benth: (c-d) Phenolic derivatives detected by fer-
ric chloride in leaf galls; (e) lipids detected by Sudan Red B in cell wall and cuticle. (f) M. hirtum (Vell.) Stellfeld. Proteins
detected by Coomassie blue in leaf galls. (g-i) Leaf galls of M. aculeatum Raddi. (g) Proteins detected by Coomassie blue.
(H) Starch detected by Lugol's reagent. (i) Carbohydrates detected by PAS. (Photos courtesy of R. M. S. Isaias.)

Once the starch that accumulated in the reserve tissue cannot be directly used either for the gallinducing larva or for the gall machinery, carbohydrate conversion is necessary. Oliveira et al. (2010c) detected the activity of the glucose-6-phosphatase, an enzyme responsible for the synthesis of intermediate compounds before the formation of sucrose in galls of Cecidomyiidae. Also, these authors detected a gradient of invertases, generally related to physiological sinks (Koch and Zeng 2002; Rehill and Schultz 2003), that fit the gradient of starch and sugars, and should provide resources to cell expansion and to the metabolism of the nutritive tissue. The detection of sucrose synthase was related to the maturation and formation of reserve tissues in gall systems. Thus, enzymatic gradients play key roles in maintaining the supply of nutrients for the developing galling larva (Bronner 1992), and also function in the maintenance of gall structure.

This citation is not listed in the References. Please check. The nutritive tissue does not present defensive secondary compounds (Hartley and Lawton 1992; Hartley 1998; Nyman and Julkunen-Tiito 2000), which may be detected in the outer cortical layers (Figure 16.6). Studies in galls induced by sawflies on willow (*Salix* spp.) showed that toxins are commonly accumulated in the outer cortex, suggesting that the insect can benefit from their defensive properties against other insects (Nyman and Julkunen-Tiito 2000). These substances may have negative effects on the growth, development, or survival of another organisms (Wittstock and Gershenzon 2002), such as the natural enemies. In galls, the role of defense against natural enemies has been commonly attributed to phenolics. However, Formiga et al. (2009) did not find any relationship between the level of phenolics in *Aspidosperma spruceanum* and the degree of gall infestation by a galling Cecidomyiidae. Moreover, Abrahamson et al. (1991) affirmed that higher phenolic concentrations restricted to the gall tissues induced by *E. solidaginis* on *S. altissima* could also potentially play a role in gall formation by influencing the hormonal control of growth. Thus, the influence of phenolics in host plant–galling herbivore systems seems to be much more complex than just constitutive chemical defense.

In Brazil, few studies on the chemistry of galls have been developed, but the chemical analysis in a Lepidoptera-Tibouchina pulchra (Melastomataceae) system showed that defensive compounds were less abundant in the nutritive tissue, and more frequent in the outer cortex of the gall, corroborating the general premise. Moreover, carbohydrates and lipids were more abundant in the tissues of the gall than in the non-galled tissues of the host plant (Motta et al. 2005). However, in some galls, such as those induced by few species of Cecidomyiidae, there is no formation of a nutritive tissue (Bronner 1992). In these cases, two types of feeding strategies can be identified. The larvae feed directly from the contents of the cells (Gagné 1994) or from hyphae of fungi that line the larval chamber (Bronner 1992). This is the case of the ambrosia galls induced by three tribes of Cecidomyiidae: Asphondyliini, Alycaulini, and Lasiopterini (Meyer 1987; Yukawa and Rohfritsch 2005). The ambrosia galls received this name in reference to the similarities in food habits of these Cecidomyiidae and the ambrosia beetles (Meyer 1987). The hyphae of fungi are introduced into plant tissues during oviposition of the Asphondyliini, or by the first instar larvae in Alycaulini and Lasiopterini (Yukawa and Rohfritsch 2005). Up to the moment, ambrosia galls were found in B. concinna, B. dracunculifolia (Arduin and Kraus 2001), and in Bauhinia brevipes (Sá et al. 2009) in Brazil. These galls do not differ in external morphology from the galls where no association with fungi was detected.

16.8 Gall Development

The development of galls has four distinct phases: induction, growth and differentiation, maturation, and dehiscence (Dreger-Jauffret and Shorthouse 1992; Arduin et al. 2005). The induction phase is characterized by a sequence of events that define the recognition of the oviposition site (tissue, organ, and host plant), and the behavior of the inducing insect. It is a critical stage, and events during oviposition and/or feeding promote crucial changes in the tissues of the host plant. Generally, the galling larvae require a reactive, meristematic tissue for the formation of galls (Mani 1964; Weis et al. 1988; Dreger-Jauffret and Shorthouse 1992); however, there are cases of gall induction on non-meristematic tissues, as in the ambrosia galls on *B. concinna* and *B. dracunculifolia* (Arduin and Kraus 2001). Also, some insects may induce galls on immature or mature tissues, and in these cases, the mature galls

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not listed in the References. may present anatomical and developmental features with distinct adaptive values (Oliveira and Isaias 2009). As a whole, the galling insect manipulates the potentialities of the host plant tissue to its own benefit. It conquers nutrition, protection, and an adequate microenvironment by generating patterns of cell redifferentiation (see Price et al. 1987). Moura et al. (2009) and Oliveira and Isaias (2010a) presented some ontogenetical analyses of gall development since the host leaf in its meristematic stage until gall maturation. These studies showed the correspondence of the tissue fates in non-galled organs and in galls of *L. camara* (Verbenaceae) and *Copaifera langsdorffii* (Fabaceae), respectively. Comparing these two gall systems, it is possible to set the ground meristem as the most plastic of the leaf tissues, capable of assuming several fates other than its primary one, the photosynthetic cells. In galls, the cells that originated from the ground meristem are redifferentiated into nutritive, protective, and also reserve tissues.

As the molecular mechanisms of gall induction and development remain mostly unknown about galls induced by insects, there is a great debate about the role of the insect and the host plant in the formation of the gall. In general, the gall-inducing stimuli originate during the feeding of the first instar larvae and more rarely during oviposition (body fluids of the female or the egg). In some groups, the role of the feeding activity of the larvae may have greater or lesser participation in gall development. For example, in Tenthredinidae, gall induction is initiated by the produced fluids of the accessory glands of the female reproductive system, injected into plant together with the eggs during oviposition (Meyer 1987). In the galls of Cynipidae, the induction process may have its origin in the fluids of the female egg or the larva (Bronner 1973; Rohfritsch and Shorthouse 1982). In Coleoptera, the galls can be induced by the larvae (e.g., Buprestidae) or during oviposition, when the eggs are laid in a cavity prepared by the female (Korotyaev et al. 2005). In some hemipteran galls, that is, Psylloidea (Burckhardt 2005) and Coccoidea (Gullan et al. 2005), the galls are usually initiated by the feeding activity of the first instars. In the galls induced by P. rolliniae (Eriococcidae) on R. laurifolia (Annonaceae), the second instar nymph induces sexually dimorphic galls (Gonçalves et al. 2005). Moreover, this species of Eriococcidae induces a stem gall for diapause to survive in the period when leaves of the host are shed (Gonçalves et al. 2009). Even though some new strategies of survival have been reported for Neotropical galling insects, the exact mechanism of the manipulation of host plant tissues remains unknown. There is evidence that the feeding action of aphids through the vascular system of the plant alters hormones and may be responsible for the initiation of the galls (Wool 2005). In Thysanoptera, gall formation is the result of the feeding activity of insects. By feeding on the plant cell content, one at a time, these insects alter the course of leaf expansion; the lamina becomes distorted because of distinct sites of hypoplasia and hyperplasia (Souza et al. 2000), and groups of necrotic cells (Mound and Arris 2005). In the case of the Thysanoptera, the epidermal or mesophyll cells near the feeding sites (Anathtakrishnan and Raman 1989) are stimulated by an unknown mechanism (Mound and Kranz 1997) to return to their meristematic potentialities and

The complexity of the gall systems may be higher when a third organism participate in the formation of the gall, as in the galls of ambrosia, or when the gall morphology is modified by inquilines and parasitoids, as is the case of many Cynipidae (Stone et al. 2002) and few Cecidomyiids (e.g., Fernandes et al. 1987). An example of this phenotype alteration was reported in the galls of *Anadiplosis* sp. whose larvae are parasitized by two plastygasterids, two eurytomids, and a tanaostigmatid (Hymenoptera). Galls due to this last parasitoid are distinguished from the others by their consistency, larger size, and different shape (Fernandes et al. 1987). If it is common sense that the maintenance of gall development and its final size and shape are under an influence of the feeding activity of the gall maker, a third trophic level inside the gall may intermediate this feeding behavior or even block it. The first case is exemplified by ambrosia galls, in which the insects feed on the fungi and not on the plant cells. Thus, it seems plausible that the signaling molecules that trigger plant tissue transformation come from the fungi, whereas in the latter case, the end or the switch of an insect feeding activity inside the chamber alters cell fates.

The phase of growth and differentiation of the gall is the period in which its biomass increases remarkably due to the increased number of cells—hyperplasia (cell division) and/or hypertrophy (increase in cell size). As stated by Moura et al. (2009) and Oliveira and Isaias (2010a), these processes take place in all three plant tissue systems, but are more evident and crucial for gall functioning in the cells that originated from the ground meristem. Both hyperplasia and hypertrophy are defined by the feeding activity of larvae, whose saliva seems to modify the cell wall and dissolve cell contents. The activity then defines the form of the larval chamber, and possibly the external shape of the gall (Rohfritsch and Shorthouse 1982). However, in the Brazilian flora, some gall phenotypes are so peculiar and the larval chamber so small that it seems less difficult to assume just the feeding activity as responsible for the gall phenotype. This is the case of the horn-shaped galls on *C. langsdorffii* (Fabaceae) (Oliveira et al. 2008), the bivalve-shaped galls on *Lonchocarpus muehlbergianus* (Ferreira et al. 1990; Oliveira et al. 2006), and the bud galls of *Guapira opposita* (Nyctaginaceae) (Araújo 2008), for instance. Perhaps, the phenolics–auxin balance in these galls may be more important than the feeding sites for the definition of the gall size and shape by the time of its maturity.

Change an expressive mass to a large mass? The maturation phase of the gall occurs when the insect is in its last instar. This is the main trophic phase of the gall inducer, and that is the time when it eats an expressive mass of nutritions. Then, the inner cortex will disappear under the control of the inducer, and the outer cortex of magall, which is more under the influence of the plant (Dreger-Jauffret and Shorthouse 1992) will have its resources totally drained. Finally, the stage of dehiscence or the opening of the gall occurs at the end of the maturation phase, when the greatest physiological and chemical changes occur in the gall tissues. By the end of this phase, the flow of nutrients and water stops.

16.9 Gall Classification

Galls can be classically classified as either organoids or histioids, due to the developmental potentialities expressed by their cells (Meyer 1987; Dreger-Jauffret and Shorthouse 1992). The galls of the organoid type are those that differ little from the growth pattern of the host organ, which even galled, does not lose its identity. The organoid galls are represented by a swelling, callus-like growth, usually induced by insects and fungi. The galls of the histioid type exhibit a great variety of abnormal structures, the growth patterns of the host organ are changed, and the rearrangement or induction of new types of tissues occur. The histioid galls can be divided into cataplasmic and prosoplasmic. The cataplasmic galls are amorphous and vary in volume and extent; they are less organized and differentiated from the host body, consisting mainly of different layers of histologically homogeneous parenchyma. Generally, the Hemiptera induce cataplasmic galls. The prosoplamic galls are highly organized, with definite size and shape. Histologically, they are more complex and composed of differentiated tissues, although the degree of tissue differentiation is variable and dependent on the inducing insect. Also, independently of the gall type, the inducing insects are usually sedentary and therefore the site of stimulation and control of morphogenesis is restricted.

Different systems of classification of morphological types of galls are adopted. One of the first classification was proposed by E. Kuster in 1903 (Larew 1982) on the basis of the position of the gall and the type of gall development. Such classification includes just leaf galls and has been currently used. It proposes six main models of gall formation (Figure 16.7). Covering galls: in this gall type, the insect becomes encapsulated within the gall, which may present an opening (ostiole/operculum) or not. Filz galls: these galls are characterized primarily by dense pubescence in their outer walls (usually leaves), which houses the inducers. Roll and fold galls: these galls present differential growth caused by the feeding habits of the insect, resulting in winding, twisting, or folding of leaves and branches, which are often swollen. *Pouch galls*: in this gall type, tissue growth occurs in a restricted area around the larva, producing an invagination by differential growth on one side of the leaf blade. The gall tissues may have different degrees of differentiation, and the epidermis of the larval chamber originates from the epidermis of the plant body. Mark galls: these are the galls in which the eggs are oviposited on the plant surface; then, the first instar larvae penetrate the tissue that proliferates and surrounds it completely. Pit galls: these galls are characterized by a slight depression where the insect feeds, sometimes surrounding a protruding halo. Sometimes the epidermis forms a vesicle (discoid gall or blister galls). Bud or Rosette galls: these models cause the growth of buds or, sometimes, the proliferation and miniaturization of new leaves. There is a marked shortening of internodes. In Figure 16.8 some types of galls found on several Brazilian host plants are illustrated.

Insect Bioecology and Nutrition for Integrated Pest Management



FIGURE 16.7 Morphological types of galls based on position of galling herbivores and gall development (Larew 1982): (a) healthy leaf lamina; (b) hairy galls; (c) mark galls; (d) discoid or vesicular gall; (e and f) pouch galls; (g) roll galls; (h and i) fold galls; (j and k) covering galls; (l) healthy shoot; (m) covering fall; (n) typical gall with several chambers; (o) healthy apical shoot; (p) rosette gall (with increased number of leaves); and (q) bud gall (reduced number of leaves). (From Dreger-Jauffret, F. and J. D. Shorthouse, Diversity of gall-inducing insects and their galls. In Biology of Insect-Induced Galls, ed. J. D. Shorthouse and O. Rohfritsch, 8-33. Oxford: Oxford University Press, 1992. Illustration courtesy of Miriam Duarte.)

16.10 Adaptive Significance

The adaptive significance of the habit of inducing galls was currently revised (Price et al. 1986, 1987; Stone and Schönrogge 2003). At least one researcher hypothesized that galls do not have any adaptive value either for the insect or for the plant (Bequaert 1924), while another one proposed that they may have an adaptive value only for the host plant (Mani 1964).

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According to the hypothesis of the adaptive value of galls for the plant, galls should limit the move-Is just a defensive ment of the insect, restricting it in space and time, and thus, the gall structure should be ju lefensive structure. Most of the evidences do not support this hypothesis since galls act as sinks, translocating nutrients from other plant parts and limiting the growth and reproduction of host plants. These two hypotheses have few defenders today because the studies in recent decades have shown that galls probably both have an adaptive significance and are a detrimental structure to the host plant. Several lines of evidence illustrate the impact of galls on the fitness of their host plants (e.g., Fernandes 1987; Fernandes et al. 1993). Three other hypotheses advocate that the gall should present an adaptive value for the insect: the nutritional, the enemy-free space, and the microenvironmental hypotheses (reviewed by Price et al. 1987).

> The nutritional hypothesis is supported by several studies that show that the galling insect is able to manipulate the host plant, inducing the formation of a nutritionally superior tissue (see Section 16.7) in comparison to the other non-galled tissues of the host plant (Shannon and Brewer 1980; Rohfritsch and This citation is not listed in the Shorthouse 1982; Bronner 1992). This nutritive tissue is also free of defensive secondary compounds Reference Please check. (Larew 1982; Price et al. 1986, 1987; Nyman and Julkunem-Tiito 2000). Studies on galls induced by tenthredinids on species of willow (Salix) in the United States showed that defensive substances, mainly phenolic compounds, are common in the outer cortex of the galls, suggesting that the insect can benefit from their defensive properties against other insects (Larew 1982; Cornell 1983; Taper and Case 1987).





FIGURE 16.8 Several morphotypes of galls in different host plants: (a) amorphous galls of thrips in Myrtaceae from Cerrado; (b) discoid galls of Cecidomyiidae in Davilla rugosa from Cerrado; (c) discoid galls of Cecidomyiidae in Sacoglotis matogrossensis from Amazonia; (d) leaf gall of Cecidomyiidae in Vismia latifolia from Amazonia; (e) insect galls in Trattinickia rhoifolia (Burseraceae) from Amazônia; (f) elliptical gall at leaf margin in Vismia latifolia from Amazonia; (g) elliptical galls in stem of Baccharis cf. trimera in Ouro Preto, MG; (h) galls of a Cecidomyiidae in Anacardium occidentale from Amazonia; (i) galls in a bud of an unidentified host plant species from Amazônia; (j) cylindrical galls of a Cecidomyiidae in an unidentified host plant species from Cerrado; (k) galls of Parkiamyia paraensis Maia in Parkia pendula; (1) spheroid hairy gall of a Cecidomyiidae in Mimosa sp. from Amazônia; (m) spherical or pineapple-like galls in Chrysothmanus nauseosus from Sonoran Desert, USA; (n) galls of Hymenoptera in Mimosa sp. from Amazonia; and (o) galls of Paradasineura admirabilis Maia in leaves of Erythroxylum suberosum (Erythroxylaceae) from Cerrado. (Photos courtesy of G. W. Fernandes.)

Sonoran Desert, USA correct?

The gall acts as a mobilizing sink of nutrients from the other tissues of the host plant (Fay et al. 1993; Larson and Whitham 1991). The enemy hypothesis argues that galling insects are less predated and/or parasitized when compared with other phylogenetically close insects, but with a different feeding habit. For example, galls induced by tenthredinids are attacked by fewer parasitoid species and have lower mortality rates than free-living ones (Price and Pschorn-Walcher 1988). Nevertheless, according to Stone and Schönrogge (2003), some other galling herbivores are more attacked than their free-living relatives.

Some external features of galls may reduce the rates of attack by natural enemies. For example, increasing size (Stone et al. 2002; Weis et al. 1985; Rossi et al. 1992) or hardness (Weis 1982; Stone et al. 2002), or the presence of trichomes may reduce the attack by parasitoids and other natural enemies. The North American system E. solidaginis-S. altissima (Abrahamson and Weis 1997) has been widely studied in recent decades, and can help understand these different strategies. The success of Eurytoma gigantea Walsh in the parasite insect gall E. solidaginis depends on the ratio between the size of its ovipositor and the thickness of the gall. When the ratio exceeds 0.95 (a parasitoid with an ovipositor 10 mm in length can lay eggs on a branch with a wall of up to 9.5 mm), the parasitoid cannot successfully make the oviposition (Weis et al. 1985). Moreover, galls with greater diameter have greater chance of Eurosta being attacked by birds (e.g., woodpecker Picoides pubescens) than smaller galls (Abrahan 6) and This citation is Weis 1992). Thus, parasitoids and predators act as a selective force ("directional") about the size of the References. Please check gall in different directions, first to increase the size of the gall and second in order to decrease it. Hence, there is a stabilizing selection favoring the differential reproduction and survival of galls of intermediate size. However, other studies did not statistically support this assertion (for a complete analysis, see Abrahamson and Weis 1997).

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The beetle weevil C. clitelae Boheman, commonly found in the Brazilian Cerrado, induces galls with several chambers on S. lycocarpum (Solanaceae) (Souza et al. 1998, 2001). Although the beetle preferably attacks small plants, the size of their galls and the number of larvae per gall increase with the size of the branch. As in the case of E. solidaginis, the larger galls of C. clitelae are most often preyed on by the Cerrado woodpecker, Colaptes campestre.

The microenvironmental hypothesis states that because galls are sessile and protected by their structure, the galling larvae are less susceptible to abiotic environmental changes, particularly temperature and humidity (Fernandes and Martins 1985; Price et al. 1987). Hygrothermal and nutritional stress, defined here as high temperature and low humidity, and nutritional quality of the plants (Fernandes and Price 1988) should be the crucial environmental factors acting on the selective evolution of galling insects. The damage caused by herbivores on their host plants, preserved in the fossil record, showed its maximum in the Middle Eocene (a period characterized by a subtropical climate; less humidity; and a dry, defined, and cold weather), indicating a high diversity of galling organisms in xeric environments (Wilf et al. 2001). Recent studies support the assertion that galling insects are richer in species and more abundant in hygrothermal and nutritionally stressed habitats, with sclerophyllous vegetation in tropical and temperate regions (Price et al. 1998).

At the habitat or environmental scale, Fernandes and Price (1988, 1991, 1992) proposed the hygrothermal stress hypothesis that predicts that species richness and abundance of galling insects is higher in stressed hygrothermal habitats (i.e., in dry and sunny habitats) usually covered by sclerophyllous vegetation, with leaves of high phenolic compounds and low levels of nutrients (Turner 1994; Fernandes and Price 1991). The hypothesis of hygrothermal stress combines arguments of the three hypotheses about the adaptive nature of the habit of inducing galls to explain the distribution patterns of galling insects in ecological time (Fernandes et al. 2005). Also, Fernandes and Price (1991) observed that the negative relationship between altitude and the richness of the species of galling insects was dependent on the type of habitat. The richness of insect species is related to altitude in xeric habitats, but not in mesic ones at the same altitude, suggesting that the relationship between altitude and species richness is spurious and that hygrothermal stress is the key factor determining species richness of galling insects. This conclusion is supported by the latitudinal pattern: the richness of the species of galling insects is greatest in intermediate latitudes (25–40° north or south), coinciding with habitats submitted to water and nutrition stresses with sclerophyllous vegetation (e.g., Cerrado, Chaparral, and vegetation of the Mediterranean type) (Fernandes and Price 1988, 1991; Blanche and Westoby 1995; Lara and Fernandes 1996; Wright and Samways 1998; Price et al. 1998).

A few patterns have been proposed on the habit of inducing galls. First, that galls may confer effective protection against climatic variation (Price et al. 1987). Second, considering that some plant nutrients become toxic at high levels, and that the gall acts as a sink of nutrients from other plant parts (Nyman This citation is ot listed in the and Julkunen-Tiitto 2000), inducing insects may have more success in stressed habitats. This second pat- References. Please check. tern is based on the fact that in these habitats, plants tend to have low nutritional status (Fernandes and Price 1991), with low concentration of nutrients, and an excess of secondary compounds (Müller et al. 1987). Furthermore, gall-inducing insects are able to overcome these defensive substances, inducing a tissue free of phenolic compounds and high in nutrients (Larew 1982; Nyman and Julkunen-Tiitto 2000). The third factor that may modulate the pattern of species richness is a differential selective pressure inflicted by natural enemies, and plant resistance between xeric and mesic habitats on galling herbivores (Fernandes 1990, 1998; Fernandes and Price 1988, 1992). In summary, galls probably have an adaptive value for insects. The evolution of the habit of inducing galls can be explained by the action of different selective forces. The end result is the formation of a tissue rich in nutrients (according to the prediction of the nutritional hypothesis), and the development of galls with external structures and varying sizes in response to environmental pressures (according to the assumptions provided by the microenvironmental and enemy-free space hypotheses).

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16.11 Concluding Remarks

In this chapter we discussed several aspects regarding insect galls and the main gall-inducing insect taxa, how insects select their host plants, how galls develop in plants, how they are classified, and their adaptive significance. In addition to these aspects, it should be mentioned that insects that induce galls can cause significant damage to wild and cultivated plants having a great economic impact. Just to mention one example, the coleopteran *Sternechus subsignathus* (Curculionidae) is known to feed on soybean plants and to cause gall formation on soybean stems; it is widely distributed, from the northeast to southern Brazil, and is regarded as a main pest of this important crop (e.g., Hoffmann-Campo et al. 1991, Silva 1998, Silva et al. 1998). The most recent review on the subject is almost 25 years old (Fernandes 1987); hence, a new revision is called for. We suggest that basic studies on bioecology and nutrition are important in order to support the managing strategies for species that has become pests.

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