

# Vascular Transport in Plants

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## Structure-Function Relationships in Sapwood Water Transport and Storage

Barbara L. Gartner and Frederick C. Meinzer

Primary production by plants requires the loss of substantial quantities of water when the stomata are open for carbon assimilation. The delivery of that water to the leaves occurs through the xylem. The structure, condition, and quantity of the xylem control not only the transport efficiency but also the release of water from storage. For example, if there is high resistance to water flow in the stem, then less water is available to the leaves, so less primary production can occur. High resistance can result from wood material with low conductivity, from having only a small amount of conductive wood, or from having very slow release of stored water to the transpiration stream. The subject of this chapter is the efficiency with which different parts of the sapwood transport, store, and release water, and how the structure of the wood affects these processes. Particularly, we describe the radial patterns of axial water transport, their anatomical and physiological causes, the effect that sapwood width and wood structure, especially density, have on water transport, and determinants of sapwood water storage properties.

We define sapwood as the xylem that is conductive to water, although sapwood can also be defined on the basis of color, respiration, and parenchyma vitality. Although our discussion refers to sapwood versus heartwood, many species also have intermediate wood, which is located between the sapwood and heartwood, and is said to have intermediate characteristics (Hillis, 1987). However, some intermediate woods may not have living cells (Hillis, 1987), and more research is needed to delineate which functions are still active in this zone for different species. Likewise, wood has a variety of types, but for simplicity we discuss only three: coniferous, and angiosperm ring-porous and diffuse-porous. These classifications capture much of the interspecific variation in gross wood structure in the temperate and arctic zones, but because most tropical species are

diffuse-porous and have extremely variable vessel groupings and/or parenchyma patterns, additional classifications may be more useful for tropical woods.

### Radial Changes in Wood Anatomical Characteristics and Hydraulic Properties

The anatomy of the wood follows systematic patterns of variation that depend on the ring number outward from the pith, the height in the tree, and the radial growth rate. Also, because the xylem transports water for several years, there may be changes in its water transport properties as the cells age. This section describes these basic patterns of wood anatomy, focusing on radial variation, and how they affect the hydraulic conductivity of sapwood.

#### Within-Bole Patterns of Wood Anatomy and Properties

In all woody plants, the anatomy of wood changes systematically along a radial (pith-to-bark) direction. The magnitude of the changes depends on the species and the type of wood (e.g., diffuse versus ring-porous). Superimposed on this variability is that caused by environmental factors such as the amount and timing of rainfall and temperature. The most obvious change to the naked eye is the pith-to-bark decrease in growth ring width. At the base of the tree, the first several rings near the pith are usually narrow, produced when the tree was growing slowly while becoming established. Beyond that zone, the rings are wide, then gradually become narrow, associated with slower growth and/or with having a larger cylinder around which to place the new wood produced by a constant-sized crown (Duff and Nolan, 1953). Depending on the species, the percentage of latewood within each ring can increase (common in conifers), decrease (common in ring-porous species), or stay the same with increasing cambial age. Diffuse-porous species are special cases because they have weaker anatomical gradients across the growth ring, so the pith-to-bark changes in growth rate probably have less of an effect on their anatomy.

The second type of radial change in wood structure is referred to as the juvenile/mature wood transition. Juvenile wood (JW) denotes the wood adjacent to the pith. Its properties (anatomical, mechanical, hydraulic, chemical composition) change dramatically from one growth ring to the next (Larson *et al.*, 2001; Senft *et al.*, 1985). In contrast, the properties of mature wood (MW) are relatively constant from ring to ring (if environment remains constant). The extent of the JW zone (in number of growth rings from the pith) depends largely on genetics (Zobel and Sprague,

1998). The juvenile wood zone is usually better correlated with number of growth rings than with distance from the pith (Zobel and Sprague, 1998). In conifers, JW may persist well past 100 years from the pith (Wellwood *et al.*, 1974), but in general the overwhelming majority of the total change will have occurred in the first 10 to 20 years. Most properties either increase or decrease extremely quickly and then reach an asymptote. The radial pattern can be somewhat different with vertical position, but changes with height for the same cambial age are usually small compared to the changes with cambial age at the same height.

In all woody plants studied, the JW shows a gradual increase in the length of the tracheids and/or libriform fibers, usually accompanied by an increase in their diameter with increasing tree age (Zobel and Sprague, 1998). The magnitude of this and other anatomical changes is much higher in gymnosperms than in angiosperms (Panshin and deZeeuw, 1980). For example, in *Pseudotsuga menziesii*, tracheid length increases from 1 to 5 mm from growth rings 2 to 25 (Megraw, 1985) and earlywood tracheid diameter increases from 22 to 40  $\mu\text{m}$  over the same age interval (Spicer and Gartner, 2001). In the ring-porous oak *Quercus garryana*, tracheid length increases from 1.0 to 1.2 mm and earlywood vessel diameter increases from 150 to 250  $\mu\text{m}$  from growth rings 2 to 25 (Lei *et al.*, 1996). Diffuse-porous species have similar increases in cell length and diameter as ring-porous ones.

In diffuse-porous angiosperms, the other radial changes are highly species-specific. As a general rule, their wood has the most constant pith-to-bark properties of any wood type. For example, red alder (*Alnus rubra* Bong) shows no significant change in wood density across the radius (Gartner *et al.*, 1997; Harrington and DeBell, 1980) or at radial growth rates that vary by a factor of 5 (Lei *et al.*, 1997). There may be some difference in the proportion of the growth ring that is vessel, libriform fiber, and parenchyma, and there can be modest increases in vessel diameter (e.g., Lei *et al.*, 1996).

In contrast to diffuse-porous species, ring-porous angiosperms have more significant changes in their wood from pith to bark. In general, these species maintain a similar earlywood width, with the decrease in ring-width at the expense of latewood (Phelps and Workman, 1994; Zhang and Zhong, 1991). Thus, in contrast to the conifers, wood density decreases and proportion of vessel area increases through the JW to the MW.

In conifers, significant changes in wood structure from the JW to MW also include a tendency toward having a higher latewood proportion, thicker cell walls in the earlywood and latewood, denser wood (mostly due to denser latewood) and a change in the cell wall ultrastructure: Microfibrils within the S2 layer decrease from 45 degrees (with respect to axial) in the JW to about 5 degrees in the MW (Larson *et al.*, 2001). The combination of a

decrease in microfibril angle and an increase in wood density result in wood that is stronger and stiffer axially in the MW than in JW. The increase in earlywood cell length and diameter and the increase in latewood proportion probably have the largest effect on hydraulics.

Within the mature wood, if the environment stays the same, the wood made in 1 year is similar to the wood made in a previous year. The exception is that in trees that are declining because of environmental degradation, disease, or very old age, the new wood can be different. For example, in *Abies alba*, declining trees had latewood zones of 1 to 2 rows, compared to a broad zone in healthy trees, and the cell wall thickness of the latewood in the declining trees tended to be lower (Schmitt *et al.*, 2003). In *Pinus mugo*, two types of root pathogen caused a decrease in growth ring width compared to uninfected individuals, but the decrease was gradual in trees infected with one type and abrupt for the other. (Cherubini *et al.*, 2002). No data were given on whether earlywood proportion or any of the cell structures were altered as the growth ring widths decreased. In the forest products industry, it is known that very old trees can have much reduced wood density in their outer rings (i.e., Wellwood *et al.*, 1974).

As the wood progresses from being outer to inner sapwood, its properties may change. The outer sapwood of MW may differ from inner sapwood in having a higher percentage of living parenchyma cells (reviewed in Gartner *et al.*, 2000), fewer cells blocked by tyloses (Cochar and Tyree, 1990), and fewer incrustated or aspirated pits (Mark and Crews, 1973; Nobuchi and Harada, 1983). The rates of change with xylem age are species- and property-specific.

Another potential difference is moisture content. There are many individual reports of moisture content variation across the radius. For example, ring-porous species are reported to have saturated earlywood vessels only in the outer growth ring, with the earlywood being embolized in older rings (Cochar and Tyree, 1990; Ellmore and Ewers, 1985; Granier *et al.*, 1994). However, the most comprehensive compendium is for the trees of Bulgaria: Nikolov and Enchev (1967) reported moisture content every centimeter across the north-south transect of the stem xylem for 12 coniferous species and 33 hardwood species. About half of the coniferous species had very constant moisture content across the sapwood, with an abrupt decrease in the heartwood (e.g., *Abies alba*, *Pinus nigricans*, and some individuals of *Pinus sylvestris*). The other coniferous species had a decline in moisture content, often close to linear, from the outer to the inner sapwood (e.g., *Juniperus excelsa*, *Taxus baccata*, *Pseudotsuga menziesii*, *Larix europaea*, and *Pinus strobus*). It was more difficult to discern the sapwood moisture content patterns in the hardwoods because it is not always clear where the sap/heart boundary is from inspection of the moisture contents. Roughly half of the species had relatively constant moisture contents across

what appeared to be the sapwood (e.g., *Quercus*, *Fraxinus*, *Celtis*, *Aesculus*). The remaining hardwoods had a variety of moisture content patterns in the sapwood, such as a gradual (*Fagus sylvatica*, *Populus*, *Alnus glabrosa*) or steep (*Robinia pseudoacacia*) decrease, or a gradual (*Ailanthus*) or steep (*Gleditsia*) increase in ring porosity versus diffuse porosity. Using both soft x-ray and cryoscanning electron microscopy, Utsumi *et al.* (2003) have shown in several conifer species (*Picea jezoensis*, *Larix kaempferi*, and *Abies sachalinensis*) that the outer ring has higher moisture content than do the inner growth rings. Similarly, Lu *et al.* (2000) showed that the outer growth ring in the angiosperm *Mangifera indica* had higher moisture content than did the other growth rings.

#### Effects of Wood Anatomy and Characteristics on Specific Conductivity

Specific conductivity ( $k_s$ ) is usually higher in the outer than the inner sapwood. As discussed here,  $k_s$  refers to the water volume per time that will pass a unit cross-sectional area of sapwood with a given pressure gradient across it. The higher  $k_s$  in outer than inner sapwood can be caused by differences in wood structure associated with a decline in radial growth rate or JW/MW changes, and/or from blockages that accumulate in the inner sapwood as it ages. The total sap flow depends on both  $k_s$  and sapwood width (see next section).

In MW, the effect of radial growth rate on  $k_s$  depends on its effect on latewood proportion. The changes in wood structure that result from the typical decrease in radial growth rate with age may be confounded with the changes occurring in the JW zone. In a study of *Pseudotsuga menziesii*,  $k_s$  was positively correlated with height growth, but there was no correlation with diameter growth (Domec and Gartner, 2003).

In diffuse-porous hardwoods, MW should have higher  $k_s$  than JW because of the gradual increase in earlywood vessel diameter (Zimmermann, 1978) and the direct relationship between flow and radius to the fourth power. In ring-porous hardwoods, increases in  $k_s$  toward the bark are caused by two factors: the increase in earlywood vessel diameter and in the decrease in latewood proportion. In hardwoods, the longer cells in MW than JW should have only a negligible effect on  $k_s$  because water moves primarily through the perforations at the ends of vessels (rather than pits), and the perforations contribute less to flow resistance than do pits. In gymnosperms, MW is expected to have higher  $k_s$  than JW both because the tracheids are wider and because they are longer. These factors more than compensate for MW's lower earlywood proportion (Mencuccini *et al.*, 1997). Tracheid length is important if a large part of the hydraulic resistance is associated with pit membranes (Petty and Pritch, 1970; Pothier *et al.*, 1989). Water must traverse twice as many pit membranes per meter of stem if the tracheids are half the length.

Because there are no development-caused differences in the anatomy of wood produced from year to year within the MW, outer sapwood should not vary in  $k_s$  from year to year. However, there is usually a decline in  $k_s$  from outer to inner sapwood, in spite of the lack of changes in the cellular structure. This decrease has been observed in conifers (e.g., Booker and Kinimonth, 1978; Constock, 1965; Domec and Gartner, 2001, 2002a; Markstrom and Hann, 1972; Spicer and Gartner, 2001) and ring-porous species (Ellmore and Ewers, 1985; see Granier *et al.*, 1994). We do not know of research on diffuse-porous species. One study showed that the pits were "immature and nearly imperforate" in the outer sapwood (Mark and Crews, 1973), from which one would predict lower  $k_s$  in the outer sapwood, with an increase inward. To our knowledge, no other research followed up the study by Mark and Crews.

The most likely cause for these declines is a higher incidence of blockages in the inner sapwood. These blockages could be in the form of air (emboli) and/or gums, resins, etc. (extractives). Indirect evidence that inner sapwood may have more embolisms than outer sapwood is found in the studies that show lower moisture content in inner than outer sapwood (above). Decrease in relative water content is associated with a decrease in  $k_s$  (Edwards and Jarvis, 1982; Pritch, 1971) and sap flow (Granier *et al.*, 2000). Because extractive content influences heartwood durability, nearly all research on extractives has focused on heartwood rather than sapwood. One article on pit membranes, however, reported an increase in membrane incrustation from outer to inner sapwood (Mark and Crews, 1973).

#### Patterns of Sapwood Width

Generally, in both conifers and hardwoods, sapwood width is positively correlated with tree health, vigor, crown class, or radial growth rate (Brix and Mitchell, 1983; de Kort, 1993; Hillis, 1987; Lassen and Okkonen, 1969; Sellin, 1996; Smith *et al.*, 1966). The tree's design criteria for sapwood quantity are unclear because although the pipe model and its modifications often explain sapwood quantity (Margolis *et al.*, 1995; Whitehead *et al.*, 1984), in many cases they do not (e.g., Gartner, 2002). The relationships are stronger between growth rate and sapwood width than between growth rate and number of rings in sapwood. That is, the amount of wood needed for physiological processes is independent of how that wood was developed.

There is little research on the width of sapwood in relation to stem age. In some species, sapwood width of individuals within similar environments is very constant. Examples are the genus *Eucalyptus* (Hillis, 1987) and the species *Pseudotsuga menziesii* (Brix and Mitchell, 1983), although it should be noted that in *P. menziesii*, the sapwood is wider in the bottom meter (Gartner, 2002), and that when the trees are several hundred years old, the sapwood width diminishes (BLG, personal observation). In contrast, in

some species, sapwood width increases with tree age. For example, in *Picea*, the sapwood width increases until the cambium attains an age of between 20 and 90 years, depending on species and dominance class of the trees (Hazenbergh and Yang, 1991; Sellin, 1996).

### How Species-Specific Characteristics of Sapwood Affect Whole-Tree Water Transport

Many of the radial and developmental changes in sapwood anatomy, structure, and hydraulic properties described in the previous section are largely species-specific and are expected to have an impact on spatial patterns of water movement within the sapwood. For example, radial profiles of axial flow may be associated with species-specific differences in hydraulic architecture that determine the nature of hydraulic connections between leaves and different layers of sapwood. Here we discuss how species-specific variation in fundamental traits such as hydraulic architecture and sapwood quantity, water storage capacity, and density influence water transport within the tree.

#### Sapwood Quantity

It is common knowledge that the sapwood cross-sectional area for a given stem diameter varies widely among tree species. For individuals with stem diameters from 0.5 to 1.0 m, radial sapwood depth can range from less than 6 cm in species such as *Eucalyptus regnans* (Wullschlegel *et al.*, 1998) and *Pseudotsuga menziesii* (Phillips *et al.*, 2002), to 10 to 20 cm in *Pinus ponderosa* (Domec and Gartner, 2003), and greater than 20 cm in a number of tropical species (James *et al.*, 2003; Meinzer *et al.*, 2001). Despite its implications for rates of whole-tree water use and sap flow per unit sapwood area (sap flux density), the consequences of this wide variation in sapwood area among trees of similar size remain largely unexplored. However, improvements in techniques for measuring sap flow have facilitated determination of the detailed radial profiles of axial flow necessary to analyze how different relationships between sapwood area and tree size among species influence water transport at different scales (e.g., James *et al.*, 2002; Jiménez *et al.*, 2000).

Plant vascular systems, and therefore water use, have been proposed to scale allometrically as power functions of body mass or size (West *et al.*, 1999):

$$Y = Y_0 M^b \quad (1)$$

where  $M$  is mass,  $b$  is a power exponent, and  $Y_0$  is a normalization constant. Although exhaustive tests of the universality of this model have yet to be conducted, it is supported by some empirical data on plant water