



PHYSIOLOGICAL ECOLOGY
A Series of Monographs,
Texts, and Treatises

T.T. KOZLOWSKI

GROWTH AND DEVELOPMENT OF TREES

Volume II Cambial Growth ,Root Growth ,and Reproductive Growth

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PHYSIOLOGICAL ECOLOGY

A Series of Monographs, Texts, and Treatises

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Volume II

Cambial Growth, Root Growth, and Reproductive Growth



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PREFACE

This two-volume treatise characterizes important features of growth and development of trees and other woody plants during their life cycles. The need for this work was indicated by greatly accelerated research and a rapidly expanding body of information on the nature and control of growth of woody plants. These volumes were planned as text or reference material for upper level undergraduate students, graduate students, investigators, and growers. The content is sufficiently interdisciplinary to make it useful to academics as well as those involved in the practice of growing trees and other woody plants for fruit crops or wood as well as for esthetic reasons. The subject matter will be of interest to arborists, foresters, horticulturists, plant ecologists, plant physiologists, plant anatomists, tree breeders and geneticists, plant pathologists, entomologists, soil scientists, meteorologists, and landscape architects.

The viewpoint in these books is largely developmental, with strong ecological and physiological overtones throughout. In organizing the chapters, an attempt was made to adhere to the following central objectives: (1) To present a comprehensive treatment of the current state of knowledge of the important events in growth of the perennial woody plant. (2) To highlight the significant changes which take place in vegetative and reproductive growth as woody plants progress from juvenility to adulthood and, finally, to a senescent state. Such an emphasis seemed especially important because ontogenetic changes often have not been treated in depth or have been overlooked in the literature on tree growth. (3) To interpret the effects of external and internal controls of vegetative and reproductive growth. Considerable attention is given to important spatial and temporal variations in growth. Among the reasons for this emphasis was my realization that cambial growth generally has been described in terms of an "annual ring" at a single stem height. As cambial growth varies markedly with stem height the need was evident for dealing with the developmental architecture of a tree axis in three dimensions. To this

end particular stress has been placed on variations in production and maturation of cambial derivatives at different stem heights and along branches. (4) To present significant reference material selected from the world literature so as to make the work authoritative and well documented.

Despite the explosive accumulation during recent years of research data, both controversies and deficiencies exist in information on several aspects of growth of woody plants. When possible an attempt was made to present conclusions that seemed most reasonable in the light of available data. Nevertheless, certain interpretations must be considered tentative, and some of the conclusions presented may be reinforced and others revised as new information becomes available.

I wish to express a debt of gratitude to a number of friends and colleagues who contributed in various ways. Particularly, I acknowledge the help of J. Johanna Clausen who read the first draft of most chapters and made many valuable suggestions. Individual chapters were also reviewed by R. F. Evert, W. E. Hillis, B. F. Kukachka, P. R. Larson, A. C. Leopold, G. C. Marks, J. D. Matthews, Daphne J. Osborne, Diana M. Smith, G. R. Stairs, R. G. Stanley, E. L. Stone, H. B. Tepper, T. A. Villiers, Y. Waisel, P. F. Wareing, H. E. Wilcox, and S. A. Wilde. To all I express my sincere appreciation for their generosity and kindly counsel.

T. T. KOZŁOWSKI

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1. Structural and Growth Characteristics of Trees
2. Seed Germination and Seedling Development
3. Maturation or Phase Change
4. Aging
5. Bud Development and Shoot Expansion
6. Leaf Growth and Development
7. Variations in Shoot Growth
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Author Index–Subject Index

ERRATUM TO VOLUME I

The third line on page 40 of Volume I should read: xylem in containing cytoplasm and in lacking *rigid* cell walls. The efficiency of

GROWTH AND DEVELOPMENT OF TREES

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Chapter 1

CAMBIAL GROWTH

Increase in girth of trees occurs primarily from meristematic activity in the vascular cambium (hereafter called cambium), a sheathing and cylindrical meristem located between the xylem and phloem of the stem, branches, and major roots. A relatively small amount of increase in girth is traceable to meristematic activity of the phellogen (also called cork cambium). Two types of cell division occur in the cambium, additive and multiplicative. Additive division involves periclinal (tangential) division of cambial cells and recent derivatives to produce secondary xylem and phloem. Multiplicative division consists of anticlinal (radial) divisions of cambial cells which provide for circumferential expansion of the cambium.

Mature Xylem and Phloem Increments

Following winter dormancy the cambium of Temperate Zone trees is re-activated as periclinal cell divisions are initiated to produce xylem centripetally and phloem centrifugally. New annual increments of xylem and phloem are thus inserted between old layers of these tissues causing the stem, branches, and major roots to increase in thickness.

XYLEM INCREMENTS

The annual rings of wood stand out prominently in stem or branch cross-sections because of rather consistent variations in cell size and density of wood formed at various times during the growing season. As mentioned in Volume I, Chapter 1 the xylem formed early in the season is composed of larger cells than that formed later. Wood formed early also is less dense than that formed late in the growing season. Because of the uniformity of composition of gymnosperm xylem, changes in cell wall thickness are closely correlated with changes in density. In angiosperms, however, the density of xylem depends not only on wall thickness but also on the proportion of

various cell types present. This proportion is relatively constant within a species and even within many genera, although it does vary within a season. In species of different angiosperm genera, however, the arrangement of cells and proportions of different cell types vary greatly.

Because of the consistent periclinal divisions of the cambium, the young undifferentiated xylem and phloem cells are regularly aligned in radial rows. In gymnosperms such a regular radial arrangement is generally maintained throughout differentiation of tracheids. In contrast, in angiosperms, the early alignment of cambial derivatives in the xylem is obscured as some cells, such as vessel members, enlarge greatly, and distort the position of rays and adjacent cells. Hence, it is not uncommon for a uniseriate ray to approach a large vessel and then bend around it (Figs. 1.1 and 1.17). In *Quercus rubra* uniseriate rays were displaced tangentially more than 100 μ by expanding vessel elements. Multiseriate rays, however, were not affected by the enlarging vessel elements (Zasada and Zahner, 1969).

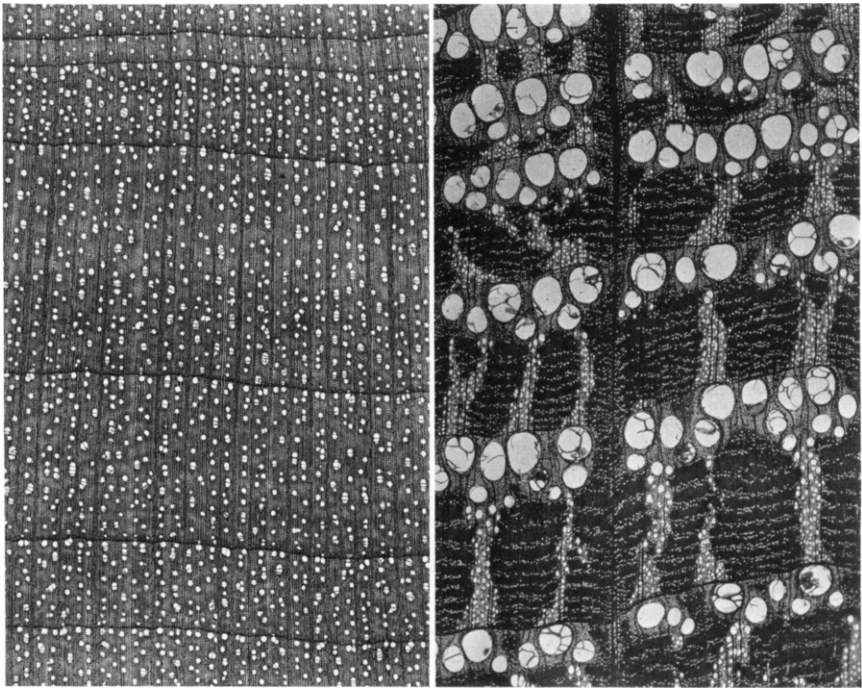


FIG. 1.1. Stem transections showing variation in vessel diameters and distribution within annual growth increments of a diffuse porous species, *Acer saccharinum* (left) and a ring porous species, *Quercus alba*. ($\times 12$.) U.S. Forest Service, Forest Products Laboratory photo.

As may be seen in Fig. 1.1 angiosperms are classified as ring porous or diffuse porous. In ring porous trees, such as *Quercus*, *Fraxinus*, and *Ulmus*, the diameters of xylem vessels formed early in the growing season are much larger than those formed later. In diffuse porous trees, such as *Populus*, *Acer*, and *Betula*, the vessels generally are of small diameter, and those formed early in the growing season are of approximately the same diameter as those formed late.

Contact Zones

Considerable variation exists in the outer contact zones of annual xylem growth increments. In areas of high rainfall and cold winters the contact zones, as seen in transections of stems or branches, between annual xylem increments are well defined in comparison to those in species growing in extreme environments. In the juvenile core of the stem of a normal tree, the transition is gradual in rings nearest the pith and becomes increasingly abrupt in the older wood. In old trees the demarcation between xylem increments generally is very sharp. Some extreme examples of cambial growth in certain species growing in the very arid region of West Texas were cited by Glock, Studhalter, and Agerter (1960). In that region, cambial activity varied among twigs from complete cessation to continuous but decreasing activity, followed by an increasing rate. Because of such variations, contacts between xylem increments were sharp, definite, indefinite, or diffuse. A single branch cross-section sometimes showed all four types of contacts. Wide variations in sharpness of contact also occurred in the longitudinal direction. Outer contact zones of annual growth increments sometimes were not as sharp as borders between intraannual rings. As borders of annual rings were sharp or diffuse, they often could not be distinguished by cell structure from the outer borders of annual increments (Glock and Agerter, 1962).

In tropical and subtropical trees annual rings often are indistinct or absent, especially in diffuse porous woods. In India, where diffuse porous species account for over 90% of all dicotyledonous woods, some species have distinct growth rings and others do not (Chapter 2). The specific anatomical features which delineate growth rings in tropical woods may vary greatly among species. In *Acacia catechu*, for example, growth rings are outlined by narrow bands of marginal parenchyma and sometimes by thick-walled fibers in the outer latewood. In *Bombax malabaricum* the growth rings are identified by radially compressed fibers and parenchyma cells in the outer latewood. The xylem increments of *Shorea robusta* have many irregularly shaped parenchyma bands which sometimes are mistaken for annual rings. These do not always encircle the tree and do not always form only once a year. When they do form annually they are not produced during the same month each year (Chowdhury, 1939).

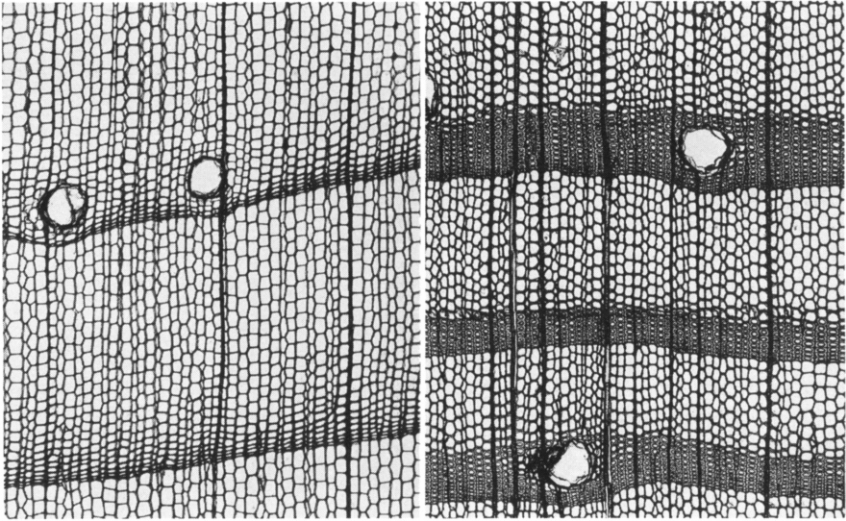


FIG. 1.2. Variations in transition from earlywood to latewood in gymnosperms. Gradual transition in *Pinus lambertiana* (left) and abrupt transition in *Pinus palustris*. ($\times 27.5$.) U.S. Forest Service, Forest Products Laboratory photo.

Earlywood and Latewood. The wood of low density usually (but not always) produced early in the season will be called “earlywood.” The part of the annual xylem increment which usually is produced late in the growing season and is of higher density than wood produced early in the season, will be called “latewood” (Fig. 1.2).

Earlywood and latewood have been used in the literature as synonyms for “springwood” and “summerwood,” but the latter terms are really misnomers because either type of wood may be produced in more than one season in the same year. Chalk (1937) suggested that the terms springwood and summerwood be abandoned but their wide usage has persisted despite their manifest shortcomings. Glock, Studhalter, and Agerter (1960) also objected to the terms earlywood and latewood because the latewood sometimes was found at the beginning of a growth layer as fragments within an annual increment, intermittent circles, and complete circles preceding the latest earlywood of an increment. They preferred to use the terms “lightwood” and “densewood,” which placed emphasis on actual structure of the tissues and were not identified with the time when tissues formed or with their relative position within a growth layer or increment.

The boundary between earlywood and latewood in the same ring can be very sharp or gradual (Fig. 1.2). The boundary is sharp in hard pines, *Pseudotsuga*, *Larix*, and *Juniperus*. Ladefoged (1952) found an abrupt early-

wood-latewood transition in ring porous angiosperms and a gradual one in diffuse porous species. Various arbitrary methods of clearly characterizing both earlywood and latewood have been advanced. One of the most popular standards is that of Mork (1928) who considered a latewood tracheid to be one in which the width of the common wall between the two neighboring tracheids multiplied by 2 was equal to, or greater than, the width of the lumen. When the value was less than the width of the lumen the xylem was considered to be earlywood. All measurements were made in the radial direction. Mork's definition originally was applied to spruce xylem but has been adopted widely for use with wood of gymnosperms. It is not useful for angiosperm woods.

PHLOEM INCREMENTS

The annual sheaths of mature secondary phloem are much thinner than the increments of secondary xylem. This is because less phloem than xylem is produced annually, old phloem tissues often are crushed, and eventually the external, nonfunctional phloem tissues are shed.

In many woody plants the phloem is divided by various features into distinguishable growth increments. However, these are not nearly as clear and distinctive as are annual increments of the xylem. Often the structural differences of early phloem are rendered indistinguishable by collapse of sieve tubes and growth of parenchyma cells.

In branches of *Juglans regia* the annual phloem rings were not crushed except for early-season phloem which was somewhat compressed. The phloem annual ring was made up of distinct tangential bands, making it possible to identify seasonal growth increments (Fig. 1.3). Each phloem increment was divisible into early- and late-season tissue. Early-season phloem, composed primarily of large sieve tubes, was separated from late-season phloem by a band of fibers. Late-season phloem was composed of a mixture of narrow sieve tubes, parenchyma cells, and sometimes an incomplete tangential band of fibers (Schaad and Wilson, 1970).

In some species the annual increments of phloem can be delineated because early phloem cells expand more than those of the late phloem (Artschwager, 1950). In *Pyrus malus* tangential bands of fiber sclereids and crystal-containing cells are characteristic boundaries of annual growth of phloem (Evert, 1963b). Early- and late-phloem increments sometimes are also identifiable by features of phloem parenchyma. For example, phloem parenchyma cells produced early have little tannin and they collapse when the phloem eventually becomes nonfunctional. In contrast, the tannin-laden, late-phloem parenchyma cells become turgid. Hence, their appearance is useful in identifying limits of annual increments. In some species the annual increments of

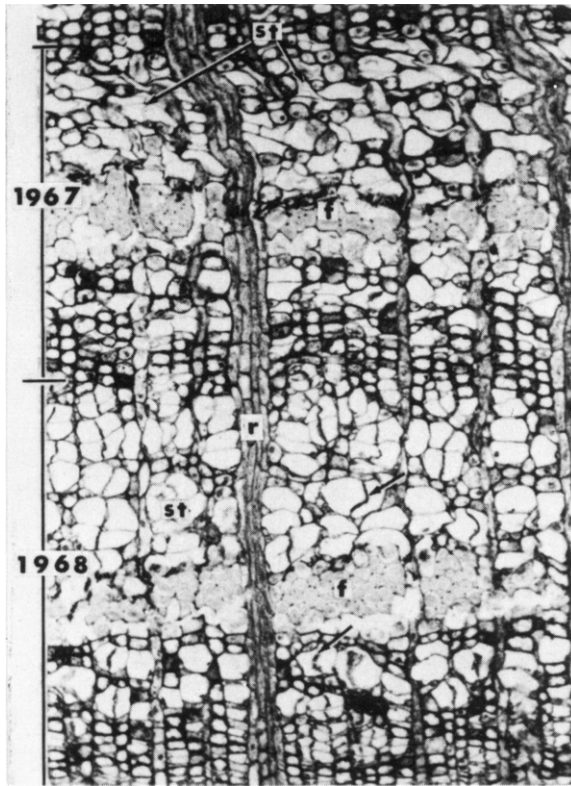


FIG. 1.3. Transection showing 1967 and 1968 season phloem increments of branch of *Juglans regia*. The degenerated sieve tubes (st) in the 1967 phloem are collapsed more than those of the 1968 phloem. f, fibers; r, ray. [From Schaad and Wilson (1970).]

phloem can be identified by the number of distinct zones of various cell types produced.

In angiosperms the seasonal timing of production and differentiation of various elements of the phloem varies considerably. In *Robinia pseudoacacia* periclinal divisions and sieve element differentiation began early (late March or early April) in Madison, Wisconsin. The first new sieve elements arose from undifferentiated, overwintering cells in the outer part of the cambial zone. Concurrently other cells divided periclinally without first expanding radially. By comparison, phloem fiber primordia usually were first produced in mid-May, by which time about half the seasonal phloem increment had already been laid down. At maturity the phloem fibers were associated with strands of crystal-containing cells. Secondary wall formation in phloem fibers and crystal-containing cells occurred slowly. Hence, mature sieve

elements were located adjacent to fibers with only partially thickened walls (Tucker and Evert, 1969).

In gymnosperms the annual increments of secondary phloem are especially difficult to outline histologically. Although differences occur in diameters of early- and late-sieve cells these often are obscured by pressures from expansion of parenchyma cells. In *Chamaecyparis* and *Thuja* the early formed fibers of an annual increment have thicker walls than do fibers formed later. According to Huber (1939) and Holdheide (1951) the early phloem of *Pinaceae* is made up almost wholly of sieve elements. As sieve elements collapse they form a dark band which outlines the boundary of the annual increment. Using such criteria, Srivastava (1963) attempted to identify annual growth increments in phloem of a variety of gymnosperms. The results were variable. Some species, including *Pinus jeffreyi*, *Picea pungens*, *P. excelsa* and *Larix decidua* had distinct growth increments. In a number of other species the boundaries of growth increments were not readily discernible either because phloem parenchyma cells were scattered or because no clear line of crushed sieve cells could be identified between successive bands of phloem parenchyma, as in *Pinus murrayana* and *Abies concolor*.

Conducting and Nonconducting Phloem

The layer of phloem which has conducting sieve tubes is exceedingly narrow. For example, the layer of conducting phloem was reported as 0.2 mm wide in *Fraxinus americana*, 0.2–0.3 mm in *Quercus*, *Fagus*, *Acer*, and *Betula*, 0.4–0.7 mm in *Juglans* and *Ulmus*, and 0.8–1.0 mm in *Salix* and *Populus* (Holdheide, 1951; Zimmermann, 1961). Because of distortions of tissues in the nonconducting phloem it is only in the narrow conducting zone that important characteristics of phloem tissues can be recognized. These include shapes of various phloem elements, presence of nacreous walls, structure of sieve plates, and variations among parenchyma cells. After sieve elements cease functioning, several important changes occur in the phloem including intensive sclerification, depositions of crystals, collapse of sieve elements, and dilatation of phloem tissues resulting from enlargement and division of axial and ray parenchyma cells. The extent to which each of these changes occurs varies with species.

Production of Xylem and Phloem

More than 90% of the cambium is comprised of elongated, spindle-shaped cells called fusiform initials. The remainder of the cambium is made up of short ray initials. Cambia may be classified as storied (or stratified) and nonstoried (or nonstratified). In storied cambia (e.g., *Diospyros*, *Robinia*,

and *Tamarix*) the fusiform initials and cambial derivatives appear in horizontal tiers in tangential view. In contrast, nonstoried cambia (e.g., *Acer*, *Pinus*, and *Populus*) have fusiform initials and derivatives with overlapping ends (Figs. 1.4, 1.5).

There has not been general agreement on a standard definition for the cambium. Whereas some investigators regard the term cambium to refer exclusively to a uniseriate layer of cambial initials, others consider the cambium to be a zone which includes both cambial initials and their recent meristematic derivatives, the xylem mother cells and phloem mother cells. The latter choice is supported by difficulty in recognizing a uniform uniseriate layer of initials and their great instability. In this chapter the entire zone of dividing cells, including the xylary and phloic initials as well as the

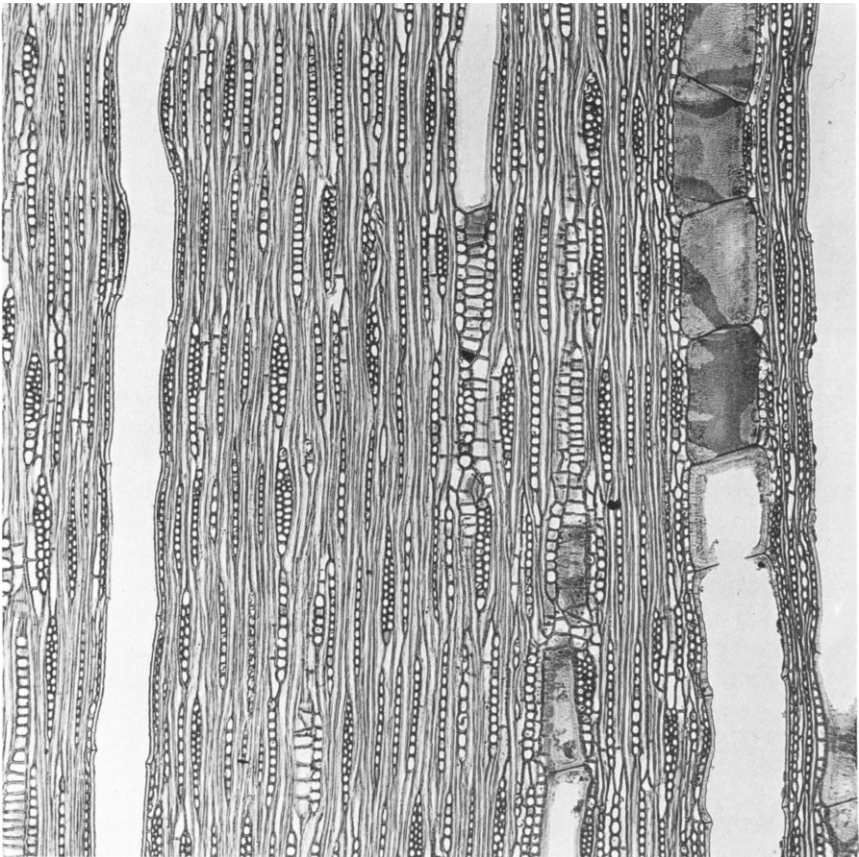


FIG. 1.4. Tangential section of xylem of *Diospyros virginiana* showing storied elements. U.S. Forest Service photo.

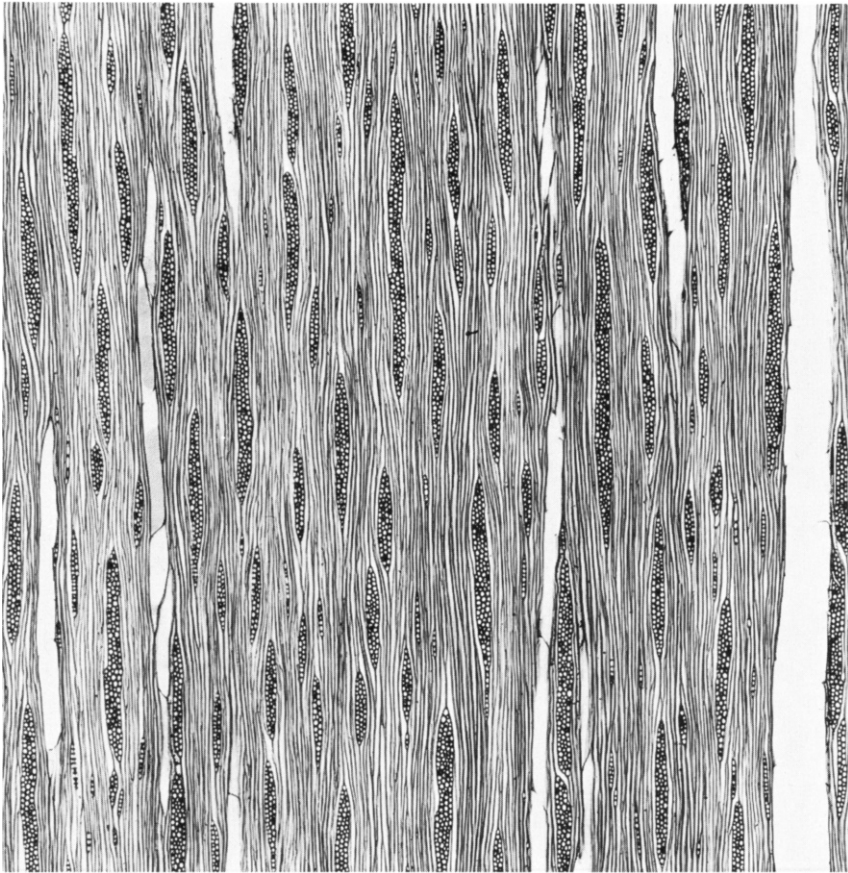


FIG. 1.5. Tangential section of xylem of *Acer rubrum* showing nonstoried elements. U.S. Forest Service photo.

uniseriate layer, will be called the cambial zone or cambium. As thus defined, the cambium in dormant trees often varies from 1 to as many as 10 cells wide (Figs. 1.6, 1.7). The width of the cambium in growing trees is extremely variable. Bannan (1962) reported the cambium to be 12–40 cells wide in fast growing trees and 6–8 cells wide in slow growing ones; in transection the cells of the cambium are arranged in radial series.

Most investigators agree that cambial reactivation in temperate zone trees actually involves two stages. The first of these, called “preliminary change” by Ladefoged (1952), is considered to be a prelude to resumption of the second phase which involves mitotic activity to produce cambial derivatives. There does not seem to be general agreement, however, on the processes

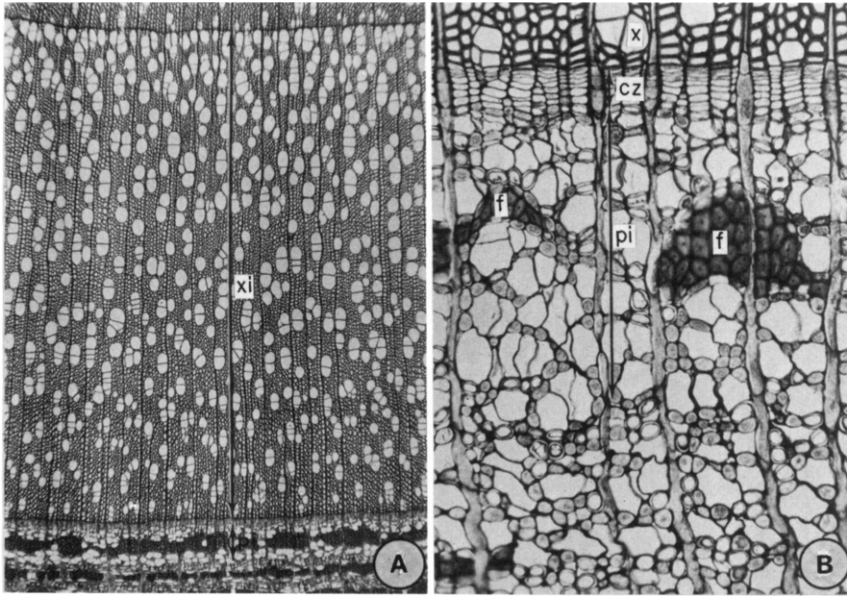


FIG. 1.6. Mature xylem and phloem increments of *Populus tremuloides*. (A) Xylem (xi) and phloem increments (pi) of trees samples in late November, 1962. (B) Outer part of 1962 xylem increment (x), the cambial zone (cz), and mostly nonconducting phloem. The phloem included all of the 1962 increment (pi) and part of 1961 increment. f, fibers. [From Evert and Kozlowski (1967).]

involved in the first or preparatory stage of cambial activity. Some observers have reported that during the first stage the cambial cells lose their dark appearance and become transparent. Although some investigators reported a general swelling of the cambial zone at the time of reactivation (Ladefoged, 1952; Wareing, 1958a), others have been unable to confirm this. For example, Alfieri and Evert (1968) found no initial general expansion of the cambial zone in *Pinus resinosa*, *P. strobus*, or *P. banksiana*. However, individual cambial cells expanded before undergoing division. An absence of a swollen cambial zone in several angiosperms has also been reported (Evert, 1960, 1963b; Derr and Evert, 1967). During reactivation of *Tilia americana* cambium, the cell walls became translucent with disappearance of lipid materials, but there was no noticeable increase in their dimensions (Deshpande, 1967). Some investigators have indicated that the preliminary change began at bud bases and moved basipetally (Ladefoged, 1952) but most data indicate that this phase begins at about the same time throughout the tree axis.

CAMBIAL GROWTH AND SHOOT ACTIVITY

Internal control of cambial growth will be considered in detail in Chapter 3 of this volume. However, as a prelude to describing cambial growth charac-