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, on 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). Extensio and net radiation (Rn) are the chapter are listed in Table 2.2, establishing the vapor pressure surrounding air. Net radiatio canopy, which causes the le pressure in the air spaces with

Nearly all transpiration via leaf cuticles and stem. Over short time periods, plan pores, while over longer time the amount of leaf area and

<table>
<thead>
<tr>
<th>Table 2.1 Terms and symbols</th>
</tr>
</thead>
<tbody>
<tr>
<td>Symbol</td>
</tr>
<tr>
<td>A_s</td>
</tr>
<tr>
<td>A_t</td>
</tr>
<tr>
<td>C</td>
</tr>
<tr>
<td>D</td>
</tr>
<tr>
<td>g_c</td>
</tr>
<tr>
<td>Gc</td>
</tr>
<tr>
<td>L</td>
</tr>
<tr>
<td>η</td>
</tr>
<tr>
<td>k</td>
</tr>
<tr>
<td>k_i</td>
</tr>
<tr>
<td>K</td>
</tr>
<tr>
<td>LAI</td>
</tr>
<tr>
<td>Q</td>
</tr>
<tr>
<td>R</td>
</tr>
<tr>
<td>R_n</td>
</tr>
<tr>
<td>Ω</td>
</tr>
</tbody>
</table>
| Ψ (Ψ_s | Water p water poten path)
sary – Their Historical

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 transpiration 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>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Typical units</th>
</tr>
</thead>
<tbody>
<tr>
<td>A_s</td>
<td>Surface area of foliage (projected or total surface)</td>
<td>m²</td>
</tr>
<tr>
<td>A_r</td>
<td>Surface area of roots</td>
<td>m²</td>
</tr>
<tr>
<td>A_s</td>
<td>Surface area of sapwood, measured at breast height (1.37 m) unless specified otherwise</td>
<td>m²</td>
</tr>
<tr>
<td>C</td>
<td>Capacitance (defined as the change in water content of plant tissue per unit change in bulk water potential of the tissue, or dV/dΨ)</td>
<td>m³ kPa⁻¹</td>
</tr>
<tr>
<td>D</td>
<td>Air saturation deficit</td>
<td>kPa</td>
</tr>
<tr>
<td>g_s</td>
<td>Stomatal conductance</td>
<td>mol m⁻² s⁻¹</td>
</tr>
<tr>
<td>G_c</td>
<td>Canopy conductance</td>
<td>mol m⁻² s⁻¹</td>
</tr>
<tr>
<td>L</td>
<td>Length of stem or hydraulic transport path</td>
<td>m</td>
</tr>
<tr>
<td>η</td>
<td>Viscosity</td>
<td>Pa s</td>
</tr>
<tr>
<td>k</td>
<td>Permeability; specific conductivity</td>
<td>m²</td>
</tr>
<tr>
<td>k_0</td>
<td>Leaf-specific hydraulic conductivity ( = k A_r⁻¹)</td>
<td>m² m⁻²</td>
</tr>
<tr>
<td>K</td>
<td>Hydraulic conductance (= Q ΔΨ⁻¹)</td>
<td>m³ Pa⁻¹ s⁻¹</td>
</tr>
<tr>
<td>LAI</td>
<td>Leaf area index</td>
<td>Dimensionless (m² m⁻²)</td>
</tr>
<tr>
<td>Q</td>
<td>Volume flow per unit time</td>
<td>m³ s⁻¹</td>
</tr>
<tr>
<td>R_n</td>
<td>Hydraulic resistance</td>
<td>Pa m⁻¹</td>
</tr>
<tr>
<td>Ω</td>
<td>Decoupling coefficient</td>
<td>Watts</td>
</tr>
<tr>
<td>Ψ (Ψ_s, Ψ_s, ΔΨ)</td>
<td>Water potential (soil water potential, leaf water potential, difference in water potential at either end of a hydraulic path)</td>
<td>MPa</td>
</tr>
</tbody>
</table>
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>
<thead>
<tr>
<th>Forest/vegetation type</th>
<th>Species</th>
<th>LAI</th>
<th>$g_s$ (mmol m$^{-2}$ s$^{-1}$)</th>
<th>$G_c$ (mmol m$^{-2}$ s$^{-1}$)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conifer boreal</td>
<td>Picea mariana</td>
<td>4.4</td>
<td>25</td>
<td>96</td>
<td>Raymont et al., 2000</td>
</tr>
<tr>
<td>temperate</td>
<td>Pinus pinaster</td>
<td>2.7</td>
<td>150</td>
<td>320</td>
<td>Louisau et al., 1996</td>
</tr>
<tr>
<td>Mediterranean temperate</td>
<td>Pseudotsuga menziesii/</td>
<td>9.0</td>
<td>50–70</td>
<td>480</td>
<td>Phillips et al., 2002; Meinzer et al., 2004c; Unsworth et al., 2004</td>
</tr>
<tr>
<td>mesic</td>
<td>Tsuga heterophylla</td>
<td></td>
<td></td>
<td></td>
<td>Ryan et al., 2000; Anthoni et al., 2002</td>
</tr>
<tr>
<td>temperate semiarid</td>
<td>Pinus ponderosa</td>
<td>2.1</td>
<td>166</td>
<td>287</td>
<td></td>
</tr>
<tr>
<td>Angiosperm boreal</td>
<td>Populus tremuloides</td>
<td>5.6</td>
<td>490</td>
<td>1200</td>
<td>Blanken et al., 1997</td>
</tr>
<tr>
<td>temperate deciduous</td>
<td>Fagus sylvatica</td>
<td>4.5</td>
<td>250</td>
<td>900</td>
<td>Herbst, 1998</td>
</tr>
<tr>
<td>temperate evergreen</td>
<td>Nothofagus menziesii/ N. fusca</td>
<td>7.0</td>
<td>160</td>
<td>440</td>
<td>Köstner et al., 1992</td>
</tr>
<tr>
<td>tropical plantation</td>
<td>Goupia glabra</td>
<td>3.7</td>
<td>180</td>
<td>600</td>
<td>Granier et al., 1992</td>
</tr>
<tr>
<td>Amazonian rainforest</td>
<td>mixed</td>
<td>6.6</td>
<td>200</td>
<td>420</td>
<td>Shuttleworth et al., 1984; Roberts et al., 1990</td>
</tr>
</tbody>
</table>

especially in environments v (Bucci et al., 2004). The response of transpiration to partial stomatal closure (Fig. 2.1, humidity), stomata are maximizing $D$. For many species, be exponentially with increasing some cases, transpiration act maximum value has been attained (et al., 1997). The responses of depending on the availability. The apparent sensitivity of largely because of differences in $g_s$, with increasing $D$ has been demonstrated to be proportional to $I$.
idely among species and forest types, dynamic and has been shown to be affected by environmental variables. Light (especially the light that penetrates the forest canopy) and temperature are often important factors in determining stomatal conductance. Stomata open and close in response to changes in the environment, particularly in response to changes in water supply and demand.

<table>
<thead>
<tr>
<th>Gc (mmol m⁻² s⁻¹)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>98</td>
<td>Rayment et al., 2000</td>
</tr>
<tr>
<td>320</td>
<td>Loustau et al., 1996</td>
</tr>
<tr>
<td>480</td>
<td>Phillips et al., 2002; Meiners et al., 2004c; Unsworth et al., 2004</td>
</tr>
<tr>
<td>287</td>
<td>Ryan et al., 2000; Anthoni et al., 2002</td>
</tr>
<tr>
<td>1200</td>
<td>Blanken et al., 1997</td>
</tr>
<tr>
<td>900</td>
<td>Herbst, 1998</td>
</tr>
<tr>
<td>440</td>
<td>Köstner et al., 1992</td>
</tr>
<tr>
<td>600</td>
<td>Granier et al., 1992</td>
</tr>
<tr>
<td>420</td>
<td>Shuttleworth et al., 1984; Roberts et al., 1990</td>
</tr>
</tbody>
</table>

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 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, at low D). The characteristic exponential decline in g with increasing D has been exploited in a model that demonstrates that the sensitivity of g to D is proportional to the magnitude of g, 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 isohydrical plants (see Section 2.2.3 for a discussion of isohydrical and anisohydrical 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.

A 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 gs, 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 dryness and the magnitude of the hydric siveness to chemical signals ( stomatal regulation in tall tree signals – in tall coniferous trees move from roots to leaves (Meinzer et al., 2002b). Th (Meinzer, 2002) and appears the plant (see next section). I sustain transpiration during pronounced drying, condition cause partial stomatal closure water deficits in the canopy.

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 resistant through stomata would thus resistance associated with low as is often the case for crop humidity near the leaf surface demand at the leaf surface fraction is partly decoupled from bination of conditions has some as a wick that passively controls apparently passive behavior n that leads to similar response types of vegetation. The degree of transpiration has been quantified from zero to one (Jarvis and Wieskes as Ω approaches 1.0 becoming decoupled from that in needle-leaved coniferous tree to 0.5 or greater in broadleaves Regardless of the degree of demand, stomata increasingly lin

At the canopy level, transpiration area (often described in terms of area), canopy structure and ac
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 Rs or is under physiological control by gs 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 gs making it appear to be driven largely by Rs. 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 gs, 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 (\( \textit{Pseudotsuga menziesii} \)) is nearly double that of ponderosa pine (\( \textit{Pinus ponderosa} \)). 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 \( g \), 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 \( \textit{CT} \) 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 \( (\Delta \Psi; \text{ or } \Psi_{\text{leaf}} - \Psi_{\text{soil}}) \) and to whole-tree hydraulic conductance \( (K) \); it is therefore inversely proportional to whole-tree hydraulic resistance \( (R) \):

\[
Q = \Delta \Psi \times K \\
Q = \Delta \Psi / R
\]

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 \( \Psi_{\text{leaf}} \) 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 \( \Psi_{\text{leaf}} \) drops to a critical level, partial stomatal closure occurs, limiting transpiration.

In the absence of transpiration, gravitational forces result in a minimum tension gradient of \(-0.01 \text{ MPa m}^{-1}\) 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 \( K \)).
typically represented by canopy boundary layer conductances. This reflects both leaf level and do not necessarily vary across anopy conductance of Douglas fir (Pinus ponderosa). Douglas fir grows in temperate forest areas. However, maximum Douglas fir; the greater stomatal area of pine forests.

and the Role of

hydraulic conductance is itself strongly structural. atmospheric conditions enclose the supply of water from the air that losses do not exceed the transpiration, it is necessary to control the use of water. 

\[
(2.1a) \\
(2.1b)
\]

t causes and effects. Does transpiration fact, the causality works both from soil through the xylem is high lowers \( \Psi_{\text{leaf}} \) and transmits columns running from the evaporation (R), However, as will partial stomatal closure occurs.

ult in a minimum tension gradi-

ent. When transpiration occurs, considerably steeper (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,

\begin{figure}
\centering
\includegraphics[width=\textwidth]{figure23.png}
\caption{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 Dorn et al. (2001) and Dorn et al. (2004). (B) Examples of species showing highly vulnerable, moderately vulnerable, and highly resistant stems 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.}
\end{figure}
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 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 \( k \) normally 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 corn Because \( k_L \) represents the balance it constrains stomatal regulatic of xylem function from cavitation thus co-vary with \( k_L \) in a cool spiration exhibits a linear dep k \( k_L \) in anisohydric species, caus the relationship between \( k_L \) a relationships between \( k_L, g_s \) and \( Bucci et al., 2005 \).

It is important to note that species or individual trees. In apex, from large to smaller (Tyree and Ewers, 1991; Ryan variation in leaf area may pa hydraulic conductivity due to e relation can vary dramatically a ferent environmental condition Black, 1999; Melcher et al., 2015) being more vulnerable than e:

Leaf level responses of \( g_s \) t tables can be summarized in t

\[ k, A_L, A_s, \text{ and } \Delta \Psi \text{ are defined path, } \eta \text{ is the temperature-dep at the leaf surface. The equat can also be applied on the st } A_L, \text{ and stand-average metrics (it involves assumptions abo } \]

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 predict- able manner in isohydric and anisohydric species (see text for details).
How Trees Influence the Hydrological Cycle in Forest Ecosystems

Reversible in some plant organs (Melcher et al., 2001; Bucci et al., 2005), the relationship between water stress in temperate forest trees, $g_s$ is dropping to levels that wouldicitate development. Thus, isohydric plants more or less constant as there is no threshold minimum by stomatal closure. Isohydric have greater capacity for embolism. Section 2.4.2 we discussed the, soil water deficits and embolisms are usually presented as key 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 ($A_s:A_L$) increases, ($k_l$) typically declines exponentially (Figure 2.4A). $A_s:A_L$ is a fundamental allometric trait that reflects the balance between transpirational demand ($A_L$) and water supply capacity ($A_s$). Both $k_l$ and $A_s:A_L$ 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 $A_s:A_L$ (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 $A_s:A_L$, 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 (Domene 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):

$$g_s = \frac{k_A \Delta \Psi}{L \eta a_L D_s}$$  \hspace{1cm} (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, $\eta$ 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 $A_t/A_h$ 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 $A_t/A_h$ 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 $A_t/A_h$ 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:

$$C = \frac{dV}{d\Psi}$$  \hspace{1cm} (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 transpiration losses before seasonal recharge occurs (Waring and Running, 1978). The behavior of deuterated water (D$_2$O) 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 if injected, and only 4 days in a with a prominent role for sap port and storage dynamics.

### 2.2.4 Water Uptake by Tree Roots

In woody plants, resistance to water resistance aboveground (Narcissus) is an important as aboveground, however, water transport and leaves.

The ability of roots to conduct water from the soil to shoots aboveground is generally limited by the root system's surface area. Water availability throughout the root system, the effective hydraulic conduit over the rhizosphere, is also critical for water transport. Root conductivity varies by species and is influenced by both osmotic and water availability. The low conductivity of water transport is generally limited by the soil's low water availability. The surface area and dem system to conduct water. \textit{(Suberization)} is the developmental process associated with a change in the water conductance associated with a change in the water conductance of a tissue. When the favorable growth characteristics of a species are poorly characterized, the surface area and dem system to conduct water, particularly in connect i

The surface area and dem system to conduct water, particularly in connect i
reservoir for water as well as a storehouse for water. In some plants, tissues can be thought of as important in determining the flow of water through the Ohm’s law analogue for a tissue, as defined as:

\( k \) (2.3)

in water potential of the tissue. Surrounding tissues into the transpiration lags between changes in (vertical) water flow through a plant (Meinzer et al., 2004; Waring et al., 1979; Holbrook and Tanaka, 2001; Maharali and Shabala). There is evidence that relative growth rate of larger amounts of stored water (2004). In absolute terms, daily in large, old-growth coniferous trees (Meinzer et al., 2004a) in the sapwood of large coniferous trees (Waring et al., 1979) with maximum sap velocity and on sapwood capacitance among species. Tracer velocity decreased with increasing sapwood capacitance species and two temperate (303, 2006). Tracer velocities for generally less than 5 m per day can be used by roots to arrive in the old-growth conifers. The tracer residence time was 7 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 belowground (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. Mycorrhizal fungi can greatly increase the effective hydraulic conductance of roots and therefore can exert considerable influence on 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 radial hydraulic 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 to ‘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, unrooted 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 10-100 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 Eissenstat, 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 \( A_r/A_i \) allows water uptake from more soil per transpiring leaf. \( A_r/A_i \) is generally greater than 1 and can vary dramatically depending on xylem vulnerability and soil texture properties (Sperry et al., 1998). For example, lodgepole pine (Pinus taeda) growing in sandy soil had an \( A_r/A_i \) ratio of 9.75 compared with 1.68 for the same species in a loam soil (Hackle 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 \( A_r/A_i \) (ranging from 1.45 to 2.37) (Nardini et al., 1999).
and Tyree, 1999). In coarse soils, soil hydraulic conductance drops more rapidly with decreases in $\Psi_{soil}$ 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 $\Psi_{soil}$ in the upper 20 cm (Warren et al., 2005). These results imply that seasonal declines in $\Psi_{soil}$ 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 of plant species, including grasses and cacti as well as shrubs and trees (Caldwell and Richards, 1989; Caldwell, 1996; 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 sarothrae) 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 from areas of high to low roots reaches a certain threshold varies among species (Baker and van Bavel, 1986; Meinzer et al., 2004b) they become an effective sink.

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

In summary, root systems' soil properties such as texture root conductivity are depend and hydraulic redistribution a plant transpiration.

2.3 Evapotranspiration

2.3.1 Evaporation and

Micrometeorologists and hydrometeorologists measure for a water transpiration (ET) cannot di: quite different. Recently, self separate these two fluxes (M 2004; Yepez et al., 2003) because they are water evaporators signature of water vapor for vapor signature over time, approach explained in More evaporative losses from an e the greater access to soil water to the upper few centimeters of ET. For example, Moreira was responsible for nearly a that soil evaporation was or desert environment. Willi in an olive orchard prior to Thus, even with wet soils in exceeds soil evaporation.
stance drops more rapidly with decreasing root surface area. Increasing root surface area can help reduce water loss through evapotranspiration.

Soil moisture decreases greater than that of stems and roots. However, roots are also more effective in maintaining conductance along the xylem. The depth of water that can be maintained in the upper 20 cm of the soil profile is controlled by root conductivity in closure and limit water uptake by the root system. The soil profile also has a significant effect on soil moisture availability.

Soil resources (nutrients and moisture) are dynamic seasonally, with nutrient concentrations in the soil profile also significant. As a result, this portion of the root system is dynamic, with nutrients moving through the soil profile seasonally. This water uptake is critical for the early growing season when upper roots, shifting later in the season, allow deeper soil layers to contribute to plant growth.

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

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

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

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

2.4.1 A Summary of Ag Structure, and Function

Many of the compositional, developmental, and structural characteristics of coniferous forests of the Pacific Northwest vary depending on the type of vegetation and the age and stage of development (Franklin et al., 2002). Often, these forests have higher productivity and establishment in dense stands than that of the previous forest type. The decoupling coefficient ($\Omega$) can be used to determine the extent to which vegetation is likely to be stressed and comparatively sensitive to climate change. If conifer regeneration is maximum within a couple of decades, the forest in humid regions, understory vegetation. Subsequent space, but total leaf area does some die, others grow much larger in size as well as begin to populate gaps. A third soil evaporation but also allows for regrowth of coniferous trees, which grow taller and have a greater water storage, even in mature forests.

In most forest types, the forest is generally more stable, less sensitive to dense, young forests of bryophytes and lichens are as 'spongy' storage of water also becomes more structural limited data.

2.4.2 Impacts of Tree Composition on Water Use

Large trees extract a huge amount of water over a longer period of time than small trees. However, the total amount of water transported through a given area can be more than 50-100 meters above the ground. Note that Equa

and therefore between transect.
and overstory components, climates. The understory is a higher relative humidity than Unsworth et al., 2004; Yepez generally less than that of the understory transpiration was sworth et al., 2004). However, transpiration was closer to one third vott et al., 2003). Similarly, 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). inspiration may be less variable are less variable over time t cause more variability in the inspiration if understory leaves apical deciduous forests, which t in temperature.

Processes through the

the preceding sections, we now the function of forests through any parts of the world, one of in of forest age-class structures. changes through the entire life of these changes impact evapo-

and 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., Post, 2004). Less well recog-

the composition, structure and

The details of developmental 30 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 gs, 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 gs 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 \( (k_x) \) is especially low at branch junctures. All of these changes tend to reduce hydraulic conductance \( (K) \), Section 2.2.2), 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., \( A_{s}:A_{g} \), 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).

In certain situations (e.g., relative to leaf diffusive resistance and conductance using measurements of synthetic capacity of foliage for an explicit linear relationship between leaf age and photosynthetic capacity, or \( A/C \) curves. For the Douglas-fir, the reduction in \( a \), height, or 20% over the height in transpiration per unit forest age classes.

### 2.4.3 Age-related Chan Storage on the Forest Stems

In general, LAI tends to decrease with age (Ryan et al., 1997). G (above) might be hypothesized with age. Alternatively, characteristic growth characteristics could counteract, preserving relative constancy.

One problem with this approach is that LAI is not a simple linear function of forest development. For example, the relationship between tree height and LAI is strongly

**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., 2002); open circles – Quercus agrarian, 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. agrarian, respectively.
In certain situations (e.g., when resistance of the canopy boundary layer is very low relative to leaf diffusive resistance), it is possible to estimate differences in stomatal conductance using measurements of stable isotope composition of leaf carbon and photosynthetic capacity of foliage from the sunlit tops of tree crowns. The estimation relies on an explicit linear relationship between isotope discrimination and the ratio of carbon dioxide concentrations internal and external to leaves (Farquhar et al., 1982). These carbon dioxide concentrations, in turn, are a function of the ratio between photosynthesis and stomatal conductance, or A/g, also known as ‘intrinsic water use efficiency’ (Ehleringer et al., 1993). Finally, relative differences in stomatal conductance can be derived using measurements of the response function of photosynthesis to internal carbon dioxide, or ‘A/C’ curves. For the Douglas fir in Figure 2.5, the change in foliage isotope composition indicates a reduction in average g, 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 Northwest where this forest type as well as a heavier litter layer of mineral soil of older forests does not occur.

In some areas interception actually increases the amount of water harvested in such forests may return to old growth (Harr, 1982).

2.4.4 Impacts of Changing Forests

Most forests undergo significant changes as they age. For example, the changing patterns in the United States, but young stands. In the case of the young, a region of broadleaf species in a than in an old-growth forest, was 40% greater for the brck old-growth forests, late-summer transpiration rates constitute forers averaged 30% lower in coniferous forests. In combination, the ant conifers, in addition to the use by the old forest that was with the preceding patterns, visual trees was consistent in tree size.

2.4.5 Implications for Climate

The Penman-Monteith equation mechanistic description of drivers that influence transpiration of its time to vegetative mation of the conductance equation is often overlooked due to these terms due to the transpiration (Section 2.2.2). Both stand development, and new (although this is commonly used).

However, our current understanding of coniferous models of the environment necessitates more robust approaches. This has been done successively by Williams *et al.*, 1996). Stabl...
(Phaeocryptopus gaeumannii) 3), so the results may say more about the potential for forest transpiration. Published data for four species of trees showed that transpiration rates for each species were lower than those reported for the forest understory (Harr, 1982).

The young forests endured a decrease in water yield following afforestation and land use change (Beadle et al., 2004), and they have been characterized as successionally important because they develop in older forests, and because of the large amounts of water stored in the older forests. The old-growth Douglas-fir forests (005) pyk et al. (2005) found that heavy rain events due to the occurrence of heavy rain events in the Pacific Northwest where this forest type grows. Thus, both interception losses from the canopy and surface runoff contribute to forest transpiration, which results in less rainfall penetration to the mineral soil of older forests during small rain events (Pyk et al., unpublished data).

In some areas, interception and condensation of fog by large 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 lower 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 (Gc 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 time, 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-Air; Williams et al., 1996). Stable carbon isotopes may offer another, more empirical, approach.
The consistent change in δ13C 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, δ13C could provide a semi-empirical approach for estimating change in Gc through forest development.

Acknowledgments

This manuscript was greatly improved thanks to careful reading and advice from Georgianne Moore and Cheley Ford. We also gratefully acknowledge helpful editorial comments from two anonymous reviewers as well as the editor of this volume. The work reported in this chapter was partially supported by the Western Regional Center (WESTGEC) of the National Institute for Global Environmental Change (NIGEC) under cooperative agreement No. DE-FC03-90ER61010, the Department of Forest Science, Oregon State University, US Environmental Protection Agency, and the USDA Forest Service Ecosystem Processes Program. This manuscript has been submitted to the Environmental Protection Agency’s peer and administrative review, and it has been approved for publication as an EPA document. Mention of trade names or commercial products does not constitute endorsement or recommendation for use. Opinions, findings and conclusions are those of the authors and do not necessarily reflect the views of the DOE or the EPA.

References


maximum tree height (Figure 2.5)
change in stomatal conductance
change of change in LAI, δ¹³C could change in Gₑ through forest

eful reading and advice from
acknowledge helpful editorial
of this volume. The work
the Western Regional Center
mental Change (NIGEC) under
Department of Forest Science, 
Agency, and the USDA Forest
has been subjected to the Envi-
view, and it has been approved
ames or commercial products
Opinions, findings and con-
reflect the views of the DOE or

in trees of a lowland tropical forest.

, Cavender-Bares J, Clearwater M, 
Ewers F, Gartner B, Hacke U, 
Ojeda-Portillo J, Lovisolo C, Martin 
Lucchini M, Mulkey S, Nardini A, 
S. Richter H, Säck L, Salleo S. 
2004. The Cohesion-Tension

ore DJ. 2002. Seasonal differences 
ponderosa pine ecosystems. Agric-
water loss. Agronomy Journal, 78, 
tation hypothesis in fast-growing 
trparis grandis plantation. Tree Physiol-
boreal aspen forest, Prince Albert 
ë, den Hartog G, Novak MD, Lee 
aspn forest: partitioning overstory 
h, 102, 28915-28927.


Future


duction of two rain forest species (bran) in French Guiana. *Annals of the Kyoto University*, **48**, 251-261.


34 Hydroecology and Ecohydrology: Past, Present and Future


