30 PLANT NUTRITION AND TRANSPORT

Leafy Clean-Up Crews

From World War I until the 1970s, the United States Army used a weapons testing and disposal site at Aberdeen Proving Grounds in Maryland (Figure 30.1). When chemical weapons and explosives became obsolete, workers burned them in open pits at the site, along with assorted plastics and other wastes.

Toxic levels of lead, arsenic, mercury, and other metals contaminated the soil and the water at Aberdeen Proving Grounds. Dozens of harmful organic compounds, such as trichloroethylene (TCE) seeped into groundwater. TCE is used as a solvent for cleaning metals. This colorless liquid can adversely affect the nervous system, lungs, and the liver in ways that can lead to coma and death. Today, the contaminated groundwater is gradually seeping toward nearby marshes and the Chesapeake Bay. Parts of the bay are now so polluted from other sources that they are a dead zone, where no marine life survives.

The Army, in concert with the Environmental Protection Agency, is now repairing the site, which is known as J-Field. Workers cannot dig up and cart off the contaminated soil; there is too much of it. As an alternative, they have planted hybrid poplars (*Populus trichocarpa x deltoides*). The trees are taking up TCE and other organic solvents and thereby cleansing the groundwater (Figure 30.1).

What is going on at Aberdeen Proving Grounds is an example of *phytoremediation*, the use of plant species to

cleanse blighted regions by taking up and concentrating or degrading contaminants.

After poplar roots take up dissolved contaminants as well as mineral ions, living cells in their tissues degrade some of them. Gaseous forms of other compounds that are still somewhat harmful are released into the surrounding air. Such airborne contaminants are the lesser of two evils. For instance, TCE persists for a long time in groundwater. It breaks down faster in polluted air.

Elsewhere, different species of plants are taking up contaminants. In some cases, they are degrading targeted compounds or releasing them into the air, as in J-Field. In other cases, microbial symbionts of plants degrade them, and plant roots take up the breakdown products.

Some kinds of plants used in phytoremediation store contaminants in their tissues. Workers then remove the plants from the site for safer, convenient disposal.

The best plants for phytoremediation take up many contaminants, grow fast, and grow big. Not many plants can tolerate toxic substances, but genetically engineered ones might expand the range of choices. For instance, the alpine pennycress (*Thlaspi caerulescens*) shown in Figure 30.1*c* absorbs ions of zinc, cadmium, and other potentially toxic minerals dissolved in soil water. Unlike most plants, its living cells store zinc and cadmium out of the way, in their central vacuole. Genetic researchers are attempting



Figure 30.1 (a) J-Field, once a weapons testing and disposal site. (b) Today, hybrid poplars are helping to remove substances that contaminate the field's soil and groundwater. (c) Pennycress, which can take up toxic metals and survive.

IMPACTS, ISSUES



to transfer a gene that confers the toxin-storing capacity of pennycress to other plants.

We use phytoremediation as your introduction to *plant physiology*, the study of how plants function in their environment. Many of the adaptations by which the toxinbusters cleanse the environment are the same ones they use to absorb and distribute water and solutes through the plant body during normal growth and development.

When considering the nature of these adaptations, it helps to remember a key point. Rarely in nature do plants have unlimited supplies of the resources they require to nourish themselves. Of every 1 million molecules of air, for example, only 350 are carbon dioxide. Most of the soils of natural habitats are frequently dry. Nowhere except in overfertilized gardens does soil water hold lavish amounts of dissolved minerals. In short, *plant structure and function are, in large part, responses to low concentrations of vital environmental resources*.

How Would You Vote?

Phytoremediation using genetically engineered plants can increase the efficiency with which a contaminated site is cleaned up. Do you support planting genetically engineered plants for such projects? See BiologyNow for details, then vote online.

Key Concepts

UPTAKE OF NUTRIENT-LADEN WATER

Many aspects of a vascular plant's structure and function are adaptive responses to low concentrations of water, mineral ions, and other environmental resources.

A plant's root system takes up water from soil and mines the soil for nutrients. For many land plants, mycorrhizae and bacterial symbionts assist in the uptake. Soils in different habitats are in different stages of development, and they affect water and nutrient availability. Sections 30.1, 30.2

WATER MOVEMENT THROUGH PLANTS

Xylem distributes absorbed water and solutes throughout the plant. Transpiration is the evaporation of water from plant parts exposed to dry air. The evaporative water loss creates a continuous negative tension in xylem that pulls unbroken columns of water from roots to leaves. The water molecules in xylem are hydrogen-bonded to one another, and they replace the ones lost. Section 30.3

WATER LOSS VERSUS GAS EXCHANGE

A cuticle and stomata help plants conserve water, a scarce resource in most land habitats. Although closed stomata stop water loss, they also stop gas exchange. Certain plant adaptations represent trade-offs between the requirements for water conservation and photosynthesis. Section 30.4

SUGAR DISTRIBUTION THROUGH PLANTS

Translocation, an energy-requiring process, distributes sucrose and other organic compounds from photosynthetic cells in leaves to all other living cells in the plant. Organic compounds are actively loaded into conducting cells of phloem and then unloaded in actively growing regions or storage regions. Section 30.5

Links to Earlier Concepts

This chapter moves you from photosynthesis in individual cells (Sections 7.3, 7.7) to functional adaptations that sustain photosynthesis. You caught glimpses of these adaptations in ecological (7.8) and evolutionary (18.9, 23.2) contexts. Here you will consider actual mechanisms of the acquisition and distribution of resources in the plant body.

You will draw on your knowledge of ionization and hydrogen bonding (2.4), water's cohesive properties (2.5), membrane transport mechanisms (5.4), and osmosis and turgor (5.5). You will use your knowledge of vascular tissues (29.2), primary stems and roots (29.3. 29.5), and the fine structure of leaves (29.4). You will once again glimpse interactions between plants and their fungal symbionts (24.6), this time in the context of plant nutrition. UPTAKE OF NUTRIENT-LADEN WATER

30.1 Plant Nutrients and Availability in Soil

LINK TO SECTION 2.4 We've mentioned nutrients in passing. But exactly what are they? A **nutrient** is any element that is essential in an organism's life because no other element can indirectly or directly fulfill its metabolic role.

THE REQUIRED NUTRIENTS

Sixteen elements are essential for plant growth. They become ionized in soil water, as Section 2.4 explains. Examples are ions of calcium (Ca⁺⁺) and potassium (K⁺). Nine elements are *macronutrients*, required in amounts above 0.5 percent of the plant's dry weight.

Table 30.1 Plant Nutrients and Symptoms of Deficiencies

	Carbon Hydrogen Oxygen	No symptoms; all three macronutrients are available in abundance from water and carbon dioxide
	Nitrogen	Stunted growth; young leaves turn yellow and die (these are symptoms of chlorosis)
	Potassium	Reduced growth; curled, mottled, or spotted older leaves; burned leaf edges; weakened plant
	Calcium	Terminal buds wither; deformed leaves; stunted roots
	Magnesium	Chlorosis; drooped leaves
	Phosphorus	Purplish veins; stunted growth; fewer seeds, fruits
	Sulfur	Light-green or yellowed leaves; reduced growth
	Chlorine	Wilting; chlorosis; some leaves die
	Iron	Chlorosis; yellow, green striping in leaves of grasses
	Boron	Terminal buds, lateral branches die; leaves thicken, curl, become brittle
	Manganese	Dark veins, but leaves whiten and fall off
	Zinc	Chlorosis; mottled or bronzed leaves; abnormal roots
	Copper	Chlorosis; dead spots in leaves; stunted growth
	Molybdenum	Pale green, rolled or cupped leaves
н		

Table 30.2 What to Ask When Home Gardening Hits a Wall

- What are the symptoms? (e.g., brown, yellow, curled, wilted, chewed leaves)
 What is the species? Is part of one plant, a whole plant, or many plants affected?
- 3. Is the planting soil loose or compact? Were amendments added? Are fertilizers used, and how often?
- 4. Is watering by hand, hose, sprinklers, drip system? When and how often?
- 5. Is the plant indoors? Outdoors, in full sun or partial or full shade? In wind?
- 6. Dig gently to expose a few small feeder roots. Are they black and mushy (overwatering), brown and dry (not enough water), or white with a crisp "snap"?
- 7. Do you see insects, or insect droppings, webs, cast skins, or slime?
- Some unique symptoms of infections rather than nutrient deficiencies: *Viral:* Leaves or petals stunted, with mottling, colored rings, distorted shapes. *Bacterial:* Tissues have a soaked, slimy texture, often a rotting smell. *Fungal:* Leaves with dry texture, discolored spots with distinct margins, usually with concentric rings (usually tan at the center, then brown, then light vellow at edge of infection).

That is the weight after all water has been removed from an organism. At least seven more elements are *micro*nutrients. They make up traces—typically a few parts per million—of the dry weight. A deficiency in any nutrient causes problems (Tables 30.1 and 30.2).

PROPERTIES OF SOIL

Soil consists of mineral particles mixed with variable amounts of decomposing organic material, or **humus**. The minerals form by the weathering of hard rocks. Humus forms from dead organisms and organic litter: fallen leaves, feces, and so on. Water and air occupy spaces between the particles and organic bits.

Soils differ in their proportions and compaction of mineral particles. The three main sizes of particles are sand, silt, and clay. The biggest sand grains are 0.05 to 2 millimeters across. You can see individual grains by dribbling beach sand through your fingers. Rub silt between your fingers and you cannot see individual particles; they are only 0.002 to 0.05 millimeter across. Clay particles are the finest of all.

How suitable is a given soil for plant growth? Is it gummy when wet because it does not have enough air spaces? Does it form hard clods when dry? The answer depends partly on its proportions of sand, silt, and clay. The more clay, the finer the soil's texture.

Each clay particle consists of thin, stacked layers of aluminosilicates with negatively charged ions at their surfaces. As water trickles through soil, clay attracts dissolved, positively charged mineral ions as well as water molecules, both of which cling reversibly to it. The charged surfaces are the reason clay is so good at latching on to many nutrients for plant growth.

Most plants do not grow well in soil with too much clay. Without enough sand and silt, clay particles pack so tightly that they exclude air. Root cells cannot get oxygen for aerobic respiration. Also, water does not soak into heavy clay soils; it tends to flow along the surface, as runoff. Runoff ends up in streams, taking soil and dissolved minerals with it. Soils having the best oxygen and water penetration are **loams**, which have roughly equal proportions of sand, silt, and clay.

Humus, too, promotes plant growth. Its negatively charged organic acids attract mineral ions of opposite charge. Also, humus swells and shrinks as it quickly absorbs and releases water. Such rapid changes aerate soil by opening up spaces that air can penetrate.

In general, soils that have 10 to 20 percent humus are best for plants. The worst soils have less than 10 percent humus or more than 90 percent humus. Bogs and swamps have notably poor soils. Soils develop slowly, over thousands of years, and they are in different stages of development in different places. They generally form in layers, or horizons, that are distinct in color and other properties (Figure 30.2). The layers help us profile the soil in a particular place. For instance, the A horizon is **topsoil**. Topsoil is the layer most essential for plant growth, and it is deeper in some places than in others. Section 48.5 shows soil profiles for some of the world's major land regions.

LEACHING AND EROSION

Leaching is the downward percolation of water, and small quantities of dissolved nutrients, through soil. Leaching is fastest in sandy soils, which are not as good as clay at binding nutrients. During spring rains and the ensuing runoff, leaching occurs more in forests than in grasslands. Why? Grass plants grow fast, and actively growing plants absorb more water.

Soil erosion is a loss of soil under the force of wind and water. Strong winds, fast-moving water, and poor vegetation cover cause the greatest losses. For example, erosion from croplands puts about 25 billion metric tons of topsoil into the Mississippi River, then the Gulf of Mexico each year. Figure 30.3 has other examples.

Either way, the nutrient losses affect plant growth and all organisms that depend on plants for survival.

Nutrients are essential elements. No other element can substitute for their direct or indirect roles in the metabolic activities that sustain growth and survival. Plants require nine macronutrients and at least seven micronutrients.

Soils consist mainly of particles ranging from large-grained sand to silt and fine-grained clay. Clay especially promotes plant growth by attracting and reversibly binding many water molecules and dissolved mineral ions.

Soil contains humus, a reservoir of organic material rich in organic acids and in different stages of decay. Most plants grow best in soils having equal proportions of sand, silt, and clay, as well as 10 to 20 percent humus.

Figure 30.3 (a) Erosion. In Chiapas State, Mexico, forests that once sponged up water from soil were cut down. Out-of-control runoff from rains cut deeper and wider gullies and carried away topsoil. (b) Why the Great Plains of North America became known as the Dust Bowl. Drought and strong winds prevail in this region. In the 1850s, native prairies were plowed under for farms. In time, a third of the once-deep topsoil and half the nutrients were blown away. By the 1930s, monstrous clouds of dust were forming. Not surprisingly, they ushered in erosion control practices.

O HORIZON

Fallen leaves and other organic material littering the surface of mineral soil

A HORIZON

Topsoil, with decomposed organic material; variably deep (only a few centimeters in deserts, elsewhere extending as far as thirty centimeters below the soil surface)

B HORIZON

Compared with A horizon, larger soil particles, not much organic material, more minerals; extends thirty to sixty centimeters below soil surface

C HORIZON

No organic material, but partially weathered fragments and grains of rock from which soil forms; extends to underlying bedrock

BEDROCK -

Figure 30.2 Example of soil horizons. These developed in a habitat in Africa.







How Do Roots Absorb Water and Mineral Ions?

LINKS TO SECTIONS 5.4, 24.6, 29.5 Mining soil for water and minerals clinging to clay particles takes energy. Where a soil's composition and texture change, new roots form, replace old ones, and infiltrate different regions. The roots are not "exploring" soil. Rather, gradients are simply stimulating their growth toward patches of soil with higher concentrations of water and minerals.

SPECIALIZED ABSORPTIVE STRUCTURES

A mature corn plant absorbs as much as three liters of water per day. Plants in general use a lot of water and dissolved mineral ions. Mycorrhizae, root nodules, and root hairs of the plant itself enhance the uptake.





Figure 30.4 Nutrient uptake at root nodules of legumes that are mutualists with nitrogen-fixing bacteria (Rhizobium and Bradyrhizobium). (a) When infected by the bacteria, root hair cells form a thread of cellulose deposits. Bacteria use the thread as a highway to invade plant cells in the root cortex.

(b) Infected plant cells and bacterial cells inside them divide repeatedly, forming a swollen mass that becomes a root nodule. Bacteria start fixing nitrogen when membranes of plant cells surround them. The plant takes up some of the nitrogen; the bacteria take up some photosynthetic compounds.

(c) Soybean plants growing in nitrogen-poor soil show the effect of root nodules on growth. Only the plants in the rows at right were inoculated with Rhizobium bacteria and formed nodules.

Mycorrhizae As Section 24.6 explains, a mycorrhiza (plural, mycorrhizae) is a form of mutualism between a young root and a fungus, in which both species gain benefits. The fungal hyphae grow as a velvety covering around the root or penetrate its cells. Collectively, the hyphae have a far larger surface area and can absorb scarce minerals from a larger volume of soil than the root can do on its own. The root's cells give up some sugars and nitrogen-rich compounds to the fungus, which gives up some minerals to the plant.

Root Nodules Certain bacteria in soil are mutualists with clover, peas, and other legumes which, like other plants, require nitrogen for growth. Gaseous nitrogen $(N \equiv N, \text{ or } N_2)$ is plentiful in air, but plants do not have enzymes that can break its three covalent bonds. The bacteria have enzymes that split the bonds, after which the atoms become rearranged as ammonia. The metabolic conversion of gaseous nitrogen to ammonia is called nitrogen fixation. Ammonia gets converted to forms that plants can absorb. As Section 47.11 explains, nitrogen fixation is a vital stage of the nitrogen cycle.

Nitrogen-fixing bacteria infect roots, then become symbionts in localized swellings called root nodules (Figure 30.4). The bacteria pilfer some photosynthetic products. The plants absorb some of the nitrogen that bacterial cells assimilated from the atmosphere.

Root Hairs As most plants put on primary growth, their root system may develop billions of root hairs (Figure 30.5). Collectively, these thin extensions of root epidermal cells enormously increase the surface area





root epidermal cells

Figure 30.5 Two views of a profusion of root hairs. These extensions of a young root's epidermal cells specialize in absorbing water and dissolved ions.



water. (**a**,**b**) Roots of most flowering plants have an endodermis (a sheet of single cells around the vascular cylinder) and exodermis (a cell layer beneath the epidermis). (**c**) Abutting walls of cells of both layers have a waxy Casparian strip that keeps water from slipping past cells. Water must move through the cytoplasm of endodermal cells. (**d**) Transport proteins in the plasma membrane of the cells selectively control water and nutrient uptake.

O Waxy, water-impervious Casparian strip (*gold*) in abutting walls of endodermal cells that control water and nutrient uptake

moves into vascular cylinder

available for absorption. These are fragile structures that do not become roots. They grow no more than a few millimeters through soil and die after a few days. New ones form just behind the root tip (Section 29.5).

HOW ROOTS CONTROL WATER UPTAKE

Section 29.5 introduced you to the tissue organization of typical roots. Turn now to how roots carry out their absorptive function. Water molecules in soil are only weakly bound to clay particles, so they readily move across root epidermis and continue on to a column of vascular tissue. This is the root's **vascular cylinder**. A cylindrical sheet of endodermal cells is all that lies between the root cortex and the cylinder's xylem and phloem—the pipelines to the rest of the plant.

Wherever endodermal cells abut, we find a band of waxy deposits. This **Casparian strip** is a barrier to the unrestricted flow of water and solutes into the vascular cylinder. It forces water and solutes to cross only at unwaxed wall regions and through the cell. They move across the plasma membrane facing the cortex, then through cytoplasm, then across the plasma membrane facing the vascular cylinder (Figure 30.6).

Like all living cells, endodermal cells have a lot of transport proteins embedded in the plasma membrane. The proteins let some solutes but not others cross the membrane. The transport proteins of endodermal cells are control points where a plant adjusts the quantity and types of solutes absorbed from soil water.

Roots of many plants also have an **exodermis**, a cell layer just beneath their surface (Figure 30.6*a*). Walls of exodermal cells commonly have a Casparian strip that functions like the one next to the root vascular cylinder.

Root hairs, root nodules, and mycorrhizae greatly enhance a plant's uptake of water and dissolved nutrients.

Roots control the type and amount of solutes that can enter their vascular cylinder. A waxy strip seals abutting cell walls in two sheetlike layers, an endodermis and exodermis. Membrane transport proteins of these cells selectively control water and nutrient uptake. WATER MOVEMENT IN PLANTS

30.3 How Does Water Move Through Plants?

LINKS TO SECTIONS 2.4, 2.5, 29.2–29.5 By now, you have a sense of how the distribution of water and dissolved mineral ions to all living cells is central to plant growth and functioning. Turn now to a model that explains how water moves throughout the plant.

TRANSPIRATION DEFINED

Plants hold on to just a fraction of the water absorbed for growth and metabolism. Most water is lost, mainly through stomata. The evaporation of water molecules from leaves, stems, and other plant parts is a process called **transpiration**.

COHESION-TENSION THEORY

Start with a basic question: How does water move from soil, into roots, and all the way up into leaves? What gets individual water molecules to the top of plants, including redwoods and other trees that may be more than 100 meters tall?

Inside a vascular plant body, water moves through a complex tissue called xylem. Section 29.2 introduced **tracheids** and **vessel members**, the water-conducting cells of xylem. Figure 30.7 gives a closer look at their structure. These cells are dead at maturity; only ligninimpregnated walls are left behind. What this means is that xylem's conducting cells cannot be expending energy to pull water "uphill."

Some time ago, the botanist Henry Dixon came up with an explanation of how water is transported in plants. By his **cohesion-tension theory**, water inside xylem is pulled upward by air's drying power, which creates a continuous negative pressure called tension. The tension extends all the way from leaves to roots. Figure 30.8 illustrates Dixon's theory. As you review this figure, consider the following points:

First, air's drying power causes transpiration: the evaporation of water from all parts of the plant that are exposed to the air, but most notably at stomata. Transpiration puts water molecules that are inside the waterproof conducting tubes of xylem into a state of tension. The tension extends from veins inside leaves, down through the stems, and on into young roots where water is being absorbed.

Second, continuous, fluid columns of water show *cohesion*, which means that they resist breaking into droplets as they are being pulled up under tension. Remember how water shows cohesion (Section 2.5)? The collective strength of hydrogen bonds among the water molecules imparts cohesion in xylem.

perforation plate



pits in tracheid



Tracheids have tapered, unperforated end walls. Pits in adjoining tracheid walls match up.

Three adjoining members of a vessel. Thick, finely perforated walls of these dead cells connect as long vessels, another type of water-conducting tube in xylem.

Perforation plate at the end wall of one type of vessel member. Perforated ends allow water to flow unimoeded.

Figure 30.7 A few types of tracheids and vessel members from xylem. Interconnected, pitted walls of cells that died at maturity form these water-conducting tubes. The pectin-coated pits may help control water distribution to specific regions. When hydrated, the pectins swell and close off water flow. During droughts, they shrink, and water moves freely through open pits toward leaves.



mesophyll (photosynthetic cells) vein

Cohesion in root, stem, leaf xylem plus water uptake in growth regions

vascular cylinder endodermis cortex water molecule root hair cell



C For as long as water molecules continue to escape by transpiration, that tension will drive the uptake of replacements from soil water.

Ongoing water uptake at roots

Third, for as long as individual molecules of water escape from a plant, the continuous tension inside the xylem permits more molecules to be pulled upward from the roots, and therefore to replace them.

Figure 30.8 Animated! Key points of the cohesion-

tension theory of water transport in vascular plants.

Hydrogen bonds are strong enough to hold water molecules together inside the water-conducting tubes of xylem. However, the bonds are not strong enough to stop the water molecules from breaking away from one another during transpiration and then escaping from leaves, through stomata.

Air's drying power causes transpiration: the evaporation of water from plant parts, especially through stomata.

By a cohesion-tension theory, transpiration puts water in xylem in a state of tension from leaf veins down to roots where water is being absorbed.

As transpiration pulls continuous, fluid columns of water upward, collective strength of hydrogen bonds between water molecules resists rupturing under the tension.

Transpiration is the evaporation of water molecules from aboveground plant parts, especially at stomata. The process

upper epidermis

WATER LOSS VERSUS GAS EXCHANGE

30.4 How Do Stems and Leaves Conserve Water?

LINKS TO SECTIONS 5.5, 7.7, 7.8, 18.9, 23.2 At least 90 percent of the water transported from roots to a leaf evaporates right out. Only about 2 percent gets used in photosynthesis, membrane functions, and other activities, but that amount must be maintained.

Think of a young plant cell. As it grows, water diffuses in and exerts turgor pressure on its soft primary wall (Section 5.5). The wall—and the cell—expands until turgor pressure is enough to counter osmotic pressure, or the tendency of water to follow its concentration gradient and diffuse into the cell. When soil dries or gets too salty, the balance can tilt badly (Section 18.9 and Figure 30.9). However, plants are not entirely at the mercy of their surroundings. They have a cuticle, and they have stomata.

THE WATER-CONSERVING CUTICLE

Even mildly water-stressed plants would wilt and die without a cuticle (Figure 30.10). Epidermal cells secrete this translucent, water-impermeable layer, which coats cell walls exposed to air. Cuticle is made of waxes,



Figure 30.9 Plant wilting. When a plant with soft green leaves is growing well, the soil water is dilute (hypotonic) compared to fluids in its living cells. Water moves osmotically into its cells, and internal fluid pressure builds up against the cell walls. Water also is squeezed out when this turgor becomes great enough to counter the attractive force of cytoplasmic fluid. (Cytoplasm usually has more solutes compared to soil water.)

In soft, erect plant parts, as much water is moving into cells as is moving out. The constant pressure keeps cells plump. When the soil dries or gets too salty, water's concentration gradient reverses and the cells lose water. Osmotically induced shrinkage of cytoplasm in the young cells results in wilting.

(a) Cells from an iris petal, plump with water. Their cytoplasm and central vacuole extend to the cell wall. (b) Cells from a wilted iris petal. The loss of turgor pressure resulted in plasmolysis; their cytoplasm and central vacuole shrank, and the plasma membrane moved away from the wall.

pectin, and fibers of cellulose embedded in cutin, an insoluble lipid polymer. A cuticle does not stop rays of light from reaching photosynthetic tissues. It does restrict water loss. It also restricts the *inward* diffusion of carbon dioxide necessary for photosynthesis, and *outward* diffusion of oxygen formed as a by-product.

CONTROLLED WATER LOSS AT STOMATA

Photosynthesis in plants requires carbon dioxide and releases free oxygen (Section 7.7). Both gases diffuse across cuticle-covered epidermis at small, collapsible openings called stomata (singular, stoma). Water also moves out, but when soil holds enough water, roots can replace the losses. Stomata of most plants close at night; CAM plants are exceptions (Section 7.7). Water is conserved, and carbon dioxide collects in leaves as cells make ATP by way of aerobic respiration.

A pair of specialized parenchyma cells define each stoma; we call them guard cells (Figure 30.11). When the pair swell with incoming water, they bend slightly and move apart. The gap between them is the stoma. When the pair lose water, the loss in turgor lets their cell walls collapse against each other, so the gap closes.

Whether stomata are open or closed is influenced by several cues, such as carbon dioxide's concentration inside a leaf, incoming light, and temperature. For example, photosynthesis starts after the sun comes up. As the morning progresses, carbon dioxide levels fall in all photosynthetic cells, including guard cells. The decrease stimulates active transport of potassium ions into guard cells. Blue light, another cue, activates kinases in each guard cell's plasma membrane. These



Figure 30.10 Upper and lower cuticle on a basswood leaf.



Figure 30.11 Stomata in action. Whether a stoma is open or closed at any given time depends on the shape of two guard cells that define this small gap across a cuticle-covered leaf epidermis. (a) This stoma is open. High turgor pressure in the guard cells caused them to bulge outward, which opened a gap between the paired cells. (b) This stoma is closed. Water diffused out of the guard cells, which caused them to collapse against each other and close the gap between them.

enzymes cause potassium ions to flow into the guard cells. Water follows the ions, and the stoma opens.

A water-stressed plant closes stomata in response to the hormone abscisic acid (ABA). Remember the Section 28.5 preview of signal reception, transduction, and response? ABA is a signal. It binds to receptors on a guard cell's plasma membrane, which causes gated channels across the membrane to open. Calcium ions flow into the cells. They cause other channels to open, so potassium ions and other substances flow out from the cytoplasm. When many ions leave, water follows its gradient and moves out of the guard cells. As the water exits, the stoma closes. It opens as potassium ions move back into the guard cells (Figure 30.12).

As this section makes clear, plant survival depends on stomatal function. Think about it when you are out and about on smog-shrouded days (Figure 30.13).

Water-dependent events in plants are severely disrupted when water loss exceeds uptake at roots for extended periods. Wilting is one observable outcome.

Transpiration and gas exchange occur mainly at stomata. These numerous small openings span all plant epidermal surfaces exposed to air, including the waxy cuticle.

Plants open and close stomata at different times to control water loss, carbon dioxide uptake, and oxygen disposal, all of which affect rates of photosynthesis and plant growth.



Figure 30.12 Hormonal control of stomatal closure. (**a**) When a stoma is open, high solute concentrations in the cytoplasm of both guard cells have raised the turgor pressure, which keeps both cells plump. (**b**) In a water-stressed plant, the hormone abscisic acid binds to receptors on the guard cell plasma membrane. It activates a signal transduction pathway that lowers the solute concentrations in the cells, which lowers the turgor pressure and causes the stoma to close.



Figure 30.13 (a) Smog in Central Europe. (b) Stomata at a holly leaf surface. (c) A holly plant growing in industrialized regions becomes covered with gritty airborne pollutants that clog stomata and prevent sunlight from reaching photosynthetic cells in the leaf.

SUGAR DISTRIBUTION THROUGH PLANTS

30.5 How Do Organic Compounds Move Through Plants?

LINKS TO SECTIONS 5.4, 5.5, 7.7, 29.2 *Xylem distributes water and minerals through plants. The vascular tissue called phloem distributes organic products of photosynthesis.*

CONDUCTING TUBES IN PHLOEM

Phloem is a vascular tissue having organized arrays of conducting tubes, fibers, and strands of parenchyma cells. Unlike xylem, it has **sieve tubes** through which organic compounds rapidly flow. *Living* cells form the long tubes, the cells of which are positioned side by side and end to end. Their abutting end walls, called



one of a series of living cells that abut, end to end, and form a sieve tube

companion cell (in the background, pressed right against the sieve tube)

perforated end plate of sieve tube cell, of the sort shown in (**b**)

Figure 30.14 (a) Part of

a sieve tube inside phloem. Arrows point to perforated ends of individual tube members. (**b**) Scanning electron micrograph of the sieve plate on the end of two side-by-side sieve tube members. sieve plates, are porous (Figure 30.14*a*,*b*). **Companion cells** are pressed against the tubes. These cells help load organic compounds into neighboring sieve tubes by active transport mechanisms.

Some organic products of photosynthesis are used in leaf cells that make them. The rest move to roots, stems, buds, flowers, and fruits (Section 7.7). Starch is the main carbohydrate storage form. Starch molecules are too big for transport across the plasma membrane of cells and too insoluble for transport. Cells convert them to sucrose, which is more easily transportable.

Experiments with insects show that sucrose is the main carbohydrate transported in phloem. Aphids were anesthetized by exposing them to high levels of carbon dioxide while they were feeding on the juices inside phloem's conducting tubes (Figure 30.15). Then researchers detached the body from the mouthparts, which they left attached to the plant. They collected and analyzed the exuded fluid. For most of the plants studied, sucrose was the most abundant carbohydrate in the fluid that was being forced out of the tubes.

TRANSLOCATION

Translocation is the formal name for the process that moves sucrose and other organic compounds through phloem. High fluid pressure drives the movement (Section 5.5). The pressure in phloem's conducting tubes is often five times higher than the air pressure inside an automobile tire.

Phloem translocates photosynthetic products along declining pressure and solute concentration gradients. The *source* of the flow is any region of the plant where organic compounds are being loaded into sieve tubes. Common sources are mesophylls—the photosynthetic



Figure 30.15 Honeydew exuding from an aphid after this insect's mouthparts penetrated a sieve tube. High pressure in phloem forced this droplet of sugary fluid out through the terminal opening of the aphid gut.



Figure 30.16 *Animated!* Translocation of organic compounds. Review Section 7.7 to get an idea of how translocation relates to photosynthesis in vascular plants.

tissues in leaves. The flow ends at a *sink*, which is any plant region where products are being used or stored. For instance, while flowers and fruits are forming, on the plant, they are sink regions.

Why do organic compounds flow from a source to a sink? According to the **pressure flow theory**, internal pressure builds up at the source end of the sieve tube system and *pushes* the solute-rich solution on toward any sink, where solutes are being removed.

Use Figure 30.16 to track what happens to sucrose as it moves from the photosynthetic cells into small leaf veins. By energy-requiring reactions, companion cells in veins load sucrose into sieve tube members. When the sucrose concentration increases in the tubes, water also moves into them, by osmosis. The rising Typical sink region Actively growing cells in a young root

fluid volume exerts more pressure on the wall of sieve tubes. With sufficient turgor pressure, sucrose-laden fluid inside the tubes is forced out of the leaf, into the stem, and on toward the sink.

Plants store carbohydrates as starch but distribute them in the form of sucrose and other small, water-soluble units.

Translocation is the distribution of organic compounds to different plant regions. It depends on concentration and pressure gradients in the sieve tube system of phloem.

Gradients last as long as companion cells load compounds into sieve tubes at sources, such as mature leaves, and as long as compounds are unloaded at sinks, such as roots.

http://biology.brookscole.com/starr11

Summary

Section 30.1 Plant nutrition requires water, mineral ions, and carbon dioxide. Mineral-laden water and the products of photosynthesis are distributed throughout the plant (Figure 30.17). Nutrients are essential elements; no other element can perform their metabolic functions.

Plants obtain nine macronutrients (such as carbon, oxygen, hydrogen, nitrogen, and phosphorus) and at least seven micronutrients (such as iron) from air, water, and soil. The properties of a given soil greatly affect the accessibility of water, oxygen, and nutrients to plants.

Section 30.2 Roots absorb water and nutrients that often are scarce in soil. Root hairs greatly increase their absorptive surface. Fungi are mutualists with young roots in mycorrhizae. Certain bacteria in root nodules are mutualists with plants. In both cases, the symbionts give up some dissolved mineral ions to the plant, which gives up some products of photosynthesis in return.

Roots exert some control over absorption. A waxy Casparian strip seals abutting walls of endodermal (and exodermal) cells that form one-cell thick cylinder inside roots. Water and dissolved mineral ions cannot reach the vascular cylinder for distribution through the plant without moving through the cytoplasm of endodermal cells. Their inward diffusion is controlled to a large extent at active transport proteins in cell membranes.

Biology SNow

See how vascular plant roots control nutrient uptake with the animation on BiologyNow.

Section 30.3 Plants distribute nutrient-laden water through tracheids and vessel members of the vascular tissue called xylem. Both cell types are dead at maturity, but their interconnected walls form narrow pipelines.

Transpiration is the evaporation of water from plant parts, mainly at stomata, into air. A cohesion-tension theory explains it as a force that pulls water upward through xylem by causing continuous negative pressure (tension) from leaves to roots. Water molecules escape from leaves, but more are pulled into the leaf under tension. Collectively, hydrogen bonds among water molecules resist rupturing; they impart cohesion, so water is pulled upward as continuous fluid columns.



Figure 30.17 Summary of interdependent processes that sustain plant growth. All living cells in plants require at least sixteen nutrients. They all produce ATP, which drives metabolic activities.

Biology 🔊 Now

Learn about water transport in vascular plants with the animation on BiologyNow. Read the InfoTrac article "How Plants Get High," Adam Summers, Natural History, March 2005.

Section 30.4 A cuticle is a waxy, waterproof cover on all plant parts in contact with the surroundings. It helps the plant conserve water on hot, dry days.

Gas exchange and transpiration occur at stomata, openings across the cuticle-covered epidermis of leaves and many stems. In response to environmental cues, ions and water move into and out of paired guard cells, which alternately plump up or collapse against each other, opening and closing the gap between them. When stomata are open, they permit gas exchange. Plants conserve water when stomata are closed.

Section 30.5 By an energy-requiring process called translocation, sucrose and other organic compounds are distributed throughout plants. Sucrose produced by photosynthesis is loaded into vessels of phloem with the help of companion cells. It is then unloaded at the plant's actively growing regions or at storage regions.

Biology 🔊 Now

Observe how vascular plants distribute organic compounds with the animation on BiologyNow.

Sel	f-Quiz	

Answers in Appendix II

1. Carbon, hydrogen, and oxygen are examples of ______ for plants.

a. macronutrients	d. essential elements
b. micronutrients	e. both a and d
c. trace elements	

2. A ______ strip between abutting endodermal cell walls forces water and solutes to move through these cells rather than around them.

a. cutin c. Casparian b. lignin d. cellulose

3. The nutrition of some plants depends on a root–fungus association known as a ______.

a. root nodule	c. root hair
b. mycorrhiza	d. root hypha

- Water evaporation from plant parts is called ______.
 a. translocation c. transpiration
 b. expiration d. tension

b. differences in source and sink solute concentrations c. the pumping force of xylem vessels

- d. cohesion-tension among water molecules
- 6. In daytime, most plants lose _____ and take up _____
 a. water; carbon dioxide c. oxygen; water
 b water; oxygen d. carbon dioxide; water
- 7. At night, most plants conserve _____, and _____ accumulates.

a. carbon dioxide; oxygen c. oxygen; water b. water; oxygen d. water; carbon dioxide



epidermal gland base of epidermal hairlike trigger

8. Match the concepts of plant nutrition and transport.

- stomata
 - nutrient b. harvesting soil nutrients c. balance water loss with carbon
- sink
- root system
- hydrogen
 - bonds
- _ translocation
- e. sugars unloaded from sieve tubes transpiration f. organic compounds distributed through the plant body

a. evaporation from plant parts

g. element with roles in metabolism

dioxide requirements d. cohesion in water transport

that no other element can fulfill

Additional questions are available on **Biology** (S) Now

Critical Thinking

1. Home gardeners, like farmers, must be sure that their plants have access to nitrogen from either nitrogen-fixing bacteria or fertilizer. Insufficient nitrogen stunts plant growth; leaves yellow and then die. Which biological molecules incorporate nitrogen? How would nitrogen deficiency affect biosynthesis and cause these symptoms?

2. You just returned home from a three-day vacation. Your severely wilted plants tell you they weren't watered before you left. Being aware of the cohesion-tension theory of water transport, explain what happened to them.

3. When moving a plant from one location to another, it helps to include some native soil around the roots. Explain why, in terms of mycorrhizae and root hairs.



4. In the sketch at *left*, label the stoma. Now think about Cody, who discovered a way to keep all of a plant's stomata open at all times. He also figured out how to keep those of another plant closed all the time. Both plants died. Explain why.

5. Allen is studying the rate of transpiration from tomato plant leaves. He notices that several environmental factors, including wind and relative humidity, affect the rate. Explain how they might do so.

6. The Venus flytrap (Dionaea muscipula) is a flowering plant native to bogs of North and South Carolina. Its twolobed, spine-fringed leaves open and close like a steel trap (Figure 30.18a-d). Like all other plants, it cannot grow well without nitrogen and other nutrients, which are scarce in bogs. Plenty of insects fly in from places around the bogs.

Epidermal glands on its leaf surfaces secrete sticky sugars that attract insects. As insects land, they brush Figure 30.18 (a) Venus flytrap (*Dionaea muscipula*), a carnivorous plant. (b) A fly stuck in sugary goo on a lobed leaf. (c) It brushes against hairlike triggers that activate the leaf, which snaps shut in half a second. (d) While a trap is open, mesophyll cells below the epidermis are compressed. Spring the trap and turgor pressure abruptly decompresses the cells. Whoosh!

against hairlike structures-triggers for the trap. When an insect touches two hairs at the same time or the same hair twice in rapid succession, the two lobes of the leaf snap shut. Digestive juices pour out from leaf cells, pool around the insect, and dissolve the prey. This plant makes its own nutrient-rich water, which it proceeds to absorb!

The Venus flytrap is only one of several species of carnivorous plants. Their mode of nutrient acquisition is a form of extracellular digestion and absorption. Not all carnivorous plants actively spring traps. Some have fluidfilled traps into which prey slip, slide, or fall and then simply drown. Given the variety and numbers of insects and other animals that attack plants, you can just imagine how endearing the carnivorous plants are to botanists. With their plucky modes of nutrition, these plants also can give you glimpses into the diversity of adaptations by which plants function in their environment.

All carnivorous plants evolved in habitats where nitrogen and other nutrients are hard to come by. They take hold even in shallow freshwater lakes and streams, which have only dilute concentrations of dissolved minerals. Insects and other small invertebrates are fair game, and so is the occasional tiny amphibian.

As a class activity, divide into research groups, each focusing on one genera of the carnivorous plants listed below. Gather data on the number of known species, their distribution, abiotic and biotic conditions in their habitats, the type and numbers of prey captured in a given interval, and mechanisms by which they capture prey. Note whether one or more species in the genera are threatened or endangered. If so, note possible causes. Present an oral or written report of your findings.

Byblis Rainbow plant Cephalotus Western Australian pitcher plant Darlingtonia Cobra lily Dionaea Venus flytrap Drosera Sundews Drosophyllum Dewy pine Nepenthes Monkey cup (Tropical pitcher plants) Pinguicula Butterworts Sarrecenia North American pitcher plants Utricularia Bladderworts