

# Vascular Transport in Plants

**N. Michele Holbrook**

Organismic and Evolutionary Biology  
Harvard University  
Cambridge, Massachusetts, USA

**Maciej A. Zwieniecki**

The Arnold Arboretum  
Harvard University  
Cambridge, Massachusetts, USA

This is a volume in the

**PHYSIOLOGICAL ECOLOGY Series**

Edited by Harold A. Mooney  
Stanford University, Stanford, California


*A complete list of books in this series appears at the end of the volume.*



**ELSEVIER**  
ACADEMIC  
PRESS

Amsterdam • Boston • Heidelberg • London  
New York • Oxford • Paris • San Diego  
San Francisco • Singapore • Sydney • Tokyo

Elsevier Academic Press  
30 Corporate Drive, Suite 400, Burlington, MA 01803, USA  
525 B Street, Suite 1900, San Diego, California 92101-4495, USA  
84 Theobald's Road, London WC1X 8RR, UK

This book is printed on acid-free paper. 

Copyright © 2005, Elsevier Inc. All rights reserved.

No part of this publication may be reproduced or transmitted in any form or by any means, electronic or mechanical, including photocopy, recording, or any information storage and retrieval system, without permission in writing from the publisher.

Permissions may be sought directly from Elsevier's Science & Technology Rights Department in Oxford, UK: phone: (+44) 1865 843830, fax: (+44) 1865 853333, e-mail: [permissions@elsevier.co.uk](mailto:permissions@elsevier.co.uk). You may also complete your request on-line via the Elsevier homepage (<http://elsevier.com>), by selecting "Customer Support" and then "Obtaining Permissions."

#### Library of Congress Cataloging-in-Publication Data

Holbrook, N. Michele (Noel Michele)  
Vascular transport in plants / N. Michele Holbrook, Maciej A. Zwieniecki.  
p. cm.

Includes bibliographical references and index.

ISBN 0-12-088457-7 (alk. paper)

1. Vascular system of plants. I. Zwieniecki, Maciej A. II. Title.

QK725.H58 2005

575.7'-dc22

2005003325

#### British Library Cataloguing in Publication Data

A catalogue record for this book is available from the British Library

ISBN-13: 978-0-1208-8457-5

ISBN-10: 0-12-088457-7

For all information on all Elsevier Academic Press publications  
visit our Web site at [www.books.elsevier.com](http://www.books.elsevier.com)

Printed in the United States of America

05 06 07 08 09 9 8 7 6 5 4 3 2 1

Working together to grow  
libraries in developing countries

[www.elsevier.com](http://www.elsevier.com) | [www.bookaid.org](http://www.bookaid.org) | [www.sabre.org](http://www.sabre.org)

ELSEVIER

BOOK AID  
International

Sabre Foundation

## Contents

Contributors	xiii
Preface	xvii
Acknowledgment	xix

## Part I Fundamentals of Transport

<b>1. Perspectives on the Biophysics of Xylem Transport</b>	<b>3</b>
<i>William F. Pickard and Peter J. Melcher</i>	
I. The Biophysics of Sap Ascent in the Xylem	4
II. Discussion	13
References	15
<b>2. Physiochemical Determinants of Phloem Transport</b>	<b>19</b>
<i>Aart J.E. van Bel and Jens B. Hafke</i>	
I. Structure-Functional Basics of Phloem Transport	19
II. Generation of a Hydraulic Pressure Gradient in Collection Phloem	21
III. Maintenance of Hydraulic Pressure Gradient in Transport Phloem	32
IV. Manipulation of the Hydraulic Pressure Gradient in Release Phloem	34
V. Radius of the Sieve Tubes	36
VI. Viscosity, Sugar Species, and Concentrations in Sieve Tubes	36
VII. Physiochemical Relationship Between Xylem and Phloem Pathway	37
VIII. Concluding Remarks	37
References	39
<b>3. Pathways and Mechanisms of Phloem Loading</b>	<b>45</b>
<i>Robert Turgeon and Brian G. Ayre</i>	
I. Minor Veins	46
II. Transport Between Mesophyll Cells	49
III. The Role of Phloem Parenchyma Cells	51

- Soh, W. Y. (1990). Origin and development of cambial cells. In *The Vascular Cambium* (M. Iqbal, ed.) pp. 37-62. Research Studies Press, Taunton/John Wiley, New York.
- Srivastava, L. M. (1963) Secondary phloem in the Pinaceae. *Univ Calif Publ Bot* **36**: 1-142.
- Stewart, C. M. (1966) Excretion and heartwood formation in living trees. *Science* **153**: 1068-1074.
- Sundberg, B. and Uggla, C. (1998) Origin and dynamics of indoleacetic acid under polar transport in *Pinus sylvestris*. *Physiol Plant* **104**: 22-29.
- Thair, B. W. and Steeves, T. A. (1976) Response of the vascular cambium to reorientation in patch grafts. *Can J Bot* **54**: 361-373.
- Thimann, K. V., Reese, K. and Nachmias, V. T. (1992) Actin and the elongation of plant cells. *Protoplasma* **171**: 153-166.
- Timell, T. E. (1980) Organization and ultrastructure of the dormant cambial zone in compression wood of *Picea abies*. *Wood Sci Technol* **14**: 161-179.
- Tuominen, H., Puech, L., Regan, S., Fink, S., Olsson, O. and Sundberg, B. (2000) Cambial-region-specific expression of the *Agrobacterium iaa* genes in transgenic aspen visualized by a linked *uidA* reporter gene. *Plant Physiol* **123**: 531-541.
- Uggla, C., Mellerowicz, E.J. and Sundberg, B. (1998) Indole-3-acetic acid controls cambial growth in Scots pine by positional signalling. *Plant Physiol* **117**: 113-121.
- van Bel, A. J. E. (1990) Xylem-phloem exchange via the rays: The undervalued route of transport. *J Exp Bot* **41**: 631-644.
- Venning, F. D. (1953) The influence of major mineral nutrient deficiencies on growth and tissue differentiation in the hypocotyl of Marglobe tomato, *Lycopersicon esculentum* Mill. *Phytomorphol* **3**: 315-326.
- Wareing, F. F. and Roberts, D. L. (1956) Photoperiodic control of cambial activity in *Robinia pseudacacia* L. *New Phytol* **55**: 356-366.
- Warren Wilson, J. M. (1978) The position of regenerating cambia: Auxin/sucrose ratio and the gradient induction hypothesis. *Proc Roy Soc London B*, **203**: 153-176.
- Whalley, B. E. (1950) Increase in girth of the cambium in *Thuja occidentalis* L. *Can J Res, Sect C* **28**: 331-340.
- Wilson, B. F. (1963) Increase in cell wall surface area during enlargement of cambial derivatives in *Abies concolor*. *Am J Bot* **50**: 95-102.
- Wilson, B. F. (1964) A model for cell production by the cambium of conifers. In *The Formation of Wood in Forest Trees* (M. H. Zimmermann, ed.) pp. 19-36. Academic Press, New York.
- Włoch, W. and Wawrzyniak, S. (1990) The configuration of events and cell growth activity in the storeyed cambium of the linden (*Tilia cordata* Mill.). *Acta Soc Bot Polon* **59**: 25-43.
- Wolking, F. (1970) Morphologie und systematische Verbreitung der lebenden Holzfasern bei Sträuchern und Bäumen II. Zur Histologie. *Holzforschung* **24**: 141-147.
- Ye, Z.-H. (2002) Vascular tissue differentiation and pattern formation in plants. *Annu Rev Plant Biol* **53**: 183-202.
- Zagórska-Marek, B. (1984) Pseudotransverse divisions and intrusive elongation of fusiform initials in the storeyed cambium of *Tilia*. *Can J Bot* **62**: 20-27.
- Zasada, J. C. and Zahner, R. (1969) Vessel element development in the earlywood of red oak (*Quercus rubra*). *Can J Bot* **47**: 1965-1971.
- Zee, S.-Y. (1968) Ontogeny of cambium and phloem in the epicotyl of *Pisum sativum*. *Aust J Bot* **16**: 419-426.
- Zhong, R., Burk, D. H. and Ye, Z.-H. (2001) Fibers. A model for studying cell differentiation, cell elongation, and cell wall biosynthesis. *Plant Physiol* **126**: 477-479.

## 15

## Structure-Function Relationships in Sapwood Water Transport and Storage

Barbara L. Gartner and Frederick C. Meinzer

Primary production by plants requires the loss of substantial quantities of water when the stomata are open for carbon assimilation. The delivery of that water to the leaves occurs through the xylem. The structure, condition, and quantity of the xylem control not only the transport efficiency but also the release of water from storage. For example, if there is high resistance to water flow in the stem, then less water is available to the leaves, so less primary production can occur. High resistance can result from wood material with low conductivity, from having only a small amount of conductive wood, or from having very slow release of stored water to the transpiration stream. The subject of this chapter is the efficiency with which different parts of the sapwood transport, store, and release water, and how the structure of the wood affects these processes. Particularly, we describe the radial patterns of axial water transport, their anatomical and physiological causes, the effect that sapwood width and wood structure, especially density, have on water transport, and determinants of sapwood water storage properties.

We define sapwood as the xylem that is conductive to water, although sapwood can also be defined on the basis of color, respiration, and parenchyma vitality. Although our discussion refers to sapwood versus heartwood, many species also have intermediate wood, which is located between the sapwood and heartwood, and is said to have intermediate characteristics (Hillis, 1987). However, some intermediate woods may not have living cells (Hillis, 1987), and more research is needed to delineate which functions are still active in this zone for different species. Likewise, wood has a variety of types, but for simplicity we discuss only three: coniferous, and angiosperm ring-porous and diffuse-porous. These classifications capture much of the interspecific variation in gross wood structure in the temperate and arctic zones, but because most tropical species are

diffuse-porous and have extremely variable vessel groupings and/or parenchyma patterns, additional classifications may be more useful for tropical woods.

## Radial Changes in Wood Anatomical Characteristics and Hydraulic Properties

The anatomy of the wood follows systematic patterns of variation that depend on the ring number outward from the pith, the height in the tree, and the radial growth rate. Also, because the xylem transports water for several years, there may be changes in its water transport properties as the cells age. This section describes these basic patterns of wood anatomy, focusing on radial variation, and how they affect the hydraulic conductivity of sapwood.

### Within-Bole Patterns of Wood Anatomy and Properties

In all woody plants, the anatomy of wood changes systematically along a radial (pith-to-bark) direction. The magnitude of the changes depends on the species and the type of wood (e.g., diffuse versus ring-porous). Superimposed on this variability is that caused by environmental factors such as the amount and timing of rainfall and temperature. The most obvious change to the naked eye is the pith-to-bark decrease in growth ring width. At the base of the tree, the first several rings near the pith are usually narrow, produced when the tree was growing slowly while becoming established. Beyond that zone, the rings are wide, then gradually become narrow, associated with slower growth and/or with having a larger cylinder around which to place the new wood produced by a constant-sized crown (Duff and Nolan, 1953). Depending on the species, the percentage of latewood within each ring can increase (common in conifers), decrease (common in ring-porous species), or stay the same with increasing cambial age. Diffuse-porous species are special cases because they have weaker anatomical gradients across the growth ring, so the pith-to-bark changes in growth rate probably have less of an effect on their anatomy.

The second type of radial change in wood structure is referred to as the juvenile/mature wood transition. Juvenile wood (JW) denotes the wood adjacent to the pith. Its properties (anatomical, mechanical, hydraulic, chemical composition) change dramatically from one growth ring to the next (Larson *et al.*, 2001; Senft *et al.*, 1985). In contrast, the properties of mature wood (MW) are relatively constant from ring to ring (if environment remains constant). The extent of the JW zone (in number of growth rings from the pith) depends largely on genetics (Zobel and Sprague,

1998). The juvenile wood zone is usually better correlated with number of growth rings than with distance from the pith (Zobel and Sprague, 1998). In conifers, JW may persist well past 100 years from the pith (Wellwood *et al.*, 1974), but in general the overwhelming majority of the total change will have occurred in the first 10 to 20 years. Most properties either increase or decrease extremely quickly and then reach an asymptote. The radial pattern can be somewhat different with vertical position, but changes with height for the same cambial age are usually small compared to the changes with cambial age at the same height.

In all woody plants studied, the JW shows a gradual increase in the length of the tracheids and/or libriform fibers, usually accompanied by an increase in their diameter with increasing tree age (Zobel and Sprague, 1998). The magnitude of this and other anatomical changes is much higher in gymnosperms than in angiosperms (Panshin and deZeeuw, 1980). For example, in *Pseudotsuga menziesii*, tracheid length increases from 1 to 5 mm from growth rings 2 to 25 (Megraw, 1985) and earlywood tracheid diameter increases from 22 to 40  $\mu\text{m}$  over the same age interval (Spicer and Gartner, 2001). In the ring-porous oak *Quercus garryana*, tracheid length increases from 1.0 to 1.2 mm and earlywood vessel diameter increases from 150 to 250  $\mu\text{m}$  from growth rings 2 to 25 (Lei *et al.*, 1996). Diffuse-porous species have similar increases in cell length and diameter as ring-porous ones.

In diffuse-porous angiosperms, the other radial changes are highly species-specific. As a general rule, their wood has the most constant pith-to-bark properties of any wood type. For example, red alder (*Alnus rubra* Bong) shows no significant change in wood density across the radius (Gartner *et al.*, 1997; Harrington and DeBell, 1980) or at radial growth rates that vary by a factor of 5 (Lei *et al.*, 1997). There may be some difference in the proportion of the growth ring that is vessel, libriform fiber, and parenchyma, and there can be modest increases in vessel diameter (e.g., Lei *et al.*, 1996).

In contrast to diffuse-porous species, ring-porous angiosperms have more significant changes in their wood from pith to bark. In general, these species maintain a similar earlywood width, with the decrease in ring-width at the expense of latewood (Phelps and Workman, 1994; Zhang and Zhong, 1991). Thus, in contrast to the conifers, wood density decreases and proportion of vessel area increases through the JW to the MW.

In conifers, significant changes in wood structure from the JW to MW also include a tendency toward having a higher latewood proportion, thicker cell walls in the earlywood and latewood, denser wood (mostly due to denser latewood) and a change in the cell wall ultrastructure: Microfibrils within the S2 layer decrease from 45 degrees (with respect to axial) in the JW to about 5 degrees in the MW (Larson *et al.*, 2001). The combination of a

decrease in microfibril angle and an increase in wood density result in wood that is stronger and stiffer axially in the MW than in JW. The increase in earlywood cell length and diameter and the increase in latewood proportion probably have the largest effect on hydraulics.

Within the mature wood, if the environment stays the same, the wood made in 1 year is similar to the wood made in a previous year. The exception is that in trees that are declining because of environmental degradation, disease, or very old age, the new wood can be different. For example, in *Abies alba*, declining trees had latewood zones of 1 to 2 rows, compared to a broad zone in healthy trees, and the cell wall thickness of the latewood in the declining trees tended to be lower (Schmitt *et al.*, 2003). In *Pinus mugo*, two types of root pathogen caused a decrease in growth ring width compared to uninfected individuals, but the decrease was gradual in trees infected with one type and abrupt for the other. (Cherubini *et al.*, 2002). No data were given on whether earlywood proportion or any of the cell structures were altered as the growth ring widths decreased. In the forest products industry, it is known that very old trees can have much reduced wood density in their outer rings (i.e., Wellwood *et al.*, 1974).

As the wood progresses from being outer to inner sapwood, its properties may change. The outer sapwood of MW may differ from inner sapwood in having a higher percentage of living parenchyma cells (reviewed in Gartner *et al.*, 2000), fewer cells blocked by tyloses (Cochard and Tyree, 1990), and fewer incrustated or aspirated pits (Mark and Crews, 1973; Nobuchi and Harada, 1983). The rates of change with xylem age are species- and property-specific.

Another potential difference is moisture content. There are many individual reports of moisture content variation across the radius. For example, ring-porous species are reported to have saturated earlywood vessels only in the outer growth ring, with the earlywood being embolized in older rings (Cochard and Tyree, 1990; Ellmore and Ewers, 1985; Granier *et al.*, 1994). However, the most comprehensive compendium is for the trees of Bulgaria: Nikolov and Enchev (1967) reported moisture content every centimeter across the north-south transect of the stem xylem for 12 coniferous species and 33 hardwood species. About half of the coniferous species had very constant moisture content across the sapwood, with an abrupt decrease in the heartwood (e.g., *Abies alba*, *Pinus nigricans*, and some individuals of *Pinus sylvestris*). The other coniferous species had a decline in moisture content, often close to linear, from the outer to the inner sapwood (e.g., *Juniperus excelsa*, *Taxus baccata*, *Pseudotsuga menziesii*, *Larix europaea*, and *Pinus strobus*). It was more difficult to discern the sapwood moisture content patterns in the hardwoods because it is not always clear where the sap/heart boundary is from inspection of the moisture contents. Roughly half of the species had relatively constant moisture contents across

what appeared to be the sapwood (e.g., *Quercus*, *Fraxinus*, *Celtis*, *Aesculus*). The remaining hardwoods had a variety of moisture content patterns in the sapwood, such as a gradual (*Fagus sylvatica*, *Populus*, *Alnus glabrosa*) or steep (*Robinia pseudoacacia*) decrease, or a gradual (*Ailanthus*) or steep (*Gleditsia*) increase from the outer sapwood inward. These patterns do not follow differences in ring porosity versus diffuse porosity. Using both soft x-ray and cryoscanning electron microscopy, Utsumi *et al.* (2003) have shown in several conifer species (*Picea jezoensis*, *Larix kaempferi*, and *Abies sachalinensis*) that the outer ring has higher moisture content than do the inner growth rings. Similarly, Lu *et al.* (2000) showed that the outer growth ring in the angiosperm *Mangifera indica* had higher moisture content than did the other growth rings.

#### Effects of Wood Anatomy and Characteristics on Specific Conductivity

Specific conductivity ( $k_s$ ) is usually higher in the outer than the inner sapwood. As discussed here,  $k_s$  refers to the water volume per time that will pass a unit cross-sectional area of sapwood with a given pressure gradient across it. The higher  $k_s$  in outer than inner sapwood can be caused by differences in wood structure associated with a decline in radial growth rate or JW/MW changes, and/or from blockages that accumulate in the inner sapwood as it ages. The total sap flow depends on both  $k_s$  and sapwood width (see next section).

In MW, the effect of radial growth rate on  $k_s$  depends on its effect on latewood proportion. The changes in wood structure that result from the typical decrease in radial growth rate with age may be confounded with the changes occurring in the JW zone. In a study of *Pseudotsuga menziesii*,  $k_s$  was positively correlated with height growth, but there was no correlation with diameter growth (Domec and Gartner, 2003).

In diffuse-porous hardwoods, MW should have higher  $k_s$  than JW because of the gradual increase in earlywood vessel diameter (Zimmermann, 1978) and the direct relationship between flow and radius to the fourth power. In ring-porous hardwoods, increases in  $k_s$  toward the bark are caused by two factors: the increase in earlywood vessel diameter and in the decrease in latewood proportion. In hardwoods, the longer cells in MW than JW should have only a negligible effect on  $k_s$  because water moves primarily through the perforations at the ends of vessels (rather than pits), and the perforations contribute less to flow resistance than do pits. In gymnosperms, MW is expected to have higher  $k_s$  than JW both because the tracheids are wider and because they are longer. These factors more than compensate for MW's lower earlywood proportion (Mencuccini *et al.*, 1997). Tracheid length is important if a large part of the hydraulic resistance is associated with pit membranes (Petty and Puritch, 1970; Pothier *et al.*, 1989). Water must traverse twice as many pit membranes per meter of stem if the tracheids are half the length.

Because there are no development-caused differences in the anatomy of wood produced from year to year within the MW, outer sapwood should not vary in  $k_s$  from year to year. However, there is usually a decline in  $k_s$  from outer to inner sapwood, in spite of the lack of changes in the cellular structure. This decrease has been observed in conifers (e.g., Booker and Kininmonth, 1978; Comstock, 1965; Domec and Gartner, 2001, 2002a; Markstrom and Hann, 1972; Spicer and Gartner, 2001) and ring-porous species (Ellmore and Ewers, 1985; see Granier *et al.*, 1994). We do not know of research on diffuse-porous species. One study showed that the pits were "immature and nearly imperforate" in the outer sapwood (Mark and Crews, 1973), from which one would predict lower  $k_s$  in the outer sapwood, with an increase inward. To our knowledge, no other research followed up the study by Mark and Crews.

The most likely cause for these declines is a higher incidence of blockages in the inner sapwood. These blockages could be in the form of air (emboli) and/or gums, resins, etc. (extractives). Indirect evidence that inner sapwood may have more embolisms than outer sapwood is found in the studies that show lower moisture content in inner than outer sapwood (above). Decrease in relative water content is associated with a decrease in  $k_s$  (Edwards and Jarvis, 1982; Puritch, 1971) and sap flow (Granier *et al.*, 2000). Because extractive content influences heartwood durability, nearly all research on extractives has focused on heartwood rather than sapwood. One article on pit membranes, however, reported an increase in membrane incrustation from outer to inner sapwood (Mark and Crews, 1973).

### Patterns of Sapwood Width

Generally, in both conifers and hardwoods, sapwood width is positively correlated with tree health, vigor, crown class, or radial growth rate (Brix and Mitchell, 1983; de Kort, 1993; Hillis, 1987; Lassen and Okkonen, 1969; Sellin, 1996; Smith *et al.*, 1966). The tree's design criteria for sapwood quantity are unclear because although the pipe model and its modifications often explain sapwood quantity (Margolis *et al.*, 1995; Whitehead *et al.*, 1984), in many cases they do not (e.g., Gartner, 2002). The relationships are stronger between growth rate and sapwood width than between growth rate and number of rings in sapwood. That is, the amount of wood needed for physiological processes is independent of how that wood was developed.

There is little research on the width of sapwood in relation to stem age. In some species, sapwood width of individuals within similar environments is very constant. Examples are the genus *Eucalyptus* (Hillis, 1987) and the species *Pseudotsuga menziesii* (Brix and Mitchell, 1983), although it should be noted that in *P. menziesii*, the sapwood is wider in the bottom meter (Gartner, 2002), and that when the trees are several hundred years old, the sapwood width diminishes (BLG, personal observation). In contrast, in

some species, sapwood width increases with tree age. For example, in *Picea*, the sapwood width increases until the cambium attains an age of between 20 and 90 years, depending on species and dominance class of the trees (Hazenbergh and Yang, 1991; Sellin, 1996).

## How Species-Specific Characteristics of Sapwood Affect Whole-Tree Water Transport

Many of the radial and developmental changes in sapwood anatomy, structure, and hydraulic properties described in the previous section are largely species-specific and are expected to have an impact on spatial patterns of water movement within the sapwood. For example, radial profiles of axial flow may be associated with species-specific differences in hydraulic architecture that determine the nature of hydraulic connections between leaves and different layers of sapwood. Here we discuss how species-specific variation in fundamental traits such as hydraulic architecture and sapwood quantity, water storage capacity, and density influence water transport within the tree.

### Sapwood Quantity

It is common knowledge that the sapwood cross-sectional area for a given stem diameter varies widely among tree species. For individuals with stem diameters from 0.5 to 1.0 m, radial sapwood depth can range from less than 6 cm in species such as *Eucalyptus regnans* (Wullschlegel *et al.*, 1998) and *Pseudotsuga menziesii* (Phillips *et al.*, 2002), to 10 to 20 cm in *Pinus ponderosa* (Domec and Gartner, 2003), and greater than 20 cm in a number of tropical species (James *et al.*, 2003; Meinzer *et al.*, 2001). Despite its implications for rates of whole-tree water use and sap flow per unit sapwood area (sap flux density), the consequences of this wide variation in sapwood area among trees of similar size remain largely unexplored. However, improvements in techniques for measuring sap flow have facilitated determination of the detailed radial profiles of axial flow necessary to analyze how different relationships between sapwood area and tree size among species influence water transport at different scales (e.g., James *et al.*, 2002; Jiménez *et al.*, 2000).

Plant vascular systems, and therefore water use, have been proposed to scale allometrically as power functions of body mass or size (West *et al.*, 1999):

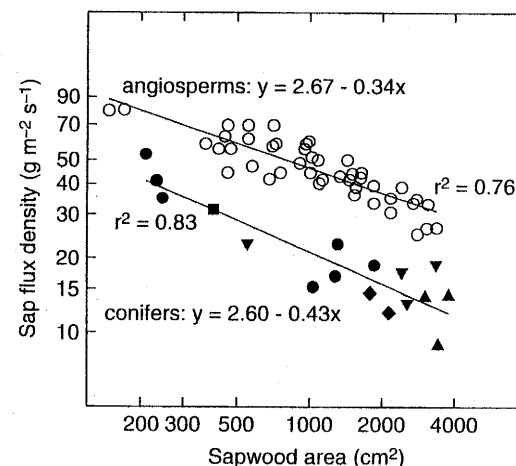
$$Y = Y_0 M^b \quad (1)$$

where  $M$  is mass,  $b$  is a power exponent, and  $Y_0$  is a normalization constant. Although exhaustive tests of the universality of this model have yet to be conducted, it is supported by some empirical data on plant water

utilization (Enquist *et al.*, 1998; Meinzer *et al.*, 2001). If the model proves to be generally valid, it would greatly simplify prediction of water utilization over a large range of tree size, and in stands comprising multiple species. Given the large range of sapwood area among trees of similar size, however, it seems clear that multiple allometric functions, rather than a single universal function, are required for predicting hydroactive xylem area as a function of tree size. Nevertheless, differing amounts of sapwood in individuals of similar size do not necessarily preclude similar rates of whole-tree water use as explained later.

Whole-tree water use can be estimated by multiplying the mass flow of sap per unit sapwood area, or sap flux density, by the cross-sectional area of sapwood at the point where flow is measured. Thus, if the allometric scaling model presented previously is valid despite large differences in sapwood area for trees of the same size, it can be hypothesized that a universal proportionality constant describes the relationship between sap flux density and sapwood area. That is, for a given sapwood cross-sectional area, sap flux density would be identical across species regardless of tree diameter. Figure 15.1 shows the relationship between maximum sap flux density in the outer 2 cm of sapwood and sapwood area for five temperate coniferous species and 24 largely tropical angiosperm species. In both groups, sap flux density initially declines steeply, then more gradually with increasing sapwood area. When the relationships are linearized, it is clear that a single function adequately describes the relationship between sap flux density and sapwood area within each group. Sap flux density was consistently greater in the angiosperms than in the gymnosperms. Whether these differences would be maintained when whole-tree water use is estimated from the product of sap flux density and sapwood area depends on the profile of axial flow over the remaining depth of the sapwood. If the differences persist at the whole-tree level, then a single allometric equation cannot be used to scale water use in both angiosperms and gymnosperms. Initial determinations of radial profiles of axial flow for some of the species represented in the figure suggest that for a given stem diameter or basal sapwood area, whole-tree water use of conifers may be substantially lower than that of angiosperms (James *et al.*, 2003; Meinzer, unpublished observations).

It is tempting to infer that the overall greater sap flux density in angiosperms than conifers (Fig. 15.1) is associated with the presence of vessels in the former versus tracheids in the latter. This is probably an oversimplification because sap flux density is not governed by the hydraulic properties of the xylem elements alone. For instance, both the whole-tree leaf area to sapwood area ratio ( $A_L:A_s$ ) and the ratio of xylem element lumen area to sapwood area are expected to influence sap flux density. The decline in sap flux density with increasing sapwood area observed in both angiosperms and conifers appears to be consistent with reports that  $A_L:A_s$

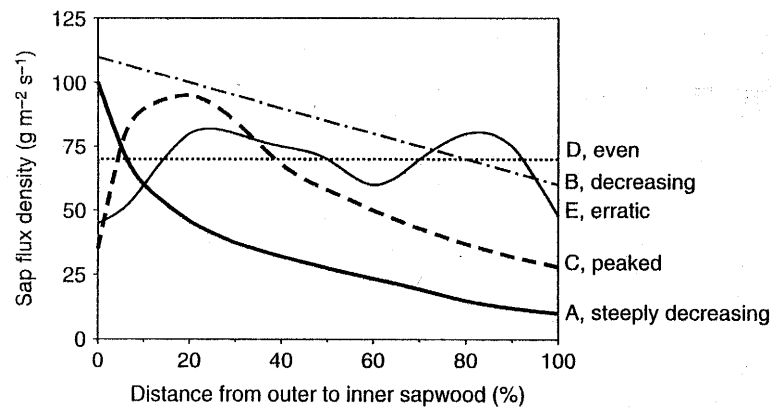


**Figure 15.1** Maximum sap flux density measured with the heat dissipation method (Granier, 1987) in the outermost 2 cm of sapwood in relation to total sapwood area for individuals of five temperate coniferous species (filled symbols) and 24 angiosperm species (open symbols). Coniferous species: (▲) *Pinus ponderosa*, (●) *Pseudotsuga menziesii*, (◆) *Thuja plicata*, and (▼) *Tsuga heterophylla* (unpublished data of Meinzer); (■) *Pinus sylvestris* (Nadezhdina *et al.*, 2002). The angiosperm species are a subset of those listed in Table 1 of Meinzer (2003).

typically decreases with increasing tree height (McDowell *et al.*, 2002). It should be noted, however, that sapwood area is not necessarily a reliable surrogate for tree height because of the species-specific differences in the relationship between sapwood area and tree size described previously. It is interesting that despite the large differences in sap flux density between angiosperms and gymnosperms over the range of sapwood area shown in Fig. 15.1, the Y-intercepts of the two regressions at zero sapwood area are similar. The differences in sap flux density are thus chiefly a consequence of the steeper negative slope for gymnosperms. If the relationships in Fig. 15.1 are governed by  $A_L:A_s$ , then it could be hypothesized that  $A_L:A_s$  may decline more steeply with increasing tree size in gymnosperms than in angiosperms. If this proves to be true, it may indicate that greater hydraulic constraints associated with tracheids than vessels require larger developmental adjustments in hydraulic architecture (e.g.,  $A_L:A_s$ ) in gymnosperms in order to maintain sufficiency of water transport to leaves (Becker *et al.*, 1999).

#### Radial Profiles of Axial Sap Flow

Numerous studies have reported a range of radial profiles of axial sap flow, but the causes of these patterns are not entirely known. The main sap flow patterns from the outer sapwood inward are even, decreasing, sharply decreasing, peaked (Phillips *et al.*, 1996), and erratic (Fig. 15.2). Even flow



**Figure 15.2** Schematic diagram of the radial patterns of axial sapflow: (A) steeply decreasing, (B) decreasing, (C) peaked, (D) even, (E) erratic. Bottom axis is the proportional distance across the sapwood, with the cambium on the far left and the sapwood/heartwood interface on the far right.

denotes similar sap flow at all measured radial depths in the sapwood. The decreasing and sharply decreasing patterns denote a gradual and more abrupt decline, respectively, from the values in the outer sapwood to those near the sap/heart border. The peaked pattern (called Gaussian by Phillips *et al.*, 1996) shows highest sap flow at some distance interior to the outer sapwood, usually within 1 to 3 cm of the cambium. Lastly, the random flow pattern shows values that go up and down across the radius in a nonsystematic manner.

To interpret radial variation in axial sap flow, more studies are needed of petiole connections to the stem xylem (Tison, 1902; Elliott, 1937; Maton and Gartner, 2005), the pathways for radial water movement in the stem xylem, and sapwood width. Water is withdrawn only from the points at which the leaf petioles attach to the xylem. In trees with leaves that survive one year or less, all the water is withdrawn through the outer ring of the sapwood. If the stem xylem has high radial resistance to water flow, then these trees should have most of the flow in the outer sapwood with a very steep decline (pattern A, Fig. 15.2). Such a pattern of sharply decreasing flow has been reported for the ring-porous deciduous trees *Quercus robur* (Granier *et al.*, 1994) and *Q. velutina* (Miller *et al.*, 1980), as well as the diffuse-porous deciduous species *Salix fragilis* (Cermak *et al.*, 1984). One might expect decreasing axial sap flow from bark inward (pattern B, Fig. 15.2) in two circumstances: trees with only current year leaves and moderate resistance to radial flow, or trees with leaves that persist for a number of years, with either moderate or strong radial resistance. This pattern of decreasing flow is commonly reported for angiosperms: the diffuse-porous deciduous

species *Cordia alliodora* (James *et al.*, 2002), *Liriodendron tulipifera* (Wulfschleger and King, 2000), the diffuse-porous evergreen species *Citrus sinensis* (Cohen *et al.*, 1981), and several species of *Populus* (Edwards and Booker, 1984) and some individuals of the *Quercus* species mentioned previously. This pattern has also been reported in two conifer species: *Pinus taeda* (Phillips *et al.*, 1996) and *Pseudotsuga menziesii* (two of the four individuals, Cohen *et al.*, 1984). Most conifers exhibit peaked flow (below), and it is possible that these conifer individuals have peaked flow but that the sensors missed the peak.

Peaked flow (pattern C, Fig. 15.2) is an interesting case because there are few mechanistic hypotheses to explain its occurrence. In conifers, peaked flow has been reported for *Picea exelsa* (Cermak *et al.*, 1992), *Picea abies* (Cermak *et al.*, 1992), *Picea engelmannii* (Mark and Crews, 1973; Swanson, 1971), a few individuals of *Pseudotsuga menziesii* (Cohen *et al.*, 1984), *Pinus contorta* (Mark and Crews, 1973), and *Pinus sylvestris* (Nadezhkina *et al.*, 2002; Waring and Roberts, 1979). In angiosperms it has been reported for the deciduous species *Prunus serotina* and *Populus canescens* (Nadezhkina *et al.*, 2002) and for the evergreen species *Rhododendron ponticum* (Nadezhkina *et al.*, 2002), *Mangifera indica* (Lu *et al.*, 2000), *Ficus insipida* (James *et al.*, 2002), and *Laurus azorica*, *Persea indica*, *Ilex perado*, *Myrica faya*, and *Erica arborea* (Jiménez *et al.*, 2000). To our knowledge, none of these angiosperms are ring-porous.

Could peaked flow be caused by deeply inserted leaves that had high transpiration rates? Probably not. Deep leaf insertion can never explain peaked flow in deciduous species. In species with long-lived leaves, leaves would probably not stay attached long enough to explain the flow: If one assumes that the peak flow is 1.5 cm from the cambium and that radial growth is 0.3 cm/year, then the foliage attached to the peak radial position would be 5 years old. It is highly unlikely that the cohort of 5-year old foliage would cause the highest flux. Possible explanations are structural, but the only structure that appears able to increase, rather than decrease conductivity once the cells are produced, is the pit membranes. Mark and Crews (1973) reported that the pit membranes were not yet open in the growth rings near the cambium in *Picea engelmannii*, and that their amount of openness correlated with the flow they observed. This observation leads to the hypothesis that the pit membrane pores need to become enlarged beyond the cambial zone, perhaps by erosion during transpiration. Yet another possible explanation is that there are more air blockages in the outer sapwood than in the location where the flow peaks, but this explanation is not consistent with reports that moisture content appears highest in the outer sapwood. In the case of *Mangifera*, the researchers reported that the peaked flow could not be accounted for by the radial patterns of wood density and relative water content (Lu *et al.*, 2000). Jiménez *et al.*

(2002) found that individuals with sparser crowns had wider radial peaks of flow, and that individuals with more dense crowns had more compact flow. More attention is needed to explain the cause of peaked flow.

Even flow (pattern D, Fig. 15.2) could be expected in trees with any pattern of leaf longevity, as long as the wood has low radial resistance. It is logical to suggest that such low radial resistance would be adaptive in species that have wide sapwood. This pattern can also be incorrectly inferred from having sap flow gauges that miss the peaks in patterns A, B, or C. It has been reported in a miscellany of species and circumstances: the diffuse-porous brevideciduous *Anacardium excelsum* (James *et al.*, 2002), the diffuse-porous deciduous species *Liquidambar styraciflua* (Phillips *et al.*, 1996), and two *Populus* species (Edwards and Booker, 1984). Additionally, it was reported for the suppressed individuals of the diffuse-porous evergreen species *Laurus azorica* and *Ilex perado* (Jiménez *et al.*, 2000), and the ring-porous deciduous species *Quercus alba*, but the researchers surmised that they missed the high flow in the outer earlywood (Phillips *et al.*, 1996).

The last pattern, erratic flow (pattern E, Fig. 15.2), could result if the wood had uneven patterns within the stem that gave zones of high sap flow and low sap flow, and then the sensors were placed in these zones, rather than integrating over more "average" wood. Such wood could develop in a ring-porous species that had slow growth rate in one location (thus high earlywood percentage) and fast growth rate in another area (thus low earlywood percentage), or in a tropical species that had broad bands of different tissues. In *Schefflera morototoni*, the erratic flow followed closely the radial pattern of lumen area (James *et al.*, 2002). In *Populus canescens* (Nadezhdina *et al.*, 2002) and in *Eucalyptus globulus* (Zang *et al.*, 1996), the researchers surmised they had measured earlywood in some spots and latewood in others.

### Sapwood Water Storage

Water stored in stems has long been recognized as an important factor in plant-water relations. In large trees, seasonal courses of capacitive discharge and recharge of water stored in sapwood have been measured and modeled (Waring and Running, 1978; Waring *et al.*, 1979). On a shorter timescale, relatively little information exists on the contribution of sapwood water storage to daily water consumption. The dynamics of discharge and recharge of water storage compartments in trees can be characterized using the lag between changes in sap flow in the upper crown (a surrogate for transpiration) and sap flow near the base of the tree (Goldstein *et al.*, 1998; Phillips *et al.*, 1997). Estimates of the contribution of stored water to daily transpiration vary widely, ranging from 10% to 20% (Goldstein *et al.*, 1998; Kobayashi and Tanaka, 2001; Lostau *et al.*, 1996) to as much as 30% to 50% (Holbrook and Sinclair, 1992; Waring *et al.*, 1979). On the other hand, it was suggested that little stored water was withdrawn from the trunk

of a *Larix decidua* tree, whereas water stored in branches accounted for 24% of the total daily transpiration (Schulze *et al.*, 1985).

Water released from both elastic compartments, such as parenchymatous tissue, and inelastic compartments, such as apoplastic capillary spaces and vessel and tracheid lumens during cavitation, can contribute to sapwood capacitance (Holbrook, 1995). Water withdrawn from living cells in stems of *Thuja occidentalis* was estimated to contribute about 6% to the total daily transpirational loss (Tyree and Yang, 1990). It has been proposed that daily cycles of cavitation and embolism followed by refilling of xylem elements may have a positive influence on leaf water balance by transiently releasing stored water into the transpiration stream (Lo Gullo and Salleo, 1992). Mounting evidence that embolism repair can occur over very short timescales, even when the surrounding intact xylem is still under tension (see Chapter 18), suggests that lumens of xylem elements constitute a dynamic and reusable water storage compartment.

Capacitance has been formally incorporated into Ohm's law analog models of water transport along the soil/plant/atmosphere continuum (e.g., Cowan, 1972; Phillips *et al.*, 1997). It is typically defined as the ratio of change in water content to change in water potential of a tissue. This relationship specifies the absolute volume of water that can be exchanged with storage tissues over the normal operating range of water potential for those tissues in a given species. Estimates of capacitance obtained from *in situ* measurements on intact trees vary from approximately 0.4 to 2 kg MPa<sup>-1</sup> for a number of coniferous and angiosperm species (Kobayashi and Tanaka, 2001; Milne, 1989; Tazikawa *et al.*, 1996; Tyree, 1988; Wronski *et al.*, 1985). It is unclear, however, whether this range of values largely reflects intrinsic, species-specific differences in the biophysical properties of the storage tissues involved, or merely differences in the size of the storage compartment, because none of the estimates was normalized for differences in tree size or the total volume of storage tissue. Species-specific values of sapwood capacitance normalized on a sapwood volume basis ranged from 83 to 416 kg m<sup>-3</sup> MPa<sup>-1</sup> among four co-occurring tropical forest tree species (Meinzer *et al.*, 2003), confirming that intrinsic differences in sapwood water storage capacity can be profound over the normal physiological operating range of stem water potential.

Despite the central role of sapwood water storage in whole-plant water relations, specific relationships between short-term cycles of capacitive discharge and recharge and the daily dynamics of stomatal behavior, transpiration, and plant water balance have not been studied until relatively recently. Capacitive exchange of water between storage compartments and the transpiration stream leads to daily fluctuations in apparent soil-to-leaf hydraulic conductance, provoking dynamic stomatal responses that maintain the balance between transpiration and hydraulic conductance, thereby

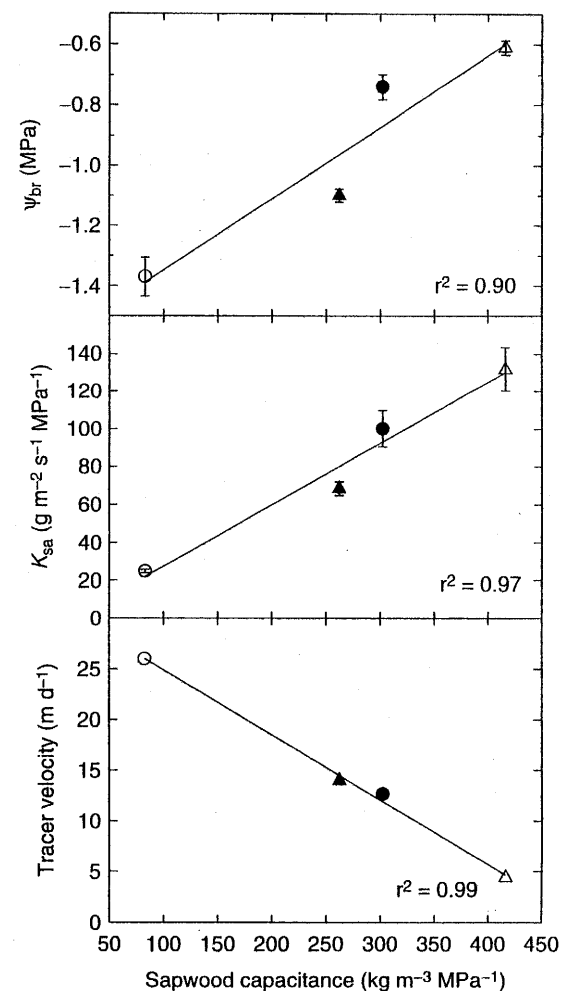
limiting daily fluctuations in leaf water potential (Andrade *et al.*, 1998; Meinzer, 2002). Consistent with this, Williams *et al.* (1996) attributed the afternoon decline in  $\text{CO}_2$  uptake in a mixed *Quercus-Acer* stand to partial stomatal closure in response to depletion of stored water, and Goldstein *et al.* (1998) reported that tropical forest trees with greater water storage capacity maintained maximum rates of transpiration for a substantially longer fraction of the day than trees with smaller water storage capacity.

In a recent study, it was shown that a suite of whole-tree water transport characteristics scaled with species-specific variation in sapwood capacitance (Fig. 15.3). Daily minimum branch water potential and soil-to-branch hydraulic conductance increased linearly with sapwood capacitance. In addition, maximum sap velocity, as estimated from the transit time of deuterated water injected as a tracer, decreased linearly with increasing capacitance. Although strong linear relationships between sapwood capacitance and features such as branch water status, whole-tree hydraulic conductance, and sap velocity do not necessarily imply direct mechanistic linkages, it was notable that based on the four species studied, the scaling of these features with capacitance appeared to be species-independent. Comparative studies of whole-plant water transport would therefore benefit from consideration of the constraints that sapwood biophysical features, such as capacitance, place on physiological functioning.

### Sapwood Density

Wood density ranges from  $<0.2 \text{ g cm}^{-3}$  in species such as *Ochroma pyramidale* (balsa) to  $>1.0 \text{ g cm}^{-3}$  in species such as *Diospyros ebenum* (ebony), and is an important determinant of xylem water transport and storage properties and whole-plant water relations. For example, the xylem tension threshold for 50% loss of specific conductivity by cavitation showed a strong positive correlation with wood density among several species spanning a relatively broad range of wood density (Hacke *et al.*, 2001). Although the relationships were distinct for angiosperms and gymnosperms, there was a common relationship between increasing wood density and increasing resistance to cavitation within each group. Wood density may also prove to be an essential normalizing variable for allometric scaling models that predict growth as a function of tree size. Growth rates of 45 co-occurring tropical tree species scaled with the  $3/4$  power of mass, but species-specific relationships with identical slopes and different intercepts did not collapse onto a common line until changes in diameter were normalized by the corresponding values of wood density (Enquist *et al.*, 1999). In view of the well-established positive correlation between biomass production and transpiration, these results imply an interaction between water transport and wood density.

Roderick and Berry (2001) developed a model to estimate how wood structure and density should affect water transport. One modeling result



**Figure 15.3** Daily minimum water potential of terminal branches ( $\Psi_{br}$ ), soil to terminal branch hydraulic conductance per unit basal sapwood area ( $K_{sa}$ ), and axial transport rate of a deuterated water tracer signal in relation to sapwood capacitance for four co-occurring tropical forest tree species (○) *Cordia alliodora*, (▲) *Ficus insipida*, (●) *Anacardium excelsum*, and (△) *Schefflera morototoni* (after Meinzer *et al.*, 2003).

was that in softwoods, wood density should be negatively correlated with temperature during the growing season, because if the temperature is lower, then the water is more viscous and a lower density wood is needed to maintain the same flux. This pattern is apparent in many conifers, which have lower wood density at higher elevation or higher latitude. The model further predicted that there would be no such correlation in hardwoods

because another term, related to the variability of conduit diameter, swamps the term in which viscosity was important. Again, this prediction is consistent with observations.

The widely reported negative correlation between sapwood saturated water content and density implies that the intrinsic capacitance of sapwood (see previously) diminishes with increasing density (Meinzer *et al.*, 2003). Low capacitance in species with dense wood could reduce the relative contribution of stored water to their daily water budget. However, compensatory behavior, such as stomatal regulation that allows stem water potential to fall to more negative values in species with denser wood, may stabilize the relative contribution of sapwood water storage to daily transpiration in species comprising a broad range of wood density.

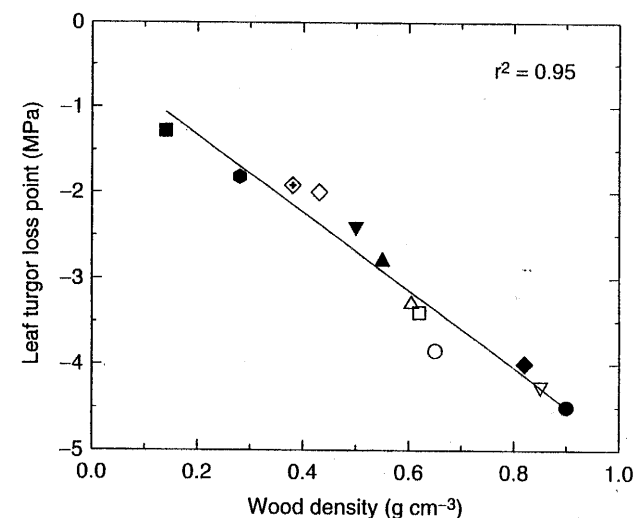
There is some evidence that the gain in cavitation resistance associated with increasing wood density is associated with a cost in terms of reduced sapwood hydraulic conductivity. In six co-occurring Hawaiian dry forest species specific hydraulic conductivity of branches increased fivefold as wood density decreased from 0.65 to 0.5 g cm<sup>-3</sup> (Stratton *et al.*, 2000). Similarly, leaf-specific hydraulic conductivity of upper canopy branches of 20 co-occurring Panamanian forest species showed a sixfold increase as wood density decreased from 0.7 to 0.35 g cm<sup>-3</sup> (Santiago *et al.*, 2004). Although numerous reports of hydraulic properties of woody stems are available, their relationship with wood density is difficult to document because corresponding values of wood density are rarely reported. Sapwood density and hydraulic conductivity averaged over entire stem cross sections may conceal within-ring variation in density and conductivity that may be associated with within-ring partitioning of water conduction and storage functions (Domec and Gartner, 2002b), or water transport and mechanical functions (Mencuccini *et al.*, 1997).

If both hydraulic conductivity and sapwood water storage capacity are negatively correlated with wood density, it is reasonable to expect that species with greater wood density may experience both larger daily fluctuations in leaf water deficits and more extreme seasonal water deficits. Consistent with this, a strong positive correlation ( $R^2 = 0.96$ ) between the magnitude of daily fluctuations in leaf water potential and wood density was noted among 27 diverse species with wood densities ranging from 0.14 to 0.9 g cm<sup>-3</sup> (Meinzer, 2003). The daily fluctuation in leaf water potential increased from c. 0.5 to 2.5 MPa over this range of wood density. The 27 species surveyed occupied habitats ranging from the humid tropics to deserts. The leaf water potential corresponding to turgor loss should be associated with the minimum leaf water potential normally experienced by a species, and therefore should provide an integrated measure of prevailing leaf water deficits. A survey of 12 species for which values of both wood density and leaf turgor loss point determined by the pressure-

volume method were available revealed a strong negative correlation between the turgor loss point and wood density (Fig. 15.4). The turgor loss point declined from c. -1.2 to -4.5 MPa over a range of wood density from 0.16 to 0.90 g cm<sup>-3</sup>. The preceding examples suggest that variation in wood density is a strong predictor of variation in a suite of characteristics related to regulation of leaf water deficits and avoidance of turgor loss, and that this feature constrains physiological options related to plant water economy, leading to functional convergence across a broad range of species.

### Prospects for Further Research

A wealth of detailed information is available on developmental and spatial variation in xylem anatomy and structure in trees. Similarly, advances in techniques for measuring sap flow have contributed to a rapidly expanding literature on spatial and temporal variation in water movement through



**Figure 15.4** Leaf water potential at the point of turgor loss in relation to wood density. (▽) *Acacia greggii* (Nilsen *et al.*, 1984); (◇) *Liriodendron tulipifera* (Roberts *et al.*, 1980); (▼) *Metrosideros polymorpha* (Stratton *et al.*, 2000); (△) *Nesoluma polynesicum* (Stratton *et al.*, 2000); (○) *Nestegis sandwicensis* (Stratton *et al.*, 2000); (◊) *Populus* spp. (Tyree *et al.*, 1978); (□) *Pouteria sandwicensis* (Stratton *et al.*, 2000); (◆) *Prosopis glandulosa* (Nilsen *et al.*, 1981); (■) *Pseudobombax septenatum* (Machado and Tyree, 1994); (●) *Rhizophora mangle* (Melcher *et al.*, 2001); (●) *Schefflera morototoni* (Tyree *et al.*, 1991); (▲) *Schinus terebinthifolius* (Stratton *et al.*, 2000). Values of wood density were obtained from Alden (1995), Meinzer (2003), and Stratton *et al.* (2000).

trees. However, improved mechanistic understanding of relationships between xylem water transport and sapwood biophysical properties is hampered by a scarcity of studies in which water movement and sapwood properties have been measured in the same individuals. Therefore, to establish mechanistic linkages between xylem structure and water transport in intact trees, comprehensive characterizations of water movement, sapwood properties, and hydraulic architecture across a broad range of scale and tree size are required. Moreover, many more species must be examined because it is clear that there is more than one evolutionary solution to the problems of water transport.

To assimilate carbon, trees lose water. The amount they lose and how it travels through the sapwood are apparently quite variable. For a given sap flux, plants can co-vary factors such as sapwood permeability (and the anatomical means by which that is achieved), sapwood area, the depth of water transport within the sapwood, the extent to which stored water is accessed (daily and seasonally), and the timing of water transport (daily and seasonally). Are there suites of characteristics that often co-vary? If so, what are their ecological and anatomical patterns? Waring and Roberts (1979) and Dye *et al.* (1991) speculated that the inner sapwood primarily supplied water to the older branches. Does pruning shift sap flux outward in the sapwood? In some but not all coniferous species, petioles break their vascular connections with the previous year's xylem and make new connections annually (Tison, 1902; Maton and Gartner, 2005). Is this pattern unusual or the norm? Does peaked flow occur because of higher driving force on inner growth rings, or higher ks there? In which ecological settings and with which other characteristics (sapwood depth, permeability, radial and temporal patterns of transport, deciduous/evergreen foliage) is capacitance most pronounced? How do species maintain the moisture content differences across the sapwood, and how do they maintain different moisture contents in the sapwood and the heartwood? An emphasis on the functional tradeoffs among these characteristics may help us see a number of distinct strategies for water transport, which would greatly help our understanding, which is currently on a species- and age-specific basis.

A special case of the previous discussion is why co-occurring tropical trees of a given diameter appear to have the same sapwood depth (Meinzer *et al.*, 2001), but temperate ones vary from one extreme to the other. Likewise, more research is clearly needed on understanding sap flux in species without annual growth rings. Because of the clear role in water transport, much of the emphasis in ecological wood anatomy has been in vessel and tracheid characteristics. However, there is a myriad of patterns of xylem parenchyma, especially in tropical hardwoods, which merit a functional understanding. For example, the longitudinal parenchyma can be

dispersed or aggregated. If it is aggregated, it can be near the vessels or apparently distanced from them ("apparently" because although it appears distanced in a cross section, the three-dimensional configuration of parenchyma, including the rays, has not been characterized). It can form tangential or radial bands, or a combination. The radially oriented parenchyma (in the rays) can be abundant or rare, and the cells can be aggregated into very wide multiseriate rays, or uniseriate rays (either of which can be tall or short). Within the rays, there can be procumbent cells and upright ones, and there can be rays within the same individual that are made up of different combinations of these geometric types. What are the roles of these different parenchyma cells and patterns? In what ecological settings are they found, and what is their role in water storage/release and water transport?

Another area that raises many questions is the striking relationship of wood density to the vulnerability of wood to embolism (Hacke *et al.*, 2001). On what structural features do these relationships depend? Given that wood density and the anatomy of the transport cells can vary independently of one another, it would not appear that there should be a relationship. For example, the density of hardwoods can vary simply by having an increase in libriform fiber cells and a decrease in parenchyma cells, with no effect on vessels. This line of research is an excellent example of recent progress in synthesizing data from diverse species and wood strategies. It shows, for example, that many hardwoods fall on one line, and that softwoods fall on another. It is also an example of a line of research that opens many questions about why the observed patterns are there. Many questions remain about structural causes of water transport and the strategies that are used in different ecological settings. These areas will continue to benefit from both the detailed species- and age-level research, and from the multispecies syntheses.

### Acknowledgments

Some of the data presented were obtained with support from National Science Foundation grant IBN 99-05012 to FCM, and with support from the Wind River Canopy Crane Research Facility located within the Wind River Experimental Forest, T. T. Munger Research Natural Area. The facility is a cooperative venture among the University of Washington, the USDA Forest Service Pacific Northwest Research Station and Gifford Pinchot National Forest. BLG wishes to acknowledge the special USDA grant to Oregon State University for wood utilization research.

## References

- Alden, H. A. (1995) *Hardwoods of North America. General Technical Report FPL GTR-83*. USDA Forest Service Forest Products Laboratory, Madison, WI.
- Andrade J. L., Meinzer F. C., Goldstein G., Holbrook N. M., Cavelier J., Jackson P. and Silveira K. (1998) Regulation of water flux through trunks, branches and leaves in trees of a low-land tropical forest. *Oecologia* **115**: 463-471.
- Becker, P., Tyree, M. T. and Tsuda, M. (1999) Hydraulic conductances of angiosperms versus conifers: Similar transport sufficiency at the whole-plant level. *Tree Physiol* **19**: 445-452.
- Booker, R. E. and Kinimonth, J. A. (1978) Variation in longitudinal permeability of green radiata pine wood. *N Z J For Sci* **8**: 295-308.
- Brix, H. and Mitchell, A. K. (1983) Thinning and nitrogen fertilization effects on sapwood development and relationships of foliage quantity to sapwood area and basal area in Douglas-fir. *Can J For Res* **13**: 384-389.
- Cermak, J., Cienciala, E., Kucera, J. and Hallgren, J.-E. (1992) Radial velocity profiles of water flow in trunks of Norway spruce and oak and the response of spruce to severing. *Tree Physiol* **10**: 367-380.
- Cermak, J., Jenik, J., Kucera, J. and Zidek, V. (1984) Xylem water flow in a crack willow tree (*Salix fragilis* L.) in relation to diurnal changes of environment. *Oecologia* **64**: 145-151.
- Cherubini, P., Fontana, G., Rigling, D., Dobberty, M., Brang, P. and Innes, J. L. (2002) Tree-life history prior to death: Two fungal root pathogens affect tree-ring growth differently. *J Ecol* **90**: 839-850.
- Cochard, H. and Tyree, M. T. (1990) Xylem dysfunction in *Quercus*: Vessel sizes, tyloses, cavitation and seasonal changes in embolism. *Tree Physiol* **6**: 393-407.
- Cohen, Y., Fuchs, M. and Green, G. C. (1981) Improvement of the heat pulse technique method for determining sap flow in trees. *Plant Cell Environ* **4**: 391-397.
- Cohen, Y., Kellhier, F. M. and Black, T. A. (1984) Determination of sap flow in Douglas-fir trees using the heat pulse technique. *Can J For Res* **15**: 422-428.
- Comstock, G. L. (1965) Longitudinal permeability of green eastern hemlock. *Forest Prod J* **15**: 441-449.
- Cowan, I. R. (1972) An electrical analogue of evaporation from, and flow of water in plants. *Planta* **106**: 221-226.
- de Kort, I. (1993) Relationships between sapwood amount, latewood percentage, moisture content and crown vitality of Douglas fir, *Pseudotsuga menziesii*. *IAWA J* **14**: 413-427.
- Domec, J. C. and Gartner, B. L. (2001) Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. *Trees* **15**: 204-214.
- Domec, J. C. and Gartner, B. L. (2002a) Age- and position-related changes in hydraulic versus mechanical dysfunction of xylem: Inferring the design criteria for Douglas-fir wood structure. *Tree Physiol* **22**: 91-104.
- Domec, J. C. and Gartner, B. L. (2002b) How do water transport and water storage differ in coniferous earlywood and latewood? *J Exp Bot* **53**: 2369-2379.
- Domec, J.-C. and Gartner, B. L. (2003) Relationship between growth rates and xylem hydraulic characteristics in young, mature, and old-growth ponderosa pine trees. *Plant Cell Environ* **26**: 471-483.
- Duff, G. H. and Nolan, N. J. (1953) Growth and morphogenesis in the Canadian forest species I. The controls of cambial and apical activity in *Pinus resinosa*. *Can J Bot* **31**: 471-513.
- Dye, P. J., Olbrich, B. W. and Poulter, A. G. (1991) The effect of growth rings in *Pinus patula* on heat pulse velocities and sap flow measurement. *J Exp Bot* **42**: 867-870.
- Edwards, W. R. N. and Booker, R. E. (1984) Radial variation in the axial conductivity of *Populus* and its significance in heat pulse velocity measurement. *J Exp Bot* **35**: 551-561.
- Edwards, W. R. N. and Jarvis, P. G. (1982) Relations between water content, potential and permeability in stems of conifers. *Plant Cell Environ* **5**: 271-277.
- Elliott, J. H. (1937) The development of the vascular system in evergreen leaves more than one year old. *Ann Bot N S* **1**: 107-127.
- Ellmore, G. S. and Ewers, F. W. (1985) Hydraulic conductivity in trunk xylem of elm, *Ulmus americana*. *IAWA Bull N. S.* **6**: 303-307.
- Enquist, B. J., Brown, J. H. and West G. B. (1998) Allometric scaling of plant energetics and population density. *Nature* **395**: 163-165.
- Enquist B. J., West, G. B., Charnov, E. L. and Brown, J. H. (1999) Allometric scaling of production and life-history variation in vascular plants. *Nature* **401**: 907-911.
- Gartner, B. L. (2002) Sapwood and inner bark quantities in relation to leaf area and wood density in Douglas-fir. *IAWA J* **23**: 267-285.
- Gartner, B. L., Baker, D. C. and Spicer, R. (2000) Distribution and vitality of xylem rays in relation to tree leaf area in Douglas-fir. *IAWA J* **21**: 389-401.
- Gartner, B. L., Lei, H. and Milota, M. R. (1997) Variation in the anatomy and specific gravity of wood within and between trees of red alder (*Alnus rubra* Bong.). *Wood Fiber Sci* **29**: 10-20.
- Goldstein, G., Andrade, J. L., Meinzer, F. C., Holbrook, N. M., Cavelier, J., Jackson, P. and Celis, A. (1998) Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant Cell Environ* **21**: 397-406.
- Granier, A. (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiol* **3**: 309-320.
- Granier, A., Anfodillo, T., Sabatti, M., Cochard, H., Dreyer, E., Tomasi, M., Valentini, R. and Bréda, N. (1994) Axial and radial water flow in the trunks of oak trees: A quantitative and qualitative analysis. *Tree Physiol* **14**: 1383-1396.
- Granier, A., Biron, P. and D. Lemoine (2000) Water balance, transpiration and canopy conductance in two beech stands. *Agr For Met* **100**: 291-308.
- Hacke, U. G., Sperry, J. S., Pockman, W. T., Davis, S. D. and McCulloh, K. A. (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* **126**: 457-461.
- Harrington, C. A. and DeBell, D. S. (1980) Variation in specific gravity of red alder (*Alnus rubra* Bong.). *Can J For Res* **10**: 293-299.
- Hazenbergh, G. and Yang, K. C. (1991) The relationship of tree age with sapwood and heartwood width in black spruce, *Picea mariana* (Mill.) B. S. P. *Holzforchung* **45**: 317-320.
- Hillis, W. E. (1987). *Heartwood and Tree Exudates*. Springer-Verlag, Berlin.
- Holbrook, N. M. (1995) Stem water storage. In *Plant Stems: Physiology and Functional Morphology* (B.L. Gartner, ed.) pp. 151-174. Academic Press, San Diego.
- Holbrook, N. M. and Sinclair, T. R. (1992) Water balance in the arborescent palm, *Sabal palmetto*. II. Transpiration and stem water storage. *Plant Cell Environ* **15**: 401-409.
- James, S. A., Clearwater, M. J., Meinzer, F. C. and Goldstein, G. (2002) Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. *Tree Physiol* **22**: 277-283.
- James, S. A., Meinzer, F. C., Goldstein, G., Woodruff, D., Jones, T., Restom, T., Mejia, M., Clearwater, M. and Campanello, P. (2003) Axial and radial water transport and internal water storage in tropical forest canopy trees. *Oecologia* **134**: 37-45.
- Jiménez, M. S., Nadezhkina, N., Cermák, J. and Morales, D. (2000) Radial variation in sap flow in five laurel forest tree species in Tenerife, Canary Islands. *Tree Physiol* **20**: 1149-1156.
- Kobayashi, Y. and Tanaka, T. (2001) Water flow and hydraulic characteristics of Japanese red pine and oak trees. *Hydrol Proc* **15**: 1731-1750.
- Larson, P. R., Kretschmann, D. E., Clark, A. I. and Isebrands, J. D. (2001) Formation and properties of juvenile wood in southern pines: A synopsis. FPL-GTR-129. USDA Forest Service, Forest Products Laboratory, Madison, WI.

- Lassen, L. E. and Okkonen, E. A. (1969) Sapwood thickness of Douglas-fir and five other western softwoods. USDA Forest Service Research Paper, FPL 124, Madison, WI.
- Lei, H., Gartner, B. L. and Milota, M. R. (1997) Effect of growth rate on the anatomy, specific gravity, and bending properties of wood from 7-year-old red alder (*Alnus rubra*). *Can J For Res* 27: 80-85.
- Lei, H., Milota, M. R. and Gartner, B. L. (1996) Between- and within-tree variation in the anatomy and specific gravity of wood in Oregon white oak (*Quercus garryana* Dougl.). *IAWA J* 17: 445-461.
- Lo Gullo, M. A. and Salleo, S. (1992) Water storage in the wood and xylem cavitation in 1-year-old twigs of *Populus deltoides* Barttr. *Plant Cell Environ* 15: 431-438.
- Loustau, D., Berbigier, P., Roumagnac, P., Arruda-Pacheco, C., David, J. S., Ferreira, M. I., Pereira, J. S., and Tavares, R. (1996) Transpiration of a 64-year-old maritime pine stand in Portugal. I. Seasonal course of water flux through maritime pine. *Oecologia* 107: 33-42.
- Lu, P., Muller, W. J. and Chacko, E. K. (2000) Spatial variations in xylem sap flux density in the trunk of orchard-grown, mature mango trees under changing soil water conditions. *Tree Physiol* 20: 683-692.
- Machado, J.-L. and Tyree, M. T. (1994) Patterns of hydraulic architecture and water relations of two tropical canopy trees with contrasting leaf phenologies: *Ochroma pyramidale* and *Pseudobombax septenatum*. *Tree Physiol* 14: 219-240.
- Margolis, H., Oren, R., Whitehead, D. and Kaufmann, M. R. (1995) Leaf area dynamics of conifer forests. In *Ecophysiology of Coniferous Forests* (W. K. Smith and T. M. Hinckley, eds.) pp. 181-223. Academic Press, San Diego.
- Mark, W. R. and Crews, D. L. (1973) Heat-pulse velocity and bordered pit condition in living Engelmann spruce and lodgepole pine trees. *Forest Sci* 19: 291-296.
- Markstrom, D. C. and Hann, R. A. (1972) Seasonal variation in wood permeability and stem moisture content of three Rocky Mountain softwoods. RM-212. USDA Forest Service, Rocky Mountain Forest and Range Experimental Station, CO.
- Maton, C. and Gartner, B. L. (2005) Do gymnosperm needles pull water through the xylem produced in the same year as the needle? *Am J Bot* 92: 123-131.
- McDowell, N., Barnard, H., Bond, B. J., Hinckley, T., Hubbard, R. M., Ishii, H., Kostner, B., Magnani, F., Marshall, J. D., Meinzer, F. C., Phillips, N., Ryan, M. G. and Whitehead, D. (2002) The relationship between tree height and leaf area:sapwood area ratio. *Oecologia* 132: 12-20.
- Megraw, R. A. (1985) *Wood Quality Factors in Loblolly Pine: The Influence of Tree Age, Position in Tree, and Cultural Practice on Wood Specific Gravity, Fiber Length, and Fibril Angle*. Tappi Press, Atlanta, GA.
- Meinzer, F. C. (2002) Co-ordination of vapour and liquid phase water transport properties in plants. *Plant Cell Environ* 25: 265-274.
- Meinzer, F. C. (2003) Functional convergence in plant responses to the environment. *Oecologia* 134: 1-11.
- Meinzer, F. C., Goldstein, G. and Andrade, J. L. (2001) Regulation of water flux through tropical forest canopy trees: Do universal rules apply? *Tree Physiol* 21: 19-26.
- Meinzer, F. C., James, S. A., Goldstein, G. and Woodruff, D. (2003) Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. *Plant Cell Environ* 26: 1147-1155.
- Melcher, P. J., Goldstein, G., Meinzer, F. C., Yount, D. E., Jones, T. J., Holbrook, N. M. and Huang, C. X. (2001) Water relations of coastal and estuarine *Rhizophora mangle*. Xylem pressure potential and dynamics of embolism formation and repair. *Oecologia* 126: 182-192.
- Mencuccini, M., Grace, J. and Fioravanti, M. (1997) Biomechanical and hydraulic determinants of tree structure in Scots pine: Anatomical characteristics. *Tree Physiol* 17: 105-113.
- Miller, D. R., Vavrina, C. A. and Christensen, T. W. (1980) Measurement of sap flow and transpiration in ring-porous oaks using a heat pulse velocity technique. *Forest Sci* 26: 485-494.
- Milne, R. (1989) Diurnal water storage in the stem of *Picea sitchensis* (Bong.) Carr. *Plant Cell Environ* 12: 63-72.
- Nadezhkina, N., Cermak, J. and Ceulemans, R. (2002) Radial patterns of sap flow in woody stems of dominant and understory species: Scaling errors associated with positioning of sensors. *Tree Physiol* 22: 907-918.
- Nikolov, S. and E. Enchev (1967) *Vlaznost na darvesinata v surovo sastojanie* (Moisture Content of Green Wood). Zemizdat, Sofia, Bulgaria.
- Nilsen, E. T., Rundel, P. W. and Sharifi, M. R. (1981) Summer water relations of the desert phreatophyte *Prosopis glandulosa* in the Sonoran Desert of Southern California. *Oecologia* 50: 271-276.
- Nilsen, E. T., Sharifi, M. R. and Rundel, P. W. (1984) Comparative water relations of phreatophytes in the Sonoran Desert of California. *Ecology* 65: 767-778.
- Nobuchi, T. and Harada, H. (1983) Physiological features of the "white zone" of sugi (*Cryptomeria japonica* D. Don)—Cytological structure and moisture content. *Mokuzai Gakkaishi* 29: 824-832.
- Panshin, A. J. and de Zeeuw, C. (1980) *Textbook of Wood Technology: Structure, Identification, Properties, and Uses of the Commercial Woods of the United States*. McGraw-Hill, New York.
- Petty, J. A. and Puritch, G. S. (1970) The effect of drying on the structure and permeability of wood of *Abies grandis*. *Wood Sci Technol* 4: 140-154.
- Phelps, J. E. and Workman, Jr., E. C. (1994) Vessel area studies in white oak (*Quercus alba* L.). *Wood Fiber Sci* 26: 315-322.
- Phillips, N., Bond, B. J., McDowell, N. G. and Ryan, M. G. (2002) Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. *Tree Physiol* 22: 205-212.
- Phillips, N., Nagchaudhuri, A., Oren, R. and Katul, G. (1997) Time constant for water transport in loblolly pine trees estimated from time series of evaporative demand and stem sapflow. *Trees* 11: 412-419.
- Phillips, N., Oren, R. and Zimmermann, R. (1996) Radial patterns of xylem sap flow in non-diffuse- and ring-porous tree species. *Plant Cell Environ* 19: 983-990.
- Pothier, D., Margolis, H. A., Poliquin, J. and Waring, R. H. (1989) Relation between the permeability and the anatomy of jack pine sapwood with stand development. *Can J For Res* 19: 1564-1570.
- Puritch, G. S. (1971) Water permeability of the wood of grand fir (*Abies grandis* (Dougl.) Lindl.) in relation to infestation by the balsam wooly aphid, *Adelges piceae* (Ratz.). *J Exp Bot* 22: 936-945.
- Roberts, S. W., Strain, B. R., and Knoerr, K. R. (1980) Seasonal patterns of leaf water relations in four co-occurring forest tree species: Parameters from pressure-volume curves. *Oecologia* 46: 330-337.
- Roderick, M. L. and Berry, S. L. (2001). Linking wood density with tree growth and environment: A theoretical analysis based on the motion of water. *New Phytol* 149: 473-485.
- Santiago, L. S., Goldstein, G., Meinzer, F. C., Fisher, J. B., Machado, K., Woodruff, D. and Jones, T. (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. *Oecologia* 140: 543-550.
- Sellin, A. (1996) Sapwood amount in *Picea abies* (L.) Karst determined by tree age and radial growth rate. *Holzforchung* 50: 291-296.
- Senft, J. F., Bendtsen, B. A. and Galligan W. L. (1985) Weak wood: Fast-grown trees make problem lumber. *J Forestry* 83: 476-484.
- Schmitt, U., Grunwald, C., Gricar, J., Koch, G. and Cufar, K. (2003) Wall structure of terminal latewood tracheids of healthy and declining silver fir trees in the Dinaric region, Slovenia. *IAWA J* 24: 41-52.
- Schulze, E.-D., Cermak, J., Matyssek, R., Penka, M., Zimmermann, R., Vasicek, F., Gries, W. and Kučera, J. (1985) Canopy transpiration and water fluxes in the trunk of *Larix* and *Picea* trees: A comparison of xylem flow, porometer, and cuvette measurements. *Oecologia* 66: 475-483.

- Smith, J. H. G., Walters, J. and Wellwood, R. W. (1966) Variation in sapwood thickness of Douglas-fir in relation to tree and section characteristics. *For Sci* **1**: 97-103.
- Spicer, R. and Gartner, B. L. (2001) The effects of cambial age and position within the stem on specific conductivity in Douglas-fir (*Pseudotsuga menziesii*) sapwood. *Trees* **15**: 222-229.
- Stratton, L., Goldstein, G. and Meinzer, F. C. (2000) Stem water storage capacity and efficiency of water transport: Their functional significance in a Hawaiian dry forest. *Plant Cell Environ* **23**: 99-106.
- Swanson, R. H. (1971) Velocity distribution patterns in ascending xylem sap during transpiration. Symposium on Flow: Its measurement and control in science and industry. Canadian Forestry Service Paper no. 4/2/171.
- Tazikawa, H., Hayami, K., Kubota, J. and Tsukamoto, Y. (1996). Variations of volumetric water content and water potential in tree stems because of transpiration. *J Jpn For Soc* **78**: 66-73.
- Tison, A. (1902) Les traces foliaires des coniferes dans leur rapport avec l'epaississement de la tige. *Memoires de la Societe Linneenne de Normandie* **21**: 61-83.
- Tyree, M. T. (1988) A dynamic model for water flow in a single tree: Evidence that models must account for hydraulic architecture. *Tree Physiol* **4**: 195-217.
- Tyree, M. T., Cheung, Y. N. S., Macgregor, M. E. and Talbot, A. J. B. (1978) The characteristics of seasonal and ontogenetic changes in the tissue-water relations of *Acer*, *Populus*, *Tsuga* and *Picea*. *Can J Bot* **56**: 635-647.
- Tyree, M. T., Snyderman, D. A., Wilmot, T. R. and Machado, J. L. (1991) Water relations and hydraulic architecture of a tropical tree (*Schefflera morototoni*): Data, models and a comparison with two temperate species (*Acer saccharum* and *Thuja occidentalis*). *Plant Physiol* **96**: 1105-1113.
- Tyree, M. T. and Yang, S. D. (1990) Water-storage capacity of *Thuja*, *Tsuga* and *Acer* stems measured by dehydration isotherms: The contribution of capillary water and cavitation. *Planta* **182**: 420-426.
- Utsumi, Y., Sano, Y., Funada, R., Ohtani, J. and Fujikawa, S. (2003) Seasonal and perennial changes in the distribution of water in the sapwood of conifers in a sub-frigid zone. *Plant Physiol* **131**: 1826-1833.
- Waring, R. H. and Roberts J. M., (1979) Estimating water flux through stems of Scots pine with tritiated water and phosphorus-32. *J Exp Bot* **30**: 459-471.
- Waring R. H. and Running, S. W. (1978) Sapwood water storage: Its contribution to transpiration and effect upon the water conductance through the stems of old-growth Douglas-fir. *Plant Cell Environ* **1**: 131-140.
- Waring, R. H., Whitehead, D. and Jarvis, P. G. (1979) The contribution of stored water to transpiration in Scots pine. *Plant Cell Environ* **2**: 309-317.
- Wellwood, R. W., Sastry, C. B. R., Micko, M. M. and Paszner, L. (1974) On some possible specific gravity, holo- and alpha-cellulose, tracheid weight/length and cellulose crystallinity relationships in a 500-year-old Douglas-fir tree. *Holzforschung* **28**: 91-94.
- West, G. B., Brown, J. H. and Enquist, B. J. (1999) A general model for the structure and allometry of plant vascular systems. *Nature* **400**: 664-667.
- Whitehead, D., Edwards, W. R. N. and Jarvis, P. G. (1984) Conducting sapwood area, foliage, and permeability in mature trees of *Picea sitchensis* and *Pinus contorta*. *Can J For Res* **14**: 940-947.
- Williams, M., Rastetter, E. B., Fernandes, D. N., Goulden, M. L., Wofsy, S. C., Shaver, G. R., Melillo, J. M., Munger J. W., Fan, S.-M. and Nadelhoffer, K. J. (1996) Modelling the soil-plant-atmosphere continuum in a *Quercus-Acer* stand at Harvard Forest: The regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. *Plant Cell Environ* **19**: 911-927.
- Wronski, E. B., Holmes, J. W. and Turner, N. C. (1985) Phase and amplitude relations between transpiration, water potential and stem shrinkage. *Plant Cell Environ* **8**: 613-622.
- Wullschlegel, S. D. and King, A. W. (2000) Radial variation in sap velocity as a function of stem diameter and sapwood thickness in yellow-poplar trees. *Tree Physiol* **20**: 511-518.
- Wullschlegel, S. D., Meinzer, F. C. and Vertessy, R. A. (1998) A review of whole-plant water use studies in trees. *Tree Physiol* **18**: 499-512.
- Zang, D., Beadle, C. L. and White, D. A. (1996) Variation of sapflow velocity in *Eucalyptus globulus* with position in sapwood and use of a correction coefficient. *Tree Physiol* **16**: 697-703.
- Zhang, S. Y. and Zhong, Y. (1991) Effect of growth rate on specific gravity of East-Liaoning oak (*Quercus liaotungensis*) wood. *Can J For Res* **21**: 255-260.
- Zimmermann, M. H. (1978) Hydraulic architecture of some diffuse-porous trees. *Can J Bot* **56**: 2286-2295.
- Zobel, B. J. and Sprague, J. R. (1998) *Juvenile Wood in Forest Trees*. Springer-Verlag, Berlin.