CAMBIAL VARIANTS IN THE ROOTS OF *GLINUS LOTOIDES* L. AND *G. OPPOSITIFOLIUS* (L.) A. DC. (MOLLUGINACEAE)

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Structure and development of successive cambia and their derivatives are studied histologically in the root of two species of *Glinus* (Molluginaceae). In both species first ring of cambium functions for a short time followed by the development of second ring from the cortical parenchyma. The subsequent cambial rings formed followed the similar pattern of development. The mature roots are composed of three to five successive rings of xylem alternating with phloem. Absence of ray initials in the cambium leads to the development of rayless xylem and phloem. Xylem consists of vessel elements, tracheids, libriform fibres, fibre tracheids and axial parenchyma. In transverse view vessels appear oval to circular and solitary in *G. lotoides* and angular, narrow and mostly in radial multiples in *G. oppositifolius*. Xylem fibres retain their nucleus even after the formation of secondary walls in both the species. Storage of starch in the lumen is a characteristic feature of fibres. The significance of successive cambia, rayless xylem and nucleated xylem fibres is discussed in relation to the plant habit.

Key words: *Glinus*, Molluginaceae, nucleated fibres, rayless xylem, successive cambia

INTRODUCTION

It has been known for many years that the secondary thickening in the axis of comparatively small number of dicotyledons proceeds in various other ways. Such pattern of secondary growth is commonly known as anomalous secondary growth, which is recently referred as cambial variant. The term cambial variant is employed as a way of referring to the less common type, anomalous may give the misleading impression of disorderly action (Carlquist 1988). There has been a growing interest on the development of cambial variants in different groups of plants (Kirchoff and Fahn 1984, Timonin 1987, Philipson 1990, Carlquist 1999*a, b*, Rajput and Rao 1998, 1999*a*, Rao and Rajput 1998, 2000), because of its significance from ecological and evolutionary point of view (Metcalfe and Chalk 1983, Carlquist 1988, Rajput and Rao 1999*a*).

Both the species of *Glinus* are diffuse prostrate herbs with thin (less than 3 mm in diameter) spreading branches, reaching 0.2 to 0.4 m in length. *G. lotoides*

usually begins to appear from the seeds in moist places in December–January and completes its lifecycle before June. Whereas, the saplings of *G. oppositifolius* grow on the wastelands in October–November and complete their lifecycle before May. Although, both *Glinus* species complete their vegetative and reproductive growth within a period of 3–6 months, their roots increase in thickness by the formation of successive cambia. However, no such cambial rings are observed in the vegetative shoots of both species. Therefore, the present investigation is aimed to elucidate the structure and development of cambial variant in the roots of two species of *Glinus* (Molluginaceae).

MATERIALS AND METHODS

Ten to fifteen pieces of roots measuring from 5 to 15 mm and branches with 2 to 2.5 mm in diameter were collected from the plants of *Glinus lotoides* and *G. oppositifolius* growing at Pavagadh in Gujarat. Immediately after the collection, samples were fixed in FAA (Berlyn and Miksche 1976), dehydrated through tertiary butanol series and embedded in paraffin. Transverse and tangential longitudinal sections of 12–15 µm thickness obtained with rotary microtome were stained in safranin-fast green combination. Some of the sections were treated with 4% acetocarmine and I_2KI for localisation of nucleus and starch, respectively.

Maceration of the xylem tissue was carried out to study general morphology and size of vessel elements and fibres. Length of the fusiform cambial cells was obtained directly from the tangential longitudinal sections. One hundred measurements were chosen randomly to obtain mean and standard deviation.

RESULTS

Structure of cambium

In both species, the mature root is composed of three to five successive rings of cambia, each formed of fusiform initials alone. The cambial cells are storied and short with the length ranging from 129–168 µm. As seen in transverse view, cambium is three to four-cell layered during the development of xylem and phloem while it differentiates completely into xylem and phloem derivatives when it becomes non-functional. The cambial rings are continuous forming a complete cylinder in *Glinus lotoides* while they appear discontinuous in *G. oppositifolius* resulting overlapping segments leading to the union and anastomosing of the adjacent rings.

Origin and development of successive cambia

The first ring of cambium develops in a manner that is typical in any dicot root. This ring of cambium functions for limited period and ceases to divide after the formation of 1.5 to 2 mm of xylem. Second ring of cambium develops following the divisions of innermost cortical parenchyma cells (Fig. 1A). The cortical parenchyma, usually four to five cell layers external to the phloem produced by previous cambium undergo differentiation following repeated periclinal divisions. This results in the formation of radial rows of cells forming complete ring of cambium (Fig. 1A,B). Those four to five layers of cortical parenchyma present between newly developed cambium and phloem of previous cambium mature into conjunctive tissues (Fig. 1A,D). Formation of further successive cambial rings followed similar pattern of its development.

Structure and development of vascular elements

In both *Glinus* species, cambium is functionally bi-directional producing both xylem centripetally and phloem centrifugally. However, development of phloem starts only after the formation of 8–10 xylem derivatives. The first elements to differentiate on xylem side in *Glinus lotoides* are always fibres. The development of relatively wider vessel element starts only after the formation of 9–12 fibres and fibriform vessels (Fig. 1C). No such pattern of vessel development is maintained in *G. oppositifolius* (Fig. 1D). The vessel development may start directly after the origin of new cambium ring or after the formation of few other elements.

As seen in transverse view, secondary xylem of both species is composed of three to five successive rings of xylem alternating with the phloem (Fig. 2A,B). However, these rings are not always continuous in *G. oppositifolius* but show union and anastomosing (Fig. 2A). Xylem consists of vessel elements, tracheids, fibre tracheids, libriform fibres and axial parenchyma while rays are absent (Fig. 2C,D). In both species, vessels show dimorphism, i.e. vessels with relatively wider lumen diameter and fibriform vessels (Fig. 2E). The latter type of vessel elements are the fusiform cells that are like imperforate tracheary elements except for the occurrence of small sub-terminal perforation plate near each end of the cells (Carlquist 1991). In *G. lotoides* the wider vessels are mostly solitary and oval to oblong with simple perforation plate on their slightly oblique to transverse end walls. The vessel element length and width vary from 127–153 μm and 69–87 μm, respectively. Whereas, in *G. oppositifolius* vessels are mostly angular and in radial multiples of 2–10 cells. The length and width of vessel elements ranges from 98–123 μm and 54–63 μm, respectively. However, the development of fibriform vessels is seen only in the xylem that is
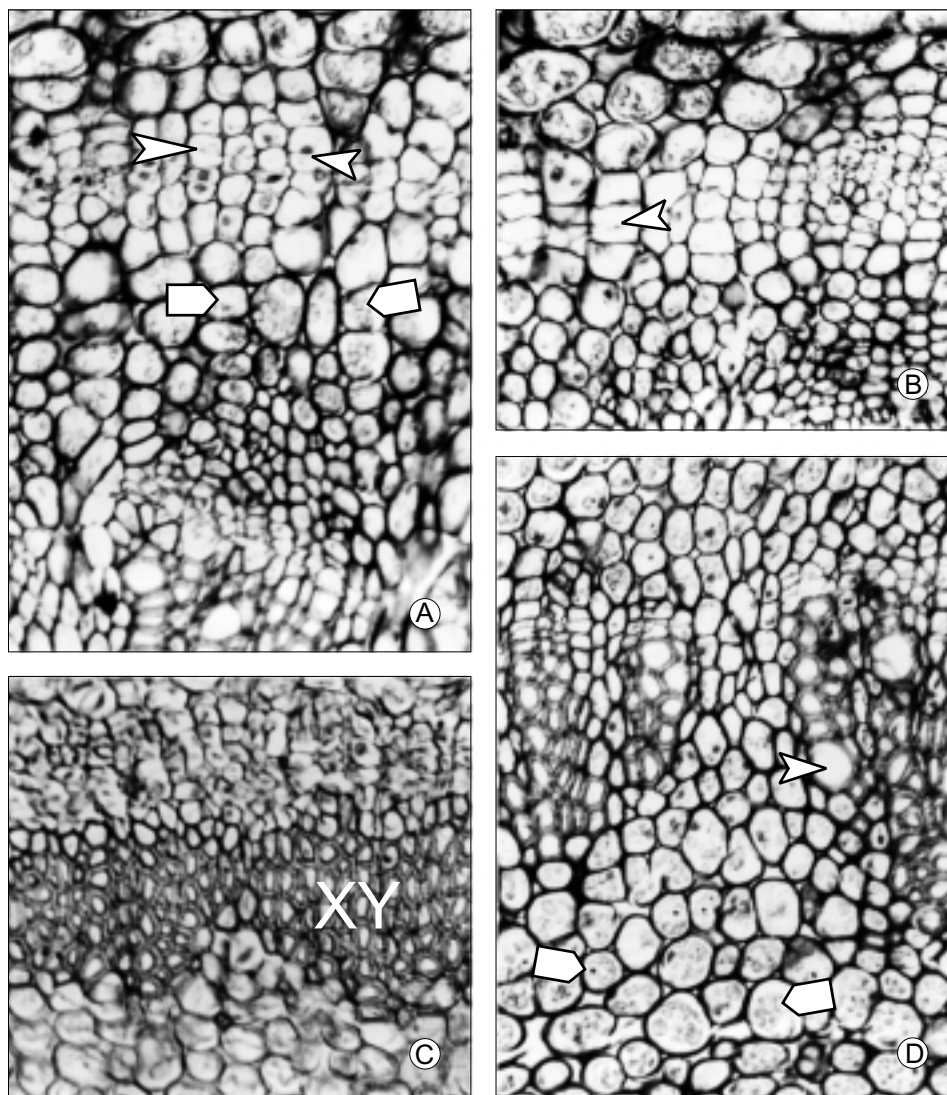
Fig. 1. Transverse view of the stem of *Glinus lotoides* and *G. oppositifolius*. – A = Development of new cambium from the cortical parenchyma (arrowheads). Arrow indicates cortical parenchyma cells between the phloem of previous cambium and developing cambium that differentiate into conjunctive tissues in *Glinus oppositifolius* (×198). – B = Repeated periclinal divisions in cortical parenchyma resulting in the formation of cambial cell layers (arrowhead), (×168). – C = Vessel-less xylem formed from new cambium in *Glinus lotoides* (×168). – D = Xylem produced in the beginning of new cambium in *Glinus oppositifolius*. Arrowhead indicates a vessel (×198)
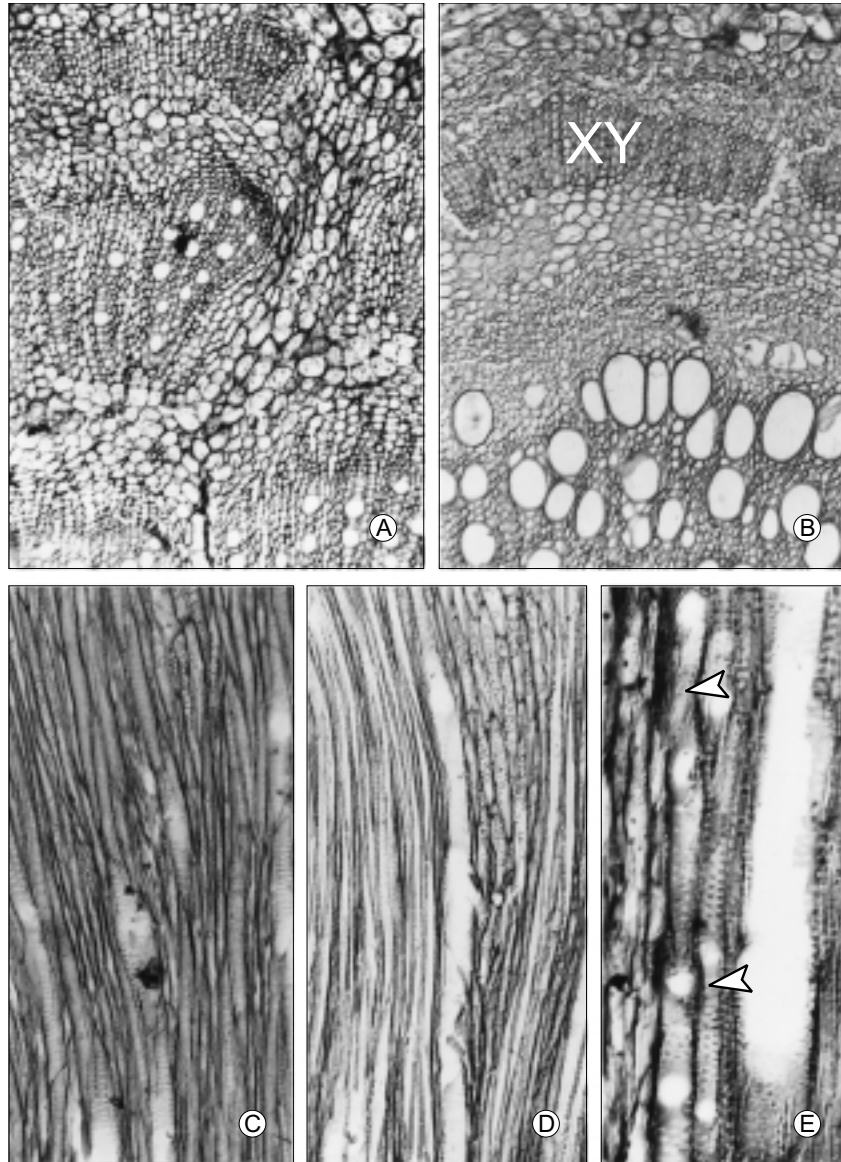
Fig. 2. Transverse (A–B), tangential (C–E) view of the stem in *Glinus lotoides* and *G. oppositifolius*. – A = Structure of xylem in mature root of *Glinus lotoides* (×48). – B = Two adjacent rings of xylem in *Glinus oppositifolius* with the outer ring showing no vessels while inner ring showing vessels with different lumen diameter (×48). – C = Rayless xylem of *Glinus lotoides* (×120). – D = Rayless xylem of *Glinus oppositifolius*. Note the variation in the vessel lumen diameter (×116). – E = Fibriform vessel formed in the beginning of xylem development (arrowheads). Note the variation in lumen diameter of the adjacent vessels (×330)

produced in the beginning of each newly developing successive cambia and it is difficult to make out in transverse view due to their narrow lumen diameter, which is almost equal to fibre diameter. Vessel elements possess alternate bordered pits on the radial walls. Not much variation in the length and width of fibriform vessel elements is noticed between the species.

Xylem in both species is composed of libriform fibres as well as fibre tracheids. They are thick walled cells with narrow lumen and tapering ends ranging from 467–547 μm and 14–18 μm in length and width, respectively. Simple pits with slit like aperture on the lateral walls of the libriform fibres formed narrow angle with the fibre axis while they are alternate, bordered and oval to circular in fibre tracheids. Xylem fibres retain their nuclei in both the species even after the deposition of secondary wall materials. The nuclei are oval to oblong or fusiform shaped ranging from 7–10 μm and 2–3 μm in length and width, respectively. Several starch grains of different sizes accumulate in the fibre lumen of both the species.

DISCUSSION

Occurrence of successive cambia in the roots is reported for the first time in two species of *Glinus* (Molluginaceae). In both species radial growth in roots occurs by the formation of concentric rings of xylem alternating with phloem while the aerial branches show normal secondary growth. The normal secondary growth that occurs in the branches may be associated with the habit of the plant. As both the species of *Glinus* are diffuse prostrate herbs with profuse branching from the ground level and lacks true stem. These branches are thin (not exceeding 1.5–2.5 mm in length) and have more or less uniform diameter.

In the species of *Glinus*, the repeated periclinal divisions in cortical parenchyma develop second ring of cambium. Prior to the initiation of second cambium ring, tangential divisions in cortex may form radial rows of parenchyma termed as secondary cortex by Carlquist (1999*a*, *b*). Such radial rows of secondary cortex are conspicuous in both *Glinus* species. However, Carlquist (1999*a*, *b*) called diffuse lateral meristem to the formation of successive cambia from such parenchyma (secondary cortex). Because the periclinal divisions do not take place in a single layer, as in vascular cambium, but at various points in the radial rows of secondary cortex. The second ring of cambium in a species with successive cambia is formed not immediately outside the secondary phloem formed by the previous cambium, but it is separated from the phloem by 4–6 layers of cortical parenchyma. This is also true in case of successive cambia formed subsequently in both the species of *Glinus*. The layers of cortical parenchyma between the newly formed cambium and phloem produced from pre-

vious cambium differentiate into conjunctive tissues. However, Carlquist (1999*a*) suggests that the term-included phloem should not be applied to the phloem of species with successive cambia. Because the conjunctive tissue is not formed from a vascular cambium and by definition it does not belong to secondary xylem.

Absence of rays tends to occur in those plants, that show scanty accumulation of secondary xylem and cambium remains functional for a short duration. In such plants successive cambia can increase stem or root diameter. Such a successive ring of xylem produced is always remains rayless (Barghoorn 1941, Carlquist 1970, Rao and Rajput 1998, Rajput and Rao 1998, 1999*a*). Both *Glinus* species show scanty accumulation of secondary xylem in each ring and root diameter increases by the activity of successive cambia. Occurrence of cambial variant is the result of loss of normal cambial activity during the evolution towards the herbaceous mode of structures (Carlquist 1970) and in this plants woodiness is in the process of increase rather than decrease. In such plants fusiform cambial cells are very short and possess highly specialised cell types in secondary xylem (Gibson 1978) and all these features are characteristics of both species of *Glinus*.

Presence of nucleated xylem fibres in *Glinus* seems to be associated with the absence of rays. Moreover, accumulation of starch in fibre lumen also suggests that in addition to mechanical support, it also acts as reservoir of photosynthetic products representing further connection between parenchyma cells and xylem fibres (Rajput and Rao 1999*b, c*). It appears that in the absence of rays, nucleated fibres in rayless xylem may play an important role in radial conduction of photosynthates. Fahn and Leshem (1963) suggested that occurrence of nucleated xylem fibres is an adaptive feature associated with diminishing supportive function exhibiting transition forms towards parenchyma cells prevailing in herbaceous plants.

Vessels with relatively wider lumen and narrow fibriform vessels are noticed in both *Glinus* species, the condition that is common in vines (Ayensu and Stern 1964, Carlquist 1988). However, fibriform vessels are also reported in non-scandent group of plants such as members of Hydrophyllaceae (Carlquist 1988). Formation of fibriform vessels is seen only in the xylem produced in the beginning of each successive ring when there is no formation of wider vessels. According to Zimmermann and Brown (1971) and Ewers (1985) narrow vessels tend to develop embolism much less readily than wide ones and wider vessels are less capable of recovery from embolism than narrow ones. However, narrow vessels have greater surface to volume ratio if degree of bonding of water to vessel wall is important in resisting embolism formation (Carlquist 1991). In functional terms, fibriform vessels have much greater

conductive safety than wider vessels and narrow vessels would continue to conduct even though wider vessels become embolised.

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