A physical analysis of sap flow dynamics in trees

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Academic dissertation

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ABSTRACT

The aim of this thesis was to analyze the water dynamics of trees by using a dynamic modeling approach. The work is of cross-disciplinary nature: tree water issues which is a subject of whole plant physiology is examined by means of physics. From physical principles five different models were derived. First, to study the sap flow and the water pressure dynamics in the xylem of tree stem, the effect of embolism on the sap flow, and the recovery of embolized conduits; and second, to analyze a sap flow measuring system based on the heat balance method.

Sap flow and water pressure dynamics are analyzed with two models that are based on the relation between xylem water tension and changes in the diameter of sapwood. This new approach is advantageous because it offers a way to compare the model predictions with the easily measured diameter changes in intact trees. The model results give new insight into the water dynamics in the stem, stating that pressure propagation is fast, but time lags of a few minutes do exist. These time lags are related to the dimensions and radial elasticity of the stem, and to the sapwood permeability. The results are in agreement with the cohesion-tension theory but partly contradict the pipe model theory of a plant form.

The embolism recovery model presents a quantitative analysis of the processes that have been suggested to recover embolized conduits while the water in surrounding conduits is under negative pressure. The model analysis reveals that under normal physiological circumstances, e.g., normal xylem water tension, osmotic pressure of living cells, or diffusion distances, the refilling process is possible if the two sides of the same living cell have different transport properties for solutes.

The model for analyzing the performance of a sap flow measuring system reveals that the method, that assumes homogenous temperature field inside the stem, is not appropriate for stems with a diameter larger than a few centimeters.

This study has shown that relatively simple models, based on physical principles, are useful in increasing our understanding of the processes and behavior of natural objects. Furthermore, model analysis leading to better understanding of dynamic systems, can guide forthcoming research and enhance the development of new instrumentation.

ACKNOWLEDGEMENTS

It was one of those long evenings in Hyytiälä in summer 1995 when I, as a young forestry student, ran into Pepe Hari in the surroundings of the greenhouse. He was quite busy with the coming great opening ceremony of the SMEAR II station but I managed to ask if he had some subject for a master's thesis. He replied that there are three topics of which one is the most interesting. 'What's that one?' I asked. 'Pitäisi selvittää, miten vesi lillii puussa', (We should find out how water is dwelling or soaking inside a tree) he replied.

Now, after ten years, we are looking forward to the coming 10th Anniversary of the SMEAR II station. During those years I have had the privilege to engage with the efforts of the group working with tree water issues. The members of this superb group are Pepe and Eero Nikinmaa from Department of Forest Ecology and Timo Vesala, Sanna Sevanto and Teemu Hölttä from Division of Atmospheric Physics, Department of Physical Sciences.

I thank the whole group and especially my supervisors Pepe, Eero and Timo, who have given support and valuable comments during the whole process. In addition, they have taught me a lot of scientific realism, forest ecology, environmental physics and the song of Lesser Whitethroat (*Sylvia curruca*). With them I have had the most interesting discussions about birds and the some other essential topics of life.

I express my gratitude to Erkki Siivola and Toivo Pohja, whose technical constructions have been invaluable in the field measurements, and to Hannu Ilvesniemi as a co-author of the first paper. Tuuli Timonen and Pirkko Harju (Botanical Museum, Univ. of Helsinki) are acknowledged for the microscope photos of Scots pine cells.

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Special thanks to my colleagues at our department for sharing this burden: Jukka Pumpanen, Eija Juurola, Pasi Kolari, Maarit Raivonen, Nina Tanskanen, Petteri Vanninen and Roope Kivekäs among others. Muchas gracias a Nuria Altimir y Albert Porcar. Albert is also acknowledged for the language revision of the summary part of this thesis. I appreciate the inspiring atmosphere among the people in both the Department of Forest Ecology, headed by Pasi Puttonen, and the Division of Atmospheric Sciences, headed by Markku Kulmala.

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Warm thanks to my relatives for all kinds of support.

My folks, Laura, Jussi, Elli and Eero, have been optimistic during all these years no matter what the speed of this process occasionally has been. Thanks for your patience.

May, 2005

Martti Perämäki

LIST OF ORIGINAL ARTICLES

This thesis consists of an introductory review followed by five research articles. In the review the articles are referred to using Roman numbers. They are reproduced with the permission of the publisher of the journals.

I. **Martti Perämäki**, Eero Nikinmaa, Sanna Sevanto, Hannu Ilvesniemi, Erkki Siivola, Pertti Hari and Timo Vesala. 2001. Tree stem diameter variations and transpiration in Scots pine: an analysis using a dynamic sap flow model. *Tree Physiology* 21: 889-897.

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

III. Timo Vesala, Teemu Hölttä, **Martti Perämäki** and Eero Nikinmaa. 2003. Refilling of a hydraulically isolated embolized vessel: Model calculations. *Annals of Botany* 91: 419-428.

IV. **Martti Perämäki,** Timo Vesala and Eero Nikinmaa. 2001. Analysing the applicability of heat balance method for estimating sap flow in boreal forest conditions. *Boreal Environment Research* 6: 29-46.

V. **Martti Perämäki**, Timo Vesala and Eero Nikinmaa. 2005. Modeling the dynamics of pressure propagation and diameter variation in tree sapwood. *Tree Physiology* 25: nnn-nnn (in press).

Martti Perämäki developed and implemented the models and produced all the simulation results in studies I, IV and V. He was also responsible for the field measurements, data analysis and literature searches in these studies. In study II the sap flow sub-model was based on the model in Study I. The embolism sub-model was developed by Teemu Hölttä and Martti Perämäki. In addition, Martti Perämäki participated in the discussions and commented on the manuscripts in studies II and III. He is the main author of articles I, IV and V.

TABLE OF CONTENTS

LIST OF TERMS

Air-seeding	Mechanism leading to embolism where a gas bubble is pulled into the cell lumen through a pit in the cell wall.
Aquaporin	Cell membrane structure controlling water and solute flow through cell membrane
Bowen ratio	Ratio of sensible to latent heat.
Cambium	Thin layer of meristematic tissue between the phloem and the xylem of a stem. Produces phloem and xylem.
Cavitation	Process where gas bubbles are formed in liquid phase in regions under low pressure.
Cell lumen	Cavity, which the cell walls enclose.
Conduit	Water-conducting cell in trees; vessels in broad-leaved trees, tracheids in conifers.
Embolism	Occlusion of a conduit by a gas bubble.
Evaporation	Conversion of water to water vapor from the soil.
Evapotranspiration	The combined evaporation from the soil surface and transpiration from plants. Represents the transport of water from the earth back to the atmosphere.
Interconduit pit	Structure in the cell wall that permits water flow between conduits but prevents gas bubbles to move from one conduit to another.
Latent heat	The energy stored in water vapor in transpiration and evaporation.
Meristem	Embryonic tissue, undifferentiated, actively dividing and growing cells.
Middle lamella	First layer formed during cell division. The outer wall of the cell. Shared by adjacent cells.
Parenchyma cell	General-purpose cell often capable of photosynthesis, and some conduction. Frequently a storage type cell for water and reserve foods.
Permeability	Degree to which a solid allows the passage of a fluid through it.

Phloem	Part of a vascular bundle consisting of sieve tubes, companion cells, parenchyma and fibers. Transports assimilates.
Reflection coefficient	Measure of the relative permeability of a membrane to a particular solute.
Sap	Water flowing in xylem conduits.
Sensible heat	Heat absorbed or transmitted by a substance during a change of temperature, which is not accompanied by a change of state.
Tracheid	Elongated xylem cell having lignified cell walls. Transports water and offers mechanical support for the stem.
Transpiration	Conversion of water to water vapor, through the plants.
Turgor	Large positive internal pressure of living plant cells giving rise to mechanical rigidity of the cells.
Vessel	Water conducting system in the xylem consisting of a column of cells.
Water tension	Negative hydrostatic pressure.
Xylem	Collective name for the cells, vessels, and fibres forming. the harder portion of the fibrovascular tissue; the wood.

LIST OF SYMBOLS AND CONSTANTS

Symbol	Unit	Description
A	m^2	stem cross-section area
E_l	mg m^{-2} s^{-1}	leaf-specific transpiration
E_r	Pa	radial elastic modulus (elasticity) of sapwood
ET	mm d^{-1}	evapotranspiration rate
G	W m^{-2}	heat flux density into the soil substrate
GEP	g C a^{-1}	gross ecosystem production, the total photosynthetic production of plants
H	W m^{-2}	sensible heat flux density
k	m^2	permeability of sapwood
A_l	m^2	leaf area
LE	W m^{-2}	latent heat flux density
p	Pa	water pressure
P_{in}	W	heating power of sap flow sensor based on SHB method
PAR	µmol m^{-2} s^{-1}	photosynthetically active electromagnetic radiation wavelength 400-700 nm
Q	kg s^{-1}	sap flow rate
Q_r	W	radial heat flux in SHB method
Q_v	W	vertical heat flux in SHB method
θ	kg m^{-3}	sapwood water content
r	m	stem radius
r_{hw}	m	radius of heartwood in stem
R_n	W m^{-2}	net radiation
RH	%	relative humidity
T	°C	temperature
VPD	Pa	vapor pressure deficit of water vapor in air
c	4.18 kJ kg^{-1}	heat capacity of liquid water
D_w	2.57×10^{-5} m^2 s^{-1}	diffusion coefficient of water vapor in air
D_c	1.60×10^{-5} m^2 s^{-1}	diffusion coefficient of carbon dioxide in air
g	9.81 kg m s^{-2}	acceleration due to gravity
γ	0.073 N m^{-1}	surface tension of water
η	0.001 Pa s (20°C)	dynamic viscosity of water
ρ	1000 kg m^{-3}	density of liquid water

1. INTRODUCTION

1.1 Distribution of forests in the world

Water stress is the most common limitation to growth of vegetation (Kozlowski et al., 1991). Especially, in the case of trees, the availability of water has a great influence on their performance. Figure 1 shows monthly gross ecosystem productivity (GEP) vs. evapotranspiration (ET) of several evergreen coniferous (a) and deciduous broadleaf (b) forest stands all over the world (Law et al. 2002). The figures indicate clear positive regression of productivity of plants on evapotranspiration.

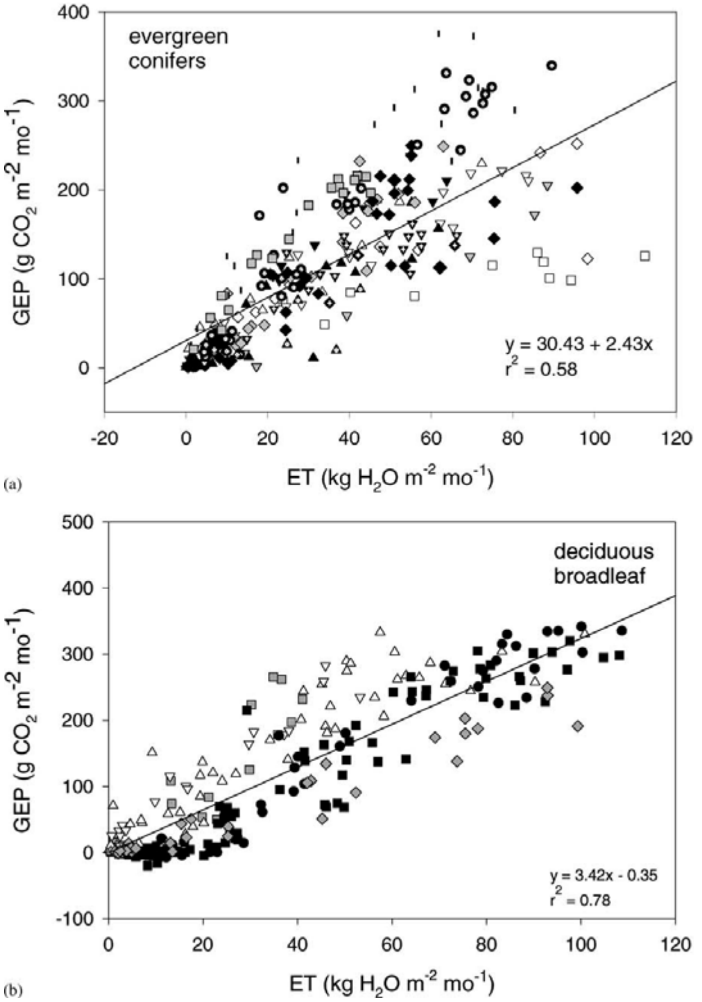

Figure **1**. Monthly gross ecosystem production (GEP) as a function of evapotranspiration (ET) in (a) evergreen coniferous forest and (b) deciduous broadleaf forest, Law et al. 2002. Reprinted with the permission of Agricultural and Forest Meteorology.

From the figures above it could be concluded that forests could be most successful in areas without water deficit. This is actually the case. The maps in Figures 2 and 3 show that forest is the natural vegetation type all over the world where potential evaporation and transpiration do not exceed precipitation and where annual average temperature is adequate. Figure 2 presents the global distribution of forests and Figure 3 illustrates aridity zones of the Earth. Arid denotes a region or climate characterized by very low rainfall, often supporting only desert vegetation. Aridity is the degree to which climate lacks effective, life-promoting moisture; opposite of humidity, in climate sense. The humid zone is most extensive, covering about 46.5 million km^2 (WRI 2002). As the figures show, almost all the humid areas are covered with forest (38.7 million km^2 in 2000, FAO 2001) and, *vice versa*, all the areas, which are covered with forest, are humid.

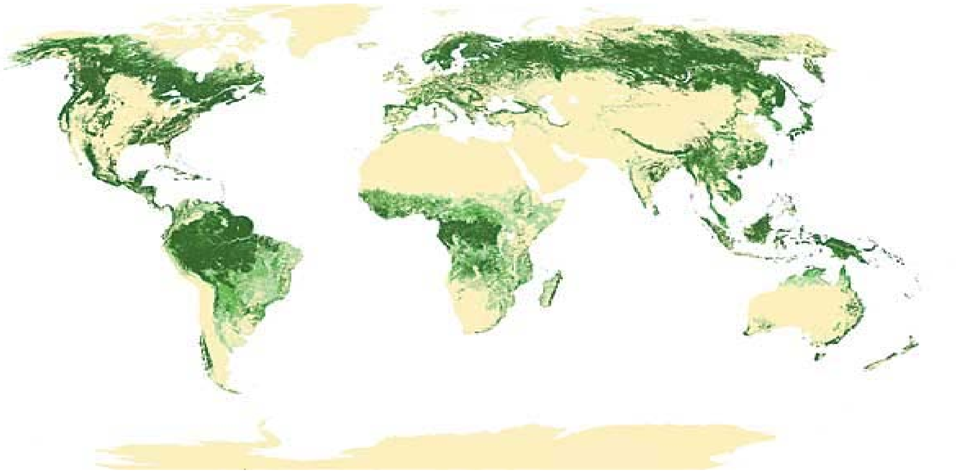

Figure **2**. The global forests distribution. Dark-green: closed forest, more than 40 per cent covered with trees more than 5 metres high. Mid-green: open (10-40 per cent coverage) and fragmented forest. Light-green: other woodland, shrubland and bushland (IUCN 2005, source FAO 2001).

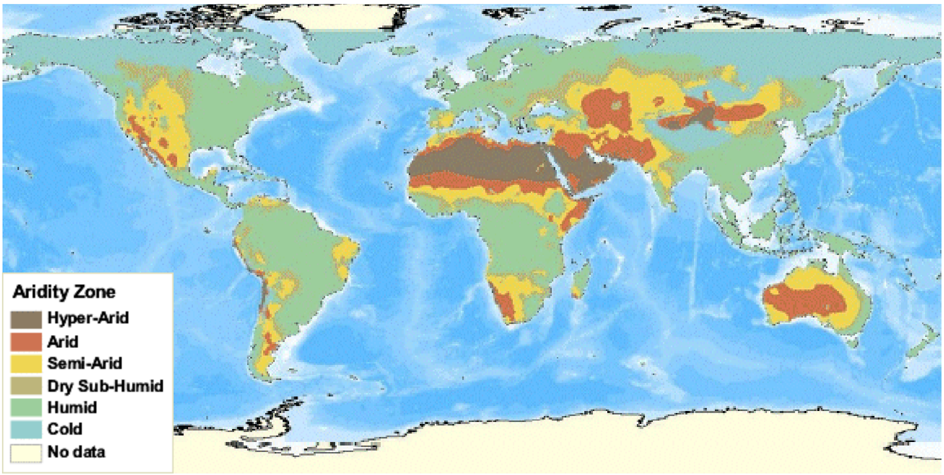

Figure **3**. The aridity zones of the world (WRI 2002).

Maximum tree height has been reported to depend on water availability (Ryan and Yoder 1997, Koch et al. 2004). The biggest trees in the world are all living in extremely humid areas: Coastal redwood (*Sequoia sempervirens* (D.Don) Endl.), which can exceed height of 100 m and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (100m) in Pacific Northwest, USA, where annual precipitation may exceed 3000 mm (Burns and Honkala 1990). In that region fog is also a major source of humidity (Dawson 1998, Burgess and Dawson 2004). In tropical rainforests, where annual precipitation exceeds 2400–2500 mm, tree heights of 60-70 m are not unusual.

1.2. Water use of trees

Transpiration at tree level

Transpiration is an inevitable consequence of photosynthesis, the most important process of plants. When stomata in leaves are open for carbon dioxide uptake they allow water molecules to escape. The primary reason for transpiration is the diffusion of water vapor molecules from the intercellular air spaces of leaf (RH ≈ 100%) through the open stomata to ambient air (Figure 4).

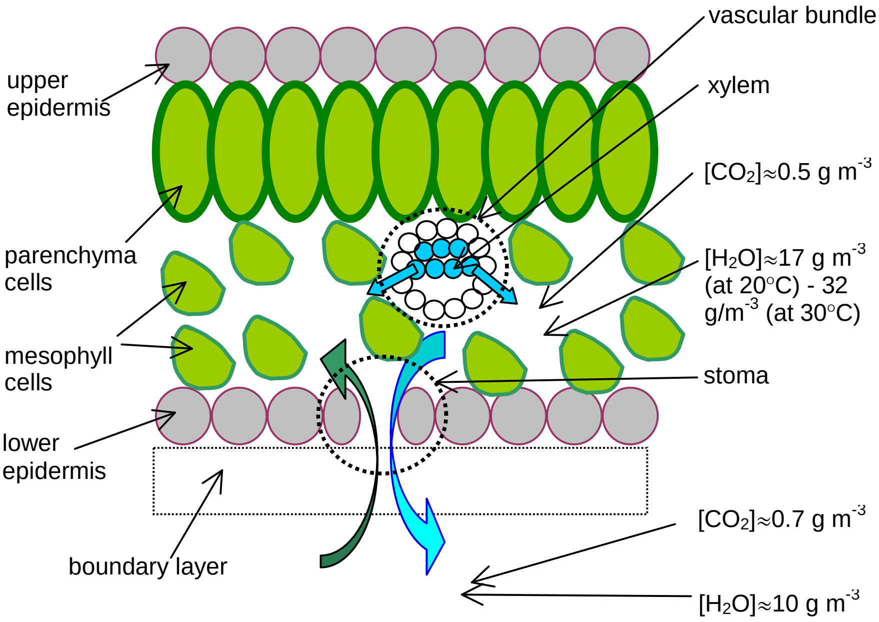

Figure **4**. A schematic illustration of the structure of a leaf and the carbon dioxide (green arrow) and water (blue arrow) fluxes between leaf air space and the ambient air.

Driving force of the diffusion is the concentration difference, which can be up to 1.1 mol m^{-3} in the case of water and about 0.0045 mol m^{-3} of carbon dioxide. Taking into account also the ratio of diffusitivies of these gases in air ($D_w/D_c \approx 1.6$, Lawlor 1993, D_w is the diffusion coefficient of water vapor in air and D_c is that of carbon dioxide) we obtain that for each carbon dioxide molecule harvested from air up to 400 molecules of water may be lost. This quite substantial transpiration per unit leaf area together with a total leaf area up to hundreds of square meters produces a significant flux of water at the tree level. The diurnal water use of a single tree can exceed 1000 kg (For a review, see Wullschleger et al. 1998). The vast majority of the water flowing in a tree is transpired in the air; less than 1 % is used in photosynthesis. In photosynthesis trees fix atmospheric carbon for energy resources and material growth. Allocation of photosynthates determines the sizes of the structural compartments (needles, branches, stem, coarse roots and fine roots) of trees (Nikinmaa 1992).

Transpiration induces sap flow, where liquid water is pulled from the soil through the stem and branches, up to the leaves where it evaporates in the air. The roots uptake water and dissolved nutrients from the soil and the wooden structure serves as a pathway for water flow from the roots to the shoots. Soil water availability, hydraulic conductance of the

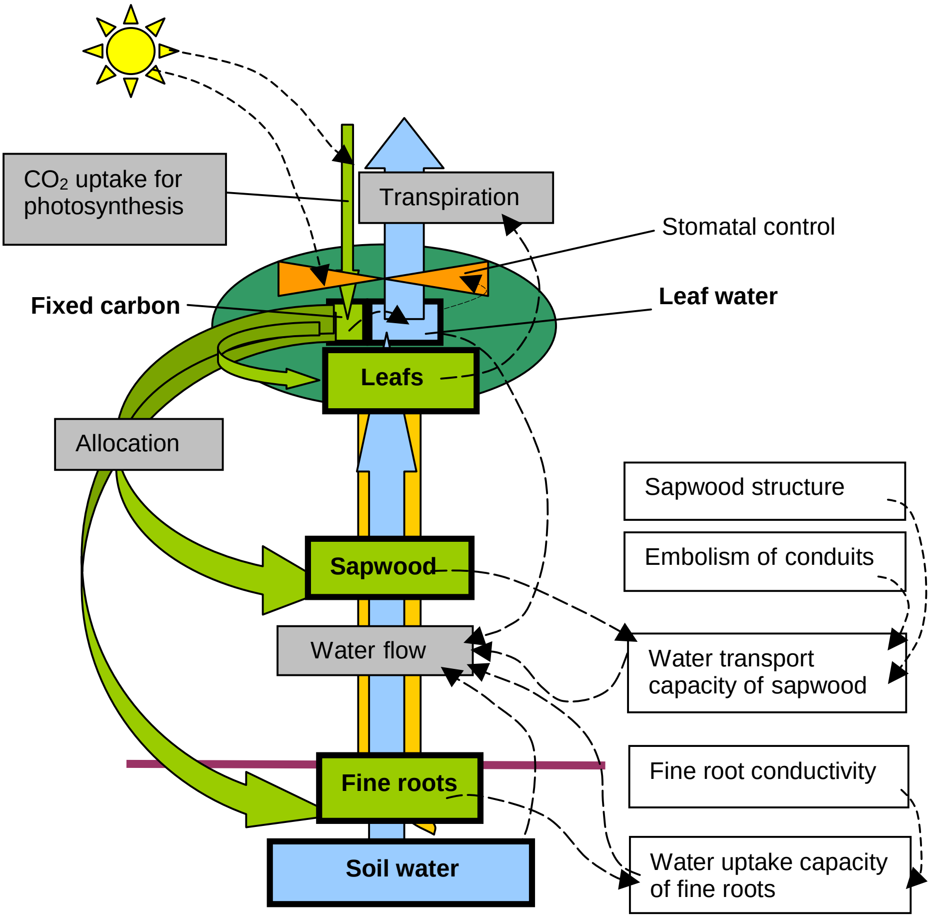

Figure **5**. A conceptual model of water related functions of a tree. State variables (amounts of leafs, sapwood, fine roots) are presented with thick-lined text boxes. Material flows are presented as blocked arrows with gray text boxes. Dashed curved lines with solid arrowheads represent influences.

transport pathway and evaporative demand of the ambient air influences the water status of the leaves, which, in turn, can impose a limitation to gas exchange by controlling the stomata (Hari et al. 1999). Stomatal control has an effect on the carbon gain and thus on the growth of the tree. Transpiration, photosynthesis, carbon allocation and growth, tree structure, and water flow are all linked to each other (Figure 5). The hydraulic pathway has to be constructed in such a way that it can feed the necessary amount of water to the leaves.

The pipe-model theory of plant form (Shinozaki et al. 1964) states that tree stem consists of a bundle of unit pipes that connect functional roots to foliage units. Non-functional pipes form heartwood. The theory proposes a linear relationship between sapwood cross-sectional area and foliage mass or area. This linear relationship has been widely used as a principle to distribute resources between stem and foliage in tree growth models (see review by Sievänen et al. 2000).

Transpiration at stand level

Transpiration consumes substantial amount of energy because the heat of vaporization of water is quite high (2260 kJ kg^{-1}). This makes the transpiration of trees an important component in the energy balance of a stand and thus in the micrometeorology of the lowest part of the atmosphere that is called planetary boundary layer (PBL). PBL is, by definition, the part of the atmosphere, in which the Earth's surface affects on the movement and the properties of air. The energy balance of a stand is:

$$R_n - G - S - Q = H + LE \qquad (1)$$

where R_n is the net radiation, G the heat flux into the soil substrate, S the rate of change of heat storage (air and biomass) between the soil surface and the top of canopy, Q the sum of all additional energy sources and sinks, H is the sensible heat which is the heat absorbed or transmitted by a substance during a change of temperature which is not accompanied by a change of state, and LE is the latent heat which contains the energy stored in water vapor in transpiration and evaporation. The contribution of canopy transpiration to the total evapotranspiration of a stand (consisting of canopy transpiration, ground vegetation transpiration and evaporation from soil) depends on the stand structure (tree species, stand density, leaf area) and on the climatic factors, and it typically varies between 30% (Jiménez et al. 1999) and 65% (Grelle et al. 1997) of the total evapotranspiration. In addition, evapotranspiration of a forest stand exceeds evapotranpiration of a clearing in the same climatic conditions. This is due to the transpiration from the forest canopy (Rannik et al. 2002). The increase of the ratio of sensible heat to latent heat (Bowen ratio) disturbs the rate of growth of the PBL (Culf 1992). Typically in boreal forests the Bowen ratio is bigger than in temperate forests leading to deeper PBL with lower water vapor concentration. This higher water vapor pressure deficit (VPD) reinforces a negative feedback on stomatal opening and transpiration and a positive feedback on sensible heat exchange (Baldocci and Vogel 1996).

The climate models used in the climate change research are very sensitive to the partitioning of energy between sensible heat and latent heat (Lundblad et al. 2001). In addition, water vapor is the most important greenhouse gas because it absorbs long wave radiation emitted by Earth. For these reasons, a better understanding of the interactions between the vegetation and the hydrological cycle is essential.

1.3. The pathway for sap flow: the xylem

The stem of a coniferous tree consists of the following parts (Figure 6):

- Pith, a result of primary growth of apical meristem.
- Xylem, result of functioning of the vascular cambium. Consists mainly of axial tracheas. The newest part of xylem is called sapwood, which serves as pathway for water and nutrient transport. Sapwood contains living ray cells. The oldest part of xylem where rays cells are dead is called heartwood.
- Cambium, an extremely narrow layer consisting of few cells only, the lateral meristem, which increases the girth of the stem. Produces xylem and phloem. Located between xylem and phloem.
- Phloem, a narrow layer consisting of living cells which transport assimilates from leaves to growing tissues.
- Bark, prevents water evaporation from phloem. Protects the stem.

Figure **6**. The structure of xylem in Scots pine. Photo: Albert Porcar, Department of Forest Ecology, University of Helsinki

Every year cambium produces a new layer of xylem, an annual ring. The annual ring consists of axial tracheids and resin ducts and radial rays. Tracheids, which are 1… 4 mm in length and tens of micrometers in diameter, die in the same year and the empty cell lumens serve as a pathway for sap flow. In the beginning of the growing period cambium produces tracheas with thin cell walls and large cell lumen (early wood, lighter area of an annual ring; later on it produces tracheas with thicker walls (late wood, darker area of an annual ring) (Figures 6 and 7). The radial rays serve as path for horizontal transport of water and assimilates. The oldest annual rings in which the cells in radial rays are dead do not transport water. This innermost part of the xylem is called heartwood. The newest annual rings constitute sapwood (Figure 6).

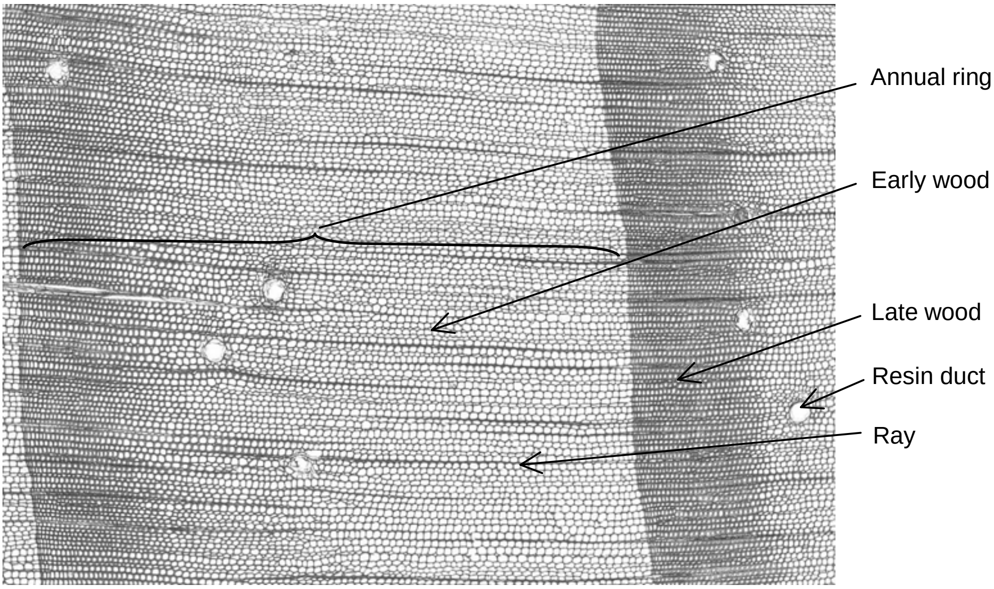

Figure **7**. A microscope photo of a stem cross-section of a Scots pine. Photo: Tuuli Timonen, Botanical Museum, University of Helsinki.

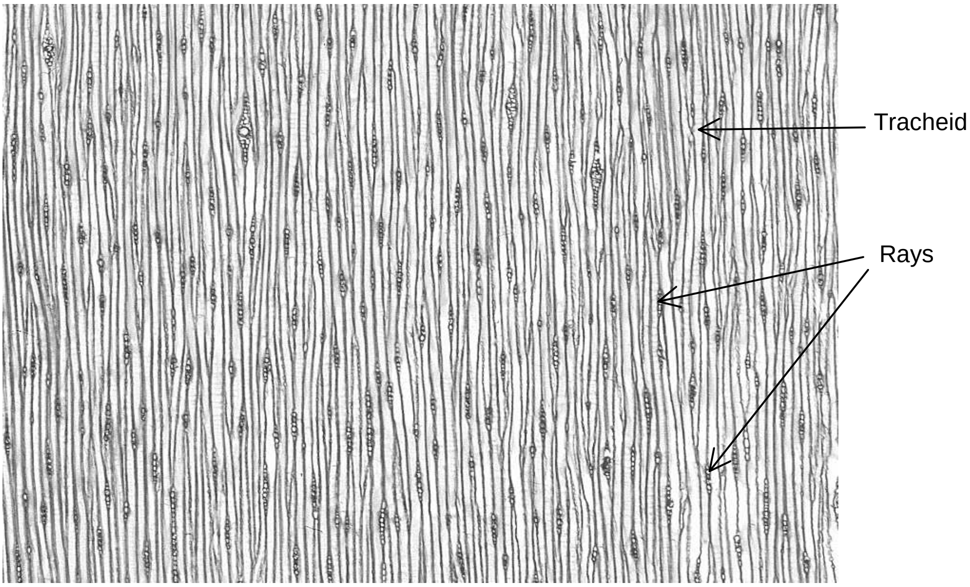

Figure **8**. A microscope photo of a tangential cut of a Scots pine stem. The groups of cells perpendicular to the longitudinal tracheids are rays with living cells. Photo: Tuuli Timonen, Botanical Museum, University of Helsinki.

The ends of the tracheids overlap in the vertical direction (Figure 8) and water flows from one tracheid to another via small pores called interconduit pits. The structure of pits varies between coniferous species. In Scots pine a pit contain a torus and margo, which is a net around the torus (Figure 9). Interconduit pits are the check valves that permit water flow between conduits but inhibit the leaking of air into the transpiration stream (Dixon 1914 cited by Sperry 2003). When there is a pressure difference between cells, the aspiration of torus against the pit aperture seals the pit and prevents the growth of gas bubble to another cell lumen.

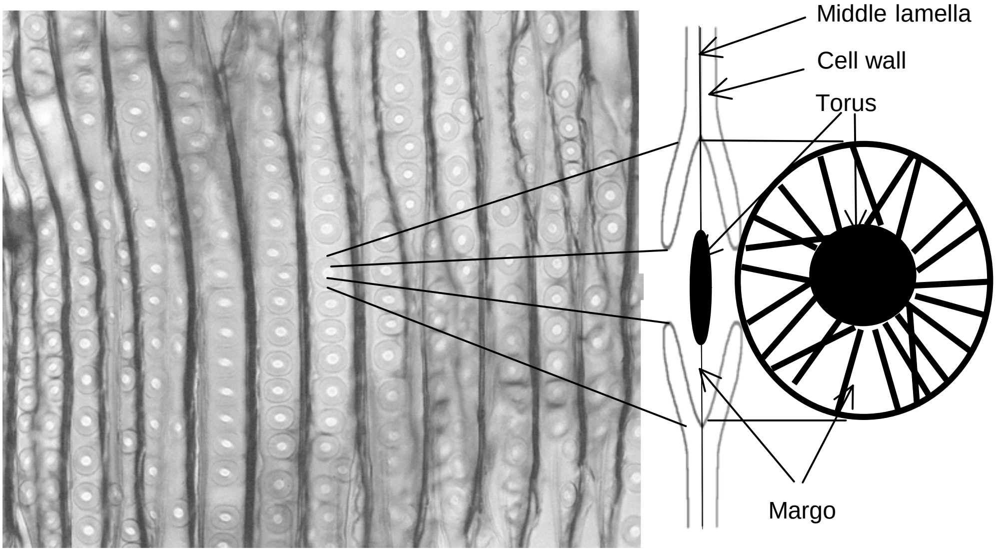

Figure **9**. A microscope photo showing the interconduit pits in the tracheid wall of Scots pine and a schematic illustration of a pit structure with torus (black centre) and margo (surrounding net-like structure). Photo: Tuuli Timonen, Botanical Museum, University of Helsinki.

1.4. From transpiration to water tension and sap flow

The physical basis for water ascent in plants derives from the structure of a water molecule, where an oxygen atom and two hydrogen atoms form an asymmetrical composition (Figure 10). This asymmetrical composition with opposite electrical charges of oxygen and hydrogen ions lead to dipolar structure, which enables water molecules to attach to each other (cohesion) and form clusters of molecules. Adhesion is the process where water molecules are attracted to polarizable or charged surfaces of other substances (wettable).

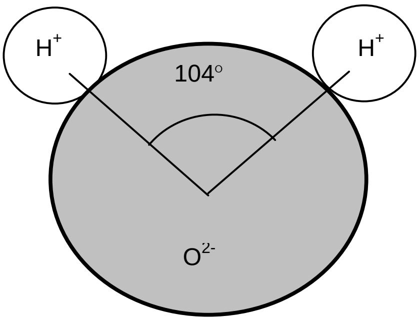

Figure **10**. A schematic illustration of the composition of a water molecule.

Water flow through sapwood of a tree is initiated in intercellular air spaces of leaves from where water molecules diffuse to ambient air (Figure 4). This causes the net evaporation of water molecules from water surfaces on parenchyma cells and increases the concavity of the surface of the water film between cells (Figure 11) or into pores in cell wall. Surface tension (relatively high for water, 0.073 N m^{-1}), which results from asymmetric forces between water molecules at the surface, tends to minimize the area of the surface and pulls the water molecules towards the surface. This results in a pressure drop in the water below the concave surface. The pressure drop is a function of the radius of the curvature and the surface tension of water (Laplace equation (Pickard 1981)):

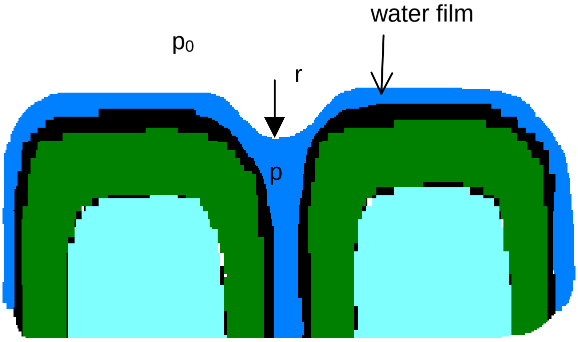

Figure **11**. Schematic illustration of curved surface of water film on parenchyma cells inside a leaf.

$$p = p_0 - \frac{2\gamma}{r} \qquad (2)$$

where p is the pressure under curved surface of water, p_0 is the ambient pressure, γ is surface tension of water, r is the radius of the concave surface. The pull i.e. tension between water molecules propagates along the continuous water chain down to soil and causes them to rise through the tracheary elements of the stem. The hydrogen bonding between adjacent water molecules keep the molecules together as a continuous chain. This is the cohesion –

tension theory of sap flow in trees, which was presented already in 1894 by H.H Dixon and J. Joly (Pickard 1981).

The cohesion theory implies that a tension gradient of 0.02…0.03 MPa m^{-1} should exist inside xylem when transpiration is present (0.01 MPa m^{-1} due to gravity and 0.01…0.02 MPa m^{-1} because of frictional pressure losses in flow). This leads to a tension of two megapascals at the top of tall trees. This predicted tension is the reason why the cohesion – tension theory remained controversial for decades: nobody had demonstrated the existence of negative pressure of water in plants and how is it possible that water columns can remain continuous under high tension for long periods of time without breaking into separate molecules. This intuitively unavoidable phase change should lead to embolism, where the conduit is filled with gas and water flow is blocked.

The existence of tension was shown at the first time in 1965 when Scholander and his co-workers introduced the pressure bomb (Scholander et al. 1965). In a pressure bomb positive pressure is used to push water out from the cut end of a leaf or a twig. The pressure at which water starts to flow out from the leaf corresponds to the negative pressure or tension inside the leaf. Tensions down to –17 MPa have been measured by the pressure bomb (Kappen et al. 1972 cited by Zimmermann et al. 2004). Later on Holbrook et al. (1995) and Pockman et al. (1995) using a centrifugal technique showed maximum sustained water tensions ranging from -1.2 to -3.5 MPa in stem segments of various species.

1.5. Implications of water tension

1.5.1. Stem sapwood diameter changes

While connected to each other with cohesive forces, the molecules in a stretched water column are attached also to the walls of tracheary elements with adhesive forces. With this mechanism the tension between water molecules is transferred also to the elastic cell walls and they bend inwards and the diameter of cell shrinks. At the scale of a stem (bundle of individual cells) this is added up to sapwood diameter changes of detectable order of magnitude (Irvine and Grace 1997).

Diurnal reversible changes of tree stem diameter have been detected since the early 20th century (MacDougal 1924). In the early days the variation of stem diameter was considered as variation in the water content in bark and phloem. Later on also variation in xylem diameter has been observed, and at the present time it is considered as a direct and immediate indicator of transpiration-induced water tension fluctuation in xylem (Irvine and Grace 1997).

1.5.2. Embolism

A phase diagram (Figure 12) shows the stable preferred physical states of water at different temperatures and pressures. At typical room temperature and pressure water is a liquid, but it becomes solid (i.e. ice) if its temperature is lowered below 0 °C, and gaseous (i.e. water vapor) if its temperature is raised above 100 °C, at the same pressure. Each line gives the conditions when two phases coexist but a change in temperature or pressure may cause the phases to abruptly change from one to the other.

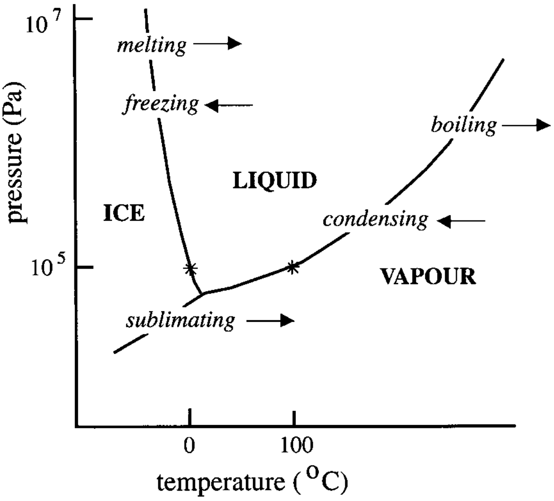

Figure **12**. A phase diagram of water.

The saturated vapor pressure of water is the partial pressure of water vapor that is in equilibrium with liquid water at a particular temperature. When saturated vapor pressure equals ambient pressure, bubbles of water vapor are formed in liquid water. If this is achieved by increasing temperature at constant pressure, the process is called *boiling*; if decreasing pressure at constant temperature it is called *cavitation* (Brennen 1995). If phase-change has not occurred when pressure-temperature combination has gone outside the stability region in the phase diagram, water is in metastable state (superheated (solid/liquid) or supercooled (liquid/vapor). Thus, liquid water, which is pulled upwards through the xylem according to the cohesion-tension theory, and which pressure is lower than 0.023 MPa (at 20 °C) is in metastable state.

Cavitation is a special case of *nucleation,* which is the process of spontaneous formation of a new phase within the volume of the pre-existing phase by random fluctuation. Phase change of a substance is explained by the classical nucleation theory (CNT) (Brennen, 1995). In cavitation, gas bubbles are formed in the liquid in regions of low pressure with constant temperature. The tiny nuclei of the new phase tend to grow rapidly if the size of the nuclei exceeds certain critical size. If the size of the nuclei is below the critical size surface tension will dissolve them. The probability of forming a void of critical size is dependent on the tension and the temperature of the water. The CNT distinguishes two types of nucleation: homogeneous and heterogeneous. In homogeneous nucleation the thermal motions of molecules within the pure liquid form microscopic voids, which can grow, but the tension for breaking the pure liquid water is hundreds of megapascals and far beyond the tensions in xylem water. In heterogeneous nucleation, interactions between water molecules and impurities or surfaces of other substances enable the formation of nuclei with critical size even at moderate tensions. Cavitation is a stochastic process and the probability of a cavitation event increases with time, hydrophobicity of the surface, and hydrophobic surface area. Wettability of a surface is expressed as the contact angle α, which a water droplet forms with a surface. If $\alpha < 90°$ the surface is wettable i.e. hydrophilic, the adhesive forces are dominating; if $\alpha > 90°$ the surface is non-wettable i.e. hydrophobic, the cohesive forces between water molecules are dominating (Pickard 1981) (Figure 13.). A single successful cavitation event with bubble growth is enough to embolize the whole conduit.

According to the nucleation theory, nucleation sites, a nucleation event, and bubble growth are required for phase-change from liquid to gas. Hence, the metastable state of liquid water is possible when conditions for nucleus formation and bubble growth are inadequate, although pressure and temperature would predict a phase change by cavitation according to the phase diagram of water.

In ecophysiological literature, the term cavitation is widely used as a synonym for *embolism* although it is only one mechanism leading to embolism, which means the occlusion of a conduit by a gas bubble. In cavitation, a phase change creates the initial nucleus of the gas bubble. In two other mechanisms leading to embolism, an existing gas bubble works as an initial nucleus for bubble growth.

In air-seeding (Zimmermann 1983), tension draws an air bubble through a pore or pit in the cell wall into the cell lumen, where water evaporates into the bubble which then enlarges and fills the whole conduit. The threshold value of pressure which leads to air-seeding is a function of pore size and surface tension of water (Laplace's equation, Eq. 2.).

The third mechanism leading to embolism is the release of existing bubbles from cracks or crevices of the cell walls (Pickard 1981). Vapor bubbles most efficiently stabilize by surface tension forces in steep non-wettable cracks or crevices of the cell wall (Figure 13). The bubble is released into the liquid when the pressure difference Δp between the bubble and the water equals to (Pickard 1981):

$$\Delta p = \frac{2\gamma}{r_c}\left|\cos(\alpha - \beta)\right| \tag{3}$$

where α is the contact angle of the three phase interface, β is half of the apex angle of the conical crevice, and r_c is the radius of the crevice.

Air-seeding and release of existing bubble are deterministic processes: when tension has reached some threshold limit the initial nucleus starts to grow and the conduit is filled with gas.

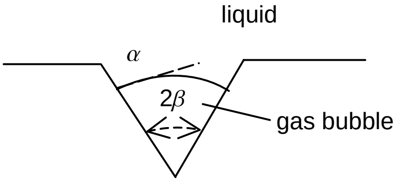

Figure **13**. A schematic illustration of a gas bubble stabilized in a conical crevice in the cell wall.

The nucleation processes described by the CNT set a limit to the strength of water to cope with tension. Theoretical *tensile strength* of pure water is -140 ... -230 MPa (Pickard 1981), but as mentioned above the existence of heterogeneous nucleation lowers substantially the maximum sustained tension. In addition, the two other mechanisms leading to embolism take place under considerably lower tensions according to the equations above.

1.5.3. Prevention of embolism

Embolism causes decrease in hydraulic conductivity by blocking the conduit with a gas bubble and therefore restricts sap flow, which, in turn, increases the water tension. It has been suggested, that this may eventually lead to 'runaway cavitation' (Tyree and Sperry 1988). On longer run, it is crucial that the excessive amount of embolism can be avoided in order to maintain the water transport capacity. As trees grow taller it is even more important because longer transport pathway increases the water tension and makes the embolism more apparent.

During evolution xylem of higher plants has undergone structural adaptation to avoid excess emboli formation (Sperry 2003). The cell lumens are small (cavitation probability increases with cell surface area). Xylem walls are air-free (Zimmermann 1984), or air bubbles are unlikely in newly produced conduits (Sperry 2003), and water uptake by roots excludes air bubbles (Zimmermann 1983). Lignified and thickened cell walls are able to avoid the wall collapse under tension (Hacke et al. 2001). Cell wall pores are small (1.2…3.3 nm) enough to prevent air-seeding under tension lower than –15 MPa (Sperry 2003). Most of the conduit walls are highly wettable because wettability of cellulose and hemicellulose, the main constituents of the conduit wall, is high (Pickard 1981). The walls contain also hydrophobic lignin, which may destabilize the xylem water under tension, but its concentration in cells of conifer xylem is highest in the middle lamella and drops to lower values closer to the lumen (Donaldson 2001). The interconduit pits are able to block the expansion of a gas bubble from one conduit to another by aspirating the torus against the pit aperture (Sperry 2003).

There are several structural adaptations to avoid hazardous water tensions. The decrease of the leaf area to sapwood area ratio with increasing stem height (McDougall et al. 2002, Vanninen et al. 1996) increases the leaf specific hydraulic conductance of the tree and decreases the maximum water tensions at tree top. The production of xylem vessels with increased permeability (Pothier et al. 1989), an increase in the fine root foliage ratio (Sperry et al. 1998; Magnani et al. 2000), and increased water storage in the stem (Phillips et al. 2003) also lead to lower water tensions.

The functional way to avoid excess embolism is to regulate the transpiration induced water tension by partial closure of the stomata. This leads to reduced CO_2 uptake and lower photosynthesis. This is typical in sunny afternoons when evaporative demand exceeds water uptake and transport capacity of the tree leading to reduced gas exchange (Figure 14). This can be seen in the asymmetric CO_2 exhange although photosynthetically active radiation, PAR (400-700 nm), which is the driving force of photosynthesis, is symmetric around noon.

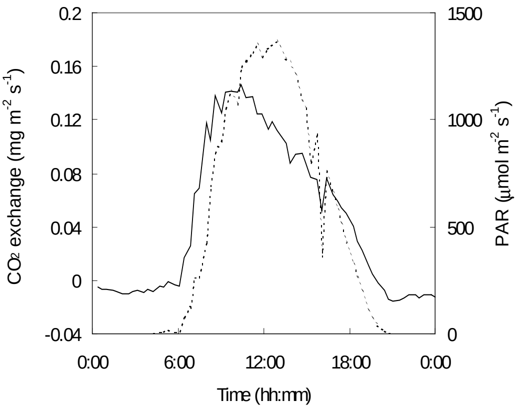

Figure **14.** Measured CO_2 exchange (solid line) of a Scots pine shoot enclosed in a cuvette and PAR (dashed line) in Hyytiälä 5.5.2004.

1.5.4. Indication of embolism

Although trees have evolved to avoid excessive embolism, the emboli formation has been found to be a regular occurrence (Perks et al. 2004). According to the current knowledge air-seeding from an already embolized conduit is the most probable mechanism of embolism. It has been proposed that with high enough water pressure difference between a gas-filled conduit and a conduit containing stretched water, the torus edge of the interconduit pit structure is pulled through the pit aperture and air-seeding occurs (Sperry and Tyree 1990, Sperry 2003).

During embolization plants produce detectable acoustic (Milburn and Johnsson 1966) and ultra-acoustic (Tyree and Dixon 1983) emissions, which are thought to result from the shock wave following a cavitation or air-seeding event (Jackson and Grace 1996). These emissions can be recorded with ultra-sonic acoustic sensors (Hölttä et al. 2005). Figure 15 presents the time course of ultra-acoustic emissions recorded from a Scots pine stem in Hyytiälä during two days in August 2000. Figure 15 illustrates also microvariation of xylem diameter which reflects the tension fluctuation due to changes in transpiration as explained above in section 1.5.1.

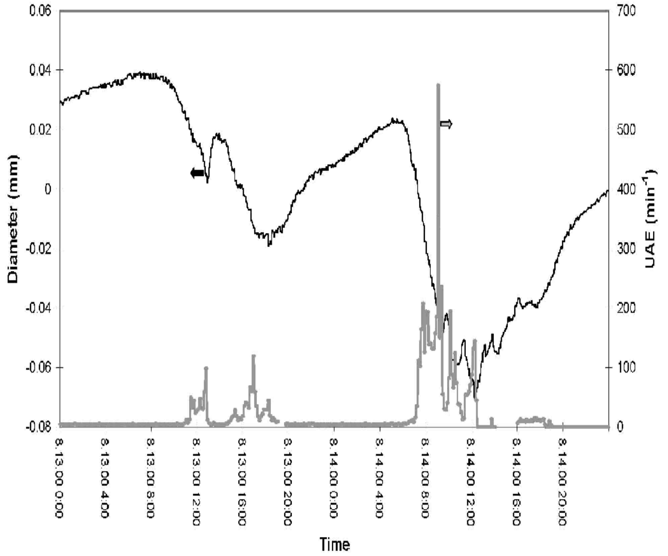

Figure **15**. Stem xylem diameter (darker line) and the observed ultra-acoustic emissions (lighter line) at the height of 2.5 m of a Scots pine stem in Hyytiälä for 13.8.-14.8.2000. From Hölttä et al. (2005).

1.5.6. Repair of embolized conduits

Embolism seems to be a usual occurrence in tree stems during periods of increasing transpiration. Because gas-filled cells cannot transmit tensions, embolized conduits are lost from the water transport system. To maintain hydraulic capacity, plants must replace embolized cells, maintain a highly redundant transport system, or repair embolized conduits (Holbrook and Zwieniecki, 1999). Pickard (1989) has suggested that embolized conduits might be restored to their functional state but this restoration has usually been connected to situations where the whole plant has been pressurized by root pressure (Tyree et al., 1986; Cochard et al., 1994; Fisher et al., 1997). In recent studies, it has been suggested that embolized conduits may be repaired also, when the water in neighboring conduits is under tension (McCully et al., 1998; Zwieniecki and Holbrook, 1998; Tyree et al., 1999; Melcher et al., 2001). Holbrook and Zwieniecki (1999) suggested that living cells in xylem parenchyma provide the driving force for refilling the embolized conduits when they are hydraulically isolated. This implies that the pressure of water in the refilling vessel is equal to the bubble gas pressure.

Later on, Holbrook et al. (2001) presented direct observations of xylem embolism and embolism repair in an intact grapevine stem by using a magnetic resonance imaging (MRI) technique. They detected about 10 individual emboli formations during a 24-hour period of active transpiration. Re-watering the plant relaxed the water tension rapidly but embolism recovery did not start until turning off the lights stopped transpiration and sap flow. Al though grapes are well known for their capacity to produce root pressure (Sperry et al. 1987) Holbrook et al. did not find any indication of this as root exudation.

1.6. Measurement of water flow

Sap flow in a tree is purely a physical phenomenon and its physics is fairly well understood (Pickard 1981). However, its quantification methods in intact trees are not problem-free. Sap flow in tree stems has been measured since the pioneering work of Huber in the early decades of the 20th century (see review by Čermák et al. 2004). The main methods used in the field apply thermodynamics: heat pulse velocity HPV (Huber 1932, cited by Čermák et al. 2004), trunk segment heat balance THB (Čermák and Deml 1972), stem heat balance SHB (Sakuratani 1981), heat dissipation HD (Granier 1985), and the most recent heat field deformation HFD (Nadezhdina et al. 1998, Nadezhdina and Čermák 1998).

The THB method is directly quantitative and needs no calibration; flow is calculated from the applied energy, the temperature change, and the specific heat of water. The THB method has been validated by volumetric techniques on several tree species. Flow rate, scaled up to stand transpiration, has shown good agreement with chamber measurements at branch level and evapotranspiration measured by the eddy-covariance method during dry conditions for a stand (Lundblad et al. 2001). The THB method is very robust and provides reliable data during long-term measurements in trees with diameters over 15 cm for a broad range of tree species, sizes and environmental conditions. It has been applied as a standard when testing other methods (Offenthaler and Hietz 1998; Nadezhdina and Čermák 1998; Lundblad et al. 2001).

The SHB method is based on the heat balance of a stem section, which is heated by a heating belt wrapped around it. The temperature increase over the heated section, the radial and vertical heat fluxes are measured, which together with the input power, are used when calculating the sap flow. It has been proposed (e.g. Shackel et al. 1992) that the SHB method is not appropriate for thick stems.

The HD is a relative method based on heat dissipation around a heated probe, and was developed from empirical laboratory calibrations (Granier 1985, 1986). Originally it was calibrated for five tree species and sawdust and it was assumed to be valid for all tree species. Later, studies have found that calibration should be done separately for each species (Smith 1996).

The HFD method is based on measurements of the deformation of the heat field around a needle-like linear heater inserted in a radial direction into the stem. The frontal view of the heat field under zero flow looks like a symmetrical ellipse due to different heat conductivity of the stem in axial and tangential directions and obtains a form of a gradually prolonging deformed ellipsoid under increasing flows. Sap flow using the HFD method is calculated from the ratio of temperature gradients around the linear heater in the axial and tangential directions. Experimentally, it was found that this ratio is proportional to the sap flow rate (Nadezhdina 1998, Nadezhdina et al. 1998).

All the above techniques have problems: either they have to be calibrated for different tree species (HD), they lack a sound physical basis and are based exclusively on empirical observations only (HD, HFD), or they have restrictions with stem size (THB, SHB).

1.7. Dynamic modeling approach

The theories of classical physics can explain phenomena in the natural environment with considerable accuracy. One could say that these theories have received a high measure of corroboration in a Popperian sense (Popper 1959). These phenomena include for example the movement of particles in a gravitational field, mass, energy and momentum transfer, and behavior of flowing fluids. They all obey basic physical principles like conservation of mass, energy and momentum. Sap flow and related phenomena are part of the physical environment and they can be studied by using methods of physics. The basic processes behind the phenomena can be modeled using mathematical equations with physical interactions and quantities, and the models can be implemented as computer programs.

Giere (1988) suggests that theoretical models are means by which scientists represent the world – both for themselves and for others. A model is an abstract entity that represents a system found in the real world. Models, as the statements defining them, come in varying degrees of abstraction. The relationship between model and real system is similarity. Hypothesis claim similarity between models and real systems, and as linguistic entities they can be true or false. A scientific theory includes both statements defining the models and hypotheses claiming a good fit between the models and some important types of real systems (Figure 16).

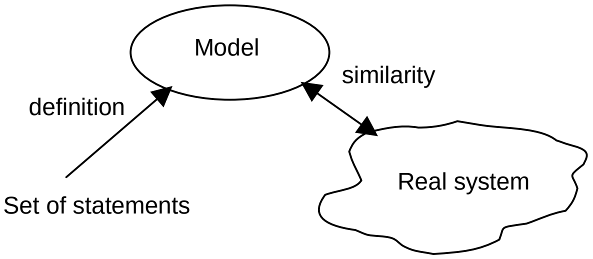

Figure **16**. Models and real systems according to Giere (1988)

Term *dynamic* refers to phenomena that produce time-changing patterns (Luenberger 1979). A dynamic system is a system whose state varies within time. Systems with flow of some substance are typical dynamic systems. A dynamic model is a model describing the time evolution of a state of the dynamic system.

The dynamic modeling approach gives us an opportunity to study functions of complicated systems. With models based on real physical interactions, it is also possible to analyze phenomena, which are difficult to measure directly. According to Bossel (1994), a key question in modeling is the structure of the model. State variables and processes should have actual counterparts in the physical world. The values of the model parameters should be obtained from direct and independent measurements.

The cohesion theory described in section 1.4. explains the water movement at the molecular level stating that individual water molecules are connected to each other by cohesive forces and these water chains are pulled upwards to the transpiring leaves. This molecular level is, however, far too detailed for quantitative modeling of sap flow and related phenomena and a more approximate approach is needed.

1.8. Other models in the literature

Water flow in a single tree has been modeled in several studies (Edwards et al. 1986, Tyree 1988, Früh 1997). All of these models are based on the capacitance analogy: the relation between water pressure p and amount of water θ is capacitance $\mathrm{d}\theta/\mathrm{d}p$ (change in water content divided by change in pressure). The problem with this approach is that the model results are not directly comparable with field measurements.

The performance of different sap flow measuring systems has been analyzed in several studies. Especially the SHB method has received considerable interest (Baker and Nieber 1989, Groot and King 1992, Grime and Sinclair 1999).

In the literature there are not many studies modeling embolism repair. Yang and Tyree (1992) considered the dissolution and movement of gas, and since their interest was the entire stem, they applied a 2-dimensional cylindrical symmetric model. However, they assumed that the pressure in the water adjacent to the bubble is equal to the stem xylem water pressure, i.e. hydraulic compartmentalization was not assumed.

2. THE AIM OF THIS STUDY

The principal aim of the present study is to extend our understanding of the dynamics of tree water relations. Five sub-studies were carried out during this process, in each a dynamic model based on known physical interactions was developed to analyze the water relations in tree stem. Sap flow and water pressure behavior was examined in **Studies I**, **II** and **V**. A particular objective of these works was to formulate sap flow model in a way that facilitates the direct comparison of simulated results with field measurements. The effect of embolism was studied in **Study II**. The aim of **Study III** was to examine under which conditions embolism repair can take place assuming that the embolized vessel is hydraulically isolated, like Holbrook and Zwienicki (1999) have suggested. In **Study IV** we examined the performance of a sap flow measuring system based on the SHB method.

The fundamental assumption behind these models is that the studied objects and phenomena are parts of the physical environment and physical interactions hold true. From physics we obtain the elementary processes in the models: convective flow of water is driven by pressure difference, diffusion of a substance is driven by concentration difference, and heat energy is transported with convective flow of sap and conduction, which is driven by temperature differences. Elastic material (wood) is shrinking under pressure. The models themselves are sets of mathematical equations describing the processes changing the state of the systems in time.

In sap flow models (**Studies I**, **II** and **V**) and in the model analyzing the Dynamax™ sap flow measuring system (**Study IV**), sapwood of tree stem is treated as a homogenous (in radial direction) porous material, with specific axial permeability for water. In the model for embolism refilling (**Study III**), the object of study is treated as a combination of individual cells. In addition, in the embolism sub-model of **Study II** the cell properties, which affect on the embolism formation, are considered as distributions. Water is treated as a fluid having properties as: mass, density, pressure, viscosity and temperature. In **Study III**, where water is treated as a solution, also concentration of sugar, is considered.

The main hypotheses tested in this work were:

- Transpiration creates curved water surfaces inside leaves. The concavity of the surface causes a water pressure drop, which rapidly propagates through the stem sapwood as predicted by the cohesion-tension theory. Pressure gradient causes the sap flow.
- Xylem pathway structure causes time lags in transport.
- The physical processes leading to embolism and embolism recovery are feasible within the normal tension variation and woody structure.
- Sap flow mechanism imposes structural limitations on tree stem.

3. MATERIALS AND METHODS

3.1. Description of the models in this study

3.1.1. About the modeling methodology

The starting point for modeling flow systems is to describe the system with a set of mathematical (differential or integro-differential) equations and boundary conditions. The equations are usually so complicated that they cannot be solved analytically and a numerical solution has to be applied. The next step is to select the discretization method i.e. a method for approximating the differential equations by a system of algebraic equations. There are two main approaches to select discretization methods: finite difference method (FD) and finite volume method (FV) (Figure 17). The FD method is the oldest method for numerical solution of partial differential equations. The starting point is the conservation equation in differential form. The solution domain is covered by a grid and at each grid point the derivatives are replaced by approximations. This results in a group of algebraic equations which can be solved (Ferziger and Peric 1996). An example of the FD methods is the Crank-Nicolson method for solving parabolic partial differential equations.

The FV method starts from the integral form of the conservation equations and they are applied into a finite number of contiguous control volumes of the solution domain. An example of these methods is the QUICK method (Ferziger and Peric 1996).

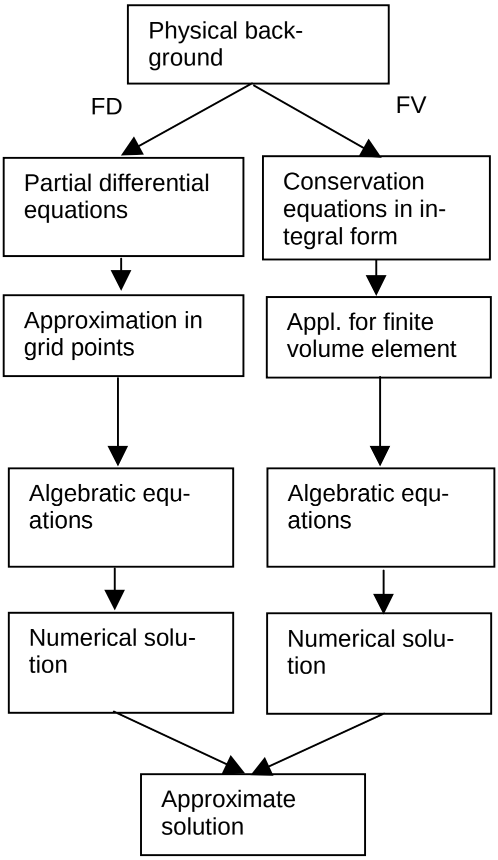

Figure **17**. Discretization methods

3.1.2. Sap flow models

Models describing sap flow (**Studies I, II** and **V**) assume that the sapwood of the tree stem is a homogeneous water-conducting elastic material and the diameter of sapwood undergoes diurnal shrinking and swelling caused by transpiration-induced fluctuating pressure i.e. tension ($p<0$) of stem sap. The change in the stem volume is assumed to match the change in water volume. Sap flow is driven by pressure gradient (Darcy's law):

$$Q = -\frac{k}{\eta}\frac{dp}{dh}A\rho \qquad (4)$$

where Q is sap flow, k is sapwood permeability, η is the dynamic viscosity of water, p is water pressure, h is length of stem segments, A is basal area of sapwood and, ρ is water density. Radius of the stem is changing with change in pressure (Hooke's law):

$$\frac{dr}{dp} = \frac{(r - r_{hw})}{E_r} \qquad (5)$$

where r is stem radius, r_{hw} radius of the heartwood and E_r is the radial elastic modulus (elasticity) of sapwood.

The mass balance of stem segment:

$$\frac{dm_{w,i}}{dt} = Q_{in,i} - Q_{out,i} - E \qquad (6)$$

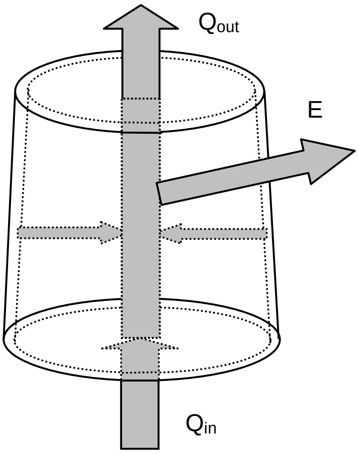

Figure **18**. A schematic illustration of a stem segment showing transpiration, sap flow, and diameter shrinkage.

where $m_{w,i}$ is the water mass in segment i, t is time, Q_{in} is the inward mass flow rate and Q_{out} is outward mass flow rate and E is transpiration from the segment. In **Studies I** and **II** the above equations where applied to a chain of elements of finite size for a short time step dt. The solution method can be regarded as a FV method.

In **Study V** the same physical background was used in the formulation of a single diffusion-advection-reaction – type of partial differential equation, which describes water pressure propagation inside a tapering ($\partial r/\partial h$) tree stem with a transpiration density S:

$$\frac{\partial p}{\partial t} = \left[\frac{E_r k}{2\eta}\left(1 + \frac{r_{hw}}{r}\right)\right]\frac{\partial^2 p}{\partial h^2} \qquad (7)$$

$$+\left[\frac{E_r}{2\eta}\left(1 + \frac{r_{hw}}{r}\right)\frac{\partial k}{\partial h} + \frac{E_r k}{\eta(r - r_{hw})}\left.\frac{\partial r}{\partial h}\right|_p + \frac{k}{\eta}\frac{\partial p}{\partial h} - \frac{r_{hw}E_r k}{r(r - r_{hw})\eta}\frac{\partial r_{hw}}{\partial h} + \rho g\frac{k}{\eta}\right]\frac{\partial p}{\partial h}$$

$$+\frac{E_r\rho g}{2\eta}\left(1 + \frac{r_{hw}}{r}\right)\frac{\partial k}{\partial h} + \frac{E_r\rho g k}{(r - r_{hw})\eta}\left.\frac{\partial r}{\partial h}\right|_p - \frac{E_r\rho g k r_{hw}}{r\,(r - r_{hw})\eta}\frac{\partial r_{hw}}{\partial h} - \frac{E_r}{2\pi r(r - r_{hw})}S$$

where ρ is water density and g is the gravity. This equation denotes that pressure is propagating by 'diffusion' (diffusion coefficient corresponds to the multiplier of the second spatial derivative of pressure) and 'advection' (advection velocity is the multiplier of the first spatial derivative of pressure) along the stem, and is depleted according to the sink term (last line in equation 7; usually negative). The diffusion term equals $Ek/2\eta$ in a stem without heartwood and approaches Ek/η with increasing heartwood percentage. The advection term introduces the effects of change in permeability ($\partial k/\partial h$), stem taper ($\partial r/\partial h$) and ($\partial r_{\mathrm{hw}}/\partial h$), and the gravity ($\rho g k/\eta$). The sink term originates from transpiration and changes in water conduction capability of the stem ($\partial k/\partial h$, $\partial r/\partial h$, and $\partial r_{\mathrm{hw}}/\partial h$). First, the FD method (Crank-Nicolson) was applied to solve the Equation 7, but it pointed out to be unstable because the advection term is too big compared to the diffusion term. Later on, the FV method (QUICK scheme) was used to obtain the approximate solution.

3.1.3. Sap flow and embolism model

In **Study II** the sap flow model in **Study I** was extended by adding an embolism sub-model and the effect of embolism on sap flow, sapwood permeability, and sapwood diameter. The embolism sub-model included three mechanisms for emboli formation: heterogeneous cavitation, air-seeding and the release of pre-existing bubbles from cell wall crevices. Heterogenous cavitation is covered by the following equations (e.g. Blander and Katz, 1975):

$$J = J_0 \exp\left[\frac{-16\pi\gamma^3 F}{3kT(p_v - p_l)^2}\right] \tag{8}$$

where J is the nucleation rate giving the number of nucleation events per unit area of the foreign surface (conduit wall or impurities) and unit time. J_0 is a kinetic pre-factor proportional to $N^{2/3}$, where N is the molecular density, k is the Boltzman factor, T is the temperature, ($p_{\mathrm{v}} - p_{\mathrm{l}}$) is the difference between saturation vapor pressure and liquid pressure, respectively, and F is a factor dependent on the contact angle:

$$F = \frac{2 + 3\cos\alpha - \cos^3\alpha}{4} \tag{9}$$

where α is the contact angle. The probability that a conduit still contains liquid after time t is $e^{-Jt\mathrm{Ah}}$, where Ah is the hydrophobic surface area of the cell lumen. Hence, the probability for cavitation is (e.g. Koop et al., 1996)

$$P = 1 - e^{-JtAh} \tag{10}$$

Parameters that affect embolism vulnerability: the wettability of conduit surfaces (contact angle), sizes of the single largest pores in the intervessel pits, and sizes of the largest crevices in the conduit walls were treated as distributions.

Air-seeding is covered by Equation 2 and the release of pre-existing bubbles is covered by Equation 3.

3.1.4. Embolism recovery model

Holbrook and Zwienicki (1999) suggested that embolism recovery (i.e. refilling of embolized conduit) is possible in conditions where water in the adjacent xylem conduits is under tension. According to their hypothesis living cells adjacent to the embolized vessel would create a driving force that draws water into the vessel lumen pressurizing the gas, which tends to dissolve into the xylem fluid and further transported away by diffusion.

Starting from their hypothesis a model describing the above processes as physical phenomena was developed (**Study III**).

The model was based on the following assumptions: In a hydraulically isolated refilling vessel, water pressure is equal to bubble gas pressure. Source of water for refilling is from water conducting vessels via living cells under turgor. Continuum of living cells act as source of solutes. Turgor driven water inflow pressurizes gas that dissolves into water and diffuses away from the embolized cell. In addition we assumed that reflection coefficient between embolized and living cell is below unity (solute transport between those cells is allowed), while the reflection coefficient between living cells and waters conduction cells equals unity (the solute transport is prohibited). The reflection coefficient represent the cell membrane aquaporins which are structures consisting of hydrophobic proteins (Tyerman et al. 2002), and there is strong evidence that they are central components in plant water relations. Figure 19 presents the system and the processes covered by the model. For detailed model equations see **Study III**.

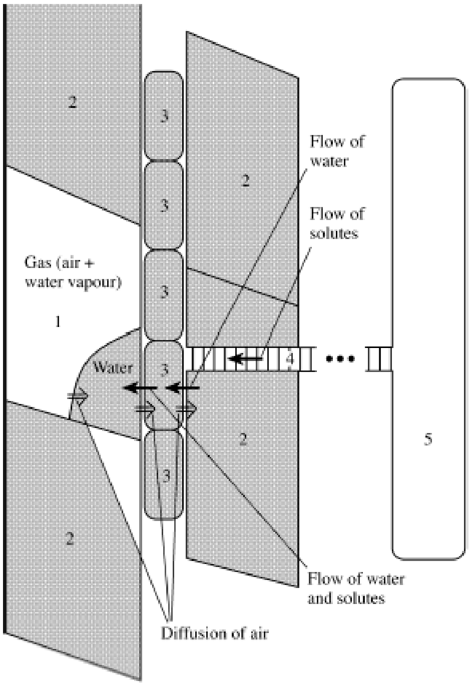

Figure. **19**. Schematic representation of the system of the refilling vessel (1), water-conducting vessels (2), living cells (3), ray cells (4) and phloem (5). The refilling vessel is hydraulically isolated from the xylem vessel. The refilling vessel contains liquid water and gas. The air dissolves in the water and diffuses out of the vessel. From Study III.

With this model, refilling process of the embolized conduit was examined in the range for the values of physico-physiological quantities (water tension in xylem, osmotic potential of the living cells, and diffusion distances).

3.1.5. Model for analyzing a sap flow measuring system

In Study **IV** a model was developed to analyze the performance of Dynamax Flow32 sap flow measuring system, which is based on the stem segment heat balance (SHB) method. The model simulates the heat propagation by conduction and convection (with a prescribed sap flow) in a stem segment, which is heated by a heating belt wrapped around the stem. Additionally, the model calculates sap flow from simulated heat transfer according to the SHB method.

3.2. Field measurements

Studies I, IV and **V** included also field measurements, which were all performed at the Helsinki University SMEAR II Station in Hyytiälä, Southern Finland (61°51´N, 24°17´E, 181 m a.s.l.). For details of the station, see Vesala et al. (1998). The site is of medium fertility and supports an even-aged Scots pine stand sown in 1962. The soil is a glacial till. The mean height of the stand was 14 m (in 2001).

3.2.1. Diameter change measurements

Xylem diameter variation of pine stems were measured with frequency of 1/300 s^{-1} (**Study I**) or 1/30 s^{-1} (**Study V**) using linear variable displacement transducers (LVDT; model A6G/1/S, Solartron Inc., West Sussex, U.K.). Each transducer was attached to a rigid steel frame mounted on the tree with attachment plates about 10 cm above the measurement point. A small area of phloem, bark and cambium was removed on opposite sides of the tree and covered with aluminum plates. One end of the frame rested on one plate and the head of the sensor was positioned on the other. Each frame and transducer was covered with a polyethylene (ST1000) shade to avoid heating by direct solar radiation (Figure 20). The frame temperatures were measured using copper-constantan thermocouples and used to correct for the effect of temperature on the expansion of the frame (Sandvik 1802 Steel). Similar setup has been used by Sevanto et al. 2002.

Figure **20**. Diamater change measurement with a linear variable displacement transducer attached to a frame and covered with polyethene shade.

3.2.2. Measurement of transpiration

In **Study I** transpiration was measured using a cylindrical trap-type cuvette enclosing a Scots pine shoot (Figure 21.). The measurement was based on the detection of the water vapor concentration change in the cuvette while this was closed for 70 s. Gas concentration was recorded every five seconds. The cuvette was open for the remaining time providing an environment close to the ambient for the shoots. When the cuvette was closed, the supply air compensated the airflow to the gas analyzer (URAS 4, Mannesman, Haartman & Brown Inc, Germany). The air in the cuvette was kept well-mixed using a small fan. Transpiration can be obtained from the mass-balance equation (Hari et al. 1999):

$$E_l = \frac{V_c \frac{d[H_2O]_c}{dt} + q_{in}[H_2O]_{in} - q_s[H_2O]_c - q_{out}[H_2O]_c}{A_l} \tag{11}$$

where E_l denotes leaf-specific transpiration of a shoot enclosed in the cuvette, $[H_2O]_c$ the H_2O concentration in the cuvette, $[H_2O]_{in}$ the concentration in the compensating flow, V_c the volume of the cuvette, q_s the air flow rate into the gas analyzer, q_{in} the compensating air flow, q_{out} the leakage from the cuvette caused by the difference between q_{in} and q_s, and A_l is the leaf area enclosed in cuvette. The cuvette measuring system (Figure 21) is described in detail in Hari et al. (1999). The shoot level transpiration was scaled up to tree level by applying the decrease of stomatal conductance as a function of light intensity inside canopy.

Figure **21**. A shoot cuvette. Photo: Pepe Hari

3.2.3. Sap flow measurements

In **Study IV** sap flow of a lower canopy Scots pine and an understorey mountain ash (*Sorbus aucuparia* L.) was measured using Dynamax Flow32™ system. Dynamax is based on the stem heat balance (SHB) theory (Sakuratani 1981). A measuring gauge is installed around stem and it heats up the stem segment with constant input power. The temperature raise ΔT over the heated segment, radial Q_r and vertical Q_v heat fluxes are measured and the sap flow Q is estimated according to

$$Q = \frac{P_{in} - Q_r - Q_v}{c\Delta T} \tag{12}$$

where P_{in} is the input power and c is the specific heat of water.

4. RESULTS

4.1. Sap flow models

Models in **Studies I** and **V** simulated water pressure dynamics and resulting sap flow in tree stems. Figure 22 presents simulated (model in **Study V**) and measured water pressure dynamics at the base of a Scots pine stem. In this case, measured water pressure was used as a boundary condition at the stem top. The model is able to predict the pressure propagation along the stem surprisingly well compared to measured values both in quantity and in pattern. Values for model parameters were obtained from literature or from independent measurements. Parameter values were not adjusted to get a better fit.

According to the analysis, the elasticity of sapwood causes a slight time lag between transpiration and pressure changes at the base of the stem. The time lag increases with increase of sapwood volume and especially with increase in height of the stem.

The increased time lag means also increased reliance on water storage in the stem, but at the same time it decreases the minimum pressures at the top of the stem. Figure 23 presents simulated water pressures of stems with heights of 30 m and 58 m with different sapwood volume to stem length ratios. Pressures were caused by identical transpiration. The figure clearly reveals that in order to increase the minimum water pressure (decrease the maximum tension) it is necessary to increase the transport capacity of sapwood. The value of minimum pressure is highly sensitive to the ratio of sapwood volume and stem length which proposes that trees can efficiently compensate for height-induced tension increase with sapwood area

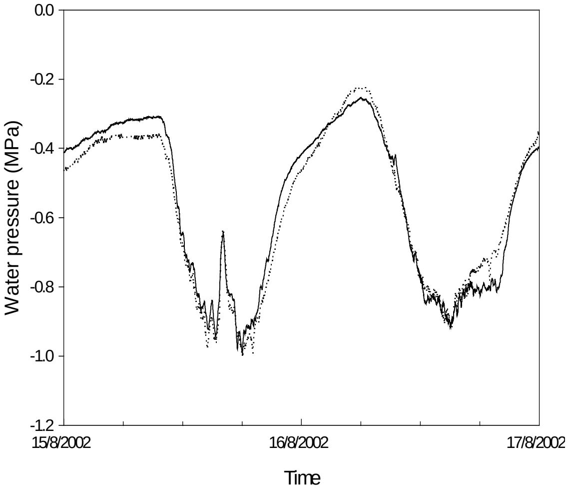

Figure **22**. Simulated (solid line) and measured (dotted line) water pressures at height of 3.6m of a Scots pine stem (heigth 28 m). Redrawn from Study V.

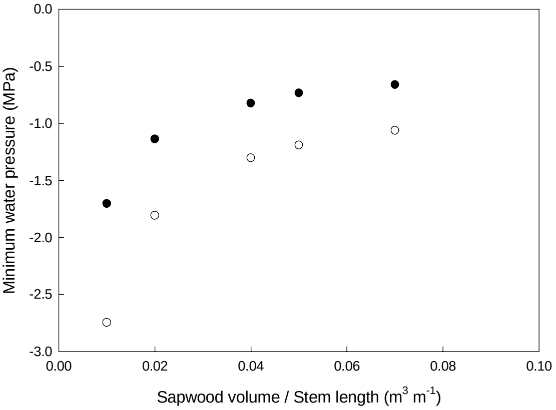

Figure **23**. Minimum simulated water pressures at the top of trees with height of 30m (filled circles) and 58m (open circles) with different sapwood volume to stem length ratios. From Study V.

increase, and maintain the same sap flow.

Another interesting result of the analysis in Study V is presented in Figure 24, which shows simulated water pressures at the top and base of an modeled tree stem with different water uptake capacities. The water uptake efficiency of fine roots has a substantial effect on the time course of the pressure change in the stem, and on the relative pressure changes at different heights of the stem. With effective water uptake the pressure change at base of stem is minimal.

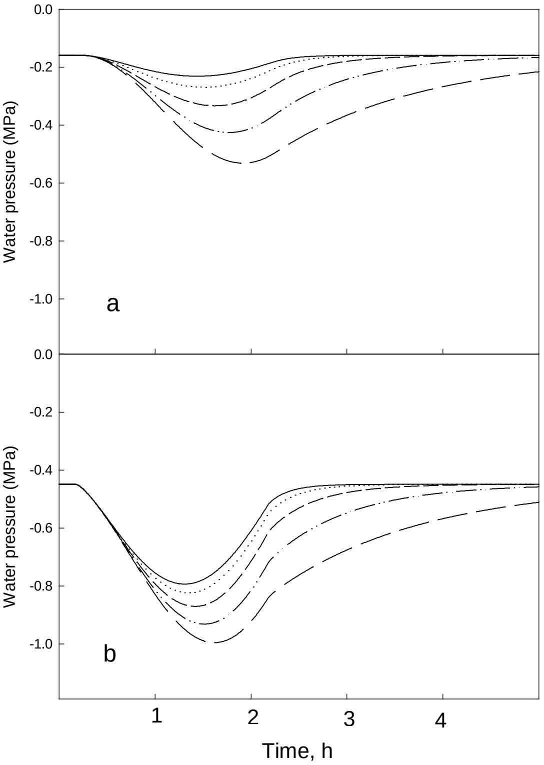

Figure **24**. Simulated water pressures at base (a) and at top of stem (b) with root permeability of 0.8 × 10 $^{-8}$ (long dashed line), 1.6 × 10 $^{-8}$ (dash-dot-dot line), 3.2 × 10 $^{-8}$ (dashed line), 6.4 × 10 $^{-8}$ (dotted line) and 12.6 × 10 $^{-8}$ m s^{-1} MPa^{-1} (solid line). Re-drawn from **Study V**.

4.2. Sap flow and embolism model

The results of the combined sap flow and embolism model revealed that the loss in permeability, caused by embolism, leads to an increasing trend in daily pressure amplitude and stem diameter change if embolism recovery is not allowed. The lowered permeability induces a larger pressure gradient according to Darcy's law (Equation 4), and therefore higher tensions are needed for transporting the same amount of water. The smaller tension values at the peak of transpiration during the first days compared with the non-embolism case result from the release of water to the transpiration stream from embolized conduits and the consequent relaxation of tension. If embolism occurs the tension peak is broader, in other words, the tension shows high values for a longer period.

4.3. Embolism recovery model

In **Study III,** the embolism repair hypothesis of Holbrook and Zwienicki (1999) was tested by developing a model to cover the essential cell structure and physical processes of embolism refilling, and performing simulations under different parameter values. The results of the model imply that embolism refilling is physically possible within reasonable time scales, under a feasible range of water tensions and the osmotic potential of living cells.

Figure 25 presents the evolution of ratio of the liquid water volume to that of the recovering vessel, for three different sizes of the recovering vessel, filled with water vapor only or with mixture of water vapor and air. It shows that the water exudation rate is initially very rapid and decreases later.

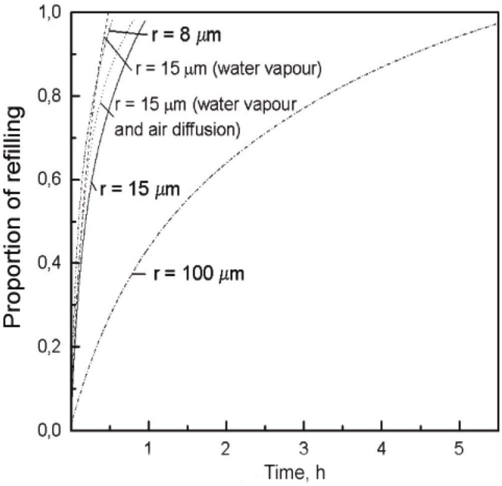

Figure **25**. Ratio of water volume to conduit volume as a function of time in the refilling conduit for different vessel radii r. From Study III.

Figure 26 shows the recovery time of an embolized cell as a function of xylem hydrostatic pressure with tree different values of osmotic potential in the living cells. This figure clearly reveals that quite high osmotic potential is needed when water pressure in xylem is low. At some specific threshold value of pressure the recovery time sharply increases and recovery is not possible without higher osmotic potential.

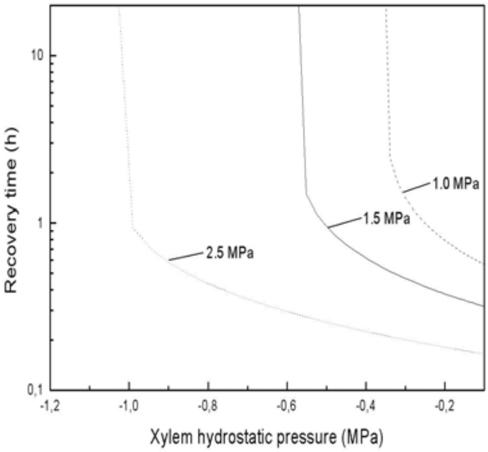

Figure **26**. Sensitivity of refilling time to pressure in water-conducting cells for three different osmotic potential in living cells. From Study III.

4.4. Model for analyzing a sap flow measuring system

The main result of the model analysis in **Study IV** is that the SHB method underestimates large flows, and the underestimation worsens with increasing stem size. The reason for this in the case of large stems, is the overestimation of stem temperature increase *ΔT* caused by heating based on the stem surface temperature measurements. Simulated steady-state temperature distributions inside the stem section are presented in Figure 27. (Big stem and high flow velocity in (a), small stem and low flow velocity in (b). In Figure 27a, in particular, the temperature distribution clearly deviates from the underlying assumption of a radially homogeneous temperature field, which the SHB method uses.

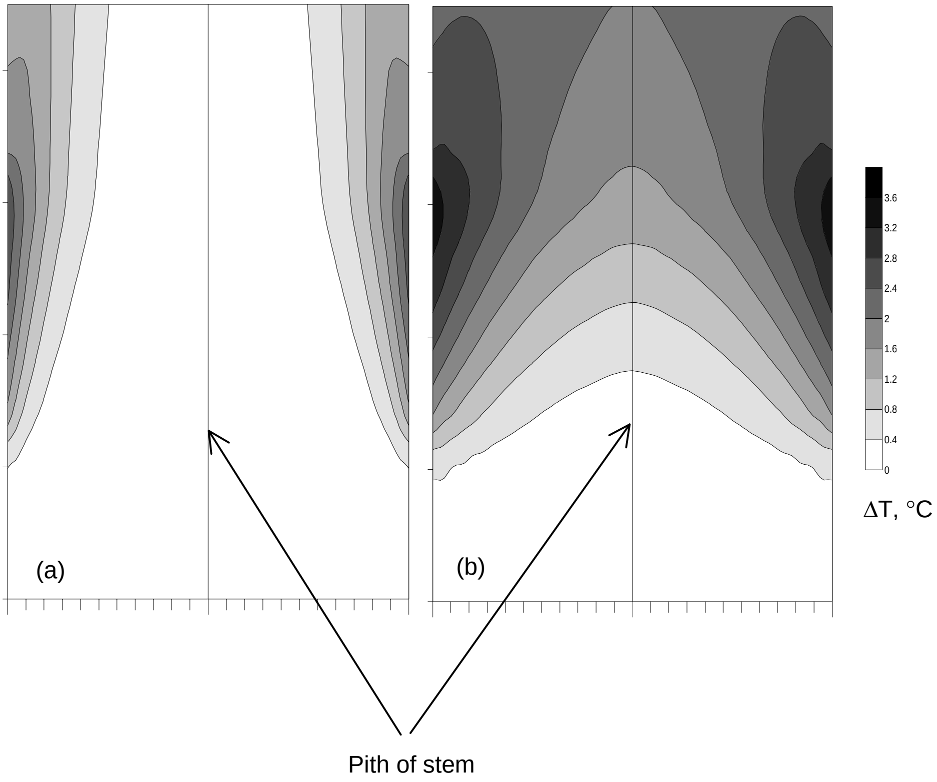

Figure **27**. Simulated temperature distributions inside the stem segment at steady state. (a) large stem, high sap flow velocity; (b) thin stem, low flow velocity. Redrawn from Study IV.

5. DISCUSSION

5.1. The modeling methodology

The primary goal of this thesis was to examine the dynamics of sap flow and related phenomena using a dynamic modeling approach. The approach is particularly suitable in this context for several reasons: the tree stem, with flowing sap, is a dynamic system and it can be expressed using state variables, which describe the actual state of the system at any moment, and processes, which cause the dynamics of the system. The state variables are clear physical entities (water mass or pressure, amount of energy in **Study IV**), and mechanisms behind the processes (mass and heat flow in **Study IV**) are rather well understood and obey well-established physical theories so that they can be expressed as mathematical equations. Values for most model parameters (e.g. stem dimensions, xylem permeability) are obtainable by independent measurements with reasonable accuracy.

Although models are always simplified representations of a particular domain of the reality (Bossel 1994), they are of great use in various fields of science. With models it is quite easy to gain information about the behavior of a complex system over different temporal and spatial scales in various environmental conditions. With measurements (especially in the field) there are always physical and economical factors which set limits to the quality and/or quantity of the obtained information. The measured results are more or less biased by measurement theory, instrument implementation and calibration, measuring practices, and human involvement. In addition, the measuring actions usually disturb or even destroy the object, especially when living biological objects are involved. Modeling methodology enables us to extend the analysis much deeper than measurements. It is also possible to create and examine the behavior of a partial system having only the most interesting properties by ignoring, for example, the environment and its effects on the system.

The most important advantage of the modeling methodology is the increase of the scientific understanding. The model development process, *per se*, clarifies our understanding about the interactions of complicated – and often non-linear – systems, and new ideas about the structure and behavior of the system can emerge. With model simulations it is possible to study for example under what conditions some non-measurable phenomenon may occur, or how long time does some process last (embolism repair in **Study III**). Models can elucidate errors in other models. Running sensitivity analysis may help us to focus our limited measurement resources more efficiently to the most dominating factors of the system and thus to improve the measuring procedure or the instrumentation. According to Oreskes et al. (1994) the primary value of models is heuristic; the model analysis can guide observations and experiments.

Verification and validation of a model are sometimes discussed as means of proving the correctness and usefulness of it. According to Giere's (1988), definition a model is an abstract, non-linguistic object which cannot be true or false. Only hypothesis claiming the similarity between a model and an object in reality can be assessed being true or false. *Verification* (from Latin, *verus*, meaning true) means: 'The action of establishing or testing the truth or correctness of a fact, theory, statement, etc.' (Oxford English Dictionary). Verification of a model means demonstrating its truth. According to Oreskes et al. (1994), only a closed system - i.e. a system whose behavior is entirely explainable from within, a system without input - can be proven to be true. Purely formal mathematical and logical statements can be shown to represent closed systems, they can be verified, their truth can be asserted.

Besides verifiable mathematical expressions, models of natural systems always require additional assumptions and incomplete known input parameters. These are called auxiliary hypotheses, and they render the system open. If the model predictions do not agree with observations, it is not possible to know whether the original or auxiliary hypothesis is faulty. Even when the model predictions agree with observations, the model can not be verified: two or more errors in the auxiliary hypotheses may cancel each other out, and it is not possible to know if that has occurred. Thus, verification of a model of natural system is simply not possible.

Validity of a model usually means that the model does not contain known or detectable flaws and it is internally consistent. Frequently a model is said to be valid if it reflects the behavior of the real system. However, it is impossible to prove that a model fulfils these requirements of validity. Bossel (1994) suggests that model validity is relative to the model purpose. Bossel requires that validity have to be demonstrated with respect to four different aspects: *behavior validity,* when the model produces qualitatively corresponding results with the original system. *Structural validity,* when the model includes the essential influence structure of the original. *Empirical validity*, when numerical model results correspond with the original. *Application validity*, when the model fulfils the requirements of the user and/or the context where model is used. These validities can be established by extensive falsification trials (Popper 1959) but they are only true until falsifying evidence appears. If a theory or model has withstood the most rigorous attempts of falsification for a long period of time it has received a high measure of corroboration (Popper 1959).

The models in the present study cannot be considered as a true and complete description of the natural phenomena involved. However, the models have gained strong corroboration because they have solid physical bases, they contain the essential elements of the objects in reality, their formulations facilitate direct comparison of simulated results with field measurements, and their results (Studies I, IV and V) agree with the results of independent observations.

5.2. Evaluation of the model performance and the model results

5.2.1. Pressure propagation and sap flow

The prominent agreement between predicted and measured diameter fluctuation at daily scale (sap flow models in **Studies I** and **V**) suggests that this novel principle, which connects the amount of water, water tension, and stem diameter, offers us a promising method to examine the dynamics of sap flow. With this model formulation we can avoid the concept of capacitance, which is used in most sap flow models found in literature (Edwards et al. 1986, Tyree 1988, Früh and Kurth 1999). Capacitance is a combined outcome of several different processes and as a whole it is ambiguous. It is deficient as a basis for sap flow modeling (Aumann and Ford 2002), not constant with respect to time, space and water tension (Jarvis et al. 1981), and difficult to measure (Holbrook 1995). The capacitate element in the models of this study (xylem shrinkage under pressure due to xylem elasticity) is based on a simple measurable physical aspect of wooden material. The results in **Studies I** and **V** also imply that sapwood diameter change can be considered as a direct and immediate indication of the water tension in the tree stem. This finding emphasizes the feasibility of this method, which can be used to record high-frequency water tension dynamics automatically with reliable and cheap instrumentation.

The results of the model in **Study V** give new insight into the water dynamics in the stem (including phloem and bark). Tension change propagates quite fast (in few minutes) through the whole sapwood down to the roots and causes the shrinkage of the sapwood diameter. The time lag in stem increases with increasing stem length, sapwood volume, stem taper, and with decreasing elastic modulus and permeability of sapwood. Soil to root hydraulic conductance (i.e. the fine root conductivity and/or the fine root surface area), seems to have a significant effect on the water pressure and sap flow dynamics of living trees. Increased tension inside the sapwood causes also radial tension propagation and water flow from the living tissue external to the xylem (Zweifel et al. 2001). Because radial permeability is several orders of magnitude smaller than axial permeability (Zwieniecki et al. 2001), and because elastic modulus of the phloem is smaller than that of the xylem (Nobel 1991), the radial tension propagation is slower than axial. This explains why diameter changes of the whole stem have been reported to lag behind xylem diameter changes (Sevanto et al. 2002). When transpiration ceases, the flow from soil fills up the sapwood quite fast, but the slower recharge of the phloem and bark water storage keeps up a tiny flow and slow tension relaxation during the night hours. This produces the ‘typical tail’ in a diurnal sap flow and diameter change curves and may explain the discrepancy between modeled and measured tension relaxation reported also in **Study I**.

The effect of stem size on the sap flow dynamics has been recently investigated in several studies. Meinzer et al. (2001) reported results of sap flow measurements of 23 phylogenetically diverse tropical forest tree species. They found that tree size affected the daily course of stem sap flow (at the height of 1.5 m), especially the time of the maximum value of sap flux. They concluded that this ‘probably reflects a common relationship between diurnal stem water storage capacity and tree size’. Similar discovery has been made by Goldstein et al. (1998) who concluded that tree size, rather than tree species, was the most important determinant of diurnal water storage, which increases exponentially with tree height. The model predictions in **Study V** are consistent with above results. The time lag between transpiration and tension changes at base of the stem (water storage) increases with tree size.

Phillips et al. (2003) measured bole and crown sap flux rates of small and large individuals of Douglas-fir, Oregon white oak (*Quercus garryana* Doug. ex. Hook.), and ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws.) in the Pacific Northwest. They reported that reliance of stored water increased with tree size, and that the use of stored water was concentrated in morning and early afternoon hours when the solar radiation was highest. They concluded that this leads to ‘an average of 18% more photosynthesis to occur in 60-m tree than if the crown flux were constrained to match the time course of bole flux’. Their reasoning is misleading. The results in **Study V** imply that the delayed bole flux in taller trees is an unavoidable physical consequence of slower tension propagation in longer stems and without this delay (i.e. use of stored water) the bole flux would match the crown flux, not the other way round. The delay means that the wooden structure of a higher tree is not able supply water to the crown at the speed of transpiration and this leads to increased water tensions in the leafs and, opposite to conclusion of Phillips et al. (2003), it is likely that photosynthesis is decreased by stomatal control. In order to avoid excessive water tensions higher trees have to increase the cross sectional area of sapwood.

5.2.2. The effect of embolism

The results in **Study II** propose that, when embolism repair is allowed for, the tension increase is damped by the water release in transpiration stream from embolized conduits. The same happens also during the first days in a case where embolism repair is not included, but over longer periods of time, cumulative increase of embolized conduits will most probably lead to runaway cavitation (Tyree and Sperry 1988). The analysis shows that the embolism might play an important role in the water and carbon balance of a tree. During periods of high transpiration water release from embolized conduits may prevent further embolism. In addition, water release may keep the stomata open and thus allow higher photosynthesis.

The analysis also shows that the contact angle required for heterogeneous cavitation on smooth and flat surfaces is very large, exceeding 170°. This implies that there has to be extremely hydrophobic areas on the conduit wall surface to produce embolism by heterogeneous cavitation. It is known that hemicellulose and cellulose, which are the main constituents of the conduit walls, are hydrophilic. This is supported by recent findings by Zwieniecki and Holbrook (2000). They measured contact angles for conduit walls of many species and found values of about 50°. According to these results smooth areas of cell wall are not a suitable surface to trigger heterogeneous cavitation and thus air-seeding (Sperry and Tyree 1990, Sperry 2003), and/or growth of existing bubbles from cell wall crevices (Pickard 1981) seem to be a more probable mechanisms for embolism.

5.2.3. Embolism recovery model

The model analysis in **Study III** shows that embolism refilling is physically possible under hydraulic isolation, while water in surrounding conduits is under negative pressure, and the idea of Holbrook and Zwieniecki (1999) may well explain the refilling process. The analysis revealed the circumstances under which the refilling process is possible. The living cells have to have an osmotic pressure of at least several hundreds kilopascals. These pressures are not atypical in living cells. The radius of the embolized conduit must not exceed 100 μm in order to allow the refilling in a feasible time scale. In addition, there has to be a route from water source (living cells) to embolized conduit, and the volume of the living cells in contact with the embolized conduit has to be adequate. A microscopic photograph in Figure 8 presents the tangential view of Scots pine xylem. The image proposes that every single tracheid is in contact with at least one ray with living parenchyma cells and, hence, a pathway for solute flow from phloem to xylem conduits for embolism recovery is provided, at least in the case of Scots pine. The most uncertain requirement for embolism recovery proposed by the model analysis is the need for different solute transport properties of the two sides of the same living cells i.e. differences in aquaporin gating allowing solutes to move to the refilling conduit but not to the conduits under tension. There is strong evidence that aquaporins are central components in plant water relations and their ability to control water and solute permeability of the membrane can be influenced by several different factors (discussed by Holbrook and Zwienicki 2003), including water tension (Ye et al. 2004). Thus, if the asymmetric aquaporin opening is workable, the scheme presented by Holbrook and Zwieniecki (1999) may give explanation to the several findings of embolism recovery under water tension (Hacke and Sperry 2003, Salleo et al. 1996, Tyree et al. 1999).

5.2.4. Analysis of the sap flow measuring system

The analysis in **Study IV** revealed that the SHB method has considerable problems associated with the non-homogeneous temperature field, when the measurements of the heat balance are conducted from the surface of the stem. The simulations point out this problem particularly for the large stems, in which the sap is flowing in the deep layers. Since the temperature difference between sap leaving and entering a segment is used to derive the sap flow, using the estimated heat carried by sap, it is clear that erroneous estimations of this difference have considerable influence on the flow estimate. As this analysis revealed this value depend on the size of the segment and the flow rate, and therefore its influence is becoming more important as larger segments are analyzed. Temperature measurements from inside the wood would improve the accuracy of the method.

5.3. How do the sap flow models apply for other species and different environment

In sap flow studies (**Studies I** and **V**), model predictions were compared with few days field measurements of two individuals of a single tree species (Scots pine). One could argue that on the basis of this limited set of tests, the models do not have the power to support any generalization and they could not be regarded as adequate descriptions of sap flow phenomena in the stem xylem. In addition, the model formulations ignore two mechanisms: embolism and radial water flow between xylem and phloem, both of which may have bigger impact in some other species. However, according to the results of **Studies I** and **V,** it seems that the quantitative effect of those two mechanisms is quite insignificant for Scots pine and presumably with other conifers with similar xylem structure. Because the models in this thesis have a sound physical base they could be regarded as an appropriate description of the tension propagation through the xylem, which in the case of other species can be slower depending on the rate of embolism and the level of coupling between xylem and phloem.

5.4. Concluding remarks

The most important result of the present work is the increased understanding of the propagation of water tension inside sapwood. The new formulation of sap flow (**Study V**) has resulted in a sound physically based model, which explains the daily swelling and shrinking of stems. It illustrates quite well how the daily dynamic of the sap flow, pressure changes, and radius fluctuations in a stem are linked with the dimensions and water transport properties of the sapwood and fine roots. The model predictions can be directly tested against simple field measurements of diameter dynamics. The model results show that pressure propagation in xylem is quite fast, but time lags between transpiration and sap flow at the stem base appear also in trees without embolism. The principal reason for time lags is the elastic shrinkage of the xylem. Although the model does not consider the phloem, the results imply that phloem and xylem are hydraulically connected, and radial water transfer between them causes slower xylem diameter recovery in the evening, when transpiration has ceased.

The present study also points out that the water uptake capacity of fine roots has a considerable effect on tension profiles in stem xylem. This result proposes that diameter change measurements together with model simulations can be used to analyze the size or performance of the fine root system. Detectable diameter variation at the base of stem indicates that resistance to water flow at the soil-to-root interface plays a substantial role in the whole soil-plant-atmosphere continuum.

Ryan and Yoder (1997) suggested a theory of hydraulic limitation to tree growth. Increased xylem path length in tall trees with long branches results in earlier stomatal control and in decreased photosynthetic production, and finally leads to cessation of growth. Furthermore, the decreased positive pressure (turgor) in living cells reduces cell expansion and growth (Koch et al. 2004). In addition, the construction of the extensive water pathway changes the allocation of biomass by requiring an increasingly bigger share of the photosynthetic production.

The results of this analysis suggest that in order to avoid limiting water tensions a tall tree should increase the carbon allocation to fine roots and sapwood at the expense of leafs, i.e., decrease the A_l:A_s and A_l:A_r ratios, where A_l is the leaf area, A_s is the cross-sectional area of sapwood, and A_r is the surface area of fine roots. This contradicts the pipe-model theory (Shinozaki et al. 1964), which assumes a constant A_l:A_s, but agrees with empirical evidence of decrease in A_l:A_s (McDowell et al 2002, Vanninen et al. 1996, Mencuccini and Grace 1996) and decrease of $\mathrm{A_l}$:$\mathrm{A_r}$ (Magnani et al. 2000) with increase in tree height. This change in allocation leads to increased respiration and decreased photosynthesis and eventually also to growth degradation. It seems that water transport sets limits to the maximum tree height, which is affected by the evaporative demand, soil properties of the site, and the species-specific sapwood permeability and the photosynthesis effectiveness.

The cohesion-tension theory has often received severe criticism (Canny 1995, Zimmermann et al. 2004). Our analysis fully supports the theory: xylem diameter fluctuation, which is a direct consequence of transpiration, shows that there is substantial water tension variation inside xylem. The tension fluctuation is transmitted by continuous water chains. Due to elasticity of xylem, there are minor time lags between transpiration and diameter change. The analysis reveals that the time lags found in intact trees are consistent with the cohesion-tension theory, and thus the conclusion contradicts that of Aumann and Ford (2002) who claimed that cohesion tension theory do not explain time lags in sap flow.

This study has shown that relatively simple models that contain only the most essential elements and processes of real systems, and explicitly or implicitly ignore several factors, can be useful in increasing our understanding of the mind- and observation-independent reality around us. The models can guide further investigations and enhance instrumentation development. In the future, the pressure propagation model (**Study V**) will be enhanced by implementing embolism phenomenon and interaction between phloem and xylem. Additional research is needed especially on the role of living cells in embolism refilling mechanisms. We also need better understanding of the mechanisms behind the influence of water tension on stomatal behaviour and the trade-off between structural costs of embolism prevention and xylem conductance. All these phenomena have an effect on sequestration of atmospheric carbon dioxide and thus growth of trees. This information is needed to improve the reliability of the tree and stand growth models under changing environmental conditions.

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