Water and Mineral Movement

Water and Mineral Movement through the Xylem

It is clear that root pressure is insufficient to push water to the top of a tall tree, although it can help. So, what does work? Otto Renner proposed the solution in Germany in 1911. Passage of air across leaf surfaces results in loss of water by evaporation, creating a pull at the open upper end of the "tube." Evaporation from the leaves produces a tension on the entire water column that extends all the way down to the roots. Water has an inherent tensile strength that arises from the cohesion of its molecules, their tendency to form hydrogen bonds with one another. The tensile strength of a column of water varies inversely with the diameter of the column; that is, the smaller the diameter of the column, the greater the tensile strength. Because plants have transporting vessels of very narrow diameter, the cohesive forces in them are strong. The water molecules also adhere to the sides of the tracheid or xylem vessels, further stabilizing the long column of water.

The water column would fail if air bubbles were inserted (visualize a tower of blocks and then pull one out in the middle). Anatomical adaptations decrease the probability of this. Individual tracheids and vessel members are connected by one of more *pits* (cavities) in their walls. Air bubbles are generally larger than the openings, so they cannot pass through them. Furthermore, the cohesive force of water is so great that the bubbles are forced into rigid spheres that have no plasticity and therefore cannot squeeze through the openings. Deformed cells or freezing can cause small bubbles of air to form within xylem cells. Any bubbles that do form are limited to the xylem elements where they originate, and water may continue to rise in parallel columns. This is more likely to occur with seasonal temperature changes. As a result, most of the active xylem in woody plants occurs peripherally, toward the vascular cambium.

Most minerals the plant needs enter the root through active transport. Ultimately, they are removed from the roots and relocated through the xylem to other metabolically active parts of the plant. Phosphorus, potassium, nitrogen, and sometimes iron may be abundant in the xylem during certain seasons. In many plants, such a pattern of ionic concentration helps to conserve these essential nutrients, which may move from mature deciduous parts such as leaves and twigs to areas of active growth. Keep in mind that minerals that are relocated via the xylem must move with the generally upward flow through the xylem. Not all minerals can re-enter the xylem conduit. Calcium, an essential nutrient, cannot be transported elsewhere once it has been deposited in plant parts.

Transpiration of Water from Leaves

More than 90% of the water taken in by the roots of a plant is ultimately lost to the atmosphere through transpiration from the leaves. Water moves into the pockets of air in the leaf from the moist surfaces of the walls of the mesophyll cells. As you saw in chapter 38, these intercellular spaces are in contact with the air outside of the leaf by way of the stomata. Water that evaporates from the surfaces of the mesophyll cells leaves the stomata as vapor. This water is continuously replenished from the tips of the veinlets in the leaves.

Water is essential for plant metabolism, but is continuously being lost to the atmosphere through the stomata. Photosynthesis requires a supply of CO_2 entering the stomata from the atmosphere. This results in two somewhat conflicting requirements: the need to minimize the loss of water to the atmosphere and the need to admit carbon dioxide. Structural features such as stomata and the cuticle have evolved in response to one or both of these requirements.

The rate of transpiration depends on weather conditions like humidity and the time of day. After the sun sets, transpiration from the leaves decreases. The sun is the ultimate source of potential energy for water movement. The water potential that is responsible for water movement is largely the product of negative pressure generated by transpiration, which is driven by the warming effects of sunlight.

The Regulation of Transpiration Rate. On a short-term basis, closing the stomata can control water loss. This occurs in many plants when they are subjected to water stress. However, the stomata must be open at least part of the time so that CO_2 can enter. As CO_2 enters the intercellular spaces, it dissolves in water before entering the plant's cells. The gas dissolves mainly in water on the walls of the intercellular spaces below the stomata. The continuous stream of water that reaches the leaves from the roots keeps these walls moist. A plant must respond both to the need to conserve water and to the need to admit CO_2.

Stomata open and close because of changes in the turgor pressure of their guard cells. The sausage- or dumbbell-shaped guard cells stand out from other epidermal cells not only because of their shape, but also because they are the only epidermal cells containing chloroplasts. Their distinctive wall construction, which is thicker on the inside and thinner elsewhere, results in a bulging out and bowing when they become turgid. You can make a model of this for yourself by taking two elongated balloons, tying the closed ends together, and inflating both balloons slightly. When you hold the two open ends together, there should be very little space between the two balloons. Now place

39.4 Dissolved sugars and hormones are transported in the phloem.

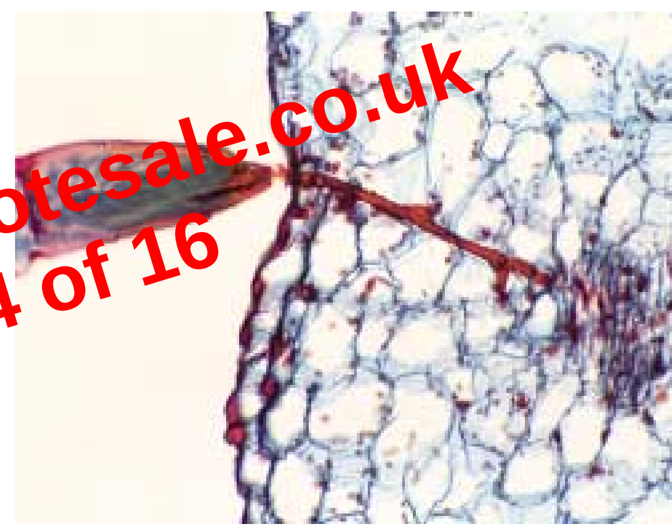
Phloem Transport Is Bidirectional

Most carbohydrates manufactured in leaves and other green parts are distributed through the phloem to the rest of the plant. This process, known as **translocation,** is responsible for the availability of suitable carbohydrate building blocks in roots and other actively growing regions of the plant. Carbohydrates concentrated in storage organs such as tubers, often in the form of starch, are also converted into transportable molecules, such as sucrose, and moved through the phloem. The pathway that sugars and other substances travel within the plant has been demonstrated precisely by using radioactive tracers, despite the fact that living phloem is delicate and the process of transport within it is easily disturbed. Radioactive carbon dioxide ($^{14}CO_2$) gets incorporated into glucose as a result of photosynthesis. The glucose is used to make sucrose, which is transported in the phloem. Such studies have shown that sucrose moves both up and down in the phloem.

Aphids, a group of insects that extract plant sap for food, have been valuable tools in understanding translocation. Aphids thrust their *stylets* (piercing mouthparts) into phloem cells of leaves and stems to obtain abundant sugars there. When a feeding aphid is removed by cutting its stylet, the liquid from the phloem continues to flow through the detached mouthpart and is thus available in pure form for analysis (figure 39.16). The liquid in the phloem contains 10 to 25% dry matter, almost all of which is sucrose. Using aphids to obtain the critical samples and radioactive tracers to mark them, it has been demonstrated that movement of substances in phloem can be remarkably fast; rates of 50 to 100 centimeters per hour have been measured.

While the primary focus of this chapter is on nutrient and water transport, it is important to note that phloem also transports plant hormones. As we will explore in the next chapter, environmental signals can result in the rapid translocation of hormones in the plant.

(a)



(a)

FIGURE 39.16
Feeding on phloem. (*a*) Aphids, like this individual of *Macrosiphon rosae* shown here on the edge of a rose leaf, feed on the food-rich contents of the phloem, which they extract through their piercing mouthparts (*b*), called stylets. When an aphid is separated from its stylet and the cut stylet is left in the plant, the phloem fluid oozes out of it and can then be collected and analyzed.

Energy Requirements for Phloem Transport

The most widely accepted model of how carbohydrates in solution move through the phloem has been called the **mass-flow hypothesis, pressure flow hypothesis,** or **bulk flow hypothesis.** Experimental evidence supports much of this model. Dissolved carbohydrates flow from a **source** and are released at a **sink** where they are utilized. Carbohydrate sources include photosynthetic tissues, such as the mesophyll of leaves, and food-storage tissues, such as the cortex of roots. Sinks occur primarily at the growing tips of roots and stems and in developing fruits.

In a process known as *phloem loading*, carbohydrates (mostly sucrose) enter the sieve tubes in the smallest veinlets at the source. This is an energy-requiring step, as active transport is needed. Companion cells and parenchyma cells adjacent to the sieve tubes provide the ATP energy to drive this transport. Then, because of the