Short Communication

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BIOTIC STRESS AND METABOLITES ACCUMULATION IN *MACAIREA RADULA* (BONPL.) DC. (MELASTOMATACEAE) INSECT GALLS

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ABSTRACT

Gall formation is known as a new plant organ that depends on biochemical and ecological interactions between the insect and host plant tissues. This relationship is controlled owing biotic stress responses generated by the inducing insect and mediated through the carbohydrates, secondary compounds, and phytohormones biosynthesis in the plant. Galls development and growth are associated with primary metabolites, whereas secondary molecules act in defense and ecological functions. These metabolites may change in response to the gall-inducing herbivores attack, leading to thenew compounds biosynthesis and the metals accumulation. This review discusses how host plants react to biotic stress caused for gall-inducing insects.

Keywords: Reactive Oxygen Species (ROS); carbohydrates; phenolic compounds.

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1. INTRODUCTION

Plants are affected by biotic and abiotic stresses variety, which can affect their growth, development, and geographic distribution [1, 2]. To survive adverse environmental conditions, they have developed several adaptive strategies, including the metabolites accumulation that perform protective functions mainly against herbivore attacks [3-5]. These organisms induce biotic stress in plants by establishing a species-specific parasitic relationship between hosts and other organisms, such as bacteria, fungi, nematodes, mites, and especially insects [6-9].

Many of these can alter plant metabolism according to the reactive sites availability, the plant life cycles synchronicity with the insect during seasonal changes [10, 11], and even throughout the day [12, 13] and induce abnormal growth with cellular hyperplasia and hypertrophy, leading to the formation of newly formed organs, the galls [14-16]. These structures can establish themselves in different plant organs such as roots, stems, flower buds, and especially leaves [7, 15, 17], creating an environment that provides food, shelter, and protection to the gall-inducing insect against natural enemies [18, 19].

The stimuli for the induction and development of these organs can be triggered by insect salivary compounds, oviposition, and the phytohormones action [9, 20, 21], which are coordinated by gene expression [22, 23]. However, the gall structure and metabolism depend on the taxon and, consequently, on the o gall-inducing insect behavior [8], as well as on how the host tissues and the galled organ respond to oxidative stress [24]. Thus, the structural and metabolic characteristics of galls have been the basis for understanding how the formation and diversification of this new plant organ occur, mainly in the insect group [25-27], and how gall-inducing host plants react to biotic stress.

2. PATTERNS IN GALL DEVELOPMENT

The galls are like nature ornaments with different shapes, sizes and colors [6]. This diversity has been widely studied, mainly regarding the growth processes, morphogenesis, and differentiation [28]. The gall morphotype is “a characteristic neoformed organ generated by the species-specific interaction between an inducing organism and a host plant” [17]. This organ can present conservative patterns, which are determined in plant meristems and manipulated by galling insects.

In the studies of Rohfritsch (1992) [18], gall development has four phases: initiation or induction, growth and development, maturation, and dehiscence or senescence. Some insects are selected to induce galls in young tissues, and this process begins with an increase in cell division and enlargement. In the early phase, there is a predominance of cell hyperplasia, whereas in the later phase cell hypertrophy predominates. During the maturation phase, the insect reaches the last larval instar, which coincides with the highest food consumption. The last phase is senescence or dehiscence, when the

insect is ready to emerge and fly. Thus, to explain the adaptive significance of this neoformation in host plants, there are three main hypotheses: the nutritional, enemy, and the microenvironment hypothesis [20]. The nutritional hypothesis argues that gall tissues offer resources of higher quality and quantity more efficiently to gall-inducing insects than to their free-living ancestors [29], while the microenvironment states that galls protect insects from unfavorable abiotic conditions, such as excessive ultraviolet radiation and temperature, which are major constraints to larval development [20]. According to the enemy hypothesis, the gall protects gall-inducing insects from predators and parasitoids [19, 20].

Neotropical galls are mostly induced by Cecidomyiidae family, but also for Cynipidae, Psyllidae, Eriophyidae, Apionidae, Gelechioidea, among others insects [30]. These insects have mouthparts associated with their specific feeding habits, which primarily fall into the chewing, scraping, and sucking guilds [8]. These different feeding activities can trigger differential growth in host tissues [8, 31-33], directly related to the biotic stress establishment [24]. This stress is qualified and quantified through the reactive oxygen species (ROS) presence, generated in plant tissues in response to gall induction [33-35].

Reactive oxygen species such as superoxide (O_2^-), hydrogen peroxide (H_2O_2) and singlet oxygen ($^1O_2$) result from the molecular oxygen (O_2) reduction [36]. These molecules trigger oxidative stress in plants and can damage the cell wall, membrane lipids, and even genetic material [37, 38]. However, they can also act as second messengers in many cellular processes, such as transdifferentiation and cellular hypertrophy during the growth and development of newly formed organs [24, 39, 40].

3. VASCULARIZATION IN GALLS

The land plants radiation was enabled by the vascular system emergence, which facilitated an increase in plant size and the diverse ecological niches colonization [41]. This conducting system specialized in the water, solutes, and macromolecules transport differentiates from the procambial meristem into two main tissues: xylem and phloem. The xylem consists of tracheary elements, tracheids and vessel elements characterized as dead, lignified cells at maturity interconnected by perforations that optimize the water and solutes flow. In contrast, phloem is composed of sieve elements, parenchyma cells, fibers, and sclereids, which are specialized in the translocation of photoassimilates synthesized during photosynthesis [42].

New organs such as galls are formed in distinct parts of the plant [7]. During this process, photoassimilates are reallocated and gall initiation and development involve the activity of auxins and cytokinins [8, 43]. Cytokinin is a controlling factor in the regeneration of vessels and sieve tubes around wounds and can influence cell differentiation in vascular tissues. This effect may vary according to cytokinin and auxin physiological levels. In addition, cytokinin may increase vascular cambium sensitivity to auxin stimulation, resulting in a higher phloem/xylem ratio, although these concentrations can vary during gall development, demonstrated in galls induced by Eurosta solidaginis (Diptera) on Solidago altissima [44]. In other studies, cytokinin was histolocalized in the outer tissue compartment of galls induced by Cecidomyiidae on Piptadenia gonoacantha [45]. This finding is one of the strategies discussed regarding how galling insects benefit their life cycle. Furthermore, cytokinin also stimulates the biosynthesis of phenolic compounds, which are partially generated in response to reactive oxygen species (ROS) [24]. Therefore, the local accumulation of phenols, auxins, and ROS may occur simultaneously, resulting in the different shapes and structures of galls. This co-occurrence of molecules can be verified using immunohistochemistry techniques [45, 46].

4. HOW THE GALL STRUCTURE WORKS: LOOKING FOR METABOLIC PATHWAYS

In gall development tissues, there are distinct cell growth and elongation patterns [28]. These can lead to the formation of an external storage compartment and an internal one, the nutritive tissue, directly responsible for the nutrition of the gall-inducing [47-49]. In general, the cells of the nutritive tissue are smaller and less elongated, with dense cytoplasm compared to the cells of the storage tissue, which are composed of hypertrophied and vacuolated cells [47, 49-51]. These differences are likely associated with the cell wall during gall development [28].

Changes in the cell wall galls composition have been studied to understand microfibril rearrangement and the degree of pectin methylesterification in different host plant systems and gall-inducing insects [28, 46, 52]. Furthermore, these polysaccharides can undergo hydrolysis, releasing oligo- and monosaccharides such as rhamnose (Rha), fucose (Fuc), arabinose (Ara), xylose (Xyl), mannose (Man), glucose (Glc), and galactose (Gal). These carbohydrates are essential components of cell walls and can regulate photosynthetic activity in galls, as well as induce the phenolic compounds biosynthesis, leading to the reddish phenomenon observed in these structures [53, 54]. Red galls in Macairea radula can accumulate more water-soluble sugars than green galls [55]. To achieve this, the gall-inducing insect continuously stimulates the metabolism of host plants to produce primary metabolites, such as proteins, lipids, and carbohydrates, available not only for the insect's diet [49, 55, 46], but also for the phenolic compounds and polyamines accumulation , which are regulated by phytohormones [56, 57], Figure 1.

All these metabolic changes that begin in the cell wall are directly related to the mechanisms controlling oxidative stress in the gall host plant system. In the galls of Aspidosperma australe and A. spruceanum, for example, the ROS concentrationis found from the initial gall cells until senescence [33]. Thus, gall establishment depends on homeostatic control and the elimination of free radicals through different pathways, both enzymatic and non-enzymatic [24]. One way to dissipate oxidative stress in plants is through the phenolic compounds biosynthesis, which can donate a hydrogen atom to neutralize ROS activity and prevent cell damage [59-62]. Furthermore, phenolic compounds are capable of sequestering metals, as well as activating antioxidant enzymes such as superoxide dismutase, catalase, ascorbate peroxidases, and peroxidases [63], which act synergistically with phytohormones induced by gall-inducing herbivores and possibly can affect the neighboring plant species survival [64, 65].

The cellular machinery used by gall-inducing insects in-

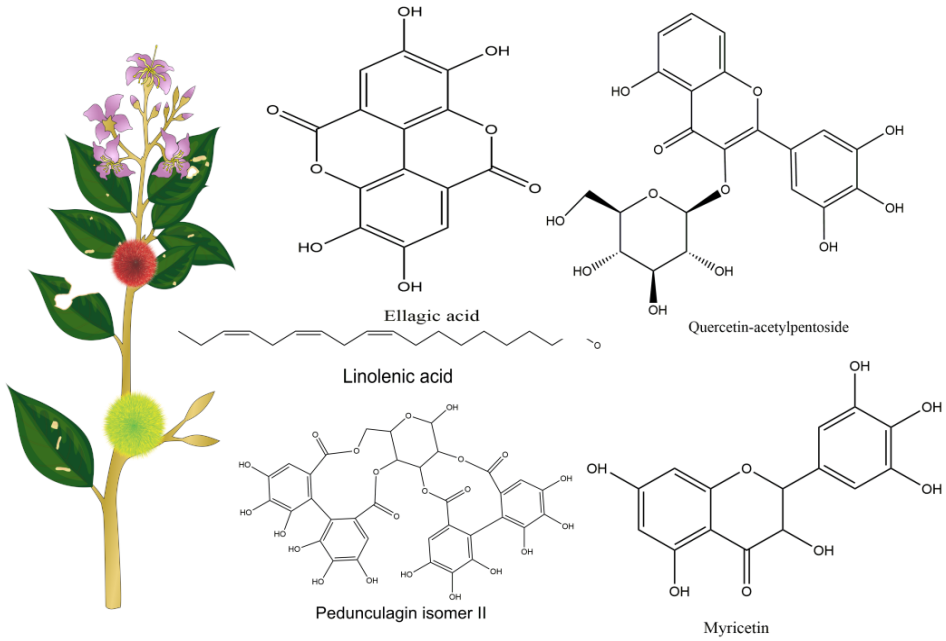

Figure 1 – Some metabolites found in galls induced on *Macairea radula* (Bonpl.) DC. (Melastomataceae) buds (Adapted from Santos, P. D. 2024. PhD thesis) [58].

volves not only enzymatic and non-enzymatic systems, but mainly the mediation and regulation by phytohormones [53]. These regulators play a crucial role in the induction, development, and establishment of insect galls, acting as primary chemical messengers [66]. These messengers can stimulate both the primary metabolites production, responsible for maintaining cellular machinery and the nutrition of gall-inducing insects, and secondary compounds, which play a relevant role in maintaining homeostasis, redox reactions, plant defense, and interactions with other organisms [24, 64, 67].

Thus, the entire the gall development and its interactions with other organisms can be governed by the action of phytohormones, mainly auxins and cytokinins. The auxin (IAA – indole-3-acetic acid) action has been linked to cell elongation, while cytokinin has been associated with cell division [68]. Other phytohormones, such as abscisic acid, gibberellins, ethylene precursors (ACC), salicylic acid, and methyl jasmonate, as well as polyamines, although participating in responses to abiotic and biotic stresses, are still poorly understood in terms of their functions in the interaction between gall-inducing insects and host plants [53]. It is known that these molecules are associated with the metals and phenolic compounds accumulation [69, 70].

5. FINAL REMARKS

The globoid gall model system induced by Palaeomystella oligophaga Becker & Adamski (Lepidoptera) in Macairea radula (Bonpl.) DC. (Melastomataceae) has been widely investigated to elucidate the metabolic associations of the insect–plant parasitic interaction. The galls in this system are initiated in the axillary buds and develop as a globoid structure on the stem with many leaf-like projections and trichomes [71]. These organs exhibit a typical nutritive tissue that accumulates lipids and proteins [72], and a storage tissue with polysaccharides and phenolic compounds accumulation [57]. The storage and nutritive tissues cell walls show differential pectins and hemicellulose distribution epitopes, evidencing distinct tissue functionalities [73]. Thus, the gall-inducing insect, throughout its different life stages, modifies the gall organ, which assumes different colors ranging from green to red [53, 54]. Part of this coloration can be explained by the primary and secondary metabolites[3,56]. It is believed that various monosaccharides are released within the gall for the secondary metabolites biosynthesis to maintain antioxidant functions and contribute to the different shapes and colors observed in galls on host plants.

AUTHORS' CONTRIBUTIONS

P.S.: writing – original draft and figure design.

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CONFLICTS OF INTEREST

The author declares that there are no conflicts of interest.

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