

## Cambial Activity in Trees

The major difference between trees on the one hand and herbs on the other is that the trees show lateral growth or growth in thickness, over and beyond the growth in length. The growth in length — called the extension growth — is due to division and elongation of cells at the tip of stem or root (Fig. 1). In trees, the subterminal regions which have ceased elongation undergo another kind of growth, the lateral growth which is due to cambium and which results in an increase in their girth. This is shown easily by a comparison of photographs of the same branch taken at different times (Fig. 2). In the photograph on the left the lowermost internode is about 1 1/2" long, and the one above it is about 2 1/2" long. After 3 weeks of growth (photograph on the right), a few more internodes have been added at the tip, but note that the bottom internode has not elongated. The one above it is now almost 3 1/2" long and also has stopped elongating, soon the one above it will stop elongating, then the one still above and so on. If cross sections of these internodes are stained with phloroglucinol-HCl which imparts a red color to wood (Fig. 3), it can be seen that the cambial activity has begun in the two internodes from the bottom. Henceforth, these internodes will only increase in girth.

The cambium is a layer of cells between wood (xylem) and bark (phloem)<sup>1</sup> which remains permanently meristematic or capable of division. In temperate climates, the cambial cells are active only in spring and summer, they cut a number of new cells toward the wood, about 1/2 to 1/4 that number toward the bark, and the new cells differentiate, respectively, as new wood and bark cells. With the beginning of autumn, the cam-

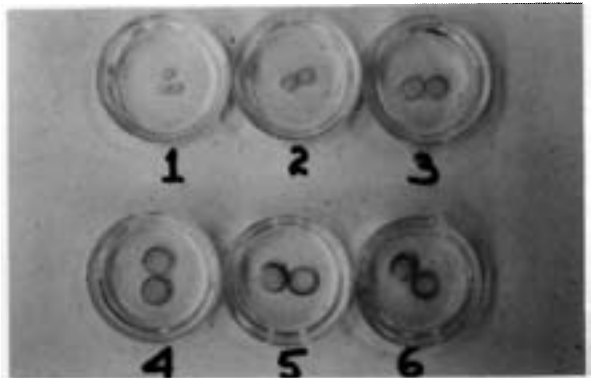
<sup>1</sup> Strictly speaking the term *wood* pertains to secondary xylem or xylem derived from the cambium as opposed to primary xylem which is derived from the procambium. The term *bark* refers to all tissues outside the cambium and includes besides primary and secondary phloem such tissues as cortex, epidermis, periderm and rhytidome. In older stems of most trees the primary phloem, cortex and epidermis are shed and the bark consists essentially of the secondary phloem, periderm and rhytidome.

<b>GROWTH AT TIP OF STEM (OR ROOT)</b>	<b>EXTENSION GROWTH</b>	<b>APICAL MERISTEM</b>
<b>GROWTH BELOW TIP</b>	<b>LATERAL GROWTH</b>	<b>CAMBIUM</b>

*Fig. 1 Two types of growth in trees, their location and meristems involved.*



*Fig. 2 Photographs of the same elderberry branch separated by a 3-week interval.*

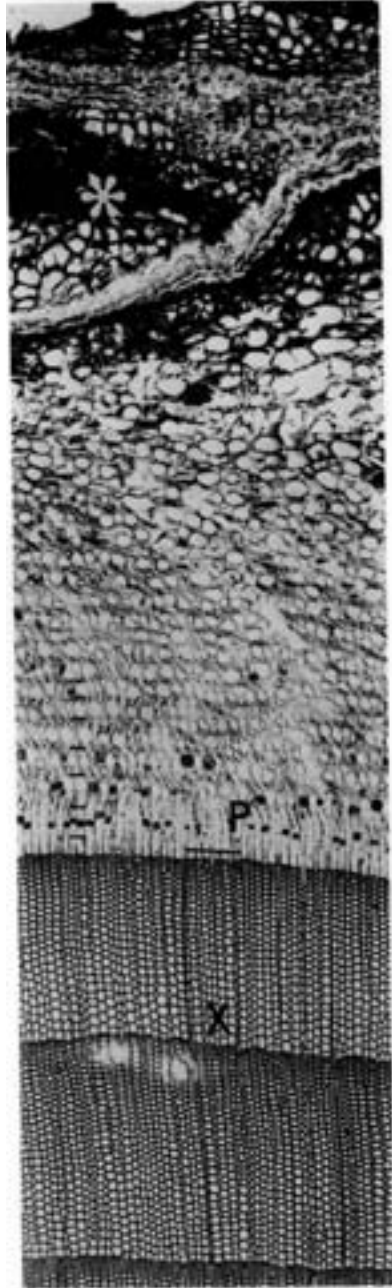


*Fig. 3 Cross sections of six internodes from the youngest (1) downwards stained with phloroglucinol/HCl to show beginning of formation of wood (internodes 6 and 5) and hence beginning of cambial activity.*

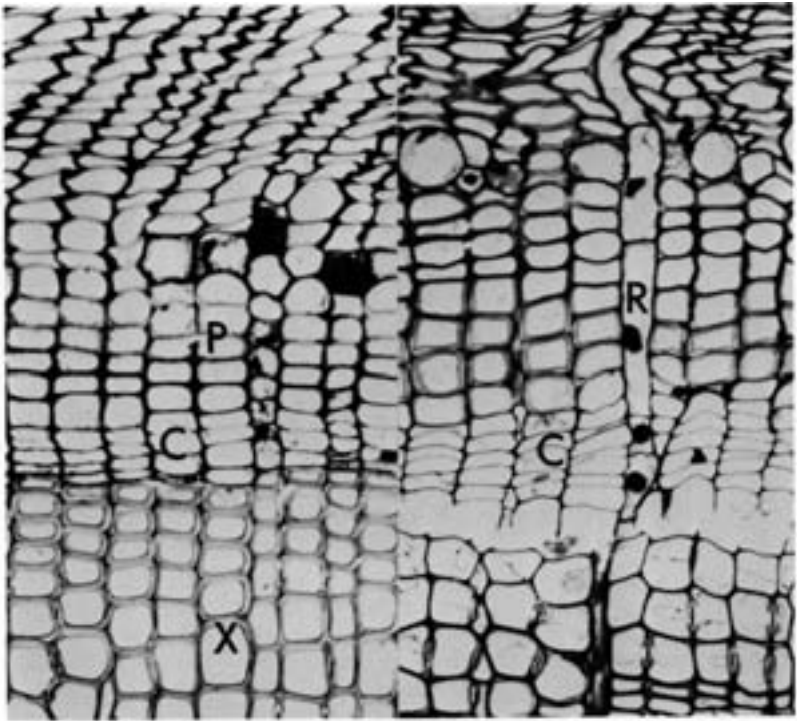
bial cells become dormant, remain in that state through the winter, and are activated again next spring. As a result of this seasonal activity of the cambium, there are growth rings in the wood, which may be considered as a record of cambial activity (Fig. 4). In contrast to the wood, the record of cambial activity is only poorly preserved in the bark (Fig. 4). First, the yearly increments in the bark are usually not distinct as growth rings. Second, they are further obliterated because of stress and distortion in mature bark due to the ever increasing diameter of the wood cylinder. Third, in most trees, the bark does not keep on accumulating from year to year as wood does; instead, the outer parts of bark are periodically cut off as bark scales by another kind of cambium, the cork cambium (Fig. 4). The formation and shedding of bark scales gives the trees their typical rough bark appearance. Some trees such as oak acquire a rough bark very early, at times within the first year; others like fir, poplar, birch, beech, and cherry may retain their smooth bark for several decades.

Wood is an important commercial product and a good deal of research has gone into it. Much less is known about bark, mainly from pharmacological work concerned with extractives; but cambium which produces both wood and bark, very little indeed is known about it. Yet the cambium is a very interesting tissue indeed. Since it produces xylem and phloem, two very different tissues, on its two sides<sup>2</sup> and since each of these two tissues is composed of different types of cells, it is of interest to students of oriented cell divisions, cell differentiation, and pattern formation in plants. Its seasonal activity in temperate climates, likewise, is of extreme interest to students of dormancy and frost resistance. Finally, a feature of cambium that has not been well recognized in the past is that it is a very dynamic tissue — it is the seat of rapid change and response to external and internal environment. In the following pages, I am going to concentrate mainly on cell types in the cambium, concept of the initiating ring, multiplicative divisions in the cambial initials and their role in plasticity of the cambium, and the effect of hormones on cambial activity and production of xylem and phloem.

<sup>2</sup> Some plants such as arborescent monocotyledons, tropical dicotyledons, and lianas show unusual cambial activity in that xylem and phloem are produced on the same side, at times in successive rings, or in different proportions in different radial sectors. Very little is known about the physiological and morphogenetical aspects of these types of cambial activity. They are not considered here.



*Fig. 4 Montage of a cross section of a stem of pine. Only two growth rings and part of a third are shown in xylem (X). In contrast several years growth, marked by small bars arranged in a row, is shown in the phloem (P). The approximate position of cambium is denoted by a longer horizontal bar. Note the distortion of tissue in outer bark and separation of outermost bark tissue by periderm (PD). The parts so separated comprise dead bark marked by an asterisk (\*) and are periodically shed as bark scales.*



Figs. 5, 6 Cross sections of stems of pine collected in winter and summer, respectively. Note that the zone of undifferentiated cell layers between the mature xylem (X) and phloem (P) is wider in summer than in winter. There is reason to believe that only one cell in a radial row acts as a cambial initial at any time. These initials maintain a certain degree of synchrony in their activity and occur more or less in a tangential line around the stem (C). The young differentiating xylem cells have weak walls and have ruptured during preparation of the material. Slippage of bark in spring and summer is due to this rupture and is indicative of cambial activity.

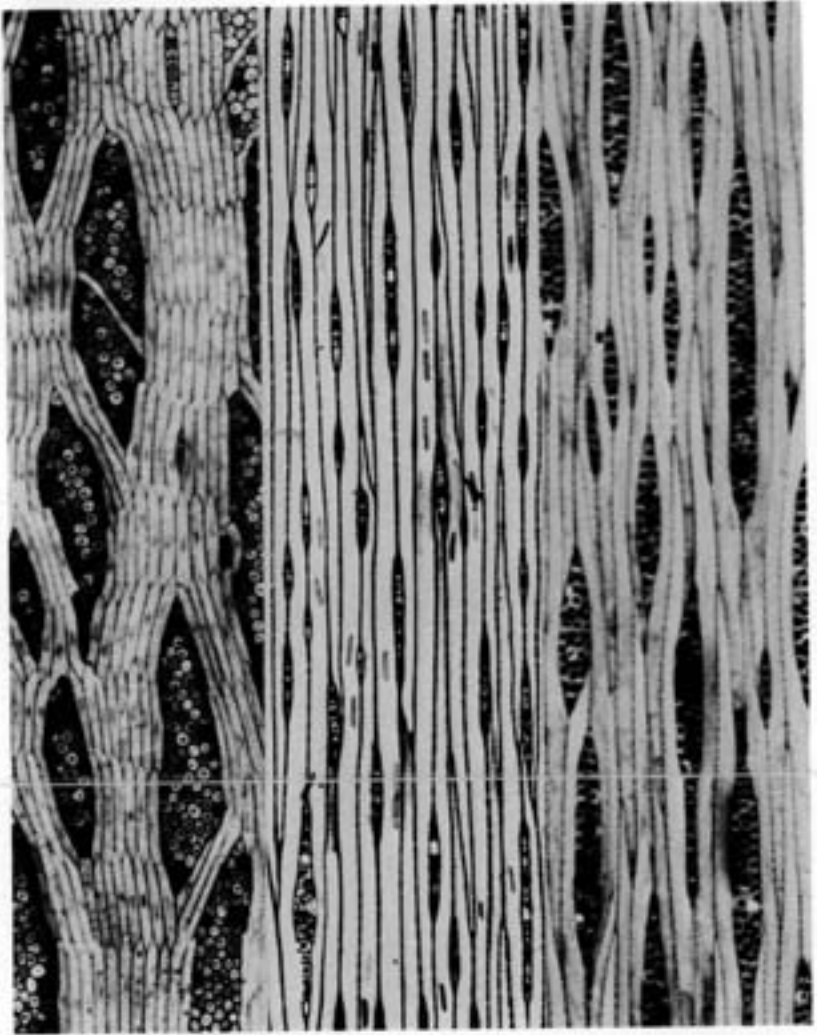
1. *Cambial layer, fusiform and ray initials*: There are theoretical reasons for maintaining that cambium is a single layer of cells (2, 3, 6) between xylem and phloem although it is not easy and often impossible to identify the cambial layer from the neighboring layers. Figures 5 and 6 represent cross sections of stems of white pine (*Pinus strobus*) sampled in winter and summer, respectively. In the winter collection 3-4 layers of undifferentiated cells intervene between the fully differentiated xylem and phloem cells. In the summer collection, the number

of layers of undifferentiated cells is much larger. Many of these, of course, are differentiating though not yet mature, xylem and phloem cells. With experience and under the higher resolution of an electron microscope it is possible to delimit the cambium both in winter and summer material to either one of 2 or 3 layers of cells. Further delimitation has proven impossible so far and perhaps is of little practical consequence.

The number of undifferentiated cell layers in winter and summer materials of different trees varies widely and in the same tree under different conditions of age, growth, and environment. For instance, in rapidly growing trees the number of undifferentiated and differentiating cell layers is usually much larger than in slow growing trees. Also, in winter collections of some trees, it may be possible to delimit the cambium to a single layer of cells.

These variations aside, the cambium basically has two types of cells (Fig. 7): 1. one type is narrow and elongated along the length of the stem and is called the *fusiform initial*; 2. the other type is short, isodiametric or horizontally elongated and clustered in groups and is called a *ray initial*. The type of cambium shown in Fig. 7 is common in most hardwoods such as birch, poplar, willow, alder, sycamore, etc. and is called *non-storied* cambium. The cambium of conifers is similar (Fig. 8), except that the fusiform initials are as a rule longer — in fact in some red woods they may be as much as 10 mm. long — and that the ray initials are usually arranged in single series. The cambia of some other hardwoods, such as ash and black locust (Fig. 9) have very short fusiform initials, as little as 0.3–0.5 mm. long, and have rather large clusters of ray initials. Irrespective of these differences between species, it is clear that basically the cambium has only two types of cells,<sup>3</sup> the fusiform and ray initials, and these two types of cells by tangential divisions produce all the different kinds of cells in wood and bark. But whereas the conducting cells such as the *vessel elements* in wood which transport water and minerals from roots up the trunk to the leaves, and *sieve elements* in the bark which transport the photosynthetic products from leaves down the trunk are produced only by the fusiform initials, parenchyma cells are produced by both. *Fibres* which provide strength to wood and bark are also produced exclusively by the fusiform initials. Besides differing in shape and size and nature of cells

<sup>3</sup> The only exception known is that of *Alseuosmia macrophylla* and *A. pusilla* which have been shown to have only fusiform initials in the cambia of their stems (5).



*Fig. 7 left Tangential longitudinal section of the cambium of birch. Note that the fusiform initials are narrow and elongated whereas the ray initials are short and clustered in groups. The derivatives of ray initials on either side extend as sheets of cells called phloem and xylem rays (Fig. 6, R).*

*Fig. 8 middle Tangential section of the cambium of pine.*

*Fig. 9 right Tangential section of the cambium of black locust.*

they produce, the fusiform and ray initials also differ in frequency of tangential divisions — the fusiform initials dividing far many more times than the ray initials in any one season.

What makes these two cells behave differently? As yet we have no explanation. There are vague suggestions of differential pressure and subtle differences at the molecular level but nothing concrete. Under the electron microscope the two types of cells show a basic similarity of structure which explains how the two may be interconverted one into the other but leaves the question — why the two behave differently — abegging.

2. *The concept of initiating ring:* The second noteworthy feature is that the production of new cells internally to the cambial ring entails a continuous net movement outward for the cambial initials and the bark tissues, and, furthermore, that the cambial initials show a remarkable degree of synchrony in their activity.

Figure 10 is a mock-up of the tangential activity of a single fusiform initial over part of a growth season. The mature (or previous years') xylem and phloem are distinguished from the current year's growth and the cambial initial is distinguished from its derivatives. The initial divides and the *internal* of the two cells — cell 1 — differentiates as a xylem element; it expands and pushes the cambial initial and mature phloem cells outwards. The cambial initial divides again, produces xylem derivative 2; derivatives 1 and 2 expand further and the cambial initial and mature phloem cells are pushed still further outwards. The cambial initial divides again but this time the *outer* of the two cells differentiates as the phloem derivative 1. The cambial initial divides again to produce xylem derivatives 3, 4, phloem derivative 2, and so on. This is, of course, a highly simplified model and does not assume tangential divisions in the young xylem and phloem derivatives. These divisions probably occur at a high rate in a growth season.

It should be remembered further that it is not simply one cambial initial that is engaged in this tangential activity. There are thousands of cells in the cambial ring — like soldiers marching in a row they are acting in concert, cutting cells toward xylem and less frequently toward phloem and as a net result moving outwards.

When soldiers march in a row and it is a hot day once in a while one of them pitches forward or backward and his neighbors move in from the sides and close rank. The same thing happens in a row of cambial cells — one of them drops out, or



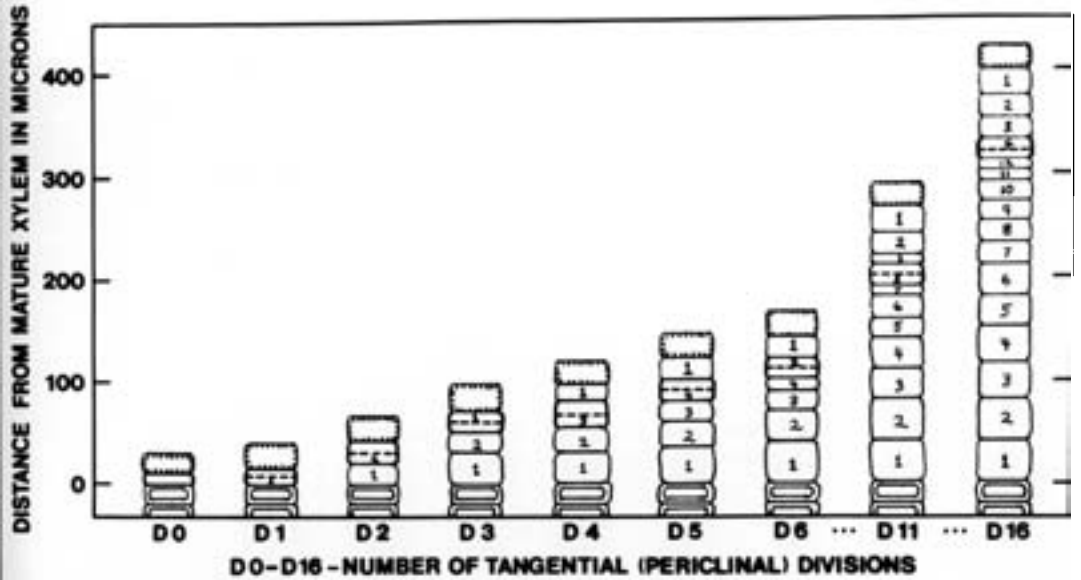
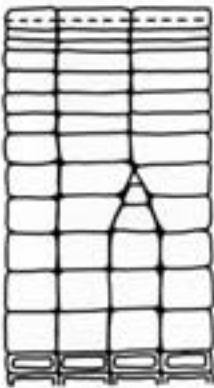
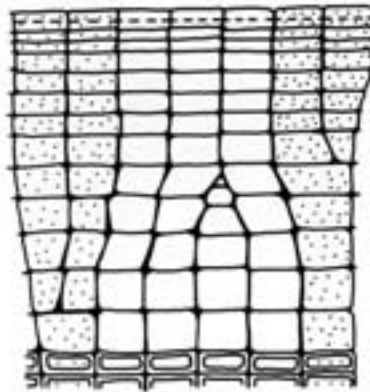


Fig. 10 An entirely hypothetical drawing showing the activity of a single cambial initial over part of a growth season. The mature or previous year's xylem and phloem are indicated by a double line and marginal stippling, respectively. The cambial initial is the cell with the broken line. Numbers indicate the order in which new xylem and phloem cells have been produced. The model does not assume tangential divisions in young xylem and phloem elements.



LOSS OF AN INITIAL



LOSS AND ADDITION OF INITIALS

Fig. 11 Loss and addition of cambial initials as seen in cross sections of xylem including the cambial initials, but excluding phloem. Markings are the same as in Fig. 10. The figure on the left dramatizes the loss of an initial by expansion of cells in neighboring rows. The figure on the right is more nearly correct and shows that the loss of an initial may be compensated for by addition of new initials elsewhere in the ring (stippled rows).

more accurately stops dividing and the neighbors close in. It is a competitive world for the cambial initials; they have to keep dividing or else either pitch forward and mature into a phloem derivative or get left behind and mature into a xylem derivative. In Figure 11, for instance, one of the initials has stopped dividing and the neighbors are shown expanded to fill the vacated space (figure on the left). Actually, this kind of expansion does not take place; instead as shown in the figure on the right, new cambial initials are added to the cambial ring. This dropping out or loss, or as we prefer to call it decline, can be sudden or protracted, but it is obvious that for each initial that declines at least one initial must be added if the cambial ring is to maintain its diameter; more than one if it is to increase in diameter. This leads us into the second type of division — the multiplicative (or anticlinal) division — that the cambial initials undergo.

3. *Multiplicative divisions*: Let us assume that a tree 20 cm. in diameter, after 50 years of growth, becomes 200 cm. in diameter, and further that the size of the cambial initials (tangential width) remains constant at 20  $\mu$ . Let us further restrict ourselves to fusiform initials. As Figure 12 shows, it can be calculated that the young tree has 10,000 initials in the cambial ring, and this number must be increased to 100,000 when the tree is 200 cm. in diameter, an increase which can be obtained if each initial multiplies a minimum of 9 times over the 50 year period. Actually the initials do increase in size (Table 1) and so the number of necessary multiplicative divisions would be less than 9. Surprisingly, however, in nearly all plants that have been investigated this number is much

Table 1. Actual measurements from *Pinus strobus*.  
Adapted from Bailey (1).

	one year old stem	60 year old stem
Radius of woody cylinder	2,000 $\mu$	200,000 $\mu$
Circumference of cambium	12,566 $\mu$	1,256,640 $\mu$
Average length of fusiform initials	870 $\mu$	4,000 $\mu$
Average tangential diameter of fusiform initials	16 $\mu$	42 $\mu$
Average tangential diameter of ray initials	14 $\mu$	17 $\mu$

CIRCUMFERENCE =  $2\pi r$   
 TANGENTIAL WIDTH OF AN INITIAL =  $20 \mu$   
 CIRCUMFERENCE OF A TREE 20cm IN DIAMETER =  $\pi \cdot 2 \cdot 10 \times 1000 \mu$   
 NUMBER OF INITIALS =  $\frac{\pi \cdot 2 \cdot 10 \times 10 \times 1000}{20} = 10,000$

AFTER 50 YRS.

CIRCUMFERENCE OF A TREE 200cm IN DIAMETER =  $\pi \cdot 2 \cdot 100 \times 10 \times 1000 \mu$   
 NUMBER OF INITIALS =  $\frac{\pi \cdot 2 \cdot 100 \times 10 \times 1000}{20} = 100,000$

$\therefore$  1 INITIAL MUST GIVE RISE TO 10 INITIALS  
 OR MULTIPLY A MINIMUM OF 9 TIMES IN 50 YEARS

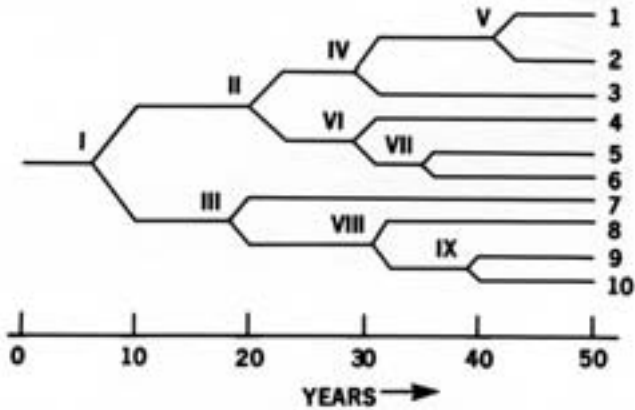


Fig. 12 The expected increase in number of fusiform initials over a 50-year growth period can be shown in the above manner. Roman numerals preceding bifurcations denote multiplicative divisions. For details see text.

greater than 9, at least 2 to 3 times as much (Fig. 13). The excess cells that are produced either decline completely or bits of them are left in the initial ring by conversion to ray initials.

Why should there be such an excessive production of new initials followed by a rejection of a large number of them? The answer to this question is unknown though it seems reasonable to assume that this device enables the cambium to adjust itself to changing conditions of growth and environment. It produces far more cells than it needs and hence can pick those that are wanted and throw out those that are not wanted.

Let me explain this by a few examples:

a. *Eccentric wood*: Trees normally grow straight but at times due to wind or snow or competition from neighboring trees they

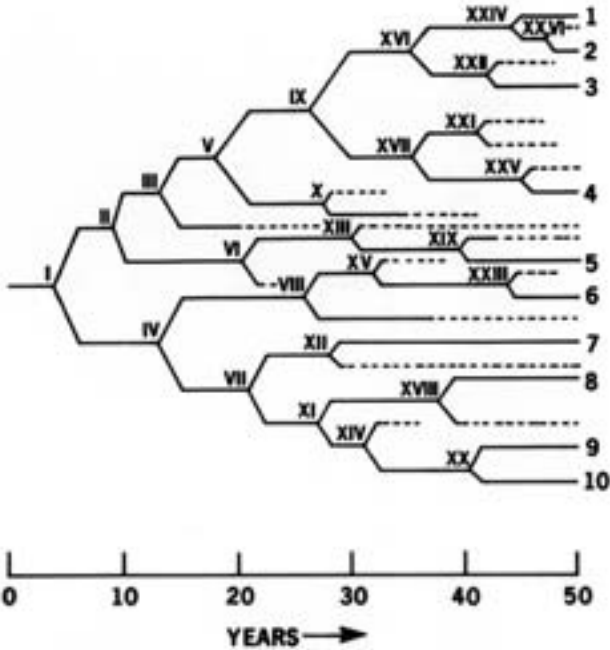


Fig. 13 This figure is similar to Figure 12, but shows that the number of multiplicative divisions is much higher than 9 and that the excess initials are lost by decline (lines which terminate somewhere and do not reach the right end) or are converted to ray initials (broken lines).

bend in a certain direction. If the tree is sawed, one sees growth rings in the wood that are eccentric rather than concentric (Fig. 14). This figure is further unusual in that it shows that the plane of eccentricity may change with time. In this stem there are at least 3 such planes which are marked by arrows. It should be noted that in the sectors marked by arrows, the cambial initials were not only producing more wood per year, but also there was a larger number of cambial initials than in the sectors on the opposite side.

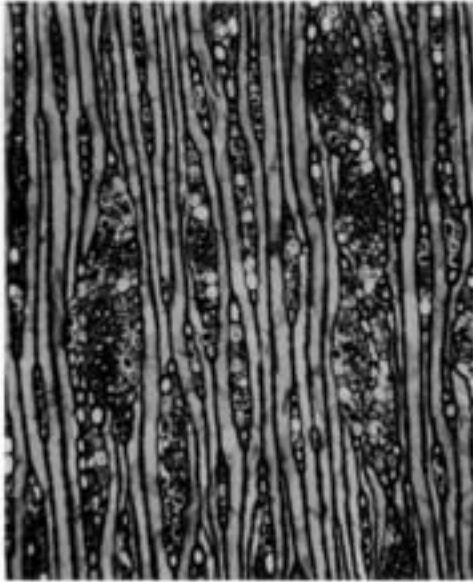
b. *Repair mechanism*: Another instance of where it is useful to have more cells than are needed is in repair of an injury. If some cells in the cambium and adjacent xylem and phloem are injured, the cambial cells on either side of the injury divide up into smaller cells, each of which behaves as an independent unit; these new initials then elongate, multiply, reject the un-

wanted pieces, elongate, multiply, further reject the unwanted pieces, and eventually give rise to straight elongated initials in a complete cambial ring.

c. *Accommodation with parasitic plants*: Still another way in which the cambial cells show adaptability is in accommodation with parasitic plants, such as mistletoes (*Phoradendron*, *Arceuthobium*) and dodder (*Cuscuta*). Seeds of these plants germinate on a host branch and send out haustorial appendages which grow in the host cortex and send out aerial stems which flower and seed. Tips of some of these appendages also come to rest against the cambial initials which respond by dividing into a number of smaller cells; the latter surround the haustorial appendage and henceforth the cells in the haustorial appendage divide tangentially and keep pace with similar divisions in the cambial initials (7). Thus, at the end of several years, sections of haustorial appendages — now known as sinkers — appear buried deep in the host wood and draw water and nutrients from the host xylem (Fig. 15). But the advantage from the host's



Fig. 14 Section of a stem showing eccentric growth rings.



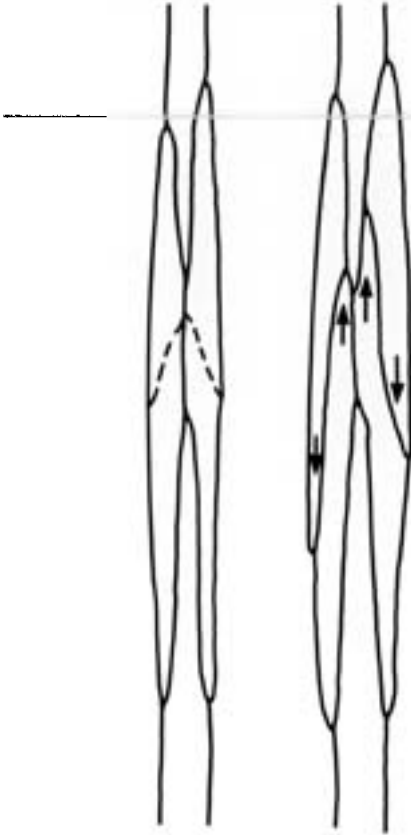
*Fig. 15 Tangential section of wood of hemlock which is infected with dwarfmistletoe. The large xylem rays are occupied by parasitic sinkers. The narrow uniseriate rays represent the normal condition.*

point of view is that an accommodation is made with the parasite and unless the infection is very severe the splitting of wood is avoided and the host is able to survive for a long time.

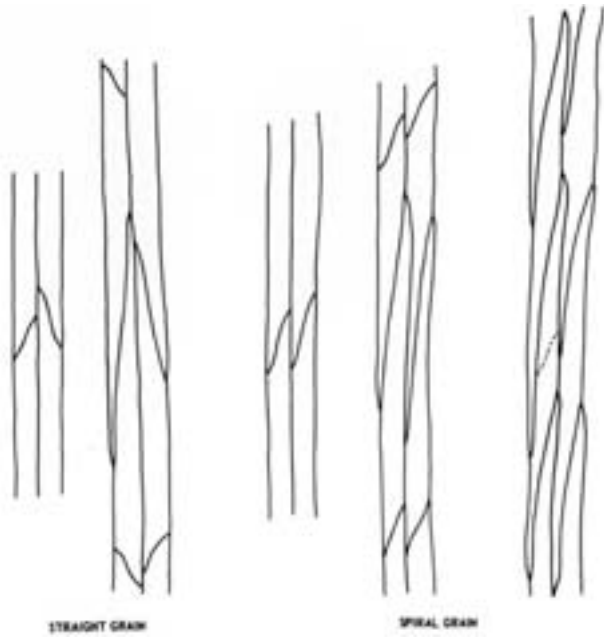
The multiplicative divisions therefore are necessary, not only to maintain the cambial ring and prevent it from bursting because of increasing diameter of the wood cylinder, but they also confer a degree of plasticity on the cambium, which would be absent otherwise. Cambium is hardly the placid tissue that monotonously keeps cutting xylem and phloem cells; it is the seat of active change, of constant multiplicative divisions, of frequent conversions between ray and fusiform initials, and of adjustment to changing conditions of growth and environment.

d. *Spiral vs. straight grain*: Another phenomenon controlled by multiplicative divisions is that of spiral vs. straight grain wood. In straight grain woods, the fibres are arranged axially in line with the longitudinal axis of the stem, but in spiral grain they are placed at an angle and seem to describe a clockwise or an anticlockwise spiral in relation to the longitudinal axis of the stem. How do the straight and spiral grains arise? They have their basis in the multiplicative divisions in the fusiform initials.

In conifers and most hardwoods such as birch, poplar, alder, willow, etc. these divisions are of the *pseudotransverse* type, such that the new cambial initials are nearly half the length of the original initial (Fig. 16). Subsequently the new initials grow at their tips until they reach the length common to the fusiform initials in that region. During this tip growth they, of course, continue to divide tangentially and produce new xylem and phloem cells. The plane of the new division determines the direction of the subsequent tip growth. Usually the divisions occur in the two planes in about equal frequency, so that on elongation the initials and the xylem and phloem derivatives maintain their more or less vertical orientation (Fig. 17). But at times the divisions occur only in one plane. This phenomenon, combined with subsequent tip growth, results in a skewering of the fusiform initials and their xylem and phloem derivatives, either in a clockwise or an anticlockwise direction. Spiral grain is mainly associated with wood but can be seen in bark if it has lots of fibres (Fig. 18). The environmental factors which cause the pseudotransverse divisions to occur in one plane are still unknown, but records show that the spiral can change direction and become straight.



*Fig. 16 Pseudotransverse divisions (shown by broken lines in the figure on left) and subsequent tip growth (direction shown by arrows in the figure on right) in fusiform initials of non-storied cambia.*



*Fig. 17 Straight and spiral grain have their basis in the planes of pseudotransverse divisions and subsequent tip growth of new initials.*

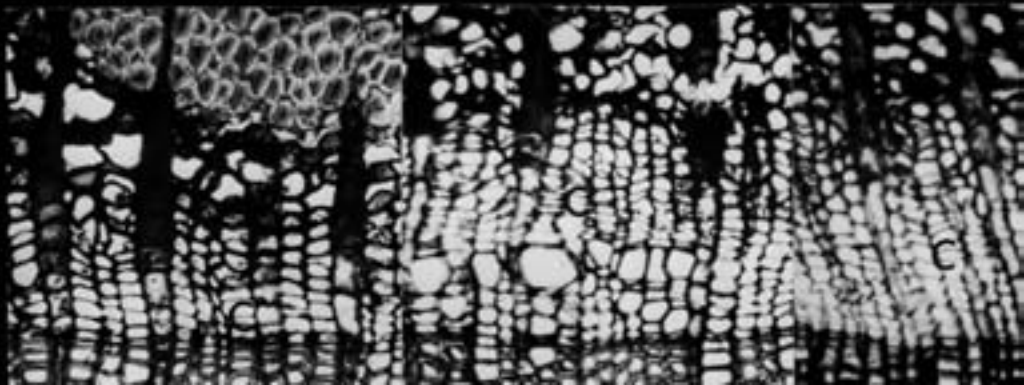


*Fig. 18 Two trees of a conifer species growing side by side in Nara near Kyoto, Japan. One shows spiral grain, the other straight grain.*



4. *Seasonal growth and xylem and phloem production*: I have mentioned earlier that in temperate climates the cambium becomes dormant in autumn and is reactivated in spring. The dormancy and reactivation of cambium are very little understood though there is reason to believe that daylength, temperature and relative concentrations of certain plant hormones play a role. With approaching autumn there is a shortening of daylight hours and a fall in temperature. If trees growing outside in the summer are transferred to growth chambers which simulate the daylength and temperature conditions of summer months, the cambium remains active and continues to produce new wood and bark cells. If these trees are then suddenly taken outside they get killed with the first frost. In contrast, the trees in the field become dormant with the onset of fall and then are able to survive very cold temperatures. In some experiments dormant twigs collected in winter were dropped in liquid nitrogen ( $-196^{\circ}\text{C}$ ) and on thawing their buds were still able to produce new branches. Just as cambial growth can be extended by appropriate control of daylength and temperature, one can also induce dormancy. In recent years a plant hormone appropriately called dormin (abscissic acid) has been extracted from buds and leaves of plants which were induced to become dormant, and, as expected, external applications of this hormone on growing trees have induced dormancy.

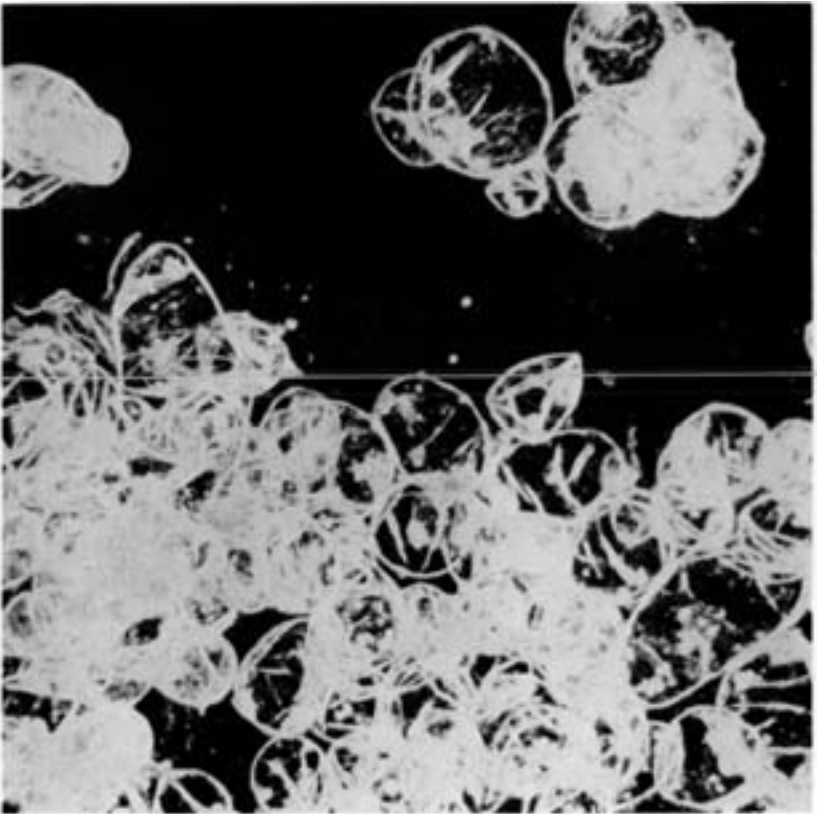
The reactivation of cambium in the spring has been related to another class of hormones, the auxins, specifically IAA. It has been suggested that in spring this hormone is present in increasing amounts in the buds and young leaves and then flows downwards, awakening the cambium so to say from its winter sleep by its magical touch (8). That IAA is involved in cambial activation is shown beautifully by a simple experiment. Twigs of poplar, birch, black locust or some other tree are collected in autumn and stored in a cold room ( $4^{\circ}\text{C}$ ) for a few months. After the cold treatment, which seems to be necessary, they are placed right side up in a small amount of water and their top ends are pasted with lanolin and with lanolin and various hormones individually and in combination. After 3 weeks, sections can be cut to see whether cambium is active and if so whether xylem is being produced, or phloem, or both, and in what proportion. From these experiments it appears that both auxin and gibberellic acid can induce cambial activity but whereas auxin promotes xylem formation, gibberellic acid seems to promote phloem formation (Fig. 19).



*Fig. 19 Cross sections of stems of poplar. A. from twigs which received only lanolin treatment, B, from twigs which received lanolin and IAA at 100<sup>ppm</sup>, and C. from twigs which received lanolin and GA at 100<sup>ppm</sup>. Note that the cambium (approximate level marked by C) is more active in B, C than in A; note also the formation of new xylem elements in B and their lack in C. Photographs are mounted such that the mature (or previous year's xylem is at the same level (Photographs courtesy of Mrs. V. Lai).*

The ultimate aim of all biology is to understand why a cell does what it does and how it does it. We want to know why fusiform and ray initials are different, why some cambial initials lose out while others persist in the ring, what triggers a cell to become a xylem or a phloem cell, and so on. Basic questions, perhaps of no economic value, but of fundamental importance to biology to which we still have no concrete answers. In an attempt to find answers to these questions, some investigators have tried to culture cambial cells. They have excised the cambial cells from the tree, and grown them in agar or liquid culture under well defined growth and nutritive conditions. But unfortunately, to date, all these attempts have failed for in culture they no longer behave as cambial cells — they lose their characteristic shape, become spherical, there are no oriented divisions and there is no oriented production of xylem and phloem (Fig. 20). There is a certain element of mob psychology involved here. Outside their own milieu or deprived of

their particular microenvironment in the tree which may include pressure, oxygen tension, and hormonal balance, these cells no longer behave as cambium. That pressure is involved is shown by some other experiments in which flaps of bark including cambium were lifted (see slippage of bark in Fig. 6), a sheet of polyethylene inserted between the flap and the stem, and measured amounts of pressure applied to the flap. The cells in the flap continued to live; the cambial cells continued to divide and produce oriented xylem and phloem derivatives (4).



*Fig. 20 Cambial cells in liquid culture. Explants from cambial region of Acer pseudoplatanus. (Slide courtesy of Dr. P. Albersheim.)*

To recapitulate I have tried to show that the cambial ring moves outward with increasing diameter of the wood cylinder and that whether or not a cell behaves as a cambial initial depends to a large extent on how well it is able to maintain itself in the initiating ring. I have further tried to show that the cambial cells are in a state of constant flux and are the seat of changes which enable the tree to adjust itself to changing conditions of growth and environment. Finally, I have tried to show that the dormancy and activation of cambium as well as differentiation of the xylem and phloem are at least in part controlled by physical factors such as daylength, temperature, and pressure and relative concentrations of at least three different types of plant hormones — dormin, auxin, and gibberellin.

These bits of information on the structure and physiology of cambium whet rather than assuage the curiosity for a greater understanding of this remarkable tissue. Arboreta, being the repositories of trees, have an important role to play in directing and supporting research on cambium. On this one hundredth anniversary of the Arnold Arboretum, I am happy and proud to say that the Arnold Arboretum has fulfilled this role admirably and, hopefully, will continue to do so in the future.

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