

Tree Physiology

Frederick C. Meinzer
Barbara Lachenbruch
Todd E. Dawson *Editors*

Size- and Age- Related Changes in Tree Structure and Function

 Springer

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Tree Physiology

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Preface

Trees are globally important because of their roles in providing fuel, food, construction materials and fiber, and their more recently recognized role in providing diverse ecosystem services such as habitat for other organisms and the oxygen we all breathe. They typically increase in size and biomass by several orders of magnitude from the seedling to adult stage. Across this growth trajectory they undergo an enormous number of changes both within their own structure, and in their interactions with the environment. Some of these changes are well-known, and others we are just beginning to understand. These changes can be in features as diverse as foliar physiology, anatomy, and chemistry; wood structure and mechanical properties; overall architecture and allometry; reproductive ability; and interactions with herbivores. Many of these changes are presumed to allow them to acclimate to the environment and endure for millennia; indeed, the ability of certain tree species to attain spectacular heights has captivated society's imagination for centuries and has driven an increasing amount of research on the biophysical factors that limit maximum tree height. The ability to acclimate and endure, however, can also restrict future response options because of a legacy of structural adjustments that constrain physiological function. Despite the importance of these changes, until recently relatively little was known about their specific causes and the extent to which they are related strictly to tree size versus age. This book presents a synthesis of the current state of knowledge about the causes and consequences of ontogenetic changes in key features of structure and function at both the individual tree and the stand level.

The book explains why it is important to distinguish among attributes intrinsically related to size versus age and why we know so little about age- versus size-specific traits. Chapters highlight some of the implications of these size- and age-related changes for commercial forestry plantations with shortening rotational ages, and for predicting how current and future forests will respond to climate and other environmental changes.

The organization of this book reflects a philosophy that universal principles are likely to govern key processes and relationships between structure and function regardless of a species' evolutionary history and where it normally grows. Thus, angiosperms and gymnosperms as well as temperate and tropical species are often

discussed in the same chapter. We have grouped the chapters into six sections beginning with a chapter that provides an historical perspective on prior research and relevant technological developments as well as a synthesis of the major topics and themes covered in the remaining chapters. This is followed by five sections organized according to processes and phenomena: reproduction and regeneration, integration of structure and function across ontogeny, photosynthetic gas exchange and carbon balance, water relations and transport processes, and scaling from individual traits to stands. Several chapters describe technological tools and innovative methodological approaches that can be used to address specific topics. Although much progress has been made in unravelling structure-function relationships in trees and forest stands during their ontogeny, important gaps in our knowledge need to be filled in order to understand the constraints on sustaining trees as viable components of ecosystems under current and future climate regimes.

We are grateful to the contributors for their willingness to participate in this project and to internal and external reviewers for their valuable comments on initial drafts of the chapters.

Frederick C. Meinzer
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Todd E. Dawson

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Part I
The Whole-Lifespan Perspective
on Integration of Structure and Function

Chapter 1

A Lifespan Perspective on Integrating Structure and Function in Trees

Thomas M. Hinckley, Barbara Lachenbruch, Frederick C. Meinzer,
and Todd E. Dawson

Abstract Trees are spectacular organisms that can accumulate a large amount of biomass, live for millennia, grow in stressful environments, and have global importance to organisms and human society as a result of their roles in contributing to diverse ecosystem services. They survive in an enormous range of environments with disturbances of various frequencies and severities, and by their very nature of being long-lived and sessile, they must possess the ability to change. This chapter provides a context for the chapters that follow, by describing a history of the investigations and of several important technological innovations that have enabled research to progress, and some of the foundations of water relations which underpin many of the later chapters. The chapter then discusses seven recurrent themes brought out by the diverse chapter authors: microclimate and other abiotic forces that change with tree and stand age; the changing structure and function employed as trees grow; what we can learn from scaling—which scaling laws pertain, when, and what is the biology or physics embedded in these laws; the tradeoffs that occur as structures and functions change through growth and development; the causes and

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correlates of the decline in productivity of trees and stands with age; the extent to which changes are plastic; and the meaning of whether changes occur relative to age versus size. The chapter concludes with a discussion on the emerging issues and questions raised in the chapters of this book. The overall aim is to give insights into the whole tree, whole lifespan perspective of the structural and functional strategies trees employ to persist in the face of internal and external factors that change as trees grow and age. This knowledge can be used to develop management approaches to manipulate trees and stands to provide a wide range of ecosystem goods and services.

1 Introduction

Using 17 chapters authored by 42 individuals, “Size- and Age-related Changes in Tree Structure and Function” captures the current state of knowledge regarding how age and size impact tree structure and function. The current chapter lays the foundations for this book with a historical perspective on how scientific curiosity, forest management, wood science, and technological innovations have led to advances in our understanding of tree and stand growth. It then gives a brief explanation of the basic plant water relations theory essential for understanding aspects of hydraulic architecture, water transport, growth and growth allometry dealt with in a number of the chapters. Next, it presents the major themes that were touched upon in the individual contributions, and lastly, the emerging issues and researchable questions on size- and age-related changes in the structure and function of trees.

Trees are spectacular organisms: they can accumulate a very substantial amount of biomass, can live for millennia, can grow in extraordinarily stressful environments, are globally important as a result of their current and historical roles in providing fuel and fiber and their more recent and emerging roles in providing diverse ecosystem services including clean air and water, conserving and cycling nutrients, capturing and storing carbon, synthesizing an extensive array of chemicals including pharmaceuticals, having living and dead structures that provide habitat for a diverse array of organisms and serving special cultural and spiritual needs. As a tree develops from seed, it expands progressively from a newly germinated seedling weighing a few milligrams to a large, complex organism containing over 3,000 Mg of dry biomass (Fig. 1.1). These and other special features of trees as compared to other plant and animal organisms have earned them a unique status throughout the history of civilization.

Because of their diverse evolutionary history, trees extend from all but the coldest and driest habitats through all terrestrial systems; and because of their ability to acclimate, they can endure for millennia. Collectively, trees employ an enormous range of reproductive, regenerative, and survival strategies. By their very nature of being long-lived and sessile, they must possess the ability to change. This change encompasses the genetic potential to alter both structure and function in association with ontogeny, as well as with abiotic and biotic factors that change



Fig. 1.1 Foliage at various life-stages in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) (left to right are cotyledons in a newly germinated seed, foliage of a young tree, and foliage from the top of an old-growth tree)

either independently or concomitantly with the aging tree and stand. The chapters in this book provide a context for understanding the features associated with “success,” and give insights into the mechanisms and strategies that facilitate their persistence in the face of these changing internal and external factors. We can then use this knowledge to predict tree and stand responses to perturbations, and to devise management approaches to manipulate trees and stands to provide a wide range of ecosystem goods and services.

The whole tree can be defined as a system of relatively fine organs (foliage and fine roots) that acquire and allocate resources and that are linked via a coarser system of roots, stems, branches and the bole to create a particular and often complex form. Changes in architectural form often result in trade-offs between structure and function that may scale according to orderly rules that we may or may not understand. These rules often begin with the trade-offs between architectural constraints and architectural opportunities, hydraulic and biomechanical safety and efficiency, vegetative versus reproductive growth, and growth rate versus longevity (e.g., Zimmermann 1983; Kennedy et al. 2010). Therefore, the visible form that a tree takes is the result of combined architectural and process rules (i.e., the hardwired or genetic component) and their interplay over time with the combined abiotic and biotic environment, which in itself changes dramatically within a day, within a crown, within a year, and over the life of the tree. During these changes in their abiotic and biotic environments, trees are responding through growth of height, diameter, crown, and roots; through physiological transitions from juvenile to reproductive and mature life history stages, and through developmental and plastic responses to a wide range of stimuli. They are also accumulating the structural and physiological legacy that potentially will restrict or alter their future response options.

In this chapter, we have attempted to present our perspective on tree growth, structure, and function to allow readers to more readily integrate the chapters

as they read them. The next three sections focus on the history of whole lifespan tree and stand ecophysiology (Sect. 2), the role of technological innovations (Sect. 3), and the foundations of plant water relations research (Sect. 4). They provide context for the findings, innovations, and connections made by authors in later chapters. Section 5 focuses on seven themes that recur in many of the chapters. We suggest this recurrence indicates the current importance of these thematic areas for understanding tree function. The next section (Sect. 6) compiles the emerging issues and questions raised in the chapters of this book. We conclude (Sect. 7) with a brief assessment of the potential utility and broader applications of the findings discussed in the remaining chapters.

2 History of Investigations into Effects of Size and Age on Trees

A starting point for the history of tree physiology or silvics might be traced back to Leonardo da Vinci who puzzled about the relationship between the ratio of the sum of twig cross-sectional areas to small branch cross-sectional areas to branch cross-sectional areas to stem cross-sectional area in an apple tree. This example of an allometric relationship has currency whether one is using the pipe theory (Shinozaki et al. 1964), the West-Brown-Enquist power relationships (West et al. 1997, 1999), or the emerging conduit packing density approach (McCulloh et al. 2010; Savage et al. 2010) when addressing conduction through a plant or through the entire soil-plant-atmosphere continuum (SPAC). Similar to da Vinci, authors interested in the allometry of hydraulics have tended to focus on plant segments and even the junctions between segments (e.g., Zimmermann 1978, 1983) rather than the whole plant. The work of Stephen Hales is often cited as the first example of the use of experiments with woody plants to test the applicability of a physical or a vitalistic theory of how water is transported within a woody plant (Hales 1727). Individuals following Hales tended to focus on finding a robust and parsimonious explanation for how water flowed through the SPAC, what controlled its flow, and how it was able through turgor to sustain cell enlargement and control stomatal opening. Early authors, such as Bruno Huber (1924) focused on merging structural – functional relationships of tree hydraulics. All these approaches have either directly or indirectly provided much of the foundation for the way scientists think today about trees from a water and carbon perspective.

Similar to those interested in the basics of tree function and structure, practicing foresters soon recognized that tree height was dependent upon age, species and the quality of the site on which the trees were growing. Site index curves, which now exist for many species (Fig. 1.2) clearly illustrate that there is a maximum height for any given species even when growing on the best of sites. In addition, certain species, such as Douglas-fir (*Pseudotsuga menziesii*), coastal redwood (*Sequoia sempervirens*) and mountain ash (*Eucalyptus regnans*) have long been noted for their ability to achieve spectacular heights and perhaps it is the existence of very tall trees

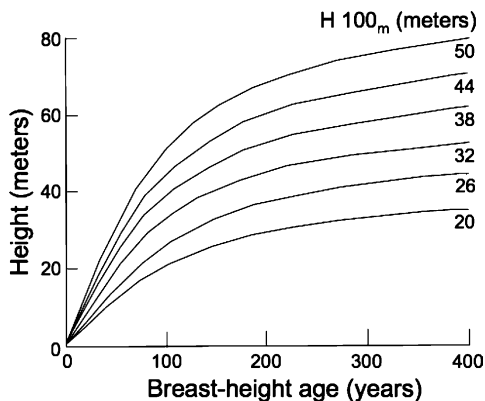


Fig. 1.2 Site index (or age versus height) curves for Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) growing in high elevation forests of the Cascades of Oregon and Washington (from DeMars and Herman 1987). Although each curve appears to be approaching an asymptote, curves have not flattened even at age 400 (see Chaps. 4, 6, 8 and 14 about height growth in Douglas-fir and other trees). It is important to note that the sample size was relatively small for trees 300 years old or older (21/240). Similar site index curves were noted for Douglas-fir growing at lower elevations on the eastside of the Cascades (Means and Helm 1985). In contrast, the range of heights at age 100 for Douglas-fir (*P. menziesii* var. *glauca*) from New Mexico was from 9 m on the poorest sites to 36.5 m on the best (Edminster and Jump 1976). Such curves have strong predictive powers, but very weak explanatory capabilities

that brings practitioners and experimenters together. Greenhill in 1881 published his still-cited paper that brings together diameter and taper to explain the form in which ship masts (tree trunks) can be found in nature, as well as how tall a tree can grow and still be stable. At about the same time, in 1895, Dixon and Joly described the Cohesion-Tension theory for water transport, which has been challenged multiple times (e.g., Zimmermann et al. 2004). Finally, after a series of ingenious experiments in the mid-1990s and a 2004 letter to the *New Phytologist* (Angeles et al. 2004), the cohesion-tension theory was accepted as the most robust and parsimonious explanation of how water moves to the top of trees, short or tall.

While the argument over the mechanism of water transport to the tops of tall trees was occurring, two elegant papers appearing in the early 1990s (Schoettle 1994; Yoder et al. 1994) demonstrated the effects of age (actually, height in these studies, which can be used as a proxy for age) on tree structure and function. Indeed, old (i.e., tall) trees were structurally different from younger trees and showed reduced photosynthesis. These observations were consistent with the declines in productivity with stand age that have been noted in the existing literature (e.g., Odum 1969; Grier et al. 1981; Gower et al. 1996; Ryan et al. 1997; see reviews by Binkley et al. 2002 and Ryan et al. 2010). Ryan and Yoder (1997) narrowed the explanation for the observations from these two 1994 papers (and others) to what is now called the hydraulic limitation hypothesis. Examinations of this hypothesis have increased in number, some supporting the original ideas and some not (Barnard and Ryan 2003; Bond 2000; Koch et al. 2004; Mencuccini et al. 2005; Burgess et al. 2006;

Burgess and Dawson 2007; Sala and Hoch 2009; Petit et al. 2011) including several chapters in this volume (e.g., Ewers et al. Chap. 18, Lachenbruch et al. Chap. 5, Mencuccini et al. Chap. 12, Sala et al. Chap. 11, Steppe et al. Chap. 9, Woodruff and Meinzer Chap. 14). It is interesting to note that a recent paper by Sillett and others (2010) suggests that there is no height-related reduction in volume increment in very large (and old) *Sequoia sempervirens* and *Eucalyptus regnans* trees. They reached this conclusion by a very detailed inventory of all of the growth increments that included all of the appendages in the massive crowns of these trees, which had not been considered previously. At the publication time of this book, these investigations continue, particularly with coast redwood (*S. sempervirens*) and further support the notion that tall and old trees continue to grow at the highest rates they ever have (Sillett, Van Pelt, Ambrose and Dawson, unpublished data). Many of the chapters in this book address the role that age may play in the observations of structure and function in tall trees. There is clearly a significant series of research questions that remain largely unanswered regarding (1) the biochemical and biophysical mechanisms that govern the interaction between age and height and how they individually and in combination result in the responses and morphologies observed and (2) a sufficient understanding of the interactions between the regulators of carbon pools, fluxes, and source – sink relationships as they play out over both small and large distances. Advancing knowledge in these areas and other will require new approaches and technology innovations as discussed next.

3 Technological Innovations

Early scientists were able to lay foundational elements that still stand today (e.g., Hales 1727; Dixon 1895; Huber 1924, etc.). However, a number of new techniques and technologies have given researchers improved access to trees and stands allowing characterization of all components in the soil-plant-atmosphere continuum including the soil (e.g., TDR, multi-sensor, frequency domain capacitance), the root system including mycorrhizal relationships (e.g., the high pressure flow meter developed by Tyree et al. (1995)), and the bole and crown. Access to tall trees was a particular problem; most often solved using mountaineering or arborist techniques. Triangular TV tower sections and scaffolding were also used, but were often relegated to canopies 45 m or less (e.g., Woodman 1971; Hinckley and Bruckerhoff 1975; Martin et al. 2001). With the advent (and use) of large construction cranes, finances became the main limitation to canopy access (e.g., Shaw et al. 2004). Many of the chapters in this book illustrate the use of a wide-range of canopy access technologies (e.g., ropes: Ishii Chap. 8; canopy construction crane: Chap. 14).

Sap flux and hydraulic conductivity can now be assessed in foliage (e.g. Brodribb and Holbrook 2003; Bucci et al. 2003) and in very small to large branches, roots, and stems (e.g., Čermák and Kucera 1981; Granier 1987; Salleo et al. 1992; Sperry et al. 1994; Burgess et al. 1998; Spicer and Gartner 1998; Čermák et al. 2007). We have methods to assess tissue water relations (e.g., Scholander—Hammel

pressure chamber, Scholander et al. 1965) and stomatal conductance (e.g., the null balance porometer: Beardsell et al. 1972; Parkinson and Legg 1972 or the leaf or shoot cuvette: Ritchie 1969; Field et al. 1982). In addition, there has been a concomitant development of infrared techniques to measure the exchange of physiologically important gases such as CO₂ and water vapor at the tissue and canopy (e.g. eddy covariance, Baldocchi 2003) scales. Analysis of stable isotopes of carbon and oxygen in CO₂ and in the hydrogen and oxygen of liquid water and water vapor allow inferences concerning physiological controls on gas exchange, sources and sinks for carbon and water and transit and residence times of water in trees (Dawson et al. 2002; Meinzer et al. 2006; Dawson and Simonin 2011). These isotope techniques have allowed investigators to measure easily, rapidly and frequently the factors associated with the movement and use of carbon and water by trees. Two of the chapters in this book explore and document the value of technology and demonstrate how some unknowns may be cracked via an imaginative application of existing technologies (e.g., chapters by Čermák and Nadezhdina Chap. 15, McDowell et al. Chap. 10). Johnson et al. (Chap. 3) explore the other end of the size spectrum and discuss the need for adapting technology for measuring physiology of the seedlings.

Technology is a two edged sword – its presence and development provide powerful ways to acquire important information and to address previously difficult to impossible questions. On the other hand, science driven by technology alone is often handicapped in scope and imagination. Several chapters in this book illustrate how relatively simple measurement techniques, when applied to interesting questions, result in powerful studies.

Another area in which technological advances have had a tremendous impact has been in characterization of wood properties. Until the 1960s, measurements of within-plant density were done with tedious direct methods to capture mass and volume of variously-sized samples; precision depended largely on how small one could cut up a tree and how well one could measure volume. In the 1960s, however, Polge (1978) introduced x-ray densitometry in which slabs or cores cut to a precise thickness were x-rayed; the intensity of the x-ray was related to the density of the material. Refinements of this technique have made it possible to document radial trends in wood density of trees and to compile data for different heights in trees or to compare trees from different silvicultural treatments. With the proper software, these systems have allowed people to compile ring-by-ring information on earlywood and latewood density as well as ring width and proportion of the ring that is latewood. Such work has been instrumental in tree breeding programs and wood quality studies (Cown et al. 2004), and maximum ring density has been used as an index of drought severity in dendrochronological studies (Cleaveland 1974; Yasue et al. 1997)

A further major advance in the study of xylem structure was the introduction of SilviScan and then SilviScan-2 (Evans 1999, 2006; Evans and Ilic 2001), a facility that scans precision-dimensioned microbeams with x-rays, light, and x-ray diffraction techniques at pre-determined step-sizes. In addition to giving the information from a typical x-ray densitometer, it produces estimates of fiber coarseness (related to cell wall thickness and lumen diameter) and orientation of the microfibrils in the thickest layer of the cell walls. With density and microfibril angle, a computer algorithm can

then estimate the wood's stiffness (modulus of elasticity) for each measurement location, typically giving radial profiles of wood properties. These advances in wood properties have made it possible for people to relate mechanical and hydraulic function to structure at a much finer scale than was possible in the past (e.g., Lachenbruch et al. 2010). Other work implementing light- and electron microscopy techniques has allowed variation in structural features of xylem conduits to be linked to variation in functional traits such as hydraulic conductivity and resistance to embolism (e.g. Pittermann et al. 2005; Wheeler et al. 2005; Domec et al. 2006; Hacke et al. 2006; Choat et al. 2008). Application of cryo-scanning electron microscopy to the study of xylem water transport has yielded important new insights on the dynamics and potential mechanisms of embolism formation and reversal in both primary and secondary xylem (e.g. Canny 1997; McCully et al. 1998; Melcher et al. 2001; Johnson et al. 2009).

4 Foundations of Plant Water Relations

For this book, it is useful to revisit the key concepts of plant water relations because much of the discussion about the role of age/height depends upon understanding how water potential varies, the biotic and abiotic factors that influence it, and how it and the tree's ability to modify it might create limits to height and reduce productivity. Qualitatively, changes in plant water status may be considered proportional to the difference between water gained through the roots (and/or redistributed from other tissues, see Chap. 13) and that transpired by the foliage (Jarvis 1975) with the additional and important caveat that no water flow from roots or storage can occur until there is a water potential gradient. Thermodynamically defined, total water potential (Ψ) is a measure of the capacity of water at a particular point to do work as compared with free, pure water (Slatyer 1967). Water potential gradients, as indicators of differential energy states of water, provide the driving force for the movement of liquid water as well as for water vapor throughout the soil-plant-atmosphere continuum (SPAC). Mathematically, Ψ can be expressed as:

$$\Psi = (\mu_w - \mu_w^{\circ}) / V_w = \Psi_p + \Psi_{\pi} + \Psi_{\tau} \quad (1.1)$$

where μ_w and μ_w° are the chemical potential of water in the system and that of free, pure water, respectively; V_w is the partial molal volume of water; Ψ_p is the pressure potential (or turgor pressure or xylem tension); Ψ_{π} is the osmotic potential (due to solutes); and Ψ_{τ} is the matric potential (due to surface forces, e.g., cell walls, soil particles).

As suggested in Eq. 1.1, Ψ is measured in terms of energy per unit volume which is equivalent to a force per unit area (commonly expressed in dynes cm^{-2} , bars or MPa). The pressure term (Ψ_p) can be positive while the others are always negative since these reduce the capacity of pure water to do work. Since the water potential of pure water at standard temperature and pressure is defined as zero, Ψ is usually equal to

or less than zero, except during periods of plant exudation (or guttation) or periods of positive root pressure, which are of negligible importance to most woody plants (Kramer 1969). Thus, Eq. 1.1 provides a framework within which all the component potentials may be accounted for when the plant properties, which lead to internal adjustments of Ψ , are discussed (e.g., Chap. 3, Chap. 14). Although Eq. 1.1 shows the solution for an instantaneous measurement at a single point in space and time, temporal and spatial dynamics can be easily added when considering either a Höfler diagram or the results of pressure-volume curves (Tyree and Hammel 1972).

A much more useful equation for the discussion of temporal and spatial variation in water potential at any point “x” in a tree can be defined as:

$$\Psi_x = \Psi_{\text{soil}} - \rho gh - \sum_{\text{soil}}^x f_i r_i \quad (1.2)$$

where ρgh is the gravitational potential (a product of the density of water, the gravity constant, and the height above water in the root zone, respectively; equal to about -0.01 MPa m^{-1} height). The frictional potential, $\sum_{\text{soil}}^x f_i r_i$, represents the summation of the products of the partial fluxes (f_i) and the partial resistance (r_i) along the pathway(s) from the soil to point “x” in the tree (Richter 1972, 1973). The water potential of the bulk soil is indicated by Ψ_{soil} . It should be remembered that for a given point “x” and time period in the tree, the bulk soil and gravitation potential are fixed (the soil value can change with time and the gravitation with height above the ground). The frictional potential is the dynamic part of this equation. It is also important to note that trees can undergo adjustments in their hydraulic architecture to partly compensate for the increasing frictional component as they get taller, but this has no effect on the gravitational component other than to increase it as a result of the increase in height. Therefore, gravity is always felt even when water is not moving and thus is not a hydraulic constraint in the usual sense of the term. An interesting note is that Eq. 1.2 was proposed by Richter after reading (and translating) the original work of Bruno Huber (1924), indicating that we continue to rely on this conceptual framing of water potential in the crowns of tall trees.

Equation 1.2 was derived by Richter (1973) from a consideration of water flow through the SPAC using the Ohm’s Law analogy where flow (q) is equated to the gradient divided by the pathway resistance (Huber 1924; van den Honert 1948). A popular, pragmatically useful, but mechanistically incorrect formulation of this analogy may be written (after van den Honert 1948);

$$q = \Delta\Psi_{\text{soil} - \text{root}} / R_{\text{soil} - \text{root}} = \Delta\Psi_{\text{root} - \text{leaf}} / R_{\text{root} - \text{leaf}} = \Delta\Psi_{\text{leaf} - \text{atmos}} / R_{\text{leaf} - \text{atmosphere}} \quad (1.3)$$

where R is the resistance along a particular pathway. Although the use of the Ohm’s Law analogy, especially as offered by van den Honert (1948) where he viewed water flow through the SPAC as a catena (or chain), has aided in the understanding and modeling of water flow through the SPAC (e.g., see Elfving et al. 1972; Hinckley and Bruckerhoff 1975; Alarcon et al. 2003; Vasconcelos et al. 2010), several precautions must be taken to avoid erroneous applications of this concept. First, the ability of various parts of the tree to act as sources and/or sinks (i.e., capacitors) is not accounted for in this formulation. Second, an assumption of steady-state, non-elastic

flow is made in which water movement through the stomata matches water uptake through the roots, hence the idea of a catena. Clearly, this cannot and does not happen. Third, stomatal gas and liquid phase resistances are not analogous, and phase changes at the leaf complicate $R_{\text{leaf-atmos}}$. Fourth, and probably most important, the Ohm's Law analogy only states that total water flow through all the roots, all the conduits of the stem, all the leaves is equal; it does not imply that flows through undefined sections of a single conduit running through the tree are numerically equal (Richter 1973). Much more sophisticated models, still initially based upon this simplified view of water flow, exist and can provide important insights into how different hydraulic conductances (1/resistance) can influence flow and vulnerability to embolism (Sperry et al. 1998). Models using very different approaches have also been successful (e.g., Aumann and Ford 2006; Lovisolo et al. 2010).

Several chapters build from these earlier and more simplistic foundations of plant water relations. It is often worth reverting to these earlier, perhaps simpler relationships in order to understand the relationships being used in these chapters. Finally, Hinckley (2004) provided a review of whole-tree physiology. The five topics there are worthy of review: (1) the nature and definition of the individual organism, (2) carbon, water, and nutrient acquisition, use, and distribution, (3) how trees and specifically large trees biophysically and biochemically "perceive" their internal and external environment and how then responses are mediated or signaled, (4) scaling and a critique of the use of branches as a surrogate for whole tree responses, and (5) the potential for "domestication" of trees.

5 Recurrent Themes in Book

These 17 chapters encompass many universal themes for the study of age- and size-related changes in tree structure and function and whether ontogenetic variation is size- or age-related. Recurrent themes include the microclimate experienced by trees of different stature and age, the extent to which morphological or functional traits change with age or size, the extent to which these changes follow simple scaling principles, tradeoffs of one trait or several traits for another trait or groups of traits, the decline of growth with tree or stand age, plastic vs. fixed control of traits with age or size, and the concept of age versus size relations for tree function.

5.1 *Microclimate*

The coverage of this book spans tree growth and development from day-old seedlings to towering giants. As a tree increases in size from a germinant to a large mature individual, its aboveground parts occupy different environments both due to growth into new microenvironments, and to changes it causes in its own environment such as self-shading (e.g., Woodman 1971; Lewis et al. 2000; Ishii et al. 2008, Chap. 10).

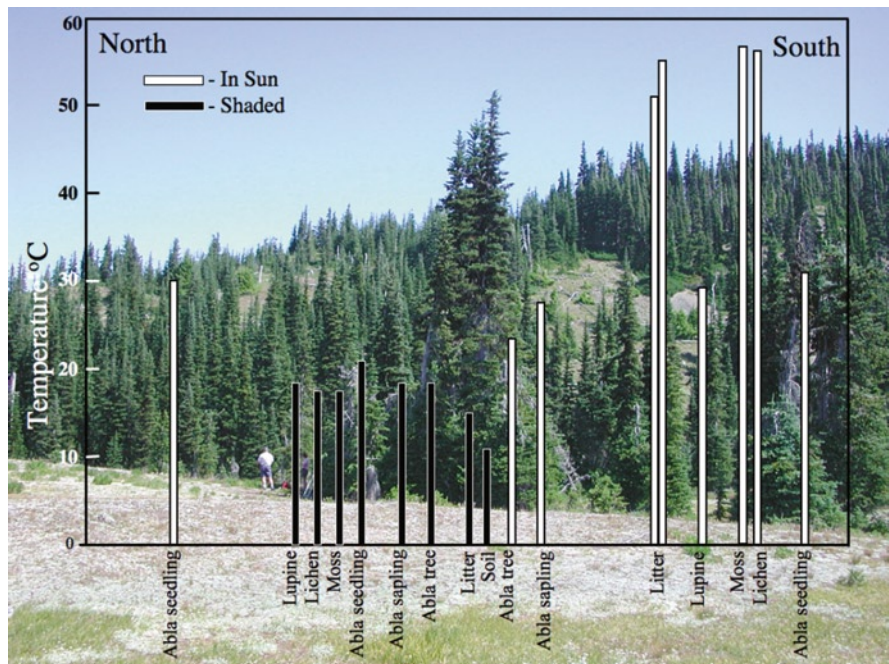


Fig. 1.3 Data are from a subalpine meadow in NE part of Olympic National Park, USA, July 28, 2005. The meadows have a 10% slope to the south and they are at 1,591 m on the SW side of a ridge that tends from the NW to the SE at Hurricane Ridge. Temperature measurements were taken with an infrared thermometer between 1,315 and 1,335 h (PDT); air temperature was between 24.1°C and 24.8°C. Measured temperatures ranged from 10.8°C to 5 cm beneath the soil surface under the sub-alpine clump to 56.3°C for dry, sunlit moss/lichen crusts on the south side of the clump. *White bars* represent things measured in direct sunlight, whereas *black bars* are for shaded measurements. Plant temperatures were largely based upon measurements of foliage temperatures

The distribution and microenvironment of belowground parts also change as touched on in Chap. 15. Chapter 3 details the extreme temperature, light and moisture regimes that new germinants may experience, as well as the patchiness of their environment in both space and time. It is not difficult to imagine the kinds of differences in micro- and mesoclimate that a tree might experience over its life, from day to night, and from summer to winter. Over the life of a bristlecone pine tree (*Pinus aristata*), it may experience almost 5,000 years of climate, and in its mature stages, it may retain foliage that was produced 28 years before. Nonetheless, microclimatic differences among seedlings or plant parts may be as pronounced as the annual differences a tree might experience in 5 millennia. A newly germinated subalpine fir (*Abies lasiocarpa*) seedling located at 1,600 m in a subalpine meadow in the Olympic National Park, Washington (Waring and Franklin 1979) would experience surface temperatures over 50°C (Fig. 1.3, see also Seymour et al. 1983), temperatures that can kill the cambium (thus girdling the developing seedling) and that exceed the upper temperature threshold for positive carbon uptake leading to

foliage death (Seymour et al. 1983; Teskey et al. 1984). Shaded plants and plants with sufficiently thick bark are not subject to such exposures. The impact of the harsh microclimate near the ground is illustrated by the fates of thousands of *Abies lasiocarpa* seeds that have been tracked for 17 growing season (Soll 1994, A. Woodward, pers. comm.) in subalpine meadows in the Olympic National Park (see Fig. 1.3 for one of the study meadows). There were initially 696 ± 469 seeds per square meter of substrate from which 12.6 seeds proceeded to the germinant stage, 9.1 survived by the end of the first growth season, and 0.43 were alive 17 years later. At this last census date, the average seedling was only 12 cm-tall while the tallest is just over 30 cm. Germination and early survival were influenced by both soil aridity and temperature.

Mature trees are faced with large within canopy gradients of light and temperature. Evergreen trees must both modify (i.e., acclimate) existing foliage and produce somewhat different new foliage as the older, lower, or more interior foliage becomes increasingly shaded (Brooks et al. 1994, 1996). In addition to light, gradients in carbon dioxide, air and foliage temperature, and humidity exist affecting the overstory and understory vegetation as well as the epiphytes and other organisms occupying these different canopy zones. For example, Garrett and Cox (1978) observed differences as great as 100 ppm between early morning and mid-day in forest carbon dioxide levels collected between 2.8 and 18.3 m in a Missouri deciduous hardwood forest. Carbon dioxide levels between 700 and 450 ppm near ground level at sunrise are not uncommon in many forest types and these values can drop to below 280 ppm in the mid to lower canopy at mid-day. Similar, but even much more pronounced gradients were noted by K. Kavanagh (unpubl. data) in a coniferous forest in Northern Idaho and also in a Northern California redwood forest (Tu and Dawson, in review). When air temperature and relative humidity at different positions in the canopy are converted to vapor pressure deficit (VPD), vertical gradients in evaporative demand are observed. Depending upon the openness of the canopy and the atmospheric conditions, very shallow or very steep gradients in VPD are noted. Near the tops of coast redwoods and giant sequoia, VPDs of about 3–4 kPa, respectively, are observed; decreasing steeply to about 0.6–1.5 kPa within 50 m of the top (Fig. 1.4). Tropical lowland and montane forests also exhibit vertical gradients, but not as steep as the two California species (Fig. 1.4). The relatively shallow gradient observed in the old-growth Douglas-fir-western hemlock forest (Fig. 1.4) is likely the result of two factors: (1) measurements were taken from a tower versus within the crowns of the trees and (2) this forest has a very strong rumple factor increasing the likelihood of strong turbulent mixing and entraining of above canopy air.

In addition to the changes imposed on their own environment as trees increase in size, the resulting increase in mass must be supported physically. This support includes not only the requirements to avoid breakage from the static load of the tree, including its foliage, reproductive structures, and occasionally snow and ice loads, but also to avoid breakage in the wind. The forces of the shifting crown extend from the upper roots to the branch tip, and act on the wood from the center of the tree (which was formed when the tree was smaller) all the way out to the surface. The impact of increasing size on biomechanics is discussed in Chap. 5.

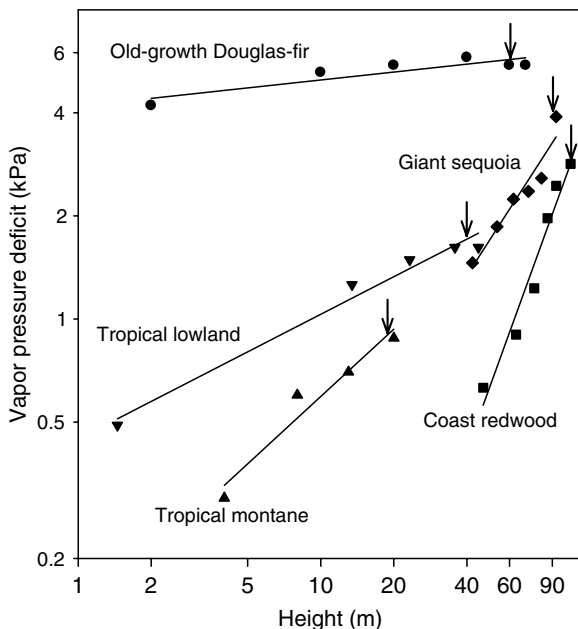


Fig. 1.4 Variation in vapor pressure deficit with height in five forest types differing in maximum canopy height: an old-growth Douglas-fir-western hemlock (*Pseudotsuga menziesii-Tsuga heterophylla*) forest in southwestern Washington State, USA, an old-growth giant sequoia (*Sequoiadendron giganteum*) forest in the Sierra Nevada Mountains, USA (Dawson, unpublished data), a coast redwood (*Sequoia sempervirens*) forest in California (Dawson, unpublished data), a tropical lowland forest in Brazil (Data from Roberts et al. 1990), and a tropical montane forest in Ecuador (Data from Motzer et al. 2005). Arrows indicate approximate maximum canopy height. Note that plot axes have log scales. Data were obtained during the dry season in each forest type

5.2 Changes in Structure, Function and Functional Relationships

Almost every chapter discusses the morphological and physiological adjustments that occur as trees get larger and/or older. Many changes are recorded in tree structure. Lachenbruch et al. (Chap. 5) propose using the radial variation in wood structure to tease out the hydraulic and biomechanical factors of importance to individuals through their growth trajectory. Similarly, Voelker (Chap. 17) uses the radial wood record present in tree rings together with regional climate to infer the factors of importance for radial growth across the lifespan of the trees. He showed, for example, that relative humidity explained half as much variation in radial growth for old as young trees, and that the age-dependency of growth varies by habitat and is much stronger at treeline than within the interior of a tree's geographic range. Another change is the enormous switch from the structure and physiology of cotyledons to

that of the true leaves, which may be associated with a spike in mortality (Chap. 3). Ishii (Chap. 8) uses the record of the canopy's structure to explain that young trees with their hierarchical structures will have less buffering capacity to disturbances than will older, larger tree with their polyarchic structure, which is essentially a population of linked hierarchical structures. Similarly, Voelker (Chap. 17) discusses that the growth of old trees seems more buffered from large variations in climate than that of young trees. McDowell et al. (Chap. 10) used a record of isotopic composition rather than physical structure to infer past physiology. They found a universal decline in stable carbon isotope discrimination with increasing height for all foliar and wood datasets. This decline occurred at a rate different from what would be expected from the effects of gravity acting on the water column alone, giving sound support to the idea of changing physiology with height.

Other changes occur by virtue of size alone, such as the fact that large trees have more self-shading inside their crowns than small trees (Chap. 10). Another example is that small trees should have more synchronized within-crown induction response to herbivory than large trees because the transmission of the signaling compounds will occur over shorter distances (Boege et al. Chap. 7). If distal water-transport conduits tend to have smaller diameters than proximal conduits (called conduit tapering), and if distal conduit diameter at the leaf petiole is fixed at a minimum level by natural selection and biophysical forces, then the size of conduits at the plant's base will be determined by plant size (Mencuccini et al. Chap. 12). Mencuccini et al. also note the increased cost of construction of a long transport system as trees get taller. Another set of examples of changes that occur by virtue of size comes from the increase in tension in the water column as trees get taller that occurs both because of the greater path length, and also from the increased hydrostatic force (the effect of gravity on the taller water column). The increase in xylem tension high in the tree causes a decrease in the turgor that can be maintained during tissue expansion, causing permanent reductions in xylem conduit and other cell sizes leading to decreased hydraulic conductivity and increased leaf mass per area and its resultant reductions in growth efficiency, increased resistance to CO₂ diffusion to the carboxylation sites, and finally, a decrease in photosynthetic rate (Chap. 9; Chap. 14; Ambrose et al. 2009, 2010; Cavaleri et al. 2010; Oldham et al. 2010). The impact of height-related reductions in turgor and leaf expansion was originally and experimentally demonstrated by Richter (1974); by using overlapping saw cuts: he was able to transform a branch that produced shade morpho-type needles to one that produced sun types. Superimposed on the approximately linear gradient of decreasing water potential with increasing height is an exponential gradient of increasing light both of which affect vertical gradients in foliar morphology and physiology (Chap. 8). McDowell et al. (Chap. 10) use a meta-analysis of stable isotope data in tall trees to separate the hydrostatic from light effects on photosynthesis and leaf morphology.

Most of the other examples of changes in structure, function, or functional relationships are those that involve structural or physiological changes that mitigate some effect of the tree's increasing size. The apparency of a plant to herbivores will