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The imbalance of redox homeostasis in arthropod-induced plant galls: Mechanisms of stress generation and dissipation ☆

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ABSTRACT

Background: Galls have specialized tissues for the protection and nutrition of the inducers, and these tissues have been studied from the developmental and histochemical perspectives. Recently, the role of oxidative stress in galls has been tested histochemically through detection of H_2O_2 in gall tissues.
Scope of Review: Developmental processes and cytological events are revisited from the perspective of the redox-potential balance in both the apoplast and symplast, especially concerning the accumulation of reactive oxygen species (ROS).
Major Conclusions: The redox potential is imbalanced differently in the apoplast and symplast at gall sites, with the apoplast having lower antioxidant-buffering capacity than the symplast. The strategies to recover redox-potential homeostasis involve the dissipation of ROS by scavenging molecules, such as phenolics, flavonoid derivatives, tocopherol, and enzyme systems.
General Significance: Insect galls are good models to test developmental hypotheses. Although the exact mechanisms of gall induction and development have not been elucidated at the biochemical and biophysical levels, modulation of the redox potential is involved in the crucial steps of gall initiation and establishment. This article is part of a Special Issue entitled Redox regulation of differentiation and de-differentiation.

1. Introduction

Galls result from intriguing and specific interactions between specialist herbivores and their host plants [62]. Insects comprise the major group of specialists in the galling habit, and can induce the morphogenesis of symmetrical structures [82] that culminate in distinct gall morphotypes, which are specific to the species of gall-inducing insect [51]. Insect-induced galls have complex tissues with typical features and functions [75,82], which deviate from the morphogenetic patterns of the host organs and are therefore elegant models for the study of developmental and physiological responses of plant cells to specific stimuli. These responses have been explored in temperate regions [5,14,84,88,89] and in the Neotropics [16,17,20,34,35,52,53,71,75]. Elicitor substances and hormones are believed to mediate plant-insect interactions [8,29,65,91,99], but the exact mechanisms of gall induction remain to be elucidated.

Galls are formed completely of plant tissues and while they may be induced in roots, stems, flowers, fruits, and seeds, they are especially numerous in leaves [62,63]. The shapes of leaf galls vary from simple, such as leaf rolling and folding, to massive globoid structures. Galls can also assume bizarre shapes such as horns or shells, e.g. the leaflet galls induced by *Euphalerus ostreoides* on *Lonchocarpus muehlbergianus*. In this gall, the mesophyll is transformed into a homogeneous cortex that accumulates phenolics, interspersed with redifferentiated vascular bundles (Fig. 1). Galls are considered to be extended phenotypes of the gall-inducing organisms, with little evidence of genetic modification, especially in insect-induced galls [21,85]. Consequently, the stimuli that trigger gall induction are most likely to be exogenous to plant cells, and may be transduced along the two cell compartments: the symplast and the apoplast. Biochemical and biophysical reactions in these compartments, i.e., the inner side of the plasma membrane and the cell-wall continuum respectively, culminate in the redifferentiation of cells, with a new organization of tissue layers. The establishment of a new redox balance within these two cell compartments involves the accumulation of reactive oxygen species (ROS), as has been demonstrated

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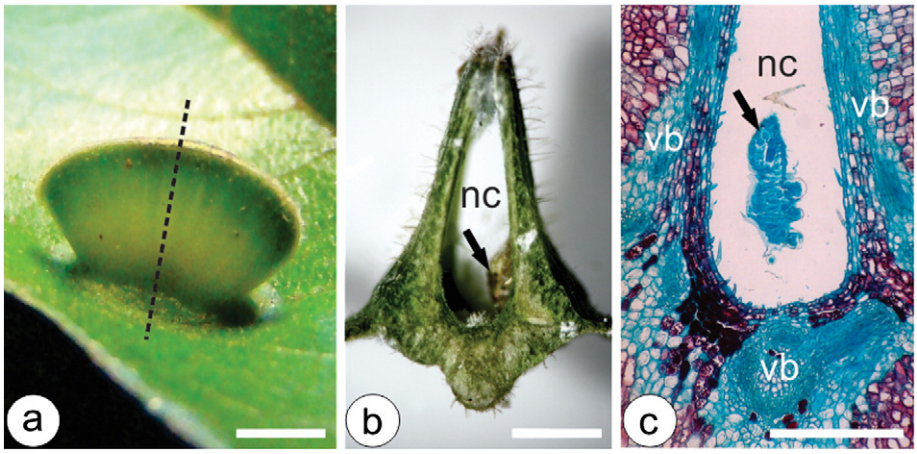

Fig. 1. Leaf gall induced by *Euphalerus ostreoides* (Hemiptera) on *Lonchocarpus muehlbergianus* (Fabaceae). **a** Macroscopic view of the bivalve-shaped gall (dotted line indicates cross-section point shown in **b**). **b** Cross section of the gall, showing a nymph (arrow) that induces the redifferentiation of the leaf parenchyma into the gall cortex, forming a continuum between non-galled and galled tissues. **c** Gall anatomical detail in cross section, showing a nymph inside the chamber (nc), and its feeding sites, the vascular bundles (vb). Bars: **a** 0.5 cm; **b** 0.25 cm; **c** 500 μm.

histochemically, and is related to the determination of new cell fates and functions [16,52,75–77]. In a general sense, the balance between ROS production and ROS scavenging in cellular compartments is assumed to affect the cell redox state, which modulates the cell reprogramming involved in the responses to the biotic stimuli of gall initiation and establishment, or triggers plant-defense mechanisms such as hypersensitivity responses (HR) [79].

2. Evidence of ROS accumulation and redox imbalance during gall establishment

High concentrations of ROS in gall tissues were detected via the 3.3' diaminobenzidine (DAB) histochemical method in four Neotropical galls [16,52,76,77], and were related to the high oxidative stress generated in response to attack by gall-inducing organisms [79]. This accumulation of ROS occurred in the cells of non-galled tissues, which are the mother cells of the gall parenchymatic cortex in *Aspidosperma australe* and *A. spruceanum* [75,76]. Agrawal (2006) suggested that the unbalancing of ROS and antioxidant production is evidence of oxidative stress. Accordingly, the higher production of ROS in galls, as demonstrated by the intensity of the reaction after the DAB test (Fig. 2), indicated that cells at gall sites are under oxidative stress and show a redox-potential imbalance. This stress is even higher during the phase of gall maturation, due to increased ROS production in the final stages of cell redifferentiation during gall establishment. Further evidence of ROS production and oxidative stress in the cells of galls is based on ultrastructural analyses. For instance, there is an increase of plastoglobules in the chloroplasts of the galls of *A. australe* compared to non-galled tissue [75]. Plastoglobules are subcompartments of the chloroplasts that may contain several kinds of lipids and proteins, including tocopherol cyclase. The activity of this enzyme indirectly protects the thylakoid membranes and the photosystems from damage caused by ROS (Porfirova et al., 2002; Kanwischer et al., 2005). Another oxidative stress-related ultrastructural alteration observed in galls is the differentiation of multivesicular, lamellar bodies, and lomasomes [83]. In the Neotropics, these cell structures were reported in the vascular and perivascular parenchyma cells in the galls of *Psidium myrtoides* [18], and in the fast-dividing nutritive cells of the galls induced by Lepidoptera on *Marcetia taxifolia* [37]. In both cases, these structures occurred at the same sites where ROS accumulate, thus corroborating the role of ROS-mediated oxidative stress in the redifferentiation of gall tissues.

Organelles involved with redox reactions and intense rates of electron flow, i.e., chloroplasts and mitochondria, are the main sources of ROS [47]. At gall sites, chloroplasts may be differentially identified in the outer cortex, where cells are typically live and photosynthesizing, and mitochondria in the inner cortex, where cells usually do not photosynthesize, being impacted most by the galling insect's activity. In the outer cortical cells, ROS production is intrinsic to plant metabolism, while in the inner cortical cells, ROS synthesis is a cellular response to the galling insect's stimuli, which lead to new tissue functions [52,75,77,78,80]. ROS are involved in gall morphogenesis (Isaias and Oliveira, 2012), in a sophisticated mechanism of imbalance of their positive and negative effects in gall tissues. Considine and Foyer [22] recently discussed the evidence for redox-dependent control of plant growth, which involves a network of interactions among ROS, antioxidants, and major regulators of the plant cell cycle. Bedetti et al. [8] demonstrated the co-occurrence of ROS, phenolics, and IAA in cells of galls on *Piptadenia gonoacantha*, which is further evidence of the coordinated control of gall growth. As a pool of new cell cycles is produced, and mechanisms to reprogram cell development are triggered [18], galls become sites of this redox-dependent controlled network of metabolites.

2.1. Galls as ROS-generating organs

ROS are commonly generated in response to insect activity, and were suggested to be the first signaling molecules involved in gall development [79]. In addition to the production of hydrogen peroxide (H_2O_2), changes must occur in both the plasma transmembrane potential (V_m), and cytoplasmic calcium concentration, followed by the production of hormones [60]. However, Foyer and Noctor [43] suggested that the cascade of signaling events following ROS production does not exist. Instead, each cell should be considered as a set of discrete compartments, with the apoplast being characterized by low antioxidant-buffering capacity compared to the symplast [43]. Even though gall development causes alterations at cytological levels, chloroplasts and mitochondria are commonly numerous and structurally preserved, as demonstrated by Ferreira et al. [37] in galls of *Marcetia taxifolia*. Moreover, even when galls are photosynthesis-deficient, such as those of *Nothotrioza myrtoidis* on *Psidium myrtoides* [16], the high metabolic rate of gall tissues is evidenced by the abundance of mitochondria [18]. Consequently, the ultrastructural analyses indicate that the cells of galls are potentially involved in the production of ROS. At the tissue level, the functional gradients established in gall cortices [75], i. e., the regulation of cell hypertrophy and tissue hyperplasia mediated by the accumulation of metabolites and the activity of

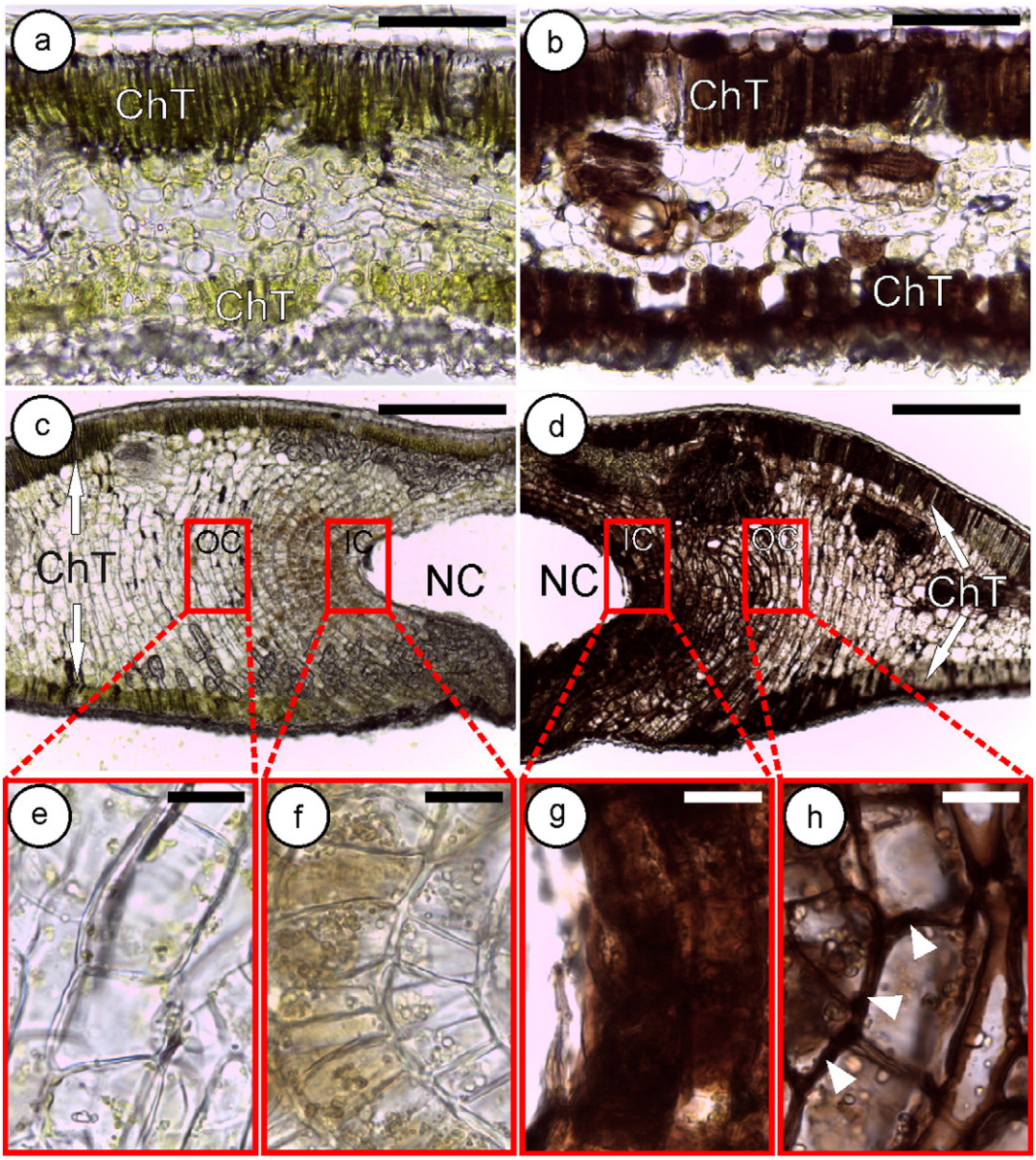

Fig. 2. Histochemical detection of reactive oxygen species (ROS) in the leaves of *Aspidosperma australe* and leaf galls induced by *Pseudophacopteron* sp. **a, b** Non-galled leaves. **c-h** Galls. **a, c, e, f** Fresh untreated tissues. **b, d, g, h** Fresh tissues treated with 3-3'-diaminobenzidine (DAB) to detect ROS. Note that both leaves and galls have chlorophyllous tissues (ChT) with high amounts of ROS. **e** Detail of the outer cortical cells (OC) of the galls, with few chloroplasts and hyaline cytoplasm. **f** Detail of the inner cortical cells (IC), with few chloroplasts and dense cytoplasm. **g** Detail of the IC with high amounts of ROS in the symplast, near the nymphal chamber (NC). **h** Detail of the OC, with ROS detection mainly in the apoplast (arrowheads). Bars: **a, b** 50 μm; **c, d** 100 μm; **e–h** 25 μm.

enzymes [16,17] support the cascade hypothesis proposed by Maffei et al. [60].

As a consequence of the low antioxidant-buffering capacity of the apoplast, ROS have been detected in the cell walls of all gall tissues, as well as in the symplast of all chlorophyllous and inner cortical cells. For instance, ROS were detected in galls of *Euphalerus ostreoides* (Hemiptera: Psyllidae) on *Lonchocarpus muehlbergianus* [52], in galls of Cecidomyiidae on *Aspidosperma spruceanum*, and in galls of Phacopteronidae on *A. australe* [76] (Fig. 2), which indicated that ROS signaling and the sites of detection are generalizable across host plants and galling-insect taxa. Currently, alterations in the cell apoplast, found in ultrastructural and immunocytochemical studies, have also been related to ROS migration from the symplast and their accumulation in cell walls [16,17,39,77,78,80]. The apoplast alterations have functional implications for the entire gall. In cell walls, ROS act synergistically with IAA to loosen the bonds between polymers [86], a mechanism essential for the neoontogenesis, *sensu* Carneiro et al. [17], of plant tissues toward gall development. Thus, the original role of ROS in non-galled cells is altered toward gall development, when the properties of rigidity, flexibility and porosity are enhanced in specific tissue layers, which requires changes in the dynamics and composition of cell walls [39,61,80].

3. Consequences of the redox imbalance in the apoplast due to gall formation

The transformation of host organs into the new developmental programs of galls involves the control of cell expansion via ROS-mediated signal transmission [4,7]. The first symptoms of redox imbalance are triggered by the ROS burst at the plasma membrane [101] and are mediated by electron acceptors such as oxygen or compounds with a catechol ring system (chlorogenic acid, caffeic acid, quercetin, and

catechin). These acceptors influence the cell-wall composition, and this culminates in the production of both reduced and oxidized forms of ascorbate (monodehydroscorbate and dehydroascorbate) in the apoplast, which are involved in cell metabolism and growth [41]. Ascorbic acid is the only antioxidant buffer of the plant cell apoplast that is capable of regulating its redox state. However, other enzymes, such as superoxide dismutase (SOD), the NADPH oxidases (NOX), peroxidases, polydiamine oxidases and oxalate oxidases [7], are also involved in this process. The dynamics of enzymatic processes and antioxidant buffering reveals that the accumulation of ROS can be toxic to plant cells, but that ROS also play important roles as signaling molecules. The growth and development of galls as well as of the non-galled organs requires the control of this antagonistic effect of ROS in plant-cell compartments.

The cell-cell communication characterizing pathogen attack is mediated by cell-wall polysaccharides [13], a signaling pathway yet to be assessed in plants under the attack of arthropods. From a structural point of view, it can be assumed that the signaling molecules triggered by the galling organism must interact primarily at the level of the apoplast compartment, the cell wall. After recognizing its host-plant species and organ, the galling herbivore must establish itself within plant tissues, which commonly requires a rearrangement of the axis of cell expansion [61]. In addition, the tissue rearrangement involves the deposition of different types of pectins and proteins during the developmental cycle of the gall [17,80]. The new patterns of cell elongation are directly linked to the reorientation of cellulose microfibrils, which requires loosening and tightening mechanisms. Several of these mechanisms involve redox reactions, with the control of wall extensibility orchestrated by low-molecular-weight oxidants and antioxidants in the apoplast [59]. This premise is supported by the work of Miller [66], who demonstrated experimentally that H_2O_2 is responsible for the rapid breakdown of the cell-wall polysaccharides. This indicates that cell-wall remodeling and ROS production in galls may be closely related, as evidenced in the galls of *Baccharis reticularia* [39].

Immunocytochemical evidence for enzymatic activity in the cell walls was reported in galls of *Baccharis dracunculifolia* [80] and of *Psidium myrtoides* [17]. The data obtained on these two gall morphotypes demonstrated that the degree of methylesterification of homogalacturonans (HGAs) decreased from young to senescent galls. One of the pathways for the demethylesterification of the cell-wall polysaccharides involves the activity of pectin-methylesterases (PMEs). The PMEs catalyze the specific demethylesterification of HGAs in plant cell walls, releasing methanol and protons, which creates negatively charged carboxyl groups in the process [72]. This mechanism indicates that variations in redox potential are linked to the methyl esters in cell walls during the cell cycles, and these variations ultimately affect the potential of cell-wall flexibility throughout gall development, constrained by the time of senescence (Fig. 3).

Some galls have a sheath of lignified cells in the cortex. Among polyphenolic derivatives, lignins are the most affected by oxidative stress, as their biosynthesis depends on the generation of ROS, especially the hydroxyl radical ($^{\bullet}OH$). The key step in lignin formation is the conversion of monolignols (*p*-coumaryl, coniferyl and synapil alcohols) into phenoxy-radicals, a reaction catalyzed by peroxidases [9]. During the transition from the phase of growth and development to

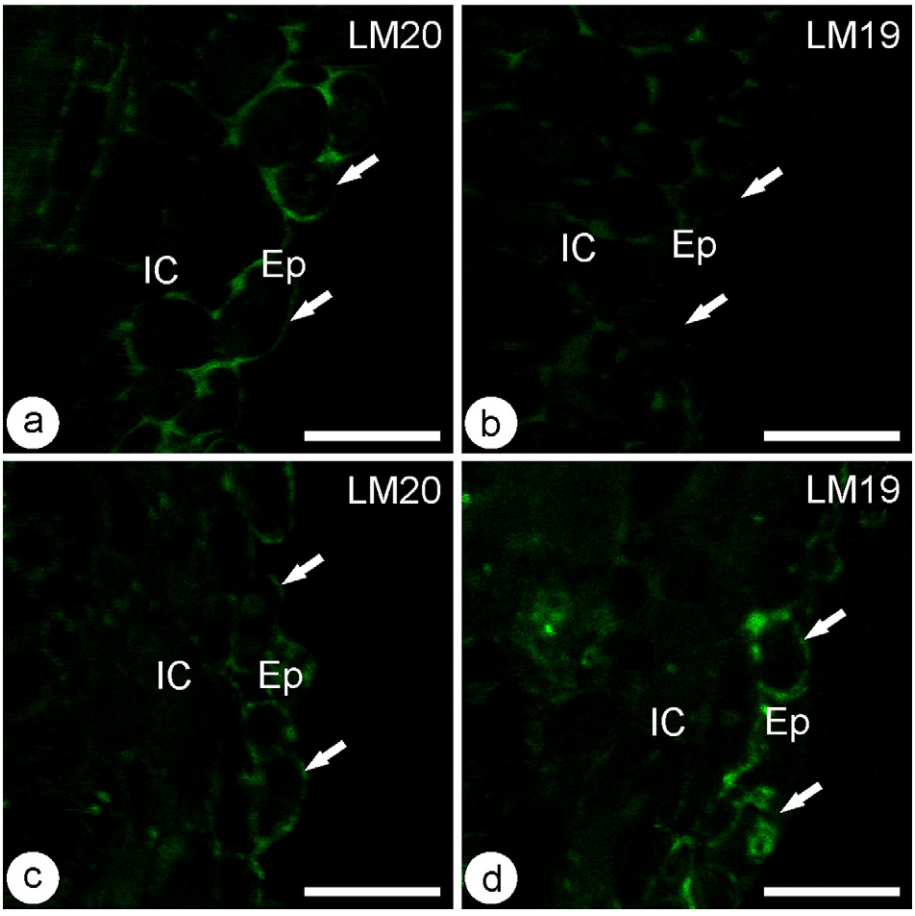

Fig. 3. Fluorescent immunocytochemical detection of homogalacturonans (HGAs) in the plant cell walls of the galls of *Nothotrioza myrtoidis* on *Psidium myrtoides*. **a, b** Mature galls. **c, d** Senescent galls. **a, c** Detection of high methyl-esterified HGAs bound by the specific monoclonal antibody LM20. **b, d** Detection of low methyl-esterified HGAs bound by the specific monoclonal antibody LM19. Mature galls show strong binding of high methyl-esterified HGAs, but weak binding of low methyl-esterified HGAs; while senescent galls show weakened binding of high methyl-esterified HGAs, and strengthened binding of low methyl-esterified HGAs by LM20 and LM19, respectively. Inner cortical cells (IC), Epidermis (Ep). Bars: 50 μm.

maturation, some plant galls, such as the intralaminar leaf galls on *A. spruceanum* [40,76], the bivalve-shaped galls on *L. muehlbergianus* [52], the fusiform stem galls on *Marcetia taxifolia* [34], and the globoid extralaminar galls on *Psidium myrtoides* [16], accumulate ROS in different cell lineages around the larval chamber. These cells differentiate into the lignified mechanical tissue layer described by Rohfritsch [88], and related to defense against natural enemies [96]. Currently, the structural roles and protective functions of mechanical layers have been contested. ROS, polyphenols, including lignins, polyphenol oxydases, and IAA were co-localized near the gall nutritive tissue [8,56] and in hypertrophied cells [16,17,34,36,52], suggesting a primary role for these compounds in gall morphogenesis [8]. Phenolics and ROS are also produced in response to methyl jasmonate, a stress hormone related to mechanical injury and pathogen attack, which stimulate the activity of phenylalanine ammonia lyase, a key enzyme of the phenylpropanoid metabolism [2,24,55].

4. Redox alterations in the symplast resulting from gall initiation

Chloroplasts and mitochondria naturally generate ROS during the processes of photosynthesis and respiration, which affect the redox potential inside the symplast [42], and then modify or permanently damage plant cell compartments [69]. The flux of electrons from the sites of photosynthesis and respiration toward molecular oxygen is followed by the production of ROS, which are buffered by antioxidant substances, responsible for redox homeostasis in plants [42]. This electron flux is increased in galls, most probably due to increased cell metabolism and respiration, and to the maintenance of the photosynthetic apparatus [78,90]. The consequent and necessary new balance of redox homeostasis in plant galls implies the existence of mechanisms of ROS scavenging to prevent hypersensitive responses (HR). The HR is a localized resistance mechanism, which takes place around the sites of oviposition and feeding of the galling insects, or the entrance of the larvae within plant cells, and is a plant counterattack against the herbivore [28,31–33]. Even though HR responses occur in some plant species, many galling herbivores successfully induce their galls despite the redox imbalance established during gall initiation, as observed in the *Fagus sylvatica* - *Hartigiola annulipes* (Diptera: Cecidomyiidae) system [33]. The quantitative evaluation of HR responses in the *Contarinia* sp. - *Bauhinia brevipes* system demonstrated that HR was the most important mortality factor for four consecutive years (>90%) [32]. Nevertheless, this is not a universal pattern of plant responses to galling stimuli. For example, in the *Pseudotectococcus rolliniae* - *Rollinia laurifolia* system, neither the natural enemies nor the HR seem to control the population of the galling herbivores; in one study, Gonçalves et al. [44] found that 93.7% of the leaves were infested, and observed no signs of HR. Similar results (98.2% infestation and no HR symptoms) were reported for the *Eriogalococcus isaias* - *Pseudobombax grandiflorum* system [61].

After gall establishment, and ROS accumulation, the degree of tissue alterations increases, but the high oxidative burst in chloroplasts is buffered, and photosynthetic rates are maintained at gall sites [78]. This buffering mechanism should include the enzymatic activity of superoxide dismutase (SOD), ascorbate peroxidase (APX) and thioredoxin peroxidase, and the involvement of ascorbic acid (ASA), glutathione, tocopherol and carotenoids [68]. The presence of all these enzymes and metabolites has not been tested in gall tissues, but the synthesis of ASA and the low levels of glutathione in galled leaves of *Terminalia arjuna* induced by *Trioza fletcheri* (Hemiptera: Psylidae) indicate that glutathione is involved in the achievement of redox homeostasis [54]. Tocopherol, an intermediary molecule that protects the thylakoid membranes and proteins associated with photosynthetic damage caused by ROS, is produced in plastoglobules (Porfirova et al. 2002, Kanwischer et al. 2005). The plastoglobules detected in large numbers and increased size at the periphery of the chloroplasts in leaves of *Aspidosperma australe*, *A. spruceanum,* and *Psidium myrtoides* [18,78] were considered to be another strategy to control the oxidative burst and maintain redox homeostasis, in cells of both non-galled and galled tissues.

The oxidative burst in chloroplasts is a symptom observed in the most often galled host-plant organs, the leaves. Leaf tissues, which are primarily adapted for photosynthesis and respiration, can produce completely new structural and functional designs as manifested in a variety of gall morphotypes. These tissues, when altered into galls, show rates of photosynthesis that indicate a positive, negative or neutral influence of the galling herbivores on their host tissues [20,30,38,58,78]. Increased photosynthesis in galls, although rarely observed, was demonstrated in a gall induced by the cynipid *Antitrophus silphii* on *Silphium integrifolium* (Asteraceae), and was related to increased water potential in the xylem as well as stomatal conductance [30]. Many studies of galls, however, indicate maintenance or reduction of photosynthesis and related parameters, such as stomatal conductance and transpiration [54,58,78]. The decrease in photosynthesis rates must also be a consequence of a reduction in the area of chlorophyllous parenchyma during the phase of gall growth and development, and lignification or suberization from the phase of gall maturation to senescence [20].

The neutrality of the effects caused by galling herbivores on host-plant tissues seems to be dependent on the maintenance of the photosynthetic apparatus at the gall sites. In such cases, besides producing carbohydrates [46], photosynthesis may play a secondary function by supplying new O_2 molecules to the system. The additional O_2 supply is especially important for galls with anomalous, functionally deficient stomata or in those where stomata are totally absent [15,52,70,74]. Some of these galls may have a suberized dermal system, and reduced intercellular spaces due to intense cell hypertrophy and tissue hyperplasia. The result of this structure is limited oxygen diffusion [49], which can be minimized by the recycling of oxygen produced by photosynthesis in the aerobic metabolism [20,46]. Independently of the effects on photosynthesis and respiration rates, oxidative stress seems to be consistently higher in galled than in non-galled leaves [54]. The analysis of chlorophyll fluorescence parameters in galls induced by *Eugeniamyia dispar* (Diptera: Cecidomyiidae) on the leaves of *Eugenia uniflora* (Myrtaceae) indicates impaired photosynthesis in gall tissues compared to non-galled tissues (Fig. 4). The low fluorescence in gall cortical parenchyma is related to the high level of ROS that damage the photosystems. Both morphologically complex galls, such as the horn-shaped galls on *Copaifera langsdorffii* (Fabaceae) [77], and simple galls, such as the lenticular intralaminar galls induced by a species of Pseudophacopteronidae (Hemiptera) on *Aspidosperma macrocarpon* (Apocynaceae) [20], seem to have low contents of chlorophyll *a* and *b*, disorganization of the thylakoid membrane system, and loss of the integrity of the grana. However, measurements of chlorophyll *a* fluorescence indicate that these galls retain their photochemistry capacity [20,78]. This maintenance demonstrates that the electron chain of photosynthesis is not impaired, and the low values of photosynthesis are consequence of low rates of CO_2 uptake.

Low rates of CO_2 fixation are expected in galls, which are consequently effective physiological sinks [10,19]. Galls induced by the cynipid *Phanacis taraxaci* accumulated up to 70% of the total carbon produced by their host plant *Taraxacum officinale* (Asteraceae) [10], indicating variation in the physiological sink even in a single host plant. The sink strength depends on the activity of sugar metabolism, which can be linked to the maintenance of gall cellular machinery and the insect's nutrition [74,75,97,98,100]. Together, these metabolic dynamics imply high rates of cellular respiration [75,90] and a sugar-dependent process [49] that is responsible for ROS production in the mitochondria [6,26,69]. Although the presence of sugars in the plant cell may increase the respiratory metabolism and ROS production, carbohydrates can react with ROS to form mannitol, as observed in transgenic tobacco plants [23,92,94]. Thus, the sugars drained to gall

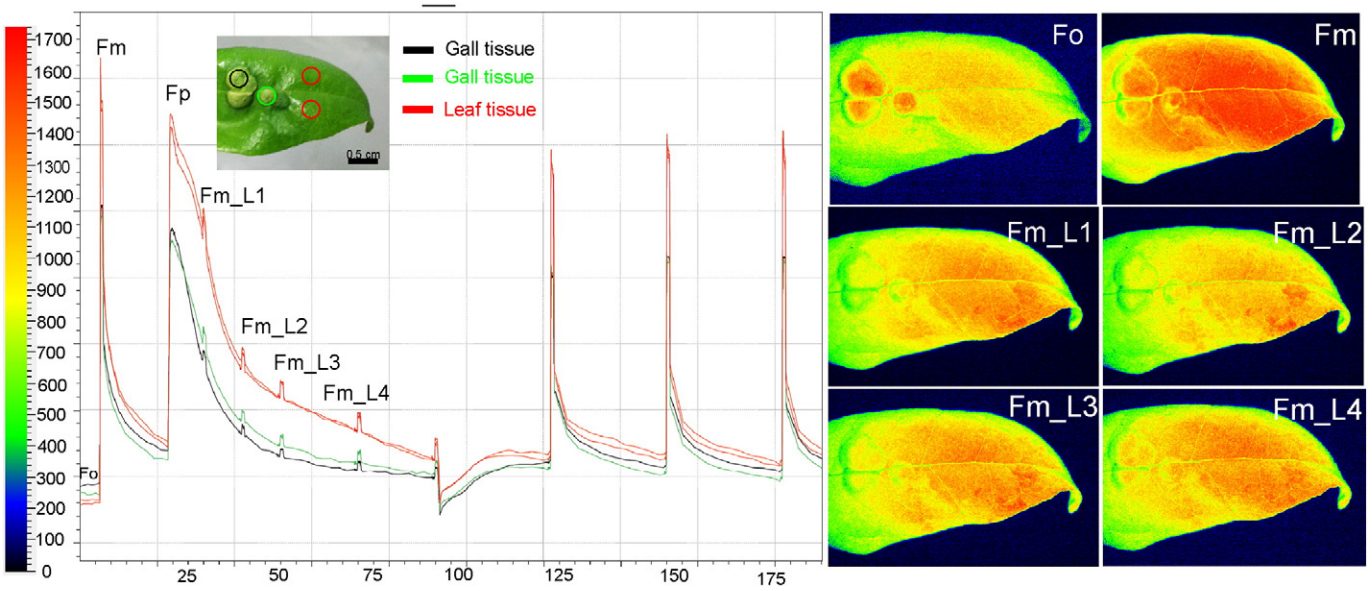

Fig. 4. Fluorescence quenching analysis performed in galled leaves of *Eugenia uniflora* (Myrtaceae), using a modulated fluorescence imaging apparatus, Fluor Handy PSI. The maintenance of the integrity of the electron chains, and the capacity of gall tissues for photosynthesis are demonstrated. A dark-adapted (30 minutes) leaf with galls was exposed to various light treatments. Fo is the minimal fluorescence in the dark-adapted state, Fp is the peak of fluorescence during the initial phase of the Kautsky effect, and Fm is the maximum fluorescence in the dark-adapted state. Fm_L1-L4 are the maximum fluorescence at intervals of 15 seconds after light-saturating pulses. The photosynthetic tissue in galls maintains its photochemistry capacity (higher values of Fm).

sites, as observed in *Copaifera langsdorffii* galls [20], may play secondary roles in the dissipation of ROS accumulated in gall tissues.

5. Phenolics accumulation follows ROS signaling at gall sites

Accumulation of phenolics has been observed in insect galls across a variety of host plants, and shows the great ability of gall-inducing organisms to cause changes in the metabolism of host-plant tissues [57,73]. Plant galls are natural sources of polyphenolic derivatives, such as tannins (hydrolyzable and proanthocyanidins) and simple phenolic acids. According to the redox theory [45], the primordial function of secondary metabolites, especially phenolic derivatives, is to protect plant cells against the noxious effects of free radicals. The scavenger effect of plant phenolics on the prevention of oxidative stresses has been tested *in vitro* [1,25,48,64]. Insect galls, as natural sources of phenolics, are good *in vivo* models to analyze the dynamics of phenolics production, their overstimulation by galling insects, and their scavenging effects.

The old dilemma of plants, whether to expend energy to grow or to defend themselves [50], relies on the competition between the production of secondary and primary metabolites. This competition can also be decisive for the establishment of chemical patterns in plant galls. Studying the galling behavior of two species of *Tanaostigmodes* (*T. ringueleti and T. mecanga*) that induce two distinct gall morphotypes on *Calliandra brevipes*, Detoni et al. [27] observed that the primary and secondary metabolism of galls differentially favored the production of nutritional metabolites over defensive ones. The gall morphotype with the largest number of inducers per chamber (*T. ringueleti* gall) has the lowest concentration of flavonoids, but accumulates the highest amounts of carbohydrates and proteins, thus supporting the nutritional hypothesis for the adaptive value of the galling habit [81]. The microenvironmental hypothesis [81,96] has been successfully tested in galls, and proved to be adaptive for the survival of gall inducers, as well [67]. Nevertheless, none of these hypotheses is exclusive, or supplants the others.

Flavonoids (including condensed tannins) are known to be chemical defenses against several abiotic stresses that are directly or indirectly related to oxidative stress in plant tissues [3,49]. The altered production of flavonoids in galled tissues can provide some clues about the relationship between oxidative stress and gall formation. There is also evidence indicating qualitative changes in the flavonoid profile of host plants due to the activity of the gall-inducing organism. For example, in *Rollinia laurifolia* (Annonaceae), the increased production of flavonoids, together with changes in their polarity [95], was attributed to the presence of the galling eriococcid *Pseudotectococcus rolliniae* [44]. The galled tissues on *R. laurifolia* showed a large increase in more lipophilic flavonoids, which may indicate protection of the cell membranes against oxidative stress. In this case, the production of more-active flavonoids at the same sites where ROS is produced could function as an adaptive mechanism to prevent oxidative damage in insect galls. Due to their constant presence in specific gall tissues, both flavonoids and simple phenolic acids have a considerable scavenger effect. This activity is more likely to explain their accumulation in galled tissues than is the defensive function that is commonly assumed [1]. Consequently, herbivorous insects can benefit from the presence of phenolics in plant tissues, because of their role in restoring the redox balance by preventing ROS accumulation, which could lead to HR at gall sites.

6. Conclusions and perspectives

Galls are the result of very specific interactions between galling herbivores and the host-plant tissues, where the redox homeostasis is very likely to be impaired. This impairment is assumed from the accumulation of ROS in the galls, which imbalances redox homeostasis in the two cell compartments, the apoplast and the symplast (Fig. 5). The accumulation of ROS in the cell walls, the apoplastic compartment, is responsible for its loosening and consequent cell redifferentiation and hypertrophy, both of which are commonly observed processes during gall growth and development. As the cell walls have low antioxidant-buffering capacity, the highest oxidative burst generated by the presence of the galling arthropod occurs in the symplast. The imbalance of redox homeostasis within the symplast of the cells at the sites of gall induction should naturally lead the tissues to a hypersensitive response and blockage of gall formation. However, mechanisms of ROS scavenging and stress dissipation at gall sites, such as (i) the presence of plastoglobules, tocopherol and antioxidants, (ii) the high accumulation of carbohydrates, and (iii) the occurrence of phenolic compounds can

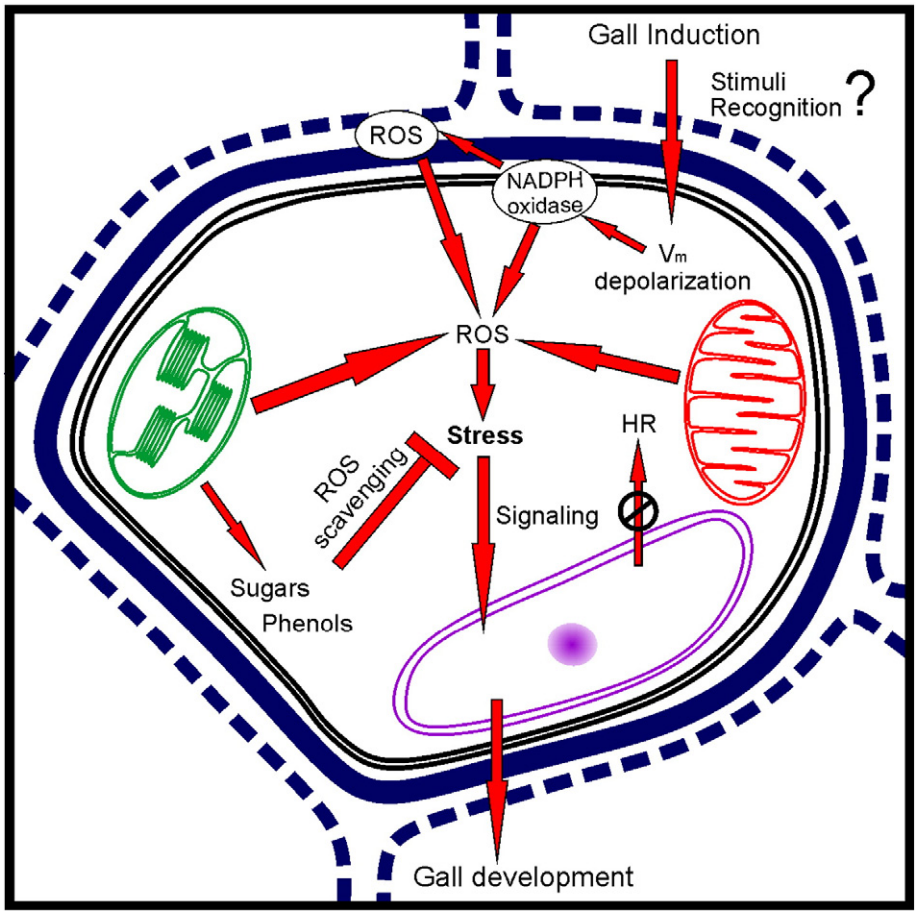

Fig. 5. Hypothetical scheme for early events in cell signaling and redox balance in the apoplast (single solid line and adjacent dotted lines = cell walls and middle lamella), and symplast (inside double solid line = protoplast) during gall induction. Changes in ion fluxes are believed to induce Vm depolarization and activation of the NADPH oxidase complex. This process leads to the production of ROS, generating oxidative stress, which is enhanced by the ROS produced by photosynthesis and respiration. The additional stress generated by gall-inducing insects imbalances redox homeostasis in the symplast. The cells react to ROS accumulation by triggering mechanisms of ROS dissipation, mediated by sugars and phenols at gall sites. These substances are believed to modulate stress in the symplast, thus preventing the occurrence of hypersensitive responses (HR). The arrows indicate positive relationships. T-shaped bars indicate the blockage of the ROS influence by scavenging molecules.

act as potent ROS scavengers, and restore the redox homeostasis in galled tissues.

Transparency document

The Transparency document associated with this article can be found, in online version.

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