

KEYNOTE: Interplay between material flows and structural properties in dynamics of tree

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Highlights: A whole tree level theoretical framework on the linkage between leaf gas exchange, long distance xylem and phloem transport and tree growth is presented.

Keywords: cambial growth, cavitation, hydraulic architecture, phloem transport, stomatal control, xylem transport

INTRODUCTION

Pressure driven transport in the xylem and phloem of trees means that leaf gas exchange, long distance material transport, growth and structural development are linked processes with feedbacks. However, the time constants of these different processes are very different which makes integrating studies of these phenomena a challenging task. Proper matching of the gas exchange, current structural growth and accumulated structure with the environmental conditions is crucial to the success and survival of trees (Brodridd 2009), particularly in the rapidly changing climate. This determines both the competitive capacity and resistivity to extreme conditions of trees.

The efficiency xylem transport is crucial for tree productivity, growth and overall performance (Bond and Kavanagh 1997). Water in the xylem is in a metastable state under negative hydrostatic pressure and thus vulnerable to phase transition by cavitation, which threatens xylem transport capacity (Tyree and Sperry 1989, Choat et al. 2012). Excessive cavitation during drought has been suggested to be main reason for tree mortality during drought (McDowell 2011). The requirements for xylem efficiency (i.e. hydraulic conductance) and safety (ability to withstand negative pressure without cavitation) are in conflict with each other; more conductive tissue tends to be more vulnerable to cavitation (e.g. Martinez-Vilalta et al. 2002). Xylem conductance increases, and vulnerability to cavitation decreases, with increasing xylem conduit size and increasing porosity of the pit membrane found between neighbouring conduits (Sperry and Hacke 2004).

Osmotic matching of the negative xylem hydrostatic pressure is involved in a number of central plant processes such as in leaf gas exchange, phloem transport and cambial growth. In phloem transport the positive turgor pressure required to drive the flow is obtained by active loading of osmotic substances, mainly sugars, to the phloem at the sources. Phloem transport and utilization of photosynthates in sinks have to maintain the rate of carbon assimilation in photosynthesis, or carbohydrate accumulation will force stomatal closure and down-regulation of photosynthesis (Paul and Foyer, 2001). The functioning of the phloem tissue in relation to environmental and structural factors is not well understood, although some theoretical predictions (e.g. Hölttä et al. 2009) and laboratory measurements (Mullendore et al. 2012) relating phloem structure to flow rate have been made. Adjustment of the stomatal opening controls leaf gas exchange in response to various environmental and internal signals. This topic has long been under rigorous study, but is still far from being understood (Buckely 2005). One obstacle is that our present understanding is based mainly on leaf level relations (Ball et al. 1987) without much consideration having been paid to whole tree level interactions and constraints.

As in the case of leaf gas exchange and phloem transport, the growth of new tissues also requires high carbohydrate availability and high turgor pressure in the different phases of growth including cell division, enlargement, and cell wall synthesis. The positive turgor pressure results from the interplay between the negative water pressure in xylem and sufficient sugar concentration in the living cambium to maintain positive pressure osmotically. In addition, carbon assimilates have a dual role in growth as apart from providing the sufficient enlarging pressure, they provide the raw material for cell wall thickening (e.g. DeSchepper and Steppe 2010, Hölttä et al. 2010, Pantin 2012). Maintenance of the balance between hydrostatic and osmotic pressures set strong boundary conditions for leaf gas exchange, within tree transport, storage, structure and growth and help to reveal how biological regulation needs to work to maintain measurable attributes, such as pressure and sugar concentration, within observed range. Resource wise, the construction and maintenance of the xylem and phloem tissue require a major proportion of the trees carbon

and nitrogen. With growth in tree height, the transport distance within the tree increases, and the transport of water (e.g. Koch et al. 2004), and perhaps even that of the assimilate products (e.g. Thompson 2006), become increasingly limiting for tree performance and growth. At the same time, the proportion of resource allocation to both of these tissues must increase.

Here we present a whole tree level theoretical framework on the linkage between leaf gas exchange, long distance xylem and phloem transport, and sink relations such as growth. Using this theoretical framework we demonstrate how xylem and phloem transport constrain whole tree level water and carbon exchange and growth in varying environmental conditions.

WHOLE TREE LEVEL LINKAGE OF LEAF GAS EXCHANGE, XYLEM AND PHLOEM TRANSPORT AND SINK RELATIONS

The interconnections and the underlying mathematical formulation amongst transpiration, photosynthesis, xylem and phloem transport, soil water status, and sink sugar status are depicted in Fig. 1. At leaf level, water is lost and carbon assimilated to and from atmosphere through stomatal openings (*). The driving forces for these fluxes are saturation pressure deficit ($C_{H_2O,i} - C_{H_2O,a}$) of water vapor in the atmosphere, and the difference in CO_2 concentration between the ambient air and the internal CO_2 concentration in the gas phase in the leaf ($C_{CO_2,a} - C_{CO_2,i}$). The utilization of CO_2 in photosynthesis (**, inside the dotted box) creates and maintains the difference in the CO_2 concentration required for assimilation. Accumulation of assimilated sugars and/or decrease in water potential in the leaf may decrease photosynthesis (**) due to stomatal and non-stomatal factors, e.g. due to down-regulation of photosynthetic machinery and decreases in mesophyll conductance (e.g. Chaves et al. 2003). The sugars assimilated by photosynthesis are passed mostly passively along the concentration gradient in trees (Turgeon 2010) from the mesophyll cells (where photosynthesis occurs) to the phloem. The photosynthesis box (**) contains many processes including the solution of CO_2 to the liquid phase and its diffusion in it, light and dark reactions of photosynthesis, and phloem loading which are not depicted in the figure.

Water loss at the transpiring surfaces in the leaves lowers the leaf xylem water potential which creates a force to draw water to the leaves though the xylem tissue from all the way from the roots and soil in the direction of the xylem water potential gradient (\dagger). The assimilated sugars loaded to the leaf phloem draw osmotically water from the adjacent xylem tissue to maintain water potential equilibrium ($\dagger\dagger$) and increase phloem hydrostatic (turgor) pressure. This positive pressure in the leaf phloem pushes water and dissolved sugars in the direction of the pressure gradient ($\dagger\dagger\dagger$) towards locations where the sugars are used in carbon sinks. Sugar utilization in the sink (***) lowers the osmotic concentration of the sap and keeps the turgor pressure low. In the absence of sugar utilization in the sink, the information of increase in sugar concentration at the sink is transmitted rapidly though the phloem to the source (leaves) due to pressure changes. Water potential equilibrium between the xylem and phloem is maintained at all locations in the tree ($\dagger\dagger$). Cambial growth (\ddagger) occurs as sugars are unloaded from phloem to cambium and this draws water osmotically from the xylem to the cambium to create pressure for cell expansion.

All these processes are coupled and constrained by one another. In steady state, the transpiration rate (E) must equal xylem sap flow rate (J_x), CO_2 assimilation rate (A) must equal the phloem sap flow rate (J_p), which in turn must equal the rate of sugar utilization at sink. The xylem and phloem are hydraulically coupled so that phloem turgor pressure plus osmotic pressure must equal the xylem water potential in all parts of the tree ($\dagger\dagger$). Xylem conductance (k_x) is dependent on xylem water potential due to embolism formation by cavitation (Tyree and Sperry 1989), and phloem conductance (k_p) is dependent on phloem sugar concentration due to viscosity, which increase highly non-linearly with sugar concentration (Hölttä et al. 2009). Conductances also depend on temperature due to the temperature dependency of viscosity. Furthermore, there seems to be a connection between phloem transport and recovery of xylem from embolism (Nardini et al. 2011). Transpiration, soil water availability, photosynthesis and sugar utilization at the sinks set the pressure gradients for xylem and phloem transport. In addition, photosynthesis is directly coupled to leaf xylem water potential and osmotic concentration, which, in turn are closely linked to avoid loss of turgor pressure and leaf dehydration. Finally, the rate of cambial growth at each height is dependent on pressure in the cambium, which is tightly linked to local phloem sugar concentration and xylem pressure. The formation of new xylem and phloem tissue in cambial growth affects the xylem water pressure and phloem turgor pressure after growth has been completed.

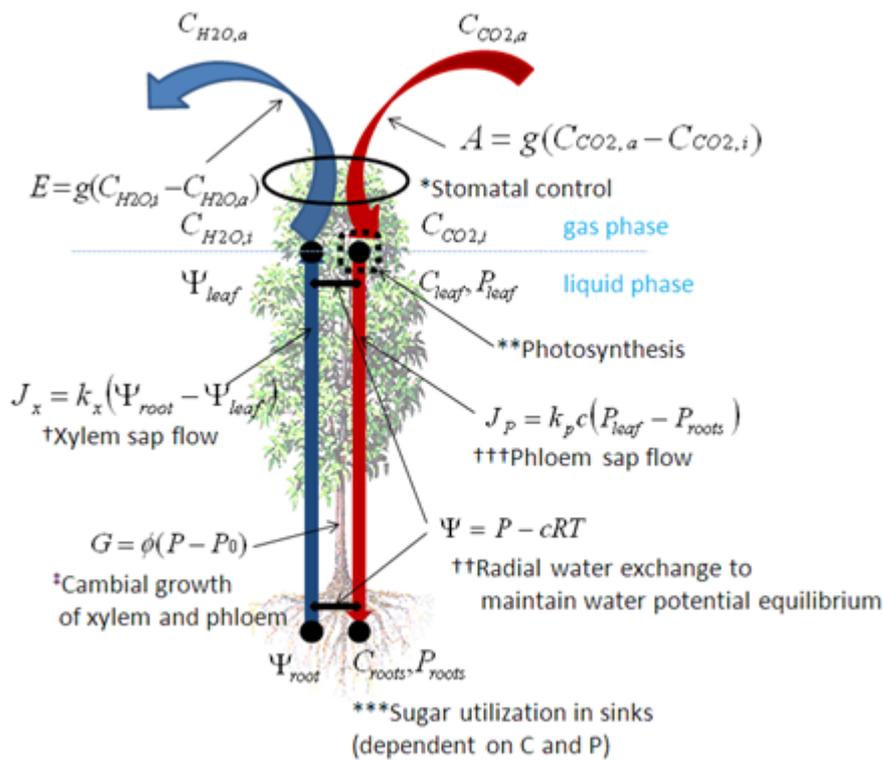


Fig. 1. Xylem and phloem transport, stomatal conductance and photosynthesis, and sink relations are interrelated. E is transpiration rate, J_x xylem sap flow rate, k_x xylem conductance, Ψ_{leaf} leaf xylem water potential, Ψ_{soil} root xylem water potential, g stomatal conductance, $C_{H2O,a}$ ambient H₂O concentration, $C_{H2O,i}$ leaf internal H₂O concentration, A photosynthesis rate, c “average” sugar concentration in phloem, k_p phloem conductance, P_{leaf} turgor pressure in leaf, P_{root} turgor pressure in root, J_p phloem sap flow rate, $C_{CO2,a}$ ambient CO₂ concentration, $C_{CO2,i}$ leaf internal CO₂ concentration, R a physical constant, T temperature, G is growth rate, Φ is cell wall (irreversible) extensibility, and P_0 is threshold pressure for cell wall extensibility.

The structure of the xylem, i.e. mainly conduit size and number and pit pore size and density, will determine vulnerability to cavitation and the specific xylem conductivity which together with xylem cross-sectional area determines xylem conductive capacity (k_x). Similarly, the structure of the phloem, i.e. sieve tube size and number, and sieve plate or pore size and number, will determine the conductive capacity of phloem which together with phloem cross-sectional area determines phloem conductivity (k_p). Phloem osmotic pressure and turgor depend, in addition, on the phloem loading and unloading dynamics as they determine the sugar concentration (c) in phloem. The former is linked to photosynthesis especially tightly in trees where the sugars diffuse from the mesophyll cells to phloem sieve tubes passively along a concentration gradient (e.g. Turgeon 2010), and the latter is linked to sugar utilization for growth, respiration and root exudates. Structural development of tree is an outcome of resource capture, allocation and turnover of structures. The rate of resource capture and allocation between productive (capturing) and non-productive organs determine the long term growth rate. Size increase will change the balance between productive and non-productive tissue. The change depends on the scaling of the xylem and phloem tissue properties but the size also influences the flow rates and the specific capacities of the active tissue. Dynamics of tissue specific activities, allocation between productive and non-productive tissue and organ turnover rate influence the rate of development and attainable final size of trees.

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