2C. Long-Distance Transport of Assimilates

1. Introduction

The evolution of cell walls allowed plants to solve the problem of osmoregulation in freshwater environments; however, cell walls restrict motility and place constraints on the evolution of long-distance transport systems. Tissues are too rigid for a heart-pump mechanism; instead, higher plants have two systems for long-distance transport. The dead elements of the xylem allow transport of water and solutes between sites of different water potentials. That transport system is dealt with in Chapter 3 on plant water relations. The other transport system, the phloem, allows the mass flow of carbohydrates and other solutes from a **source** region, where the **hydrostatic pressure** in the phloem is relatively high, to a **sink** region with lower pressure.

Plants differ markedly in the manner in which the products of photosynthesis pass from the mesophyll cells to the sieve tubes (**phloem loading**) through which they are then transported to a site where they are unloaded and metabolized (Fig. 1). Plants also differ with respect to the major carbon-containing compounds that occur in the sieve tubes, which is the complex consisting of sieve elements and companion cells. For reasons that are explained in this chapter, there is a close association between the type of phloem loading (symplastic or apoplastic) and the type of major carbon compound (sucrose or oligosaccharides) transported in the phloem. Sucrose is a sugar composed of two hexose units, whereas an oligosaccharide comprises more than two units. In addition, there appears to be an association between the pattern of phloem loading (symplastic vs. apoplastic) and the ecological distribution of species and between phloem structure and plant habit (vine vs. tree or shrub). It is this association between phloem transport and ecological adaptation that we explore in this chapter.

2. Major Transport Compounds in the Phloem: Why Not Glucose?

In animals, glucose is the predominant transport sugar, albeit at much lower concentrations than those of predominant sugars in the sieve tubes of higher plants. In plants, **sucrose** is a major constituent of phloem sap, whereas glucose and other monosaccharides are found only in trace concentrations. Why not glucose?

A comparison of the physical properties of glucose and sucrose does not provide a compelling reason for the predominance of sucrose. A good long-distance transport compound, however, should be **nonreducing**, so as to avoid a nonenzymatic reaction with proteins or other compounds during its transport. This excludes compounds

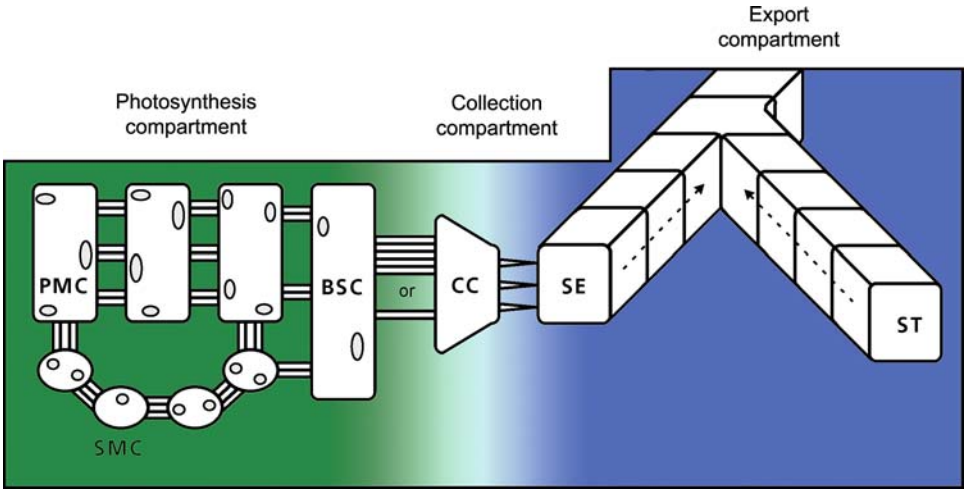

FIGURE 1. Sucrose and other products of photosynthesis (photosynthates) are generated in palisade (PMC) and spongy (SMC) mesophyll cells. They are either symplastically (top) or apoplastically (bottom) moved to the companion cells (CC) and/or sieve elements (SE) of the minor vein phloem and are subsequently exported to sink regions of the plant. Plasmodesmata connect all cell types, but the roles they play in the various transport steps differ in different species. In particular, the number of plasmodesmata connecting bundle sheath cells (BSC) to companion cells varies greatly. In some plants there are many, as depicted at the top. In others there are relatively few, as shown at the bottom. The ultrastructure and biochemistry of the companion cells in minor veins also differs considerably in different plants, an indication of different loading strategies (as discussed in the text). The plasmodesmata between companion cells and sieve elements are especially wide and accommodate the passage of much larger molecules. Once inside the sieve elements, photosynthates are carried away in the export stream. The minor veins merge to create larger veins with connected sieve tubes (ST). Though not depicted here, all sieve elements have adjoining companion cells.

such as glucose and fructose, which contain an aldehyde group, which is readily oxidized to a carboxylic acid group; hence they are known as **reducing sugars**. A good transport compound should also be protected from enzymatic attack until it arrives at its destination. In this way the flow of carbon in plants can be controlled by the presence of key hydrolyzing enzymes in appropriate sink tissues. Thus, **sucrose** appears to be a preferred compound because it is "**protected**".

Other "protected" sugars include the oligosaccharides of the raffinose family: raffinose, stachyose, verbascose. These sugars are formed by the addition of one, two or three galactose molecules to a sucrose molecule (Fig. 2). They are major transport sugars in a wide range of species. Other transport compounds are the sugar alcohols (sorbitol, mannitol, dulcitol) (Fig. 2), e.g., in Apiaceae [e.g., *Apium graveolens* (celery)], Rosaceae [e.g., *Prunus persica* (peach)], Combretaceae, Celastraceae, and Plantaginaceae, and oligofructans [e.g., in *Agave deserti* (century plant)] (Wang & Nobel 1998). Despite the diversity in composition of the phloem transport fluid among species, nearly all species are similar in their very low concentrations of monosaccharides (glucose, fructose) (Turgeon 1995).

In addition to sugars, phloem sap contains a range of organic acids, amino acids, and inorganic ions. Concentrations of Ca, Fe, and Mn in the phloem sap are invariably low; this may be related to the fact that these nutrients tend to precipitate at the relatively **high pH** that characterizes phloem sap (Fig. 6.1B in Chapter 6 on mineral nutrition). As a result, growing leaves and fruits must predominantly import these nutrients via the xylem. If the Ca concentrations in the xylem sap and the transpiration rates are low, some fruits [e.g., of *Solanum lycopersicum* (tomato) and *Capsicum annuum* (capsicum)] may show Ca-deficiency symptoms (Marschner 1995). Similarly, legume seeds may show seed disorders when the import of Mn becomes too low, and calcifuge species show yellowing of their youngest leaves, due to a restricted uptake of Fe at high soil pH (Sect. 2.2.6 of Chapter 6 on mineral nutrition). That is, plant organs that predominantly import specific nutrients via the xylem may show **deficiency symptoms** when transpiration rates are low, when the concentration of

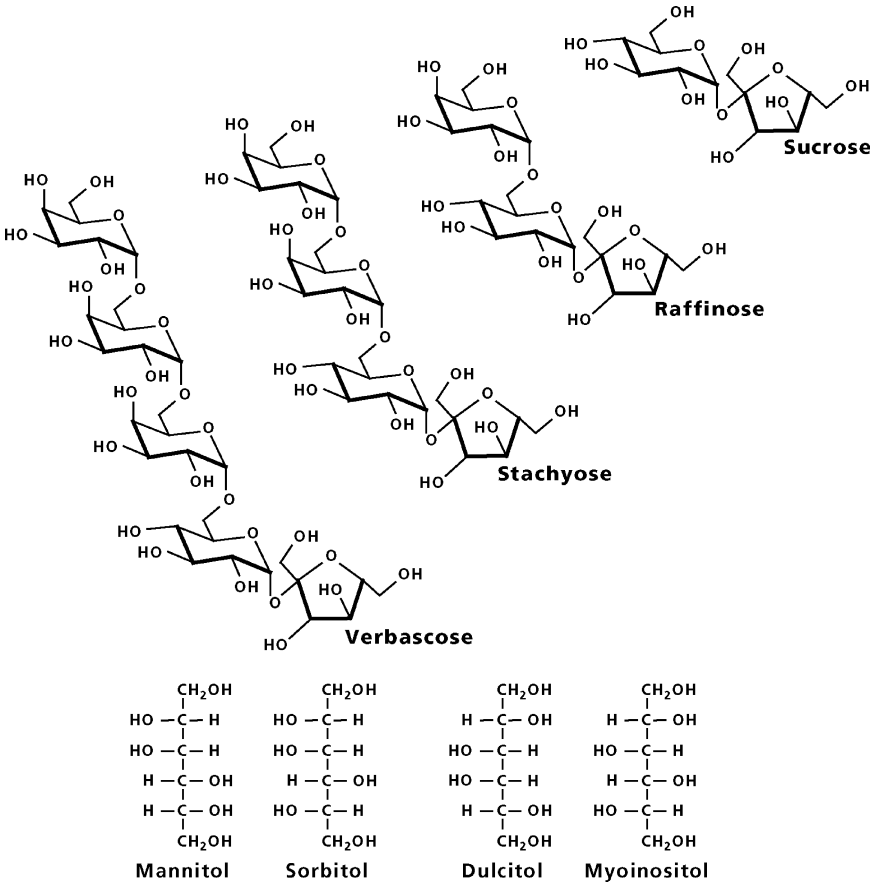

FIGURE 2. The chemical structure of the major sugars and some sugar alcohols transported in sieve tubes. Note that not all of these compounds occur in the phloem sap of every species.

these specific nutrients in the xylem is very low, due to restricted uptake, or both.

Most plant viruses can also move over long distances in the phloem (e.g., Roberts et al. 1997). Moreover, alarm signals involved in induced systemic resistance, hormones, and microRNA (miRNA) molecules, which are a class of developmental signaling molecules, are also transported via the phloem (Van Bel 2003, Juarez et al. 2004, Lough & Lucas 2006).

3. Phloem Structure and Function

In the process of transporting assimilates from the site of their synthesis (the **source**) to the site where they are used (the **sink**), the products of photosynthesis must move from the mesophyll cells to the transport system: the **sieve elements**. Sieve elements are living cells with characteristic sieve areas in their cell walls. When pores connect adjacent cells, they are commonly differentiated into **sieve plates**, with pores ranging in diameter from 1–15 μm.

In the gymnosperm *Sequoiadendron giganteum* (giant redwood) the source-sink distance of the phloem path can be as much as 110 m, due to the enormous height of the tree. This example is extreme, because sinks mostly receive assimilates from adjacent source leaves, but it illustrates the point that transport sometimes occurs over vast distances, for example to growing root tips far removed from source leaves. Long-distance transport in the phloem occurs by **mass flow**, driven by a difference in **hydrostatic pressure**, created by phloem loading in source leaves and unloading processes in sink tissues.

When sieve tubes are damaged and the pressure declines, sieve plates tend to be blocked. Short-term sealing mechanisms are triggered by Ca and involve

proteins, e.g., **forisomes** in legumes (Furch et al. 2007). Long-term sealing involves blocking with a glucose polymer, **callose**.

3.1 Symplastic and Apoplastic Transport

How are the products of photosynthesis in the mesophyll loaded into the sieve tubes? There are two ways in which solutes can pass from one plant cell to another. One is through **plasmodesmata**. This is known as symplastic (or symplasmic) transport. (The **symplast** is the internal space of cells, surrounded by plasma membranes. Since plasmodesmata are lined by the plasma membrane, cells connected by plasmodesmata form a symplastic continuum.) Solute passage through plasmodesmatal channels is passive, unassisted by proteins that mediate active transport. Therefore, symplastic transport cannot, by itself, establish a solute concentration gradient.

The second route available for solute movement from one cell to another is through the apoplast. (The **apoplast** is the space outside the plasma membranes, including the cell walls and the xylem conduits.) If solute molecules originate inside cells, as photosynthates do, then apoplastic (or apoplasmic) transport involves release of the solute from the symplast into the cell wall space, followed by uptake into recipient cells. The uptake step may involve specific transporters located in the plasma membrane, and often occurs against a concentration gradient. In some cells that are responsible for high solute flux the walls are invaginated to increase the surface area of the plasma membrane and uptake capacity. These are known as **transfer cells** (Offler et al. 2003). Uptake may also occur nonselectively by endocytosis (Samaj et al. 2004).

Since the solute concentration of the phloem is often much higher than that of the mesophyll tissue, it is not surprising that, in many plants, sucrose is loaded into the phloem from the apoplast. However, in other plants, photoassimilate molecules follow an entirely symplastic pathway into the phloem (Sect. 3.3).

3.2 Minor Vein Anatomy

The veins in leaves of dicotyledonous species branch progressively to form a reticulate network. Up to six or seven branching classes (orders) can be recognized in some species. The largest vein is the **midrib** (class I) and the smallest few classes are called **minor veins**. Minor veins are much more extensive than the major veins, and thoroughly permeate the mesophyll tissue. Few mesophyll cells are more than 6 or 8 cells away from a minor vein. Clearly, the minor venation is responsible for most, if not all, phloem loading of photoassimilates.

Since structure is often a meaningful guide to function, the comparative anatomy of the minor veins should provide clues to the mechanisms of

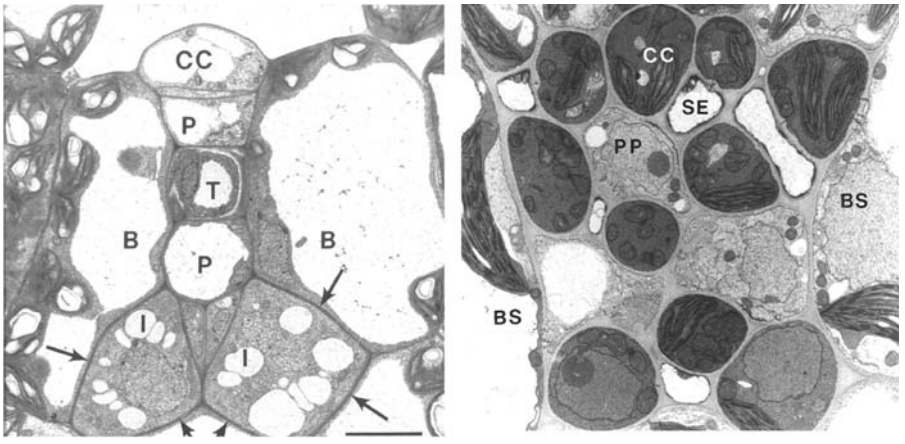

FIGURE 3. (*Left*) Minor vein from sink-source transition region of a leaf of *Cucumis melo* (melon). Abaxial phloem contains two intermediary cells (I) and immature sieve elements (not labeled) adjacent to a parenchyma cell (P). The interface of intermediary cells and bundle-sheath cells is indicated by *arrows*. A developing tracheid (T) and adaxial companion cell (CC) with its immature sieve element (not labeled) are also present. Bar = 5 μm (Volk et al. 1996). (*Right*) Transverse section of a typical *Arabidopsis thaliana* (thale cress) minor vein, with five sieve elements. BS, bundle sheath cell; CC, companion cell; PP, phloem parenchyma cell; SE, sieve element; T, tracheary element; VP, vascular parenchyma cell. Bar = 2 μm (Haritatos et al. 2000).

the loading process in different species. Gamalei (1989, 1991) studied the minor-vein anatomy of over 1000 higher plant species. He recognized different degrees of **plasmodesmatal connectivity** between the mesophyll cells and the minor vein phloem in different species. In the herb *Senecio vernalis* (eastern groundsel) the frequency is around 0.03 plasmodesmata μm^{-2} interface area, against 60 in the tree *Fraxinus ornus* (manna ash). Gamalei grouped plants into arbitrarily defined types. **Type 1** plants exhibit about three orders of magnitude more plasmodesmatal contacts than **type 2,** while intermediates between the two extremes (types 1-2a) differ by about one to two orders of magnitude in plasmodesmatal frequency. Within Gamalei's types there are subgroups. Type 1 plants with the highest plasmodesmatal counts have specialized **companion cells** known as **intermediary cells** (Fig. 3). Intermediary cells are especially large, with many small vacuoles and extremely large numbers of asymmetrically branched plasmodesmata connecting them to bundle sheath cells. They are so different in many respects from the rest of the type 1 plants that they should probably be treated as a separate group. Type 2 is also heterogeneous. Type 2a **companion cells** have smooth cell walls, whereas those of type 2b have **transfer cells** with highly invaginated plasma membranes (Fig. 3).

Plasmodesmatal frequency is often a strong family characteristic; for example, all studied species in the Magnoliaceae (magnolia family) are type 1, those in the Aceraceae (maple family) are type 1-2a; and those in the Liliaceae (lily family) are type 2. The minor veins of most monocots have low plasmodesmatal frequencies. Trees tend to have more plasmodesmata in the loading pathway than herbaceous plants, but this is not a strict correlation, because both herbaceous and tree species are found in some families. For example, *Fragaria* (strawberry) and *Malus* (apple) are both in the Rosaceae (rose family) and both are type 1-2a plants.

3.3 Sugar Transport against a Concentration Gradient

As noted in Sect. 1, one of the characteristics of the phloem is that the solute concentration, and thus the **hydrostatic pressure**, is high (Fig. 4). How is this high solute concentration generated?In many species, sucrose is actively loaded into the phloem from the apoplast by specific **transporters** located in the plasma membranes of the **companion cells** and/or **sieve elements** (Fig. 5A). By taking advantage of the steep **proton gradient** between the apoplast and the cytosol of the sieve elements, with pH values of approximately 5 and 9, respectively, sucrose is continually pumped into the phloem by secondary active transport, maintaining a concentration several times that found in mesophyll cells. Since sucrose-proton co-transporters are found in the plasma membranes of most plant cells, it is

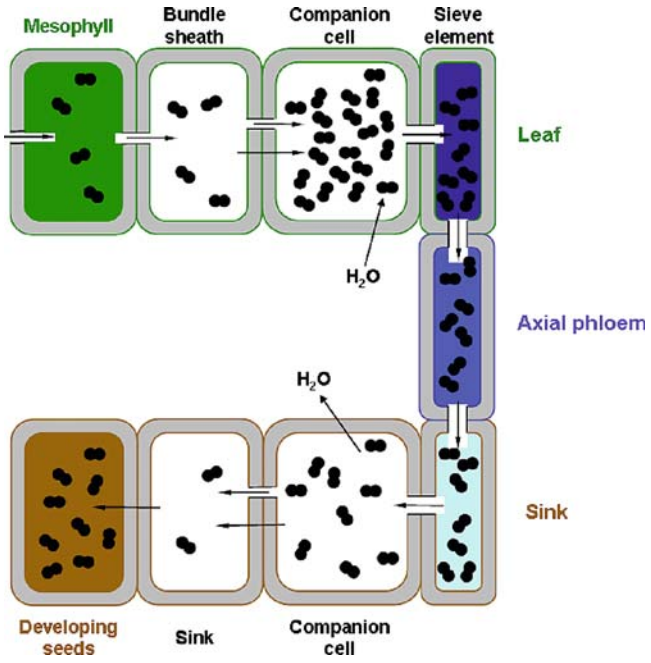

FIGURE 4. Phloem transport. Cell walls are shown in gray. Sucrose molecules (double circles) are produced in mesophyll cells by photosynthesis and diffuse into bundle sheath cells of the minor veins through plasmodesmata. In the minor veins they enter the companion cells and sieve elements by one of several mechanisms, either through plasmodesmata, or across the apoplast (see Fig. 4). Water enters the phloem due to the low water potential, keeping the hydrostatic pressure above that in the sink phloem. Bulk flow of water carries sucrose, and other solutes, from the source leaf to sink tissues where it unloads into sink cells, either through plasmodesmata or via the apoplast. In some sinks, such as embryos of developing seeds, sucrose enters the apoplast after it is unloaded from the phloem and is actively pumped into the sink cells. Courtesy R. Turgeon, Cornell University, Ithaca, U.S.A.

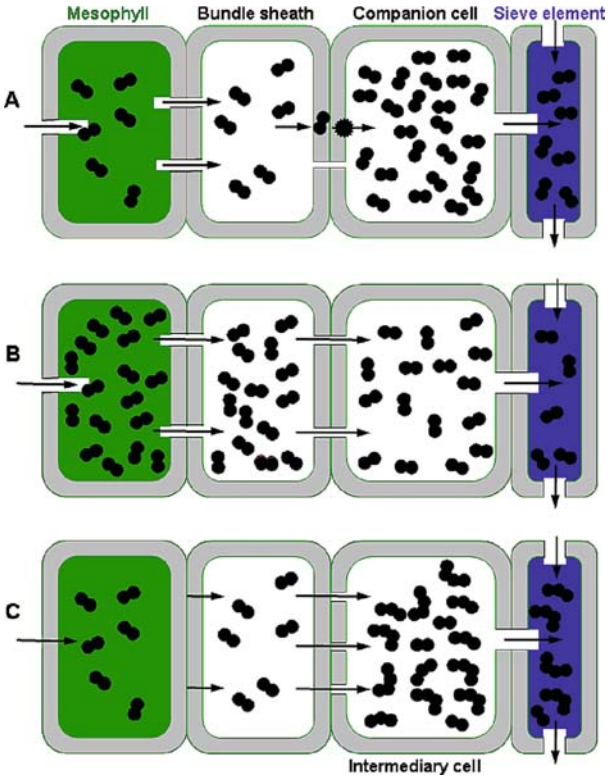

FIGURE 5. Phloem-loading pathways and mechanisms. (A) Apoplastic loading. Sucrose from mesophyll cells (M) diffuses through plasmodesmata to bundle sheath cells (BS) and into the minor veins. Inside the veins, it enters the cell-wall space (apoplast, in grey) near the phloem, and is loaded into the companion cells (CC) and/or sieve elements (SE) by secondary active transport. A sucrose transporter is shown as a star. Phloem parenchyma cells (not shown) are part of the pathway in the vein, and may be the most important site of sucrose efflux into the apoplast. Apoplastic loading is the most common strategy in flowering plants. (B) Diffusion. A downhill sucrose concentration gradient allows diffusion from the cytosol of mesophyll cells, through the bundle sheath and companion cells, and into the sieve elements. Sucrose is carried away in the sieve tubes to the sinks, resulting in continued diffusion. Phloem parenchyma cells are not shown here, but may also be part of the diffusion pathway in the vein. (C) Polymer trapping. Sucrose diffuses through numerous, narrow plasmodesmata from bundle sheath cells into specialized companion cells called intermediary cells (IC), where it is converted to raffinose (trisaccharide) and stachyose (tetrasaccharide). This keeps the sucrose concentration in the intermediary cells low and prevents back diffusion to the mesophyll. The sugars pass from intermediary cells into the sieve elements through larger plasmodesmata. Courtesy R. Turgeon, Cornell University, Ithaca, U.S.A.

reasonable to assume that **apoplastic phloem loading** evolved from a general retrieval mechanism that returns to the cytoplasm sucrose that has leaked out of cells.

If sucrose is loaded into the phloem from the apoplast, one would expect little symplastic continuity with the mesophyll; otherwise the loaded sucrose would leak back through the plasmodesmata to the cells it came from, creating a futile pump/leak system. Indeed, all type 2 plants (those with a low plasmodesmatal frequency) that have been studied load from the apoplast. Many of these plants have highly invaginated plasma membranes (type 2b **transfer cells**) that maximize surface area for this transport. What about the plants with **intermediary cells** (Fig. 5A) that have numerous **plasmodesmata** between the mesophyll and minor vein phloem (Gamalei's type 1 and type 1–2a)? One possibility is that, in these species, sucrose simply diffuses along an entirely symplastic pathway from the mesophyll, without creating an uphill gradient into the phloem (Fig. 5B). If so, the concentration of sucrose must be higher in the mesophyll than in the phloem. This appears to be the case in *Salix babylonica* [(weeping willow), a type 1 species with numerous plasmodesmata], which has a high concentration of sucrose in the leaves, but a lower concentration in the phloem of the stem (Turgeon & Medville 1998).

In species with **intermediary cells**, yet another strategy prevails (Fig. 5C). All plants with intermediary cells transport their photoassimilates primarily as **raffinose** and **stachyose** which suggests that the synthesis of these sugars (tri- and tetra-saccharides, respectively; Fig. 2) is somehow part of the phloem-loading mechanism. A model put forward to explain this is known as **polymer trapping** (Turgeon 1991, 1996). Sucrose supposedly diffuses into the intermediary cells from the bundle sheath through the numerous plasmodesmata that connect these two cell types. Inside the intermediary cells, most of the sucrose is converted to raffinose and stachyose, which accumulate to high concentrations, because these sugars are too large to diffuse backward through the plasmodesmata. This keeps the sucrose concentration lower in the intermediary cell than in the mesophyll, and allows continued diffusion. Thus, the plasmodesmata between bundle sheath cells and intermediary cells act as valves. The plasmodesmata between the intermediary cells

and the sieve elements are larger, which permits entry of the sugars into the long-distance transport stream.

Most effort in this field has been devoted to sucrose loading, since sucrose is the major transport compound in most plants. We know less about the loading of sugar alcohols, in the species that transport them, and even less about the loading of other organic compounds and ions. Unraveling these mechanisms is an ongoing research effort.

4. Evolution and Ecology of Phloem Loading Mechanisms

The ancestral mechanism of phloem loading in flowering plants is not known for certain because we cannot be sure that "basal" groups (those that diverged early in the evolution of the angiosperms) have retained their ancestral characteristics (Fig. 6). However, most basal plants have numerous minor vein plasmodesmata (type 1) (Gamalei 1989, Turgeon et al. 2001). Type 2 plants, and plants with intermediary cells, are more phylogenetically derived; these traits having evolved independently on a number of occasions (Turgeon et al. 2001). The strategies employed by other vascular plants, including the gymnosperms, are not known.

What are the selective pressures that have led to the emergence of the different forms of phloem loading? There is no clear answer to this question, but we can make a start by studying the growth characteristics and habitats of existing plants. Families with **intermediary cells** are heavily represented in the **tropics** [e.g., Cucurbitaceae (gourd family)] although a few are cosmopolitan [Scrophulariaceae (figwort family)] and some individual species occur in the arctic. There appears to be no correlation of intermediary cells with growth rate or with the woody or herbaceous growth habit. The rest of the type 1 species are essentially all woody (trees or shrubs) and can be found in all climates, except the arctic. Type 2 plants can have many forms, but they tend to be herbaceous and are more heavily represented in temperate and colder regions.

What do the differences between phloem-loading types signify? An early hypothesis that symplastic loading is somehow more sensitive to the cold than apoplastic loading does not appear to be valid. The absence of type 1 plants in the arctic is probably due to the fact that there are very few woody species of any kind in those extremely cold environments, for reasons that have nothing to do with phloem loading. In addition, laboratory experiments do not support the concept of cold sensitivity in type 1 species with intermediary cells (Schrier et al. 2000). Although plants with intermediary cells seem to be favored in the tropics, it should not be assumed that this has anything directly to do with temperature. There are many other correlates of life in the tropics that need to be considered.

Sugar alcohols present another problem. Plants from many families produce **sugar alcohols** in their leaves, though only a few appear to transport significant amounts of these compounds in the phloem. There is convincing evidence that sugar alcohols confer tolerance to **boron** deficiency because they complex and solubilize this otherwise insoluble mineral and allow it to be transported in the phloem from leaves to meristematic regions, where it is needed for growth (Hu et al. 1997). It has also been suggested that sugar alcohol synthesis and export may channel away excess reducing energy from photosynthesis in times of stress (Loescher & Everard 2000).

5. Phloem Unloading

When considering how sugars and other materials unload from the phloem, it is useful to make the distinction between **axial sinks** (tissues adjacent to the axial, long-distance transport phloem in shoots and roots) and **terminal sinks** (tissues that are either actively growing or storing large quantities of photoassimilates, such as shoot and root tips, growing leaves, and growing fruits) (Fig. 7).

In terminal sinks, where the unloading rate is generally high, solutes unload from the phloem through **plasmodesmata**. Water must follow through **aquaporins**, which are strongly expressed in sink tissues such as the seed coat of *Phaseolus vulgaris* (common bean) (Zhou et al. 2007). The unloading rate is apparently controlled by the radii of the plasmodesmata and by solute concentration and/or hydrostatic pressure differences between the phloem and surrounding cells. In some terminal sinks, the unloaded solute passes **symplastically** through a number of sink cells. It is subsequently released into the apoplast, from which it is actively retrieved by recipient cells. This is the route necessarily taken by sugars in **seeds** since the maternal plant and embryo are different generations and have no connecting plasmodesmata. In this case, sucrose exits the phloem of the seed coat via plasmodesmata, passes symplastically through a layer of cells, and is released into the apoplast

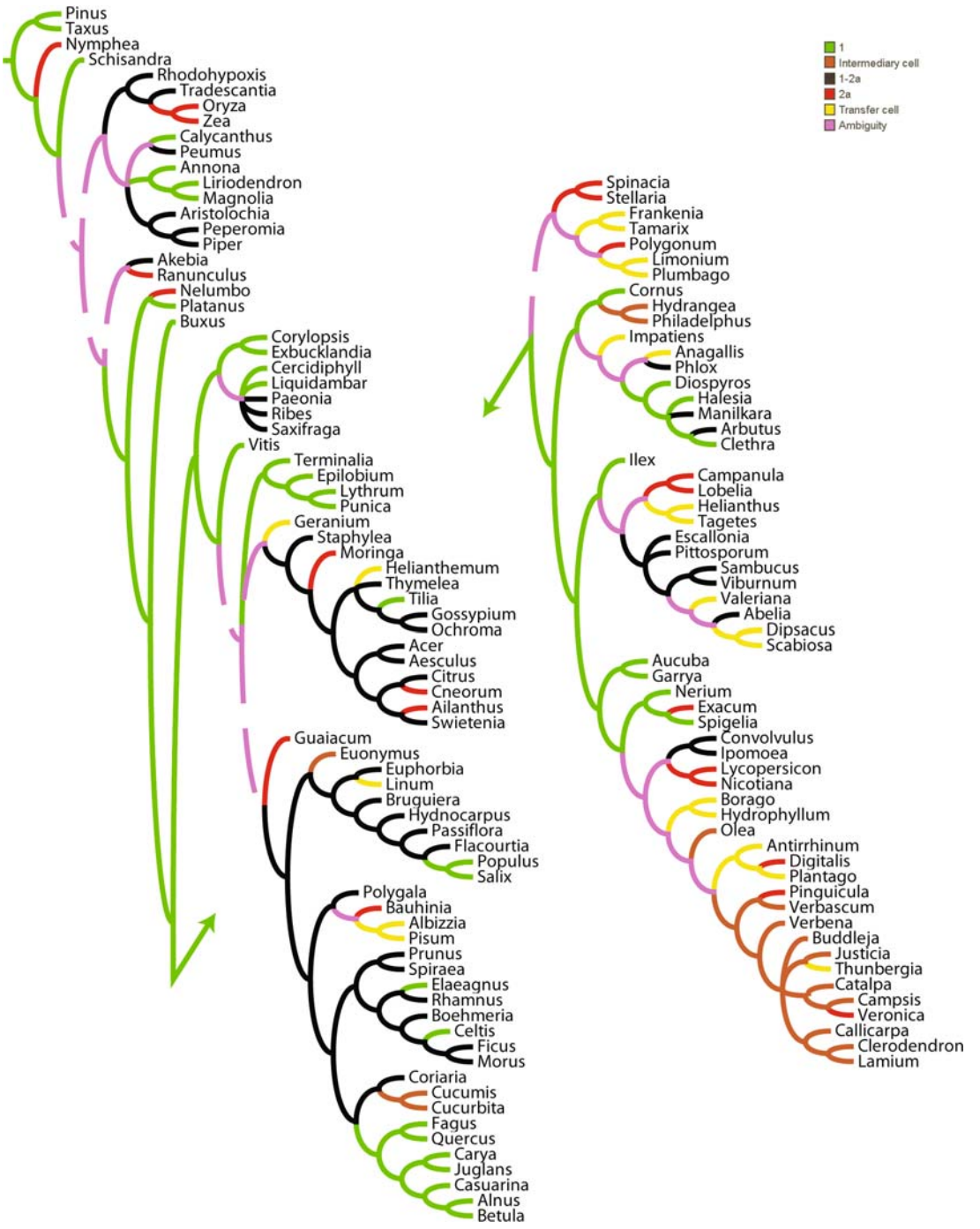

FIGURE 6. Minor vein companion cell characteristics for 137 taxa mapped onto a phylogenetic tree. Wherever possible, genera for which phloem anatomy is known are coded directly in the matrix, but for some representatives there is no equivalent genus in the molecular matrix. In some of these cases, a closely related confamilial genus is coded for the phloem character. All taxa scored as missing for the phloem loading character are automatically pruned from the consensus tree, producing a tree topology that is a fully congruent subset of the topology with all taxa. The tree has been split at the point indicated by the arrows, with the more ancestral taxa at the left (Turgeon et al. 2001). Copyright The Botanical Society of America.

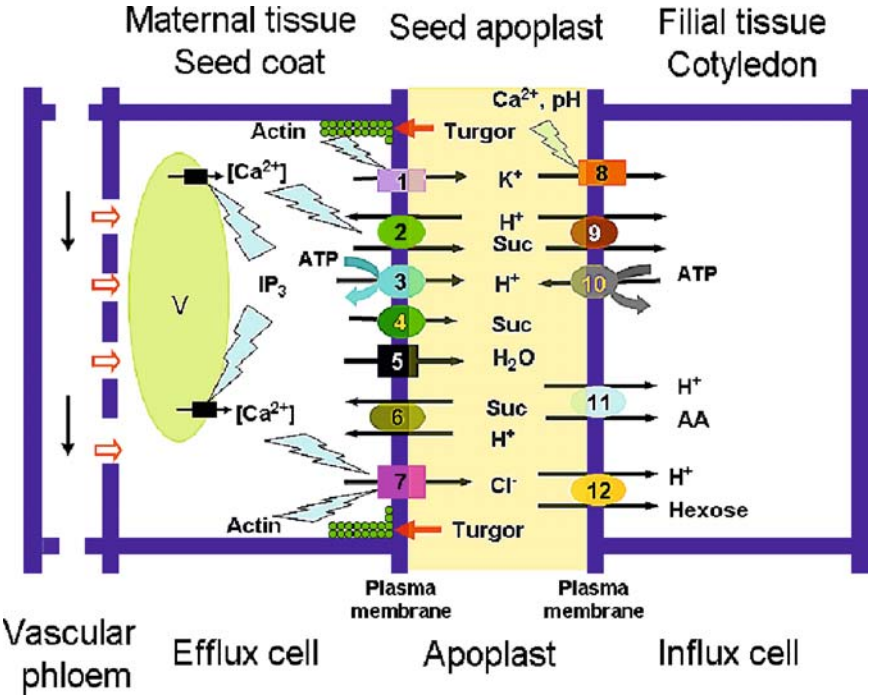

FIGURE 7. **Phloem unloading, followed by transport into developing seeds. The diagram shows membrane transporters involved in transferring phloem-imported nutrients from seed coats to cotyledons of developing grain legume seeds. Phloem-imported nutrients are transported through plasmodesmata to the seed coat efflux cells. Here, membrane transporters in plasma membranes lining the efflux cells release nutrients to the seed apoplast. Currently known transporters are: (1) nonselective channels; (2) sucrose/H^+ antiporters; (3) H^+-ATPases; (4) sucrose facilitators; (5) aquaporins; (6) sucrose/H^+ symporters; (7) pulsing Cl^- channels. Nutrients are taken up from the seed apoplast by membrane transporters located in plasma membranes of cotyledon cell complexes. Currently known transporters include: (8) nonselective cation channels; (9) sucrose/H^+ symporters; (10) H^+-ATPases; (11) amino acid/H^+ symporters; (12) hexose/H^+ symporters. An elevated cell turgor (arrow), due to enhanced uptake of nutrients from the seed apoplast, activates Cl^- and nonselective channels, and possibly also activates Ca^{2+} release, leading to an increase in the cytosolic Ca^{2+} concentration, which serves as a signal to activate sucrose/H^+ antiporters and Cl^-channels (Zhang et al. 2007, *Functional Plant Biology* 34: 314—331, Copyright CSIRO Australia).**

surrounding the embryo. The embryo then scavenges the sucrose by active transporters in the plasma membranes of the cotyledons.

Unloading in axial sinks follows either the **symplastic** or **apoplastic** routes, depending on the species, the specific sink, and the stage of development. When the path of small fluorescent dyes is followed down a root, the dye does not exit the axial phloem, indicating that the plasmodesmata are too narrow to accommodate even small solute molecules (Oparka et al. 1994). Therefore, sugars and other solutes must be released into the **apoplast**. However, as indicated above, when the dye in the phloem reaches the meristematic tissue at the tip of the root, it rapidly unloads through **plasmodesmata**.

Unloading into cotton fibers provides an example of a shift in unloading routes during development. Cotton fibers (single cells of the seed coat epidermis) grow extremely rapidly. Initially, unloading from the phloem and post-phloem transport into the fiber cell is entirely **symplastic**. However, during the most rapid growth phase the plasmodesmata in the wall of the fiber close for about 6 days, and sucrose instead enters the **apoplast**. This allows active sucrose transporters in the plasma membrane of the fiber to drive up osmotic and turgor potentials to the high values needed for rapid cell expansion (Ruan et al. 2001). Once this active growth phase is over, the plasmodesmata open again.

Phloem unloading in sink leaves illustrates the need to consider anatomy, physiology, and development to assemble a complete picture of events (Turgeon 2006). Very young leaves are sinks: they obtain most of their carbohydrate from older leaves. As this photoassimilate enters a young leaf in the phloem it unloads from relatively large veins; the smaller veins are not yet mature (Turgeon 1987, Roberts et al. 1997). As the leaf grows, it reaches a positive carbon balance and then begins to export. Just before it does so, the small veins mature. These **minor veins** are used for photoassimilate **loading**. Therefore, there is a division of labor between veins of different size classes, large ones for **unloading** in young leaves, small ones for loading in mature leaves.

In some organisms structures have evolved to parasitize the phloem-transport system. Rapid phloem unloading occurs when a **phloem-feeding organism** (e.g., an aphid) injects its stylet into a sieve tube. The hydrostatic pressure in the sieve pushes the contents of the sieve tube into the aphid. The aphid absorbs predominantly nitrogenous compounds and excretes much of the carbohydrate as "**honeydew**". The aphids ingest phloem sap without eliciting the sieve tubes' normal response to injury (Sect. 3). Sealing mechanisms are prevented by chemical constituents in aphid saliva injected into sieve tubes before and during feeding (Will et al. 2007). Another special site where phloem unloading occurs is the **haustoria** of**holoparasites** that depend on their host for their carbon supply. The release of solutes from the phloem of the host is strongly stimulated by the presence of such a parasite, by an as yet unidentified mechanism (Sect. 4 of Chapter 9D on parasitic associations). In some species, e.g., *Lupinus albus* (white lupin) the phloem bleeds spontaneously upon cutting (Pate & Hocking 1978). Phloem sap collected in this way or as honeydew has provided valuable information on the composition of phloem sap (Sect. 2).

Phloem unloading is affected in a rather special manner by**root nematodes** (e.g., the parasitic nematodes *Meloidogyne incognita* and *Heterodera schachtii*), which can act as major sinks (Dorhout et al. 1993). Unloading from the sieve element companion cell complexes occurs specifically into the "syncytium", the nematode-induced feeding structure within the vascular cylinder of the root. The infective juvenile nematode selects a procambial or cambial cell as an initial syncytial cell, from which a syncytium develops by integration of neighboring cells. The developing nematode depends entirely on the expanding syncytium, withdrawing nutrients from it through a feeding tube. Unlike in the root tip, the transport of sugars from the phloem to the syncytium in this host-pathogen relationship is apoplastic. The syncytium is not connected via plasmodesmata with the normal root cells. In an as yet unidentified manner, the nematode induces massive leakage from the phloem, thus reducing the transport of phloem solutes to the rest of the roots (Böckenhoff et al. 1996).

6. The Transport Problems of Climbing Plants

Vines can be viewed as "mechanical parasites". They invest too little in wood to support themselves, and thus depend on other plants for mechanical support. Xylem (wood) tissue has both a transport and a mechanical support function. As discussed in Sect. 5.3.5 of Chapter 3 on plant water relations, vines have fewer but longer and wider xylem vessels in their stem per unit stem cross-sectional area. They also have fewer lignified phloem fibers than do trees and shrubs and less phloem tissue per unit of distal area (Fig. 8). How do vines achieve sufficient phloem transport capacity?

Compared with trees and shrubs, vines have **wider sieve tubes** (Fig. 8). Since the hydraulic conductance, by Hagen-Poiseuille's law for ideal capillaries, is proportional to the fourth power of the conduit radius (Sect. 5.3.1 of Chapter 3 on plant water relations), the larger diameter compensates for the smaller total area. The obvious advantage of fewer sieve tubes with a larger diameter is that relatively few resources need to be allocated to producing phloem in the stem, which is therefore light, preventing the supporting plant from toppling over. For a similar investment in stem, the climbing plant will reach a greater height than a nonclimbing plant. If few sieve tubes with large diameters are so advantageous for climbing plants, why do not *all* plants have such wide tubes in their phloem? There is likely a disadvantage in having large-diameter sieve tubes, in that physical damage to a small number of sieve tubes causes a larger proportional loss of transport capacity. Such damage may be mechanical or due to phloem-sucking arthropods or pathogens. As in the xylem of plants with contrasting strategy (Sect. 5.3.5 of Chapter 3 on plant water relations), there may be a trade-off between transport **capacity** and **safety**.

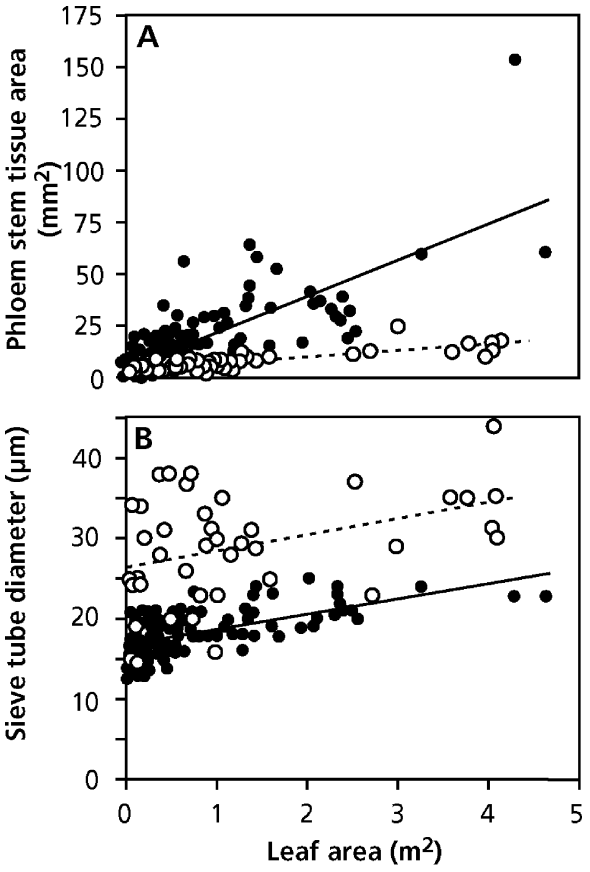

FIGURE 8. Phloem area (A) and maximum diameters of sieve tubes (B) of contrasting *Bauhinia* species. Values are plotted as a function of the leaf area distal to the investigated stem section for stems of lianas (dashed line, open symbols) and congeneric trees and shrubs (*solid line, closed symbols*) (Ewers & Fisher 1991).

7. Phloem Transport: Where to Move from Here?

After several years of debate on whether phloem loading occurs via an apoplastic or a symplastic pathway, it is now agreed that both pathways occur, depending on species. Are there disadvantages and disadvantages associated with the apoplastic or symplastic pathway? The proton-pumping activity of the transfer cells involved in apoplastic loading requires a substantial amount of metabolic energy. It remains to be demonstrated, however, that this energy requirement is greater than that for the polymerization that occurs in the intermediary cells of plants with symplastic phloem loading. Disadvantages associated with the apoplastic pathway are not immediately obvious.

Phloem unloading can also occur either apoplastically or symplastically, depending on the kind of sink and on species. Phloem unloading in sinks is an important aspect of crop yield, since increases in yield in newer varieties are often determined by the amount of resources transported to harvestable sinks, rather than by the total amount of resources acquired. It is therefore important to develop a good understanding of phloem transport. Unraveling both loading and unloading mechanisms continues to offer major challenges.

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