



Plant anatomy: history and future directions

The anatomy of neotropical galls and the untold lessons about the morphogenetical potentialities of plants

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Abstract

Plant anatomists perceive the plant body as the dynamic result of complex developmental processes which may deviate during gall development. Gall development involves local responses forming a morphophysiological *continuum* with the host plant organ, which can be addressed by anatomical studies. We revisited the history of galls in Brazil, as well as their morphogenetical potentialities and integration with entomological, chemical, physiological, and ecological approaches. The Fabaceae, Myrtaceae, Melastomataceae, and Asteraceae are the main hosts of the Brazilian gall morphotypes, which can be classified according to their three-dimensional shapes. Anatomical tools have been used to map cell and tissue fates in gall morphotypes, revealing the potential of plant tissue systems to overexpress or inhibit standard plant development. In-depth anatomical, cytological, histochemical, and immunocytochemical techniques have greatly expanded the knowledge of gall traits and plant cell responses. The new structures of galls hosted on leaves, stems, roots, and reproductive organs show consistent tissue specialization regarding the dermal and ground tissue systems, with the gall's vascular system being connected to preexisting or newly formed bundles of the host plant. Due to the diverse stressors imposed on plant tissues, gall anatomy reveals adaptive responses that can be addressed from several perspectives, including citizen science initiatives.

Key words: cell fates, ontogenesis, structure and function.

Resumo

Anatomistas vegetais percebem o corpo da planta como resultado de processos dinâmicos e complexos que podem ser desviados ao longo do desenvolvimento da galha. Este desenvolvimento envolve respostas locais, mas em um *continuum* morfofisiológico com o órgão hospedeiro, o que pode ser estudado do ponto de vista anatômico. Revisitamos a história das galhas no Brasil, suas potencialidades morfofisiológicas e integração com abordagens entomológicas, químicas, fisiológicas e ecológicas. No Brasil, espécies de Fabaceae, Myrtaceae, Melastomataceae e Asteraceae são as principais hospedeiras de diversos morfotipos de galhas classificados com base em suas formas tridimensionais. Ferramentas anatômicas usadas para mapear o destino de células e tecidos nas galhas revelam o potencial dos sistemas de tecidos vegetais para superexpressar ou inibir o desenvolvimento vegetal padrão. Técnicas anatômicas, citológicas, histoquímicas e imunocitoquímicas aprofundadas expandiram o conhecimento das características das galhas e das respostas das células vegetais. As galhas hospedadas em folhas, caules, raízes e órgãos reprodutivos têm especialização tecidual consistente nos sistemas de tecido dérmico e fundamental, com o sistema vascular das galhas conectado àqueles da planta hospedeira. Devido a diversos estressores impostos aos tecidos vegetais, a anatomia das galhas revela respostas adaptativas que podem ser abordadas por diversas perspectivas, incluindo iniciativas de ciência cidadã.

Palavras-chave: destinos celulares, ontogênese, estrutura e função.

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Introduction

Plant anatomy is a crucial component of plant biology, and plant anatomists are the researchers who best understand the plant body as a dynamic structure shaped by continuous and complex processes. All plant cells, tissues, and organs go through such processes, resulting from metabolic interactions responsive to abiotic and biotic factors of the environment (Mauseth 1988). Among the biotic factors, there are organisms that induce galls and influence plant development, resulting in the diverse shapes of galls found in nature (Ferreira *et al.* 2019), known as gall morphotypes (Isaias *et al.* 2013).

Gall development involves cell hypertrophy and hyperplasia processes, as well as cell redifferentiation in the host plant organ, culminating in the formation of new organs with specialized tissues (Mani 1964). For example, the typical nutritive tissue and the sclerenchyma are common anatomical features of the Diptera, Hymenoptera, and Lepidoptera galls (Ferreira *et al.* 2017, 2019; Guedes *et al.* 2023a). In contrast, a nutritive-like tissue occurs in some Hemiptera galls (Ferreira *et al.* 2019). Plant morphologists and physiologists may explore galls as models for the understanding of plant developmental programs (Shorthouse & Rohfritsch 1992) based on the premise that the anatomical examination of galls showcases how plants, under specific stimuli, can undergo reprogramming to grow atypical structures. The structural and metabolic patterns of these atypical organs can deviate significantly from the typical course of plant development (Isaias *et al.* 2014b; Ferreira *et al.* 2019; Guedes *et al.* 2023a). Moreover, the restricted cellular changes observed in galls underlie the focus on structural and physiological studies (Carneiro *et al.* 2017), although according to an integrative perspective (Jorge *et al.* 2018), since the connection between the gall tissues and the non-galled tissues of the host plants are part of a morphophysiological *continuum* (Mani 1964; Isaias *et al.* 2014b).

Brazil stands out as the epicenter of scientific production in Cecidology, the study of galls. Historical records date back to the early 20th century when Tavares (1909) published the first data on the host plant-galling insect systems in the Brazilian flora. From the early 1980's onwards, the first anatomical diagnoses of galls described how cells and tissues involved in the development of different gall morphotypes are reprogrammed toward the expression of new phenotypes (Arduin *et al.* 1989,

1991; Arduin & Kraus 1995, 2001) repetitively found in nature (Isaias *et al.* 2013, 2014a). From the perspective of the influence of the gall inducers' taxa (Bronner 1992; Rohfritsch 1992), many galls from Brazil have been found to fit previously described patterns of Nearctic and Palearctic galls. However, as diverse as the Brazilian flora is, many peculiarities, herein understood as host plant morphogenetical constraints and potentialities, have been reported as novelties due to in-depth anatomical investigations (*cf.* Arduin *et al.* 1991, 2005; Ferreira *et al.* 2019; Teixeira *et al.* 2022).

Anatomical traits, together with histochemical profiles, have been used as diagnostic features of the new functions assumed by plant cells and tissues at the sites of gall development. In contrast to the plant's structural modules specialized for photosynthesis, storage of water and metabolites, and support of other organs, the physiological processes of plants aim at the maintenance of new tissue homeostasis, enabling the development and maintenance of galls as ectopic new organs (Mani 1964) such as the horn-shaped gall on *Copaifera langsdorffii* Desf. (Fabaceae) leaves (Carneiro *et al.* 2017). The physiological demands imposed by gall tissues have been interpreted as a complex set of metabolic pathways that guarantee the balance of reactive oxygen species (ROS), which ends up triggering the first steps of gall induction (Isaias *et al.* 2015). Furthermore, consistent data about the anatomical development of galls are crucial for a better elucidation of the genetic dynamics involved in this interaction (Schultz *et al.* 2019). From the first descriptive steps to the functional approaches about gall structure, Brazilian cecidology has progressed from understanding gall anatomy to addressing functional traits. On this basis, we review here the history of gall anatomy in Brazil and its integration with entomological, chemical, physiological, and ecological approaches, and we point out future perspectives regarding the focus of this line of research.

The 20th Century and the first studies on gall anatomy in Brazil

After the initial records of the presence of galls in Brazil reported by Tavares (in 1909), several studies on gall anatomy were undertaken over the years, with emphasis on graduate programs on Botany (Fig. 1) at the University of São Paulo (USP) under the regency of Jane E. Kraus. In the 1980's, as mentioned above, the first consistent descriptive studies on the morphoanatomy and

the ontogenesis of Neotropical galls generated the first results, which were published during the next decade and at the beginning of the 21st century (Arduin *et al.* 1989, 1991, 2005; Arduin & Kraus 1995, 2001; Kraus *et al.* 1993, 1996, 1998, 2002; Souza *et al.* 2000).

The 21th Century: Brazil stands out as the epicenter of scientific production in Cecidology

By the end of the 2000's, the establishment of a research group on the Structure, Chemistry, and Physiology of Neotropical Galls at the Federal University of Minas Gerais (UFMG), registered in the “Conselho Nacional de Desenvolvimento Científico e Tecnológico” - CNPq (Brazilian National Council for Research) and headed by Rosy M. S. Isaias (CNPq 2023), promoted a higher level of the study of galls. The richness and diversity of galls in the Neotropical region are well known, and Fabaceae, Myrtaceae, Melastomataceae, and Asteraceae are the main host plant families reported in gall inventories of the Brazilian flora (Isaias *et al.* 2021). In this scenario, particularly important is the analysis of the inventories of gall diversity and richness reported during the period from 1990 to 2010. However, this analysis reveals a profusion of confusing data regarding the morphological terminology used to describe the galls. Similar shapes were often referred to by different, inaccurate names, thus making any type of comparative analysis very difficult due to many

inconsistencies (Isaias *et al.* 2014a). The solution came from the initiative of using names of standard tridimensional forms to refer to gall morphotypes, facilitating the recognition of galls and host plants in nature. The recognition of host plants on the basis of gall morphology is a trustworthy and efficient taxonomic tool since each host plant-gall inducer system has a peculiarly associated morphotype (Isaias *et al.* 2013, 2014a). Despite the variety of shapes, the development of galls involves a similar functionality based on the search for a buffered environment that ensures increased protection of gall-inducing organisms against adverse biotic and abiotic environmental conditions, as well as higher-quality nutrition compared to free-living herbivores, as demonstrated by comprehensive empirical data and tests of hypotheses (Price *et al.* 1987).

The effort to improve the terminology used for gall shapes resulted in an illustrated and annotated checklist of Brazilian gall morphotypes (Isaias *et al.* 2013), which provides the standardization of gall shapes by dividing 43 referenced shapes into seven morphotypes. Among the tridimensional standard shapes (Figs. 2-3), the globose (Figs. 2a; 3a), lenticular (Figs. 2b; 3b), and conical morphotypes (Figs. 2c; 3c) were found to be the most common (Isaias *et al.* 2013). In addition to providing a standardized terminology, this effort also helps overcome problems generated by the lack of taxonomic identity of the gall inducers and enables comparative analyses of the data presented in the inventories of gall richness and distribution in Brazil (Isaias *et al.* 2014a) and worldwide.

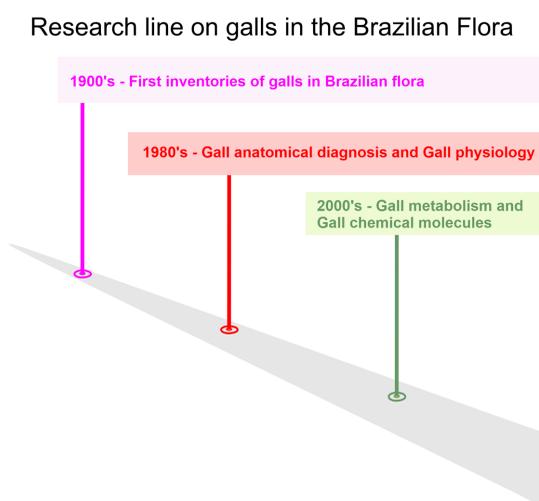


Figure 1 – Time line illustrating the areas of contribution to the research line on galls in the Brazilian flora.

The organization of gall tissues -
from the host organ
to the new structure

In terms of developmental pathways, galls can be useful models for morphogenetic studies. Mapping cell and tissue fates in different galls reveals the potential of the three plant tissue systems to express neoformations, which are also linked to new physiological traits. The developmental anatomy of galls in the Neotropics reveals that the gall inducer stimuli may be balanced by the host plant morphogenetical constraints (Isaias *et al.* 2014b; Ferreira *et al.* 2019), as demonstrated in the Cecidomyiidae galls on *Baccharis reticularia* (Asteraceae) and in the *Calophya mammifex* galls on *Schinus polygama* (Anacardiaceae) (Guedes *et al.* 2018). With non-galled tissues as control samples, the analysis of gall tissues can indicate

the origin and fates of the differentiated cells along cecidogenesis, so that many of these silenced and stimulated effects can be revealed (Fig. 4).

Prominent changes in the three plant tissue systems usually indicate various degrees of overexpression of preexisting traits, but the differentiation of sclereids interspersed within the gall parenchyma is not observed in non-galled leaves of other species, such as *Aspidosperma spruceanum* (Apocynaceae) (Formiga *et al.* 2011). On the other hand, an example of an impaired developmental feature of galls is the pericycle, a cell layer adjacent to procambial derivatives whose meristematic potential can be fundamental for gall development since it is responsible for the differentiation of fibers lining the vascular system, forming a protective layer. Impaired lignification of pericycle cell walls is relatively common in galls (Meyer & Maresquelle 1983), as observed in several leaf galls on *B. concinna* and *B. dracunculifolia*-Cecidomyiidae (Diptera) (Arduin & Kraus 2001), *Ficus microcarpa* (Moraceae)-*Gynaikothrips ficorum* (Thysanoptera) (Souza *et al.* 2000), *Piptadenia gonoacantha* (Fabaceae)-Cecidomyiidae (Diptera) (Arduin & Kraus 1995), and *Struthanthus vulgaris* (Loranthaceae)-Hymenoptera (Kraus *et al.* 2002). This is particularly evident in galls induced by sap-sucking organisms, whose main feeding sites are neofomed vascular bundles around the gall chamber. These vascular bundles are surrounded by parenchymatous cells near the phloem and the xylem, instead of being covered by pericyclic fibers (Carneiro *et al.* 2015; Ferreira *et al.* 2019). In addition, the sclerenchyma in triozid-induced

galls (Fig. 3a) and other insect-induced galls often differentiates from ground tissues and not from the pericycle (Carneiro *et al.* 2014; Ferreira *et al.* 2019; Guedes *et al.* 2023b).

The numerous plasmodesmata in living sclereids indicate the possible translocation of substances toward the feeding site of the inducer or related to the maintenance of cecidogenesis (*cf.* Meyer & Maresquelle 1983; Hori 1992). This is also observed in neotropical galls (Kraus *et al.* 1993; Oliveira *et al.* 2010) and in plants in general, whose sclerenchyma cells (both fibers and sclereids) may not be dead at maturity (Evert 2006). More recently, the lignification process has been acknowledged as a pathway that scavenges free radical molecules, representing a physiological defense mechanism against excessive oxidative stress (Oliveira *et al.* 2017), as further considered in the present text.

In galls without a typical nutritive tissue around the larva chamber, anatomical and cytological investigations have shown the presence of nutritive-like cells differentiated from the vascular and perivascular parenchyma (most probably, the pericycle), which are the feeding sites of the gall inducers, in this case, triozid phloem-feeders (Carneiro & Isaias 2015). Vascular neofomation is quite important for the redirection of metabolites toward the gall developmental sites. In most galls, the neofomed vascularization is connected to the vascular system of the host organs (Meyer & Maresquelle 1983), but vascular cells can have different origins. For instance, in leaf galls on the *Guarea macrophylla* (Meliaceae)-

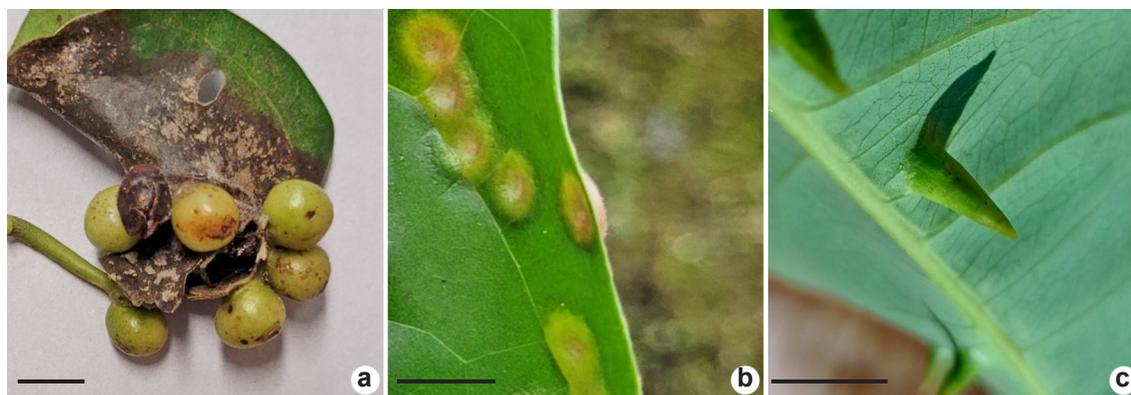


Figure 2 – a-c. Main gall morphotypes reported in the Brazilian flora – a. globoid gall on *Psidium laruotteanum* Cambess. (Myrtaceae) induced by *Nothotrioza acuminata* Burckhardt 2022 (Hemiptera, Triozidae); b. lenticular gall on *Piper* sp. (Piperaceae) by an unidentified inducer; c. conical gall on *Byrsonima* sp. (Malpighiaceae) induced by an unidentified Cecidomyiidae (Diptera). Scale bars = 1 cm.

Cecidomyiidae (Diptera) system (Kraus *et al.* 1996), the vascular system differentiates directly from procambial cells, whereas in other galls the vascular systems may derive from the vascular parenchyma of preexisting vascular bundles or from the ground parenchyma cells in the cortical region of the developing gall (Carneiro & Isaias 2015; Bragança *et al.* 2021).

The vascular parenchyma cells may also be hyperplastic, separating the conductive elements of the xylem from the phloem, which appear as isolated bundles immersed in the gall parenchyma, as observed in the Cecidomyiidae galls on *S. vulgaris* (Arduin *et al.* 1991). Changes in cell number, area,

and developmental patterns particularly occur in some host plant-gall inducer systems, where the phloem portion of the vascular bundles can be wider than the xylem portion, and vessel elements with helical thickening can predominate (Kraus *et al.* 1993). Also, the differentiation of tracheids where only procambial cells should be found, as in the root galls of *Cattleya guttata* (Orchidaceae),

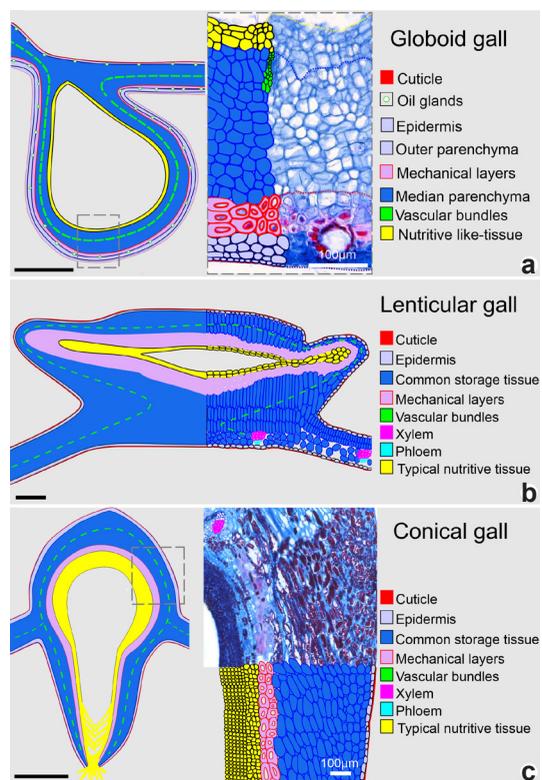


Figure 3 – a-c. Diagrams of the anatomical profiles of the main gall morphotypes reported in the Brazilian flora – a. globoid gall of *Nothotrioza myrtooidis* (Hemitera, Triozidae) on *Psidium myrtooides* (Myrtaceae) leaves - Adapted from Carneiro *et al.* (2014); b. lenticular gall of Cecidomyiidae (Diptera) on *Inga ingoides* (Fabaceae) leaves - Adapted from Bragança *et al.* (2021); c. conical gall of Cecidomyiidae (Diptera) on *Byrsonima variabilis* (Malpighiaceae) leaves - Authors’ archive, demonstrating tissue organization. Scale bars: 3a = 2 mm; 3b = 100 μm; 3c = 2 mm.

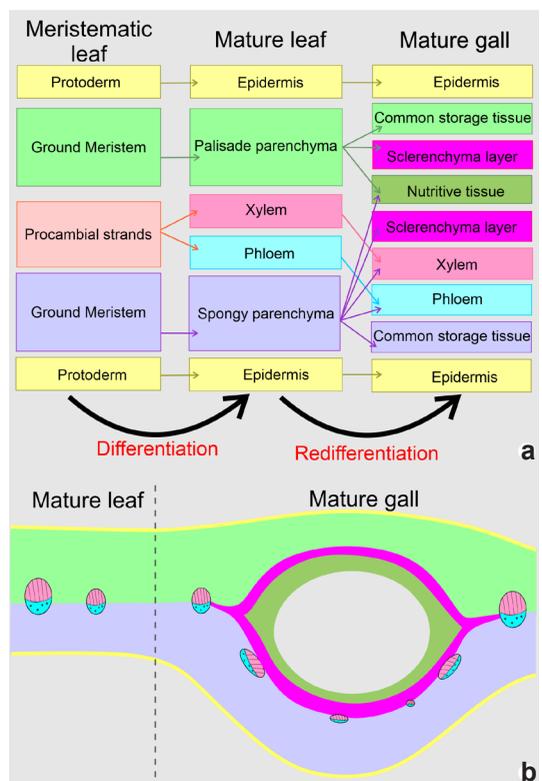


Figure 4 – a-b. Diagrams of the cell lineages (origins and fates) in the tissues of mature leaves (NGL) and hypothetical mature galls (MG) – a. diagrams demonstrating that dermal, ground, and vascular tissue systems of NGL originate by the differentiation of leaf meristematic tissues (protoderm, ground meristem, and procambial strands), while the dermal, ground, and vascular tissues of MG originate from the redifferentiation of epidermal and parenchyma leaf cells; b. diagram of the MG in continuum with the NGL lamina, showing the epidermis (yellow), vascular bundles (pink and blue), the dorsiventral mesophyll with palisade (light green) and spongy parenchyma (purple) in NGL; and the epidermis (yellow), common storage tissue (purple and light green), vascular bundles (pink and blue), sclerenchyma layer (dark pink), and typical nutritive tissue (dark green) in MG.

indicates that gall induction may lead to the premature differentiation of the vascular system (Kraus & Tanoue 1999).

The new organogenesis alters the ordinary patterns of the host plants

Any plant organ can host galls induced by several taxa of organisms; most galls associate with eudicotyledons, but, more rarely, they may also be found in association with monocotyledons and ferns. While, indeed, monocotyledons seem to rarely host galls, ferns seem to be a neglected group of plants in terms of gall studies, especially when the first inventories of gall occurrence in the Brazilian flora are analyzed (Farias *et al.* 2020). Consequently, few papers deal with the morphological data of galls induced on ferns. Initial records have reported anatomical changes caused by a micromoth on the stems of *Microgramma squamulosa* (Polypodiaceae) (Kraus *et al.* 1993), whose inducer was then described as *Tortrimosaiica polypodivora* (Lepidoptera: Tortricidae) (Brown *et al.* 2004). Recently, more accurate searches in field trips have revealed many ferns hosting diverse gall morphotypes (Santos & Maia 2018) and new anatomical studies have been conducted on fern galls. The structure of galls induced by *T. polypodivora* has been revisited since complex galls of this type are also induced on *M. vacciniifolia* (Martins *et al.* 2023) and on *M. mortoniana* in addition to *M. squamulosa*. Additionally, galls on *Niphidium crassifolium*, another Polypodiaceae species, have been recently studied anatomically and biogeographically based on herbaria records, with their anatomical characteristics showing that such galls are induced by Diptera: Cecidomyiidae in plants occurring across a wide geographical range (Bragança *et al.* 2023).

Despite the taxonomical identity, all gall hosts are stimulated by their associated inducers in different ways that determine gall shape, size, and functions (Mani 1964; Rohfritsch 1992). Nevertheless, even though gall morphology is considered to be the extended phenotype of its inducer, the sites of oviposition (Formiga *et al.* 2011; Carneiro *et al.* 2015; Teixeira *et al.* 2022), *i.e.*, the plant organs, influence gall development. Leaves are galled the most, but stems, roots, and reproductive plant organs may also host galls, with tissue specialization following a simple general pattern involving the three tissue systems. The dermal system assumes a protective role (when covering the outer surface) or a nutritive role (when

lining the larval chamber); the ground system constitutes a storage parenchyma with interspersed sclereids and/or a sclerenchymatic sheath around the innermost parenchyma layers that form nutritive tissues; and the vascular system is formed either by preexisting or neoformed bundles which supply water and nutrients to both the gall and the inducer (See Figs. 3-4). Such general anatomical characteristics are common to most galls, but peculiarities attributed to galls occurring in specific organs may also occur.

Galls on roots are less frequent either owing to a reduced number of gall inducers living in the soil or to lack of information due to poor sampling. As orchids usually have aerial roots, the visualization of their root galls is easier, rendering them good models for identifying some anatomical aspects of root anatomy manipulation by the gall inducers. In root galls induced by Hymenoptera on *Cattleya guttata* (Orchidaceae), the velamen and the central vascular cylinder remain unchanged, except for their displacement toward the root apex. The overdifferentiation of cortical parenchyma cells is the most prominent feature in this root gall, and the non-differentiation of the root cap cells highlights an impairment of root standard anatomy (Kraus & Tanoue 1999). These impairments have also been reported for non-galled root galls on *Ansellia gigantea* (Orchidaceae) under dry winter conditions (Noel 1974), demonstrating a convergent structural response of the roots of Orchidaceae species to both abiotic and biotic stressors. Another peculiarity of the root galls on *C. guttata* is the differentiation of tracheoidal cells surrounding the larval chamber (Kraus & Tanoue 1999). Tracheoidal cells are a common structural trait of Orchidaceae (Burr & Barthlott 1991) that provides further mechanical support and aid to water-retention mechanisms in non-galled orchid organs (Olatunji & Nengim 2008), a characteristic that may also apply to the context of gall structure.

Additionally, the ontogenesis of root galls on *C. guttata* reveals the presence of a group of meristematic cells formed in an atypical region of the plant body such as the parenchyma. The formation of meristematic centers is well-known in plant tissue culture (Kruglova *et al.* 2023), with these areas being crucial for the development of new morphological plant structures such as the galls. Gall induction usually stimulates cell divisions and growth in existing meristems or in totipotent tissues such as the parenchyma, and may lead to the differentiation of ectopic meristems, as observed

in the horn-shaped galls on *Copaifera langsdorffii* (Fabaceae) (Carneiro *et al.* 2017), in the bud rosette galls on *Guapira opposita* (Nyctaginaceae) (Fleury *et al.* 2015), and in the amorphous galls on *Miconia* spp. (Melastomataceae) (Ferreira *et al.* 2017). The formation of meristematic centers shows that cecidogenesis affects processes of cell differentiation, including dedifferentiation, confirming that galls are new plant organs (Mani 1964).

Galls on stems and leaves commonly lead to the most marked changes in the ground tissue system, whose cell fates can be altered not only toward parenchyma cells accumulating water and primary and secondary metabolites, but also toward the differentiation of new cell types. As far as the development of stem galls is concerned, the host stem structure is affected to different degrees depending on the site of oviposition and on the taxa of the gall inducer. When the adult's ovipositor or a recently hatched larva enters the stem tissues, usually near the stem apex, shoot elongation may be compromised, as observed for the galls induced by *Tortrimosaica polypodivora* (Lepidoptera, Tortricidae) on *Microgramma mortoniana* (Polypodiaceae) (Lehn *et al.* 2020) and on *M. squamulosa* (Kraus *et al.* 1993). When the entry of *T. polypodivora* larvae does not compromise the apical cell at the shoot apex, the elongation of the stem is not affected, as is the case for the Lepidoptera galls induced on *Marcetia taxifolia* (Melastomataceae) (Ferreira & Isaias 2013) and for the *Neolasioptera* sp. (Diptera, Cecidomyiidae) galls induced next to the stem apex of *Eremanthus erythropappus* (Asteraceae) (Jorge *et al.* 2022a), whose stems continue to grow above the site of gall development.

The development of globoid stem galls in the *Neolasioptera* sp.-*E. erythropappus* system involves a change in vascular cambium activity. The anatomical consequences are the production of less numerous but larger vessel elements and the overproduction of vascular parenchyma cells. In functional terms, the vascular traits of the *Neolasioptera* sp. stem galls on *E. erythropappus* result in increased water flow that supplies both the galls and the non-galled portions of the stems which continue to grow above the galls, allowing the maintenance of shoot development even after gall infestation (Jorge *et al.* 2022a). The similar atypical activity of the vascular cambium is also observed in *Peumus boldus* (Monimiaceae) due to the development of *Dasineura* sp. stem galls.

In this case, the differentiation of the xylem is detrimental to the phloem, with overproduction of xylem parenchyma cells with poorly lignified cell walls that can store water and nutrients, while the differentiation of the phloem is inhibited (Guedes *et al.* 2022, 2023b). In these two systems, changes in the activity of the vascular cambium do not affect xylem conductivity or the activity of the shoot apical meristem (Jorge *et al.* 2022a; Guedes *et al.* 2023b).

As an example of the importance of the site of oviposition, galls on stem internodes may develop due to the ability of the female inducers to oviposit through leaf gaps, in the stem cortex or in axillary buds, but also due to the ability of the gall-inducing larvae to dig through the stem cortex toward the pith parenchyma, as described for *Calophya rubra* stem galls on *S. polygama* in Chile (Guedes *et al.* 2018). The access through leaf gaps avoids lignified tissues such as pericyclic fibers and xylem and favors the establishment of galls in stems, which are naturally harder than leaves. As the first instar nymphs establish and begin to feed, cell hypertrophy and hyperplasia in the parenchyma pith is stimulated to generate the gall (Guedes *et al.* 2018). In the *C. rubra* stem galls, as well as in other stem galls (Ferreira & Isaias 2013; Ferreira *et al.* 2022; Jorge *et al.* 2022a, b), phellogen activity confers further protection to the gall inducers by the production of additional cork (phellem) layers on the outer surface of the galls in a process similar to the cork production in non-galled stems in secondary growth. Further meristematic activity in stem galls reveals that the activity of cambium-like meristems in the gall cortex results in a complex, thickened and vastly reinforced structure, as observed for the galls induced by *Eucecidoses minutanus* (Lepidoptera) on the buds of *Schinus engleri* (Anacardiaceae), whose shoots are transformed into galls (Ferreira *et al.* 2022). Thus, the meristematic activity of galls should be further explored as a potential source of many structural novelties, especially if studied using the ontogenetical approach.

Galls on leaves involve the redirection of the structure, standardly adapted to photosynthesis, toward supporting the life cycle of the inducers, providing food, shelter, and a buffered microenvironment (Stone & Schönrogge 2003). The chlorophyllous parenchyma (spongy and palisade) is often the tissue most modified by cell hypertrophy and/or hyperplasia. Notably, these changes primarily occur in the spongy parenchyma,

whose cells respond more quickly to the outer stimuli than the palisade parenchyma, with the loss of intercellular spaces. Such responses of parenchyma homogenization have been reported in the galls induced by distinct insects on *S. vulgaris* (Arduin *et al.* 1991; Kraus *et al.* 2002), *Guarea macrophylla* (Meliaceae) (Kraus *et al.* 1996), and *Psidium myrtoides* (Myrtaceae) (Carneiro *et al.* 2014, 2015). The loss of dorsiventrality in leaf laminae hosting galls is another important consequence of gall development, which was elegantly diagnosed in leaf folding galls induced by Thysanoptera on *Ficus microcarpa* (Moraceae) (Souza *et al.* 2000) and *Myrcia splendens* (Myrtaceae) (Jorge *et al.* 2018).

Changes of parenchyma cell fates, as in the case of galls induced by Diptera (Cecidomyiidae), Lepidoptera, and Hymenoptera, result in the formation of highly specialized nutritive tissues. The cytoplasm of nutritive cells is rich in metabolites (see ahead), fragmented vacuoles, hypertrophied nuclei and nucleoli, and abundant organelles (Bronner 1977, 1992; Meyer & Maresquelle 1983; Rohfritsch 1992; Ferreira *et al.* 2019). In general terms, typical nutritive tissues are characterized by the accumulation of starch, lipids, or proteins and form one or more continuous layers around the larval chamber (Ferreira *et al.* 2017). The accumulated nutrients form specific gradients depending on the inducer's taxon and on the stage of development (Oliveira *et al.* 2010; Carneiro *et al.* 2014, 2015; Carneiro & Isaias 2015). The presence of an active inducer is necessary to initiate and maintain the cytohistochemical characteristics of the nutritive tissue; in the absence of the larva (death by predation or parasitoidism), the nutritive cells lose their metabolic and ultrastructural characteristics (Bronner 1992). Even though classical works refer to Lepidoptera galls typically having no nutritive tissue, a recent review has indicated that the formation of a typical nutritive tissue is a common anatomical trait of Lepidoptera galls (Guedes *et al.* 2023b). The nutritive cells of these galls are located around the larval chamber, have an abundant cytoplasm and large nuclei with one or more nucleoli, and are in intense division, being smaller in size than the surrounding parenchyma. Thus, they have characteristics similar to those described for the nutritive tissues of galls induced by other groups of insects, with lipids as the main storage reserve. The gall-inducing Hymenoptera and Lepidoptera (Motta *et al.* 2005; Vieira & Kraus 2007), as is true for other chewing insects, stimulate the accumulation of lipids in the

nutritive cells of their galls, which may be tested by the reaction with one of the Sudan's reactivities (Vieira & Kraus 2007; Rezende *et al.* 2019).

Peculiar cases of gall anatomy regarding the taxa of the inducers

The Diptera: Cecidomyiidae-induced galls are the most common in the Brazilian flora, with 265 of them having been described (Maia 2021), while the Hymenoptera and Thysanoptera galls are not so commonly reported in the inventories (Maia 2012). Thysanoptera-induced galls may not be formed by specialized tissues; instead, they may be characterized by necrotic spots, sites of cell hypertrophy, and hyperplasia in the ground system. Thus, for instance, the ordinary functionality of the leaves for photosynthesis and respiration is altered toward protecting and nurturing the colony of *Gynaikothrips ficorum* (Thysanoptera) on *F. microcarpa* (Souza *et al.* 2000).

An intriguing characteristic is that gall shapes and sizes are usually constant, but sexually dimorphic galls may occur, as is the case for Eriococcid-induced galls, whose male-induced galls are smaller and simpler than the large, more complex, galls induced by females (Gonçalves *et al.* 2005). This sexual dimorphism results from the differences in chemical signalers (Gullan *et al.* 2005), which make the Eriococcid galls good models for determining the origin of gall shapes and their cytological potentialities. In the *Annona dolabripetala* (= *Rollinia laurifolia*) (Annonaceae)-*Pseudotectococcus rollinae* (Hemiptera) system, female-induced galls have a longer life cycle and consequently higher stimuli for the development of parenchyma cells than male-induced galls (Gonçalves *et al.* 2005, 2009). The anatomy of the the *Pseudobombax grandiflorum* (Malvaceae)-*Eriogalococcus isaias* (Hemiptera) system shows less evident differences between male- and female-induced galls regarding the shape of the gall chamber and cell wall lignification in a wider area on top of the chamber of the galls induced by *E. isaias* females (Magalhães *et al.* 2015). In this case, the gall morphotype is the same independently of the sex of the inducers, but the mapping of the cell origin and fate has been used to support the different determination of gall induction by females and males. In the other taxonomic groups of insect-induced galls, the shapes rarely vary according to sex, as surprisingly observed in Cecidomyiidae-induced galls on *Matayba guianensis* (Sapindaceae) (Gonçalves *et al.* 2022).

Gall anatomy elucidates gall functional traits

Together with a greater investment in anatomical studies, histochemical, immunocytochemical, and cytological analyses have expanded the knowledge of gall functional traits, revealing potential cell responses in each plant tissue system. The dermal system is the first line of contact of the gall inducer with its host plant, where oviposition and the feeding activity of the larvae occur. Salivary secretions may induce increasing cell divisions, which may indicate the return of the epidermal cells to the meristematic condition. Also, changes in the patterns of determination of cell origin and fates in the epidermal cell mosaic (Glover 2000) result in the overexpression or impairment of trichome and stomata differentiation, with these structures being less dense or malformed. Trichomes may buffer the environmental abiotic factors, and their overdifferentiation, hyperplasia and/or hypertrophy are anatomical traits used to distinguish different morphospecies of Cecidomyiidae galls on *Mimosa gemmulata* (Fabaceae) (Costa *et al.* 2022a) and *Croton floribundus* (Euphorbiaceae) (Teixeira *et al.* 2022). Stomata malformation indicates the incapacity of the leaf lamina to photosynthesize and to perform cellular respiration, as observed in leaf galls on *F. microcarpa* (Souza *et al.* 2000), and *Aspidosperma* spp. (Lemos-Filho *et al.* 2007). In addition, the larger stomata of *Clinodiplosis profusa* (Diptera, Cecidomyiidae) and *Eugenia uniflora* (Myrtaceae) galls may allow higher gas exchange rates and tissue aeration in galls than in host leaves (Castro *et al.* 2023). Periderm can replace epidermis as the protective outer layer, expressing an unusual program in leaf development, but observed on leaf galls on *S. vulgaris* (Arduin *et al.* 1989; Kraus *et al.* 2002) and *Guarea macrophylla* (Kraus *et al.* 1996).

The galls induced by different organisms on superhosts of galling herbivores reveal the potential of each parasite to drive cecidogenesis in particular ways (Cornell 1983), with the superhosts of galling herbivores thus representing adequate models for addressing hypotheses about plant potentialities. Their associated gall inducers may cohabit not only the same plant individual, but in some cases the same plant organ, as observed in *Copaifera langsdorffii*-Cecidomyiidae (Diptera) systems, requiring seasonal syndromes in order to share the same plant potentialities over a one-year time

(Oliveira *et al.* 2013). The different anatomical profiles of the gall morphotypes on *C. langsdorffii* indicate different impacts and constraints regarding the same plant potential (Oliveira *et al.* 2008).

The study of galls on *Lonchocarpus muehlbergianus* (Fabaceae) has provided a new understanding of gall anatomy and histochemistry since its gall inducer, *Euphalerus ostreoides* (Hemiptera, Psyllidae) was previously considered incapable of inducing the differentiation of nutritive cells (Oliveira *et al.* 2006). However, this understanding began to change when these galls were found to have peculiar ultrastructural characteristics in the cells that accumulate carbohydrates. Carbohydrates were already known to accumulate in the tissues of galls induced by *E. ostreoides* (see Oliveira *et al.* 2006), but no cellular or subcellular characteristics of such galls had been previously described. Further investigations of these galls by Isaias *et al.* (2011) demonstrated that the ultrastructural features of cells where the carbohydrates accumulate and where the gall inducer feeds were similar to those of true nutritive tissues formerly described by Bronner (1992) for Cecidomyiidae (Diptera) and Cynipidae (Hymenoptera) galls. This was the first time that histochemical profiles and ultrastructural analyses were used together to describe a nutritive-like tissue, *i.e.*, a tissue that is similar in structure and function to those described in the classical literature for other insects, but does not fully fit the concept of “true nutritive tissues” described by Bronner (1992). The fact that nutritive-like tissues were reported for galls induced by a sap-sucking insect, classically believed to induce non-nutritive galls, was considered a paradigm shift.

Further investigations on the “nutritive nature” of hemipteran galls have shown the accumulation of primary metabolites and highly specialized ultrastructure of cells in galls induced by *Nothotrioza myrtoides* and *N. cattleyani* (Hemiptera, Triozidae) on *P. myrtoides* and *P. cattleyanum* (Myrtaceae) (Carneiro *et al.* 2014, 2015), when the terminology “nutritive-like cells” and “nutritive tissues” was used for the first time to describe cell types of galls induced by sap-sucking insects. Beyond the nutritional aspects concerning plant cell manipulation, the analyses of *L. muehlbergianus* galls demonstrated the accumulation of oxonium salts, a novelty for flavonoidic derivatives described in galls, highlighting the ability of the gall inducer to manipulate the chemical profile of the plant

(Oliveira *et al.* 2006). The phenolic derivatives mediate plant-herbivore interactions along several pathways and, as the investigations on gall anatomy, histochemistry and immunocytochemistry have evolved, the association of phenolics with plant growth regulators and as ROS scavengers for the maintenance of tissue homeostasis has been discussed.

The role of metabolites - from chemical defenses to signalers of gall development

More than being astringent molecules that turn plant tissues unpalatable and deter herbivore attacks, phenolics interact with other molecules taking part in crucial steps of gall development. The effects of the fluctuation in the levels of phenolics in plant and gall tissues may influence gall metabolism and the maintenance of tissue homeostasis (Isaias *et al.* 2015). In galls, the phenolic compounds contribute to absorbing and neutralizing free radicals, which seem to be one of the main roles of these compounds in gall tissues (Detoni *et al.* 2010, 2011; Isaias *et al.* 2015).

Phenolic compounds have been related to the defensive role against parasites and/or parasitoids (Harborne 1980), fungi or other agents in galls. Later, they were suggested to be involved in hormonal regulation, inhibiting indole-3-acetic acid (IAA) oxidases, thus indirectly increasing the accumulation of auxins (Hori 1992), which are phytohormones responsible for cell hypertrophy (Cleland 1995). As naturally phenolic-rich structures, galls are good models demonstrating the interaction of phenolics and phytohormones due to the increased and local cell hypertrophy and hyperplasia. Histochemical tests were used for the detection of this interaction (Leopold & Plummer 1961), with the Ehrlich's reagent revealing the accumulation of IAA together with catechol, chlorogenic acid or caffeic acid by the development of different colors. By the application of this reagent, the double accumulation of phenolic compounds and IAA could be detected in the parenchyma of Cecidomyiidae galls on *P. gonoacantha* (Bedetti *et al.* 2017, 2018). Curiously, the sites with the most intense staining of the phenolics-IAA complex are also the sites with the highest cell hypertrophy, thus supporting the growth-promoting effect of phenolic accumulation in galls (Hori 1992). Analyses of the horn-shaped galls on *C. langsdorffii* (Carneiro *et al.* 2017), for example, demonstrated that the distribution of phytohormones along

the developmental process is crucial for the determination of the gall bizarre shape. Together with auxins, cytokinins in gall tissues were histochemically and immunocytochemically detected at hyperplastic sites, confirming the role of these two phytohormones in the determination of gall shapes (Bedetti *et al.* 2017, 2018). Galls have been used for proposing hypothetical models of plant organogenesis involving ROS-phenolics-IAA-cytokinins based on empirical evidence. These proposals are valuable for the understanding of possible plant responses to a wide variety of biotic and abiotic stressors.

Gall responses to environmental conditions

Environmental conditions such as water availability, light intensity, and temperature variations have effects on the diversity of gall structures (Stone & Schönrogge 2003), as documented in galls in the restrictive coastal environments of the Brazilian *Restinga* (Isaias *et al.* 2017; Arriola *et al.* 2018; Costa *et al.* 2022b). The effects of water availability and light intensity on gall structure have been recently investigated, demonstrating a high investment in water-storage parenchyma, a site of ion accumulation, in leaf galls on *Avicennia schaueriana* (Acanthaceae)-*Meunieriella* sp. (Diptera, Cecidomyiidae) system. In these galls, salt excess is removed by epidermal salt glands, favoring internal ion balance (Nobrega *et al.* 2021), a specific environmental adaptation to the variable salinity and flooding of mangrove environments. In the case of the *Mimosa tenuiflora* (Fabaceae) - *Lopesia mimosae* (Diptera, Cecidomyiidae) system, cell wall porosity mediated by methyl-esterified homogalacturonans seems to favor water flux toward the storage parenchyma, favoring gall development in the *Caatinga* environment (Nogueira *et al.* 2022). The hyperplasia and cell hypertrophy of the ground tissue system are also influenced by light conditions, with effects on sun and shade galls of *C. profusa* on *E. uniflora* (Castro *et al.* 2023).

In addition to abiotic factors, the diverse guild of organisms associated with galls such as parasitoids, inquiline, predators, and successors (Luz & Mendonça-Júnior 2019) can affect gall structure. The attack by these organisms may cause the collapse of nutritive cells, the loss of cell membrane integrity (Rezende *et al.* 2019), and precocious gall senescence (Costa *et al.* 2022c). In contrast to the effect of parasitoids, the

additional feeding stimuli of inquiline may induce an increase in gall tissue thickness (Rezende *et al.* 2019, 2021). The successors, such as ants, may occupy post-senescent galls, and, interestingly, their movements when entering and exiting the gall seem to reactivate cambium activity and stimulate the differentiation of an ectopic phellogen lining the larval chamber, as demonstrated for *E. erythropappus* stem galls (Jorge *et al.* 2022a). This post-senescence case of activity in gall tissues has been used to raise the interest of young students in nature and science using storytelling strategies (Jorge *et al.* 2022b, 2023).

Studies of gall anatomy based on the histochemistry, immunocytochemistry, cytology, physiology, and chemistry of Brazilian host plant-gall inducer systems are progressing towards the interpretation of structural and functional traits not only at the species-specific level but also in terms of environmental bases since gall development is a highly multifactorial phenomenon (Fig. 5). Thus, we propose that gall development should be interpreted as the result of taxon-dependent changes caused by the different galling organisms, but also by the various constraints and potentialities peculiar to each plant species and to each plant organ. As a product of complex ecological phenomena, gall structure should also be considered in terms of biotic and abiotic factors (Fig. 5) since galls are not parasite-free and are found across different biomes in Brazil and worldwide. Based on this perspective, plant anatomists have adhered to the open field of

interdisciplinary research that is still growing and innovating. From a broader perspective, data of gall occurrence in Brazilian phytophysiognomies is of paramount importance for the progression of gall studies toward understanding functional traits, adaptive anatomical features under current and future scenarios of climate changes.

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Data availability statement

In accordance with Open Science communication practices, the authors inform that all data are available within the manuscript.

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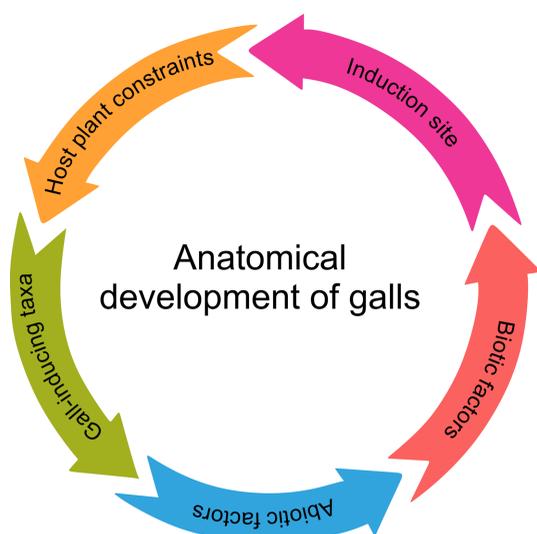


Figure 5 – Diagram of the factors involved in the determination of the anatomical development of galls.

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