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Original Article

Phloem flow and sugar transport in *Ricinus communis* L. is inhibited under anoxic conditions of shoot or roots

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ABSTRACT

Anoxic conditions should hamper the transport of sugar in the phloem, as this is an active process. The canopy is a carbohydrate source and the roots are carbohydrate sinks. By fumigating the shoot with N_2 or flooding the rhizosphere, anoxic conditions in the source or sink, respectively, were induced. Volume flow, velocity, conducting area and stationary water of the phloem were assessed by non-invasive magnetic resonance imaging (MRI) flowmetry. Carbohydrates and $\delta^{13}C$ in leaves, roots and phloem saps were determined.

Following flooding, volume flow and conducting area of the phloem declined and sugar concentrations in leaves and in phloem saps slightly increased. Oligosaccharides appeared in phloem saps and after 3 d, carbon transport was reduced to 77%. Additionally, the xylem flow declined and showed finally no daily rhythm. Anoxia of the shoot resulted within minutes in a reduction of volume flow, conductive area and sucrose in the phloem sap decreased. Sugar transport dropped to below 40% by the end of the N_2 treatment. However, volume flow and phloem sap sugar tended to recover during the N_2 treatment.

Both anoxia treatments hampered sugar transport. The flow velocity remained about constant, although phloem sap sugar concentration changed during treatments. Apparently, stored starch was remobilized under anoxia.

Key-words: *Ricinus*; carbohydrates; flooding; isotopic signature; phloem; xylem.

INTRODUCTION

The primary products of photosynthesis – sugars – are translocated within plants mostly by the phloem system. The classic ‘Druckstrom-’ (pressure flow) theory (Münch 1930) divided the phloem system in three parts: loading/collection, transport and unloading/release phloem. Sugars are loaded in the sieve tubes of the collection phloem in source tissues and unloaded/escape from the sieve tubes of the release phloem in sinks. The resulting turgor difference across the phloem drives mass flow in the source-to-sink direction (e.g. van Bel 2003; Lalonde *et al*. 2003; Gould *et al*. 2005; Pickard & Abraham-Shrauner 2009; Knoblauch & Oparka 2012; De Schepper *et al*. 2013). Along the translocation pathway – the transport phloem – sugars and water are continuously lost from and retrieved into the sieve tubes (van Bel 1993; De Schepper *et al*. 2013). Additionally, the phloem may be a pathway for signal transport (De Schepper *et al*. 2013; Turnbull & Lopez-Cobollo 2013).

In most plants, sucrose is the major osmotically active solute in the phloem and thus also provides the driving force for mass flow in the phloem (Lalonde *et al*. 2004). All plant species transport sucrose in the phloem. Some species transport detectable amounts of raffinose, stachyose and/or sugar alcohols, which can exist in even higher concentrations than sucrose (Lalonde *et al*. 2004). Next to sugars, amino N compounds and potassium largely account for phloem sap osmotic concentrations and hence pressure differences between source and sink.

In general, phloem loading and unloading can occur symplastic or apoplastic (Lalonde *et al*. 2003; De Schepper *et al*. 2013). Sucrose, and probably certain amino acids, is loaded via the apoplastic pathway into minor veins by proton symporters localized in plasma membranes of sieve element/companion cell complexes. The transport systems across the membranes are energized by proton-motive force (van Bel 2003; Lalonde *et al*. 2003; Turgeon 2010). In contrast, oligosaccharides seem to be loaded symplastically. The so-called polymer trapping involved in this loading pathway is also active from a thermodynamical point of view, although it does not involve active transport of ions or molecules across a membrane (Turgeon 2010). In the initial step, sucrose diffuses via plasmodesmata from the mesophyll into the companion cells, where raffinose and stachyose, which cannot diffuse back, are synthesized (Turgeon 2010; De Schepper *et al*. 2013). In summary, most phloem loading processes are energy dependent and therefore sensitive to conditions which hamper the synthesis of ATP, such as low oxygen concentrations. In addition to the energy demand for

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