Transport Phloem: Low Profile, High Impact

Transport phloem in veins, petioles, stems, and roots makes up the major part of the phloem stretch. Nevertheless, the transport trajectory has gained a much less distinct profile than the phloem zones involved in loading and unloading in sources and sinks. Yet, the tasks of transport phloem may be diverse and have a strong impact on whole-plant physiology. Given that transport phloem in medium-sized herbs (50 cm) encompasses at least 99% of the axial phloem stretch, its importance as a distribution and signal relay center may exceed an intuitive estimate by far. This subspecial issue highlights some of the functional peculiarities of transport phloem.

IMPACT OF RELEASE/RETRIEVAL ALONG THE PHLOEM PATHWAY

The classic Münch hypothesis (Münch, 1930) distinguished three phloem domains executing different tasks. In the source region, sieve tubes were engaged in loading in the sink region in unloading of photoassimilates. Along the translocation pathway between source and sink ends, sieve tubes were considered to be almost hermetically sealed. This static image may have set the stage for a depreciation of transport phloem functions.

A more dynamic concept of mass flow through the sieve tubes hardly changed lack of interest in transport phloem functions beyond that of photoassimilate displacement. This so-called volume flow model says that sieve tubes are essentially leaky and that solute and solvent are lost and retrieved along the sieve tubes (Eschrich et al., 1972). Its validity for intact plants was later demonstrated by $^{13}$C experiments, e.g. 6% of the photo-assimilates was lost, and 3.4% was retrieved every centimeter along the phloem pathway in bean (Phaseolus vulgaris) plants (Minchin and Thorpe, 1987). These and other findings indicate that transport phloem has a dual function (van Bel, 1996). It carries photoassimilates from sources to terminal sinks such as root/shoot tips. Concurrently, transport phloem is responsible for maintenance and growth (e.g. cambium) of tissues in the plant axis (axial sinks). Thus, events in transport phloem dictate solute distribution between terminal and axial sinks.

In this issue, Ayre et al. (2003) demonstrate the dramatic consequences of release/retrieval for longitudinal displacement of materials. Raffinose and stachyose are withdrawn from the phloem stream to a much lesser extent than galactinol and octopine. As a result, long-distance transport of the galactosyloligosaccharides is much more efficient than that of octopine and, above all, galactinol. The sieve tube track seems to act as a chromatograph column, given the inverse relationship between lateral withdrawal and longitudinal flow. However, this comparison falls short because the materials released back into the sieve elements (SEs) after metabolic processing often differ from those having escaped. Obviously, carbohydrate transformation along the pathway has a strong impact on amount and nature of the photoassimilates arriving in sinks. By acting so, transport phloem may be directly involved in remote control in plants because sugars themselves regulate gene expression in sinks (Rolland et al., 2002).

IMPACT OF SYMPLASMIC TRANSPORT ALONG THE PHLOEM PATHWAY

Special attention requires the spatial position of SEs and companion cells (CCs), their volume ratios, and their symplasmic coupling along the pathway (van Bel, 2003). In transport phloem, the reduced plasmodesmal density as compared with other cell interfaces indicates a symplasmic bottleneck between CC and phloem parenchyma cells (PPCs; Kempers et al., 1998). That the few symplasmic channels between C Cs and PPCs are virtually closed is inferred from the containment of phloem-mobile fluorochromes in sieve tubes along the translocation path in intact plants in several species. However, the plasmodesmata between CC and PPC seem to be open under sink-limiting conditions, when excess photoassimilates are stored in stem parenchyma (Patrick and Offler, 1996).

The latter may apply when the transport phloem in a translocating potato (Solanum tuberosum) stolon switches to an unloading state in a tuberizing stolon (Viola et al., 2001). A more drastic reconstruction of the symplasmic network is demanded during sink-source transition in leaf maturation. In the sink stage, a simple vascular system with a few major vein orders, assigned to unload substances, develops acropetally. During source-to-sink transition, a reticulate vein minor vein system, responsible for phloem loading, differentiates basipetally between the existing veins (Turgeon, 1990). The coincident import-to-export transition goes along with dramatic changes in the symplasmic organization of the major veins (Roberts et al., 1997). Selective closure and secondary modification of plasmodesmata (Roberts et al., 2001) transform the higher order major veins from importing into exporting channels. The sink-source transition requires an activation of Suc carriers in collection phloem and transport phloem as shown in tobacco (Nicotiana tabacum) transformants with green fluorescent protein expression under control of the phloem-specific AtSUC2 promoter (Wright et al., 2003).

THE SYMPLASMIC CONFIGURATION OF TRANSPORT PHLOEM MAY ALSO IMPACT ON OTHER EVENTS

Evidence is mounting that phloem provides a pathway for all sorts of signaling substances, including...
proteins and RNA (Lucas et al., 2001). Some of these macromolecules may be able to enter meristematic tissues and exert control on gene expression. It is not excluded that transport phloem is not merely involved in translocation of macromolecules but is also engaged in generation, transformation, or multiplication of macromolecular signals.

Furthermore, MP (movement protein)-related viral behavior along the transport path has profound consequences for patterns of virus spread. Several systemic viruses are able to cross the symplasmic bottlenecks at the CC/PPC interface from the PPC side (tobacco mosaic virus; Chen et al., 2000) or from the CC side (Itaya et al., 2002). Others such as potato leaf roll virus (Derrick and Barker, 1997), however, remain restricted to the SE/CCs.

**IMPACT OF APOPLASMIC TRANSPORT ALONG THE PHLOEM PATHWAY**

Given the cellular arrangement of transport phloem in higher plants, SEs are only partly covered by CCs. Direct contact with a large apoplasmic interface requires a set of uptake devices. Hence, transporters and channels are expected to reside almost equally frequent in the plasma membrane of SEs and CCs of transport phloem (van Bel, 1996). Thus far, localization of transport proteins in SE/CCs does not always meet these expectations. The distribution of membrane-bound transporters is not consistent between species and even not within one species (Yoshimoto et al., 2003). For instance, no uniform deployment of Suc transporters in transport phloem was found. Using different strategies, Suc transporters were identified on the plasma membrane of CCs and CCs of transport phloem (van Bel, 1996). One may speculate that part of the sugars necessary to complete cellular outfit of SEs makes sieve tube channels in transport phloem vulnerable to oxygen radicals, UV light, and reductive substances such as Glc (Raven, 1991). Lack of atmospheric oxygen may affect the respiratory capacity of SE/CCs. Expectedly, respiration is particularly endangered in transport phloem, which is often deeply embedded in heterotrophic tissues. In this issue, van Dongen et al. (2003) describe specific adaptations of the metabolic machinery of SE/CCs to a low-oxygen environment.

When plants are subject to drought stress, sieve tubes are endangered to lose the capacity of pressure flow. In such a situation, a more negative osmotic potential in the sieve tubes is required. As demonstrated by Cernusak et al. (2003), sugar content of the sieve tubes is enhanced in response to drought stress. One may speculate that part of the sugars necessary to restore sieve tube turgor is derived from cells lining the sieve tube channels in transport phloem.

**IMPACT OF STRESS FACTORS ALONG THE PHLOEM PATHWAY**

Sieve tubes are obvious high-risk zones requiring supplementary measures to secure survival. The incomplete cellular outfit of SEs makes sieve tubes

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**LITERATURE CITED**


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