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Two different gall morphotypes for two different galling insect species in *Protium icicariba*, Burseraceae[§]

Dois diferentes morfotipos de galhas de duas espécies diferentes de insetos galhadores em *Protium icicariba*, Burseraceae

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Abstract Gall induction in plants is considered the most complex association in nature, where the insect gains in redirecting the physiology and growth of attacked organs, in order to create an appropriate environment that provides food, shelter and protection for the development of their larvae. Both structural and chemical changes have great influence in maintaining the life cycle of galling insect. So this study aims to evaluate the structural reaction of the gall induced by a galling insect from the family Cecidomyidae and another belonging do the family Psyllidae in *Protium icicariba* (DC) Marchand. The morphology and structure of the galls was assessed by stereoscopic and transmitted light microscopy. In the cecidomyiid gall, the presence of non-cutinized inner epidermis and pits in plant cells in tissues whose walls were lignified, are the main instruments in the transfer of water and water-soluble substances from the cells of the fundamental parenchyma, where there are the vascular bundles, towards the larval chamber, what allows the larvae to feed. Psyllidae evidenced an interaction in which it acts as a sap-sucking insect during larval and nymphal development. In both galls, the outer wall of the gall and the internal wall of the larval chamber composed in part by sclerenchyma, with gall tissue induced Cecidomyidae e Psyllidae in *P. icicariba* suggest a strong relationship with the physical defense against external enemies.

Keywords: cecidogenesis, Cecidomyiidae, plant-insect interaction, Psyllidae, sandbank.

Resumo A indução de galhas em plantas é considerada a mais complexa associação na natureza, onde o ganho dos insetos consiste em redirecionar o crescimento e fisiologia de órgãos atacados, de modo a criar um ambiente favorável, que forneça alimento, abrigo e proteção para o desenvolvimento de suas larvas. Tanto alterações estruturais quanto químicas têm grande influência na manutenção do ciclo de vida dos galhadores. Assim, este trabalho tem o objetivo de dimensionar do ponto de vista estrutural e químico a constituição reacional da galha induzida por Cecidomyiidae e Psyllidae em *Protium icicariba* (DC) Marchand. A morfologia e a estrutura das galhas foi avaliada em microscopia estereoscópica e de luz transmitida. A presença de epiderme não cutinizada e as pontoações em paredes celulares lignificadas na galha de Cecidomyiidae, são os meios principais para a transferência de água e substâncias hidrosolúveis das células do parênquima fundamental, onde se localizam os feixes vasculares, para dentro da câmara larval favorecendo o acesso da larva à alimentação. Psyllidae evidenciou uma interação em que atua como um inseto sugador de fotoassimilados do floema durante o desenvolvimento de suas larvas e ninfas. A parede externa da galha e a parede interna da câmara larval composta em parte por esclerênquima, no tecido com galha induzida por Cecidomyiidae e Psyllidae em *P. icicariba* sugerem forte relação com a defesa mecânica contra os inimigos externos.

Palavras-chaves: cecidogênese, Cecidomyiidae, interação inseto-planta, Psyllidae, restinga.

Introduction

Gall induction in plants is considered the most complex association between insects and plants in nature, where the gain of the insects is to redirect the growth and physiology of the attacked plant organs, to create a favorable internal environment, providing food, shelter, and protection for the development of their larvae (Shorthouse *et al*. 2005). Galling insects are herbivores that represent the ending point of the generalist - specialist gradient, being too specific about the choice of the host (Fernandes and Price 1992, Price *et al*. 1998)

Contrasting to generalist herbivores with free life that can move among different habitats and feed on different plant species during their lives, galling insects trend to live most of their lives within the host plant species, inducing changes in the host plant tissues. However, they are free to choose among different body parts offered by their hosts, possibly inducing galls on leaves, stems, thorns, flowers, fruits, and roots (Fonseca *et al.* 2006).

Some studies have shown that there is variation in abundance and composition of assemblages of herbivorous insects associated with plants at different ontogenetic stages (Fonseca *et al*. 2006, Campos *et al*. 2006). Thus, the behavior, physiology, and ecological adaptations of herbivores select the stage of plant development, which provide them with better rates of survival and reproduction. Therefore, the process of development of the host plant is the main selective pressure on this type of interaction (Fonseca e Benson 2003).

The main force driving the ontogenetic change sequences in plant-insect interaction is the process of the plant host development, which continuous changes the quality of the resource associated with the behavioral, physiological, and ecological selectivity of herbivores, leading to the best set of conditions for their survival and reproduction. In addition, biotic interactions with higher trophic levels and abiotic conditions will modulate densities of species during ontogeny (Fonseca *et al*. 2006).

Many insects have a remarkable ability to modify host plant tissues and induce atypical growth called galls (Mani 1964, Redfern and Shirley 2002). Galls are sophisticated structures comprised of living cells from the host plant, considered as the extended phenotype of inductor, wherein it is capable of inducing abnormal growths in host plant tissues by means of a kind of specific stimulus (Mani 1964, Redfern and Shirley 2002, Stone and Schönrogge 2003, Shorthouse *et al*. 2005).

Until now, there are many ecological and histological studies foccused on the adaptive significance of the habit of galling (Rohfritsch and Shorthouse 1982, Price *et al*. 1987, Stone and Schönrogge 2003, Raman *et al*. 2005, Shorthouse *et al*. 2005), and development induced by insects (Rohfritsch 1992) galls process. Featuring highly specialized life styles, these insects are apparently parasites , monophagous , sessile, and immersed in plant tissues for a somehow long period of their life cycle (Shorthouse *et al.* 2005). The recognition of several species of gall inducers in recent years suggests that midges are still in an evolutionary dynamic state, with extensive adaptive radiation (Price 2005).

Species of *Protium* L. have given their epithets to the description of new species of galling insects, so that the type of galling insect species became steps of analytical keys to species of galling insects (Maia 2013). Thus, this paper aims to describe and to characterize clearly delimited stages of development of two different gall morphotypes, concerning their morphological and anatomical events, and their distinct galling insect species that occur in the leaflets of *Protium icicariba* (DC) Marchand (Burseraceae).

Methods

Galls were morphologically characterized concerning their shape, color, site of occurrence in the host plant, number of internal chambers, and indumentum. In the case of leaflet galls, the side of their occurrence was signaled if in the adaxial or abaxial side of leaflet. Structural and *in situ* chemical assessment of galls were made at the Laboratory of Functional Ecology - UVV.

Morphological analyzes were performed on fresh leaflets without galls, with young, mature, and, in one case, with senile galls. Sample of leaflets with young galls were separated in glass pots protected with an inframillimetric mesh sheath, to monitor the emergence of adult insects. Part of the galls were dissected to obtain insect immature stages. The larval specimens were identified with the aid of specialized literature (Maia e Fernandes 2004, Narahara *et al*. 2004, Bregonci *et al*. 2010, Rodrigues e Maia 2010, Maia 2013) and photographed in stereoscopic microscope.

Investigation *in situ* of the nature of the reddish impregnations in the galls was made through microextraction of the affected area in methanol and ethanol, and subsequent exposure to aqueous HCl 1%, NH_4OH 1% and AlCl3 5% (Costa 1972, Harborne 1984).

Anatomical analysis used leaflets without and with the two morphotypes of studied galls in different stages of development, that were fixed by immersion in a FAA 50 (Jensen 1962), since their collection in field. After near 40 minutes, the immersed leaflets were taken under a vacuum chamber for two hours to enhance the fixing solution penetration in plant tissues (Jensen 1962). Just after, leaflets were washed in distilled water and immersed in a solution of ethanol 70% for conservation.

Transversal sections were handmade for leaflet lamina nearby the two galls morphotypes, while transversal and longitudinal sections were made for the galls in different maturation stages (Johansen 1940). Gall handmade sections were diaphanized in a water solution of sodium hypochlorite 2% (1:1), washed with distilled water, and neutralized during five minutes with a water solution of acetic acid 5%. After neutralization, sections were washed in distilled water until complete disappearance of ascetic acid scent, and then they were stained with the double coloration with Astra Blue and Safranine (Bukatsch 1972), at the proportion of 4:1. Stained sections were mounted in bidistilled glycerin and photographed in light microscopy at the Laboratory of Functional Ecology, at UVV.

Figure 1 Psyllid galls induced in leaflet lamina of *Protium icicariba* (DC) Marchand in adaxial view. **a**: juvenile (arrow) and mature (double arrow) galls; **b**: mature wart-like emergences (arrow) pigmented in vinous color by anthocyanins.

Results and discussion

Psyllid galls involve the whole leaflet lamina. They appear on the adaxial side (Figure 1a) as wart-like emergences (Figure 1b) and in abaxial side they showed anthocyanin pigmented areas with two up to five nymphs (Figure 2a), filling gall chambers that were shaped as campanualte cavity (Figure 2b). They are glabrous, greenish in the initial stages of larvae development, and become vinous by the presence of a hydrophilic pigment identified as anthocyanin in mesophyll tissue involved in gall structure and its surroundings, that appeared since the intermediate stages of larvae development (Figure 2).

Cecidomyiid galls may start in both adaxial and abaxial sides (Figure 3a) of the leaflet lamina. They are turbine-like glabrous, greenish during the major part of their development, but they can show, in maturity or in senility, vinous striae by the presence of anthocyanins (Figure 3b).

Psyllidae's gall has a single larval chamber that is not closed by the plant tissue, but by the body of the nymph itself (Figure 2a), that act as a sap-feeding insect during both larval and nymphal development (Yana *et al*. 2010, Burckhardt and Queiroz 2012). On the abaxial surface where the oviposition has occurred, the eggs (Figure 4a) and the four larval stages (Figure 4b-d) are wrapped in a white waxy material, which was also observed in the vicinity of body of nymphs (Figure5a-b) or even their exuvia (Figure 5c-d) after the final ecdysis. Nymphs obliterate the entrance of the larval chamber even when adults hatche (Figure 5e-f).

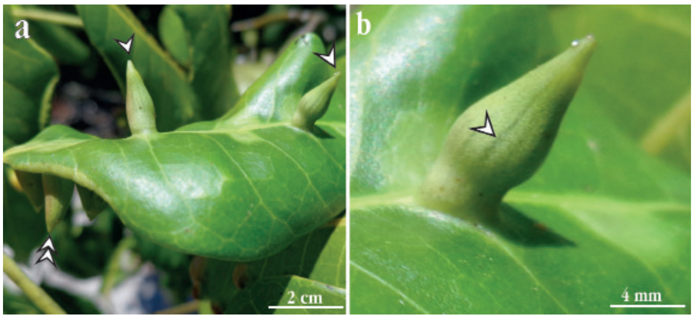

Figure 3 Cecidomyiid galls induced in the leaflet lamina of *Protium icicariba* (DC) Marchand. **a**: Near mature turbinate galls in adaxial (arrow) and adaxial (double arrow) sides; **b**: vinous striae of anthocyanin (arrow) in a near mature gall.

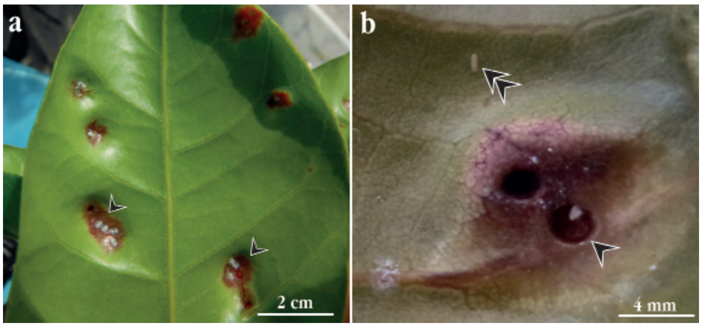

Figure 2 Psyllid galls induced in leaflet lamina of P*rotium icicariba* (DC) Marchand in abaxial view **a**: galling areas in mature stage, showing two up to five nymphs in an anthocyanin pigmented area (arrow); **b**: empty larval chamber (arrow) after adult emergency surrounded by pigmented in vinous color by anthocyanins, and a larvae stage (double arrow)

The galls of Cecidomyiidae have a single larval chamber with only one larvae of the inductor (Figure 6a-b). In mature galls there are three larval stages (Figure 6a-e) up to the hatching of adult insects (Figure 7a-b). The first larval stage shows yellowish color and incomplete development of ventral gut (Figure 6a-b). The second larval stage has a more pronounced segmentation, yellow color with well developed ventral digestive tract of black color (Figure 6c-d). The third stage is already shows a more marked improvement with the change of body color to orange and the formation of exoskeleton that will give rise to the cephalothorax and the pair of wings (Figure 6e). The adult is a Diptera with membranous wings, rockers well developed, three pairs of ambulatory legs with black and white streaks and a pair of antennae (Figure 7).

Maia (2001) reported in a study of galls on sandbanks, the

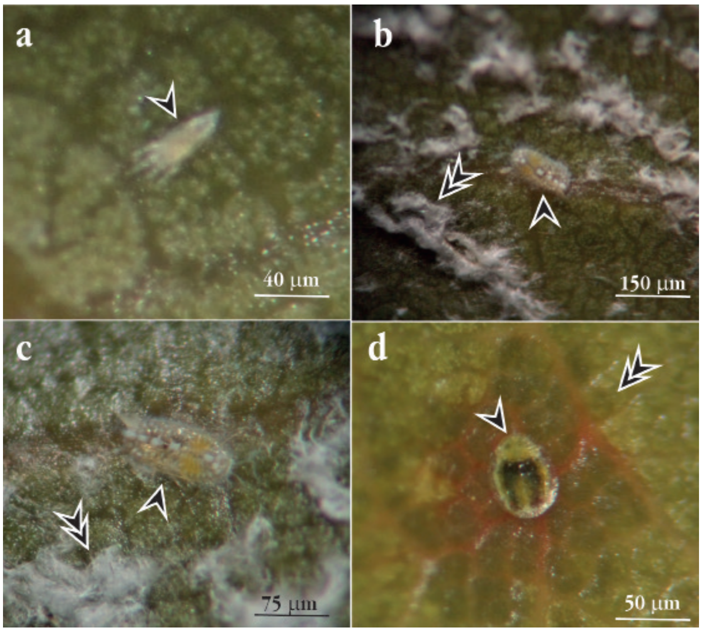

Figure 4 Psyllidae galls inducction in the leaflet lamina of *Protium icicariba* (DC) Marchand. **a**: egg (arrow); **b**: larvae in first stage (arrow) surrounded by a white waxy material (double arrow); **c**: larvae in second stage (arrow) still surrounded by a white waxy material(double arrow); d: nymph in initial stage (arrow) and the anthocyanin area arround the galling place (double arrow)

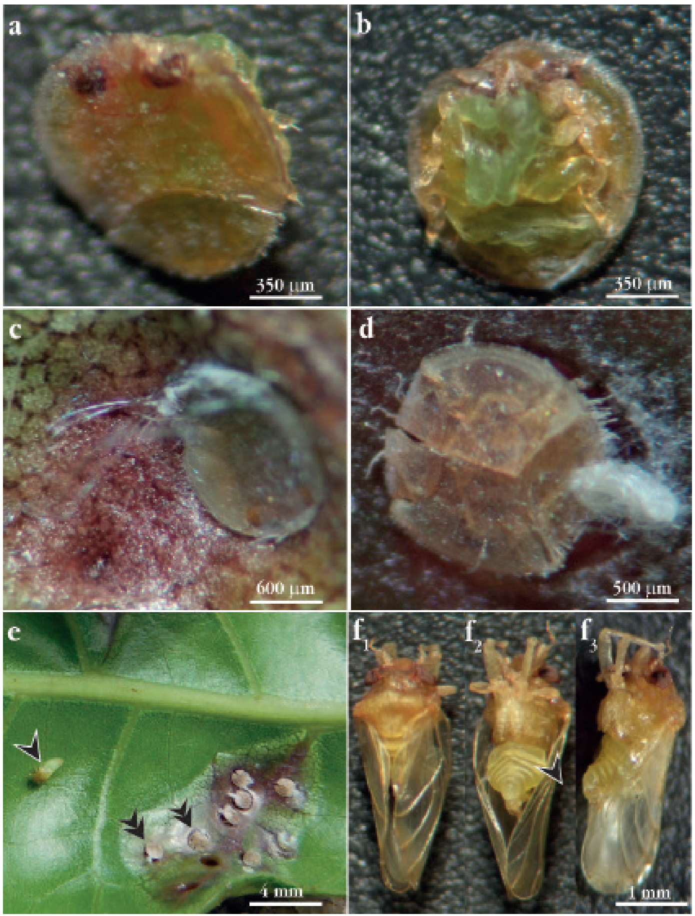

Figure 5 Psyllidae galls inducction in the leaflet lamina of *Protium icicariba* (DC) Marchand. **a**: nymph in dorsal view; **b**: nymph in ventral view; **c**: exsuvia in doral view; **d**: exsuvia in ventral view; **e**: adult insect (arrow) recently hatched on abaxial side of leaflet and exsuvias obliterating the entrance of gall chamber (double arrow); **f**: views of adult insect - ($\mathbf{f}_1$) dorsal, ($\mathbf{f}_2$) ventral, ($\mathbf{f}_3$) lateral.

occurrence of eight gall morphotypes associated with *Protium*: two types in *Protium brasiliensis*, two in *Protium heptaphyllum*, and four in *Protium icicariba*. In another study Maia *et al*. (2002) had described two new species of Cecidomyiidae to *Protium icicariba*: *Dactylodiplosis icicaribae* Maia 2002, and *Lopesia simplex* Maia 2002. Maia (2013) recognizes four kinds of gall on leaves and fruit of one morphotype in *P. icicariba*, based on their research and in some other authors. However, the gall morphotypes described here is still unknown to *P. icicariba*.

The ungalled leaflets, as well as the ungalled parts of leaflets bearing galls, show a typical dorsiventral mesophyll, with adaxial palisade parenchyma and abaxial spongy parenchyma, and with a sclerenchyma sheath that involves vascular bundles and connects the two epidermis (Figure 8a). Both galls have only one larval chamber and a remarkable feature that happens in their development is the dedifferentiation of palisade and spongy parenchyma into a fundamental parenchyma, and the proliferation of sclerenchyma in the neighborhood of the galls of Psyllidae (Figure 8b) and Cecidomyiidae (Figure 4c) insect species.

Psyllid gall is a result of a saccular growing (Raman 2011), involving the whole lamina from abaxial to adaxial epidermis (Figure 9a), in such a way that the abaxial epidermis becomes the inner surface of the larval chamber (Figure 8a). Cecidomyiid gall involves a metaplasied cell proliferation (Raman 2011), forming a turbine-like gall whose external epidermis corresponds to either the adaxial or the abaxial leaflet epidermis, depending on which lamina side the initiation occurred, but the inner larval chamber epidermis is a neoformed structure (Figure 9b). Internal epidermis in larval chamber of psyllid gall shows intense cutinized deposition in external periclinal wall, as well as conspicuous cuticle flanges in anticlinal walls (Figure 10a), while cecidomyiid gall shows an one-layer epidermis without cuticle deposition neither in anticlinal nor periclinal walls (Figure 10b), and no nutritional tissue was found.

The loss of differentiation of palisade and spongy parenchyma into a fundamental parenchyma may be a derived character of galling inducer that involves a deep modification in

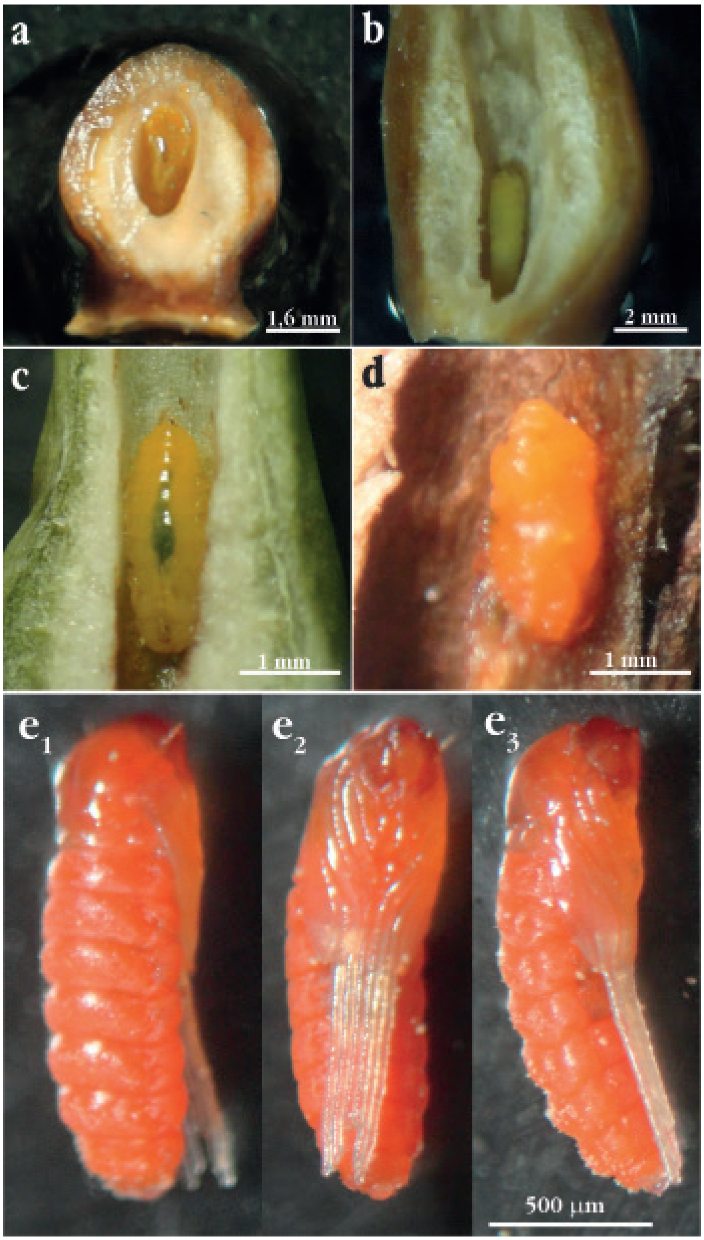

Figure 6 Cecidomyiidae galls inducction in the leaflet lamina of *Protium icicariba* (DC) Marchand. **a**: larvae in first stage; **b**: larvae in second stage; **c**: larvae in second stage evidencing its guts; **d**: larvae in third stage, showing and orange color; **e**: views of pupae ($\mathbf{e}_1$) dorsal, e) ventral, ($\mathbf{e}_3$) lateral.

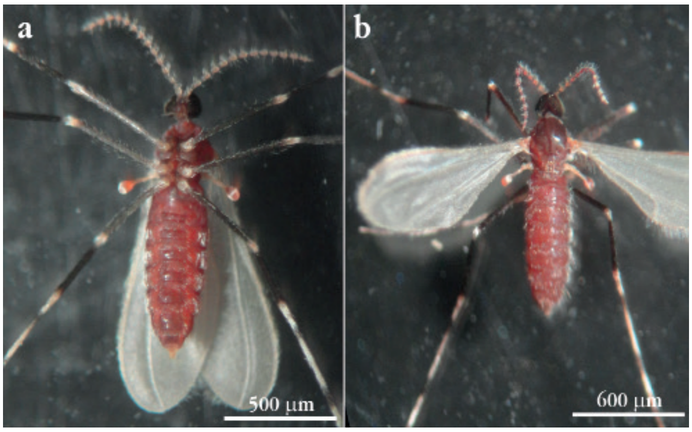

Figure 7 Cecidomyiidae galls inducction in the leaflet lamina of *Protium icicariba* (DC) Marchand. Views of adult insect **a**: ventral; **b**: dorsal.

leaflet mesophyll of *P. icicariba*. This fact may be understood as a reciprocal adaptation involving the host plant and the galling inducer, and in evolutionary terms, galls may be taken as extended phenotypes of galling insects, due to their influence and control over plant tissues during gall ontogeny (Dawkins 1982, Stone e Schönrogge, 2003).

The non-cutinized epithelium that cover the internal surface of the larval chamber of Cecidomyiidae's gall may be one of the main indicators of a symplastic way of transference of water and hydrosoluble substances available in fundamental parenchyma towards the larval chamber, allowing larval feeding. Besides that, the pits in the plant cells with lignified walls may add a complementary way of transferring water and water-soluble substances towards the larvae chamber in a complementary way (Evert 2005). In an anatomical study of epidermis in *Pistacia terebinthus* galled leaves, induced by three aphid different species had shown that the multiseriate epidermis observed in the three galls represented a structural barrier to outer water input, creating a dry and hydrophobic environment that was crucial to galling insect survival (Álvarez *et al*. 2009).

These galls in the leaflets of *P. icicariba* are a typically a consequence of a set of modifications in the leaflet mesophyll tissues that are induced by the presence of insect larvae stages (Schoonhoven *et al*. 2005). While Psyllidae induces the formation of an ectopic campanualte chamber that progressively deeps and involves body and legs of the growing larvae growing, Cecidomyiidae induction consists of set of cell proliferation and differentiation that involves the whole larvae in development (Raman 2007).

The presence of anthocyanin, a glycosil-flavonoid phenolic pigment, may be also a consequence of gall induction, since morphological modifications are also followed by biochemical responses involving both primary and secondary metabolites (Hartley 1998, Herrera e Pellmyr 2002, Schaller 2008). Several secondary metabolites have been found in the host plant tissues, such as flavonoids, tannins, anthocyanins, phenolic acids, free aminoacids and glycids (Hartley 1998, Yang *et al*. 2003). The presence of anthocyanins was restricted to the galling tissues for Cecidomyiidae's gall, or was also spread to their immediate neighborhood, for Psyllidae's gall. No matter in some cases

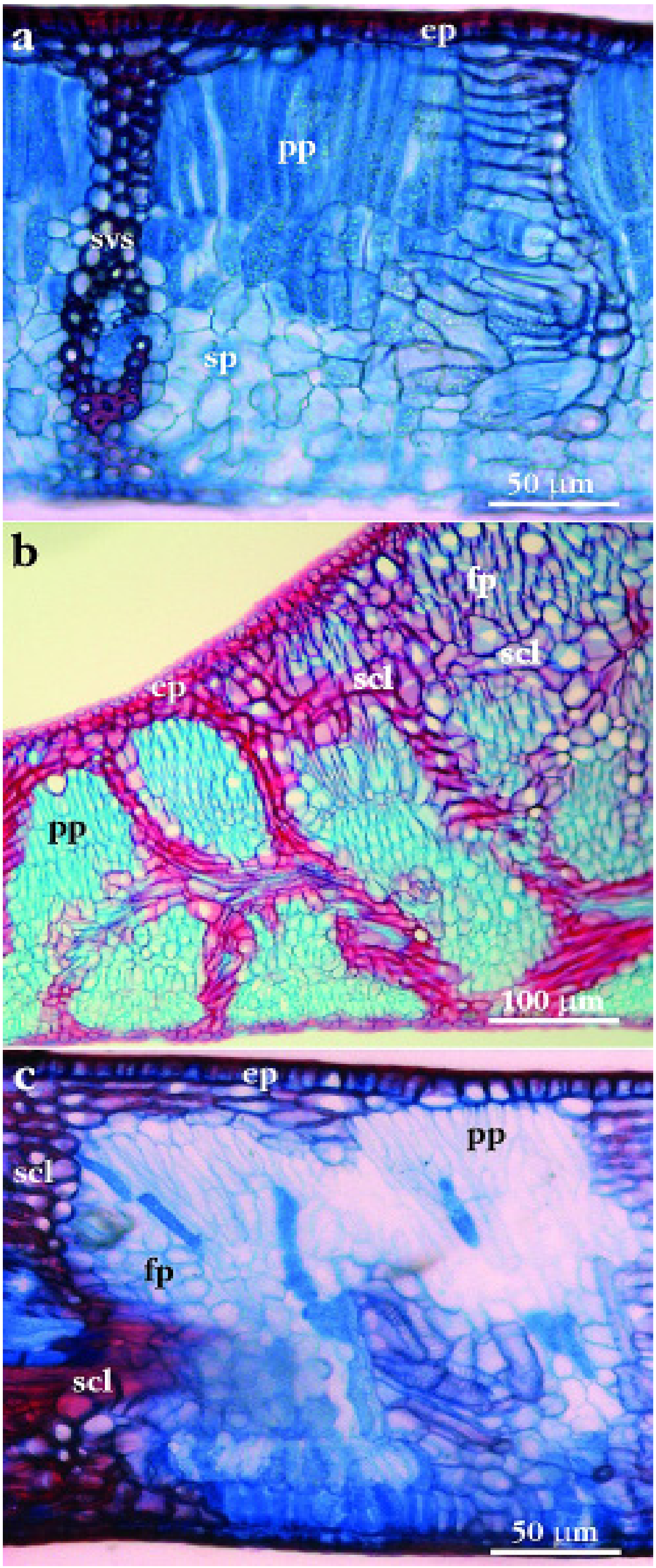

Figure 8 Leaflet mesophyll of *Protium icicariba* (DC) Marchand in transversal section. **a**: region without galls, showing a typical dorsiventral pattern with palisade parenchyma (pp) under the adaxial epidermis (ep), and spongy parenchyma (sp) in the abaxial side, and a sclerenchyma sheath that connects abaxial and adaxial epidermis (ep) and involves the vascular bundle. **b**: region near a psyllid gall; **c**: region near a cecidomyiid gall, evidencing the loss of the typical dorsiventral pattern with substitution of palisade and spongy parenchyma by a fundamental parenchyma (fp), and increasing of sclerenchyma (scl).

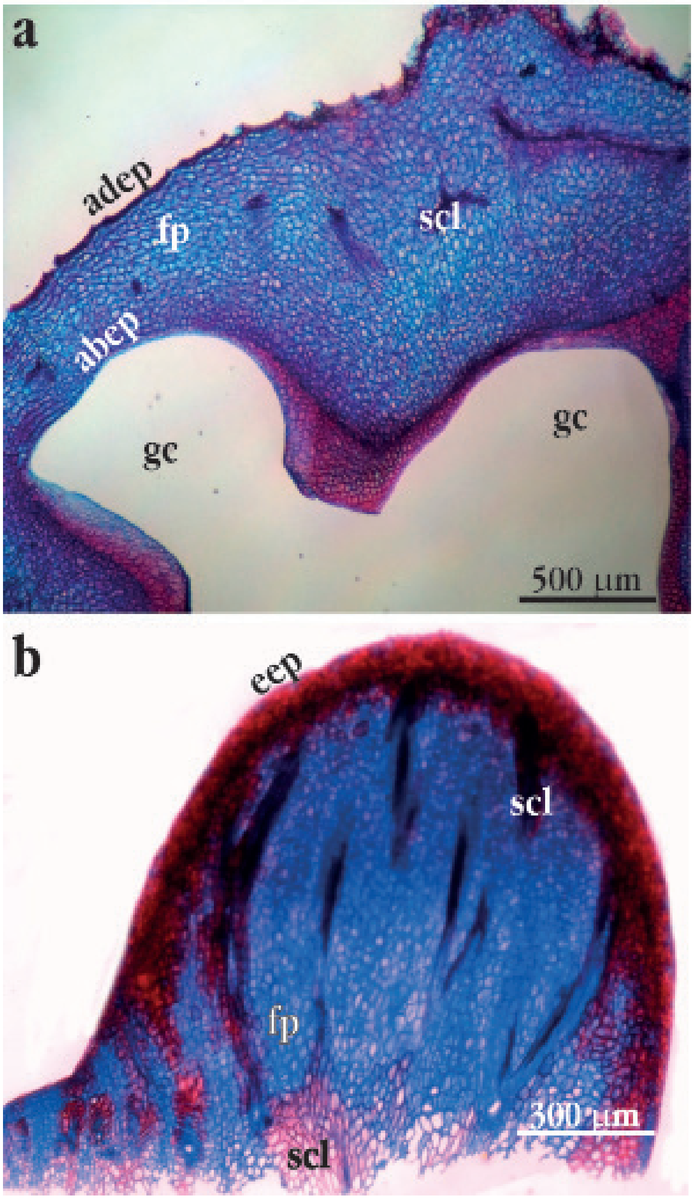

Figure 9 Galls in leaflets of *Protium icicariba* (DC) Marchand in longitudinal section. **a**: Psyllid galls, showing chambers (gc) produced by saccular growing of mesophyll, preserving epidermis orientation, with abaxial epidermis (abep) covering inside the chamber, keeping the adaxial epidermis (adep) as the most outside surface. Mesophyll loses its dorsiventral pattern under the adaxial epidermis (ep), and spongy parenchyma (sp) in the abaxial side, and a sclerenchyma sheath that connects abaxial and adaxial epidermis (ep) and involves the vascular bundle. **b**: cecidomyiid gall at first stage of larvae development, evidencing the loss of the typical dorsiventral pattern with substitution of palisade and spongy parenchyma by a fundamental parenchyma (fp), and increasing of sclerenchyma (scl).

these biochemical changes may systemically affect the whole plant, in some others, such as in both of these galls, their occurrence may be limited to the galling tissues (Schoonhoven *et al*. 2005).

Anthocyanins present in both galls belong to the major group of phenolic compounds (Harborne 1984) and have been clearly associated in some cases with the presence of galls (Purohit *et al*. 1979, Abrahamson and Weis 1997). However, in some others galls, phenolics may be diminished (Hartley 1998) or inducing-gall insect may even do not affect phenolic production in plant tissues (Nyman and Julkunen-Tiitto 2000). The presence of phenolic compounds in a plant tissue has been generally considered a part of plant defense strategy against herbivores (Mani 1964, Price *et al*. 1987, Price 1990). Nevertheless, defense is not the unique role of alelochemicals (Price *et al*. 1987).

Besides, of being involved in signaling for pollination, phenolics take part in regulation of phytoregulators, in protection against ultraviolet radiation, in metabolic defenses against oxidative stress, and have an important role in lignification process (Harborne 1998, Lee and Gould 2002, Steyn *et al*. 2002, Hoch *et al*. 2003, Grace 2005). Therefore, it is possible that even in cases of slight metabolic changes

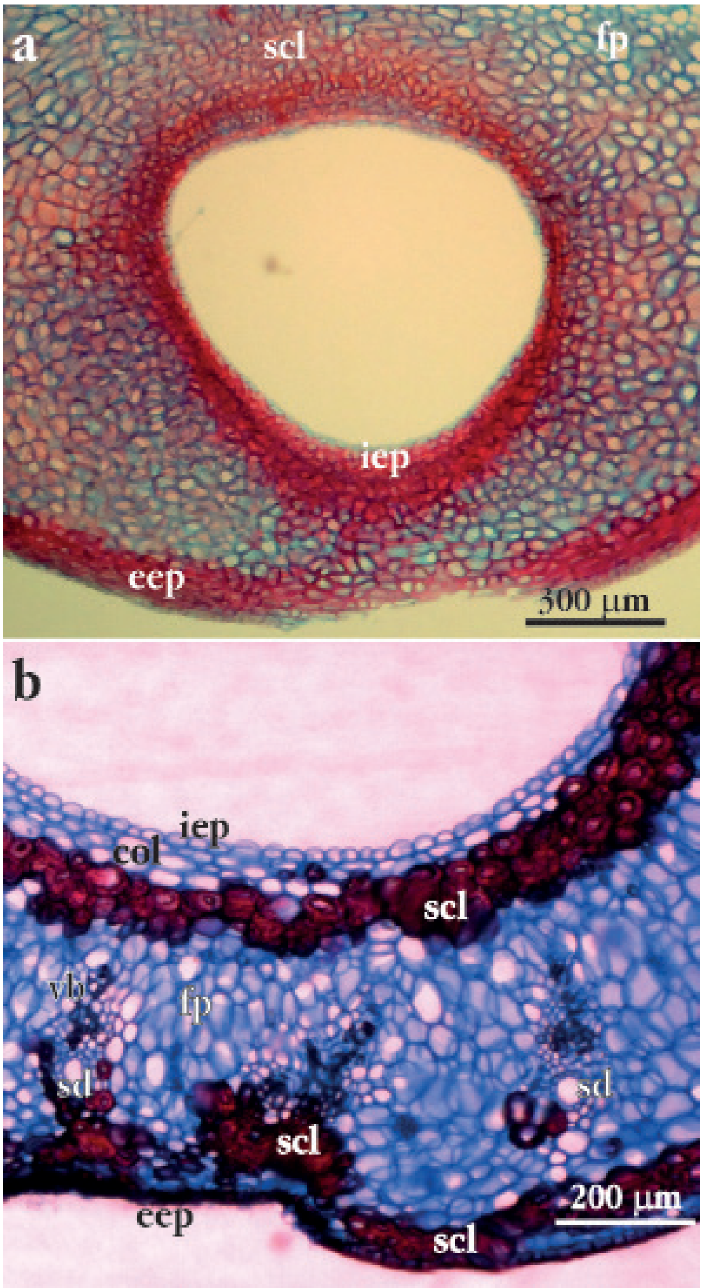

Figure 10 Galls in the leaflets of *Protium icicariba* (DC) Marchand in transversal section across the longest chamber axis. **a**: psyllid gall, showing the external (eep) and internal (iep) epidermis, the fundamental parenchyma (fp) and regions of sclerenchyma irregularly distributed. **b**: cecidomyiid gall showing the external and high suberized epidermis (eep), two sclerenchyma layers that are filled with a fundamental parenchyma (fp), with secretory ducts (sd). An inner non-suberized epidermis delimitates the larval chamber, and a two or three cell layer of collenchyma fill the space between the inner epidermis (iep) and sclerenchyma layer (scl).

in their biosynthesis, phenolic derivatives may affect essential process of plant growing and development (Formiga *et al*. 2009).

Phenolic compounds may also favor the galling insect interfering with hormonal balance related to the cecidogenetic field. It has been proven that some phenolic derivatives act synergistically with auxin in stimulating growth (Takahama, 1988). The presence of some phenols may inhibit, for example, the indolyl acetic acid – IAA oxidases, thus increasing he auxin action involved in cellular hypertrophy process that occurs during gall formation (Fosket 1994). Therefore, the presence of phenols is not an efficient barrier to oviposition by the inductor, or the development of galls (Soares *et al*. 2000).

Commonly, galls have a high content of mineral nutrients, carbon, and energy, and accumulate secondary metabolic substances, such as phenolics (Formiga *et al*. 2009). Among the total phenols, there is a range of signaling molecules which quantitative variation may indicate different response patterns of plants to biotic factor,s such as the action of galling herbivores and abiotic factors, which may indirectly influence the success in introducing and developing these herbivores (Fernandes and Price 1992, Hartley 1998, Nyman and Jukulnen-Tiitto 2000).

Formiga *et al*. (2009) suggested that the stimulatory effect of cecidogenesis on the production of phenolic compounds in healthy tissue and galled leaves of *Aspidosperma spruceanum* is highest when their biosynthesis ia not previously stimulated by environmental conditions, or in other way, abiotic factors could be acting together with the galling process in modulating the chemical response of the host plant.

As the vast majority of phenolic derivatives has their origin in the shikimate pathway, especially in post-phenylalanine synthesis, insolation is an important factor in its production. This phenomenon may be explained by the fact that the key enzyme in the production of shikimate-derived phenolics, the phenylalanine-ammonialyase (PAL), suffer transcriptional stimulation by UV radiation present in sunlight. Therefore, the production of shikimate derivatives can be considered a protective mechanism against light stress (Jones 1984).

Considering these findings, the presence in the gall of a non-cutinized inner epidermis and pits in plant cell in tissues with lignified walls are the main arguments that support the idea of transference of water and water-soluble substances from the cells of the fundamental parenchyma towards the larval chamber, allowing larval access to food. The development of anthocyanin in the leaflet tissue involved in galling process seems not to interfere in the development of both insects and may be related to oxidative stress that occur in plant leaflet. In cecidomyiid galls, the abundant sclerenchyma bellow the outer epidermis and before the internal wall of the larval chamber, suggest a strong relationship f these features with the physical defense against external enemies, probably in a next trophic level of that relationship.

Acknowledgments

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