Initiation and structure of the secondary vascular system in *Phytolacca dioica* (Phytolaccaceae)

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Abstract:
Phytolacca dioica (L.) is characterized by anomalous secondary thickening by means of supernumerary cambia. After a period of primary growth and the formation of an initial (normal) vascular cambium, supernumerary cambia are initiated outside of the primary vascular cylinder. The initiation of the first supernumerary cambium takes place through approximately the number of nodes equal to the denominator of the phyllotactic fraction characterizing a given axis. At each node a segment of supernumerary cambium is initiated opposite the leaf traces supplying the leaf inserted at that node. The segments of differentiated cambium arc preceded by regions of obliquely and antielinally dividing cells. In the single juvenile axis studied supernumerary cambial segments also appear above the node to the cathodic side of the entering leaf traces, and opposite the medullary bundle immediately anodic to these traces. Vascular eonnections among the primary and supernumerary vascular cylinders occur between leaf insertions on the same orthostiehy. The levels at which these connections oceur vary among stems. The switch from ordinary to anomalous secondary growth may be caused by a change in tissue response to stimuli produced by leaves.

Une croissance secondaire anormale a l'aide de cambiums surnuméraires caractérise le *Phytolacca dioica* (L.). Après une période de croissance primaire et la formation d'un cambium (normal) vasculaire initial, des cambiums surnuméraires naissent a l'extérieur du cylindre vasculaire primaire. L'initiation du premier cambium surnuméraire se fait pour un nombre de noeuds approximativement égal au dénominateur de la fraetion phyllotaetique caractérisant un axe donné. A chaque noeud, un segment de cambium sumuméraire prend naissance en face des traces foliaires qui alimentent la feuille inserée a ce noeud. Les segments de cambium différencié sont précédés par des regions of les cellules se divisent dc fawn oblique et antieline. Dans]'unique axe juvénile étudié, des segments surnuméraires (le cambium apparaissent aussi au-dessus du noeud du Me cathodique des traces foliaires pénétrant et en face du faisceau médullaire immédiatement anodique a ces traces. Des anastomoses parmi les cylindres vasculaires primaire ct surnuméraires se font entre les insertions foliaires se trouvant sur la même orthostichie. Les niveaux où se font ces connections varient entre les tiges. Le passage de la croissance secondaire ordinaire a la croissance secondaire irrégulière est peut-être cause par un changement dans la reaction des tissus en réponse a des stimuli d'origine foliaire.

Article:

INTRODUCTION

The structure of the primary and secondary vascular systems of *Phytolacca dioica* (L.) differs from that of most dicotyledons. The primary vascular system contains medullary bundles and has recently been investigated by Kirchoff and Fahn (1984). The secondary vascular system is characterized by anomalous secondary thickening taking place by means of supernumerary cambia (Solereder 1908; Metcalfe and Chalk 1950). The functioning of these cambia has been described by Wheat (1977), and the differentiation of the first supernumerary cambium (SC) has been described in *P. americana* by Mikesell (1979).

While there has been considerable interest in the mode of action of supernumerary cambia (Artschwager 1920; Maheshwari '1930; Esau and Cheadle 1969; Philipson et al. 1971; Pufawska 1973; Baird and Blackwell 1980; Yarrow and Popham 1981; among others), little attention has been paid to the influence of leaves on the. initiation of these cambia. Since leaves are known to be the source of the stimuli responsible for the resumption of cambial activity in the spring (Sachs 1981), it is reasonable to expect a relationship between leaf arrangement and the initial formation of a cambium. There are, however, few studies which explore this relationship. A principal reason for this is most likely the difficulty in identifying the exact transition region from procambium to cambium (Larson and Isebrands 1974). This difficulty is overcome in plants with supernumerary cambia where the first SC generally arises outside the primary phloem (Fahn 1982). The cell divisions that initiate this cambium are, thus, easy to recognize, and such plants are ideal subjects for the study of the relationship between leaves and the initiation of secondary growth.

The goals of the present investigation of *P. dioica* are twofold: (i) to study the initiation of the first SC and its relationship with the arrangement of leaves on the axis and (ii) to study the distribution of vascular connections between supernumerary vascular cylinders.

MATERIALS AND METHODS

Shoots of *Phytolacca dioica* were collected from plants growing on the grounds of the Givat Ram campus of The Hebrew University of Jerusalem and the School of Gardening and Landscaping in Petah Tiqwa. Nine axes with 3/8 and one with 2/7 phyllotaxy were used in this study. For the study of cambial development pieces of stem were fixed in FAA (90 mL 70% EtOH, 5 mL glacial acetic acid, 5 mL 40% formaldehyde), sectioned at 100 on a Reichert sliding microtome, stained in Alcian green—safranin (AGS) (Joel 1983), and dehydrated and mounted in Cedrax or dehydrated and mounted in Karo syrup (Johansen 1940). Connections between vascular eylinders were traced by three methods: (1) FAA-fixed stem segments were sectioned at 100 p.m, stained in AGS, and mounted in Karo syrup; (ii) FAA-fixed stem segments were perfused under vacuum with a dilute solution of safranin, sectioned at 2001µm, and mounted in 50% glyeerin; and (iii) fresh pieces of stcm werc perfused with Koh-i-noor rapidograph ink
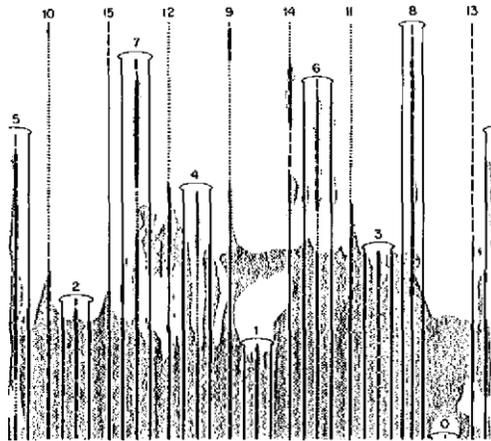
FlG. 1. Diagram of the longitudinal course of initiation of the first supernumerary cambium. The vasculature has been greatly simplified in this diagram. The median and two lateral traces are shown for nodes 0-8. Only the median trace is shown leading to the higher nodes (9-15). Broken lines, median leaf trace partially inserted in the vascular cylinder; dotted lines, median leaf trace in a medullary position; thin solid lines, leaf traces completely inserted in the vascular eylinder; shaded areas, locations of the supernumerary cambium.

(a particulate ink which does not pass from one vessel to another) or Parker Super Quink ink (a nonparticulate ink which will pass between vessels). Ink was applied to the cut distal ends of stem segments and pulled through the stem by vacuum. The distal portions of the supernumerary cylinders were cut away from the primary cylinder and their cut ends sealed with Duro silicon sealer so that ink could enter only the primary cylinder. The treated stems were either sectioned by hand for immediate observation or sectioned on a Reichert sliding micro- tome and photographed every 1 or 2 mm.

Preliminary surgical experiments were carried out on juvenile axes of *P. dioica* growing in pots at the Botanical Gardens of The Hebrew University of Jerusalem, Givat Ram campus. Incisions were made in the axis either above (one axis) or below (three axes) the transition zone between primary and initial secondary growth. No supernumerary cambia were prcsent at the level of an incision. The axes were colleeted and fixed in FAA between 2 and 4 weeks after the beginning of the experiments. Cross sections were cut at 100 1μm on a Reichert sliding microtome, stained in AGS, and mounted in Kara syrup.

RESULTS
Primary vascular system
The primary vascular system of *Phytolacca dioica* has previously been described in detail (Kirchoff and Fahn 1984). Here, we will briefly summarize only those features of the primary body which relate to the present research.

An axis with 3/8 phyllotaxy contains eight sympodia each connecting the median traces of leaves separated by eight inter- nodes. In the distal region of juvenile axes each median leaf trace enters the pith at the level of leaf insertion and traverses eight internodes in a medullary position before joining the vascular cylinder.

In the basal regions of the juvenile axes and frequently throughout the length of adult flowering axes the median leaf traces entering the axis become, at first, incorporated into the vascular

cylinder and only after traversing a number of inter- nodes in this position pass into the pith as medullary bundles. Eight nodes below their entrance into the axis these median traces, also, leave the pith and rejoin the vascular cylinder. At this level the medullary bundles split into two or three vascular strands in both types of axes.

Secondary growth in the initial vascular cylinder

Before the initiation of the first SC an ordinary (initial) vascular cambium is formed in the primary vascular cylinder. This cambium produces secondary xylem and phloem in the fascicular regions (Fig. 2). Since primary xylem maturation is basipetal while formation of the initial cambium is acropetal, there is an inverse relationship between the amount of primary and secondary xylem in a trace at any level. For a distance of eight nodes below the insertion of a leaf there is an increase in the amount of secondary xylem in the traces to that leaf and a corresponding decrease in the amount of primary xylem. Leaf traces in the region immediately below the insertion of a leaf contain predominantly primary and little or no secondary xylem. Continuing downward the amount of secondary xylem increases until, eight nodes below leaf insertion, more than half of the xylem is secondary. Below this level the relative amount of secondary xylem in the bundles continues to increase but fluctuates widely from level to level. This change from a steady to a variable increase in the amount of secondary xylem may be related to the entrance of the medullary bundle into the vascular cylinder, which occurs eight nodes below leaf insertion.

Measurements of the relative amount of secondary xylem show greater fluctuations between levels in flowering axes than between levels in the distal parts of juvenile axes. This phe-nomenon supports the above-mentioned supposition that the change of position of the median leaf trace from the pith to the vascular cylinder affects the activity of the cambium. In flowering axes, as mentioned above, the median trace is often incorporated in the vascular cylinder for a distance of some nodes before entering the pith, whereas in the distal parts of juvenile axes the median trace occupies a medullary position throughout all eight internodes.

Origin of the first supernumerary cambium
Flowering axes
(i) Basic pattern

Mature flowering axes bear flowers in terminal racemes and are renewed by the growth of an axillary bud. Since these axes are determinate, the position of the first SC advances acropetally in the axis.

The first SC is initiated beneath the insertion of a leaf, opposite its traces, in the parenchyma occupying the space between the phloem groups and the pericyclic fibers (Fig. 2). Since a new segment of cambium is initiated opposite the traces of each successive (lower) leaf, a complete cylinder of SC is eventually built up. The number of nodes through which this process occurs is approximately equal to the denominator of the phyllotactic fraction characterizing a given axis (Fig. l).

Below each node, in the uppermost portions of the transition zone between normal and anomalous secondary growth, the first supernumerary cambium is restricted to the regions directly opposite the median traces (Fig. 1, nodes 8, 7; Fig. 3). At lower nodes cambial segments

also appear opposite the lateral leaf traces (Fig. 1, node 6; Fig. 4). The transition from isolated cambial segments to a complete cylinder takes place through the initiation of cell divisions in regions not directly below leaves (Fig. l).

The supernumerary cambia function bidirectionally, producing collateral vascular strands embedded in conjunctive tissue. Phloem production starts before the beginning of xylem production. The first xylem cells to be produced are fibers. These findings agree with those of Wheat (1977). Fiber differentiation in the vascular strands of the first supernumerary cylinder follows the same pattern as the initiation of the first SC.

(ii)Connections between the initial and first supernumerary cambia
Only the connections between the initial and first supernumerary cambia found immediately below leaves, and those found in association with the passage of median leaf traces into and out of the pith, will be dealt with here. The distribution of other cambial connections may be determined from the distribution of vascular connections between supernumerary vascular cylinders, dealt with below.

As mentioned above, the first SC is initiated beneath the insertion of a leaf, opposite its median trace. At this level the median leaf trace is partially incorporated in the vascular cylinder, and the initial segment of the SC is often connected to the initial vascular cambium on one or both sides of the median trace (Fig. 3), There may also be connections between the fascicular cambia of the lateral traces and the first SC occurring on the sides of the leaf trace region.

In the region where a medullary bundle passes from the vascular cylinder into the pith (Fig. 1, median traces 4, 5, 6, 7), or from the pith to the vascular cylinder (Fig. 1, median traces 11, 12, 14), a segment of the first SC becomes longitudinally continuous with the initial vascular cambium (Figs. 5, 9). Where a median leaf trace passes from the vascular cylinder into the pith (Fig. 1, median traces 4, 5, 6, 7), connections are formed between the SC opposite this trace and the fascicular cambia of the primary vascular strands adjacent to the median trace (Figs. 9b, 9c). Immediately below this the segment of the SC opposite the median trace becomes disconnected from the rest of the SC and is incorporated in the initial cambial cylinder (Fig. 9d). Below this level it functions as part of the initial vascular cambium (Figs. 9d, 9e). Thus, a gap in the super-numerary cambium is formed (Fig. 9d). Supernumerary cambial divisions outside the initial cambium are resumed at a lower level (Figs. 9e and 1, median traces 4 and 6). A similar connection between the initial and supernumerary cambia occurs in the region where a medullary bundle rejoins the initial vascular cylinder. This takes place eight nodes below the entrance of the median leaf trace into the axis (Fig. I, median traces I I , 12, 14). In this case a segment of the cambium of the primary vascular cylinder passes outwards and becomes a segment of the first SC. The longitudinal course of this connection is the reverse of that described above.

In addition to these effects, the position of the median leaf trace may also affect the SC segments in the regions opposite the lateral leaf traces. As the median leaf trace passes from the vascular cylinder into the pith, SC divisions opposite the regions of the laterals may disappear (Fig. 1, traces of leaf 6).

(iii)Cell divisions preceding the formation of the first supernumerary cambium

Regions of anticlinal and oblique cell divisions occur distal to differentiated segments of the first SC (Fig. 6). Short strips of cambiumlike structure may develop in these regions but extend less than 100 μm in the longitudinal direction and are often oriented anticlinally or obliquely. As the differentiated segments of the SC are approached in transverse section, the cell divisions become more frequent and more and more periclinally oriented, until all divisions are periclinal and a complete cambial segment is formed. This process occurs both in regions where connections between the initial and the first SC take place as well as in regions of the developing SC cylinder where no connections occur.

Juvenile axis
There are several differences between the pattern of initiation of the first SC in flowering axes and that in the distal part of the single juvenile axis studied. As mentioned above, the median leaf traces of the latter do not join the vascular cylinder at the level of leaf insertion but enter the pith directly. In this region supernumerary cambial segments first appear opposite the lateral traces. As in the flowering axis there are also lateral connections between the initial and first supernumerary cambia. However, there are no longitudinal connections.

In addition to the SC segments that appear beneath the insertion of leaves there are two areas where SC segments appear at the nodes. Just above a node a small segment of SC appears to the cathodic (opposite the direction of the rise of the phyllotactic helix) side of the entering leaf trace (Fig. 10). This is often the most well developed cambial segment at this level, but it is restricted to the immediate region of the node. At approximately the same level, or slightly below, SC segments also appear in the region opposite the medullary bundle immediately anodic (in the direction of the rise of the phyllotactic helix) to the entering leaf trace (Fig. 10). These segments become less evident basipetally. In other respects the initiation of the SC in the juvenile axis is similar to that in the flowering axis.

Connections between the initial and supernumerary vascular cylinders
Vascular connections occur both within a vascular cylinder and between cylinders. Three types of connections occur between the supernumerary vascular cylinders: (i) whole vascular strands passing from one cylinder to another; (ii) one or a few vessels associated with phloem passing from cylinder to cylinder; and (iii) connections formed by fibers only.
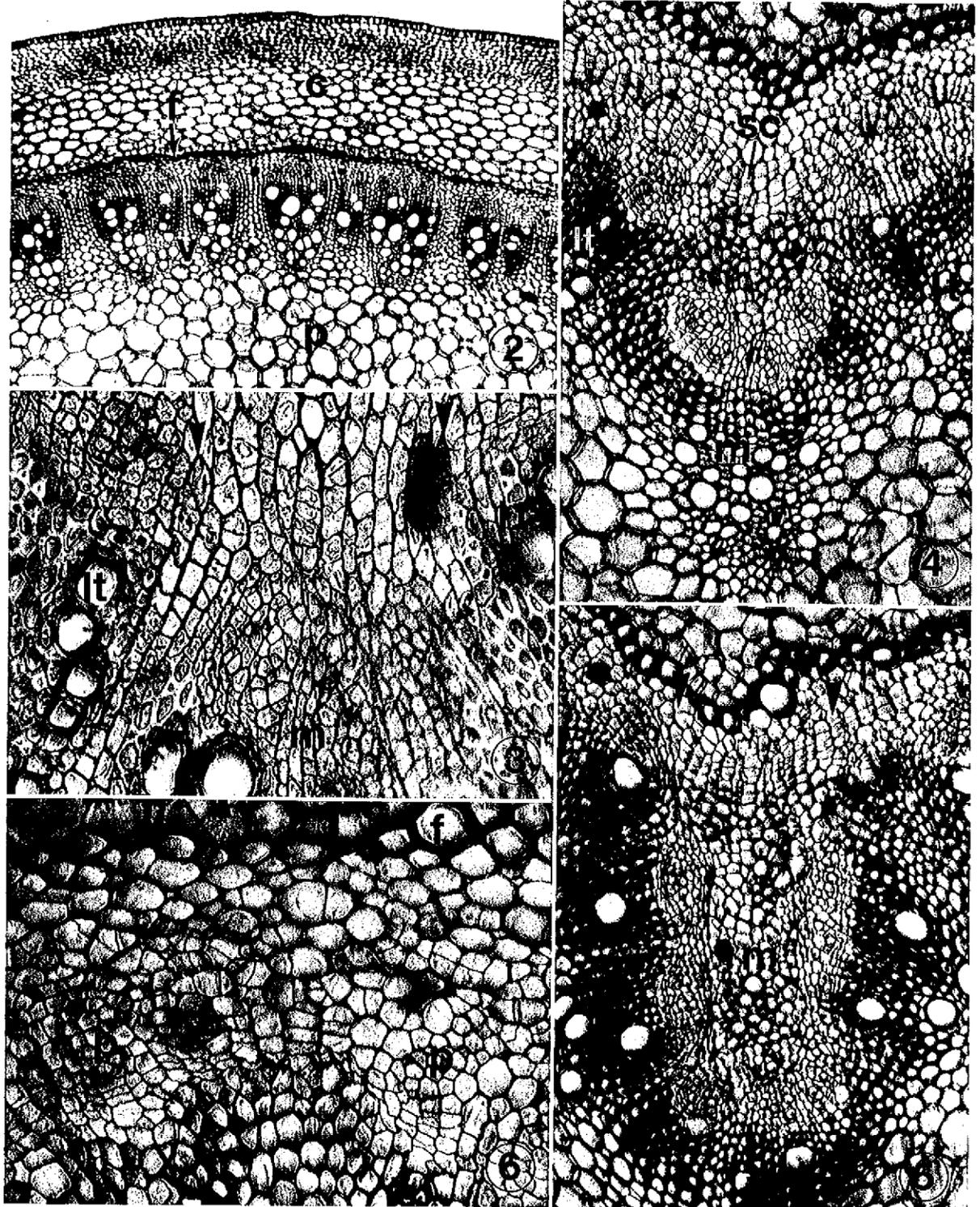
Experiments in which particulate ink was drawn through stem segments demonstrate that single vessels can apparently cross from the initial to the first, second, and third supernumerary vascular cylinders (Fig. 8). In certain regions, generally in the internode immediately below the insertion of a leaf, the passage of vascular bundles from cylinder to cylinder causes the cylinders to merge (Fig. 7).

While there is an association between leaf arrangement and vascular connections between cylinders, the levels at which these connections take place vary. The locations of the vascular connections were studied in three stems with 3/8 phyllotaxy and are presented here along one orthostichy through eight internodes. (i) In the flowering axis with one supernumerary vascular cylinder the majority of the vascular connections occur between five and eight internodes below the insertion of a leaf. (ii) In the flowering axis with two supernumerary vascular cylinders, connections between cylinders are especially prevalent immediately below a node and occur

sporadically throughout the remaining seven internodes. Connections between the two supernumerary vascular cylinders are more frequent than those between the primary and the first supernumerary cylinders. (iii) In the juvenile axis with three supernumerary vascular cylinders, connections between the primary and the first supernumerary vascular cylinders occur throughout the first three internodes below the insertion of a leaf. In this axis, connections between the supernumerary cylinders occur only in the region of the insertion of a leaf and in the first internode below this.
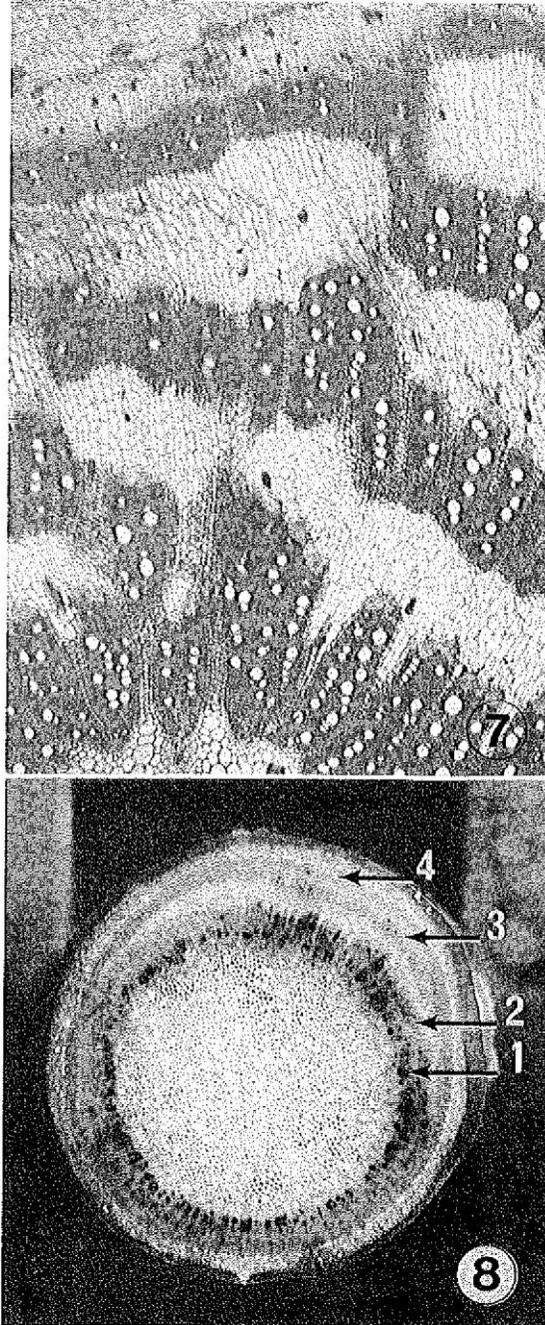
Preliminary surgical experiments
In the three axes in which initial secondary growth had begun

FIGS. 2-6. Cross sections of stems of *Phytolacca dioica*. Fig. 2. Structure of the axis before the initiation of a supernumerary cambium. *c,* cortex; *f,* pericyclic fibers; v, vascular cylinder; *p,* pith. x67. Fig. 3. A segment of the first supernumerary cambium (between arrowheads) outside a median leaf trace *(n)*. Connections between the intrafascicular cambia of the lateral leaf traces *(It)* and the segment of the first supernumerary cambium occur below the arrowheads. x307. Fig. 4. A segment of the first supernumerary cambium *(sc)* outside median *(m)* and lateral *(It)* leaf traces. x 189. Fig. 5. Connections between the primary and first supernumerary cambia (arrowheads)

opposite a median leaf trace (m) which is passing into the pith. x126. Fig. 6. Anticlinal and oblique divisions occurring above a differentiated segment of the first supernumerary cambium. f, pericyclic fibers; p, phloem; x, xylem. x301.

before the experiment a SC formed outside the primary cylinder on the sides of the incision. This cambium was most strongly developed at the level of the cut and its activity decreased basipetally and acropetally. No SC formed in the axis with only primary growth at the level of the incision. There was, however, an advance in the developmental stage of the region of the

FIGS. 7 and 8. Cross sections of stems of *P. dioica* with several supernumerary vascular cylinders. Fig. 7. Merging of vascular cylinders due to vascular connections between cylinders. x30. Fig. 8. Rapidograph ink in the vessels

of the primary (I) and three super- numerary *(2-4)* vascular cylinders. The ink was applied only to the primary vascular cylinder. For explanation see text. X5.3

axis to the sides of the incision as evidenced by the appearance and activity of the primary vascular cambium and the differentiation of mature pericyclic fibers. Mature fibers were not evident elsewhere at this level.

DISCUSSION

The results presented here show a clear correlation between leaf arrangement and the initiation of the first SC in *Phytolacca dioica*. In flowering axes this cambium is built up through the coalescence of cambial segments initiated beneath leaves. This
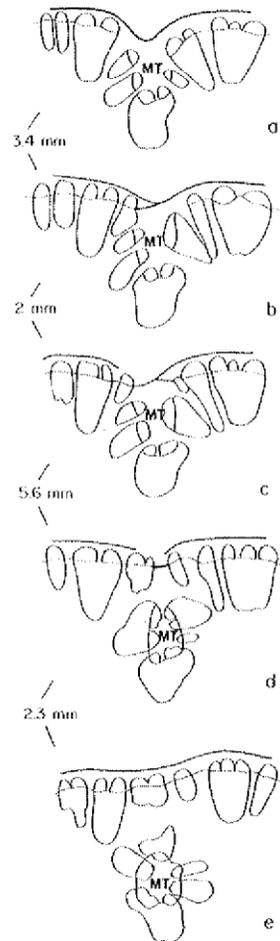

Fig.. 9. Diagrams of cross sections at various levels of an axis showing continuity between the first supernumerary cambium (thick lines) and the primary fascicular and interfascicular cambia (thin lines). A median leaf trace (MT) is shown passing from a position partially inserted in the vascular cylinder *(a)* to a medullary position (e). The measurements refer to the distances between the sections reproduecd here.
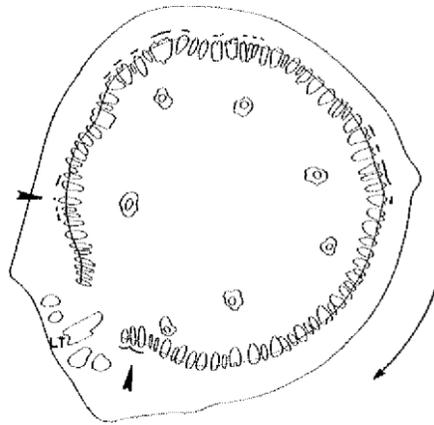
FlG. 10. Diagram of a section of a juvenile axis with 2/7 sinistrorse phyllotaxy showing the regions of initiation of the first supernumerary cambium (thick lines). The diagram represents the arrangement of the tissues just above a node. The supernumerary cambial segments in the regions indicated by the arrOwheads are initiated at the level of the entering leaf traces (LT). The other supernumerary cambial segments are associated with higher leaves. Arrow, direction of rise of the phyllotactic hclix.

process takes place through approximately the number of inter- nodes equal to the denominator of the phyllotactic fraction characterizing a given axis. In juvenile axes the first SC is built up through approximately the same number of internodes, but cambial segments are initiated in two additional positions in the region of each node: (i) just above the node, to the cathodic side of the entering leaf traces and (ii) just above the node, in the region opposite the medullary bundle immediately anodic to the entering leaf traces (Fig. 10). These latter supernumerary cambial segments become weaker basipetally.

There are several reports in the literature of a relationship between leaf arrangement and the beginning of anomalous or normal cambial activity. Zamski (1981) is unable to find a relationship between number of leaves and number of successive cambia in *Avicennia* (*Avicennia*ceae). Horak (1981) finds that the initial appearance of the first supernumerary increment in *Stegnosperma* (Phytolaccaceae) occurs in a node associated with a major branch. He suggests that gradients of growth- regulating substances and nutrients are important in the ini- tiation of the first supernumerary cambium. Dobbins (1971, 1981) comes to a similar conclusion about the beginning of anomalous cambial activity in *Doxantha unguis-cati* and *Clytostoma callistegoides* (Bignoniaceae). In these species segments of the vascular cambium opposite major vascular strands cease or greatly reduce their production of xylem and increase their production of phloem.

The only indication of a relationship between leaves and the initiation of more than one SC is found by Zamski and Azenkot (198la) in *Beta vulgaris* (Chenopodiaceae). They find that the first three leaves after the cotyledons induce the formation of the first supernumerary cambium and that the small leaf traces from the first four leaves induce the second SC. As growth continues and the number of supernumerary cambia increase, they do not find any relationship between leaves and the initiation of the additional supernumerary cambia.

Fahn and Zimmermann (1982) find that the first SC in *Atriplex halimus* (Chenopodiaceae) is initiated in continuation with the active, initial, fascicular cambium. They suggested that the signal for the initiation of this and the additional supernumerary cambia might come from

developing leaves by way of the vascular system. In the present research we were able to confirm an influence of leaves on the initiation of the first SC; however, we observed that this cambium is not always initiated as a continuation with the initial, fascicular cambium. When connections are initiated between the two cambia they are preceded by a region of anticlinally and obliquely dividing cells.

The effect of a horizontal incision made in the axis of *P. dioica* is to advance the adjacent tissues to a developmental stage characteristic of an older region of the axis. This is similar to the response elicited in *Ricinus communis* (Euphorbiaceae) seedlings by making a deep wound in the hypocotyl (Fahn et al. 1972), and most likely represents a typical response to wounding.

The simplest conclusion that is consistent with the pattern of cambial initiation reported here is that there is an age-related change in the competence of the tissues of *P. dioica* to respond to differentiation inducing stimuli moving along the plant axis. Naturally occurring stimuli are produced in the leaves and transported basipetally in the stem (Sachs 1981).

Vascular connections between supernumerary vascular cylinders have previously been noted in a number of plants (Fahn and Shchori 1968; Wheat 1977; Mikesell 1979; Zamski 1979, 1980; Zamski and Azenkot 1981a, 1981b; Horak 1981; Fahn and Zimmermann 1982). There have, however, been no previous attempts to relate these connections to the insertion of leaves. Our results show that such a relationship exists in *P. dioica* However, there is considerable variation between stems in the levels at which connections occur below leaves. Since connections between supernumerary vascular cylinders have to be preceded by connections formed between the cambia of these cylinders, the distribution of the vascular connections is a record of previous cambial connections. At present, the factors determining the exact level at which these connections take place are not understood.

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