upon wall sculpture would detract from the value of these terms. The relative time of maturation within the vascular system gives the most consistent basis for classification of the primary xylem into protoxylem and metaxylem (Esau, 1943; Goodwin, 1942).

SECONDARY XYLEM

Distinction from Primary Xylem

Like the division of the primary xylem into protoxylem and metaxylem, the classification into primary and secondary xylem is problematical. This classification, too, is of little value unless it is conceived in relation to the growth of the plant or of a plant organ as a whole (chapters 1, 4). Briefly, the primary xylem is the xylem differentiating in conjunction with the growth of the primary plant body and derived from the procambium. The secondary xylem is a part of the accessory secondary body superimposed over the primary and formed by the vascular cambium.

The secondary xylem is formed by a relatively complex meristem, the cambium, consisting of fusiform and ray initials, and is, therefore, composed of two systems, the *axial* (vertical) and the *ray* (horizontal) systems (figs. 11.10, 11.11), an architecture not characteristic of the primary xylem. In the dicotyledons the secondary xylem is commonly more complex than the primary in having a wider variety of component cells. The sculpture of the secondary walls of the primary and secondary tracheary elements has been considered earlier in this chapter. The elements of the late part of the metaxylem may intergrade with the secondary elements, since both may be similarly pitted.

Frequently the arrangement of cells, as seen in transverse sections, is stressed as a criterion for distinguishing the primary from the secondary xylem. The procambium and the primary xylem are said to have a haphazard cell arrangement, and the cambium and the secondary xylem, an orderly arrangement, with the cells aligned parallel with the radii of the secondary body. This distinction is highly unreliable, for in many plants the primary xylem shows just as definite radial seriation of cells as the secondary (Esau, 1943; chapter 15).

In many woody dicotyledons the length of tracheary cells reliably separates the primary from the secondary xylem (Bailey, 1944*b*). Although the helically thickened tracheary elements are generally longer than the pitted elements of the same primary xylem, these pitted elements are still considerably longer than the first secondary tracheary elements. Indeed, this difference may be so conspicuous that one can speak of a nonconformity between the two parts of the xylem (Bailey, 1944*b*). The apparent break in the continuity of development may be caused, not only by the elongation of the metaxylem cells during their differentiation and lack of a comparable elongation of the cambial derivatives but also by possible transverse divisions of the procambial cells just before the initiation of cambial activity. In the gymnosperms, too, the last primary xylem elements are longer than the first secondary elements (Bailey, 1920).

The change from longer to shorter tracheary cells at the beginning of secondary growth is one of the steps in the establishment of mature characteristics of the secondary xylem. Various other changes accompany this step, for example, those involving the pitting, the ray structure, and the distribution of axial parenchyma. By these changes, the secondary xylem eventually attains the evolutionary level characteristic of the species. Since the evolutionary specialization of the xylem progresses from the secondary to the primary xylem, in a given species the latter may be less advanced, or more juvenile, with regard to the evolutionary specialization. It appears that dicotyledons which are not truly woody —even if they possess secondary growth—show a protraction of juvenile characteristics into their secondary xylem (paedomorphosis, Carlquist, 1962). One of the expressions of this juvenility is a gradual, instead of a sudden, change in length of tracheary elements.

Basic Structure

Axial and Ray Systems. The arrangement of cells into the vertical, or axial, system, on the one hand, and the transverse, or ray system, on the other, constitutes one of the conspicuous characteristics of the secondary wood (figs. 11.10, 11.11). The rays and the axial system are arranged as two interpenetrating systems closely integrated with each other in origin, structure, and function. In conducting xylem the rays most commonly consist of living cells. The vertical system contains, depending on the species of plant, one or more of the different kinds of nonliving tracheary elements, fibers, and parenchyma cells. The living cells of the rays and those of the axial system are interconnected with each other, so that one can speak of a continuous system of living cells permeating the wood. Moreover, this system often is connected, through the rays, with the living cells of the pith, the phloem, and the cortex.

Since the longitudinal axis of the vertical system is parallel with the longitudinal axis of the stem or the root in which the xylem occurs, transverse and longitudinal sections of the organ coincide with the same kind of sections of the vertical system. The rays, on the contrary, have their longitudinal axes parallel with the radii of the approximately cylindrical bodies of stem and root and their branches. Consequently, transverse and radial longitudinal sections of the plant axis show the rays in longitudinal section, whereas tangential longitudinal sections expose the rays in their transverse section. If statements are made that xylem is sectioned transversely and longitudinally (radially or tangentially), the plane of sectioning is referred to the organ as a whole and, therefore, also to the axial system of the xylem.

The rays are characterized as having length, width, and height. The length is measured between the cambium and the innermost end of the ray. The width of the ray corresponds to its tangential extent and is commonly expressed in the number of cells in this direction. The height of a ray is its extent in the direction parallel with the longitudinal axis of stem or root.

The rays vary much in their dimensions in different plants and may be of more than one size in the same plant. If a ray is one cell wide, it is termed *uniseriate* (pls. 31, 32). The contrasting type is the *multiseriate* ray (pl. 33*C*), which may be a few cells to many cells wide (if the ray is two cells in width, it is called *biseriate*). A multiseriate ray, as seen in a tangential section of the xylem, tapers toward the upper and lower margins, where it is commonly uniseriate. Thus a wide ray appears lenticular or fusiform in its transectional outline. Both kinds of ray may be low or high. Although the height and width of rays often undergo considerable change through the successive layers of secondary xylem, the kind and extent of change induced are characteristic of a given species. The length of a ray, on the other hand, is an indefinite characteristic for three reasons: first, new rays are constantly initiated as the axis increases in circumference; second, some rays are discontinued; and, third, the length of the ray is affected by the vigor of growth.

Storied and Nonstoried Woods. In chapter 6 a distinction was made between storied, or stratified, and nonstoried, or nonstratified, cambia, with reference to the arrangement of the fusiform initials in tangential sections. Nonstoried cambia produce nonstoried woods (figs. 11.10, 11.11, pl. 31–33). The xylem derived from a storied cambium may be storied (pl. 35*A*, *B*) or only partly so, if the original stratification is obscured by changes during the differentiation of the xylem. One of the most common of such changes is the elongation of the elements in the vertical system. Tracheids, fiber-tracheids, and libriform fibers generally become longer than the fusiform cambial cells from which they were derived (chapter 6). The apices of these elements extend by intrusive growth beyond the limits of their own horizontal tier and