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Gall insects: Introduction and mechanism of Gall induction

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ABSTRACT

The modification of plant structures through hypertrophy and/or hyperplasia lead to development of galls which can be induced by various biotic agents such as viruses, bacteria, fungi, algae, nematodes, rotifers, copepods and insects. Galls provide a better utilisation of underutilised niche, thus have been reported to be helpful for insect survival and evolutionary processes. Around 13,000 species of gall-inducing insects are known worldwide, representing about 2% of the total number of insect species. These insect- gall inducers belong to different families of Hemiptera, Thysanoptera, Coleoptera, Hymenoptera, Diptera and Lepidoptera. Even though, their wider distribution throughout the world, they have not yet explored fully. The plant defence – insect offense interaction in the gall- host interaction depends on various factors such as production of effectors, release of phytohormones, indirect and direct plant defence mechanisms which need to be studied for better understanding. There is need to decipher the mechanism of gall induction to manage the insects economically.

Keywords— *Hypertrophy, Hyperplasia, Gall-inducing insects, Plant defence, Phytohormones*

1. INTRODUCTION

The earliest record of galls dates back to the time of Theophrastus, Pliny the Elder, Hippocrates. In the book *Historia Naturalis XXVI*, he used the word "the Merciful," or "gall" to designate the structure induced in oak trees by wasps from the family Cynipidae (Meyer, 1987). Furthermore, ancient authors also have been described the emergence of insects from such structures, yet Marcello Malpighi (1628–1694), Antony van Leeuwenhoek (1632–1723), and Jan Schwammerdam (1630–1680) concluded that gall development was linked to the oviposition of an insect in late 17^{th} century. Galls or otherwise, vegetative tumours are physiologically modified plant tissues that are formed either by hyperplasia (increased cell number) and/or hypertrophy (increased cell size) induced by parasitic or pathogenic organisms (Mani, 1964; Dreger-Jauffret and Shorthouse, 1992). The inducer organisms of galls can be, viruses, bacteria, fungi, algae, nematodes, rotifers, copepods, and plants from the family Loranthaceae (popularly known as mistletoes), but are mainly caused by insects (Mani, 1964; Raman *et al.*, 2005).

Patterns of evolution of these gall makers vary yet, approximately 13,000 species of insect gallers known in the world, (Dreger-Jauffret & Shorthouse, 1992; Raman *et al.*, 2005). The radiation of gall inducers has been studied in diverse insects, but still a long way to study these different dynamics of host-plant insect interaction. Gall inducers have evolved independently in seven orders of insects mostly from the most common and well-studied groups, such as aphids (Aphididae, Homoptera), midges (Cecidomyiidae, Diptera), sawflies (Tenthredinidae, Hymenoptera) and cynipids (Cynipidae, Hymenoptera). The ability to control plant physiology, growth and differentiation has been well evolved, which is an example of adaptive radiation according to Simpson's (1953) theory. As per this theory, the underutilised niches provide ecological opportunities to the insects for exploitation, thus development of new niches lead to radiation of new species/ genera, which ultimately leads to speciation. The traits possessed by new lineage of insects are known as key characters that provide beneficial advantage to the newly radiating group such as gall inducers in this case. For e.g. the accidental deposition of eggs by the Cynipid gall wasps, ancestors of modern gall makers by probing the leaf buds in search of stem boring insects, lead to acquire a new niche. The mixed stimulus of the oviposition and parasitization lead to induction of galls in plants.

1.1 Galls: A brief introduction

Galls are one of the physiological modifications caused by various insects/non insects for their own benefit. The modified plant growth pattern, alternation in the structure and physiology of the plant to alter the vegetative structure to produce a food source that is rich in nutrients and free from chemical defences together with a protective structure that is isolated from the environment is the primary and main cause of gall development (Larew, 1992; Labandeira *et al.*, 1994; Labandeira and Phillips, 2002; Stone *et al.*, 2008). Galls are used for their pharmacological properties. Aleppo galls (spherical galls formed on the twigs of *Quercus infectoria* by gall-wasp larvae) has been reported to contain 50% to 60% galactonic acid and significant levels of gallic and ellagic acids, which are used for treatment of diarrhoea, oral swelling, and haemorrhoids. Some colouring pigments present in galls are also being exploited for dying hair and other tissues, and as writing ink (Fernandes *et al*., 1988). Some galls induced by insects have also been used for their aesthetic and medicinal values. In South America, the indigenous Aguaruna- Jívaro people of the Peruvian Amazon use leaf galls from *Licania cecidiophora* (Chrysobalanaceae) to make necklaces (Berlin and Prance, 1978). Recently, interest in studies on occurrence of galls and associated organisms has increased because of their potential uses as biological control agents for invasive plants and as bioindicators of environmental quality and health (Fernandes, 1987; Fernandes and Price, 1988; Stone and Schönrogge, 2003; Julião *et al*., 2005).

2. PREFERENCE FOR GALL INDUCTION

Although the host plant finding process ensures the insects to find suitable host for gall induction, but some plant factors also regulate the initiation and development of galls. Most gall makers have strong level of fidelity or constancy but some species are not so restricted and can induce galls on plant species other than their preferred hosts (Abrahamson *et al.*, 1991; White & Korneyev, 1989; Raman *et al.*, 1996; Frenzel *et al.*, 2000; Wool, 2005). Furthermore, shifts in hosts within same / different families also have been observed. A majority of cecidomyiid genera induce galls on specific host-plant genera (Gagne and Jaschhof, 2004), some of the larger cecidomyiid taxa (e.g., Asphondylia, Contarinia, Dasineura, and Lasioptera) display a diverse host range across different plant families (Yukawa & Rohfritsch, 2005).

3. POSITION OF GALL MAKERS IN THE HERBIVORE GUILD

Herbivorous or phytophagous insects are those that consume living parts of plants, constitute the largest portion of all extant species diversity. Nearly 50% of all herbivorous organisms are insects (Gullan and Cranston, 2005) belong to the orders Phasmatodea, Orthoptera, Thysanoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera, and Hymenoptera (Triplehorn and Johnson, 2005). Herbivorous insects can be grouped in terms of the variation in the number of host plants they utilize. For e.g. monophagous insects utilize a single plant taxon; oligophagous insects utilize a few plant taxa that are usually phylogenetically related (i.e., from the same genus or family); and polyphagous insects utilize a wide variety of host plant species that are not phylogenetically related (Price, 1997). Insects can also be separated into functional groups according to the type and form of utilization of a particular resource. These groups are called guilds (Root, 1967); that is, they consist of species that exploit the same food class (or other type of resource) in a similar way. The species within a guild may or may not be phylogenetically related (generally, they are not).

Table 1: Different types of principal herbivorous guilds according to Price, 1997

Exophytic herbivorous insects	Endophytic herbivorous insects
i. Chewers and suckers feed externally on the host plant and are therefore called free-living or exophytic herbivorous insects ii. Chewers belong to the orders Orthoptera (grasshoppers, crickets), Coleoptera (beetles, weevils), Lepidoptera (butterflies and moths), and Hymenoptera (wasps) possess mouthparts specialized for chewing and consume tissues from roots, stems, leaves, flowers, and fruits iii. Sucking insects possess mouthparts that are modified to consume sap from plant vessels or the liquid contents of plant cells. These insects can feed on- i. Xylem sap, which is found in the xylem vessels (cells that carry nutrients and mineral salts from the soil to the plant) ii. Phloem sap, which is found in phloem sieve tubes (cells that distribute carbohydrates and amino acids throughout the plant) iii. Intracellular contents of vegetative cells in various organs of the host plant iv. Sucking insects are found in the order Hemiptera (true bugs, leafhoppers, and aphids). v. Many chewing and sucking insects are specialized feeders on seeds commonly referred to as seed predators which feeds on seeds of nutrient-rich compared with other plant tissues. vi. Belong to orders Hymenoptera, Coleoptera, Hemiptera, and Lepidoptera. Among coleopteran seed predators, members of the subfamily Bruchinae (Chrysomelidae), which predate on plants from Fabaceae	i. The three remaining guilds (miners, drillers, and gall makers) consist of insects whose larvae feed internally on plant tissues. Therefore, they are called endophytic insects ii. Mining insects are those whose larvae live in and feed on plant tissue between the epidermal layers (Dempewolf, 2005). Mines are canals formed by insects feeding inside the parenchyma or epidermal tissue of a plant whose external walls remain intact. The tissue that is most often consumed is the palisade parenchyma in the mesophyll. ii. Drilling insects are differentiated from gall-making insects as they don't modify tissues, and feed deeper within the plant tissue, forming cavities called galleries found in the orders Coleoptera, Lepidoptera, and Hymenoptera (Coulson and Witter, 1984). iv. Gall-forming insects are defined as herbivorous insects that, to complete their life cycles, obligatorily induce pathological modifications in the tissue of their host plants (galls) (Espírito-Santo and Fernandes, 2007) v. The interaction between the insect and the host plant results in hypertrophy and/or hyperplasia of the plant tissue found in (Hemiptera, Thysanoptera, Coleoptera, Hymenoptera, Lepidoptera, and Diptera), with the exception of Orthoptera

4. GALL-INDUCING INSECT TAXA

Around 13,000 species of gall-inducing insects are known worldwide, representing about 2% of the total number of insect species (Dreger-Jauffret and Shorthouse, 1992; Raman *et al*., 2005). However, recent estimates have extrapolated this value to nearly 120,000 species of gall-forming insects (Espírito-Santo and Fernandes, 2007). The habit of inducing galls in plants has evolved independently several times among the phytophagous insects (Roskam, 1992; Gullan *et al.*, 2005), occurring in at least 51 families distributed in six different orders, and is found in all biogeographic regions. The species richness and species diversity yet need be explored.

Table 2: Different gall forming insect orders with their geographical distribution and host plant families

Insect order	Belongs to	Geographical distribution	Host plant families
Hemiptera (11 families, principally in the suborder Sternorrhyncha)	**Superfamily Psylloidea** includes around 3000 described species	Tropical and temperate regions of the southern hemisphere (especially in tropical Asia and the Australian region) (Gullan *et al.* 2005).	Asteraceae, Myrtaceae, Melastomataceae, Fabaceae, Lauraceae, Polygonaceae, Moraceae and Salicaceae.
	Superfamily Coccoidea 20 families, among which 230 gall-forming species *Pseudotectococcus rolliniae* Hodgson and Gonçalves (Eriococcidae) in *Rollinia laurifolia* (Annonaceae).	Neotropics	Myrtaceae (around 130 species), Fagaceae, Asteraceae, Ericaceae, and Verbenaceae (Gonçalves *et al.*, 2005, 2009)
	Superfamily Aphidoidea 440 species of gall-forming		Host plant *Rhus glabra* (Anacardiaceae)
Thysanoptera	Subfamily Phlaeothripinae	Tropical Asia and the Australian region	
Coleoptera	Superfamilies Chrysomeloidea and Curculionoidea	Brazilian Cerrado biome	Asteraceae, Solanaceae, Brassicaceae, and Fabaceae (Souza *et al.*, 1998, 2001; Craig *et al.*, 1991)
Hymenoptera	(Tenthredinidae, Cynipidae, Agaonidae, Tanaostigmatidae, and Eurytomidae)		
	Family Tenthredinidae	Nearctic region	Angiosperm families (Salicaceae, Rosaceae, Caprifoliaceae, and Grossulariaceae); One gymnosperm family (Pinaceae)
	Family Cynipidae		
	Family Cecidomyiidae	All biogeographic regions	Fagaceae, Fabaceae, Rosaceae, and Aceraceae (Csóka *et al.*, 2005)
	Super family Chalcidoidea (Six families: Agaonidae, Eulophidae, Eurytomidae, Pteromalidae, Tanaostigmatidae, and Torymidae in Neotropical region) (La Salle, 2005)		
	Agaonidae	Tropical regions (Price, 1997)	Genus *Ficus* (Moraceae) (Galil and Eisikowitch, 1968; Wiebes, 1979; Weiblen, 2002)
	Tanaostigmatidae	Neotropical regions	Trees of the families Fabaceae, Polygonaceae, Lecythidaceae, and Rhamnaceae (La Salle, 1987, 2005)
	Subfamily Eurytominae	tropical regions	Families Myrtaceae, Campanulaceae, Boraginaceae, Orchidaceae, and Pinaceae
Lepidoptera	Gelechiidae and Tortricidae (47 and 39 species, respectively)	All biogeographic regions	41 families of host plants, especially Asteraceae, Salicaceae, and Fabaceae (Miller, 2005)
Diptera	Cecidomyiidae subfamily Porrycondilinae	Neotropical and Nearctic regions	Asteraceae, Melastomataceae, Aquifoliaceae, Acanthaceae, Fabaceae, and Onagraceae
	Tephritidae**)** subfamily Tephritinae		
	Chloropidae	Palearctic and Nearctic regions	Poaceae, Cyperaceae

5. MECHANISM OF GALL INDUCTION

Through horizontal gene transfer from the associated micro-organisms, the gall inducers produce galls and facilitate herbivory (Giron and Glevarec, 2014; Spíchal *et al.*, 2012; Kaiser *et al*., 2010; Giron *et al.*, 2007) such as Ambrosia gall midges that are commonly associated with fungal symbionts produce and proceed for development of galls (Huang *et al.*, 2015; Hansen and Moran, 2014). This successful life history trait has evolved genetically multiple times leading to survival of the insect. This type of host plant- insect interaction has been reported to manipulate the source-sink dynamics and thus reconfigure the metabolism of hosts (Oates *et al.*, 2015). For e.g. aphid (*Pemphigus betae*) infesting narrowleaf cottonwood (*Populus angustifolia*), has been reported increased concentration of sugars, carbon-containing compounds and nitrogen-containing compounds (Compson *et al.*, 2011). Thus, it can be confirmed that galls provide enhanced nutrition to the insects. The plant primary cell wall is structurally complex of cellulose and micro-cellulose micro-fibrils embedded in pectin polysaccharides matrix (Formiga *et al.*, 2013). But induction of galls by the insects alter the compositional dynamics of the cell wall (Suzuki *et al.*, 2015; Tooker and Helms, 2014; Favery *et al.*, 2015; Gheysen and Mitchum, 2011). Fundamentally the inducers control the host cellular machinery throughout the period of development by secreting of various elicitors and inducing phytohormonal changes (Stone and Schönrogge, 2003).

6. ROLE OF EFFECTORS IN INSECT GALLING

Current model that describes the pattern identification by the immune cells, thus provide the detailed description of induction and development of galls (Deslandes and Rivas, 2012). Following the recognition of microbe-associated molecular patterns (MAMPs), the Plant pattern-triggered immunity (PTI) is initiated. The suppression of PTI by pathogen-secreted effectors (effector-triggered susceptibility, ETS) occurs before the interaction of host plant and gall making insects. ETS is countered by the recognition of these effectors by intracellular R proteins (effector-triggered immunity, ETI). With the onset of time, pathogen evolves new effectors to avoid detection by the plant and the plant evolves new R proteins to improve surveillance. This model has also been accepted currently for plant-insect interactions (Stuart, 2015) and herbivore- and egg-associated molecular patterns (HAMPs and EAMPs), as well as effectors that elicit PTI and ETI, respectively, have been identified (Sheth and Thaker, 2014; Unsicker *et al.*, 2013; Büchel *et al*., 2012).

7. ROLE OF PHYTOHORMONES IN INSECT GALLING

Galls have been reported to produce by 2 different mechanisms such as hypertrophy and hyperplasia. Tooker and Helms studied the role of phytohormones in induction and development of galls by manipulating the host machinery for the first time. Two of the hormones addressed in the review, auxins and cytokinins, are well-known growth regulators that have been repeatedly implicated in insect gall development and their role in plant-galling insect interactions has also been established. The de novo transcriptome comparison between galled and ungalled leaves of *Metrosideros polymorpha* (Myrtaceae) by *Trioza spp*. (Hemiptera: Triozidae), a galling psyllid. Bailey *et al.*, (2015) concluded the significant enrichment of auxin-response genes associated with galling in this system.

8. PLANT DEFENCE RESPONSES AGAINST GALLING INSECTS

There is a need to understand the insect offense-plant defence in the plant – gall inducer interactions (Bruinsma *et al.*, 2009). The dynamic interaction of pests and plants, starting from the information transmission and interpretation by signalling machinery and a coherent and coordinated response by the plants finally (Troncoso *et al.*, 2012). The defence system in plants are finally activated to overcome the insect behaviour. These defences may be broadly divided into direct and indirect responses (Furstenberg-Hagg *et al.*, 2013).

Table 3: Different types of plant defence responses against galling insects

Induced direct defences	Induced indirect defences
i. Induced direct defences involves the synthesis of toxic proteins or secondary metabolites that directly affect the pest. ii. e.g. plants are able to produce a wide range of chemicals to defend themselves against insect herbivory. iii. Secondary metabolites that show insecticidal activity generally target specific insect biological systems such as the nervous and digestive systems cytochrome P450s, glutathione S-transferases, peroxidases, ferritins, catalases, and peroxy-redoxins are also involved.	i. Indirect defences involve the release of volatile cues that allow the plant to interact with the pest, neighbouring plants, or predators and parasitoids of the pest ii. e.g. The blue gum chalcid wasp, *Leptocybe invasa*, induced changes in the volatile terpene profile of a resistant or susceptible host

9. CONCLUSION

The host plant defence- gall inducer offense interactions causes the development of galls in plants leading to the abnormalities. Thus, the changes in plant cell structure through hypertrophy and/or hyperplasia, followed by different phytohormonal changes are the primary cause of gall formation. Furthermore, the metabolic changes achieved by the host finding females for its oviposition, nutrition and development are the foremost regulator of gall dynamics in plants. These gall inducer- plant interaction needs further elaborated study for deciphering the complicated phenomenon.

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