Proc. Indian Acad. Sci., Vol. 88 B, Part II, Number 2. March 1979, pp. 103–107,

On the developmental morphology of the leaf fold galls of *Maytenus senegalensis* (Lam) Excell., (Celastraceae), induced by *Alocothrips hadrocerus* (Karny) (Thysanoptera: Insecta)

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MS received 20 June 1978

Abstract. The galls of *Maytenus senegalensis* (= *Gymnosporia heyneana* Lawson) induced by *Alocothrips hadrocerus* are histologically unique when compared with the other thrips galls. Principal cecidogenetic phenomena are hypertrophy and hyperplasia. The incidence of tannin containing as well as sclerenchymatous cells, and the epidermal proliferation are discussed in relation to gall development.

Keywords. *Maytenus senegalensis*; *Alocothrips hadrocerus*; hypertrophy; hyperplasia; tannin cells and sclereids.

1. Introduction

Ananthakrishnan and Jagadish (1969) have reported the leaf galls of *Maytenus senegalensis* (= *Gymnosporia heyneana* Lawson) induced by *Alocothrips hadrocerus*. As only brief descriptions of external morphology are available (Mani 1973; Ananthakrishnan 1978), a more critical assessment of gall formation has been attempted with the availability of various developmental stages.

2. Materials and methods

Normal and galled leaves were collected from Thenmalai Hills (800–1,000 m), Kerala State, and were fixed in FAA. They were processed through the customary methods of dehydration and embedding. The sections (12–15 μm) were stained with safranin and methylene blue.

3. Observations

The young differentiating leaves of *Maytenus*, as a result of the feeding injury by *Alocothrips*, show periclinal divisions in the cells of the primordial palisade tissue. The primordial spongy mesophyll cells occurring close to the abaxial epidermis are peculiarly hypertrophied and are stretched along the periclinal axis. These activities contribute in a general way to the inward folding of the laminar margin. Tannin containing cells occur in abundance during the initial stages of cecidogenesis (figure 1). Owing to further proliferation the primordial palisade cells lose their morphological identity and give rise to 5 or 6 layers of closely arranged parenchymatous cells of varied dimensions constituting the feeding zone* close to the gall chamber harbouring the insects. The spongy mesophyll cells, on the other hand, undergo hypertrophy resulting in cells of enormous size with large nuclei. At this stage, the adaxial epidermal cells exhibit meristematic activity showing periclinal divisions, thus adding to the thickness of the gall (figure 2), — a phenomenon also known in the thrips galls on the leaflets of *Vitis lanceolaria* (Karny *et al* 1913). The normal, dorsiventrally differentiated, mature leaves of *Maytenus* show in transverse sections one layer of short palisade cells and 8–10 layers of spongy cells with large air spaces and sparsely distributed tannin containing cells (figure 3). Mature galls show a great increase in the number of the constituent cell layers with the cells being very closely arranged. Further, the cells are greatly enlarged due to cellular hypertrophy and are filled with dense tannin contents. Following the few layers of parenchyma bordering the gall (insect) chamber, a thick band of sclerenchyma occurs which is made up of sclereids with very thick secondary walls and simple

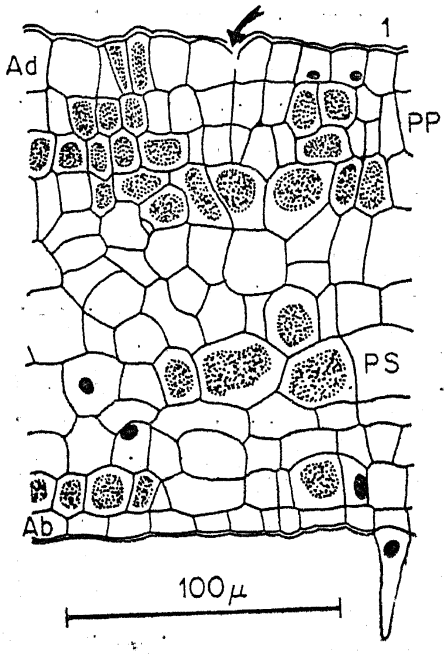


Figure 1. Portion of a differentiating leaf showing the feeding injury by thrips (arrow) (stippled areas indicate tannin). (For legends see caption for figure 5.)

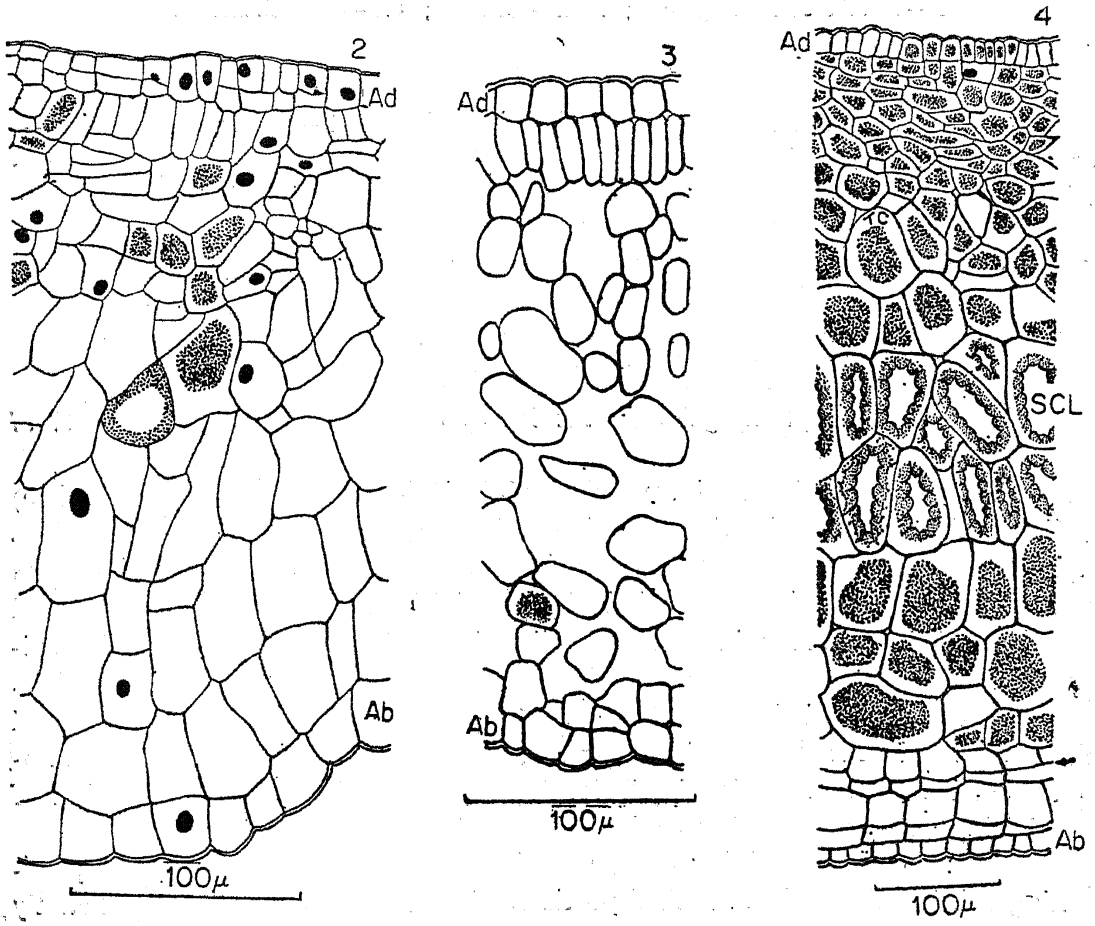
* The gross morphology of this region suggests that it could be the 'nutritive zone' (Meyer 1969). However, cytological confirmation is needed.

pits. The few layers following the sclereid band are also tanniniferous. At such a late stage of gall development, one or two layers of parenchyma adjoining the abaxial epidermis become meristematic, so that, through periclinal divisions they add cells to the thickness of the gall (figure 4).

4. Discussion

Gall development in *Maytenus* involves: (i) marginal infolding, (ii) stretching of the folded region, (iii) thickening of the gall-lamina, and (iv) maturation. Maturation is characterised by abundance of tannin containing cells and development of a sclereid band (figures 5a–d). The principal cecidogenetic phenomena are hypertrophy and hyperplasia.

Karny *et al* (1913) have shown that the process of development among thrips galls in general envisages inhibition of normal histogenesis of the (affected) organ, and cellular hypertrophy, while the adaptive phenomena are significantly absent. In the galls of *Maytenus*, hypoplasy is manifested to a lesser magnitude as in the thrips galls of *Casearia* (Raman *et al* 1978), since the gall initiation occurs at a stage when the mesophyll is differentiated into primordial palisade and spongy



Figures 2–4. 2. Portion of a developing gall showing epidermal proliferation and hypertrophy of the mesophyll cells. **3.** Portion of the mature normal leaf. **4.** Portion of the mature gall. (Stippled areas indicate tannin) (arrow shows meristematic activity). **(For legends see caption for figure 5).**

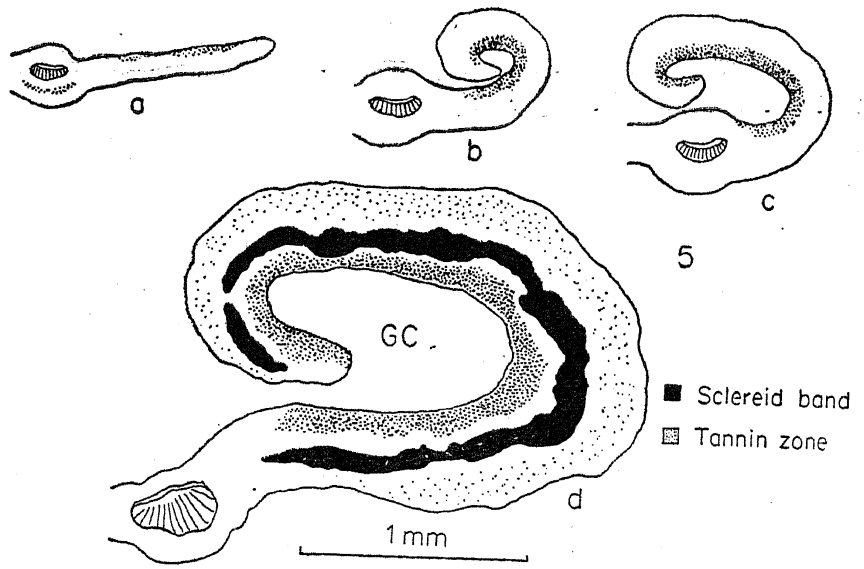


Figure 5 a–d: Gall development in *Maytenus*. (Ab—Abaxial epidermis; Ad—Adaxial epidermis; PP—Primordial palisade cells; PS—Primordial spongy cells; TC—Tannin containing cells; SCL—Sclereids; GC—Gall chamber).

tissue regions, although the final phase of leaf development — laminar expansion — is yet to occur. Analysing the overall picture of gall structure among thysanoptero-cecidia, and the leaf fold/roll gall types in particular (Ananthakrishnan 1978), the galls of *Maytenus* are unique in their histological organization in that they display adaptive differentiation of newer tissue types. The incidence of a sclereid band indicates it to be a feature of distinction (Ananthakrishnan and Raman 1977), since such a histological condition is absent in the other galls induced by Tubulifera (Thysanoptera), although occurrence of sclereids had been known in the terebrantian (Thysanoptera) galls on the leaves of *Cordia* (Krishnamurthy *et al* 1977).

Tran Thanh Van *et al* (1974) have confirmed the incidence of cell divisions (in vi*ro) in differentiated superficial tissues (epidermal and sub-epidermal cells) of various angiosperms. They have shown the existence of a number of division centres regulating the predominantly anticlinal cell division patterns in the epidermal systems of (i) individual epidermal cells, (ii) epidermal cell groups, and (iii) epidermis as a whole. In the adaxial epidermal cells of *Maytenus* galls, cell divisions are predominantly periclinal, yet follow the same regulatory processes in individual cell levels and in the levels of cell groups; but perhaps due to the partial autonomy* envisaged as a result of gall development, the third level of regulation of cell divisions at the level of the epidermis-as-a-whole is however lacking.

Abundant tannin containing cells, sclereids of distinct morphology and proliferating epidermal cells in the galled portions of the lamina — differing significantly

* The reorientation of normal morphogenetic potentialities, *with limitations*, as manifested during the galling process.

from the normal leaf structure — establish that the influence of the cecidozoa is able to relieve the differentiating mesophyll cells from the correlative/inhibitory phenomena of normal histogenesis.

Acknowledgement

Thanks are due to the University Grants Commission for the award of a research grant.

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