

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

T.M. Hinckley (✉)
School of Forest Resources, University of Washington, Seattle, WA 98195, USA
e-mail: hinckley@u.washington.edu

B. Lachenbruch
Department of Wood Science and Engineering, Oregon State University,
Corvallis, OR 97331, USA

F.C. Meinzer
USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way,
Corvallis, OR 97331, USA

T.E. Dawson
Departments of Integrative Biology & Environmental Science, Policy and Management,
University of California – Berkeley, Berkeley, CA 94720, USA

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

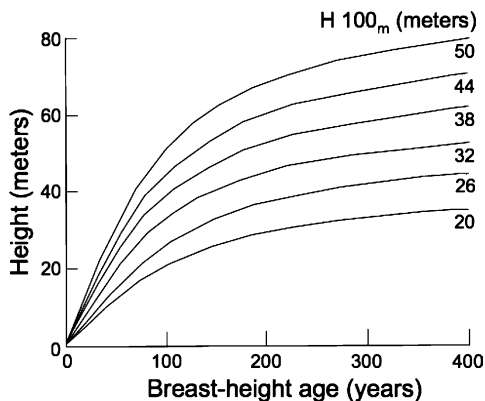


Fig. 1.2 Site index (or age versus height) curves for Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) growing in high elevation forests of the Cascades of Oregon and Washington (from DeMars and Herman 1987). Although each curve appears to be approaching an asymptote, curves have not flattened 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).

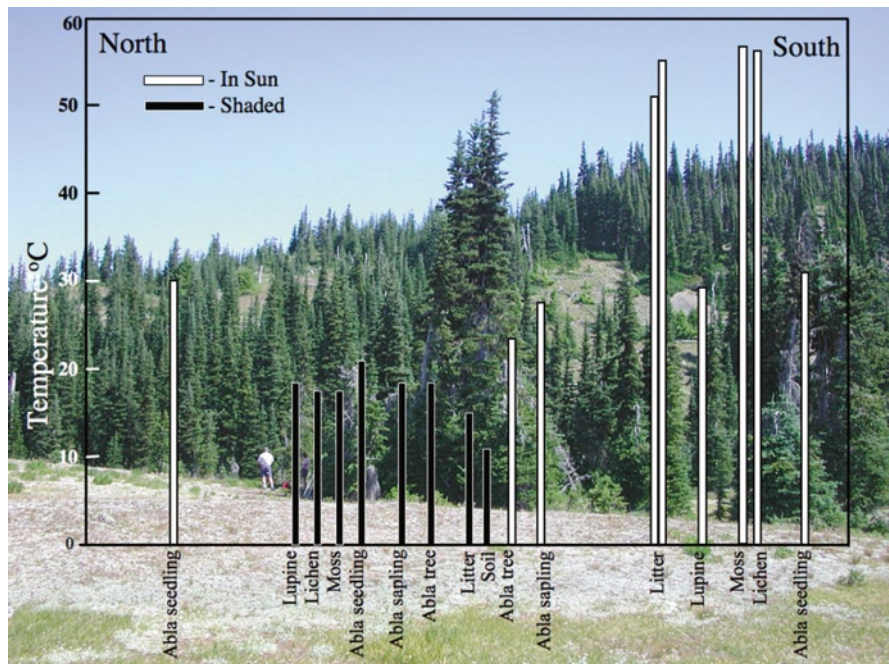


Fig. 1.3 Data are from a subalpine meadow in NE part of Olympic National Park, USA, July 28, 2005. The meadows have a 10% slope to the south and they are at 1,591 m on the SW side of a ridge that tends from the NW to the SE at Hurricane Ridge. Temperature measurements were taken with an infrared thermometer 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 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.

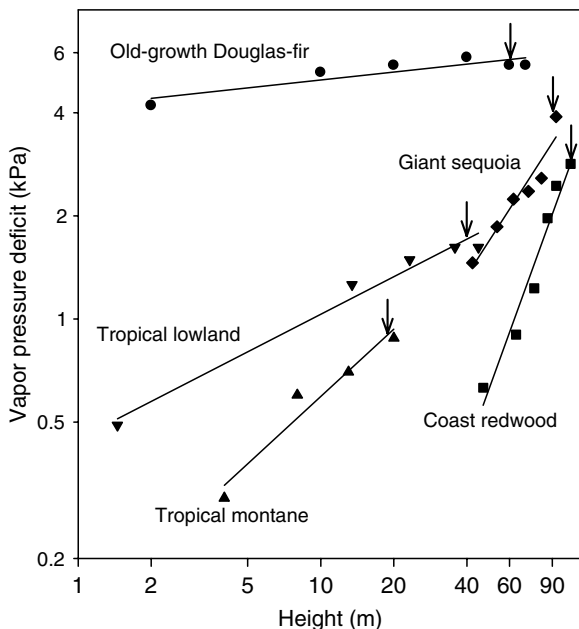


Fig. 1.4 Variation in vapor pressure deficit with height in five forest types differing in maximum canopy height: an old-growth Douglas-fir-western hemlock (*Pseudotsuga menziesii*-*Tsuga heterophylla*) forest in southwestern Washington State, USA, an old-growth giant sequoia (*Sequoiadendron giganteum*) 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

generally increase as a plant grows and develops (Chap. 7). It would be expected that trees have an increased tolerance to herbivory as they grow, and/or have dispersal and germination strategies to mitigate their increased apparency. Two such strategies are germination close to the parent, assuming the parent is more herbivore-resistant than the germinant, or germination at long distance from the parent, increasing its chances of moving away from the herbivores. The production of epicormic branches (from buds that had long been dormant) in some species appears to partially compensate for the increasing resistance for water flow in large old trees (Chap. 8) and possibly also compensates for the increasing ratio of respiration to photosynthesis in these large trees. Lastly, tall, old trees appear to have a higher hydraulic capacitance, permitting greater reliance on stored water to transiently replace transpirational losses and buffer fluctuations in xylem tension (Scholz et al. Chap. 13).

At the stand level, it is appropriate to ask which traits can best predict tree function with age. Ewers et al. (Chap. 18) showed that getting the correct estimate of stand stomatal conductance is key, and that either leaf area or sapwood area have more accurate predictive capability than sap flux per xylem area. Succession can be viewed as an age-related change at the stand level, and Anten and Selaya (Chap. 16) show that the light level is the most important environmental change through succession in tropical forests. Early successional species have adaptations that are useful in the highly resource competitive environment in which they live (thin leaves, strong shade avoidance response, thin wide-ranging roots). Late successional species have adaptations that are useful in the more variable light environment in which they grow but that also enable them to survive the stresses of the lower resource environment.

Some of the changes in structure or function that occur throughout the tree's lifetime are related to changes in its biotic environment. The clearest examples of this sort of change come from the relationship of ontogeny to plant defenses against herbivory (Chap. 7). Indirect defenses include traits that facilitate the visitation or colonization by mutualistic animals that defend plants against herbivores. The reliance on these indirect defenses can change during ontogeny because a tree may need to be sufficiently large to acquire mutualists. Similarly, seedlings may have facilitative or competitive interactions with other trees through a variety of factors including pathogens and mycorrhizae (Chap. 3). Another example of biotic factors that may shape the age- or size-related changes in trees is differential effect herbivory may have on reproductive success: female plants, bearing a higher reproductive effort, may be less tolerant of herbivory than male plants (Chap. 2). Lastly, height relative to surrounding vegetation is often more important than absolute height: consider the greater importance for males than females to be tall for pollen transfer (Chap. 2) and consider the effects of being an emergent tree on the risk of wind damage (Chap. 4), and the effects of shading from its own and adjacent crowns. The preceding examples represent situations in which changes in functional traits and functional relationships during growth could not be studied in isolation from biotic factors of the environment.

5.3 *Scaling of Structure and Function with Size*

Another theme in many of the chapters is that some processes scale with tree size, whereas other processes occur at different sizes or ages. Mencuccini et al. (Chap. 12) gave the example of the pipe model, which scales relatively well with size (as leaf area/stem cross-sectional area) only when a stem contains no heartwood. They also summarize eight models for long-distance transport in xylem or phloem, telling explicitly whether the model is scalable by tree size, and explaining the manner in which functions are scaled. Day and Greenwood (Chap. 4) stated that there is no predictable ontogenetic trajectory for a number of physiological traits such as photosynthetic rate, water use efficiency, specific leaf mass, ratio of shoot to root mass and metabolic efficiency. Such lack of correlation means that age-related scaling models may need input from all ontogenetic stages. King (Chap. 6) showed that the aboveground mass allocation of trees appears to follow different scaling rules at different life stages.

With regard to scaling of resilience to disturbances, large trees and stands of large trees may have a greater capacity to buffer themselves than smaller trees and stands of smaller young trees. Therefore, it would be inappropriate to scale up the response of a young stand to a perturbation to that of an old stand of large trees. Not only do young and old trees and stands have different responses to disturbance, but Ewers et al. (Chap. 18) reported that stand age has a large effect on forest transpiration. For example, accurate modeling of stand transpiration requires substantially different old-growth and young stand values of the canopy average reference stomatal conductance and average sensitivity of canopy conductance to vapor pressure deficit.

5.4 *Tradeoffs*

The changes in tree structure and function that occur throughout growth (Sect. 5.2) are presumably those that give the highest fitness through promotion of survival and reproduction, regardless of whether they follow simple scaling rules (Sect. 5.3). Many of these changes are likely to involve tradeoffs that may be difficult to uncover. These tradeoffs are considered explicitly in some scientific formulations and are implicitly assumed without considering alternatives in others. In an explicit discussion of the optimal design of a transport system for tall trees Mencuccini et al. (Chap. 12) suggest that among the answers of what should be maximized are total conductance of the tree or organ-level efficiency; tree growth; total net carbon gain; and tree level efficiency of use of a particular resource. Such explicit consideration can move the field forward tremendously. We can also be misled by preconceptions that a trait is traded off for another when in reality entirely different factors may be of importance (Chaps. 2 and 5). Moreover, many features have more than one role in a tree, so it is a challenge to take multi-functionality into account as in the case of the cost of construction of a xylem conduit wall, which functions both in hydraulic reinforcement and mechanical stability of the tree (Chap. 12).

Adaptations and tradeoffs that serve an individual well at one life stage may be mal-adaptive to survival at another life-stage (Chap. 4). A similar comparison could

be made involving “young” (early successional) species and “old” (late successional) species. The early successional species tend to have a high allocation to leaves, enabling them to have high assimilation rates for a period of time. The late successional species, with lower leaf allocation and more allocation to mechanical support have slower growth but then have a longer life span, for they can maintain higher assimilation rates in the later years of life than can the early successional species that are mal-adapted to the late-successional habitat (Chap. 16).

5.5 Decline in Productivity of Individual Trees and Stands

Many chapters discuss and evaluate hypothetical causes for the well-documented decline in productivity of individual trees and stands with age. These hypotheses include declining photosynthetic rates (Chap. 11) the age-related increasing cost of reproduction (Thomas Chap. 2) or of structural support (Chap. 6). The decreasing photosynthetic rate observed in taller trees could result from many factors, including a feedback inhibition of photosynthesis resulting from reduced sink demand for carbohydrates associated with the impact of reduced turgor on expansion of cells in leaves and shoot tips (Chap. 14). Evidence from studies that characterize pool sizes of non-structural carbohydrates suggests that carbon does not limit growth of old trees, and that other causes of size-related growth reductions must be sought (Chap. 11) such as difficulty in sustaining adequate rates of long-distance transport of nutrients and assimilates. Ishii (Chap. 8) points out that the study of these limiting factors is made more difficult by extremely complex architecture of the oldest trees: what is the appropriate functional architectural unit of study in old trees? As pointed out above (Sect. 2), Sillett et al. (2010) showed an increase in the growth of mature (>800 years old) redwood trees, a trend opposite to many previous reports. They emphasized that the reason they saw an opposite trend is that because estimates in most past studies relied on ground-based measurements and not on measurements obtained in the upper crown where most of the growing biomass is. Thus, even though shoot extension in tall trees may be limited by reduced turgor, the multiplication of meristematic regions (apical and lateral buds, cambium) in large trees may allow total volume growth to continue unabated. These findings raise yet another question: are we making our growth measurements in the appropriate places in large and old trees? Without access to time or the entire tree, how does one access total biomass increment by a tree or a stand, and how does one include the belowground portion?

5.6 Plasticity

Several chapters deal with whether the observed differences between young and old trees are fixed traits or plastic responses to the changing environment sensed by the plant. Day and Greenwood (Chap. 4) distinguish between traits regulated by factors that are intrinsic vs. extrinsic to the meristem. Those traits regulated by intrinsic

factors are manifested by permanent ontogenetic changes in meristem behavior (i.e. “fixed” developmental patterns), whereas traits regulated by extrinsic factors, are plastic responses that can follow changes in the environment. They provide a list of the predominant intrinsically and extrinsically regulated traits in germinants, seedlings, saplings, young-mature, and old-growth trees. (Note that Johnson et al. Chap. 3 state that seedlings exhibit a high degree of phenotypic plasticity in traits associated with water transport and light, whereas Day and Greenwood’s summary says seedlings exhibit very little phenotypic plasticity.) Similarly, the chapter on radial changes in wood characteristics (Chap. 5) shows examples of species in which certain wood traits appear to be intrinsically controlled and others in which the control is plastic. A good example is wood density: in many species, it increases by growth ring number until it reaches an asymptote. In many of the pines, the density value is more closely correlated with growth ring number than with the diameter of the cambium at the time the wood was produced. This suggests that the changes follow a fixed trajectory, by age. Other species have clear plastic responses. Many lianoid species, for example, show a radical increase in wood density when the self-supported young stem encounters support and begins lianoid growth.

If a tree experiences a defoliating event such as herbivory, its ability to replace the lost biomass is termed compensation. Compensation is a form of plastic reaction to the disturbance. Boege et al. (Chap. 7) state that in general saplings are able to compensate to a greater degree than are seedlings, presumably by virtue of sapling’s larger photosynthetic area, reserves, and bud banks.

Several authors mentioned traits that appear to follow specific rules, but that have variants on the basic pattern that are related to environment. Examples include the effects of crowdedness or wind on whether trees grow with geometric similarity, (Chap. 6), and the offset between height-related declines in carbon isotope discrimination for sunlit and shaded foliage (Chap. 10) (Fig. 1.5).

5.7 *Age vs. Size*

Several chapters make distinctions between age- and size-related features. Thomas (Chap. 2) stated that monocarpic plants reproduce a given age rather than size, although Day and Greenwood (Chap. 4) state that precocious flowering is regulated by both size and maturation state. Tree size is more important than meristem age for the growth rate of buds from grafted meristems (Chaps. 8 and 4). Size (height) is more important than age for processes driven by turgor such as leaf expansion and shoot extension (Chaps. 9 and 14) and for processes driven by xylem tension such as vessel and tracheid features that confer resistance to embolism (Chap. 5). Size has also been linked to mechanical influences on radial variation in stems (Chap. 5).

Lachenbruch et al. (Chap. 5) list the most apparent similarities and differences between hypothetical trees of the different size but the same age, and different age but the same size. The list is long and includes a wide range of traits (Table 1, Chap. 5). Had there been only one trait that differed and many that were the same (i.e. “small trees have less stress on the stem periphery than do large trees; all other traits were

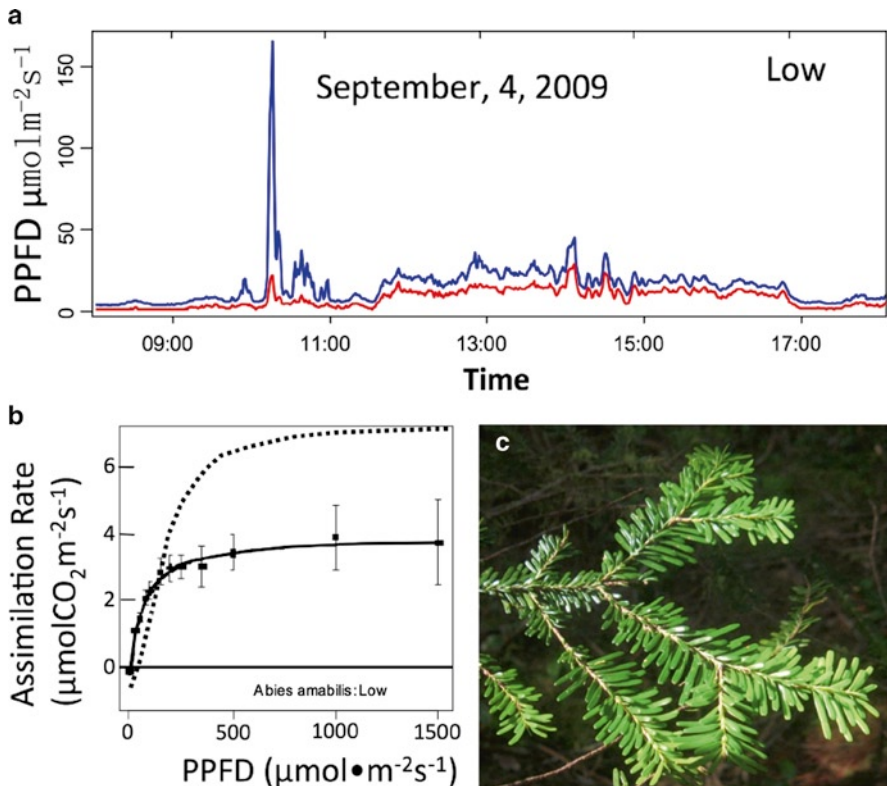


Fig. 1.5 (a) Daily pattern of direct beam radiation (*blue line*) and diffuse radiation (*red line*) in a dense western hemlock stand (*Tsuga heterophylla*) in the NW part of the Olympic Peninsula, Washington State. (b) Assimilation versus photosynthetic photon flux density curve (*solid line*) for shade foliage (see panel c) from *Abies amabilis* saplings growing under the stand in panel (a) The *dashed line* is for sun foliage for an *Abies amabilis* sapling growing in a thinned stand. (c) Photograph of typical shade foliage and branch from *Abies amabilis* (Data from Ma 2010)

the same between small and large trees”) then logic would allow us to hypothesize that the size-related changes were driven by the stress on the stem periphery. The list demonstrates, however, that there is not any one obvious factor that is driving changes for either size- or age-related changes.

6 Emerging Issues and Open Questions

A number of gaps in our knowledge, mechanistic questions, and integrative issues remain and likely will continue to grow. Two key levels of integrative issues remain in our minds. The first involves the pronounced changes in structure and function that occur over the life cycle of a tree. The second issue involves the controls on integration over time and space of carbon, water and nutrient functioning, its changes

in integration, and feedbacks at multiple scales within a tree. In addition to these themes, some authors have called for more standardization in techniques, terminologies, and the way in which different measures are reported (Chaps. 13 and 15) and warn of the importance of being explicit about the variables under discussion (Chap. 12).

6.1 Gaps in Knowledge

Authors have pointed out that more work is needed to clarify differences in patterns among taxonomic groups, biomes, and specific life stages. Most of the chapters distinguished between angiosperms and gymnosperms, noting that they often followed different developmental and physiological rules. Boege et al. (Chap. 7) state that to understand the macro-evolutionary patterns of the ontogeny of defense, a phylogenetic context is needed. Indeed, it is intriguing when angiosperms and gymnosperms have similar (rather than different) ranges of values for a trait, such as intrinsic capacitance, C , of xylem tissue (Chap. 13). This similarity suggests that the trait (or something strongly correlated with it) is of importance for fitness, as well as being governed by laws of physics. Other examples are the maximum height of trees, and the near-universal pattern of asymptotic increases in tracheid or fiber cell length with cambial age (Chap. 5). Much of the research discussed in this book comes from research on tropical angiosperms or temperate angiosperms and gymnosperms; more work is needed in other ecosystem types (boreal, dry tropical, and other special ecosystems) and in other woody growth forms (shrubs, prostrate and climbing plants and hemiepiphytes). This information will help us ask more informed questions, to ultimately better understand, predict, and manipulate species, stands, and ecosystems. For example, the knowledge that tropical angiosperms had higher carbon isotope discrimination than did either temperate gymnosperms or angiosperms (Chap. 10) gave insights into the strong effect of precipitation and the lack of freezing temperatures on this variable.

Most research has focused on saplings to mature trees, and young to mature stands of economic value, with relatively less research on the seedling to sapling stage, reproductive effects on tree growth, and senescence, or very young and very old forests. There is little research on the physiology of newly emerged seedlings, in spite of the importance of the regeneration niche for establishment of new individuals (Chap. 3). Likewise, in spite of a large body of theory on life history strategies and their use in predicting growth and reproductive dynamics of trees and stands, there is relatively less research that integrates reproductive costs into our understanding of age-related changes in tree ecophysiology (Chap. 2) and the challenge of how to measure “costs” remains as well.

Senescence is not discussed very explicitly in this book, perhaps because of the nature of the individual contributions, but also perhaps because of less research in this area. It was mentioned in the context of monocarpy, a reproductive strategy in which the plant dies soon after reproduction (Chap. 2), as maximum height attainable

for biomechanical considerations (Chap. 6) and for early vs. late successional species (Chap. 16). Mortality was mentioned in the context of establishment success (Chap. 3), questions about vulnerability during specific ontogenetic transitions, such as when shade-tolerant conifer saplings transition into the upper canopy (Chap. 4), and the effects of herbivory at life stages that differ in plant architecture and metabolic stores (Chap. 7). Ishii (Chap. 8) discussed the buffering effects of large, complex canopies on the impacts of disturbance on individuals, but did not discuss tree death, and Anten and Selaya (Chap. 16) discussed the modeling results of leaf longevity vs. longevity of trees growing under the forest canopy and in gaps of different sizes. The physiological data on factors such as carbon isotope discrimination (Chap. 10) and tolerance to herbivory at the oldest ages will be particularly interesting in the light of trends toward increased non-structural carbon stores in mature trees (Chap. 11).

6.2 Questions About Integration and Feedbacks

Numerous questions remain surrounding the integration of woody plant growth over space and time, including the changes, controls and feedbacks associated with the usage of carbon, water and nutrients. The most basic question is how does the tree regulate the development of appropriate structures that work together, in an apparently coordinated manner? This question includes the mechanisms of coordination (like epigenetic changes at the meristem, or plastic responses), as well as the causal agent or signal to direct the appropriate development and physiological responses (Chaps. 4 and 7). The second question is what variables does a tree or a tree part sense in order to develop and function differently at different stages? Does it “know” its size or age, are there intrinsic directional changes in the meristem that tend to correlate with size or age, or does it sense its size or age more indirectly from the environment (such as by sensing bending stresses near the cambium)? Root to shoot distances and the number of divisions a given meristem has undergone all likely play some role. The phloem is largely overlooked in this book: Mencuccini et al. (Chap. 12) point out the importance of developing suitable empirical methods to estimate the physiological properties of phloem (fluxes of water and solute fluxes, turgor pressure, hydraulic conductivity) so that the integration and interactions between xylem and phloem can be studied.

Below are some of the specific questions related to integration or feedbacks that were raised in the chapters. To better understand the degree to which the age-related decline in productivity is related to the geometrical distribution of biomass, we need data on life-long trajectories of tree allometry that we can compare to the allometric patterns generated by models that embed our hypotheses (Chap. 6). An empirical approach could make use of individual trees, comparing mass distribution before and at periods after the removal of their tops.

The newly emerging picture of carbon economy suggests that trees may not be specifically carbon-limited in their growth. Many more cases will need to be studied

to understand the range of species and conditions for which this is true, and also to integrate this knowledge with our current paradigms in which resource availability directs the organismal physiology and resulting growth or reproduction (Chap. 12). Sala et al. (Chap. 11) highlight the need to find the most sensitive and informative time and tissues in which the study of non-structural carbon (e.g. carbohydrates) concentrations best reflects the actual imbalance between sources and sinks. It is possible that some of this stored carbon becomes inaccessible at some point: the study of heartwood non-structural carbon stores would be enlightening in species with extremely large stores of starch in their sapwood, such as *Toxicodendron radicans*, (Rock 1972). A more general picture of the degree to which trees are carbon-limited throughout their lifetime would have immediate application to better understand resiliency to disturbance of individuals and stands of different ages.

The decline in assimilation and tree growth with age may be related to physical factors and feedbacks, but also to intrinsic changes in tissues. More research using rootstocks and scions of different sizes and ages will provide more insights (Chap. 9). Measuring growth at the points in a tree crown where most of it is happening also needs to be done more frequently because it is revealing that apparently “old trees” are not showing growth declines at all (Sillett et al. 2010). Such experimental methods and others may help us answer questions about whether tree growth at different developmental stages has the same sensitivity to biophysical drivers. This age-specific information will be of great value for models of tree productivity and net primary productivity under different climate projections (Chap. 17).

6.3 Questions About Changes in Structure and Function over the Tree's Life-Cycle

There are also many remaining questions about the changes in structure and function that occur during the tree's life cycle. Many of these questions are aimed at understanding the effect of a factor on a trait through time. The factors may relate to phylogeny, genetics, previous history, the physical environment (its stability, its change, or the tree's changed perception of the environment), biotic interactions that themselves may change as the tree grows, or a particular observable characteristic displayed by the organism such as its xylem anatomy. The affected traits are also varied, and can include functional traits (such as water transport) or a population-level characteristic (like survivorship). Many of the questions are not easy to address, and for this reason, experimental methods must be designed carefully. It is exceedingly easy to misinterpret tradeoffs (Chap. 12). Thomas (Chap. 2) discussed an example in which rainfall had a positive effect on growth and a negative effect on acorn production and could have been interpreted as a negative correlation of growth and acorn production (Knops et al. 2007), when in fact, the correlation did not represent causation. Another example is when a trait (e.g. embolism) affects more than one function (it may have provided stored water; it may decrease water transport) (Chap. 12).

7 Conclusions

This book brings together current information from diverse fields on the age- and size-related changes in structure and function in trees, successional groups of trees and stands, as well as providing frameworks for understanding, characterizing, and further researching age- and size-related changes. Many voids in our knowledge were exposed, and ideas for how to move forward are presented. We know that we have not covered all of the relevant topics or all of the tree species where relevant work has been done. Nonetheless, the findings from the types of research that are presented in the chapters that follow do highlight the state of our knowledge in many areas of tree research and its many applications. In all cases, the work presented is designed to lead to a better understanding of how trees work. For example, by understanding how xylem structure integrates the sometimes-conflicting requirements of water transport and biomechanics at multiple stages of life within an individual, we have created a working model for how these functions are integrated in other systems. In some cases, the information could potentially be used by breeders to increase biomass productivity, increase fruit production, or decrease losses to herbivory. In other cases, information could be used to better understand the magnitude of vulnerabilities to different biotic or abiotic factors at different life stages, which could lead to management strategies to encourage or discourage a population to flourish. These same insights could be very helpful in predicting and shaping performance and biogeography of species and assemblages of species at the individual and population levels under current and changing climate regimes. An example is the insights provided by Woodruff and Meinzer (Chap. 14), who state that “It is noteworthy that elevated carbon dioxide levels will not benefit trees if they are turgor limited as opposed to carbon limited. Furthermore, increased temperatures and/or droughts are likely to exacerbate turgor-related constraints on growth.” It is with the goal of bringing together this information and inspiring others to continue contributing to the growing understanding and use of whole lifespan biology of trees that the editors and authors put forward this volume.

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