



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



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ARTICLE INFO

Article history:

Received 16 September 2014

Received in revised form 12 March 2015

Accepted 15 March 2015

Available online 24 March 2015

Keywords:

Apoplast

Gall

Morphogenesis

Reactive oxygen species

Redifferentiation

Symplast

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 H₂O₂ 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.

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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

[☆] This article is part of a Special Issue entitled Redox regulation of differentiation and de-differentiation.

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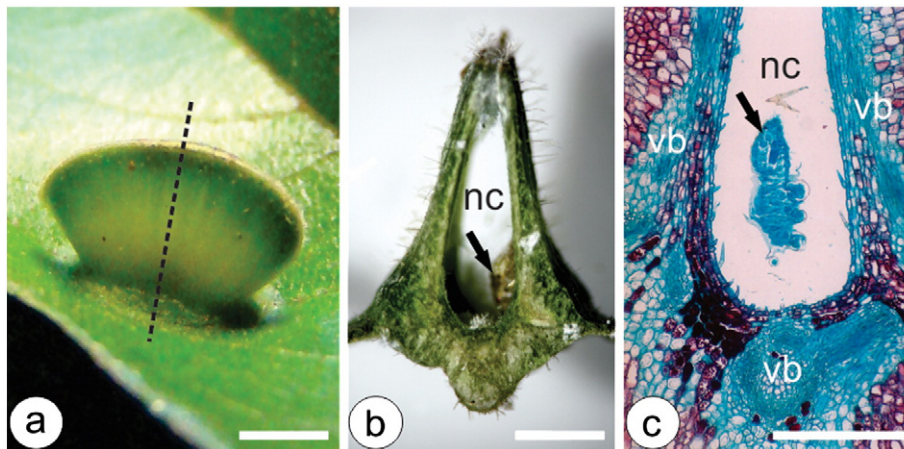


Fig. 1. Leaf gall induced by *Euphalerus ostreoides* (Hemiptera) on *Lonchocarpus muelbergianus* (Fabaceae). **a** Macroscopic view of the bivalve-shaped gall (dotted line indicates cross-section point shown in **b**). **b** Cross section of the gall, showing a nymph (arrow) that induces the redifferentiation 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 μ m.

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 myrtilloides* [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 (Isaías 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 myrtilloides* on *Psidium myrtilloides* [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

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