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CAMBIAL DYNAMICS *VIS - A - VIS* LARVAL EMPLACEMENT IN SHOOT- AXIS GALLS

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Among the phytophagous insects the gall moulding ones are endowed with the versatility of selecting their specific host plants as well as preferring specific site within the host organ for building the larval chamber. The present paper highlights the correlations of the loci of the gall-larva in the cortex, secondary xylem, pith and eventual behavioural patterns of the vascular cambium. The gradients of cecidogenetic impulses emitted by the feeding activity of the larva seems to be the key factors for the differential behaviour of the cambium in the shoot-axis galls.

Keywords: Cecidogenetic factors; Gall insects; Histogenetic patterns; Larval cavity; Shoot- axis galls; Vascular cambium.

Introduction

One of the perplexing phenomena often encountered in the study of insect-plant relationships is the pronounced tendency of the insects to be associated with particular host plant species or a group of related taxa. This eventuality of host specificity has evolved into what is known as *monophagism, a* phenomenon well established among gall forming insects rather than non- gall forming phytophagies.The selective location of the gall-insects within the plant organs has a definite bearing on the feed-back reactions of the host tissues, which are also specific and fixed. Houard[1] in his classical treatment of plant- galls has paid due attention to the studies of stem-galls with specific accent on the positional effects of the gall- inducing larva in the stem.This concept seems to have remained unpursued by the subsequent investigators. In the present paper, the reciprocal correlations of the specific larval location and equally specific responses of the vascular cambium are highlighted by citing some shoot- axis galls studied by the author[2].

Meterials and Methods

Shoot-axis galls on eight different host plant species were selected for the present study (Figs. 1-8). These galls were incited by different groups of insects and the galls comprise different categories of larval locations such as cortex, interxylary zone and pith. The host plants, the insect groups and the position of the larva in the galls are tabulated below:

Table 1.

S.No.	Plants	Insects	Larval Position
1	*Ammania rotala* CI. (Lythraceae)	*Nanophyes* sp. Coleoptera	Cortex
2	*Atalantia monophylla* (L.) Correa. (Rutaceae)	Unknown Diptera	Secondary Xylem
3	*Capparis sepiaria* Linn. (Apocynaceae)	Unknown Lepidoptera	Secondary Xylem
4	*Syzygium cumini* (l.) Skeels (Myrtaceae)	Unknown Diptera	Secondary Xylem
5	*Eupatorium adenophorum* Spreng (Asteraceae)	*Procecidochares utilis* Stone Diptera	Pith
6	*Tephrosia villosa* (L.) Pers. (Papilionoideae)	*Dactylethra candida* Staint Lepidoptera	Pith
7	*Carissa spinarum* Linn. (Apocynaceae)	Unknown Diptera	Pith
8	*Phyllanthus polyphyllus* willd. (Euphorbiaceae)	*Betuosa stylophora* Swinhoe Lepidoptera	Pith

Galls and normal stems of corresponding age were fixed in FAA. Dehydration and paraffin wax infiltration were carried out as per customary methods[3]. Rotary microtome sections of 10-12 μm thickness were stained with tannic acid, Ferric- Choride plus safranin[4] or Toluidine blue O[5]. Camera lucida drawings were drawn to appropriate scales. Insects associated with galls were identified with the help of the monograph , Plant galls of India[6].

Obeservations

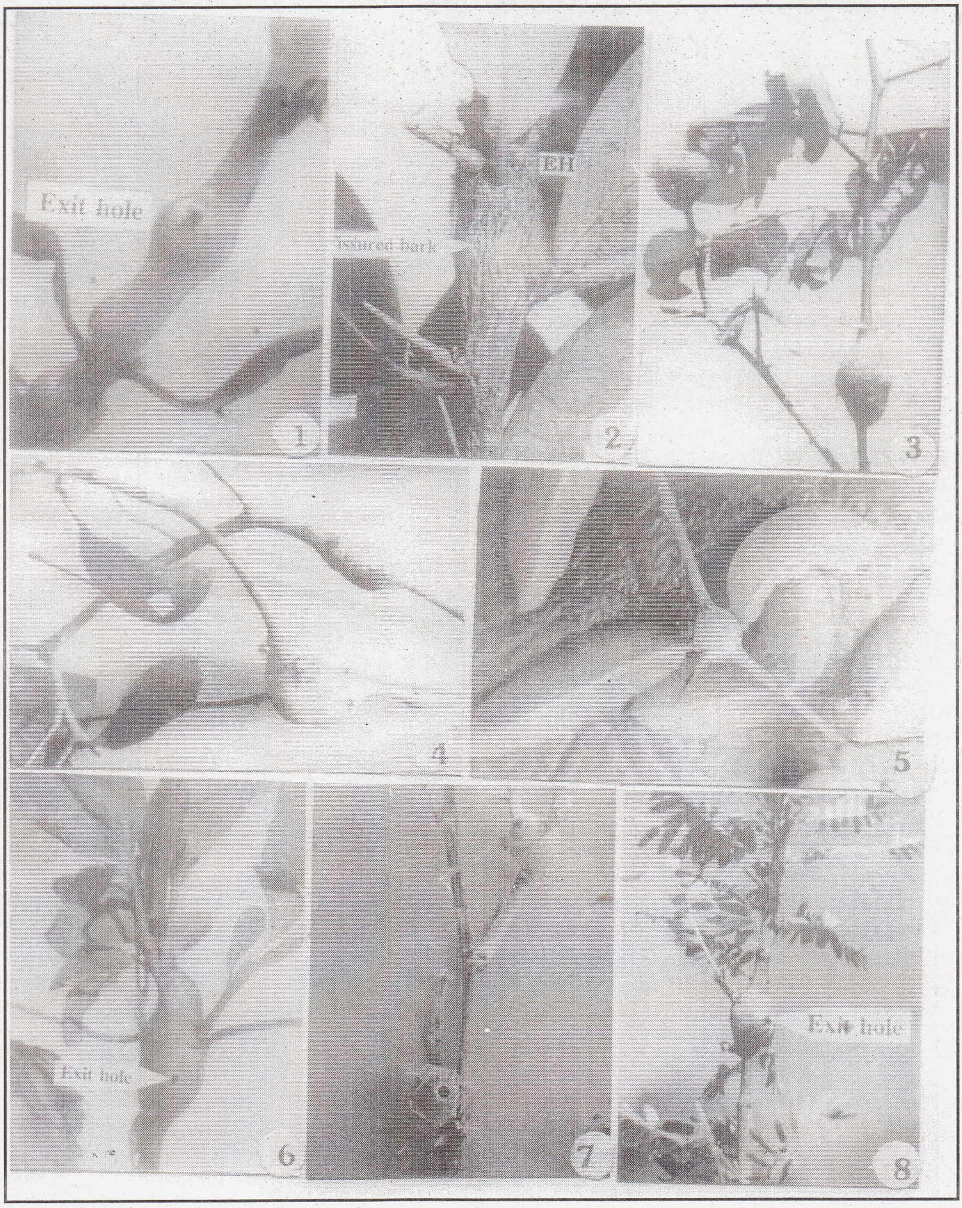
1. Gall with cortical position of larva: On *Ammannia rotala,* a Coleopteran insect, *Nonophyes* incites quite prominent, soft, brightly coloured ' rinden' gall on the nodal or internodal region (Fig.1.) The weevil larva after gaining entry in to the stem establishes its domain in the aerenchymatous cortex. The feeding stimulus emanating from the larva renders the aerenchyma tissue encompassing the larva to proliferate abnormally producing massive callus like mass of tissue. The gall projects as a lateral bump and remain aloof of the vascular cylinder (Fig.9). Development of densely cytoplasmic 'nutritive tissue' permeated by 'irrigating strands' around the larval chamber is an added advantage of the gall.

2. Gall with interxylary larva: In the galls on *Atalantia monophylla Capparis sepiaria* and *Syzygium cumini* the larval chambers are interxylary in position.The gall on *A. monophylla* has multiple larval chambers disposed all around the stem in the xylem cylinder. Eventually the growth of the gall is radially symmetrical (Fig.2). In *C. Sepiaria* and *S. cumini* the larval chamber is usually single and unilateral, so that the development of the gall is asymmetrical and lopsided (Figs.3,4). The abnormal growth responses of the cambium and other ground tissues occur more or less uniformly around the multilocular gall on *A. monophylla;* consequently the resulting gall assumes ellipsoidal symmetry (Fig.10). In *C. sepiaria* and *S. cumini,* the larval emplacement is unilateral and only the segment of the cambium contiguous to the larval chamber receives the cecidogenetic impulse and reponds in terms of aggravated activity and subsequent unilateral growth of the gall (Figs. 11,12). In these galls, the larval chamber is encompassed by a dense zone of "nutritive tissue" on which the larva feeds through which the cecidogenetic stimulus is probably transmitted to the cambial zone.

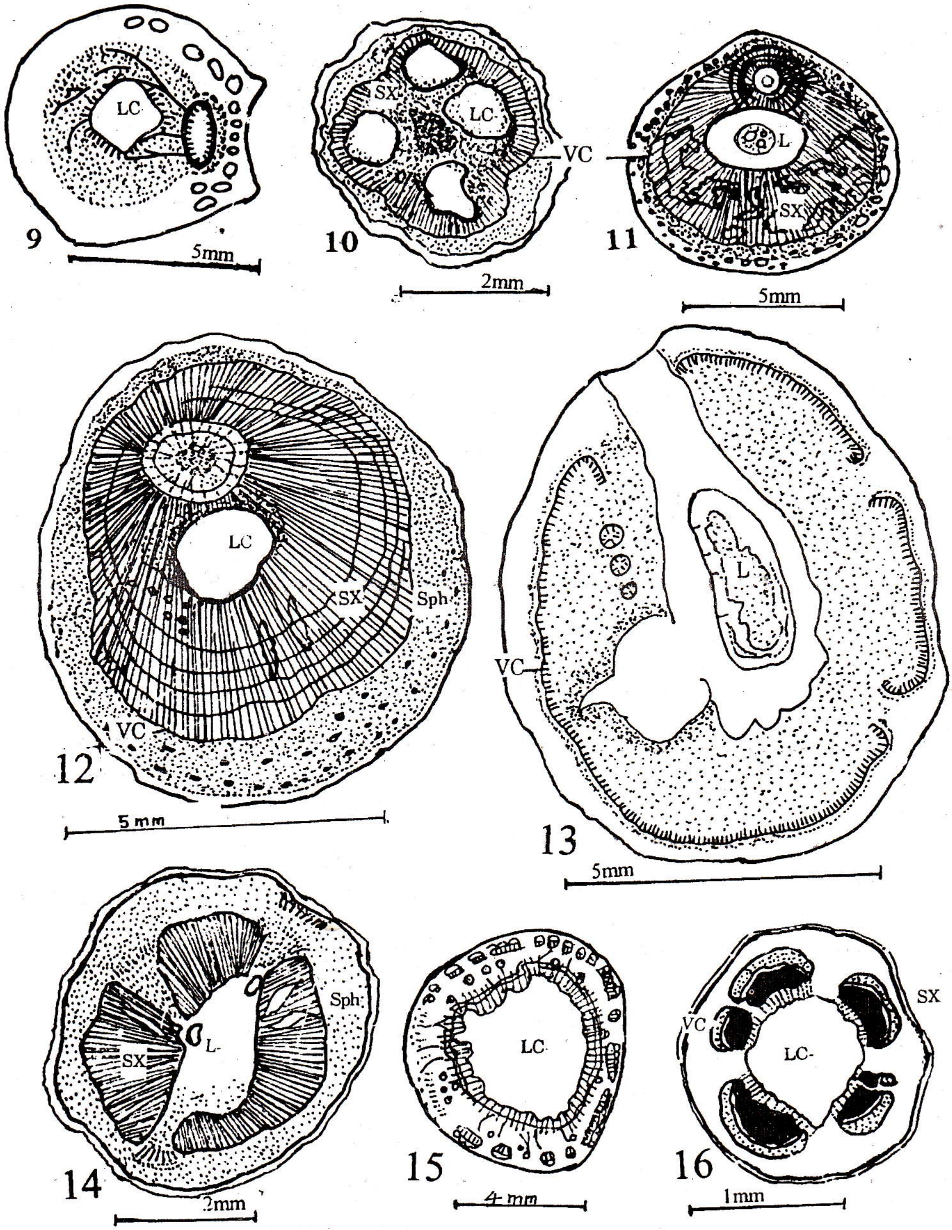
The vascular cambium juxtaposing the larval chamber deflects conspicuously from its normal pace of activity and from usual cyto-differentiation sequence. The cambial initials in the gall undergo additive and multiplicative division with great impetus producing inflated quantum of xylem tissues. Th enhanced activity of the cambium is accompanied by hyperlastic and hypertrophic activities of the ground tissues. The total effects of these changes culminate in the dovelopment of gall. The histological syndromes in the gall tissues, xylem tissue in particular, include inhibitions of lignification of the xylem elements, reduction in the porosity leading to homogeneity of the xylem, vessels, when present, diminished in dimensional values, shifting of the vertical alignment of the xylem elements to horizontal posture, dilation of the xylem rays, twisting and whirling of the xylem elements and precocious development of periderm over the gall.

3. Gall with medullary larva: The third category of gall comprise *Tephrosia villosa; Carissa spinarum* and *phyllanthus polyphyllus* in which the larvae are medullary in position. The larvae feed on the pith cells, and later on the boundary xylem tissue if pith cells are exhausted on *T. villosa*, a moth larva of *Dactylethra candida* (Lepidoptera) forms pyriform, nut like gall on the terminal part of the shoot (Fig.7). The gall grows in thickness up to 10mm on a stem that is less than 2mm thick. This dramatic increase in the perimeter of the gall is accomplished by diffuse and uniform hyperplasy and hypertrophy of the dermal and cortical tissues which keep abreast with the profound multiplicative divisions and tangential dilation of the cambial cylinder. Additive divisions of the cambial initials are minimised so that only a thin cylinder of vascular tissues is formed (Fig.15). The pith cells bounding the larval chamber assumes meristematic potentials and build up mantle of nutritive tissue, many 'irrigating strands' originating from the main vascular cylinder enrich the nutritive tissue, on which the moth larva is ensured with sustainable provision of nutrition within the gall.

In *Carissa spinarum,* a Dipteran gall midge larva evokes ellipsoidal gall on the



Figs.1-8. Shoot axis Galls exomorphic features; 1. *Ammannia rotala*. 2. *Atalantia monophylla*. 3. *Capparis sepiaria*. 4. *Syzygium cumini*. 5. *Carissa spinarum*. 6. *Eupatorium adenophorum* 7. *Tephrosia villosa*. 8. *Phyllanthus polyphyllus*.



Figs.9-16. Shoot axis Galls transections. 9. Cortical larval chamber: *Ammannia rotala.*

Figs: 10-12. Inter-xylary larval chambers: 10. *Atalantia monophylla,* 11. *Capparis sepiaria.* 12. *Syzygium cumini.*

Figs: 13-16. Medullary larval chambers: 13 *Eupatorium adenophorum,* 14. *Carissa spinarum,* 15. *Tephrosia villosa,* 16. *Phyllanthus polyphyllus.* L. Larva; LC. larval chamber, sph. Secondary phloem; sx. Secondary xylem; vc. Vascular cambium.

nodal or internodal region of branches (Fig.5). The larva colonises in the pith region and feeds on the parenchymatous pith. In quite contrast to the situation as in *T. villosa* gall, the cecidogenesis in *C. spinarum* involves different mode of cambial behaviour. Influenced by the feeding stimulus of the larva, the cambium functions in the greatest impulse and produce a dense wide cylinder of xylem uniformly around the gall (Fig.14). No distinct nutritive tissue or irrigating strands are evident in the gall. Thus, the growth of the gall is accomplished to tally by exaggerated xylogenesis. However, the xylem tissue of the gall is deprived of normal lignification, porosity and cyto-differentiation.

Procecidochares utilis (Diptera) incites soft, brightly coloured gall on the tender terminal part of the shoot- axis on *Eupatorium adenophorum* (Fig.6). The gall harbours a single medullary larval chamber; the larva feeding on the pith parenchyma engenders cecidogenetic stimulus that diffuses out in radial plane. A wide zone of pith cells ensheathing the larval chamber dedifferentiate into nutritive tissue that furnishes sustainable source of nutrition to the larva. The waves of cecidogenetic stimulus spread beyond the pith and extend up to the cortical zone, elating the ground tissue to proliferate at randomized planes. The vascular cambium is fragmented along several loci due to the pressure exerted by the proliferating ground tissue and broken segments assume strange configurations like circle, wavy string, loops etc (Fig.13) functioning of the cambial segments is normal in that it produces inner xylem and outer phloem. However the quantum of the vascular tissues produced is much lower than that of the stem.

Gall on *Phyllanthus polyphyllus* is caused by Lepidopteran larva, *Betuosa stylophora*. The gall has a single wide medullary larval chamber and the gall is radially symmetrical with shallow ridges and furrows (Fig.8). The moth larva is an aggressive feeder and bites and chews the entire pith tissue. The larva continues to feed on the bordering xylem tissue. It corrodes the xylem cylinder along four 'or five places and where the cambial derivatives are stimulated to undergo extensive proliferation causing cleavage of the cylinder into corresponding number of segment. The parenchymatous components of the wounded xylem as well as the inter-segmental parenchymatous tissue become actively meristematic and proliferate centripetally into a broad radial files of nutritive tissue; the meristematic behaviour of the nutritive tissue continues for a prolonged period (Fig.16). The growth of the gall is brought about by the accelerated activity of the cambium of the segmented xylem masses, as well as dilation of the cortical parenchyma coupled with hyperplasia leading to wide, fissured periderm which renders the gall with charateristic rough surface.

Discussion

The phytophagous insects which incite galls preferentially galls on shoot-axes of plants, also exhibit selective tendency in choosing the specific locus in the stem. The rationale behind the option of the insects for specific niche in the shoot-axis can not be ascertained with certainity. One reason that will not fail to strike our attention for the specific locus of larval chamber in the stem galls seems to be the chemical composition of the nutrition that the insect larva prefers. The type of mouth parts, feeding behaviour and the life span of the larva may also be complementary factors. Whatever be the logic behind the selection of specific place in a gall, the position of the larva in the gall seems to impulse the vascular cambium to behave in different pattern. The impact of the gall invoking stimulus on the vascular cambium and eventual repercussion to the stimulus have been given due to accent by Houard[1] and Mani[7]. The larval position and consequent cambial reprisal have been the basis for proposing a classification of shoot- axis galls by Jayaraman[8]. The observations made on a few shoot- axis galls during earlier studies[2] lend support to the prepositions put forth by the earlier investigators. In the gall on *A. rotala* the larval chamber is cortical in position and the radially diffusing gall evoking impulse gets defused as it reaches the cambial zone, so that the vascular meristem does not get involved in cecidogenesis thus the gall is totally cortical in origin[9].

In the galls on *A. monophylla, C. sepiaria* and *S. cumini,* where the larvae are interxylary in position, the waves of gall formulating factors diffuse in centrifugal direction. On its course of centrifugal movement, the stimulus meets the cambial zone its optimal state of concentration, a condition that favours to impulse the cambium to function at enormous impetus. Subsequent growth of the gall may be in radial symmetry, if the gall is multilocular disposed all around the gall, as exemplified by the gall on *A. monophylla* (Fig. 10). In the galls on *C. sepiaria* and *S. cumini* the larval chambers are single unilateral and interxylary. Consequently, the diffusion of the gall stimulus is unilateral and the resultant gall are unilateral in growth, brought about by circumscribed activation of a cambial segment. Similar type of observation has been made by Mani and Jayaraman[10] on *Metrosideros and Hydnocarpus which* accede to the results of the present studies.

The galls with the larval chambers in the pith may be conceived to be the most specialized ones in terms of structural complexity and affording the gall insects a domain safer as well as of sustainable nutritive source. In the shoot axis galls studied by Jayaraman[11] on *Achyranthes, Astronidium, Coccinia, Mamordica* etc. the pith which harbours the larva, contributes substantially to the growth of the gall, while the cambium increases in perimeter and keeps in pace with growth of the gall. This type of cecidogenetic process stands parallel to the gall on T. *villosa* studied at present. Proliferation of the ground tissue at random usually results in the fragmentation of the cambium into many segments, which may further be thrown into forms like ring, loop or lash. This pattern of gall development occurs in E. *adenophorum* as well as in galls on *Sopubia trifida* and *Acacia suma*[8]. In *P. polyphyllus* the cleaved cambia segments remain *in situ* and produce considerable quantum of secondary xylem, of course with some structural deficiencies. The ellipsoidal nodal gall on *C. spinarum* is unique in that the cambial cylinder does not break during cecidogenesis, it undegoes extensieve additive divisions producing a bulk of continuous cylinder of secondary xylem and multiplicative divisions to increase the perimeter of the gall. The moth larva in *P. polyphyllus* is an aggressive feeder, chews and wound the xylem cylinder, whereas in *C. spinarum* the larva is minute insect with restricted feeding capability. So cleavage of the vascular cylinder may be partly due to feeding vigour of the insect in additin to hyperplastic potentials of the host tissues.

The aberrant micromorphological configurations of xylem components in the stem galls seems to be a widespread phenomenon observed by a few investigators[12,13]. The causal factors and the mechanism underlying such abnormalities remain little understood. Normal fuctioning of the cambium and regular course of cytodifferentiation of the cambial derivatives into vessels, fibres and xylem parenchyma depend upon certain critical chemical factors that include auxins, gibberellins, cytokinins, carbohydrates and possibly ethylene[14]. These substances are made available to the cambium and its derivatives from phloem translocating streams[15]. Deficiency in one or more of these factors will hinder the normal functioning as well as differentiation of the cambium and its products. The wounding and feeding activities of the gall-insects brings about an imbalance in the biochemical pool of the shoot axis tissues. When once the chemical composition of the meristematic plant tissues is meddled with, such changes may intercept the cambium either at the functional level or at the differentiation level of the cambial derivatives. Thus the histogenetic scenaria and the histological spectrum of the gall and on the shoot axes can be explained in terms of positional effects of the larvae coupled with the diffusing gradients of the chemically mediated cecidogenetic impulses emitted by the gall incitants.

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