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Cambial anatomy and absence of rays in the stem of *Boerhaavia* species (Nyctaginaceae)

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Structure of vascular cambium and its derivatives in *Boerhaavia diffusa* L., *B. verticillata* Poir. and *B. rependa* Willd. (Nyctaginaceae) was studied by anatomical methods.The stem revealed anomalous secondary growth characterised by the development of successive rings of xylem and phloem. The cambium was exclusively composed of fusiform initials giving rise to rayless secondary vascular tissues. While undergoing periclinal divisions cambium appeared nonstoried but remained storied when the divisions ceased. Each successive ring of cambium was originated from the outermost phloem parenchyma cells. The cambial ring was functionally segmented into fascicular and interfascicular regions, the former mainly producing conducting elements of xylem and phloem and the latter giving rise to parenchyma cells. The parenchyma cells on the xylem side developed into conjunctive tissue following thickening and lignification of cell walls. However, in *B. verticillata* and *B. rependa* the parenchyma cells on the pholem side also became lignified. In *B. diffusa* parenchyma cells did not undergo lignification. As a result, alternate bands of lignified and parenchyma bands became distinct in the stem. Vessel elements were short with simple perforation plate on slightly oblique to transverse endwall. Sieve tube members were slightly shorter as compared to the fusiform cambial cells.

Key words: *Boerhaavia*, plant anatomy, raylessness, vascular cambium

INTRODUCTION

Boerhaavia L. (Nyctaginaceae) has attracted the attention of plant anatomists due to the presence of medullary bundles and supernumerary cambium in the stem. Sabnis (1921) studied three species of *Boerhaavia* for the first time and that was probably the first contribution on Nyctaginaceae in India. He gave a brief description of anomalous growth in the stem. Maheshwari (1930) made detailed studies on primary and secondary growth in *B. diffusa* L. Bhargava (1932) studied the anatomy and embryology of *B. rependa* Willd. and found it to be identical to that of *B. diffusa*. The nodal anatomy of *B. diffusa* was described by Pant and Mehra (1961). Although *Boerhaavia* is basically herbaceous, its habit differs among the species studied. *Boerhaavia diffusa* is a diffuse herb with prostrate stems reaching 2–3 feet. *Boerhaavia rependa* is a diffuse subscandent herb, reaching 3–6 feet while *B. verticillata* Poir. is a decumbent or climbing herb reaching 6–8 feet in height. This paper deals with the anatomical details of development and structure of cambium, xylem and phloem and rayless nature in the stem of *B. diffusa, B. verticillata* and *B. rependa*.

MATERIALS AND METHODS

Segments of both young and mature stems measuring 4–10 mm in diameter were collected from *Boerhaavia diffusa*, *B. verticillata* and *B. rependa* growing naturally in the northern part of Maharashtra State (Bhorkheda) and the central part of Gujarat State (Vadodara). From each species 6–8 pieces of stem measuring 4–6 cm in length were collected. Three to four plants were sampled for each species. Samples were fixed in FAA and processed for microtomy by conventional methods (Berlyn & Miksche 1976). Transverse and longitudinal sections of 10–15 µm thickness were stained with a tannic acid-ferric chlorid lacmoide combination (Cheadle *et al.* 1953). An iodine-potasium iodide (Johansen 1940) test was used for the histochemical localisation of starch. To obtain the length of vessel elements and xylem fibres, small pieces of stem were macerated with Jeffrey's fluid (Berlyn & Miksche 1976) at 55–60°C for 12–24 hrs. The average length of fusiform cambial cells and sieve tube members was obtained directly from the tangential longitudinal sections of stem. To obtain the mean value, hundred random measurements were taken. Vessel frequency was counted in 0.5 mm^2 area of xylem in transverse section by using a projection microscope.

RESULTS

Structure of cambium

In all three species of *Boerhaavia* the cambium is exclusively composed of axially elongated fusiform initials. It is storied (Fig. 1A) when non-dividing and non-storied (Fig. 1B) in the functional state. The fusiform cambial cells are short, uninucleate with dense cytoplasm and beaded radial walls. The cell length does not show significant difference among the species studied. It ranges from 128 µm to 150 µm, 122 µm to 145 µm and 126 µm to 148 µm in *B. diffusa*, *B. verticillata* and *B. rependa,* respectively. The cambial cells undergo periclinal divisions giving rise to xylem and phloem without rays. (Fig. 1C).

Development of cambium

In all three species, the fascicular and interfascicular segments of the first cambial ring maintain their identity giving rise to conducting elements and interfascicular parenchyma respectively on both sides. The second ring of cambium differentiates from phloem parenchyma cells produced by the preceding cambium (Fig. 1D). The second and subsequent cambial rings in the stem developed similarly to the first ring, producing distinct bundles of conducting elements of xylem and phloem from fascicular region and parenchyma cells from interfascicular region (Figs. 1E and F). Each cambium in ring is narrow with two to three layers of cells arranged in radial rows. The cambial cells lose their identity following their differentiation into parenchyma cells in non-dividing cambial zone (Fig. 1G). The disappearance of cambial cells results in direct contact between the xylem and phloem tissue (Fig. 1G).

Structure of phloem

The secondary phloem is composed of sieve tube members, companion cells and axial parenchyma. In transverse section it appears as tangential bands alternating with the xylem in *Boerhaavia diffusa* (Figs. 1H and E) and as islands of sieve elements with associated parenchyma cells in *B. verticillata* and *B. rependa* (Figs. 1I and J). Compared with fusiform cambial cells the length of sieve tube members decreases slightly in all the species. The sieve tube members have slightly inclined end walls with simple sieve plates and are found associated with a companion cell. The phloem becomes non-functional following deposition of callose on sieve plates. The obliteration of sieve tube elements and disappearance of cambial cells seem to occur simultaneously.

Structure of xylem

There are three to five rings of xylem in the stems. Each ring is composed of bundles of vessels with associated parenchyma cells and fibres alternating with lignified conjunctive tissue.

In *Boerhaavia diffusa,* the xylem rings are distinct, alternating with phloem bundles and tangen-

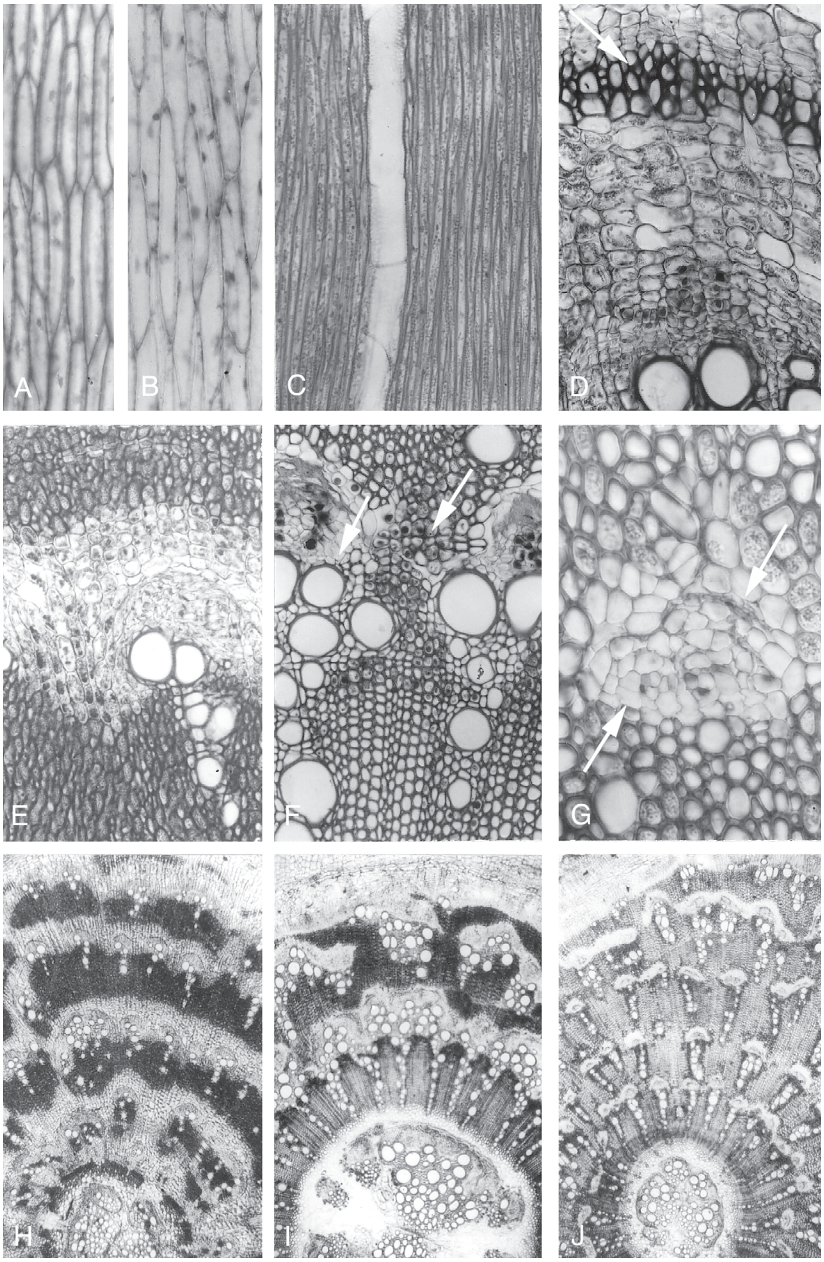

Fig. 1. *Boerhaavia* spp. (A–C, I and J apply to all three species studied). A–G: Transverse sections. H–J: Tangential longitudinal sections. — A: Storied arrangement of fusiform cambial cells of non-dividing cambium (× 80). — B: Cambium showing non-storied arrangement of cambial cells (× 80). — C: Rayless secondary xylem with vessel and fibres (× 84). — D: Newly formed outermost cambial ring with recently developed xylem (arrow) in *B. diffusa* (× 200). — E: A close view of part of two successive xylem rings enclosing pholem of *B. diffusa*. Note the conducting elements of xylem and phloem confined to the fascicular region of cambium (× 80). — F: Cessation of cambium in fascicular region (arrow) while xylem development is continued by interfascicular cambium (arrow head) in *B. verticillata* (× 84). — G: Complete differentiation of cambium (arrow) into phloem parenchyma in *B. verticillata* and obliteration of sieve elements (arrow head) (× 200). — H: Successive rings of xylem and phloem in the stem of *B. diffusa* (× 20). — I: The second cambial ring in association with distinct patches of xylem and phloem surrounded by interfascicular cells (× 20). — J: Successive rings of cambium with associated islands of xylem and phloem (× 20).

tially adjacent unlignified parenchyma cells (Figs. 1H and E). In *B. verticillata* and *B. rependa* the xylem rings in older stems are not distinct as the interfascicular parenchyma between the rings becomes lignified (Fig. 1F). Thus in the stem, the interfascicular regions appears radially continuous with lignified cells. This leads to the formation of islands of phloem tissue surrounded by lignified cells.

The rayless xylem of *Boerhaavia* is composed of vessel members, axial parenchyma and fibres (Fig. 1C). Vessels are angular to oval or oblong in transverse view. They are solitary or in radial to tangential multiples of three to ten often forming clusters. Their number ranges from 12–20 in *B. diffusa*, 15–31 in *B. verticillata*, and 9–15 in *B. rependa* per 0.5 mm^2 in transverse area of xylem with a radial diameter ranging from 49–96 μm, 37–136 μm and 25–112 μm in *B. diffusa, B. verticillata* and *B. rependa* respectively. The perforation plate at the end of each vessel element is simple on the slightly oblique to transverse end walls of vessel elements. Inter-vessel bordered pits are round to oval and alternate. In all the species, the vessel diameter increases parallel with the cambial cell division in each successive cambial ring (Figs. 1E and F). The axial parenchyma is vascicentric and sparse. The length of fibres ranges from 260–465 μm, 248–527 μm and 310–584 μm in *B. diffusa, B. verticillata* and *B. rependa* respectively. Histochemical studies revealed heavy deposition of starch in axial parenchyma and fibres in all the three species.

DISCUSSION

The stem of *Boerhaavia* shows anomalous secondary thickening via formation of successive rings of cambium (Maheshwari 1930). The cambium in all the three species is composed of only fusiform cambial initials which are storied when non-dividing and not-storied when actively dividing. The storied and non-storied nature of the cambium in the same stem appears to be related to the developmental changes occurring in the cambial cells. The absence of ray initials in the cambium results in the development of rayless xylem and phloem in the stem. The loss of rays occurs in plants having herbaceous habit with limited cambial activity, very short fusiform cambial cells and highly specialised cell types in secondary xylem (Carlquist 1970, Gibson 1973, 1978, Rao & Rajput 1997). Raylessness also tends to occur in plants showing anomalous secondary thickening (Metcalfe & Chalk 1983). Anomalous secondary growth results, in some groups at least, from loss of normal cambial activity during evolution toward an herbaceous mode of structure. It is considered that successive cambia can produce a larger stem or root diameter than a single cambium (Carlquist 1970). However, in the present study the stem diameter does not exceed more than 15 mm inspite formation of successive rings of cambium.

The functional behaviour of sieve elements is found to be similar to that of normal phloem with rays. Functional sieve tube members possess p-protein (slim plugs) while nonfunctional sieve tube members are devoid of cell content and accumulate callose on the sieve plate. These characters are considered as a signs of non-functioning sieve tube members (Davis & Evert 1970, Evert 1984, Deshpande & Rajendrababu 1985, Vishwakarma 1991).

Shorter and wider vessel elements are the characters of xeromorphic species and increase in length of vessel elements is associated with mesomorphy. However, these changes are not phenotypic modifications, but a result of genetically controlled mechanism of adaptation to mesomorphy and vis-a-vis to xeromorphy (Carlquist 1970). Compared with cambial cells, the length of vessel elements decreases slightly, but width increases by four to seven times in *Boerhaavia*. Xylem fibre and axial parenchyma serve as storage tissues, but as to how radial conduction takes place is obscure. The production of limited xylem and alternating bands of xylem and phloem may limit active radial transport of reserved metabolites. On the other hand, the exchange of material may take place via pits present on the tangential walls of the axial elements.

Maheshwari (1930) reported that the cells of the cambial zone completely differentiated into its derivatives when new cambia arose from phloem parenchyma, which were produced in the beginning of activity. However, our study reveals that the radial arrangement of cells in the cambium is maintained as long as the sieve elements are functional. The complete differentiation of cambial cells and obliteration of sieve elements seem to occur simultaneously. The differentiation of conducting elements of xylem and phloem from fascicular region of cambium and parenchyma cells from interfascicular region of cambium indicate that morphogenetic behaviour of cambial ring in *Boerhaavia*.

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