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ANATOMY AND ONTOGENESIS OF FOLIAR GALLS INDUCED BY *ODINADIPLOSIS ODINAE* (DIPTERA: CECIDOMYIIDAE) ON *LANNEA CORAMANDELICA* (ANACARDIACEAE)

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Abstract

Samples of healthy leaves and galls induced by *Odinadiplosis odinae* on *Lannea coramandelica* were submitted to routine techniques to investigate morphological and anatomical alterations taking place during gall development. The persistent galls on the midvein and the lateral veins are globose to subglobose/oval, hard, indehiscent, woody, sessile, solid, solitary and light brown in colour with a warty surface. Both palisade and spongy cells proliferate around the larval path. The neoformed parenchyma results from hypertrophy and hyperplasia of the spongy parenchyma cells initially but later the palisade also undergoes hyperplasia. Some of the cells bordering the larval path turn necrotic while certain other cells show meristematic activity due to the stimulus of wounding. The larvae seem to have settled either in the central parenchymatous region or sometimes in the lateral laminar region adjoining the midrib. The medullary cells surrounding the chamber are usually smaller and colourless and the cortical cells are filled with phenolic substances. Parenchyma cells between the vascular bundles also get neoformed and newly differentiated tracheary elements are distinctly observed.

KEY WORDS: Foliar gall. gall anatomy, anatomical alteration, *Odinadiplosis odinae*, ontogenesis.

Introduction

Galls are known to be distinct morphological structures observed in a great number of algae, bryophytes, gymnosperm and angiosperm. The number of gall-inducing insects in a global context is high, estimated at about 133,000 species (ESPIRITO-SANTO & FERNANDES, 2007; RAMAN *et.al*., 2009). Galls are known to originate following a stimulus of an invader organism like algae, lichens, bacteria, viruses, fungi, nematodes, mites and insects. Host plant tissues respond to challenges imposed by pathogens and insects in beneficial

or detrimental ways (BOSTOCK *et al*., 2001). Galls develop as an extension of the host-plant phenotype (RAMAN, 2011, 2012). They provide nutrition and shelter to the inducing insects and sometimes even its progeny. The insect activates a perturbation in growth mechanism and alters the differentiation processes in the host plant, modifying the plant's architecture to its advantage (RAMAN, 2007).

According to MANI (1973) and RAMAN (2007) gall-inducing ability among the known insects of the Indian subcontinent is found in Thysanoptera, Hemiptera, Diptera and Hymenoptera, and in relatively few species in Lepidoptera and Colcoptera, a pattern that matches the global pattern (RAMAN *et.al.,* 2009). Most of the insect induced galls are known to occur on species belonging to Fabaceae, Moraceae, Lauraceae, Myrtaceae, Combretaceae, Dipterocarpaceae, Anacardiaceae and Asteraceae (RAMAN *et. al.,* 2005). Anatomical studies on leaf galls induced by Cecidomyiidae family (Diptera) indicate high modifications at the cell and tissue levels (ROHFRITSCH, 1992; KRAUS *et al.,* 2003). Conspicuous palisade parenchyma proliferation and cell hypertrophy were reported in *Piptadenia gonoacantha* (Mart.) J.F. Macbr. (Fabaceae) (ARDUIN & KRAUS, 1995) whereas in galls induced on *Gurea macrophylla* subsp. *Tuberculata*(Vell.) T.D. Penn. (Meliaceae) the spongy parenchyma cells also divide and become rounded with small intercellular spaces (KRAUS *et al.,* 1996). Gall formation on the leaves of *Baccharis concinna* G.M. Barrosa (Asteraceae) caused alterations in pericyclic fibers, losing their ordinary secondary walls noticed in healthy leaves (ARDUIN & KRAUS, 2001).

The present work is a complementary study of RAMAN & DEVDAS (1977) which aims to describe the morpho-anatomical alterations taking place during the different developmental stages of foliar galls in *Lannea coramandelica* (Hoult.) of Anacardiaceae, provoked by the infestation of Cecidomyiidae *Odinadiplosis odinae*.

Material and Methods

Study area and species

Galls and normal plant materials for the present study were collected from the grassland in Bandheli, a forest division in Godhra in Gujarat state. The plant was authentically identified with the help of the BARO herbarium of Maharaja Sayajirao University of Vadodara.

Sampling

Mature infested and non-infested leaves of *Lannea coramandelica* were collected. The youngest gall development stage was determined based on the smallest diameter, observed as a small bulge on the leaf. The leaves and galls were fixed and taken to laboratory for morphological and anatomical analysis.

Morphological and anatomical analysis

Galls of different developmental stages were observed under a dissecting microscope while still attached to the leaf and photographed with the help of a Sony cyber shot DSC-T10 camera.

Galls with oviposition scars and in successive stages of development were fixed on the spot in FAA (FAA:70% ethanol-90ml, 40% formalin-5ml, glacial acetic acid-5ml) and brought to the laboratory. Galls of the different developmental stages were separated into glass vials and dehydrated with an ethanol series, and

embedded in paraffin (JOHANSEN, 1940). Transverse serial sections, 12-14µm thick, were cut with a Leica rotary microtome. The histological sections were contrasted with 1% Toluidine blue (dissolved in 1% aqueous borax solution) and safranin- fast green (SASS, 1951). Slides were mounted in DPX mountant, and further observed and photographed under different magnifications with the help of a Leica DME research microscope.

Results

Morphological alterations in the leaf

Morphological alterations during the different developmental stages of galls have been represented in Figs.1a-g. Galls are initiated on the abaxial surface of the leaflets and with an increase in size they become distinctly visible on the adaxial surface also. Initiation of the gall formation results from the oviposition on leaves by the insect *Odinadiplosis odinae*. Eggs are normally deposited close to the veins. The first visible change is a decolorisation and reddening of the site where the eggs are deposited (Fig. 1a, arrow). Chemical stimulus brings about degeneration of surrounding cells forming a small necrotic cavity on the leaflet (Fig.1b). Gradually the decolorized area increases in size and forms a small rounded structure (Figs. 1c, d). The larvae that hatch from the eggs deposited on the midvein or close to it grow into the tissue forming small elliptical pits with a corky outline (Fig.1d). By feeding, biting and piercing, the larvae settle down in the central region of the midrib. Due to the stimulus of this wounding, the surrounding cells become meristematic resulting in hyper- and hypotrophied cells, resulting in turn in an increase in the size and formation of the mature galls.

Morphology of mature gall

Galls form mainly on the midvein and the lateral veins of the leaflet (Fig. 1e). Rachis also shows the formation of gall. These persistent galls on the midvein and the lateral veins are globose to subglobose/oval, hard, indehiscent, woody, sessile, solid, solitary or sometimes fused becoming woody and light brown in colour with a warty surface (Figs. 1f, g) at a later stage. Leaflets with mature galls are almost completely without the lamina portion which appears to have completely degenerated with sometimes the distal portion of the lamina remaining (Fig. 1f). Though the characteristic galls occur scattered on the leaf veins throughout the laminar surface, they tend to agglomerate at the midvein region, giving a moniliform appearance (Fig. 1f) and crinkling of leaves. The corky surface of the gall irregularly cracks, exposing dark brownish cortical tissue (Fig. 1g). The galls are equally visible on both sides of the vein and a number of galls may be seen at their various stages of development (Fig. 1e). A single mature gall sometimes showed 3-4 chambers.

Anatomy of Uninfested lamina

Anatomical features of a normal uninfested leaf are depicted in Figs. 2a, b. Leaves are dorsiventral. Some of the upper epidermis is tanniniferous and sparsely distributed (Figs. 2a, b). The epidermal cells are cubical in transection and are covered with a very thick cuticle. Cells of the lower epidermis are cubical and very small compared to upper epidermal cells. These cells are also tanniniferous. Stomata are confined to the lower epidermis.

The mesophyll is distinctly distinguished into 1- 2 layers of palisade (Fig. 2a). The two layers of palisade cells are of the same size and have a few layers of spongy tissue. The upper palisade layer shows dense chloropl-

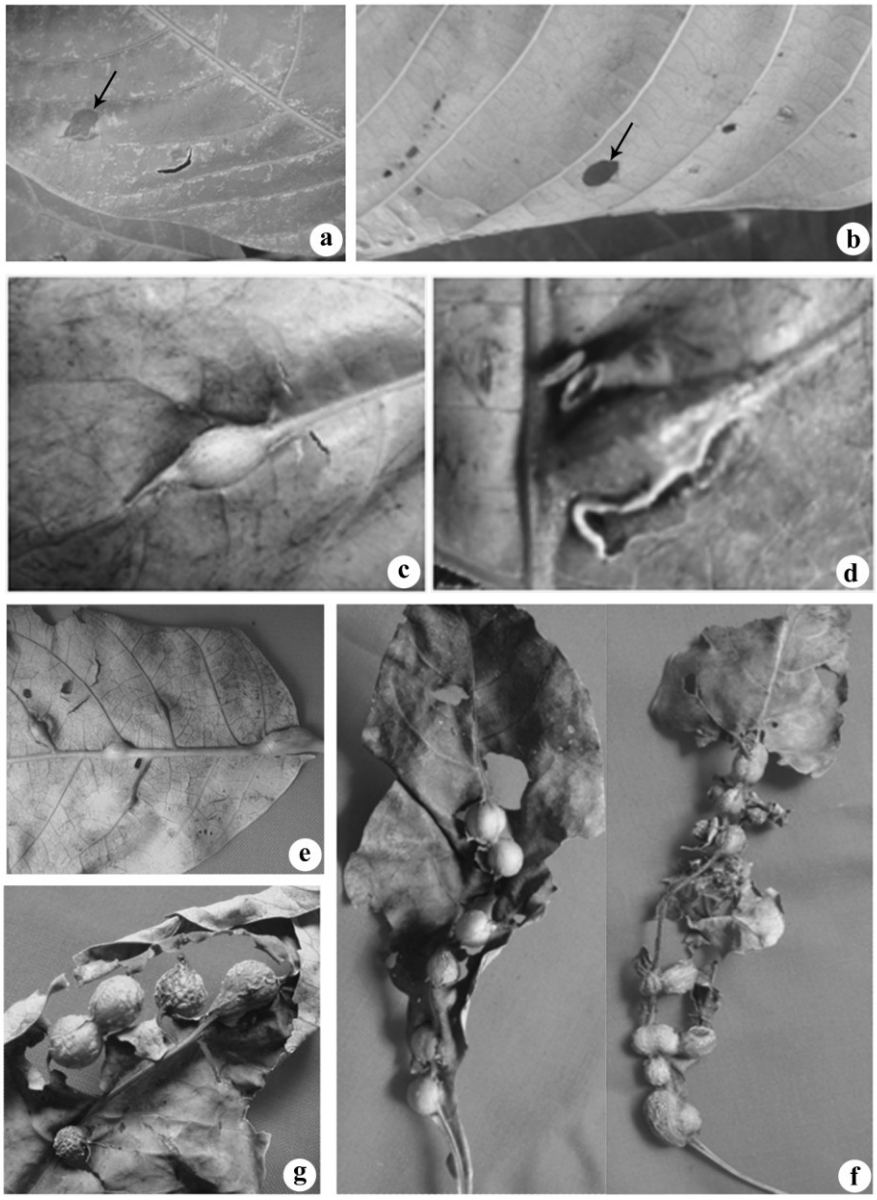

Figure 1. a - Decolorisation and reddening of the leaflet (arrow); b - Necrotic cavity formed on the leaflet (arrow); c - Gall visible on adaxial surface; d - Formation of pit with corky outline on the leaflet; e - Galls of different developmental stages on midvein and lateral veins; f - Deformed crinkled leaflet; g - Warty surface of gall (arrow).

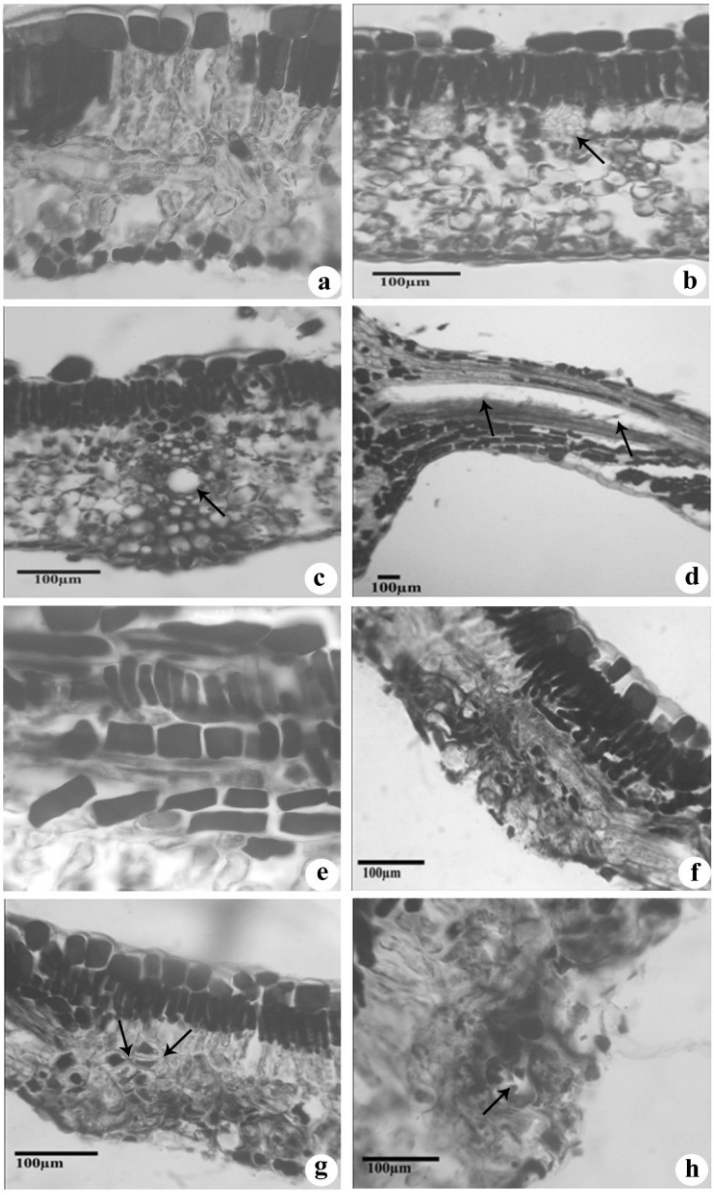

Figure 2. a - Transection of leaflet; b - Presence of tannin in epidermal cells, presence of sphaeraphides (arrow) in pallisade tissue; c - Presence of resin canal (arrow) in the phloem region; d - Formation of large cavities (arrows) through the entire lamina extending up to the midrib leaflet; e - Tanniniferous pallisade parenchyma cells; f - Penetration of pathogen through lower epidermis; g - Periclinal division of pallisade parenchyma forming new cell layers (arrows); h - Densely stained gall chamber.

ast compared to the lower palisade layer. The spongy cells are oval round, loosely arranged with large intercellular spaces. Spongy cells below the palisade layer intermittently show the presence of sphaeraphides (Fig. 2b, arrow). Often the palisade layer is interrupted by large idioblastic cells. The palisade tissue extends up to the middle part of the vein on the adaxial side. The pallisade layer extends over the lateral veins embedding them in the spongy tissue (Fig. 2c). The vein comprises a large resin canal in the phloem region which faces the lower epidermis (Fig. 2c, arrow) and is flanked by a few layers of collenchyma. The midrib is biconvex in outline. Epidermal cells are rectangular and coated with cuticle. The sphaeraphides are larger than the ones observed below the palisade layer. Petiolules are crescentic in outline. 14-15 vascular bundles are arranged peripherally.

Anatomy of infested lamina

In the lamina the larval chambers are not situated wholly within a definite zone and may extend up to the midrib. An Infested lamina shows the presence of large cavities tunnelling through the entire lamina extending up to the midrib (Fig. 2d, arrow). In the cell lining the cavity appears to be hypertrophied and filled with tanniniferous compound (Fig. 2e). New tracheary elements are also noticed. Penetration of the pathogen occurs through the lower epidermis disrupting the normal anatomical features (Figs. 2f, g). Hypertrophy and hyperplasia of the tissue surrounding the area of the pathogen entry is prominently observed. The palisade cells are largely unmodified but the cells of spongy parenchyma contiguous to the palisade parenchyma are elongated anticlinally and are also tanniniferous. These cells divide mainly in the periclinal direction, forming new cell layers (Figs. 2g, h, arrow). Cells surrounding the gall chamber distinctly appear to be densely stained and arranged in radial files, a condition appearing consequent upon cell divisions occurring parallel to the insect chamber, and largely by the renewed activity of the spongy parenchyma.

Anatomy of uninfested midrib

The unaffected midrib of *Lannea coramandelica* has a ring of vascular bundles ranging from 8- 10 in number arranged in a crescent form (Fig. 3a). The abaxial side is bordered by 2-3 layers of collenchyma.The vascular ring is flanked by resin canals. The cortex consists of nearly 7 layers of parenchyma cells, some of which are filled with tannin. The vascular bundles are collateral with inner xylem and outer phloem and a large resin canal occurring outside at the centre of the latter. The pith is made up of large compact thin-walled parenchyma cells interrupted by a resin canal. Crystalline inclusions sphaeraphides occur in a few outer cortical collenchymatous cells and in a few phloem elements. Epidermal cells are small, barrel-shaped and filled with tannins (Fig. 3c).

Anatomy of infested midrib

The epidermal layer of the galled midrib is highly modified. The midrib develops a corky surface, and develops gall channels (Fig. 3b, arrow) and a gall (Fig. 3b, arrowhead) chamber within the midrib. It initiates with periclinal and anticlinal divisions in the epidermis and the hypodermal layer below it (Fig. 3d). Repeated divisions and an increase in the number of cells break the epidermal layer (Fig. 3e). The cells formed are anticlinally elongated and oriented in radially arranged rows (Fig. 3f). Covered with a secretion the epidermal layer becomes multilayered and periderm is formed (Fig. 3g). The epidermal cells lose their tanniniferous content and undergo division. After oviposition the insect probably secretes a secretion to protect the egg. The larvae move by piercing and feeding on the epidermal cells, thereby destroying them (Figs. 4a, b). The larvae that hatch from the eggs deposited on the leaflets grow into the plant tissue and reach the centre of the midrib or settle down in the outer parenchymatous region. Following this the cells surrounding the

pathway show great alterations (Figs. 4c, f). Some of the cells become necrotic while certain others above them show dense contents (Figs. 4d, e arrow) while yet others show degeneration along the pathway (Fig. 4f). Some of the cells show meristematic activity which is probably due to the stimulus of wounding (Fig. 4e). External to the larval chamber, a parenchymatous zone of hypertrophied and tannin containing cells 25-30 thick is present. The cecidogenic stimulus involves wound healing along the larval path, hypoplasia of ground tissue and extensive hyperplasia of neighbouring cells. Sections of mature galls show the larval cavity bordered by remnants of a once functional nutritive parenchymatous zone. The well-developed neoformed parenchyma is characterized by a cortical and a medullar region. The medullary cells surrounding the chamber are usually smaller and colourless and the cortical cells are densely stained because of the presence of phenolic substances (Fig. 5a). Parenchyma cells between the vascular bundles also get neoformed (Figs. 5b, c). The medullary parenchyma cells are arranged in radial files (Fig. 5c) indicating repeated periclinal divisions in the formation of new cell layers. The size of the thin walled parenchyma cells reduces towards the chamber. The resin canals become larger and scattered, lining the parenchymatous layer surrounding the chamber (Fig. 5a). New atypical tracheary elements are formed close to the larval chamber (Fig. 5e, arrow). Surrounding the degenerating cells tanniniferous cells are present (Fig. 5f). The larval path is invariably closed by newly differentiated parenchyma. After the establishment of a nutritive region 13-15 cells thick, growth is uniform all around the larval chamber increasing the size of the gall and making it globose in shape.

Discussion

The gall insects exhibit a very large degree of specificity not only with the reference to host plants, but also to plant organs and plant tissues, and they take advantage of the fundamental property of the plant to react, whereby even the differentiated tissues could be converted into a meristematic state (JAYARAMAN, 1980). By inducing a gall, the insect ensures nutrition and shelter for shorter or longer periods of its life. Gall-inducing insects generally show novel traits in their nutritional physiology and population dynamics (RAMAN *et al.,* 2005).

The gall midges known to infest different taxa of Anacardiaceae belong to the Cecidomyiinae (RAMAN *et. al.,* 2009). Larvae of Cecidomyiidae are known to have a sucking mouth type by which they ingest plants (SOLINAS, 2011). Anatomical studies on leaf galls induced by the Cecidomyiidae family (Diptera) indicate profound modifications at the cells and tissue levels (BRONNER, 1992; ROHFRITSCH, 1992; KRAUS *et al*., 2003; CAMILLA *et al*., 2009). Prominent palisade parenchyma proliferation and cell hypertrophy has been reported in *Piptadenia gonoacantha* (ARDUIN & KRAUS, 1995) whereas in galls induced on *Guarea macrophylla* sub sp. *tuberculata* the spongy parenchyma cells also divide and become round with small intercellular spaces (KRAUS *et al*., 1996). In *Lannea coramandelica* both palisade and spongy cells proliferate around the larval path. The neoformed parenchyma results from hypertrophy and hyperplasia of the spongy parenchyma cells initially but later the palisade also undergoes hyperplasia. Therefore the spongy parenchyma cells respond more rapidly to the insect stimulus than the preferred sites of insect attack which is at the abaxial surface of the leaflet, so the cecidogenic field is nearer to the spongy parenchyma.

The presence of phenolic substances in cells surrounding the larval chamber and the superficial portion of the neoformed parenchyma in *Lannea coramandelica* point to chemical defence in this gall. This feature was observed in dipteran foliar galls (ARDUIN *et al*., 1991; CAMILLA *et al*., 2009). According to CORNELL (1983) the presence of phenolics indicates a chemical defence mechanism because they are thought to inhibit the feeding of herbivorous insects, or the parasite community of the insect gall (TAPER & CASE, 1987).

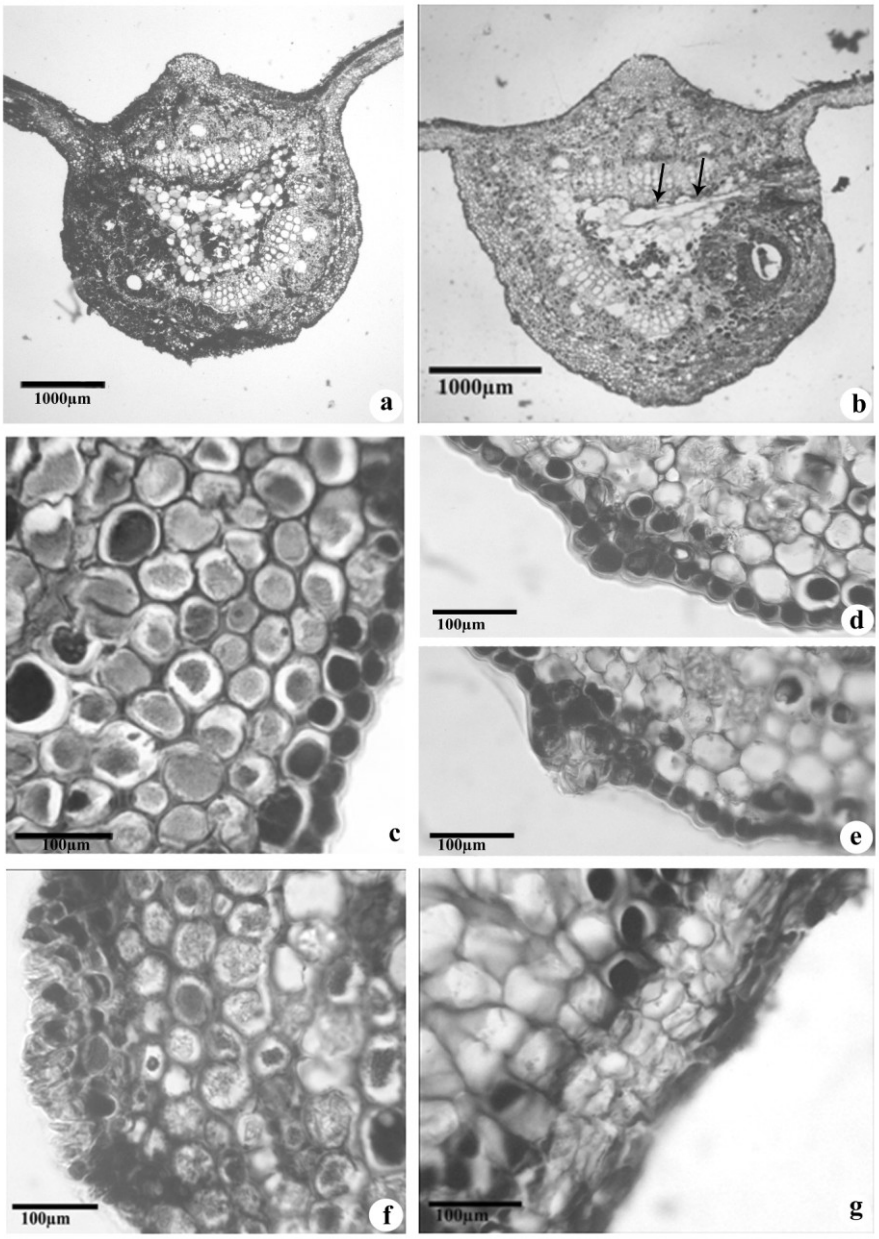

Figure 3. a - Transverse section of midrib of uninfested leaf; b - Gall channels (arrow) and chamber (arrowhead); c - Epidermal and hypodermal layers of midrib; d - Divisions initiated in epidermal cells; e - Rupture of epidermal layer; f - Anticlinally elongated and radially arranged rows of epidermal cells; g - Formation of periderm.

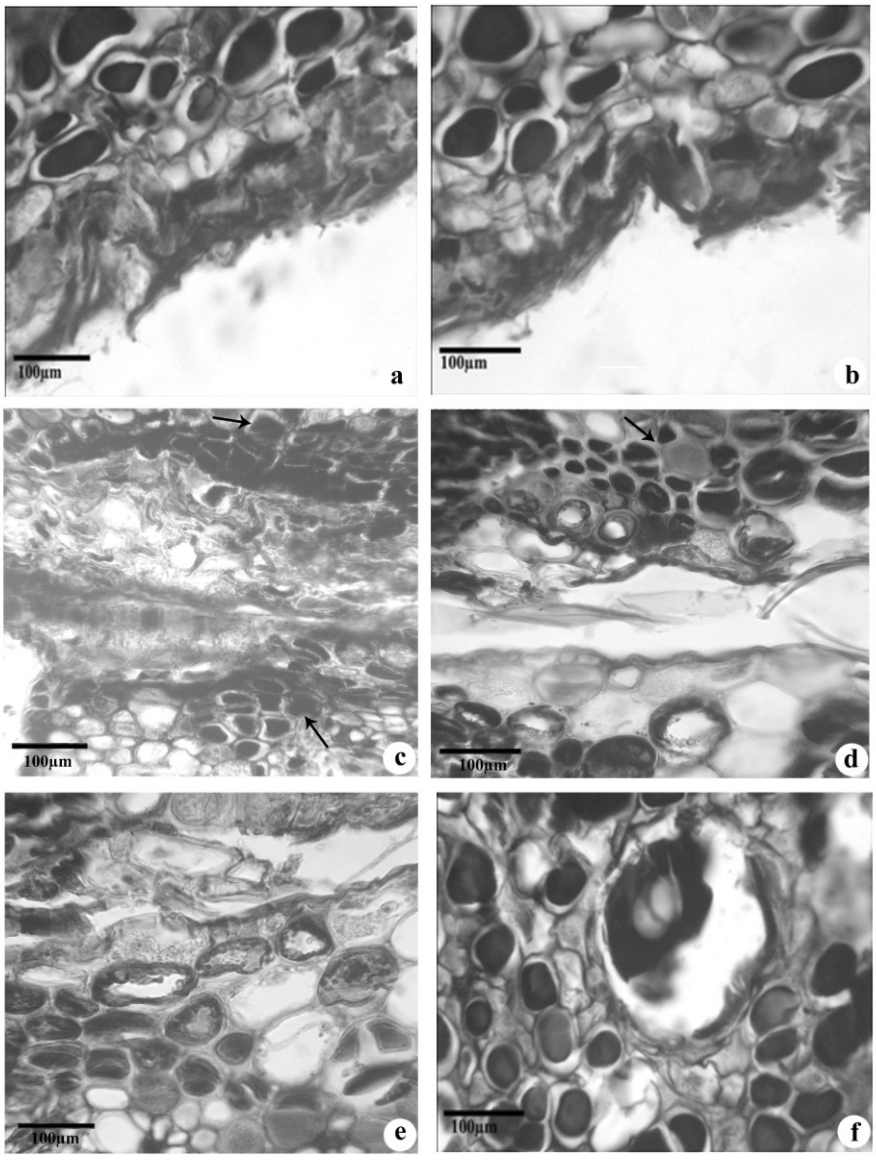

Figure 4. a, b - Midrib showing divisions in epidermal cells and the pathway of pathogen entry; c - Necrotic cells surrounding the pathway; d - Degeneration of cells surrounding the pathway; e - Cells surrounding the pathway showing densely stained contents; f - Developmental stage of the larval chamber in the infected leaflet.

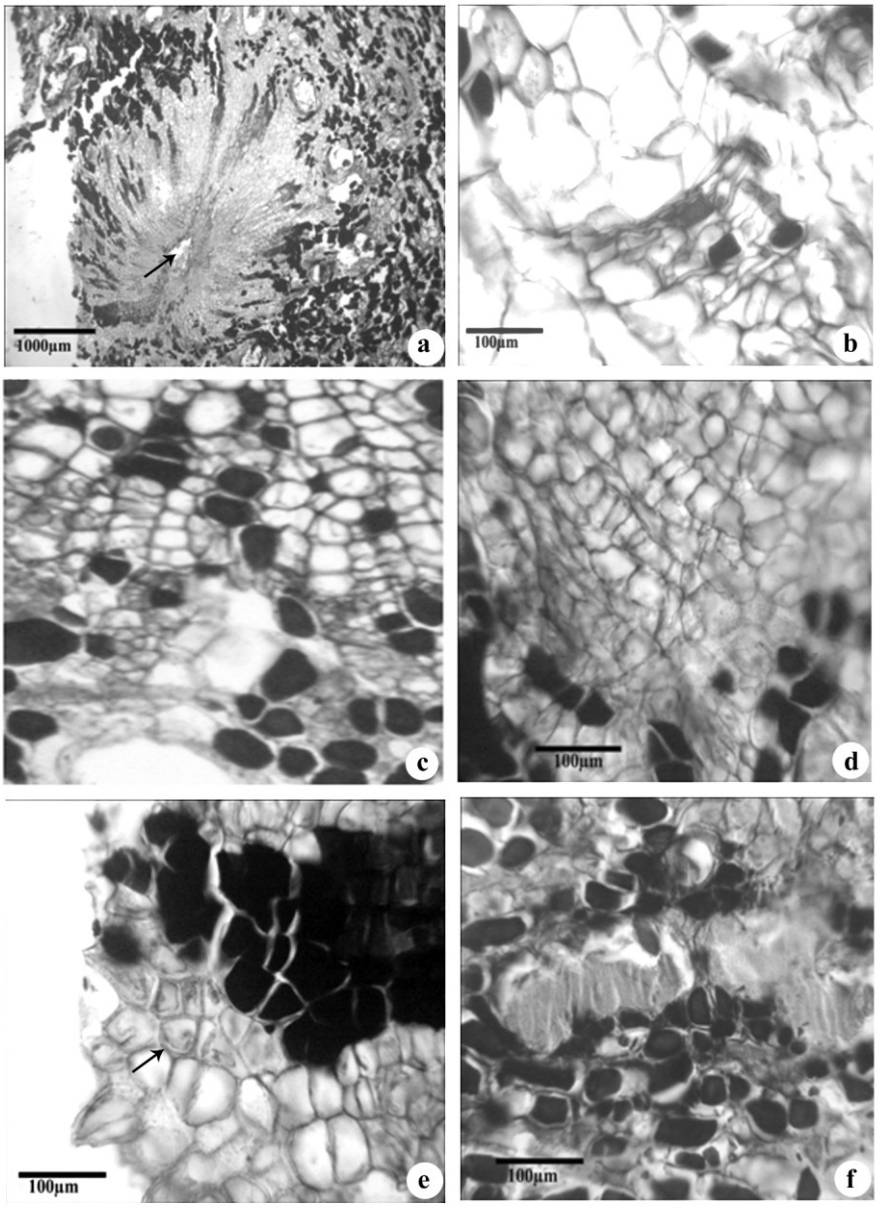

Figure 5. a - Colourless parenchymatous medullary cells surrounding the gall chamber (arrow); b, c - Parenchyma cells between the vascular bundles neoformed; d - Radially arranged medullary parenchyma cells formed due to repeated periclinal division; e - Formation of new atypical tracheary elements (arrow) close to the larval chamber; f - Development stage of the larval chamber in the infected leaflet. Larval chamber surrounded by densely stained contents.

Another relevant characteristic feature observed in *Lannea coramandelica* is the formation of periderm on the midvein of the leaf infested by *Odinadiplosis odinae.* The presence of periderm on healthy leaves is rare and it is suggested that leaf periderm is a consequence of insect or mechanical injuries or that it develops beneath microorganisms (FAHN, 1990). However some galls are reported to develop periderm (MEYER & MARESQUELLE, 1983; KRISHNAN & FRANCESCHIE, 1988). The formation of periderm is discussed by MEYER & MARESQUELLE (1983) as a form of mechanical protection.

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 galls - a phenomenon frequented in the galls caused by midges and by moths (ARNOLD, 1966a,b,c) and by weevils (KRISHNAMURTHY *et al*., 1977).

The host response to the feeding or ovipositional stimulus is something unique that alters plants' morphogenetic responses. Many cecidogenous insects, which infest the leaves, prefer to feed on the veins and petioles of plants, most probably because of their selective food requirements (GUPTA, 2011). This phenomenon has been very clearly depicted in *Lannea coramandelica* infested by *Odinadiplosis odinae.* The mode of piercing and sucking the cell contests during the major part of their development together with the possible divergence of the chemical action from the larvae is the probable cause for the development of the galls.

Insects attack plant tissues resulting in the alteration of the subcellular environment and the placement of those tissues in a state of chemical shock. This shock evokes osmotic changes in the cell attacked, establishing the earlier recognizable stage in gall induction. To neutralize the stress arising consequent to osmotic changes, aggravated by wounding, the plant responds by developing usually one, sometimes 2-3, metaplasied cell(s). Localized metabolic changes diffuse from the metaplasied cell(s), but not throughout either the involved plant organ (e.g. leaves) or the plant (ROHFRITSCH, 1978, 1980, 1992). When the shock is of low intensity, the plant responds with "certain" chemical-molecular factors that disperse from the metaplasied cell(s) triggering gall development. When the shock factor is of high intensity, the cells under the influence of the insects (e.g. *Dasineura marginemtorquens*, Diptera: Cecidomyiidae; *Daktulosphaira vitifoliae*, Hemiptera: Phylloxeridae) die rejecting the inducing insect and thus defending the plant tissue (OLLERSTAM *et al*., 2002; RAMAN *et al*., 2009). The shock factor appears to differ in the lamina and the midvein region of *Lannea coramandelica*. The shock appears to be of higher intensity in the lamina region compared to the midvein. This is probably the reason why the metaplasied cells of the lamina die rejecting the inducing insect while the cells of the midvein respond by triggering gall development as continuing stimulus from the insect is essential to control gall shape and structure (ROHFRITSCH, 1971).

Gall development involves two contracting events: the insect stresses the host organ, and the host counters it with new physiological activities supplemented by newly differentiated tissues. Development of tracheary elements is distinctly observed in *Lannea coramandelica.* Development of galls on *Alstonia scholaris* showed newly differentiated phloem elements in the hypertrophied tissues (SUSY *et al.,* 2011).

Occurrence of a typical tracheary element has been reported in bacterial gall cultures (SPURR *et al*., 1964), galls caused by fungi (AKAI, 1951) and nematodes (SWAMY & KRISHNAMURTHY, 1971). Morphologically and developmentally these atypical elements resemble the tracheary elements differentiating after wounding - designated as wound vessel elements (ROBERTS & 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 & 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, which initially occurred only in close proximity to the larval path and in mature galls extending all round the larval chamber in a very uniform manner.

In *Lannea* observed elements of vascular tissue differentiated towards the centrally located larval chamber. The galls of *Salix,* LOUX & MEYER (1968) have shown anastomosing radially oriented vascular traces, while in the leaf galls of *Aeschyanthus* (KRISHNAMURTHY & RAMAN, 1972) the galls were restricted to the laminar regions. In the galls of *Lannea* and *Salix* (LOUX & MEYER, 1968) the tracheary elements differentiated much earlier to the development of a 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 derivatives may be due to the entry and feeding by the larva as shown by MILES (1968).

The present study has shown that the galls of *Lannea* caused by *Odinadiplosis odinae* are not an uncontrolled tumor growth. Their ontogeny follows a well-defined sequence, and produces an equally well-defined morpho-anatomical structure. Our findings confirm the conclusions of TAFT & BISSING (1988) that not only the presence of the inducer leads to a rupture of the cellular process of the host, but it also results in an active redirection of the existing ontogenic patterns to the benefit of the inducers. The anatomical studies on the gall induced by *Odinadiplosis odinae* on *Lannea* complement what is currently known regarding gall biology and contribute to the body of knowledge about the plasticity of plant tissues stimulated by biotic factors.

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АНАТОМИЈА И ОНТОГЕНЕЗА ЛИСНИХ ГАЛА ПРОУЗРОКОВАНИХ АКТИВНОШЋУ *ODINADIPLOSIS ODINAE* (DIPTERA: CECIDOMYIIDAE) НА ЛИСТОВИМА *LANNEA CORAMANDELICA* (ANACARDIACEAE)

СУЗИ АЛБЕРТ, СВИТ РАНА и ДАРА ГАНДИ

Извод

Узорци здравих листова и гала изазваних *Odinadiplosis odinae* на *Lannea coramandelica* су подвргнути рутинским техникама да би се истражиле морфолошке и анатомске промене које се дешавају током развоја гала. Гале на средњој и бочним венама листа су лоптасте или овалне, дрвенасте, сесилне, појединачне, светло браон боје брадавичасте површине. Ларве оштећују и палисадне и сунђерасте ћелије. Новоформирани паренхим је последица хипертрофије и хиперплазије у почетку код сунђерастих ћелија паренхима, али касније и палисада који такође пролази кроз хиперплазију.

Ларва се сатционира у централном делу паренхима или понекад у бочном ламинарном делу на нерву. Медуларне ћелије окружује комора, која је обично мања, безбојна а кортикалне ћелије су пуне фенолних супстанци. Паренхимске ћелије између васкуларног снопова формирају нову форму и јасно се уочавају нови трахеални елементи.

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