

On the developmental morphology of the rosette galls of *Acacia leucophloea* Willd., (Mimosaceae) induced by *Thilakothrips babuli* Ramk. (Thysanoptera: Insecta)

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MS received 14 March 1983; revised 30 July 1983

Abstract. *Thilakothrips babuli* induces rosette (artichoke) galls on the axillary buds of *Acacia leucophloea*. As a result of feeding by the building populations of thrips, axillary shoot meristems are destroyed, and primordial palisade tissues of the leaflets and cortical tissues of the shoot axis are transformed into nutritive cells of specialised morphology. Very similar to the galls induced by mites, midges, chalcids, and chloropids, *Thilakothrips*-induced *Acacia* galls also have a characteristic morphology, involving the inhibition of elongation of the shoot axis and crowding of maldeveloped leaflets. While describing the cecidogenesis in relation to the biology of the gall maker, an attempt has been made to discuss the morphological convergence among shoot apex galls.

Keywords. Thrips; *Acacia leucophloea*; *Thilakothrips babuli*; Rosette galls; developmental morphology.

1. Introduction

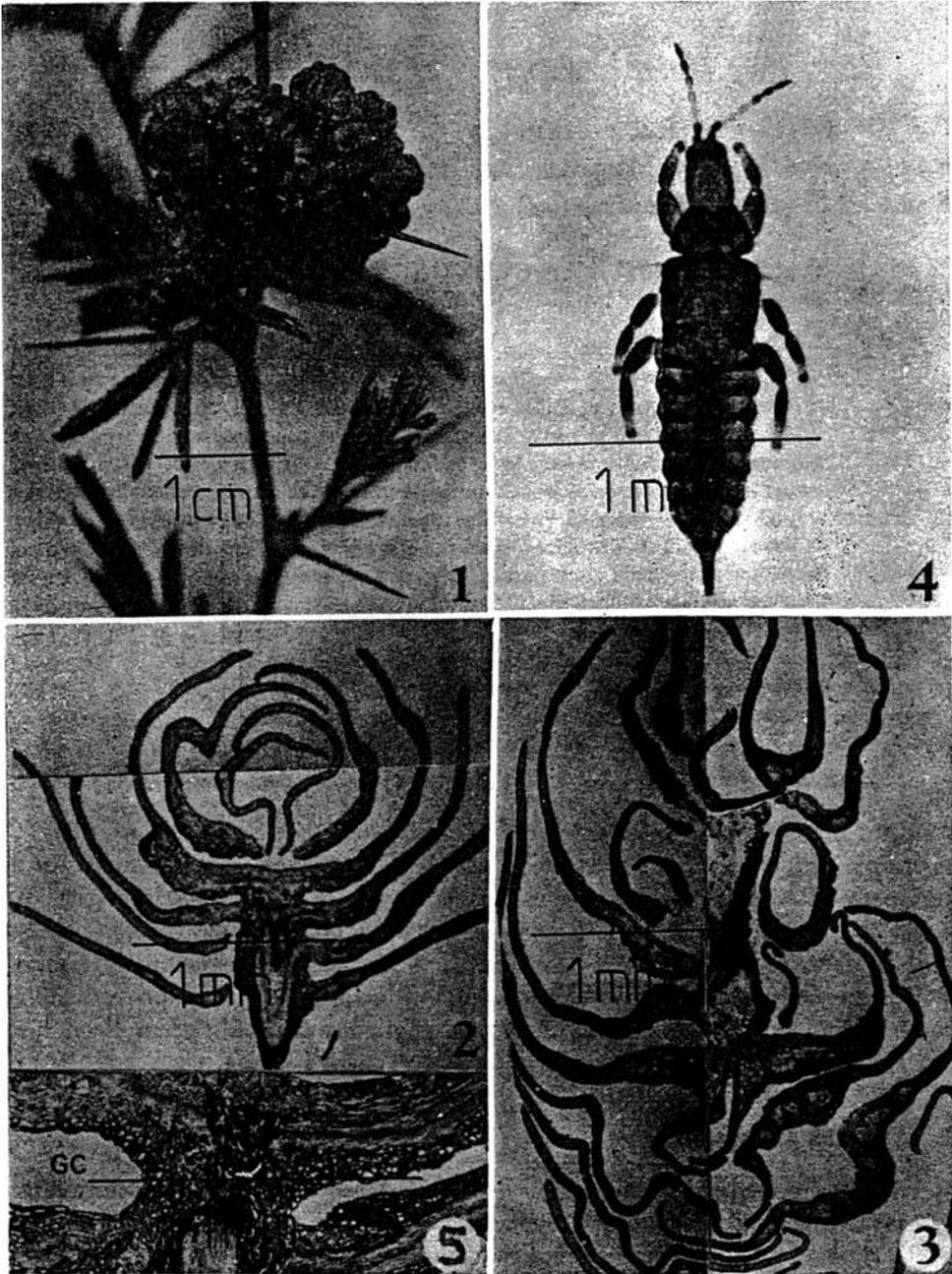
Cecidogenous thrips — *Acacia* association appears striking since more than 30 species of thrips are known to induce galls of diverse morphological patterns on a number of species of *Acacia* in Australia (Mound 1971; Ananthakrishnan 1978). From the Indian subcontinent, Ramakrishna (1928) reported bud galls, known as rosette galls, on *Acacia leucophloea* induced by *Thilakothrips babuli*. *Thilakothrips*-induced *Acacia* galls are unique as bud galls (figure 1) involving rachis, leaflets and portions of the shoot system (figures 2-3) as different from the common leaf galls of Thysanoptera (Ananthakrishnan 1980).

2. Material and methods

Normal and galled shoots of *Acacia leucophloea* were fixed in FAA (formalin; glacial acetic acid; ethanol). Depending upon their relative dimensions and approximate population count supplements, the FAA-fixed galls were graded into various developmental stages and processed through customary methods of dehydration and embedding in wax. Serial sections (6-10 μ m) were stained with safranin-methylene blue and safranin-fast green combinations.

3. Biology of *Thilakothrips babuli*

With the production of new shoots in *Acacia leucophloea* during late April or early May, a few diapausing apterous adults of the preceding generation migrate and

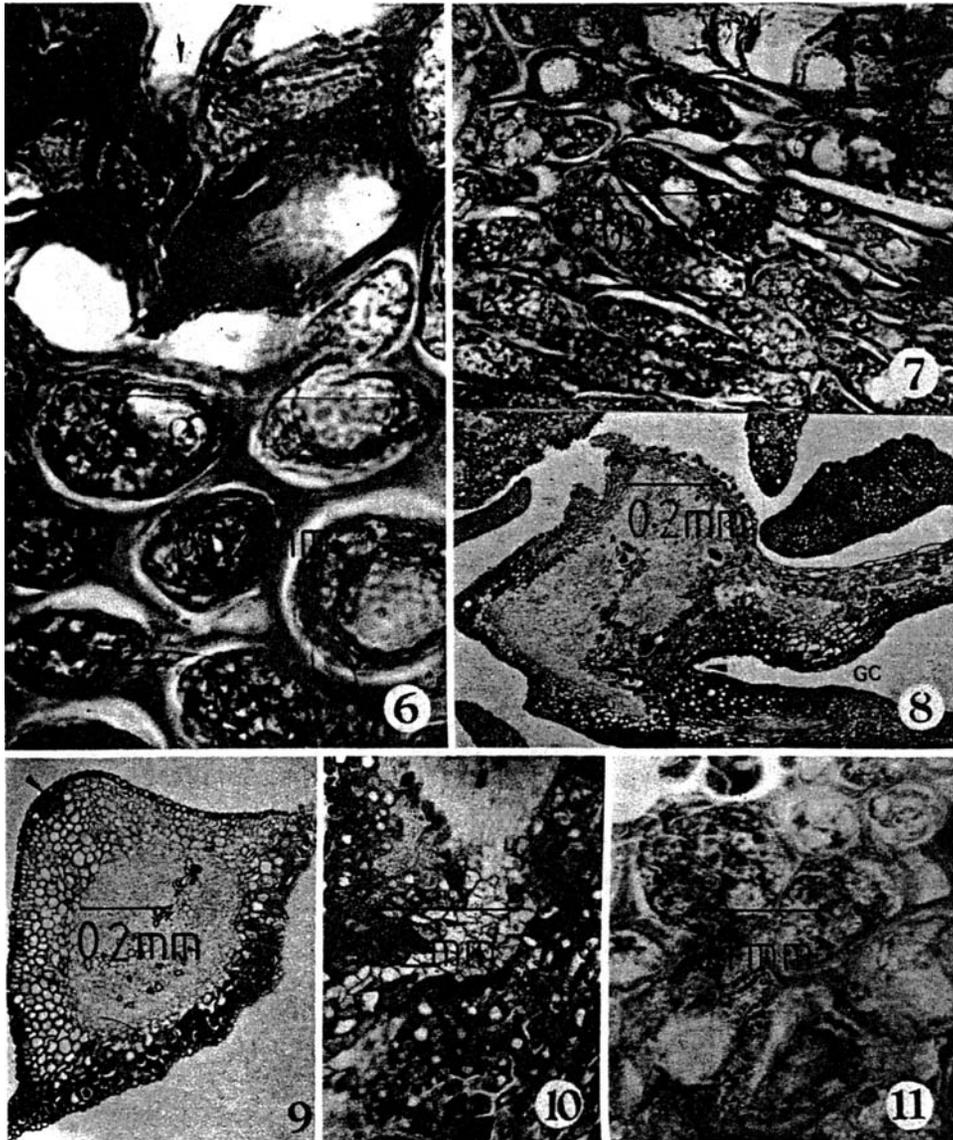


Figures 1-5. 1. Gall of *Acacia leucophloea*. 2. Mature gall in LS. 3. TS mature gall. 4. *Thilakothrips babuli* (♀). 5. LS young gall (GC - Gall chamber).

inhabit the developing buds. As a result of continuous feeding, the developing buds are galled and gall-development is directly proportional to the building-up of the *Thilakothrips* population. *T. babuli* is highly seasonal and induces galls over a period of 45 days, particularly during the summer months, May and June. Gravid females of *T. babuli* (figure 4) lay 25-34 eggs; the larvae emerge out and become adults in 22 days. The emergence of adults from the 2nd pupae coincides with the formation of young foliar primordia of the host-plant. As with all the gall-formers (Mani 1964) the period of emergence of adults coincides with the optimum range of host development which in turn underlines the basic necessity of the host tissue for the development and oviposition of the gall-maker (Varadarasan and Anantha-krishnan 1981).

4. Developmental morphology of the gall

As a result of the feeding damage (figures 5,11) by a few gravid females migrating from the hibernation sites, gall development commences, ultimately ending in a rosette gall with a highly telescoped main axis and a number of elongated, widened, and thickened (in varying degrees) leaflets. With an increase in number, thrips not only inhabit the apical region of the stem but also spaces between the leaflets. Invariably the apical region of the axillary shoot is completely destroyed by the feeding of thrips. Consequently a characteristic nutritive zone develops both in the superficial layers of the leaflets and in the outer cortical regions of the stem. In leaflets, the feeding is invariably restricted to the adaxial side and this stimulates the palisade cells to divide periclinally, contributing to the thickness of the gall-leaflets (figure 8 — arrow). The epidermal cells and the palisade undergo hyperplasy as well as lateral stretching, facilitating the elongation of gall-leaflet (figures 12,13). The resultant cells constitute the compactly arranged nutritive zone with prominent nuclei and dense cytoplasm (figure 6). With the maturing of the leaflets, concurrent with the development of the gall, the nutritive cells show two different profiles depending on their location. When the cells are closer to the midrib region, they are very large, almost isodiametric, and are characterised by prominent cytoplasm and nuclei (figure 6). On the other hand, the nutritive cells that occur along the extended laminar regions appear greatly stretched along the radial axis and contain some golden-yellow amorphous inclusions (figure 7). In general, the modifications in the morphology of the leaflets are profound, when compared with the normal leaflet (figure 14) the leaflets are elongated in different axes: (i) elongated laterally without any pronounced central thickening (figure 16), (ii) elongated laterally to a moderate degree but thickened to a very great extent in the midrib region, also showing extensive vascular hypertrophy (figure 17), (iii) elongated along only one of the laminar halves to a profound degree (figure 15), (iv) elongated along both the laminar halves displaying a prominent fold (figure 18), and (v) elongated and thickened to a great extent without any folding (figure 19). Whereas these are the general patterns of morphological variations in the leaflets constituting the gall, different grades of thickening have also been observed within a single gall, depending on the position of the leaflet. During gall development the youngest leaflet closer to the axillary shoot apex shows greater thickening as well as an increase in tannin content along

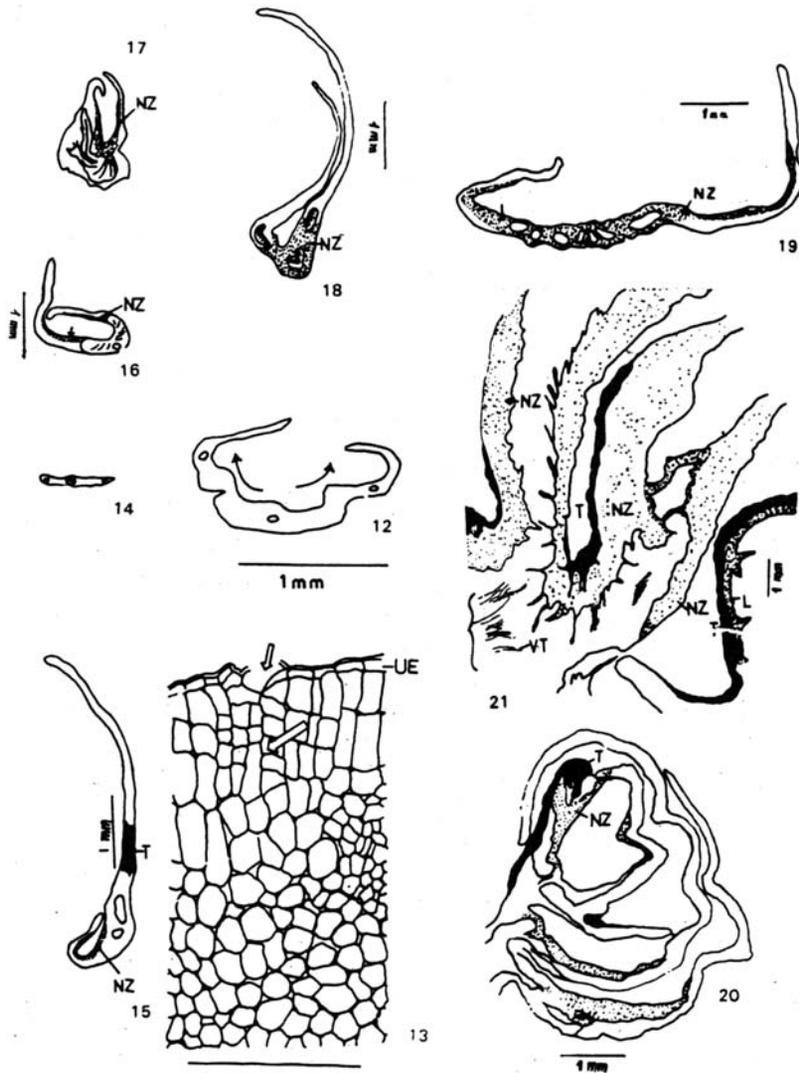


Figures 6-11. 6. TS young gall leaflet (feeding injury - arrow). 7. Nutritive cells — (midrib zone) in a young gall leaflet TS (nutritive cells — laminar zone). 8. TS young gall leaflet (GC — Gall chamber; arrow — nutritive cells). 9. Young gall stem in TS (arrow — feeding site; Darker cells — Tanniferous cells). 10. Young gall stem in TS (arrow — hyperplasy of cortical cells). 11. TS young stem (nutritive cells).

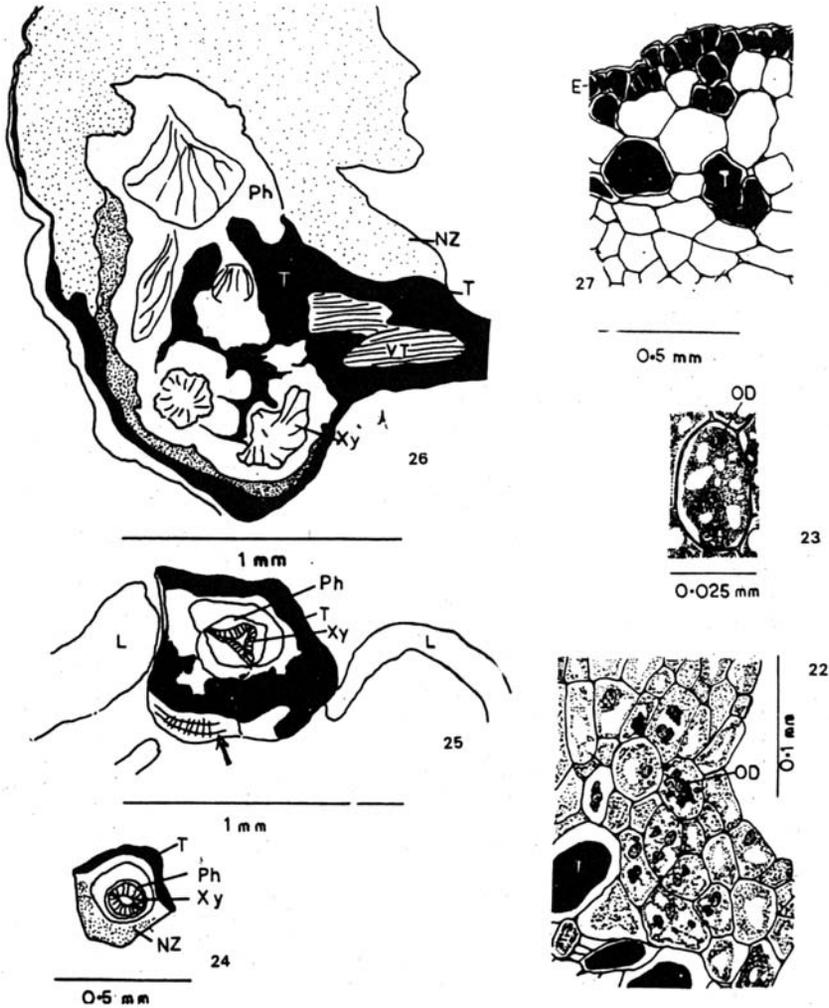
the abaxial epidermis and mesophyll; the thickening gradually gets reduced from the innermost leaflet to the outer one, although elongation is profound in the leaflets away from the shoot apical region (figure 20). Oblique sections of galls show peculiar fusion patterns of leaflets, thus establishing a 'closed' gall system (figure 20), a phenomenon rather unusual among the thrips galls. Leaflets occurring at these sites invariably show development and organization of nutritive

cells of the morphology described earlier. Tannin accumulates in cells in which thrips no longer feed (figure 21).

The infected regions of the main stem show hypertrophy and hyperplasy of the cortical cells (figures 9,11 — arrow). As a result of feeding of thrips, the epidermal and the subjacent layers of the cortex become differentiated into nutritive cells which show large nuclei, dense cytoplasm, and groups of oil droplets (figures 22,23). The cortical cells contribute to the bulk of the galled stem by repeated divisions (figure 10). On account of the proliferation of the interxylary parenchyma (figures 24-26) and phloem, the vascular cylinder becomes disrupted into



Figures 12-21. 12. Young gall leaflet in TS (arrow — inrolling of lamina). 13. Young gall leaflet in TS (arrows — injury and proliferation of the palisade zone). 14. TS mature normal leaflet. 15-19. Gall leaflets in TS (T — tanniferous zone; VB — Hypertrophied Vascular Bundle). 20. Mature gall in LS (oblique section). 21. Mature gall in LS (accumulation of tannin in old non-functional nutritive zone).



Figures 22-27. 22. Cortical region of gall stem in TS (nutritive cells). 23. A cell enlarged from figure 22 to show abundant cytoplasm and vacuoles. 24. Young gall stem in TS. 25. Mature gall stem TS (arrow — meristematic activity). 26. Old gall stem TS. 27. Cortical region of old gall stem TS (E — Epidermis; T — Tannin).

Abbreviations: OD — oil droplets; NZ — nutritive zone; Ph — phloem; T — tanniferous cells; Xy — xylem; VT — vascular trace; E — epidermis.

numerous isolated strands. The old stem-gall areas show abundant accumulation of tannin which permeate through the central core of the stem (figure 27).

Accumulation of tannin is yet another interesting feature in these galls, which is frequent in normal tissues of *Acacia* spp. as well. Curiously in the gall-tissues, however, tannin accumulates in the regions where thrips have ceased to feed. This aspect is more clearly evident in the stem regions of the gall (figures 26, 27). In the young stems, with the organization of the nutritive zone, the tanniniferous zone develops on the opposite side (figure 24). Whether tannin production is inhibited in the nutritive area or occurs in regions where thrips do not feed as a result of the organization of the nutritive zone, is not clear.

Cecidogenesis in *Acacia* galls involves the inhibition of histogenesis, especially in the leaflets and to a moderate extent in the stem regions and the subsequent hypertrophy and hyperplasy. Whereas the shoot apex becomes destroyed, the continued feeding of thrips affects the leaflets occurring beneath; it also inhibits the growth of the shoot axis which naturally results in the telescoped nature of the stem.

5. Discussion

By virtue of being formed on the axillary vegetative buds, *Acacia leucophloea* galls differ significantly from the other *Acacia* galls known to be formed on the phyllodes as large pouches (Mound 1971). By their number, mode of nutrition, and the life-cycle pattern well-synchronised with the developmental phase of the host-plant, *Thilakothrips* affect the axillary shoot meristems, and eventually the normal growth and organogenesis of the host-shoots. This is similar to the cecidogenetic influence of mites such as *Cecidophyopsis psilapsis* (Nal.) Keiffer, *C. ribis* Westw., *Phytophus avellanae* (Nal.), and *Aceria thomasi* (Nal.) inducing artichoke galls on the shoot apices of *Taxus baccata* L., *Ribes nigrum* L., *Corylus avellana* L., and *Thymus serpyllus* respectively (Dreger-Jauffret 1977). Leaflets of *Acacia* galls, examined here, show different degrees of maldevelopment possibly because the affected organ is a bud with foliar primordia in different stages of development. Besides the tendency to form 'closed' gall-systems, patterns of modifications in the leaflets with a number of intergrades from simple crinkles to folds and rolls, are indeed impressive. Variations in the leaflets of the gall-shoot pertain not only to size, but also to morphological elaboration in terms of the regenerative capacity and the inherent growth potential. This is well substantiated by the more-active growth centres in the foliar areas than in the axis areas, the latter showing inhibition of elongation.

The general morphogenetic pattern in these thrips-induced *Acacia* galls conforms to that of the bud-galls induced not only by mites (Westphal 1977; Dreger-Jauffret 1977), but by cecidomyiids (Jauffret *et al* 1970), cynipids, chloropids, and chalcids (Dreger-Jauffret 1977) as well, showing identical telescoping effect of the shoot axis. This is probably because of the destruction of the shoot apical meristem during early or late stage of gall-development. Besides, more than one gall maker is involved in cecidogenesis, requiring the organization of specialised nutritive tissue. Probably, a functional compromise is achieved among the destruction of the apical meristem, the organization of nutritive cells all over the gall region, and the normal organogenetic effort of the host in order to contribute to the rosette form of the gall.

Curiously, the galls formed on the shoot apices of diverse host plants display almost identical gall-forms, in spite of being induced by cecidozoa of different orders, indicating a morphological convergence. This is specially significant since galls formed on other plant organs such as leaf, stem, etc., by cecidozoa of the same order are generally significantly different morphologically (Westphal 1977; Meyer 1969).

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