6

The Vascular Cambium

LOCATION IN THE PLANT

The vascular cambium is the lateral meristem that forms the secondary vascular tissues. It is located between the xylem and the phloem (fig. 1.3, pl. 21) and, in stems and roots, commonly has the shape of a cylinder. When the secondary vascular tissues of an axis are in discrete strands, the cambium may remain restricted to these strands in the form of strips (*Cucurbita*, pl. 63*C*). It also appears in strips in most petioles and leaf veins that show secondary growth.

CELL TYPES

The tissues derived from apical meristems contain many cell types which differ strikingly from the meristematic cells in shape and size. In contrast, there is a general resemblance between the cambium cells and their derivatives, and the shape and arrangement of cells in the secondary xylem and the secondary phloem are foreshadowed in the shape and arrangement of the cambial cells (pl. 21; chapters 11, 12).

The vascular cambium contains two types of cells: elongated cells with tapering ends, the *fusiform initials* (that is, spindle-shaped initials), and nearly isodiametric, relatively small cells, the *ray initials* (figs. 6.1, 6.2; pl. 22). The exact shape of the fusiform initials of *Pinus silvestris* has been determined as that of long, pointed, tangentially flattened cells with an average of 18 faces (Dodd, 1948). The fusiform initials give rise to all the cells of xylem and phloem that are arranged with their long axes parallel to the long axis of the organ in which they occur; in other words, they form the longitudinal or axial systems of xylem and

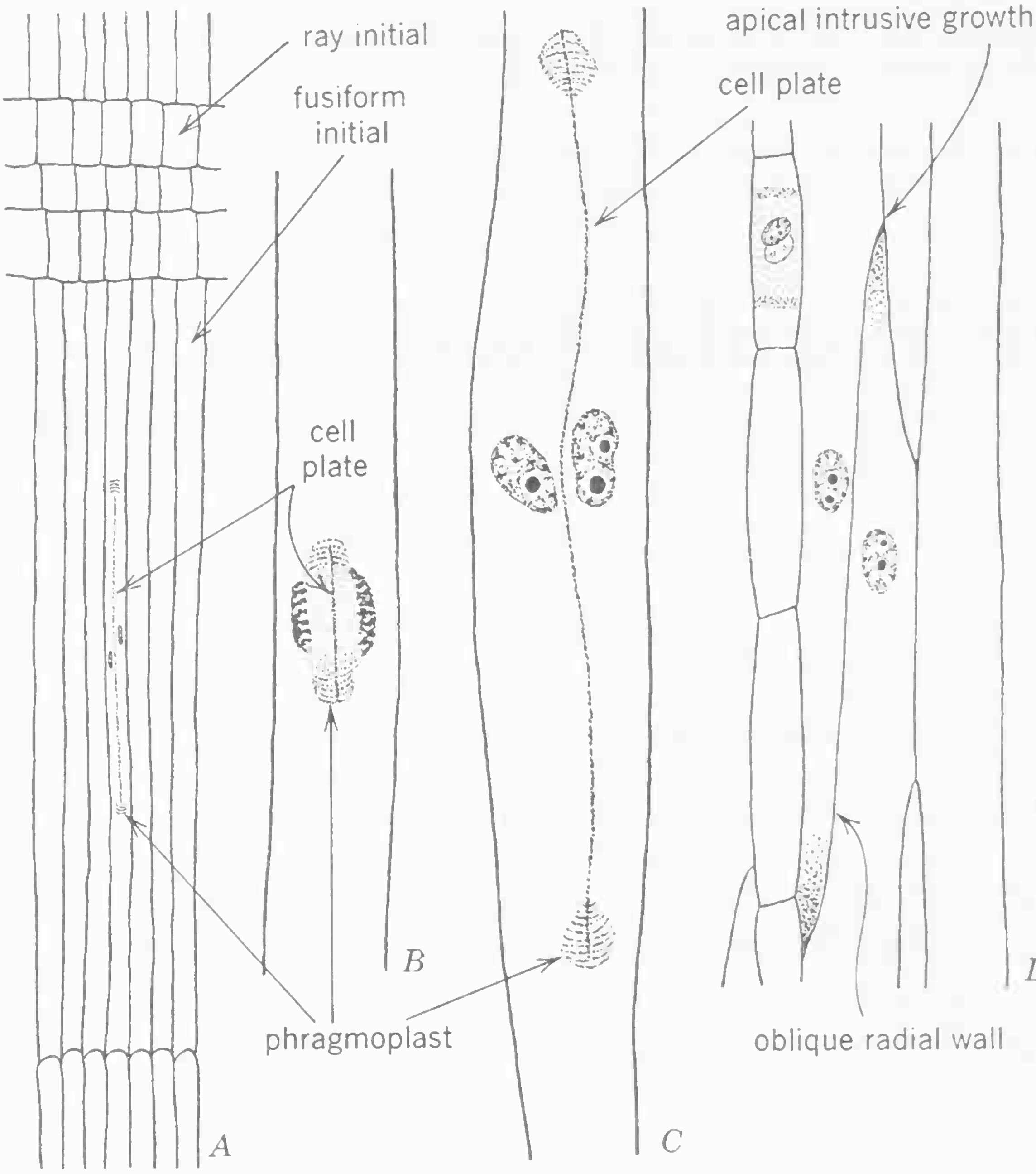

FIG. 6.1. Cytokinesis in vascular cambium of *Nicotiana tabacum* as seen in radial (*A–C*) and tangential (*D*) sections of stem. *A–C*, tangential divisions in side view. *B*, early stage of division; *C*, later stage. *D*, ray initial in tangential division, with the cell plate appearing in surface view, and an oblique radial wall recently formed in fusiform initial. Densely stippled areas in *D*, apices of the two new cells which were growing by apical intrusive growth, one downward, the other upward. (*A*, ×120; *B*, *C*, ×600; *D*, ×300.)

phloem (chapters 11, 12). Examples of elements in these systems are tracheids, fibers, and xylem-parenchyma cells in the xylem; sieve cells, fibers, and phloem-parenchyma cells in the phloem. The ray initials give origin to the ray cells, that is, elements of the transverse or ray system of the xylem and the phloem.

Table 6.1 gives information on the comparative characteristics of the two kinds of initials in *Pinus strobus*. These initials differ from each other most notably in length and volume, the fusiform cells being much larger than the ray initials. However, in one dimension, the radial, the ray initials surpass the fusiform. In the 60-year-old stem both kinds of

Table 6.1 Dimensions of Cambial Initials of *Pinus strobus* (Adapted from Bailey, 1920*b*)

Age of axis in years	Kind of initial	Diameters in microns			Volume in microns^3	Ratio between volumes of nucleus and cell
		Vertical	Radial	Tangential		
1	Ray	22.9	17.8	13.8	5,000	1:14
1	Fusiform	870.0	4.3	16.0	60,000	1:60
60	Ray	24.8	26.6	17.0	10,000	1:12
60	Fusiform	4000.0	6.2	42.4	1,000,000	1:286

length within species, partly in relation to growth conditions. They also show length modifications associated with developmental phenomena in a single plant. Generally, the length of fusiform initials increases with the age of the axis, but after this length reaches a certain maximum it remains relatively stable (table 6.1; Bailey, 1920*a*; Bannan, 1960*b*; Bosshard, 1951). The changes in the size of fusiform initials bring about similar changes in the secondary xylem and phloem cells derived from these initials. The ultimate size of these cells, however, depends only partly on that of the cambial initials, because changes in size also occur during the differentiation of cells (chapter 4).

The cambial cells are highly vacuolated (pls. 21*B*, 22; Bailey, 1930). Their walls have primary pit-fields with plasmodesmata. The radial walls are thicker than the tangential walls particularly during dormancy, and their primary pit-fields are deeply depressed.

CELL ARRANGEMENT

During active growth in the cambium, the initials and their immediate derivatives form a zone of similar unexpanded meristematic cells, the *cambial zone* (pl. 21*A*). As seen in transections the cells in the cambial zone are arranged in radial series. On either side of the cambial zone, cambial derivatives expand and gradually assume the characteristics of the various xylem and phloem cells. Experiments with strips of bark partially detached from the stem indicate that mutual pressure of tissues is important in controlling the orderly pattern of differentiation of the cambial products (Brown and Sax, 1962). The prevailing concept is that the initials are arranged in one layer, one cell in thickness. In a strict sense, only the initials constitute the cambium (Bailey, 1943), but frequently the term is used with reference to the cambial zone, because it is difficult to distinguish the initials from their recent derivatives (pl. 21*B*; Bannan, 1955).

In tangential views the arrangement of cambial cells shows two basic patterns. In one, the fusiform initials occur in horizontal tiers with the ends of the cells of one tier appearing at approximately the same level (pl. 22*B*). Such meristem is called *storied* or *stratified cambium*. It is characteristic of plants with short fusiform initials. In the second type, the fusiform initials are not arranged in horizontal tiers, and their ends overlap (pl. 22*A*). This type is termed *nonstoried* or *nonstratified cambium*. It is common in plants with long fusiform initials. Intergrading types of arrangement occur in different plants. The nonstratified type is considered to be phylogenetically more primitive than the stratified. The former is found in fossil pteridophytes, in fossil and living gymnosperms, and in structurally primitive dicotyledons; the latter, in highly specialized dicotyledons (Bailey, 1923). In primitive cambia the initials vary in length more than in the more specialized meristems.

CELL DIVISION

The phloem and the xylem are formed by tangential (periclinal) divisions of cambial initials. The vascular tissues are laid down in two opposite directions, the xylem cells toward the interior of the axis, the phloem cells toward its periphery. The consistent tangential orientation of the planes of division during the formation of vascular tissues determines the arrangement of cambial derivatives in radial rows (pl. 65). Such radial seriation may persist in the developing xylem and phloem (fig. 6.3*A*), or it may be disturbed through various kinds of growth readjustments during the differentiation of these tissues (xylem in pl. 21*A*).

Tangential divisions that occur during the formation of xylem and phloem cells are not limited to the initials but are encountered also in varied numbers of derivatives, sometimes several times within the progeny of the same derivative (fig. 6.3*B*; Bannan, 1955, 1957; Evert, 1963). During the winter rest, xylem and phloem cells mature more or less close to the initials; sometimes only one cambial layer is left between the mature xylem and phloem elements. But some vascular tissue, frequently only phloem, may overwinter in an immature state in the cambial zone.

As the xylem cylinder increases in thickness by secondary growth, the cambial cylinder enlarges in circumference. The principal cause of this enlargement is the increase in the number of cambial cells in a tangential direction, followed by a tangential expansion of these cells. In stratified cambia the increase in the number of fusiform initials occurs by radial (anticlinal) longitudinal divisions. In nonstratified cambia, however, the fusiform initials divide by more or less oblique anticlinal walls (the so-called pseudotransverse walls), and then the resulting cells elongate at their apices (apical intrusive growth; figs. 6.1*D*, 6.4*D–H*) until each cell is as long as, or longer than, the mother cell. Some investigators use the term *multiplicative* divisions with reference to the anticlinal divisions that increase the number of initials, as contrasted with the *additive*, periclinal, divisions that contribute cells to the xylem and the phloem (Bannan, 1956; Duff and Nolan, 1957).

In the longitudinal divisions of the cambial initials and their derivatives, cytokinesis is a process extended in time and space. The cell plate is initiated between the two new nuclei and then spreads through the entire length of the cell, preceded by the phragmoplast fibers (figs. 6.1, 6.2).

DEVELOPMENTAL CHANGES

Detailed studies of the vascular cambium of conifers have shown that the increase in circumference of the meristem is accompanied by profound changes in size, number, and arrangement of cells. Table 6.2 illustrates some of the quantitative changes that occur in the nonstratified cambium of a pine stem as the stem increases in girth. Both the fusiform and the ray initials are greatly multiplied in number. The fusiform initials enlarge notably along their tangential diameters, whereas the ray initials become only slightly larger in this dimension. There is also a remarkable increase in the length of the fusiform initials. The increase in number of the fusiform initials, as seen in transections, results from intrusive apical elongation (fig. 6.4*A–C*) following the multiplicative oblique radial divisions (fig. 6.4*D–H*). Since the rays in the pine are mostly uniseriate (one cell in width), the increase in the number of ray initials, as shown for the older stem in table 6.2, is a result, not of divisions of the existing ray initials, but of the addition of new ray initials.

New ray initials arise from fusiform initials or their segments. These additions maintain a relative constancy in the ratio between the rays and the axial components during the increase in the circumference of the vascular cylinder (Braun, 1955). New rays have fewer cells than older. A ray may be one cell wide and one cell high in the beginning; later, the initial divides or more initials are added to the first. The ray thus increases in height and may increase in width if multiseriate rays are characteristic of the plant. Some investigators report that new ray initials may be cut off the apices or cut out of the sides of fusiform initials (Braun, 1955; Evert, 1961). In a herbaceous species of *Hibiscus* rays were found to be derived by transverse divisions of one of the two fusiform cells resulting from an anticlinal division of a fusiform initial