Morphology, anatomy and development of the midrib galls on the leaflets of *Lannea coramandelica* (Hoult.) Merrill (Anacardiaceae) caused by *Odinadiplosis odinae* Mani (Diptera)

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Abstract. A midge, *Odinadiplosis odinae* Mani induces galls along the midribs of the leaflets of *Lannea coramandelica* (Hoult.) Merr. (=*Odina wodier* Roxb.). Gall initiation takes place at a very early stage of leaf development, incited by the larvae from the superficially deposited eggs, migrating into the leaf tissue. Bulk of the gall is formed by the proliferation of the interfascicular or parenchymatous ground tissue. Vascular bundles occur widely separated and during the early stages of cecidogenesis, a few atypical tracheary elements appear which later develop into a very complex anastomosing network of vascular elements around the larval chamber with the maturation of the gall. The functional nutritive zone becomes sclerenchymatous with the ageing of the gall.

Keywords. *Odinadiplosis odinae*; *Lannea coramandelica*; midrib galls; Anacardiaceae.

1. Introduction

*Odinadiplosis odinae* Mani (Diptera) has been known to induce galls on the midrib and lateral veins (figure 1) of the leaflets of *Lannea coramandelica* (Hoult.) Merr., (Anacardiaceae) a large tree widely distributed in India (Mani 1948; 1959; 1973). Since various stages of development of the galls were available, an attempt was made to study some aspects of morphology and the process of cecidogenesis.

2. Materials and methods

Galls, in various stages of development, were collected locally and fixed in FAA. Serial sections were cut at 12-15\(\mu\) thickness, after customary methods of dehydration and embedding, and were stained with tannic acid—iron chloride—safranin and tannic acid—iron chloride—haematoxylin combinations. Xylem elements were macerated with Jeffrey’s fluid and were stained with toluidine blue.

3. Observations

Small pores 35-40\(\mu\) wide, generally along the adaxial, occasionally on the abaxial side of the midrib of tender foliage indicate early stages of gall initiation.
maturation, the gall assumes a gradual elliptic-ovate outline, usually spreading along the longer axis of the midrib or the lateral vein (figure 1). Mature galls are large (1 cm × 0.9 cm) attaining more or less a globular shape. The gall is indehiscent, hard, with a coryck surface cracking irregularly and exposing dark brownish cortical tissue (figure 2).

Midribs of the unaffected leaflets show (figure 6) in transverse sections 5-9 collateral vascular bundles arranged more or less in a circle, each bundle being externally flanked by a resin canal. Mature midrib regions along the adaxial side show a centrally elevated collenchymatous region, gradually invading the laminar mesophyll on either side. The abaxial side is bordered by 2 or 3 layers of collenchyma, while the rest of the cortex is filled with thin-walled parenchyma cells. Crystalline inclusions occur in a few outer cortical collenchymatous cells and in a few phloem elements. The epidermal cells are tanniniferous and sparsely distributed. Branched or unbranched trichomes are also present.

Transverse sections of mature galls which are circular in outline show a large central larval cavity, bordered by remnants of once functional nutritive parenchymatous

Figures 1-3. 1. A leaflet, galls on petiolule, midrib and lateral veins. 2. Same, galls on midrib, gall surface corky. 3. T.S. mature gall, a portion of the peripheral region, cameral cells.
Figures 4-5. 4. same, a portion, vascular network around larval chamber, and nutritive zone. 5. same, atypical tracheary elements. (LC—larval chamber, NZ—nutritive zone).
zone. Although these cells appear degenerated, they are distinctly arranged in regular radiating files. Encircling the nutritive zone there is a thick band of scelerenchyma; the constituent sclereids being of different sizes and shapes, varying in wall thickness and occasionally with completely obliterated lumen. External to this larval chamber is the 25-30 cells thick parenchymatous zone of hypertrophied, hyperplasied and tannin containing cells. Tanniniferous cells are abundant especially along the peripheral regions of the gall (figure 3). Resin canals appear reduced in size owing to the extraordinary growth at the outer regions. They are sometimes completely obliterated. Vascular bundles are widely separated and scattered all round the periphery of the gall. Curiously short, or sometimes squat atypical tracheary elements are seen establishing a network (figures 4, 5) around the larval chamber making direct or indirect vascular connections with the isolated vascular bundles of the galled midrib. These elements show annular wall thickening. The perforation may occur either at both or at one of the terminals along the tangential wall or may be totally absent. Pore size varies considerably with the size of the xylem element. It has been observed that these atypical tracheary elements originate from parenchymatous cells of the ground tissue located between the vascular bundles. These cells distinctly possess large nuclei and dense cytoplasm, which later degenerate and the cells develop annular wall thickening.

The initial stages of infection occur at an early stage of leaf differentiation. The larvae that hatch from the eggs deposited on juvenile leaflets gnaw into the plant tissue (figures 7, 8). Some of the cells bordering the larval path turn necrotic while certain other cells show meristematic activity due to the stimulus of wounding (figures 9, 10). The larvae seem to settle down either in the central parenchymatous region or in the outer parenchymatous region (figure 11) or sometimes in the lateral laminar region adjoining the midrib. This feature is followed by the meristematic activity in the cells around the feeding larva, evidenced by periclinal divisions around the larval cavity. These cells stain densely and are prominently nucleated, which later establish the nutritive zone (figure 13). When the larva is situated at the central parenchymatous region, cells of the interfascicular parenchyma undergo similar differentiation to establish the nutritive zone. The larval path is invariably closed by the newly differentiated parenchyma. At this stage of gall development, large, densely cytoplasmic parenchymatous cells of the ground tissue show newly differentiating atypical tracheary elements, occurring between the already present vascular bundles of the midrib. After the establishment of the 13-15 cells thick nutritive region, growth is uniform all round the larval chamber, resulting in a more or less globular gall with a circular outline in transections (figure 14). Mature gall, immediately around the functional nutritive zone encircling the larva, a narrow band of sclereids which becomes broader, with the degeneration of the cells of the nutritive zone has been observed.

4. Discussion

Galls are initiated at an early stage of ontogeny of the leaflet of Lannea in conformity with the situation occurring in many other midge galls (Mani 1965), establishing a centrally placed larval cavity surrounded by the nutritive zone, ensheathed by a sclerenchymatous band. Various developmental stages and mature gall structure
indicate an involvement and proliferation of the interfascicular parenchyma or the central parenchyma cells in forming the bulk of the gall — a phenomenon frequented in the galls caused by midges (Arnold 1966a; 1966b), by moths (Arnold 1966c) and by weevils (Krishnamurthy et al 1977).

Occurrence of atypical tracheary elements has been reported in bacterial gall cultures (Spurr et al 1964), galls caused by fungi (Akai 1951) and nematodes (Swamy and Krishnamurthy 1971). Morphologically and developmentally these atypical elements resemble the tracheary elements differentiating after wounding — designated as woundvessel elements (Roberts and Fosket 1962). These wound vessel elements are supposed to be redifferentiating from previously mature parenchyma cells in response to a new stimulus, while the xylem differentiating in the normal plant organ is the culmination of procambial development. Atypical tracheary elements of *Lannea* galls also exhibit many characteristics in conformity with the observations of Roberts and Fosket (1962), the initiation probably taking place with the larval entry, further triggered by the continued feeding stimulus of the inhabiting larva. This fact is supported by our observations of these elements, that initially occur only in close proximity to the larval path and in mature galls extend all round the larval chamber in a very uniform manner.

Vascular irrigation of the gall, very distinct in the galls of *Lannea* by the develop-
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ment of an anastomosing network of tracheary elements around the larval chamber indicates its vascularization pattern. Elements of vascular tissue differentiate in a centripetal manner towards the centrally located larval chamber. The complexity in the vascular irrigation may be due to the location of the gall along the veins, where normally more of vascular tissue occurs. In the galls of Salix, Loux and Meyer (1965) have shown similar instances of anastomosing radially oriented vascular traces, while in the leaf galls of Aeschynanthus (Krishnamurthy and Raman 1972) the galls which are restricted to the laminar regions such a vascular complexity is absent. Further, similarity occurs with reference to the ontogeny of the newly developing tracheary elements between the widely separated vascular bundles, in the galls of Lannea and Salix (Loux and Meyer 1965) where the tracheary elements differentiate much earlier to the development of the sclerenchymatous zone around the larval cavity.

With the development of abundant tannin containing cells and sclereids, galls of Lannea also show a common phase of resistance, and the increase in phenol derivatives may be due to the entry and feeding by the larva as shown by Miles (1968).

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