# Gall insect-host plant relationships—An ecological perspective

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**Abstract.** Compared to other phytophagous insects, the gall insects are specialised in view of their imperative demand for a particular type of food in terms of a specific host; this is further supported by their specialised trends in establishing a coordinated, functionally efficient system involving (i) the biogenesis of the host plant organ, and (ii) the life-cycle of the gall-maker. The 'inherent potential' (genetic-?) of the gall-insect to establish an independent, yet a discrete habitat, modifying the host plant tissue to enjoy a self-contained nutritional guild, facilitated by the host selection patterns, appears especially different from the other non-cecidogenous phytophages.

Besides the autecological factors such as the changing climate, chemical and physical changes in the host tissue, and patchyness of food plant resources, which are of great importance to the cecidogens, of particular significance are the community interactions within gall systems involving many arthropod participants like inquilines, parasites, predators, and other casual visitors. As specialised organisms and with limited population size per unit area, the gall insects seem to run the risk of random extinction, although their efficient development of strategies to survive appears significant.

**Keywords.** Gall insects; phytophagy; ecology.

## 1. Introduction

Like that of any phytophagous insect, the existence, physiology, behaviour, ecology, and evolution of a gall insect are remarkably influenced by the host plant, which offers food and shelter in a special way. Although there could have been a time when the Spermatophyta remained unprotected and therefore were fed upon by many phytophagous insects (Feeny 1975), probably over the years, most of the spermatophytes became non-hosts (de Ponti 1982), thus paving the way for more-intimate relationships as a result of careful and skilful utilisation of the available plant resources by the insects. Although the phloem-feeding Hemiptera were well established in the Permian (Smart and Hughes 1973), accumulating evidences of the leaf-mining habit among particular groups of phytophagous insects from the Eocene (Hickey and Hodges 1975; Crane and Jarzembowski 1980) indeed suggest the behaviour of insects to seek new food sources and the larvae opting for 'specialised' but limited feeding sites during the upper Cretaceous, when the diversification and establishment of Angiosperms took place, with a progressive integration of the faculties of exploitation by the insect and the susceptibility of the plant. It is in this perspective that the cecidogenous trait of some of the insects appears significant that the gall forming tendency could have branched off as a major offshoot from the phytophagous habit, particularly in view of the sophistication in terms of host selection and the adaptive strategies (Faith 1979; Ananthakrishnan 1982; Raman and Ananthakrishnan 1983b) the gall insects display.

## 2. The host plant as an environment

Almost all the gall inducing insects and mites are host-, organ-, and tissue-specific (Shorthouse 1982) and they take advantage of the fundamental property of the plants to react, whereby even the differentiated tissues could be converted into meristematic state. The host's response to the feeding or ovipositional stimulus is something unique that the plant's morphogenetic responses are altered, being relieved from the in-built correlative factors of plant development. Sufficient information exists on the structural readjustments and specialised differentiation patterns in insect/mite induced gall systems (Maresquelle and Meyer 1965; Meyer 1969; Rohfritsch 1971); yet the development of nutritive cells through dedifferentiation is one of the most outstanding features of gall formation. Further, the galls in general show a number of specialised adaptations including the differentiation of vascular elements and sclereids which are of great significance to the effective functioning of gall guilds. The growth patterns as in a cecidogenetic system involve, on the whole, a blending of homeogenetic as well as heterogenetic phenomena (Lang 1973) for an effective functioning under an abnormal biological demand, i.e., to provide 'facilities' for an alien organism. The host, for example, shows heterogenetic adaptations like the transformation of parenchyma cells into sclereids and tracheary elements (Meyer 1968; Raman and Devadas 1977). This highlights the operation of different polarity gradients during the phase of interaction. Moreover, a compromise among the field effects—the repulsive factors between the sites of normal histogenesis *vis à vis* the sites of cecidogenesis—, controlling the external form and internal organisation are displayed in a great magnitude. On the whole, the inductive phenomena of the host, *viz* the homeogenetic, heterogenetic, and field effects function in varying intensities in every gall system, thus contributing to the totality of each gall. In other words, the insect-induced galls are organised proso-plasmatic structures, representing an obscure situation of normality (in terms of organised form) in abnormality. However, the localised nature of the 'transformed' area and the specific nature of the target cells evoke interest. It is believed that in all the angiosperm cells, a polarised cytoplasm exists that determines the ability of cells, and in turn that of the organs to be polarised in a specific way, and the orientation of the polarity follows a gradient from the active meristem to regions of cellular elongation. This, when extended to galls by insects and mites, indicates the diffusion of a polarity gradient from the nutritive cell areas to the areas away (Mani 1964). Attempts to quantify growth as in insect gall systems (Shorthouse 1973; Wiebes-Rijks 1974, 1982; Lintott 1975; Gopinathan 1984) have revealed an increase in the relative growth rates, wherein the target levels of growth are attained quickly, indicating the efficiency and rapidity in the developmental rates of gall systems. Thus a gall represents the functional efficiency of the host as a producer of new material and also gives a measure of the host's economy in working (Blackman 1919) to counter abnormal situations. This is effectively moderated by the differential elaboration of the tissues in the gall system: functional elaboration in the cells closer to the feeding sites (Bronner 1978) and morphological elaboration of the cells away from the nutritive zone.

## 3. Nutritional ecology and host/habitat selection

In general, most of the activities such as the performance, timing and extent of reproduction, dispersal activity, probability of survival, and quality of the offspring

produced (de Wilde and de Loof 1973a, b; Slansky 1982) are primarily controlled by the amount, rate and quality of food consumed by the insects. This becomes more specific and highly relevant among the cecidogenous insects, because of their specialised behaviour, since a major part of the life cycle is intimately linked with a gall and most of the development is completed therein deriving nutrition from the gall tissue. Environmental evaluation for colonization and decision-making (Slansky 1982) is best displayed in gall insects which show sophisticated levels of these behavioural patterns. For instance, populations of *Thilakothrips babuli* within the rosette galls on the axillary buds of *Acacia leucophloea* (Varadarasan and Ananthakrishnan 1982; Raman and Ananthakrishnan 1983a) are restricted to a short period of 3 months. When the rosette galls begin to dry up, thrips population also declines leaving behind a few apterous adults, which remain in the dry galls and diapause. When *Acacia* puts forth new flower buds, the apterous adults leave the diapausing site and migrate to form new galls. Another interesting example would be the choosing of alternative courses of action by cecidogenous species in a flower head system as illustrated by Zwölfer (1979), who believes in the operation of a high selection pressure for the evolution of strategies to mitigate the effects of competition. Species, particularly those belonging to the same genus, coexisting on the same floral locus evolve evasion strategies by developing differences in the selection of oviposition or larval feeding sites, or in the timing of larval development (Zwölfer 1975). Perhaps the most efficient evasion strategy would be character displacement of developing races or biotypes, as is possibly existing in the cecidogenous *Bemisia tabaci* distributed almost throughout the world (Mound and Halsey 1978) on a variety of host plants.

The host selection patterns of almost all the gall insects need to be examined in a new perspective of sterol availability from the plants to enable the insects to develop growth hormones. *Taxomyia taxi*, inducing galls on *Taxus baccata*, moults only after a pad of nutritive tissue has erupted from the infested apex and has accumulated large amounts of fat and starch indicating the nutritive tissue to be a sink for metabolities (Lovett 1970). Excision of galled shoot in most cases prevented larval ecdysis. Ecdysterone level in these galls increased from June to mid-August (as in Southwick, England) and this could represent that a chemostimulant is needed for the progress of larval develop-ment (Lovett 1981). Although Svaboda *et al* (1975) have cautioned about the dangers of making generalizations concerning sterol metabolism in insects, Lovett's (1981) suggestion based on the circumstantial evidence as in *Taxomyia* work provides ample scope to imagine the relevance of gall insects being specific to particular hosts, thus offering close-knit opportunities to maintain values for the life history performance.

By virtue of being highly specific to particular hosts involving very intimate relationships of an efficient host-finding behaviour and organised development of a habitat, the gall insects appear to have tactfully 'surmounted the nutritional hurdles' in the words of Southwood (1975). Aiming at the maximal larval survival and by a well regulated phagostimulatory behaviour based on the orientation and utilization of visible and chemical cues, the cecidogenous female selects the oviposition site and lays its eggs. In spite of any possible spatial isolation, the eggs laid occur in an extremely ideal food area, which is able to subserve the immediate demands of the emerging larvae. The juvenility of the host tissues is yet another important factor that provides ample opportunities for regeneration and thus is able to create a highly desirable locus of nutrition (Rohfritsch 1974, 1976; Bronner 1978; Raman and Ananthakrishnan 1983c). For example, the emergence and migration of stem mothers of *Pemphigus betae*

are precisely synchronised with the bud burst of *Populus angustifolia* (Whitham 1980); the size of the mature leaf is critical to the ultimate fitness of the colonising stem mother, and Whitham (1978) further contends that the locus of the galling is a very important factor, because the galling at the leaf blade/petiole junction achieved the highest reproductive success, while the stem mothers occupying gall positions along the distal regions of *Populus* leaf registered low success, since the suprapetiolar region of the leaves, the gateway regulating the inflow and outflow of material, ensures greater nutrient availability. This is particularly significant in a cecidogenous system, where the gall insect attacks meristematic and venal regions of the host organs suggesting the basic necessity for nitrogenous material for a high energy conversion efficiency. Or, could it be so, that they avoid toxins as Way and Cammell (1970) have shown non-cecidogenous aphids feeding on dying foliage thus achieving spatial avoidence? In this system, the stem mothers, because of their galling habit, realised at least 84 % of the potential fitness. Whitham (1980) attributes that regardless of the specific mechanism employed by stem mothers to select superior habitats this level of precision indicates that the gall insects effectively assess and integrate the variables of individual habitat quality, the distribution of habitat qualities, and the density of competition in each habitat. And this can be extended to other gall insects as well, since very identical behavioural patterns appear to occur among gall midges such as species of *Semudobia* on species of *Betula* in western Europe (Roskam and van Uffelen 1981).

While cecidogenous systems are highly complex and intriguing because of the elegant behaviour of the insect, tissue resistance though rare, as in some individuals within populations of the susceptible host taxon appears interesting. In the *Picea excelsa–Chermes abietes* system, some of the individuals of *Picea* are resistant to cecidogenous *Chermes* (Tjia and Houston 1975; Thelenhorst 1972). Analysing this interesting host behaviour Rohfritsch (1981) has illustrated that the host tissue in the susceptible individuals gives rise to a nutritive zone, while in the resistance plant the attacked cells are 'hypersensitive', leading to plasmolysis, cell collapse, precipitation of phenolic substances, and finally necrosis. Curiously, in spite of the abnormal behaviour in spring and autumn by the host tissues, this spruce (*P. excelsa*) has been shown to be a good host to another gall making species *Chermes strobilobius*.

## 4. Gall community: structure and interactions

It is believed that the community involving interactions between species are often ecologically unstable (May 1974), and unless the interactions are examined explicitly, it becomes difficult to assess whether the ecological instability could lead to genetic instability. In spite of this conceptual vagary, a plant gall system evoked and organised by an insect appears stable. The stability is so significant that it prompts the idea that gall insects solicit genetic expressions from their host cells (Rohfritsch and Shorthouse 1982). Attempting to bridge the gap between the individual behaviour as evident in the gall maker and the niche structure as seen in the gall associated arthropod community, the roles of the inquilines, predators, and parasites seem important. The system presents itself to be complex involving the functioning of more than one organism (Brewer and Johnson 1977; Wangberg 1978; Varadarasan and Ananthakrishnan 1981). In the *Diplolepis* induced galls on *Rosa*, Shorthouse (1973) has demonstrated the functioning of the inquiline (*Periclistus*) larvae that are able to activate and modify

the tissue developed by *Diplolepis*. Similarly, *Androthrips flavipes*, recorded in as many as 15 thrips-induced galls (Ananthakrishnan 1978) and shown to be an inquiline-predator (Ananthakrishnan and Varadarasan 1977), effectively regulates the developing colonies of the gall maker thrips. Adept with very agile body action and swift movements, these associates are well-suited for inhabiting specialised habitats such as galls, where the opportunities to locate and feed on gall insects are ample especially in view of the restricted space; besides these, *Androthrips* also shows a short life cycle duration, which enables a successful predatory habit. Resorting to cannibalism, this predatory inquiline keeps the number low so that over-crowding—a dangerous factor in a gall system—is avoided. Large-bodied insects such as *Montandoniola moraguesi* also play an important role in the gall communities. When compared with the functioning of the small-bodied predatory insects such as *Androthrips, Montandoniola* compensates by consuming more of gall insects (Raman *et al* 1978). The participation of endophagous and ectophagous parasitoids, both displaying well-defined courses of action can be illustrated with the example of *Eurytoma* inhabiting *Urophora* galls (Zwölfer 1979). The endophagous *E. robusta* oviposits when the gall reaches more or less the full size. This strategy adapted by 2 species of *Eurytoma* to achieve maximum utilisation of the resources is indeed impressive. The early action of *E. serratulae* elicits protection through the development of the host which develops cuticular sclerotization to escape the attack of the aggressive competitor, *E. robusta*. The restricted nature of the food supply coupled with rapid population growth rates of gall-maker as in some of the Homoptera-induced gall systems suggests the existence of an unusual defensive behaviour in keeping 'territories' (Whitham 1979). Since the population densities approach the carrying capacity of the environment and because of parthenogenesis, *Pemphigus betae*, cecidogenous on *Populus angustifolia*, defends its microterritory leading to individuals being displaced through competitive interactions. Examining *Baccharis pilularies – Rhopalomyia californica* system, and the associated parasites like *Torymus koebelei*, *T. baccharidis*, *Platygaster californica*, *Zatropis capitis*, *Mesopolobus* sp., and *Tetrastichus* sp., Ehler (1982) proposes that some form of interspecific competition occurs especially between the most superior competitor in that gall systems (*T. koebelei*) and an intermediate competitor (*P. californica*) affecting the performance of each other. These kinds of biological systems involving a highly specific and organised community and necessarily depending on the development of galls raise a number of questions. In principle, there is a three-level trophic interaction among the participants—producer, gall maker and parasite—and the interaction behaviour of the competitors as in these systems needs to be assessed in terms of the competitives superiority or inferiority, as well as in terms of *r*-to-*k* continuum (MacArthur and Wilson 1967) to understand and elucidate the optimal evolutionary strategies employed by these organisms.

## 5. Conclusions

The insect-plant interactions on the criterion of gall induction appears unique particularly when examined on the biogeographic factors. The highly specific nature of gall insects to particular hosts does throw significant light on their behavioural pattern of colonising biogeographically specific areas. For instance, the isolation of cecidogenous thrips to arborescent hosts of tropical and subtropical zones (Raman and

Ananthakrishnan 1984; Ananthakrishnan 1978), the epiphyllous bud-gall inducing coccids on the foliage of asiatic *Shorea*-s of Indo-Malayan region (Anthony 1980), and the flower inhabiting *Semudobia* to *Betula*-s of boreal and temperate Holarctic (Meusel *et al* 1965) evoke interest, suggesting the complexity of the trophic relationships in cecidogenous systems, as well as the emerging properties characterising the whole ecosystems. It remains to be seen whether these intricate relationships have anything remarkable to contribute to the process of coevolution. This is important and relevant here because plant gall/insect association is one of the intimate biological associations. However, in the cecidogenous systems such as that of *Semoudobia-Betula* (Roskam 1979), confusing pictures emerge. In any case, detailed analyses of the host spectrum of gall insects may provide additional evidence to identify the affinities among host species, since many defined groups of gall insects are characteristically bound to defined groups of plant hosts. However, the interplay of two unrelated organisms as in insect gall systems highlights the evolution of a remarkably efficient interacting system: the plant mobilising all the possible resources to protect itself initially, and then undergoing a series of adaptive changes to enable the survival and sustenance of the insects; and the insect, on its part displaying feeding specialization to create a new habitat. In this background, the gall insects are highly specialised in their search, and it is also possible to imagine that they had no potential or an imperative need to search for new hosts, particularly when they got established. The nutritional behaviour of *Monarthropalpus buxi*, cecidogenous on *Buxus sempervirans* having the potential to induce galls on *Buxus nana* and *B. bullata* only under experimental infestations (Brewer and Skuhravy 1980), gives a clue that the gall insects are basically conservative, and perhaps because of the lack of necessary gene-pool readjustments to produce necessary enzyme systems, they are not able to adapt to newer environments in terms of new hosts. This trait of conservation could become significant, since a genotype with a high frequency in one generation will automatically be changing its environment and paying the way for its decline at some future point of time. Notwithstanding the possible 'conservatism', the nature of host selection, the creation of a highly refined, self-sufficient microenvironment and the constant fitness of the interacting genomes, appear highly specialised.

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