Review

Manipulation of host plant cells and tissues by gall-inducing insects and adaptive strategies used by different feeding guilds

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ABSTRACT

Biologists who study insect-induced plant galls are faced with the overwhelming diversity of plant forms and insect species. A challenge is to find common themes amidst this diversity. We discuss common themes that have emerged from our cytological and histochemical studies of diverse neotropical insect-induced galls. Gall initiation begins with recognition of reactive plant tissues by gall inducers, with subsequent feeding and/or oviposition triggering a cascade of events. Besides, to induce the gall structure insects have to synchronize their life cycle with plant host phenology. We predict that reactive oxygen species (ROS) play a role in gall induction, development and histochemical gradient formation. Controlled levels of ROS mediate the accumulation of (poly)phenols, and phytohormones (such as auxin) at gall sites, which contributes to the new cell developmental pathways and biochemical alterations that lead to gall formation. The classical idea of an insect-induced gall is a chamber lined with a nutritive tissue that is occupied by an insect that directly harvests nutrients from nutritive cells via its mouthparts, which function mechanically and/or as a delivery system for salivary secretions. By studying diverse gall-inducing insects we have discovered that insects with needle-like sucking mouthparts may also induce a nutritive tissue, whose nutrients are indirectly harvested as the gall-inducing insects feeds on adjacent vascular tissues. Activity of carbohydrate-related enzymes across diverse galls corroborates this hypothesis. Our research points to the importance of cytological and histochemical studies for elucidating mechanisms of induced susceptibility and induced resistance.

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1. Introduction

Many species of herbivorous insects have evolved the ability to modify tissues of their host plants to produce highly specialized structures known as galls. The induction of galls represents an adaptation of the insect to the host plant, as well as an adaptation of the plant to the insect (Berryman and Ferrel, 1988). As diverse are the gall-inducing organisms, so are their host plants. Whether there are unifying features of galls and gall induction has been debated for many years (e.g., Mani, 1964; Price et al., 1987; Hartley, 1998; Stone and Schönrogge, 2003; Shorthouse et al., 2005; Raman, 2011; Isaias and Oliveira, 2012). In spite of it, some general conclusions on gall-inducing insect-plant interactions can be drawn: (1) typically gall inducing insects are strict specialists and therefore have had to face many constraints imposed by their host(s) and the environment (e.g., Price et al., 1987; Fernandes, 1990; Julião et al., 2014a); (2) as a result, a great variety of life strategies is observed (e.g., Cornell, 1983; Shorthouse and Rohfritsch, 1992; Rohfritsch, 1992); (3) complex larval behaviors are responsible for many different gall structures (Shorthouse and Rohfritsch, 1992; Rohfritsch, 1992) and (4) phylogenetic constraints and female ovipositing behavior have strong effects on gall-inducing insect population dynamics (Price et al., 1990). Peculiarities in anatomical, biochemical and physiological features have prompted some authors to view complex insect-induced galls as entirely new and unique plant organs because they have diverged so dramatically from the normal trajectory of host plant development (e.g. Shorthouse et al., 2005; Oliveira and Isaias, 2010a).

Galls induced by insects vary in all possible traits: color, shape, size, phenology, hardness, chemistry, internal structure, and abundance in nature. While morphologically simple galls are represented by slight swellings of leaf or stem tissues, complex galls may be elaborate structures with external surfaces covered by diverse features, e.g., secretory trichomes that trap and kill natural enemies of the gall-inducing insects (Fernandes, 1987), spines or even glands that secret honeydew to attract ants that act as bodyguards (e.g. Fernandes et al., 1999), and production of oxalate crystals that surround the larval chamber of cynipids, making its location by ovipositing parasitoids difficult (Fernandes et al., 1990). These remarkable changes in plant development provide evidence that gall-inducing insects are among the Earth's most sophisticated herbivores (Shorthouse et al., 2005).

Many gall-inducing insect species have been documented and many more will be found. Espírito-Santo and Fernandes (2007) postulated that the number of gall-inducing insects worldwide may reach 133,000 species. This estimate was based on the reported average of gall-inducing species richness per plant species and, alone, indicates the biological importance of this group. Their astonishing diversity was recently corroborated in a study on the diversity of gall-inducing insects on the harsh canopies of the Amazonian rain forests (e.g. Julião et al., 2014a). From an economic point of view, gall-inducing insects are also of major relevance. Many of these insects represent serious threats to agriculture or forestry, while others provide benefits as biological control agents of invasive plant species (Fernandes, 1987).

Our knowledge on the way host plants react to gall-inducing insects relies on cytological and histochemical profiles of diverse neotropical insect-induced galls. Current text reviews: (1) the diverse and numerous insect-induced galls found in a variety of habitats in the neotropics, (2) the importance of synchronizing host plant phenology and colonization by gall-inducing insects, and (3) the results of our cytological and histochemical studies on insect-induced galls of the neotropics. Based on this discussion we propose 'themes' underlying gall induction and development and insects nutrition accessed by histochemical analysis of gall tissues. A range of neotropical plant species associated to gall-inducing insect species was used to illustrate this review (Table 1). When the insect species is undescribed, we used gall morphotypes (Isaias et al., 2013) along with information on the order/family and feeding guild of the insect that induces the gall.

2. An overview of neotropical gall-inducing insects

Gall-inducing insects are distributed worldwide, with the orders Diptera, Hymenoptera, and Hemiptera being dominant, while the most common gall-inducing families are likely the Cecidomyiidae, Cynipidae, and Psylloidea, respectively. The frequency of these taxa varies among the biogeographical regions, but in the Neotropical region, the majority of gall-inducing species belong to the family Cecidomyiidae (Gagné, 1994; Fernandes and Santos, 2014). Other taxa that are frequently found include the Cynipidae, Psyllidae, Eriophyidae, Apionidae, and Gelechioidea (Cuevas-Reyes et al., 2014; Hanson et al., 2014; Medianero et al., 2014; Quintero et al., 2014). A review on the ecology and distribution of gall-inducing insects in the neotropics is found in Fernandes and Santos (2014).

Independent of the biogeographical region, the degree of sophistication of the galling habit may have arisen under selection imposed by host plant defense mechanisms against natural enemies, and may vary among habitats and environments. Although many host plants and many different habitats are found in the neotropics, analogous diversity of strategies occurs in other regions of the world. A greater diversity of gall-inducing insects is found in xeric habitats as opposed to mesic habitats (e.g., Fernandes and Price, 1988, 1991), at lower altitudes (e.g., Fernandes and Price, 1988, 1991; Lara et al., 2002; Quintero et al., 2014), and on the xeric canopy compared to the more humid understory (Julião et al., 2014a,b; Medianero et al., 2014). Mechanisms that contribute to this differential distribution are still being studied, but so far results point to the major influence of natural enemies (parasites, herbivores, and pathogens), plant resistance (e.g., Fernandes and Price, 1992; Ribeiro-Mendes et al., 2002; Ribeiro and Basset, 2007; Ribeiro et al., 2014), host plant species richness (e.g., Fernandes, 1992), density of host plants (Gonçalves-Alvim and Fernandes, 2001), dynamics of plant meristems (Espírito-Santo et al., 2012), and super-host plants (e.g., Fernandes and Price, 1991; Formiga et al., 2011, 2015). The super host plants, such as *Copaifera langsdorffii* (Table 1), support a high richness of gall-inducing species and are relatively common in the neotropics.

The knowledge on the relationships between Neotropical gall-inducing insects and their host plants has vastly improved during the last two decades. Earlier botanical studies primarily focused on pure descriptive anatomical and morphological studies (e.g. Fernandes et al., 1990). In contrast, recent studies have addressed questions related to host tissue manipulation and gall ontogenesis in the light of evolution and adaptation (Oliveira and Isaias, 2010a, b; Isaias et al., 2014a).

3. Life history strategies of gall-inducing neotropical insects

Gall-inducing insects must synchronize their colonization activities with the phenology of host tissues, once they are sessile and in close association with their specific host plants. Precise synchronization provides the best morphological and physiological conditions of plant tissues for insect colonization, survival and growth.

For some neotropical gall-inducing species, fine-tuned synchronization results in univoltine life histories. This strategy is associated with hosts that flush new leaves only once a year, which is the case of the gall inducers *Nothotrioza* spp. and *Pseudopha-*

Table 1
Check list of Neotropical host-gall inducing insects systems discussed and their feeding guild.

Host species	Insects species/morphotype	Order:Family	Feeding guild	References
Copaifera langsdorffii (Fabaceae)	Horn-shaped gall Cup-shaped gall Midrib-gall Intralamminar gall Suberized spherical gall Flat gall	Diptera:Cecidomyiidae	Scraper	Oliveira et al. (2013). Oliveira and Isaias (2009), Oliveira et al. (2011a)
Aspidosperma spruceanum (Apocynaceae)	Intralaminar gall	Diptera:Cecidomyiidae	Scraper	Campos et al. (2010); Oliveira et al. (2010), Formiga et al. (2009)
Piptadenia gonocantha (Fabaceae)	Pinnula lenticular Rachis fusiform gall	Diptera:Cecidomyiidae	Scraper	Bedetti et al. (2014)
Marcetia taxifolia (Melastomataceae)	Pistil-shaped gall	Diptera:Cecidomyiidae	Scraper	Ferreira and Isaias (2014)
Marcetia taxifolia (Melastomataceae)	Fusiform stem gall	Lepidoptera	Chewing	Ferreira and Isaias (2013)
Bauhinia ungulata (Fabaceae)	Leaf-folding galls	Lepidoptera	Chewing	Bedetti et al. (2013)
Tibouchina pulchra (Melastomataceae)	Globoid leaf galls	Lepidoptera	Chewing	Vecchi et al. (2013)
Ficus microcarpa (Moraceae)	*Gynaikothrips ficorum*	Tysanoptera: Phlaeothripidae	Chewing	Souza et al. (2000)
Psidium cattleianum (Myrtaceae)	*Nothotrioza cattleiani*	Hemiptera: Triozidae	Sucking	Butignol and Pedrosa-Macedo (2003)
Lonchocarpus muehlbergianus (Fabaceae)	*Euphalerus ostreoides*	Hemiptera: Psyllidae	Sucking	Oliveira et al. (2006), Isaias et al. (2011)
Psidium myrtoides (Myrtaceae)	*Nothotrioza myrtoidis*	Hemiptera: Triozidae	Sucking	Carneiro et al. (2013)
Aspidosperma macrocarpon (Apocynaceae)	*Pseudophacopteron longicaudatum*	Hemiptera: Phacopteronidae	Sucking	Malenovský et al. (2015), Castro et al., 2013
Aspidosperma tomentosum (Apocynaceae)	*Pseudophacopteron longicaudatum*	Hemiptera: Phacopteronidae	Sucking	Malenovský et al. (2015)
Aspidosperma australe (Apocynaceae)	*Pseudophacopteron aspidospermi*	Hemiptera: Phacopteronidae	Sucking	Campos et al. (2010), Oliveira and Isaias (2010b)
Pseudobombax grandiflorum (Malvaceae)	*Eriogallococcus isaias*	Hemiptera: Eriococcidae	Sucking	Magalhães et al. (2015)
Rollinia laurifolia (Annonaceae)	*Pseudotectoccus rolliniae*	Hemiptera: Eriococcidae	Sucking	Gonçalves et al. (2005, 2009)
Matayba guianensis (Sapindaceae)	*Bystracoccus mataybae*	Hemiptera: Eriococcidae	Sucking	Hodgson et al. (2013)
Schinus polygamus (Anacardiaceae)	*Calophya duvauae*	Hemiptera: Calophyidae	Sucking	Dias et al. (2013)

copteron longicaudatum with their associated host species. These insects have only a narrow window of opportunity to attack the shortly available meristematic tissues, hence favoring the evolution of a univoltine life cycle. The double co-generic systems *Nothotrioza cattleiani–Psidium cattleianum* (Butignol and Pedrosa-Macedo, 2003), and *Nothotrioza myrtoidis–Psidium myrtoides* illustrate this synchronization nicely (Carneiro et al., 2013). In both *Nothotrioza* spp.–*Psidium* spp. systems, the emergence of adults is closely synchronized with leaf flushing, and just young leaves are adequate sites of oviposition and gall establishment (Butignol and Pedrosa-Macedo, 2003; Carneiro et al., 2013). Similar phenological synchronization occurs in the *P. longicaudatum–Aspidosperma macrocarpon* system (Malenovský et al., 2015), with the peaks of leaf falling coinciding with the emergence of adults from mature galls, and leaf flushing occurring during the period of induction of new galls (Castro et al., 2013).

Some species of Neotropical gall-inducing insect species induce galls on deciduous host plants, and developed peculiar life cycle strategies. This is the case of the eriococcids *Eriogallococcus isaias*, *Pseudotectococcus rolliniae*, and *Bystracoccus mataybae* that attack *Pseudobombax grandiflorum* (Malvaceae), *Rollinia laurifolia* (Annonaceae), and *Matayba guianensis* (Sapindaceae), respectively. These gall inducers establish on immature leaves during the period of leaf flushing and leave the mature galls just before leaf falling during the dry season. To survive the dry season, when no leaves are available on the host plants, these three eriococcid species use the stems of their host plants to overwinter. In the stems of *R. laurifolia* and *M. guianensis*, galls for dormancy are induced by *P. rolliniae* and *B. mataybae,* respectively (Gonçalves et al., 2005, 2009; Hodgson et al., 2013). On the other hand, the gall-inducing species *E. isaias* shelters in depressions on the stem bark of *P. grandiflorum* as it is not capable of inducing galls for dormancy or attacking other host species (Magalhães et al., 2015). These host plants-gall-inducing eriococcids systems reveal a novel phenomenon of gall-inducing

insects, which is the capacity of first instar nymphs to induce stem galls for dormancy, while the second instar nymphs induce leaf galls.

In some multivoltine systems the gall-inducing larvae are able to induce galls not only in young but also in mature tissues of their host plants. Thus, these gall-inducing species are able to explore the full spectrum of responsiveness (*sensu* Weis and Abrahamson, 1988) of plant parenchymatic cells to the gall-inducing stimuli (Oliveira and Isaias, 2009). Such ability was recorded on the systems represented by different gall-inducing herbivores and their hosts *Baccharis concina*, *Baccharis dracunculifolia*, *Aspidosperma spruceanum*, *Aspidosperma australe*, and *Copaifera langsdorffii* (Arduin and Kraus, 2001; Oliveira and Isaias, 2009; Campos et al., 2010).

Although univoltine and multivoltine insect species occur simultaneously in the field, multivoltinism seems to be especially important for those species that associate to superhosts of gall-inducing herbivores (Isaias et al., 2013), as far as the sharing of the same plant potentialities is concerned. *C. langsdorffii* (Fabaceae), for instance, shelters at least nine Cecidomyiidae gall-inducing species. Oliveira et al. (2013) reported three well-defined seasonal syndromes in this system in which the gall-inducing insects select host niches according to the availability of water. The first syndrome reveals that the abundance of the horn-shaped and of the cup-shaped galls decrease during the dry season. The second syndrome reveals that other four gall-inducing insect species (associated to the hairy spherical, midrib, crown-shaped, and intralaminar galls) adjust their cycles to leaf flushing. The third syndrome involves three gall-inducing insect species (associated to the glabrous spherical, suberized spherical, and flat galls), which occur homogeneously along the year, with a slight peak of abundance in July (Fig. 1). These syndromes may reflect strategies towards the occupation of distinct temporal niches during the phenological cycle of the same host plant (Oliveira et al., 2013).
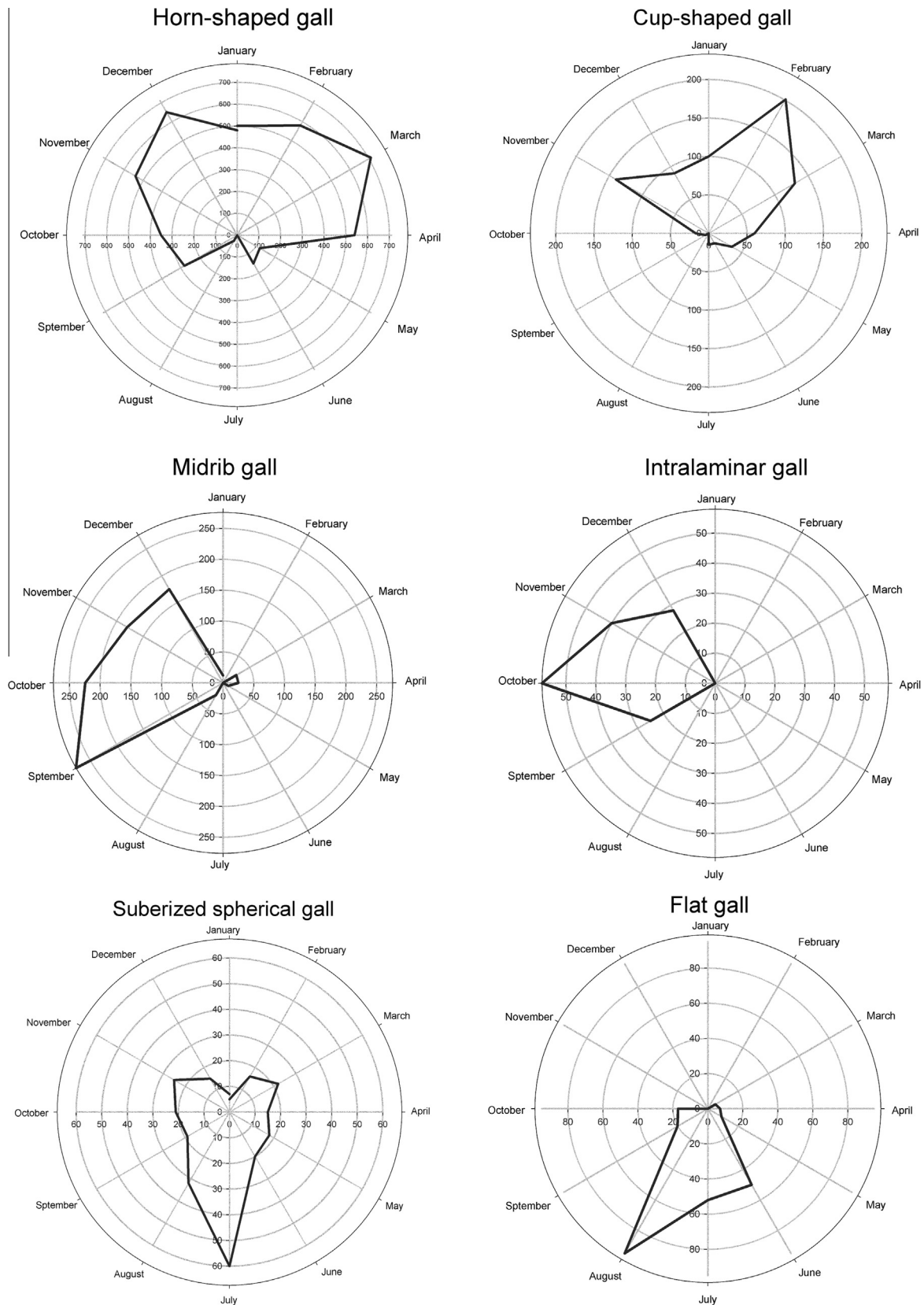
Fig. 1. Monthly patterns of abundance for six gall morphotypes induced by unidentified species of Diptera: Cecidomyiidae on *Copaifera langsdorffii* (Fabaceae). The observation of these morphotypes concomitant with plant phenology over the year evidenced three seasonal syndromes, which permitted the galling insects to share the same host plant. The Horn-shaped gall and Cup-shaped gall are the most abundant morphotypes and are induced concomitantly to leaf sprouting, in a period of high water availability in the host plant. The Midrib gall and the Intralaminar gall have peaks of abundance in September and October, respectively, they have short cycles, and they are induced after the leaf sprouting. The Suberized spherical gall and the Flat gall are most abundant in July and August, a period of leaf senescence and leaf falling with low water availability in the host plant. (Adapted from Oliveira et al. 2013).

4. Events involving reactive oxygen species (ROS), growth regulators and phenolics during gall initiation

A cascade of events involving ROS, growth regulators and phenolics has been proposed to contribute to subcellular signaling during the very first developmental steps leading to gall induction (Bedetti et al., 2014; Guiguet et al., 2016), especially for several Neotropical gall systems (Isaias et al., 2015). For galls induced by *Pseudophacopteron aspidospermi* (Hemiptera) on *A. australe* (Malenovský et al., 2015), the high oxidative stress detected in young (first cell division and elongation, slightly visible spot) and mature galls has been linked to the establishment of histological and cytological gradients, and consequently, to the differentiation of protective and nutritive tissues (Oliveira and Isaias, 2010b; Oliveira et al., 2010). The elevated synthesis and accumulation of phenolics in galls could be a primary response to ROS production for they act as important ROS-scavenging molecules (Aboul-Enein et al., 2007; Del Río and Puppo, 2009). The biosynthesis of phenolics in galls has often been related to the defense against natural enemies, including parasitoids, herbivores and fungi (Cornell, 1983; Fernandes and Price, 1988, 1991; Hartley, 1998). Phenolics are also increased in some host lineages and even augmented independently in stressed environments (Coley et al., 1985; Fernandes and Price, 1991). It is not surprising therefore that gall-inducing insects are the most common herbivores of plants in stressed environments (e.g. Fernandes and Price, 1988, 1991; Julião et al., 2014b).

We propose that the important role of phenolics in gall induction has profound consequences for the manipulation of the host tissues and resulting gall-inducing success. Besides minimizing the effects of the oxidative burst by ROS (Oliveira et al., 2011a,b; Isaias et al., 2015), phenolics may increase the levels of auxins (mainly the Indole-3-Acetic Acid, IAA) by interacting with auxin oxidases, provoking cell hypertrophy, i.e. an increase in cell size (Bedetti et al., 2014). Dias et al. (2013) detected the accumulation of phenolics by histochemical assays in the host tissues surrounding the eggs of *Calophya duvauae* (Hemiptera: Calophyidae) oviposited on the abaxial epidermis of the leaves of *Schinus polygamus* (Anacardiaceae), the site of gall initiation. The simultaneous occurrence of phenolics, ROS, and IAA at the gall site after the insects oviposition and during gall growth has been histochemically detected in Cecidomyiidae galls on *Piptadenia gonoacantha* (Bedetti et al., 2014), providing evidence for the hypothesis of phenolic-regulated type of cell growth. These data reinforce that the physiologies of plants and gall-inducing insects could be synergistically tied to trigger and maintain the chemical signaling responsible for the development of the new steps that lead to the development of the gall phenotype (Fig. 2).

5. Gall induction stimulates physiological and structural alterations on the host

Processes related to oviposition or feeding by early larval stages are crucial for the stimulation of cytological and anatomical responses of host plants (Shorthouse and Rohfritsch, 1992; Rohfritsch, 1992; Stone and Schönrogge, 2003), and have enormous evolutionary consequences for population dynamics (Price et al., 1990). Different taxa of gall-inducing insects show distinct mouthparts and feeding behaviors. In some cases, these include periods of quick feeding alternated with periods of resting to conserve energy, such as gall-inducing lepidopterans (Chapman and De Boer, 1995). These larvae often have cyclic feeding patterns that include initiation, maintenance and termination of their activity (Chapman and De Boer, 1995). The consumption of the nutritive tissue of galls induced by chewing insects leads to the development of sites of fast differentiation of new nutritive cells. Such response is evidenced in the Neotropical lepidopteran galls on *Tibouchina pulchra* (Vecchi et al., 2013), *Marcetia taxifolia* (Ferreira and Isaias, 2013), and *Bauhinia ungulata* (Bedetti et al.,
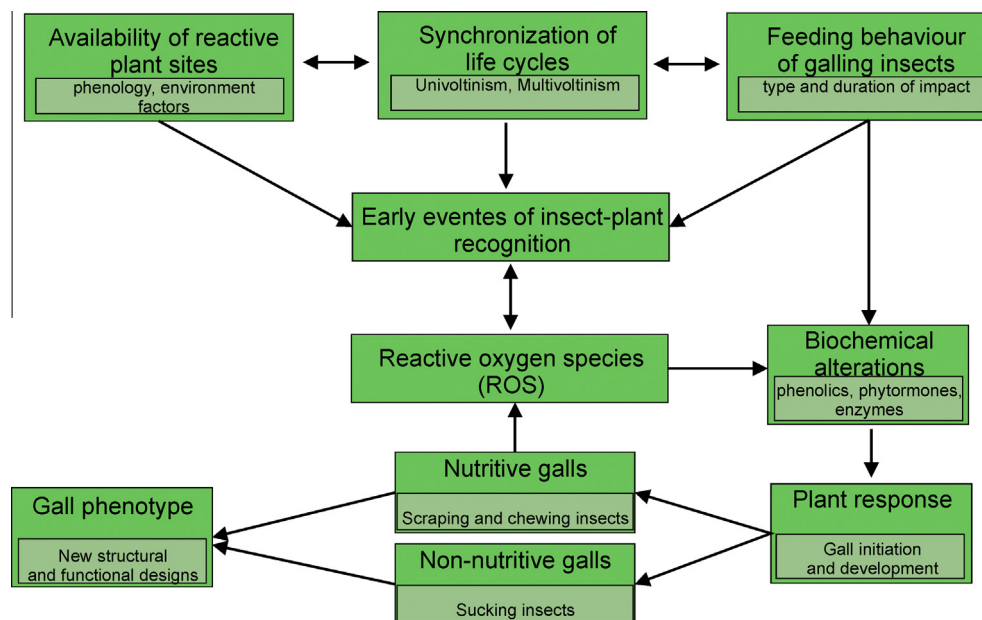

Fig. 2. Schematic diagram of the synergistic effects of plant and insect elicitors for gall initiation and development. Dark green colors indicate plant-controlled levels. Light green colors indicate insect-controlled levels. Gradient tones between green and light green indicate the insect-plant interactions on the response. Events of plant cell recognition are dependent on three factors: the availability of plant reactive sites, the synchronization of the life cycles of host plants and gall-inducing insects, and the distinct feeding behaviors of gall-inducing insect taxa. Reactive oxygen species may be among the first signaling molecules to trigger different events. In one side, high concentration of ROS may lead to cell death, and consequently the failure of gall establishment; on the other side, low concentration of ROS may lead to biochemical alterations, which modulate plant cell responses, and gall development. Such cell responses lead to the morphogenesis of nutritive and non-nutritive galls with specific phenotypes related to peculiar structural and functional designs. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
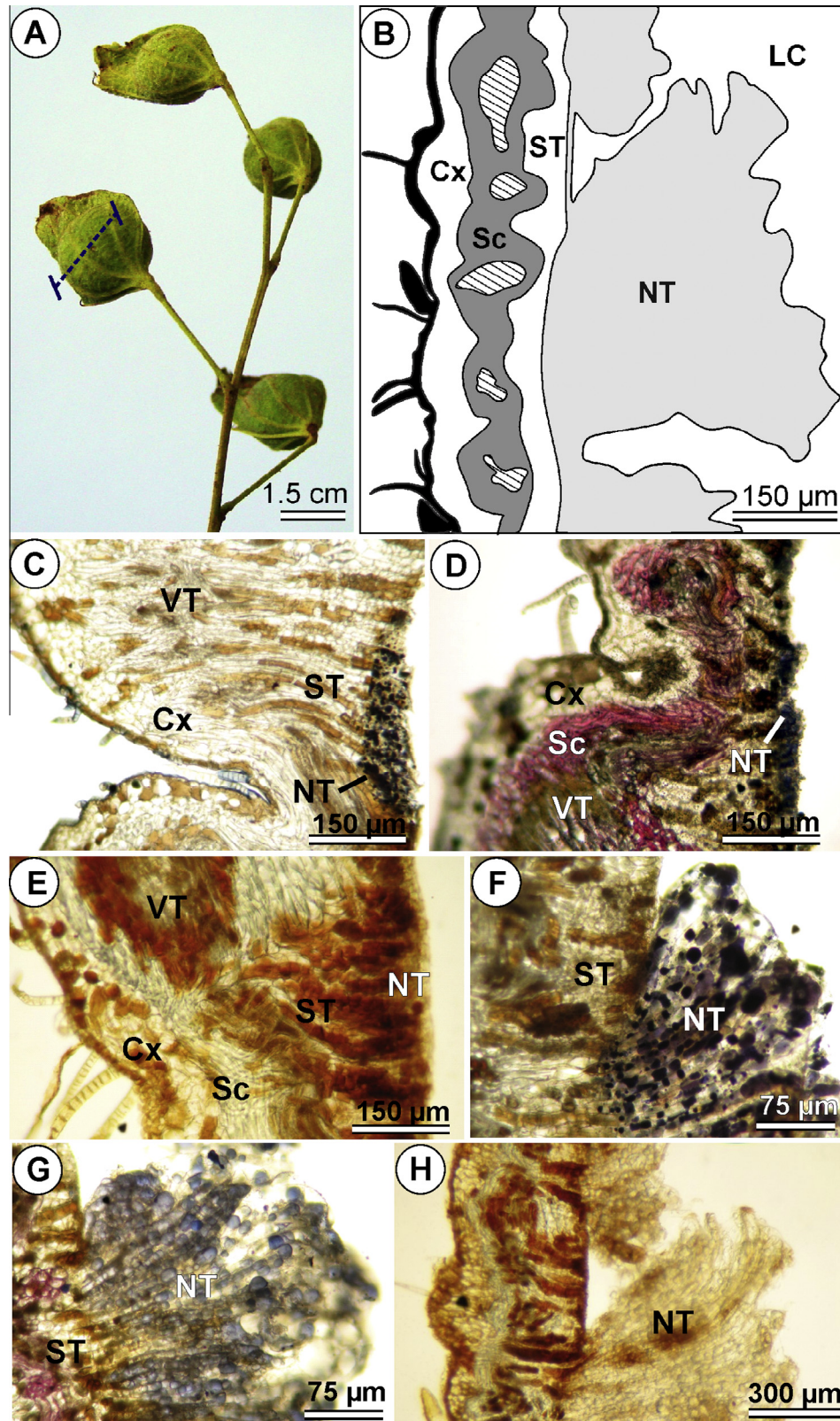
Fig. 3. Galls induced by an unidentified Lepidoptera on *Bauhinia ungulata* (Fabaceae: Caesalpinioideae). (A) Leaf-folding galls (the dotted line indicates the transverse plane of the sectioning made to the histochemical tests illustrated in C–H. (B) Diagram indicating tissue organization in transverse section. Epidermis (black), cortex (Cx), schlerenchyma layer (Sc) with vascular tissues embedded (hatched), storage nutritive tissue (ST), and typical nutritive tissue (NT) lining the larval chamber (LC). (C)–(H) Histochemical detection of lipids, terpenoids and reducing sugars in nutritive tissues of the gall, as described by Bedetti et al. (2013). (C)–(E) Galls with non-parasitoidized lepidopteran larva. (F)–(H) Galls with hymenopteran parasitoids and a dead lepidopteran larva. (C) Lipids detected by Sudan black B in typical nutritive tissue (NT) lining the larval chamber. (D) Terpenoids detected by α-naphtol/*p*-phenilenediamine (NADI) in typical nutritive tissue (NT). (E) Reducing sugars detected by Fehling's reagent in some cortical cells (Cx), vascular tissue (VT), and storage nutritive tissue (ST). (F)–(H) Hyperplasia of the typical nutritive tissue due to the death of the inducer and cessation of its feeding in parasitoidized galls (Bedetti et al. 2013). The hyperplasic nutritive tissue also accumulates lipids (F) and terpenoids (G), but does not accumulate reducing sugars (H).

2013) (Fig. 3). Galls induced by Lepidoptera, have been characterized as non-nutritive (see next section) in the temperate region (Dreger-Jauffret and Shorthouse, 1992) due to the feeding habit of their larvae that causes the rapid consumption of nutritive tissues, which could only be characterized using plant microtechniques. However, galls induced by distinct species of Lepidoptera on *B. ungulata* and *M. taxifolia* do differentiate true nutritive tissues (Bedetti et al., 2013; Ferreira and Isaias, 2013). *B. ungulata* galls are formed by leaf-folds that delimit a larval chamber. These galls have typical tissue organization, with outer epidermis, parenchymatic cortex and sclerenchyma wit interspaced vascular bundles. The nutritive tissue is divided into a storage nutritive tissue, and typical nutritive tissue lining the larval chamber, where the larvae actively feeds (Fig. 3). Histochemical tests detect the presence of lipids, terpenoids and reducing sugars in tissues nearest to the gall chamber, as described by Bedetti et al. (2013), and corroborate the existence of a true nutritive tissue. The outermost nutritive zone (storage nutritive tissue) accumulates starch and reducing sugars, while the innermost nutritive zone (typical nutritive tissue) accumulates lipids (Fig. 3) (Giron et al., 2016). This tissue zonation implies a distinct impact of insect feeding on the accumulation of metabolites, which ends up the conversion of carbohydrates into lipids and cell replication. Similar gradients of starch and lipids were observed in other galls induced by chewing insects (Meyer, 1987; Rohfritsch, 1992; Bronner, 1992), and indicate convergent cell responses to the voracious feeding of such insects.

In contrast to the chewing larvae of Lepidoptera and Hymenoptera, phloem feeders such as the Hemiptera, may feed constantly for several days or even for all their nymphal and/or adult stages (Tjallingii, 1995). Such feeding behavior turn galls into strong sinks of photoassimilates (Hartley, 1998), as observed for the galls induced by *P. longicaudatum* (Hemiptera) on *A. macrocarpon* (Castro et al., 2013; Malenovský et al., 2015), and *N. myrtoidis* on *P. myrtoides* (Carneiro et al., 2014a). In this last host-insect system, the histochemical profile was assessed, and the gall accumulates several primary metabolites like sugars, proteins and lipids, for instance, indicating the establishment of a strong sink towards the gall site. In addition, cytological studies revealed, for the first time, the redifferentiation of nutritive cells in the vascular and perivascular parenchyma in hemipteran galls (Carneiro and Isaias, 2015), based on the ultrastructural features of these cells, and on the activity of carbohydrate-relates enzymes detected histochemically. These cells are cytoplasm-rich cells with small vacuoles, hypertrophied nuclei and nucleoli, numerous cytoplasmic organelles, abundant RNA, carbohydrates, and high enzymatic activity, characteristic features of nutritive cells. They are located in the innermost cell layers of the galls, where *N. myrtoidis* may insert its mouth apparatus either directly on sieve tube elements or in these perivascular nutritive cells, and assess nutritive substances.

Among the gall-inducing insects, the Cecidomyiidae are the most specialized to the gall-inducing habit (Gagné, 1994). Cecidomyiids may activate and deactivate different parts of their salivary glands (Gagné, 1994), thus stimulating plant tissues differently along their life cycles. Different substances accumulated in the storage and nutritive cells in cecidomyiid galls like starch, reducing sugars and proteins are involved in the nutrition of the insect larvae, in the maintenance of cell machinery at the gall site (Oliveira et al., 2010), or can even be displayed as an aposematic trait (Inbar et al., 2010).

Plant cell responses at the gall-inducing sites have been widely tested experimentally, as far as the accumulation and the suppression of specific metabolites are concerned. Nevertheless, the set of signaling molecules that integrates information at the level of plant-insect interactions remains a mystery. As galls are completely formed by plant cells, the specificity of the relationship between gall-inducing insects and host plants have been suggested

to be modulated by hormones (Tooker and Helms, 2014). The synthesis of ethylene (ET) is stimulated by several factors, such as chemical stimuli or mechanical lesions (O'Donnel et al., 1996), which are inflicted in gall tissues by the feeding activity of the gall-inducing herbivores or during oviposition. Depending on the concentration, ET can alter the developmental patterns of plant tissues, and induce lateral expansion (Taiz et al., 1983), which is diagnosed in some gall systems. Lateral cell elongation is detected during the development of several galls, such as the bivalve-shaped gall induced by *Euphalerus ostreoides* on *Lonchocarpus muehlbergianus* (Oliveira et al., 2006; Isaias et al., 2011), the globoid gall induced by *N. myrtoidis* on *P. myrtoides* (Carneiro et al., 2014b), and also the pistil-shaped gall induced by a cecidomyiid, and in the stem fusiform gall induced by a lepidopteran, both on *M. taxifolia* (Ferreira and Isaias, 2013, 2014).

During gall initiation and/or development, cell hypertrophy and tissue hyperplasia, i.e., an increase in cell number, are the main processes involved (Fig. 4) (Isaias et al., 2014b). The processes of cell growth and division point towards the implication of auxins as well as cytokinins (CKs) in the induction of plant galls by insects and their development, and suggest that gall-inducing herbivores manipulate the balance of phytohormones to force the plant to create the gall (Tooker and Helms, 2014; Favery et al., 2016; Zhang et al., 2016). High levels of IAA and CKs (especially trans-zeatin family) were found in the saliva, bodies or accessory glands of many gall-inducing insects and other plant-manipulating insects (Hori, 1992; Mapes and Davies, 2001; Dorchin et al., 2009; Straka et al., 2010; Yamaguchi et al., 2012; Tooker and De Moraes, 2011; Giron et al., 2013). The IAA is the only growth regulator histochemically detected in specific sites of the galls induced by a cecidomyiid on *P. gonoacantha* (Bedetti et al., 2014). IAA occurs specifically during the stages of growth, development and maturation, and is absent in senescent galls, which suggests the manipulation of the IAA levels by the contact of the gall-inducing herbivore with plant cells.

Besides modifying the levels of IAA in the gall-inducing sites, gall-inducing herbivores and other plant-manipulating insects are able to manipulate the levels of CKs, presumably to maintain the sink status of plant tissues (Giron et al., 2013; Zhang et al., 2016). The CKs are responsible for stimulating cell divisions (Taiz and Zeiger, 2009), i.e. tissue hyperplasia. Hyperplasia was reported for galls induced by Thysanoptera (Souza et al., 2000) (Fig. 4), Hemiptera (Oliveira et al., 2006; Carneiro et al., 2014b), Lepidoptera (Ferreira and Isaias, 2013), and Diptera (Moura et al., 2008, 2009; Formiga et al., 2011), indicating that this response is most probably a convergent morphogenetical potential of the host plants, which is conservatively manipulated by gall-inducing herbivores of phylogenetically different taxa. Most of the gall morphotypes have sites of cell hypertrophy and tissue hyperplasia, indicating that auxins and CKs may be imbalanced at specific sites, which is yet to be histochemically confirmed.

Current studies on neotropical gall-inducing systems lead to the conclusion that the stimulation of plant growth regulators by gall-inducing insects is taxa-independent. The morphological patterns proposed for the galls induced by insects in the temperate region (Rohfritsch, 1992) do not include the whole spectrum of patterns found in the neotropics. An explanation for it is that the much more diverse interactions of gall inducers and host plants in the tropical region led to a much broader range of gall morphologies. The repertoire of interactions of gall-inducing insects and their neotropical host plants is enormous, and as such presents a high potential for more novelties, in addition to those ones brought to light in this review. We argue that strong emphasis should be placed on studying cytological alterations, patterns of metabolite accumulation and related enzymatic activity at the early stages of the interactions, and on more broad systems and ecological
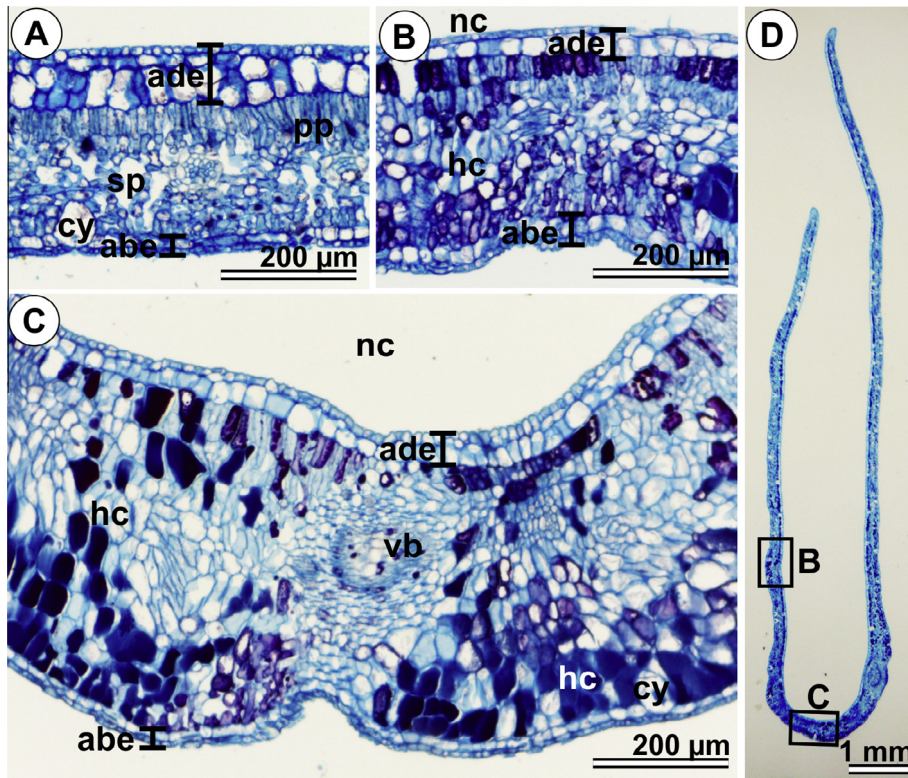
Fig. 4. Transverse anatomical sections of leaf and galls induced by *Gynaikothrips ficorum* (Thysanoptera: Phlaeothripidae) on *Ficus microcarpa* (Moraceae). (A) Non-galled leaf of *F. microcarpa* evidencing palisade and spongy parenchymas, and multisseriate epidermis. (B)–(C) Detail of the folding gall with sites of cell hypertrophy and hyperplasia of palisade and spongy parenchyma. (D) Transversely sectioned folding gall. The rectangles B and C show where the details of figures B and C are situated. *Abbreviations:* abe = abaxial epidermis. ade = adaxial epidermis. pp = palisade parenchyma. sp = spongy parenchyma. cy = cystolith (extension of the cell wall, with a cellulose matrix and covered by inorganic crystals such as calcium carbonate; structures common in some typical cells of *Ficus* genus, with unknown function). hc = hypertrophied cells. vb = vascular bundle. nc = nymphal chamber. Staining: astra blue and safranin.

scenarios. Indeed, this is another dimension yet to be addressed in botanical studies of gall-inducing insects and their host plants.

6. Role of enzymes activities in nutrition and non-nutritional neotropical galls

Classically, insect galls have been divided into those that induce nutritive and non-nutritive cells (Bronner, 1992). This division implies that the metabolic requirements of the gall-inducing insects are guaranteed either by the nutritional supply accumulated in the host plant cells surrounding the larval chamber or by the solutes sucked directly from phloem cells (Bronner, 1992). The plant cells lining the larval chambers are in direct contact with the gall-inducing insects, and are the first sites of cytological reactions. The redifferentiation of true nutritive tissues in the innermost cell layers of nutritive galls depends on the taxa of the gall-inducing insect, and on the strength of the physiological sink established during gall induction and development.

The galls induced by Cecidomyiidae and Cynipidae are the archetype for nutritive galls. These galls present conspicuous nutritive tissues with cytological features related to the high metabolism of the gall tissues, and to their high capacity of sinking photoassimilates to the gall sites. In the horn-shaped galls induced by a Cecidomyiidae on the leaflets of *C. langsdorffii* (Fabaceae), starch grains were detected both by cytological and histochemical analyses in the reserve nutritive tissue, while reducing sugars were detected in the typical nutritive cells around the larval chamber (Oliveira et al., 2011a). These reducing sugars are product of the hydrolization of starch by the enzymatic activity of invertases and sucrose synthase in the nutritive cells of the galls, as demon-

strated in galls induced by a Cecidomyiidae on the leaves of *A. spruceanum* (Oliveira et al., 2010).

Another kind of physiological relationship commonly observed in the neotropical gall-inducing fauna is established between the sucking insects and their host plants, which end up in the differentiation of typically non-nutritive galls. The feeding sites of these insects may be restricted to phloem cells, where they insert their stylets to feed on the host sap. The galls of sucking insects are considered structurally simple (*sensu* Formiga et al., 2015), and without any histochemical gradients (Bronner, 1992). An unexpected novelty was the detection of nutritional metabolites in gall tissues induced by the sucking insect *E. ostreoides* (Hemiptera) (Oliveira et al., 2006; Isaias et al., 2011), *P. aspidospermi* (Hemiptera) (Oliveira and Isaias 2010a; Malenovský et al., 2015), *N. cattleiani* and *N. myrtoidis* (Carneiro et al., 2014a; Carneiro and Isaias, 2015), and different species of Aphididae on *Pistacia* spp. (Álvarez et al., 2009; Muñoz-Viveros et al., 2014). In the galls induced by these insect species, starch and lipids are detected in the outer and inner cortices of the galls, establishing intriguing histochemical gradients. The mobilization of these substances to the developmental sites of galls is a key-process, which has been elucidated by the study of carbohydrate-related enzymes, such as phosphorylase, glucose-6-phosphatase, invertases and sucrose synthase. The activity of such enzymes was histochemically detected for the first time in the galls induced by sucking insects on *A. australe* (Oliveira and Isaias 2010a), and was also reported for the galls on *Psidium* spp. (Carneiro et al. 2014a; Carneiro and Isaias, 2015). The specific sites of enzyme activity play a role in mediating the translocation of carbohydrates in and towards the vascular bundles, or alternatively towards the storage parenchyma.

The metabolism of the non-nutritive galls should be, on the other hand, much more intricate due to the physiological demands imposed by sucking gall-inducing insects over plant cells both near and far from their feeding sites. The activity of phosphorylase, an enzyme related to the breakdown and/or polymerization of starch (Gerbrandy and Verleur, 2001), was detected both in immature and mature galls on *A. australe*, another supposedly non-nutritive gall. In addition, the activity of glucose-6-phosphatase was detected in the cells lining the larval chamber (Oliveira and Isaias, 2010b), which indicates a site of the synthesis of sucrose (Baroja-Fernandez et al., 2003). The product of sucrose breakdown by sucrose synthase is the UDP-glucose, which takes part in the biosynthesis of some polysaccharides, such as starch, and in cell respiration (Asano et al., 2002). On the other hand, the invertases detected in gall tissues are associated to high respiratory metabolism and oxidative stress. The activity of invertases may also elicit cell divisions and the orchestration of the regular cell growth needed for the development of the specific gall morphotypes (*sensu* Isaias et al., 2013, 2014a). In addition, the similar results on enzymatic activities observed in galls induced by Cecidomyiidae on leaves of *A. spruceanum* (Oliveira et al., 2010), and of *C. langsdorffii* (Oliveira et al., 2011a) corroborate the gall-inducing Hemiptera and Cecidomyiidae influence on plant enzymatic metabolism towards their nutrition.

7. Conclusions and future perspective

The specific events inherent to the induction and development of galls reveal a set of plant cell responses linked to adaptive behavioral and manipulation strategies by the gall-inducing insect. These interactions involve structural, physiological, and chemical manipulations by the insect and specific reactions by the host cells. Histochemical and physiological assays have helped us to understand the chemical battle involving the mobilization of nutritive compounds to nourish the developing insect and defensive substances produced by the host plants to fight gall induction and development (e.g., Oliveira et al., 2006, 2010, 2014; Ferreira and Isaias, 2014). Gall-inducing insects are basically sessile during the feeding stage (Price et al., 1987), and therefore are totally dependent on the stability and force of the nutrient sink that is established within host plant tissues. Hence, of critical importance is the capacity to fine tune and manipulate host plant physiology, as well as synchronizing feeding behavior with the phenology of host plant (Fernandes et al., 1990; Yukawa, 2000; Espírito-Santo et al., 2012). The availability of reactive plant sites for gall induction implies an adequate nutritional status (Dorchin et al., 2009; Castro et al., 2013), as well as synchronization between the life cycle of the gall-inducing insects and plant phenology (Weis and Abrahamson, 1988; Yukawa, 2000; Magalhães et al., 2014). The adjustment of the life cycle of the gall-inducing insect with the physiology and phenology of the host plants can lead to distinct strategies by gall-inducing herbivore, including the number of generations in a given period of time.

From the perspective of the host plant, the production of controlled levels of reactive oxygen species (ROS) seems to represent the first signaling step during the process of gall induction (Oliveira et al., 2014). ROS trigger the accumulation of phenolics in cells surrounding the site of gall induction (e.g., Dias et al., 2013), this, in turn, stimulates the first set of cellular responses to gall induction in association with growth regulators such as auxins (Bedetti et al., 2014). Once under the control of the gall-inducing insect, the plant cells and tissues reprogram their development leading to new structural and functional designs, the gall morphotypes (Isaias et al., 2013, 2014b).

For the success of gall development, the enzymatic modulation of carbohydrates is essential, as has been shown for diverse Neotropical gall-inducing insects taxa. Studies on mechanisms of recognition and responses to oxidative stress represent a new frontier for understanding of physiology of gall induction. In order to fully develop this perspective, further cytological studies are needed to assess how species of gall-inducing insects deal with the varied physiology and metabolism of host plants.

Acknowledgments

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