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Secondary Growth of the Stem of *Celosia argentea* L. and *Aerva sanguinolenta* (L.) BLUME (*Amaranthaceae*)

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With 2 figures

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Summary

RAJPUT K. S. 2001. Secondary growth of the stem of *Celosia argentea* L. and *Aerva sanguinolenta* (L.) BLUME (*Amaranthaceae*). – Phyton (Horn, Austria) 41 (2): 169–177, with 2 figures. – English with German summary.

Structure and development of vascular cambium was studied histologically in the stem of *Celosia argentea* L. and *Aerva sanguinolenta* (L.) BLUME (*Amaranthaceae*). In both the species secondary growth resulted in the development of successive rings of cambia. The cambium is storied consisting only of fusiform initials giving rise to rayless vascular tissues at least in the early part of secondary growth. In the later part of the secondary growth, development of vertically elongated rays were observed in *Celosia argentea.* Each successive ring of cambium developed from the axial parenchyma at a distance of about four to six cell layers external to the phloem produced by the previous cambium. Functionally the cambium was bi-directional producing xylem centripetally and phloem centrifugally. Developmentally each cambium ring was divided into two distinct types : i. small segments of cambium producing conducting elements of xylem and phloem, and ii. wider segments of cambium giving rise to thick-walled conjunctive tissues centripetally and thin-walled parenchyma centrifugally in *Aerva sanguinolenta* and thin-walled parenchyma on both xylem and phloem side in *Celosia argentea.* This variation in cambial behavior resulted in the formation of successive rings of xylem alternating with

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phloem and axial parenchyma in *Aerva sanguinolenta* and vascular bundles embedded in ground mass of axial parenchyma in *Celosia argentia*.

Zusammenfassung

RAJPUT K. S. 2001. Sekundäres Dickenwachstum in den Stämmen *Celosia argentea* L. und *Aerva sanguinolenta* (L.) BLUME (*Amaranthaceae*). – Phyton (Horn, Austria) 41 (2): 169–177, 2 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Es wurde der Aufbau und die Entwicklung des vaskulären Kambiums im Stamm von *Celosia argentea* L. und *Aerva sanguinolenta* (L.) BLUME histologisch untersucht. In beiden Arten resultiert das sekundäre Dickenwachstum aus einer Bildung von aufeinanderfolgenden Kambialringen. Das Kambium ist so aufgebaut, dass es nur aus fusiformen Initialen besteht, welches zu strahlenlosen vaskulären Geweben führt; dies betrifft zumindest den frühen Teil des sekundären Dickenwachstums. In der späteren Entwicklung des sekundären Dickenwachstums kann bei *Celosia argentea* eine Entstehung von vertikalen Strahlen beobachtet werden. Jeder aufeinanderfolgende Kambiumring entsteht aus axialem Parenchym in einer Entfernung von ungefähr 4 bis 6 Zellschichten außerhalb des Phloems, welches vom vorhergehenden Kambium gebildet wurde. Das Kambium produziert das Xylem zentripetal und das Phloem zentrifugal. Entwicklungsmäßig ist jeder Kambiumring in zwei markante Bereiche unterteilt. 1. Schmale Abschnitte des Kambiums, welche die Leitelemente des Xylems und Phloems bilden und 2. breite Segmente des Kambiums, welche dickwandige Zellkomplexe centripetal und dünnwandige Parenchyme centrifugal bei *Aerva sanguinolenta* abgeben; bei *Celosia argentea* werden nur dünnwandige Parenchyme sowohl auf der Xylem als auch auf der Phloemseite abgegeben. Dieser Unterschied im Verhalten der Kambien bewirkt die Bildung von aufeinanderfolgenden Xylemringen, abwechselnd mit Phloem und axialem Parenchym in *Aerva sanguinolenta* und bei *Celosia aregentia* von Gefäßbündeln die in einer Grundmasse von axialem Parenchym eingebettet sind.

Introduction

The important functions of rays are radial transport of reserve materials and water as well as storage and strengthening (VAN BEL 1990, HARMS & SAUTER 1992). Regeneration after wounding (KURODA & SHIMAJI 1984, LEV-YADUN & ALONI 1995) and aeration, the radial transport of gases (HOOK & al. 1972, RAJPUT & RAO 1998a) are specifically achieved by the rays. In the compartmentalization of wounds, the rays also participate by forming the radial wall of the compartment (SHIGO 1984). In spite of all these important functions, a tiny portion of dicotyledons is found to be devoid of rays among them, the Amaranthaceae (BARGHOORN 1941, GIBSON 1978, CARLQUIST 1988, RAO & RAJPUT 1998, RAJPUT & RAO 1999a).

This family is well known to possess secondary growth, which is abnormal in all the investigated cases (BALFOUR 1965, RAJPUT & RAO 1999a), although opinions have differed on the mode of its formation (DE BARY 1884, DAUSTER 1925, PFEIFFER 1926, JOSHI 1937, METCALFE & CHALK 1950, BALFOUR 1965, TIMONIN 1988). In all investigations attention has been

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directed mainly to the origin of the meristem responsible for the secondary growth, but the occurrence of rayless xylem was neglected. Moreover the cambium of Amaranthaceae is considered functionally unidirectional (PHILIPSON & WARD 1965, PHILIPSON 1990). The present investigation is therefore, focused on the functionally bi-directional nature of the cambium and of the occurrence of rayless xylem in *Celosia argentia* L. and *Aerva sanguinolenta* (L.) Blume (*Amaranthaceae*).

Materials and Methods

Four to eight internodal segments of the main stem measuring 3–20 mm in diameter were collected in July, September and March from ten plants of *Aerva sanguinolenta* L. and *Celosia argentia* (L.) Blume (*Amaranthaceae*) growing at Bhorkheda in north Maharashtra. These samples were immediately fixed in FAA (BERLYN & MIKSCHE 1976). Transverse, radial and tangential sections of 15–20 µm thickness were obtained with rotary and sliding microtome and stained with safranin fast/green combination (JOHANSEN 1940) for general studies. Some of the sections were also stained with 4% acetocarmine and potassium iodide for nucleus and starch localization, respectively.

Macerations of xylem were also prepared to study general morphology and size of vessels and fibers. One hundred objects were chosen randomly to obtain mean and standard deviation.

Results

Both *Celosia argentia* and *Aerva sanguinolenta* are the annual erect herbs reaching four to six feet in height and 10–20 mm in diameter. With the onset of rains in June, new saplings develop from the seeds and later flower in September-October. Fruit maturation and its dispersal occur in the subsequent months of December and January, respectively. These plants show leaf yellowing and shrinkage of stem in February-March, which ultimately results in a complete drying of the plants in April when it is dry and hot (average temperature 40 °C).

Structure of cambium

The stem is composed of three to five successive cambium rings comprised entirely of fusiform cambial initials at least in the early part of secondary growth. However, in *Celosia argentia* some of the fusiform cambial cells undergo further division and result in the development of vertically elongated rays. In *Aerva sanguinolenta* no such ray formation is observed throughout the life span of the plants. The cambium is storied with relatively short fusiform cambial cells varying from 87–179 µm in length. In transverse view, the cambium appears to be two to three layered when non-dividing, and four to six layered during the development of xylem and phloem. Functionally each cambium is divided into two distinct types: i. The segment of cambium producing conducting elements of xylem

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and phloem, and ii. The segment of cambium producing thick-walled conjunctive tissues toward the xylem in *A. sanguinolenta* and thin walled conjunctive tissues on both xylem and phloem side in *C. argentia*.

Development of vascular cambium

In both the species studied, the first ring of cambium ceases to divide after a limited period of activity. The second ring of cambium develops from the axial parenchyma cells at a distance of about three to six cell layers outside the phloem produced by the previous cambium (Fig. 1A, B). However, during the development of new cambium one or two parenchyma layers undergo repeated periclinal divisions and result in the formation of three and four layered wide bands of cells (cambium) arranged in radial files (Fig. 1B, C). The four to five layers of parenchyma between the newly developed and previous cambium differentiate into conjunctive tissues. The formation of subsequent cambia followed similar pattern of development as described above. In *A. sanguinolenta* development of new cambium ring is observed only after the cessation of cell divisions in previous cambium while in *C. argentia* the development of new cambium is seen even though the previous cambium is functionally active and giving rise to xylem and phloem elements (Fig. 1A).

Structure and development of vascular elements

In both the species, each cambium is bi-directionally functioning and producing xylem centripetally and phloem centrifugally (Fig. 1C, D). The development of xylem and phloem is not synchronous. It may occur simultaneously in some of the segments (Fig. 1C), in other segments the xylem development precedes that of phloem. However, the ratio of xylem to phloem development varies from 6:1 to 8:1 (Fig. 1 D). This variation gives an impression of unidirectional nature of the cambium. As aforementioned, the development of each cambium is of two distinct types (Fig. 1E, F). In *C. argentia,* the segment of cambium responsible for the development of conjunctive tissues differentiates exclusively into thin walled parenchyma on both the xylem and phloem side (Fig. 2A), while in *A. sanguinolenta* it forms thick-walled elements towards xylem and thin-walled parenchyma cells toward phloem. (Fig. 2B). This variation in the differentiation of vascular elements from the cambium results in the formation of a continuous ring of xylem alternating with a phloem ring in *A. sanguinolenta* and vascular bundles embedded in ground tissue in *C. argentia*.

Xylem is composed of vessel elements, tracheids, axial parenchyma and fibres while xylem rays are absent throughout the life span of *A. sanguinolenta* and they developed in *C. argentia* when the plants reached the flowering stage (Fig. 2C, D). These rays are mostly uniseriate, but multiseriate rays are also observed which are composed of upright cells. Vessels

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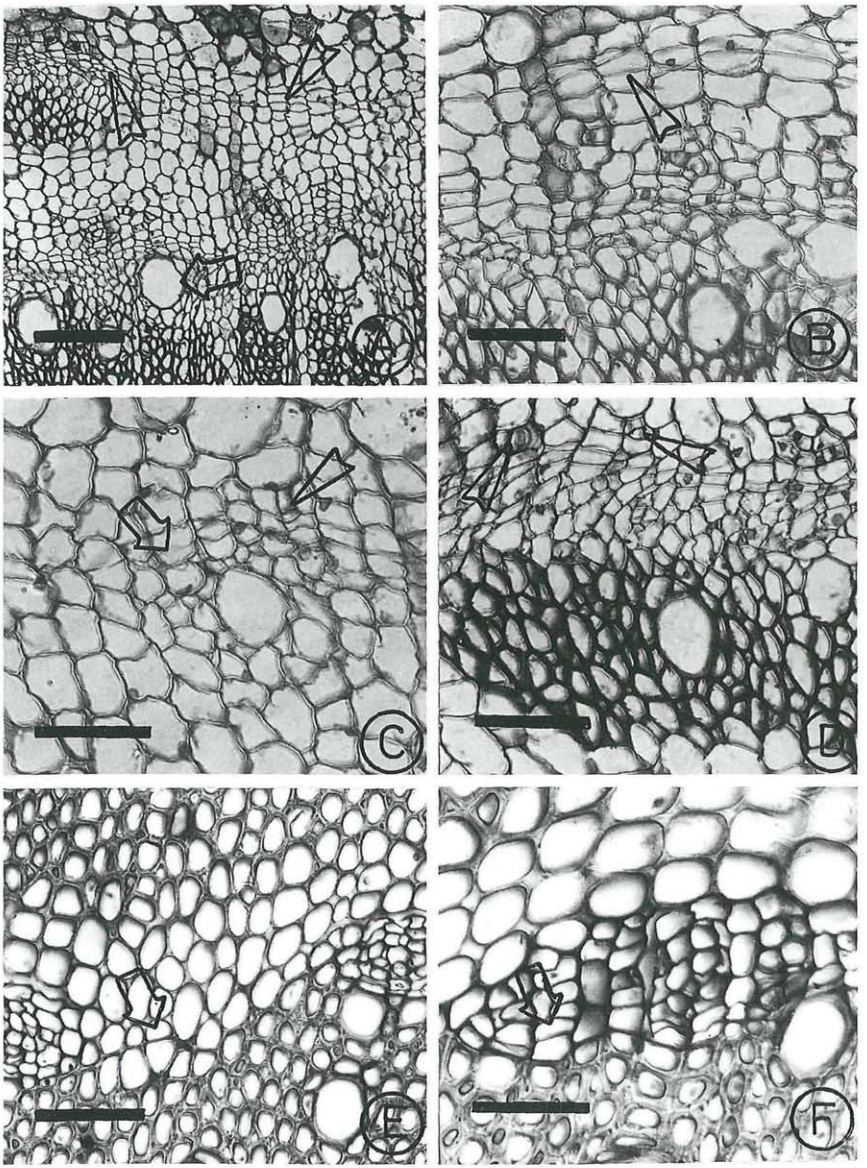

Fig. 1 A–F. Transverse view of cambium and xylem of *Celosia argentia* and *Aerva sanguinolenta*. A: Development of new cambium ring in *Celosia argentia* external to the previous cambium (arrowheads). Note the differentiating xylem elements (arrow) from the previous cambium. B: Enlarged view of newly developing cambial ring in *C. argentia* (arrowhead). C: Simultaneous development of xylem and phloem (arrowhead) in *C. argentia* showing bi-directional nature of cambium. D: Newly developed cambium showing relatively more xylem development than phloem in *C. argentia*. Arrowhead indicates sieve tube element. E: Interfascicular cambium differentiates completely into conjunctive tissues in *Aerva sanguinolenta* (arrow). F: Fascicular cambium maintains its radial arrangement even after the cessation of cell division in *A. sanguinolenta*. DV: Differentiating vessel. Fig. 1 A–F Scale Bar = 100 μm

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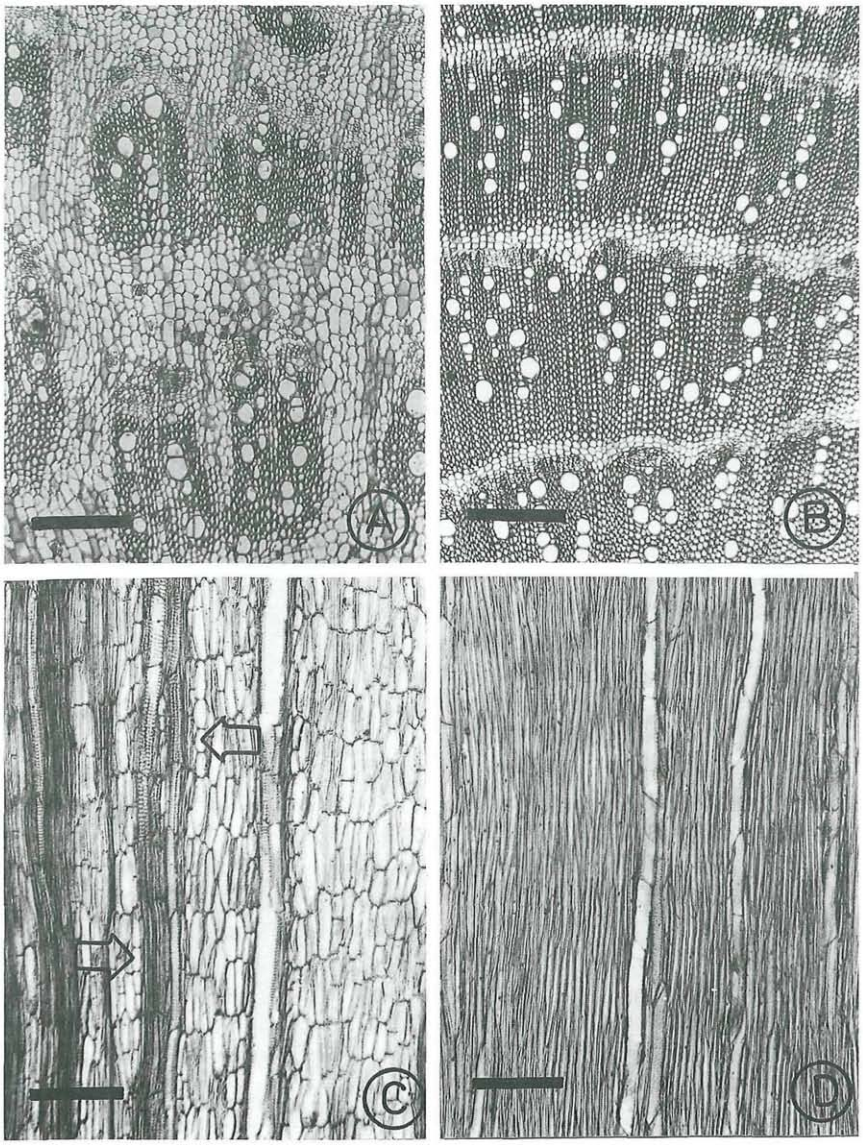

Fig. 2. Transverse (A, B) and tangential longitudinal (C, D) view of xylem in *C. argentia* and *A. sanguinolenta*. A: Structure of xylem in mature stem of *Celosia argentia*. B: Structure of xylem in the mature stem of *A. sanguinolenta*. C: Vertically upright rays (arrow) formed in the later part of xylem development in *Celosia argentia*. D: Rayless xylem of *Aerva sanguinolenta*. Fig. 2 A–D Scale Bar = 150 μm

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are oval to circular with alternate bordered pits on their lateral walls. They possess simple perforation plate on their slightly oblique to transverse end walls. Vessels are either solitary or in radial multiples of two to four. The length of vessel elements vary from 74–168 μm and width from 55–98 μm. Fibers are non-septate with simple pits on their radial walls. Xylem fibres retained their living protoplast and nucleus even after the development of secondary wall. The nuclei are oval to oblong and fusiform measuring from 6–12 μm in length and 3–4 μm in width, whereas fibre length measures from 658–783 μm and their width from 18–22 μm.

Discussion

The pattern of secondary thickening in *Amaranthaceae* deviates from that of many dicotyledons investigated (BALFOUR 1965, FAHN & ZIMMERMANN 1982). Much attention has been paid to the question whether each growth increment of secondary vascular tissue arises from a separate cambium layer or from a residuum of the previous cambium (BALFOUR 1965, PHILIPSON & WARD 1965, BAIRD & BLACWELL 1980, FAHN & ZIMMERMANN 1982). However, the composition and development of their derivative tissues remained neglected (RAO & RAJPUT 1998, RAJPUT & RAO 1998b, 1999a). DE BARY 1884 and BALFOUR 1965 have studied the development of secondary meristem thoroughly in *Celosia argentia* and *Celosia thompsoni*. However, there is no mention about the absence of a radial system in xylem and phloem in the early part of secondary growth and the occurrence of nucleated xylem fibres.

In all the members of Amaranthaceae, cambia are reported to be functionally unidirectional (BALFOUR 1965, PHILIPSON & WARD 1965). In the present investigation, both the species showed bi-directional differentiation of xylem and phloem. Similar observations were also been made in *Pupalia lappacea* (RAJPUT & RAO 1999a), a member of the same family. In the species investigated, the time of xylem and phloem differentiation is not necessarily synchronized. Phloem development may start simultaneously or after the development of few xylem derivatives. However, the less intense production of phloem elements as compared to xylem gives a false impression of a functionally unidirectional cambium (RAJPUT & RAO 1999a).

Rayless xylem has also been reported in some genera and is restricted to a small portion of dicotyledons (GIBSON 1978, CARLQUIST 1988, LEV-YADUN & ALONI 1995, RAO & RAJPUT 1998, RAJPUT & RAO 1999a). Raylessness may be total, i.e. rays are not formed at all during the entire life span of the plants, or it may be temporary, i.e. raylessness is restricted to the juvenile wood (LEV-YADUN & ALONI 1995). In *Aerva sanguinolenta* rays are found to be absent even in the samples collected at the end of the growing season while they appear in *Celosia argentia* in the later part of secondary growth

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when the plants show flowering. Rayless xylem has also been reported in some members of the *Amaranthaceae* (METCALFE & CHALK 1950, RAJPUT & RAO 1999a). However, rays if produced in species with rayless xylem occur only in the outer portion of secondary xylem as noted by BARGHROORN 1941 for *Geranium trident*s and *Plantago webbii* as reported by CARLQUIST 1988. Such rays are also shown here for *Celosia argentia*. According to GIBSON 1978, raylessness in dicotyledonous wood is most frequently observed in species with reduced cambial activity, short fusiform initials and highly specialized cell types in secondary xylem. These characteristic features occurred in both the species studied.

It has been considered that rayless xylem tends to occur in groups of plants in which normal cambial activity is lost during the course of evolution towards herbaceous mode of structure (CARLQUIST 1988). Furthermore, raylessness may represent a way of increasing mechanical strength in short-lived stems, in which the selective value for the radially oriented parenchyma is minimal. It appears true that both the species studied here are annual erect herbs.

Fibres with living protoplast are considered to be an adaptive feature, exhibiting transition forms towards parenchyma cells prevailing in the herbaceous plants (FAHN & LESHEM 1963, RAJPUT & RAO 1999b). Occurrence of nucleated fibres may be associated with the rayless nature of the stem and the fibres may be functioning both as mechanical and storage tissues (RAJPUT & RAO 1999a, b).

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