Chapter 5
Radial Variation in Wood Structure and Function in Woody Plants, and Hypotheses for Its Occurrence

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Abstract Woody stems, branches, and roots display large progressive changes in structure and function from the pith outwards, a pattern known as the core/outerwood or juvenile/mature wood pattern. For example, the typical radial pattern (TRP), characterized mostly for commercial softwoods, includes increases in wood density by a factor of up to 1.5, tracheid width by a factor of 2, and tracheid length by a factor of up to 4. These large changes will have substantial effects on the success or failure of the plant. Our knowledge of the drivers and the universality of the typical radial pattern are minimal in spite of 150 years of research that has been concentrated mostly on commercial softwoods. This chapter (1) provides a brief description of the nature and magnitude of the structural and functional changes along the radius of woody stems, (2) clarifies whether ring number from the pith or size best explain the typical radial pattern, and (3) introduces and briefly evaluates hypotheses for the functional significance of the radial patterns, with developmental, hydraulic, and mechanical hypotheses. The chapter indicates major knowledge gaps in different biomes and plant types, and provides examples of systems in which research advances could be made. An improved knowledge of why wood develops into the structures we observe will provide a basis for better predictions of woody plant behavior across environments. It is also essential for tree breeders in developing adapted stock for different environments, and foresters and wood processors in predicting end-product quality.

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1 Introduction

Throughout their lives, animals reinvent themselves by replacing their cellular structure at various rates. Juvenile characteristics are lost even in bone. Trees and other woody plants, on the other hand, do not reabsorb their structural elements, so that their entire morphological history is recorded in the wood as the cells die. Apart from the deposition of materials to form heartwood, block conduits, and increase the resistance to decay by microorganisms, little else happens to the original wood structure throughout the life of the plant – which can sometimes be thousands of years. Therefore, the wood properties at a specific location within a plant reflect any plastic response to the environment superimposed on the plant's ontogenetic stage at the time when the wood was formed. The anatomical, chemical, physical and mechanical properties of wood vary considerably within plants; these variations exist between different plant parts (such as main stems, branches, and roots) and within any given plant part. If these wood properties reflect adaptations to the plant's needs, then the study of their variation may help us to identify the most important factors that through natural selection have shaped plants, and especially their xylem, at different stages of their lives.

As a plant grows, a given point within it will experience changes in both its external environment and its internal physiology (Day et al. 2002; Day and Greenwood 2011). It is likely that plants experience shifts in the relative importance of various hydraulic and mechanical demands that vary systematically with the position in the plant and with time. Firstly, a small plant will experience the environment at a finer scale than will a larger plant with respect to many factors (such as water and light availability). Secondly, a small plant will also have a lesser ability to buffer its interactions with the environment (such as transient high evaporative demand, short-term low temperatures, and localized disturbance from herbivory or stem breakage) because of its lesser biomass for storage (Scholz et al. 2011), and its smaller spatial extent for averaging patchy resources and disturbances (Johnson et al. 2011). Lastly, any location in a plant will experience changing hydraulic and mechanical demands as the biomass distal and/or proximal to it changes in extent (through growth, reproduction or breakage) and/or physiology (such as stomatal behavior or root uptake capacity). Therefore, it is likely that species have evolved mechanisms to produce xylem that functions appropriately for the stresses encountered at any given stage of growth. Because xylem serves a number of roles, there will be tradeoffs among the many potential roles that the xylem can play. For example, Meinzer et al. (2009) showed that species with low capacitance (water storage) and dense wood tend to have high daily maximum xylem tensions and structural adaptations that help them resist embolism at these tensions. In contrast, species with higher capacitance and less dense wood are able to use the stored water to avoid the transient high maximum xylem tensions, and they have wood that is less resistant to embolism at the high tensions (which will rarely occur). Other examples for specific situations include the within-plant tradeoff of specific hydraulic conductivity and resistance to embolism (Domec et al. 2008, 2009) and the between-plant tradeoff of basic density and vulnerability to embolism (Hacke et al. 2001; Rosner et al. 2008; Meinzer et al. 2010), or decreases in specific conductivity that can occur if compression wood is produced (Spicer and Gartner 1998; Mayr and Cochard 2003).

In this chapter we concentrate on the radial variation in wood structure and properties within main stems (i.e. differences in the xylem from the pith toward the bark) of angiosperm and gymnosperm trees, which are generally more pronounced than variation within the same growth ring along the stem (Zobel and van Buijtenen 1989). The radial patterns of wood structure may reflect the changing hydraulic and mechanical demands placed upon woody plants as they grow, thus providing a relatively simple case study in structure and function. Because the structure is recorded in the wood, one can infer the function with assumptions, as elaborated here. We acknowledge that patterns may vary by species and environment, and even along the compass directions of the same annual ring (e.g. Lachenbruch et al. 2010), but this variation may illustrate, rather than take away from, the thesis that the variation has a functional significance. The focus on radial variation is a good starting place because of the relatively large amount of information available, and because it can be of economic importance if we can manipulate it. Moreover, to a first approximation, the vertical pattern of wood properties (from the tip downward to the base) is similar to the radial pattern (from the pith outward) allowing use cambial age information from a basal disk to estimate vertical distributions of properties.

Within a tree, the wood located in the region close to the pith, which generally exhibits relatively large radial gradients in properties, is commonly referred to as ‘corewood’ owing to its location near the pith or ‘juvenile wood’ on account of the young age of the vascular cambium at the time that it was formed, whereas wood located outside this zone is often referred to as ‘outerwood’ or ‘mature wood’ (Fig. 5.1, and Cown 1992; Zobel and Sprague 1998). Note that the terms ‘juvenility’ and ‘maturity’ in wood are unrelated to the same terms used to describe the ability of a plant to reproduce. Some of the earliest observations of radial variation in wood properties were reported by Sanio (1872) who found that the length of tracheids in Scots pine (*Pinus sylvestris*) stems and branches increased from pith towards the bark reaching a final value in a quasi-asymptotic manner. The typical radial pattern of variation (called TRP in this chapter) is discussed in more detail in Sect. 2.2, but briefly, it involves rapid inter-annual changes in characteristics such as cell length, lumen diameter, cell wall thickness, microfibril angle in the S2 layer of the cell wall (MfA, measured with respect to the cell’s axial direction) and density in the first few years of tree growth. Eventually, a cambial age or distance from the pith is reached at which these radial changes are extremely gradual or are swamped by variation caused by the environment. The age of transition between corewood and outerwood, which is very dependent on the analysis methods used and the characteristic under consideration, is often reported as somewhere between 5 and 20 years (Bendtsen 1978; although Abdel-Gadir showed the age ranged from 15 to 38 in a sample of *Pseudotsuga menziesii*), after which if there are still continued changes in traits, they are very slight and are not of notable economic value. The time scale over which this occurs can be very long indeed.

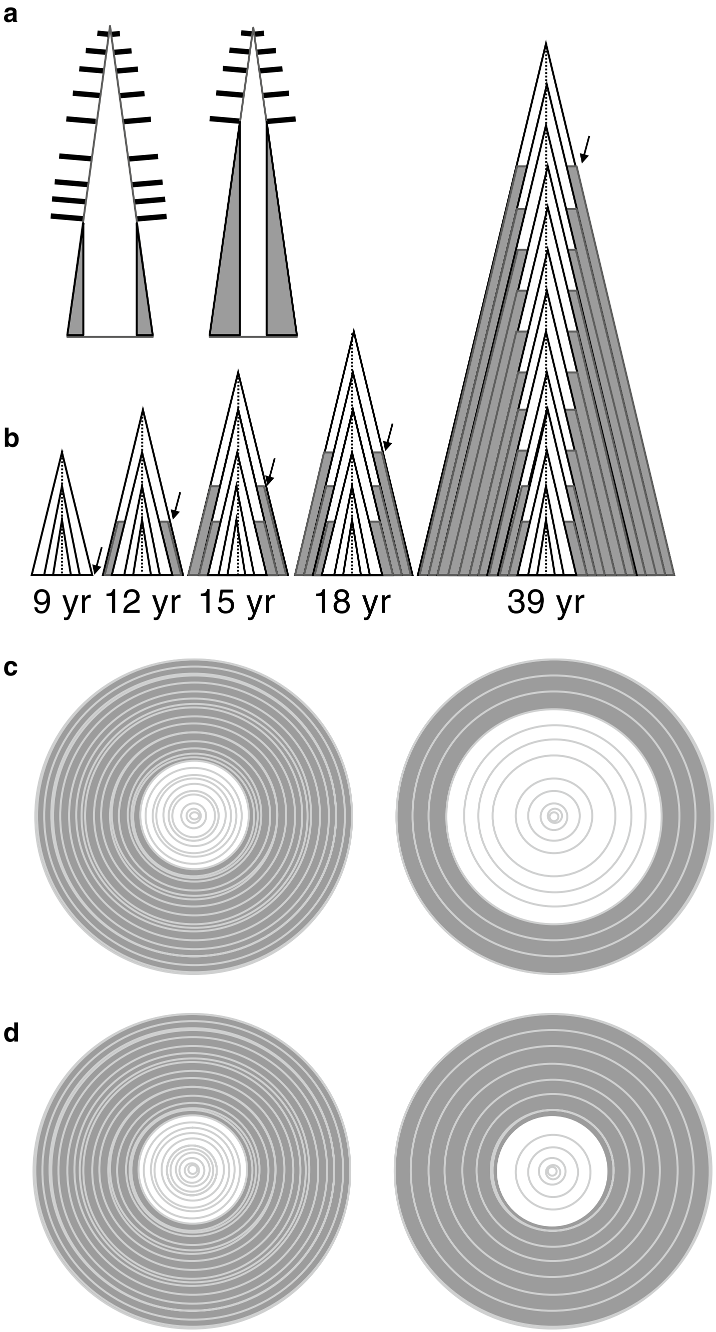

Fig. 5.1 Mechanistic hypotheses for the location of the corewood/outerwood transition. Corewood is *white*, and outerwood is *gray*. (**a**) Location determined by the position of the live crown. (**b**) Location determined by cambial age. Shown schematically for transition age of 9 years, with each sheath of the tree representing 3 years' growth. At any stage of tree growth, corewood is produced at cambial age of ≤9 years and outerwood is produced at cambial age of >9 years (*arrow*). (**c**) Location determined by cambial age. Shown schematically for transition age of 9 years for a slow-grown and a fast-grown tree. (**d**) Location determined by diameter

For example, Gerry (1916) reported that tracheid length in Douglas-fir (*Pseudotsuga menziesii*) was still increasing slowly in the 400th growth ring from the pith, while Baas et al. (1986) found that tracheids in *Pinus longaeva* were still increasing in length after more than 2,000 years, with no sign of leveling off. These typical radial patterns are not seen in all species, a fact that may provide us with plant material for use in comparative studies to better understand why (and under which circumstances) the TRP exists.

Although published studies on wood anatomy date back almost 150 years, the research concerning radial variation is not well-distributed taxonomically: it has been concentrated in the conifers that have an abrupt transition from earlywood to latewood (such as *Pinus taeda*, *P. radiata*, and *Pseudotsuga menziesii*), which include most of the valuable timber species that are used in construction. In these species, knowledge of the radial variation has been used in tree breeding programs and has helped silviculturalists anticipate the wood quality they are producing. It has also been very useful for processing and utilizing the lumber. In contrast, we have much less information on all of the following: conifers with a gradual transition (such as members of the Cupressaceae, and several genera in Pinaceae such as *Abies*, *Picea*, and *Tsuga*), hardwoods with diffuse-porous wood that is often reputed to be relatively uniform across the cross-section (such as *Alnus rubra* or hybrid poplar) and which are not used to the same extent for strength properties, hardwoods with ring-porous wood structure which tend to produce an earlywood band of constant width, and thus whose many properties are largely tied to variation in the width of the latewood band, and tropical hardwoods, including not only trees, but woody plants that have phases with different degrees of mechanical support (such as lianas and hemi-epiphytes). Data are also rare on shrubs, whose wood density is often high and whose growth form is often distinct from that of a tree. In general, the TRP is much less marked in hardwood trees than conifer trees.

Moreover, there have been very few adaptive explanations of the TRP. The early literature on wood variation mainly focused on anatomical characteristics that could be examined through transmitted light microscopes and on mechanical properties of boards cut from different radial positions within a tree. Quite sophisticated methods, some automated, are now available for characterizing radial variation, and unlike most of the work undertaken during the twentieth century, there is now careful physiological work in addition to anatomical and mechanical work characterizing radial changes in structure and function. Much of this chapter is concerned with what we can infer from knowing whether the radial variation in function is more closely related to ring number from the pith (cambial age) or size (more strictly referred to as radius or overall diameter). We use the term ‘size’ rather than stem radius because the tree’s functions (related to allometry, physiology, and/or mechanics) depend on its three-dimensional form rather than a simple linear or quadratic function of radius. For example, tree size is related to traits such as how deep is the canopy and at what range of water potentials does the tree transpire (for water needs), the extent to which the canopy’s mass is offset (for bending stresses), or the stem’s taper (for axial load).

This chapter has three main objectives:

- To provide a brief description of the nature and magnitude of the typical structural and/or functional changes along the radial direction of a stem at any height (the TRP). We will use breast height as the standard height in order to reduce the number of factors discussed, but most of this discussion would pertain to locations higher or lower in the bole as well.
- To clarify whether ring number from the pith or size best explains the TRP in self-supporting trees that are not subjected to any unusual mechanical environments.
- To briefly introduce and evaluate hypotheses for the functional significance of the structural variation exhibited in the TRP. We also suggest plant material/environment systems in which these hypotheses can be further tested.

If the evaluations proposed here improve our knowledge of why wood develops into the structures we observe, we will have a good basis for better understanding the woody plant habit and predicting its behavior in various environments. Moreover, knowledge of the extent and location of variation in wood properties within a stem is of importance to foresters and wood processors as it has major implications for end-product quality.

2 Radial Variation's Terminology, Patterns, and Effects on Wood Utilization

In this section, we review the terminology, location, and structure of corewood and outerwood and its effects on wood utilization. We then briefly discuss three mechanistic theories to explain the typical radial pattern (TRP) that is observed in selected wood properties.

2.1 Terminology

The terminology used to describe the wood found at different positions within a tree has been the source of much debate (e.g. Larson 1969; Amarasekara and Denne 2002; Burdon et al. 2004). In the wood technology and wood science literature, wood located near the pith is commonly referred to as juvenile wood, and wood found further from the pith as mature wood. However, Larson (1969) argued that the term juvenile wood is a misnomer as it can only adequately describe the type of wood formed in young trees and not the wood formed higher up in the stem of older trees. He stated that it would be appropriate to refer to this type of wood from a positional perspective as 'core wood' or from a developmental perspective as 'crown-formed wood'. In fact, the term 'crown-formed wood' has been in existence since at least the 1930s, when it was used by Trendelenburg (1935, cited in Paul 1957) to describe the core of low density wood in a tree, and reflects the effect that proximity to the active crown has on the properties of the wood that is formed. 'Crown-formed wood' has the disadvantage of not distinguishing between wood that is truly in close proximity to foliage and/or terminal meristems, and wood that is instead near long branches, which may not be influenced by crown-derived hormones. While the terms 'juvenile wood', 'core wood' and 'crown-formed wood' have often been used synonymously, Amarasekara and Denne (2002) proposed that the term 'crown-formed wood' should be used to describe fluctuations in wood structure associated with the size of the crown, which are superimposed upon the trends due to cambial age. There are also overlaying patterns resulting from the effects of gravity and wind (e.g. Chiba 2000). These perspectives were advanced further by Burdon et al. (2004) who developed two separate concepts: juvenility versus maturity to describe axial variation in wood properties; and corewood versus outerwood to describe variations from pith to bark. They argued that these terms should be used in conjunction with each other, rather than as alternatives. For example, wood located near the pith at the base of the tree would be referred to as juvenile corewood, while further up the tree it would be referred to as mature corewood. We will use the term corewood to refer to the wood located near the pith at all heights in a tree where there is considerable radial variation in wood properties, and outerwood to refer to the wood exterior to the core. We will also use the term typical radial pattern (TRP) to describe the radial variation at any given height.

2.2 The Typical Radial Pattern (TRP)

Radial variation exists not only in the length of cells within a stem, but in most other cell characteristics. In softwoods, growth rings near the pith usually consist of a large proportion of earlywood tracheids (which have larger diameter and thinner cell walls than latewood tracheids), that gradually transitions to a larger proportion of latewood tracheids with increasing ring number from the pith. Earlywood tracheid diameter increases with cambial age and together these two properties control most of the variation in density, which is the most widely studied physical wood property. (Unless stated otherwise, we will use the term density to mean basic density, which is dry mass per unit green volume.) Tracheid shape and length have relatively minor effects on density, and the density of the cell wall itself is almost constant at approximately 1,530 kg m^{-3} (reviewed in Siau 1984). Automated x-ray densitometers have greatly aided in data acquisition on radial density patterns. For conifers in the Pacific Northwest of North America, mean ring-level density generally follows a pattern where there is an initial decrease for the first 5–20 growth rings outward from the pith, followed by a rapid increase until a maximum value is reached asymptotically (Kennedy 1995). The typical pattern in many hard pines, including *Pinus radiata* and *P. taeda*, as well as a number of other species is to have no initial decrease in density, just a rapid increase in density with ring number, followed by a leveling off (Turnbull 1948, reviewed in Zobel and van Buijtenen 1989). With the advent of rapid x-ray diffraction technology such as SilviScan (Evans et al. 1999), within-tree variation in

MfA has been studied in great detail for a number of species. In softwoods, MfA generally declines rapidly in the first few growth rings out from the pith before it approaches a minimum value asymptotically (Cave and Walker 1994; Mansfield et al. 2009); however, other radial patterns do exist.

There is no universal position within a stem at which wood properties reach a quasi steady-state value; the progression from corewood to outerwood is usually gradual, and the steady-state values as well as the pattern themselves can vary between wood properties, as well as between individual trees and sites (Cown et al. 1991; Fabris 2000). Therefore, for convenience, the extent of the corewood zone (i.e. the number of rings from the pith or the area that it occupies at a given height in a tree) can be defined by an arbitrarily assigned threshold in a systematically changing property. In many cases, the number of rings from the pith has been used to identify the extent of the corewood zone, but in other cases, distance from the pith has been used (see Sect. 3). In southern pines (primarily *Pinus taeda* and *Pinus elliottii*) its extent is commonly based on visual assessments of latewood percentage (Larson et al. 2001). Its extent has also been delimited using densitometry (which gives an estimate of wood density that is in turn related to mechanical properties) (e.g. Abdel-Gadir et al. 1993; Fabris 2000), or fiber or tracheid length (e.g. Shiokura 1982; Mansfield et al. 2009). More recently, microfibril angle has been used to identify corewood because of its influence on wood stiffness, shrinkage potential and dimensional stability (e.g. Cown et al. 2004).

The radial extent of corewood differs by species, between individuals within a species, by height within the stem, and with the property used to define it (Zobel and Sprague 1998). For example, in *Pinus taeda*, the juvenile core is generally taken to consist of the inner ten growth rings (Larson et al. 2001), whereas in lodgepole pine (*Pinus contorta*) Mansfield et al. (2009) found that the transition from corewood to outerwood occurred at 31, 18 and 15 years based on the analysis of radial profiles of wood density, tracheid length and MfA, respectively. For a particular property the age at which the transition from corewood to outerwood occurs within a species appears to be under a degree of genetic control (e.g. Gapare et al. 2006). Irrespective of the property or properties used to define the extent of the corewood zone, the change from corewood to outerwood is usually not abrupt. Almost all woods of self-supported woody plants show a transition from corewood to outerwood, which can be called the transition zone (Zobel and Sprague 1998). The discussion of this zone, or the properties of the wood contained within it, adds little to our insights while adding to the complexity of an already uncertain concept and, therefore, will not be pursued further in this chapter.

Differences between corewood and outerwood have been studied for many species, particularly conifers. Zobel and Sprague (1998) summarized the general characteristics of corewood and outerwood in both conifers and hardwoods. Here we present what we are calling the typical radial pattern (TRP), which is most likely biased by the larger number of studies on softwoods than hardwoods, and on traits of traditional importance to wood processors and tree breeders (such as wood density and microfibril angle) rather than on other physical and biological traits (such as critical strain, or peak transpiration/sapwood area). This pattern is typical for self-supported plants;

those plants that are supported externally for some or all of their life will not necessarily conform to the TRP, nor will those that have other unusual mechanical loads such as from a prevailing wind, or from self-weight if the whole stem is leaning. As more growth forms, habitats, and environments are studied, many of the generalizations about the TRP may well shift significantly. The main TRP discussed in this paper includes the following differences in key characteristics of corewood compared to outerwood:

- Shorter cells with smaller diameter and thinner cell walls.
- Smaller contribution (in conifers) of the S2 wall layer to the double cell wall thickness.
- Lower specific gravity. In some pine species (mostly hard pines) the specific gravity of outerwood can be as much as double that of corewood, but 10–20% differences are more common.
- High microfibril angle (40–50° is common for softwoods such as pines; 25–35° is more common for hardwoods such as eucalypts, poplar and birch).
- Low modulus of elasticity and strength due to lower specific gravity and higher microfibril angle. Specific stiffness (the ratio of modulus of elasticity to specific gravity) is also generally lower in corewood.
- High spiral grain angle (the angle of the longitudinal cells with respect to the stem's axis). In many species spiral grain reaches a maximum in the first few rings from the pith, and then declines to a low value in the outerwood.
- Higher lignin and lower cellulose content.
- Higher incidence of reaction wood, i.e. compression wood in softwoods and tension wood in hardwoods.
- Greater propensity for distortion when wood is dried because of higher longitudinal shrinkage (associated with high microfibril angle), spiral grain angle and incidence of reaction wood.
- Greater susceptibility to internal checking (Ball et al. 2005).

These properties listed above have been studied because of their effect on wood utilization. The following characteristics of corewood have been found by tree physiologists:

- Lower specific conductivity (Mencuccini et al. 1997; Spicer and Gartner 2001; Domec et al. 2005).
- Lower vulnerability to embolism in conifers (e.g. Domec and Gartner 2002, 2003; Domec et al. 2005; Rosner et al. 2006).

In addition, gene expression studies are showing that there are differential activities and products produced by the cambium at different ages; essentially, rather than explaining why the physical and physiological traits exist, these studies are providing a new set of traits that follow the TRP. For example, Cato et al. (2006) showed that the expression of many genes of developing tissues have monotonic gradients from the cambial zone of corewood to that of outerwood in *Pinus radiata*. Similarly, Paiva et al. (2008) sampled *Pinus pinaster* trees along a height (and thus cambial age) gradient. They showed that the relative expression of genes for processes of importance in the corewood region (a cluster of 71 genes) was higher in cambial material from the top than the bottom of the tree, and that the relative expression of genes for processes of importance in the outerwood region (a cluster of 53 genes) was higher at the bottom than the top of the tree.

There is usually markedly less radial variation in wood anatomy within hardwoods than within softwoods (Panshin and deZeeuw 1980; Zobel and Sprague 1998), although Wiemann and Williamson (1988) found that tropical pioneer angiosperm species can have very high radial variation in wood density. Diffuse-porous species have patterns that are roughly similar to those in softwoods, and generalized curves were presented by Maeglin (1987), showing that fiber length, cell diameter and wood density increased with ring number from the pith while MfA decreased. A study in *Alnus rubra* showed, however, that some diffuse-porous species have no significant variation in density from pith to bark, in spite of an increase in vessel proportion and a decrease in fiber proportion (Gartner et al. 1997). In ring-porous species (those species with markedly wider vessels at the beginning than the end of the growth ring), there is a very large difference between earlywood and latewood densities. This fact coupled with the tendencies to have narrower growth rings at higher ring number from the pith but to maintain approximately constant earlywood width, results in ring-porous hardwood species tending to decrease in density from the pith outward (Lei et al. 1996; Woodcock and Shier 2002).

Several characteristics can be classed as exhibiting a radial pattern, but which are actually integrative values that depend not only on the currently produced structure, but on the structure elsewhere in the tree. One example is leaf-specific conductivity, which is a measure of how conductive the xylem is relative to the leaf area that it supplies. In most trees, the corewood has lower leaf-specific conductivity than the outerwood (Zimmermann 1978; Ewers and Zimmermann 1984; Domec et al. 2005). However, leaf-specific conductivity at a particular location depends on both the conductivity at that location and all of the leaf area distal to that point. Another example is the growth stress at a location (the force per unit cross-sectional area which the xylem exerts on its surrounding wood). Longitudinal growth stresses display strong radial gradients, with the outer layers (xylem in the outer part of the radius) contracting and inner layers (xylem within about the inner 2/3 of the radius) expanding upon removal from surrounding tissues (Jacobs 1945; Boyd 1950; Archer 1986). These values, however, depend on the characteristics of the wood that had already been laid down: the growth stress exerted by the newest growth layer will result in a different stress profile within the stem depending on what the previous profile had been (Fournier et al. 1990).

2.3 Effects of Radial Variation on Wood Utilization

Much of the interest in the radial variation in wood properties and the size of the corewood zone arises from their importance to the wood processing industry. As a result there is a substantial body of literature on both the effects of different silvicultural practices on the size of the corewood zone (particularly the percentage of log volume occupied by corewood) as well as on the effects of corewood on the performance of different products for a large number of tree species, mostly commercially-important softwoods. We highlight some of the major corewood/outerwood differences and the implications for manufacturers; interested readers are directed to the reviews by Zobel and van Buijtenen (1989), Zobel and Sprague (1998), and Larson et al. (2001). Without genetic and silvicultural intervention, the proportion of corewood in the commercial forest resource worldwide will inevitably continue to increase for several reasons. The proportion of timber originating from plantations has increased substantially in the last few decades but outerwood in many cases does not yield much higher prices than corewood. Therefore, to maximize the rate of return on investment in land and silviculture, there has been a move toward harvesting trees much younger than in the past, and also in increasingly using the trees that are removed during thinning operations.

Corewood is generally regarded as being of lower quality than outerwood for most structural uses, although it is actually preferred for certain products such as medium density fiberboard and for some types of paper. Zobel and Sprague (1998) caution that the large number of publications focusing on the adverse properties of corewood have led to it being labeled as “bad wood”, whereas they argue that from a utilization perspective it should be considered as “different wood” with advantages of its own. The relatively low density of juvenile softwood affects pulp and paper properties mainly through the greater collapsibility of the tracheids. Kraft pulp handsheets produced from corewood have higher tensile strength but lower tear strength than those produced from outerwood. Printing paper produced by the thermo-mechanical process from young radiata pine (*Pinus radiata*) has high structural uniformity, optical performance and surface smoothness (Burdon et al. 2004). The strength properties of medium density fiberboard panels produced from the corewood of black spruce (*Picea mariana*) were found to be superior to those of panels produced from outerwood taken from the same trees (Shi et al. 2005).

Corewood does, however, present real problems for sawmills producing structural timber. For these uses, the low density and high microfibril angle of corewood results in timber with low modulus of elasticity (low stiffness) and bending strength (Bendtsen and Senft 1986), an often high incidence of compression wood (Barger and Ffolliott 1976; Timell 1986), and a longitudinal shrinkage as much as ten times greater than that of outerwood (Voorhies and Groman 1982). This results in poor dimensional stability, meaning high shrinkage or swelling in response to changes in ambient humidity. These strong property gradients lead to warping and twisting of timber that contains both corewood and outerwood. Such dimensional instability can cause significant serviceability problems in timber structures, even if it only affects a small number of the pieces of timber within a structure. Numerous studies have shown that engineered wood products such as oriented strand board have poorer performance if they are made from corewood (e.g. Cloutier et al. 2007);

however, corewood can be placed in certain locations in some engineered wood products where it will not adversely affect overall performance (e.g. in the middle layers in laminated veneer lumber or glulam beams; e.g. Kretschmann et al. 1993). Corewood also tends to have a higher proportion of knots by virtue of its location in the tree and geometry; these knots negatively impact grade recovery and strength, but are not the subject of this chapter.

3 Developmental Controls of the Typical Radial Pattern

Gradual radial changes in many xylem properties are the rule, rather than the exception, in most woody plant species that have been investigated, but what mechanism is responsible for these changes? Are the patterns ontogenetically fixed, or are they plastic, triggered by factors that vary as the plant increases in size? The radial pattern may be of adaptive value regardless of whether the control is ontogenetic or plastic because natural selection can favor a similar radial pattern through either developmental route. Knowledge of the nature of the driver, however, can tell us whether the variation we observe is genetic or is related to the environment that the plant lives in, and can also give us tools to use if we want to alter the pattern of wood development. In this section, we review terminology that make more explicit the meaning of ‘fixed’ and ‘plastic’ control, then present three hypotheses for the mechanism responsible for the TRP. While we acknowledge that it is likely that a combination of fixed and plastic mechanisms is involved, for simplicity we will examine the potential mechanisms separately. We then focus on rings from the pith vs. diameter (a special case of ‘age vs. size’) and ask why it may be useful to understand which factor is more important, and then give examples of studies that supported the importance of either ring number or diameter for determining the TRP. The examples show that for both conifers and hardwoods, in some cases age is more strongly correlated with a trait and in other cases it is size. It is not surprising to find such variability in the control (fixed or plastic) or the type of factors (age or size) that describe the development of the TRP in the woody plants: given the physiological, developmental, and mechanical interactions that occur within woody plants, one would not expect an extremely simple set of rules to orchestrate the development of adaptive patterns in all trees and under all circumstances.

Day and colleagues (Day et al. 2002; Day and Greenwood 2011) define three models of potential pathways controlling age-related changes in the development of plant shoots. *Intrinsic control* results from internal factors (those within the meristem itself) that result from programmed changes in gene expression (the typical meaning of ‘ontogenetically fixed’ or ‘developmentally controlled’). Environmental (plastic) control can be broken down into two types. *Extrinsic control* results from external factors (those beyond the meristem—but that can include environmental as well as within-plant signals) that act on the products of the meristem such that they develop differently (for example, the effect of light on developing leaf tissue). In

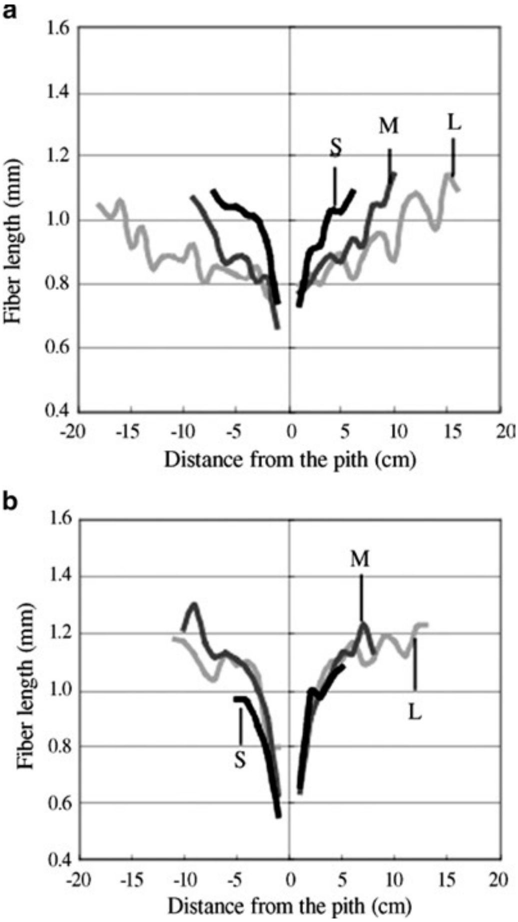

Fig. 5.2 Radial distribution of fiber length at breast height from small (S), medium (M), and large (L) diameter plantation grown trees. (**a**) *Eucalyptus grandis* (14 years old, mean DBH of 21.7, 28.0, and 37.9 cm, respectively, n = 6 trees/size class) showing dependence of fiber length on cambial age, not stem diameter. (**b**) *Acacia auricuriformus* (11 years old, mean DBH of 14.1, 19.1, and 25.8 cm, respectively, n = 4 trees/size class) showing dependence of fiber length on stem diameter, not cambial age (From Kojima et al. 2009. Used with permissions)

this case, the meristem remains inherently the same over time, but the signals change. *Extrinsic-intrinsic control* results from changes in gene expression that are induced by environmental factors. Extrinsic-intrinsic control appears to be more common than extrinsic controls.

Although the theory makes clear distinctions among these controls, in practice we are not always able to discern which type of control is acting, and so our ability to distinguish among these types of control is somewhat blurred. An ontogenetically fixed (intrinsically controlled) pattern could be manifested by a tight correlation of a trait with cambial age but a poor correlation with diameter (e.g. Fig. 5.2a), as discussed by Day et al. (2002). A fixed pattern could also be manifested by the reverse, a tight correlation with diameter but a poor correlation with cambial age (e.g. Figs. 5.2b and 5.3). In the first case, the cambium's algorithm would be triggered by a time-related metric such as the number of dormancy periods experienced, and in the second case, by a diameter-related algorithm

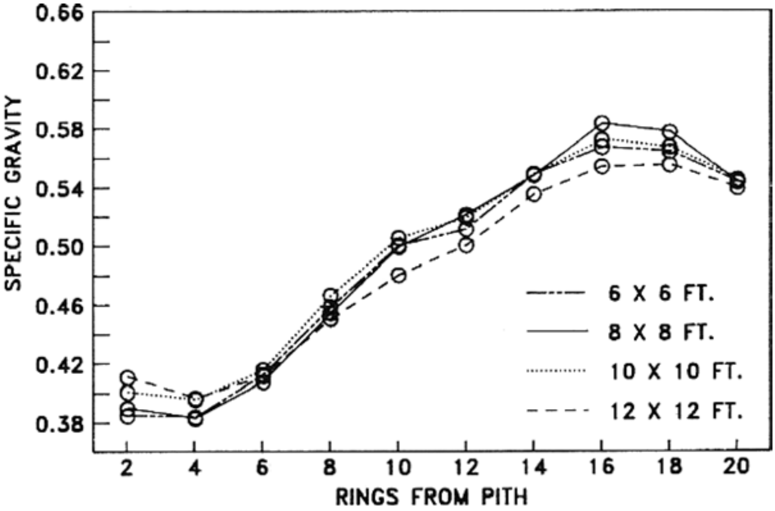

Fig. 5.3 Influence of tree spacing on the radial pattern of wood specific gravity at breast height in *Pinus taeda* (loblolly pine) growing in the Piedmont of South Carolina showing the dependence of specific gravity on cambial age, not stem diameter. Mean diameter at breast height (and height) of trees at the closest spacing was 20.3 cm (20.9 m) and at the widest spacing was 28.7 cm (22.5 m) (From Clark and Saucier 1989. Used with permissions)

such as number of periclinal divisions that the cambium has undergone. It should be noted that a good correlation with diameter but a poor correlation with cambial age could also result from plastically-controlled development, if the growth algorithm was triggered by a force acting beyond the cambium itself, such as a bending stress. In this case, the magnitude of the force depends on factors such as the amount of biomass distal to the xylem sample, as well as its geometric distribution. Unlike a size-related pattern that is ontogenetically controlled, a plastically-controlled one could be altered with manipulations of the driving force, such as staking plants in the example in which the TRP is driven by changes in bending stresses.

To investigate the extent of ontogenetic (intrinsic) vs. plastic (intrinsic/extrinsic) control of wood development, Lenz et al. (2010) estimated the heritability of eight traits that follow the TRP for rings 1–16 in *Picea glauca*. If a trait was highly heritable, then its control was most likely ontogenetic, and likewise if it had low heritability, then its control was most likely plastic. Near the pith, there was little evidence to support ontogenetic control: none of the traits were strongly heritable, with the highest heritability values there being 0.3–0.4 (for earlywood radial cell diameter and earlywood and latewood MfA). Heritability then increased markedly for earlywood traits from the first to the 16th growth ring for five of the eight traits studied (wood density, specific fiber surface, cell wall thickness, tangential cell diameter, radial cell diameter), with heritability at ring

16 exceeding 0.7 for three of these traits. The authors inferred that ontogenetic control becomes more important for these traits at increasing ring number. Similar research on other factors and in other taxa would be very valuable for determining the degree to which the patterns can be changed through genetic selection vs. through environment.

3.1 Mechanistic Hypotheses Explaining the Location of the Corewood/Outerwood Transition

Proposed mechanisms controlling the TRP are the number of rings from the pith (pattern ontogenetically fixed), diameter (usually treated as a plastic response, but as shown above, could also be ontogenetically fixed), and the location with respect to the position of the live crown (plastic). We refer to these hypotheses as mechanistic, as distinct from the adaptive hypotheses (Sect. 4) that explain the functional advantages of such radial variation.

3.1.1 Transition Occurs in Response to Ring Number from the Pith (Cambial Age)

This hypothesis proposes that the transition from corewood to outerwood is related to the age of the cambial initials (synonymous with the terms ‘cambial age’, and ‘number of growth rings from the pith’) at a particular height within the stem (Fig. 5.1b, c); the TRP is intrinsically controlled. At young cambial ages (in a young tree or higher up the stem in an older tree), the products of the cambial initials have xylem properties that are characteristic of corewood (e.g. short cells with narrow diameter and relatively high MfA). As a tree grows outward, the older cambial initials at the base of the tree are the first to reach the transition from corewood to outerwood as shown by these properties, while younger cambial initials higher in the tree are still producing corewood (Fig. 5.1b) but will be reaching the transition in the future. As discussed in more detail in Sect. 3.3, there are many examples in which ring number is a better predictor of the trajectory of the TRP than is stem diameter, in both softwoods (e.g. Herman et al. 1998; Clark and Saucier 1989) and hardwoods (e.g. DeBell et al. 1998).

3.1.2 Transition Occurs in Response to Stem Diameter

This hypothesis proposes that the transition from corewood to outerwood is related to stem diameter (Fig. 5.1d). One possible explanatory mechanism for this is that the cambial cells in a small-diameter stem would need to have a much higher proportion of anticlinal divisions (those that produce tangentially-aligned cambial cells) than would those in a larger stem to produce a new radial increment. However, true anticlinal divisions are rare; cells generally divide pseudo-transversely (i.e. rather than having a cell divide into two thin cells of the same length, the cell divides into two shorter cells, one above the other, but with some overlap of the bottom and top of the resulting cells). This mode of cell division would depress the apparent tendency for cambial initials to increase in length with increasing cambial age, and would explain the gradual increase in cell dimensions as the cambium develops a lesser radius of curvature at larger sizes (discussed in DeBell et al. 1998). Indeed, Bannan (1967) found that tracheids arising from pseudotransverse divisions are considerably shorter and therefore the radial pattern of tracheid length can be interpreted in terms of the relative frequency of pseudotransverse divisions.

However, diameter is actually a one-dimensional trait that serves as an index of the size of the tree (see King 2011), in which the size also encompasses its mass, height, center of mass, foliage quantity, and other factors. While the signal to transition from to corewood to outerwood could be fixed such as the total number of cell divisions in the cambium (which would give an index of diameter) or the current number of divisions/number of cells in the cambium (which would give an index of the cambium's radius of curvature, and thus its distance from the pith), it could also be plastic, triggered by a factor such as self-weight, compression, tension, or torsion sensed in the cambial zone or hormones produced in a specific location (such as crown or root).

3.1.3 Transition Occurs in Response to Location with Respect to the Live Crown

The *crown position* hypothesis proposes that crown-produced auxins favor production of corewood, and their absence favors production of outerwood (Fig. 5.1a and Larson 1969). Larson (1969) further states that xylem in the crown region has a greater proportion of earlywood and thinner cell walls overall. There are no definitive studies that are strongly supportive of this hypothesis, although some are mildly supportive (e.g. Amarasekara and Denne 2002; Gartner et al. 2005).

Crown position may well be an important factor for determining the radial pattern of xylem traits, and it may follow the mechanism describe here, but it could, alternatively follow other mechanisms. For example, the production of plant growth regulators in the crown or the sensitivity of the cambium to these regulators could be related to factors such as the rate of change in water potential, the amount of available water storage, or the quantity of sunlight that reaches the bark (Gartner 1996). The crown-position hypothesis is the basis for suggestions that silvicultural treatments which affect the depth of the live crown, such as pruning or manipulation of stand density (i.e. through initial spacing and/or thinning), will lead to different patterns of corewood and outerwood in same-aged trees (see the critical review in Briggs 1995). We do not discuss this hypothesis further in this paper, but it may be a fruitful area of future research.

3.2 *Why Ask Whether Age or Size Is a Better Predictor of Traits?*

As stated before, ring number from the pith is related to the age of the cambium at a given height, and diameter at that location is related to the size of the tree, so these characteristics can represent age and size. Clarification of whether the TRP is more closely related to ring number from the pith or diameter for a particular wood property, species, and environment may give insight to physiologists seeking to understand the factors that have influenced wood structure and function, on both the short-term and the evolutionary time scales. Limits to the inferences, however, include the possibility (a) that age and size are correlated with one another so strongly that we will learn little from knowing with which variable a trait has the stronger correlation, (b) that age (or size) exhibits the stronger correlation with the trait of interest but that size (or age) was a simpler path for natural selection to use, and (c) that an observed correlation with age or size is spurious and the relationship is actually evolutionarily neutral.

Assuming that these caveats are noted, we can address the implications of size vs. age correlations. As an example, if age is more strongly correlated with a morphological trait than is size, we can infer that evolution favored an age-related factor (such as the hydraulic redundancy provided by having numerous growth rings) over some size-related factor (such as the physical stress caused by the canopy in the wind) as the better predictor of appropriate function. Physiologists can then develop and test hypotheses in accordance with age rather than size to further understand plant biology. Knowledge of whether traits are more closely correlated with number of rings from the pith or with diameter can be very useful to forest managers in situations in which the incidence of corewood will affect value or use (Kojima et al. 2009). This knowledge can be used to manipulate tree growth to maximize log value. It can also be used to predict the value of logs knowing the management history, to better schedule when to harvest a stand, and to better target log sales and processing for their appropriate use.

3.3 *Is There a Small Set of Potential Drivers of Age- or Size-Dependent Changes in Xylem Traits?*

It is instructive to list the most apparent similarities and differences one would expect between a small and a large tree of the same age, and a young and an old tree of the same size. If the lists are short, it may be simple to infer the factors of importance for the plant during passage from one size or age to the next. These factors could then be explored with respect to the radial changes in wood properties. While not exhaustive, Table 5.1 illustrates that there are numerous candidate functions on which natural selection may have acted, and that there is no one set of similarities or differences from which we can infer why a certain species and trait is more closely correlated with one of the independent variables (age or size) than with the other.

Table 5.1 Similarities and differences between trees that differ in age but not size, or in size but not age, and their relevance for development of hypotheses to explain radial variation in xylem structure. These attributes do not take into account any mitigating differences in wood structure or function, such as the centrifugal increase in modulus of elasticity and cell length

Small tree compared to large tree of same age[a]	
Similarities	Potential relevance
Both have been subjected to environmental factors for the same length of time (e.g. freeze-thaw cycles, oxidation)	Both may exhibit similar deterioration or changes due to physical and chemical environment
Both have same likelihood of experiencing infrequent extreme events (e.g. fire, extreme wind, ice-storms, pest outbreaks, oxidation)	Both are at similar risk for damage (although magnitude of damage is probably size-related)
Both have had same number of growth and dormancy periods	Both have had same number of cues, if species has mechanism to count periods to assess age
Both may have same number of plies (growth increments), and same number of branch clusters if determinate growth	Both may have similar numbers of growth rings through which water must traverse from inner to outer wood
Both have had same number of years to reach current architecture	Both should have similar morphology and perhaps physiology at same-aged locations, if meristems have age-dependent behavior
Both may have expended reproductive effort	Small tree may have further reduced growth
Differences	*Potential relevance*
Small tree has shorter internodes if determinate growth	Small tree may have more closely spaced branches, foliage, reproduction
Small tree has shorter stem overall	Small tree may have less hydraulic resistance due to force of gravity and due to path length
Small tree has fewer total divisions at meristem over lifetime	Small tree may be more homogeneous genetically and may track the environment more poorly, if meristematic divisions are associated with somatic mutations
Small tree has lower lever arm, smaller crown relative to stem, less self-weight/stem cross-sectional area	Small tree may need less investment in structural support
Small tree has more growth layers per cm of wood	Small tree may have tougher stem if latewood zones retard crack propagation
Small tree may have lower leaf area	Small tree may have lower absolute carbon gain, less leaf redundancy so more vulnerable to leaf loss (from herbivores, pathogens, physical factors)
Small tree may have narrower sapwood, shallower or less dispersed rooting and/or less stored water per leaf area	Small tree may be more subject to drought stress if drought conditions are limiting

(continued)

Table 5.1 (continued)

Young tree compared to old tree of same size[b]	
Similarities	Potential relevance
Both have same physical environment – wind, light, temperature	Both have same spatial patterns of wood properties if species responds plastically to these factors
Both have undergone roughly same number of division in meristems	Both have same spatial pattern of wood properties, if species has intrinsic meristematic controls that change with size (as number of divisions)
Both have same spatial distribution of mechanical stresses in all the axes: axially, radially, and tangentially along bole, and along individual branches and roots (if distribution of elastic properties were the same in both trees)	Both have wood designed to same mechanical safety factor if species can anticipate (probably through intrinsic controls) or react to (through extrinsic controls) magnitude of stresses
Both may have same water potentials (assuming similar leaf area, root area, and specific conductivities)	Both have wood designed to same hydraulic safety factor if species can anticipate (probably through intrinsic controls) or react to (through extrinsic controls) magnitude of drought stress
Both may have roughly same abilities to capture assimilate (assuming similar leaf area, fine root area, and whole-plant architecture)	Both may have similar growth efficiencies, carbon to allocate to defenses, re-growth after damage, etc.
Differences	*Potential relevance*
Young tree has experienced environment for shorter period	Young tree has had less time to deteriorate from ongoing, predictable processes
Young tree is less likely to have experienced any particular environmental perturbation	Young tree is less likely to have been damaged by extreme events
Young tree has had fewer growth and dormancy periods	Young tree is developmentally behind, if development is influenced by years
Young tree has fewer but wider layers ('plies'), and either the earlywood, latewood or both will be present in wider expanses	Young tree may have different stress distribution, access to stored water, risk (due to diff. amount of redundancy in structure), depending on importance of plies to these factors
Young tree has had fewer years to reach current whole-plant architecture	Young tree is more heterogeneous, has less redundancy in structure if determinate growth (ex: loss of one branch whorl causes a greater biomass loss)
Young tree may not have expended reproductive effort	Young tree may have more vigor
Young tree architecture may be more hierarchic, with older tree consisting of repeated hierarchic units	Young tree's productivity possibly less tied to demography of the units, and thus less buffered

[a] Comparisons are of idealized trees that arrive at different sizes for the same age but that grew without constraints related to tree social status (such as being dominant vs. suppressed). For illustration, consider small (5 m) vs. large trees (30 m) of the same age (50 years)

[b] Comparison of idealized trees that require different ages to attain the same size but that grew without constraints related to environment (such as differences in rainfall). For illustration, consider young (10 years) vs. old (50 years) trees of the same size (10 m)

3.4 Examples of Age- or Size-Related Xylem Traits

One type of experiment of use for testing age vs. size dependence is to find or develop plant material with a common age but that differs in size. (It would be redundant to also compare trees of the same size but different age because this situation is also found by dissecting the larger tree back to the point at which it had the same size, but different age, as the smaller tree.) The criterion of same-aged but different sized trees is often met in silvicultural trials that have variable thinning, fertilization, or irrigation. It may also be met in a cohort of trees that have established following a disturbance.

In the conifers, most such studies have shown that ring number from the pith is more closely correlated than is diameter to the values of traits, although there are examples of each outcome (reviewed in Zobel and Sprague 1998, pp. 9–11). For example, in thinning or spacing trials, the transition from corewood to outerwood was more closely related to ring number for wood density in two species of southern pine (*Pinus taeda* and *P. elliottii,* Clark and Saucier 1989) (Fig. 5.3) and for tracheid length in two species of spruce (*Picea mariana* and *P. glauca*, Yang 1994). A similar study with Norway spruce (*Picea abies*) also showed that tracheid length and MfA were more closely related to ring number from the pith, but that tracheid diameter was more closely related to diameter (Saranpaa et al. 2000). Many studies also show no effect of radial growth rate on wood density. Zobel and van Buijtenen (1989), summarizing 59 studies on hard pines, reported that 59% of the studies showed no significant relationship between radial growth rate and wood density, 19% showed a large negative relationship, 15% showed a small negative relationship, and 7% showed a positive relationship. One must be cautious in labeling this a TRP, however, because density can be driven by changes in latewood proportion that could have more to do with tree spacing and foliage area, rather than changes in latewood or earlywood density (e.g. Cown 1973, 1974).

In hardwoods, there are too few studies to conclude which pattern is more common, but as with conifers, there are examples of both age and diameter having the strongest influence. Two projects studied the radial pattern of wood density in tropical hardwoods of different size but the same age: plantation trials in a secondary successional species in Brazil (de Castro et al. 1993), and cohorts of four self-seeded pioneer species in Costa Rica (Williamson and Wiemann 2010). In most cases in both studies, the small-diameter trees had significantly greater slope of the density on radial distance relationship than did the larger-diameter trees of the same cohort. Moreover, there were no significant differences between the densities of the outer wood in the smallest vs. the largest individuals in most of the species-stand combinations, indicating that density was more closely related to cambial age than to diameter. Studies have also compared the radial patterns of fiber length in trees whose radial growth rates were manipulated. In some studies (e.g. *Populus*, DeBell et al. 1998, and two *Eucalyptus* species, Kojima et al. 2009), fiber length was more closely related to cambial age than to diameter (Fig. 5.2b). However, Kojima et al. (2009) studied four taxa (two *Acacia* species and two accessions of one species of *Paraserianthe*s, formerly *Albizia*) in which fiber length was more closely related to size than to cambial age (e.g. Fig. 5.2a).

4 Hypotheses for Why Trees Develop Radial Changes in Wood Properties

The TRP is sufficiently common for us to infer that it has evolved through natural selection to help the plants survive and reproduce. This inference is not necessarily correct, of course: patterns can develop randomly, or as incidental by-products of another function upon which selection has acted. An example of an incidental by-product is the color of wood, which is not thought to be of adaptive value itself, but to result incidentally from the materials of which wood is formed and by which it is chemically defended.

In this section we present three hypotheses for the evolutionary drivers of the TRP related to developmental constraints (*D*), maintaining adequate water distribution (*H*), and maintaining structural integrity of the tree subjected to its own body forces as well as external loads such as wind (*M*) (summarized in Table 5.2). We then give examples of comparisons to help us link specific structures and functions with the *H* and *M* constraints. Although we treat these hypotheses separately, it is unlikely that any plant was shaped through evolution solely by one of these types of constraint. The magnitude of different constraints surely vary among species, plant parts (e.g. stems vs. roots), and cambial ages, and in the xylem of individuals in different habitats. As pointed out by Zimmermann et al. (2004) in their review of hydraulic mechanisms, trees are most likely to have evolved ways to use all the available physical and biological avenues to maximize their chances of survival. This includes the ability to respond to both long-term and short-term environmental changes, where ‘environment’ refers to all external influences including climate, gravity, day length, latitude, terrain, soil properties, competition from other plants and predation—and, of course, silvicultural conditions related to regimes such as spacing, thinning, and pruning. For this reason, making inferences about which constraint was the most important may be difficult: disparate constraints and tradeoffs may dampen any signature of one constraint over another. Thus, we may learn the most about the adaptive significance of wood structure and function through comparisons of wood that developed in extremes of the *H* and *D* constraints—through manipulation of plants, or choosing plants living in extreme hydraulic or mechanical environments.

4.1 Development (D): Production of Sequentially More Optimal Xylem as Cambium Matures

Hypothesis D (developmental constraints) states that the TRP strategy is a by-product of the need for the young cambium to mature before it can produce the most adaptive wood (Table 5.2). This view suggests that a developmental constraint prevents the meristem from producing the ‘good’ wood from the beginning and that corewood has no particular adaptive value other than that the tree must produce it before its cambium matures to the point of producing the outerwood.

Table 5.2 Adaptive hypotheses for the purposes of the typical radial pattern (TRP) in secondary xylem of woody plants

Purpose of TRP	When young or small	When old or large	Structure and/or function involved
D: Byproduct of the need for the young cambium to mature before it can produce the most adaptive wood[a]	The cambial initials have derived from the apical meristem, where cells are small, and so they are constrained to produce small, short cells with high microfibril angle	By virtue of the number of cambial divisions already made, the initials have had opportunities to 'mature' gradually, making products that are now optimal for the tree	All characteristics, including morphological and physiological
H: To permit higher resistance to embolism in corewood, and to permit higher specific conductivity in outerwood[b]	Need to allow more negative pressure before hydraulic or mechanical failure because young axes have less readily available stored water (and thus, less buffering capacity) than outerwood, because of their smaller mass, and in young plants, smaller root system	Need more water transport capacity to compensate for increased resistance caused by friction over longer path and gravity on taller path	Cell lumen diameter, cell wall thickness, cell length, pit characteristics, MfA
M: To permit a higher critical strain in corewood, and to permit greater strength and stiffness in outerwood[c]	Small diameter trees need to be flexible to bend through large angles in response to applied loads (e.g. from wind), and to have a high critical strain so it won't fracture with this bending. Low stiffness wood also permits more effective stem re-orientation by the growth stresses associated with reaction wood	As trees increase in size, stem needs increased wood strength and stiffness in order to avoid failure from both self-weight from the stress produced when the stem is bent by applied wind or snow loads	MfA and wood density, which in turn affect critical strain, stiffness and strength

[a] Related to developmental (*D*) constraints on type of wood the young cambium can produce
[b] Related to maintaining hydraulic (*H*) integrity of the water distribution network
[c] Related to maintaining structural (*M*) integrity of the tree

This hypothesis can explain all characteristics that change along the radial transect, as long as the outerwood is presumed to have universally superior function over the corewood. The TRP reflects the decreasing intrinsic control and the increasing production of wood that is optimal for the tree (Fig. 5.4).

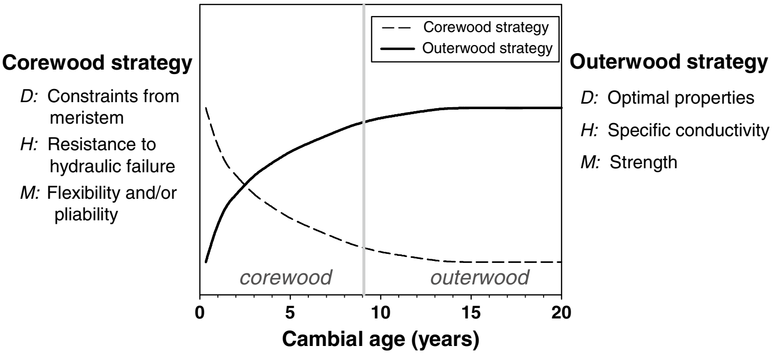

Fig. 5.4 Schematic diagram of hypotheses for why trees develop radial changes in wood properties, showing the changing strategy expressed in the corewood (*dashed curve*, *left axis*) and the strategy expressed in the outerwood (*solid curve*, *right axis*). See Sect. 4 for explanations of the developmental (*D*), hydraulic (*H*), and mechanical (*M*) hypotheses

A general understanding of the vascular cambium supports this hypothesis if the size and shape of the cambial initials constrains the size, shape, and ultrastructure of the cambium's products. The apical meristem lays down cells that differentiate to become the vascular cambium. These vascular cambium cells (the fusiform cambial initials) produce secondary xylem immediately exterior to the growth that had been laid down by the apical meristem. It is logical to expect that these first fusiform initials will be relatively short. Bailey (1920) showed that for branch and stem segments of 13 gymnosperm taxa the tracheid length was about the same length as (or up to 10% longer than) the cambial initials, although he did not survey wood immediately adjacent to the pith. Therefore, these first fusiform initial cells in conifers, if short, may be incapable of producing the extremely long axial cells that are found in outerwood, unless their products are capable of a large amount of intrusive growth. In angiosperms, however, Bailey (1920) reported that fiber tracheids were often more than twice as long as the fusiform initials, showing their ability to exhibit this high intrusive growth.

Hypothesis D is supported by data for some characteristics, particularly for the first several growth rings from the pith, which often appear to be the same size regardless of environment. For example, Christensen-Dalsgaard et al. (2008, discussed below) show a cross-section of a distal root 1 m from the bole, in which they observed that vessel diameters increased markedly for the first 2 mm, even though their calculations show no change in the mechanical strain across the time period during which this wood is developed. From this discrepancy the authors state that these early changes may well result from ontogenetic requirements rather than adaptive responses (either plastic or evolved). They did not estimate hydraulic needs for the small plants, however, so the patterns could have conformed to the hydraulic constraints hypothesis (below). Another example is that it is often noted that growth ring structure often 'takes a few rings to settle down.' For example, ring-porous woods may look diffuse-porous in the first several growth rings, and in conifers it is often much more difficult to distinguish earlywood from latewood in the early rings using either lumen diameter or cell wall thickness as criteria. Another example is the typical pattern of increasing cell lengths in the first several growth rings, suggestive that the cambium can only make short cells near the pith.

Hypothesis D is not supported by several kinds of evidence. First, this hypothesis assumes that the corewood characteristics are not of value. This assumption is violated by physiological evidence that corewood's hydraulic characteristics (such as its high resistance to embolism) are helpful for survival (e.g. Domec and Gartner 2002, see Sect. 4.2), and mechanical evidence that compression wood, which helps a stem re-orient when it is bent, is more common in corewood than outerwood (Pillow and Luxford 1937).

Secondly, structural evidence often shows that the cambium is capable of producing very abrupt radial changes in anatomy, suggesting that the cambial products are not entirely constrained. Compression wood can be detected within days of a stem's being bent (reviewed in Timell 1986, pp. 680–686). When individuals that transition from self-supported to semi- or totally-supported experience a change in their mechanical environment, they often exhibit coincident radial anatomical changes (Ménard et al. 2009). An example is shown with the tropical liana *Condylocarpon guianense*. Rowe and Speck (1996) present a cross-section in which the inner 0.9 mm of xylem is extremely dense and has vessels that average about 50 μm in diameter. Immediately adjacent is xylem that is not dense in which vessels average about 200 μm in diameter. This abrupt change in anatomy implies plasticity with very rapid cambial response.

Lastly, *Hypothesis D* is not supported by data for characteristics that largely are invariant across the radius. Root tracheids provide such an example: in several studies in conifers, the tracheids in the first rings adjacent to the pith are similar in length to those found in the outerwood (Sanio 1872; Matsumura and Butterfield 2001; Peterson et al. 2007). Peterson et al. (2007) reported that the tracheids in the first two growth rings from the pith averaged 3.8–4.7 mm in length for the *Pseudotsuga menziesii* roots examined; the same roots had a mean of 3.8–4.1 mm at 40–41 rings from the pith. Other studies show that conifer root wood produced in the first cm (Matsumura and Butterfield 2001, *Pinus nigra*, *P. radiata*) or the first 8–13 years (Sanio 1872, *Pinus sylvestris*) has very long tracheids. In hardwoods, Sun and Suzuki (2001) reported a lack of radial variation in vessel element and fiber lengths for two of the five mangrove species investigated; the main environmental difference was that the two species that lacked the radial gradient lived in sites with less wind, less force from shifting tides, and less inundated sites than did the other three species. Certain rosette plants also lack a radial gradient in axial cell length (e.g. Carlquist 1962). This research shows that the young cambium is not necessarily canalized into producing short axially-oriented cells. More research is needed to help us tease apart the relative contributions of intrinsic controls vs. plastic responses to environment for the many traits that do exhibit radial changes throughout the secondary xylem.

4.2 Hydraulics (H): Maintaining Adequate Water Distribution as Cause for the TRP

Hypothesis H (hydraulic constraints) states that the TRP strategy permits corewood to withstand high negative pressures and allows the outerwood to have high specific conductivity. There is ample evidence of a tradeoff between resistance to embolism and specific conductivity (Domec and Gartner 2002; Rosner et al. 2008; Domec et al. 2008), depending on the scales compared (Meinzer et al. 2010). The rationale for *Hypothesis H*, detailed below, is that young/small axes have little access to stored water, and they may not have a steady supply of water from their root systems, suggesting plants could benefit from allowing high negative pressures in the corewood before conduits fail mechanically or hydraulically. Large/old axes, in contrast, can buffer the water potentials with stored water and soil water to a greater extent (Scholz et al. 2011). However, as trees grow, resistance to water transport will increase from both the longer and taller path, suggesting that old/large trees could benefit from high specific conductivity in the outerwood (Table 5.2). The TRP reflects the changing strategy from hydraulic safety to efficiency as the tree increases in age/size (Fig. 5.4).

4.2.1 Corewood

First, young/small trees may need to operate with more negative water potentials than old/large trees because they are likely to have less developed root systems and therefore less certainty of access to a steady water supply. Secondly, young/small plants have been shown to have less water storage, and thus to be less capable than larger plants at modulating their water tensions (Scholz et al. 2011). Phillips et al. (2003) showed that young trees can have lower volume of sapwood per leaf area, and that there is a decreasing reliance on stored water with increasing plant size in two coniferous and one hardwood species. Cermak et al. (2007) showed that in old-growth *Pseudotsuga menziesii* trees, most of the stored water comes from stem sapwood, with the largest amount coming from the lower stem. The spikes in tension gradient were buffered to a larger extent lower in the stem (in the outerwood) than higher up (in the corewood). Thirdly, if the corewood is located higher on the stem than is the outerwood, the upper position will experience greater xylem tension because of the resistance from the greater path length, and because of the effect of gravity acting on the taller water column.

Hydraulic failure in the corewood can occur through air-seeding of embolisms or through conduit collapse. In either case, the driving force is a water tension that exceeds some critical value, and plants need be protected from both failure modes simultaneously. Physiological and acoustic measurements in conifers show that corewood (Domec and Gartner 2002; Domec et al. 2009; Rosner et al. 2006, 2008, 2009) and branches (e.g. Domec and Gartner 2002; Mayr et al. 2003; Dunham et al. 2007) are often more resistant to embolism than is outerwood. Anatomical evidence also suggests this higher resistance to embolism and/or collapse in corewood than outerwood. Hacke et al. (2001) calculated a wall reinforcement factor to explain collapse of a simplified conduit, using engineering equations for a plate that has the width of the cell lumen diameter (*t*) and the thickness of the double cell wall (*b*). This wall reinforcement factor, $(t/b)^2$, is positively correlated with conduit collapse, but it is also positively correlated with the resistance to embolism (Hacke et al. 2001). Domec et al. (2009) showed that two coniferous species maintain higher safety factors to air-seeding of their xylem than to collapse, but that the values relative to one another are similar (at about 2:1) throughout the plant. Moreover, these two species had higher $(t/b)^2$ in corewood than in outerwood. The higher MfA of corewood (i.e. running at more of an angle to the cell axis than in outerwood) may also contribute to the higher collapse-resistance of corewood; a model such as that by Innes (1995) could be parameterized to test the sensitivity of collapse to MfA. Moreover, resistance to embolism is positively correlated with structural features that are observed more frequently in corewood than outerwood, such as small pit apertures, low pit frequencies, and narrow tracheids (Pittermann and Sperry 2003; Domec et al. 2006) and low capacitance (water storage, Meinzer et al. 2009; Barnard et al. 2011).

On first glance, some of the research on internal checking appears to run counter to *Hypothesis H*, but in fact, it may not. There has been much research on breakage in xylem in which the wood separates within a growth ring along the radial plane, termed internal checking, intra-annual cracks, frost cracks, and collapse. It has been studied from points of view of wood utilization, material science, dendrochronology, tree nutrition, and tree physiology. Some studies report that these breakages occur more frequently in the inner part of the cross-section than in the outer part, and that they occurred (based on resin or growth intrusions) when the wood was sapwood rather than heartwood (Cherubini et al. 1997; Pang et al. 1999, discussed in Ball et al. 2005). When it occurs in wood that is at moisture contents above the fiber saturation point, the stress is generated by transpiration or wood-drying and is transferred to the inside of the conduit walls where the water tension pulls inward (e.g. Innes 1995; Booker 1999; Grabner et al. 2006). If it pulls to failure of the cell wall, it will cause a check or crack. Rosner et al. (2010) called this stress the tension stress to distinguish it from shrinkage stress (which occurs only in very rare pockets of the stem of living plants where the wood is drier than the fiber saturation point). It is likely that the internal checking, if more prevalent in corewood than outerwood, is caused by additive factors beyond the water tension in the wood, which may not differ significantly from the corewood to the outerwood (e.g. Domec et al. 2009). Through elegant experimentation, Rosner et al. (2010) deduced that the cell wall deformation from tension stress was much lower in corewood than outerwood for all water tensions more negative than about 1 MPa in *Picea abies*. The lesser deformation in the corewood was related to its higher wall reinforcement, $(t/b)^2$. Thus, at a given tension stress, the corewood will deform less than the outerwood. All things being equal, a modeling approach from material science showed that wider growth rings (as are usually found in the corewood) will be more prone to this internal checking (Nairn 2010). Other studies have shown that internal checking is more prevalent in wood with lower earlywood density (Grabner et al. 2006) or with altered cell wall infrastructure (Putoczki et al. 2007) or chemistry (Downes and Turvey 1986).

4.2.2 Outerwood

Old/large trees need to have high specific conductivity (K_s) to meet their water transport demands. As shown above, the corewood will have lower K_s because of the heightened importance in corewood of embolism resistance, and the negative relationship between resistance to embolism and K_s. Specific conductivity, K_s (kg s^{-1} m^{-1} MPa^{-1}), is defined in Eq. 5.1 as

$$K_s = F\,L\,P^{-1}A_s^{-1} \tag{5.1}$$

in which F is water flow rate (kg s^{-1}), L is segment length (m), P is the pressure difference across the segment's length (MPa), and A_s is the segment's sapwood cross-sectional area (m^2). Higher (K_s) in outerwood is almost always observed.

Leaf-specific conductivity (K_l) is similar to K_s but it is normalized by the distal leaf area (A_l, that it supplies with water) rather than by the sapwood area (across which the water flows) (Eq. 5.2):

$$K_l = F\,L\,P^{-1}A_l^{-1} \tag{5.2}$$

Therefore,

$$K_l = K_s A_l^{-1} A_s \tag{5.3}$$

Leaf-specific conductivity (K_l) typically increases greatly with stem diameter (Tyree and Zimmermann 2002) by a factor of 3–10. In an extreme example K_l increased by a factor of 300 from outerwood at the tip to the corewood at the base (Tyree et al. 1991; Tyree and Ewers 1991). Leaf area/sapwood area ($A_l A_s^{-1}$) often (but not always) decreases as trees grow, by a factor of 20% over a height range of 50 m (McDowell et al. 2002). Assume for this exercise that there is no change. If a tree were constructed entirely from wood with the K_s of corewood, then to achieve a 300-fold increase in K_l from its smallest to its largest stem diameter, it would need 300 times more sapwood than observed— i.e. have a basal stem diameter of 6.9 m rather that 0.4 m—or else maintain only 1/300th of its leaf area. Clearly, trees benefit by having an increase in K_s from the corewood to the outerwood.

Data are largely supportive of *Hypothesis H*, that K_s increases from corewood to outerwood (Spicer and Gartner 2001; Domec and Gartner 2002), and that these are related to the tree's changing hydraulic needs as it grows from young/small to old/large. While this hypothesis touches on functional behavior caused by the morphology of cells (length, diameter), inter-conduit pits, and their membranes, it is not centered on MfA or density, both of which are known to change in the TRP. The following mechanical hypothesis relates to MfA and density, which in turn affect wood stiffness and strength.

4.3 Mechanics (M): Maintaining Adequate Structural Integrity as Cause for the TRP

Hypothesis M (mechanical constraints) states that the TRP strategy permits small stems (and branches) to bend without breaking in response to applied loads such as those from wind and snow; provides old/large trees with the strength needed to withstand the forces due to their self-weight as well as from applied loads such as from wind, ice, and snow; and facilitates more effective use of growth stresses to re-orientate the stem (Table 5.2). The strength and rigidity of the stem are functions of its size (diameter) and wood properties (Niklas 1992), and the tree is genetically programmed to adjust both of these in order to maintain adequate mechanical stability for a given situation. A number of studies have investigated the scaling that occurs between diameter and height (or length in the case of branches) to ensure that a tree maintains its structural integrity (e.g. Greenhill 1881; McMahon and Kronauer 1976; King and Loucks 1978; Wilson and Archer 1979; Bertram 1989; Niklas 1994; King 2011). In the case of branches, Bertram (1989) suggested that the more slender form of peripheral branch segments enables them to bend in response to wind and to reduce the associated drag, while the more robust form of non-peripheral segments is due to the need to resist greater bending loads. Material properties also play an important role, particularly if structural integrity is to be maintained using a minimum of material. While some studies have considered material properties in scaling analyses (e.g. Anten and Schieving 2010), in most studies the radial variation in these properties within a tree has been ignored. We hypothesize that the TRP is necessary to enable a tree to change its strategy from compliance to resistance in terms of its response to applied loading as it increases in size (Fig. 5.4).

4.3.1 Corewood

Stems and branches of small diameter can avoid large wind loads by becoming streamlined and therefore presenting a smaller frontal area to the wind (Bertram 1989; Vogel 1989; Steinberg 2002). Not only is this aided by the increased flexibility of peripheral branch segments (Bertram 1989), but also by the increased flexibility of the upper part of the stem in more mature trees (Hedden et al. 1995). Therefore, it is an advantage for the tree to be flexible below a given diameter over the whole height of the tree. The alternative, a stem of small diameter that remains relatively rigid in the wind, would require wood with higher stiffness and strength to avoid breakage due to the larger wind (or other) force acting on it. These concepts can be illustrated by using a simple model where a tree stem or branch is represented as a cantilever beam of uniform diameter (d) and modulus of elasticity (E) along its length subjected to a lateral point load (P) at its free end. The deflection x at any point z along the height (H) of the idealized stem is given by:

$$x(z) = \frac{32P(z^3 - 3Hz^2)}{3\pi Ed^4} \qquad (5.4)$$

It is readily apparent from Eq. 5.4 that for a given applied force (*P*), an increase in stem diameter (*d*) results in a reduced tree deflection ($x(z)$). Furthermore, for a given diameter the amount that a tree deflects under an applied load is inversely proportional to the modulus of elasticity (*E*) of the wood. Therefore, wood with a lower value of *E* would allow a tree stem to deflect more. *E* is strongly dependent on microfibril angle and density (e.g. Cave and Walker 1994; Barnett and Bonham 2004; Lachenbruch et al. 2010); wood with a high MfA and low density has low stiffness and in softwoods Cave and Walker (1994) reported that *E* can increase by a factor of 3–5 during the first 30 years of growth.

The large deflections permitted by this strategy will result in an additional bending moment due to the offset mass of the stem and crown; when the tree is small, these second-order effects due to the displaced mass are comparatively small and it is at lower risk of mechanical instability caused by such large deflections. However, for this strategy to be successful the corewood requires a high fracture strain ($\varepsilon_{\max}$) to allow the tree to bend through a large angle without rupture of the wood fibers. The strain in the outermost part of the stem depends on the magnitude of the deflection (*x*) as well as the length over which the deflection is acting and the stem diameter (*d*). For the simple case of the cantilever beam with uniform circular cross-section, the surface strain (ε) at the base resulting from a deflection (*x*) at the tip is given by:

$$\varepsilon = \frac{3xd}{2H^2} \tag{5.5}$$

By re-arranging Eq. 5.5, it is apparent that the maximum amount a tree can deflect before failure is governed by the fracture strain of its wood. Lichtenegger et al. (1999) advanced this further and showed theoretically that in order for the tip of a stem or branch to bend by a certain amount without buckling or fracture of the wood requires the optimization of $\varepsilon_{\max}^2 E$. While data on the radial variation of fracture strains are rare, particularly for wood in the saturated condition found in a living tree, Reiterer et al. (1999) present data for Norway spruce which show an almost fivefold increase in $\varepsilon_{\max}^2 E$ with a change in MfA from 5° up to 30°. Therefore, the high MfA found in the first few growth rings from the pith, would allow corewood to undergo large amounts of deformation with a lower risk of mechanical failure. This strategy is assumed to be further aided by the higher spiral grain angle often found in corewood, which enables considerable energy absorption to occur in young stems as they bend and twist in the wind (Kubler 1991; Skatter and Kucera 1997; Schulgasser and Witztum 2007).

4.3.2 Outerwood

As a tree gets larger, body forces (i.e. those associated with self-weight) will increase, but the wind load will also increase as the crown increases in size and the tree increases in height (larger force × longer moment arm = larger bending moment at the base of the stem) (Niklas 1992). Lichtenegger et al. (1999) showed that for the case of an applied lateral load (F_L), the height that a tree of a given diameter can grow is limited by the strength of its wood ($\sigma_{\max}$), i.e.

$$H < \frac{2I}{dF_L}\sigma_{\max} \tag{5.6}$$

where I is the second area moment of inertia ($= \pi d^4 / 64$ for a beam with circular cross section). This is supported by empirical observations (e.g. Putz et al. 1983) showing that trees which fail by stem fracture in wind storms have less strength (as well as lower wood density and stiffness) than trees that are uprooted. For the case of a vertical compressive force (F_G), Lichtenegger et al. (1999) showed that the maximum height that a vertical column of a given diameter can reach before buckling occurs is a function of E, i.e.

$$H < \frac{\pi}{2}\sqrt{\frac{EI}{F_G}} \tag{5.7}$$

Clearly, these two situations do not occur independently. When a tree is displaced by a lateral wind load, there will be an additional bending moment due to the offset mass of the stem and crown, termed the p-delta effect (Megson 2005). This can lead to instability as the p-delta effect increases the deflection of the tree, which in turn further increases the p-delta effect. This is particularly the case for tall, slender trees. In this situation, the tree is on the verge of falling over when the increase in deflection means that the toppling moment from the p-delta effect just exceeds the restoring moment provided by the rigidity of the stem. Increased strength is required to resist this additional moment due to the p-delta effect, and additional rigidity is required to reduce the risk of instability. The first requirement can be satisfied if wood strength increases as tree size increases. This is consistent with measured radial profiles of wood strength that show a substantial increase from pith to bark (e.g. Bendtsen and Senft 1986; Evans II et al. 2000).

When a tree adds new wood to the outside of the stem the rigidity of the stem (EI) increases not only because diameter increases, but also because this new material is as stiff or stiffer than material previously laid down (i.e. there is an asymptotic radial increase in wood stiffness up to a maximum value). Because this new material is added furthest from the neutral axis of the stem (assumed here to coincide with the pith), the overall stiffness of the stem is highly dependent on the stiffness of the outermost material (Lundstrom et al. 2008). If the tree only added wood with the same value of E as found in the first few growth rings, it would need to add considerably more material to achieve the same overall rigidity. However, there is an upper limit to the value of E that can be achieved, which is dependent on the product of the relative proportion of cell wall material in a tracheid and the E value of this cell wall material. The relative proportion of cell wall material in a tracheid will be limited by hydraulic conductivity requirements, while the E value of this cell wall material will be limited by MfA; once MfA reaches a value of around 10º, further reductions in MfA will only have a relatively small effect on cell wall stiffness. From a biomechanical perspective, it is also unlikely to be advantageous for a tree to keep producing increasingly stiff wood as it grows. This is due to the requirement for strain compatibility in the longitudinal direction within the stem (Archer 1986), which means that the bending stresses due to applied loads such as wind will be resisted by the stiffest material. If the tree continues to add successive increments of increasingly stiff material, then the bending stresses will be transmitted through the outermost thin layer of high stiffness material. This situation can be avoided if E remains approximately constant with increasing radial position after it has reached its maximum value; such a radial profile of wood stiffness will ensure that bending stresses are distributed over a larger area.

The radial profile of wood stiffness typically found in trees also enables trees to more effectively use their growth stresses to re-orient their stem or branches (Alméras and Fournier 2009). Such re-orientations are either a negative gravitropic response (e.g. bending of the stem to correct a lean or to induce upward inclination and/or minimize downward inclination of a branch), or a phototropic response to asymmetric light conditions (Matsuzaki et al. 2006). In the case of tree stems and branches that have finished elongating, the gravitropic response occurs via the internal bending moment generated by the asymmetric pattern of growth stresses in their wood (Archer 1986; Alméras and Fournier 2009). This asymmetric growth stress pattern is due to the presence of reaction wood. For example, in conifers compression wood is formed in response to a lean (Timell 1986). Compression wood has an unusually thick S2 cell wall layer with a very high MfA so that on maturing, the cell will tend to lengthen (Archer 1986; Schulgasser and Witztum 2007), resulting in a longitudinal compressive growth stress which a tree uses to “push” its leaning stem back to the vertical position. The bending moment provided by the addition of a new growth layer is a function of the growth stress differential generated by the asymmetric distribution of reaction wood in this layer and the effective distance that this acts from the neutral axis of the stem (Timell 1986). In turn, the change in curvature that this moment is able to generate is inversely related to the stem diameter and is positively related to the ratio of E in the new growth layer to the effective stiffness of the inner section of the stem (Alméras and Fournier 2009). This ratio increases with an increasing radial gradient in wood stiffness, so that trees with a large radial gradient in wood stiffness are able to use their growth stresses more effectively than trees having a smaller gradient.

While more detailed studies are required to fully test *Hypothesis M*, the principle that the radial changes in wood properties from corewood to outerwood are related to the tree’s changing requirements for mechanical support as it grows from young/small to old/large is supported by other published studies (e.g. Bertram 1989; Woodcock and Shier 2002, 2003). Woodcock and Shier (2002, 2003) suggest that radial increases in wood density are characteristic of early-successional species and reflect a pattern of growth in which there is a shift in allocation of resources from growth in height, associated with production of low-specific gravity wood, to greater structural reinforcement of the stem, associated with the production of denser wood.

If trees germinate in the understory, this additional reinforcement may be required as they reach the canopy and are subjected to increasing stresses associated with wind loading. The strongest radial gradients occur in tropical pioneer species that have very low density wood near the pith (Wiemann and Williamson 1988). Woodcock and Shier (2002) suggest for those species in which there is a radial decrease in wood density, that the structural reinforcement can be achieved by diameter growth. This latter argument is also supported by Larjavaara and Muller-Landau (2010) who argue that a large stem of low-density wood can have greater strength at lower construction cost than a thinner stem of high-density wood. However, this conclusion is based on the assumed relationships between wood stiffness, strength and density. Because wood stiffness and strength are functions of both density and MfA (Evans and Ilic 2001; Via et al. 2009; Lachenbruch et al. 2010), radial increases in these two properties could still occur in species showing a radial decrease in density if the reduction in MfA was sufficient.

4.4 Comparative and Experimental Approaches to Inferring Hydraulic and Mechanical Causes of the TRP

The diversity of wood patterns and environments in nature suggest that with careful comparisons, we may be able to infer the relative importance of developmental, hydraulic, and/or mechanical constraints on the TRP. The clearest comparisons for inferring the relationship of xylem structure to a type of constraint may be manipulations that develop, or natural comparisons that display, extreme levels of an environmental factor that one could categorize as hydraulic or mechanical. This approach can be used for different species, genotypes, individuals, and plant parts of individuals. Alternatively, one can start by identifying species, genotypes, individuals, and plant parts that differ in anatomy or properties, and work the other direction to infer drivers for these differences. Both approaches will help us avoid study of patterns in which the structure is a rather neutral reflection of multiple factors resulting in a compromise wood structure (either plastic or fixed but evolved) that bears little clear signature of any one driving force.

Note that these experiments need to be designed to study the radial variation, and not simply the ecological wood anatomy of the trait itself. The former is rarely done (with the exception of work in tree breeding programs for specific cases in commercially-important woods that exhibit ‘problems’ with corewood), whereas the latter is a mainstay in physiological ecology. For example, most studies on within-plant variation in structure and function only characterize the outer wood of a given position (i.e. Dunham et al. 2008; Lintunen and Kalliokoski 2010) rather than the radial variability. Many of the studies only characterize selected factors of importance to either hydraulics or mechanics, but not both, and they may not be the characteristics of most interest for distinguishing among the hypotheses in Table 5.2. For example, Peterson et al. (2007) looked at radial patterns in tracheid length and wood density for trunks, root, and branch of four 65-year old *Pseudotsuga menziesii* trees to learn if there is a TRP in all three plant parts. They concluded there are distinct radial patterns, but they did not ask whether hydraulic or mechanical issues appeared more important in one location than another. Several studies have characterized the TRP of hydraulic and mechanical characteristics, but have not used another factor such as water availability or diameter to tease out the adaptive significance of the observed patterns (e.g. Mencuccini et al. 1997). Therefore, targeted research on within-plant variability is necessary to help us understand why plants produce the observed radial patterns in wood structure and plant function.

4.4.1 Comparisons of Species or Genotypes That Vary in Radial Pattern

One experimental approach is to compare taxa that differ in the radial pattern of a set of wood traits, and ask (correlatively) what characteristics of the species or environment may be responsible for these differences. On a large scale, consider softwoods vs. hardwoods, softwoods having much greater radial variation in wood density, cell length, and microfibril angle than hardwoods. Both taxa can attain similar sizes. At first glance, this suggests that the TRP is unlikely to be related to mechanical considerations. However, the radial pattern of growth stresses also differs greatly between softwoods and hardwoods (Fournier et al. 1990), and in the outer wood, softwoods have much lower growth stresses than hardwoods, both of which could compensate for the mechanical considerations above, again, putting mechanics as a possible adaptive driver of the TRP. On a smaller scale, many tests of the hydraulic and mechanical hypotheses could be undertaken.

There is also much potential in comparing between genotypes that show variation in their radial pattern of a target characteristic. Clonally-reproduced plant material can provide replicate individuals within a treatment. One could study the correlations of the TRP of wood density, MfA, propensity to produce reaction wood, or height/diameter ratio, to learn whether they track environment, appear to have intrinsic control, or show signs of doing both simultaneously. There are many excellent and comprehensive studies with wood properties of commercial value, particularly with components of wood density in pines (e.g. Cown and Ball 2001; Cown et al. 2002), that have been interpreted in part to partition the variation into intrinsic (‘genetic’) and environmental (‘phenotypic’) variation. Breeding programs that seek to decrease the type and/or quantity of lignin, thereby producing wood with a lower stiffness, could also be used in this type of research. Increasingly, we will be able to use genomics approaches for studying these vegetative changes (Greenwood et al. 1989; Brunner and Nilsson 2004; Willmann and Poethig 2005; Cato et al. 2006; Paiva et al. 2008).

4.4.2 Comparisons of Individuals or Species from Different Environments

Another approach is to compare radial patterns for individuals or species that have contrasting mechanical or hydraulic environments to infer the role of those radial differences on function. These environments can be found or produced experimentally. Mechanical environments may derive from wind, ice loads, self-weight, mechanical stimulation, effects of neighbors, bending, compression, tension, addition of weights, reduction of force with pulleys, inclination at various angles, etc. Likewise, hydraulic environments may derive from drought, freezing, leaf area/sapwood area, root area/leaf area, short vs. long paths for the water transport, wood with low vs. high hydraulic resistance, nutrient status/soil fertility, etc. The plant material can also involve clones (common in forestry, agriculture, and horticulture) to provide closely-related plants that differ in an hydraulic aspect (such as leaf area/sapwood area) or a mechanical aspect (such as the tendency to lean). If groups growing in different hydraulic and mechanical environments have similar radial wood patterns, one can infer that the constraint is intrinsic (such as for earlywood and latewood densities in ten families of 22-year old *Pinus radiata*, grown at seven sites, Cown and Ball 2001). If, for example different hydraulic environments are associated with different radial patterns, one can interpret that the pattern is related to a putative hydraulic function. Another twist to this type of study would be to study radial patterns in monocarpic vs. polycarpic species to ask if there is an effect of reproductive effort on the structure and function; the monocarpic species would have no reproductive effort until the end of their lives (Thomas 2011).

Many observations have been made on individuals or species that differ hydraulically or mechanically from the typical plant. Mature lianas, for example, typically provide little of their own mechanical support, but some individuals may remain self-supporting (e.g. Gartner 1991a, b). A comparison of free-standing and supported individuals of *Croton pullei* indicated that the mechanical environment constrained growth form: if an individual had to support itself, its wood was stiff throughout the radial transect, but if an individual was supported by external objects, there was a radial progression (or even a switch) to having less stiff (Gallenmüller et al. 2001) and less hydraulically conductive wood (Carlquist 1991). The less stiff outerwood contrasts with the pattern typical of softwoods, but the more conductive outerwood is consistent with what is seen in softwoods (Spicer and Gartner 2001).

4.4.3 Within-Plant Comparisons, with Known Environmental or Radial Differences

Yet another approach for inferring whether the TRP is caused more by mechanical or hydraulic constraints is to study radial variation among plant parts within an individual where those plant parts are known to have contrasting mechanical or hydraulic environments. An example in tropical hardwoods compared radial patterns of hydraulic conductivity and longitudinal strain at several locations in three species of buttressed trees (Christensen-Dalsgaard et al. 2008). Theoretical conductivity was estimated from measurements of vessel frequency and vessel diameter on wood samples from the upper trunk (above the buttress), from the buttress near its top where it attaches to the trunk (proximal buttress), and from the buttress near its base and far from the trunk (distal buttress). They estimated the strain that would have been present when the wood was developing for the inner, middle, and outer radial positions of the proximal and distal buttresses. The proximal buttress had very high levels of strain that were similar at all radial positions. The distal buttress, in contrast, had very low strain in the inner position, higher strain at the middle position, and much higher strain at the outer position. These strains, however, were still much lower than the strain in the proximal buttresses. (They were estimated at 15% and 35% of the strain values of the middle and outer positions, respectively, of the proximal buttress). In the trunk above the buttresses in all three species, theoretical conductivity increased markedly from the inner to the outer wood of the trunk, as expected for the TRP. Theoretical conductivity showed no meaningful radial change in the proximal buttresses, but increased markedly from the inner through middle and then outer radial position for the distal buttresses. The research suggests that the radial variation in hydraulic characteristics was induced by the mechanical environment, with very different hydraulic patterns at these three locations.

Just as the buttresses can have quite different mechanical demands at different locations and cambial ages, many lianoid and hemiepiphytic species also will have within-plant variation in mechanical demands. Lianas, for example, are often self-supporting when young. This pattern is reflected in large radial changes in wood anatomy (reviewed in Carlquist 1991) including dense wood with small vessels near the pith, and new wood of lower density (Caballé 1998) and dramatically lower stiffness when the plant becomes supported (Rowe and Speck 1996; Ménard et al. 2009). Rowe and Speck (1996) noted that the properties did not progress smoothly from bottom to tip of an axis, giving evidence that the radial changes are functional responses to the mechanical environment, rather developmentally-induced trends.

Domec and Gartner (2002) made a within-plant comparison of safety factors to embolism and buckling in the temperate softwood *Pseudotsuga menziesii*. This study examined trunkwood from 4- and 10-year old saplings and 98-year old trees. Samples from the outer sapwood were tested for vulnerability to embolism, and the authors used the air entry point for calculations of safety factor, which is the inflection point early on the sigmoidal vulnerability curve at which wood has a sudden decrease in conductivity. Density of this outer sapwood was also determined, empirical relationships with density were used to estimate modulus of elasticity (E), and this estimated E was used with tree geometry to estimate the critical buckling height of the tree. The safety factor for the air entry point was low throughout the tree, and hovered near unity, meaning that the trees were on the verge of becoming embolized. In contrast, the safety factor for buckling was much higher (ranging from 1.5 to 10), suggesting that the trees were at greater risk from hydraulic rather than mechanical failure. Moreover, simplistic modeling of corewood in the place of outerwood and outerwood in the place of corewood showed much larger effects of wood type for hydraulic safety factors than for mechanical safety factors. This result is suggestive that the selection pressure is currently higher for hydraulics than mechanics. It may have previously evolved in such a way that the mechanical challenges were largely met.

A further type of within-plant comparison could involve study of the radial patterns within the sequentially-produced ramets of plants such as *Rubus alceifolius*, which make a series of increasingly robust self-supporting shoots that increase markedly in pith area, stem cross-sectional area, and internode length (Baret et al. 2003). As one shoot begins to wither, the next shoot is developing. The interpretation is that the first shoot is water-limited, but that sequentially-produced shoots are less water-limited. The growth culminates with the production of a shoot that initially is self-supporting. It grows very long, and develops vine-like mechanical (and probably hydraulic) characteristics at its developing and arching tip. One could predict that the first shoot will have radial wood properties that are adapted to producing a small upright stem, and each subsequently-produced ramet could have a radial pattern reflective of less hydraulic constraint. Another system of interest could be original axes vs. re-sprouts (such as after coppicing or a burn, e.g. Utsumi et al. 2010). One could expect the re-sprouts to have much more water available/leaf area, and so a much lessened hydraulic constraint. What would this signature be on the radial wood pattern?

5 Conclusions

Woody plants experience very different environments as they get older and larger. In most cases they display pre-set (ontogenetic) or plastic changes in their xylem's structure and function. It is presumed that the observed characteristics of corewood and outerwood mostly represent evolutionary 'solutions' to the particular design tradeoffs facing the individual as it gets older and often larger. This chapter has shown that these solutions may change with size and age, and they are more varied than has been widely understood. Until recently, much of the research on these radial patterns has focused on characteristics of importance for wood utilization, and perhaps for that reason, there was an underlying assumption that corewood, which is more flexible and weaker than outerwood in the axial direction, is the best that a young cambium can make, and that as the cambium matures, it can produce the stiffer, stronger xylem that is of higher quality for the tree as well as for humans. The view in this paper is that the radial progression of structure and function has evolved to increase the chances of survival of the whole plant at all stages of vegetative growth. In some cases the TRP will have evolved more for hydraulic than mechanical purposes and in other cases it will have evolved for mechanical rather than hydraulic purposes. The extraordinary plasticity of the cambium ensures that the tree can respond rapidly to environmental variation by favoring one or more mechanisms over others, thereby greatly altering hydraulic and mechanical functionality. This view is an extension of Larson's (1962) prescient work in which he stated that we can only advance our understanding of wood quality through looking at how the environment affects the plant biology, rather than the wood directly.

This paper shows that the particular radial patterns are variable in hardwoods vs. softwoods, and among growth forms, species, environments, and plant parts. There are sets of traits that are most common for a given category of plants (such as plastic response to the mechanical environment in semi-self-supporting species), but the literature is scant on some of these categories and so our knowledge is quite incomplete. The paper also shows that there are numerous examples of changes that are determined ontogenetically and other examples in which the changes are plastic; both types of example can be found in softwoods and hardwoods. With what is now known, it is not easy to predict whether changes are intrinsically or plastically controlled, with a few exceptions (such as the tendency for MfA and tracheid length in aboveground stems to be under intrinsic control). It is important to note that while this paper focuses on radial changes, there are also changes that occur with height that were considered beyond our scope.

The paper presents three frameworks. The first framework (Sect. 3.1) discusses the possible triggering mechanisms responsible for the production of the radial changes in wood. Elucidation of these proximal mechanisms could be very useful for management of forests to increase the value of logs and wood. The second framework (Sect. 3.3) delineates a range of abiotic, developmental, mechanical, and architectural attributes that are likely to be similar, and another set of attributes that are likely to differ, between same-aged small and large plants, and same-sized young and old plants. This framework shows that no selective factors stand out above others to help us interpret the TRP. The third framework (Sect. 4) introduces three hypotheses for why woody plants have evolved a TRP. Our intention was to illustrate that there are numerous hypotheses for patterns, and, indeed, we would not expect one hypothesis to describe the functioning of a plant at all times. With careful comparisons, we should be able to better elucidate the conditions during which different types of radial variation are adaptive.

These changes in xylem structure and function are not trivial. They make substantial contributions to the success or failure of the plant. We will benefit greatly from an understanding of the physiology and structure of xylem as humans continue to impact the environment; as natural plant ranges are disrupted and more plants are left with maladapted traits in their altered environments; as economic pressures push foresters to both accelerate growth and harvest trees younger; as processing technologies for wood change the material requirements for products; as agricultural practices change in response to economic factors, availability of natural resources, prevalence of competing vegetation, pathogens, and herbivores; as industrial agriculture and horticulture increasingly develop new clonal materials that need to be evaluated; as new uses for plants are adopted such as for biofuels, carbon sequestration, and as chemical factories; and as scientists increasingly relate gene function to development, structure, and function. The appreciation of the diverse functions of xylem and its heterogeneity will help physiologists move forward on many fronts. The vascular cambium that produces xylem is also producing phloem (Mencuccini et al. 2011), and so future work at the whole plant, whole lifespan level will benefit from the study of xylem and phloem together, at developmental, anatomical, and ecophysiological levels.

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