Insect gall systems: Patterns, processes and adaptive diversity

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Resource manipulation and endophagy are typical of insect–plant gall interactions, galls acting as physiological sinks providing insects with quality nutrients. Diverse biochemical and morphogenetic processes result in a fascinating array of galls induced by an equally wide array of insects, providing a favourable microenvironment. Phenolic compounds play an essential role in gall initiation, besides the ability of gallers to manipulate nitrogen levels to their own advantage. Social behaviour of some gall insects is reflected in the division of labour evident in polymorphs which are functionally different.

INSECTS are known to alter the developmental profiles of plants, manipulating plant tissues to form morphologically distinct abnormal outgrowths or galls varying in form and structure in accordance with the concerned plant species and the insect galler. Galls are miniecosystems or mini food webs and gall induction is a major specialized type of herbivory providing adequate information on insect–plant interactions. In these interactions nutrition and environmental protectants are essential criteria shedding light on their adaptive nature and ecological significance. They are phenotypic entities that develop under the influence of both plant and insect genotypes and being developmental abnormalities induced by environmental stimuli, galls are considered as *extended phenotypes*[1]. They are adaptations enabling gall insects to feed on high quality plant tissues, the gall maker having precise control over gall differentation and development. Most galls involve inhibition of development, differentiation, growth and tissue suppression along with activation of some tissues. While Hymenopteran and Dipteran galls dominate the gall scenario, equally fascinating gall diversity is evident in galls formed by thrips, aphids, mites and coccids. Involvement of two or more species of the same or different group of insects is a common phenomenon. Such interspecific diversity results in polymorphic forms, in many cases resulting in division of labour. Factors affecting gall size include the number of larvae, diversity of galls, portions of infested leaf, physiological state of environment and host genes.

Gall formers have a genetically biased host preference and a high degree of host specificity is typical of galls, the plant tissues responding to the stimulus particularly at a time when they are juvenile, meristematic and undifferentiated. A specific demand of the galler therefore is the availability of reactive host tissues which are temporally and spatially restricted. The size, structure and metabolism of the galls are under the control of the gall-forming organisms which may range from an individual to many, when they form guilds. With the induction of galling, perfect coordination exists between the galler and the host plant, the former being under strong selection pressure to adapt to the phenology of the plant.

Adaptive diversity

Natural selection acts concurrently upon the insect to stimulate the development of nutritive and protective tissues and on the plant to resist the insect stimulus which may be chemical, mechanical or behavioural. Changes in the plant developmental patterns should make it more difficult for a galler to manipulate the plant into making a gall, simple or complex. The developmental processes of the host have to be manipulated to produce structures that will enable feeding, shelter and escape. The extent to which gall insects manipulate growth varies considerably from induction of cell proliferation to the production of complex structures not normally produced by the plant. From the benefits that the gall makers derive from their interactions with host plants it is suggested that gall-making ability is an adaptive trait subject to modification by natural selection. Variations in gall phenotype influence fitness of insects and gall phenotypic variations are affected by genetic variations in the insect population[2]. Intraspecific exploitation competition is an equally common feature in galls, with large populations resulting in strong selection pressure in choosing oviposition sites on which the fitness of the larvae depend. This is particularly the case when a high degree of polymorphism exists, as in thrips galls. While there is no disputing the fact that galling places a drain on the energy and nutrient status of the host,

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opinions tend to vary regarding the adaptive value of galls. Though in general both the plants and insects are benefited, the view still prevails that the primary advantage is to the galler. Since the gall is isolated in space and time and is forced into extreme specialization[3], the plant is considered to be the beneficiary. However the nutrition hypothesis[4] on the other hand suggests that the potential advantage is to the galler, with the cytology and histochemistry of nutritive tissues of the gall favouring the galler. Phylogenetic relationships are much stronger with about whole families of arthropods with the gall-forming habit[5], offering potential advantage to the galler in this plant–insect interaction. The nutrient hypothesis in its modified form[6] indicates that the nutrient modification in the gall varies with the gall species and 'gall formation represents a very precise and species specific manipulation of host plant chemistry and may involve a reduction or increase in critical nutrients within the gall to improve insect performance'. The gall environment favours insects with improved nutrition, reduced defence chemicals, as well as limited access to natural enemies.

Gall forming has been referred to as an adaptive syndrome involving endophagy and resource manipulation, gall distribution involving spatial and temporal differences which are essentially resource based[7]. As survivorship, developmental rate and fecundity determine fitness, the fact that insects reproduce effectively in galls and multiply rapidly reflect the adaptive trends in gall formation.

Source–sink interactions and nutrition

Galls act as physiological sinks for drawing in resources from surrounding plant sources. Early gall development depends on the concerned insect sinks increasing allocation for storage reserves and later development of the progeny in the gall is dependent on resources from the galled leaf and from neighbouring leaves. 'Vascular plumbing' of host plants influences flow of assimilates from the source to the sink and the relationships so established between a gall and its host are in turn influenced by the gall site. Role of source–sink interactions is basic to the ecology of gall–insect interactions and the relationships so established between a gall and its host are in turn influenced by the gall site[8]. Studies on aphid galls have shown that they function as sinks throughout their development, the source of the phloem sap imported into their galls being dependent on seasonal development. Work in this direction has shown that the total allocation to a gall from all neighbouring leaves in some aphid-induced galls is estimated at 38.2% based on studies of C14 assimilates from a single leaf[8]. The capacity of aphids to act as mobilizing sinks was affected by the position of the galls. Some of the assimilates which accumulate in the gall and are then fed by the insects are transported to the gall from plant tissues that are some distance away. Galls are therefore unique in that they appear to 'exhibit control on the within-plant movement of assimilates'[9]. The diversity of the source–sink interactions in different galls is an aspect that deserves closer scrutiny.

The unusual concentrations of highly nutritive substances within gall tissues, the vulnerability of cecidozoa and the presence of cells with near-meristematic conditions provide a favourable habitat for the development of microcommunities from bacteria and fungi to insects and mites. Tissues close to the gallers show cytological and morphological changes which are beneficial to the feeding and development of the insect. For instance, the nutritive cells in young galls have denser cytoplasm, increased vacuoles often fragmented into smaller vacuoles, larger nuclei and hypertrophied nucleoli and modified chloroplasts (Figures 1 and 2). The ergastoplasm is rich in roughly surfaced endoplasmic reticulum[10]. The attributes of the nutritive tissue progressively change from the edge of the larval chamber onwards forming a 'cytological gradient'[11], very typical of cynipid galls and absent in cecidomyiid galls in which a characteristic nutritive tissue and a storage nutritive tissue are present. The presence of an active larva is absolutely crucial for the development and maintenance of the nutritive tissue. Relative to the ungalled plant there is a remarkable differentiation of the plant tissues clearly indicative of resource modification.

Gall diversity profiles

Variations in gall morphology also contribute to the adaptive nature of gall growth to enable reduction in the energy expended. The size of the gall also varies, small galls often resulting from low plant reactivity to gall-inducing stimuli or due to the decreasing population diversity of the gall makers. In many galls, insect attack patterns also vary, as also the life cycle strategies mostly

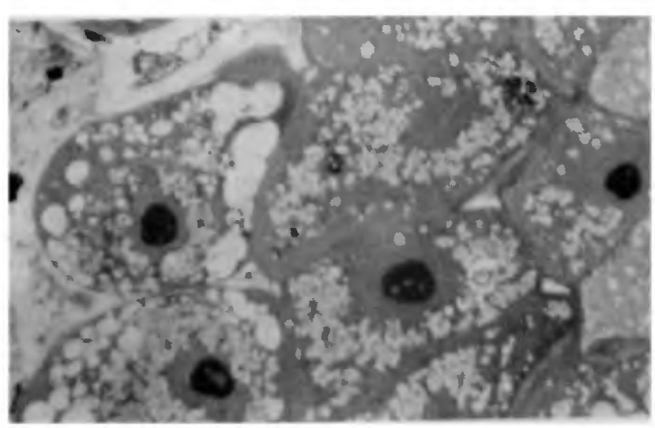

Figure 1. Nutritive cells of a young gall showing increased vacuoles.

due the hypersensitive reaction[12] of plants which ultimately influence their distribution. The incidence of gall variability supplemented by numerous intergrades indicate that galls are induced at different stages of the organ involved and by the cumulative effect of the population. In thrips galls, gall initiation that occurs during the differentiation phase of the leaf results in complete reorientation of normal development, while those that have crossed the stage of determination result in partial galls with weak feeding impact. Gall initiation in sawflies occurs during oviposition. The patterns of cell proliferation and resulting gall form vary with species and host plants.

Galls are essentially single, very rarely multichambered, prosoplasmic structures undergoing differentiation, their diversity ranging in complexity from simple pits and blisters, through leaf curl, fold and rolls to bud, horn, rosette and pouch galls. While gall makers are confined to the Hemiptera, Thysanoptera, Coleoptera, Hymenoptera and Diptera, the latter two groups harbour a large number of species involved in making diverse types of galls varying in form and structure. A high degree of specialization is seen in cecidomyiids or gall-forming Diptera, which show a multitude of gall types. Tephritid flies also produce galls, some of which are important in the biological control of weeds. While considerable gall diversity exists at the interspecific level, a fascinating array of complications at the intraspecific level is also evident as in the horn galls of *Schefflera*[13].

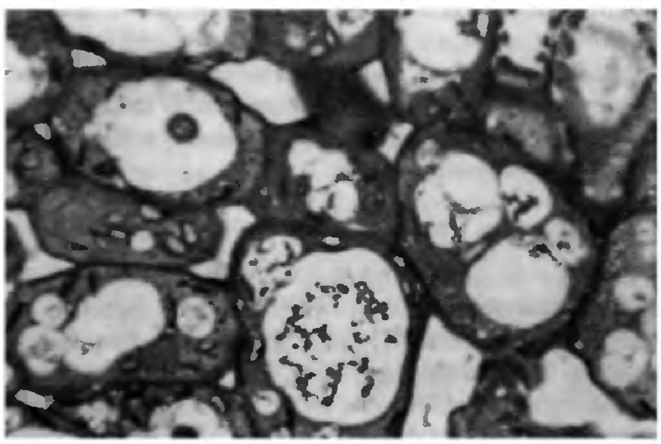

Figure 2. Developing nutritive cells.

Gall insects modify minute areas of host plants by soliciting unusual gene expressions from adjacent cells in such a way that new developmental events result. Thus the insect through its activities is able to reveal new morphological potentialities of the host plant which were initially directed against it[2]. Gall morphogenesis occurs only for a relatively brief period during growth of responding plant parts. Gall makers not only damage the host plants of tissues that they consume, but also cause them to alter tissues that would otherwise be useful. Early attacking species may alter growth of the affected organ so as to reduce the number of gall sites. Galls are therefore harmoniously organized entities with an orderly arrangement of cell layers and determinate growth which result in structures with particular sizes and shapes (Figure 3)[9].

Gall complexity results from variation in the degree of hyperplasy and hypertrophy (Figures 4 and 5). Patterns of gall development in general vary with, the cecidomyiid, the sawfly model and the cynipid models. The cecidomyiid model is the most plastic and is very common and represents all degrees of evolution of the insect–gall plant relationships demonstrating variability in gall induction. Heterogony or occurrence of alternation of generations of the same spcies including two types of galls occurs in the development of cynipid galls[9].

Gall initiation: Nature of insect stimuli

Gall phenotypes that provide clues to their adaptive significance are their chemical composition involving

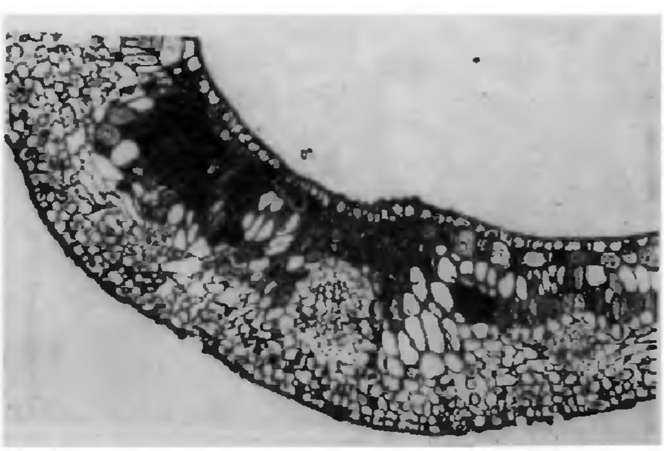

Figure 3. Profile of a gall showing hyperplasy and hypertrophy.

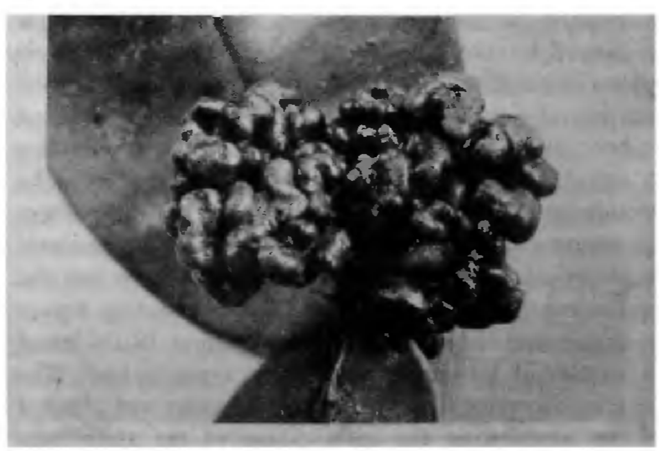

Figure 4. A complex tortuose gall of *Memexylon*.

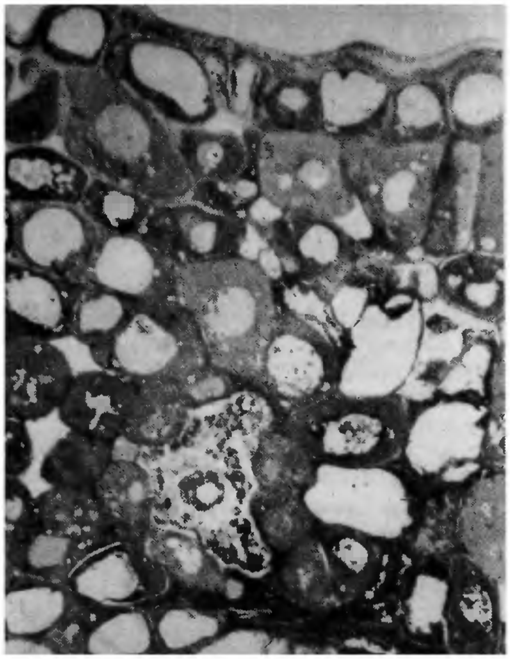

Figure 5. Cell enlargement and differentiation.

nutritive and defensive elements. Hartley and Lawton[6] have shown that cynipid gall forms may be able to manipulate host nitrogen levels to their own advantage and secondary metabolites, notably phenolic compounds, play an essential role in gall formation, in the sense that they can suppress or induce galling in accordance with their mileu. As galls are formed, secondary chemicals get isolated from the nutritive tissues and are concentrated in the peripheral tissues at proportions ten times higher than that in non-galled leaves[14].

Studies on the cotton stem galls caused by *Pempherulus affinis* have shown that maximum levels of total phenols and OD-phenols are present in the resistant cotton cultivar MCU5 as against the lower phenolic profiles in the cultivar LRA. With the onset of galling, gallic acid and gentisic acid appear in the multigalled stems and presumably result in low growth and fecundity indices of *P. affinis*. Single-galled stems are highly preferred by *P. affinis* because of the low phenolic profiles, in particular, low tannin and gossypol contents[15].

Indoleacetic acid (IAA) in the saliva of insects is considered to be an 'inducer' of galls. 'Cell conditioning' precedes gall induction[16]. Polyphenol oxidase (PPO) is a component of the saliva of insects and PPO phenolic compounds increase in plant tissues attacked by insects. The complex role of phenolic compounds and phenol oxidases may indicate that plant–PPO system has a more fundamental significance in gall production. Amino acids, essentially lysine, histidine and tryptophan might function as 'conditioners' for gall induction. They tend to make the tissue more plastic and raise their sensitivity to the gall inducer. Therefore when saliva contains higher levels of IAA, and amino acids and a low level of phenolic compounds, there is inhibition of gall induction. Cell enlargement is influenced by the role of IAA in the synthesis of RNA and protein in plants[16].

Suggestion has also been made that insects inject plasmids and viroids into the plant genome and take over gene regulation to produce a gall[17,18]. Elevated levels of RNA in nutritive tissues, acid phosphatase, glucose-6-phosphatase, invertase, amylase and phosphorylase are also common in galls[19]. Away from the action feeding sites and near the gall exterior, tissues often accumulate high tannin levels and other defensive chemicals over time.

Polymorphs and role in social behaviour

The enclosed nature of galls with highly valuable resources providing food and shelter for a lifetime creates circumstances where behavioural adaptation for defence and other forms of cooperation may be favoured by selection. Such an association within galls indicates aspects of their genetic system, morphology, development, behaviour and ecology. Associated with wing polymorphism in species of *Thilakothrips, Alocothrips, Byctothrips, Oncothrips, Kladothrips*, etc. are modifications of head, thorax and foreleg armature, the latter indicative of intra- and inter-specific fighting[20]. The involvement of major females and minor females as well as oedymerous and gynaecoid males in *Arrhenothrips, Mallothrips*, etc. as well apterous and macropterous forms provides considerable opportunities for increasing incidence of mating patterns and resulting oviposition diversity and sex ratios[21]. In short, because of their haplodiploid genetic system and their ecological relationships with plants and natural enemies gall thrips exhibit complex social behaviour.

Social behaviour in gall thrips reflects the presence of functionally diverse morphs, the more common ones being those showing extreme foreleg allometry, also associated with wing polymorphism, often functioning as soldiers in the defence of the gall, particularly in combating invading members of inquiline species[22]. Gall thrips on *Acacia* species exhibit 'a remarkable diversity of complex agonistic, cooperative and habitat manipulation behaviour directly related to the nature of their domiciles'[20]. Some of the more important aspects related to intraspecific fighting, a preadaptation for evolution of soldiers showing considerable diversity, relate to wing reduction, increased armature of foreleg which are typical of some gall thrips.

In short, gall thrips by dint of their haplodiploid genetic system and their ecological relationship with plants and natural enemies exhibit complex social behaviour including soldier caste, pleometrosis (joint colony forms), group foraging and group defence[20].

Conclusion

Gall induction unquestionably is a complex phenemenon involving recanalization and reorientation of plant development by the galler, an adaptation for exploitation and diversification of nutritive tissues which may be in the form of isolated patches of cells or a specialized zone forming a new physiological environment around the galler. The physiological nature of the insect stimulus and the nature of plant responses are still open questions and the nature of such responses has a profound influence in the evolution of adaptive diversity owing to the selection pressure in the loci that influence reactions. The independent development or the ability of the gall insects to reorient the growth mechanisms of the host plant is impressive, creating favourable and sustainable nutritional and insect shelter guilds. Gall insect–host plant association seems to exemplify an advanced or specialized level of trophic strategy. The nature of the selection pressures on the different interacting species would determine the rate and direction of gall phenotype evolution. While the type of interactions between the galler and the host plants will tend to vary with different galling organisms, the growing importance of tritrophic interactions cannot be ignored. The host plant sufficiently influences the susceptibility of natural enemies which often use host plant cues for locating their victims.

Host plant reaction endows the galler with benefits which could be the result of adaptive evolution. Host responses must be influenced by the genome of the galler and it is here that further intensive investigation is required. The galler has the potential advantage in insect–plant relationships and morphological, developmental and chemical aspects lend adequate support to the adaptive value of insects. Perfect coordination between the galler and the host plant is necessary for their continued existence.

Intraspecific host plant variation tends to result in insect polymorphism and this may preadapt for host shifts, though in the majority of the cases galls are highly host specific since they have genetically based host preference and lack the ability to shift hosts on a non-genetic basis[7]. The evolution of polymorphism, and consequent social behaviour are aspects which go a long way towards a better appreciation of the pre-adaptation and selection pressure of the galler. The reproductive behaviour of polymorphs considerably influences the fecundity and results in mating patterns, leading to recognizable variations in the subsequent production of morphs.

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