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Invited review

Hydraulic functioning of tree stems—fusing ray anatomy, radial transfer and capacitance

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Not long ago, textbooks on plant physiology divulged the view that phloem and xylem are separate transport systems with exclusive functions. Phloem was flowing downwards providing roots with carbohydrates. Xylem transported water upwards from roots to leaves. This simplified view has changed forever. Today we have a much-refined understanding of the complex transport mechanisms, regulatory functions and surprisingly ingenuous solutions trees have evolved to distribute carbohydrates and water internally to fuel growth and help mediate biotic and abiotic stresses. This review focuses on functional links between tissues of the inner bark region (i.e., more than just phloem) and the xylem, facilitated by radially aligned and interconnected parenchyma cells, called rays. Rays are usually found along the entire vertical axis of tree stems, mediating a number of transport processes. We use a top-down approach to unveil the role of rays in these processes. Due to the central role of rays in facilitating the coupling of inner bark and xylem we dedicate the first section to ray anatomy, pathways and control mechanisms involved in radial transport. In the second section, basic concepts and models for radial movement through rays are introduced and their impacts on water and carbon fluxes at the whole-tree level are discussed. This section is followed by a closer look at the capacitive function of composite tissues in stems where gradual changes in water potential generate a diurnal 'pulse'. We explain how this pulse can be measured and interpreted, and where the limitations of such analyses are. Towards the end of this review, we include a brief description of the role of radial transport during limited availability of water. By elucidating the strong hydraulic link between inner bark and xylem, the traditional view of two separate transport systems dissolves and the idea of one interconnected, yet highly segregated transport network for carbohydrates and water arises.

Keywords: dendrometer measurements, phloem–xylem exchange, ray parenchyma, tree water transport.

Introduction

Trees are often described as silent observers, destined to grow in one particular place where they develop from a germinating seed until they die. They have no lungs, eyes, brain, intestines, heart, blood or nerves similar to us. Yet, today we accept that trees respire (e.g., Chapin et al. 2012), can read the clock (e.g., Resco de Dios et al. 2013), and communicate with each other (e.g., Baldwin and Schultz 1983, Pearse et al. 2013) and with even other life forms like fungi (Bouwmeester et al. 2007). They age (e.g., Mencuccini et al. 2014), defend themselves (e.g., Bennett and Wallsgrove 1994), express environmentally entrained and oscillatory rhythm (Lüttge and Hertel 2009) and have a 'pulse' without a heart. Here we define this pulse as the product of cyclic pressure variations, driven by the diel cycle of transpiration (and to a lesser degree by photosynthesis), which in turn is the result of the diel cycle of solar irradiance, temperature and dryness of the atmosphere. We acknowledge that also seasonal cycles can cause a pulse-like signal. These are not the subject of the present review.

The pulse-analogy has been used to describe similarities between a medical practitioner and a tree physiologist, both taking a pulse to understand how and why their 'patient' responds in certain ways to biological or environmental stimuli (Burgess 2008). Initially focused on interpreting axial water-flow dynamics in xylem of trees, we would like to extend the pulse-analogy by including knowledge about dynamic processes that involve radial transfer of water between xylem and inner bark. We use inner bark as a unifying term that encompasses a number of different tissue types, namely phellogen, axial parenchymal tissue, phloem and vascular cambium. We assume that at this point we have lost the medical fraternity.

The pulse originates from transport dynamics of water and organic, as well as inorganic compounds in the open vascular system of trees (Figure 1). The transport dynamics of water involve four components: (i) transpiration from leaf surfaces and subsequent mostly acropetal transport of water from roots to leaves; (ii) circulation of water from xylem to collection phloem at the leaf level, basipetal movement in phloem and circulation from release phloem into sinks such as cambial tissues, flowers, fruits and roots; (iii) Münch counterflow inside the xylem opposite to the direction of phloem transport; and (iv) emptying and refilling of stored water from symplastic and apoplastic spaces in sapwood and inner bark. While replacement of water lost during transpiration makes up the largest volumetric flow of water in trees, processes listed under points (ii) and (iv) are substantially involved in creating the pulse.

Traditionally, it was believed that the loading and unloading of sugars into and out of the phloem and its usage in processes related to respiration, repair and growth, determine the circulation of water between xylem and phloem and the resulting pulse. Yet, more recently it was shown that also the radial transfer of water between inner bark and xylem (e.g., Zweifel et al. 2001, Sevanto et al. 2011, Pfautsch et al. 2015*a*) can play an important role in the origin of the pulse. The force required for this radial transfer is mostly generated by transpiration and the associated differences in water potential in xylem and inner bark (Figure 2).

Many books and reviews have been written on either functioning of phloem (e.g., van Bel 2003*a*, Dinant and Lemoine 2010, Thompson and van Bel 2013, van Bel and Thompson 2013, De Schepper et al. 2013*a*) or xylem (e.g., Bollard 1960, Tyree and Zimmermann 2002, Sperry 2003, Zyalalov 2004), yet syntheses of their hydraulic interactions are much less common (e.g., Stroock et al. 2014). For this reason, the present review focuses on functional links between inner bark and xylem that involve hydro- and/or osmodynamic changes in pressure, excluding diel

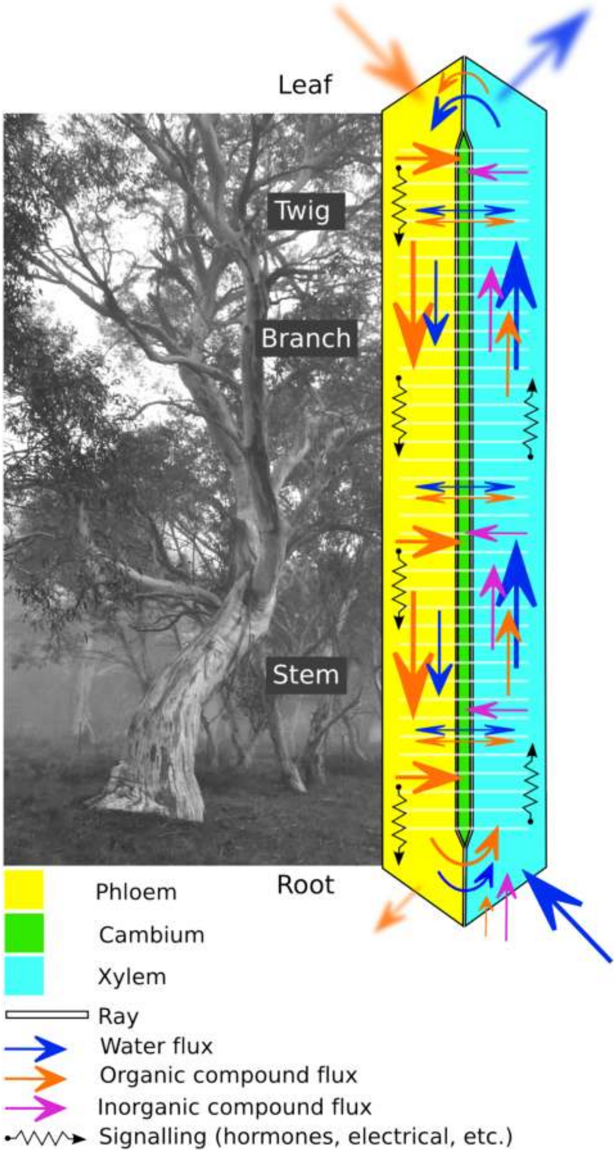

Figure 1. Conceptual representation of fluxes and signal transduction in the open vascular system of a tree, depicting the strong interconnection of the xylem and transport phloem. The relative size of each flux is represented by the size of arrows. Flux directions and sizes shown only apply to a sunny summer day. Sharp-edged arrows represent fluxes of solid or liquid materials, blurred arrows those of gases. A large influx of water at the root level is accompanied by a quantitatively smaller influx of inorganic and organic substances. Simultaneously, a small efflux of organic substances can occur in solid (e.g., organic acids, sugars) and gaseous (e.g., CO_2) form. In the xylem a large flux of water transports organic and inorganic substances, as well as signals (e.g., hormonal, electrical, changes in pressure, changes in concentration of compounds, etc.) upwards through the stem, branches and twigs to the leaves. Wood rays (gray horizontal lines) connect xylem and transport phloem along the entire vertical axis of the stem where they facilitate a bidirectional flux of water, as well as organic and selected inorganic substances. Although rays traverse the cambium, they also supply this meristem with resources necessary for cell growth and respiration. At the leaf, transpiration is responsible for the large efflux of water vapor leaving the tree. Where xylem and phloem cells are in close contact in leaves, a small and predominately unidirectional flux of water and organic compounds can be observed from xylem to phloem. CO_2 taken up by the leaf is incorporated into organic substances through biochemical processes in the chloroplasts. These organic substances (mostly sugars) are loaded into the collection phloem. The flux of organic substances through transport phloem is proportionally much larger than that found in xylem. In turn, the flux of water in transport phloem is proportionally much smaller. In addition, a small flux of inorganic compounds (e.g., ions) exists in transport phloem. The proportion of signals conducted by the phloem is potentially larger and more diverse compared with the flux of signals in the xylem. A relatively small flux of water and organic substances from release phloem into xylem is maintained in roots.

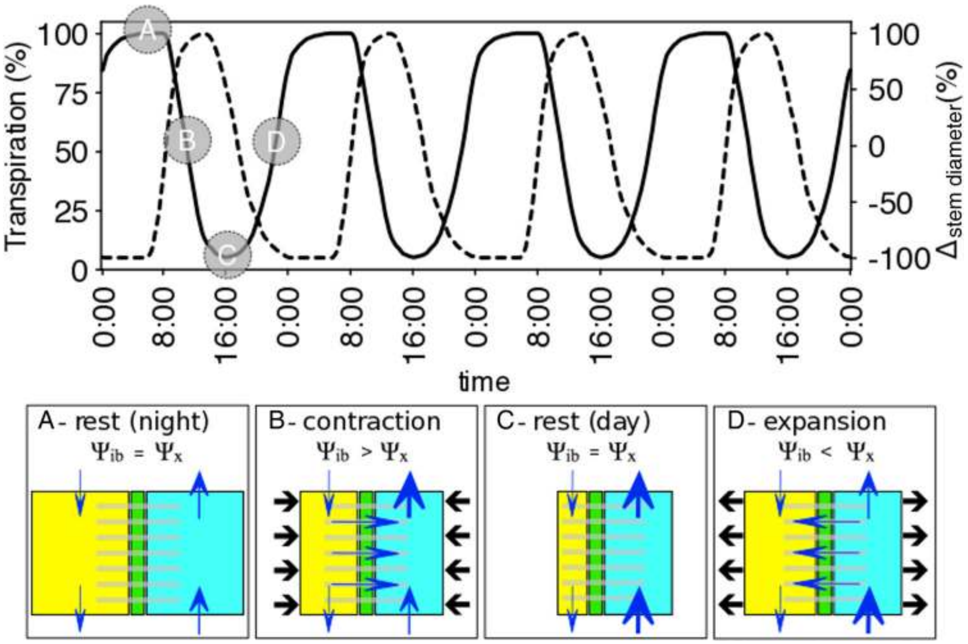

Figure 2. Schematic view of four diel cycles of transpiration (dashed line) and the consequential 'pulse' in tree stems (solid line). In the example provided the pulse results from differences in water potential between xylem (Ψ_x) and inner bark (Ψ_{ib}). The resulting fluxes of water between the tissue types are responsible for radial variation in stem diameter ($\Delta_{\text{stem diameter}}$). $\Delta_{\text{stem diameter}}$ is typically diametrically opposed and slightly lagged to transpiration. Each pulse oscillation typically has four distinct phases marked A, B, C and D. Each phase is represented in the lower panels, detailing hydration status of tissues (indicated by size of rectangles representing inner bark and xylem) and relative volume as well as direction of water fluxes. Colors used represent plant tissues and fluxes as in Figure 1. (A) An extended rest phase can be observed late at night, when tissues are fully hydrated and Ψ_{ib} is in equilibrium with Ψ_x. At this time influxes are equal to effluxes in each tissue type, although the volume of water passing through xylem is larger compared with that in inner bark. (B) With a steep increase of transpiration during the morning, efflux largely exceeds influx of water in xylem, causing water to flow from inner bark into xylem through rays, leading to a contraction of inner bark (indicated by black arrows), and often but to a lesser degree also a contraction of xylem. At the point of maximal contraction, a short rest phase is reached (C) after which expansion of the stems begins (D). Following stomatal closure and associated reductions in transpiration, tissues begin to rehydrate, leading to an expansion of inner bark and xylem that continues until rehydration is complete (back to A).

growth dynamics that have recently been summarized by Steppe et al. (2015). Inner bark includes phloem tissue and special attention will be given to this important plant organ. Theory predicts that both physiological and biophysical functions between inner bark and xylem are tightly linked. For example, regulation of osmotic potentials in phloem tissue impacts water potential in xylem (Ψ_x), and vice versa (Hölttä et al. 2006, 2009*a*).

Phloem is commonly separated into three units based on the dominant function: collection, transport and release phloem (e.g., Lucas et al. 2013). Although all three units are constructed from living sieve-element/companion cell complexes (from here on termed SE-CCC) and parenchyma cells, the ratio among the cell types as well as total thickness of the composite tissue varies according to the main function to be performed. For example, collection phloem consists of high numbers of companion cells to facilitate phloem loading; high numbers of sieve tube elements are typically found in transport phloem to facilitate translocation of solutes (van Bel 2003*a*, De Schepper et al. 2013*a*, Patrick 2013).

This review is mostly concerned with inner bark that contains transport phloem, as it is the section of phloem where a pulse can easily be recognized. We explain the importance of radial transfer of water and solutes to regulate water and carbon fluxes inside trees and summarize current knowledge on how to interpret the pulse of trees using theoretical and empirical approaches. We show that even mortality of trees may be linked to interactions between xylem and inner bark. Throughout the text we identify unknown aspects of radial transfer that, once addressed, will help in interpreting the function and health of our green patients.

Xylem and phloem

The force required to lift water against gravity, in some tree species for more than 100 m, originates largely from transpiration of water from leaves. To date the Cohesion–Tension Theory by Dixon and Joly (1895) captures best the underlying physical processes of water transport in xylem. Their theory explains how hydrogen bonds formed between water molecules (cohesion) and negative pressure (tension) in xylem conduits generated by loss of water molecules from leaves result in the upward movement of a continuous water column. The majority of water transported upwards in trees is lost during transpiration and only a relatively small proportion of liquid water will enter SE-CCC of the collection phloem that is in close contact with xylem cells in the veinlets of leaves. This water serves as carrier of organic molecules to various sinks and as a medium to distribute signals throughout the plant.

Until today, the 'Pressure Flow Hypothesis'—a concept based on an osmotically generated pressure gradient as a cause of mass flow in phloem (Münch 1930)—serves as the physical and physiological foundation to explain movement of solutes within this complex organ. Yet recently, its applicability in tall trees with very long transport pathways has been questioned (see Turgeon 2010). Knoblauch and Peters (2010) may be correct by stating that our physical understanding of the 'bread-and-butter' function of phloem remains poor by exposing a number of unresolved issues that involve the long-distance transport of carbohydrates. Yet many different plant species have been studied to produce an incredible amount of the literature that embraces functions of phloem related to nutrition (e.g., Millard et al. 2006, Pfautsch et al. 2009, 2015*b*), transport of carbohydrates (e.g., van Bel 1990, 2003*a*, 2003*b*), micro-, as well as macro-elements and messenger molecules (e.g., Hannapel et al. 2013, Lucas et al. 2013, Pallas and Gómez 2013, Spiegelman et al. 2013), viruses (e.g., Hipper et al. 2013), as defense tool against pathogens (e.g., Will et al. 2013), and as a pathway for electrical signals (see references in Dinant and Lemoine 2010). Significant advances have also been made in research that assesses gene expression and characteristics of transporters and mechanisms related to loading and unloading of substrates (Lalonde et al. 2004, De Schepper et al. 2013*b*, Lucas et al. 2013).

Although these functions were studied in a range of woody and non-woody plants, the radial transport of water between inner bark that includes the phloem and xylem appears universal in woody plants, regardless of age, size or stature. Thus a thorough description of anatomy and physiological functioning of rays seems appropriate to be provided first.

Anatomy and physiology of wood rays

Linking inner bark with xylem

Since the initial work on phloem–xylem transfer phenomena (Stout and Hoagland 1939) we now have compelling visual evidence for bidirectional transport of water and nutrients between inner bark and xylem of angiosperms (Sano et al. 2005, Sokolowska and Zagórska-Marek 2012, Pfautsch et al. 2015*a*). Similar evidence for gymnosperms is yet to be produced. The early work of Ziegler (1965) and Höll (1975) established that radial transport is predominantly organized by movement through the symplastic space of rays. Ziegler used radioactively labeled sugars and ions to show that their movement in rays was considerably faster than expected if solutes were displaced solely by diffusion. The importance of plasmodesmata for radial transport of water was further confirmed by experiments with dry wood (Matsumura et al. 1998). After being called an 'undervalued pathway' 25 years ago (van Bel 1990), it is now clear that rays play an important role in whole-tree hydraulic regulation. Besides their role in translocation of solutes, the extensive work by Jörg Sauter and colleagues revealed the role of rays in metabolic processes related to seasonality of storage and remobilization of carbohydrates (e.g., Sauter and Neumann 1994, but see references in van Bel 1990).

Pfautsch et al. (2015*a*) presented a method that can assess in situ the movement of water from inner bark through rays into xylem by linking measurements of high precision point-dendrometers and leaf water potential with dye injections into inner bark tissue. Their study showed that dye entered ray parenchyma cells and travelled from phloem via the cambial zone into mature xylem (see Figure 3). Their study confirmed that water transport in rays varies in accordance with Ψ_x. Although water and dye may have entered rays using different pathways (e.g., aquaporins, sucrose transporters, diffusion), their ex situ experiment confirmed that the dye inside the rays was translocated by bulk flow of water and not by simple diffusion, in agreement with the work of Ziegler mentioned above. This observation provides further evidence that rays are actively involved in whole-tree hydraulic regulation in angiosperms. To date, two studies have investigated the radial conductivity of rays in sapwood of a range of gymnosperms (Domec et al. 2006, Barnard et al. 2013). Both studies concluded that radial conductance in this section of rays did not play a significant role in hydraulic regulation and functioning in *Pinus* and *Pseudotsuga* species.

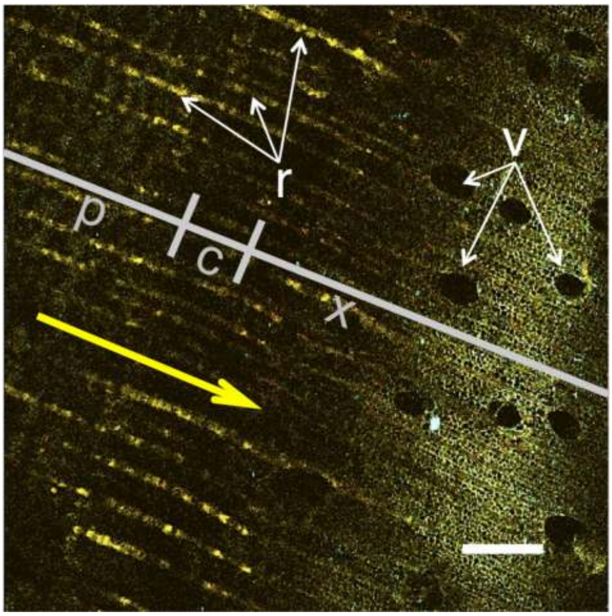

Figure 3. Confocal micrograph showing the transport of Fluorescein in ray parenchyma cells of *Eucalyptus saligna* Smith. Fluorescein was injected into inner bark tissue from where it was transported symplastically in rays from phloem, through cambial into xylem tissue. See Pfautsch et al. (2015*a*) for more details. c, cambial zone; p, phloem tissue; r, wood rays; v, xylem vessels; x, xylem tissue. The yellow arrow depicts direction of dye flow. Scale bar = 200 µm.

Anatomy of wood rays

Systematic analyses of ray anatomy across woody species date back to the pioneering work of Kribs (1935) that was completed by Carlquist (1988, 2001). The radial system of rays is formed from ray-initials embedded in the cambial zone. Depending on species, age and position within rays the orientation of individual ray cells can be upright or radially elongated (*procumbent*; Carlquist 2009, 2013). We refer to Lev-Yadun and Aloni (1995) for further information on the differentiation of rays. Ray cells are living, thin-walled parenchyma cells that interconnect by plasmodesmata to form the ray. Each cell contains a nucleus, vacuole, mitochondrion, cytoplasm and other organelles that help control cell function and metabolism (Frey-Wyssling and Bosshard 1959). They can also contain calcium oxalate crystals, cystoliths and silica bodies (Carlquist 2001). Ray cells share pit-connections with surrounding axial parenchyma and fiber cells in sapwood (Carlquist 2007*b*). These pit connections allow transfer of storage compounds into and out of axial parenchyma. Ray parenchyma cells in sapwood usually have lignified secondary cell walls that, once dried, can provide surprisingly high radial tensile strength (Burgert and Eckstein 2001). Yet, the radial and longitudinal tensile strength of rays in fresh wood is approximately half of that in dry wood (Burgert et al. 1999). Similar information on ray cells embedded in living bark tissue is missing. Along the entire length of transport phloem and regardless of angio- or gymnosperm species, uni- and/or multiseriate strands of these radially aligned parenchyma cells connect xylem with tissues of the inner bark.

The volume of rays in woody tissue of hard- and softwoods can vary from 5 to 33% (Siau 1984) and from 3 to 12% (Panshin and De Zeeuw 1980), respectively. Their capacity to store water in secondary xylem increases in parallel with their height and length (Carlquist 2001). The functional and anatomical diversity of rays appears limited in gymnosperms and it has been speculated that diversification of ray functioning was an evolutionary necessity to increase angiosperm competitiveness across diverse habitats (Carlquist 2009). This specialization helps explain the results of Domec et al. (2006) and Barnard et al. (2013) (see above) and underpins the relatively larger importance of rays in hydraulic regulation in angiosperms compared with gymnosperms.

Physiology of wood rays

Five distinct transport processes involving ray parenchyma cells can be identified (after Sauter 1982): (i) loading of solutes (and water) from the SE-CCC and surrounding tissues into the ray; (ii) bidirectional, radial transport inside the rays; (iii) passing through the ray-initials in the cambial zone; (iv) unloading of solutes (and water) into the xylem and (v) exchange processes with wood fibers and axial parenchyma cells in secondary xylem.

Water can easily diffuse through the plasma membranes from SE-CCC into rays and back following gradients of Ψ (see Principles of radial flow of water between xylem and inner bark). Relatively little is known about the loading/unloading mechanisms of solutes (mostly carbohydrates) between these cell types. In conifers the SE-CCC can be in direct plasmic contact with ray parenchyma cells or indirectly via Strassburger cells. Another pathway involves unloading from SE-CCC into phloem parenchyma before loading into ray parenchyma cells. This pathway requires solutes to pass the apoplast between phloem and ray parenchyma cells and this mechanism (i.e., apoplastic loading) is believed to be the dominant route of carbohydrate transfer in angiosperms (Sauter 1982, van Bel 1990). A membrane-bound ATPase generates the required proton gradient to drive sucrose-proton co-transport in and out of participating cells (Sauter 1982). Empirical evidence for apoplastic loading comes from tracer injections into inner bark tissue with subsequent uptake of the tracer into ray parenchyma (Pfautsch et al. 2015*a*).

Once inside the ray, solute transport follows gradients of Π, whereby acto-myosin-induced widening of plasmodesmata assists in transfer between individual ray parenchyma cells. The internal transport in ray cells could be assisted by cytoskeletal structures of microtubule and microfilament bundles that extend to the cambial zone where they collapse and become available as building materials for cambial growth (Chaffey and Barlow 2001). In the xylem section of the ray carbohydrates can be accumulated in vacuoles or granules or be exported into surrounding axial parenchyma cells where they can be stored as fuel for prospective requirements, such as bud development (e.g., Sauter and van Cleve 1994).

Compared with the limited understanding of transport between SE-CCC and ray cells, the mechanisms and cellular structures involved in bidirectional exchange processes between rays and xylem conduits are relatively well known and are reviewed by van Bel (1990). Briefly, solutes leave the symplast of ray parenchyma by substrate-mediated proton co-transport into the apoplastic space between the ray and conduit. During this process they must pass a ‘safety layer’ that comprises of the same electron density as primary cell walls and is constructed from pecto-cellulosic composite materials (see references in van Bel 1990). The exact role of this safety layer is yet to be discovered, but its involvement in prevention of tylosis spreading into ray cells as well as a hydrostatic support for the adjacent contact pits has been suggested (van Bel 1990). Following a concentration gradient the solutes pass through these pit membranes that are made of loosely woven networks of cellulose fibers (Siau 1984). These pits occur in high numbers across contact fields (Figure 4).

While this section on rays provided the anatomical foundation necessary to understand the basic organization of radial flow, the following section will explain current theory, modeling approaches and empirical findings that concern this flow. The focus will range from cells to the whole-organism level, showing how rays are involved in signal propagation and how gradients in water and osmotic potential generate the pulse in tree stems.

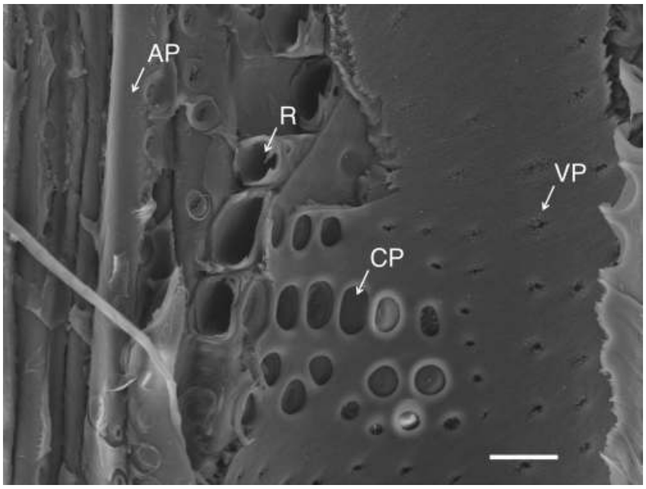

Figure 4. Scanning electron image (working distance = 6.3 mm; acceleration voltage = 10 kV) of the contact field between ray parenchyma (R) and the inner wall of a xylem vessel in sapwood of *Eucalyptus regnans* F. Muell. (L517). Visible are large contact pits (CP) where rays intersect the vessel wall in a tangential direction. Also visible are numerous vestured pits (VP) that connect the vessel with axial parenchymal (AP) cells. Scale bar = 10 μm.

Concepts, theory and modeling of radial transfer

Principles of radial flow of water between xylem and inner bark

The direction and rate of water movement (J, m^3 s^{-1}) between the xylem and inner bark is determined by the water potential difference between xylem (Ψ_x, MPa) and inner bark (Ψ_{ib}), and hydraulic conductance between them (k, m^3 MPa^{-1} s^{-1}):

$$J = k(\Psi_x - \Psi_{ib}) \tag{1}$$

Disregarding gravity, water potential consists of pressure potential (P) and osmotic pressure (Π):

$$\Psi = P - \Pi \tag{2}$$

Osmotic pressure consists of four components, namely its molar concentration of solutes c, the gas constant R, the temperature T (measured in K) and the reflection coefficient for solutes across cell membranes d (unitless). The osmotic pressure is estimated here according to the Van't Hoff's relation, which is a good approximation for dilute solutions (Nobel 1999). For a perfectly semipermeable membrane $d = 1$. For substances found included or excluded from plant cells, for example sucrose, d across a cell membrane is at least close to one (Nobel 1999), and this value has been used in modeling studies of xylem and phloem water exchange (e.g., Génard et al. 2001, Steppe et al. 2006, Sevanto et al. 2011, Mencuccini et al. 2013, but see Cabrita et al. 2013 for an exception).

Area-specific hydraulic conductance L is defined as the hydraulic conductance k divided by the cross-sectional area A through which transfer occurs:

$$L = \frac{k}{A} \tag{3}$$

The radial conductance L (m^3 m^{-2} MPa^{-1} s^{-1}) between the xylem and inner bark has been found to be of the order 10^{-8} to 10^{-7} m^3 m^{-2} MPa^{-1} s^{-1} in trees (e.g., Génard et al. 2001, Steppe et al. 2006, Sevanto et al. 2011, Mencuccini et al. 2013). Area-specific hydraulic conductance is largely dependent on temperature due to the influence of temperature on the viscosity of phloem sap (e.g., Steppe et al. 2012 for a controlled laboratory study, Mencuccini et al. 2013 for a field study) as well as on aquaporin activity (Steppe et al. 2012). Additionally, solute concentration will influence viscosity and thus can be expected to impact area-specific conductance. The direction of radial water transfer, however, changes transiently according to the water status of the xylem and inner bark.

Although d is frequently assumed to be close to 1, in reality, SE-CCC are not perfectly semipermeable and have been found to be somewhat 'leaky' (e.g., Thorpe et al. 2005). This means that solutes are lost both by advection with the radial exchange of water between xylem and inner bark (Pfautsch et al. 2015*a*) and also by diffusion from SE-CCC directly (e.g., Patrick 1997). Solutes can also be re-loaded back into sieve elements (e.g., Thorpe et al. 2005). Mechanisms for the continuous leakage and retrieval of carbohydrates out and back into the phloem have been proposed several times (Minchin and Thorpe 1987, Gould et al. 2004, van Bel and Hafke 2005, De Schepper et al. 2011) and are consistent with observations of losses of ^{11}C at constant flow velocity along transport phloem of oak trees (De Schepper et al. 2013*b*).

Mathematically, the case of leaky SE-CCC translates into d being <1. Cabrita et al. (2013) demonstrated in a modeling study that leaky SE-CCC would markedly affect radial transfer of water and bulk flow inside SE-CCC. The solute leakage-retrieval mechanism could also effectively act as a 'solute-relay' mechanism if solutes are leaked on one side of a sieve plate and reloaded on the other (e.g., van Bell 2003*a*, De Schepper et al. 2013*a*). Theoretically, this could result in local turgor pressure gradients within transport phloem and help to constrain turgor pressure differences between sources and sinks.

Time scales for radial transfer of water

Equation (1), describing the radial transfer of water J between the inner bark and xylem, can be employed to estimate the time-scales of the process. The changes in tension in xylem act as the driving force for the radial transfer of water stored in inner bark towards the transpiration stream or back towards the bark. This in turn changes the water potential of the inner bark ($J > 0$ when water flows from xylem to inner bark and $\Psi_x > \Psi_{ib}$). We further define $\Psi_{ib} = P_{ib} - \Pi_{ib}$ as the turgor and osmotic pressure components of the inner bark water potential, respectively. Following Hooke's Law, the changes in bark turgor pressure over time caused by the hydraulic radial transfer can be expressed as (cf. Mencuccini et al. 2013, Eq. (S1)):

$$\frac{dP_{ib}}{dt} = \frac{E_{ib}J}{AR^*_{ib}} \tag{4}$$

where R^*_{ib} is a reference bark radius (i.e., the bark radius on one side), A the area of hydraulic flow between inner bark and xylem for an inner bark volume V^*_{ib} (i.e., $V^*_{ib} = AR^*_{ib}$) and E_{ib} the apparent elastic modulus of the tissue. Substituting the expressions for J in Eqs (1) and (3) into Eq. (4) and simplifying, the following first-order ordinary differential equation of a linear time-invariant system can be formulated:

$$\frac{dP_{ib}}{dt} = a(\Psi_x - (P_{ib} - \Pi_{ib})) \tag{5}$$

where a is defined as

$$a = \frac{E_{ib}}{R^*_{ib}}L \tag{6}$$

This treatment of the problem follows Mencuccini et al. (2013, Eq. (S1)), even though the derivation presented here is novel. The advantage of the present derivation is that it retains Ψ_x as the external driving force for the radial transfer of water between inner bark and xylem and it focuses on the examination of the time dynamics of the water relation components of inner bark. This derivation allows achievement of an analytical solution of the problem.

Ψ_x is a function of time t and a is the inverse of the time constant of the system. Π_{ib} can vary over time (e.g., as a function of vertical changes in phloem solute transport), or can be treated as a constant—as in the following numerical example where it is set at $\Pi_{ib} = 2$ MPa. These equations treat the inner bark as a hydraulic storage that passively follows changes in the external forcing variable, namely Ψ_x.

The differential equation in Eq. (5) can be solved analytically under some conditions. By way of illustration, we can assume that Ψ_x changes diurnally as a function of $\mathrm{Sin}[2\pi t]$ around a starting value of $\Psi_x = -1$ MPa, assuming that Ψ_x cycles with amplitude of 2 MPa units from a daily minimum of −2 MPa to a daily maximum of 0 MPa. We also set the boundary condition for turgor pressure at P_{ib} $(t = 0) = 1$ MPa. In this case, the general solution of Eq. (5) in terms of Ψ_{ib} as a function of time t and parameter a can be obtained by integration as

$$\Psi_{ib} = \frac{e^{-at}(2a\pi + e^{at}((a^2 + 4\pi^2) - 2a\pi\cos[2\pi t] + a^2\sin[2\pi t]))}{a^2 + 4\pi^2} - 2 \tag{7}$$

The sine and cosine functions in Eq. (7) give the oscillations imposed by Ψ_x whereas the initial negative exponential gives the delay in the response of bark water relations to the forcing by Ψ_x. An illustrative example of the predicted behavior of bark and xylem water potentials and diameters for different sets of parameter values is provided in Figure 5. Based on Eq. (7), the water potential of inner bark always lags behind xylem water potential and shows a reduced amplitude, depending on the values of a.

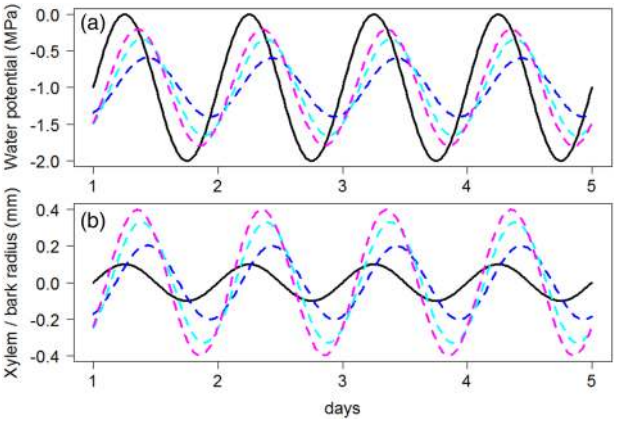

Figure 5. Theoretical illustration of predicted changes in bark properties in relation to changes in xylem properties over a time interval of four diel cycles. (a) Changes in bark and xylem water potentials. The black curve is xylem water potential, and the pink, blue and turquoise curves represent bark water potentials for three different parameter settings. (b) Changes in bark and xylem radii. The black curve is xylem radius, and the pink, blue and turquoise curves represent bark radius for three different parameter settings. The following set of parameters was used for the simulations: xylem radius = 100 mm; bark radius = 10 mm; bark elastic modulus = 20 MPa; bark radial hydraulic conductivity = 10 e^{-8} (turquoise), 20 e^{-8} (blue) or 30 e^{-8} (pink) m MPa^{-1} s^{-1}. One period of the xylem water potential cycle equals 2π. See text for further explanations.

For large values of a (e.g., $a \approx 10$, corresponding to a time constant of 0.1), the lag becomes very small and the amplitude of fluctuations in Ψ_{ib} is almost identical to fluctuations in Ψ_x. Since the value of a is determined by the radius of inner bark, as well as radial hydraulic conductivity and elastic modulus (Eq. (6)), large and fast changes in Ψ_{ib} can occur for combinations of thin, rigid and conductive inner bark tissues. It is possible that this arrangement constrains the time constant of the inner bark. For example, for a constant thickness, the gains obtained by having a woody and rigid inner bark may be offset by a lower radial conductivity. Similarly, it is possible that very thick inner bark may require higher values of the bulk radial conductivity L. Despite the smaller water potential fluctuations in the bark and xylem diameters being larger than bark diameters, the larger elasticity of the bark and the high values of radial conductivity can result in bark diameter changes being larger than xylem radius changes, such that most of the movements observed on the stem are the product of the pulse occurring in the bark, not the xylem.

As stated above, available empirical information suggests $L \approx 10^{-8}$ m MPa^{-1} s^{-1} (e.g., Sevanto et al. 2002, 2003, 2011, Hölttä et al. 2006, Mencuccini et al. 2013), whereas the apparent elastic modulus of inner bark is in the order of 10 MPa (e.g., Alméras 2008, Sevanto et al. 2011, Mencuccini et al. 2013). For a quantitative application of these relationships, it is necessary to account for additional mechanical effects not included in this simplified model, such as anisotropy of inner bark in three dimensions (i.e., the difference between tangential and radial elastic moduli), the different mechanical behavior of cell walls and water in transmission of the elastic strains and a non-negligible Poisson's ratios in bark material (cf. Alméras 2008).

The approach followed here of employing Eq. (1) to describe the radial transfer as a function of water potentials and radial hydraulic conductivity is similar to the phenomenological representation of a coupled resistor–capacitor that was developed in earlier studies (e.g., Wronski et al. 1985). However, the use of a fixed-capacitance concept can be avoided by directly measuring diameter changes of stem and inner bark to provide a more direct link to our current understanding of the physical and biological controls of membrane conductivity.

Modeling the hydraulic nexus of xylem and inner bark

Current conceptual and numerical models often incorporate the exchange of water between inner bark and xylem along a gradient of water potential (Steppe et al. 2006, Sevanto et al. 2011, Mencuccini et al. 2013). However, others assume equilibrium of water potentials in the tissues involved (Thompson and Holbrook 2003*a*, Lacointe and Minchin 2008, Hall and Minchin 2013). Although assuming equilibrium conditions, the latter models implicitly assume water exchange between xylem and inner bark. These models are based on the a priori assumption that conductance between the xylem and inner bark is so high that there is no loss in water potential when water moves between the tissues.

Models of phloem transport have mainly resorted to numerical solutions, because the flow equations are too complicated to be solved analytically. However, analytical solutions have been found for steady-state cases when a set of simplifying assumptions and boundary conditions at the sources and sinks were used (e.g., Phillips and Dungan 1993, Pickard and Abraham-Shrauner 2009, Jensen et al. 2012). Fermer et al. (1975) predicted with a dynamic model that pressure and sugar concentration signals can propagate faster than the rate of mass flow, and that dynamics of xylem water potential, in addition to the dynamics of sugar loading and unloading, influenced the fluctuation of the pressure and solute-concentration signals. Thompson and Holbrook (2003*b*) formulated the rate of movement of these pressure signals as a function of axial decline in P and osmotic concentration.

Empirical evidence for the occurrence of very rapid transfer of pressure-concentration signals is however rare. The majority of the existing reports stress instead that lateral transfer of carbohydrates to storage sites tends to decouple short-term photosynthetic production from sink activity (e.g., Thorpe and Minchin 1996, van Bel and Knoblauch 2000). For example, the removal of rapidly growing fruits of *Capsicum annuum* L. did not depress photosynthesis for several hours afterwards (Hall and Milthorpe 1978). Similarly, stem carbohydrate reserves have been shown to represent a main source of substrate for stem growth in both annual plants (Biscoe et al. 1975) and deciduous trees (Barbaroux and Bréda 2002, Gessler et al. 2004, Helle and Schleser 2004, Weigl et al. 2008, Maunoury-Danger et al. 2010, Offermann et al. 2011). However, this may not always be the case, as experiments have shown that interruption of carbohydrate fluxes can severely reduce radial growth (e.g., Daudet et al. 2005). Observations of fast-travelling signals may have been hampered by the speed with which these changes can take place. For example, Gould et al. (2005) used a sieve-element pressure probe prepared by gluing a pressure probe to an exuding aphid stylet. Reductions in phloem loading were caused by the replacement of the air supply with nitrogen. A decline in phloem osmotic and hydrostatic pressure, caused by lower sucrose concentrations, was evident at time scales of minutes, as predicted by Münch theory. Similarly, Minchin et al. (1994) used labeled, short-lived ^{11}C to show that rapid changes (in the order of tens of minutes) in partitioning of carbon took place after shading of leaves or cooling of roots. Any transport system will also convey information about rapid changes in its water potential (or positive turgor, in the case of the phloem), as water is nearly an incompressible liquid. Changes in turgor of a compressed liquid will occur more or less immediately, depending on other properties such as elasticity of cell walls and radial conductivity between xylem and inner bark via rays.

Resistance to transport in phloem has been modeled using the diameter of the sieve-element lumens and the size and number of pores in the sieve plates (e.g., Thompson and Holbrook 2003*a*), although the situation is complicated by the fact that the pores in the sieve plates may be occluded due to sampling artifacts (e.g., Knoblauch and Oparka 2012). Additional resistance to phloem transport also originates from the larger viscosity of phloem sap in relation to the xylem sap. Naturally, viscosity of phloem sap increases with increasing concentration of sugars and decreasing temperatures. Increasing concentration of sugars creates a larger turgor pressure and results in a larger sugar transport rate for a given phloem sap flow rate. However, if phloem sap becomes too concentrated its flow rate will decrease due to an increase in viscosity.

Theoretically, a phloem sugar concentration that maximizes the sugar transport rate does exist (Lang 1979, Jensen et al. 2012), but its exact value is dependent on the assumptions made (temperature, rates of loading and unloading, physical shape of SE-CCC, etc.), and composition of the sap. Jensen et al. (2012) predicted the optimal sugar concentration based on maximizing the flow rate to be ~30% v/v, and found this to match well with concentrations typically found in plants. Interestingly, Woodruff (2014) found that the relative proportions of fructose and glucose increased in relation to sucrose with increasing water stress in tall Douglas-fir trees. This effect could help preventing sap from becoming too viscous as fructose and glucose change the viscosity of the solution less than sucrose for a given change in osmotic pressure.

As of today, many questions related to phloem transport remain and it appears helpful to turn our attention briefly to xylem where an analogous situation can be found. In the xylem, vessel tapering and changes in the leaf-to-sapwood area are known to be involved in limiting the negative consequences of increasing transport distances with size (e.g., Mencuccini and Grace 1995, West et al. 1999). Empirical as well as theoretical studies have reported very similar changes in the diameter of phloem sieve tube elements as a function of position within the tree (Petit and Crivellaro 2014, Jyske and Hölttä 2015) and with tree size (Mencuccini et al. 2011). In addition, the phloem cross-sectional area was found to scale closely with the current year xylem cross-sectional area (Jyske and Hölttä 2015). So, to what degree are anatomical adjustments in sieve tube elements promoting safety and continuity of phloem transport over long distances? We would like to remind the keen reader here that in contrast to transport in xylem, gravity aids phloem transport with increasing tree height.

Although the basics of solute translocation in phloem according to the Münch hypothesis are rather well understood, at least in theory (see van Bel 2003*a*), other mechanisms of phloem functioning remain fuzzy. This uncertainty begins when linking phloem transport to whole-tree function (e.g., Ryan and Asao 2014). As stated above, short-term changes in sink dynamics appear decoupled from photosynthetic carbon fixation rates. However, over longer time intervals phloem transport does couple leaf gas exchange and sink dynamics. Processes such as leaf photosynthesis, local woody tissue photosynthesis, phloem sugar loading, sugar to starch polymerization, phloem unloading and sugar consumption by sinks during growth and respiration are all dependent on local carbohydrate status, which is propagated through the phloem in trees. This scenario presents a large range of conditions where our understanding of regulatory processes is incomplete.

The understanding and modeling of the xylem and phloem transport at the whole-tree level is complicated by the fact that this particular system has many feedback and feed-forward loops (such as cavitation and changes in phloem sap viscosity). Moreover, we have to deal with processes that operate at different time scales due to varying transport resistances and capacitances related in part to the elasticity of the tissues. Typically, environmental conditions as well as production and consumption of sugars change much faster than solute concentration and osmotic pressure in phloem. It follows that phloem transport rarely remains at the steady-state conditions that would be required to study some of the above-mentioned unknowns.

Capacitance as source for the pulse

Estimates of capacitance at the tree scale

In trees, capacitors are locations from where stored water can be mobilized to mitigate increasingly large rates of transpiration without excessive decreases in Ψ_x. In this context, capacitance is the change of water content of a tissue per unit change in water potential, either in absolute or in relative units. Sites of water storage have been categorized into three components (Tyree and Zimmermann 2002): (i) capillary water, (ii) water released from living cells due to their elasticity and (iii) water released by cavitation. The majority of capillary water is utilized and stored mainly at Ψ_x close to zero so its physiological significance is likely small (Tyree and Yang 1990). This is owed to the inverse relation between the tension required to drain a capillary and diameter of the volume of water stored in the capillary space as described by Laplace's Law. The amount of water released by cavitation can be very large at the relevant range of Ψ_x (Hölttä et al. 2009*b*) but this mechanism has a downside since hydraulic conductivity decreases in concert, and refilling of embolisms may take time and metabolic energy, or not occur at all. This section will focus therefore largely on water released from living cells.

A significant number of estimates of tree internal water storage exist in the literature and have been summarized by Scholz et al. (2011). The most frequently employed methods to derive estimates of internal water storage consist of determining the water release isotherms of wood (i.e., Tyree and Yang 1990), which is a variant of the pressure–volume technique (i.e., Tyree and Hammel 1972) applied to the sapwood of trees (e.g., Meinzer et al. 2003, Scholz et al. 2007). Another approach was developed by Vergeynst et al. (2015), where data from acoustic emissions caused by cavitation were combined with measurements of changes in diameter and volumetric water content of branches to yield estimates of capacitance. Other approaches determine time lags in sap flux densities between sensors at different heights in a tree (e.g., Phillips et al. 1997, Goldstein et al. 1998, Meinzer et al. 2004, Čermák et al. 2007, Köcher et al. 2013) or between sensors at the bottom of a tree and the vapor fluxes measured above the canopy using eddy covariance techniques (Kumagai et al. 2009). Estimates of tree water storage based on the calculation of the time lags between fluxes at different heights are a function, among other things, of the amount of water that is extracted from storage tissues relative to transpiratory losses, but also of the changes in environmental conditions at different canopy heights. Disentangling these two components may be difficult but informative (Burgess and Dawson 2008). It was noted that studies that estimated water storage using Granier-type sensors might be biased by the slow response time of this sensor type to changes in flow rates (Burgess and Dawson 2008). One approach that circumvents this issue is the use of isotopically labeled 'heavy water' to estimate capacitive effects (James et al. 2003, Meinzer et al. 2006).

Comparing the total volume of water from stores with total daily water use of trees can help approximate the physiological significance of capacitance. Using a mathematical approach based on measurements of tree water use, Pfautsch and Adams

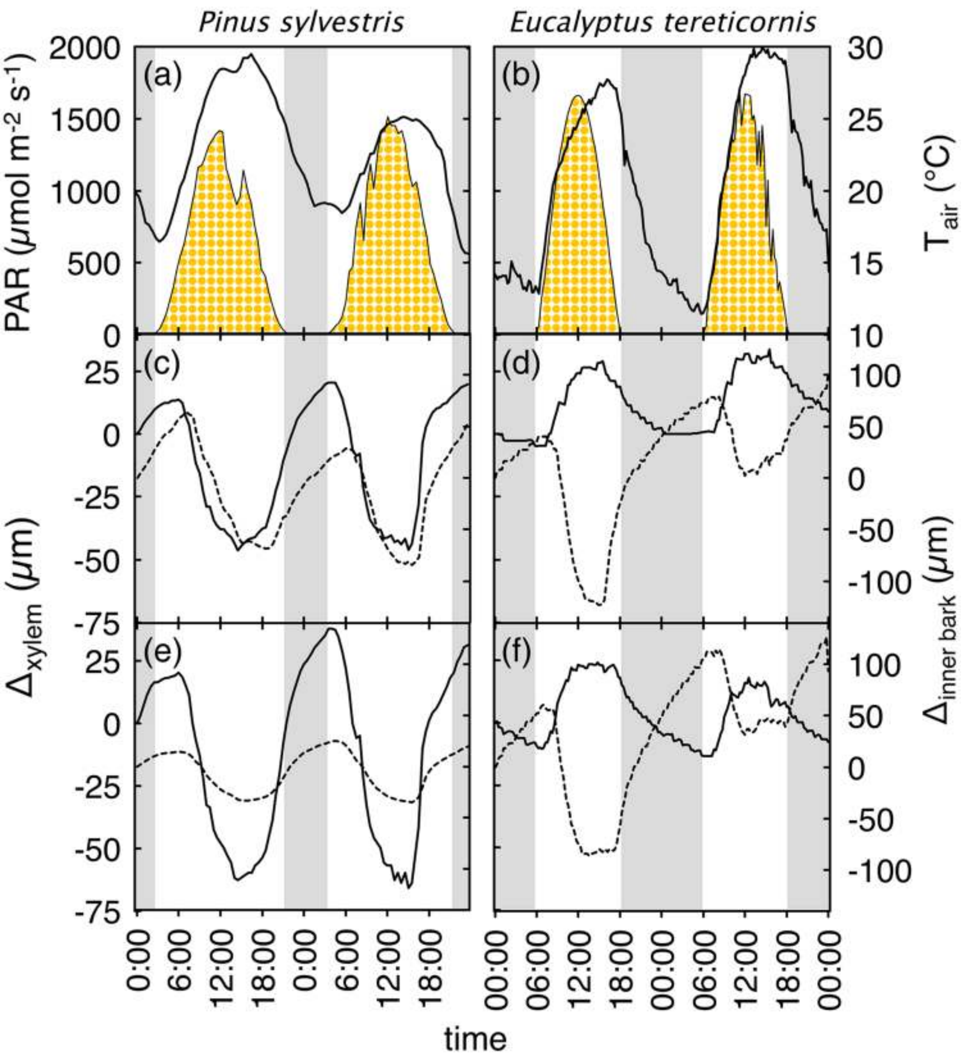

Figure 6. Representation of different strategies of hydraulic coupling between xylem and inner bark in stems of a gymnosperm species ($n = 3$ trees, 15 m tall) and an angiosperm species ($n = 2$ trees, 8 m tall). Error bars are omitted for clarity. (a and b) Environmental conditions (air temperature (T_{air}) = black line, yellow dotted area = photosynthetic active radiation (PAR)). Data in (a) represent conditions of 8–9 July 2006 at the SMEAR II research site in Hyytiälä, southern Finland; data in (b) were recorded 17–18 March 2014 at the Hawkesbury Forest Experiment, Richmond, Australia. Solid lines in (c–f) depict change in xylem radius (Δ_{xylem}), dotted lines the change in diameter of inner bark ($\Delta_{inner\ bark}$), using the respective value of each trace measured at midnight of the first day as reference point zero. Data in (c) and (d) were collected from the stem in the upper canopy section, data in (e) and (f) were recorded at the stem base.

(2013) demonstrated that tall eucalypt trees increasingly depended on stored water to maintain hydraulic integrity during drought and heat wave conditions. The authors showed that relative to the volume of water transported during the day, nocturnal water transport increased following hot days with high vapor pressure deficit. These observations emphasize the importance of nocturnal water transport in restoring capacitance (e.g., Zeppel et al. 2014).

The amount of water retrieved from stores inside mature trees can account for up to one-third of daily water loss due to transpiration (Čermák et al. 2007) although this proportion was found to be much higher in some studies (e.g., Goldstein et al. 1998, Zweifel et al. 2001). The importance of stored water for whole-tree hydraulic functioning increases with tree size (Scholz et al. 2011), buffering some of the decrease in whole-tree hydraulic conductance (Goldstein et al. 1998, Phillips et al. 2003). The increasing relevance of capacitance with increasing tree height can also be understood from the scaling of leaf area to tree mass with a scaling exponent of three-quarters (West et al. 1999), indicating that transpiration rates increase less compared with the volume of trees.

Significance of bark and xylem diameter changes for estimates of capacitance

That trees do have a 'pulse' has been known since the work of Mallock (1919) and MacDougal (1924), which related changes in stem diameter to the water status of trees. The invention of precision band dendrometers (Reineke 1932) has been instrumental to measuring the pulse, and countless reports exist that relate water deficits to stem contraction (see review by Clark et al. 2000). This technology has been essential to understand growth dynamics of trees and helped increase the accuracy of growth models for forests across all biomes. However, using band dendrometers does not allow for a deeper understanding of how environmental conditions impact radial transfer of water and hydraulic functioning of trees more broadly. This is owed to the fact that the recorded signal cannot be separated into an inner bark and a xylem component. Here particularly the development of highly sensitive point dendrometers (e.g., Clark et al. 2000, Zweifel et al. 2000), but also the use of frequency domain reflectometry (e.g., Hao et al. 2013), magnetic resonance imaging (e.g., Windt et al. 2006), laser scanning confocal microscopy (Pfautsch et al. 2015*a*) and an increased modeling capacity (e.g., Mencuccini 2003, Hölttä et al. 2006, 2009*a*, Steppe et al. 2006) has propelled our understanding to new levels.

The contribution of xylem tissue to stem diameter change can vary from being quite small (e.g., Zweifel et al. 2000, Sevanto et al. 2011), to being one-third (Sevanto et al. 2002) and in at least some cases even surpass the dimensional changes of inner bark (Zweifel et al. 2014). The exact contribution can be determined by simultaneous measurements of whole stem and xylem diameter changes. The change in xylem diameter can be subtracted from dynamics of the whole stem (e.g., Sevanto et al. 2002), resulting in data streams that exclusively describe the dynamic changes in diameter of xylem and inner bark. However, even following this refined procedure, the signal attributed to inner bark still consists of two components: the irreversible and plastic component due to growth, and the reversible and elastic component due to changes in water content. Typically, the majority of changes in water content are the result of changes in water potential (e.g., De Schepper and Steppe 2010, Sevanto et al. 2011, Mencuccini et al. 2013), although in some cases the changes in osmotic concentration seem to dominate (Vandegehuchte et al. 2014, Zweifel et al. 2014).

To date, simultaneous measurements of radial variation of inner bark and xylem diameters have revealed two different patterns. The characteristic contraction of the inner bark during the day is congruent between the two examples shown in Figure 6, but xylem dynamics differ substantially between the selected gymno- and angiosperm species. According to the theory on hydraulic functioning presented above and in Figure 5, data from gymnosperm species confirm that a decline in Ψ_x causes xylem to contract (e.g., Zweifel et al. 2000, Sevanto et al. 2002, 2008), matching data traces in Figure 6c and e. Following a phase lag that depends on Ψ_x, contraction of inner bark follows, in sync with model predictions (Figure 6c and e). These patterns are consistent for the upper and lower sections of tree stems. However, in the example shown, the amplitude of change in xylem thickness was larger at the base of trees (103.5 vs 66.9 μm), whereas that of inner bark was larger at the upper stem (148.6 vs 60.0 μm). This may be owing to differences in the proportional contribution of inner bark and xylem tissues to total stem radius at a given sample height.

The second pattern, observed in *Eucalyptus* species (Figure 6d and f but also see Zweifel et al. 2014, Pfautsch et al. 2015) shows a markedly different pattern. The contraction and expansion of xylem and inner bark are diametrically opposed—incongruent with patterns recorded using other angiosperm species (e.g., Sevanto et al. 2011). When inner bark contracts during the day, xylem radius increases. Moreover, the amplitude of radial change at the upper stem and at the base is remarkably similar, yet much lower in xylem (i.e., upper stem = 38.5 μm; base = 37.6 μm) compared with that of inner bark (upper stem = 225.4 μm; base = 212.1 μm). In addition, the contraction or expansion of inner bark tissues lags minimally behind the opposite dynamic of xylem, indicating a tighter coupling in these diffuse porous angiosperms compared with the gymnosperm species.

While Zweifel et al. (2014) attempted to explain the unfamiliar pattern observed in eucalypts with radial transfer of water from inner bark into non-lignified, elastic immature xylem cells, a different mechanism could be proposed that involves reversal of radial transport of carbohydrates. As Ψ_x declines, water and carbohydrates are drawn from phloem towards xylem in rays. While water enters the xylem vessels, the carbohydrates accumulate in rays and neighboring xylem parenchyma cells where they slowly increase the osmotic potential of rays (Π_r), resulting in influx of water, hence expansion of the xylem. Once Π_{ib} exceeds Π_r and Ψ_x increases due to stomatal closure, water and carbohydrates from xylem and ray parenchyma cells are drawn back into the inner bark. Although there is no empirical evidence for such a mechanism, it closely aligns with work of Nardini et al. (2011) that links movement of carbohydrates with hydraulic functioning of the stem. Certainly, future research should rectify the different patterns observed.

The volume of water released elastically from living cells of any tree species may be estimated from dendrometer measurements. The recorded patterns result mostly from de- and rehydration of stem and bark tissues, assuming the change in volume corresponds to the volumetric change in water. This assumption has been found to be reasonable as long as no phase change (i.e., cavitation) occurs (e.g., Simonneau et al. 1993, Zweifel et al. 2000) and as long as the air fraction of the inner bark is small and does not change markedly. For example, in bark of walnut such a phase change occurred after bark had contracted 400 μm (Cochard et al. 2001). The changes in bark volume can be derived geometrically from diameter changes (Čermák et al. 2007):

$$dV = \{\pi[(R^{*}_{ib} + dR_{ib})^2 - R^{*2}_{ib}]\}\ l \tag{8}$$

where d*V* is change in volume and *l* is length. Alternatively, if dimensional changes are not measured, the amount of water released elastically from storage can be calculated from the change in pressure (dP_{ib}), elastic modulus of the tissue (E) and tissue volume (V):

$$dV = \frac{dP_{ib}}{E} V \quad (9)$$

For a typical E of 20 MPa (Nobel 1999), a change of 0.5 MPa in water potential corresponds to a 2.5% change in volume, which is the typical diurnal order of magnitude for relative change in phloem volume calculated from stem diameter changes at the base of a tree (e.g., Sevanto et al. 2002, 2011, Mencuccini et al. 2013). Within a tree, the relative amount of water (i.e., dV/V) taken from storage tends to be proportionally larger moving towards the tree apex and for smaller stem/branch diameters (e.g., Wronski et al. 1985, Sevanto et al. 2002, Čermák et al. 2007, McCulloh et al. 2014). This is caused by several effects, including the apparent change in the ratio of elastic bark tissue (lower E) to the rigid xylem tissue towards apical sections of stems and branches (Jyske and Hölttä 2015).

As mentioned above, assessing the contribution of inner bark separately from that of the wood to the tree internal water storage requires separate monitoring of the xylem and the inner bark displacements, which is not frequently carried out. Alméras (2008) tabulated the results from the few studies where the contributions of wood and inner bark to total plant volume changes—and therefore water storage—could be obtained. The contribution of the inner bark (as a proportion of the contribution of inner bark plus wood) to total internal water storage varied between a minimum of 46% observed in a beech sapling (Alméras et al. 2006) to a maximum of 95% for cotton plants studied by Molz and Klepper (1973). It is worth noting that this analysis did not account for the changes in inner bark osmotic concentration due to phloem transport (Mencuccini et al. 2013) or for xylem diameter changes and consequent water release following cavitation (e.g., Rosner et al. 2010). The approaches based on monitoring of stem diameter variations have additional limitations, in that the quantification is valid only for the cross section at which the point measurements are made. Given that the thickness of the bark varies significantly along the vertical axis of a tree, direct measurements using point dendrometers would need to be collected from several positions along the entire flow path of water, including stem and branches, to quantify internal water storage at the scale of the entire tree.

Taking an ecological perspective on capacitance, one would expect the importance of capacitance to vary along a gradient of water limitation from mesic to xeric environments. Evidence supports such an expectation. The capacity to develop successive cambia that generate concentric internal phloem tissue has been shown to increase with the degree of water stress that plants, including trees, shrubs and lianas, regularly experience (Robert et al. 2011). Here stress is defined as either direct shortage of fresh or dependence on saline water (e.g., mangroves). The production of additional, internal phloem tissue results in increased water storage capacity due to the high elasticity of phloem parenchyma cells (Carlquist 2007*a*). The fact that production of secondary phloem is not an omnipresent feature in woody plants from water-limited environments may be explained by a cost–benefit analysis of maintaining multiple vs singular layers of cambial tissues (Robert et al. 2011). Such analyses are currently missing.

Radial transfer and drought

Water transported under tension in xylem is in a metastable state, meaning that it remains liquid below its vapor pressure. The water column in a single vessel can rupture when microscopic voids of air that are trapped in conduits expand as a result of increasing tension between water molecules. The process is known as 'air seeding' and leads to conduit embolism with subsequent loss of conductivity in the xylem (e.g., Salleo et al. 2000). It is this metastable state of water transport that poses a real threat, as excessive embolism can ultimately lead to tree mortality (Brodribb and Cochard 2009).

The capacity to reverse xylem embolism is likely to differ among plant organs along the pathway of water (i.e., in roots, stem, twigs, petioles, leaf veins; Bordersen and McElrone 2013). Refilling of xylem embolism in the woody parts of trees potentially involves actively generating positive pressure in the phloem and/or radial transport of carbohydrates from phloem into xylem, although a new theory that uses the disjoining pressure concept of thin-films has just surfaced (Gouin 2015). A variant of the first mechanism to reverse embolism in xylem conduits has also been suggested. This mechanism involves use of carbohydrates produced in xylary chloroplasts, which could suffice to provide local energetic and carbohydrate requirements for the repair of embolized conduits (Steppe et al. 2015 and references therein). It is well known that phloem girdling reduces embolism refilling below the girdle (Salleo et al. 1996, Zwieniecki and Holbrook 2009, Nardini et al. 2011); girdling has been suggested to hinder embolism refilling, possibly due to decreases in phloem pressure and decreases in radial transport of solutes to xylem. Some role of carbohydrates in the repair of embolism seems thus likely, be it as metabolic source for energy or to generate osmotic gradients.

The water necessary to transport carbohydrates in phloem must originate from xylem. It is thus reasonable to speculate that the capacity for radial transfer of water plays a major role in surviving drought. A rising number of theoretical and empirical studies of tree mortality suggest that water limitation can impair the transfer of water and carbohydrates (e.g., McDowell and Sevanto 2010, Sala et al. 2010, Mitchell et al. 2014, Sevanto et al. 2014). Both, water and carbohydrates seem necessary components for reversal of embolism (Nardini et al. 2011, Secchi and Zwieniecki 2011) and possibly wider osmotic regulation. Nardini et al. (2011) hypothesized that after a calcium-induced depolymerization of starch, ‘simple sugars’ are actively deposited into the embolized vessel. Here they act as osmolytes that draw water and additional carbohydrates from the phloem through ray parenchyma into the vessel. This mechanism is yet to be experimentally confirmed. Manipulative experiments are necessary to identify the regulatory mechanisms that determine when water is used to support CO_2 uptake, facilitating mobilization of stored carbohydrate reserves in parenchymal tissues or to dilute highly concentrated phloem sap.

Indirect support for the theory presented by Nardini et al. (2011) comes from recent experiments that investigated gene expression in petioles of grape vine leaves during recovery from water stress (Perrone et al. 2012). The researchers detected up-regulation of gene categories related to secondary metabolism, including genes involved in sugar metabolism and transport as well as some aquaporin genes. The importance of aquaporins in embolism repair of trees has been verified (Secchi and Zwieniecki 2010, 2014). In addition, Salleo et al. (2009) as well as Secchi and Zwieniecki (2011) found that starch reserves in xylem tissues were depleted after subjecting bay trees or poplars to cycles of severe drought stress. In addition to radial transfer of water initiated by changes in Π_{ib} it was also suggested that water released during phloem unloading (i.e., Münch water) could provide the necessary pressure and radial flux necessary to reverse embolism (Milburn 1996). Finally, we would like to note that Bordersen and McElrone (2013) collated a valuable review on possible additional mechanisms to reverse xylem embolism that do not involve radial transfer of solutes and water.

Conclusions

Trees have highly complex transport systems for water and solutes. These systems, the xylem and the phloem are so intimately linked by rays that it is questionable whether we can continue to depict them as separate systems, rather than a single, highly segregated one. Bidirectional exchange processes between phloem and xylem via the rays are critical to maintain hydraulic function of trees. Other processes like drought mitigation, photosynthetic activity and allocation of carbon are impacted as well. We have shown here that the readily measurable pulse of tree stems, their diurnal rhythm of expanding and contracting, is the result of radial transfer of water between phloem and xylem. This pulse beats particularly strong during periods of sufficient water availability, demonstrating that capacitance is part of daily physiological and hydraulic cycles. While our knowledge on theoretical functioning of the involved processes is increasing, we lack empirical evidence of these functions. This is particularly the case for mature, field-grown trees as the many manipulative glasshouse studies are limited to small, potted trees. Certainly, data generated to improve predictive models of forest function under increasing environmental stresses will not improve the health of our patients per se. However, an improved understanding of the pulse of trees will strengthen our capacity to predict the future of tree-dominated ecosystems under changing environmental conditions.

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Conflict of interest

None declared.

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