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Stem Development, Medullary Bundles, and Wood Anatomy of *Croton Glandulosus Var. Septentrionalis* (Euphorbiaceae)

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STEM DEVELOPMENT, MEDULLARY BUNDLES, AND WOOD ANATOMY OF CROTON GLANDULOSUS VAR. SEPTENTRIONALIS (EUPHORBIACEAE)

by

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Summary

Anatomy and development of vascular tissues in the annual stems of *Croton glandulosus* var. *septentrionalis* are described. In primary stages of growth the stem possesses a eustele of bicollateral bundles; internal phloem is notably more extensive than the external. In addition to a vascular cambium and secondary xylem that form in the usual fashion, additional cambia add cells to the internal phloem portion of the bicollateral bundles, forming well-marked medullary bundles at the perimeter of the pith. At first, the perimedullary cambial strands produce only internal secondary phloem; later, internal secondary xylem is also formed in some stems. When internal secondary xylem is present, the medullary bundles have an inverted orientation, i.e., phloem innermost (towards centre of pith) and xylem outermost (near protoxylem). Cells of the medullary bundles include sieve tube elements, vessel elements, and fibres. Normal (external) secondary phloem is weakly developed. Normal secondary xylem contains short vessel elements with simple perforation plates and alternate intervascular pits, libriform fibres, narrow heterocellular rays, and lacks axial parenchyma.

Key words: Croton, Euphorbiaceae, internal phloem, medullary bundles, stem development, wood anatomy

Introduction

Croton L. is a large genus of Euphorbiaceae comprising nearly 1000 species of trees, shrubs, and herbs found throughout the warm regions of the globe and achieving great diversity in the neotropics (Webster 1992, 1993). *Croton glandulosus* L. is a taxonomically complex assemblage of some 21 described varieties found from eastern North America, the West Indies, and South America to southern Brazil and northern Argentina; it has been classified in section *Geiseleria* (Webster 1993). The northernmost element of this species complex is *Croton glandulosus* var. *septentrionalis* Muell. Arg. (Fig. 1), a vigorous weedy annual herb found from Maryland, to Iowa, Florida, and Texas. The plants grow one to two feet tall and branch freely.

Stems of most species of *Croton* are noteworthy for the presence of internal phloem (Pax 1884; Froembling 1896; Gaucher 1902; Léandri 1939). In addition to these plants, Metcalfe and Chalk (1983) list nine more genera of Euphorbiaceae said to possess this feature and earlier literature indicates that internal phloem or bundles of phloem-like cells are widespread in uniovulate members of the family (e.g, Pax 1884; Froembling 1896; Gaucher 1902, Pax & Hoffmann 1931). The most comprehensive descriptions of stem anatomy for *Croton* and related genera are found in Froembling's (1896) survey (summarised in Solereder 1908 and Metcalfe & Chalk 1950, 1983), but there appears to have been no previous study of stem development in this genus. Preliminary observations of stems of *Croton glandulosus* var. *septentrionalis* confirmed the presence of medullary bundles containing phloem, but also revealed, for the first time, some with secondary xylem as well. Thus, the present study was undertaken to provide a detailed first report of stem ontogeny of this species, with an emphasis on its vascular tissues, especially the unusual structures encountered in the pith region.

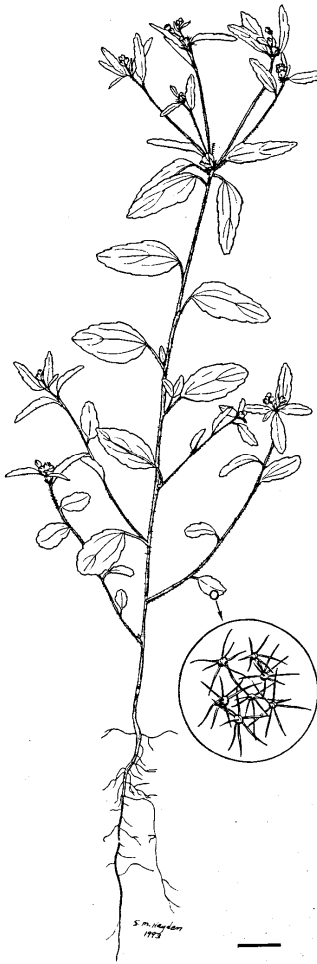


Fig. 1. *Croton glandulosus* var. *septentrionalis*, habit, shortly after onset of flowering. Scale bar = 2 cm.

Materials and Methods

Specimens were collected from the authors' residence in the suburbs of Richmond, Virginia. A series of spring-collected seedling stems provided developmental stages from shortly after expansion of the cotyledons through primary growth, and early stages of secondary growth. Summer and autumn-collected plants yielded stout pencil-thick stems with late stages of secondary growth. Collection data and voucher specimens are as follows: U.S.A., Virginia, Chesterfield Co.: Hayden 2082 (9 July 1988) (URV); Hayden 2634 (26 May 1990) (URV); Hayden 2892 (23 Sept. 1990) (URV).

All tissues were fixed in FAA. A total of 15 seedling and herbaceous stems were dehydrated in tertiary butanol, embedded in paraffin, and sectioned at 10 µm on a rotary microtome. Paraffin sections were stained in aniline blue and counter-stained with safranin. Six larger stems were sectioned at 30 µm on a sliding microtome and stained in various combinations of hematoxylin, aniline blue and safranin. Secondary xylem from the base of two of the larger stems was macerated by means of Jeffrey's fluid (equal volumes of 10 percent nitric acid and 10 percent chromic acid). Numerical values reported in the wood description are derived from these two sets of macerations as well as sections prepared from the same stems; these values are based on 50 measurements per specimen of vessel element length, diameter, and fibre length, 30 measurements per specimen of end wall angle, and 10 measurements or counts per specimen for all other features. SEM observations were made from sections cut on a sliding microtome at 50 µm, dehydrated in ethanol, critical point dried with liquid CO_2, and sputter coated with a gold/palladium mixture.

The epicotyl of *Croton glandulosus* var. *septentrionalis* ascends through several nodes, eventually terminating in a flower cluster subtended by a verticil-like group of smaller flower-bearing stems (Fig. 1). In order to control for potential ontogenetic variation, i.e., variation with position along the stem, our anatomical observations were routinely focused on the basal portion of the epicotyl, specifically, the most proximal (i.e., first) node and internode above the cotyledons; un-

less stated otherwise all descriptions pertain to this region. Two of the six mature stems were sectioned at multiple (four or five) intervals spaced evenly between the cotyledons and the first distal cluster of branches to provide information on potential developmental (i.e., positional) variation.

Results

Primary growth

Primary growth in the stem of *Croton glandulosus* var. *septentrionalis* produces a eustele composed of bicollateral bundles (Figs. 2–5). Epidermis is uniseriate and bears few stomates but has numerous stellate hairs (Fig. 1, inset) with multiseriate stalks. Cortex consists of collenchyma and parenchyma cells; in older stems, groups of thick-walled laticifers bearing clear latex are prominent in the cortex (Fig. 12). Each vascular bundle consists of three groups of cells, external primary phloem, primary xylem, and internal primary phloem (Fig. 3). In the mature primary body, internal phloem is generally more extensive than external phloem (Fig. 3). Internal and external phloem are similar in their total lack of sclerenchyma, but external primary phloem has scattered tannin-bearing idioblasts that are absent in the internal phloem (Figs. 2, 4, 5). Primary xylem development is exarch and consists of single or double files of lignified conducting elements separated by unlignified xylem parenchyma. Protoxylem walls of tracheary elements are helically thickened (Fig. 11); scalariformly thickened or pitted elements are frequent in the metaxylem. Internal phloem excluded, the pith consists solely of parenchyma cells (Figs. 2–5). Druses occur scattered throughout the cortex and pith (Figs. 3–5). Through maturation of the primary body, pith cells are generally devoid of starch (Fig. 3). Pith cells from stems with secondary growth, however, are densely packed with starch grains (Figs. 8, 10).

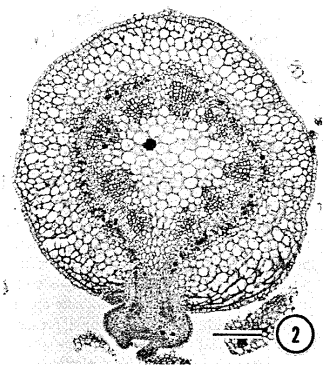
Developmentally, internal phloem is first detectable as a small clump of densely cytoplasmic cells that differentiate shortly after the first elements of protoxylem and external phloem. Additional internal phloem forms internally adjacent to the protoxylem as primary growth continues.

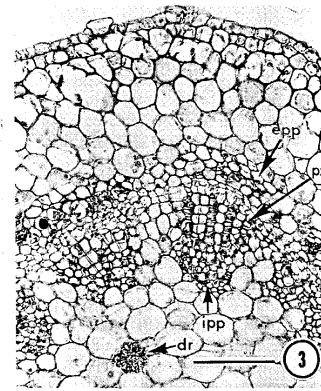
Nodes conform to the three-trace trilacunar configuration (Fig. 5). Each trace remains bicollateral as it diverges from the stele and enters the petiole (Fig. 4). Longitudinal sections of young stems reveal the presence of sieve tube elements in both internal and external phloem. Sieve tube elements are identifiable by virtue of their simple sieve plates stained darkly with aniline blue and conspicuous mucous slime plugs (Fig. 11). To the extent detectable in our light microscope preparations, sieve cells of the internal and external primary phloem are structurally similar. Sieve pores were not observed, probably a consequence of their presumed small size and the failure to control fixation for optimal preservation of fine details in phloem. No lateral sieve areas were observed on sieve tube elements. We assume that small cells among the sieve tube elements of both internal and external phloem are companion cells, but the preparations made do not permit positive confirmation of this assumption.

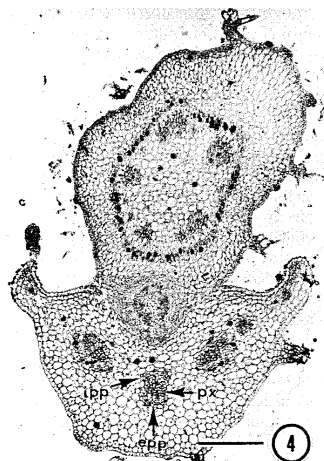
Secondary growth

The origin of the vascular cambium located between the last-formed cells of metaxylem and the external phloem proceeds in a completely normal fashion; the same can be said of the accumulation of secondary xylem (Figs. 13, 15). The amount of externally produced secondary phloem is sparse and, like the primary phloem, it lacks sclerenchymatous elements (Fig. 12), but otherwise its mode of development seems normal. However, an atypical secondary ontogeny occurs between the protoxylem and internal phloem. The combined activity of normal and atypical cambia transforms the vascular system of the plant from a eustele of bicollateral bundles to a vascular cylinder of normal secondary xylem and phloem with the addition of anomalous medullary bundles. The anomalous medullary bundles consist of the original cells of internal primary phloem plus additional secondary vascular tissues. In order to distinguish between normal secondary growth and events that occur in the vicinity of the internal phloem, the latter will be referred to as perimedullary secondary growth.

The cambia responsible for perimedullary secondary growth occur as discrete strands







Figs. 2–5. Seedling stems of *Croton glandulosus* var. *septentrionalis* (Hayden 2634) just after expansion of first true leaf. – 2: Eustele at upper portion of first node. – 3: Bicollateral bundles, same section as Fig. 2. – 4: Bicollateral leaf traces in petiole base of first true leaf. – 5: Departure of bicollateral leaf traces below first node. – Scale bars of 2 & 5 = 150 µm; of 3 = 100 µm; of 4 = 250 µm. – dr = druse; epp = external primary phloem; ipp = internal primary phloem; lt = leaf trace; px = primary xylem.

that arise between the earliest-formed protoxylem elements and outermost cells of the internal primary phloem. Perimedullary secondary growth is restricted to the medullary bundles. Cells of the interfascicular regions (areas formerly between bundles of internal primary phloem) are passive and either remain unchanged (Figs. 6–8) or, in robust older stems, become crushed by proliferation of cells formed in the inner portion of the bicollateral bundle (Fig. 9).

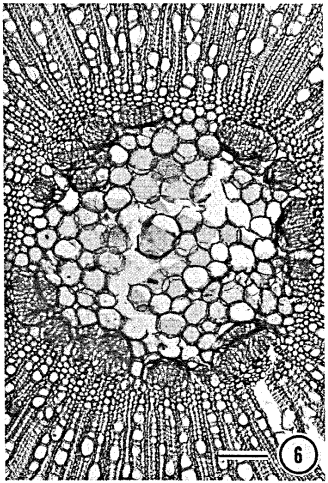
We have observed stages of perimedullary secondary growth only in stems that had at least some normal secondary xylem. In early stages of perimedullary secondary growth divisions apparently produce only internal (centripetal) derivatives which mature as internal secondary phloem; internal secondary xylem is not formed in early stages. The new cells formed by perimedullary secondary growth are constrained to develop within the confined space of the pith which, at this stage, is completely surrounded by a cylinder of wood. One readily observable consequence of perimedullary secondary growth is the obliteration (crushing) of primary phloem cells toward the interior of the medullary bundle (Figs. 6–8). The accumulation of crushed cells becomes ever greater as perimedullary secondary growth proceeds.

The cambial nature of perimedullary growth is evident from the radial alignment of the derivative cells (Figs. 7, 10). The observation of slime plugs in radial files (Fig. 7) further indicates that each sieve cell of the group developed at the same height in the stem, a further confirmation of the cambium-like nature of perimedullary secondary growth. Unlike the normal cambium, however, we have seen no evidence of the production of ray tissue in perimedullary secondary growth. Further, we have seen no evidence of anticlinal (multiplicative) divisions in cambia of medullary bundles.

The phloem-only stage of perimedullary secondary growth may be restricted to a single source of cambium-like cells as implied by the above description. However, as many as half the internal bundles of a given stem section may possess multiple clumps of phloem cells separated from each other by partitions of crushed cells (Figs. 6, 8). In some cases it appears that multiple clumps of phloem cells are the result of the vagaries of which cells succumb to crushing by the forces resulting from formation and expansion of new cells in the bundle; in this fashion, the innermost phloem elements may become isolated from the remainder of the bundles. In other cases, especially bundles with complex patterns of intact and crushed phloem elements (Fig. 8), we cannot rule out the possibility of multiple cambia.

In some stems, there is a second phase of perimedullary secondary growth that produces internal secondary xylem elements in addition to the internal secondary phloem cells previously described. The newly formed xylem elements are produced centrifugally, i.e., towards the protoxylem elements. Consequently, the positions of xylem and phloem in perimedullary bundles at this stage of development are inverted relative to that of normal stem bundles in dicotyledons. Initiation of this second phase of development is highly variable from specimen to specimen. The earliest stage observed, a single xylem element in a perimedullary bundle, was found in a spring-collected seedling stem that had surpassed 3 cm in height and had produced approximately a 0.5 mm radius of normal secondary xylem, but had not yet initiated flowering. Some late summer collections of flowering stems with as much as a 3 mm radius of normal secondary xylem are completely devoid of internal secondary xylem (Figs. 6, 13), while others of comparable size and collected at the same time may have one to several perimedullary secondary bundles bearing internal secondary xylem. In one late summer stem the perimedullary bundles had expanded to occupy virtually the entire volume of the former pith, the original pith parenchyma being crushed along with early-formed cells of the internal primary phloem (Fig. 9). Internal secondary xylem consists of vessel elements and fibres; ray and axial parenchyma are absent.

Sections taken at various heights along the main stem reveal expected aspects of developmental/positional variation. Qualitatively, the structure of all upper portions of the stem correspond to that of the base, but one finds successively earlier developmental stages as one progresses apically. Another difference is re-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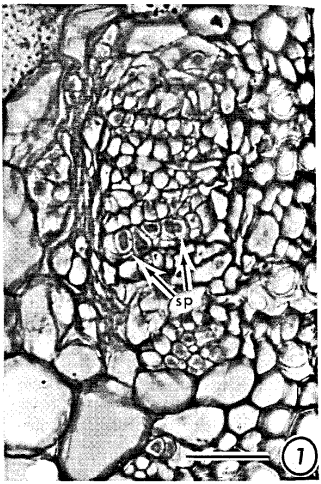
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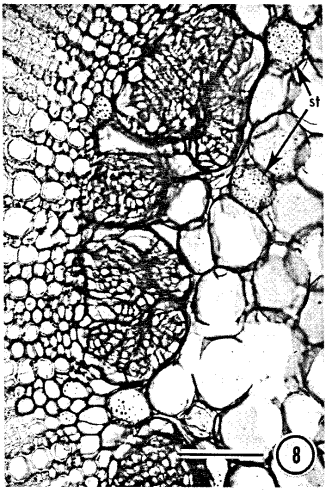
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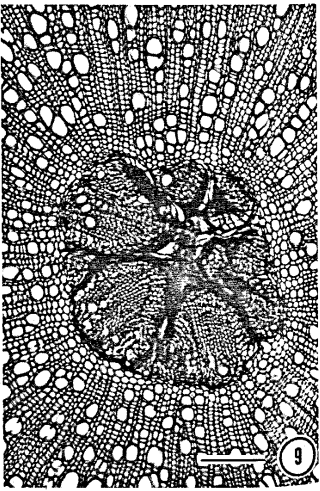
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lated to the normal slight increase in primary stem diameter that occurs from seedling stages to maturity; thus, pith diameter and the number of perimedullary bundles is smaller at the base of the plant than in apical regions.

Periderm

A thin periderm was observed in older stems. Periderm arises from cortical cells immediately subjacent to the epidermis (Fig. 12). Phellem cells are thin-walled and devoid of deposits. In addition to periderm formation, accommodation to increasing stem diameter in secondary growth is also accomplished by diffuse growth, evidenced by numerous partitions encountered in cells of the outer cortex (Fig. 12).

Wood anatomy

Vessels are distributed more or less evenly across the single growth ring present in the annual stems, however, vessels are less frequent and somewhat smaller in later formed secondary xylem than that formed early in the season (Figs. 13, 15). Vessel distribution is 45 percent solitary, 32 percent radial multiples, and 23 percent clusters; clusters are usually radially elongate (Fig. 16). Vessel outlines range from rounded to somewhat angular, the latter condition being found in clusters. Vessel walls have an average thickness of 2.6 µm. Average tangential diameter of vessels is 26 µm (10–51 µm). Perforation plates are predominantly simple (Fig. 17); however, a few scalariform perforations with only 2 or 3 bars can be found near the protoxylem. On average, end walls are inclined 59 degrees from the horizontal (25–85 degrees). Intervascular pits are circular to elliptical, alternate, and have an average vertical diameter of 6 µm; vessel to ray pits are similar. Vessel element length varied notably in the two specimens for which this feature was measured: an average of 237 µm (78–362 µm) for one, and 396 µm (170–600 µm) for the other. Vessel elements are often ligulate, the ligules averaging 71 µm long.

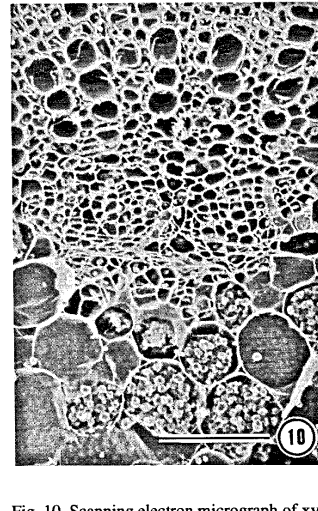
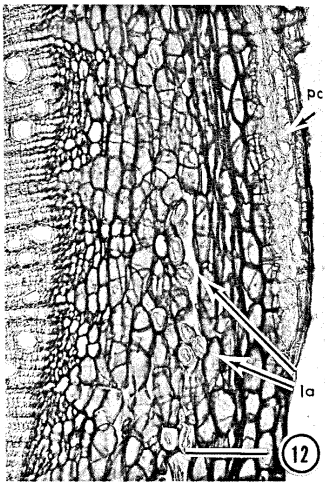
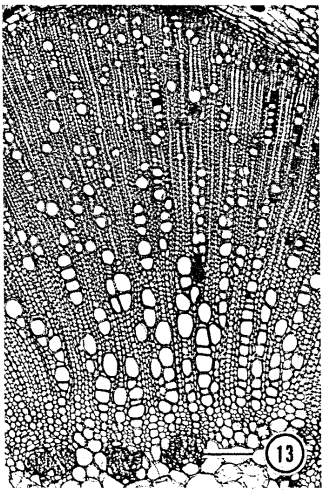


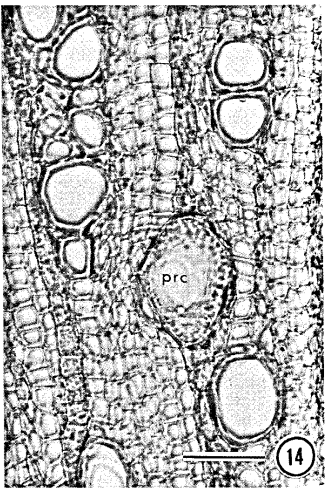
Fig. 10. Scanning electron micrograph of xylem, phloem-only medullary bundle, and pith of *Croton glandulosus* var. *septentrionalis* (Hayden 2892). Scale bar = 100 µm.

Imperforate tracheary elements are predominantly libriform fibres that have an average length of 582 µm (300–820 µm). Fibre lumens occupy more than half of the cell's diameter. Fibres with gelatinous walls are common, occurring in broad tangential arcs (Fig. 15) in most specimens examined. Some of the small diameter elements of pore groups prove to be vascular tracheids (Figs. 14, 16), but these cells are, overall, rare.

Figs. 6–9. Medullary bundles in mature stems of *Croton glandulosus* var. *septentrionalis* (Hayden 2892). – 6: Pith and phloem-only bundles. – 7: Phloem-only medullary bundle with radial alignment of slime plugs in sieve tube elements. – 8: Complex phloem-only medullary bundles. – 9: Inverted medullary bundles containing secondary xylem, pith nearly occluded. – Scale bar of 6 = 150 µm; of 7 = 50 µm; of 8 = 100 µm; of 9 = 250 µm. – sp = slime plug; st = starch grains.







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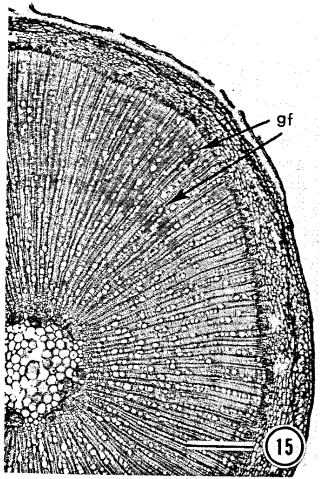

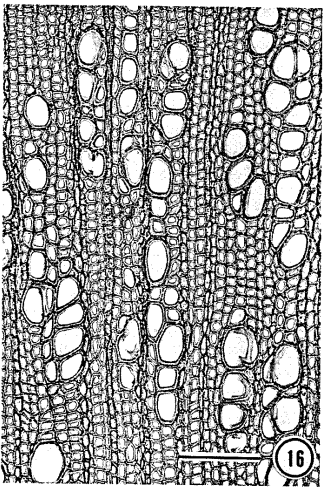

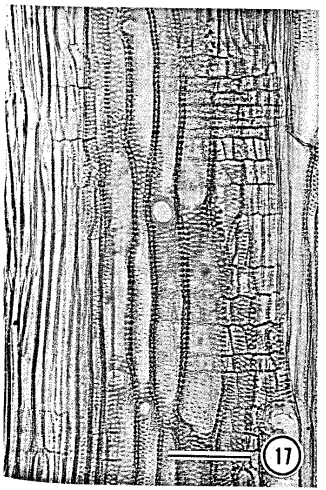

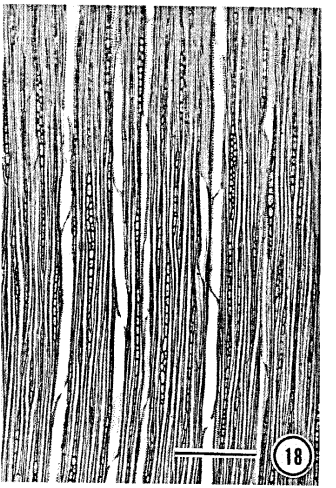

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Axial xylem parenchyma is essentially absent.

Rays are heterocellular and consist primarily of erect cells with occasional procumbent cells toward the centre of the ray (Fig. 17). Rays are 66 percent uniseriate and 34 percent multiseriate (Fig. 18). Uniseriate rays have an average width of 10 µm and are generally less than 10 cells or 350 µm in height, although a few rays more than twice this height were encountered. Multiseriate rays are mostly biseriate, less commonly 3-seriate, and have an average width of 18 µm. Multiseriate rays routinely range up to 35 cells high, rarely higher, and have an average height of 572 µm. Perforated ray cells are regularly encountered (Fig. 14). Starch was observed in ray cells only in regions near the primary xylem. Neither secretory canals nor laticifers were observed in the ray system.

Discussion

Internal phloem and medullary bundles

Previous literature (Froembling 1896) provides only limited information on stem structure of *Croton glandulosus* (variety unspecified). Froembling (1896) noted internal phloem at the periphery of the pith, but he did not describe the successive addition of phloem elements to the medullary bundle, neither did he mention internal secondary xylem nor the inverted orientation of xylem-containing bundles. Froembling did mention the occurrence of sclerenchyma fibres associated with internal phloem in *Croton glandulosus* and several other species; none was observed in this study except, of course, the fibrous component of the xylem formed in medullary bundles in late developmental stages. Froembling's reference to fibres may be attributable to taxonomic differences in the material studied, or, possibly, failure to interpret the fibres as components of internal secondary xylem. Fibres have been reported as components of the internal phloem of several other euphorbiaceous genera (Pax 1884; Gaucher 1902).

Available literature indicates the existence of some subtle differences in the structure of internal phloem of various species of *Croton*. In addition to presence or absence of fibres discussed above, Léandri (1939) noted that tanniniferous cells (cf. those observed in the external phloem in this study) are often, but not always present in the internal phloem of *Croton* species. The amount of internal phloem in any given stem is also reported to vary from species to species (Gaucher 1902), but it is clear from our studies that age of the stem may affect such assessments. Finally, internal phloem is reported to be absent in several species of *Croton* section *Astraea* (Froembling 1896).

The occurrence of internal phloem, medullary bundles, or other phloem-like tissues at the periphery of the pith is widespread among uniovulate members of Euphorbiaceae (Gaucher 1902; Solereder 1908; Metcalfe & Chalk 1983). In addition to *Croton* and its closest relatives, well-developed internal phloem has

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Figs. 11–14. Stem features of *Croton glandulosus* var. *septentrionalis*. – 11: Longitudinal section through pith, internal phloem, and protoxylem, note sieve plates and slime plugs (Hayden 2634). – 12: External phloem, cortex, epidermis, and periderm of a mature stem; note laticifers; same section as Fig. 15 (Hayden 2892). – 13: Phloem-only medullary bundles, primary xylem, and secondary xylem (Hayden 2892). – 14: Transverse section of wood with perforated ray cell (Hayden 2892). – Scale bars of 11 & 14 = 50 µm; of 12 = 100 µm; of 13 = 150 µm. – la = laticifer; pd = periderm; pp = pith parenchyma; prc = perforated ray cell; sp = slime plug.

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Figs. 15–18. Wood of *Croton glandulosus* var. *septentrionalis* (Hayden 2892). – 15: Transverse section; same section as Fig. 12. – 16: Transverse section. – 17. Radial section. – 18: Tangential section. – Scale bar of 15 = 500 µm; of 16 & 17 = 100 µm; of 18 = 200 µm. – gf = gelatinous fibres.

been recorded in *Alchornea* Swartz, *Caelebogyne* J. Smith, *Conceveiba* Aublet, *Mabea* Aubl., *Pera* Mutis, *Sebastiana* Spreng., *Senefeldera* Martius, and some species of *Mallotus* Loureiro (Gaucher 1902; Metcalfe & Chalk 1983). Medullary bundle cells in some uniovulate euphorbs appear phloem-like but lack sieve areas (Pax 1884; Gaucher 1902). Such apparently vestigial phloem tissue has been described as 'cambiform' (Pax 1884; Pax & Hoffmann 1931), suggesting the persistence of perimedullary secondary growth in plants with poorly developed sieve plates in their internal 'phloem'. It is noteworthy that both vestigial and well-developed internal phloem are reported in all three subfamilies of uniovulate Euphorbiaceae, i.e., Acalyphoideae, Crotonoideae, and Euphorbioideae in the classification of Webster (1975). The systematic potential of this anatomical feature seems obvious, but to apply it meaningfully would require much more data on stem structure in uniovulate euphorbs than is presently available.

Bicollateral bundles occur in stems of a number of dicotyledons, in some cases, characterising entire families, in other cases restricted to isolated genera or species (see lists in Metcalfe & Chalk 1950, 1983). Perhaps the best known examples include Cucurbitaceae, the families of Myrtales, and several families of Asteridae (as classified by Cronquist 1981). Based on the summaries in Metcalfe & Chalk (1950), it is interesting to note that cambial conversion of the inner portion of bicollateral bundles into medullary bundles is not known in Cucurbitaceae and Myrtales, but does occur in some members of Apocynaceae, Asclepiadaceae, Convolvulaceae, Gentianaceae, Loganiaceae (Buddleioideae excluded), Solanaceae, and one non-asterid family, Polygonaceae. Among these families, anomalous xylem production resulting in the formation of inverted medullary bundles has been reported sporadically, including the following (Metcalfe & Chalk 1950; and others, as cited): *Apocynum* (Holm 1910) and *Willughbeia* (Apocynaceae); *Leptadenia* (Asclepiadaceae) (Singh 1943); many genera of Convolvulaceae (Mikesell & Schroeder 1984; Carlquist & Hanson 1991); *Gelsemium* (Loganiaceae); *Gentiana* (Gentianaceae); *Rumex* (Polygonaceae) (Joshi 1936; Maheshwari 1929; Maheshwari & Singh 1942); and also *Campsis* (Bignoniaceae) (Handa 1936). The case of *Gentiana* is notable in that external phloem is described as weakly developed, much as was found in *Croton glandulosus* var. *septentrionalis*.

As noted by Maheshwari (1929), in his discussion of *Rumex*, the inverted medullary bundles of all the genera named above, having developed in the perimedullary region by cambium-like proliferation from bicollateral bundles, seem to constitute a special category of medullary bundle. The type of bundle found in these plants and in *Croton* may bear no homology with deeply seated medullary bundles of other plants, especially bundles with the normal orientation of xylem and phloem. For example, the medullary bundles of cacti which are found throughout the pith and develop from discrete procambial strands (Mauseth 1993) differ fundamentally from the bundles of *Croton* which form by perimedullary secondary growth.

Physiological studies of internal phloem in various plants offer a basis for hypotheses concerning the function of the structures found in *Croton glandulosus* var. *septentrionalis*. A number of studies employing radioactive tracers and/or fluorescent dyes have indicated that internal phloem may exhibit directional or temporal differences in translocation compared to the external phloem of the same plant (Bonnemain 1969; Fredon & Bonnemain 1970; Couillault & Bonnemain 1973). Further, observation of preferential feeding by aphids has suggested differences in the composition of the cell sap between internal and external phloem (Botha et al. 1975; Botha & Evert 1978). Judging by its accumulation of starch, pith of *Croton glandulosus* var. *septentrionalis* is evidently a storage organ of considerable significance for the plant. Our light microscope illustrations of woody stems grossly under-represent starch content since large quantities of starch were released during sectioning. Somewhat better retention of starch is visible in the SEM image (Fig. 10), but starch has been lost from this section, too. The internal phloem of bicollateral and medullary bundles is efficiently located for transport of assimilates to and from the pith, which we hypothesize to be its major function.

Such a direct pathway to cells of the pith is presumably more efficient than the pathway available to plants with only external phloem, i.e., through the cambium and across the secondary xylem via ray cells. The predominance of upright ray cells would render radial transport in *Croton glandulosus* var. *septentrionalis* inefficient and, in fact, starch grains were noticeably absent from xylem ray cells (except for a few cells near the pith) even though all specimens were fluid preserved. Since this species is an annual it has no winter dormancy and no need for subterranean storage of reserve assimilates; the relatively weak development of external phloem may well be sufficient to support growth and metabolism of the root system.

Wood anatomy

Although *Croton* is, essentially, a genus of woody plants, only a minority of species are actually arborescent and few of these produce timber that has come to the attention of wood anatomists. Several aspects of wood structure reported for various species of *Croton* in Janssonius (1934), Record (1938), Léandri (1939), and Metcalfe & Chalk (1950) conform with the above description of *C. glandulosus* var. *septentrionalis*: numerous, narrow vessels frequently in radial alignment; libriform fibres with frequently gelatinous walls; and strongly heterocellular uni- or biseriate rays that are generally less than 25 cells tall (sometimes taller, as reported here and in Janssonius 1934). *Croton glandulosus* var. *septentrionalis* is noteworthy, however, in its virtual absence of axial xylem parenchyma, in contrast to the diffuse, banded, and aliform patterns reported for other species. Record (1938) and Carlquist (1988) report the presence of secretory canals in rays of *Croton* (species not mentioned) and Rudall (1987, 1989) has noted laticifers in rays of *C. conduplicatus* H.B.K., *C. panamensis* Muell. Arg., and an unidentified species, but no such structures were observed in *Croton glandulosus* var. *septentrionalis*.

Suggestions for further study

Results of the present study suggest several avenues for further investigation. The three-dimensional pattern of medullary bundles in mature stems, their relation to branches, and presumed assimilate sinks such as flowers and fruits remains unknown, but must be considered before the function of these bundles can be understood thoroughly. Similarly, a detailed cytological examination of the phloem of *Croton glandulosus* would seem necessary in this regard. Also, our knowledge of the medullary cambium itself is, at best, rudimentary; additional structural and physiological studies are indicated. As mentioned earlier, *Croton* is a large genus, and thus affords many opportunities for comparative anatomical study beyond Froembling's (1896) original survey. The perspective provided by the present study highlights the necessity of examining multiple stages of stem development in any comparative study of *Croton* or, for that matter, any plant with perimedullary secondary growth.

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