Ontogeny of cambium in *Amaranthus caudatus* L. and *Achyranthes aspera* L.

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Abstract. Young seedlings have two independent vascular systems which subsequently get fused with each other. The cambium originates in the form of patches in the pericycle of the root on 6th day of its growth in *Amaranthus caudatus* and on 10th in *Achyranthes aspera*. Later on, a complete ring is formed within the pericycle which subsequently differentiates acropetally and basipetally in the hypocotyl and root. This cambium is short-lived, bidirectional and has no relation with the fasicular cambial strips of differentiating vascular bundles. Successive cambia, originated from the innermost cells of the cortex, are also bidirectional in activity and have short span of life.

Keywords. Cambium ontogeny; *Amaranthus caudatus*; *Achyranthes aspera*.

1. Introduction

Centrospermae has attracted the attention of anatomists since long due to the presence of several rows of vascular bundles of secondary origin or having alternate rows of secondary xylem and secondary phloem (see De Bary 1884; Eames and MacDaniels 1947; Matcalfe and Chalk 1950; Esau 1977). The presence of these vascular bundles or rings is usually related to the occurrence of successive cambia (Esau and Cheadle 1969; Bhamie 1972; Zamski 1979). Normally a vascular cambium arises in the stem by the fusion of fasicular and interfasicular cambial strips, but in certain members of Centrospermae e.g., *Bougainvillea spectabilis*, *Mirabilis jalapa* and *Atriplex hortensis*, a cambium arises in the pericyclic region and has no relation with fasicular cambial strips as it originates before the differentiation of normal vascular bundles (Stevenson and Popham 1973; Micksell and Popham 1976; Gray and Popham 1981). In view of this, developmental anatomy of seedlings and structural configuration in the internodes of the stem of *Amaranthus caudatus* L. and *Achyranthes aspera* L. have been undertaken to have a better understanding of the origin of the first and successive cambia as well as the stelar configuration of seedlings.

2. Materials and methods

Seeds of *A. caudatus* and *A. aspera* were procured locally. Seedlings of different ages and pieces of internodes of the main stem were fixed in absolute alcohol: acetic acid (3:1). Usual method of paraffin embedding with ethyl alcohol and xylene was employed and microtome sections 10–12 μm thick were cut. Safranin-fastgreen combination was used for staining. Some handsections of internodes were also prepared.
3. **Observations**

3.1 **Seedling anatomy**

Cross-sections of the root on 6 and 10 days old seedlings of *A. caudatus* and *A. aspera* show a diarch xylem and two radially arranged phloem patches (figures 1, 6). Pith is absent. The metaxylems of these are centrally fused (figures 1–3). In the lower

![Diagram of seedling anatomy](image)

*Figures 1–12. 1–5. Serial transections of a 6 day old seedling of *A. caudatus*; note the occurrence of initiating cambial patches in figures 2 and 3, 4 and 5 respectively, 6–10. The same of 10th day old seedling of *A. aspera*; note the initiating cambial patches in figures 6 and 7 and enhancement of xylem elements in figure 7 and differentiation along with the adjacent of proto- and meta-xylem in figures 7 and 8 as well as 6 differentiating and fully developed bundles in figures 9 and 10. 11. Central portion of figure 1 magnified to show periclinaly divided and somewhat stratified cells of initiating cambium. 12. A portion from a t.s. of internode of *A. aspera* depicting two successive cambia. (cm1 – 1st cambium; cm2 – 2nd cambium; Co – cotyledon; Cr – cortex; ep – epidermis; end – endodermis; i. cm – initiating cambium; ph – phloem; pro – procambium; scl – sclerenchyma; sc. ph – secondary phloem; sc. xy – secondary xylem; xy – xylem; vb – vascular bundle).*
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3.2 Origin of cambium

Seedlings of 6, 10, 14, 18 and 24 days old have been studied to locate the site of the origin of the first cambium. The cross-sections of 6 and 10 days old seedling's root of A. caudatus and A. aspera have a differentiation of the cortical and vascular region by the formation of a presumptive endodermis-like layer (figure 11). The cells of this layer are barrel-shaped, regularly arranged and have slight thickened inner tangential walls. Casparian strips develop subsequently on their radial walls. Internally this layer is followed by a layer of thin-walled smaller meristematic cells which perhaps refers pericycle due to their position. These cells divide periclinally, the derivatives radially flattened, somewhat rectangular in shape and are arranged in stratified rows (figure 11). In the beginning the initiating cambium is recognized in patches just adjacent to phloem (figures 2, 6, 7, 11, 13–16). It is absent in the upper hypocotyl region. A 10 days old seedling of A. caudatus and 14 days old seedling of A. aspera though have a cambium in roots, it is in the form of discontinuous patches in the middle region of the hypocotyl (figures 13–17). A continuous cambium in the hypocotyl has been recognized when the seedlings of A. caudatus and A. aspera have attained the age of 14 days and 24 days respectively. This cambium gives rise to some secondary parenchyma followed by secondary phloem on its outer side and secondary xylem elements along with conjunctive tissue on its inner side.

3.3 Origin of successive cambia

Cross-sections of young internodes have 8–10 irregularly arranged and two centrally placed medullary bundles in A. caudatus and A. aspera respectively. The pith is bound by cambium and its derivatives. This, in turn, is being followed by an endodermis, cortex and epidermis. A. aspera has sclerenchymatous patches in between endodermis and phloem (figure 12) and collenchymatous patches in the cortex below the ridges as the stem is quadrangular. The two medullary bundles are free in the proximal 5 or 6 internodes but are being fused in the middle of internodes to form an amphiphylic strand in the rest of the distal internodes. Later on, the cambial strips (Amaranthus) and the entire cambial ring (Achyranthes) ceased to be active. New strips or a new ring of cambium originated from the outermost cells of the secondary phloem (figure 12). The newly formed cambial strips in Amaranthus get themselves further differentiated inwardly and become fused with the active cambial strips of the previous cambium forming a zig-zag cambium. This process is repeated and several successive irregular or smooth cambia originate one after another. They give rise to regularly arranged bundles in A. caudatus and rings of secondary xylem and phloem in A. aspera. All the cambia happen to be bidirectional in

they activity. Cambial cells of inactive cambial ring can be easily recognized due to their narrow, appressed, radially arranged somewhat stratified cells in a cross-section (figures 12, 18). The fasicular cambial strips of medullary bundles are of limited activity.
4. Discussion

Three points which can be profitably discussed here are: (i) the site of the first cambium; (ii) activity and origin of successive cambia; and (iii) stelar configurations of seedlings.

Regarding the origin of cambium in the members of Centrospermae there are different viewpoints. De Bary (1884) has opined that a ring of cambium develops on the outer margin of the phloem while the primary bundles are still at the stage of differentiation. Artschwager (1920) has stated that cambium patches get differentiated in the pericyclic region opposite the vascular bundles and partly as interfascicular cambial strips. Maheshwari (1930) has found cambial ring forming by the fusion of interfascicular and interfascicular cambial strips of the outermost ring of vascular bundles of 3 rings present within Boerhaavia diffusa. Balfour (1965) has been of the opinion that in Amaranthaceae, a cambium originates in the extrafascicular region of the stem in the parenchyma cells present on the periphery of primary phloem. In Bougainvillea spectabilis, Mirabilis jalapa and Atriplex hortensis, wherein the ontogeny of cambium has been studied in the seedlings of various stages, the first cambium originates in the pericyclic region (Stevenson and Popham 1973; Miksell and Popham 1976; Gray and Popham 1981). Present findings regarding the ontogeny of cambium have corroborated the work of Popham and his students as the cambium has been found to be pericyclic in origin. It has no relation with the fascicular cambium of the axial bundles which differentiate inbetween the xylem and phloem. Fasicular cambial strips have limited activity as in the medullary bundles of Boerhaavia (Maheshwari 1930).

There are two different views regarding the origin and activity of successive cambia. According to one, the first formed cambium remains permanently active throughout the life of the plant (De Bary 1884; Wilson 1924; Boureau 1957). A modification of this view has been proposed by Balfour (1965) who maintains that the first formed cambial ring remains active as it is self perpetuating on its outer side. The secondary phloem gets differentiated within it and subsequently its outermost layers give rise to a new cambium. Her work has influenced Philipson and Ward (1965) to categorize cambium as bidirectional and unidirectional. Centrospermae according to them have unidirectional cambium as secondary xylem and secondary phloem are produced on the same side. The advocates of the second view have opined that first formed cambium has limited activity and after its cessation another cambium develops just adjacent to the secondary phloem mostly from the innermost cortical layers either as complete or partial ring or in patches which subsequently form a ring (Artschwager 1920; Maheshwari 1930; Joshi 1937). Esau and Cheadle (1969) after reinvestigating Bougainvillea spectabilis have reported that anomalous distribution of vascular tissue is due to origin of successive cambia one after another. This concept has been upheld by Bambie (1972), Pannikar and Bambie (1974), Stevenson and Popham (1973), Miksell and Popham (1976), Zamski (1979) and Gray and Popham (1981) in various taxa of Centrospermae. Present observations on the origin of successive cambia and their activity fully substantiate the idea of Esau and Cheadle (1969). Concentric rows of vascular bundles can be easily explained due to these cambia.

Regarding the fusion of medullary bundles in the distal internodes of Achyranthes, the present findings are in accordance with those of Joshi (1934) and Srivastava (1960). Joshi (1934, 1937) has asserted that amphixylic vascular bundle represents a derived and advanced condition.
In young seedlings, the epicotyl axis has vascular supply in the form of procambium. Maturation of xylem starts in the basipetal direction. In young seedlings, the vasculature of shoot is independent of root-hypocotyl-cotyledon. Later on, the vasculature of stem gets superimposed and fused with that of root-hypocotyl-cotyledon. The present observations thus support Thoday's (1939) interpretation, who has envisaged the double origin of vascular system in the seedlings of angiosperms. Such two independent systems have been described from a number of plants (Weaver 1960; Pillai and Sukumaran 1969; Bhambie and Nigam 1976; Gupta and Bhambie 1978; Goyal and Pillai 1979; Dubey et al 1981).

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