

Chapter 2

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

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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 laminae, while the median layers may later 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 target 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.

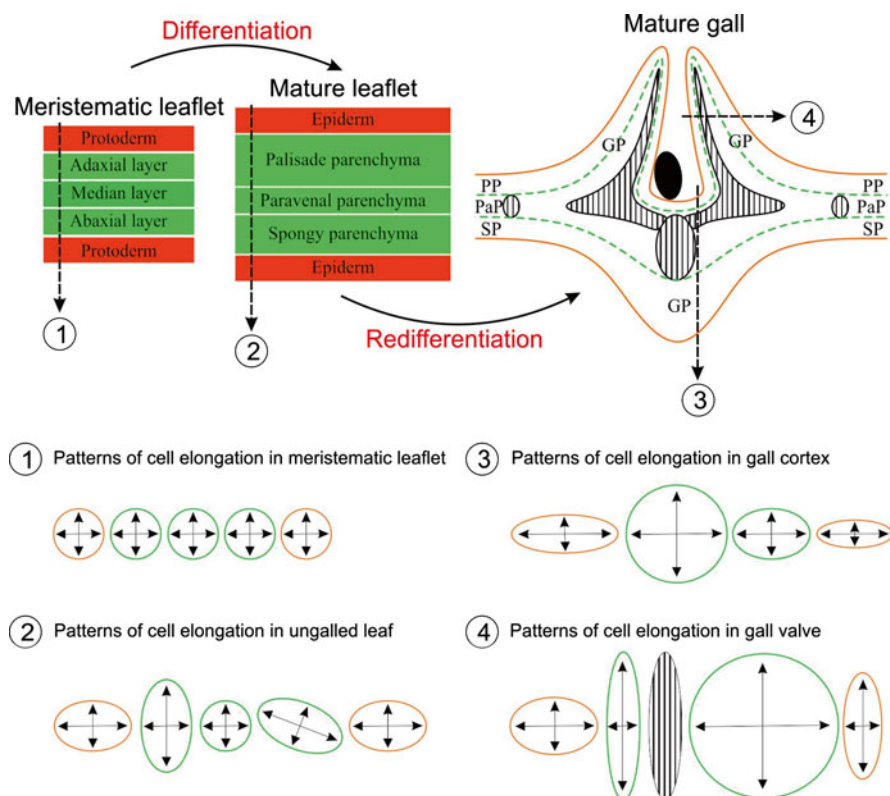


Fig. 2.1 Development of the galls induced by *Euphalerus ostreoides* (Hemiptera: Psylloidea) in *Lonchocarpus muehlbergianus* (Fabaceae). Non chlorophyllian tissues (orange lines) and chlorophyllian tissues (green lines) differentiate from leaf meristem until gall maturation, with distinct axis of cell 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 Gallling 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

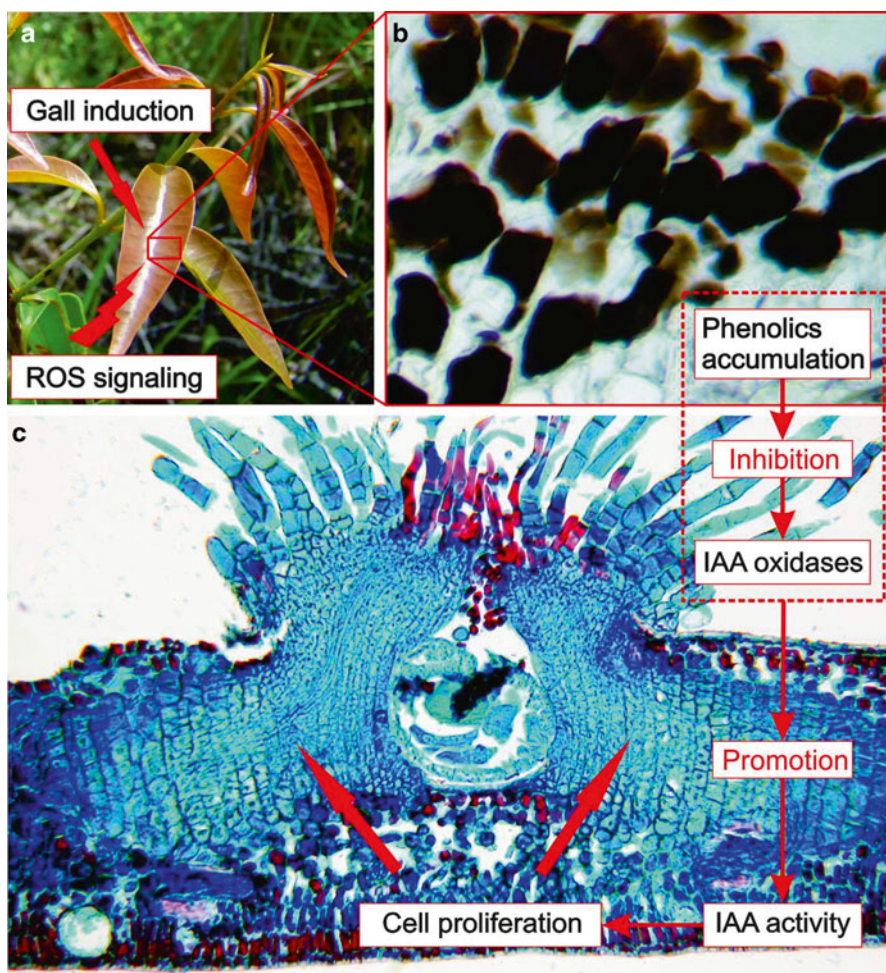


Fig. 2.2 Schematic representation of the cascade of events that leads to gall formation. (a) During gall induction, ROS production enhances, which is believed to be the first signaling step for gall development. (b) At the sites of gall induction, phenolic compounds quickly accumulate (Note the cell 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 esterase, receptors of glutamate, of gamma-aminobutyric acid (GABA), and components of endocannabinoids 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 (Hülkamp 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 hyperplastic 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* (Apocynaceae). 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

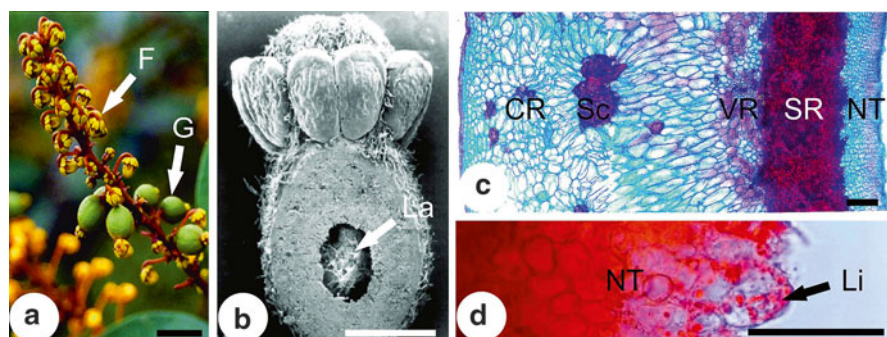


Fig. 2.3 Galls induced by an unidentified Lepidoptera on pedicels of *Byrsonima sericea* (Malpighiaceae). (a) Inflorescence with ungalled flowers and pedicel galls. (b) A scanning electron micrograph of a galled pedicel evidencing a larva inside the larval chamber. (c) Transverse section of an intermediate 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 μ m, (d) = 50 μ m

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 meristemes. 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,

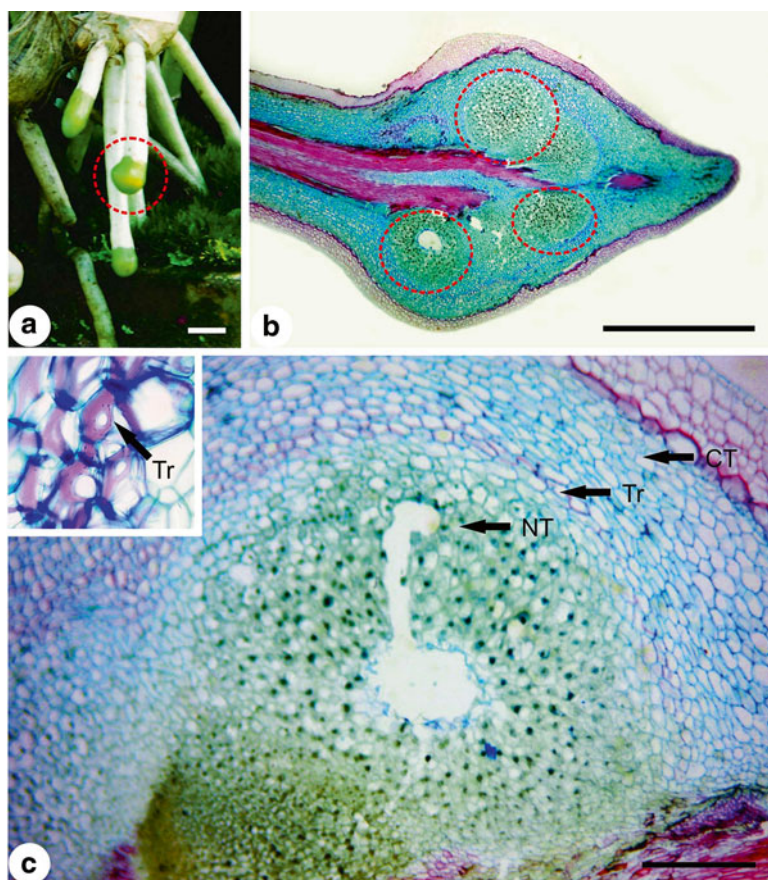


Fig. 2.4 Galls induced by *Calorileya nigra* (Hymenoptera: Chalcidoidea) on the roots of *Cattleya guttata* (Orchidaceae). (a) Macroscopic aspect of the attacked root apex (*dotted circle*). (b) General view of a longitudinally sectioned root apex with many inducers (*dotted circles*). Concentric tissue 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 μ m

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 gall-inducing 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 Gibeau 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 Pseudophacopterionidae 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

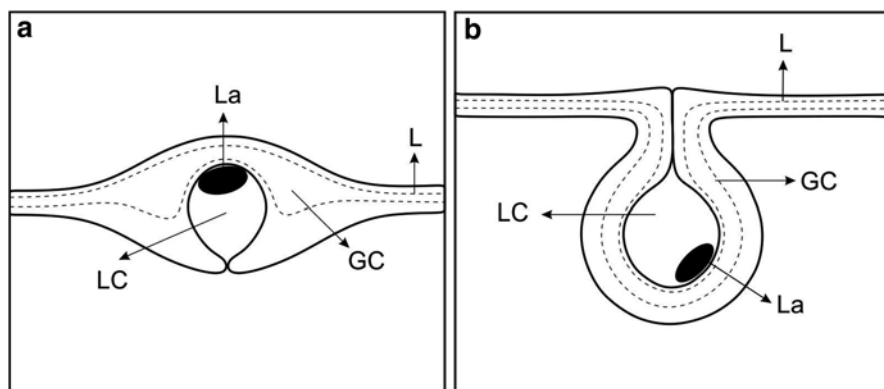


Fig. 2.5 Schematic representation of the cross section of intralaminar leaf gall of *Aspidosperma australe* (Apocynaceae) (a) and extralaminar leaf gall of *Psidium myrtilloides* (Myrtaceae) (b). Dotted lines represent different cell lineages in a continuum between non-galled leaf tissues and gall tissues. 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 langsdorffii* (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 mid-rib 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*–*Schimatodiplosis 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*–*Schimatodiplosis 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

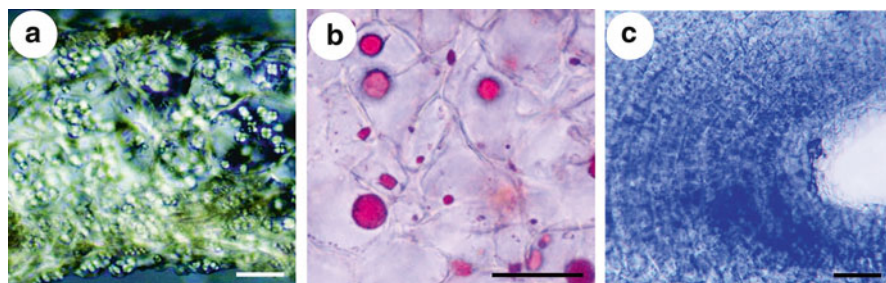


Fig. 2.6 Detection of (a) starch (Polarized Light – bright spots) in the globoid leaf gall on *Machaerium nycitans* (Fabaceae); (b) histochemical detection of lipids (Sudan III – red droplets) in globoid leaf gall on *Psidium myrtilloides* (Myrtaceae) and (c) proteins (Coomassie blue – blue precipitate)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

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 hypertrophic or hyperplastic 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*–*Schimatodiplosis 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 macrocapitata* (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 Isaías 2010b), on *A. spruceanum* (Oliveira et al. 2010), and on *Lonchocarpus muhelbergianus* (Isaías 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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