



Review

Manipulation of host plant cells and tissues by gall-inducing insects and adaptive strategies used by different feeding guilds



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ABSTRACT

Biologists who study insect-induced plant galls are faced with the overwhelming diversity of plant forms and insect species. A challenge is to find common themes amidst this diversity. We discuss common themes that have emerged from our cytological and histochemical studies of diverse neotropical insect-induced galls. Gall initiation begins with recognition of reactive plant tissues by gall inducers, with subsequent feeding and/or oviposition triggering a cascade of events. Besides, to induce the gall structure insects have to synchronize their life cycle with plant host phenology. We predict that reactive oxygen species (ROS) play a role in gall induction, development and histochemical gradient formation. Controlled levels of ROS mediate the accumulation of (poly)phenols, and phytohormones (such as auxin) at gall sites, which contributes to the new cell developmental pathways and biochemical alterations that lead to gall formation. The classical idea of an insect-induced gall is a chamber lined with a nutritive tissue that is occupied by an insect that directly harvests nutrients from nutritive cells via its mouthparts, which function mechanically and/or as a delivery system for salivary secretions. By studying diverse gall-inducing insects we have discovered that insects with needle-like sucking mouthparts may also induce a nutritive tissue, whose nutrients are indirectly harvested as the gall-inducing insects feeds on adjacent vascular tissues. Activity of carbohydrate-related enzymes across diverse galls corroborates this hypothesis. Our research points to the importance of cytological and histochemical studies for elucidating mechanisms of induced susceptibility and induced resistance.

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1. Introduction

Many species of herbivorous insects have evolved the ability to modify tissues of their host plants to produce highly specialized structures known as galls. The induction of galls represents an adaptation of the insect to the host plant, as well as an adaptation of the plant to the insect (Berryman and Ferrel, 1988). As diverse are the gall-inducing organisms, so are their host plants. Whether there are unifying features of galls and gall induction has been debated for many years (e.g., Mani, 1964; Price et al., 1987; Hartley, 1998; Stone and Schönrogge, 2003; Shorthouse et al., 2005; Raman, 2011; Isaias and Oliveira, 2012). In spite of it, some general conclusions on gall-inducing insect-plant interactions can be drawn: (1) typically gall inducing insects are strict specialists and therefore have had to face many constraints imposed by their host(s) and the environment (e.g., Price et al., 1987; Fernandes, 1990; Julião et al., 2014a); (2) as a result, a great variety of life strategies is observed (e.g., Cornell, 1983; Shorthouse and Rohfritsch, 1992; Rohfritsch, 1992); (3) complex larval behaviors are responsible for many different gall structures (Shorthouse and Rohfritsch, 1992; Rohfritsch, 1992) and (4) phylogenetic constraints and female ovipositing behavior have strong effects on gall-inducing insect population dynamics (Price et al., 1990). Peculiarities in anatomical, biochemical and physiological features have prompted some authors to view complex insect-induced galls as entirely new and unique plant organs because they have diverged so dramatically from the normal trajectory of host plant development (e.g. Shorthouse et al., 2005; Oliveira and Isaias, 2010a).

Galls induced by insects vary in all possible traits: color, shape, size, phenology, hardness, chemistry, internal structure, and abundance in nature. While morphologically simple galls are represented by slight swellings of leaf or stem tissues, complex galls may be elaborate structures with external surfaces covered by diverse features, e.g., secretory trichomes that trap and kill natural enemies of the gall-inducing insects (Fernandes, 1987), spines or even glands that secrete honeydew to attract ants that act as bodyguards (e.g. Fernandes et al., 1999), and production of oxalate crystals that surround the larval chamber of cynipids, making its location by ovipositing parasitoids difficult (Fernandes et al., 1990). These remarkable changes in plant development provide evidence that gall-inducing insects are among the Earth's most sophisticated herbivores (Shorthouse et al., 2005).

Many gall-inducing insect species have been documented and many more will be found. Espírito-Santo and Fernandes (2007) postulated that the number of gall-inducing insects worldwide may reach 133,000 species. This estimate was based on the reported average of gall-inducing species richness per plant species and, alone, indicates the biological importance of this group. Their astonishing diversity was recently corroborated in a study on the diversity of gall-inducing insects on the harsh canopies of the Amazonian rain forests (e.g. Julião et al., 2014a). From an economic point of view, gall-inducing insects are also of major relevance. Many of these insects represent serious threats to agriculture or forestry, while others provide benefits as biological control agents of invasive plant species (Fernandes, 1987).

Our knowledge on the way host plants react to gall-inducing insects relies on cytological and histochemical profiles of diverse neotropical insect-induced galls. Current text reviews: (1) the diverse and numerous insect-induced galls found in a variety of habitats in the neotropics, (2) the importance of synchronizing host plant phenology and colonization by gall-inducing insects, and (3) the results of our cytological and histochemical studies on insect-induced galls of the neotropics. Based on this discussion we propose 'themes' underlying gall induction and development and insects nutrition accessed by histochemical analysis of gall

tissues. A range of neotropical plant species associated to gall-inducing insect species was used to illustrate this review (Table 1). When the insect species is undescribed, we used gall morphotypes (Isaias et al., 2013) along with information on the order/family and feeding guild of the insect that induces the gall.

2. An overview of neotropical gall-inducing insects

Gall-inducing insects are distributed worldwide, with the orders Diptera, Hymenoptera, and Hemiptera being dominant, while the most common gall-inducing families are likely the Cecidomyiidae, Cynipidae, and Psylloidea, respectively. The frequency of these taxa varies among the biogeographical regions, but in the Neotropical region, the majority of gall-inducing species belong to the family Cecidomyiidae (Gagné, 1994; Fernandes and Santos, 2014). Other taxa that are frequently found include the Cynipidae, Psyllidae, Eriophyidae, Apionidae, and Gelechioidea (Cuevas-Reyes et al., 2014; Hanson et al., 2014; Medianero et al., 2014; Quintero et al., 2014). A review on the ecology and distribution of gall-inducing insects in the neotropics is found in Fernandes and Santos (2014).

Independent of the biogeographical region, the degree of sophistication of the galling habit may have arisen under selection imposed by host plant defense mechanisms against natural enemies, and may vary among habitats and environments. Although many host plants and many different habitats are found in the neotropics, analogous diversity of strategies occurs in other regions of the world. A greater diversity of gall-inducing insects is found in xeric habitats as opposed to mesic habitats (e.g., Fernandes and Price, 1988, 1991), at lower altitudes (e.g., Fernandes and Price, 1988, 1991; Lara et al., 2002; Quintero et al., 2014), and on the xeric canopy compared to the more humid understory (Julião et al., 2014a,b; Medianero et al., 2014). Mechanisms that contribute to this differential distribution are still being studied, but so far results point to the major influence of natural enemies (parasites, herbivores, and pathogens), plant resistance (e.g., Fernandes and Price, 1992; Ribeiro-Mendes et al., 2002; Ribeiro and Basset, 2007; Ribeiro et al., 2014), host plant species richness (e.g., Fernandes, 1992), density of host plants (Gonçalves-Alvim and Fernandes, 2001), dynamics of plant meristems (Espírito-Santo et al., 2012), and super-host plants (e.g., Fernandes and Price, 1991; Formiga et al., 2011, 2015). The super host plants, such as *Copaifera langsdorffii* (Table 1), support a high richness of gall-inducing species and are relatively common in the neotropics.

The knowledge on the relationships between Neotropical gall-inducing insects and their host plants has vastly improved during the last two decades. Earlier botanical studies primarily focused on pure descriptive anatomical and morphological studies (e.g. Fernandes et al., 1990). In contrast, recent studies have addressed questions related to host tissue manipulation and gall ontogenesis in the light of evolution and adaptation (Oliveira and Isaias, 2010a, b; Isaias et al., 2014a).

3. Life history strategies of gall-inducing neotropical insects

Gall-inducing insects must synchronize their colonization activities with the phenology of host tissues, once they are sessile and in close association with their specific host plants. Precise synchronization provides the best morphological and physiological conditions of plant tissues for insect colonization, survival and growth.

For some neotropical gall-inducing species, fine-tuned synchronization results in univoltine life histories. This strategy is associated with hosts that flush new leaves only once a year, which is the case of the gall inducers *Nothotrioza* spp. and *Pseudopha-*

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