Morphological and anatomical studies of the floral gall of
Pongamia glabra Vent. Fabaceae (= Papilionaceae)

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Abstract. The morphological and anatomical studies of the floral galls of Pongamia glabra reveal the involvement of the entire floral primordia, telescoping of the internodes of the peduncle resulting in the agglomeration of galls, morphogenetic phenomena of hypertrophy, hyperplasia, dedifferentiation and redifferentiation, lack of polarity of certain cells and tissues as shown by the concentric, plicate and reticulate types of arrangement of vessels of the reaction xylem, development of irrigating strands and sclerosed cells towards the larval cavities and formation of crystals and tanniniferous idioblasts. The nutritive tissue around the larval cavity is rich in starch grains. The short vessels of the normal and reaction xylem with simple porous perforations and minute alternate lateral wall pittings indicate an advanced level of specialisation of secondary xylem, despite the modifications of the flowers due to galling.

Keywords. Pongamia glabra; floral gall; morphology; anatomy; Papilionaceae.

1. Introduction

Pongamia glabra Vent. is a taxon well-known for its susceptibility to leaf galling (Mani 1973). In the family Fabaceae, to which this taxon belongs, 90 different galls have been reported so far but most of them pertain to the leaves. In Pongamia glabra four kinds of galls caused by four different organisms have been reported. These are leaf gall caused by Eriophyes cheriani Masse., ovary gall by Asphondylia pongamiae Felt, stem and leaf gall by Myricomyia pongamiae Mani, and stem gall by an unknown Agromyzidae (Diptera). Whereas all the four galls have been reported on this taxon from south India, only the mite gall on the leaf has been recorded from north India and from Sumatra and Java (Mani 1973).

The present study concerns the morphology and anatomy of a hitherto unreported new type of floral gall of Pongamia glabra caused by an unidentified dipteran.

2. Materials and methods

The materials were collected and fixed at Mayuram, Thanjavur district, Tamil Nadu, south India in January 1968. Sections were cut at thickness of 10–12 μm
using sledge and rotary microtomes. Following the customary methods of dehydration, infiltration, embedding and sectioning (Johansen 1940), two sets of slides were prepared using safranin-aniline blue, and safranin–fast green and the third set using only toluidine blue. The materials were also macerated using Jeffrey's reagent and stained with safranin (Johansen 1940). Unstained sections were examined in polarised light to detect the presence of crystalline bodies.

3. Observation

3.1. Morphology of the galls

The mature floral galls of *Pongamia glabra* are spherical, solid, ligneous, sessile, indehiscent, greyish to greyish green up to 2 cm in diameter and occurring more or less in compact irregular whorls on the peduncle. On account of fusion with the adjacent ones, they appear as lobed masses (figure 1). In the absence of any indication of either sears or remnants of floral parts on the surface of these galls, it is presumed that this kind of gall seems to represent the involvement and modification of the entire floral primordia themselves. Sometimes proliferation of the affected floral primordia brings about stalked condition and superposed arrangement of the galls (figure 1) and also the formation of obtusely conical sessile bodies which are directly seated upon the parent galls (figures 1, 3). The internodal regions of the peduncles may also become telescoped with the result the galls assume an ultimately crowded and congested disposition. It is interesting to observe that at the time of collecting the galls, the entire tree was seen to bear only galled inflorescences with the result no normal flower was encountered.

3.2. Anatomy of the gall

A solitary mature gall in longsections and transections appears more or less circular in outline. Its periphery is constituted by 3–4 phelloid layers (figures 4 A–I, 16). The cortex is narrow and consists of parenchyma; it is delimited internally by a narrow discontinuous zone of nearly isodiamic and/or slightly elongated sclereids. Between this sclereid zone and the inner zone of vascular tissues, there is a relatively broad parenchymatous zone. The pith is broad and is composed of isodiamic parenchyma cells. The xylem occurs as a prominent continuous band except for the gaps which might have been caused perhaps by the entry of the larvae towards the pith. Each gall has 1–7 larval cavities. Although these are usually restricted to the pith region, they do sometimes occur within or outside the vascular region. Each larval cavity irrespective of its location is surrounded by a zone of 15–20 layers of parenchyma cells which constitute the nutritive tissue. In addition the larval cavities that are located within the xylary region possess one or several layers of sclerosed cells to form the crescentiform structure (figures 4 G–I, 13). But in larval cavities developing within the non-vascular region such internal sclerosed layers are totally absent (figure 4 J).

The xylary tissues of the mature galls are not only secondary in origin but represent a combination of both normal and reaction tissues. The latter can be readily distinguished from the former by their mode of development and different patterns of arrangement. The reaction xylem is associated with and develops
Figures 1-2. 1. Agglomerate floral galls on peduncles of *Pongamia glabra* Vent. (× 1/5 natural size). 2. Surface macerated galls showing the orientation of xylary tissues in the subsurface region and the location of larval cavities (LC) with larva. P-peduncle.
consequent upon the cecidozoan influence. The components of the normal secondary xylem are vertically arranged whereas those of the reaction xylem (present in the intervening regions of the normal secondary xylem) are oriented at right angles to the former revealing a tangentially storeyed arrangement of the vessels (figure 6). Likewise the vessels of the normal secondary xylem are also storeyed. Furthermore, the vessels and imperforate tracheary tissues of the reaction xylem present outside the xylary regions exhibit a variety of interesting patterns of arrangement. Of these, three major types namely, concentric, plicate and reticulate types appear to be worthy of consideration. In the concentric type—the vessels are arranged in variable number of concentric layers (figure 8) resembling the previously reported “tracheary knots” (Stewart 1914), “woody nodules or burrs” (Butler and Jones 1949), “whirlpool” (Akai 1950) and “whorls” (Littau and Black 1952). In the plicate type, the arrangement of vessels reveals regular, sharply crested wave-like appearance (figure 9). In the reticulate type, the vessels are loosely and variously arranged forming an anastomosing system (figure 10).

The three kinds of arrangement of vessels observed in the reaction xylem of the extraxylary region are an unique feature in the present material. Thus, on the basis of these observations it is quite possible to distinguish the vessels of normal secondary xylem with a vertical alignment from those of reaction xylem characterized by their concentric, plicate, reticulate and other kinds of transitional patterns of arrangement. The vessels of normal xylem are all vertically oriented throughout but appear to assume different kinds of arrangement similar to those of reaction xylem in the subsurface layers of the mature gall (figure 2).

In respect of mode of development the normal secondary xylem is formed by the activity of the vascular cambium, and the reaction xylem is a product of de-
Figure 4. Serial T.S. of the gall (A-H) and a L.S.
Figures 5-7. 5. T.S. of normal peduncle showing tannin idioblasts in the phloem, xylem, and pith. 6. A portion of gall-normal secondary xylem (NSX) and reaction secondary xylem (RSX). Note tangential alignment of vessels in the latter. 7. Portion of gall-procambial strands at arrows.
differentiation of ground parenchyma as well as xylem parenchyma which is triggered by larval stimulation.

The vessels in the reaction xylem are simple porous just as those of the normal xylem, but the location of the pores in the former is predominantly subterminal or lateral (figure 11 B - d), whereas it is always terminal in the latter (figure 11 A). The lateral wall pittings are minute and alternate which in the vessels of the normal xylem, are polygonal and compactly arranged whereas in the reaction xylem, they are oval or elliptical without compact arrangement (figure 11 C, D). The vessels of the reaction xylem are longer (137 μm) and broader (37·3 μm) than those of the normal xylem (length 102 μm and breadth 33·4 μm, the values statistically tested). As far as the location of these two kinds of xyla is concerned, the normal xylem unlike the reaction xylem is situated a little away from the larval cavities and is free from the influence of the cecidogenic factor(s).

Divisions in xylem parenchyma cells followed by elongation and maturation give rise to short radial files of vessels. A part of the ground parenchyma (designated here as gall parenchyma) develops into prominent procambial strands, a part of which differentiates into vessels (figure 7) and the rest into prosenchyma cells with thick pitted walls. Thus the vessels become ultimately embedded in the prosenchyma (figure 7). The gall parenchyma which does not undergo the above mentioned developmental changes differentiates into sclerenchymatous tissue. Thus the gall parenchyma is potentially capable of developing into procambial strands, prosenchyma and sclerenchyma, but the vessels in the reaction xylem have a dual origin (from xylem parenchyma and gall parenchyma).

The strands of vessels and parenchyma of the reaction xylem thus formed in the nonvascular regions of the gall become directed towards the larval cavities despite their various contours and configurations and ultimately dip into the nutritive tissue (figure 12) by way of ploughing through the sclerotic shell surrounding the larval cavity. Such strands of the reaction xylem are comparable to the “faisceaux irrigateurs” (Loux and Meyer 1967) as the vessels in these strands can be presumed to translocate nutrients to the parasitic larva (figures 4 G, 1; 12).

3.3. Nutritive tissue

The nutritive tissue that encircles the larval cavity consists of 15–20 layers of cells (figure 13) which are small, isodiametric and conspicuously vacuolated. Cells of this tissue containing abundant starch grains are sandwiched between the larval cavity on one side and the sclerosed layers on the opposite side (figures 13, 14).

Crystals of different geometric shapes such as cubical, bipyramidal, hexagonal and rectangular occur in the cortical (figure 15) and medullary regions of the gall, but they are significantly absent in and around the larval cavities.

Tanniniferous idioblasts have been noted in abundance in phloem, secondary xylem and pith of normal peduncle (figure 5) and they are present only in the outermost phelloid layers of the gall (figure 16).

On the basis of structural and developmental characteristics two kinds of sclerosed cells are recognised. One kind of cells is found in the cortical region of the gall and is formed as a result of normal course of differentiation. They develop exceedingly thick walls marked by ramiform pits and narrow lumen.
Figure 11. Vessels from normal (A) and reaction (B₁₀) secondary xyle showing difference in size, location of perforations and lateral wall pittings of vessels in the normal (C) and reaction (D) xylem.
Figures 15-16. 15. Cortical region of gall—crystals (C) and sclereids (S) under polarized light. 16. Peripheral region of gall-pheloid layers (PL) and the cortex (C).
The second kind of sclerosed cells is characterized by slightly thickened walls with simple pits and large lumina. The latter results from redifferentiation of gall parenchyma under cecidogenic influence.

4. Discussion

Non-availability of the different stages of the floral galls of *Pongamia glabra* has precluded the possibility of studying the developmental aspects of the gall and its tissues.

As mentioned earlier the galls are presumably initiated at the primordial stage of the flower. This is quite evident from the total absence of scars and/or any rudiments of the floral parts on the surface of the gall. One visible effect of galling is the shortening of the peduncle due to the telescoping of the internodes leading ultimately to the agglomeration of the galls.

The floral galls investigated here are unique and a new type as they are a modification of the entire floral primordia and in this respect they differ from floral galls already reported in this taxon as being either stalked and derived from infected ovaries (Ayyar 1921; Mani 1959, 1964, 1973) or modifications of the thalamus (Channabasavanna 1952–53).

In the present material, multiple infection seems to be the rule which is so far unknown in the floral galls of this taxon except for an earlier report of the bilocular condition in some ovary galls caused by two larvae (Mani 1973).

Hypertrophy and hyperplasia are considered as two major processes in cecidogenesis. The latter appears to be predominant in the parenchymatous tissues in the present material. The significance of hypertrophy in causing the cell walls to become thinner thereby facilitating the movement of the substances (Strebler 1971) cannot be ignored in the present materials. In conformity with the sequence of events in cecidomorphogenesis as suggested by Hough (1953), in the floral galls of *Pongamia glabra* there seems to be in the first place dedifferentiation of the parenchyma in the affected part, particularly in the pith parenchyma, followed by hypertrophy and hyperplasia which give rise to the bulk of the gall parenchyma. This, in turn, leads to the development of different types of reaction tissues by way of dedifferentiation and redifferentiation such as the nutritive tissue, sclerotic tissue, irrigating strands and xylary tissue. As already explained, the vessels of the reaction xylem are aligned in different patterns. These observations amply substantiate Hough's (1953) conclusion that 'the gall structure is, in fact, the result of interplay of both dedifferentiation and redifferentiation of which the latter is a major phenomenon in galls'.

Lack of polarity in the orientation of the vessels of the reaction xylem seems to be another conspicuous feature in this gall. Cases of similar kind have earlier been reported both under natural and experimental conditions by Vöchting (1908), De Ropp (1950), Hough (1953), and others (further references see Sinnott 1960, Arnold (1966) and Miles (1969). De Ropp (1950) states that the crown gall bacteria acting on the meristematic cells bring about a permanent change leading to the formation of a tumor meristem which exhibits total lack of polarity. However, in insect galls Hough (1953) and Miles (1968) report that the polarity in respect of various tissues is different from that of the corresponding normal organs.
In the process of formation and subsequent ramification, the procambial strands of the present gall typically resemble the tumor meristem of the crown gall (De Ropp 1950) and also the "anarchial bundles" of the fungal tumors (Caporali 1976). Within these strands, the formation of vessels takes place on the homeo-genetic induction pattern which is analogous to the differentiation of tracheary elements in the pith of the wounded stems of Coleus (Sinnott and Bloch 1945).

The presence of starch grains in the nutritive tissue of the Pongamia gall, as in the galls induced by the cecidomyiids and cymipids indicates a high metabolic activity (Loux and Meyer 1967). The significance of a starchy nutritive tissue for the 'imprisoned' cecidozoan larva could be appreciated from the Gilmour's (1955) statement: "most of the insects cannot survive for long in the absence of a dietary supply of carbohydrates."

Although reaction xylem has been recognized and reported under pathological and certain physiological conditions by many authors in the higher vascular plants, it is unique in the floral galls of P. glabra on account of its diverse patterns of arrangement of the vessels.

The pattern of arrangement of vessels of both normal and reaction xyla is the same in the subsurface layers of the mature gall, although it differs in the remaining regions of the gall. This unusual arrangement of vessels of normal xylem in the subsurface layers is probably caused by the limited growth and curved contour of the gall. The galls resemble "wood knot or burrs" (Butler and Jones 1949) in the arrangement of tissues in general and vessels in particular.

The vessels of both normal and reaction xyla are very short (102-137 μm) and storeyed. Furthermore, the simple porous vessels with minute, alternate, lateral wall pittings are supposed to represent an advanced level of specialization of the secondary xylem in a normal organ (Bailey 1923; Frost 1931). But it is interesting to observe that the floral galls, despite their drastic external modifications and internal changes, should retain the above mentioned advanced xylary features unaffected.

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* Original not seen.