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How Trees Influence the Hydrological Cycle in Forest Ecosystems

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2.1 Introduction

Ultimately, the quest of ecohydrology (or hydroecology) is to apply fundamental knowledge from hydrology, ecology, atmospheric science, and related disciplines to solve real world problems involving biological systems and hydrologic cycles. Achieving this goal requires sharing information across disciplines, and this chapter is structured toward that end. Our aim is to present current ecological concepts concerning the ways that the structure and function of forest vegetation influence hydrologic processes. To cover this topic in a single chapter, we emphasize some aspects of the interactions between forest trees and hydrology, especially transpiration, over others, such as moisture interception by forest canopies. Other important topics are not covered at all, such as the influence of forest trees and the myriad flora and fauna associated with them on soil hydraulic properties, and root channels as preferential water flow paths in soils. Research is needed to develop a broader conceptual understanding of these belowground processes, especially over long time periods.

Forests occupy approximately one-third of the Earth's land area, accounting for over two-thirds of the leaf area of land plants, and thus play a very important role in terrestrial hydrology. Our discussion emphasizes temperate coniferous trees in North America because that is where we have the most experience, but the processes discussed are

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generally applicable to all forest trees, and the tables and figures include information about rates and processes for a variety of species and ecosystems in order to provide perspective on the upper and lower boundaries. Section 2.2 explores transpiration from top (leaves) to bottom (roots), emphasizing the importance of tree hydraulic architecture to transpiration. Section 2.3 expands consideration of evapotranspiration from trees to forest ecosystems. The chapter concludes (Section 2.4) by applying concepts presented in earlier sections to the question of how hydrological processes in forests change as they age – a topic of great relevance as humans alter the age class distribution of forests around the world through land management activities.

2.2 Key Processes and Concepts in Evapotranspiration – Their Historical Development and Current Status

2.2.1 The SPAC

The 'Soil-Plant-Atmosphere Continuum', or SPAC, is a key concept in studies of plant water use. The notion of the SPAC emerges from the cohesion–tension (CT) theory of water movement through plants (Dixon and Joly, 1894), and the recognition that water moves from soil into roots, through plants and into the atmosphere along thermodynamic gradients in water potential (see van den Honert, 1948); these processes are described in detail later in this section. Although the CT theory has been disputed (e.g., Canny, 1995; 1998), it has held up to robust examination (Holbrook *et al*., 1995; Pockman *et al*., 1995; Sperry *et al*., 1996) and is now widely accepted (Angeles *et al*., 2004).

An electric circuit analogy is often used to characterize physical controls on the movement of water into and through plants and to the atmosphere (van den Honert, 1948). In its simplest form, the pathway can be visualized as a chain of resistances connected in series. The total hydraulic resistance, therefore, is the sum of the individual resistances along the path, including the aerodynamic boundary layer resistances associated with canopy elements, the boundary layer at the leaf surface, stomatal pores, through the xylem pathway of the plant, across root membranes to the soil, and through the soil. Whereas micrometeorologists prefer to view the SPAC in terms of resistances, plant physiologists typically use the inverse of resistance, or conductance, because transpiration increases linearly with conductance at a constant vapor pressure gradient.

While the SPAC model provides a powerful conceptual basis for understanding plant–water relations, it also tends to constrain ecological concepts and models of hydrological cycles to a one-dimensional perspective, limited to vertical fluxes. In this respect, most ecological models and analyses of water balance differ fundamentally from hydrological models and analyses, which typically consider three-dimensional flows of liquid water over and through a landscape. On the other hand, hydrological models are often limited to gravity-driven flowpaths of liquid water, often ignoring or oversimplifying the influences of vegetation on the water cycle. An especially fruitful arena for ecologists and hydrologists to work together is in merging modern, mechanistic models of plant water use, which are almost always one dimensional, with three-dimensional hydrological models (Bond, 2003).

2.2.2 Transpiration

The ratio of transpiration to biomass accumulation varies across plant growth forms, but forest trees typically lose 170 to 340 kg of water vapor for every kg of biomass accumulated (Larcher, 1975). Extensive research has established that the air saturation deficit (D) and net radiation (R_n) are the principal drivers of transpiration (symbols used in this chapter are listed in Table 2.1). Air saturation deficit directly affects transpiration by establishing the vapor pressure gradient between the vapor-saturated leaf interior and the surrounding air. Net radiation indirectly affects transpiration through heating of the canopy, which causes the leaf-to-air vapor pressure gradient to increase as the vapor pressure in the air spaces within leaves increases exponentially with leaf temperature.

Nearly all transpirational vapor loss occurs through the stomatal pores – water losses through leaf cuticles and stems are typically negligible except in unusual circumstances. Over short time periods, plants control transpiration by regulating the size of stomatal pores, while over longer time periods water balance is regulated largely by changes in the amount of leaf area and species composition.

Table 2.1 *Terms and symbols*

Symbol	Description	Typical units
A_L	Surface area of foliage (projected or total surface)	m^2
A_r	Surface area of roots	m^2
A_s	Surface area of sapwood, measured at breast height (1.37 m) unless specified otherwise	m^2
C	Capacitance (defined as the change in water content of plant tissue per unit change in bulk water potential of the tissue, or $dV/d\Psi$)	$m^3\,kPa^{-1}$
D	Air saturation deficit	kPa
g_s	Stomatal conductance	$mol\,m^{-2}\,s^{-1}$
G_c	Canopy conductance	$mol\,m^{-2}\,s^{-1}$
L	Length of stem or hydraulic transport path	m
η	Viscosity	Pa s
K	Permeability; specific conductivity	m^2
k_L	Leaf-specific hydraulic conductivity ($= k\ A_L^{-1}$)	$m^2\,m^{-2}$
K	Hydraulic conductance ($= Q\ \Delta\Psi^{-1}$)	$m^3\,Pa^{-1}\,s^{-1}$
LAI	Leaf area index	Dimensionless ($m^2\,m^{-2}$)
Q	Volume flow per unit time	$m^3\,s^{-1}$
R	Hydraulic resistance	$Pa\,s\,m^{-3}$
R_n	Net radiation	Watts
Ω	Decoupling coefficient	dimensionless
Ψ (Ψ_{soil}, Ψ_{leaf}, $\Delta\Psi$)	Water potential (soil water potential, leaf water potential, difference in water potential at either end of a hydraulic path)	MPa

Maximum and mean stomatal conductances (g_s) vary widely among species and forest types (Table 2.2). Stomatal pore size, and therefore g_s, is dynamic and has been shown to respond rapidly to numerous environmental and physiological variables. Light (especially in blue wavelengths) and D are key components of the aerial environment that exert opposing effects on g_s. Stomatal conductance exhibits a characteristic saturating or asymptotic response to increasing light. Light-saturation points for g_s of different types of forest trees vary considerably, with g_s of coniferous forest trees typically saturating at photosynthetic photon flux densities (*PFD*) substantially lower than those of temperate and tropical broadleaf trees. Both the light saturation of g_s and maximum g_s are highly variable due to adaptation of foliage to the local light environment. Although it is widely assumed that stomata of woody species are tightly closed at night, resulting in negligible nocturnal transpiration rates, a number of reports indicate that nocturnal transpiration can be substantial, often contributing 25% or more to the daily total (Green *et al*., 1989; Benyon, 1999; Donovan *et al*., 1999; Oren *et al*., 1999a; Sellin, 1999; Feild and Holbrook, 2000),

Table 2.2 *Examples of maximum stomatal (g_s) and canopy (G_c) conductance of different types of forest vegetation*

Forest/vegetation type	Species	LAI	g_s (mmol m^{-2} s^{-1})	G_c (mmol m^{-2} s^{-1})	Reference
Conifer					
boreal	*Picea mariana*	4.4	25	98	Rayment *et al*., 2000
temperate	*Pinus pinaster*	2.7	150	320	Loustau *et al*., 1996
Mediterranean temperate mesic	*Pseudotsuga menziesii*/ *Tsuga heterophylla*	9.0	50–70	480	Phillips *et al*., 2002; Meinzer *et al*., 2004c; Unsworth *et al*., 2004
temperate semiarid	*Pinus ponderosa*	2.1	166	287	Ryan *et al*., 2000; Anthoni *et al*., 2002
Angiosperm					
boreal	*Populus tremuloides*	5.6	490	1200	Blanken *et al*., 1997
temperate deciduous	*Fagus sylvatica*	4.5	250	900	Herbst, 1998
temperate evergreen	*Nothofagus menziesii*/ *N. fusca*	7.0	160	440	Köstner *et al*., 1992
tropical plantation	*Goupia glabra*	3.7	180	600	Granier *et al*., 1992
Amazonian rainforest	mixed	6.6	200	420	Shuttleworth *et al*., 1984; Roberts *et al*., 1990

especially in environments where nighttime relative humidity remains relatively low (Bucci *et al*., 2004).

The response of transpiration to increasing *D* is regulated (Schulze *et al*., 1972) through partial stomatal closure (Figure 2.1). Thus, when light is adequate and *D* is low (i.e., high humidity), stomata are maximally open and transpiration increases linearly with increasing *D*. For many species, beyond a critical level of *D*, stomatal conductance declines exponentially with increasing *D*, causing transpiration to level off at a maximum rate. In some cases, transpiration actually decreases at very high evaporative demand once a maximum value has been attained (Farquhar, 1978; Mott and Parkhurst, 1991; Franks *et al*., 1997). The responses of both stomatal conductance and transpiration to *D* change depending on the availability of soil moisture (Figure 2.1).

The apparent sensitivity of g_s to *D* varies widely among tree species (Figure 2.2A), largely because of differences in their hydraulic characteristics (discussed in next section) and species-specific differences in leaf anatomical traits such as stomatal pore depth and density (which determine maximum g_s at low *D*). The characteristic exponential decline in g_s with increasing *D* has been exploited in a model that demonstrates that the sensitivity of g_s to *D* is proportional to the magnitude of g_s at low *D* in the same manner across a

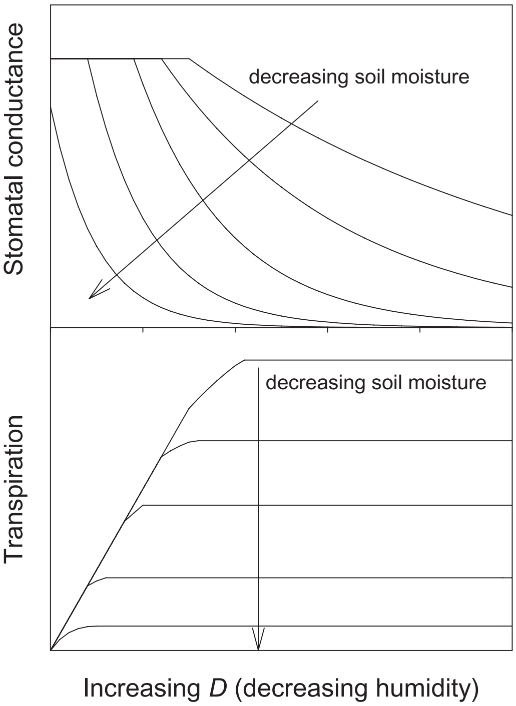

Figure 2.1 *A generalized view of the responses of stomatal conductance and transpiration to soil and atmospheric water deficits for* isohydric *plants (see Section 2.2.3 for a discussion of isohydric and anisohydric behavior in plants)*

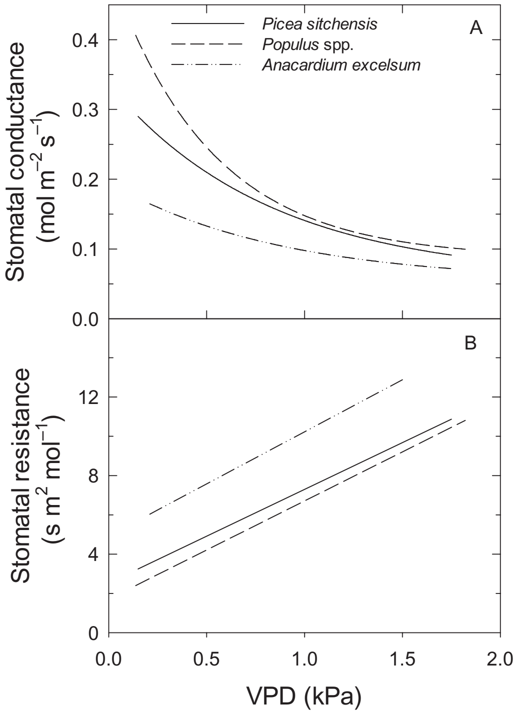

Figure 2.2 *Stomatal conductance (A) and resistance (B) in relation to the leaf-to-air vapor pressure deficit (VPD) for a temperate conifer (*Picea sitchensis*; Schulze and Hall, 1982), temperate broadleaf (*Populus *spp.; Meinzer* et al.*, 1997), and a tropical broadleaf (*Anacardium excelsum*; Meinzer* et al.*, 1993) species*

broad range of species and conditions (Oren *et al.*, 1999b). Apparent species-specific differences in stomatal sensitivity to D are diminished when the reciprocal of g_s, stomatal resistance, is plotted against D (Figure 2.2B). Because stomatal resistance changes linearly with pore radius, nearly parallel linear responses of resistance to D imply similar sensitivity of stomatal aperture to variation in D, whereas different y-intercepts (minimum resistance) imply differences in leaf anatomy and hydraulic properties of the species.

There is still no comprehensive understanding of how stomata integrate external and internal signals to regulate transpiration. Although stomata are obviously autonomous to some degree in responding directly to external variables such as PFD and D, the amplitude of stomatal responses is constrained by internal variables. Stomatal responses to increasing soil water deficits exemplify the complex regulatory interactions that ultimately limit forest transpiration during periods of drought. As the soil dries, two types of signal, hydraulic and chemical, may be generated and transmitted to the leaves. Hydraulic signals consist of increases in xylem tension that are rapidly propagated to the leaves as a result of changes in root/soil hydraulic resistance (Section 2.2.4) or soil water potential. Chemical signals may consist of changes in levels of plant growth regulators such as abscisic acid that are exported in the transpiration stream from the roots to the leaves, where they cause partial stomatal closure (Davies and Zhang, 1991). Chemical signals may be generated during incipient soil drying well in advance of hydraulic signals (Gollan *et al*., 1986), and the magnitude of the hydraulic signal (xylem tension) may determine stomatal responsiveness to chemical signals (Tardieu and Davies, 1993). The role of chemical signals in stomatal regulation in tall trees is uncertain because of the slow propagation of chemical signals – in tall coniferous trees it may take two weeks or more for chemical signals to move from roots to leaves (Meinzer *et al*., 2006) – relative to nearly instantaneous hydraulic signals. Regardless of the signals or response mechanisms involved, it appears that under a broad range of conditions stomata regulate transpiration to prevent leaf water potentials from dropping below some species-specific minimum (Bond and Kavanagh, 1999), although that minimum may vary slightly with tree size or age within a species (McDowell *et al*., 2002b). This behavior balances vapor and liquid phase water transport (Meinzer, 2002) and appears to ensure integrity of the liquid water transport pathway in the plant (see next section). Even in deeply rooted tree species that are able partially to sustain transpiration during periods of drought by tapping soil layers that never undergo pronounced drying, conditions sensed by roots in the dry upper soil generate signals that cause partial stomatal closure, leading to relative seasonal homeostasis of maximum leaf water deficits in the canopy (Domec *et al*., 2004; Warren *et al*., 2005).

The extent to which transpiration is passively driven by environmental variables such as R_n or is under physiological control by g_s has been debated. Differences in interpretation of the role played by stomata in limiting transpiration are related to the nature of the pathway of water movement in the vapor phase. Closer inspection of the vapor pathway and its associated resistances shows that stomatal control of transpiration is strongest when boundary layer resistance is small in relation to stomatal resistance. Vapor diffusion through stomata would thus represent the controlling resistance. High boundary layer resistance associated with low wind speed, short stature, large leaves, or dense canopies (as is often the case for crop plants and grasslands), will promote local equilibration of humidity near the leaf surfaces, thereby uncoupling the vapor pressure and evaporative demand at the leaf surface from that in the bulk air. Under these circumstances, transpiration is partly uncoupled from g_s, making it appear to be driven largely by R_n. This combination of conditions has sometimes led to the characterization of well-watered vegetation as a wick that passively conducts water from the soil to the atmosphere. However, this apparently passive behavior may conceal pronounced stomatal regulation of transpiration that leads to similar responses of transpiration to environmental drivers across different types of vegetation. The degree of decoupling between stomatal conductance and transpiration has been quantified with a dimensionless decoupling coefficient (Ω) ranging from zero to one (Jarvis and McNaughton, 1986). Stomatal control of transpiration diminishes as Ω approaches 1.0 because the vapor pressure at the leaf surface becomes increasingly decoupled from that in the bulk air. Typical values of Ω range from near 0.1 in needle-leaved coniferous trees with low stomatal and high boundary layer conductance to 0.5 or greater in broadleaf trees; they are higher in dense, herbaceous vegetation. Regardless of the degree of decoupling of transpiration from g_s when soil water is abundant, stomata increasingly limit transpiration as soil water deficits develop.

At the canopy level, transpiration is influenced by additional variables that include leaf area (often described in terms of leaf area index, or LAI, the ratio of leaf area to ground area), canopy structure and aerodynamic properties that determine canopy boundary layer

K2

properties. At this scale, controls on transpiration are typically represented by canopy conductance (G_c), a term that combines stomatal and boundary layer conductances. Variation in canopy conductance among forest types thus reflects both leaf level and higher order properties (Table 2.2), and these properties do not necessarily vary across ecosystem types in a consistent way. For example, the canopy conductance of Douglas fir (*Psuedotsuga menziesii*) is nearly double that of ponderosa pine (*Pinus ponderosa*). This is consistent with the environments they grow in – Douglas fir grows in temperate mesic regions, whereas ponderosa pine grows in much drier areas. However, maximum g_s of ponderosa pine is significantly greater than that of Douglas fir; the greater stomatal conductance of the pines is more than offset by lower leaf area of pine forests.

2.2.3 Liquid Water Transport Through Trees and the Role of Hydraulic Architecture

Canopy conductance controls transpiration; however, canopy conductance is itself strongly influenced by the hydraulic architecture of trees and forests. Atmospheric conditions create a demand for water, and hydraulic architecture influences the supply of water from the soil. Ultimately, stomata regulate transpiration to ensure that losses do not exceed the supply capacity. In order to understand how vegetation controls transpiration, and to predict how alterations to vegetation will alter evapotranspiration, it is necessary to understand how hydraulic properties of trees influence their use of water.

According to the CT theory, the volume flow per unit time (Q) of liquid water through plants (the 'supply' for transpiration) is directly proportional to difference in water potential between leaves and soil ($\Delta\Psi$; or $\Psi_{\text{leaf}} - \Psi_{\text{soil}}$) and to whole-tree hydraulic conductance (K); it is therefore inversely proportional to whole-tree hydraulic resistance (R):

$$Q = \Delta\Psi * K \tag{2.1a}$$

$$\mathrm{Q} = \Delta\Psi / R \tag{2.1b}$$

Application of Equation (2.1) can be misleading about causes and effects. Does transpiration control $\Delta\Psi$, or does $\Delta\Psi$ control transpiration? In fact, the causality works both ways. The driving force ($\Delta\Psi$) for liquid water movement from soil through the xylem is generated by the transpirational loss of water vapor, which lowers Ψ_{leaf} and transmits tension, or negative pressure, through continuous water columns running from the evaporative surfaces in the leaves to the soil (Tyree and Zimmermann, 2002). However, as will be demonstrated below, when Ψ_{leaf} drops to a critical level, partial stomatal closure occurs, limiting transpiration.

In the absence of transpiration, gravitational forces result in a minimum tension gradient of $-0.01\,\text{MPa}\,\text{m}^{-1}$ through the vertical dimension of trees. When transpiration occurs, frictional resistances make the vertical tension gradient considerably steeper (Tyree and Zimmermann, 2002). Following Equation (2.1), the magnitude of tension at a given point in the xylem depends upon the water potential of the soil from which the water has been taken up, the cumulative hydraulic resistance to that point, the flow rate, and the height above the ground (for the purposes of this illustration, gravitational forces can be included with R or K).

The development of substantial tension makes xylem water transport potentially vulnerable to disruption by cavitation and embolism (Tyree and Sperry, 1989). Cavitation is the separation of the water column within a xylem conduit (tracheid or vessel) forming a vapor-filled partial vacuum, whereas embolism results from the entry of air into a xylem conduit with or without prior cavitation. Both phenomena block water transport in the affected conduit. The vulnerability of xylem to loss of conductivity from cavitation and embolism is a key component of tree hydraulic architecture. Vulnerability curves relating percent loss of hydraulic conductivity to negative pressure in the xylem have been determined for numerous tree species. Within individual trees, xylem vulnerability typically decreases along a gradient from roots to trunk to terminal branches (Figure 2.3A), corresponding to gradients of increasing tension from roots to branch tips. Not surprisingly, xylem vulnerability varies widely among tree species growing under different ecological conditions (Figure 2.3B), and it is an important determinant of the limits to species distribution (embolism can occur as a result of freezing as well as water stress). Xylem embolism was formerly thought to be largely irreversible over the short term; however,

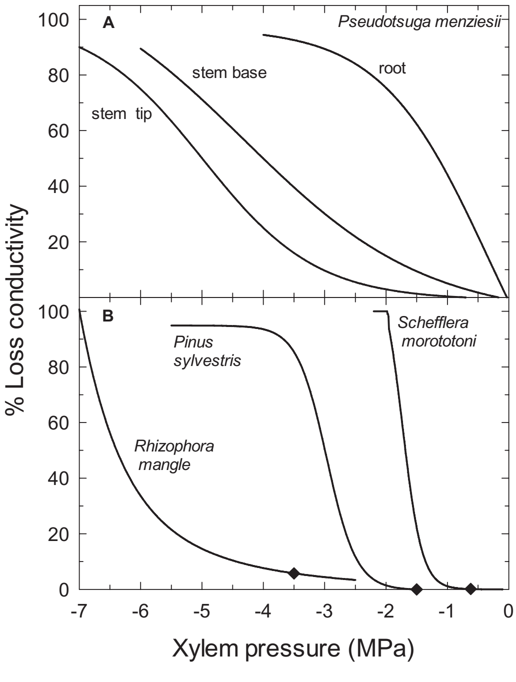

Figure 2.3 *Xylem vulnerability curves showing loss of hydraulic conductivity as a function of xylem pressure (tension). (A) Axial gradient of decreasing vulnerability from roots to terminal branches in a temperate conifer. Data from Domec and Gartner (2001) and Domec* et al. *(2004). (B) Examples of species showing highly vulnerable, moderately vulnerable, and highly resistant stem xylem. In all of the examples, stomata regulate minimum leaf water potential (diamonds) to prevent excessive loss of conductivity. Data from Cochard (1992), Melcher* et al. *(2001), and Meinzer* et al. *unpublished observations*

increasing evidence is emerging to show that it is rapidly reversible in some plant organs (Zwieniecki and Holbrook, 1998; Tyree *et al*., 1999; Melcher *et al*., 2001; Bucci *et al*., 2003).

Plants can be aggregated into two groups based on the relationship between water potential and g_s. In *isohydric* species, which include most temperate forest trees, g_s is regulated to prevent the water potential of xylem from dropping to levels that would provoke excessive loss of conductivity as soil water deficits develop. Thus, isohydric species have a minimum midday water potential that remains more or less constant as soils dry (Figure 2.4B, diamonds). In *anisohydric* species there is no threshold minimum water potential, and transpiration is not as tightly regulated by stomatal closure. Isohydric species may tend to be more vulnerable to embolism and have greater capacity for embolism repair than do anisohydric species (Vogt, 2001). In Section 2.4.2 we discussed species-specific relationships between stomatal conductance, soil water deficits and atmospheric vapor pressure deficit. These environmental controls are usually presented as empirically derived characteristics of species, but in fact they are strongly associated with plant hydraulic architecture as they regulate the transpirational flux of water so that water

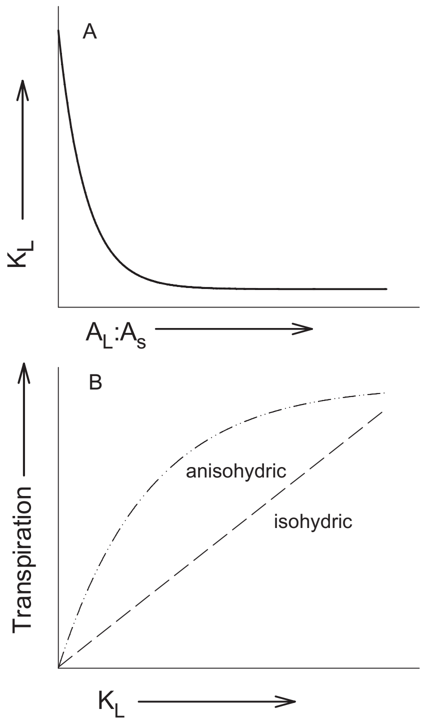

Figure 2.4 *(A) Typical relationship between leaf-specific conductivity (k_L) and the leaf area : sapwood area ratio (A_L : A_S), an index of transpirational demand in relation to water supply capacity. (B) Stomatal regulation causes transpiration to increase with k_L in a predictable manner in isohydric and anisohydric species (see text for details)*

potentials do not fall to a damaging level. The upper limit to transpiration from a community of isohydric plants is therefore strongly influenced by their vulnerability to cavitation as well as g_s and LAI.

The hydraulic resistance (or its inverse, conductance) of stems is determined in part by the permeability (k) of wood (many authors use *specific conductivity* for this property), which is primarily determined by the length and diameter of xylem cells. Leaf-specific conductivity (k_L) is k normalized by leaf area distal to the stem ($k\ A_L^{-1}$). As the ratio between leaf area and sapwood area (A_L:A_s) increases, (k_L) typically declines exponentially (Figure 2.4A). A_L:A_s is a fundamental allometric trait that reflects the balance between transpirational demand (A_L) and water supply capacity (A_s). Both k_L and A_L:A_s can be expressed at multiple scales from terminal branches to entire trees. Co-occurring tree species often share a common relationship between k_L and A_L:A_s (Bucci *et al*., 2005). Because k_L represents the balance between the demand for and efficiency of water supply, it constrains stomatal regulation of transpiration within limits that avoid catastrophic loss of xylem function from cavitation and embolism. Stomatal conductance and transpiration thus co-vary with k_L in a coordinated manner (Figure 2.4B). In isohydric species, transpiration exhibits a linear dependence on k_L. Transpiration increases asymptotically with k_L in anisohydric species, causing minimum leaf water potential to vary with k_L. As with the relationship between k_L and A_L:A_s, co-occurring tree species often share common relationships between k_L, g_s and transpiration (Meinzer *et al*., 1995; Andrade *et al*., 1998; Bucci *et al*., 2005).

It is important to note that k_L and xylem vulnerability are not static properties within species or individual trees. In many trees, k_L decreases from the base of the stem to the apex, from larger to smaller diameter branches, and with increasing tree age and size (Tyree and Ewers, 1991; Ryan *et al*., 2000; McDowell *et al*., 2002a). In addition, seasonal variation in leaf area may partially conserve k_L during dry periods that cause reduced hydraulic conductivity due to cavitation (Bucci *et al*., 2005). Xylem vulnerability to cavitation can vary dramatically among populations of the same species growing under different environmental conditions (Tognetti *et al*., 1997; Kavanagh *et al*., 1999; Sparks and Black, 1999; Melcher *et al*., 2001), and even within the same growth ring, with latewood being more vulnerable than earlywood (Domec and Gartner, 2002).

Leaf level responses of g_s to the combination of architectural and environmental variables can be summarized in the following equation (Whitehead, 1998):

$$g_s = \frac{kA_s\Delta\Psi}{L\eta A_L D_s} \qquad (2.2)$$

k, A_s, A_L, and $\Delta\Psi$ were defined above; L is the length of the stem or the hydraulic path, η is the temperature-dependent viscosity of water, and D_s is the air saturation deficit at the leaf surface. The equation is typically applied to individual leaves or plants, but can also be applied on the stand level by substituting basal sapwood area for A_s, *LAI* for A_L, and stand-average metrics for the other variables. Although this equation is 'inexact' (it involves assumptions about steady-state processes that are not strictly true, and root resistances – see below – are difficult to incorporate), it yields many insights into the relationships between plant canopies, their environment and transpiration. Across a range of environments with different humidities, for example, g_s may be conserved through adjustment in A_L:A_s via change in allocation patterns. Such adjustments have been measured in Scots pine (*Pinus sylvestris*) (Mencuccini and Grace, 1995). Likewise, pruning part of a canopy decreases A_L:A_s, and often results in increased g_s in remaining foliage. Thus, in response to partial defoliation, leaf-level transpiration rates increased in loblolly pine (*Pinus taeda*), resulting in more or less constant rates of water flow through sapwood (Pataki *et al*., 1998). This also helps to explain the good relationships often found between transpiration and the sapwood conducting area. In another application, McDowell *et al*. (2002b) found that tall Douglas fir trees have higher wood permeability (k) and lower A_L:A_s compared with smaller trees, partially compensating for the impact that increased L would otherwise have on g_s.

The sapwood of large trees may serve as a storage reservoir for water as well as a conduit. The hydraulic capacitance of sapwood and other plant tissues can be thought of as a component of hydraulic architecture in that it plays an important role in determining the dynamics of water movement through trees. Following the Ohm's law analogue for water movement along the SPAC, the capacitance (C) of a tissue is defined as:

$$C = \mathrm{d}V / \mathrm{d}\Psi \tag{2.3}$$

where $\mathrm{d}V/\mathrm{d}\Psi$ is the volume of water released per change in water potential of the tissue. An increase in xylem tension will thus pull water from surrounding tissues into the transpiration stream. This release of stored water can cause pronounced lags between changes in transpiration in the tree's crown and changes in axial (vertical) water flow through stems (Goldstein *et al*., 1998; Phillips *et al*., 2003; Ford *et al*., 2004; Meinzer *et al*., 2004a). Trees typically exhibit diel (24-hour) cycles of capacitive discharge of stored water followed by complete recharge (or nearly so) during periods of reduced transpiration later in the day or overnight. Daily reliance on stored water as a percentage of total transpiration varies widely, ranging from about 10 to 50 % (Waring *et al*., 1979; Holbrook and Sinclair, 1992; Loustau *et al*., 1996; Kobayashi and Tanaka, 2001; Maherali and DeLucia, 2001; Phillips *et al*., 2003; Meinzer *et al*., 2004a). There is evidence that relative reliance on stored water increases with tree size in some species (Phillips *et al*., 2003), but not in others (Meinzer *et al*., 2004a), and that trees use larger amounts of stored water in drought conditions (Phillips *et al*., 2003; Ford *et al*., 2004). In absolute terms, daily utilization of stored water ranges from about 20–50 kg in large, old-growth conifers (Phillips *et al*., 2003) to 80–100 kg or more in large tropical trees (Meinzer *et al*., 2004a). During seasonal drought, water withdrawn from storage in the sapwood of large coniferous trees may be sufficient to replace up to 27 mm of transpirational losses before seasonal recharge occurs (Waring and Running, 1978). The behavior of deuterated water (D_2O) injected into trees as a tracer of water movement suggests that maximum sap velocity and water residence time in the tree are strongly dependent on sapwood capacitance among both vessel- and tracheid-bearing trees independent of species. Tracer velocity decreased linearly and tracer residence time increased exponentially with increasing sapwood capacitance among 12 trees representing four tropical angiosperm species and two temperate coniferous species (James *et al*., 2003; Meinzer *et al*., 2003, 2006). Tracer velocities for the angiosperm trees were as high as 26 m per day, but generally less than 5 m per day in the conifers, implying that transit times for water taken up by roots to arrive in the upper crown would be at least three weeks in the tallest old-growth conifers. The tracer residence time was 79 days in a 1.43-m-diameter Douglas fir tree, the largest individual injected, and only 4 days in a 0.34-m-diameter tropical tree. These results are consistent with a prominent role for sapwood water storage in determining whole-tree water transport and storage dynamics.

2.2.4 Water Uptake by Roots

In woody plants, resistance to water flow in the root system can equal or even exceed resistance aboveground (Nardini and Tyree, 1999; Sperry *et al*., 1998; Tyree *et al*., 1998). Thus, the mechanisms and physical constraints regulating root water uptake are at least as important as aboveground constraints. Due to the difficulties of belowground investigations, however, water transport has not been studied as intensively in roots as in stems and leaves.

The ability of roots to supply water for plant transpiration depends on the hydraulic conductance of the root system (determined by fine-root conductivity and total fine-root surface area), the distribution of roots within the soil profile along with the ability to produce new roots dynamically as soil water is used and replenished, and soil water availability throughout the rooting zone. Hyphae of mycorrhizal fungi can greatly increase the effective hydraulic conductance of roots and therefore can exert considerable influence over transpiration (Hobbie and Colpaert, 2004). The hydraulic conductivity of soil in the rhizosphere is also critically important to root water uptake.

Root conductivity varies because water flows into roots through multiple pathways that are influenced by both osmotic and hydraulic drivers (Steudle, 1994, 2001). Roots generally have very high axial ('lengthwise') conductivity; thus, overall conductance of root systems is generally limited by radial ('crosswise') conductivity as water enters the root from the soil. The low radial conductivity is largely due to a special feature of root anatomy that forces most of the water to cross cell membranes. By forcing water to cross a cell membrane, plants are able 'sieve out' undesirable chemical compounds and favor others, but the flow of water is impeded considerably.

The surface area and demography of fine roots greatly influences the ability of the root system to conduct water. Water uptake primarily occurs in young, unsuberized roots (*suberization* is the development of a waxy, protective layer around roots, and is usually associated with a change in color). The radial hydraulic conductivity of these young roots is 10- to 100-times higher than in older roots. Fine roots continuously emerge, age and die through the favorable growing season and, as with leaves above ground, their physiological characteristics change with age, although at present these developmental changes are poorly characterized (Wells and Eissenstadt, 2003).

The surface area of fine roots is an important parameter in models of plant water transport, particularly in connection with the transpiring surface area of leaves. Increasing root surface area per unit leaf area (A_r:A_l) allows water uptake from more soil per transpiring leaf. A_r:A_l is generally greater than 1 and can vary dramatically depending on xylem vulnerability and soil texture properties (Sperry *et al*., 1998). For example, loblolly pine (*Pinus taeda)* growing in sandy soil had an A_r:A_l ratio of 9.75 compared with 1.68 for the same species in a loam soil (Hacke *et al*., 2000), whereas five different species of oak (*Quercus* spp.) growing under similar conditions with adequate water but differing in drought tolerance did not differ as much in their A_r:A_l (ranging from 1.45 to 2.37) (Nardini

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and Tyree, 1999). In coarse soils, soil hydraulic conductance drops more rapidly with decreases in Ψ_{soil} than in finely textured soils (Bristow *et al*., 1984). Increasing root surface area can help alleviate this conductance limitation in coarse soils.

The axial conductivity of roots can be as much as 40-times greater than that of stems due to the greater diameter of water transport cells, and deeper roots are more conductive than shallow roots, providing a continuum of decreasing conductivity along the xylem pathway (Kavanagh *et al*., 1999; McElrone *et al*., 2004). However, roots are also more vulnerable to cavitation than are shoots (Doussan *et al*., 1998; Kavanagh *et al*., 1999; Sperry and Ikeda, 1997). Sperry *et al*. (1998) speculated that surface roots may act as a kind of hydraulic 'fuse'; root xylem failure that is localized in the dry upper soil may allow deeper roots in wetter soil to continue transporting water. Seasonal loss of root conductivity in upper soil has been correlated with decreased stomatal conductance even though deep roots had access to water (Domec *et al*., 2004). Similarly, the rate of water depletion throughout the soil profile is correlated with the Ψ_{soil} in the upper 20 cm (Warren *et al*., 2005). These results imply that seasonal declines in Ψ_{soil} and root conductivity in the upper soil may generate signals that induce stomatal closure and limit water uptake even though most water is coming from deeper parts of the soil profile.

Rooting depth and the distribution of roots through the soil profile also has a significant impact on access to water throughout the growing season. Soil resources (nutrients and water) are not evenly distributed within the soil profile and are dynamic seasonally. Generally, the majority of roots are concentrated in the upper soil where nutrient concentrations are high (Jackson *et al*., 1996; Warren *et al*., 2005). As a result, this portion of the soil is the first to dry out during periods without rain both from direct evaporation and root water uptake (Brooks *et al*., 2006; Warren *et al*., 2005) leaving most of the roots in the driest portion of the soil. However, roots are also located much deeper in the soil and sometimes into rock layers (McElrone *et al*., 2004; Rose *et al*., 2003; Zwieniecki and Newton, 1996), especially in areas with low soil moisture. Thus water uptake rates per unit root surface area shift seasonally down the profile. In the early growing season when water is plentiful, the majority of uptake comes from the upper roots, shifting later in the season to the relatively fewer deeper roots (Brooks *et al*., 2006; Warren *et al*., 2005; Hacke *et al*., 2000).

When roots are in contact with soils that vary spatially in moisture content, they may act as conduits for water redistribution through the soil, driven by gradients in soil water potential. The process of water transport from deep to shallow soil layers through roots, termed *hydraulic lift*, has been demonstrated in a large number plant species, including grasses and cacti as well as shrubs and trees (Caldwell and Richards, 1989; Caldwell, 1990; Caldwell *et al*., 1998; Dawson, 1993; Moreira *et al*., 2003; Yoder and Nowak, 1999). It occurs horizontally as well as vertically (Brooks *et al*., 2002; Burgess *et al*., 1998; Schulze *et al*., 1998), so the more general term 'hydraulic redistribution' (HR) is now preferred. Downward HR can enhance the rate of recharge of deeper soil layers following rainfall events that are not sufficient to saturate the rooting zone (Burgess *et al*., 2001; Ryel *et al*., 2003). HR is most common among deeply rooted species, but can occur even in shallow-rooted species when soil moisture conditions are conducive. Broom snakeweed (*Gutierrezia sorothrae*) rooted to a depth of only 60 cm hydraulically lifts about 15 % of the water it transpires (Wan *et al*., 1993; Richards and Caldwell, 1987).

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The process generally occurs only at night or during periods of heavy cloud cover (Caldwell and Richards, 1989) when stomata are closed, and when there are strong gradients in soil moisture content. Roots then provide a low-resistance pathway for water flow from areas of high to low soil moisture. When the water potential in the shallow roots reaches a certain threshold above the water potential in the surrounding soil (this threshold varies among species), water begins to exude from the roots and into the soil (Baker and van Bavel, 1986; Richards and Caldwell, 1987; Caldwell, 1990; Dawson, 1993). Meinzer *et al*. (2004b) found that when upper soil layers dry to about –0.4 MPa, they become an effective sink for water from deeper layers.

The amount of water moved by HR is relatively small – less than 0.5 mm m^{-1} soil depth day^{-1} – (Brooks *et al*., 2006), but may have a significant impact on the rate of soil drying since water uptake from those layers has also slowed considerably at soil water potentials below –0.4 MPa. HR can replace 40–80 % of the daily water used from those upper layers (Brooks *et al*., 2002; Brooks *et al*., 2006, Domec *et al*., 2004; Meinzer *et al*., 2004b). Brooks *et al*. (2002) found that HR delayed soils in coniferous forests from reaching water potentials equal to the minimum midday leaf water potential (point at which no water can be obtained from that soil layer) by an additional 16–21 days depending on the system. This delay in soil drying can be critical in decreasing root cavitation and preserving root function in these upper soils (Domec *et al*., 2004).

In summary, root systems appear to be highly responsive to soil water availability and soil properties such as texture. Rooting depth, total fine root surface area and specific fine root conductivity are dependent on species and site conditions. In addition, root cavitation and hydraulic redistribution also play important roles in regulating root water uptake and plant transpiration.

2.3 Evapotranspiration in Forest Ecosystems

2.3.1 Evaporation and Transpiration

Micrometeorologists and hydrologists often combine evaporation and transpiration into one measurement for a watershed, largely because the methods used to determine evapotranspiration (ET) cannot distinguish between the two fluxes, yet the two processes are quite different. Recently, stable isotopic techniques have become available for helping to separate these two fluxes (Moreira *et al*., 1997; Wang and Yakir, 2000; Williams *et al*., 2004; Yepez *et al*., 2003) because water transpired from leaves is more enriched isotopically than is water evaporated from soil (Yakir *et al*., 1993). By measuring the isotopic signature of water vapor from leaves and the soil, and measuring the atmospheric water vapor signature over time, it is possible to separate these fluxes using a mixing model approach explained in Moreira *et al*. (1997). Trees have the potential greatly to increase evaporative losses from an ecosystem because of the increase in evaporative surface and the greater access to soil water through roots. Evaporation from soils is generally restricted to the upper few centimeters; thus, in forests, transpiration generally accounts for most of ET. For example, Moreira *et al*. (1997) found that in the Amazon forest, transpiration was responsible for nearly all of the loss in water vapor. Wang and Yakir (2000) found that soil evaporation was only 1.5–3.5 % of the evapotranspiration flux from crops in a desert environment. Williams *et al*. (2004) found that soil evaporation changed from 0 % in an olive orchard prior to irrigation, to 14–31 % for the 5 days following irrigation. Thus, even with wet soils in a system with relatively low canopy cover, transpiration far exceeds soil evaporation.

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2.3.2 Transpiration from the Understory

Transpiration can be further divided between understory and overstory components, which can experience very different environmental microclimates. The understory is a relatively sheltered environment with lower radiation and higher relative humidity than the overstory (Blanken and Black, 2004; Scott *et al*., 2003; Unsworth *et al*., 2004; Yepez *et al*., 2003). As a result, transpiration of the understory is generally less than that of the overstory. In a mesic coniferous forest with an LAI of 9.6, understory transpiration was approximately one tenth of the ecosystem vapor flux (Unsworth *et al*., 2004). However, in a semiarid woodland with LAI of 1.6, understory transpiration was closer to one third to one half of the ecosystem flux during wet periods (Scott *et al*., 2003). Similarly, in larch (*Larix gmelinii*) and pine (*Pinus sylvestris*) forests in Siberia where 40 % of the radiation reaches the understory, understory transpiration can amount to 25–50 % of the ecosystem vapor flux (Hamada *et al*., 2004).

Seasonal variability of understory transpiration is dependent on the seasonal variability of surface soil moisture, R_n and D. In a semiarid woodland, understory transpiration was more variable than overstory transpiration over time because the understory plants had shallow roots in soil layers with highly variable moisture availability, whereas the overstory had deep roots with access to more consistent and reliable water (Scott *et al*., 2003). However, in more mesic coniferous forests, understory transpiration may be less variable over time as understory radiation and surface soil moisture are less variable over time (Unsworth *et al*., 2004). A deciduous overstory will also cause more variability in the understory environment that could influence understory transpiration if understory leaves are present when overstory leaves are not, especially in tropical deciduous forests, which have large seasonal variation in rainfall but little variation in temperature.

2.4 Applying Concepts: Changes in Hydrologic Processes through the Life Cycle of Forests

As an example of an application of concepts presented in the preceding sections, we now explore some of the ways that changes in the structure and function of forests through developmental stages impact hydrologic processes. In many parts of the world, one of the most dramatic impacts of forest land use is the alteration of forest age–class structures. The structure and function of forests undergo significant changes through the entire life cycle (Franklin *et al*., 2002; Bond and Franklin, 2002), and these changes impact evapotranspiration (Harr, 1982; Hicks *et al*., 1991; Keppeler and Ziemer, 1990; Zimmerman *et al*., 2000; Law *et al*., 2001; Moore *et al*., 2004), fog and rainfall interception and losses (Pypker *et al*., in press; Zinke, 1967), and streamflow (Harr *et al*., 1975; Hicks *et al*., 1991; Jones and Grant, 1996; Thomas and Megahan, 1998). The dramatic impacts of forest harvest and early regeneration on hydrology have been well documented (e.g., Hewlett and Hibbert, 1961; Swank *et al*., 2001; Jones and Post, 2004). Less well recognized are slow but profound changes that may occur as the composition, structure and function of the new forest continue to develop.

We focus on coniferous forests of the western USA. The details of developmental stages are different in other forest types, but most undergo changes in species composition, structural complexity and water storage capacity, and there are common elements in the impacts of these changes on hydrology.

2.4.1 A Summary of Age-related Changes in Forest Composition, Structure, and Function

Many of the compositional, structural and functional changes that occur through forest development can strongly influence hydrology. After a major disturbance, coniferous forests of the Pacific Northwest regenerate quickly, but their density and early growth varies depending on the type of disturbance and legacies from the previous forest (Franklin *et al*., 2002). Often, fast-growing grasses and broadleaf shrubs and trees, which typically have much higher maximum g_s compared with later successional species, are established in dense stands. Even though the LAI of this pioneer vegetation may be lower than that of the previous forest, vegetation water use may be as high or higher. However, the decoupling coefficient (Ω; Section 2.2.2) between transpiration and D in the pioneer vegetation is likely to be greater than in later developmental stages because of the low stature and comparatively smooth canopy structure.

If conifer regeneration is abundant, the coniferous crown closes and LAI reaches a maximum within a couple of decades – this is less than 5% of the natural life cycle of the forest. In humid regions, the crown at this point is usually dense, and there is little understory vegetation. Subsequently, as trees grow taller, the crown is ‘pushed up’ in space, but total leaf area does not change much. Trees start to compete with each other: some die, others grow much larger, and small, shade-tolerant, trees (mostly conifers) begin to populate gaps. A thick organic layer forms on the soil surface, which minimizes soil evaporation but also intercepts precipitation. Roots and mycorrhizal hyphae of shade-tolerant trees explore the organic layer and even large woody debris, which can provide a considerable water reservoir that is not utilized by the initial cohort of non-shade-tolerant trees. As the trees grow larger, their biomass also stores increasing amounts of water (Section 2.2.3). This stored water can be important in maintaining transpiration in large trees during seasonal drought, although it is a small component of total site water storage, even in mature forests.

In most forest types, the canopies of older forests become structurally complex both vertically and horizontally, increasing in aerodynamic conductance and interception relative to dense, young forests. In most humid regions, older forests harbor an abundance of bryophytes and lichens that strongly influence the interception of precipitation, serve as a ‘spongy’ storage of water and also moderate the canopy microclimate. Root systems also become more structurally complex over time, but generalizations are difficult due to limited data.

2.4.2 Impacts of Tree Size on Stomatal Conductance and Whole-tree Water Use

Large trees extract a huge quantity of water from the soil (more than 100 kg day^{-1} for a large conifer) and transport it against gravity and through tiny xylem conduits to foliage that is 50–100 meters above the ground. Increasing height results in a longer hydraulic path length; note that Equation (2.2) predicts an inverse relationship between g_s and L, and therefore between transpiration and L, if all other factors remain constant. The complex, 'tortuous' branching pattern of older trees makes the transport even more difficult, because xylem conductivity (k_s) is especially low at branch junctures. All of these changes tend to reduce hydraulic conductance (K, Section 2.2.3) as trees grow larger (Ryan *et al.*, 2000; Phillips *et al.*, 2002), although the potential impacts are compensated to some extent by other adjustments (e.g., A_L:A_S, Section 2.2.4; McDowell *et al.*, 2002a).

As predicted from Equation (2.2), age-related changes in tree hydraulic architecture often affect stomatal conductance at the leaf level. Many studies have shown that g_s is reduced in older trees, although this is not found universally (Bond, 2000). The change in stomatal conductance is indicated most clearly by a change in the composition of carbon isotopes (δ^{13}C) in foliage over a range of tree sizes (Figure 2.5). Although there are several possible explanations for the isotopic change, in most cases the best explanation is a decrease in g_s in older trees (Yoder *et al.*, 1994; Koch *et al.*, 2004). Direct measurements of water fluxes in conifer stems also show that transpiration per unit leaf area is reduced in older trees, especially in conditions of relatively high water availability in soil and low to moderate D (Ryan *et al.*, 2000; Phillips *et al.*, 2002; Irvine *et al.*, 2004). As a result, transpiration increases exponentially with tree size during the early stages of tree growth, but later reaches an asymptotic maximum (Meinzer *et al.*, 2005). However, there are exceptions to these general trends (see, for example, Barnard and Ryan, 2003).

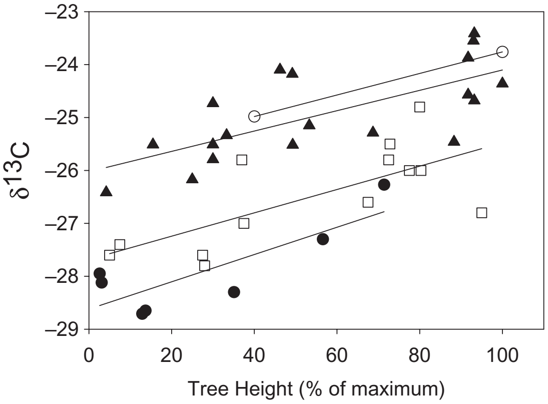

Figure 2.5 *Carbon isotope composition of foliage from the tops of nonsuppressed trees of different heights. Each symbol represents a different species: closed circles –* Pinus sylvestris *(unpublished data courtesy of Maurizio Mencuccini); open squares –* Pinus ponderosa *(Yoder* et al.*, 1994); closed triangles –* Pseudotsuga menziesii*, each point is a mean of five samples (unpublished data collected by Bond* et al. *Wind River, WA and McDowell* et al.*, 2002b); open circles –* Quercus oregana*, each point is a mean of seven samples (unpublished data collected by McDowell* et al.*, Corvallis OR). Heights are expressed relative to the maximum for the species at the site sampled (heights of Scots pine were estimated from tree ages). Slopes of the relationships between δ^{13}C and percent maximum height are 0.22, 0.19 and 0.257 and 0.20 for* P. sylvestris*,* P. ponderosa*,* P. menziesii *and* Q. oregana*, respectively*

In certain situations (e.g., when resistance of the canopy boundary layer is very low relative to leaf diffusive resistance), it is possible to estimate differences in stomatal conductance using measurements of stable isotope composition of leaf carbon and photosynthetic capacity of foliage from the sunlit tops of tree crowns. The estimation relies on an explicit linear relationship between isotope discrimination and the ratio of carbon dioxide concentrations internal and external to leaves (Farquhar *et al*., 1982). These carbon dioxide concentrations, in turn, are a function of the ratio between photosynthesis and stomatal conductance, or A/g, also known as 'intrinsic water use efficiency' (Ehleringer *et al*., 1993). Finally, relative differences in stomatal conductance can be derived using measurements of the response function of photosynthesis to internal carbon dioxide, or 'A/C_i' curves. For the Douglas fir in Figure 2.5, the change in foliage isotope composition indicates a reduction in average g_s of a little over 2% for each 10-percentile change in height, or 20% over the height range of the forest, which in turn suggests a similar reduction in transpiration per unit leaf area as long as the microclimate is similar across the forest age classes.

2.4.3 Age-related Change in Transpiration, Interception and Water Storage on the Forest Stand Level

In general, LAI tends to decrease somewhat in aging forests after they achieve maximum LAI (Ryan *et al*., 1997). Given that leaf-level transpiration also decreases with age (above), it might be hypothesized that transpiration on the stand level might also decline with age. Alternatively, changes in stand density, species composition or understory characteristics could counterbalance the age-related shifts in LAI and leaf-level transpiration, preserving relative constancy in plant water use.

One problem with this analysis is the assumption that transpiration is closely related to LAI. Although LAI is usually a good predictor of change in transpiration in initial stages of forest development as vegetation cover increases following a disturbance, transpiration does not correspond well with changes in LAI in later developmental stages (Zimmermann *et al*., 2000). Changes in sapwood basal area, on the other hand, appear to explain much of the variation in transpiration in stands of different ages (Dunn and Connor, 1993; Zimmermann *et al*., 2000; Moore *et al*., 2004), consistent with the notion that transpiration is strongly influenced by the supply capacity of the hydraulic system (*K*; Section 2.2.3). The presence of very large trees in old forests can give a deceptive sense of their water conducting capacity. Moore *et al*. (2004) found that although the total basal area in an old-growth Douglas-fir forest was more than twice that of a 45-year-old forest (about 85 vs 35 $\mathrm{m^2\,ha^{-1}}$, respectively), the old forest had lower sapwood basal area (17 vs nearly 22 $\mathrm{m^2\,ha^{-1}}$ for the old and young forests, respectively). In this study, age-related changes in species composition, tree height, and sapwood basal area all limited seasonal transpiration in the old-growth forest compared with that of the younger stand. Due to their additive influence, the young forest used nearly three times as much water over a growing season compared with the old forest.

In contrast to the findings of Moore *et al*. (2004), a replicated study of three old (about 450 years) and three young (about 25 years) Douglas-fir stands in western Washington, USA, revealed no significant difference in stand level transpiration between the age classes during the growing season (Bond *et al*., unpublished). However, the young stands had recently been heavily infected by a foliar pathogen (*Phaeocryptopus gaeumannii*) that is known to reduce transpiration (Manter *et al*., 2003), so the results may say more about the effects of the pathogen than stand age on transpiration. Published data for four conifer species show an average decrease in maximum daily transpiration of about 4% for each ten-percentile increment in forest height (Figure 2.6), although there is a great deal of variability in the data. However, age-related differences in maximum daily transpiration do not necessarily translate into lower total water use on a yearly or seasonal basis. In a water-limited ponderosa pine ecosystem, young forests exhausted soil water reserves earlier in the growing season than did old forests. The young forests endured a longer period of drought than did older forests, and over the growing season water use was similar between the age classes (Irvine *et al*., 2004).

Interception water losses were the chief cause of reduced water yield following afforestation of pasture or farmed land with eucalypts (Whitehead and Beadle, 2004), and increased interception also affects site water balance in regenerating forests after harvest. As with developmental changes in transpiration, leaf area is an important determinant of change in interception in the early stages of stand development, but it is less important in subsequent stages. A large epiphytic community often develops in older forests, and the mosses and bryophytes are able to intercept and store very large amounts of water; epiphytes double the water storage capacity in canopies of old-growth Douglas-fir forests relative to young forests with similar LAI (Pypker *et al*., 2005). Pypker *et al*. (2005) found that differences in interception were small during moderate to heavy rain events due to other changes in canopy structure, but interception losses were much greater from old forests during intermittent and small rain events, which can occur frequently in the Pacific

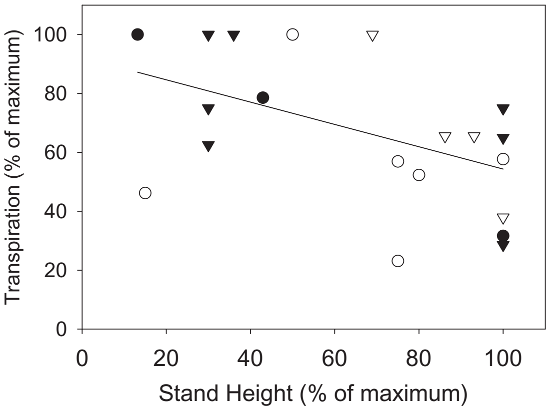

Figure 2.6 *Response of maximum stand-level transpiration to increasing stand height. Each symbol represents a different species: closed circles –* Pinus ponderosa *(Irvine* et al.*, 2004); open circles –* Pinus sylvestris *(Zimmermann* et al.*, 2000); closed triangles –* Pseudotsuga menziesii *(Phillips* et al.*, 2002); open triangles –* Picea abies *(Köstner* et al.*, 2002). Height is expressed as a proportion of estimated maximum for the species and site; transpiration is daily maximum, expressed as a proportion of the maximum in each dataset. The overall* r^2 *is 0.24*

Northwest where this forest type grows. Thus, both interception losses from the canopy as well as a heavier litter layer in the older forests result in less rainfall penetration to the mineral soil of older forests during small rain events (Pypker *et al.*, unpublished data).

In some areas interception and condensation of fog by mature conifer canopies can actually increase the amount of moisture reaching the soil (Dawson, 1998), and extensive harvests in such forests may result in increased precipitation 'downwind' from the harvest (Harr, 1982).

2.4.4 Impacts of Change in Species Composition on Transpiration in Aging Forests

Most forests undergo significant changes in species composition over their normal lifespan. In some cases the changes are dramatic, and often characterized as successional patterns; in others the changes are more subtle. In the conifer-dominated Pacific Northwest of the United States, broadleaf trees and shrubs are often heavy water consumers in young stands. In the case study by Moore *et al.* (2004) outlined above, the sapwood basal area of broadleaf species in a young (45-year-old) Douglas-fir forest was six times greater than in an old-growth forest, and seasonal water use normalized by sapwood basal area was 40% greater for the broadleaf species than for conifer species of the same age. In old-growth forests, late-successional, shade-tolerant conifers with high leaf areas and low transpiration rates constituted most of the sapwood basal area. These shade-tolerant conifers averaged 30% lower water use, again normalized by sapwood area, than the pioneer conifers. In combination, the reduction in broadleaf vegetation and increase in shade tolerant conifers, in addition to lower overall sapwood basal area, resulted in a seasonal water use by the old forest that was only about one-third that of the young forest. In agreement with the preceding patterns, Meinzer *et al.* (2005) found that daily transpiration of individual trees was consistently greater in broadleaf than in coniferous species at a given tree size.

2.4.5 Implications for Predictive Models

The Penman–Monteith equation (Monteith, 1965) is widely accepted as the definitive mechanistic description of relationships between vegetation properties and environmental drivers that influence transpiration, and is arguably one of the most important contributions of its time to vegetation science. However, the difficulty involved in accurate estimation of the conductance terms (G_c and boundary layer) in the Penman–Monteith equation is often overlooked, even though estimates of transpiration for forests are sensitive to these terms due to the strong coupling between stomatal conductance and transpiration (Section 2.2.2). Both canopy stomatal and boundary layer conductance change over stand development, and neither is easily measured or predictable as a function of LAI (although this is commonly done).

However, our current understanding of plant physiological processes suggests using more robust approaches. One approach is to estimate canopy conductance using mechanistic models of environment and plant hydraulic architecture, as described in this chapter. This has been done successfully in at least one model, SPA (Soil–Plant–Atmosphere; Williams *et al.*, 1996). Stable carbon isotopes may offer another, more empirical, approach.

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The consistent change in $\delta^{13}C$ in relation to relative maximum tree height (Figure 2.5) suggests that this parameter could be a useful predictor of change in stomatal conductance through stand development. Together with measurements of change in LAI, $\delta^{13}C$ could provide a semi-empirical approach for estimating change in G_c through forest development.

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References

Andrade JL, Meinzer FC, Goldstein G, Holbrook NM, Cavelier J, Jackson P, Silvera ••. 1998. Regulation of water flux through trunks, branches and leaves in trees of a lowland tropical forest. *Oecologia*, **115**, 463–471.

Angeles G, Bond B, Boyer B, Brodribb T, Brooks JR, Burns MJ, Cavender-Bares J, Clearwater M, Cochard H, Comstock J, Davis S, Domec J-C, Donovan L, Ewers F, Gartner B, Hacke U, Hinckley T, Holbrook NM, Jones HG, Kavanagh K, Law B, Lopez-Portillo J, Lovisolo C, Martin T, Martinez-Vilalta J, Mayr S, Meinzer FC, Melcher P, Mencuccini M, Mulkey S, Nardini A, Neufeld HS, Passioura J, Pockman WT, Pratt RB, Rambal S, Richter H, Sack L, Salleo S, Schubert A, Schulte P, Sparks JP, Sperry J, Teskey R and Tyree M. 2004. The Cohesion-Tension Theory. *New Phytologist* (Letters), **163**, 451–452.

Anthoni PM, Unsworth MH, Law BE, Irvine J, Baldocchi D, Moore DJ. 2002. Seasonal differences in carbon and water vapor exchange in young and old-growth ponderosa pine ecosystems. *Agricultural and Forest Meteorology*, **111**, 203–222.

Baker JM, van Bavel CHM. 1986. Resistance of plant roots to water loss. *Agronomy Journal*, **78**, 641–644.

Barnard HR, Ryan MG. 2003. A test of the hydraulic limitation hypothesis in fast-growing *Eucalyptus saligna*. *Plant, Cell and Environment*, **26**, 1235–1245.

Benyon RG. 1999. Nighttime water use in an irrigated *Eucalyptus grandis* plantation. *Tree Physiology*, **19**, 853–859.

Blanken PD, Black TA. 2004. The canopy conductance of a boreal aspen forest, Prince Albert National Park, Canada. *Hydrological Processes*, **18**, 1561–1578.

Blanken PD, Black TA, Yang PC, Neumann HHNZ, Staebler R, den Hartog G, Novak MD, Lee X. 1997. Energy balance and canopy conductance of a boreal aspen forest: partitioning overstory and understory components. *Journal of Geophysical Research*, **102**, 28915–28927.

Bond BJ. 2000. Age-related changes in photosynthesis of woody plants. *Trends in Plant Science*, **5**, 349–353.

Bond BJ. 2003. Hydrology and ecology meet – and the meeting is good. *Hydrological Processes*, **17**, 2087–2089.

Bond BJ, Franklin JF. 2002. Aging in Pacific Northwest forests: A selection of recent research. *Tree Physiology*, **22**, 73–76.

Bond BJ, Kavanagh KL. 1999. Stomatal behavior of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential. *Tree Physiology*, **19**, 503–510.

Bristow KL, Campbell GS, Calissendorff C. 1984. The effects of texture on the resistance to water movement within the rhizosphere. *Soil Science Society of America Journal*, **42**, 657–659.

Brooks JR, Meinzer FC, Coulombe R, Gregg JW. 2002. Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests. *Tree Physiology*, **22**, 1107–1117.

Brooks JR, Meinzer FC, Warren JM, Domec JC, Coulombe R. 2006. Hydraulic redistribution in a Douglas-fir forest: lessons from system manipulations. *Plant, Cell and Environment*, **29**, 138–150.

Bucci SJ, Scholz FG, Goldstein G, Meinzer FC, Sternberg LDSL. 2003. Dynamic changes in hydraulic conductivity in petioles of two savanna tree species: factors and mechanisms contributing to the refilling of embolized vessels. *Plant, Cell and Environment*, **26**, 1633–1645.

Bucci SJ, Scholz FG, Goldstein G, Meinzer FC, Hinojosa JA, Hoffmann WA, Franco AC. 2004. Processes preventing nocturnal equilibration between leaf and soil water potential in tropical savanna woody species. *Tree Physiology*, **24**, 1119–1127.

Bucci SJ, Goldstein G, Meinzer FC, Franco AC, Campanello P, Scholz FG. 2005. Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plant water potential in Neotropical savanna trees. *Trees*, in press.

Burgess SSO, Adams MA, Turner NC, Ong CK. 1998. The redistribution of soil water by tree root systems. *Oecologia*, **115**, 306–311.

Burgess SSO, Adams MA, Turner NC, White DA, Ong CK. 2001. Tree roots: conduits for deep recharge of soil water. *Oecologia*, **126**, 158–165.

Caldwell MM 1990. Water parasitism stemming from hydraulic lift: a quantitative test in the field. *Israel Journal of Botany*, **39**, 395–402.

Caldwell MM, Richards JH. 1989. Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia*, **79**, 1–5.

Caldwell MM, Dawson TE, Richards JH. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia*, **113**, 151–161.

Canny MJ. 1995. A new theory for the ascent of sap – cohesion supported by tissue pressure. *Annals of Botany*, **75**, 343–357.

Canny MJ. 1998. Transporting water in plants. *American Scientist*, **86**, 152–159.

Cochard H. 1992. Vulnerability of several conifers to air embolism. *Tree Physiology*, **11**, 73–83.

Davies WJ, Zhang J. 1991. Root signals and the regulation of growth and development of plants in drying soil. *Annual Review of Plant Physiology and Molecular Biology*, **42**, 55–76.

Dawson TE. 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Oecologia*, **95**, 565–574.

Dawson TE. 1998. Fog in the California redwood forest: ecosystem inputs and use by plants. *Oecologia*, **117**, 476–485.

Dixon HH, Joly J. 1894. On the ascent of sap. *Philosophical Transactions of the Royal Society of London B*, **186**, 563–576.

Domec J-C, Gartner BL. 2001. Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. *Trees*, **15**, 204–214.

Domec J-C, Gartner BL. 2002. How do water transport and water storage differ in coniferous earlywood and latewood? *Journal of Experimental Botany*, **53**, 2369–2379.

Domec J-C, Warren JM, Meinzer FC, Brooks JR, Coulombe R. 2004. Native root xylem embolism and stomatal closure in stands of Douglas-fir and ponderosa pine: mitigation by hydraulic redistribution. *Oecologia*, **141**, 7–16.

Donovan LA, Grise DJ, West JB, Papport RA, Alder NN, Richards JH. 1999. Predawn disequilibrium between plant and soil water potentials in two cold-desert shrubs. *Oecologia*, **120**, 209–217.

Doussan C, Vercambre G, Pagès L. 1998. Modelling of the hydraulic architecture of root systems: an integrated approach to water absorption–distribution of axial and radial conductances in maize. *Annals of Botany*, **81**, 225–232.

Dunn GM, Connor DJ. 1993. An analysis of sap flow in mountain ash (*Eucalyptus regnans*) forests of different age. *Tree Physiology*, **13**, 321–336.

Ehleringer JR, Hall AE, Farquhar GD. 1993. *Stable isotopes and plant carbon-water relations*. Academic Press: San Diego.

Farquhar GD. 1978. Feedforward responses of stomata to humidity. *Australian Journal of Plant Physiology*, **5**, 787–800.

Farquhar GD, O'Leary MH, Berry JA. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology*, **9**, 121–137.

Feild TS, Holbrook NM. 2000. Xylem sap flow and stem hydraulics of the vesselless angiosperm *Drymis granadensis* (Winteraceae) in a Costa Rican elfin forest. *Plant, Cell and Environment*, **23**, 1067–1077.

Ford CR, Goranson CE, Mitchell RJ, Will RE, Teskey RO. 2004. Diurnal and seasonal variability in the radial distribution of sap flow: predicting total stem flow in *Pinus taeda* trees. *Tree Physiology*, **24**, 951–960.

Franklin JF, Spies TA, Van Pelt R, Carey AB, Thornburgh DA, Berg DR, Lindenmayer DB, Harmon ME, Keeton WS, Shaw DC, Bible K, Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management*, **155**, 399–423.

Franks PJ, Cowan IR, Farquhar GD. 1997. The apparent feedforward response of stomata to air vapour pressure deficit: information revealed by different experimental procedures with two rainforest trees. *Plant, Cell and Environment*, **20**, 142–145.

Goldstein G, Andrade JL, Meinzer FC, Holbrook NM, Cavelier J, Jackson P, Celis A. 1998. Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant, Cell and Environment*, **21**, 397–406.

Gollan T, Passioura JB, Munns R. 1986. Soil water status affects stomatal conductance of fully turgid wheat and sunflower leaves. *Australian Journal of Plant Physiology*, **13**, 459–464.

Granier A, Huc R, Colin F. 1992. Transpiration and stomatal conductance of two rain forest species growing in plantations (*Simarouba amara* and *Goupia glabra*) in French Guyana. *Annals of Forest Science*, **49**, 17–24.

Green SR, McNaughton KG, Clothier BE. 1989. Observations of night-time water use in kiwifruit vines and apple trees. *Agricultural and Forest Meteorology*, **48**, 251–261.

Hacke UG, Sperry GS, Ewers BE, Ellsworth DS, Schafer KVR, Oren R. 2000. Influence of soil porosity on water use in *Pinus taeda*. *Oecologia*, **124**, 495–505.

Hamada S, Ohta T, Hiyama T, Kuwada T, Takahashi A, Maximov TC. 2004. Hydrometeorological behaviour of pine and larch forests in eastern Siberia. *Hydrological Processes*, **18**, 23–39.

Harr RD. 1982. Fog drip in the Bull Run municipal watershed, Oregon. *Water Resources Research*, **18**, 785–789.

Harr RD, Harper, WC, Krygier JT. 1975. Changes in storm hydrographs after road building and clear-cutting in the Oregon coast range. *Water Resources Research*, **11**, 436–444.

Herbst M. 1998. Stomatal behaviour in a beech canopy: an analysis of Bowen ratio measurements compared with porometer data. *Plant, Cell and Environment*, **18**, 1010–1018.

Hewlett JD, Hibbert AR. 1961. Increases in water yield after several types of forest cutting. *International Association Scientific Hydrology Bulletin*, **6**, 5–17.

Hicks BJ, Beschta RL, Harr RD. 1991. Long-term changes in streamflow following logging in western Oregon and associated fisheries implications. *Water Resources Research*, **27**, 217–226.

Hobbie EA, Colpaert JV. 2004. Nitrogen availability and mycorrhizal colonization influence water use efficiency and carbon isotope patterns in *Pinus sylvestris*. *New Phytologist*, **164**, 515–525.

Holbrook NM, Sinclair TR. 1992. Water balance in the arborescent palm, *Sabal palmetto*. II. Transpiration and water storage. *Plant, Cell and Environment*, **15**, 401–409.

Holbrook NM, Burns MN, Field CB. 1995. Negative xylem pressures in plants: a test of the balancing pressure technique. *Science*, **270**, 1193–1194.

Irvine J, Law BE, Kurpius MR, Anthoni PM, Moore D, Schwarz PA. 2004. Age-related changes in ecosystem structure and function and effects on water and carbon exchange in ponderosa pine. *Tree Physiology*, **24**, 753–763.

Jackson RB, Canadell J, Ehleringer JR, Mooney HA. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia*, **108**, 389–411.

James SA, Meinzer FC, Goldstein G, Woodruff D, Jones T, Restom T, Mejia M, Clearwater M, Campanello P. 2003. Axial and radial water transport and internal water storage in tropical forest canopy trees. *Oecologia*, **134**, 37–45.

Jarvis PG, McNaughton KG. 1986. Stomatal control of transpiration: scaling up from leaf to region. *Advances in Ecological Research*, **15**, 1–49.

Jones JA, Grant GE, 1996. Peak flow responses to clear-cutting and roads in small and large basins, western Cascades, Oregon. *Water Resources Research*, **32**, 959–974.

Jones JA, Post DA. 2004. Seasonal and successional streamflow response to forest cutting and regrowth in the northwest and eastern United States. *Water Resources Research*, **40**: W05203, doi:10.1029/2003WR002952.

Kavanagh KL, Bond BJ, Aitken SN, Gartner BL, Knowe S. 1999. Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings. *Tree Physiology*, **19**, 31–37.

Keppeler ET, Ziemer RR. 1990. Logging effects on streamflow: Water yield and summer low flows at Caspar Creek in Northwestern California. *Water Resources Research*, **26**, 1669–1679.

Kobayashi Y, Tanaka T. 2001. Water flow and hydraulic characteristics of Japanese red pine and oak trees. *Hydrological Processes*, **15**, 1731–1750.

Koch, GW, Sillett SC, Jennings GM, Davis SD. 2004. The limits to tree height. *Nature*, **428**, 851–854

Köstner BMM, Falge E, Tenhunen JD. 2002. Age-related effects on leaf area/sapwood area relationships, canopy transpiration and carbon gain of Norway spruce stands (*Picea abies*) in the Fichtelgebirge, Germany. *Tree Physiology*, **22**, 567–574.

Köstner BMM, Schulze E-D, Kelliher FM, Hollinger DY, Byers JN, Hunt JE, McSeveny TM, Meserth R, Weir PL. 1992. Transpiration and canopy conductance in a pristine broad-leaved forest of *Nothofagus*: an analysis of xylem sap flow and eddy correlation measurements. *Oecologia*, **91**, 350–359.

Larcher W. 1975. *Physiological Plant Ecology*. Springer-Verlag: New York.

Law BE, Goldstein AH, Anthoni PM, Unsworth MH, Panek JA, Bauer MR, Fracheboud JM, Hultman N. 2001. Carbon dioxide and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer. *Tree Physiology*, **21**, 299–308.

Loustau D, Berbigier P, Roumagnae P, Arruda-Pacheco C, David JS, Ferreira MI, Pereira JS, Tavares R. 1996. Transpiration of a 64-year-old maritime pine stand in Portugal. 1. Seasonal course of water flux through maritime pine. *Oecologia*, **107**, 33–42.

Maherali H, DeLucia EH. 2001. Influence of climate-driven shifts in biomass allocation on water transport and storage in ponderosa pine. *Oecologia*, **129**, 481–491.

Manter DK, Bond BJ, Kavanagh KL, Stone JK, Filip GM. 2003. Modelling the impacts of the foliar pathogen, *Phaeocryptopus gaeumannii*, on Douglas-fir physiology: net canopy carbon assimilation, needle abscission and growth. *Ecological Modelling*, **164**, 211–226.

McDowell NG, Barnard H, Bond BJ, Hinckley T, Hubbard RH, Ishii KB, Meinzer FC, Marshall JD, Magnani F, Phillips N, Ryan MG, Whitehead D. 2002a. The relationship between tree height and leaf area : sapwood area ratio. *Oecologia*, **132**, 12–20.

McDowell NG, Phillips N, Lunch C, Bond BJ, Ryan MG. 2002b. An investigation of hydraulic limitation and compensation in large, old Douglas-fir trees. *Tree Physiology*, **22**, 763–774.

McElrone AJ, Pockman WT, Martinez-Vilalta J, Jackson RB. 2004. Variation in xylem structure and function in stems and roots of trees to 20 m depth. *New Phytologist*, **163**, 507–517.

Meinzer FC. 2002. Co-ordination of liquid and vapor phase water transport properties in plants. *Plant, Cell and Environment*, **25**, 265–274.

K2

Meinzer FC, Goldstein G, Holbrook NM, Jackson P, Cavelier J. 1993. Stomatal and environmental control of transpiration in a lowland tropical forest tree. *Plant, Cell and Environment*, **16**, 429–436.

Meinzer FC, Goldstein G, Jackson PJ, Holbrook NM, Gutierrez MV. 1995. Environmental and physiological regulation of transpiration in tropical forest gap species: the influence of boundary layer and hydraulic properties. *Oecologia*, **101**, 514–522.

Meinzer FC, Hinckley TM, Ceulemans R. 1997. Apparent responses of stomata to transpiration and humidity in a hybrid poplar canopy. *Plant, Cell and Environment*, **20**, 1301–1308.

Meinzer FC, James SA, Goldstein G, Woodruff D. 2003. Whole-tree water transport scales with sapwood capacitance in tropical forest canopy trees. *Plant, Cell and Environment*, **26**, 1147–1155.

Meinzer FC, James SA, Goldstein G. 2004a. Dynamics of transpiration, sap flow and use of stored water in tropical forest canopy trees. *Tree Physiology*, **24**, 901–909.

Meinzer FC, Brooks JR, Bucci SJ, Goldstein GH, Scholz FG, Warren JM. 2004b. Converging patterns of uptake and hydraulic redistribution of soil water in contrasting woody vegetation types. *Tree Physiology*, **24**, 919–928.

Meinzer FC, Bond BJ, Warren JM, Woodruff DR. 2005. Does water transport scale universally with tree size? *Functional Ecology*, **19**, 558–565.

Meinzer FC, Brooks JR, Domec J-C, Gartner BL, Warren JM, Woodruff DR, Bible K, Shaw DC. 2006. Dynamics of water transport and storage in conifers studied with deuterium and heat tracing techniques. *Plant, Cell and Environment*, **29**, 105–114.

Meinzer FC, Woodruff DR, Shaw DC. 2004c. Integrated responses of hydraulic architecture, water and carbon relation of western hemlock to dwarf mistletoe infection. *Plant, Cell Environment*, **27**, 937–946.

Melcher PJ, Goldstein G, Meinzer FC, Yount DE, Jones T, Holbrook NM, Huang CX. 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. 1995. Climate influences the leaf area/sapwood area ratio in Scots pine. *Tree Physiology*, **15**, 1–10.

Monterith, JL, 1965. Evaporation and environment. *Symposium Society Experimental Biology*, **19**, 205–234.

Moore GW, Bond BJ, Jones JA, Phillips N, Meinzer FC. 2004. Structural and compositional controls on transpiration in a 40- and 450-yr-old riparian forest in western Oregon, USA. *Tree Physiology*, **24**, 481–491.

Moreira MZ, Sternberg L da SL, Martinelli LA, Cictoria RL, Barbosa EM, Bonates LCM, Nepstad DC. 1997. Contribution of transpiration to forest ambient vapor based on isotopic measurements. *Global Change Biology*, **3**, 439–450.

Moreira MZ, Scholz FG, Bucci SJ, Sternberg L da SL, Goldstein G, Meinzer FC, Franco AC. 2003. Hydraulic lift in a Netropical Savanna. *Functional Ecology*, **17**, 573–581.

Mott KA, Parkhurst DF. 1991. Stomatal responses to humidity in air and helox. *Plant, Cell and Environment*, **14**, 509–515.

Nardini A, Tyree MT. 1999. Root and shoot hydraulic conductance of seven *Quercus* species. *Annals of Forest Science*, **56**, 371–377.

Oren R, Phillips N, Ewers BE, Pataki DE, Megonigal JP. 1999a. Sap-flux-scaled transpiration responses to light, vapor pressure deficit, and leaf area reduction in a flooded *Taxodium distichum* forest. *Tree Physiology*, **19**, 337–347.

Oren R, Sperry JS, Katul GG, Pataki DE, Ewers BE, Phillips N, Schäfer KVR. 1999b. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant, Cell and Environment*, **22**, 1515–1526.

Pataki D, Oren R, Phillips N. 1998. Responses of sap flux and stomatal conductance of *Pinus taeda* L. trees to stepwise reductions in leaf area. *Journal of Experimental Botany*, **49**, 871–878.

Phillips N, Bond BJ, McDowell NG, Ryan MG. 2002. Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. *Tree Physiology*, **22**, 205–211.

Phillips NG, Ryan MG, Bond BJ, McDowell NG, Hinckley TM, Cermák J. 2003. Reliance on stored water increases with tree size in three species in the Pacific Northwest. *Tree Physiology*, **23**, 237–245.

K2

Pockman WT, Sperry JS, O'Leary JW. 1995. Sustained and significant negative water pressure in xylem. *Nature*, **378**, 715–716.

Pypker TG, Bond BJ, Link TE, Marks D, Unsworth MH. 2005. The importance of canopy structure in controlling the interception loss of rainfall: Examples from a young and old-growth Douglas-fir forests. *Agricultural and Forest Meteorology*, **130**, 113–129.

Pypker TG, Unsworth M, Bond BJ. The role of epiphytes in rainfall interception by forests in the Pacific Northwest: Field measurements at the branch and canopy scale. *Canadian Journal of Forest Research*. In press.

Rayment MB, Loustau D, Jarvis PG. 2000. Measuring and modeling conductances of black spruce at three organizational scales: shoot, branch and canopy. *Tree Physiology*, **20**, 713–723.

Richards JH, Caldwell MM. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia*, **73**, 486–489.

Roberts J, Cabral OMR, De Aguiar LF. 1990. Stomatal and boundary-layer conductances in an Amazonian terra firme rain forest. *Journal of Applied Ecology*, **27**, 336–353.

Rose KL, Graham RC, Parker DR. 2003. Water source utilization by *Pinus jeffreyi* and *Arctostaphylos patula* on thin sois over bedrock. *Oecologia*, **134**, 46–54.

Ryan MG, Binkley D, Fownes JG. 1997. Age-related decline in forest productivity: pattern and process. *Advances in Ecological Research*, **27**, 213–262.

Ryan MG, Bond BJ, Law BE, Hubbard RM, Woodruff D, Cienciala E, Kucera J. 2000. Transpiration and whole-tree conductance in ponderosa pine trees of different heights. *Oecologia*, **124**, 553–560.

Ryel RJ, Caldwell MM, Leffler AJ, Yoder CK. 2003. Rapid soil moisture recharge to depth by roots in a stand of *Artemisia tridentata*. *Ecology*, **84**, 757–764.

Schulze E-D, Hall AE. 1982. Stomatal responses, water loss, and CO_2 assimilation rates of plants in contrasting environments. In *Encyclopedia of Plant Physiology, New Series*, Vol. 12B. Eds O.L. Lange, P.S. Nobel, C.B. Osmond, H. Ziegler. Springer-Verlag: New York, pp. 181–230.

Schulze E-D, Lange OL, Buschbom U, Kappen L, Evenari M. 1972. Stomatal responses to changes in humidity in plants growing in the desert. *Planta*, **108**, 259–270.

Schulze E-D, Caldwell MM, Canadell J, Mooney HA, Jackson RB, Parson D, Scholes R, Sala OE, Trimborn P. 1998. Downward flux of water through roots (i.e. inverse hydraulic lift) in dry Kalahari sands. *Oecologia*, **115**, 460–462.

Scott RL,Watts C, Payan JG, Edwards EA, Goodrich DC, Williams DG, Shuttleworth WJ. 2003. The understory and overstory partitioning of energy and water fluxes in an open canopy, semiarid woodland. *Agricultural and Forest Meteorology*, **114**, 127–139.

Sellin A. 1999. Does pre-dawn water potential reflect conditions of equilibrium in plant and soil water status? *Acta Oecologica*, **20**, 51–69.

Shuttleworth WJ, Gash JHC, LLoyd CR, Moore CJ, Roberts J, Marques ADO, Fisch G, Silva V De Paula, De Nazare Goes Ribeiro M, Molion LCB, De Abreu Sa LD, Nobre JC, Cabral OMR, Patel SR, De Moraes JC. 1984. Eddy correlation measurements of energy partition for Amazonian forest. *Quarterly Journal of the Royal Meteorological Society*, **110**, 1143–1162.

Sparks JP, Black RA. 1999. Regulation of water loss in populations of *Populus trichocarpa*: the role of stomatal control in preventing xylem cavitation. *Tree Physiology*, **19**, 453–459.

Sperry JS, Ikeda T. 1997. Xylem cavitation in roots and stems of Douglas-fir and white fir. *Tree Physiology*, **17**, 275–280.

Sperry JS, Saliendra NZ, Pockman WT, Cochard H, Cruziat P, Davis SD, Ewers FW, Tyree MT. 1996. New evidence for large negative xylem pressures and their measurement by the pressure chamber method. *Plant, Cell and Environment*, **19**, 427–436.

Sperry JS, Adler FR, Campbell GS, Comstock JP. 1998. Limitation of plant water use by rhizosphere and xylem conductance: results form a model. *Plant, Cell and Environment*, **21**, 347–359.

Steudle, E. 1994. Water transport across roots. *Plant and Soil*, **167**, 79–90.

Steudle, E. 2001. The cohesion–tension mechanism and the acquisition of water by plant roots. *Annual Review of Plant Physiology and Molecular Biology*, **52**, 847–875.

Swank WT, Vose JM, Elliot KJ. 2001. Long-term hydrologic and water quality responses following commercial clearcutting of mixed hardwoods on a southern Appalacian catchment. *Forest Ecology and Management*, **143**, 163–178.

Tardieu F, Davies WJ. 1993. Integration of hydraulic and chemical signalling in the control of stomatal conductance and water status of droughted plants. *Plant, Cell and Environment*, **16**, 341–349.

Thomas RB, Megahan WF. 1998. Peak flow responses to clear-cutting and roads in small and large basins, western Cascades, Oregon: A second opinion. *Water Resources Research*, **34**, 3393–3403.

Tognetti R, Michelozzi M, Giovanelli A. 1997. Geographical variation in water relations, hydraulic architecture and terpene composition of Aleppo pine seedlings from Italian provenances. *Tree Physiology*, **17**, 241–250.

Tyree MT, Ewers FW. 1991. Tansley review No. 34. The hydraulic architecture of trees and other woody plants. *New Phytologist*, **119**, 345–360.

Tyree MT, Sperry JS. 1989. Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology*, **40**, 19–36.

Tyree MT, Velez V, Dalling JW. 1998. Growth dynamics of root and shoot hydraulic conductance in seedlings of five neotropical tree species: scaling to show possible adaptation to different light regimes. *Oecologia*, **114**, 293–298.

Tyree MT, Zimmermann MH. 2002. *Xylem Structure and the Ascent of Sap*. Springer: New York.

Tyree MT, Salleo S, Nardini A, Lo Gullo MA, Mosca R. 1999. Refilling of embolized vessels in young stems of laurel. Do we need a new paradigm? *Plant Physiology*, **120**, 11–21.

Unsworth MH, Phillips N, Link T, Bond BJ, Falk M, Harmon ME, Hinckley TM, Marks D, Paw U KT. 2004. Components and controls of water flux in an old-growth Douglas-fir-western hemlock ecosystem. *Ecosystems*, **7**, 468–481.

van den Honert TH. 1948. Water transport in plants as a catenary process. *Discussions of the Faraday Society*, **3**, 146–153.

Vogt UK. 2001. Hydraulic vulnerability, vessel refilling, and seasonal courses of stem water potential of *Sorbus aucuparia* L. and *Sambucus nigra* L. *Journal of Experimental Botany*, **52**, 1527–1536.

Wan CG, Sosebee RE, McMichael BL. 1993. Does hydraulic life exist in a shallow-rooted species? A quantitative examination with a half-shrub *Gutierrezia sarothrae*. *Plant Soil*, **153**, 11–17.

Wang X-F, Yakir D. 2000. Using stable isotopes of water in evapotranspiration studies. *Hydrological Processes*, **14**, 1407–1421.

Waring RH, Running SW. 1978. Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth Douglas-fir. *Plant, Cell and Environment*, **1**, 131–140.

Waring RH, Whitehead D, Jarvis PG. 1979. The contribution of stored water to transpiration in Scots pine. *Plant, Cell and Environment*, **2**, 309–317.

Warren JM, Meinzer FC, Brooks JR, Domec J-C. 2005. Vertical stratification of soil water storage and release dynamics in Pacific Northwest coniferous forests. *Agricultural and Forest Meteorology*, **130**, 39–58.

Wells CE, Eissenstadt DM. 2003. Beyond the roots of young seedlings: the influence of age and order on fine root physiology. *Journal of Plant Growth Regulation*, **21**, 324–334.

Whitehead D. 1998. Regulation of stomatal conductance and transpiration in forest canopies. *Tree Physiology*, **18**, 633–644.

Whitehead D, Beadle CL. 2004. Physiological regulation of productivity and water use in *Eucalyptus*: A review. *Forest Ecology and Management*, **193**, 113–140.

Williams DG, Cable WL, Hultine KR, Hoedjes JCB, Yepez EA, Simonneaux V, Er-Raki S, Boulet G, de Bruin HAR, Chehbouni A, Hartogensis OK, Timouk T. 2004. Evapotranspiration components determined by stable isotope, sap flow and eddy covariance techniques. *Agricultural and Forest Meteorology*, **125**, 241–258.

Williams M, Rastetter EB, Fernandes DN, Goulden ML, Wofsy SC, Shaver GR, Melilli JM, Muhger JW, Fan SM, Nadelhoffer KJ. 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 and Environment*, **19**, 911–927.

Yakir D, Berry JA, Giles L, Osmond CB. 1993. The δ^{18}O of water in the metabolic compartment of transpiring leaves. In Ehleringer JR , Hall AE, Farquhar GD. (eds) *Stable Isotopes and Plant Carbon-Water Relations.* Academic Press: San Diego, pp. 529–540.

Yepez EA, Williams DG, Scott RL, Lin G. 2003. Partitioning overstory and understory evapotranspiration in a semiarid savanna woodland from the isotopic compostion of water vapor. *Agricultural and Forest Meteorology*, **119**, 53–68.

Yoder CK, Nowak RS. 1999. Hydraulic lift among native plant species in the Mojave Desert. *Plant and Soil*, **215**, 93–102.

Yoder BJ, Ryan MG, Waring RH, Schoettle AW, Kaufmann MR. 1994. Evidence of reduced photosynthetic rates in old trees. *Forest Science*, **40**, 513–527.

Zimmerman R, Schulze E-D, Wirth C, Schulze E-D, McDonald KC, Vygodskaya NN, Ziegler W. 2000. Canopy transpiration in a chronosequence of Central Siberian pine forests. *Global Change Biology*, **6**, 25–37.

Zinke PJ. 1967. Forest interception studies in the United States. In Sopper WE, Lull HW (eds), *International Symposium on Forest Hydrology*. Pergamon Press: New York, pp. 137–161.

Zwieniecki MA, Holbrook NM. 1998. Diurnal variation in xylem hydraulic conductivity in white ash (*Fraxinus americana* L.), red maple (*Acer rubrum* L.) and red spruce (*Picea rubens* Sarg.). *Plant, Cell and Environment*, **21**, 1173–1180.

Zwieniecki MA, Newton M. 1996. Seasonal pattern of water depletion from soil-rock profiles in a Mediterranean climate in southwestern Oregon. *Canadian Journal of Forest Research*, **26**, 1346–1352.