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2

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

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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

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Table 2.1 *Terms and symbols*

Symbol	Descript
A_L	Surface surfac
A_r	Surface
A_s	Surface breast otherv
C	Capacita water chang tissue,
D	Air satur
g_s	Stomatal
G_c	Canopy
L	Length path
η	Viscosit
k	Permeal
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)

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in order to provide perspective
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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	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

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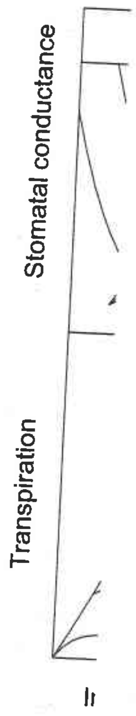

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y (G_c) conductance of different

G_c (mmol m^{-2} s^{-1})	Reference
98	Rayment *et al.*, 2000
320	Loustau *et al.*, 1996
480	Phillips *et al.*, 2002; Meinzer *et al.*, 2004c; Unsworth *et al.*, 2004
287	Ryan *et al.*, 2000; Anthoni *et al.*, 2002
1200	Blanken *et al.*, 1997
900	Herbst, 1998
440	Köstner *et al.*, 1992
600	Granier *et al.*, 1992
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

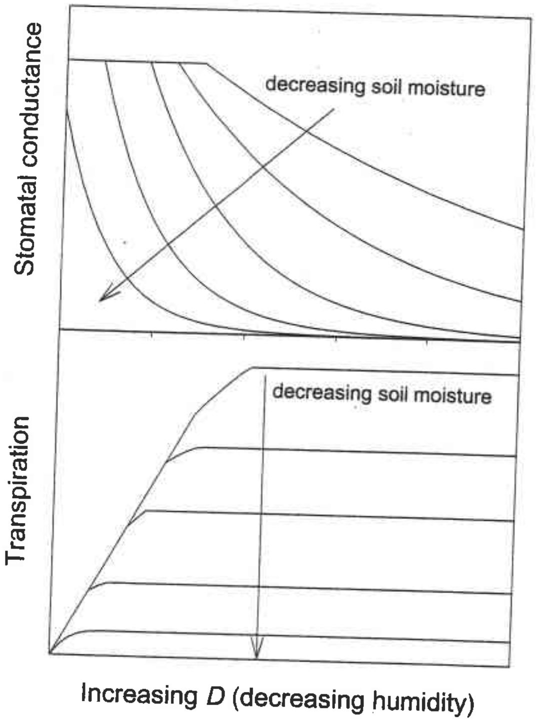

Figure 2.1 *A generalized view of the responses of stomatal conductance and transpiration to soil and atmospheric water deficits for isohydric plants (see Section 2.2.3 for a discussion of isohydric and anisohydric behavior in plants)*

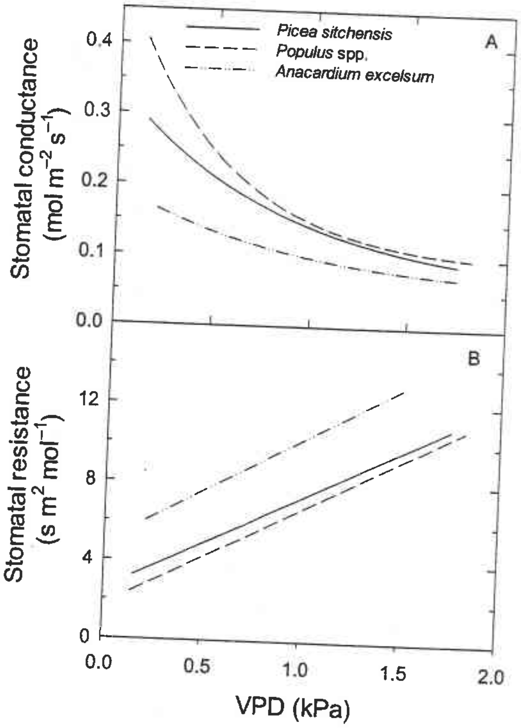

Figure 2.2 *Stomatal conductance (A) and resistance (B) in relation to the leaf-to-air vapor pressure deficit (VPD) for a temperate conifer (*Picea sitchensis*; Schulze and Hall, 1982), temperate broadleaf (*Populus *spp.; Meinzer* et al.*, 1997), and a tropical broadleaf (*Anacardium excelsum*; Meinzer*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

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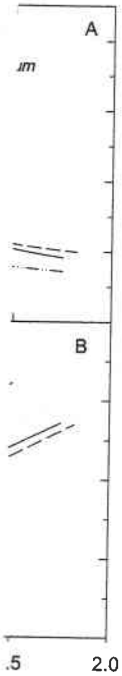

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cause partial stomatal closure (Davies and Zhang, 1991). Chemical signals may be generated during incipient soil drying well in advance of hydraulic signals (Gollan *et al.*, 1986), and the magnitude of the hydraulic signal (xylem tension) may determine 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 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 $\Psi_{leaf} - \Psi_{soil}$) 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 $-0.01\,\mathrm{MPa\,m^{-1}}$ 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).

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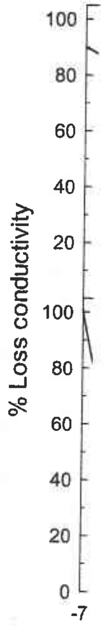

Figure 2.3 *Xylem vulnerabilit*
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The development of substantial tension makes xylem water transport potentially vulnerable to disruption by cavitation and embolism (Tyree and Sperry, 1989). Cavitation is the separation of the water column within a xylem 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,

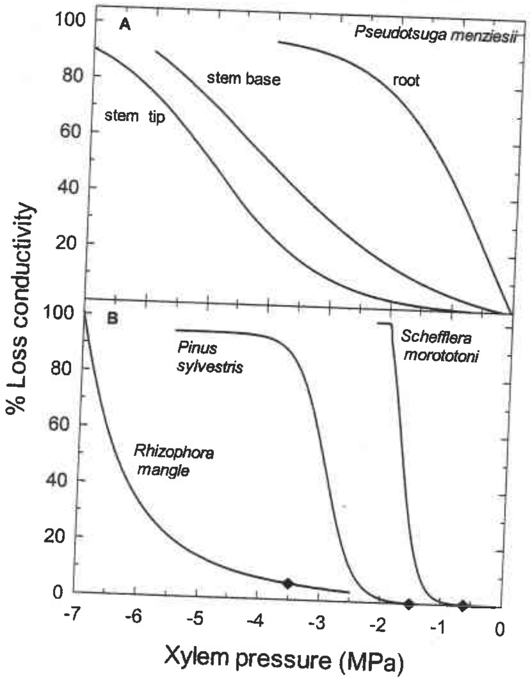

Figure 2.3 *Xylem vulnerability curves showing loss of hydraulic conductivity as a function of xylem pressure (tension). (A) Axial gradient of decreasing vulnerability from roots to terminal branches in a temperate conifer. Data from Domec and Gartner (2001) and Domec et al. (2004). (B) Examples of species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

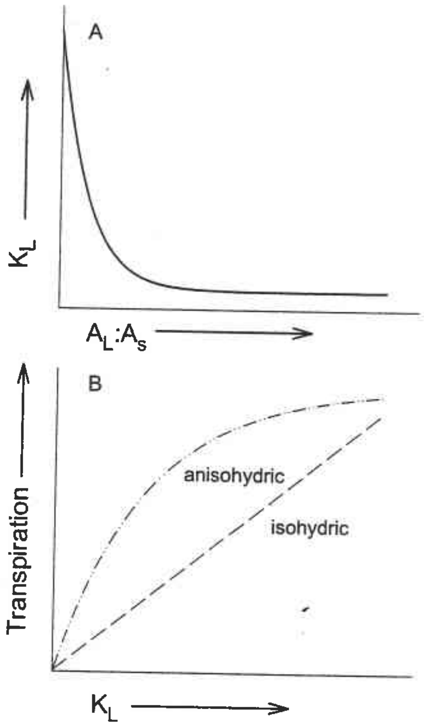

Figure 2.4 (A) Typical relationship between leaf-specific conductivity (k_L) and the leaf area : sapwood area ratio ($A_L : A_S$), an index of transpirational demand in relation to water supply capacity. (B) Stomatal regulation causes transpiration to increase with k_L in a predictable manner in isohydric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

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potentials do not fall to a dam munity of isohydric plants is th tion as well as g_s and LAI.

The hydraulic resistance (or the permeability (k) of wood (which is primarily determined conductivity (k_L) is k normali between leaf area and sapwoc tially (Figure 2.4A). A_L:A_s is between transpirational demar can be expressed at multiple s tree species often share a comr Because k_L represents the balar it constrains stomatal regulatio of xylem function from cavitat thus co-vary with k_L in a coor spiration exhibits a linear depe k_L in anisohydric species, caus the relationship between k_L a relationships between k_L, g_s an Bucci *et al.*, 2005).

It is important to note that species or individual trees. In apex, from larger to smaller (Tyree and Ewers, 1991; Ryan variation in leaf area may pa hydraulic conductivity due to tation can vary dramatically a ferent environmental conditior Black, 1999; Melcher *et al.*, 2 being more vulnerable than ea

Leaf level responses of g_s t ables can be summarized in th

k, A_s, A_L, and $\Delta\Psi$ are defined path, η is the temperature-dep at the leaf surface. The equat can also be applied on the sta A_L, and stand-average metrics (it involves assumptions abou resistances – see below – are relationships between plant ca of environments with differe

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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):

$$g_s = \frac{kA_s\Delta\Psi}{L\eta A_L D_s} \tag{2.2}$$

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 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

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2.2.4 Water Uptake by

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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 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).

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

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2.3 Evapotranspiration

2.3.1 Evaporation and

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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 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.

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-

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tion, structural complexity an
in the impacts of these chang

2.4.1 A Summary of Ag
Structure, and Function

Many of the compositional, s
development can strongly in
forests of the Pacific Northw
varies depending on the ty
(Franklin *et al.*, 2002). Often,
typically have much higher
established in dense stands. E
than that of the previous fore
the decoupling coefficient (Ω
vegetation is likely to be gre
stature and comparatively sm
If conifer regeneration is
maximum within a couple o
the forest. In humid regions,
understory vegetation. Subs
space, but total leaf area doe
some die, others grow muc
begin to populate gaps. A thi
soil evaporation but also inte
tolerant trees explore the org
a considerable water reserv
tolerant trees. As the trees g
water (Section 2.2.3). This s
large trees during seasonal
storage, even in mature fore
In most forest types, the
vertically and horizontally, i
tive to dense, young forests
of bryophytes and lichens t
as a 'spongy' storage of wat
also become more structural
limited data.

2.4.2 Impacts of Tree
Whole-tree Water Use

Large trees extract a huge
large conifer) and transport
that is 50–100 meters abov
path length; note that Equa
and therefore between tra