35 Plant Structure, Growth, and Development

▲ **Figure 35.1 Fanwort *(Cabomba caroliniana).***

Key Concepts

Overview

No Two Plants Are Alike

To some people, the plant in **Figure 35.1** is an intrusive aquatic weed that clogs streams, rivers, and lakes. Others consider it an attractive addition to an aquarium. Whatever else the lanwort *(Cabomba caroliniana)* may be, it is a striking example of **plasticity**—an organism's ability to alter or "mold" itself in response to local environmental conditions. The underwater leaves have a feathery appearance, an adaptation that may provide protection from the stress of moving water. In contrast, the surface leaves are pads that aid in flotation. Both leaf types have genetically identical cells, but the dissimilar environments cause dilferent genes involved in leaf formation to be turned on or off- Such extreme developmental plasticity is much more common in plants than in animals and may help compensate for their lack of mobility. As Natasha Raikhel puts it in the interview preceding this chapter, "Plants have to be exquisite to survive because they can't run." Also, since the form of any plant is controlled by environmental as well as genetic factors, no two plants are exactly alike.

In addition to plastic structural responses by individual plants to specific environments, entire species have by natural selection accumulated characteristics of morphology, or external form, that vary little among plants within the species. For example, some species of desert plants, such as cacti, have leaves that are so highly reduced as spines that the stem is actually the primary photosynthetic organ. This reduction in leaf size, and thus in surface area, results in reduced water loss. These leaf adaptations have enhanced survival and reproductive success in the desert environment.

This chapter focuses on how the body of a plant is formed, setting the stage for the rest of this unit on plant biology. Chapters 29 and 30 described the evolution and characteristics of bryophytes, seedless vascular plants, gymnosperms, and angiosperms. This chapter and Unit Six in general focus mainly on vascular plants—especially angiosperms because flowering plants comprise about 90% of plant species and are the base of nearly every terrestrial food web. As the world's population increases, the need for plants to supply food, fuel, fiber, medicine, lumber, and paper has never been greater, heightening the importance of understanding how plants grow and develop.

Concept 35.1

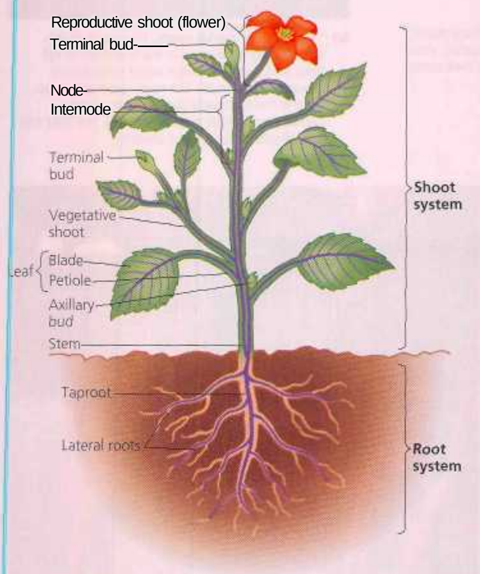
The plant body has a hierarchy of organs, tissues, and cells

Plants, like multicellular animals, have organs composed of different tissues, and these tissues are composed of cells. A **tissue** is a group of cells with a common function, structure, or both. An organ consists of several types of tissues that together carry out particular functions. In looking at the hierarchy of plant organs, tissues, and cells, we will focus first on organs as the most readily observable features of plant structure.

The Three Basic Plant Organs: Roots, Stems, and Leaves

The basic morphology of vascular planis reflects their evolutionary history as terrestrial organisms that inhabit and draw resources from two very different environments—below-ground and above-ground. Plants must absorb water and minerals from below the ground and CO_2 and light from above the ground. The evolutionary solution to this separation of resources was the development of three basic organs: roots, stems, and leaves. They are organized into a root system and a shoot system, the latter consisting of stems and leaves **(Figure 35.2).** With few exceptions, angiosperms and other vascular plants rely completely on both systems for survival. Roots are typically nonphotosynthetic and would starve without the organic nutrients imported from the shoot system. Conversely, the shoot system depends on the water and minerals that roots absorb from the soil.

Later in the chapter, we will discuss the transition from vegetative shoots (shoots that are nonreproductive) to reproductive shoots. In angiosperms, the reproductive shoots are flowers, which are composed of leaves that are highly modified for sexual reproduction.



▲ **Figure 35.2 An overview of a flowering plant.** The plant body is divided into a root system and a shoot system, connected by vascular tissue (purple strands in this diagram) that is continuous throughout the plant. The plant shown is an idealized eudicot.

As we take a closer look at roots, stems, and leaves, try to view these organs from the evolutionary perspective of adaptations to living on land, In identifying some variations in these organs, we will focus mainly on the two major groups of angiosperms: monocots and eudicots (see Figure 30.12).

Roots

A root is an organ that anchors a vascular plant (usually in the soil), absorbs minerals and water, and often stores organic nutrients. Most eudicots and gymnosperms have a taproot system, consisting of one main vertical root (the taproot) that develops from an embryonic root. The taproot gives rise to lateral roots, also called branch roots (see Figure 35.2). In angiosperms, the taproot often stores organic nutrients that the plant consumes during flowering and fruit production. For this reason, root crops such as carrots, turnips, and sugar beets are harvested before they flower. Taproot systems generally penetrate deeply into the ground.

In seedless vascular plants and in most monocots, such as grasses, the embryonic root dies and does not give rise to a main root. Instead, many small roots grow from the stem, with each small root forming its own lateral roots. The result is a fibrous root system—a mat ol generally thin roots spreading out below the soil surface, with no root standing out as the main one (see Figure 30.12). Roots arising from the stem are said to be adventitious (from the Latin *adventidus*, extraneous), a term describing any plant part that grows m an unusual location. A fibrous root system is usually shallower than a taproot system. Grass roots are particularly shallow, being concentrated in the upper few centimeters of the soil. Because grass roots hold the topsoil in place, they make excellent ground cover for preventing erosion. Large monocots, such as palms and bamboo, are mainly anchored by sturdy rhizomes, which are horizontal underground stems.

The entire root system helps anchor a plant, but in most plants the absorption of water and minerals occurs primarily near the root tips, where vast numbers of tiny root hairs increase the surface area of the root enormously **(Figure 35.3).** A

◀ **Figure 35.3 Root hairs and root tip.** Growing by the thousands just behind each root tip, root hairs increase the surface area for the absorption of water and minerals by the roots.

root hair is an extension of a root epidermal cell (protective cell on a plant surface). Root hairs are not to be confused with lateral roots, which are multicellular organs. Absorption is often enhanced by symbiotic relationships between plant roots and fungi and bacteria, as you will see in Chapters 36 and 37.

Many plants have modified roots. Some oi these arise froi n roots, and others are adventitious, developing from sterr s and, in rare cases, leaves. Some modified roots provide mo e support and anchorage, while others store water and nutrien s or absorb oxygen or water from the air **(Figure 35.4).**

T Figure 35.4 Modified roots. Environmental adaptations may result in roots being modified for a variety of functions, Many modified roots are aerial roots that are above the ground during normal development.

(a) Prop roots. The aerial roots shown here in maize are examples of prop roots, so named because they support tall, top-heavy plants. All roots of a mature maize plant are adventitious after the original roots die. The emerging roots shown here will eventually penetrate the soil.

(b) Storage roots. Many plants, such as sweet potatoes, store food and water in their roots.

(c) "Strangling" *aerial* roots. The seeds of this strangler fig germinate in the branches of tall trees and send numerous aerial roots to the ground. These snake-like roots gradually wrap around the hosts and objects such as this Cambodian temple ruin. Eventually, the host tree dies of strangulation and shading.

(d) Buttress roots. Aerial roots that look like buttresses support the tall trunks of some tropical trees, such as this ceiba tree in Central America.

(e) Pneumatophores. Also known as air roots, pneumatophores are produced by trees such as mangroves that inhabit tidai swamps. By projecting above the surface, they enable the root system to obtain oxygen, which is lacking in the thick, waterlogged mud.

Stems

A **stem** is an organ consisting of an alternating system of **nodes,** the points at which leaves are attached, and **internodes,** the stem segments between nodes (see Figure 35.2). In the angle (axil) formed by each leaf and the stem is an **axillary bud,** a structure that has the potential to form a lateral shoot, commonly called a branch. Most axillary buds of a young shoot are dormant (not growing). Thus, elongation of a young shoot is usually concentrated near the shoot apex (tip), which consists of a **terminal bud** with developing leaves and a compact series of nodes and internodes.

The proximity of the terminal bud is partly responsible for inhibiting the growth of axillary buds, a phenomenon called **apical dominance.** By concentrating resources toward elongation, apical dominance is an evolutionary adaptation that increases the plant's exposure to light. But what if an animal eats the end of the shoot? Or what if, because of obstructions, light is more intense to the side of a plant than directly above it? Under such conditions, axillary buds break dormancy; that is, they start growing. A growing axillary bud gives rise to a lateral shoot, complete with its own terminal bud, leaves, and axillary buds. Removing the terminal bud usually stimulates the growth of axillary buds, resulting in more lateral shoots. That is why pruning trees and shrubs and "pinching back" houseplants will make them "bushier."

Modified stems with diverse functions have evolved in many plants as environmental adaptations. These modified stems, which include stolons, rhizomes, tubers, and bulbs, are often mistaken for roots **(Figure 35.5).**

Leaves

The **leaf** is the main photosynthetic organ of most vascular plants, although green stems also perform photosynthesis. Leaves vary extensively in form but generally consist of a flattened **blade** and a stalk, the **petiole,** which joins the leaf to a node of the stem (see Figure 35.2). Among angiosperms, grasses and many other monocots lack petioles; instead, the base of the leaf forms a sheath that envelops the stem. Some monocots, including palm trees, do have petioles.

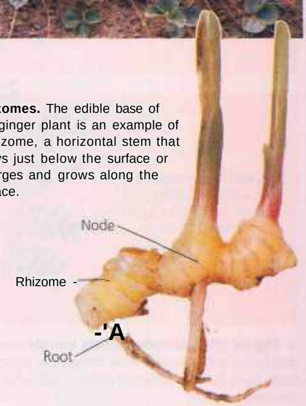
Monocots and eudicots differ in the arrangement of veins, the vascular tissue of leaves. Most monocots have parallel major veins that run the length of the leaf blade. In contrast,

Figure 35.5 Modified stems.

(a) Stolons. Shown here on a strawberry plant, stolons are horizontal stems that grow along the surface. These "runners" enable a plant to reproduce asexually, as plantlets form at nodes along each runner.

(b) Bulbs. Bulbs are vertical, underground shoots consisting mostly of the enlarged bases of leaves that store food. You can see the many layers of modified leaves attached to the short stem by slicing an onion bulb lengthwise.

(c) Tubers. Tubers, such as these red potatoes, are enlarged ends of rhizomes specialized for storing food. The "eyes" arranged in a spiral pattern around a potato are clusters of axillary buds that mark the nodes.

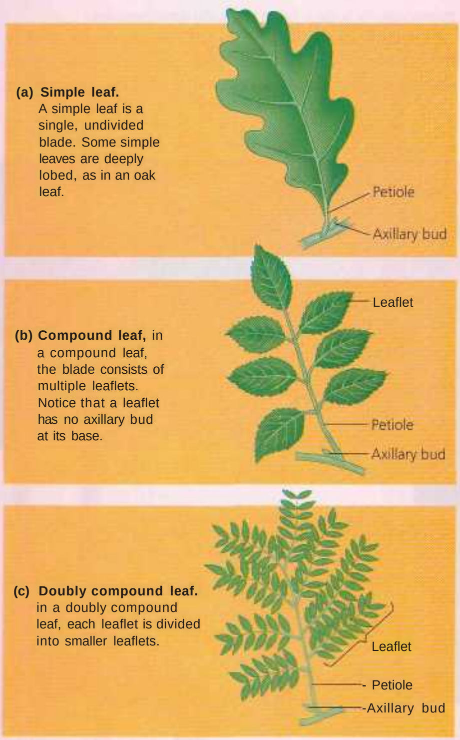


(d) Rhizomes. The edible base of this ginger plant is an example of a rhizome, a horizontal stem that grows just below the surface or emerges and grows along the surface.

eudicot leaves generally have a multibranched network of major veins (see Figure 30.12).

In identifying and classifying angiosperms, taxcmomists rely mainly on floral morphology, but they also use variations in leaf morphology, such as leaf shape, spatial arrangement of leaves, and the pattern of a leaf's veins. **Figure 35.6** illustrates a difference in leaf shape: simple versus compound leaves. Most very large leaves are compound or doubly compound. This structural adaptation may enable large leaves to withstand strong wind with less tearing and also confine some pathogens that invade the leaf to a single leaflet, rather than allowing them to spread to the entire leaf.

Most leaves are specialized for photosynthesis. However, some plant species have leaves that have become adapted by evolution for other functions, such as support, protection, storage, or reproduction **(Figure 35.7).**



(a) Simple leaf. A simple leaf is a single, undivided blade. Some simple leaves are deeply lobed, as in an oak leaf.

(b) Compound leaf, in a compound leaf, the blade consists of multiple leaflets. Notice that a leaflet has no axillary bud at its base.

(c) Doubly compound leaf. in a doubly compound leaf, each leaflet is divided into smaller leaflets.

A Figure 35.6 Simple versus compound leaves. You can distinguish simple leaves from compound leaves by looking for axillary buds. Each leaf has only one axillary bud, where the petiole attaches to the stem.

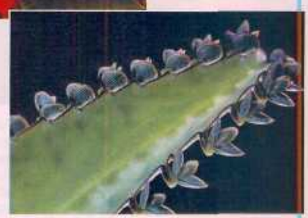
• Figure 35.7 Modified leaves.

(a) Tendrils. The tendrils by which this pea plant clings to a support are modified leaves. After it has "lassoed" a support, a tendril forms a coil that brings the plant closer to the support. Tendrils are typically modified leaves, but some tendrils are modified stems, as in grapevines.

(b) Spines. The spines of cacti, such as this prickly pear, are actually leaves, and photosynthesis is carried out mainly by the fleshy green stems.

(c) Storage leaves. Most succulents, such as this ice plant, have leaves modified for storing water.

(d) Bracts. Red parts of the poinsettia are often mistaken for petals but are actually modified leaves called bracts that surround a group of flowers. Such brightly colored leaves attract pollinators.

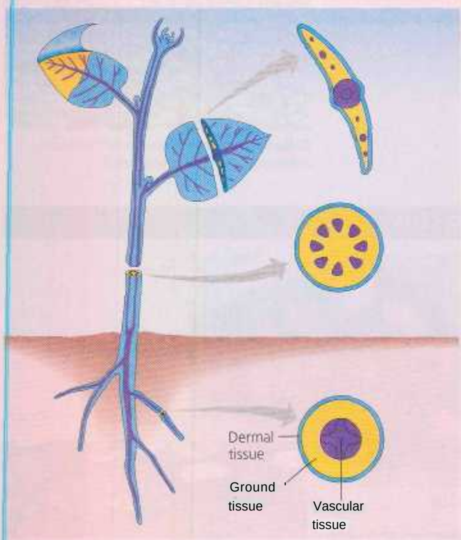


(e) Reproductive leaves. The leaves of some succulents, such as *Kalanchoe daigremontiana,* produce adventitious plantlets, which fall off the leaf and take root in the soil.

The Three Tissue Systems: Dermal, Vascular, and Ground

Each plant organ—root, stem, or leaf—has dermal, vascular, and ground tissues. A tissue system consists of one or more tissues organized into a functional unit connecting the organs of a plant. Each tissue system is continuous throughout the entire plant body, but specific characteristics of the tissues and their spatial relationships to one another vary in different organs (**Figure 35.8**).

The dermal tissue system is the outer protective covering. Like our skin, it forms the first line of defense against physical damage and pathogenic organisms. In nonwoody plants, the dermal tissue usually consists of a single layer of tightly packed cells called the epidermis. In woody plants, protective tissues known as periderm replace the epidermis in older regions of stems and roots by a process discussed later in the chapter. In addition to protecting the plant from water loss and disease, the epidermis has specialized characteristics in each organ. For example, the root hairs so important in the absorption of water and minerals are extensions of epidermal cells near root tips. In the epidermis of leaves and most stems, a waxy coating called the cuticle helps prevent water loss—an important adaptation



▲ **Figure 35.8 The three tissue systems.** The dermal tissue system (blue) covers the entire body of a plant. The vascular tissue system (purple) is also continuous throughout the plant, but is arranged differently in each organ. The ground tissue system (yellow), responsible for most of the plant's metabolic functions, is located between the dermal tissue and the vascular tissue in each organ.

to living on land. Later we will look at specialized leaf cells that regulate CO_2 exchange. Leaf trichomes, which are outgrowths of the epidermis, are yet another example of specialization. For instance, trichomes in aromatic leaves such as mint secrete oils that protect plants from herbivores and disease.

The vascular tissue system carries out long-distance transport of materials between roots and shoots. The two vascular tissues are xylem and phloem. Xylem conveys water and dissolved minerals upward from roots into the shoots. Phloem transports organic nutrients such as sugars from where they are made (usually the leaves) to where they are needed—usually roots and sites of growth, such as developing leaves and fruits. The vascular tissue of a root or stem is collectively called the stele (the Greek word for "pillar"). The arrangement of the stele varies, depending on species and organ. In angiosperms, the stele of the root is in the form of a solid central vascular cylinder. In contrast, the stele of stems and leaves is divided into vascular bundles, strands consisting of xylem and phloem. Both xylem and phloem are composed of a variety of cell types, including cells highly specialized for transport.

Tissues that are neither dermal nor vascular are part of the ground tissue system. Ground tissue that is internal to the vascular tissue is called pith, and ground tissue that is external to the vascular tissue is called cortex. The ground tissue system is more than just filler. It includes various cells specialized for functions such as storage, photosynthesis, and support.

Common Types of Plant Cells

Like any multicellular organism, a plant is characterized by cellular differentiation, the specialization of cells in structure and function. In plant cells, differentiation is sometimes evident within the protoplast, the cell contents exclusive of the cell wall. For example, the protoplasts of some plant cells have chloroplasts, whereas other types of plant cells lack functional chloroplasts. Cell wall modifications also play a role in plant cell differentiation. **Figure 35.9**, on the next two pages, focuses on some major types of plant cells: parenchyma, collenchyma, sclerenchyma, the water-conducting cells of the xylem, and the sugar-conducting cells of the phloem. Notice the structural adaptations that make specific functions possible. You may wish to review Figures 6.9 and 6.28, which show basic plant cell structure.

Concept Check 35.1

1. How does the vascular tissue system enable leaves and roots to combine functions to support growth and development of the whole plant?
2. Describe at least three specializations in plant organs and plant cells that are adaptations to life on land.
3. Describe the role of each tissue system in a leaf.

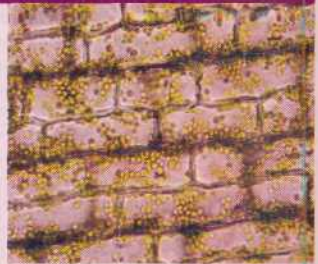
For suggested *answers, see* Appendix A.

Figure 35.9

Exploring Examples of Differentiated Plant Cells

PARENCHYMA CELLS

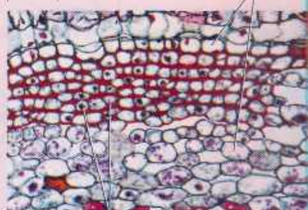
Mature **parenchyma cells** have primary walls that are relatively thin and flexible, and most lack secondary walls. (See Figure 6.28 to review primary and secondary layers of cell walls.) The protoplast generally has a large central vacuole. Parenchyma cells are often depicted as "typical" plant cells because they appear to be the least specialized stiTicturally Parenchyma cells perform most of the metabolic functions of the plant, synthesizing and storing various organic products. For example, photosynthesis occurs within the chloroplasts of parenchyma cells in the leaf. Some parenchyma cells in stems and roots have colorless plastids that store starch. The fleshy tissue of a typical fruit is composed mainly of parenchyma cells. Most parenchyma cells retain the ability to divide and differentiate into other types of plant cells under special conditions—during the repair and replacement of organs after injury to the plant, for example. It is even possible in the laboratory to regenerate an entire plant from a single parenchyma cell.



Parenchyma cells in *Elodea* leaf, with chloroplasts

COLLENCHYMA CELLS

Grouped in strands or cylinders, **coUenchyma cells** help support young parts of the plant shoot. CoUenchyma cells have thicker primary walls than parenchyma cells, though the walls are unevenly thickened. Young stems and petioles often have strands of coUenchyma cefls just below their epidermis (the "strings" of a celery stalk, for example). CoUenchyma cells lack secondary walls, and the hardening agent lignin is absent in their primary walls. Therefore, they provide flexible support without restraining growth. At functional maturity, coUenchyma cells are living and flexible, elongating with the stems and leaves they support—**unlike** sclerenchyma cells, which we discuss next.

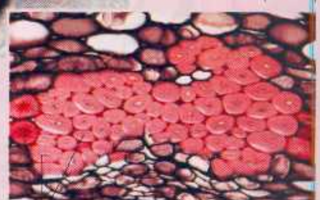


CoUenchyma cells (in cortex of *Sambucus*, elderberry; cell walls stained red)

SCLERENCHYMA CELLS

Also functioning as supporting elements in the plant, but with thick secondary walls usually strengthened by lignin, **sclerenchyma** cells are much more rigid than coUenchyma cells. Mature sclerenchyma cells cannot elongate, and they occur in regions of the plant that have stopped growing in length. Sclerenchyma cells are so specialized for support that many are dead at functional maturity, but they produce secondary walls before the protoplast dies. The rigid walls remain as a "skeleton" that supports the plant, in some cases for hundreds of years. In parts of the plant that are still elongating, the secondary walls of immature sclerenchyma are deposited unevenly in spiral or ring patterns. These forms of cell wall thickenings enable the cell wall to stretch like a spring as the cell elongates.

Two types of sclerenchyma ceUs called **sclereids** and **fibers** are specialized entirely for support and strengthening. Sclereids, which are shorter than fibers and irregular in shape, have very thick, lignified secondary walls. Sclereids impart the hardness to nutshells and seed coats and the gritty texture to pear fruits. Fibers, which are usually arranged in threads, are long, slender, and tapered. Some are used commercially, such as hemp fibers for making rope and flax fibers for weaving into linen.



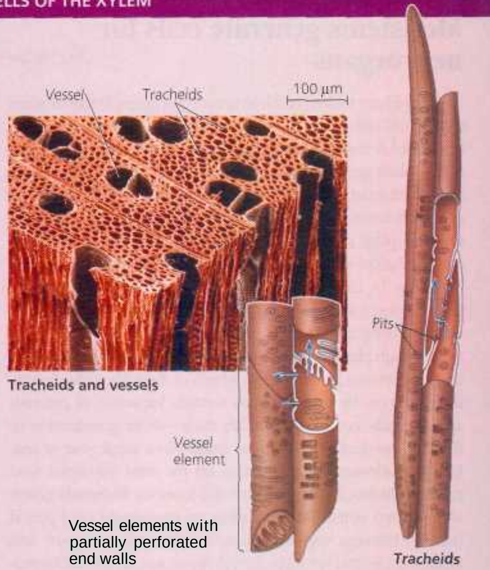
Fiber cells (transverse section from ash tree)

WATER-CONDUCTING CELLS OF THE XYLEM

The two types of water-conducting cells, tracVieids and vessel elements, ars tubular, elongated cells that are dead at functional maturity. Tracheids are found in the xyleni of all vascular plants. In addition to tracheids, most angiosperms, as well as a few gymnosperms and a few seedless vascular plants, have vessel elements. When the protoplast of a traeheid or vessel element disintegrates, the cells thickened cell walls remain behind, forming a nonliving conduit through, which water can. flow. The se ^ondary walls of iracheids and vessel elements are often interrupted by pi s, thinner regions where only primary walls are present (see Figure 6. i8 to review primary and secondary walls). Water can migrate laterally between neighboring cells through pits.

Tracheids are long, thin cells with tapered ends. Water moves from cell to cell mainly through the pits, where it does not have to cross thick secoadary walls. The secondary walls of tracheids are hardened with lignin, wkich prevents collapse under the tensions of water transport and also provides support.

Vessel elements are generally wider, shorter, thinner walled, and less tapered than tracheids. They are aligned end to end, forming long micropipes known as vessels. The end walls of vessel elements have perforations, enabling water to flow freely through, the vessels.



Tracheids and vessels

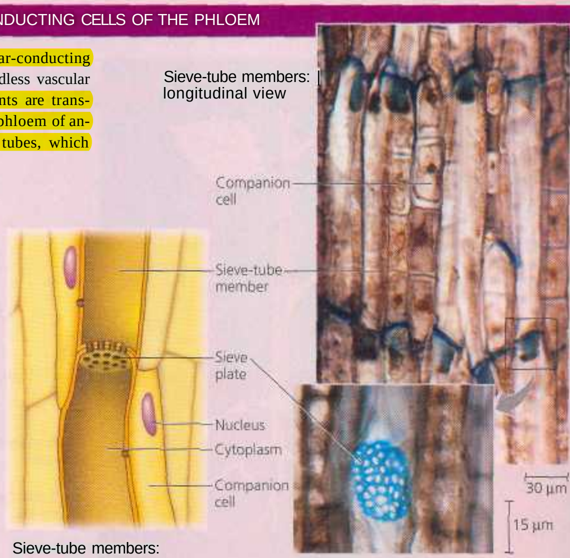
Vessel elements with partially perforated end walls

Tracheids

SUGAR-CONDUCTING CELLS OF THE PHLOEM

Unlike the water-conducting cells of the xylem, the sugar-conducting cells of the phloem are alive at functional maturity. In seedless vascular rjlants and gymnosperms, sugars and other organic nutrients are transported through long, narrow cells called sieve cells. In the phloem of ansiosperms, these nutrients are transported through, sieve tubes, which cprisist of chains of cells called sieve-tube members.

Though alive, sieve-tube members lack such organdies as the nucleus, ribosomes, and a distinct vacuole. "This reduction in cell contents enables nutrients to pass more easily through the cell. The end walls between sieve-tube members, called sieve plates, have pores that facilitate the flow of fluid from cell to cell along the sieve tjube. Alongside each sieve-tube member is a nonconducting cell called a companion cell, which is connected do the sieve-tube member by numerous channels, the flasmodesmata (see Figure 6.8). The nucleus and ribosomes of the companion cell may serve not only that cell Lself but also the adjacent sieve-tube member. In some lants, companion cells in leaves also help load sugars nto the sieve-tube members, which then transport the ugars to other parts of the plant.



Sieve-tube members: longitudinal view

Sieve-tube members: longitudinal view

Sieve plate with pores