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How Trees Influence the Hydrological Cycle in Forest Ecosystems

Barbara J. Bond, Frederick C. Meinzer and J. Renée Brooks

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

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 bi forest trees typically lose 170 lated (Larcher, 1975). Extensi and net radiation (R_n) are the chapter are listed in Table 2. establishing the vapor pressure surrounding air. Net radiatio canopy, which causes the lea pressure in the air spaces with

Nearly all transpirational v through leaf cuticles and stem Over short time periods, plan pores, while over longer time the amount of leaf area and sp

Table 2.1 Terms and symbols

Symbol	Descript
A_L	Surface : surfac
A_r	Surface :
A_s	Surface : breast otherv
C	Capacite water chang tissue,
D	Air satur
g_s	Stomatal
G_c	Canopy
L	Length c path
η	Viscosity
k	Permeak
k_L	Leaf-spe (= $k A$)
K	Hydraul
LAI	Leaf are.
Q	Volume
R	Hydraul
R_n	Net radi
Ω	Decoup
Ψ (Ψ_{soil} , Ψ_{leaf} , $\Delta\Psi$)	Water p water poten path)

gures include information about in order to provide perspective transpiration from top (leaves) hydraulic architecture to transpiration from trees to forest ecosystem concepts presented in earlier forests change as they age – a distribution of forests around the

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key concept in studies of plant cohesion–tension (CT) theory of and the recognition that water nosphere along thermodynamic these processes are described in en disputed (e.g., Canny, 1995; il., 1995; Pockman *et al.*, 1995; *et al.*, 2004).
erize physical controls on the atmosphere (van den Honert, ized as a chain of resistances efore, is the sum of the indi- mic boundary layer resistances he leaf surface, stomatal pores, ranes to the soil, and through SPAC in terms of resistances, nce, or conductance, because a constant vapor pressure

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

especially in environments v (Bucci *et al.*, 2004).

The response of transpiration to partial stomatal closure (Figure 2.1, humidity), stomata are maximizing D . For many species, g_s decreases exponentially with increasing D . In some cases, transpiration approaches its maximum value as D approaches its maximum value (Bucci *et al.*, 1997). The responses of g_s to D are highly variable depending on the availability of soil water.

The apparent sensitivity of g_s to D is largely because of differences in species-specific differences in stomatal density (which determine maximum g_s) and the response of g_s to D has been shown to be proportional to $1/D$.



Figure 2.1 A generalized view of soil and atmospheric water potential of isohydric and anisohydric trees.

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1999; Feild and Holbrook, 2000),

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G_c ($\text{mmol m}^{-2} \text{s}^{-1}$)	Reference
98	Rayment <i>et al.</i> , 2000
320	Loustau <i>et al.</i> , 1996
480	Phillips <i>et al.</i> , 2002; Meinzer <i>et al.</i> , 2004c; Unsworth <i>et al.</i> , 2004
287	Ryan <i>et al.</i> , 2000; Anthoni <i>et al.</i> , 2002
1200	Blanken <i>et al.</i> , 1997
900	Herbst, 1998
440	Köstner <i>et al.</i> , 1992
600	Granier <i>et al.</i> , 1992
420	Shuttleworth <i>et al.</i> , 1984; Roberts <i>et al.</i> , 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

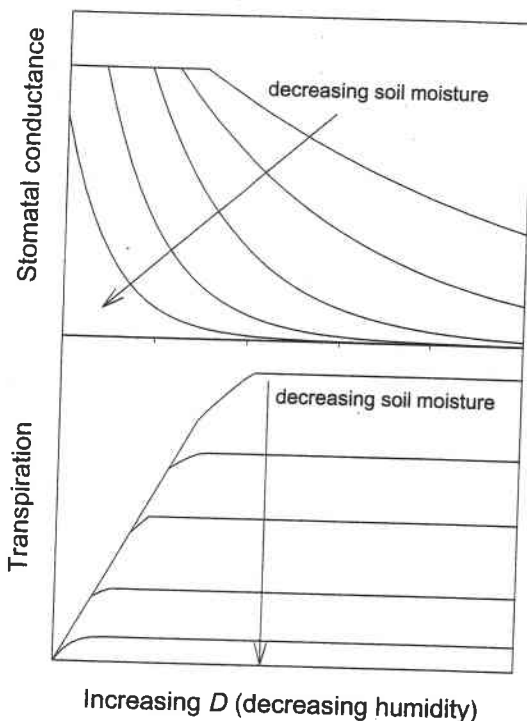


Figure 2.1 A generalized view of the responses of stomatal conductance and transpiration to soil and atmospheric water deficits for isohydric plants (see Section 2.2.3 for a discussion of isohydric and anisohydric behavior in plants)

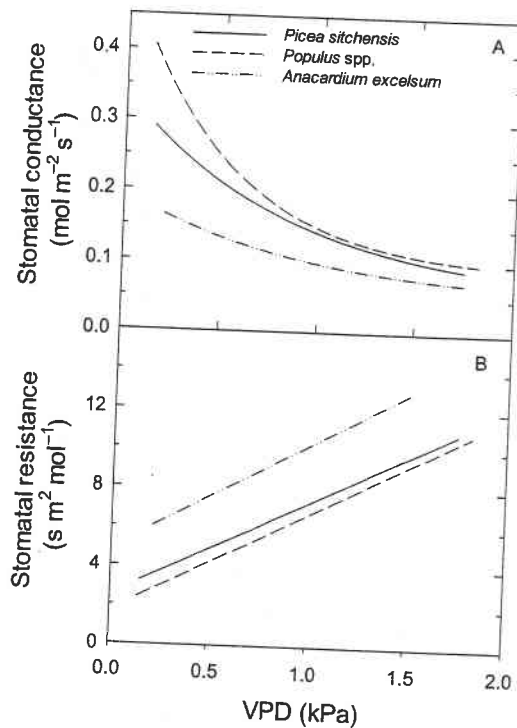


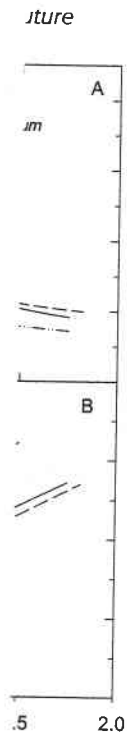
Figure 2.2 Stomatal conductance (A) and resistance (B) in relation to the leaf-to-air vapor pressure deficit (VPD) for a temperate conifer (*Picea sitchensis*; Schulze and Hall, 1982), temperate broadleaf (*Populus spp.*; Meinzer et al., 1997), and a tropical broadleaf (*Anacardium excelsum*; Meinzer 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 during incipient soil drying and the magnitude of the hydraulic signal is sensitive to chemical signals (stomatal regulation in tall trees – in tall coniferous trees – move from roots to leaves (Meinzer et al., 1999), although that minimum (McDowell et al., 2002b). The plant (see next section). It sustain transpiration during pronounced drying, condition cause partial stomatal closure water deficits in the canopy (McDowell et al., 2002b).

The extent to which transpiration is under physiological control of the role played by stomatal pathway of water movement and its associated resistances when boundary layer resistance through stomata would thus resistance associated with low humidity near the leaf surface demand at the leaf surface fraction is partly uncoupled from combination of conditions has some as a wick that passively conducts water, leading to similar response types of vegetation. The degree of decoupling has been quantified from zero to one (Jarvis and McNeill, 1986) as Ω approaches 1.0 becoming increasingly decoupled from that in needle-leaved coniferous tree to 0.5 or greater in broadleaves. Regardless of the degree of decoupling, stomata increasingly linearly respond to D . At the canopy level, transpiration area (often described in terms of leaf area), canopy structure and aerodynamic resistance



B) in relation to the leaf-to-air vapor pressure deficit (D) for *Pinus sitchensis*; Schulze and Hall, 1997), and a tropical broadleaf

99b). Apparent species-specific changes in the reciprocal of g_s , stomatal resistance, changes linearly with D imply similar boundary layer properties of the species. Stomata integrate external and internal signals and are obviously autonomous to environmental factors such as PFD and D , the amplitude of the signal. Stomatal responses to increasing D are interactions that ultimately limit transpiration as soil dries, two types of signal, hydraulic and chemical, propagate to the leaves as a result of soil water potential. Chemical signals such as abscisic acid move from 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_a 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_a . 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

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):

$$Q = \Delta\Psi * K \quad (2.1a)$$

$$Q = \Delta\Psi / R \quad (2.1b)$$

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 MPa 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 sublethal damage to xylem is vulnerable to disruption by cavitation, the separation of the water column into a vapor-filled partial vacuum, within a conduit with or without prior embolism in an unaffected conduit. The vulnerability to embolism is a key component of xylem hydraulic architecture. The percent loss of hydraulic conductivity is determined for numerous tree species. The percent loss of hydraulic conductivity decreases along a gradient from the top of the tree to the base, corresponding to gradients of increasing xylem vulnerability varies with environmental conditions (Figure 2.3B), and the distribution of embolism can occur throughout the tree. Embolism was formerly thought

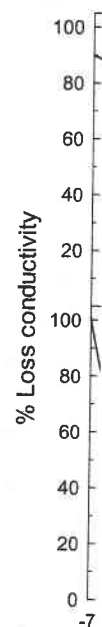


Figure 2.3 Xylem vulnerability to embolism (cavitation) of xylem pressure (tension). (A) Minimal branches in a temperate tree. (B) Examples of xylem pressure (tension) in highly resistant stem xylem. In (A) xylem pressure (tension) is potential (diamonds) to prevent embolism (Melcher et al. (2001), and Me

typically represented by canopy boundary layer conductances. This reflects both leaf level and do not necessarily vary across canopy conductance of Douglas lerosa pine (*Pinus ponderosa*). Douglas fir grows in temperate rier areas. However, maximum Douglas fir; the greater stomatal f area of pine forests.

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py conductance is itself strongly rests. Atmospheric conditions ences the supply of water from re that losses do not exceed the i controls transpiration, and to anspiration, it is necessary to air use of water. ime (Q) of liquid water through al to difference in water pote- nole-tree hydraulic conductance ydraulic resistance (R):

$$(2.1a)$$

$$(2.1b)$$

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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,

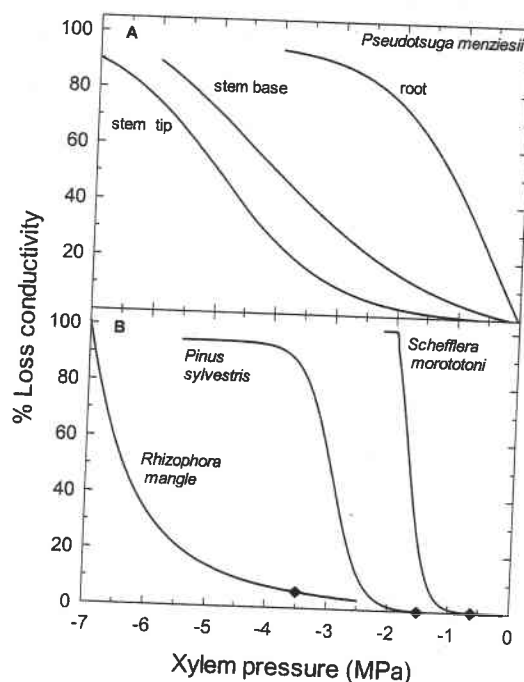


Figure 2.3 Xylem vulnerability curves showing loss of hydraulic conductivity as a function of xylem pressure (tension). (A) Axial gradient of decreasing vulnerability from roots to terminal branches in a temperate conifer. Data from Domec and Gartner (2001) and Domec et al. (2004). (B) Examples of species 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 2.3B, 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

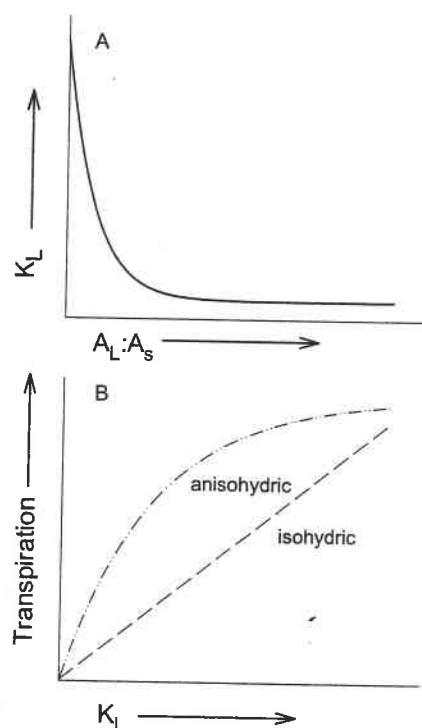


Figure 2.4 (A) Typical relationship between leaf-specific conductivity (k_L) and the leaf area:sapwood area ratio ($A_L:A_s$), an index of transpirational demand in relation to water supply capacity. (B) Stomatal regulation causes transpiration to increase with k_L in a predictable manner in isohydric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

potentials do not fall to a damaging level as well as g_s and LAI.

The hydraulic resistance (or the permeability (k) of wood (which is primarily determined by conductivity (k_L)) is k normalized between leaf area and sapwood area (Figure 2.4A). $A_L:A_s$ is between transpirational demand and water supply capacity. Because k_L represents the balance between transpiration and water supply, it constrains stomatal regulation of xylem function from cavitation and thus co-vary with k_L in a coordinated manner. In anisohydric species, because the relationship between k_L and g_s is not tightly regulated, the relationships between k_L , g_s and $A_L:A_s$ are more variable (Bucci *et al.*, 2005).

It is important to note that these relationships vary among species or individual trees. In anisohydric species, at the apex, from larger to smaller trees, the relationship between k_L and g_s varies (Tyree and Ewers, 1991; Ryan *et al.*, 1999). Variation in leaf area may partially offset variation in hydraulic conductivity due to cavitation, but transpiration can vary dramatically at different environmental conditions (Black, 1999; Melcher *et al.*, 2001). Anisohydric species are being more vulnerable than isohydric species.

Leaf level responses of g_s to environmental variables can be summarized in the

k , A_s , A_L , and $\Delta\Psi$ are defined as the water potential path, η is the temperature-dependent parameter at the leaf surface. The equation can also be applied on the stand level, A_L , and stand-average metrics (it involves assumptions about the relationships between plant characteristics and environmental conditions with different

versible in some plant organs
cher *et al.*, 2001; Bucci *et al.*,

the relationship between water
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in Section 2.4.2 we discussed
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trolls are usually presented as
ey are strongly associated with
onal flux of water so that water

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):

$$g_s = \frac{k A_s \Delta \Psi}{L \eta A_L D_s} \quad (2.2)$$

k , A_s , A_L , and $\Delta \Psi$ are defined in Table 2.1; 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

conductivity (k_L) and the leaf
nal demand in relation to water
n to increase with k_L in a predict-
for details)

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:

$$C = dV / d\Psi \quad (2.3)$$

where $dV/d\Psi$ 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 injected, and only 4 days in a with a prominent role for sap port and storage dynamics.

2.2.4 Water Uptake by

In woody plants, resistance to resistance aboveground (Narc Thus, the mechanisms and pl as important as aboveground tions, however, water transp and leaves.

The ability of roots to-sur conductance of the root syste surface area), the distributio produce new roots dynamic availability throughout the ro the effective hydraulic condu over transpiration (Hobbie a rhizosphere is also critically

Root conductivity varies b are influenced by both osmo ally have very high axial ('l systems is generally limited from the soil. The low rad anatomy that forces most of a cell membrane, plants are others, but the flow of water

The surface area and dem system to conduct water. V (suberization is the develop associated with a change in is 10- to 100-times higher t die through the favorable g ological characteristics chan are poorly characterized (W

The surface area of fine r port, particularly in connect surface area per unit leaf ar leaf. $A_r:A_l$ is generally great nerability and soil texture (*Pinus taeda*) growing in s same species in a loam soi (*Quercus* spp.) growing ur drought tolerance did not di

ch adjustments have been measured (Nardini and Tyree, 1995). Likewise, pruning increased g_s in remaining foliage. Transpiration rates increased in loblolly pine. Relationships of water flow through sapwood and transpiration often found between transpiration and application, McDowell *et al.* (1998). Good permeability (k) and lower resistance to flow for the impact that increased

reservoir for water as well as a plant tissues can be thought of as an important role in determining the Ohm's law analogue for a tissue is defined as:

(2.3)

in water potential of the tissue. Surrounding tissues into the transpiration stream. Pronounced lags between changes in (vertical) water flow through roots (Nardini *et al.*, 2004; Meinzer *et al.*, 2004). Capacitive discharge of stored water during periods of reduced transpiration as a percentage of total water (Waring *et al.*, 1979; Holbrook and Tanaka, 2001; Maherali and Tyree, 2004). There is evidence that relative water content of species (Phillips *et al.*, 2003), and larger amounts of stored water (Nardini *et al.*, 2004). In absolute terms, daily transpiration in large, old-growth conifers (Nardini *et al.*, 2004a). In the sapwood of large conifers, transpirational losses before seasonal dormancy of deuterated water (D_2O) are such that maximum sap velocity and sapwood capacitance among species. Tracer velocity decreased with increasing sapwood capacitance among species and two temperate species (Nardini *et al.*, 2003, 2006). Tracer velocities for sapwood are generally less than 5 m per day for sapwood up by roots to arrive in the sapwood of 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, unsubsided roots (*subsidization* 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

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 sorostrae*) 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).

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. Flow from areas of high to low soil moisture reaches a certain threshold varies among species (Baker and van Bavel, 1986; Meinzer *et al.*, 2004b) and they become an effective sink.

The amount of water moved is day^{-1} (Brooks *et al.*, 2006), since water uptake from those below -0.4 MPa . HR can replenish soil water (Brooks *et al.*, 2002; Brooks and Brooks *et al.*, 2002) found that potentials equal to the minimum obtained from that soil layer. This delay in soil drying can function in these upper soils.

In summary, root systems and soil properties such as texture and root conductivity are dependent on hydraulic redistribution and plant transpiration.

2.3 Evapotranspiration

2.3.1 Evaporation and

Micrometeorologists and hydrologists have one measurement for a water balance: evapotranspiration (ET) cannot distinguish between these two fluxes (Moreira *et al.*, 2004; Yepez *et al.*, 2003) because water evaporation signature of water vapor from the soil is different from the vapor signature over time, an approach explained in Moreira *et al.* (2004). The greater access to soil water by the upper few centimeters of soil leads to the upper portion of ET. For example, Moreira *et al.* (2004) was responsible for nearly a third of that soil evaporation was or was not in a desert environment. Williams *et al.* (1999) found that in an olive orchard prior to irrigation, even with wet soils in the soil, ET exceeds soil evaporation.

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; Yezpez *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 to greatly 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.

ature

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only 60 cm hydraulically lifts
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periods of heavy cloud cover
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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 composi-

tion, structural complexity and in the impacts of these changes.

2.4.1 A Summary of Age Structure, and Function

Many of the compositional, structural and functional changes in forest development can strongly influence the development of forests of the Pacific Northwest varies depending on the type of forest (Franklin *et al.*, 2002). Often, coniferous forests typically have much higher structural complexity than established in dense stands. Even more than that of the previous forests, the decoupling coefficient (Ω) of vegetation is likely to be greater for mature forest stature and comparatively smaller for younger forests.

If conifer regeneration is at its maximum within a couple of decades of the forest. In humid regions, understory vegetation. Subsequently, space, but total leaf area does not decrease as some die, others grow much faster to begin to populate gaps. A thick canopy of soil evaporation but also intense transpiration of tolerant trees explore the organic matter a considerable water reservoir for tolerant trees. As the trees grow, water (Section 2.2.3). This slows down large trees during seasonal carbon storage, even in mature forests.

In most forest types, the canopy changes vertically and horizontally, increasing relative to dense, young forests of bryophytes and lichens that act as a 'spongy' storage of water that also become more structurally complex and limited data.

2.4.2 Impacts of Tree Structure on Whole-tree Water Use

Large trees extract a huge amount of water (large conifer) and transport it to heights that is 50–100 meters above the ground path length; note that Equations 2.1 and 2.2 and therefore between transpiration and

y and overstory components, climates. The understory is a higher relative humidity than ; Unsworth *et al.*, 2004; Yepez ; generally less than that of the 5, understory transpiration was sworth *et al.*, 2004). However, iration was closer to one third ott *et al.*, 2003). Similarly, in in Siberia where 40% of the can amount to 25–50% of the

dent on the seasonal variability d, understory transpiration was ause the understory plants had availability, whereas the over- able water (Scott *et al.*, 2003). nspiration may be less variable re are less variable over time) cause more variability in the nspiration if understory leaves opical deciduous forests, which 1 in temperature.

Processes through the

the preceding sections, we now nd function of forests through any parts of the world, one of n of forest age–class structures. changes through the entire life id these changes impact evapo- nd Ziemer, 1990; Zimmerman ! rainfall interception and losses Harr *et al.*, 1975; Hicks *et al.*, 998). The dramatic impacts of e been well documented (e.g., d Post, 2004). Less well recog- the composition, structure and

The details of developmental go changes in species composi-

tion, 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 ($\delta^{13}C$) 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).

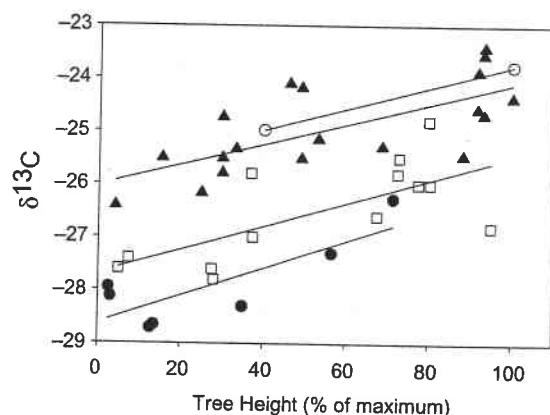


Figure 2.5 Carbon isotope composition of foliage from the tops of nonsuppressed trees of different heights. Each symbol represents a different species: closed circles – *Pinus sylvestris* (unpublished data courtesy of Maurizio Mencuccini); open squares – *Pinus ponderosa* (Yoder *et al.*, 1994); closed 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 $\delta^{13}C$ and percent maximum height are 0.22, 0.19, 0.257 and 0.20 for *P. sylvestris*, *P. ponderosa*, *P. menziesii* and *Q. oregana*, respectively

In certain situations (e.g., $\delta^{13}C$ relative to leaf diffusive resistance, r_s) conductance using measurements of the synthetic capacity of foliage for an explicit linear relationship between $\delta^{13}C$ and r_s indicates a reduction in average height, or 20% over the height in transpiration per unit forest age classes.

2.4.3 Age-related Change in Carbon Storage on the Forest Stand

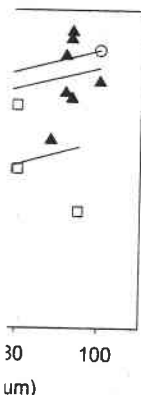
In general, LAI tends to decrease with age (Ryan *et al.*, 1997). Given the above, it might be hypothesized that LAI decreases with age. Alternatively, changes in leaf characteristics could counteract the reduction in LAI, preserving relative conductance.

One problem with this analysis is that LAI is not constant over the stages of forest development. Transpiration does not correspond to LAI (Zimmermann *et al.*, 2000), but can explain much of the variability in LAI (Connor, 1993; Zimmermann *et al.*, 1993). That transpiration is strongly related to LAI (Section 2.2.3). The presence of their water conductance and basal area in an old-growth forest (about 85 vs 35 m² ha⁻¹ for related changes in species composition and seasonal transpiration in the forest). Due to their additive influence over a growing season compared to the findings

In contrast to the findings of Bond (1997) and three young forest classes during the growing season

s the transport even more diffi-
branch junctures. All of these
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in most cases the best explana-
Koch *et al.*, 2004). Direct mea-
transpiration per unit leaf area
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example, Barnard and Ryan,



tops of nonsuppressed trees of
: closed circles – *Pinus sylvestris*
open squares – *Pinus ponderosa*
menziesii, each point is a mean of five
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ts pine were estimated from tree
cent maximum height are 0.22,
P. menziesii and *Q. oregana*,

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 m² ha⁻¹, respectively), the old forest had lower sapwood basal area (17 vs nearly 22 m² 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

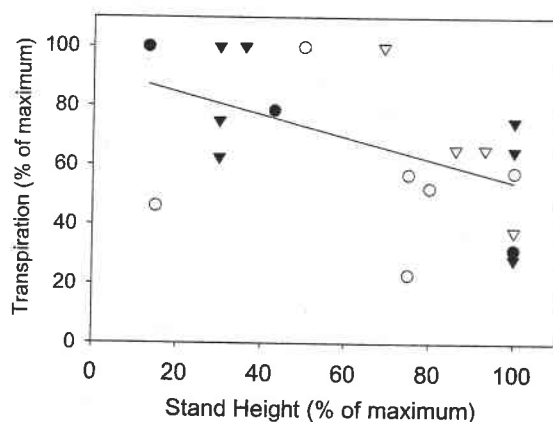


Figure 2.6 Response of maximum stand-level transpiration to increasing stand height. Each symbol represents a different species: closed circles – *Pinus ponderosa* (Irvine *et al.*, 2004); open circles – *Pinus sylvestris* (Zimmermann *et al.*, 2000); closed triangles – *Pseudotsuga menziesii* (Phillips *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 has a heavier litter layer and mineral soil of older forests.

In some areas interception actually increases the amount of harvests in such forests may result (Harr, 1982).

2.4.4 Impacts of Changing Aging Forests

Most forests undergo significant change. In some cases the change is in the pattern; in others the change is in the amount. In the west of the United States, broadleaf species in young stands. In the case of broadleaf species in a young stand, the area of broadleaf species in a young stand is greater than in an old-growth forest, was 40 % greater for the broadleaf species in old-growth forests, late-successional transpiration rates constituted 30 % lower water use by the old forest that was consistent with the preceding patterns, individual trees was consistently smaller.

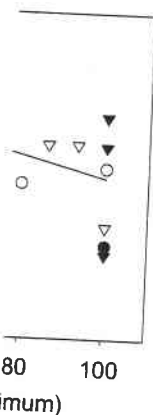
2.4.5 Implications for

The Penman–Monteith equation is a mechanistic description of the drivers that influence transpiration of its time to vegetation. The equation is often overlooked relative to these terms due to the complexity of the equation (Section 2.2.2). Both stand development, and net primary production (although this is commonly

However, our current understanding is more robust approaches. On the other hand, mechanistic models of environmental change have been done successfully (Williams *et al.*, 1996). Stable

(*Phaeocryptopus gaeumannii*) 3), so the results may say more iration. Published data for four daily transpiration of about 4% (2.6), although there is a great differences in maximum daily transpiration use on a yearly or seasonal growing forests exhausted soil water use. The young forests endured a the growing season water use

ed water yield following afforestation and Beadle, 2004), and generating forests after harvest. is an important determinant of development, but it is less important in older forests, and develops in older forests, and the very large amounts of water; of old-growth Douglas-fir forests (2005). Pypker *et al.* (2005) found that heavy rain events due to transpiration were much greater from old forests occur frequently in the Pacific



to increasing stand height. Each s ponderosa (Irvine *et al.*, 2004); closed triangles – Pseudotsuga (Köstner *et al.*, 2002). Height species and site; transpiration is in each dataset. The overall r^2 is

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.

The consistent change in $\delta^{13}\text{C}$ 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, $\delta^{13}\text{C}$ could provide a semi-empirical approach for estimating change in G_c through forest development.

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