

Effects of cold-girdling on flows in the transport phloem in *Ricinus communis*: is mass flow inhibited?

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ABSTRACT

The effects of cold girdling of the transport phloem at the hypocotyl of *Ricinus communis* on solute and water transport were investigated. Effects on the chemical composition of saps of phloem and xylem as well as of stem tissue were studied by conventional techniques and the water flow in the phloem was investigated by NMR imaging. Cold girdling reduced the concentration of sucrose but not that of inorganic solutes or amino acids in phloem saps. The possibility that cold treatment inhibited the retrieval of sucrose into the phloem, following leaching from the sieve tubes along a chemical gradient is discussed. Leaching of other solutes did not occur, as a result of missing promoting gradients in stem tissue. Following 3 d of cold girdling, sugar concentration increased and starch was synthesized and accumulated in stem tissue above the cold girdling region and along the cold-treated phloem pathway due to leaching of sugars from the phloem. Only in the very first period of cold girdling (<15–30 min) was mass flow inhibited, but recovered in the rest of cold treatment period to values similar to the control period before and the recovery period after the cold treatment. It is concluded that cold treatment affected phloem transport through two independent and reversible processes: (1) a permanent leaching of sucrose from the phloem stem without normal retrieval during cold treatment, and (2) a short-term inhibition of mass flow at the beginning of cold treatment, possibly involving P proteins. Possible further mechanisms for reversible inhibition of water flow are discussed.

Key-words: *Ricinus communis*; cold girdling; NMR-imaging; phloem; water flow.

INTRODUCTION

One of the most important features that have allowed higher plants to conquer dry land are the phloem and

xylem which transport water, photo-assimilates, nutrients and signals over long distances within the plant. The phloem is responsible for the transport of metabolic products and for the recycling of mineral nutrients from the shoot to the root or within the shoot from mature leaves to younger growing parts. The phloem can be divided into three functional areas: loading, transport and unloading phloem (van Bel 1993, 2003a, b). While the loading phloem is responsible for active loading of photoassimilates into the phloem, the unloading phloem delivers assimilates to sink tissues, and the transport phloem translocates water and solutes from source to sink. In the transport phloem, which generally can be found from the main leaf veins downwards, release as well as loading (retrieval) of sugars takes place (Patrick 1997; van Bel 1998, 2003a, b; Komor 2000; Lalonde *et al.* 2003; Gould, Minchin & Thorpe 2004). Along the way the transport phloem provides the surrounding tissue with assimilates for processes such as maintenance and growth.

The forces that drive phloem transport and dictate the direction of flow originate in the source–sink relations between the phloem and the tissue surrounding it (van Bel 1998, 2003a, b; Bancal & Soltani 2002; Henton *et al.* 2002; Thompson & Holbrook 2003; Lalonde *et al.* 2003; Gould *et al.* 2004). It has been shown that in the phloem, but also in the xylem, complex and fragile gradients in pressure and osmotic potential exist that are easily disturbed by invasive experimentation (van Bel 1998, 2003a, b; Bancal & Soltani 2002; Lalonde *et al.* 2003). It is widely accepted that these potential gradients drive long-distance transport in the phloem as well as the xylem, even though the current debate around the validity of the cohesion tension theory (Zimmermann *et al.* 2004) has demonstrated that not everybody agrees on the question of how large the water potential gradients in xylem vessels can be.

Long-distance phloem transport within intact plant systems is especially difficult to measure because only few techniques are suitable and because of the extreme sensitivity of the phloem to wounding. In a number of studies dyes or radioactive tracers were applied or injected to investigate transport in the phloem (see *inter alia* Patrick 1997; Knoblauch & van Bel 1998; Oparka & Turgeon 1999; Komor 2000). Additionally, the small vessel sizes, the slow flow velocities and the small flowing volume per unit of

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