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Modeling xylem and phloem water flows in trees according to cohesion theory and Münch hypothesis

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Abstract Water and solute flows in the coupled system of xylem and phloem were modeled together with predictions for xylem and whole stem diameter changes. With the model we could produce water circulation between xylem and phloem as presented by the Münch hypothesis. Viscosity was modeled as an explicit function of solute concentration and this was found to vary the resistance of the phloem sap flow by many orders of magnitude in the possible physiological range of sap concentrations. Also, the sensitivity of the predicted phloem translocation to changes in the boundary conditions and parameters such as sugar loading, transpiration, and hydraulic conductivity were studied. The system was found to be quite sensitive to the sugar-loading rate, as too high sugar concentration, (approximately 7 MPa) would cause phloem translocation to be irreversibly hindered and soon totally blocked due to accumulation of sugar at the top of the phloem and the consequent rise in the viscosity of the phloem sap. Too low sugar loading rate, on the other hand, would not induce a sufficient axial water pressure gradient. The model also revealed the existence of Münch “counter flow”, i.e., xylem water flow in the absence of transpiration resulting from water circulation between the xylem and phloem. Modeled diameter changes of the stem were found to be compatible with actual stem diameter measurements from earlier studies. The diurnal diameter variation of the whole stem was approximately 0.1 mm of which the xylem constituted approximately one-third.

Keywords Münch hypothesis · Phloem translocation · Sap flow · Stem diameter change

Introduction

Two parallel conduit systems are responsible for water, nutrient, and assimilate product transport in plants. Transpiration driven water flow occurs through the xylem. According to the cohesion theory, water evaporates at the leaf surfaces and is pulled by cohesive forces that create a water pressure gradient through a continuous pathway of water-conduits extending from leaves to the roots. Transport of assimilation products from mature leaves to the stem, roots, immature leaves, and other organs occurs via the phloem. Sugars are transported in the phloem along a continuous pathway of sieve space made out of sieve elements (sieve cells) that are connected to each other either by sieve plates or by small pores.

The driving force and mechanisms for phloem transport have been under dispute. The pressure-flow model, as proposed by Ernst Münch in the 1930s, is now quite commonly agreed to explain phloem translocation and has also gained experimental support (Knoblauch and van Bel 1998). According to the pressure-flow model the active loading of solutes at the mature leaves, “sources”, lowers the osmotic potential of the semipermeable sieve elements and draws in water from the surrounding tissue. This causes the hydrostatic water pressure, i.e., turgor pressure, to rise. Unloading of solutes at the sink areas raises the osmotic potential of the sieve elements and water is pushed out. This pressure gradient drives the bulk water flow in the phloem from the solute sources to sinks, and solutes move by convection along with the water stream. No membranes are crossed in the axial direction, and thus osmotic potential differences do not contribute to axial water movement in the phloem. The majority of the axial resistance to water flow is caused by pore plates or pores between the sieve elements (Thompson and Holbrook 2003a).

The two conduit pathways, the xylem and phloem, have mainly been studied as separate systems. However, they

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are next to each other in the vascular bundles in tree leaves and in small roots. Also, in the tree organs with secondary thickening they are connected through a narrow band of cambial cells and a number of intrusions of living and dead cells penetrating the xylem tissue in radial direction in the wood rays. As xylem and phloem are hydraulically interconnected, there should be water exchange between them in the direction of the water potential gradient. Models by e.g., Tyree et al. (1974), Ferrier et al. (1975), Smith et al. (1980), Phillips and Dungan (1993), Thompson and Holbrook (2003a) have demonstrated that the pressure-flow hypothesis can produce a net transport of photosynthates in the phloem. In these models, the phloem has mainly been considered as a separate compartment and disconnected from the influence of the transient transpiration stream in the xylem. Ferrier et al. (1975) and Daudet et al. (2002) have modeled the effect of a sinusoidal variation of xylem water pressure on phloem translocation. However, explicit water exchange between the xylem, and phloem and water flow in the xylem, i.e., full “Münch circulation”, has not been modeled to our knowledge.

Simultaneous treatment of xylem and phloem flows is physiologically interesting. Both the flow rate of water and that of sugar to and from the leaves set requirements on the stomatal regulation of the transpiration stream. Stomatal regulation directly influences the tension in the xylem tissue and is influenced by the xylem transport capacity (Sperry and Pockman 1993; Hubbard et al. 2001). On the other hand, the stomatal control influences the sugar loading capacity and thus phloem transport by influencing the CO₂ intake rate. Ferrier et al. (1975) concluded that sugar loading has more importance on the Münch pressure flow than variation in the xylem pressure but also the latter can have significant influence on the flow pattern. However, the diurnal pattern of transpiration is quite inevitable in most land plants while starch formation offers a possibility to more constant sugar loading. It is an interesting question whether the observed rates of transpiration may have significant influence also on the phloem transport and consequently have impact on stomatal control, as has been suggested by Schultze (1991).

Since both xylem and phloem flows are pressure gradient driven, we can expect to see variation in the dimensions of the respective tissue that depend on their elastic properties, which is due to adhesion between water columns and water conducting cell surfaces. These have, indeed, been observed both in xylem (Irvine and Grace 1997; Offenthaler et al. 2001; Perämäki et al. 2001) and recently also in phloem (Sevanto et al. 2002, 2003). Our ability to observe the diameter variation is offering us convenient and nondestructive means to monitor these two flows in the field conditions. Previous diameter measurements have shown that the living bark tissue has considerable diurnal thickness variation in spite of its limited width (Sevanto et al. 2002). Explicit treatment of diameter variation in the model improves our possibilities to test the model behavior against readily available field observations as demonstrated earlier by Perämäki et al. (2001) for xylem sap flow and by Sevanto et al. (2003) for the whole stem. In this study, we

have paid special attention in simulating the diameter variations of the wood core and the whole stem that includes in addition to wood also the living bark tissue but excludes the cork layer. This is done for model validation purposes, as there exists simultaneous field measurements of xylem and stem diameter variations in previous studies by Sevanto et al. (2002, 2003).

In this study we present a mathematically simple model of the very complex, coupled xylem and phloem transport system in a structurally simplified scheme. A new feature of the model is that it treats simultaneously these two flows. Unlike in previous phloem translocation models, water movement in axial and radial directions is explicitly modeled to effect water pressure. This allows us to investigate the interaction of the xylem and phloem in variable environmental conditions and also if water equilibrium between these components is achieved as was suggested by Thompson and Holbrook (2003b). In the results we demonstrate the diurnal dynamics of water pressure, sap flows, and consequent diameter changes resulting from the model when transpiration, soil water tension, and loading and unloading rates of sugars are used as input data to the model. We also consider how the movement of water and sugar in the phloem are affected when values of the parameters, such as permeability to sap flow and boundary conditions, such as the amount of sugar loading and transpiration are varied in carrying out sensitivity analysis. An important feature of our model is that it allows us to analyze the range of conditions under which water circulation according to Münch hypothesis works.

Materials and methods

The model tree is divided into different functional components in the radial direction: xylem, cambium, phloem sieve cells, and other living bark tissue (Fig. 1). For the sake of simplicity, we omit the ray cells from the analysis, and thus each component has a homogeneous radial distribution of water pressure. Each component is separated from adjacent components by a semipermeable membrane, i.e., reflection coefficient of the membrane is 1. Solutes cannot move across the membranes, so osmotic pressure differences contribute to the water potential differences driving the radial water flow. Axially the model tree is divided into N equally long elements in each radial component. Both in the phloem sieve cells and in the xylem, axial water flow is caused by a hydrostatic pressure gradient. There is no axial water flow in the cambium and living bark tissue. In the xylem, water pressure gradient is induced by water removal at the topmost element of the transport matrix, which propagates tension in the water column that drives water along the pressure gradient. At the bottommost xylem element water is drawn from the soil. Roots are excluded from the model. Solving the axial water flows and diameter variations in the xylem and phloem follows the procedure of Perämäki et al. (2001). In the calculation we assume source at the top and sink at the bottom. Thus, sugars are loaded into phloem sieve cells at the top and unloaded at

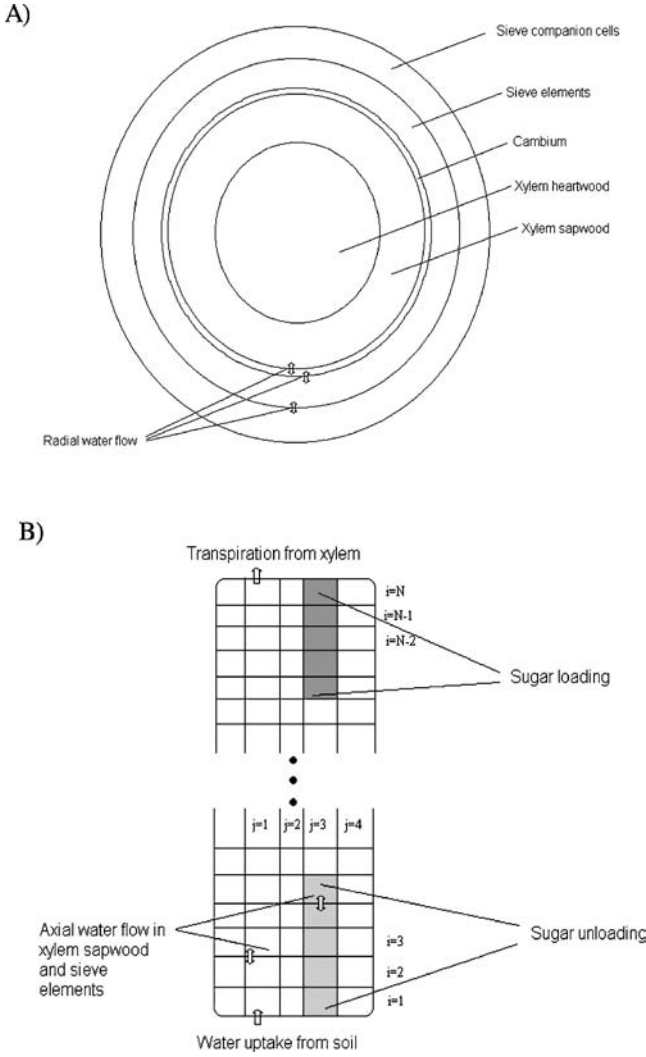


Fig. 1 A schematic representation of the model tree in (a) radial (b) axial direction. Loading occurs in the five topmost phloem elements and unloading occurs in five bottommost phloem elements. For numerical solutions each tree compartment is assumed radially homogeneous and is vertically discretized into N ($=40$) elements. The sieve companion cells and sieve elements constitute the phloem. Roots are excluded in the model

the bottom of the stem, and the consequent changes in hydrostatic, i.e., turgor, pressure, induces the water pressure gradient. The solutes flow in the phloem sieve cell elements by convection at the same speed as water.

The mass balance equation (Siau 1984)

$$\frac{dm_{i,j}}{dt} = Q_{ax,in,i,j} - Q_{ax,out,i,j} + Q_{rad,in,i,j} - Q_{rad,out,i,j}, \quad (1)$$

is solved for each axial element in each radial component. The subscript i refers to axial elements from $i=1$ to $i=N$ and the lower index j refers to radial components: xylem, cambium, phloem sieve cells, living bark tissue (Fig. 1). $m_{i,j}$ is

the mass of water in element i in component j , $Q_{ax,in,i,j}$ and $Q_{ax,out,i,j}$ are the corresponding values of the axial inflow and outflow rates ($m^3 s^{-1}$), and $Q_{rad,in,i,j}$ and $Q_{rad,out,i,j}$ are the radial inflow and outflow rates.

The axial water inflow rate for the xylem and phloem sieve elements is calculated using Darcy's law (Siau 1984)

$$Q_{ax,in,i} = \frac{k}{\eta} \frac{P_{i-1,j} - P_{i,j} - P_h}{l} A_{ax,i,j} \rho, \quad (2)$$

which combines water flow with the pressure gradient in a segment (Perämäki et al. 2001). Here $P_{i,j}$ is the water pressure of element i in component j , k (m^2) is the axial water permeability, η is the dynamic viscosity ($N sm^{-2}$) of water, l is the length of the element, $A_{ax,i,j}$ is the axial cross-sectional area of the water-conducting surface between elements i and $i-1$ in component j , and ρ is the density of water. P_h is the term resulting from the gradient in hydrostatic pressure induced by gravitation. ($P_h = \rho gl$, where ρ is water density and g is acceleration due to gravity, $g=9.81 ms^{-2}$). The axial outflow rate $Q_{ax,out,i,j}$ for each element is equal to the inflow rate of the element above it. In the xylem, outflow from the topmost element $Q_{ax,out,N,j}$ equals transpiration, and water pressure under the bottommost element equals the soil water potential (see Fig. 1b). In the phloem the outflow from the topmost element and inflow to the bottommost element equal zero.

The radial flow rate of water ($m^3 s^{-1}$) between adjacent components becomes (Nobel 1991)

$$Q_{rad,in,i,j} = L_r [P_{i,j-1} - P_{i,j} - \sigma(C_{i,j-1} - C_{i,j})RT] A_{rad,i,j}, \quad (3a)$$

where $A_{rad,i,j}$ is the surface area of the radial interface between the components j and $j-1$, and L_r ($mPa^{-1} s^{-1}$) is the radial hydraulic conductivity of the interface surface. $P_{i,j}$ is the hydrostatic pressure in element i in component j , $C_{i,j}$ is the solute concentration in element i in component j

$$C_{i,j} = \frac{n_{i,j}}{V_{i,j}}, \quad (3b)$$

where $n_{i,j}$ is the molar amount of solute in the volume $V_{i,j}$, σ is the reflection coefficient between the components, which identically equals one (i.e., semipermeability) between radial components, R is the universal gas constant ($8.314 J mol^{-1} K^{-1}$), and T is the absolute temperature. Note that Eq. 3 holds in cylindrical coordinates as well as Cartesian coordinates when the surface area term $A_{rad,i,j}$ is calculated accordingly. Here van't Hoff approximation is used to calculate the osmotic pressure of the phloem solution.

If we assume no phase transitions in the wood, Hooke's law then gives the relationship between the change in water mass $m_{i,j}$ and pressure $P_{i,j}$ for each element in each component (Perämäki et al. 2001)

$$\frac{dP_{i,j}}{dt} = E_{r,j} \frac{1}{V_{i,j} \rho} \frac{dm_{i,j}}{dt}, \quad (4)$$

where $E_{r,j}$ is the elastic modulus of wood tissue of component j in the radial direction. The elastic modulus is constant in the longitudinal direction.

As the details on the loading and unloading of sugar are not known, we assume constant loading at the sources and constant sugar concentration at the sinks. The equation describing the change in the amount of solutes is

$$\frac{dn_{s,i,j}}{dt} = (Q_{ax,in,i,j} - Q_{ax,out,i,j}) C_{i,j} \rho + L_i - U_i, \quad (5a)$$

where $n_{s,i,j}$ is the molar amount of solutes in element i in the phloem sieve cells, L_i is the constant loading rate of sugar in element i (and is zero outside the sugar loading zone), and U_i is the sugar unloading rate in element i . The unloading rate at the sugar sink zone is made solute concentration dependent and is explicitly written as

$$U_i = (C - C_0) \times 10^{-9} \text{ mol s}^{-1}, \quad (5b)$$

where C_0 is a reference concentration. U_i is zero outside the sugar sink zone. Finally, a geometric equation for cylindrical stem segments reveals the relationship between changes in diameter and water content of a component (Perämäki et al. 2001)

$$\frac{dd_{i,j}}{dt} = \frac{2}{\pi \rho l d_{i,j}} \frac{dm_{i,j}}{dt}, \quad (6)$$

where $d_{i,j}$ is the diameter of element i in component j . Diameter changes are assumed to be completely reversible. In practice, diameter changes are calculated for the xylem and the whole stem for comparisons with the corresponding field measurements. Diameter changes are calculated

individually for each component, and the diameter of the whole stem equals the sum of the diameter changes of the individual components.

Model simulations and parameters

Equations (1)–(6) are solved numerically using the fourth-order Runge–Kutta method (Press et al. 1989). The water pressure, water mass, and diameter of each segment are updated after each time step. A time step of 0.01 s is used. A value of 40 is used for N , the number of axial elements in each component. The time step and the number of elements N are chosen so that reducing the time step or increasing the number of elements does not have any noticeable influence on the results. Parameters used in the model simulations are listed in Table 1. The parameters are either measured from a model tree, a 35-year old Scots pine (*Pinus Sylvestris* L.) tree in SMEAR II station in Hyytiälä, Southern Finland (61°51'N, 24°17'E) (Vesala et al. 1998) or estimated from literature.

Measured parameters include the tree dimensions. The maximum transpiration rate is measured from the model tree by shoot chamber measurements (Hari et al. 1999). Transpiration is made to follow the positive part of the sine wave during the day, from 6 am to 6 pm, with a maximum value of 0.9 g s⁻¹ for the total leaf area at midday, while being zero at night, from 6 pm to 6 am. The loading zones, at the topmost segments, and unloading areas, at the bottommost segments, are both 1/8th, (i.e., 5 segments) of the stem length (1.125 m).

Estimated parameters include the radial hydraulic conductivity between the xylem and phloem. The radial hydraulic conductivity is estimated to be the same as radial water conductivity through the cell walls. Nobel (1991) states that water conductivity coefficient for plant

Table 1 Parameter and boundary condition values that are used in the model^a

Tree dimensions	
Height of the tree	12 m (measured)
Xylem diameter	160 mm (measured)
Nonconducting heartwood diameter	120 mm (measured)
Phloem diameter	1.6 mm (measured)
Tree parameters	
Xylem axial permeability	$1.5 \times 10^{-12} \text{ m}^2$ (Irvine and Grace 1997; Mencuccini et al. 1997)
Xylem elastic modulus	1000 MPa (Irvine and Grace 1997; Mencuccini et al. 1997)
Sieve tube axial permeability	$6.0 \times 10^{-12} \text{ m}^2$ (Thompson and Holbrook 2003a)
Sieve cells elastic modulus	30 MPa (Nobel 1991)
Sieve companion cells elastic modulus	10 MPa (Nobel 1991)
Radial hydraulic conductivity	$1 \times 10^{-13} \text{ mPa}^{-1} \text{ s}^{-1}$ (Zwieniecki et al. 2001)
Cambium elastic modulus	10 MPa (Nobel 1991)
Reference concentration at sugar sink	0.1 MPa (Sheehy et al. 1995)
Boundary conditions	
Maximum transpiration rate	0.9 g s ⁻¹ (measured)
Soil water tension	0 MPa (Perämäki et al. 2001)
Sugar loading rate	$2.5 \times 10^{-5} \text{ mol s}^{-1}$ (Sevanto et al. 2003)

^aAfter each value is stated whether the parameter is measured or the literature source used in its estimation

cells ranges from about 10^{-13} to $2 \times 10^{-12} \text{ m s}^{-1} \text{ Pa}^{-1}$. Zwieniecki et al. (2001) measured the radial conductivity of *Fraxinus americana* to be of the order $2 \times 10^{-13} \text{ m s}^{-1} \text{ Pa}^{-1}$ and we use this value in our model. Also Génard et al. (2001) use a similar value for radial hydraulic conductivity between the xylem and a water storage component. The xylem axial permeability ($1.5 \times 10^{-12} \text{ m}^2$) in lower and middle parts of the stem is estimated from literature (e.g., Irvine and Grace 1997; Mencuccini et al. 1997), and is set to $3.75 \times 10^{-13} \text{ m}^2$ in the five topmost elements to account for conductivity changes in the wood along the axis (Zimmermann 1983). The xylem permeability is assumed to be constant in time, although in reality it is influenced by embolism and subsequent refilling of xylem elements as the effects of embolism are not included in the model. The values of the xylem permeability and transpiration are also confirmed to produce a reasonable maximum xylem tension, which is comparable to an actual measured value of approximately -2 Mpa . The sieve tube axial permeability ($6.0 \times 10^{-12} \text{ m}^2$) is estimated from literature (e.g., Thompson and Holbrook 2003a). The values of axial permeability for both the xylem and phloem are of macroscopic scale, where the effects of sieve plates, pit membranes, and other microscopic structure have been incorporated into them. The values for radial elasticity of the various compartments (see Table 1) are estimated from literature (Irvine and Grace 1997; Mencuccini et al. 1997) for the xylem, and (Nobel 1991) for the living cells. The soil water potential is kept constant at 0 MPa . (Perämäki et al. 2001).

The sugar loading rate is estimated to be $2.5 \times 10^{-5} \text{ mol s}^{-1}$. This estimate is in accordance with actual daily CO_2 influx measurements in Sevanto et al. (2003), which are done with shoot chambers from a few branches in our model tree (Hari et al. 1999). These measurements are then scaled over the whole tree by assuming that the entire net CO_2 intake is converted into sucrose. The reference concentration for the unloading rate C_0 (Eq. 5b) is made equivalent to a 0.1 MPa osmotic pressure, a typical value found at the base of the phloem (e.g., Sheehy et al. 1995).

The dynamic water viscosity at each element in the phloem sieve tissue is calculated as a function of the solute concentration. The following equation (Morison 2002) is used to calculate the dynamic viscosity of the phloem sap

$$\eta = \eta_0 \exp\left(\frac{4.68 \times 0.956\phi}{1 - 0.956\phi}\right), \quad (7)$$

where η is the dynamic viscosity, η_0 is the reference viscosity of pure water, and ϕ is the volume fraction of sucrose in the phloem sap. Morison (2002) states the equation to be valid for sucrose volume fractions of up to 65%, which equals an osmotic pressure of 7.5 MPa . The viscosity is also a function of temperature, but here we assume a constant temperature of 25°C . In the xylem, the viscosity is constant η_0 ($1.0019 \times 10^{-3} \text{ Nsm}^{-2}$ the value for pure water), as there are only small amounts of solutes in the sap.

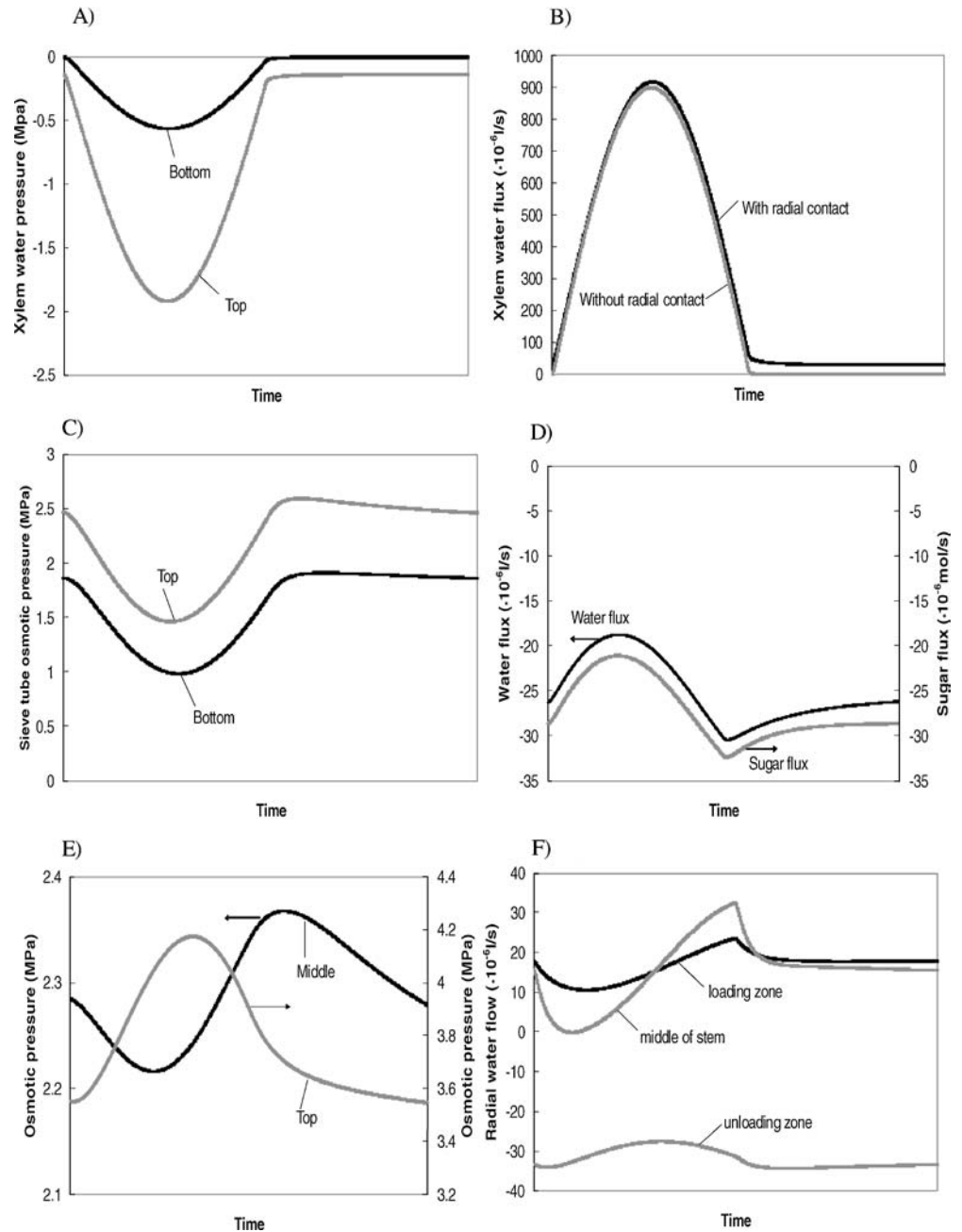
We also examine, in the sensitivity analysis section, how phloem translocation is affected when the cross-sectional area of the sieve tube and also radial interface with xylem is increased in the loading area. The phloem tissue forms a narrow, rapidly renewing band around the xylem in woody axes, while functional xylem tissue accumulates gradually to larger cross-sectional areas. Along the woody axes from the tree base till branch tips the sapwood cross-sectional area remains effectively fairly constant according to the pipe model theory (Hari et al. 1986). However, since the conducting axis divides into numerous branches, simple geometry implies that the conducting phloem tissue should increase relative to xylem toward the top. In leaf veins, where most of the loading takes place the xylem and phloem tissue have approximately equal cross-sectional area (Mauseth 2003). To imitate this structure, the phloem cross-sectional area in the uppermost sieve tube element is made equal to that of the xylem, which still remains constant at all heights. The cross-sectional area is then linearly reduced throughout the loading zone, so that it attains its original value at the bottommost loading elements. The area between the phloem and xylem, where water exchange occurs, is increased accordingly in the loading zone. At the topmost element the water-conducting area between the phloem and xylem is calculated assuming branching to 1000 separate circular conduits. The area is then linearly decreased to the lowest loading zone element.

Results

Base case dynamics

Figure 2a–f shows the development of water pressure, sugar concentration, and water and sugar flows in the xylem and phloem during a period of 1 day for the base case simulation. In the xylem, water pressure and the axial water flow follow the transient transpiration (transpiration not shown) with a short time lag of few minutes (Fig. 2a and b). The maximum diurnal water tension reached in the xylem depends mainly on the magnitude of the transpiration, soil water tension, and xylem axial permeability. Phloem translocation has also an effect on the xylem water flow (Fig. 2b) as there is a small amount of water flow in the xylem during the night even in the absence of transpiration, and also the xylem water flow has more time lag to transpiration compared to the case where the phloem continuity is omitted. The phloem water potential (Fig. 2c) adjusts very quickly to changes in the xylem water potential. However, as a result of constant sugar loading and unloading, the phloem is always at lower potential in the loading zone and at higher water potential in the unloading zone, inducing constant radial water exchange between the xylem and phloem in the direction of water potential gradient. Water (lighter line) and solutes (darker line) flow downward continuously in the phloem and upwards in the xylem, but the transient flow rate varies diurnally with the transpiration rate (Fig. 2d). Both flows decrease when transpiration increases, as transpiration reduces the axial water pressure

Fig. 2 **a** Diurnal evolution of the xylem water pressure at the top (*light line*) and bottom (*dark line*). **b** Diurnal evolution of xylem axial water flow at the middle of the stem (*dark line*). Also, a case for xylem water flow, where there is no radial conductivity between the xylem and phloem as shown (*light line*). **c** Diurnal evolution of water pressure at the top (*light line*) and bottom (*dark line*) of phloem sieve elements. **d** Diurnal evolution of axial water (*dark line*) and sugar (*light line*) flow in the phloem sieve tube at the middle of the stem. Negative values refer to downward flux. The *arrows* point to the corresponding *y*-axes. **e** Diurnal evolution of sugar concentration induced osmotic pressure in the phloem sieve cells at the top (*light line*) and middle (*dark line*) of the stem. **f** Diurnal evolution of the sum of radial water flow to/from the phloem sieve cells for the loading zone (*dark line*) elements, unloading zone (*light line*) elements, and the intermediate (*light line*) elements. Negative values refer to flux from phloem to xylem and positive values to flux from xylem to phloem. All results are shown developing in time for a period of 24 h



gradient in the phloem by inducing an opposite direction pressure gradient in the xylem. The loading and unloading of sugars maintain the axial water pressure gradient and the consequent phloem water and sugar flow. The average water flow rate is about 0.5 m h^{-1} , which is similar to values calculated in other modeling exercises (e.g. Sheehy et al. 1995; Taiz and Zeiger 1998; Thompson and Holbrook 2003a). Diurnal patterns are also noticeable in the sugar concentration induced osmotic pressure (Fig. 2e). Sugar accumulates temporarily at the top of the stem when the sugar-loading rate exceeds the sugar flux. Water moves in the radial direction from the xylem through the cambium to the phloem in the phloem-loading zone, and from the phloem through the cambium to the xylem in the un-

loading zone (Fig. 2f). In the middle of the stem, water exchange is much smaller per unit length. The diurnal rate of radial water flow between xylem and phloem follows the same pattern as axial water flow in the phloem, as the water circulates continuously according to the Münch hypothesis and moves rapidly through the cambium layer.

Sensitivity to changes in parameters and boundary conditions

Figure 3 presents the average daily sugar flux when the sugar loading rate value is varied. The sap flux increases at small sugar-loading rates along with the sugar-loading

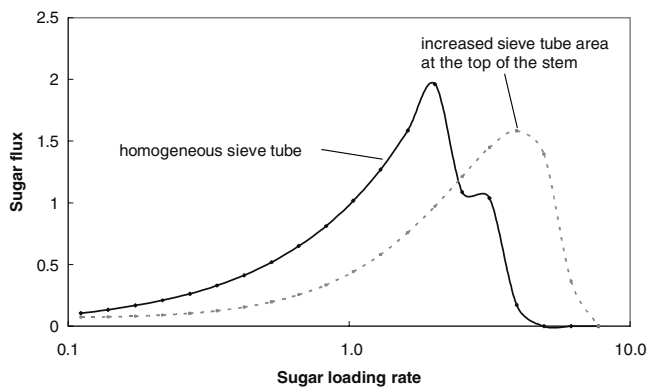


Fig. 3 The average axial sugar flow rate at the middle of the phloem sieve tube as a function of the sugar-loading rate (*solid dark line*). All values are presented in relation to the base case, i.e., value 1 represents the base case in both x - and y -axis. Positive values in the y -axis correspond to solute flow down, i.e., from the sugar-loading zone to the unloading zone. Sensitivity analysis for the case with increased cross-sectional area (as explained in the Materials and methods Section) at loading zone is also shown (*dotted line*)

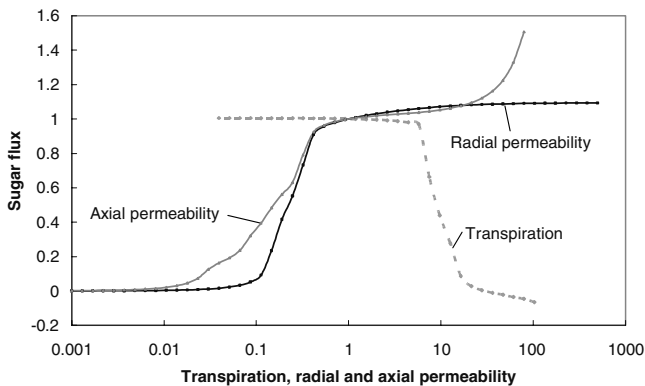


Fig. 4 The average axial sugar flow rate at the middle of the phloem sieve tube, when transpiration (*light dotted line*), radial permeability between the phloem and xylem (*dark uniform line*), and sieve tube axial permeability (*light uniform line*) of the sieve tube are varied from the base case value. All values are presented in relation to the base case, i.e., value 1 represents the base case in both axes. Positive values in the y -axis correspond to solute flow down, i.e., from the sugar-loading zone to the unloading zone

rate due to elevated turgor pressure as more water is drawn in to the sieve tube at the loading zone. The sugar flux reaches a maximum value at a sugar-loading rate of approximately twice the base case value. If sugar loading is elevated beyond this, sugar flux starts to decrease rapidly as substantial sugar accumulation and viscosity rise occur at the loading zone. In the case of the increased sieve tube cross-sectional area (the dotted line in Fig. 3), the amount of transported sugar is smaller than in the case of homogeneous sieve tubes at small sugar loading rates, but grows higher at larger loading rates.

Figure 4 shows the effects on sugar flux when transpiration rate, radial and axial permeability are varied individually. Phloem sugar transport rate decreases uniformly when transpiration increases or the radial or axial permeability decrease. Elevated transpiration reduces phloem sap flux by lowering xylem water pressure and this is then quickly re-

flected to the phloem. During high transpiration xylem pulls water from the sieve elements and their turgor pressure is reduced. The turgor pressure drop is more evident at the top of tree during diurnal transpiration peaks, which reduces the axial pressure gradient and raises the viscosity of the sap through accumulation of sugars. When transpiration is lowered from the base case value, water and sugar flows are very slightly enhanced. The sap flow is approximately as sensitive to changes in the phloem axial permeability as to changes in the radial permeability. As radial permeability is lowered, phloem sugar transport decreases due to reduced water exchange with the xylem following the decreased water input at the top of the phloem and water removal at the base of the phloem. This also drives sugars to accumulate at the top of the phloem. A decrease in the radial permeability will also hinder the water flow in the xylem during the absence of transpiration, i.e., so called “Münch counterflow” (e.g., Tanner and Beevers 2001). The total amount of diurnal water and sugar flux increase only slightly when the radial permeability is raised from the base case value. When the phloem permeability is lowered phloem sugar

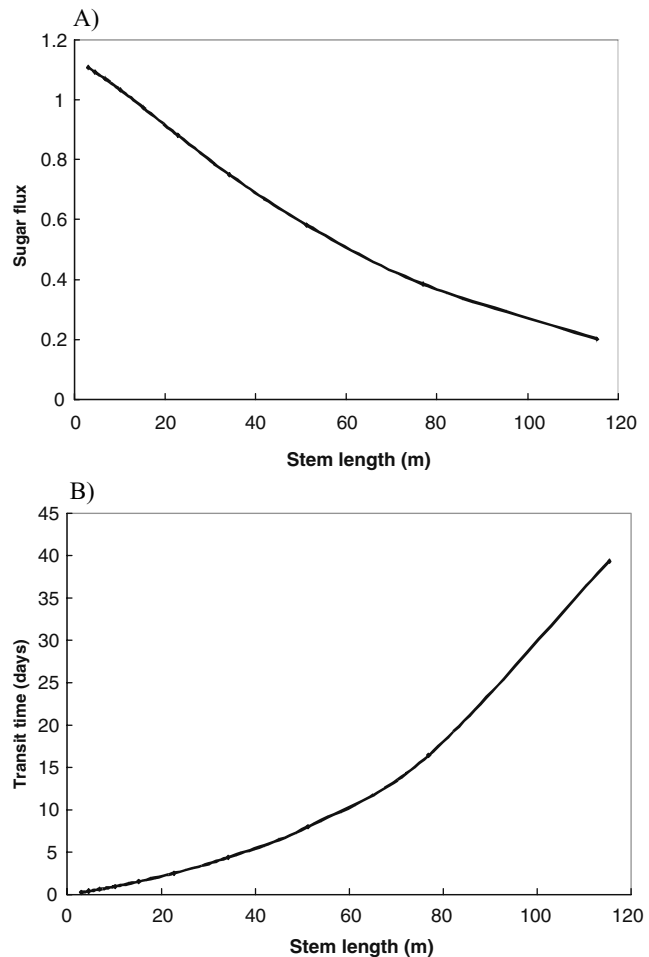


Fig. 5 a The sugar flow rate through the tree as the height of the stem is varied. The sugar flow rate is presented in relation to the base case, i.e., value 1 represents the base case in both axes. **b** The transit time, i.e., the time needed for sugar to travel through the stem, as the height of the stem is varied

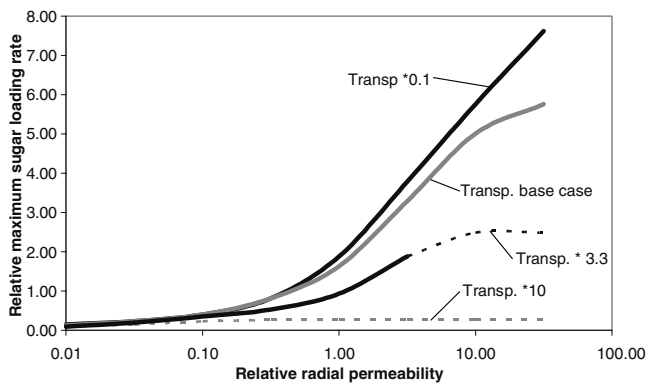


Fig. 6 The maximum sustainable sugar-loading rate as a function of radial permeability for different transpiration schemes. The maximum sugar-loading rate is defined to be reached when the sugar concentration reaches a value of 7.5 MPa. At this value, the phloem sap becomes so viscous that resistance of the sieve tubes increases 1000-fold. Different *lines* show different transpiration values and the corresponding minimum xylem water tensions at the sugar-loading zone. *Dotted parts* of the *lines* show negative turgor pressure. The sugar loading rates, radial permeability, and transpiration are shown relative to their base-case values

and water flows decrease due to sugar accumulation and sap viscosity rise. Phloem translocation would function also with increasing phloem transport distance. Figure 5a shows the effect of a change in the sieve tube length, i.e., in tree height, to the sugar flow rate while the loading and unloading zone lengths were kept as in the base case. The sugar flow rate does not decrease much, but the transit time (Fig. 5b), i.e., time needed for sugar to travel the complete distance from the sources to the sinks, increases more significantly, since it is the product of flow rate and sieve tube length.

The limits of phloem translocation capacity were also studied by varying several boundary conditions and variables simultaneously. Figure 6 illustrates the maximum sugar-loading rate that can be sustained before the translocation system is blocked due to excessive sugar accumulation, as a function of the radial permeability with varying transpiration levels. The maximum sustainable sugar-loading rate is calculated by gradually increasing sugar loading until sugar accumulation is so extensive that phloem sap flow is practically prevented by viscosity. Transpiration levels of 0.1, 1, 3, and 10 compared to the base case transpiration are shown. These transpiration levels drop the xylem water pressure to -0.4 MPa, -2.0 MPa, -6.0 MPa, and -20 MPa in the uppermost xylem compartments, respectively. The results show that transpiration has a noticeable effect on the sugar loading that can be transported in the sieve tube, and the effect grows especially strong when the radial permeability between the xylem and phloem is increased. With high transpiration and high radial permeability turgor in the sieve tubes drops to below zero (dotted font).

Finally we varied the sugar loading function to a form, which maintains the sugar concentration at a constant value in the sugar-loading zone. Figure 7a shows the amount of sugar transport rate as a function of the sugar concentration induced osmotic pressure at the sugar-loading zone

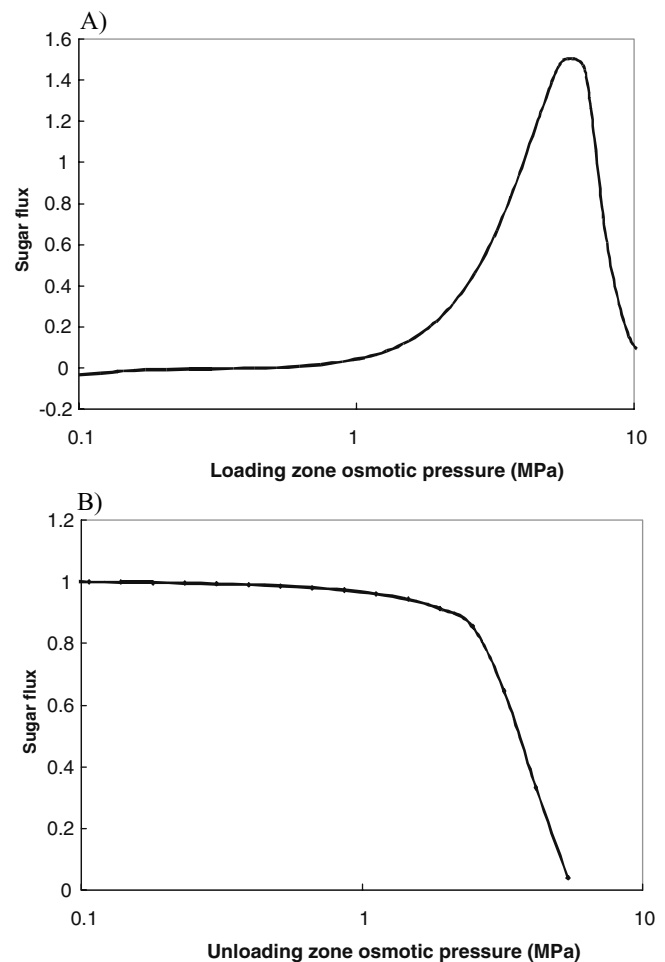


Fig. 7 a Sugar flow rate through the sieve tube, when the sugar concentration is kept at a constant value at the loading zone. The value of the constant sugar concentration is varied along the *x*-axis. The sugar flux is shown relative to the base case value. **b** Sugar flow rate through the sieve tube, when the sugar concentration is varied at the unloading zone

while other parameters were as in the base case. The graph demonstrates that there is sugar concentration, where the sugar flux reaches its maximum value. At smaller concentrations the axial pressure gradient in the phloem is too low to induce a higher flow and at higher concentrations the resistance in the sieve tube grows too high due to rise in the sap viscosity. The maximum transport value in this case is at a loading zone concentration of approximately 6 MPa. Figure 7b shows the effect of varying the unloading zone reference osmotic pressure, i.e., factor C_0 in Eq. 5b. Practically this means that the unloading zone osmotic pressure is kept at this reference value. We see that the sugar flux decreases uniformly as the sugar concentration and osmotic pressure at the unloading zone is increased as axial pressure gradient in the sieve tubes decreases and sap viscosity increases.

Diameter variations

Diameter changes of the xylem (Fig. 8) explicitly follow the pattern in xylem water pressure (Fig. 2a) as can be expected

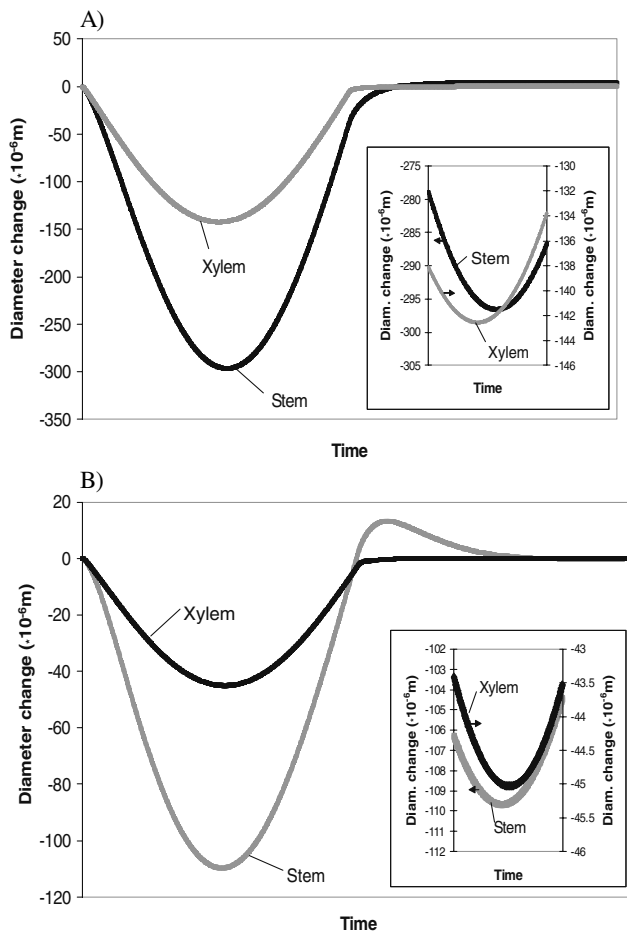


Fig. 8 The diameter changes at the (a) top and (b) bottom of the xylem and the whole stem. All results are shown developing in time for a period of 24 h. The *inserts* show the daily minimums in diameter in detail. The inserts show a 2 h time period. The *arrows* point to the corresponding y-axes

from Eqs. 4 and 6. The diameter change is expressed in relation to an initial value at the beginning of the period, and it signifies how much the xylem and whole stem diameter has changed from its initial value. In the diameter variation calculations the sugar-unloading rate is kept constant with the same value as the sugar-loading rate. The elasticity and volume of each component determines the magnitude of diameter change compared with the change in water pressure. The diameter change of the whole stem is a mixture of the pattern of xylem and phloem water pressure development. The whole stem diameter variation has the same basic pattern as the xylem diameter variation: they are both following the transpiration. The inserts show a 2 h time period to demonstrate the time lag between the xylem and whole stem diameters. The stem diameter is lagging behind the xylem diameter at the top and leading the xylem at the bottom (see inserts in Fig. 8a and b). This same pattern has also been observed in field measurements (Sevanto et al. 2002, 2003). Comparing the relative amplitudes of the xylem and stem diameter variations, we find out that the stem diameter variation is about three times larger than the xylem diameter variation. This indicates that about one-third of

the whole stem diameter change was due to changes in xylem and two-thirds to the living tissue outside the xylem, i.e., almost exclusively the phloem. This relation in the diameter variation amplitudes was also observed in field measurements. Also, the magnitudes of the absolute values of the diurnal diameter amplitude variations (about 0.3 mm at the top of the stem and 0.1 mm at the top of the xylem) match earlier field measurements (Sevanto et al. 2002).

Discussion

Recent studies with sieve element—companion cell complexes have consolidated the Münch hypothesis as the most probable explanation of the long distance transport of assimilate products in plants (e.g., Knoblauch and van Bel 1998; Van Bel 2003). It results from interplay between transpiration driven xylem flow and osmotically driven phloem flow. That such interaction should function sets several requirements and limitations not only for both the regulation of transpiration and physiology of sugar loading and unloading, but also on the tree structure as our modeling exercise points out. The hydraulic architecture of trees has received a lot of attention as an important mechanism in controlling the water distribution within tree crowns (Zimmermann 1983). The modeling showed that tree level phloem architecture may be equally important but has received far less attention. The recent reviews by van Bel (2003) and Lalonde et al. (2003) have shown that we are gradually starting to understand the physiology of phloem transport but van Bel (2003) also points out that the linking of the physiology with environmental variation is a further challenge in this field. During normal daily variation of tree environment the xylem tension can reach levels of many megapascals. This study shows that coupled long distance transport models are needed to appreciate their significance at the whole tree level. As Schultze (1991) has pointed out the requirements of regulating the xylem and phloem flows could be the driving reason for stomatal control of transpiration (and photosynthesis) in leaves. Sufficiently low water tensions are maintained in the leaf to avoid excess embolism. However, very high tensions could also prevent water crossing to phloem inducing limitation on stomatal conductivity.

Sensitivity of transport to tree properties and environmental conditions

The sensitivity analysis reveals that of the various boundary conditions and variables, phloem translocation in our model is most sensitive to changes in the amount of sugar loading. If the sugar-loading rate is too small, sap flow in the phloem is hindered by decreased turgor pressure at the top of the sieve elements and dilution of the phloem sap. At high loading rates the sap flow is slowed down due to accumulation of sugar and the consequent rise of viscosity at the top of the phloem. Viscosity of the phloem sap is a steeply growing exponential function of the sugar concentration

and varies also substantially with height. In the base case simulation the viscosity of the phloem sap is over 10 times higher than the viscosity of pure water. Viscosity deviation has severe effects on the phloem translocation capacity but its variation has not, to our knowledge, been explicitly modeled as a function of sugar concentration in the whole physiological range of possible sugar concentrations before, except by Bancal and Soltani (2002).

The model shows that there is “an optimal value” for the sugar-loading rate for maximum sugar translocation to balance between the two scenarios of drop in turgor pressure and the dilution of the sap solution, and the rise in viscosity. This “optimal value” is evidently dependent on the structure of the transport system and environmental conditions. With our parameter choices, this optimal value is about 5 mol s^{-1} resulting in an osmotic pressure of 6 MPa at the loading zone. As the phloem cross-sectional area at the loading zone is made higher (Fig. 3) then this “optimal value” is shifted to even higher sugar loading rates. With this ad hoc structural variation more sugar loading is permitted without an increase in the solute concentration, but sugar transport is inefficient at smaller solute loading rates as larger volume of sieve elements keep the turgor pressure and the axial pressure gradient in the sieve elements lower.

Phloem translocation does not require transpiration to function, and the daily amount of sugar transport is only slightly reduced in the case of moderate transpiration increase. However, transpiration has a noticeable impact on the amount of sugar loading that can be sustained (Fig. 6). Water tension buildup will reverse the direction of the phloem flow during the daily peak transpiration if transpiration is raised to more than five times the base case value. An increase in transpiration to more than three times of the base case value is liable to drop the turgor pressure below zero during the daily transpiration peak as water is “sucked” to the xylem. This suggests that the water tension in leaf might be controlled by stomatal conductivity also to facilitate Münch flow. The turgor drop and phloem sap flow direction reversal are faster and stronger if the radial permeability is high and if the sugar-loading rate is not sufficient to resist the “pull” from the xylem.

The different permeability components, radial permeability between the phloem and xylem, and the axial permeability of the phloem sieve cells and the xylem have to be high enough for efficient phloem translocation as the radial and axial water flows are coupled in water circulation. Our sensitivity studies show that the water and solute flows were not inversely proportional to the transport distance as Thompson and Holbrook (2003a) found out, but bulk sugar translocation was found to work quite well with increased distance. This maybe because with our choice of parameters, the axial resistance to the sap flow in the phloem was not the limiting factor to sugar translocation. Also, the axial turgor gradient grows with increasing stem length due to sugar accumulation at the top of the stem, and this increase in the driving force of translocation partly compensates for the increase in transport distance.

Münch counterflow

The continuous sugar loading and unloading also during the absence of transpiration results in the transpiration-independent water flow in the xylem during the night (Fig. 2b). The axial xylem pressure gradient and “Münch counterflow” is induced by withdrawal of water from the xylem to the phloem at the top and the influx of water from the phloem to the xylem at the bottom of the stem. Also, experimental evidence of Münch counterflow has been found (e.g., Kockenberger et al. 1997; Tanner and Beevers 2001). It is important especially for large trees since it provides a transport mechanism for nutrients from roots to canopy even in low transpiration conditions. There is convincing evidence that growth is possible even in no transpiration conditions (Pedersen and Sand-Jensen 1997; Tanner and Beevers 2001). These studies even concluded the lack of transpiration was not likely to constrain the transfer of nutrients from root to shoot in herbaceous plants. Münch’s counterflow in our simulation was equal to the phloem flow and almost 5% of the maximum transpiration flow. This is similar to the result estimated earlier (Pedersen and Sand-Jensen 1997; Tanner and Beevers 2001).

Whole plant level regulation

In this study we have considered the transport of the bulk solution in the phloem. It has been shown in previous studies (Ferrier et al. 1975; Thompson and Holbrook 2004) that “information” about local changes in sugar concentration or turgor pressure, can travel considerably faster than the actual bulk solution itself. Fast information transmission is viewed important as excessive sugar loading and turgor pressure drop can be avoided by whole plant level regulation of sugar loading and unloading in response to changes in turgor or osmotic pressure in the sieve tube. Concentration wave propagation could be viewed as one possibility for “information transmission”. In our study, the concentration wave speed, i.e., the speed that a concentration peak will propagate, is about 1 m h^{-1} (calculated from Fig. 2e). A much faster “information signal” along the phloem sieve tube between the sources and sinks is the sieve tube pressure front propagation, which propagates at a rate of approximately 25 m h^{-1} (calculated from Fig. 2c). Also, Thompson and Holbrook (2004) suggest that turgor pressure would be a better information signal for sugar loading and unloading, as it is more uniform along the whole translocation pathway. Measurements of diameter variation have also indicated very rapid propagation of pressure along the xylem and with a small time lag in the phloem (Perämäki et al. 2001; Sevanto et al. 2003).

Also, other possibilities have been suggested for whole plant level regulation. Minchin and Thorpe (1987) suggested that the sugar concentration along the phloem transport path would be a result of balance between release and retrieval of sugars between sieve element, companion cells, and phloem parenchyma cells. These stored sugars could subsequently be used as energy for maintaining

the phloem flow (van Bel 2003). Such a system would also provide a flexible transport system even for locally occurring short distance flows that may be required during developmental processes (Pate and Jeschke 1995). In this case, phloem transport would be much more controlled as simply a passive pathway between sources and sinks. These questions are, however, beyond the scope of this study and require further research.

Limitations of the model and conclusions

Our model describes a complex system with many different variables. This being the case, the model is highly generalized. Also, the structural description is generalized. The location of the sources and sinks could vary considerably from our assumptions (Pate and Jeschke 1995). Also, the temporal dynamics of phloem loading depends on the assimilate production and on the actual loading mechanism, whether it is symplastic or apoplastic and its detailed modeling is a task by itself (e.g., Lalonde et al. 2003). Also, in the simulations we consider only sucrose. As pointed out by Thompson and Holbrook (2003a) other solutes, especially potassium, which can be present in high concentration and still not have similar increase in viscosity as is caused by sugars, could have an important role in maintaining the phloem flow.

However, this study shows that in realistic conditions Münch water circulation occurs and the model gives basic information about the effects of different parameters and boundary conditions to water circulation in trees. The hydraulic linking between the xylem and phloem and their connection with the carbon uptake and transpiration regulation makes trees highly integrated in terms of carbon uptake and allocation and requires more study in the future. In the future, the study of radial water exchange between the xylem and phloem might potentially also lead to more understanding on how water and solute flow from the xylem could facilitate the refilling process of embolized xylem conduits. Many studies (e.g., Milburn 1996; Salleo et al. 1996; Vesala et al. 2003; Salleo et al. 2004) have discussed this possibility, but further analysis of possible mechanisms and dynamics has not been done.

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