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## 6

## Patterns of Xylem Variation within a Tree and Their Hydraulic and Mechanical Consequences

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### I. Introduction

Xylem is nonuniform in its structure and function throughout the plant stem. Xylem structure varies from pith to bark, from root to apical meristem, from stem to branch, at nodes vs internodes, and at junctions of branches, stems, or roots compared to the internodal regions nearby. At smaller scales, anatomy varies systematically within one growth ring and it varies among the layers of the cell wall. Xylem properties vary by the plane in which they are examined, owing to cell shape, cell orientation, and the orientation of microfibrils in the cell walls. As concluded by Larson (1967, p. 145), "more variability in wood characteristics exists within a single tree than among [average values for] trees growing on the same site or between [average values for] trees growing on different sites."

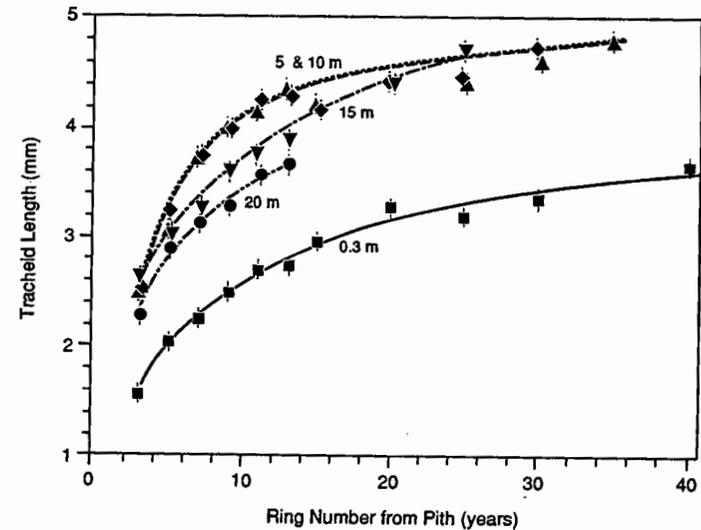
This structural heterogeneity results in spatial variation in hydraulic and mechanical performance of the xylem. Whereas wood technologists have long acknowledged the importance of wood variability (e.g., Northcott, 1957; Dadswell, 1958; Larson, 1962; Cown and McConchie, 1980; Beery *et al.*, 1983; Megraw, 1985; Schniewind and Berndt, 1991), this heterogeneity often has been overlooked by botanists, who have tended to view stems as homogeneous organs ("biomass") with only a passive role in the biology of the plant. This chapter details the patterns of variation in xylem structure found within a woody plant, and emphasizes what is known and what is not known about the functional consequences of this variation for shoot water movement and mechanics.

## II. Typical Patterns of Xylem Variation

This section reviews the typical structure of xylem within a tree, but the reader should refer to other sources such as Panshin and de Zeeuw (Ch. 7, 1980) or Koch (pp. 305–349, 1985) for more detailed descriptions. There is more information on softwood (gymnosperm) than hardwood (woody angiosperm) anatomy, and therefore many of the paradigms of wood anatomy are based on softwoods. In fact, most of that research has probably occurred in only two genera, *Pinus* and *Pseudotsuga*. In spite of the extreme differences in xylem anatomy of softwoods and hardwoods, the wood in both types of plant apparently fulfills the same basic functions. Softwood xylem is made of about 90–94% tracheids by volume, with most of the remaining cells in ray parenchyma (Petric and Scukanec, 1973), whereas hardwoods have a much greater variety of cell types and configurations. Hardwoods can have libriform fibers, tracheids, and vasicentric tracheids (all in the same size range as softwood tracheids), vessel elements (up to an order of magnitude wider than tracheids), and numerous types of parenchyma cells and arrangements (Panshin and de Zeeuw, 1980). Vessel volume in North American hardwood tree species ranges from 6 to 55%, with 29–76% fiber volume, 6–31% ray volume, and 0–23% volume of axial (longitudinally oriented) parenchyma (French, 1923, as cited in Panshin and de Zeeuw, 1980). Tracheids, which are cells with closed ends, range from 1 to 7 mm long (Panshin and de Zeeuw, 1980). Vessels, which are made of stacks of open-ended vessel elements, are variable in length. In diffuse-porous species, most vessels are shorter than 10 cm, but in ring-porous species many of the vessels are longer, with the longest frequently as long as the stem itself (Zimmermann and Jeje, 1981).

Within a growth ring there are systematic changes in cell length, frequency of cell type, and cell wall structure (Panshin and de Zeeuw, 1980), but the most apparent differences are in xylem density and the abruptness of density changes within a ring. In general, ring-porous hardwoods (e.g., *Fraxinus*, *Quercus*, and *Ulmus*) and abrupt-transition softwoods (e.g., the hard pines, such as *Pinus taeda* and *P. rigida*) have the most abrupt change in density across the growth ring, followed by gradual-transition softwoods (e.g., *Picea*) and then diffuse-porous hardwoods (e.g., *Acer*, *Alnus*, and some *Populus*). Softwoods can have 500% denser wood in latewood than earlywood (*Thuja plicata*; p. 271 in Panshin and de Zeeuw, 1980) and even a diffuse-porous hardwood can have 10–20% denser wood at the end of the growth ring than at the beginning (*Populus × euroamericana*; Babos, 1970).

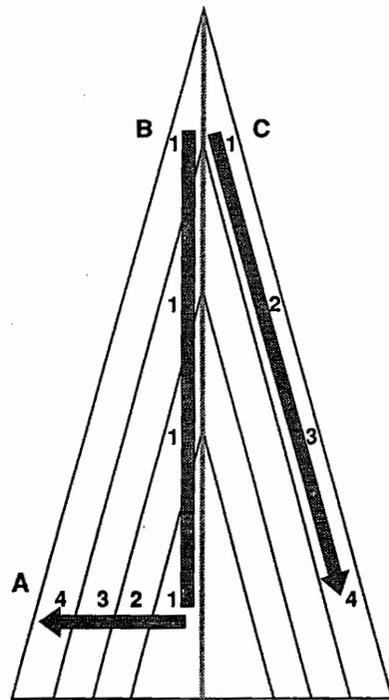
Wood near the pith (called core wood, juvenile wood, or crown-formed wood) differs anatomically from that nearer the bark (called outer wood, mature wood, or stem-formed wood; reviewed in Panshin and de Zeeuw, 1980; Megraw, 1985; Zobel and van Buijtenen, 1989). Outer wood has



**Figure 1** Variation in tracheid length as a function of cambial age and height in *Pinus taeda* (mean of 33 trees). Tracheid length increases with increasing cambial age (ring number from the pith), and its value at any cambial age is a function of height. [Reprinted from Megraw (1985) with permission from TAPPI.]

longer (Fig. 1), sometimes wider (Olesen, 1982) longitudinal cells than core wood. In *Alnus rubra*, a species showing no variation in density from pith to bark (Harrington and DeBell, 1980), the average fiber length increased by 39% from the first to the twentieth growth ring, where it leveled off (H. Lei and B. L. Gartner, unpublished observations). In ring-porous hardwoods (e.g., *Quercus alba*; Phelps and Workman, 1994) and some softwoods, outer wood has a lower proportion of latewood. However, outer wood has a higher proportion of latewood than does core wood in the majority of softwoods [e.g., *Pinus taeda* (Megraw, 1985) and *Pseudotsuga menziesii* (Abdel-Gadir *et al.*, 1993)]. In addition, outer wood often has narrower growth rings than core wood, thicker latewood cell walls, and a lower incidence of spiral grain (cells oriented at a consistent angle to vertical) or compression wood (see below).

This radial (pith-to-bark) variation results from wood produced by a cambium at one height that increases in age with each growth ring (Fig. 2, transect A). As shown by Duff and Nolan (1953), woody plants also exhibit variation in the vertical axis, whether cambial age is held constant (Fig. 2, transect B), or whether wood is produced in the same year but by cambia of different ages (Fig. 2, transect C). As a first approximation, the same



**Figure 2** Schematic diagram of a longitudinal section of a 4-year-old stem, showing sampling transects (numbers represent years from pith at a location; stippled line represents the pith). (A) Wood produced by the same cambium at one height with increasing cambial age and during different years; (B) wood produced by cambia of the same age but with differing height and during different years; (C) wood produced by cambia of increasing age and decreasing height during the same year.

pattern is found in the vertical direction (transect C) as in the radial direction (transect A) because the younger cambium (at the tip or center of the tree) makes different products than does the older cambium (at the base or perimeter of the tree).

The pattern of variation due to vertical position not related to cambial age (Fig. 2, transect B) depends on the taxon, and is superimposed on the variation due to cambial age (transect A) to give the actual patterns of transect C. Common patterns in transect B are an increase in tracheary diameter from the base of the stem to near the base of the live crown, then a decrease to the apex (Dinwoodie, 1961), or a steady decrease from the base of the stem to its apex. For hardwoods, vessel density increases as vessel

diameter decreases within an individual (Larson, 1962). The parallel patterns of anatomy along transects A and C (Fig. 2) may not pertain to axial or ray parenchyma: in hardwoods, the amount and type of parenchyma may be highly variable within the individual, with the highest proportions reported at the base of the stem (e.g., Patel, 1965; also see Pate and Jeschke [8] in this volume).

Typical heartwood (following the softwood paradigm) has no living cells, is nonconductive, and develops in the oldest xylem. Sapwood has some living cells, is conductive, and occupies the outer sheath of a stem, or the entire cross-section in a younger plant. An old tree may have core wood that is heartwood and core wood that is sapwood, and outer wood that is heartwood and outer wood that is sapwood. In softwoods, the conversion of sapwood into heartwood always involves death of the cytoplasm of all living cells, which may include longitudinal or ray parenchyma, and fiber cells. In hardwoods, the transition may be less distinct, with some cells remaining alive in the inner region, known as "ripewood" rather than heartwood (Hillis, 1987). Depending on the taxon, conversion can also involve many of the following (Hillis, 1987): a decrease in sugars and starches; embolism of the tracheary elements; a decrease in moisture content in softwoods, or an increase or decrease in moisture content in hardwoods (Table 3-3, p. 3-10, U.S. Forest Products Laboratory, 1987); deposition of secondary chemicals onto nearby cell walls; or production of tyloses into tracheary cell lumens.

The wood in branches is different from the wood in main stems. This degree of difference must depend on the growth form of the plant, but more research is needed to clarify this point. Compared to main stems, branches have shorter, narrower tracheary elements (Ikeda and Suzaki, 1984), generally denser wood (but in some reports, less dense wood), narrower growth rings, and more numerous rays (Table I). Vessel density is higher but vessel volume is lower in branches than trunks (Fegel, 1941; and see Table I). The stem-branch and branch-branch junctions are commonly sites of decreased diameter of tracheary elements (Salleo *et al.*, 1982b), but other anatomical patterns have also been described (see Section III.D). Table I also shows that roots have different anatomical characteristics than stems. Moreover, unlike stems, roots rarely possess reaction wood (Wilson and Archer, 1977). In fact, there may be more within-plant variability in secondary xylem structure between roots and other plant parts than within the shoot; the magnitude and functional significance of these differences need more research.

Reaction wood develops in response to gravity where stems or branches are out of their vertical "equilibrium positions" (Wilson and Archer, 1977). Reaction wood is usually present on the underside of branches or leaning stems in softwoods (compression wood), and on the upper side of branches or leaning stems in hardwoods (tension wood). Opposite wood, with its own

**Table 1** Comparative Anatomy of Root, Trunk, and Branch for Diffuse- and Ring-Porous Hardwoods and Softwoods\*

Characteristic	Diffuse-porous hardwoods			Ring-porous hardwoods			Conifers		
	Root	Trunk	Branch	Root	Trunk	Branch	Root	Trunk	Branch
Specific gravity	0.46	0.49	0.54	0.46	0.54	0.57	0.38	0.36	0.49
Growth rings/cm	7.9	4.6	9.8	9.4	5.1	10.2	7.9	5.9	15.0
Tracheid diameter ( $\mu\text{m}$ )							30	27	31
Vessel diameter ( $\mu\text{m}$ )	90	100	71	78	60	40			
Vessel density (No./mm <sup>2</sup> )	22	54	60	48	118	200			
Vessel volume (%)	13	27	18	29	27	22			
Ray volume (%)	19	14	15	16	11	13	5	5	5

\*Specific gravity is based on oven-dried weight and fresh volume. There were four ring-porous species (*Fraxinus americana*, *F. nigra*, *Ulmus americana*, and *Quercus borealis* var. *maxima*), eight diffuse-porous species (*Prunus serotina*, *P. pennsylvanica*, *Betula lutea*, *Populus tremuloides*, *Tilia americana*, *Fagus grandifolia*, *Acer saccharum*, and *A. rubrum*), and eight coniferous species (*Pinus strobus*, *Pinus resinosa*, *Picea rubens*, *Picea mariana*, *Larix laricina*, *Tsuga canadensis*, *Abies balsamea*, and *Thuja occidentalis*). (From Fegél, 1941.)

unique anatomical and mechanical properties, may develop in the same growth ring but on the opposite side of the reaction wood (see discussion in Wilson and Archer, 1977). Growth rings may be wider on the side with reaction wood than opposite wood. Another type of wood, flexure wood, results from repetitive motion of the gymnosperm stem, not from a permanent offset (Telewski, 1989), and it has slightly higher density and smaller cell lumens than normal wood.

Compression wood has higher density, thicker cell walls, different cell wall ultrastructure, and often smaller diameter cell lumens than normal wood. The earlywood/latewood transition of compression wood becomes gradual in species with abrupt transitions in their normal wood, and it becomes abrupt in species with gradual transitions in their normal wood (Panshin and de Zeeuw, 1980). Tension wood has lower vessel density, narrower vessels, different cell wall ultrastructure in the fiber, and less ray or longitudinal parenchyma than normal wood, with most modifications in the beginning of the growth ring (Scurfield, 1973; Panshin and de Zeeuw, 1980). There appears to be a gradation in anatomy from opposite to normal to reaction wood, such that distinctions among the three may be somewhat arbitrary (Dadswell and Wardrop, 1949).

### III. Variation in Water Transport

The anatomical variation just described results in systematic variation in efficiency of water transport through the stem. The hydraulic properties

discussed here are hydraulic conductivity ( $k_h$ ) and specific conductivity ( $k_s$ ), in the axial direction, as follows:

$$k_h = V/[t(\Delta P/l)] \quad (1)$$

$$k_s = k_h/A_{\text{stem}} \quad (2)$$

where  $V$  is the volume of water,  $t$  is time,  $\Delta P$  is the pressure difference between the two ends of the stem segment,  $l$  is length of the stem segment, and  $A_{\text{stem}}$  is stem cross-sectional area. The variable  $A_{\text{stem}}$  can be defined to include only the portion of the stem that later conducted stain, all sapwood, or the whole stem cross-section (including or excluding the pith). Hydraulic conductivity ( $k_h$ ) is a measure of how much water comes out of a stem segment (diameter unspecified) per unit time per pressure gradient. Specific conductivity ( $k_s$ ) is a measure of how much water a stem segment will transport per unit time per pressure gradient, normalized by its cross-sectional area. If a twig and a trunk of the same length were made of hydraulically identical material, the trunk would have higher  $k_h$  than the twig but the same  $k_s$ . The effects of wood anatomy on xylem embolism are considered by Sperry ([5] in this volume).

#### A. Within a Growth Ring

Most research on hydraulics within a growth ring has focused on hardwoods. The hydraulic function of different parts of a hardwood growth ring is controlled by their anatomy: vessel diameter (flow is proportional to radius to the fourth power; Poiseuille's law), vessel density, time span over which vessels are conductive given their environment, permeability of inter-vessel pits, and vessel lengths. Ring-porous species usually have the same vessel density throughout the growth ring (Carlquist, 1988), with wider vessels at the beginning than the end of the growth ring. On that basis one would expect much higher specific conductivity ( $k_s$ ) of wood at the beginning of the growth ring. Indeed, Ellmore and Ewers (1985) calculated that for the ring-porous species *Ulmus americana*, 96% of the flow would be through the beginning of the growth ring if flow were governed by Poiseuille's law alone.

The ring-porous habit involves production of xylem with two spatially separated hydraulic strategies in each growth ring (high  $k_s$  with short functional life span, and low  $k_s$  with long functional life span), whereas the diffuse-porous habit results in a more uniform tissue (intermediate  $k_s$ , variable life span). Within an individual, the wider vessels conducted water for a shorter period than the narrower vessels (Salleo and Lo Gullo, 1986; Hargrave *et al.*, 1994). Ring-porous species (with some wide long vessels) were much more susceptible to freezing-induced embolism than were diffuse-porous species (with only narrow, short vessels; Sperry and Sullivan, 1992). Of 43 north-temperate tree species sampled in late winter, the ring-porous species were the most embolized followed by diffuse-porous species and

then conifers (Wang *et al.*, 1992). Interestingly, the date of leafing out was inversely related to the degree of late winter embolism: the least embolized species were the fastest to leaf out (Wang *et al.*, 1992). A common xylem pattern in regions with a mediterranean climate is to have smaller vessels and tracheids that are interwoven among the larger vessels, purportedly to provide some water throughout the canopy once the larger vessels have embolized owing to drought (Carlquist, 1985). The double-staining experiments of Hargrave and colleagues (1994) support this hypothesis with evidence for spatial intermingling of large embolized vessels and smaller non-embolized ones in droughted, but not in irrigated, *Salvia mellifera*, a chaparral shrub.

Even in conifers there is evidence of two spatially separated hydraulic strategies: pit membranes of earlywood tracheids are more likely to "aspilate" (indicating that the conduit has embolized) than the pit membranes of latewood (Wardrop and Davies, 1961). The current interest in temporal and spatial patterns of embolism in softwoods shows that there is much to learn even about the hydraulic strategy of woods as simple in structure as softwoods.

There are numerous other intraring xylem arrangements in hardwoods besides ring-porous and diffuse-porous, such as those characterized by vessel grouping (solitary, chains, or bands), ray frequency and type, or presence and pattern of longitudinal parenchyma (Carlquist, 1988). Except for the surveys documenting the proportion of a flora that may contain them (e.g., Carlquist and Hoekman, 1985; Baas and Schweingruber, 1987), these arrangements have been little studied in an ecological context. Function, within-individual variability, and the degree of plasticity in exhibiting these arrangements are largely unknown.

### B. From Pith to Bark

Outer wood has a higher  $k_s$  value than core wood because of the radial gradient in anatomy resulting from development (see Section II) and because the center of an old stem has heartwood. This results in the portion of the stem with the highest  $k_s$  being the closest to the external environment, and thus the most vulnerable to fluctuating temperatures, physical injury, and attack by biotic agents.

Water does not flow readily between growth rings (Ewart, 1905; Ellmore and Ewers, 1985). In softwoods, pits are larger and more frequent in the radial walls of tracheids than in the tangential walls (Koran, 1977; Panshin and de Zeeuw, 1980), promoting water movement within a growth ring rather than between growth rings. Nonetheless, *Picea mariana* has tangential pitting in tracheids of the last four rows of latewood and the first row of earlywood (Koran, 1977), facilitating some water flow between growth rings.

**1. Developmental Changes** The radial changes in anatomy that occur during cell development (e.g., increasing vessel and tracheid lengths and widths, alteration in earlywood to latewood ratio) have been well described, but their effects on hydraulics have not. The experiments to determine the pattern of radial changes in  $k_s$  are not done easily, because xylem position and age are confounded. There should be an increase in  $k_s$  going from pith to bark, owing to tracheary dimension alone (this is especially true in hardwoods), but the outcome could be different, for example, if the ratio of earlywood to latewood increases with radius (e.g., a ring-porous *Quercus*) rather than decreases (e.g., a *Pseudotsuga menziesii*).

**2. Heartwood and Sapwood** Heartwood supports no appreciable water flow, and therefore all the axial flow occurs in the sapwood. However, not all zones of sapwood have the same  $k_s$ ; there is an abrupt increase in embolized tracheids in the sapwood adjacent to the sapwood/heartwood boundary (Hillis, 1987). Sperry and colleagues (1991) discovered that pit membranes are partially degraded in the older vessels of *Populus tremuloides* near the boundary of the ripewood (see Section II) and the sapwood. This degradation lowers the xylem tensions required for embolism and may initiate heartwood formation.

The costs or benefits of spatial patterns of sapwood area have been only rarely studied from the plant's perspective (Ryan, 1989). Apparent benefits of a large sapwood cross-sectional area are that it permits high stem  $k_h$  and thus maintenance of a large leaf area, and that it permits storage and reuse of water (Waring and Running, 1978; and see Holbrook [7] in this volume), nutrients, and carbohydrates. An apparent cost is the maintenance respiration for the larger volume of xylem parenchyma (Ryan, 1990; Ryan *et al.*, 1995).

### C. From Root to Crown

The hydraulic trends from base to tip of a stem (e.g., Booker and Kininmonth, 1978) reflect the anatomical variation, with higher  $k_s$  in locations that have a higher proportion of earlywood and wider conducting elements. If the species produces distinct core wood, then the top of the tree will differ hydraulically from the base of the tree (see Fig. 2). Empirically, researchers have generally found the pattern of  $k_s$  reported by Farmer (1918a, p. 223): "Young or immature wood always gives a relatively low reading [of  $k_s$ ] and of quite uncertain value." This finding is in spite of the fact that a typical growth ring has a higher proportion of earlywood near the top of a tree than near the base (Larson, 1962). In the shrub *Toxicodendron diversilobum*, the  $k_s$  of apical segments of wood (2–3 years old) averaged 45% of that of basal segments of wood (averaging 10.5 years old; Gartner, 1991a). To characterize the hydraulic strategy of a plant will require

research throughout its lifetime on its transpiration rates and stem transport capabilities resulting from growth, development, and injury.

The shortness of average vessels and tracheids protects a stem from losing much of the hydrosystem from a point injury or a single embolism. This feature explains the results of double saw-cut experiments (described at least as far back as 1806; see Zimmermann, 1983), in which the foliage remains alive despite a cut half-way through the trunk on one side, and a cut half-way through the trunk on the opposite side a few centimeters higher. Nonetheless, experiments in noninjured trees have shown that sap generally spreads very little laterally from the rank and file of vessels or tracheids in which it enters (reviewed in Kübler, 1991), although in some species that rank and file may have a characteristic path of ascent (e.g., spiral to the right, spiral to the left, or winding; Vité and Rudinsky, 1959).

#### D. Between Stems, Branches, and Nodes

Consistent with their smaller tracheary elements, branches generally have lower  $k_s$  values than their parent axis (e.g., Ewers and Zimmermann, 1984a,b; Gartner, 1991a). Moreover, there is usually a localized decrease in calculated or measured  $k_s$  for junctions between a branch and its lower order stem (e.g., Ewers and Zimmermann, 1984b), nodes vs internodes in young stems (Farmer, 1918b; Rivett and Rivett, 1920; Salleo *et al.*, 1982a,b; Tyree *et al.*, 1983; Salleo and Lo Gullo, 1986), the branch and the reproductive parts (Darlington and Dixon, 1991), and the branch and its deciduous leaves (Larson and Isebrands, 1978). Two possible causes of this decreased  $k_s$  are a greater proportion of mechanical tissue at branch junctions (see Section IV.A.2), and selection for segmentation (Section III.E). Lower  $k_s$  at junctions can result from various anatomical combinations such as a decrease in diameter and number of vessels in the leaf-branch abscission zone of *Populus deltoides* (Larson and Isebrands, 1978), an increase in vessel diameter but a decrease in vessel numbers in nodes vs internodes of *Vitis* (Salleo *et al.*, 1982b), or a discontinuity between vessels in the vegetative and the reproductive stem of *Rosa hybrida* (Darlington and Dixon, 1991).

#### E. Segmentation and the Relationship between Wood Anatomy, Hydraulics, and Architecture

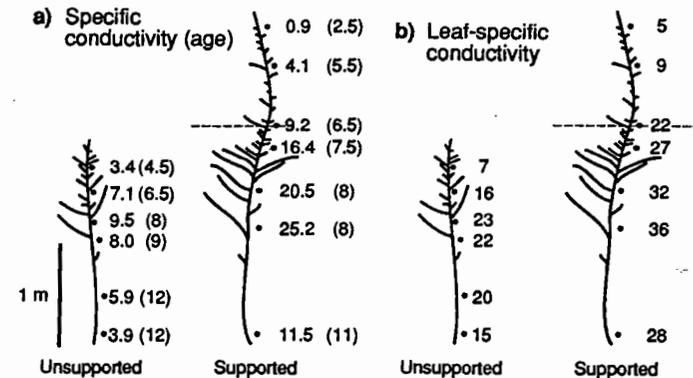
The segmentation hypothesis of plant hydraulics (Zimmermann, 1978, 1983) states that the hydraulic architecture of a plant (the geometry and performance of its xylem relative to its distribution of ports of water loss, mainly the leaves) permits certain zones of the plant to survive drought stress while other zones die. Regardless of the hydraulic architecture of the plant, distal axes will have more negative water potentials than will proximal axes during steady state transpiration. But hydraulic constrictions, thought to result from the arrangement and structure of xylem cells, may enhance cavitation in some localities relative to others. Organs such as branches

(e.g., Kolb and Davis, 1994), fruits (e.g., Darlington and Dixon, 1991), leaves (e.g., Sperry, 1986), or above-ground shoots (e.g., Aloni and Griffith, 1991) that are distal to zones of hydraulic constriction will die under conditions of severe water stress. These deaths will decrease the evaporative area supplied by the parent axis, promoting its survival.

The amount of water that actually flows through a stem depends on its xylem conductance and its flow rate. Conductance is controlled by the wood structure, whereas flow rate is controlled at least in part by leaf-level factors such as leaf number, size, and albedo; stomatal aperture and density; and sensitivity of the stomata to the environment. Given the function of xylem in supplying water for transpiration, one would expect some relationship between stem water transport and transpiration. The Huber value (Huber, 1928) was one such relationship, describing the ratio of stem area (including heartwood) to leaf area (or mass) in a plant. The pipe model (Shinozaki *et al.*, 1964) suggested that a unit of sapwood will supply water for one unit of leaf area. A more refined relationship, that of leaf-specific conductivity ( $k_l$ ), takes into account the conductivity of that sapwood:

$$k_l = k_s / A_{leaf} \quad (3)$$

This value describes how conductive the wood is relative to the potential evaporative surface, the leaf area ( $A_{leaf}$ ). For a given order branch and height,  $k_l$  can be relatively constant for different individuals or species in the same environment, even when other factors differ, such as  $k_s$  (Fig. 3) (Gartner, 1991a; Chiu and Ewers, 1992; Kolb and Davis, 1994), rooting



**Figure 3** (a) Specific conductivity ( $k_s$ ,  $10^{-3} \text{ m}^2 \text{ sec}^{-1} \text{ MPa}^{-1}$ ) and (b) leaf-specific conductivity ( $k_l$ ,  $10^{-7} \text{ m}^2 \text{ sec}^{-1} \text{ MPa}^{-1}$ ) of two neighboring *Toxicodendron diversilobum* shoots, one shrubby (unsupported) and one viney (supported). Above the dashed line, the vine is unsupported. Stem age is shown in parentheses. Whereas  $k_s$  is much higher in supported than unsupported individuals for a given aged segment,  $k_l$  does not vary significantly. [Modified from Gartner (1991a) with permission from Springer-Verlag.]

depth (S. D. Davis, personal communication), growth form (Fig. 3) (Gartner, 1991a; Chiu and Ewers, 1992), wood structure (Shumway *et al.*, 1993), or total path resistance (Shumway *et al.*, 1993). Undoubtedly, better relationships will be established for stem/leaf hydraulic function to indicate the hydraulic design criteria of plants.

It is unknown whether the crown physiology, phenology, and architecture drive development of the stem hydraulics (Larson, 1962), the reverse, or whether both occur in a feedback loop (Ford, 1992). Nonetheless, stem architectural development is clearly related to  $k_s$  and  $k_b$  in many reported cases. Branches have lower  $k_b$  than lower order stems and trunks. Tyree and Alexander (1993) argue that the lower  $k_b$  of branches, not the localized constrictions of  $k_b$  or  $k_s$  at branch junctions, contributes most to segmentation. Larson and Isebrands (1978) explained the death and abscission of deciduous leaves according to principles consistent with the segmentation hypothesis. Darlington and Dixon (1991) describe anatomy of the sympodial species *R. hybrida*, in which one lateral becomes reproductive (with vessels discontinuous from the main shoot) while the other remains vegetative (with vessels continuous with the rest of the plant body). This arrangement allows continued vegetative growth during drought at the expense of reproductive growth. Farmer (1918b) said that in ash trees (no scientific name given), the leader is replaced by a lateral almost annually. Measurements by Farmer showed that the lateral (which will become the leader) has a higher  $k_s$  than the leader (which will lose dominance). Similarly, *Tsuga canadensis* has weak apical control (its leader is replaced by a lateral in at least 31% of the years; Hibbs, 1981) and there is little hydraulic difference between the tip of the main stem and the lateral branches (Ewers and Zimmermann, 1984b). In contrast to ash and *T. canadensis*, sycamore (no scientific name given) has a persistent leader and its  $k_s$  remains higher than the  $k_s$  of its laterals (Farmer, 1918b). A vigorous *Abies balsamea* tree with strong apical control had higher  $k_b$  along the main stem, and particularly at the apex, than did less vigorous individuals having lower apical control (Ewers and Zimmermann, 1984a).

#### IV. Variation in Stresses, Structure, and Density

##### A. Stress Distributions

Stems experience short- and long-term stress (force per unit area) from a variety of causes such as gravity, wind, weight of snow or a maturing fruit, removal of a branch, partial failure of the anchorage system, or growth and development (the latter classified as "growth stress"; Jacobs, 1945). The effect that a force has on the structure depends on where the force is applied, the material properties of the structure, the geometry of the structure, and the degree to which it is "fixed" (unmovable) at its base. Note

that the material properties of wood are variable on scales from  $10^{-3}$  to 10 m and that as a first-order approximation, wood density is positively and nearly linearly correlated with strength properties (Table 4-8, p. 4-28, U.S. Forest Products Laboratory, 1987).

One of the ways in which a plant senses the environment is through stress, most likely through sensing the strain (relative change in length of a line in a deformed body) that stress generates. The strain could indicate, for example, that a stem is flexing (perhaps from wind), the stem has little compressive or tensile stress (as in the case of a vine on an external support), or the stem is leaning.

**1. Typical Normal Stress Distributions** This discussion deals with normal (not shear) stresses: radial, axial, and bending. At the scale of the growth ring, the denser wood bears more of the stress than less dense wood if both have the same strain, because the denser wood has more cell wall material per cross-sectional area. Therefore, a plant with large intraring variation in density will have a more variable axial stress distribution than a plant with relatively uniform density.

For a tapered columnar beam of a homogeneous material, the normal bending stress throughout the cross-section is at a maximum at the surface. However, for at least part of the season there will be higher axial and bending stresses in the preceding year's latewood than in the current growth (earlywood) and at the vascular cambium (the contribution of bark will be variable). The mechanical theory of uniform stress states that at each height a woody stem develops a cross-sectional shape that tends to equalize the average bending plus axial stresses (Morgan and Cannell, 1994; see also Mattheck [3] in this volume). This theory, combined with the previous statement, suggests that the time-averaged bending stress at the cambium at a given height is somewhat lower than the time-averaged bending stress several millimeters toward the pith. However, this stress diminution probably has a trivial effect on wood development because at the wind speeds likely to be encountered most of the time in most forests, the majority of the stress is axial, not bending (Morgan and Cannell, 1994), and because the same phenomenon occurs throughout the entire circumference.

The vertical location of peak stress depends on the geometry of the beam, where the load is applied, and whether the force is acting in compression, bending, or torsion (see texts on theory of beam column for analytical solutions, e.g., Chajes, 1974; Chen and Atsuta, 1976, 1977). Leiser and Kemper (1973) modeled bending stress for young trees with wind loads on the canopy, and concluded that stress is maximum in the lowest one-third of the height if the stem is moderately tapered, grading to the very base if the stem is a right cylinder. In actual trees, normal bending stresses are also concentrated at locations where the stem cross-section is eccentric. Within the canopy, bending stresses are concentrated at junctions between

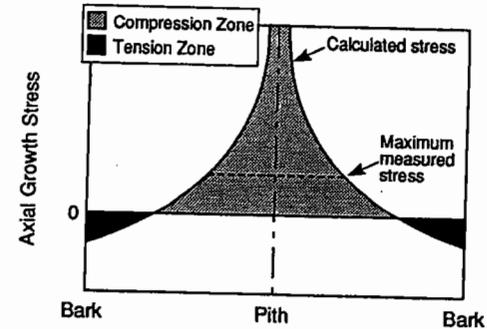
branches or between branches and stems, but some of the hypothetical stress concentration at the branch-stem junction is dissipated by the orientation of the grain (e.g., Mattheck, 1990; Hermanson, 1992).

Options for lowering stresses on the structure (tree) are to decrease the stress encountered or to increase the resistance to the stresses. The first option, decreasing the normal stress encountered, can be accomplished by means such as occupying a less windy site, reducing leaf area to decrease wind or snow load, remaining shorter to project a shorter lever arm, being lighter in weight, or modifying branches to prevent their blowing to one side of the stem, thereby causing a large overturning moment. The second option, increasing resistance to the stresses, can be accomplished by having stiffer material or a greater resisting area (becoming wider).

**2. Radial, Tangential, and Axial Growth Stresses** The maturation of sequential sheaths of xylem cells produces stress in the older xylem along each of the three axes. The static stresses at any location change as the plant grows because that location changes its position relative to the perimeter of the stem. Cell walls can be thought of as fiber-reinforced composites, with cellulose as the fiber and lignin as the matrix. The microfibrils are oriented in helices with distinct angles of ascent in the different cell wall layers (Wardrop and Preston, 1947). These angles, which direct many of the physical properties of wood (Cave and Walker, 1994), are under both environmental and genetic control (Wardrop and Preston, 1950). Mathematical models have shown that the stresses generated during maturation are consistent with the explanation that as cell walls mature, the microfibrils shorten and the matrix between them swells (Archer, 1987). Thus, the orientation of the microfibrils and the quantity of lignin should play major roles in the direction and magnitude of stresses generated.

Tangential stress is tensile at the center of a stem, zero at about half the radius, and compressive at the cambium (Fournier *et al.*, 1994). Radial stress is also tensile at the center of the stem but declines to zero at the cambium (Fournier *et al.*, 1994). Nonetheless, Hejnowicz (1980) shows for both hardwoods and softwoods that the small radial stresses near the cambium facilitate intrusive growth of developing axial cells.

Some species, such as *Eucalyptus* and *Fagus*, develop large axial growth stresses. This condition is well documented because of the nuisance and danger to loggers: during sawing the saw commonly becomes stuck in the stem, and occasionally an enormous longitudinal segment of wood will burst out of the bole. Axial growth stresses are compressive in the center of a woody stem and decline with distance from the pith to become tensile in about the outer third of the radius (e.g., Boyd, 1950; and see Fig. 4). In some species, the maximum compressive stresses near the center of the stem are much lower than those determined from theory (Fig. 4), with the extra stress probably dissipated through viscoelastic creep (Boyd, 1950) and/or minute compression failures (Dadswell, 1958). There are many



**Figure 4** Theoretical distributions of axial growth stress across the cross-section of a tree stem. The dashed line shows maximum measured longitudinal stresses, which are much lower than those calculated from theory. [Modified from Boyd (1950) with permission from the *Australian Journal of Applied Science*.]

ways in which tree stems may fail, but if the first failure occurs on the compressive (downhill) side of the tree, then the growth stresses should act to help trees resist breakage: the tension prestressing will reduce the total compressive bending stress on the downhill side of the tree compared to the case with no such tension prestressing (Boyd, 1950).

Reaction wood relies on the generation of growth stresses and the firm bonding of adjacent cells for its action (Wilson and Archer, 1977). The mechanism of stress generation is thought to be similar to that discussed above for cell maturation in general. Compression wood, on the lower side of a leaning stem, has microfibrils in the S<sub>2</sub> layer of the cell wall oriented at about 45° with respect to the cell axis; normal wood generally has microfibrils at about 10–20° (Dadswell and Wardrop, 1949). The bulking of the cell wall during maturation causes the cells to attempt to elongate (Scurfield, 1973), and concomitantly a tension develops along the microfibrils, also causing cells to attempt to elongate. These processes place a tensile force on the lower side of the stem that will tend to right the stem (Archer, 1987). Furthermore, a small reorientation of the stem can shift the canopy enough such that it has a shorter lever arm and/or is more evenly balanced over the root crown. The generation of compressive forces during cell wall maturation in tension wood derives from the tension generated along the microfibrils (Okuyama *et al.*, 1990; Yamamoto *et al.*, 1993), which are in a near axial orientation (Wardrop and Dadswell, 1955). These compressive forces on the upper side of the leaning stem will tend to pull the stem upright.

There remain many puzzles about reaction wood, normal wood, opposite wood, flexure wood, and the wood of branches vs stems. The lumens of conducting cells are narrower in reaction wood than normal wood, but the increment of wood is wider (Scurfield, 1973); what is the effect on supply

of water to the foliage? Rays and other parenchyma are less abundant in tension wood (Scurfield, 1973); is less parenchyma needed, is the parenchyma more efficient, or is the plant made more vulnerable in some way by its reduced parenchyma volume? Why do some species have a greater tendency to produce reaction wood than others, and what accounts for the numerous patterns of reaction wood, especially in angiosperms (Wilson and Archer, 1977; Panshin and de Zeeuw, 1980)? How much of typical branch wood is actually a type of reaction wood? More research is needed on the incidence, magnitude, generation, and location of normal stresses in stems, their roles in development, and their consequences for the biology of the plant.

### B. Within a Growth Ring

Within-growth ring variation in density will affect mechanics, although the extent to which these variations are important to the biology of a plant is unknown. Trees with distinct annual growth rings have significantly denser latewood than earlywood, even if diffuse-porous (Section II). The seasonal patterns of wood production and density are less understood in plants lacking annual rings. One approach to understanding the functional significance of different patterns of wood within a growth ring is to model wood as a laminate having low and high stiffness areas (corresponding to the earlywood and latewood) to predict modulus of elasticity and zones of failure (reviewed in Bodig and Jayne, 1982). A second approach is to determine empirically the effect of natural variation in anatomy (e.g., proportion of ray or earlywood tissue) on a mechanical property (e.g., modulus of elasticity, maximum stress and strain) of wood when tested in a certain axis (e.g., Schniewind, 1959; Beery *et al.*, 1983; Bariska and Kucera, 1985). These approaches could be used by botanists to gain insights on evolutionary costs or constraints of different wood patterns. Wood technologists have used neither the correlative nor the modeling approach exhaustively, perhaps because most engineering needs are met by tabulated values of allowable strengths based on performance standards. The tables themselves (e.g., U.S. Forest Products Laboratory, 1987) are not directly relevant to tree physiologists because the origin of the wood usually is not stated, and because the values represent moisture contents of in-service lumber (8–15%; mass of water in wood/wood dry mass) rather than moisture contents found in live trees ( $\geq 30\%$ ).

The case of earlywood provides a simple example of a mechanical function of a specialized pattern of xylem cells. Because the earlywood zone has relatively thin cell walls, it contributes little to the axial strength of wood (Dinwoodie, 1975). Earlywood has a lower tensile axial breaking strength than does latewood, and earlywood fails brashly (perpendicular to the cell axis), breaking the cells, whereas latewood failures are jagged, following a

path between cells, such that few cells break (Kennedy and Ifju, 1962; Nordman and Qvickström, 1970).

A second example of mechanical function related to the pattern of xylem cells comes from research on lianas. Müller (1866, as cited in Haberlandt, 1914, pp. 690–696) hypothesized that the cable-like construction of some lianas, in which longitudinal strands of conducting tissue are separated from one another by parenchyma, makes use of the different strengths of these tissues, with parenchyma acting as padding for the conducting tissues should the liana sway (by wind) or fall (by failure of its external support). In support of this hypothesis, Putz and Holbrook (1991) found that liana stems withstood much more torsional stress (they could be twisted through more revolutions) before water stopped flowing than did tree stems of similar diameter. A quick glance through an atlas showing cross-sections of diverse dicotyledonous woods (e.g., Schweingruber, 1990; Ilıc, 1991) or the Obaton (1960) treatise on “anomalous” patterns in wood production in lianas demonstrates the plethora of xylem patterns. Our understanding of the functional significance of any of these patterns is almost nil.

### C. From Pith to Bark

The radial gradient in xylem density appears to fall into several different patterns. It is unknown whether the typical pattern of a species results from selection for some biomechanical and/or hydraulic optimum, whether it is a plastic response to the changing environment perceived by the changing plant, or whether it is developmentally controlled but unrelated to selection for mechanics or hydraulics. The general pattern for hard pines, *Larix*, *Pseudotsuga*, and the mid- to high-density diffuse-porous hardwoods is low-density wood near the pith, with an increase in density for some number of years, and then a leveling off or a decline in the rate of increase (summarized in Panshin and de Zeeuw, 1980, and Zobel and van Buijtenen, 1989). Many tropical hardwood species appear to have lower density near the pith than those from temperate zones, while attaining similar densities to temperate-zone species in the outer wood (Wiemann and Williamson, 1989; Butterfield *et al.*, 1993). With this pattern, the core wood is weaker in tension and compression and more flexible (lower modulus of elasticity) than outer wood.

*Tsuga heterophylla* and some of the low-density diffuse-porous hardwoods such as *Populus* tend to have highest density at the pith with a gradual decrease toward the bark. For softwoods in the Cupressaceae and most soft pines the general pattern is high density near the pith, a dip in density for several growth rings, and then an increase again to a constant or slowly increasing value (Panshin and de Zeeuw, 1980; Zobel and van Buijtenen, 1989).

Many vines have a fourth pattern, that is, production of denser wood

where they are self-supported and less dense wood around this dense core once they find support (Haberlandt, 1914; Carlquist, 1991; Gartner, 1991a). Ring-porous hardwoods often show the same pattern as do vines, caused by outer wood having a higher proportion of the growth ring occupied by wide vessels (summarized in Zobel and van Buijtenen, 1989). Last, some diffuse-porous tree species such as *Alnus rubra* appear to have no change in density with age (Harrington and DeBell, 1980) or growth rate (H. Lei and B. L. Gartner, unpublished data).

Models on mechanical trade-offs of stem width and wood density (see Givnish [1] in this volume) in tandem with models on the effects of density and stem width on water conduction could help explain the range of wood densities and stem widths in nature. A small decrease in wood density may result in a small decrease in the ability of a stem to resist compression and bending (e.g., Gartner 1991b), but a large increase in specific conductivity (Gartner, 1991a). Such a negative correlation between sapwood  $k_s$  and wood density has been reported for *Pinus radiata* (Booker and Kininmonth, 1978).

The several percent higher density of heartwood than sapwood that results from deposition of secondary compounds should have no direct effect on the mechanics of the live tree. However, the secondary compounds make the heartwood more resistant to decay. A solid stem (i.e., interior not decayed) is more stable than a hollow one, particularly if the outer layer is O shaped rather than C shaped (broken; Ch. 9 in Chen and Atsuta, 1977). Thus, one mechanical justification for protection of heartwood from decay is that heartwood provides mechanical stability in case the sapwood layer becomes disrupted.

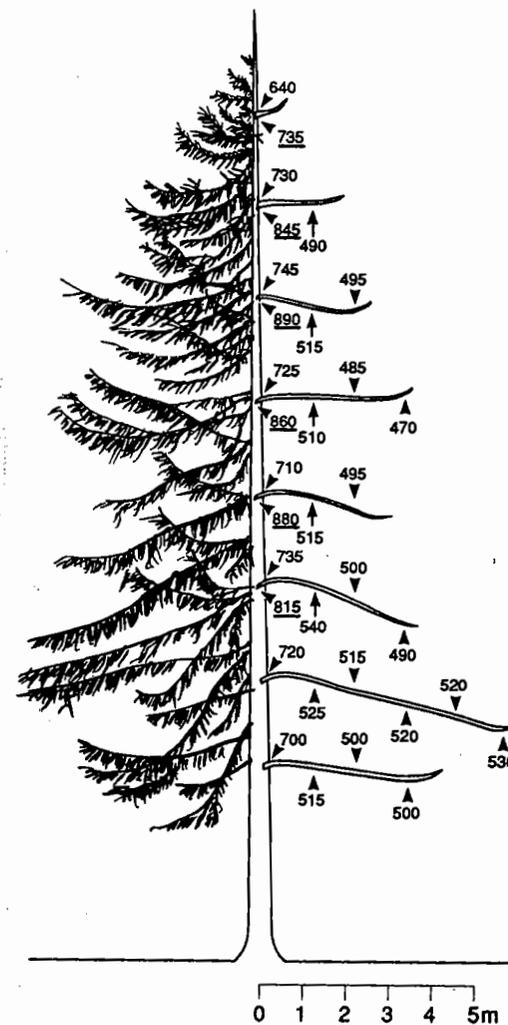
#### D. From Root to Crown

The pattern of xylem density from the base to the tip depends mainly (but not always entirely) on the pattern found from pith to bark because the vertical profile reflects the simultaneous production of outer wood at the base (if a plant is old enough) and core wood at the tip. In hardwoods, the magnitude of density variation with height is relatively low compared to softwoods (Zobel and van Buijtenen, 1989). Descending the stem within the growth ring produced in the same year (Fig. 2, transect C), density of hardwoods can decrease (as in a ring-porous species), increase, or increase and then decrease. The common pattern for hard pines and *Pseudotsuga* is greater density at the base than the tip (Panshin and de Zeeuw, 1980; Zobel and van Buijtenen, 1989). Denser wood at the base of a stem, together with the widening of the stem base that is often observed (butt swell), can contribute to mitigating the stress concentration there.

#### E. Between Stems and Branches

Branches often have denser wood than do stems (Fegel, 1941; and see Table I), meaning that branch material is stronger on a volumetric basis

than stem wood. At least in softwoods, larger diameter branches have higher density than smaller-diameter ones, branches have higher density near their base than toward their tip, and knots have very high density (Fig. 5) (Hakkila, 1969). The presence of reaction wood at branch junc-



**Figure 5** Variation in wood density ( $\text{kg}/\text{m}^3$ ) within and between branches in *Picea abies*. Along one branch, density is highest at the knot (the junction of branch and main stem; underlined values) and decreases toward the branch tip. Between branches, density is highest in large, more basal branches. [Modified from Hakkila (1969) with permission from the Finnish Forest Research Institute.]

tions may partially explain the lower  $k_s$  value there than in normal wood, although reaction wood is not always present at branch junctions.

## V. Conclusions

Xylem in stems and branches is constructed of nonuniform material that is systematically distributed throughout a plant. In some cases, the nonuniformity allows the material to function mechanically and hydraulically in manners appropriate to its location such that it contributes to the success of the plant. Different aspects of the variation are probably controlled by the environment, cambial age, distance from the leaves, physiological status of the plant, and even plant size, for size may contribute to the scale of environmental fluctuations that the plant senses. This chapter has emphasized optima for mechanics and hydraulics separately, but the trade-offs between the two (Long *et al.*, 1981; Gartner, 1991a) must be considered more fully. In the ranges of wood densities and water demands that plants have, we do not even know whether there are trade-offs between mechanics and hydraulics, partly because one must define the hydraulic and mechanical criteria in order to try such analyses.

Little is known about the effect on plant function of different combinations or patterns of xylem cell types (e.g., vessel groupings or parenchyma banding in relation to vessels). Baseline surveys of ecological wood anatomy provide starting points for experimental work on relationships between wood structure, environment, and growth form. For example, in different regional floras it has been reported that vines tend to have more paratracheal parenchyma than do trees (Carlquist, 1991), shrubs have more vessels per grouping and a higher incidence of vasicentric tracheids than do trees (Carlquist and Hoekman, 1985), and shrubs are less commonly ring-porous than are trees (Baas and Schweingruber, 1987). What clues do these patterns give us to relate structure to function, and physiology to habitat and population biology? What are the most common xylem patterns in areas that are arid (Lindorf, 1994), have frequent freeze-thaw cycles, have short growing seasons, are subject to frequent fires, have cyclic herbivore outbreaks? How does the wood compare in congeners that are drought deciduous, evergreen, and winter deciduous? How does ramet demography relate to xylem anatomy: do short-lived stems have throw-away xylem strategies compared to long-lived stems? Are there syndromes of bark/xylem anatomy? Thin-barked species may be more susceptible to physical and biotic injury to the sapwood; do these species tend to have more parenchyma or other xylem adaptations to mitigate damage?

Experimental research is beginning to elucidate the physiological, ecological, and structural roles of stem xylem. Like the roots, leaves, and flow-

ers, the stem profoundly influences the biology of the plant. Further studies in the physiological ecology of wood can impart new insights into areas such as physiology, plasticity, demography, and patterns and dynamics of architecture. Such research will also benefit efficient production and utilization of forest products, manipulation of woody crops, and management of forested lands.

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