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DYNAMICS OF WATER AND SOLUTE TRANSPORT IN TREES

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ACADEMIC DISSERTATION

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Abstract

Two parallel conduit systems transport water and assimilate products in trees. First, the transpiration-driven water flow occurs through the xylem, the woody tissue composed of dead elongated cells. Second, the transport of assimilate products from leaves to the other parts of the tree occurs via the phloem, bark tissue composed of conducting sieve elements and living companion cells. Water is drawn in from the xylem to the phloem at the top of the tree and is pushed back into the xylem at the bottom, according to the Münch hypothesis. As the forces needed to pull water from the soil in the xylem are generated at the transpiring surfaces of the leaves, the water pressure in the transpiration stream is commonly dropped below the saturation vapor pressure. Water is then in a meta-stable state and it is prone to form water vapor bubbles when the cohesive or adhesive forces between water molecules fail to keep the water column intact. Gas bubble formation is limited to individual water conduits as embolised, i.e. non-conducting and gas-filled conduits are sealed from the water conducting ones to prevent the embolisms from spreading. However, when water tension rises through increasing transpiration demand, gas can be sucked from embolised conduits to water conducting ones through pores in the membranes separating the conduits in a process of air seeding. The embolisms created are not necessarily permanent ones, but can be refilled by mechanisms, which are so far mostly unknown.

The purpose of this thesis was to study the different physical processes that are included in the water and solute transport in trees and the interaction of these processes. Much of the dynamics of these processes have not been quantified previously. Water and solute transport processes in trees are of interest, as their functioning can set limits to water and carbon exchange with atmosphere, and they also play a part in the structural development of the tree. This thesis consists of five papers, of which three are modeling studies and two are experimental (field and laboratory) studies. The modeling papers consist of a model of water flow in the xylem where water transport is coupled with embolism, a model of how embolised conduits could possibly be refilled, and a model for phloem translocation and its interaction with the xylem. The field experimental study demonstrates a method for monitoring embolism formation in the xylem with simultaneous ultra-acoustic and stem diameter variation measurements. Stem diameter variation is an indicator of xylem water tension as the volume of the woody tissue contracts in and expands in relation to changes in water tension. The stem diameter variation measurements are developed further in this thesis to accurately account for thermal expansion effects, which cause errors in these measurements.

The results of this study include details of dynamics of various mechanisms leading to embolism, and how embolism affects the xylem water flow. More embolism was found to occur during increasing rather than during decreasing tensions in field conditions, but decreasing tensions also showed some embolism. Münch circulation of water between the phloem and xylem was found to function as has been hypothesized and phloem sap translocation was found to be most sensitive to the amount of sugar that was loaded into the phloem. Refilling of embolised conduits was found to be possible in a time-scale of a few hours under an osmotic induced refilling scheme.

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List of publications

This thesis consists of an introductory review, followed by five research articles. Papers are reproduced with the kind permission of the journals concerned.

Paper I Hölttä T., Vesala T., Perämäki M. and Nikinmaa E. (2002) Relationships between Embolism, Stem Water Tension, and Diameter Changes. *Journal of Theoretical Biology* 215: 23–38.

Paper II Hölttä T. Vesala T., Nikinmaa E., Perämäki M., Siivola E. and Mencuccini M. (2005) Field measurements of ultra-sonic acoustic emissions and diameter variations. A new insight into the relationship of xylem tensions and embolism. *Tree Physiology* 25: 237–243.

Paper III Sevanto S., Hölttä T., Hirsikko A., Vesala T. and Nikinmaa E. (2005) Thermal expansion of green wood: an analysis of temperature corrections for tree stem diameter variation measurements. Accepted for publication in *Boreal Environmental Research*.

Paper IV Vesala T., Hölttä T., Perämäki M. and Nikinmaa E. (2003) Refilling of a hydraulically isolated embolised vessel: Model calculations. *Annals of Botany*. 91: 419–428.

Paper V Hölttä T., Vesala T., Sevanto S., Perämäki M. and Nikinmaa E. (2005) Modeling xylem and phloem water flows in trees according to cohesion theory and Münch hypothesis. Accepted for publication in *Trees*.

1. Introduction

Water transport in trees is commonly explained by the cohesion-tension theory, first proposed in 1896. According to this theory, the evaporation of water at the leaf surfaces pulls a continuous water column against a gravitational gradient through a continuous pathway of xylem conduits reaching all the way down to the roots (Nobel, 1991). As a consequence, water pressure in the xylem is decreased below saturation vapor pressure, i.e. water is under tension. That water transport occurs constantly in this thermodynamically meta-stable state in nature is extraordinary and has made the research topic puzzling. The water column is mostly kept intact by cohesive forces between water molecules and by adhesive forces between water molecules and the surrounding conduit walls. The xylem water, i.e. sap, is vulnerable to a failure of these forces and to spontaneous phase-transition through cavitation under these conditions.

Also other mechanisms can cause the water column to break and individual water conducting vessels to become gas filled. These mechanisms include air penetration to the water conduits from adjacent conduits or air spaces through little pores, what is referred to as air seeding, or the release of stabilized gas bubbles from cracks and crevices from the vessel walls (Tyree, 1997). Regardless of the initial mechanism, as individual water-conducting vessels are filled by water vapor or air, and they become embolised. Embolised vessels become hydraulically isolated from water conducting vessels and cease conducting water (Zimmermann, 1983; Holbrook & Zwieniecki, 1999). Thus water in the transpiration stream has to find alternate pathways around the embolised vessels, and as a result, the hydraulic conductivity of the xylem is reduced.

The occurrence of embolism appears to be quite common in natural conditions and it can be detected and quantified by various experimental methods (e.g. Sperry et al., 1988; Jackson & Grace, 1996). Embolism occurs as the xylem water tension increases through increased transpiration or soil drying. The vulnerability to embolism can vary significantly among different species. Recent experiments have also confirmed that embolisms can be repaired at least in some species, and this occurs even while water is under considerable tension (Tyree et al., 1999; Holbrook & Zwieniecki, 1999). In this process, water is forced back into the gas filled conduits, but the mechanisms of refilling embolised conduits are mostly unknown and are currently under debate.

A separate transport system in trees for assimilate product translocation from the leaves to other parts of the tree is the phloem. The phloem is constructed of a continuous pathway of sieve cells that are connected to each other either by sieve plates, or by small pores. The pressure-flow theory is commonly accepted to explain phloem translocation (Taiz & Zeiger, 1998). The loading of sugars to the phloem near the leaves reduces the osmotic potential, and draws in water from the surrounding tissue and raises the water pressure, i.e. turgor pressure. Similarly, the unloading of sugars elsewhere lowers water pressure. According to the pressure flow theory, this axial water pressure gradient in the phloem sieve cells is the driving force for phloem translocation. The phloem water is under positive pressure as opposed to the xylem. The two pathways, xylem and phloem, are usually separated only by a very thin layer of cambium tissue and still developing xylem cells, and the water exchange occurs between them. According to the “Münch hypothesis” water is circulated between the xylem and phloem so that water moves from the xylem to the phloem at the top of the tree and from the phloem to xylem at the bottom (Taiz & Zeiger, 1998). Neither of the theories, the cohesion-tension theory or the pressure flow theory, have been unambiguously proven

to be the sole mechanism for water and solute transport. Debate still exists about the validity of the cohesion tension theory, mainly because it requires the existence of high xylem water tensions, especially for tall trees. Alternate theories or possible additional mechanisms to the cohesion tension theory, have been proposed, such as the role of the surrounding living tissue or osmotic effects in raising the water (e.g. Zimmermann et al., 1993; Canny, 2001; Zimmermann et al., 2004), but no substantial evidence for these theories have been presented and even the basis of these theories have not been found to be thermodynamically sound (e.g. Comstock, 1999). Thus the cohesion-tension (Tyree, 1997; Steudle, 2001) and pressure flow theories (Taiz & Zeiger, 1998) are widely accepted. Also the results acquired in this study are found not to contradict the underlying principles of these theories.

The interest for studying water and solute transport processes in trees and other plants is not only to understand basic biological phenomena, or the curiosity that the water transport system of trees and most plants rely on meta-stable water. The water and solute transport systems play an important regulatory factor for water and carbon exchange at the leaves. Small openings in the leaves, the stomata, balance the carbon uptake against water loss with the atmosphere, and the water transport pathway from the soil to the leaves is an important factor in stomatal regulation. The threat of failing to keep water columns intact under tension and transport a sufficient amount of water to the leaves will force the tree to close the stomata (e.g. Salleo et al., 2000; Cochard et al., 2002), thereby decreasing the photosynthetic productivity. As trees and other plants cover a large part of the earth's surface, they play a major role in the global water and carbon cycle. Furthermore, structural development of the tree is affected by the water and solute transport capacity, as the conduit systems requires a part of the biomass allocation (e.g. Mencuccini, 2002; Taneda & Tatenno, 2004). This study provides details as to how these transport processes and failures in them physically occur. Much of the dynamics of embolism formation and repair, as well as the exchange between the xylem and phloem shown in this study have not been previously quantified.

The articles forming this study analyze the above processes using modeling and measurements performed both in the laboratory and field conditions. All of these different processes, except for embolism refilling, have been a subject of study for a long time already, but their details are still largely unknown and even the underlying theories are under debate. One reason for this is that negative pressures are generally quite rare in natural conditions, and they are also hard to quantify experimentally. Measurements are difficult due to the small sizes of the cells, and due to the disturbances they cause. All of the subjects which are under study here are linked together by the movement of water in the tree. *The aim* of the study has been to quantify the dynamics of xylem and phloem water flow, embolism and embolism refilling, and to link these processes by studying their interaction with each other. *The first theme* of the study concentrated on quantifying the dynamics between transient xylem water tension and embolism on a diurnal and also on a day-to-day scale. This is done by modeling water flow and embolism in the xylem (**paper I**), and also by analyzing field measurements (**paper II**). In the field measurements, stem diameter variation is used as an indicator of xylem water tension, as due to the elasticity of the wood material, its diameter varies according to the water pressure. The accuracy of diameter variation measurements have been improved by accounting for the discrepancy that thermal expansion of the stem causes in the measurements (**paper III**). This includes defining the radial thermal expansion coefficients of wet fresh wood for different tree species as they have been

previously unknown. Embolism is monitored by ultra-acoustic emission sensing. *The second theme of the study* was to determine the conditions necessary for the refilling of embolised conduits and the dynamics of the processes that possibly are involved in refilling (**paper IV**). *As a third theme*, the Also water and solute flows in the phloem and the water exchange between the phloem and xylem have been modeled in this study (**paper V**). We wanted *to test* if, as well as under what conditions, water circulates in the tree as the Münch hypothesis suggests and how sugars are translocated from the leaves to the sugar sinks. *Other aims* have been to find out conditions necessary for refilling of embolised conduits and the dynamics of the processes that possibly are involved in refilling (**paper II**). Finally, the accuracy of diameter variation measurements have been improved by accounting for the discrepancy that thermal expansion of the stem causes in the measurements (**paper V**). This includes defining radial thermal expansion coefficients of wet fresh wood for different tree species as they have been previously unknown.

2. Theory

Water flow in the xylem and diameter change measurements

Transpiration induces a sub-atmospheric, usually a negative water pressure at the cell-wall spaces in the sub-stomatal cavities of the leaves/needles, from where water diffuses into to the atmosphere. This draws water in a continuous column all the way from the soil. Mass water flow in the xylem occurs along a pressure gradient and can be described by Darcy's law (Siau, 1984)

$$Q = \frac{k}{\eta} \frac{dP}{dx} A \rho, \quad (1)$$

where k is the water permeability of the conduit complex, η is the dynamic viscosity of water, dP/dx is the pressure gradient, A is the cross-sectional area of the conduit complex, and ρ is the density of water. The pressure gradient consists of both the gravitational and the viscous effects. The usage of Darcy's law is justified because water flow in both the xylem and phloem is laminar due to the slow flow velocities of typically less than $1. \text{ m h}^{-1}$. Also some solutes are transported in the xylem along with the water flow from the soil, but the solute concentration in the xylem is so small that the xylem sap is treated as pure water in the calculations. In the case of phloem flow, the concentration of solutes is much higher, and their affect on the viscosity of the phloem sap have to be taken into account.

The relation between pressure and water content change in a control volume V resulting from the water mass flow can be estimated according to (Nobel, 1991)

$$dP = E_r \frac{dm}{V\rho}, \quad (2)$$

where E_r is the radial elastic modulus of wood, dm is the change in the water mass in the volume, and ρ is the density of water.

The negative water pressures in the xylem are very difficult to measure directly. A direct method of measuring water pressure inside the xylem during negative water pressure is the pressure probe (e.g. Tomos & Leigh, 1999), which is penetrated into

an individual conduit lumen. An indirect method, the Scholander-Hammel pressure bomb, has been more widely used to measure xylem tension (Tyree, 1997). In this method a branch or leaf is excised from a plant. This causes a rapid release of water tension in the xylem conduits, and water from the xylem conduits is then pushed into the surrounding tissue. The sample is then pressurized, and the magnitude of positive pressure needed to force water back to its original position before excision is thought to be equal to the xylem water tension. These two measurement methods somewhat contradict each other, as the large tensions supported by the cohesion theory can be measured with the pressure bomb, whereas the pressure probe has been unable to measure large water tensions. There is still ongoing debate about the validity of these measurement methods, but the pressure bomb is generally thought to be more reliable, as there are problems in directing the pressure probe directly into the lumen of a water-transporting conduit and not causing cavitation at the same time (Tyree, 1997; Steudle, 2001).

Another indirect and less used method of estimating water pressure in the xylem is to measure variation in the stem xylem diameter. It is known that the diurnal diameter variation of the xylem coincide with variation in xylem water tension (Irvine & Grace, 1997) and also with transpiration (Perämäki et al., 2001). Since the xylem and also phloem are elastic tissue, their diameter changes according to the water pressure. As the changes in the diameter are very small, a linear relationship between the diameter and pressure change can be assumed, i.e. Hooke's law can be used (Perämäki et al., 2001). The diameter change of the xylem and the whole stem can be calculated from the pressure change using simple geometry

$$dd = \frac{1}{E_r} \frac{2V}{\pi dd} dP, \quad (3)$$

where dd is the change in stem diameter and l is the height of the component over which the diameter changes. It follows that the stem diameter decreases as the water pressure drops. If the radial elastic modulus of the stem sapwood is known, then changes in diameter can be directly converted into changes in water pressure according to equation (3). As equation (3) calculates only changes in water pressure, the initial values of tension and diameter at any single point in time are needed to calculate the absolute values of tension.

The diameter changes also due to thermal expansion and radial growth of the stem. The growth effect can be ignored when we are studying the diameter change over the xylem only, but in the experimental results, the thermal expansion effects have to be corrected for. As the magnitude of the dimension change of the wood due to thermal expansion is almost comparable in magnitude to the diameter change due to pressure variation, it is important to accurately determine the thermal expansion coefficient of wood. While the thermal expansion coefficients have been determined accurately for dry timber wood in the common species, there is plenty of confusion about the same coefficients for wet, fresh wood. Some have even suggested that the thermal expansion coefficient is negative (Salmén, 1990), i.e. that the diameter of wet wood shrinks when the temperature is raised. The problem associated in determining the thermal expansion coefficient of moist wood is that water tends to migrate out of the wood cells when heated. **Paper III** develops the method for measuring the radial thermal expansion coefficient of wet fresh wood. This method ensures that water movement out of the sample during the measurement is prevented.

Water flow over a membrane

For calculating water exchange over a membrane, the following equation can be used (Nobel, 1991)

$$Q = L[P_1 - P_2 - \sigma(C_1 - C_2)RT]A \quad (4)$$

where Q is the mass water flow over the membrane, A is the surface area of the radial interface over the membrane and L ($mPa^{-1}s^{-1}$) is the hydraulic conductivity of the interface surface, P is the hydrostatic pressure, C is the solute concentration, σ is the osmotic reflection coefficient of the interface, and the subscripts 1 and 2 refer to the adjacent sides of the membrane and the flow direction (positive value for Q) is from 1 to 2. For a semi-permeable membrane, the reflection coefficient is equal to unity and solutes cannot move across the membrane. For a permeable membrane, solutes move across as easily as water and the reflection coefficient is zero in this case, i.e. no osmotic effects occur.

Phloem water flow

Sugar loading into the sieve cells at the top of the tree decreases the osmotic potential locally. This decreases the total water potential compared to the surrounding cells and water is drawn into the sugar-loading zone according to equation (4) through a semi-permeable membrane. As a result of this inflowing water, the water pressure, i.e. turgor pressure, is raised at the top of the phloem. Likewise, unloading of solutes at the sink zone raises the osmotic potential of the sieve elements and water is exuded out to the surrounding tissue, which causes a decrease in the water pressure. This sugar loading and unloading induced axial water pressure gradient drives the bulk water flow in phloem from the sugar sources to sinks according to equation (1). No osmotic effects influence the phloem water flow in the axial direction, as there are no membranes to cross. The solutes move along with the water stream-wise. Diffusion of solutes is likely to occur also, but it is much slower. The biological loading and unloading mechanisms of solutes to and from the phloem are beyond this study. While phloem and xylem water flow have been studied separately, only a few studies (Ferrier et al., 1975; Daudet et al., 2002) have been conducted to find out the interaction between the xylem and phloem flows. **Paper V** of this study analyses the water and pressure exchange between the xylem and phloem. Interaction between the xylem and phloem are investigated more explicitly than in previous studies, as the present study quantifies the water mass exchange between the xylem and phloem, and the consequent pressures changes.

Embolism

Water can withstand large tensions before cohesive forces between molecules rupture under ideal conditions. Tension is a measure of how much the water pressure has dropped below saturation water vapor pressure, and it is thus equal in magnitude to the negative water pressure in addition to the saturation vapor pressure. The classical nucleation theory calculates that water tension can be raised up to 140 MPa (Brennen,

1995) before cavitation occurs homogeneously in the bulk of the liquid. However, in practice this limit is never reached, as small impurities, solid surfaces, dissolved gases and other disturbances will cause nucleation at much smaller tensions even under laboratory conditions (Smith, 1994). The tensions are much larger than those found in trees, as water tensions in trees remain almost always under 10 MPa and are much lower in most species. It is thus very likely that embolism also occurs in the xylem by some mechanism other than by homogeneous cavitation in the bulk xylem without any impurities or external disturbance.

Embolism in the xylem can, at least in theory, be induced by various mechanisms. Various possible mechanisms are illustrated in Figure 1. Any gas volume larger than a critical size in a liquid will grow in size according to the laws of thermodynamics to become a macroscopic bubble. This critical size radius is defined by Laplace's equation (Brennen, 1995)

$$R = \frac{2\gamma}{P_g - P_L} \quad (5)$$

where γ is the surface tension of the liquid/gas interface, P_g is the gas pressure inside the void, and P_L is the liquid pressure. Gas voids smaller than this are crushed by surface tension forces. We have categorized the mechanisms for inducing gas bubbles larger than the critical size into two groups, stochastic and deterministic processes.

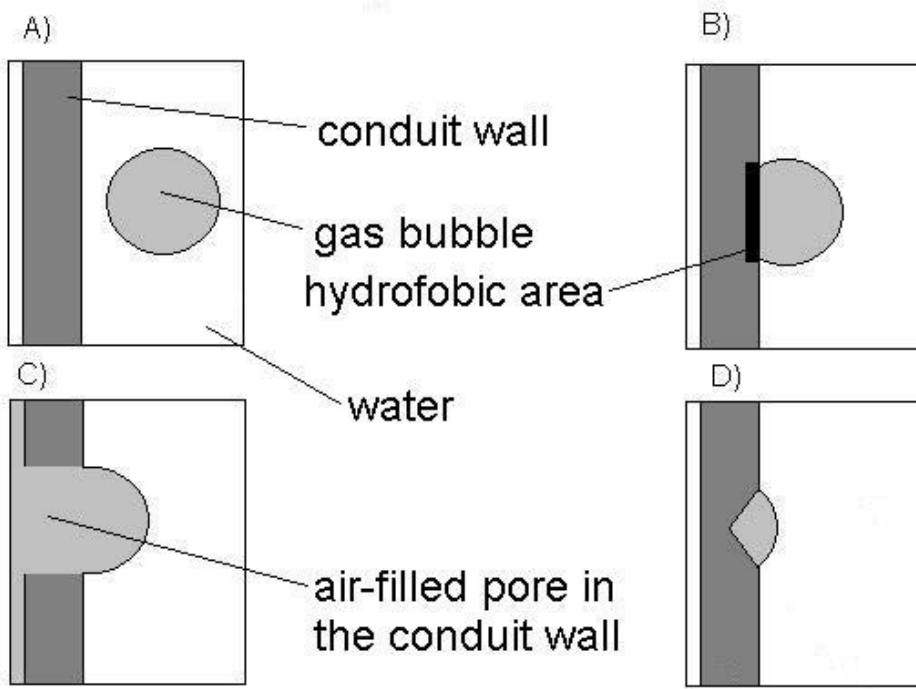


Figure 1. Different mechanisms potentially leading to embolism. a) homogeneous cavitation b) heterogeneous cavitation c) air seeding d) release of pre-existing bubbles from cracks in the conduit wall.

Stochastic processes include actual nucleation phenomena where vapor voids of the critical radius or larger are developed by thermodynamic fluctuations in the liquid. Stochastic processes leading to embolism are homogeneous and heterogeneous cavitation, see Fig. 1 a and b. Homogeneous cavitation is a failure of cohesive forces between water molecules, where a vapor void forms inside the bulk liquid and in heterogeneous cavitation at a liquid/solid surface interface. Heterogeneous cavitation results from a failure of the adhesive forces between the water molecules and conduit walls. Also impurities in the liquid can be sites for heterogeneous cavitation. The nucleation rate J , cavitation events per unit volume and time, can be calculated by the classical nucleation theory to be to (Brennen, 1995)

$$J = J_0 \exp\left(-\frac{E_{cr}}{kT}\right) \quad (6)$$

where E_{cr} is the energy required in forming a critical size vapor nucleus, k is the Boltzmann factor, T is the temperature and J_0 is a pre-factor proportional to the molecular density in case of homogenous cavitation and proportional to the molecular density elevated to the power of $2/3$ in the case of heterogeneous cavitation. The factor kT is the typical kinetic energy of the water molecules. The classical nucleation theory is under debate, and also other theories, like the density functional theory e.g. (Debenedetti, 1990), are being developed to account for inaccuracies in it. As the water tension required for homogeneous cavitation is much larger than what is found in trees, only the occurrence of heterogeneous cavitation is thought to be possible in trees. More detailed formulas for calculating the probability of heterogeneous cavitation as a function of water tension, temperature and conduit wall properties are presented in **paper I**.

Deterministic processes leading to embolism are, for example, air seeding and the release of stabilized gas bubbles from cracks and crevices from the vessel walls. For these processes, an explicitly defined threshold exists for the process to occur. They are not actual nucleation processes, as the critical size gas bubble is not induced by phase transition. **Paper I** presents our argument that they are not cavitation in the physical sense of the word, although this term is widely used in the literature, for instance in the case of air seeding. In air seeding, the maximum pressure difference ΔP between a gas-filled and water-conducting vessel can be

$$\Delta P = \frac{2\gamma}{r} \cos \theta \quad (7)$$

where r is the radius of the largest gas-filled pore between the two vessels, and θ is the contact angle between the vessel wall and water. If the pressure difference ΔP exceeds this, then a bubble is sucked into a water conduit and embolism occurs. Air seeding is generally thought to be the most common cause of embolism (Sperry & Tyree, 1988) but the possible role of other mechanisms should also be investigated.

As a result of embolism, the hydraulic conductivity of the xylem is decreased, as embolised conduits are no longer able to conduct water. They consequently become isolated from water filled conduits and water has to find alternate paths around the embolised conduits. The reduction in permeability does not necessarily correspond to the relative number of embolised conduits, but this can be a first approximation (e.g. Hacke & Sauter, 1996). By examining equation (1), we also see that if the amount of water flux remains unaltered after embolism events, then the pressure gradient in the xylem has to increase. This would in turn induce more embolism as the water pressure

in the xylem would drop and a cycle of “run away embolism” (Tyree & Sperry, 1988) would develop. According to this scheme, an increase in embolism and a decrease in water pressure would feed each other and eventually all conduits would become embolised. To avoid this scenario, transpiration must be reduced by stomatal closure, which also reduces photosynthesis simultaneously.

During embolism plants produce detectable acoustic (Milburn, 1966) and ultrasonic (Tyree & Dixon, 1983) emissions that result from pressure waves following the events. In the ultrasonic detection range, background noise can be reduced more efficiently than at audio frequencies. This ultrasonic range is used in **paper II**. Embolism can also be detected using other methods, for example, by measuring the hydraulic loss it induces. Vulnerability curves, where the amount of loss in hydraulic conductivity is measured as a function of the xylem water pressure, have been constructed for the most common species e.g. (Tyree & Sperry, 1989). This method, however, is tedious to execute and destructive for the tree, as branch or stem segments have to be cut from the tree to perform the measurements and this method is therefore unsuitable for continuous field measurements.

Refilling

Embolisms have been found to refill in various experiments, but the details associated with the processes leading to refilling are not yet known. Refilling has also been found to occur in some species during transpiration while the xylem is under considerable water tension (e.g. Tyree et al. 1999; Melcher et al., 2001). What makes the refilling process problematic is that water must be forced into the gas-filled conduit, where pressure is close to atmospheric, from the surrounding tissue, where the water potential is negative. The flow of water through the membrane can be calculated using equation (4), as is done in **paper IV**. There have been many suggestions in the literature as to how this could be achieved including the active secretion of salts/solutes from the adjacent living cells to embolised vessels (Holbrook & Zwieniecki, 1999; Grace, 1993), or the flow of solutes through opened water channels from adjacent living cells into embolized vessels (Tyree et al., 1999). These solutes would decrease the osmotic potential of the refilling vessels, and the total water potential of the refilling vessel could drop below that of the surrounding xylem conduits and/or living cells and thereby draw water in. Moreover, it has been suggested that the role of the phloem and high water pressure generated by reverse osmosis in living vessels serves as a source of solutes and/or water under positive pressure (Salleo et al., 1996; Milburn, 1996; Salleo et al., 2004) as a refilling mechanism. In addition, surface tension forces aid in the solution of the gas bubbles. But this effect is very small when the refilling process is not already near to completion, as the effect grows stronger when the curvature of the water gas/liquid phase interface increases when gas bubbles become very small. In the beginning of the process, the effect depends on the size of the tapered ends of the refilling conduit, and is not sufficient by itself to explain refilling under tension. As the refilling process is near to completion, it is necessary that all gas voids in the refilling vessel have to be dissolved before hydraulic conductivity is re-established with the adjacent conduits (Holbrook & Zwieniecki, 1999). Otherwise, these residual gas pockets would seed new embolisms when hydraulic conductivity is established to the adjacent water-filled conduits.

3. Materials and methods

Both computer modeling and experimental measurements done in the field and laboratory are included in this thesis. The computer modeling for **papers I, IV, and V** have been done using Fortran 90 programming language. The field measurements for **paper II** were conducted in SMEAR II (Station for Measuring Forest Ecosystem-Atmosphere Relations, University of Helsinki) (**61°51'N, 24°17'E, 181 m asl**) research station in Hyytiälä, southern Finland. The site has an even aged stand of Scots Pine (*Pinus Sylvestris* L.) which was established from the seed in 1962. The mean height and diameter of the trees is 13 m and 13 cm, respectively. Detailed information about the research station can be found in (Vesala et al., 1998). **Paper III** includes the laboratory measurements conducted in the Department of Physical Sciences at the University of Helsinki.

Modeling

Modeling sap flow in the xylem and phloem

Sap flow both in the xylem and phloem (**papers I and V**) are modeled as bulk flow driven by a water pressure gradient according to equation (1) and mass conservation. For calculation purposes, the model tree is axially divided into 40 equally long elements. Transpiration from the top-most xylem element and soil water tension under the bottom-most xylem element is fed as input into the model. The changes in water pressure for each element are calculated by equation (2). The parametrization for **papers I and V** have been done using a model tree in the SMEAR II station with measured dimensions and some parameters and boundary conditions. Parameters which have not been measured have been estimated from the literature.

In **paper I**, where the effects of embolism on water flow are considered, embolism formation is calculated according to equation (7) for air seeding and with more detailed versions of equation (6), which are presented in **paper I**, for heterogeneous nucleation. A schematic outline of the model is given in Figure 2. The properties of water-conducting vessels, which influence the vulnerability to embolism, are given to vary according to the normal distribution. The various effects of embolism on the water balance of the tree are then calculated as presented by the equations in **paper I**. These modeled effects include the water release from the conduits following embolism, the drop in the xylem permeability due to embolism, and the effect of embolism on the diameter of the stem. Also the effects of refilling of the embolised conduits on the water status of the xylem are calculated in some model runs. The actual refilling process is not modeled in **paper I**. Instead, refilling is modeled to occur at a constant rate as the water pressure reaches a certain level.

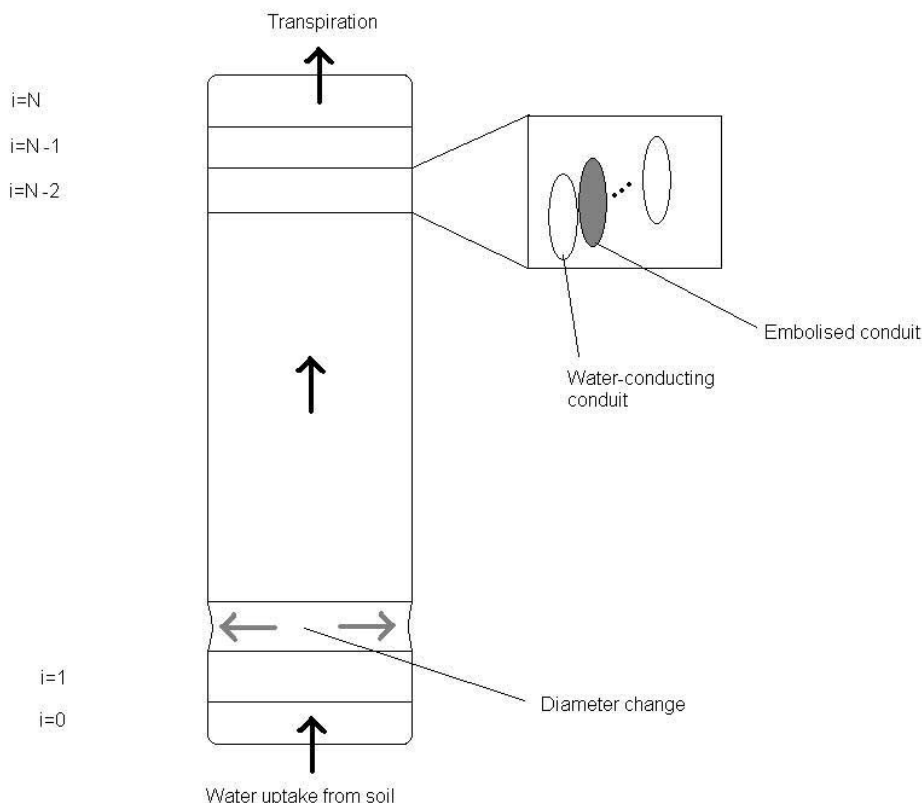


Figure 2. A schematic outline of the xylem flow and embolism model in the tree stem. The stem is divided into N components in the axial direction. Each component has a transient amount of embolised conduits.

In the case of the simultaneous calculation of both phloem and xylem sap flows, the radial water exchange between the xylem and phloem are calculated according to equation (4). The simultaneous modeling of these two flows has not been explicitly done before, although phloem flow has been modeled substantially (e.g. Thompson et al., 2003). The cambium tissue between the xylem and phloem, and sieve storage cells are also included in the model, both with semi-permeable membranes surrounding them. This semi-permeability assures that osmotic potential differences induce water exchange and that solutes do not move across the membranes. Sugar is loaded into the phloem at the five topmost elements and unloaded at the five bottommost elements. These equations are solved numerically by the Runge-Kutta method (Press et al., 1989) using a time step approach. The viscosity, included in equation (1), is made concentration-dependent (Morison, 2002). Furthermore, the diameter changes in this study are calculated for the xylem and phloem, as there are field measurements of diameter variations from previous studies (Sevanto et al., 2003) that can be compared to diameter changes predicted by the model.

Modeling embolism refilling

The refilling process of an embolised conduit by air in a system, which consists of a refilling vessel, water-conducting vessels and living cells, is modeled in **paper IV**. The model is presented schematically in Figure 3. The model assumes that living cells act as solute sources and that they are able to draw in water from the water-conducting xylem vessels. It is required that the water and solute permeability and reflection coefficient are changing asymmetrically on the two sides of the same living cell. Water and solute start to flow into an embolised vessel when the reflection coefficient, see equation (4), between a living cell and an embolised conduit drops below unity, possibly by the opening of water-channels, aquapores. This causes the exudation of water and solutes into the gas-filled conduit from the living cell and a drop in its total water potential below that of the bulk xylem. As the water potential in the living cell drops due to this, it draws more water from the surrounding water-conducting vessel. As water exudates into the refilling conduit, the gas in the refilling conduit is confined in a smaller volume and its pressure rises. The elevated gas pressure causes gas dissolution to the liquid water. Now, as the partial pressure of air dissolved in the water inside the refilling vessel is higher than the atmospheric one, air diffuses out of the refilling vessel to the atmosphere. Also taken into consideration is the solute transport from the phloem and refilling of a water vapor filled conduit in contrast to an air-filled one. No active transport of solutes has to be assumed in any of the processes.

The rates of these different processes in the model, water exudation, solute movement, water and gas pressure changes, dissolution of gas, and gas diffusion, are calculated according to equations found in **paper IV**. These rates are then multiplied by a small time step, and the values are updated, i.e. the Euler method of differentiation is used. The basic simulations consist of the evolution of the water/gas ratio in the refilling vessels. Gas pressure and the osmotic potential in the refilling vessel and of the osmotic potential and water pressure in the living cell are also calculated, and some of these parameters can be compared to available experimental results (e.g. Tyree et al., 1999; Zwieniecki & Holbrook, 2000). Since in reality, many of parameters and actions under consideration are not well known, sensitivity analysis to them is performed. So the model shows under what conditions xylem refilling is possible and how long time the complete refilling process takes.

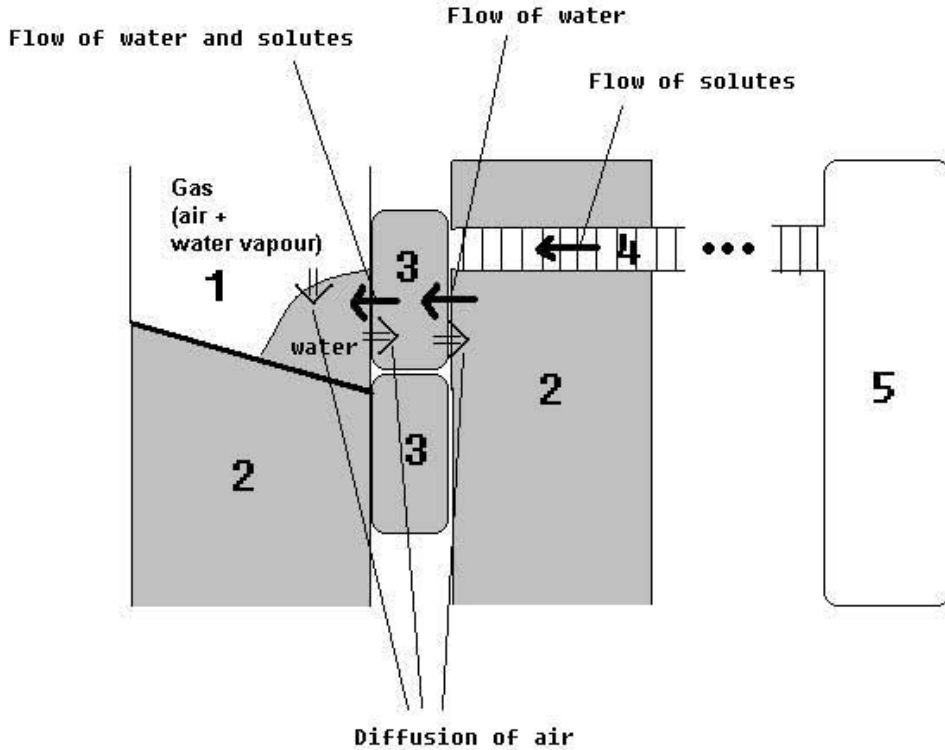


Figure 3. A schematic outline of the embolism refilling model. The different components include the refilling vessel (1), water-conducting vessels (2), living cells (3), ray cells (4) and phloem (5). The refilling vessel is hydraulically isolated from the xylem vessel. The refilling vessel contains liquid water and gas. The air dissolves in the water and diffuses out of the vessel.

Measurements

Ultra-acoustic emission and diameter change measurements

We have used the ultra-acoustic method to detect embolism in **paper II**. Variations of stem xylem diameter variations were measured with linear displacement transducers (LVDT; model AX/5.0/S, Solartron Inc., West Sussex, U.K.) to estimate water pressure variation in the xylem stem in **paper II**. The diameter change data is corrected for thermal expansion by subtracting their calculated effect on the stem diameter. The linear displacement transducers used to measure the stem diameter were attached to the tree with rigid steel frames after the bark and phloem were removed from these locations that were resting on screws attached to the outer 0.5 cm of xylem. In addition, pressure bomb measurements were made to estimate the absolute value of the water pressure in the tree. For the UAE measurements, 4615 DSM (Drought Stress Monitor) was used with I15I transducers (Physical Acoustic Systems, Princeton, NJ, USA) attached to the trunk of a tree and to the branches after the bark and phloem were removed to prevent attenuation of the signal. Laboratory tests were also conducted to estimate the total number of water conduits within the hearing distance of the sensors by allowing

a wood sample to dry completely until all conduits were embolised. The number of observed UAE's would be an estimate of the total number of water conduits within a sensor's hearing distance. For details on the instrumentation the readers should refer to (e.g. Jackson & Grace, 1996) for the UAE measurements and to (Perämäki et al., 2001) for the diameter change variations.

The diameter changes and ultrasonic-acoustic emissions were measured simultaneously on a 35-year-old 12-meter high Scots Pine (*Pinus sylvestris*) tree to estimate the diurnal and day-to-day patterns of embolism and stem xylem tension. Both measurements have a time resolution of one minute. This assures that rapid changes in both water tension and embolism rate and thus the dynamics of the embolism process can be observed. More focus in the paper is devoted to the transient changes in the water pressure and embolism rather than to their absolute values.

Determining thermal expansion coefficient

To determine the radial thermal expansion coefficient of wet wood, we developed a measuring system in **paper III** including a heat bath with a controllable temperature, and linear displacement transducers to measure the diameter variation. The measuring system is depicted in Figure 4. The wood specimen would be sunk into the heat bath while the temperature would be varied very slowly. This assures that the water contents of the wood remain unchanged. The linear displacement transducer would be attached to the wood species by steel frames to measure the change in diameter. Thermocouples were used to measure the temperatures of the steel frame and the wood. A hole was drilled in the wood so that the thermocouple could be pushed inside the stem to acquire a more representative value of the stem temperature. The thermal expansion of the steel frames was also measured and so that its effect would be subtracted from the results.

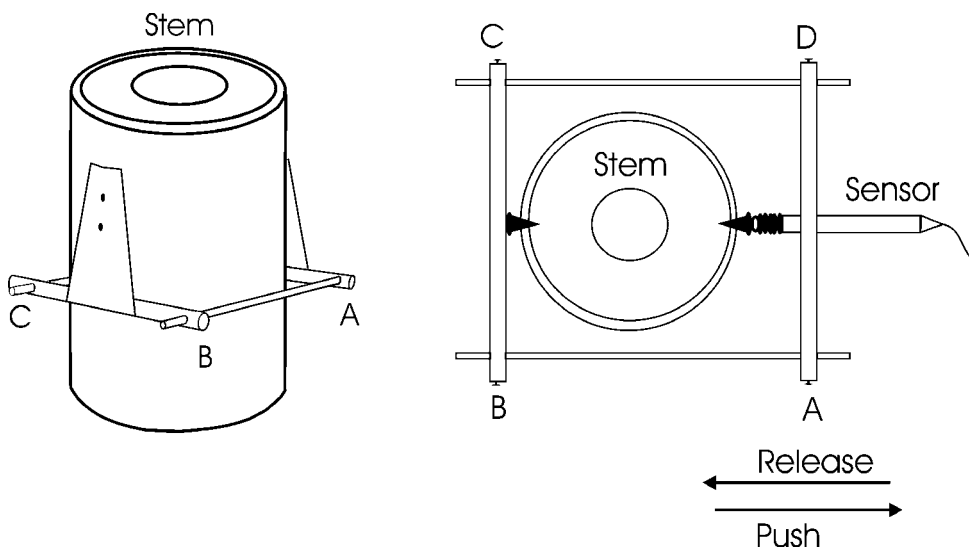


Figure 4. Measuring system of the thermal expansion coefficient of wood including the steel frame, linear displacement transducers, and a cylindrical segment of the stem.

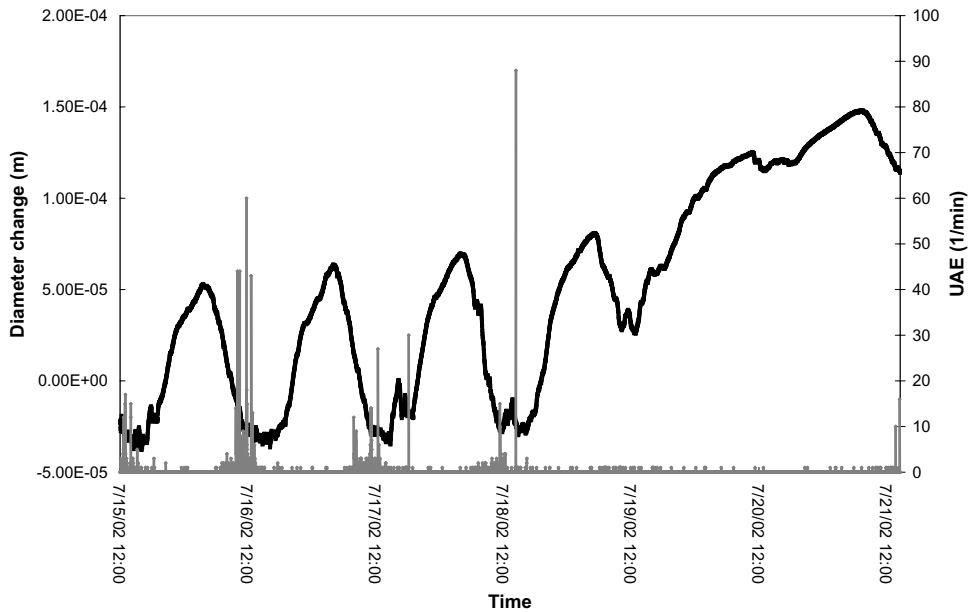
4. Results and discussion

Xylem sap flow and embolism

The xylem sap flow and embolism model presented in **paper I** demonstrates that even a moderate amount of embolism has a significant effect on xylem water balance. Embolism relieves tension temporarily as water is freed to the transpiration stream when it is pushed out of the embolising conduits. The growth of the embolism rate is then temporarily prevented. A reduction in hydraulic conductance is seen as a rise in water tension on the following days as larger pressure gradients are needed to transport a certain amount of water, which is fixed by stomatal conductivity and the vapor pressure deficit. If the amount of embolism grows too high then transpiration must be reduced to avoid “run-away” embolism. The embolism model showed that even a very moderate occurrence of embolism is seen in diameter change measurements as a deviation of diameter variation from the transpiration, which it normally follows by a very short time lag. The stem diameter swells after embolism events due to the water release into the transpiration stream. Embolism also enhances the amplitude of the daily diameter variation as a result of lowered water permeability if transpiration remains unchanged, assuming that the elasticity of the xylem would not change due to embolism. If refilling of embolised conduits occurs, then the embolising conduits in a way act as storage or capacitance elements. They release water during high transpiration when the need for water in the transpiration stream is large. Then water is pushed back into them during the night when xylem tension is lower and the need for water is less. Refilling is seen in the diameter change measurements as a slower swelling of the stem in the afternoon and evening when the water stores are refilled. Perämäki et al. (2005) reported this type of slow recovery in the diameter variation data. Part of this slow recovery of diameter could be connected to embolism recovery.

According to the model in **paper I**, different mechanisms leading to embolism should show a lightly different time evolution. As deterministic processes like air seeding have well defined threshold tensions for embolism occurrence for individual conduits, they should show embolism only on increasing water tension. This is because all conduits would have already embolised during increasing tensions when the tension thresholds for embolism for the individual conduits were already reached before the daily maximum tension. Embolism by stochastic processes, such as heterogeneous cavitation, should also be induced during decreasing water tensions in the afternoon, as the amount of embolism is also dependent on the time that a tension persists, and there is not an explicit tension threshold for a conduit to become embolised.

Figure 5 shows an example of simultaneous diameter change and UAE measurements. The measured ultra-sonic acoustic emissions followed the xylem diameter decreases on a short time scale. This clearly indicates that individual peaks in embolism occurred simultaneously with peaks in water tension. Analyzing the data from the whole measuring period, we observed that ultra-acoustic emissions occurred mainly at decreasing stem diameters, i.e. increasing water tensions when water tension was high. The fact that a majority of the events occurred during increasing water tensions indicates the dominant role of deterministic processes in inducing the embolisms. Still, many embolism events (about 30 % during the whole measuring time) occurred at decreasing xylem water tensions, indicating a contradiction with a scenario that depicts embolism as purely deterministic air-seeding induced.



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Figure 5. Stem xylem diameter (darker line) and the observed ultra-acoustic emissions (lighter histogram) at 2.5 meters height in the stem of a Scots Pine tree for the measuring period of 15.7 - 22.7.2002 at SMEAR II research station in Hyytiälä, southern Finland. The diameter is shown relative to a reference diameter at the beginning of the measuring period. The water tension increases as the diameter decreases, and the relationship between them is assumed to be linear.

The total amount of embolism remained quite small, under 10 % of the sapwood xylem cells at a given control volume during a period of two weeks. There was very much variation between days. Periods with high xylem diameter, i.e. low water tensions, (19.7–21.7 in Figure 5) showed very little or no embolism. Also tension and embolism history seemed to affect the amount of daily embolism. After periods of relatively numerous embolism events, either higher tensions than before, or wet periods with embolism refilling, were needed before new embolisms were observed. This was observed both in the model (**paper I**) and in the measurements (**paper II**). Embolisation events seemed to occur during short time spells in our measurements. Increase in stem diameter, which indicates a release of tension after peaks in embolism, can be observed in our study, but we cannot be conclusive that this was due to the water release from embolised conduits as is suggested by the model.

Phloem flow

Our combined xylem and phloem model demonstrates that water circulation between xylem and phloem can occur physically feasible with realistically chosen parameters and environmental conditions. The continuous loading of sugar at the top of the stem keeps the water flowing at the top stem from the xylem to phloem, and unloading at the bottom from the phloem to the xylem continuously, just as the Münch hypothesis

predicts. Figure 6 shows the resulting water potentials in the xylem and phloem and the flow direction of water. Water flow in the axial direction follows the hydrostatic pressure gradient and in the radial direction, the water potential gradient. The direction of all flows remains the same throughout the day. The phloem flow and water circulation is slightly larger during the night in the absence of transpiration. Also the modeled diameter changes of the xylem and whole stem corresponded well with the experimental studies of (Sevanto et al., 2002; Sevanto et al., 2003), so that the magnitudes and time lags were very similar in both.

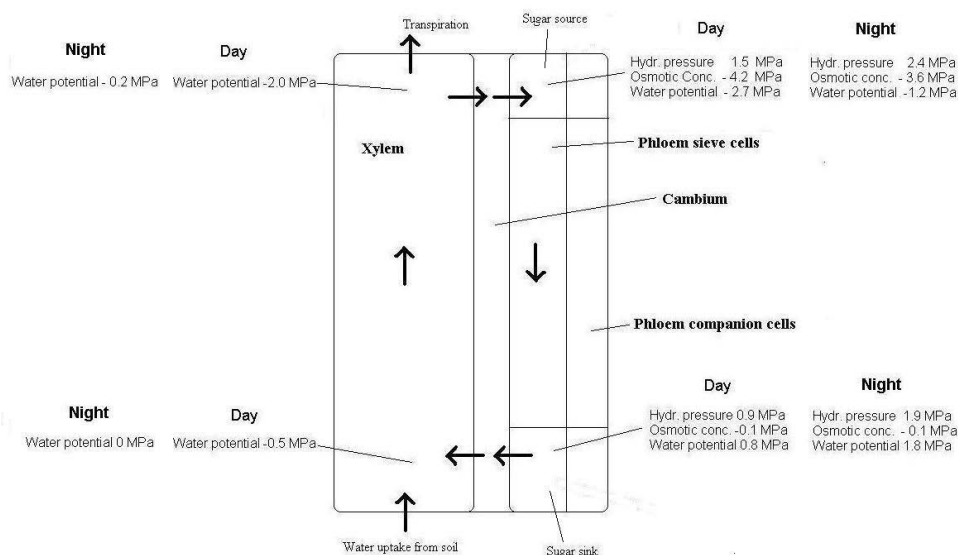


Figure 6. Water potentials resulting from the coupled xylem and phloem flow model during the day (during peak transpiration) and during the night (in the absence of transpiration). Transpiration (sine-wave like during the day, zero at night) and sugar loading and unloading rates (constant throughout the day) are fed as input to the model. The direction of resulting water flows are indicated by arrows. Water potential is the sum of the hydrostatic pressure and osmotic pressure induced by the osmotic concentration. Water flows follow the hydrostatic pressure gradient in the axial direction and the water potential gradient in the radial direction.

The model shows that phloem translocation is fairly sensitive to the sugar concentration in the phloem, which is controlled by the sugar loading and unloading rates. Too much sugar loading raises the viscosity of the sap and disrupts the sap flow. The viscosity then rises very high at sugar concentrations only little bit higher than those found in the phloem in experimental studies (Taiz & Zeiger, 1998), as viscosity has a fourth order dependence on the sugar concentration. This means that if the sugar concentration in the phloem would be higher, then the resistance to sap flow would grow too much for the phloem translocation to function efficiently. The structural relationship between phloem and xylem cross-sectional area seems to allow higher loading of sugars from the leaf than would otherwise be possible. Axially, the phloem vs. xylem area strongly decreases from the transpiring leaf downwards. This is beneficial since sugar accumulation in leaves could down-regulate the photosynthetic capacity. Too little sugar loading, on the other hand, is not sufficient to maintain a sufficient axial

water pressure gradient in the phloem, which is the driving force for the phloem flow. Our model shows that there is an optimal sugar-loading rate in the phloem, where viscosity is kept restricted but the pressure gradient is high enough.

Phloem sap flow is also disrupted if transpiration grows too high, as then the water potential is reduced especially at the top of the tree, and the flow driving axial pressure gradient in the phloem is reduced. The sensitivity of phloem translocation to transpiration variation increases as the hydraulic conductivity between the xylem and phloem is elevated. With too high transpiration and insufficient sugar loading, the tree also faces the danger of the phloem turgor pressure dropping below zero, which the tree must prevent by regulation. Phloem translocation also functions well in the absence of transpiration. At night, in no transpiration conditions, there is still residual water flow in the xylem. This xylem flow is called “Münch counterflow” and to our knowledge, it has not been explicitly modeled before, although experimental evidence of “Münch counterflow” has been found when transpiration has been artificially prevented (Tanner & Beevers, 2001; Kockenberger et al., 1997).

Refilling

The refilling model shows that embolism refilling according to the presented scheme is physically possible under negative water pressures if certain conditions are met. These include an asymmetric aqua pore opening which causes a decrease in the reflection coefficient on the side of the living cell and refilling vessel interface while the living cell and xylem conduit membrane would remain semi-permeable. The most limiting factors to complete refilling were the initial living cell osmotic potential and the ratio of the volume of the adjacent living cells to that of the embolised vessel. These conditions were greatly eased when the phloem was allowed to supply the xylem with solutes. The parameters associated with the air diffusion process would slow down the refilling but not limit the conditions for its completion. The time scale needed for refilling by the presented mechanism is a few hours and varies a lot when the parameter values are changed. The simulated gas pressure within the refilling vessel was in accordance with recent experimental results and low enough to retain hydraulic isolation until the whole refilling process is completed. Our model therefore predicts somewhat higher osmotic potentials in the refilling vessel than experiments have shown (e.g. Tyree et al., 1999). However, even Tyree et al. (1999) were in doubt whether these experiments have been truly able to measure the undiluted sugar concentration inside the refilling vessels.

Thermal expansion coefficient

The thermal coefficients of all the species used in the measurement were positive and lower than that of dry timber. The average values for the coefficient of thermal expansion varied between $7.6\text{--}17.9 \times 10^{-6} \text{ }^{\circ}\text{C}^{-1}$ for different species. Heating and cooling gave similar results for all the species and no hysteresis was observed. The thermal expansion coefficients of wood are of the same order of magnitude as the coefficient for steel. Correction for thermal expansion in the field measurements of the tree stem diameter variations are dominated by the difference in the temperature of the frame and the stem. The exact values for the thermal expansion coefficients are used when correcting the diameter variation measurements.

5. Review of publications

Paper I focuses on the relation between xylem water pressure, xylem diameter change and embolism. These processes and their interaction are modeled. Embolism mechanisms are modeled as physical processes based on water tension and actual properties of the water conduits and the underlying differences between varying embolism mechanisms is taken into account. The effect of embolism and embolism refilling on the water balance of the tree is considered. Furthermore, the details of how embolism can be seen in the diameter change measurements are modeled.

Paper II presents an experimental method for measuring xylem water tension and embolism simultaneously by using xylem diameter change and ultra-sonic acoustic measurements. The experimental set-up allows non-destructive and good time precision measurements under natural field conditions. Analysis of the results concentrates on the short time dynamics of water tension and embolism and how they are inter-related. More embolism events were found to occur during decreasing stem diameters, i.e. increasing water tensions but also increasing diameters, i.e. decreasing water tensions showed embolism. Also the inter-daily patterns of water tension development and embolism formation are analyzed.

Paper III presents an experimental method for determining the thermal expansion coefficients for wet, fresh wood. These coefficients are important as they are used in the diameter variation measurements to correct the results for thermal expansion effects. The coefficients were measured for several tree species. The experimental setup included a heat bath in which the wood samples were immersed and a linear displacement transducer to measure changes in the samples diameter while the temperature of the heat bath was varied. The thermal expansion coefficients of all the species were found to be positive and smaller than for dry timber.

Paper IV presents a model that calculates the refilling process of embolised conduits. This model is based on water and solute exudation from living vessels to refilling conduits. Air in the embolised conduit is dissolved in water and it diffuses out of the stem. The model calculates the dynamics of the process and under what conditions refilling is possible according to this scheme. Refilling was made possible by the positive pressures developed in the living cells adjacent to the refilling vessel when the exchange of solutes across the interface was allowed. No active transport of solutes was needed. The described refilling scheme requires hydraulic isolation of the refilling conduit from the functioning xylem conduits, and also this condition was found to be met.

Paper V describes a model that is developed to study water and sugar translocation in the phloem, and circulation of water among the xylem and phloem according to the “Münch hypothesis”. The model also calculates how the varying of the external boundary conditions and parameters affects phloem sugar translocation, and in what conditions the phloem flow and circulation of water will cease to function. Phloem flow was found to be much more sensitive to changes in sugar loading and unloading than to changes in transpiration. The model also resulted in xylem water flow in the absence of transpiration, i.e. so called “Münch counterflow”. The stem diameter changes resulting from sap flows both in the xylem and the whole stem were modeled to provide verification material for the model to be compared to field measurements.

6. Conclusions

Processes related to water and solute movement in the tree have been quantified by modeling and measurements in this study. It has been shown how xylem and phloem flow, embolism formation and embolism refilling can be described as physical processes linked to measurable physical properties of the water conduits and the thermodynamic state of sap using the concepts of the cohesion tension theory. This study also develops the diameter change measuring method further. A new application for this method, the experimental study of dynamics between the xylem diameter variation and embolism formation, has been introduced. Similar relations in embolism formation to xylem diameter variation were seen in the modeling studies. In addition, quantifying the effects of thermal expansion on the tree stem on the measurements has developed further the accuracy of the diameter variation measurement method. The quite approximate level of the describing the macrostructure of the tree, and lack of knowledge concerning the many of microscopic properties at the cell level can be considered shortcomings of the models in this study. On the other hand, the affect the individual parameters on the processes were quantified by performing sensitivity analysis on them. This has also allowed the mapping of the range of possible structural and environmental conditions in which xylem and phloem translocation and embolism refilling can function.

The processes of xylem and phloem sap flows, embolism formation and embolism refilling are coupled closely together in this study. Previously, these processes have mainly been analyzed as separate processes although in reality they are connected as water and solutes are exchanged between them, as has been shown in this study. In addition, the same environmental drivers, especially transpiration, influence all of these processes. All of the individual papers, except **paper III** in this thesis, have considered these interactions between the different processes. **Paper I** shows how embolism formation and refilling affect the transient xylem water flow, and that transpiration must be reduced through stomatal closure to prevent extensive embolism formation if the embolism refilling does not occur. Also maintaining the phloem translocation capacity could affect stomatal control, as **paper V** demonstrates. The details of stomatal control are, however, beyond this study, as it is a complicated phenomenon dependent also on many other variables such as light, atmospheric water vapor deficit and temperature conditions. The role of stomatal regulation to optimize photosynthesis production and translocation and on the other hand, to avoid excess water loss and embolism, may possibly in the future be linked to the processes studied here. Moreover, the refilling of embolised xylem conduits could very well be associated with the water and solute exchange between the phloem and the xylem. As **paper V** shows, water is constantly being exchanged between the xylem and phloem, and this radially transported water from the phloem to xylem can potentially be a source of the water and solutes needed for the refilling of the embolised conduits in the xylem. More rigorous studies of this will be needed in the future, where combining the now existing models in **papers IV** and **V** may prove to be a useful tool.

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