Impacts of gall induction on the structure and physiology of *Caryocar brasiliense* Camb. (pequi) leaves

Impactos da indução de galhas na estrutura e fisiologia de folhas de *Caryocar brasiliense* Camb. (pequi)

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ABSTRACT

Gall induction commonly causes macro and microscopical effects in host leaves, such as a reduction in area, a spacing of chlorophyllian tissue, and a decrease in photosynthetic capacity linked to alterations in the contents of photosyntethizing pigments, as well as distinct histochemical profiles. These aspects were evaluated on galls induced by *Eurytoma* sp. (Hymenoptera) on leaves of *Caryocar brasiliense* and revealed the topographic disposition of the reserve substances in the galled tissues. This disposition indicates an ideal microenvironment for the *Eurytoma* sp. development and corroborates Nyman's (2000) proposal for the determination of tissue zones in galls. The outer cortex and its phenolics accumulation confer protection, while the carbohydrates accumulation in the inner cortex fits for nutrition. Unexpectedly, the levels of infestation positively affect the host leaves by increasing their potential photosynthetic area. Also, photosynthetizyng pigments may guarantee basal levels of photosynthesis and accessory pigments, such as the carotenoids, may play the crucial antioxidant role in the gall chemical battle.

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RESUMO

A indução de galhas comumente causa efeitos macro e microscópicos nas folhas hospedeiras, tais como, redução de área, dos espaços intercelulares e da capacidade fotossintetizante ligadas a alterações nos conteúdos dos pigmentos fotossintetizantes, e nos perfis histoquímicos. Estes aspectos foram avaliados em galhas induzidas por *Eurytoma* sp. (Hymenoptera) em *Caryocar brasiliense* (Caryocaraceae) e revelaram a distribuição topográfica das substâncias de reserva nos tecidos da galha. Esta disposição revela um microambiente ótimo para o desenvolvimento do *Eurytoma* sp. e corrobora a proposta de um zoneamento histoquímicos nas galhas. O acúmulo de fenólicos no córtex externo confere proteção, enquanto os carboidratos acumulados no córtex interno estão funcionalmente ligados à nutrição. Inesperadamente, os níveis de infestação afetaram positivamente as folhas hospedeiras pelo aumento da área potencialmente fotossintetizante. Os pigmentos fotossintetizantes podem garantir níveis basais de fotossíntese, enquanto os pigmentos acessórios, tais como os carotenóides, podem ter função crucial como agentes oxidantes na batalha química da interação.

INTRODUCTION

The world of plant galls is just one among the countless interactions that take part in the ecological web that supports the biodiversity of our planet (Russo 2006), and as so represent microenvironments located inside a complete individual – the host plant. Cecidology, the study of galls, unites entomology, botany, and parasitology, and also reveal an intricate structural and physiological web of processes. The interaction between *Caryocar brasiliense*, the pequi, and *Eurytoma* sp. (Hymenoptera) is herein focused on the impacts of the insect's behavior on the development of its host organ – the leaf. These impacts are expected to be negative for galls and are clearly cases of parasitism.

It is believed that gall induction should cause the reduction in leaf area as observed by Gonçalves *et al*, (2005) in *Rollinia laurifolia* (Annonaceae). Concomitant to the impact on leaf area, a reduction in photosynthetic capacity should be linked to a decrease in the contents of photosyntethizing pigments. The alterations in pigment contents influences the fluorescence of chlorophyll and the photosynthetic activity in galls, as was demonstrated by Castro *et al*

(2013) in *Copaifera langsdorffii* (Fabaceae) (*in press*) and by Oliveira *et al* (2011) in *Aspidosperma australe* (Apocynaceae) (Oliveira *et al* 2011). This relationship strongly supports the analyses of photosynthetic pigments as an indicative tool of gall physiological status and the establishment of a potential source-sink flux.

Independently or not of the flux of photoassimilates, the accumulation of primary and secondary metabolites on gall tissues may be representative of the physiological impact of gall induction, improving their nutritional status (Motta *et al.*, 2005). Carbohydrates (Bronner, 1992; Hartley, 1998; Oliveira and Isaias 2010a, Oliveira *et al* 2010, Castro *et al* 2013), phenolics, lignins and flavonoids accumulation (Motta *et al.*, 2005, Oliveira *et al.*, 2006, Formiga *et al* 2009, Formiga *et al* 2011) has been documented in galls, and are integrative parts of the nutritional and defensive peculiarities of the structure. The chemical battle generated in gall sites has been attributed to the increase in reactive oxygen species (Oliveira and Isaias 2010a, Oliveira *et al* 2010). This increased accumulation should be a particular response to phenolics accumulation (Hartley 1998, Formiga *et al* 2009). This proposal was pointed out by Nürnberger & Scheel (2001) as one of the most important responses to parasitism. As part of the chemical battle between the galling herbivore and the host plant, antioxidative substances such as the carotenoids (Krause, 1988; Thiele *et al.*, 1998) and flavonoids (Harborne & Williams, 2000) must compensate the oxidative stress originated in response to cecidogenesis.

Gall development is dependent of the structural and chemical status of host tissues by the time of oviposition. The leaves of *C. brasiliense* accumulates reducing sugars, steroids, triterpenoids, seschiterpenic lactones, saponins, and phenolic compounds, such as tannins, and flavonoids (Marques, 2001; Ferreira *et al.*, 2005). Based on the accumulation of such compounds and the potential of the galling herbivores to drain substances towards the host organ, this study verified the impact of gall induction on the phtosynthetizing leaf area of *C. brasiliense*. The maintenance of potential photosynthesis was inferred by the analyses of pigment contents in relation to the infestation levels, and the relocation of nutritive resources and chemical defenses like phenols was histochemically evaluated.

MATERIAL AND METHODS

Estimation of infestation and leaf area – The percentage of galled leaves were calculated in three trees of *C. brasiliense* on the campus of Universidade Federal de Minas Gerais in Montes Claros, Minas Gerais (43°50'26.8"W, 16°40'54.5"S) between March 2005 and March 2006. Twenty non-galled and galled leaves per

tree were randomly collected and the number of galled leaflets per leaf was evaluated. The area of 10 non-galled and galled leaves and the percentage of galled area per leaf was calculated monthly with the software EasyQuantify®.

Photosynthesizing pigments- The pigments of disks (0.5 cm in diameter) from non-galled leaves, non-galled tissues of galled leaves and galled tissues were extracted in 80% acetone (v/v) after maceration and centrifugation. All samples were weighted and their areas were calculated. The contents of chlorophylls *a* and *b* and carotenoids were obteined using the equation proposed by Lichtenthaler and Wellburn (1983).

Histochemical tests – Histochemical tests were performed in fresh-hand sections and in material embedded in Paraplast® (Kraus & Arduin, 1997). Lipids were tested with Sudan red B (C.I. 26050), starch with (Brundett *et al.*, 1991) Lugol's reagent (Johansen, 1940), and reducing sugars with Fehling's reagent (Sass, 1951). Phenolic derivatives were detected in samples fixed in 2% ferrous sulfate in formalin (Johansen, 1940), mono and polymeric flavonoids (proantocianidins) were tested in hand made sections of fresh material fixed in 1 % cafein-sodium benozoate in 90% buthanol, and transferred to p-dimethylamminocinnamaldehyde (DMACA) for 2h (Feucht et al., 1986), and lignins were tested with 1% acidified phologlucinol (Jensen, 1962). Control-tests and sections *in natura* were used to compare with positive and negative results.

Statistical tretament - All data were submitted to variance analysis, Pearson correlations and Tukey test (P ≤ 0,05).

RESULTS AND DISCUSSION

Infestation level and the impact on leaf area - The trees of *Caryocar brasiliense* had a medium level of infestation (40.6% ±16.44) when compared to other host species such as *Rollinia laurifolia*, with 93.8% of leaves galled by *Pseudotetococcus rolliniae* (Gonçalves *et al.* 2005), and *Myrciaria dubia*, with 94% of stems galled by *Tuthillia cognata* (Barbosa *et al.* 2004). Most leaves presented just one galled leaflet (42.4%), while 26.4 and 31.2% presented 2 or 3 galled leaflets. In addition, the impact of gall induction on leaves of *C. brasiliense* is as reduced as the infestation level.

The area of non-galled leaves were 225.04 ± 6.43cm², and the galled leaves had a significant increase of 11% in area, with 249.94 ± 6.48cm² (fig. 1), and just 1.32% of their area occupied by galls. The results obtained with mature leaves are consequence of the common preference for gall induction on young leaves, which may have favored a greater leaf expansion due to the realocation

of resources to galled sites. Moreover, the leaf marginal meristem should have been stimulated. This increase in area was significant just in leaves with less than 8% of their area occupied by galls, while those leaves with 16% of galled area had a reduction in area (fig. 2). These data were similar to those of Gonçalves *et al.* (2005) on *Rollinia laurifolia- Pseudotectococcus rollinae* system. Either the area of non-galled or galled leaves increased in relation to the percentage of galled leaves on a single tree (r = 0.41; P = 0,0058 e r = 0.61; P = 0,0000), which may indicate a compensatory mechanism of galled plants as proposed by Welter (1989). These should be consequence of an increase in photosynthesis on non-galled tissues as an indirect effect of herbivory. Nevertheless, the contents on photosynthetizing pigments in *C. brasiliense* galls do not corroborate this proposal.

Photosynthesizing Pigments – Photosynthesis in galls has been studied in the Neotropical flora (Fernandes et al., 2010, Oliveira et al., 2011, Castro et al., 2013), and can be inferred by the comparison of the pigment contents in non-galled and galled leaves. The contents of total chlorophyll, chlorophyll a, chlorophyll b, xantophylls + carotenoids, and chlorophyll *a/ b*, total chlorophyll/carotenoids on *C. brasiliense-Eurytoma* sp. system were lower in galls when compared to non-galled leaves and non-galled portions of galled leaves (table 1). As the area of galled leaves was higher than that of non-galled leaves, photosynthesis does not seem to be negatively impacted by the gall induction. The intriguing positive impact of gall induction on the leaf area of *C. brasiliense* may be consequence of the translocation of photoassimilates from non-galled leaves to galled ones as proposed by Larson & Whitham (1991). This increase in potential photosynthetizing area may compensate the loss in the adaptive value of the host plant due to the galling herbivore activity.
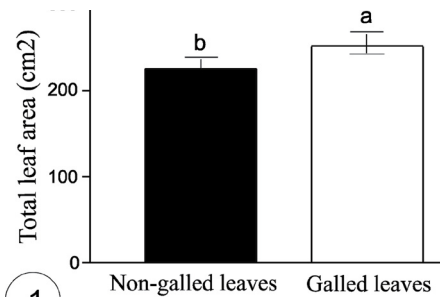
Figure1. Impact of gall induction on the leaf area of *Caryocar brasiliense* Camb. (Caryocaraceae).

$y = 227,37 + 4,01x - 0,25 x^2 (R^2 = 0,73)$
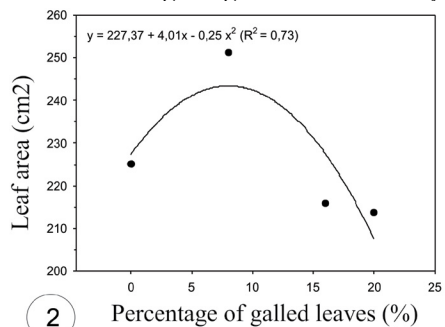
Figure 2. Effect of distinct infestation levels on total area of leaves of *Caryocar brasiliense* Camb. (Caryocaraceae).

The carotenoids contents were higher on non-galled portions or non-galled leaves than on galls (table 1). The production of pigments increased due to the level of infestation either in non-galled leaves (r = 0.74; P = 00038) or in non-galled portions (r = 0.63; P = 0.0077), which can cause a positive impact because of their antioxidant properties. The excess of ROS should end up in tissue death due to an hypersentitive response (HR), as proposed by (Isaias and Oliveira, 2011). The reduced content of photosynthetizing pigments in the gall tissues does not necessarily indicates their degradation. In *C. brasiliense* gall structure (Castro *et al.*, 2012), these seems to be consequence of the gain in mass, cell hypertrophy and hyperplasia, common processes of gall development (Mani, 1964; Oliveira and Isaias, 2010b; Isaias et al., 2011), and the spacement of pigments in the gall tissues. This relationship has been already reported in the Neotropics for *Aspidosperma australe*-Psyllidae and *Copaifera langsdorffii*-Cecidomyiidae gall systems (Oliveira et al., 2011; Castro et al., 2012). The true proof of the maintenance of photosynthetic activity deserves the analyses of fluorescence of chlorophyll *a*.

Table 1. Average values of chlorophyll *a*, *b* and total, xantophylls+carotenoids (mg.g^{-1}) chlorophyll *a*/*b* relationship and chlorophyll/carotenoids in non-galled leaves (NL), non-galled portion of galled leaves (NGL), and galls (G) of *Caryocar brasiliense*

Samples	Pigments					
	chlorophyll *a*[*]	chlorophyll *b*[*]	Total chlorophyll [**]	Xantophylls + Carotenoids[**]	chlorophyll *a*/*b*[*]	chlorophyll / Carotenoids[**]
NL	858.13a	250.85a	1108.98a	209.10a	3.49a	5.58a
NGL	802.01a	250.35a	1052.38a	207.21a	3.32a	5.26a
G	226.38b	104.83b	331.21b	78.77b	2.38b	4.21b

Values followed by the same letter in the same line do not have significantly differences by the Tukey test.

[*] e [**] - significant, respectively, at 1 and 5% of probability.

Histochemical profiles - Positive reactions for lipids were evidenced only in the cuticle of either non-galled or galled tissues (fig 3-C). Reducing sugars accumulated in the outer cortex of galls, a topographical maintenance of its accumulation by the tissues of origin, i.e., the palisade parenchyma and secondary and mid veins (fig 4A-C). Histochemical detection of reducing sugars is not common for Hymenopteran galls, but determines the nutritive profile of Cecidomyiidae galls (Bronner 1992). Nevertheless, starch, the reserve substance of Dipteran galls was not detected either in non-galled or galled tissues of *C. brasiliense*. The non-accumulation of lipids and starch in the nutritive and reserve tissues of *C. brasiliense* galls differs from the pattern proposed by Bronner (1992) for Hymenopteran galls.
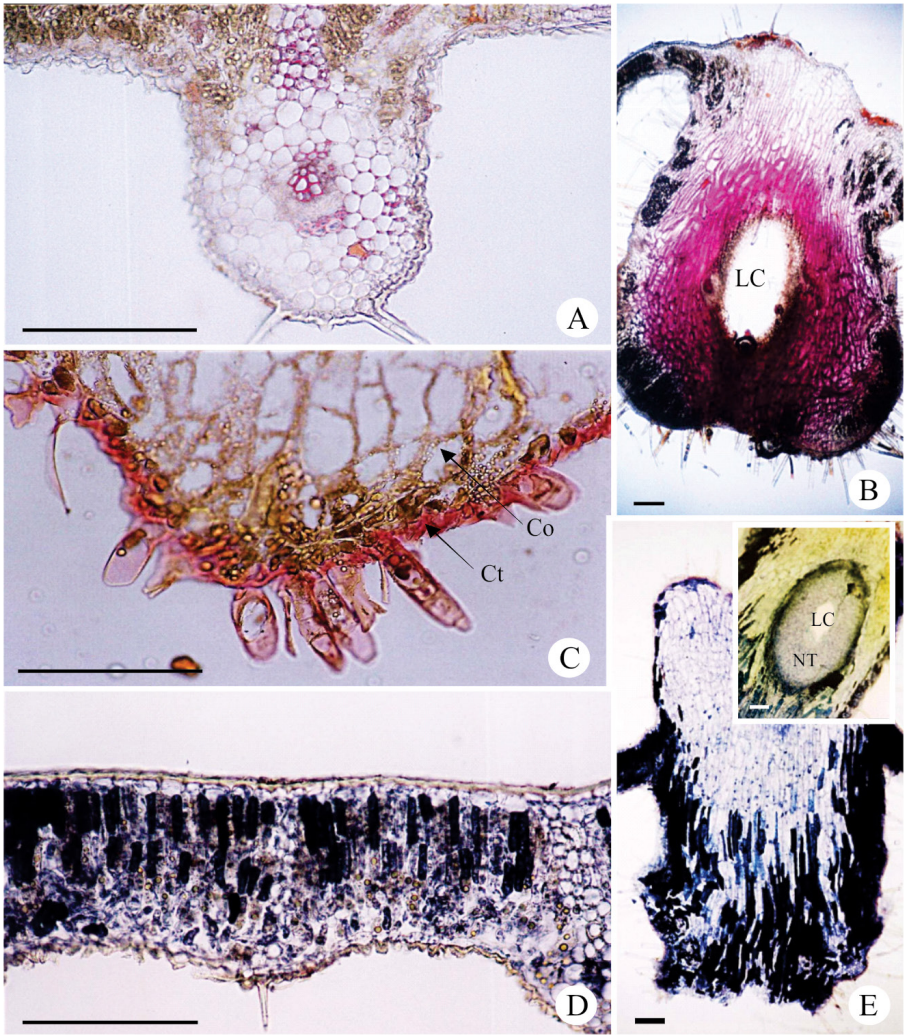
Figure 3. Histochemical profile of *Caryocar brasiliense* Camb. (Caryocaraceae). (A and D) Non galled leaflet. (B, C, E and F) Gall. (A-B) Lignins. (A) Detected in the vascular bundles and in a bundle sheath of a secondary vein. (B) Detected in gall cortex around the larval chamber. (C) Lipids in the cuticle on gall epidermis. (D-F) Flavonoids. (D) Detected in the chlorophyllian parenchyma. (E) Detected in gall cortex. (F) Less intense detection in nutritive tissue. LC = Larval chamber; Co = cortex; Ct = cuticle; NT = nutritive tissue. [Bars = 100 µm].
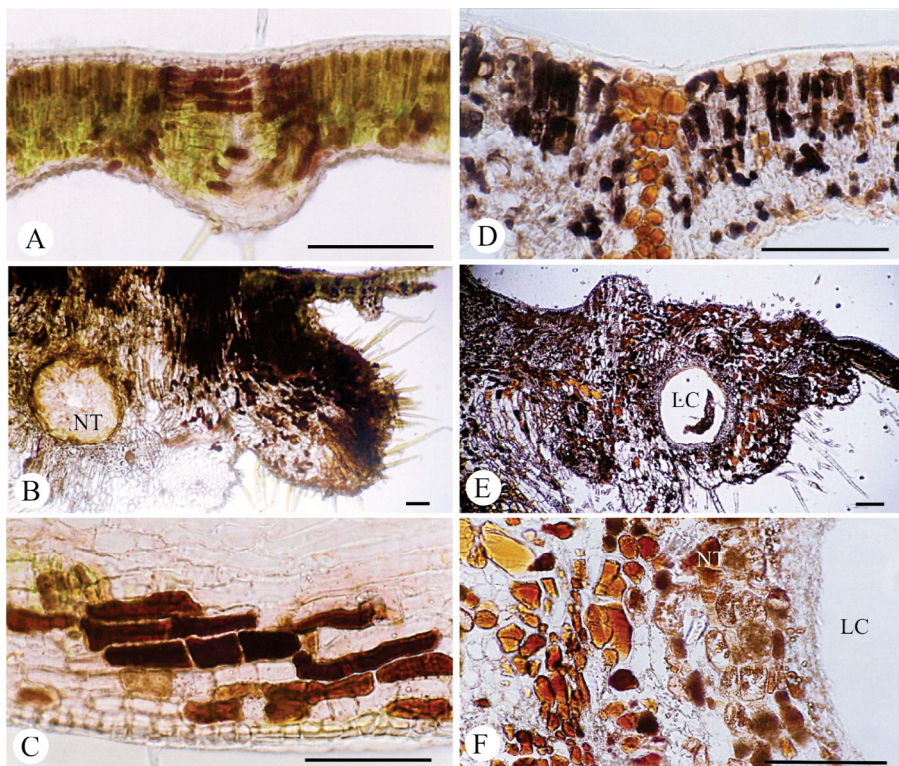
Figure 4. Histochemical profile of *Caryocar brasiliense* Camb. (Caryocaraceae). (A and D) Non-galled leaflet. (B, C, E and F) Gall. (A-C) Reducing sugars. (A) Detected in mesophyll and vascular bundles. (B) Detected in gall cortex. (C) Detected in cortical cells next to the epidermis. (D-E) Phenolic derivatives. (D) Detected in the cortex of second order veins, and ground system. (E-F) Detected in gall cortex. LC = larval chamber; NT = nutritive tissue. [Bars = 100 μm in A, B, E and F; 50 μm in C and D].

Lignins, which were deposited only in vascular tissues of non-galled leaves, were detected in the inner cortex, limiting the nutritive tissue (fig. 3 A-B). The poor lignification of *C. brasiliense* tissues (Castro *et al.*, 2012) may facilitate the first steps of the herbivore establishment. The neoformation of sclereids protect the galling larvae (Stone & Schönrogge, 2003), and is a physiological expression of programmed cell death (PCD) indirectly associated to ROS accumulation. The lignification of the cortical cells has been commonly related to a mechanical protection in several galls (Raman, 1991; Kraus *et al.*, 1994, 1996, 2002; Oliveira *et al* 2006, Oliveira and Isaias 2010b, Isaias *et al.* 2011,

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Formiga *et al* 2011), and its association with a physiological response of PCD is recent. The relationship between high concentrations of H2O2 and PCD events was based on the results of Potikha *et al.* (1999) with cotton fibers, where destructive reactions in membranes, proteins and nucleic acids were evidenced.

Phenolic and flavonoidic derivatives commonly function as anti-herbivore compounds (Mani, 1964; Abrahamson *et al.*, 1991; Formiga 2009). Nevertheless, their presence did not block the establishment of the *Eurytoma* sp. on *C. brasiliense* tissues. Flavonoidic derivatives were detected in the ground system of non-galled leaves, mainly in palisade parenchyma, and in gall cortex and nutritive tissue (Figure 3D-E). Phenolic derivatives concentrated in non-galled vascular sheath and palisade parenchyma, and were detected in gall cortex and epidermis (Figure 4D-F). The topographic position of the phenolics in peripheral tissues of the galls (Mani, 1964; Fernandes & Martins, 1985; Oliveira et al 2006, Formiga et al 2009) corroborates its defensiveness role against the galling herbivore's natural enemies (Mani, 1964; Oliveira , 2006).

CONCLUSIONS

The topographic disposition of reserve substances in galled tissues of *C. brasiliense* indicates its ideal microenvironment for *Eurytoma* sp. development and corroborates Nyman's (2000) proposal for the determination of tissue zones in galls. Phenolics accumulation in the outer cortex confers protection against natural enemies, while the carbohydrates accumulation in the inner cortex promotes nutrition for the galling herbivore. Unexpectedly, the levels of infestation positively affect the host leaves of *C. brasiliense* and photosynthesizing pigments may guarantee basal levels of photosynthesis, and play the crucial antioxidant role in gall chemical battle.

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REFERENCES

Abrahamson, W.G., Mccrea, K.D., Whitwell, A.J., Vernieri, L.A. (1991). The role of phenolics in goldenrod ball gall resistance and formation. *Biochemical Systematics and Ecology.* 19 (8): 615-622. (novembro)

Barbosa, M.L.L., Acioli, A.N.S., Oliveira, A.N., Silva, N.M. Canto, S.L.O. (2004). Ocorrência de Tuthillia cognata Hodkinson, Brown & Burckhardt, 1986 (Hemiptera: Homoptera, Psyllidae) em plantios experimentais de camu-camu Myrciaria dubia (H.B.K.) Mc Vaugh em Manaus (Amazonas, Brasil) *Acta* Amazônica. 34 (1): 115-119.

Bronner, R. (1992). Biology of insect induced galls, in: Shorthouse, J.D. & Rohfritsch, O., eds.*The role of nutritive cells in the nutrition of cynipids and cecidomyiids,* Oxford University, Oxford. p. 118-140. Brundett, M.C., Kendrick, B., Peterson, C.A. (1991). Efficient lipid staining in plant material with Sudan Red 7B or Fluoral Yellow 088 in polyethylene glycol-glycerol. *Biotechnic & Histochemistry.* 66: 111-116.

Castro, A.C., Oliveira, D.C., Moreira, A.S.F.P., Lemos-Filho, J.P., Isaias, R.M.S. (2012). Source-sink relationship and photosynthesis in the horn-shaped gall and its host plant Copaifera langsdorffii Desf. (Fabaceae). *South African Journal of Botany* 83: 121-126

Castro, A.C.R., Leite, G.L.D., Isaias, R.M.S. Morphological patterns of a hymenopteran gall on the leaflets of Caryocar brasiliense Camb. (Caryocaraceae). *American Journal of Plant Sciences* 3: 921-929.

Fernandes, G.W., Martins, R.P. (1985). Tumores de plantas: as galhas. *Ciência Hoje.* 19: 58-62.

Ferreira, K.M., Oliva, M.A., Hernandez-Terrones, M.G. (2005). Caracterização histoquímica da folha de pequi (Caryocar brasiliense Camb.). In: *Congresso Nacional de Botânica* Curitiba. Resumos: 56, Curitiba: UFPR.

Formiga, A.T., Gonçalves, S.J.M.R., Soares, G.L.G., Isaias, R.M.S. (2009). Relações entre o teor de fenólicos e o ciclo de galhas de Cecidomyiidae em Aspidosperma spruceanum Muel. *Acta* Botânica *Brasilica.* Arg. (Apocynaceae). 23: 93-99.

Formiga, A.T., Soares, G.L.G., Isaias R.M.S. (2011). Responses of the host plant tissue in Aspidosperma spruceanum Arg. (Apocynaceae). *American Journal of Plant Science.* 2: 350-358.

Gonçalves, S.J.M.R., Isaias, R.M.S.; Vale, F.H.A., Fernandes, G.W. (2005). Sexual dimorphism of Pseudotectococcus rolliniae Hodgson & Gonçalves (Hemiptera Coccoidea Eriococcidae) influences gall morphology on Rollinia laurifolia Schltdl. (Annonaceae). *Tropical Zoology* 18: 161-169.

Harbone, J., Williams, C.A. (2000). Advances in flavonoid research since 1992. *Phytochemistry*. 55: 481-504.

Hartley, S.E. (1998). The chemical composition of plant galls: are levels of nutrients and secondary compounds controlled by the gall-former? *Oecologia*.113: 492-501.

Isaias, R.M.S., Oliveira, D.C. (2011). Gall Phenotypes Product of Plant Cells Defensive Responses to the Inducers Attack. In: Mérillon, Jean Michel; Ramawat, Kishan Gopal. (Org.) *Plant Defence: Biological Control*. 1ed. New York: Springer, 12: 273-290.

Isaias, R.M.S., Oliveira, D.C., Carneiro, R.G.S. (2011). Role of Euphalerus ostreoides (Hemiptera: Psylloidea) in manipulating leaflet ontogenesis of *Lonchocarpus muehlbergianus* (Fabaceae). Botany. 89: 581-592.

Jensen, W.A. (1962). *Botanical histochemistry: principles and practice*. San Francisco: W.H. Freeman, 408 p.

Johansen, D.A. (1940). *Plant microtechnique*. New York: McGraw-Hill Book Co. Inc, 523 p.

Kraus, J.E., Arduin, M. (1997). *Manual básico de métodos em morfologia vegetal*. Seropédica: EDUR, 198 p.

Kraus, J.E., Solórzano Filho, J.A., Arduin, M., Isaias R.M.S. (1994). Respostas morfogenéticas de plantas brasileiras a insetos galhadores In: Fortunato, R.; Bacigalupo, *Proceedings of the VI Congresso Latinoamericano de Botânica*. Mar del Plata, Argentina.

Kraus, J.E., Sugiura, H.C., Cutrupi, S. (1996). Morfologia e ontogenia em galhas entomógenas de Guarea macrophylla subsp. tuberculata (Meliaceae) *Fitopatologia Brasileira*, 21 (3): 349-356.

Kraus, J.E., Tanoue, M. (1999). Morpho-ontogenetic aspects of entomogenous galls in roots of Cattleya guttata (Orchidaceae) *Lindleyana* 14 (4): 204-213.

Krause, G.H. (1988). Photoinhibition of photosynthesis. An evaluation of damaging andprotective mechanisms. *Physiologia Plantarum*. 74: 313-349.

Larson, K. C. (1998). The impact of two gall-forming arthropods on the photosynthetic rates of their hosts. *Oecologia*. 115: 161-166.

Larson, K.C., Whitham, T.G. (1991). Manipulation of food resources by a gall-forming aphid: the physiology of sink-source interations. *Oecologia*. 88: 15-21.

Lichtenthaler, H., Wellburn, A. (1983). Determinations of total carotenoids and chlorophylls a and b of leaf extracts in different solvents. *Biochemical Society Transactions*. 11 (5): 591-592.

Mani, M.S. (1964). *Ecology of plant galls*. The Hague: Dr. Junk Publishers, 434p.

Marques, M.C.S. (2001). *Estudo fitoquímico dos extratos de pequi (Caryocar brasiliense Camb.)*. Dissertação (Mestrado em Agroquímica/Agrobioquímica) – Universidade Federal de Lavras, Lavras, 91 p.

Motta, L.B., Kraus, J.E., Salatino, A., Salatino, M.L.F. (2005). Distribution of metabolites in galled and non-galled foliar tissues of Tibouchina pulchra. *Biochemical Systematics and Ecology*. 33: 971-981.

Nürnberger, T., Scheel, D. (2001). Signal transmission in the plant immune response. *Trends in Plant Science*. 6 (8): 372-379.

Nyman, T., Widmer, A., Roininen, H. (2000). Evolution of gall morphology and host-plant relationships in willow-feeding sawflies (Hymenoptera: Tenthredinidae). *Evolution*. 54: 526-33.

Oliveira, D.C., Christiano, J.C.S., Soares, G.L.G., Isaias, R.M.S. (2006). Reações estruturais e químicas de defesa de Lonchocarous muehlbergianus (Fabaceae) e ação do galhador Euphalerus ostreoides (Hemiptera, Psyllidae), *Revista Brasileira de Botânica (Impresso)*. 29:657-667.

Oliveira, D.C., Isaias, R.M.S. (2010a). Cytological and histochemical gradients inducing by sucking galls of Aspidosperma australe Arg. Muel. (Apocynaceae). *Plant Science*, 178: 350-358.

Oliveira, D.C., Magalhães, T.A., Carneiro, R.G.S., Alvin, M.N.A., Isaias, R.M.S. (2010). Do Cecidomyiidae gall induced by Aspidosperma spruceanum (Apocynaceae) fit the pre-stablished cytological and histochemical patterns? *Protoplasma*. 242: 81-93.

Oliveira, D.C., Isaias, R.M.S. (2010b). Redifferentiation of leaflet tissues during midrib gall development in Copaifera langsdorffii (Fabaceae). *South African Journal of Botany*. 76: 239-248.

Oliveira, D.C., Isaias R.M.S., Moreira, A.S.F.P., Lemos-Filho, J.P. (2011). Is the oxidative stress caused by Aspidosperma spp. galls capable of altering leaf photosynthesis? *Plant Science*. 80:489-495.

Potikha, T.S., Collins, C. C., Johnson, D. I., Delmer, D. P. & Levine, A. (1999). The involvement of hydrogen peroxide in the differentiation of secondary walls in cotton fibers. *Plant Physiology.*119: 849-858.

Raman, A. (1991). Cecidogenesis of leaf galls on Syzygium cumini (L.) Skeels (Myrtaceae) induced by Trioza jambolanae Crawford (Homoptera: Psylloidea). *Journal of Natural History.*25: 653-663.

Russo, R. (2006). Field guide to plant galls of California and other Western States. Univ. California Press, 397p.

Sass, J.E. (1951). *Botanical microtechnique*, 2nd ed. Ames: Iowa State College Press, 391p.

Stone, G.N., Schönrogge, K. (2003). The adaptative significance of insect gall morphology. *Trends in Ecology and Evolution*. 18 (10): 512-522.

Thiele, A.; Krause, G.H.; Winter, K. (1998). *In situ* study of photoinhibition of photosynthesis and xantophyll cycle activity in plants growing in natural gaps of the tropical forest. *Australian Journal of Plant Physiology,* 25: 189-195.

Welter, S. C. (1989). Arthropod impact on plant gas exchange. In: Bernays EA (ed) Insect-plant interactions, CRC, Boca Raton, Fla, 1: 135-150.150.