Plant, Cell and Environment (2001) **24**, 491–503

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Simultaneous measurement of water flow velocity and solute transport in xylem and phloem of adult plants of *Ricinus communis* over a daily time course by nuclear magnetic resonance spectrometry

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ABSTRACT

A new method for simultaneously quantifying rates of flow in xylem and phloem using the FLASH imaging capabilities of nuclear magnetic resonance (NMR) spectrometry was applied in this study. The method has a time resolution of up to 4 min (for the xylem) and was used to measure the velocity of flows in phloem and xylem for periods of several hours to days. For the first time, diurnal time course measurements of flow velocities and apparent volume flows in phloem and xylem in the hypocotyl of 40-d-old *Ricinus communis* L were obtained. Additional data on gas exchange and the chemical composition of leaves, xylem and phloem sap were used to assess the role of leaves as sinks for xylem sap and sources for phloem. The velocity in the phloem ($0{\cdot}250 \pm 0{\cdot}004$ mm s^{-1}) was constant over a full day and not notably affected by the light/dark cycle. Sucrose was loaded into the phloem and transported at night, owing to degradation of starch accumulated during the day. Concentrations of solutes in the phloem were generally less during the night than during the day but varied little within either the day or night. In contrast to the phloem, flow velocities in the xylem were about 1·6-fold higher in the light ($0{\cdot}401 \pm 0{\cdot}004$ mm s^{-1}) than in the dark ($0{\cdot}255 \pm 0{\cdot}003$ mm s^{-1}) and volume flow varied commensurately. Larger delays were observed in changes to xylem flow velocity with variation in light than in gas exchange. The relative rates of solute transport during day and night were estimated on the basis of relative flow and solute concentrations in xylem and phloem. In general, changes in relative flow rates were compensated for by changes in solute concentration during the daily light/dark cycle. However, the major solutes (K^+, NO_3^-) varied appreciably in relative concentrations. Hence the regulation of loading into transport systems seems to be more important to the overall process of solute transport than do changes in mass flow. Due to transport behaviour, the chemical composition of leaves varied during the day only with regard to starch and soluble carbohydrates.

Key-words: chemical composition; fast nuclear magnetic resonance imaging., long-distance transport; phloem flow; xylem flow

INTRODUCTION

Characterization of long-distance transport systems is fundamental to understanding the physiology of higher plants. In the xylem and phloem, water and solutes are transported by a mass flow. Transported solutes vary widely in composition (e.g. inorganic ions taken up from the environment by the roots, organic compounds produced by plant metabolism) and, in the phloem in particular, photo-assimilates are transported as energy in chemical form. For a number of physiological questions, knowledge of transport velocities and rates of transport are of basic interest. Additionally, the rate of response of transport in xylem and phloem to rapid changes in environmental conditions (such as light, temperature, humidity) is integral to many aspects of plant metabolism but poorly understood owing to lack of quantitative methods. Current knowledge of the 'driving forces' for xylem and phloem transport of water and solutes is still based on gradients in hydrostatic pressure and water potential for the xylem (but see Benkert *et al*. 1995 and Thürmer *et al*. 1999), and chemical potential (gradients in concentrations of photo-assimilates, the pressure-flow theory of translocation, Münch 1930) for the phloem. Gas exchange of water vapour, CO_2 and O_2 and associated processes are central to the regulation of long-distance transport in plants. Both phloem and xylem systems are reasonably complex and susceptible to manipulation. For these reasons, it has remained difficult to investigate the long-distance transport systems of plants *in situ*.

Heat-based methods have been used to trace movement of xylem sap and can yield reasonably accurate measures

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