

## Thrips-Plant Gall Association with Special Reference to Patterns of Gall Diversity in Relation to Varying Thrips Populations\*

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The impact of populations of thrips on the size, shape and morphological complexities of galls necessarily involves: (a) timing of gall initiation; (b) numbers of thrips in varying phases of gall formation; (c) extent of receptivity of tissues in relation to population density; (d) mode of action of primary and meristematic tissues; (e) visible changes in gall complexity and correlation of external topography with internal cellular dynamics.

The concept of gall maturity has been defined in terms of maximum limitations of reactivity as evident from the development of corrugations, granulations, excrescences, and other surfacial complexities. Thrips galls are outstanding in their reaction to the population of thrips within them, and an attempt has been made to discuss these aspects with reference to several thrips galls from the view point of increasing complexities.

**Key Words:** Thrips, Galls, Populations, Diversity

### Introduction

Over three hundred species under about 90 genera of thrips are gall inhabiting, and two-thirds of these are from the Orient. The major thrips gall-bearing plant families are Araliaceae, Euphorbiaceae, Melastomaceae, Moraceae, Myrtaceae, Piperaceae, Rubiaceae, Urticaceae and Vitaceae (Ananthakrishnan 1978). Available information on the comparative morphology of thrips galls clearly indicates that thrips galls are mostly morphologically simple, being

leaf-fold or leaf-roll galls, but bud, pouch, rosette, coralline, and horn-galls are not uncommon (Ananthakrishnan & Jagadish 1968, Ananthakrishnan 1978). On the whole, about 50% are leaf-rolls, mostly epiphyllous, rarely hypophyllous, 25-30% leaf-folds, and the rest comprise the more complex categories. In view of an apparent morphological convergence in external form, and an internal histological divergence, sufficient potential exists for an analysis of the organizational

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patterns of galls, particularly in relation to the varying populations of thrips in terms of age of the gall. Evidence is here presented of the view that the population of the gall maker, besides being a controlling factor in cecidogenesis, has a decisive role on gall morphology, offering a sufficient range of morphological variability.

The adaptation and evolution of cecidogenesis thrips are reflected by the restriction of thrips galls to leaves with their localization to specific areas. This is further confirmed by monophagism having reached a climax stage well evidenced by the restriction of thrips species to specific host plants as well as by the maintenance of gall form through generations. This feature presupposes the possible coevolution of insects and host plants. This is further substantiated by several instances of closely related host plant species associated with closely related thrips species such as *Liothrips-Schefflera* (Araliaceae), *Crotonothrips-Memecylon* (Melastomaceae), *Gynaikothrips-Ficus* (Moraceae), *Liothrips-Piper* (Piperaceae), and *Oncothrips-Acacia* (Mimosae).

Intraspecific variation is a frequent feature in thrips galls, adding to the complexity in organizational patterns, particularly in view of gall form being controlled by the developmental stage of the organ concerned. The time of gall initiation is very important in cecidogenesis, and the structural diversity such as the total expression of galling effect, and incomplete or partial expression resulting in incomplete or partial galls respectively, according as to whether they are induced at a very early stage or a later stage in leaf development. Gall initiation occurring during differentiation phase of the leaf results in the complete reorientation of the normal morphogenetic activity of the leaf. With the developing leaves having crossed the stage of 'determination', combined with a weak feeding impact due to small populations of thrips, an incomplete or partial

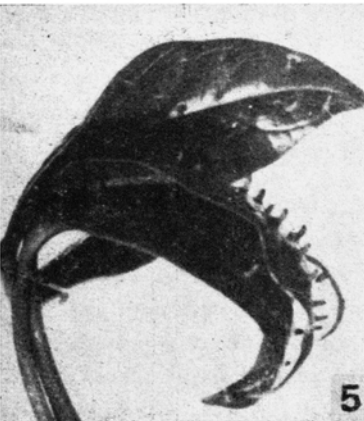
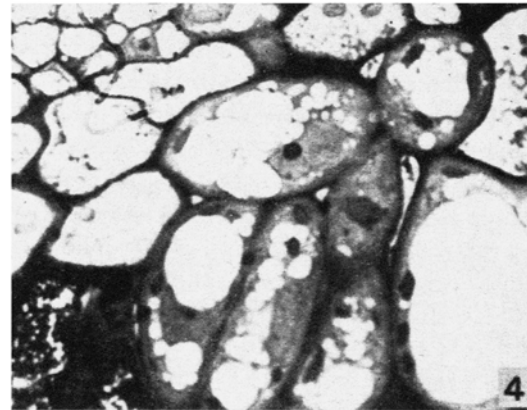
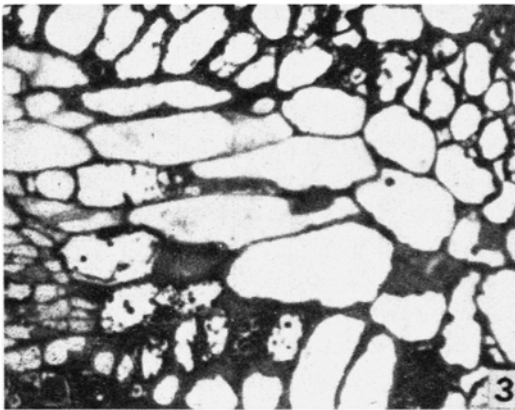
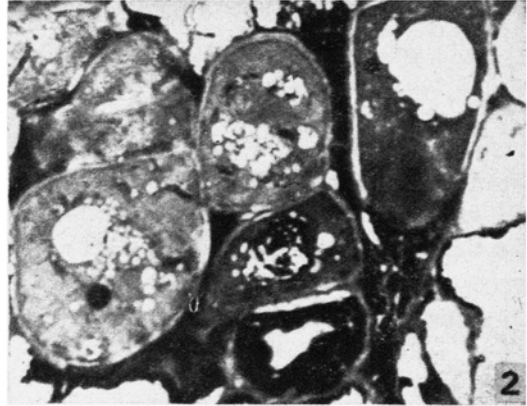
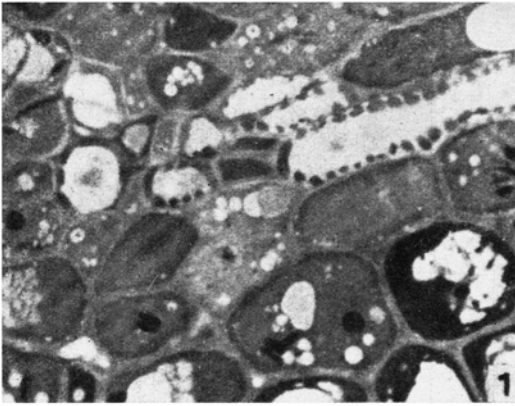
morphogenetic reorientation results in partial galls (Raman et al. 1977). As a result of high thrips populations as well as their being confined for prolonged periods in a limited area, simple and complex galls arise on the same plant. The simple, tubular, as well as fleshy, branched galls on *Schefflera racemosa*, Harms present two extreme forms of gall, the simple, smooth, as well as rough; tuberculate galls of *Pavetta hispidula* W. & A. (\**Teuchothrips longus*), *Memecylon edule* Roxb. (\**Crotonothrips dantahasta*), *Walsura piscidia*, Roxb. (\**Psenothrips priesneri*), and *Casearia tomentosa* Roxb. (\**Gynaikothrips flaviantennatus*), the incomplete or partial as well as complete marginal rolls of *Cordia obliqua* Willd. (\**Aneurothrips priesneri*), and *Maytenus senegalensis* (Lam.) (\**Alocothrips hadrocerus*) and the increasingly complex and corrugated nature of the galls of *Calycopteris floribundus* Lam., *Memecylon lushingtoni* Gams., *Acacia leucophloea* Willd. etc., with increasing populations of thrips are all striking instances of diversity in gall form.

The impact of such changes in form is reflected also by the nature of the gall tissues. Though many thrips galls have definite morphological patterns, an analysis based on the tissue dynamics in the context of gall development appears significant.

Depending both upon the time of infection as well as of the impact of thrips activity, varying organizational patterns in terms of tissue displacement result in galls. In the simple morphological types as in the galls of *Planchonia valida* (Barringtoniaceae) only portions of the lamina are crinkled without any pronounced change in the tissue morphology, the galled areas showing only large air spaces and lateral stretching of the epidermal cells in response to the attack of *Cercothrips nigrodentatus*. A definite meristematic zone is absent in thysanoptero-

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\*Gall-maker



**Figure 1** *Casearia tomentosa* young gall—Hypertrophy of vascular parenchyma ( × 854)  
**Figure 2** *Casearia tomentosa* old gall—Hyperplasia of mesophyll cell ( × 1250)  
**Figure 3** *Mimusops elengi* young gall—Hypertrophy of vascular parenchyma ( × 375.6)  
**Figure 4** *Mimusops elengi* old gall—Hyperplasia of mesophyll cells ( × 375.6)  
**Figure 5** *Schefflera racemosa* galls—Young developing stages  
**Figures 6 & 7** *Schefflera racemosa* galls—Complex and fleshy due to high population of thrips

cecidia, but the cells show specific division patterns facilitating the gall development. In fold galls such as those of *Mimusops elengi* L., longitudinally elongated parenchymatous mesophyll cells exhibit anticlinal divisions facilitating upward and lateral stretching of the leaf blade. Species of *Cordia*, *Maytenus*, and *Casearia* develop into rolls if infection is early, or folds when late, and accountably the organizational patterns differ. While there is no hypertrophy in both complete and partial galls of *Cordia*, there is epidermal and subepidermal hypertrophy in *Maytenus*, and the blade rolls due to periclinal divisions adding thickness to the galls. Raman and Ananthkrishnan (1978) have indicated that regulation of the meristematic behaviour of the epidermal system of the gall zones seems to operate only at the individual cell and cell group levels resulting in a localised effect, so that cellular disturbance is attributed only to a limited area without any systemic effects. In both cases, the mesophyll fails to differentiate and in *Cordia* the mesophyll cells become completely sclerified with various types of sclereids with various degrees of pitting and cell wall thickening. In *Maytenus*, mesophyll is compact with two to three layers of strongly thickened stone cells in the form of a longitudinal strip. In the mature galls the entire mesophyll is sclerified. In the hypophyllous roll galls of *Pavetta hispidula* W. & A. predominantly periclinal divisions occur showing considerable increase in cell layers (with about 17-60 layers) due to epidermal and mesophyll hypertrophy. Abnormal tracheary elements are frequently formed by the transformation of the parenchyma cells. In the roll galls of *Casearia*, however, both anticlinal and periclinal divisions occur with hypertrophy of the vascular elements, a phenomenon also seen in the roll galls of *Loranthus elasticus*. However, the development of leaf folds or partial leaf rolls with lateral stretching of cells with late infection as well as increased

hypertrophy and hyperplasy is characteristic of early infection of *Pavetta* galls.

However, in *Schefflera* we come across striking organizational patterns both in external form and internal structure. Simple tubular galls showing only 7-12 layers of compactly arranged parenchyma cells do not harbour thrips continuously, but only for a short initial period. Complex fleshy, twisted, and branched galls harbour large numbers of thrips for a considerable period, and by their feeding provide a continuous stimulus resulting in the leaf attaining morphological abnormalities, with lobulations and bizarre branchings due to activities of the localised populations of thrips. This incidentally results from the reactivation of the differentiated parenchyma showing 25-35 layers with few chloroplasts and with tracheary elements broader and with closely packed elements.

The age of the gall and the involved thrips population are essential in interpreting the nature of tissue reactions which result in diverse organizational patterns. The populations of thrips inclusive of larvae and adults in the complex galls appear to be 3-15 times more than that in the simpler galls. Raman et al. (1978) have clearly indicated that the population build-up in such galls as *Casearia tomentosa* is up to the 15th day of gall development but declines with the age of the gall, the variability in populations per gall ranging from 2-65 individuals. The population of the gall maker has a decisive influence on the morphology of the galls. Table 1 provides an indication of the population of thrips in immature and mature galls as well as the nature of tissue reactions.

A clear segregation of thrips into sap-sucking, pollen-feeding, and gall-forming categories is obvious, but further trends of specialization particularly among the cecidogenous thrips does not appear speculative. It may, however, be said that the gall-forming tendency among Terebrantia is

Table 1 Population trends in terms of the age of the gall

Gall (Gall thrips)	Age of the gall in days (Total population of gall thrips)		Population of thrips			Tissue reaction		No. of cell layers added in the gall tissue (No. of cell layers in the normal tissue)			
	Immature gall	Mature gall	Immature gall	Mature gall		Hypo- plasy	Hyper- trophy				
				Larva	Adult						
<i>Mimusops elengi</i> ( <i>A. ramakrishnae</i> )	6-10 (19-37)	15-21 (60-92)	2-6	2-4	14-21	18-26	+	+	moderate	13-18 (4-6)	
<i>Ventilago maderasapatana</i> ( <i>S. orientalis</i> )	8-10 (7-20)	20-25 (69-93)	—	5-8	18-23	11-16	+	+	+	12-16 (5-6)	
<i>Pevetia hispidula</i> ( <i>T. longus</i> )	9-10 (22-24)	23-25 (130-159)	—	9-10	45-61	19-32	+	+	+	17-60 (8-10)	
<i>Memecylon edule</i> ( <i>C. dantahasta</i> )	10-13 (13-25)	20-25 (59-63)	2-4	3-6	15-19	19-21	+	+	+	22-25 (9-12)	
<i>Calycopteris floribundus</i> ( <i>A. cochinchinensis</i> )	— (93-136)	— (480-1400)	60-80	10-45	250-400	650-800	+	+	+	moderate	47-75
<i>Acacia leucophloea</i> ( <i>T. babuli</i> )	4-8 (14-31)	20-24 (49-85)	1-2	2-3	18-32	21-28	+	+	+	+	30-35 (7-9)
<i>Cordia obliqua</i> ( <i>A. prietneri</i> )	5-10 (4-7)	15-30 (29-105)	2-5	1-3	14-24	7-57	moderate	+	moderate	10-15 (6-8)	
<i>Casearia tomentosa</i> ( <i>G. flaviantennatus</i> )	5-10 (13-22)	15-30 (46-61)	6-11	8-11	2-17	14-25	+	+	moderate	+	15-20 (8-10)

comparatively weak, limited to very few species of host plants, forming generally only leaf rolls. In Tubulifera the gall-forming trait is much stronger not only involving a larger number of better adapted species but also showing a remarkable host specificity culminating in closely related species forming galls on closely related plants. Undoubtedly, the existence of thrips galls on a range of host plants starting from the ferns through Gymnosperms to Angiosperms presents an extremely complex picture.

The process of gall formation is, therefore, the climax stage in the insect-host plant relationships, as this principally involves a highly specialised host preference and selection on the part of the insect, and an interesting response including a number of adaptive phenomena on the part of the host plant. As visualised by Dethier (1970)

although the relationship could have arisen as a consequence of the interaction of two independently mutating systems involving a tremendous diversity in the association patterns, the insect-host plant association with special reference to gall formation still remains an enigma. As Southwood (1968) has well pointed out the mutations are of course, independent, but ecologically the two systems are interlinked and, as is frequent in the evolution of interactions between organisms, 'contest evolves to compromise'. This, in the galling phenomenon, appears significantly so.

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