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Anatomy of the Primary-Secondary Transition Zone in Stems of *Populus deltoides*

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Summary

The transition from primary to secondary stem tissues occurs as a continuum, and a precise anatomical definition of the transition does not exist. A definition was derived for *Populus deltoides* based on the birefringent properties of the fiber wall. This definition was quantitatively reproducible in the 9 plants tested, and the secondary transition was found to occur in the internode associated with the first mature leaf from the apex. The primary-secondary transition did not occur uniformly around the periphery. It was first observed in the vascular bundles opposite the incoming trace, and from there it progressed in a counter-clockwise direction. Within the transition internode, each vascular bundle and each tissue comprising the bundle differentiated in accord with the physiological age and the phyllotactic disposition of the developing leaf to which it led. Within any one vascular bundle, differentiation occurred first in the metaxylem vessels and associated fibers, followed closely by extension of fibers into the interfascicular regions and centripetal differentiation of the phloem fibers. The ontogenetic sequence of differentiation for each of the principal tissues of the secondary transition zone is described.

Introduction

In all vascular plants that develop by secondary stem thickening there is a transition from primary to secondary tissues. Primary stem tissues serve as the principal translocatory pathways to the developing apex and lateral organs, whereas the secondary tissues perform physiological functions required for prolonged growth of the plant and also stabilize and strengthen the plant body. During development, the plant organs and tissues proceed through a definite series of events that lead from a state of physiological immaturity and dependence to one of physiological maturity and function. As a consequence of development, the transition from primary to secondary tissues presents a continuum in both anatomical structure and physiological function.

The initiation of secondary stem tissues is usually correlated with the cessation of internodal elongation [Esau 1965]. Internode elongation, in turn, is correlated with leaf maturity. We have previously demonstrated [Larson, Isebrands 1971] that the appearance of secondary xylem coincides with the cessation of lamina expansion in *Populus deltoides* seedlings. Although the cessation of either internode elongation or lamina expansion is an acceptable criterion for certain developmental

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purposes, these measures lack anatomical specificity. For example, simply identifying the last internode to mature provides no indication as to the rate at which secondary differentiation is progressing in the internode or the level that it has attained.

Objections can also be raised regarding most anatomical criteria. Esau [1943; 1965] has pointed out the problems in attempting to differentiate between the procambium and cambium as a criterion for secondary differentiation. Similar difficulties are encountered with criteria based on the length of the vascular elements [Bailey 1944] or the initiation of phellogen [Bond 1942]. Difficulty in defining the primary-secondary transition on the basis of discrete anatomical characteristics results from the continuum that exists between primary and secondary tissues. Ontogenetically, these tissues originate by the same meristematic process, and there is seldom a sharp dividing line between them. Furthermore, secondary differentiation does not proceed uniformly around the stem periphery, but instead proceeds acropetally according to the phyllotactic disposition of the vascular bundles.

The primary-secondary transition zone is familiar to most wood anatomists and much has been written on the differentiation of specific anatomical elements within it. However, the sequence in which these differentiation processes occur within the transition zone has not been described. A definition of the primary-secondary transition that can be usefully employed in developmental studies of wood formation is also lacking. To be useful, such a definition should be based on criteria readily obtained by sampling and highly reproducible among plants.

The objectives of the present study were to anatomically define the primary-secondary transition in *Populus deltoides*, to test its reproducibility among plants, and to describe the series of ontogenetic events within the transition zone.

Methods

Eastern cottonwood (*Populus deltoides* Bartr.) plants were raised from seed as previously described [Larson, Gordon 1969]. Plants were collected for anatomical observation when they reached a plastochron index (PI) of 16.0 to 17.0 [Larson, Isebrands 1971] (Table 1). At PI 16.0, the 16th leaf from the base, designated the index leaf, was exactly 2.0 cm long, whereas at PI 16.57 the index leaf had advanced 0.57 of a plastochron beyond the 2.0 cm length. Leaves in the ontogenetic series down the plant were numbered according to leaf plastochron index (LPI). For example, the index leaf on a plant of PI 16.0 would have a LPI of 0.0, the next older leaf LPI 1.0, and so on down the stem. Similarly, the index leaf on a plant of PI 17.0 would be exactly 2.0 cm in length and would have a LPI of 0.0. A leaf at LPI 0.0 has recently emerged from the apex, and its lateral margins are still inrolled for about one-half the lamina length, whereas a leaf at LPI 6.0 has a fully expanded lamina and is considered mature. Plants and leaves of similar PI and LPI, respectively, are at comparable morphological stages, thus providing rigorous selection criteria within an experiment.

At harvest, the stem of each plant was divided into internodes and the internodes into segments (Table 1). Internodes selected for sampling bracketed the

Table 1. Quantitative relationship in plastochrons between leaf maturity and internode maturity in cottonwood

1 Tree No.	2 PI of plant	3 LPI of mature leaf	4[1] Transition segment No.	5[2] LPI	6[3] Variance in plastochrons
1	16.57	6.57	6c	7.07	−0.50
2	16.81	6.81	6a	6.81	0.00
3	17.00	6.00	6b	6.25	−0.25
4	17.00	7.00	7a	7.00	0.00
5	16.57	6.57	6b	6.82	−0.25
6	16.73	6.73	6c	7.23	−0.50
7	16.78	6.78	6a	6.78	0.00
8	17.23	6.23	6c	6.73	−0.50
9	16.00	6.00	5d	5.75	+0.25

[1] Internodal segment in which the secondary transition occurred. Internodes were divided into quarters, and labeled basipetally a—d.

[2] LPI of Column 4 adjusted to coincide with LPI of mature leaf in Column 3.

[3] Adjusted LPI of secondary transition (Col. 5) minus LPI of mature leaf (Col. 3). Variance was minus because the secondary transition progressed acropetally whereas the LPI was computed basipetally.

presumptive secondary transition predicted by leaf maturity [Larson, Isebrands 1971]. Selected internodes were next sub-divided into quarters so that the secondary transition could be identified more precisely; preliminary sampling indicated that the transition might occur at any position within an internode depending on the morphological stage of leaf development. The quarter segments from each internode were labeled basipetally *a* through *d* to conform with the LPI, and with Segment *a* coinciding with the node.

The quarter-internode segments from Trees No. 1 — 7 were fixed in Craf III, embedded in paraffin, and stained with chlorazol black E. Ten microsections, cut from the top of each segment on a rotary microtome, were used to quantitatively locate the secondary transition.

The stem of Tree No. 8 was not divided into internodes. Instead, the entire stem section between leaves at LPI 4.23 to 9.23 was fixed in Craf III, embedded in celloidin, serially sectioned at 30 μm and stained with safranin 0. These sections were used to follow the gradual anatomical changes within the transition zone.

The stem of Tree No. 9 was divided into quarter-internode segments, fixed in 3% glutaraldehyde in phosphate buffer (*p*H 7.4), post-fixed with osmium tetroxide, and embedded in epon-araldite for sectioning on the ultramicrotome. The secondary transition was isolated in Segment *d* of the internode below leaf LPI 5.0 (Table 1). The upper one-half of Segment 5*d* was serially sectioned at 2 μm in the longitudinal plane from the periphery through the pith, and the lower one-half serially sectioned at 2 μm in the transverse plane. The sections were stained with toluidine blue 0. These sections were used to follow minute changes within the transition zone and for photomicrography.

Results and discussion

Definition of transition and transition zone

Because of the objections cited in the Introduction, it may be difficult to define the primary-secondary transition in terms entirely acceptable to all wood anatomists. Nevertheless, it would be extremely useful to have an index of the transition that could be reproducibly verified from tree to tree. The following definition, based on polarization optics, was therefore derived for developmental investigations of cottonwood: The transition from primary to secondary internodal tissue occurred when fibers with birefringent walls were first detected both within and between adjacent traces forming the vascular cylinder, with the exception of those traces last to enter the stem and all traces situated between them (Fig. 1). This definition can be rigorously applied to the acropetal continuum in internodal maturation to be described later.

In this paper, the term "secondary transition" will refer to the specific transverse plane to which the forementioned definition of the transition applies. There will be only one transverse plane at any *one point in time* that will satisfy our definition, even though the acropetal progression of secondary differentiation does not proceed uniformly in all bundles of the vascular cylinder. Consequently, it must be recognized that within the specific transverse plane defined as the secondary transition, differentiation will be more advanced in some vascular bundles than in others. The term "secondary transition zone" will refer to the region above or below the secondary transition in which gradual anatomical changes occur. Secondary wall formation in vessel elements and fibers will refer to the deposition of secondary wall substance as determined by polarization optics, and not to the blocking out of these elements following cellular division.

Relation of the secondary transition to leaf maturity

Previous work with cottonwood indicated that secondary differentiation coincided with leaf maturity [Larson, Isebrands 1971]. In an attempt to quantify this relationship, data from all 9 plants of the present study were analyzed (Table 1). In every case but one, maturity occurred in the sixth leaf below the index leaf (the index leaf has a LPI of 0.0); in Tree No. 4, maturity occurred in the seventh leaf below the index leaf (Column 3).

The quarter-internode segment in which the secondary transition was registered is shown in Column 4, and the LPI of the internode segment in Column 5. The latter was computed by adjusting the internode segment in which the secondary transition occurred to the LPI of the mature leaf shown in Column 3. The variance, in plastochrons, between leaf maturity and internode maturity is shown in Column 6.

The rationale for derivation of Column 6 was as follows: If internodal maturity is visualized as progressing acropetally, the theoretical point of maturation should be at the node (Internode Segment *a*) when the leaf attains full expansion and matures. The variance arose from approximations of leaf maturity (determined by measuring leaf lengths at 24-hour intervals) and internode maturity (determined to the nearest one-quarter internode). In spite of these approximations, leaf and

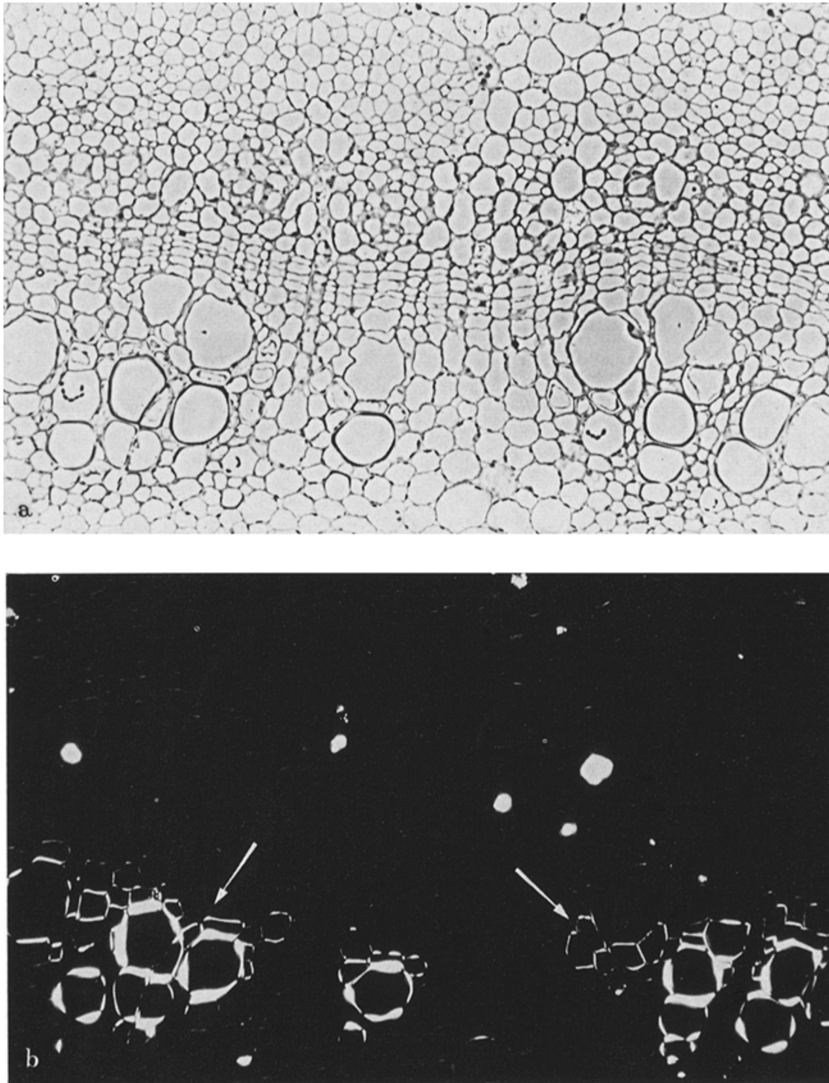

Fig. 1. Phase (a) and polarized light (b) photomicrographs of the secondary transition in transverse section. Fibers with birefringent walls are evident within and between adjacent traces of the vascular cylinder (arrows). Numerous fibers are also present that have not yet begun secondary wall thickening. Magn. 252 : 1

internode maturity coincided well, even in Tree No. 4 with a PI of 17.0 in which the mature leaf was at LPI 7.0. The data therefore indicate that leaf maturity, as measured by the leaf plastochron index, can be used as a reliable estimate of both internode maturity and the secondary transition in developmental studies of wood formation in cottonwood. The data also indicate that a valid anatomical criterion of the secondary transition is provided by secondary wall formation of the blocked-out xylem elements.

Phyllotaxy and the continuum of differentiation within the internode

Every vascular bundle within an internode is associated with a trace emerging from a leaf at a higher level on the stem[1]. In an elongating shoot, all of the leaves, and the vascular traces associated with them, are at different stages of development. Consequently, the transition from primary to secondary tissues is not uniform within the transition internode, but rather, it proceeds according to the phyllotaxy of the bundles. Because of these differences in development, it was necessary to reconstruct the phyllotaxy of the principal vascular bundles traversing the transition internode (Fig. 2) before the secondary transition could be described and Table 2 constructed.

In Figure 2, all vascular bundles for a complete orthostichy of 8 leaves, from LPI 6.23 through LPI −1.23 in Tree No. 8 (Table 1), have been identified from the serial sections; for convenience, the fractional LPI notation has been deleted for all bundles in Figure 2 and in the discussion. Since a cottonwood leaf contributes 3 traces to the stem, each of the laterals has been identified. In addition, the positions at which traces from the first leaf (LPI 7.23) of the next lower orthostichy will enter the stem have been indicated to aid interpretation. Although secondary differentiation progressed acropetally from the subjacent internode, it was convenient in examining the serial sections to proceed basipetally from primary tissue, through the transition zone, to the fully mature secondary tissue. The basipetal sequence will be adhered to in describing the anatomical changes that occur within the secondary transition zone (Table 2).

The term orthostichy has been used to designate an 8-leaf growth unit, although, as pointed out by Sinnott [1960], the perfect symmetry required by the concept of orthostichies seldom exists. Minor deviations from the theoretical $^3/_8$ phyllotaxy may be noted in Figure 2. Such deviations resulted from transpositions that occurred during development of the anastomosing trace system.

Table 2 reveals a general trend that applied to all tissues examined. Within the internode in which the transition occurred (LPI 6.23) secondary differentiation was most advanced in those bundles above the site where the next lower leaf (LPI 7.0) would arise; hence, the most mature region in a physiological sense. Differentiation of all tissues proceeded counterclockwise from this region and was most retarded in those bundles emerging from the next higher leaf (LPI 6.0). The fact that differentiation actually began to the left of 7.0 C and then advanced counterclockwise was undoubtedly related to the direction of the phyllotactic spiral in the tree examined. The microsection shown in Figure 2 was taken below the secondary transition and was included to illustrate vascular phyllotaxy. It cannot be used to judge the counterclockwise progression of development.

The pattern of secondary differentiation in cottonwood is strikingly similar to the cessation of internode elongation in *Pisum* as reported by Griffiths and Malins [1930]. In *Pisum*, elongation ceased first at the base of the internode on the stem side just above the point leaf insertion (comparable to our LPI 7.0), and it continued longest on the side in which the next leaf trace above entered the

[1] Following Hanstein [1858], that portion of a trace bundle extending into the leaf and down to the vascular cylinder will be referred to as a "trace", and that portion extending through the internode as a "bundle". Phloem fibers will be referred to as "groups".

stem (comparable to our LPI 6.0). From these observations, the authors concluded that final cell extension in a shoot axis is completed in a number of steps, each corresponding to a growth unit defined by phyllotaxy. Bernheim [1930] also noted zones of growth within individual internodes.

Maturation of the internodal tissues in a systematic pattern according to phyllotaxy results from physiological gradients related to the developmental stage of the leaf from which each trace emerged. Because of these gradients, the bundles entering the transition zone will be observed in varying degrees of completion. Nevertheless, all cells that differentiate from the cambium following the cessation of internode elongation will be secondary elements regardless of the

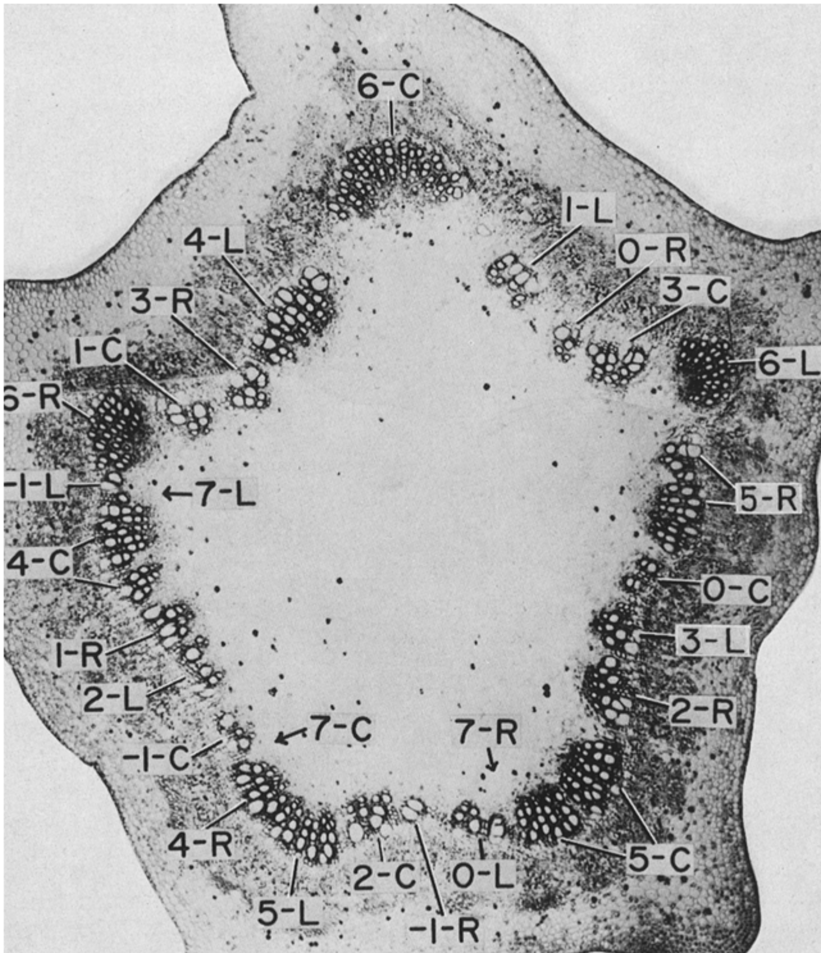

Fig. 2. Transverse section below the secondary transition from Tree No. 8 showing the phyllotactic arrangement of vascular bundles for one orthostichy of 8 leaves. Each bundle is labeled (Center, Right or Left) according to the leaf plastochron index (LPI) of the leaf to which it leads. The locations at which traces from the next lower leaf (LPI 7.0) will enter the vascular cylinder are also indicated

Table 2. Basipetal course of differentiation through the secondary transition zone of Tree No.8[1]

Micrometers	Secondary differentiation[2]
0	Secondary walls of xylem fibers associated with trace bundles thickening in 4.0 C. Parenchyma between bundles exhibit some radial alignment.
800	Slight thickening, particularly in cell corners, in scattered xylem fibers counterclockwise from 4.0 C to 3.0 L.
1200	Trace 6.0 C enters vascular cylinder.
1600	Obvious secondary wall thickening of xylem fibers in bundles extending counterclockwise from 4.0 C to 5.0 L; differentiation also extending into interfascicular region adjacent to each bundle. Incipient wall thickening of xylem fibers in remaining bundles except incoming traces of LPI 6.0. Incipient wall thickening in phloem fiber groups associated with maturing bundles.
2000	Trace 6.0 R enters vascular cylinder.
2400	Trace 6.0 L enters vascular cylinder. Transition according to definition in text (Fig. 1a, b); fibers with birefringent walls present both within and between all principal bundles except those from LPI 6.0. Differentiation also lags in bundles between 6.0 R and 6.0 C., and particularly between 6.0 C and 6.0 L. Medullary rays blocked out in both xylem and phloem.
3200	Secondary walls of phloem fibers thickening in groups located between 4.0 C and 5.0 L; differentiation proceeds centripetally within each fiber group (Fig. 8). Xylem, phloem and phloem fibers clearly delineated into tissue units.
4150	Xylem fibers well developed in all bundles except those of LPI 6.0; bundles between 6.0 C and 6.0 L still lagging in development. Differentiation of fibers in interfascicular regions proceeding rapidly with most bundles opposite incoming traces completely united. Phloem fibers associated with bundles from 6.0 L counterclockwise to 6.0 R maturing rapidly.
5100	Walls of xylem fibers thickening in 6.0 R.
5500	Walls of xylem fibers thickening in 6.0 L.
6600	Walls of xylem fibers thickening in 6.0 C. Walls of phloem fibers thickening to some degree around entire periphery, except those associated with 6.0 C.
8900	All tissues around periphery maturing; interfascicular fibers and vessel elements now form completely closed cylinder. Trace 6.0 C exhibits well-developed fibers. Phloem fibers in region between 6.0 C and 6.0 L still lagging in development.
12,500	Trace 7.0 C enters vascular cylinder. Groups of phloem fibers fully mature between 4.0 C and 5.0 C; remaining blocked-out groups mature to varying degrees. All remaining tissues around periphery mature.

[1] Differentiation proceeds acropetally, but the basipetal course has been used to conform with the LPI system. The fractional LPI notation has been deleted for convenience. Fig. 2 has been included to illustrate the vascular phyllotaxy referred to in Table 2. It cannot be used to follow the progress of differentiation.

[2] Secondary differentiation of fibers and vessel elements refers to the deposition of secondary wall substance as determined by polarization optics. The starting point in the transition internode was arbitrarily established.

relative age or state of maturity of the individual bundle. These events have been followed in detail in stems of *Helianthus* by Thoday [1922] and Priestley and Scott [1936], and the concept has been reviewed by Esau [1954] and Wardlaw [1965]. Cottonwood conforms to this general concept.

The ontogenetic sequence of differentiation within the internode

When examining the serial sections in basipetal sequence, secondary wall formation was first observed in the fibers closely associated with the mature metaxylem vessels of the bundles, and from there it gradually extended tangentially into the interfascicular regions and centrifugally toward the cambium (Table 2). During the phase of interfascicular differentiation, the phloem fibers in the cortical region of the stem also began to differentiate, and demarcation of the medullary ray tissue between the principal traces became especially prominent. The xylem and phloem elements together with the contiguous group of phloem fibers external to them occurred as a wedge of tissue. The tissues comprising each of these tissue units appeared to arise from a common primary bundle and to differentiate in unison (Fig. 3).

All differentiation processes were gradual and continuous, and in each tissue and tissue unit differentiation proceeded in essentially a counterclockwise direction from the point of origin. Because of the overlap in tissue differentiation, it is incorrect to think of these as discrete differentiation processes although they will be considered as such for purposes of discussion.

Secondary differentiation always occurred in previously blocked-out tissues. That is, the cellular elements arose from the procambium during elongation as noted by Wetmore et al. [1964]. However, a cambium was also present in the transition internode, and derivatives that were destined to differentiate into elements possessing definite secondary characteristics upon maturity were also blocked-out. These elements were generally found in the most advanced bundles arising from the older leaves. Because radial seriation occurs early in procambial development, it is not a valid criterion for secondary growth [Bond 1942; Thompson, Heimsch 1964].

Xylem differentiation

Considering the gradients just described, it should be possible to locate bundles within the secondary transition zone that contain vascular elements representing the entire ontogenetic series. Furthermore, because cambial activity is somewhat restricted prior to the transition, these elements should occur side-by-side within some bundles. The first protoxylem elements with annular or spiral wall sculpturing are produced prior to any internodal growth. They function for a very short time and are then passively stretched during internodal elongation. In *Pisum*, early protoxylem elements have been found that were stretched through an entire internode [Griffiths, Malins 1930]. Similar distorted elements were found to occur in cottonwood (Fig. 4).

Protoxylem elements are succeeded by metaxylem [Frey-Wyssling 1940] as internode elongation declines, and varying degrees of functional and non-functional

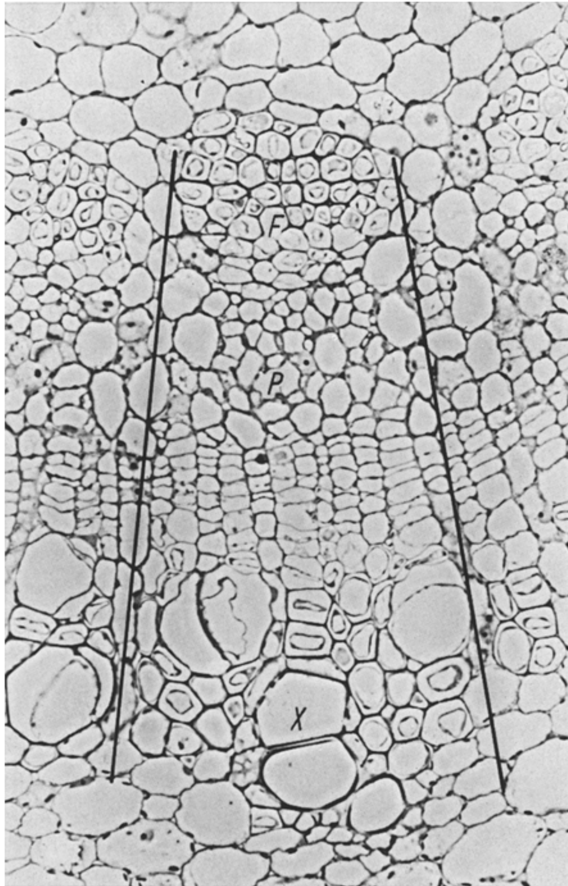

Fig. 3. A tissue unit consisting of a wedge of xylem (X), phloem (P) and phloem fibers (F). Each tissue unit (between solid lines) appears to arise from a common primary bundle. Transverse section from below the secondary transition. Magn. 320 : 1. Phase

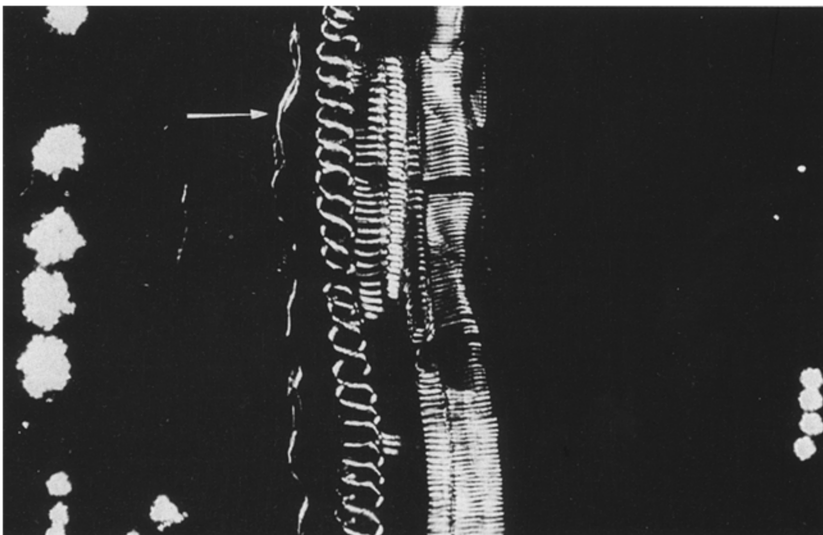

Fig. 4. Protoxylem elements are stretched to varying degrees during internodal elongation. The one on the left (arrow) was stretched through an entire internode. The elements exhibit both annular and spiral wall sculpturing. Magn. 315 : 1. Polarized light

elements may be found in the secondary transition zone. The last metaxylem elements produced prior to the transition in cottonwood were large in diameter and highly variable in length (300 μm to 580 μm), due both to stretching and apical intrusive growth. Within the transition zone, new vessel elements with secondary characteristics often formed adjacent to the last metaxylem of the vascular bundles (Fig. 5). These secondary vessel elements were large in diameter and short in length (140 μm to 290 μm when the tapered tips were included).

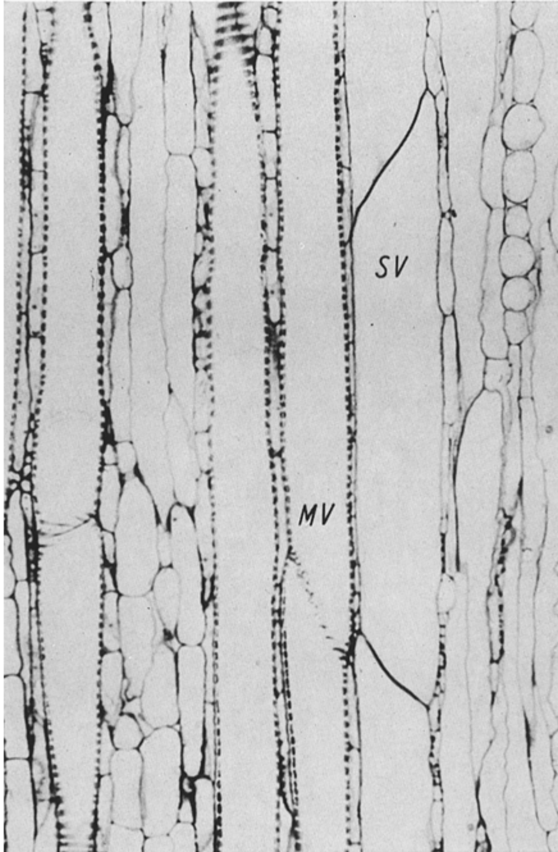

Fig. 5. Within the transition zone, secondary vessel elements (SV) often abut directly on the last-formed metaxylem (MV) of a vascular bundle. Magn. 252 : 1. Bright field

Bailey [1944] noted the significant decrease in length from the last-formed primary to the first-formed secondary xylem, and suggested that it might be a reliable means for distinguishing the outer boundary of primary xylem. In carefully prepared longitudinal sections from the transition internode of cottonwood the short, secondary elements could be observed. However, they were difficult to identify on transverse sections, and it was impossible to establish the secondary transition from longitudinal sections because of the variation from bundle to bundle around the periphery.

Fibers in the interfascicular regions began to differentiate by deposition of secondary wall substance shortly after those associated with the vascular bundles (Table 2). Differentiation advanced continuously and tangentially from the vessel groups of the bundles and formed wedges of fibers that extended into the interfascicular regions (Fig. 6). Although differentiation proceeded into previously blocked-out tissue of the interfascicular regions, cambial activity was apparently limited up to the time of transition. The cambial zone rarely exceeded 4 to 6 cells in width and mitotic figures were seldom encountered.

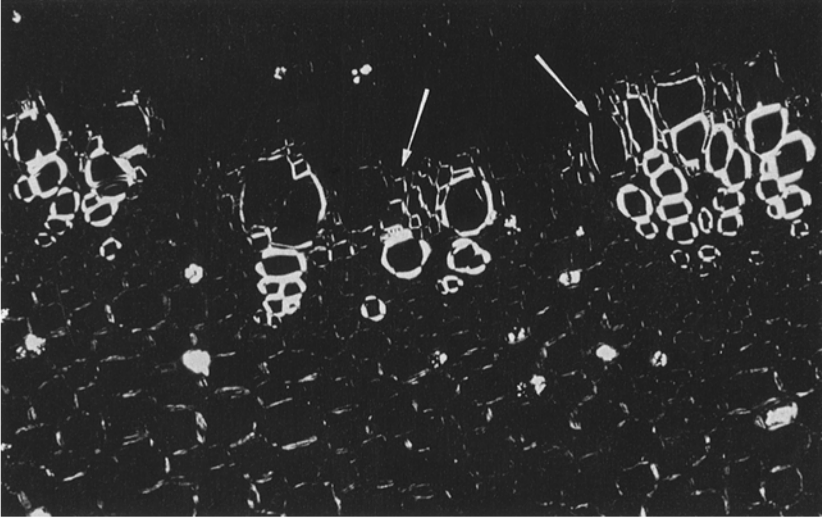

Fig. 6. Fibers differentiating tangentially into the blocked-out interfascicular tissue regions between adjacent bundles (arrows). Transverse section just below the secondary transition zone. Magn. 160 : 1. Polarized light

During the counterclockwise progression of interfascicular differentiation, closely adjacent bundles were united quickly while more remote ones lagged. Occasionally, fibers differentiated within an apparently isolated interfascicular region. These areas could usually be associated with the phloic component of a bundle devoid of either proto- or metaxylem vessels. The few immature secondary vessels found in the interfascicular region were invariably associated with such bundles.

Phloem differentiation

Bailey's [1944] proposed definition of secondary growth pertained exclusively to the xylem, and Esau [1965] has noted that comparable data on the relative lengths of primary and secondary sieve elements are not available. Sieve elements classified as metaphloem in the secondary transition zone of cottonwood ranged from 210 μm to 400 μm in length. Shorter sieve elements typical of the secondary phloem, ranging from 110 μm to 185 μm in length, were occasionally encountered adjacent to those of the metaphloem.

Phloem fiber differentiation

A group of sclerenchymatous fibers occurred external to each vascular bundle adjacent to the protophloem. The metaphloem of cottonwood, like other species examined [Esau 1950], does not contain fibers. Obliterated protophloem elements were found on the inner face of these fiber groups (Fig. 7). Because of the phloic components, each of the fiber groups could be associated with a tissue unit. Occasional fiber groups, representing incomplete tissue units, occurred in conjunction with bundles consisting of phloem with no xylem counterpart as described by Esau [1954] and O'Neill [1961] for *Linum* and *Lupinus*, respectively.

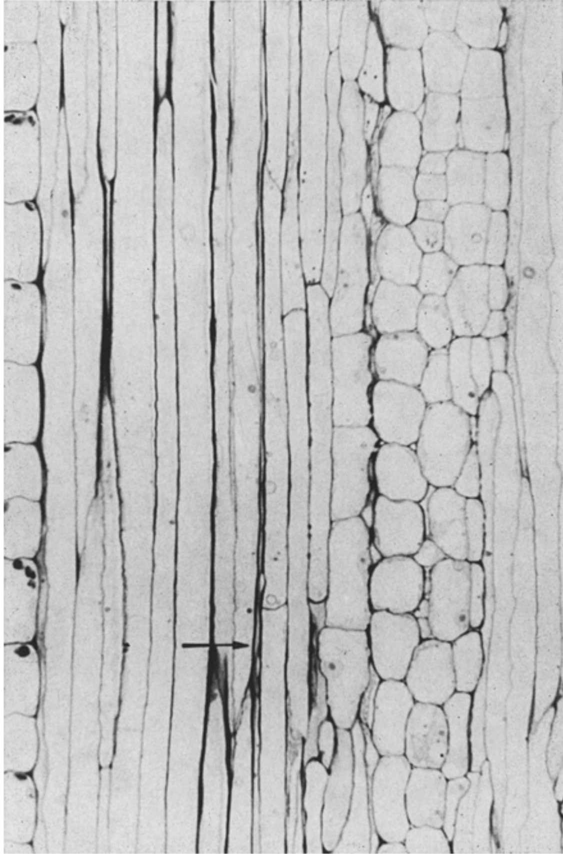

Fig. 7. Partially obliterated protophloem element (arrow) located between the inner face of a phloem fiber group (left) and the metaphloem (right). The protophloem element was stretched during internodal elongation. Magn. 400 : 1. Bright field

Secondary wall thickening of the phloem fibers began simultaneously with and progressed parallel to that of the interfascicular fibers. That is, phloem fibers with birefringent walls were noted at about the time that differentiating fibers from the same tissue unit were observed extending into the interfascicular regions.

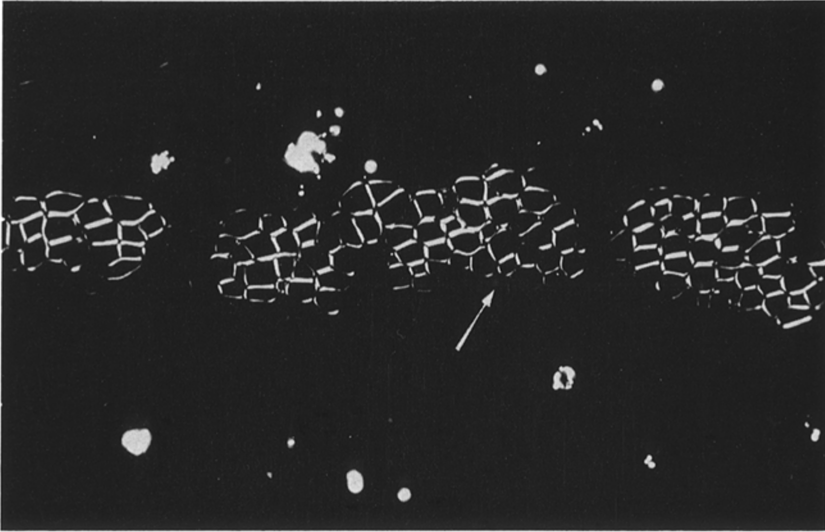

Fig. 8. Phloem fiber group at an advanced stage of maturation showing some centripetal differentiation still occurring in the blocked-out tissue (arrow). Magn. 320 : 1. Polarized light

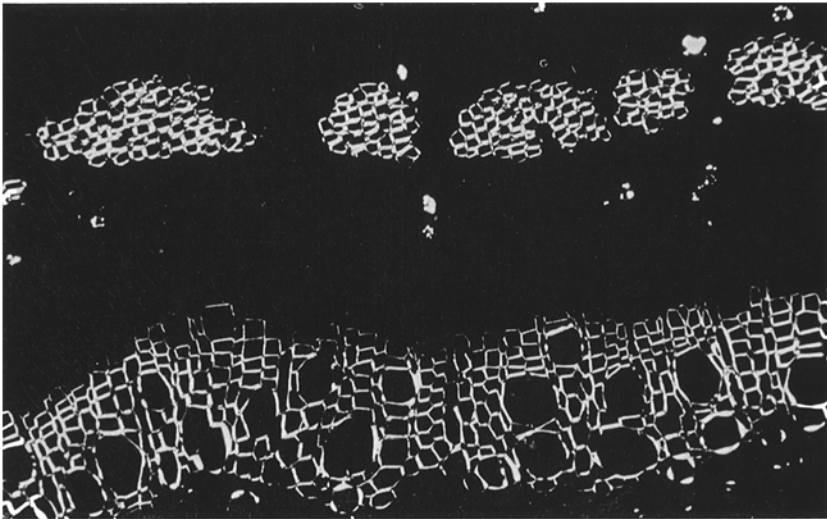

Fig. 9. Completely closed woody cylinder below the secondary transition zone consisting of birefringent fibers and vessel elements. Mature groups of phloem fibers occur in the external portion of the phloem. Magn. 160 : 1. Polarized light

Subsequent differentiation of phloem fibers in other tissue units proceeded essentially counterclockwise as described previously. Phloem fibers within a group of blocked-out elements always differentiated centripetally (Fig. 8).

Conclusion

It is evident from this discussion that a precise, clear-cut transition from primary to secondary stem tissues does not exist. The secondary transition occurs in the internode just beneath the most recently matured leaf. Within this transition internode, each vascular bundle and each tissue comprising the bundle differentiates in accord with the physiological age and the phyllotactic disposition of the developing leaf to which it leads. As a consequence, certain bundles differentiate in advance of others. That is, although each bundle develops acropetally in continuity with more mature tissues, those opposite the incoming trace are developmentally more advanced. When this bundle arrangement is observed in a basipetal series of sections, the counterclockwise progression of differentiation is encountered. Our definition of the secondary transition is based on certain anatomical criteria that appear within this continuum of development on a specific transverse plane *at the time of sampling.*

The primary vascular bundles emerging from the leaves coalesce to form a woody cylinder in the secondary transition zone. From this point downward, the individual bundles lose their identity (Fig. 9), but they persist as components of the anastomosing vascular system extending throughout the stem and roots. The entire system can therefore be viewed as an aggregation of vascular bundles regulated in its development by the foliar organs. Although the system develops as a continuum, certain physiological gradients culminate in association with leaf maturity resulting in marked anatomical changes in the transition internode.

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