12

Phloem

CONCEPT

The phloem is the principal food-conducting tissue of the vascular plants. The phloem and the xylem are, as a rule, spatially associated with each other (fig. 12.1, pl. 28) and together constitute the vascular system of the plant body. Like the xylem, the phloem is composed of several different kinds of cells, concerned with different functions, and therefore it, too, exemplifies a morphologically and physiologically complex tissue.

The basic components of the phloem are the sieve elements, several kinds of parenchyma cells, fibers, and sclereids. In plants possessing a laticiferous system, elements of this system may be found in the phloem also. Various idioblasts, specialized morphologically and physiologically, are encountered in the phloem. In this chapter only the principal components of the phloem are considered in detail.

Information on the structure of the phloem is relatively incomplete, and knowledge of the phylogeny of this tissue is fragmentary. Various circumstances are responsible for this deficiency. The phloem shows unique cytologic characteristics which require exacting techniques for investigation. The phloem cells, other than the fibers and the sclereids, do not develop such rigid, persisting walls as the xylem elements, and, after the phloem ceases to act as a conducting tissue, it becomes much modified, functionally and structurally. The most pronounced changes occur in the conducting elements themselves, for they become disorganized to various degrees. Thus, in contrast to the xylem, for which a large body of comparative data is available (chapter 11), the phloem early loses its original nature and appearance, and in such a state it can-

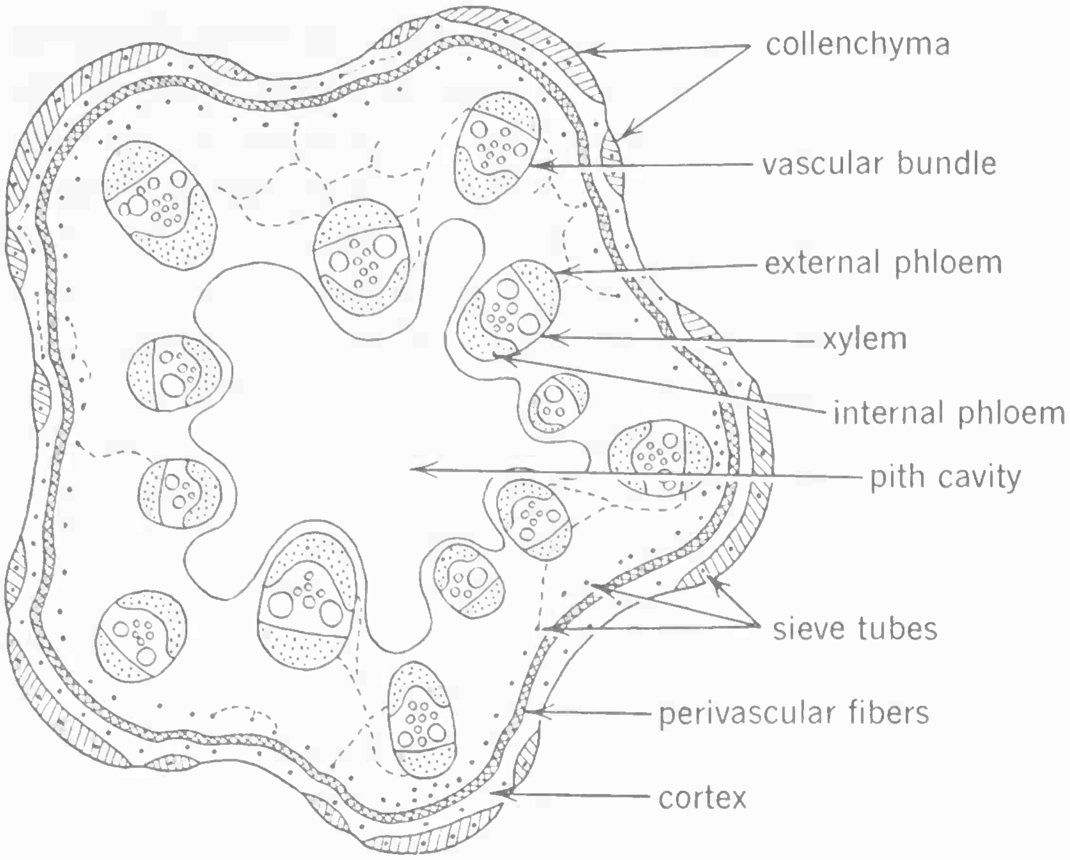

FIG. 12.1. Transection of *Cucurbita* stem. Herbaceous vine with discrete vascular bundles, each having external and internal phloem (bicollateral bundles). Vascular region is delimited on the outside by sclerenchyma (perivascular fibers). Cortex is composed of parenchyma and collenchyma. There is an epidermis. A cavity has replaced the pith. Small strands of extrafascicular sieve tubes and companion cells traverse parenchyma of vascular region and cortex. (×8.)

not be properly studied with regard to its structural details. The lack of firmness is also related to the generally poor preservation of phloem in fossils (Andrews, 1961; exceptionally well preserved phloem was found in *Tetraxylopteris*, pl. 29*B*; Beck, 1957). In much of the commercial utilization of xylem this tissue is not separated into its individual components, and the proper evaluation of its economic qualities requires the knowledge of its structure as a tissue. The commercial importance of the phloem, on the other hand, is determined largely by its content of fibers and such organic substances as tannins, spices, latex, and drugs, all products that are separated or extracted from the tissue. Thus the commercial utilization of the products of the phloem is not a strong stimulus for the study of the phloem as a tissue.

Historically, too, the significance of the xylem as a conducting tissue was recognized earlier than that of the phloem (Esau, 1961). In the phloem, the fibers attracted the first attention and, as was outlined in chapter 10, the tissue received the name of *bast*—a word related to the verb to bind—because the fibers formed in it were used for binding. After the sieve element was discovered by Hartig in 1837, the true nature of the tissue was gradually revealed. In 1858 Nägeli gave it the name of *phloem* (derived from the Greek word for bark), thus eliminating the emphasis upon the presence of fibers in this tissue. In time phloem became the generally accepted term for the food-conducting tissue of vascular plants. Nevertheless, substitute terms are still being used, particularly in German (*Leptom, Siebteil, Cribralteil*) and French (*liber, tissu criblé*) literatures. The term *leptom* deserves special mention. It refers, since Haberlandt (1914), to the soft-walled conducting part of the phloem, including sieve elements, companion cells, and parenchyma cells. The parallel term for the xylem is *hadrom*, which refers to the conducting part of the xylem including the tracheary and parenchymatic elements but excluding the fibers.

Sometimes, with reference to stems and roots, it is convenient to treat as a unit the phloem and all the tissues located outside it. The nontechnical term *bark* is employed for this purpose. In stems and roots possessing only primary tissues bark most commonly refers to the primary phloem and the cortex. In axes in a secondary state of growth it may include the primary and the secondary phloem, various amounts of cortex, and the periderm (chapter 14).

From the researches on phloem conducted since the discovery of the sieve element and periodically reviewed from different points of view by various authors (Crafts, 1961; De Bary, 1884; Strasburger, 1891; Perrot, 1899; Schmidt, 1917; Huber, 1937; Esau, 1939, 1950, 1961; Swanson, 1959), the concept has become established that the main characteristic of the phloem is the presence of highly specialized cells, the sieve elements, which together with the accompanying parenchymatic members of the tissue are concerned with the translocation of elaborated food materials, and that the structural peculiarities of the sieve elements are related to their function. Furthermore, the fibers, if present, came to be regarded as components of the phloem tissue, just as wood fibers are components of the xylem tissue.

CLASSIFICATION

Like the xylem, the phloem is classified as primary or secondary on the basis of its time of appearance in relation to the development of the plant or the organ as a whole. The primary phloem is initiated in the embryo, is constantly added to during the development of the primary plant body, and completes its differentiation when the primary plant body is fully formed. Like the primary xylem, the primary phloem differentiates from procambium. If a dicotyledon or a gymnosperm plant has secondary growth, the vascular cambium that forms secondary xylem toward the interior of the stem or root produces secondary phloem in the opposite direction, that is, toward the periphery of the stem or root.

Although most commonly the phloem occupies a position external to the xylem in the axis, or abaxial in the leaves and leaf-like organs, certain ferns and many dicotyledonous families (Apocynaceae, Asclepiadaceae, Convolvulaceae, Cucurbitaceae, Myrtaceae, Solanaceae, Compositae) have a part of the phloem located on the opposite side of the xylem as well (figs. 12.1, 15.1*B*, pl. 38*A*). The two parts of the phloem are called *external* and *internal* phloem, respectively. They may be termed also *abaxial* (that is, away from the axis) and *adaxial* (that is, toward the axis) phloem. In the leaves these terms refer the position of the phloem to the stem, or axis, to which the leaf is attached. In the stems and roots the axis of reference would be an imaginary one, passing longitudinally through the center of the organ. (In the root, internal phloem occurs at levels where a pith is present.)

The term internal phloem replaces *intraxylary phloem* (Committee on Nomenclature, 1957). The latter term is sometimes confused with *interxylary phloem* referring to phloem strands or layers included in the secondary xylem of certain dicotyledons, that is, to the *included phloem.* The included phloem is called *concentric* when it appears in layers alternating with xylem layers, *foraminate* when it appears in strands surrounded by xylem tissue (chapters 15, 17; anomalous growth).

In dicotyledons the internal phloem is initiated somewhat later than the external. Nevertheless, it constitutes a part of the primary phloem system. It resembles the external primary phloem in development, composition, and structure and arrangement of cells (Esau, 1939). Generally, it is not increased in amount by cambial activity (Jean, 1926).

ELEMENTS OF THE PHLOEM

Sieve Elements

Parallel with the classification of the tracheary elements into the phylogenetically primitive tracheids and the more advanced vessel members, the conducting elements of the phloem, called collectively *sieve elements,* may be segregated into the less specialized *sieve cells* (fig. 12.7, pl. 42) and the more specialized *sieve-tube members* (or *sieve-tube elements;* fig. 12.8, pl. 43). The term *sieve tube* designates a longitudinal series of sieve-tube members, just as the term vessel denotes a longitudinal series of vessel members. In both classifications the characteristics of the wall structures—pits and perforation plates in the tracheary elements, *sieve areas* and *sieve plates* in the sieve elements—serve to distinguish the elements of the two kinds of categories.

Sieve Areas and Sieve Plates. The morphologic specialization of the sieve elements is expressed in the development of the sieve areas on their walls and in the peculiar modifications of their protoplasts. The sieve areas (the term implies a resemblance to a sieve) are wall areas with clusters of pores, through which the adjacent sieve elements are interconnected by strand-like prolongations of their protoplasts (figs. 12.2, 12.3; pls. 38*C*, *D*; 39, 40). Thus the sieve areas are comparable to the primary pit-fields with plasmodesmata that occur in primary walls of living parenchyma cells. In fact, the sieve areas are specialized primary pit-fields. The diameter of the pores in the sieve areas ranges from a fraction of a micron to 15 and probably more in some dicotyledons (Esau and Cheadle, 1959). Accordingly, the strand-like contents of

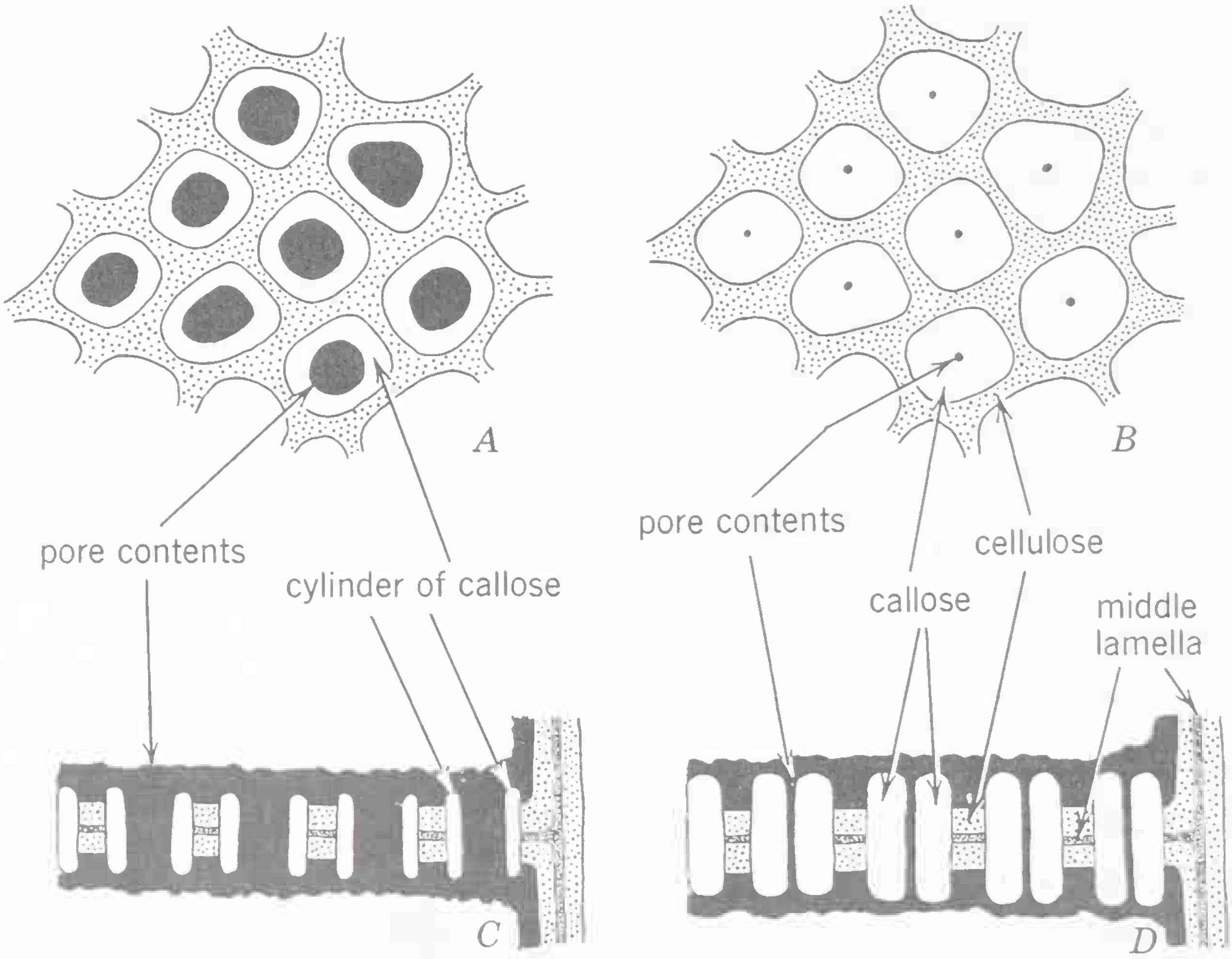

FIG. 12.2. Interpretation of structure of a sieve area in an angiosperm sieve tube. Each drawing represents a part of a sieve area with several pores. Surface views in *A*, *B*, sectional views in *C*, *D*. The protoplasmic contents of the sieve elements covering the sieve areas in *C* and *D* are shown in black; so are also the strands connecting these contents across the sieve areas. *A*, *C*, illustrate younger sieve areas; *B*, *D*, older sieve areas. In *B*, *D*, the amount of callose lining the pores is larger and the pores narrower than in *A*, *C*.

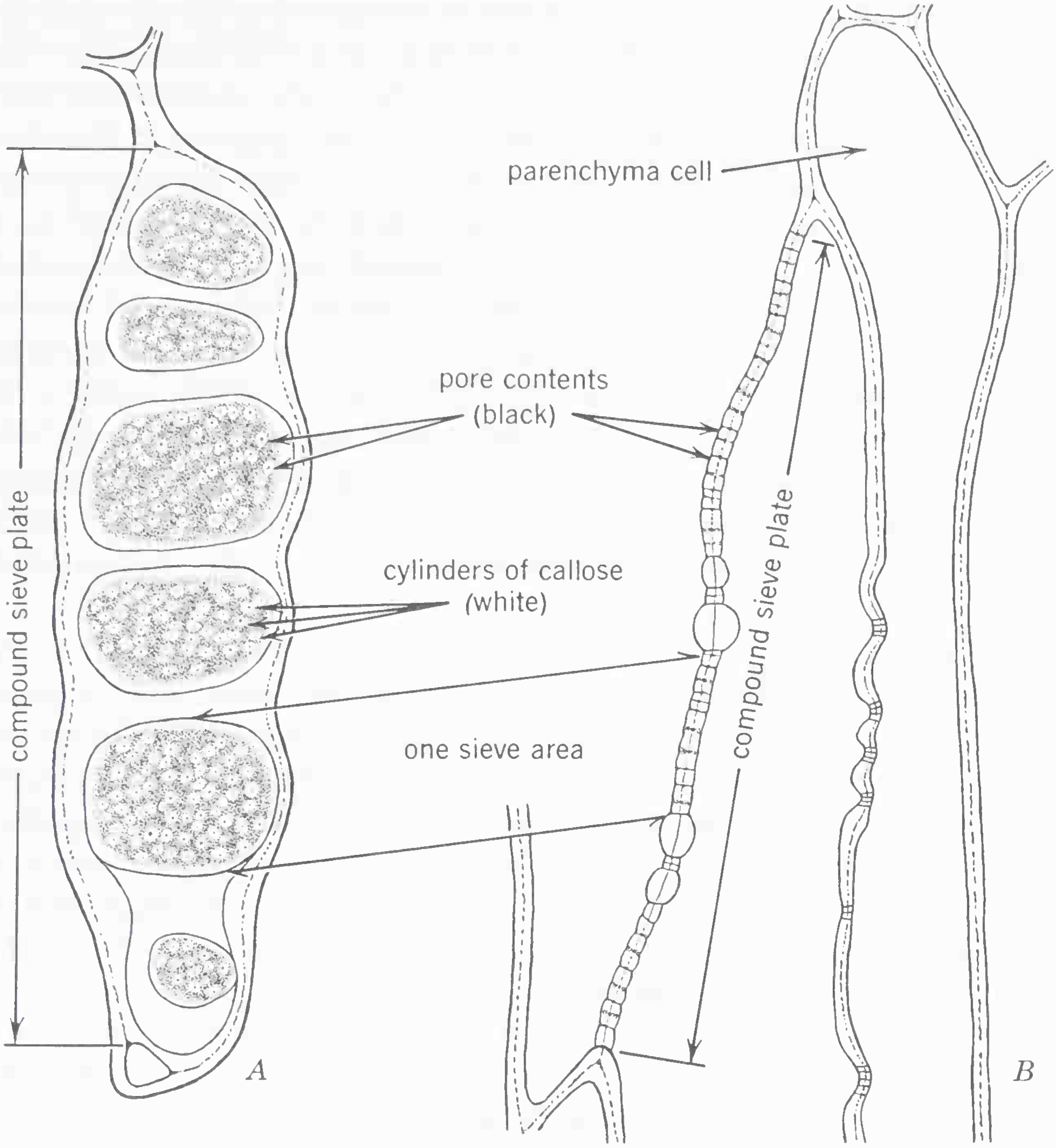

FIG. 12.3. Compound sieve plate of *Nicotiana* (tobacco) in surface view (*A*) and in longitudinal section (*B*). In each sieve area, numerous pores are each lined with callose. Sieve areas occur in depressions of sieve-plate wall. Depressions with plasmodesmata occur in wall between sieve element and parenchyma cell in *B*. (*A*, ×1,070; *B*, ×930. After Esau, *Hilgardia* 11, 1938.)

the pores range from the size of plasmodesmata to considerably larger (pl. 38*C*, *D*).

In sectioned material the sieve-area strands are commonly seen associated with the carbohydrate *callose,* a polymer of glucose residues united into spirally wound chains in β-1-3 linkages (Kessler, 1958; in contrast, cellulose occurs as straight chains of glucose residues in β-1-4 linkages; chapter 3). Callose stains a clear blue with anilin blue and resorcin blue and, in small amounts, may be detected by its characteristic fluorescence after treatment with dilute anilin blue (Currier, 1957).