

# HEARTWOOD FORMATION AND NATURAL DURABILITY— A REVIEW

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(Received April 2002)

## ABSTRACT

This paper reviews recent literature on the formation of heartwood and on the components that affect natural durability. It includes discussion about the function of heartwood in living trees, factors influencing the natural durability of heartwood, the process of heartwood formation, and variations in heartwood quantity and quality. Heartwood formation is a regular occurrence in tree stems, and heartwood may have many different properties from sapwood, including natural decay resistance. A greater understanding of the heartwood formation process could allow control of heartwood production. Recent research involving enzymatic analyses have provided valuable insight into the biochemical processes involved in heartwood formation. Further study of the role natural durability plays in living trees would help to bring together many of the disparate strands of research relating to heartwood.

*Keywords:* Decay resistance, extractives, heartwood, natural durability, sapwood.

## INTRODUCTION

Heartwood is a normally occurring part of the xylem in trees. Heartwood has properties that can significantly influence its usefulness to the end user of wood products; notable among these is natural resistance to deterioration by insects, marine borers, and microorganisms. Understanding the formation of heartwood in trees may ultimately allow foresters to influence the heartwood formation process by using various silvicultural practices. It may also enable forest geneticists to enhance durability through selection and/or molecular biological techniques.

This review builds upon the reviews of

Scheffer and Cowling (1966), Bamber and Fukazawa (1985), and Hillis (1987). In this review, we emphasize recent literature relating to the function of heartwood in the tree, the process of heartwood formation, and the factors that influence heartwood formation, while building upon previous reviews.

## THE FUNCTION OF HEARTWOOD AND SAPWOOD IN TREES

It is important to consider wood quality in terms of wood as part of a living tree (Larson 1962). Thus, in order to understand heartwood formation and how it can be modified, it is first important to comprehend the role of heartwood and sapwood in the tree.

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Anatomists [IAWA] defines heartwood as "the inner layers of the wood, which, in the growing tree, have ceased to contain living cells, and in which the reserve materials (e.g., starch) have been removed or converted into heartwood substance" (IAWA 1964, p. 32). In some species, heartwood may be distinguished from sapwood by a darker color, lower permeability, and increased decay resistance. Heartwood often has different moisture content than sapwood; in conifers heartwood is usually drier than sapwood, but the relative moisture contents of the two regions in hardwoods are species specific (see Table 3.3 in USDA-FS Forest Products Laboratory 1999).

Heartwood is formed in gymnosperm and angiosperm tree species, although in some cases it may be difficult to detect (e.g., *Abies* spp.) or may only develop in very old sapwood (e.g., *Alnus* spp.) (Panshin and de Zeeuw 1980). The presence of heartwood may optimize sapwood volumes, conserve resources, and provide structural support.

Sapwood is defined by the IAWA (1964) as "the portion of the wood that in the living tree contains living cells and reserve materials" (IAWA 1964, p. 43). It contains the wood that is part of the transpiration stream of the tree, and it generally has high moisture content. Sapwood also contains energy reserve materials such as starch. Its permeability is facilitated by the presence of unspirated, unencrusted pits. Sapwood contains few toxic extractives and is generally susceptible to decay.

The primary role of sapwood in a tree is to conduct water from the roots to the crown (Gartner 1995). According to the pipe model (Shinozaki et al. 1964), sufficient sapwood is required to supply the foliage with water, and the amount of foliage on a tree often is strongly correlated to the amount of sapwood (Berthier et al. 2001; Ryan 1989; Dean and Long 1986; Whitehead et al. 1984).

Sapwood also serves as a storage site for water and for energy reserve materials such as starch (Hillis 1987; Ryan 1989), and as a site for living cells that can respond to injury through production of more tissue or defensive

compounds (Boddy 1992). However, there are also costs associated with maintaining sapwood in a tree. Living parenchyma cells respire and consume considerable amounts of "maintenance" energy [an estimated 5%–13% of annual net photosynthate in some species (Ryan et al. 1995)]. In addition, energy stored in sapwood parenchyma may be utilized in response to injury (Shain 1995). Thus, it may be hypothesized that sapwood in excess of the amount required to satisfy foliar demands is converted to heartwood to decrease energy demands.

Sapwood permeability is also a factor in the balance between the amount of foliage and sapwood. The concept of a "homeostatic balance" between these parameters has led people to speculate that the modification of one variable (e.g., leaf area) might result in changes in sapwood area (Margolis et al. 1988; Whitehead et al. 1984).

The "transition zone" between heartwood and sapwood has been defined as "A narrow, pale-colored zone surrounding some heartwoods and injured regions, often containing living cells, usually devoid of starch, often impermeable to liquids, with a moisture content lower than the sapwood and sometimes also than the heartwood" (Hillis 1987, p. 16). This zone is also known as the "white zone" and "dry zone" (Nobuchi and Harada 1983). This zone is not apparent in all species, nor is it always observed in those species in which it occurs (Hillis 1987). The IAWA (1964) defines "intermediate wood" as "The inner layers of the sapwood that are transitional between sapwood and heartwood in color and general character" (IAWA 1964, p. 46). The term, "intermediate wood" is often confused with, or used interchangeably with, the term "transition zone" (Hillis 1987).

"Extractives" is a term used to describe the nonstructural compounds present in wood. The term originates from the fact that many of these substances can be removed with neutral, organic solvents or water (Sjostrom 1993). However, Gang et al. (1998) point out that "extractives" may be a misnomer, be-

cause, in some cases, phenolic compounds present in heartwood are not easily removed.

#### *Structural support*

Wood properties, including density, vary from pith to bark (Panshin and de Zeeuw 1980). Wood density in conifers generally increases with distance from the pith. Hardwoods are more variable; density increases with distance from the pith in some, and remains unchanged or decreases in others. Strength is closely correlated with density; thus strength differences may exist between heartwood and sapwood. However, heartwood does not differ structurally from sapwood; any significant strength differences result from radial changes in wood density and cell wall ultrastructure, not from whether the sample is heartwood or sapwood, per se (Panshin and de Zeeuw 1980).

If the structure of a tree is considered to be a cantilevered cylinder, then the highest tensile and compressive stresses will occur in the outer growth rings. Thus, heartwood is less important than the sapwood for structural support. Indeed, it is not unusual to observe hollow trees that have stood for many years. However, there are indications that heartwood is necessary for structural support. Long et al. (1981) found that sapwood cross-sectional area was more or less constant below the crown of *Pseudotsuga menziesii* trees. They concluded that this sapwood was insufficient for the mechanical support of older trees, and that the additional xylem contained in the heartwood provided the necessary compressive strength. Mattheck (1995) showed that hollow trees will break only when the outer shell of wood is less than one-third of the total radius. Heartwood may compose part of this critical wood shell in thinner sapwood species. Mencuccini et al. (1997) found that heartwood made little contribution to the stiffness of *Pinus sylvestris* stems. However, this tree species maintains relatively thick sapwood bands, which would minimize the mechanical role of heartwood. Heartwood would extend farther

from the neutral axis in trees with thinner sapwood, and would be composed of more of the stronger, mature wood, simply because of radial changes in wood properties.

#### *Recycling nutrients*

A variety of species recycle nutrients from newly forming heartwood back into sapwood, in a process likened to nutrient resorption from senescing leaves (Bamber and Fukazawa 1985). Recycled nutrients can represent a significant nutrient source; Attiwell (1980) calculated that heartwood conversion supplied 31% of the entire phosphorous demand of *Eucalyptus obliqua* trees.

Andrews et al. (1999) studied nutrient recycling in the sapwood and heartwood of *Chamaecyparis thyoides* and found that nutrient levels in sapwood of trees growing on sites with lower soil nutrient concentrations were maintained at levels comparable with more nutrient-rich sites. Heartwood was relatively low in these elements in trees on nutrient-poor sites. Thus, heartwood formation may allow trees to concentrate nutrients in sapwood.

#### *Repository for toxic substances*

Stewart (1966) suggested that heartwood forms in response to a build-up of toxic by-products of metabolism. Death of the parenchyma cells in the heartwood could result from the build up of these toxins. For example, cambial cells are negatively affected by trace amounts of tannins (a common heartwood extractive) (Jacquiot 1947). Indeed, Carodus (1971) measured high levels of carbon dioxide (a waste product of respiration) in xylem, indicating that a build-up of respiratory wastes occurs in this zone.

However, *in-situ* formation of new chemical compounds at the sapwood/heartwood boundary, observations of the patterns of heartwood development, and the low toxicity of some heartwoods suggest that heartwood does not function primarily for waste storage (Bamber and Fukazawa 1985).

#### FACTORS INFLUENCING THE NATURAL DURABILITY OF HEARTWOOD

"Natural" durability is commonly measured by exposing wood to decay fungi under accelerated conditions (e.g., ASTM 1993), although wood may also be tested for resistance to termites, beetles, and marine borers. The natural durability of sapwood is generally low, but the heartwood of some species can be very resistant to biodeterioration. There are also variations in natural durability between and within the heartwoods of individual trees, as will be discussed later.

Living sapwood has active and passive defense mechanisms. Active defenses are those that are induced by an attack or wound, while passive defenses are produced prior to infection. The CODIT concept has been proposed to describe the patterns of active and passive defenses in trees (Shigo 1984). When heartwood forms, death of the parenchyma eliminates the active defenses (Shain 1995), leaving only passive mechanisms of resistance to pathogens.

#### *Extractives*

Toxic extractive compounds in heartwood are recognized to be the most important factor in determining the natural durability of wood (Bamber and Fukazawa 1985; Hillis 1987; Scheffer and Cowling 1966). Durable wood from which extractives are removed becomes susceptible to decay (Scheffer and Cowling 1966; Smith et al. 1989). Similarly, adding heartwood extractives to normally decay-prone wood can render it decay-resistant (Kamden 1994; Onuorah 2001; Smith et al. 1989).

However, extractive concentrations in heartwood do not necessarily correspond to natural durability, as measured by standard methods (Kumar 1971; Hillis 1987). In some cases, decay resistance is poorly correlated with variations in the heartwood compounds that are largely responsible for preventing decay (DeBell et al. 1999; Hillis 1987). In other cases, extractives exhibit activities that are spe-

cific to the organisms that normally attack the living tree (Etheridge 1962; Ohsawa et al. 1992; Wilcox 1969). In addition, some durable heartwoods may contain multiple low-toxicity extractive compounds that interact synergistically (Schultz et al. 1995; Shultz and Nicholas 2002). Finally, some species (e.g., *Larix* spp.) produce large amounts of extractive material that apparently provide little or no protection to the wood (Srinivasan et al. 1999).

Whereas total extractive content in a species is correlated with decay resistance, the micro-distribution of extractives also influences performance. Extractives that are impregnated into the cell wall are more effective in deterring microorganisms than are those in the cell lumen (Hillis 1987; Kleist and Schmitt 1999).

The structure, toxicity, and specificity of various heartwood substances have been extensively studied (e.g., Anderson et al. 1962, 1963; Fitzgerald and Line 1990; Freydl 1963; Hart 1981; Hillis 1972, 1987; Kumar 1971; Ohsawa et al. 1992; Rao 1982; Rowe and Connor 1979; Rudman 1963; Scalabert 1991; Scheffer and Cowling 1966; Schultz et al. 1990, 1995). The micro-distribution of extractives has received less attention, largely because of the difficulty of accurately assessing extractive content in situ.

#### *Reduced attractiveness to decay organisms*

Heartwood may be less attractive than sapwood for some pathogens simply because it lacks the requisite nutrients, or because the nutrients it contains may be less accessible (Scheffer and Cowling 1966). For example, starch is required for the successful reproduction of *Lyctus* beetles in wood (Parkin 1938; Humphreys and Humphreys 1966; Wilson 1933). These insects rarely attack heartwood, which is free of starch. Sapstain and mold fungi feed on free sugars and starch in the sapwood, and their penetration into heartwood may be limited, in part, by the absence of readily assimilable carbohydrates (Findlay 1959). Wilson (1933) observed that sapwood with less starch suffered less discoloration.

Similarly, Taylor and Cooper (2002) found that sapstain and mold fungi did not grow as well on *Pinus resinosa* sapwood with reduced starch content as on sapwood with normal amounts of starch.

#### *Mechanical barriers*

It also is logical to suppose that mechanical barriers to attack may prevent or slow wood decay in some species by physically blocking the penetration of insects or fungal hyphae. For example, aspirated and encrusted pits are also a feature of heartwood. Although wood-destroying fungi are capable of moving through pit membranes, aspirated pits reduce moisture movement, slowing wetting and presumably creating conditions less conducive to decay.

Verrall (1938) concluded that the resin exuded in response to wounding of *Pinus resinosa* reduced the risk of decay by its water repellency, rather than by inherent toxicity. DeVries and Kuyper (1990) suggest that decay resistance in *Taxus* spp. was determined more by physical characteristics (longitudinal permeability) than by its chemistry. Extractives clearly make important contributions to the natural durability of wood; however, the relative importance of extractives (like gums) as mechanical barriers vs. in their other roles (relating to toxicity, wettability, etc.) is poorly understood.

Tyloses are another factor that may impede wood decay. They are a regular feature of heartwood vessels in many hardwood species, but they also occur in the sapwood of these species and in some conifers (Gerry 1914). Gerry (1914) observed a correlation between the regular occurrence of tyloses and high decay resistance in hardwoods of the United States, although there were exceptions to this trend. Bell (1980) suggested that tyloses function as part of the defensive strategy of trees by blocking the movement of pathogens along vessels and by allowing toxic extractives to accumulate without being diluted by the transpiration stream.

#### THE PROCESS OF HEARTWOOD FORMATION

##### *The events associated with heartwood formation*

Although heartwood transformation is not completely understood, many of the component processes have been studied. A number of changes may occur as sapwood becomes heartwood. Some of these events are clearly evident in the resulting heartwood (e.g., parenchyma death and extractive formation), while others are more ephemeral (e.g., changes in enzyme activity).

*Death of parenchyma.*—Complete parenchyma cell death, by definition, marks the transformation of sapwood into heartwood. Changes in parenchyma viability have been recorded by measuring respiration or by observing cytological changes. Shain and Mackay (1973) stated that most evidence suggests that parenchyma activity gradually declines with increasing distance from the cambium. However, their work demonstrated a spike of metabolism by parenchyma (by measuring oxygen consumption) in the transition zone during the dormant season. Shigo and Hillis (1973) concluded that there was a spike of metabolism in the transition zone related to the various processes involved with the transformation to heartwood. Nobuchi et al. (1979) described three patterns of parenchyma decline in sapwood of various species. In Type I, all parenchyma survive from the cambium to the heartwood/sapwood boundary. In Type II, there is a gradual decline in parenchyma, beginning in the middle sapwood. In Type III, parenchyma cell death begins in the outer sapwood, and continues to the heartwood boundary; there is no sharp boundary at the heartwood/sapwood transition. Fukazawa et al. (1980) also defined three patterns of parenchyma "maturation," but further subdivided the groups by the season during which the changes took place.

Pruyn et al. (2002b) observed greater CO<sub>2</sub> evolution in outer sapwood than in inner sapwood, and higher sapwood parenchyma respiration at the base and crown of the tree than

at 1 m above the ground. They hypothesized that respiration was related to proximity to carbohydrate sources.

Changes in the nuclei of sapwood parenchyma have been related to heartwood formation in a number of species including *Cryptomeria japonica*, *Melia azedarach*, *Pinus sylvestris*, *Larix decidua*, *Pseudotsuga menziesii*, and *Robinia pseudoacacia* (Hillis 1987). Changes in the shape of nuclei of the parenchyma before they disappear have been used to develop indices to describe the extent of parenchyma decline. These indices include the nuclear slenderness ratio (Frey-Wyssling and Bosshard 1959), the nuclear irregularity index (Yang 1992), and the nuclear elongation index (Yang et al. 1994).

*Gas accumulation.*—Carrodus (1971) applied carbon dioxide to *Acacia mearnsii* sapwood and observed that heartwood-type extractive compounds were formed. High carbon dioxide levels and low oxygen levels have been observed in heartwood, suggesting that heartwood extractive formation is related to the high level of carbon dioxide (a by-product of metabolism) within the trunk. However, Hillis (1987) reported that carbon dioxide inhibited polyphenol synthesis in various species. Shain and Hillis (1973) suggested that ethylene gas, and not carbon dioxide, was responsible for initiating the formation of heartwood extractives.

*Desiccation.*—Heartwood is often significantly drier than sapwood in conifers; in angiosperms, no consistent pattern exists, although there are often moisture content differences between the two tissues (Bamber and Fukazawa 1985; Hillis 1987). The transition zone may have lower moisture content than either heartwood or sapwood (Nobuchi and Harada 1983), and the transition in moisture content between these different tissues can be abrupt (reviewed in Hillis 1987). Often, desiccation of sapwood is associated with the formation of heartwood extractive compounds in sapwood (Jorgensen 1962; Jorgensen and Balsillie 1969; Shain and Hillis 1973; Torelli 1984).

The lower moisture contents of heartwoods are not low enough to prevent fungal decay. Fungal activity is limited only when *free* water is completely absent from wood (moisture content < 30%). Heartwood moisture content is typically above this level (USDA-FS Forest Products Laboratory 1999), suggesting that moisture contents change when heartwood forms, but not enough to prevent fungal attack.

*Lack of water transport.*—The transport of water from the roots to the crown is one function of stems. All of this transport in living trees occurs in the sapwood. However, not all parts of the sapwood are equally important in conduction, nor is conduction the only function. Heartwood transports no water. Embolism of the water-conducting conduits and closure of the pits connecting cells are both associated with lack of conduction in wood.

*Embolism.*—Water movement through sapwood is generally explained by the “cohesion-tension” theory: A continuous string of water is pulled up the tree by evaporation at the leaves. Because of the tensile stress in the water column, the water in the cell lumens in the sapwood is under considerable tension. The entry of a gas bubble into any lumen—an “embolism”—will break the string and the conduction of water along that pathway will cease (Zimmermann 1983). Embolisms reduce the number of functioning sapwood cells, producing more negative water potentials that further increase the risk of embolism.

Embolisms and their removal are believed to be continuous processes in sapwood maintenance. It has been proposed that the living cells of the sapwood are responsible for embolism reversal (Zwieniecki and Holbrook 1998; Wilson and Gartner 2002), but there is also some evidence against this explanation (Borghetti et al. 1991).

Sperry et al. (1991) observed degraded pit membranes (allowing embolism) in a *Populus* species and concluded that their breakdown was the cause of heartwood formation. However, similar processes have not been observed in other species. In fact, pit connections be-

tween cells often become tightly sealed during heartwood formation, greatly reducing wood permeability.

Shigo and Hillis (1973) suggested that changes in moisture content lead to the production of ethylene, which in turn stimulates heartwood formation (see below). However, Taylor and Cooper (2002) induced dramatic moisture content changes in the sapwood of *Pinus resinosa* through girdling, and heartwood production was not observed.

*Pit closure.*—Bordered pit pairs are specialized connections between adjacent xylem cells. The membrane separating the two cells contains a thickened torus in gymnosperms and some angiosperms (Carlquist 1988). "Aspiration" occurs when the torus moves to one side of the pit pair, blocking the connection and inhibiting fluid flow. Aspiration is believed to take place when free water is withdrawn from a lumen; the surface tension of the receding water layer draws the torus to the side (Panshin and de Zeeuw 1980). In the living tree, it is thought to occur when water tension becomes so high that the pit membrane can not exclude air bubbles. The bubble is sucked into a tracheid or vessel, the bubble expands to fill the tracheid or vessel, and that tracheid or vessel has less tension than the cells around it. The pit membranes are pushed away from the embolized cell because of the tension differences in the water column in an action that aspirates the pits.

Aspirated pits have been observed in a number of coniferous species (Fujii et al. 1997; Krahmer and Côté 1963) and in a few hardwoods (Dute and Rushing 1987, 1990). Harris (1954) observed bordered pits in *Pinus radiata* and found that the percentage of aspirated pits gradually increased from the cambium inward, reaching about 50% at the sapwood/transition zone boundary. At that point, the percentage of aspirated pits increased abruptly to about 90%. Fujii et al. (1997) found that the percentage of aspirated pits varied in the heartwood of samples of *Cryptomeria japonica* from different trees. They suggested that this variability was related to the

relatively high moisture content of the heartwood in that species, although this correlation was not shown in their results.

Pits can be blocked by encrustation with extractives (Krahmer and Côté 1963; Panshin and de Zeeuw 1980) in the heartwood of some species in a process that can be independent of aspiration (Fujii et al. 1997). Encrustation occurs abruptly at the border between the sapwood and the transition zone (Yamamoto 1982).

Pit closure by aspiration and/or encrustation may reduce the ease of movement of decay organisms through the wood. Pits are the paths of least resistance to hyphal movement, and pit closure should make this movement more difficult in softwoods because the solid torus must be penetrated in aspirated pits, instead of the netlike margo (Boddy 1992).

*Ethylene production.*—Bamber (1976) suggested that the centripetal movement of a heartwood-inducing substance stimulated heartwood formation. Since then, numerous authors have investigated the possible roles of ethylene and various enzymes in heartwood formation. Ethylene is a phytohormone that can be produced by all plant tissues in small amounts (Hillis 1987) and is associated with such processes as fruit ripening, and flower and leaf senescence. Ethylene also has been linked to increases in enzyme activity and to the production of heartwood polyphenolic extractives (Hillis 1987). Greater ethylene production related to heartwood formation (at the heartwood/sapwood boundary or in the transition zone) has been observed in the dormant season in a number of species (Hillis 1987), but the relationship, if any, between ethylene production and the quantity or quality of extractives is unknown.

*Enzyme activity.*—Enzymes that have been associated with heartwood formation include malic and glucose-6-phosphate dehydrogenases (Shain and Hillis 1973); tyrosinase and peroxidase (Nelson 1977); acid phosphatase, adenosine triphosphatase, glucose-6-phosphatase, lipase, glucose-6-phosphate dehydrogenase, succinate dehydrogenase and peroxidase

(Baqui and Shah 1985); phenylalanine ammonia-lyase (PAL) and chalcone synthase (CHS) (Magel et al. 1991); lipase and phospholipases (Hillinger et al. 1996); sucrose synthase (SuSY) and neutral invertase (NI) (Hauch and Magel 1998); and 6-phosphogluconate dehydrogenase (Magel et al. 2001). These various enzymes have been observed to be active in the vicinity of the transition zone or the sapwood/heartwood boundary, and have been implicated in the breakdown of the storage materials starch and fat and in the formation of heartwood-type extractives (e.g., Baqui and Shah 1985; Hillinger et al. 1996; Hauch and Magel 1998, Dehon et al. 2001).

Nair and Shah (1983) observed increased acid phosphatase, ATPase, and succinate dehydrogenase activities following the induction of heartwood by the application of the herbicide paraquat to *Azadirachta indica*. Succinate dehydrogenase and acid phosphatase were also observed during naturally occurring heartwood formation in the same species (Nair 1988).

Enzymes present in the sapwood have also been implicated in the non-microbial staining of sapwood after harvest. Forsyth and Amburgey (1992) noted that such staining often begins at the heartwood/sapwood boundary and progresses into the sapwood.

*Depletion in storage compounds.*—Heartwood is known to be low in energy reserve compounds such as sugars, starch, or lipids (Bamber and Fukazawa 1985; Hillis 1987). Gradual decreases in reserve materials in the sapwood from the cambium inwards are frequently observed (e.g., Saranpaa and Holl 1989; Magel et al. 1994, 1995). Nobuchi et al. (1987a) also observed gradual decreases in some species with wide sapwood, but found relatively constant levels throughout the sapwood of other species with narrow sapwood. Magel et al. (1994, 1995) observed gradual decreases in energy compounds in the narrow sapwood zone of *Robinia pseudoacacia*; however, relatively high levels of these compounds were still at the heartwood boundary, although they were absent from the adjacent heartwood.

Changes to—but not depletion of—lipid droplets in parenchyma cells have been observed in association with heartwood development in some species (Hillis 1987).

*Removal or accumulation of elemental nutrients.*—Trees may recycle nutrients from senescing sapwood back into living parts of the tree. Okada et al. (1993a, b) identified three patterns of radial nutrient distribution: In Type 1, element concentrations increased outward from the pith across the heartwood/sapwood boundary. In Type 2, the pattern is reversed. In Type 3, there is a peak in element concentration at the heartwood/sapwood boundary. Alkali metals and halogens typically follow Type 1 or 3 patterns, whereas alkaline earth metals follow a Type 2 pattern. Softwoods generally contain higher elemental concentrations in their heartwood, while the hardwoods studied contain higher concentrations in their sapwood.

Myre and Camire (1994) organized nutrient distribution in *Larix* species into three groups: “mobile” (P and K), “intermediately mobile” (Mg and Zn), and “immobile” (Ca and Mn). They observed that sapwood contained relatively high concentrations of mobile nutrients, while heartwood contained high concentrations of intermediately mobile and immobile nutrients. They suggested that an increased number of exchange sites, changes in pH, and translocation of nutrients towards the pith may account for these differences.

Andrews and Siccama (1995) observed decreases in the concentrations of calcium and magnesium from the pith to the outer heartwood. They speculated that this pattern reflected changes in the availability of these nutrients in the soil over time. The significance of differences in elemental distribution between sapwood and heartwood is unclear. Substantial amounts of an element can make the wood harder and more resistant to insect or marine borer attack, and can alter the wood/moisture relationship. Generally, however, the differences noted in these studies were not of a magnitude that would produce these effects.

*Formation of extractives.*—Heartwood ex-



tractives are responsible for the distinctive color, odor, and luster of some heartwoods. Because color is evident to the naked eye, the presence of a color change in the xylem is often used as the indicator of heartwood formation, even though other changes associated with heartwood formation (e.g., parenchyma death) may not have occurred (Nobuchi et al. 1984).

Heartwood extractives form at the heartwood/sapwood boundary (or in the transition zone) using locally available compounds and materials translocated from the phloem and sapwood (Hillis 1987). The chemistry of extractive biosynthesis has been investigated in a variety of species (e.g., Burtin et al. 1998; Dellus et al. 1997; Magel et al. 1995). Magel and others (reviewed in Magel 2000) have identified two types of heartwood formation, based on patterns in the production of phenolic extractives. In Type 1, or *Robinia*-type, extractives accumulate in the transition zone. In Type 2, or *Juglans*-type, the precursors to extractives gradually accumulate in the sapwood, and these precursors are transformed in the transition zone.

Streit and Fengel (1994) observed that extractives formed in the transition zone impregnated the cell walls, beginning in the middle lamella, and subsequently impregnated the secondary cell walls. They likened this process to lignification. Hergert (1977) coined the term "secondary lignification" for this phenomenon, and Jouin et al. (1988) reported more lignin in the heartwood than the sapwood of *Quercus*. However, Magel et al. (1995) and Gang et al. (1998) were careful to note that the formation of heartwood compounds is a different process than lignification, the process by which lignin is laid down in the formation of xylem cell walls. Magel (2000) refers to "secondary lignification" as "pseudo-lignification," and her analysis of this process has indicated that there are intimate chemical associations between heartwood extractives and the wood structural components.

It is clear that the pattern of extractive mi-

crodeposition plays a role in durability. For example, the impregnation of extractives from the heartwood of durable species into nondurable sapwood improved durability, but not to the extent of the original heartwood (Smith et al. 1989).

*Formation of tyloses.*—Tyloses are bubble-like projections from parenchyma into the lumens of adjacent vessels of some hardwoods, and occasionally in conifers (Gerry 1914), that are composed of material similar to the cell wall of adjacent cells (Chattaway 1949). Tyloses are believed to form as the result of enzymatic hydrolysis breaking down the pit membrane between a parenchyma cell and an adjacent vessel. This allows a portion of the parenchyma protoplast to extrude into the vessel lumen (Murmanis 1975). Tyloses inhibit fluid flow, which can limit moisture uptake and may physically impede the movement of pathogens through wood.

#### *The relationships between heartwood formation processes*

The temporal, spatial, and causal relationships between heartwood processes have received less attention than have the various processes themselves. Working with a number of species, Frey-Wyssling and Bosshard (1959) suggested that there is a gradual decrease in parenchyma activity in the sapwood going towards the heartwood. Aerobic respiration breaks down in the transition zone and anaerobic conditions develop. These conditions lead to the hydrolysis of starch, and once the starch is depleted, colored extractives are produced.

Fahn and Arnon (1962) studied the sapwood to heartwood transition in *Tamarix aphylla*. They noted that, when going from the cambium to the heartwood border in sapwood, starch grains disappeared first, followed by inactivity of the parenchyma, and finally disintegration of the parenchyma nuclei.

Bamber (1976) suggested that parenchyma death was the result, not the cause of heartwood formation. This idea is supported by the observations of Nobuchi et al. (1984), who

found that heartwood extractives were formed before parenchyma death in *Robinia pseudoacacia*.

When observing changes to parenchyma in *Pinus* species, Yamamoto (1982) determined that heartwood formation began with various changes to the parenchyma cells, followed by encrustation of bordered pits, and reductions in reserve materials and moisture content. Heartwood formation concluded with the degradation of the parenchyma nuclei.

Nobuchi, Harada, and their colleagues studied temporal and spatial relationships between some heartwood variables in their research. Moisture content decreases, and pits aspirate at the sapwood/transition zone boundary in *Cryptomeria japonica*. The parenchyma die in the transition zone, and extractives appear at the transition zone/heartwood boundary (Nobuchi and Harada 1983; Nobuchi et al. 1987b). Nobuchi et al. (1984) tracked temporal and spatial relationships between heartwood processes in *Robinia pseudoacacia* and found viable parenchyma inside the "heartwood" (defined as the colored region) for much of the summer and fall. Starch was depleted from sapwood adjacent to the heartwood, but only during the summer. A similar pattern was seen in the presence of large lipid droplets in the parenchyma, and these observations imply that heartwood formation is gradual, not instantaneous.

The biochemistry of heartwood formation has been studied extensively in *Robinia pseudoacacia* by Magel and her coworkers, and their work has been summarized in Magel (2000). Magel (2000) describes heartwood formation as a programmed cell death that has similarities to the senescence of leaves.

#### *The time of year of heartwood formation*

The time of year that heartwood forms has been the subject of some debate. Difficulties in determining the time of heartwood formation include choosing which variable to measure, where to look for it, and how to sample

the same individual repeatedly without affecting the measurement.

Much evidence suggests that heartwood forms in the dormant season. Shain and Hillis (1973) measured increased ethylene in the transition zone in the winter in *Pinus radiata*. Shain and Mackay (1973) found increased respiration and enzyme activity in the dormant season in the transition zone with the same species. Nelson (1977) studied ethylene concentration, enzyme activity, and nitrogen content in *Juglans nigra* and *Prunus serotina*, and concluded that heartwood formation occurs in the dormant season. Magel et al. (1991, 1995) and Hauch and Magel (1998) found that enzyme activity related to heartwood extractive synthesis in the transition zone was highest in the autumn in *Robinia pseudoacacia*.

Yamamoto (1982) studied the "maturation" processes in parenchyma in the inner sapwood and transition zone of *Pinus* species, concluding that "the season of heartwood formation is not the period when cambial growth is vigorous, but is the period when cambial activity declines" (Yamamoto 1982, p. 288). Similarly, Yang (1992) observed changes in ray parenchyma nuclei in the inner sapwood of *Pinus banksiana*, *Picea mariana*, and *Populus tremuloides*, in the northern hemisphere. He found that the greatest change in these nuclei occurred in August, July–August, and August–October, respectively, and also concluded that heartwood formation was initiated at those times. However, Fukazawa et al. (1980) stated that, while some parenchyma necrosis took place in the dormant season, other parenchyma senescence patterns were independent of season.

Baqui and Shah (1985) did not observe seasonal patterns in heartwood-related enzyme activity in *Acacia auriculiformis*, and concluded that heartwood formation occurred throughout the year. Bergstrom et al. (1999) found no change in the concentration of a heartwood extractive at the heartwood/sapwood boundary in *Pinus sylvestris*, and thus concluded that there was no particular time of year for heartwood formation.

Most reports used color differences to mark the boundary between heartwood and sapwood. This demarcation is convenient, but it defines heartwood as the area where colored extractives are present, rather than the region of dead parenchyma. It is also a mistake to treat the colored zone as a fixed target, since changes in the position of the colored boundary over time may better delineate "the season of heartwood development" than observations of activity in one fixed area of the xylem. Nobuchi et al. (1984) showed that different components of the heartwood formation process happen at different times, and in different locations in relation to the colored zone. The colored boundary of the heartwood in *Robinia pseudoacacia* (in the northern hemisphere) moves outward from July to September. Starch grains are depleted from, and lipid droplet patterns change in, the sapwood adjacent to the heartwood, just before the expansion of the colored zone. The parenchyma in the newly formed heartwood slowly die from September through the following spring. These studies indicate that heartwood formation is a stepwise process, occurring over much of the year, that ends with cell death.

#### VARIATIONS OF HEARTWOOD DISTRIBUTION AND QUALITY IN TREES

The amount of heartwood within and between trees and species has received considerable study. Patterns of variations in the quality—e.g., the chemical makeup or natural durability—of heartwood are less well understood.

##### *Macro-distribution of heartwood*

*Heartwood volume.*—Sapwood width, and consequently heartwood proportion, varies greatly between species. As extreme examples, *Catalpa speciosa* has 1–2 annual rings of sapwood, whereas there are 80–100 sapwood rings in *Nyssa sylvatica* (Sargent 1926). Sapwood width also varies within species, due to genetic, environmental, and tree age differences.

Smith et al. (1966) observed decreasing sapwood thickness with height in *Pseudotsuga menziesii*. In contrast, sapwood widths have been observed to be constant from the base of trees to the crown (Brix and Mitchell 1983; Megraw 1986; Nobuchi et al. 1987b; Gominho and Pereira 2000), although the number of sapwood rings decreases with height. Thus the heartwood portion often tapers from the ground up (e.g., Yang et al. 1994); however, heartwood width in some *Pinus* species increases from the base to about 1–3 m, and then decreases to the top of the tree (Wilkes 1991; Stokes and Berthier 2001). Sapwood volume can have important consequences with regard to water transport and stem storage, but there appears to be no consistent heartwood/sapwood relationship among many species.

*Extractives content.*—The outer heartwood at the base of the tree in most species studied is the most decay-resistant heartwood (Anderson et al. 1963; Scheffer and Cowling 1966). This pattern has been associated with a decrease in extractive content towards the pith and up the tree (Hillis 1987).

There are exceptions to this trend, especially when individual components are considered. Hillis (1987) refers to work that found no trends in the radial distribution of extractives in the heartwood of *Pseudotsuga menziesii*, *Pinus ponderosa*, and *Pinus radiata*. Nobuchi et al. (1987b) found that heartwood extractives were highest at the heartwood/transition zone boundary in boles of *Cryptomeria japonica*. However, extractive concentrations in the crown area increased towards the pith. Chui and MacKinnon-Peters (1995) found relatively high concentrations of extractives in heartwood of young larch trees.

Morita et al. (1995) observed slightly increased concentrations of extractives in the upper portions of the heartwood of one *Cryptomeria japonica* tree. They also found that, although extractives concentrations generally decreased towards the pith, two of the component chemicals increased in concentration. Mosedale et al. (1996a) studied heartwood extractive patterns in *Quercus* species and ob-

served that the concentration of total soluble ellagitannins showed a logarithmic decline from the heartwood boundary towards the pith, while individual ellagitannins varied in their response. Burtin et al. (1998) found that concentration of phenolic compounds in the wood of *Juglans* species peaked around the transition zone, whereas the remaining compounds had greater concentrations in the heartwood.

The pattern of lower extractives near the pith may reflect the degradation of extractives over time or an increase in extractive deposition with age. DeBell et al. (1999) found that lower extractive levels near the pith of *Thuja plicata* were associated with juvenile wood, and that aging of the wood seemed to have little effect. Nault (1988) found similar patterns in the same species. Van der Kamp (1986) observed that staining fungi that occur naturally in heartwood could reduce thujaplicin content in *Thuja plicata*, although this reduction was not associated with reduced decay resistance. Gartner et al. (1999) found no radial or horizontal patterns of decay resistance in young *Pseudotsuga menziesii* trees. However, the correlation between decay resistance and total heartwood extractive content can be poor, suggesting that more subtle differences in extractive composition or distribution may be important.

#### *Micro-distribution of heartwood extractives*

Extractives are located mostly in the rays (Hillis 1972). Côté et al. (1966) observed that when arabinogalactan of *Larix occidentalis* was removed by extraction with water, the volume of the wood remained nearly constant, suggesting that almost all of the polysaccharide was located outside the cell wall (i.e., in the lumen). However, extractives can also form coatings on the cell wall and on the pits, and can penetrate the cell wall itself. In some cases, differences in heartwood dimensional stability have been attributed to the presence of cell wall extractives (Bosshard 1968; Hillis 1972).

Côté et al. (1966) found that earlywood in *Larix* contained more arabinogalactan than did latewood. They attributed this pattern to larger lumen size in the earlywood cells. Extractive levels peaked at the middle of the earlywood zone of *Pseudotsuga menziesii* and were minimal at the beginning and end of the annual ring (Squire et al. 1967). By contrast, Lloyd (1978) observed more extractives in the latewood portion of the annual ring of *Pinus radiata*. This distribution was explained by Harris (1965) as a result of the exudation of resin from transverse resin canals after heartwood was formed, because latewood cells were less likely to aspirate when heartwood forms. Kuo and Arganbright (1980) reported that the proportion of heartwood extractives in the cell wall (as opposed to the lumen) increased in the inner portions of the heartwood of a *Sequoia sempervirens* tree and a *Libocedrus decurrens* tree. Pensar (1967) reported that the extractives in the earlywood of *Picea abies* contained a slightly higher proportion of extractives than the latewood. The resin acids and other terpenoids were concentrated in the resin canals of *Picea*, while fatty acids, glycerides, waxes, and sterols were located in the ray parenchyma cells (Kimland and Norin 1972). Although these reports imply differences in micro-distribution of various extractives, there are few methods for delineating extractive distribution in situ. As a result, most relationships are inferred by extraction studies of whole wood sections.

#### CONTROL OF HEARTWOOD FORMATION AND DURABILITY

There has been relatively little work on factors controlling heartwood quantity and even less on heartwood quality (i.e., natural durability).

#### *Sapwood area homeostasis*

The concept of a dynamic relationship between sapwood area, sapwood permeability, and foliage area is not new (e.g., Gartner 1991; Margolis et al. 1988; Whitehead et al.

1984). Much of the research into this hypothesis has been directed toward estimating foliage biomass and modeling stand and ecosystem dynamics (e.g., Margolis et al. 1995). If there is a homeostatic balance between sapwood area and leaf area, then it is a logical extension that the amount of sapwood (and thus the proportion of heartwood) can be influenced by the manipulation of the other variables.

Leaf-area-to-sapwood-area ratio ( $A_e:A_s$ ) may vary with species (Grier and Waring 1974), soil water availability (White et al. 1998), average relative humidity (Mencuccini and Grace 1995), tree age (Dean and Long 1986), tree vigor (Sellin 1996), stand density (Shelburne et al. 1993), soil nutrient availability (Brix and Mitchell 1983), and height in the tree (White et al. 1998). The influence of each of these factors on heartwood formation will be addressed separately in the following discussion.

In most of the research into changes in  $A_e:A_s$ , it is not stated whether sapwood area changes when  $A_e:A_s$  ratios change. Shelburne et al. (1993) suggested that leaf area changes are primarily responsible for the differences in  $A_e:A_s$  observed between stands of different basal areas. This assertion suggests that sapwood area (and hence heartwood area) is not easily modified by adjustments to the "homeostatic balance." Langstrom and Hellqvist (1991) observed reductions in the area of conducting sapwood in pruned young *Pinus sylvestris* trees. The reaction time was found to be quite slow; the homeostatic balance was not completed four years after the treatment. The authors were also careful to state that the sapwood that was no longer conducting was "immobilized sapwood" and not heartwood. It has not yet been demonstrated clearly that heartwood volumes can be manipulated by alterations to the homeostatic balance.

#### *Inter-specific variations in heartwood*

Species differ widely in their relative amounts of heartwood, as well as in the quan-

tity and composition of the extractives. The between-species differences in the durability of wood has long been of interest to users of wood products. The natural durability of wood of many species has been evaluated by a multitude of methods in many species (reviewed in Scheffer and Morrell 1998).

It is difficult to describe consistent trends in the natural durability of the wood of different species. Many tropical species, but not all, are durable with respect to biodeterioration, but there are also very durable species in temperate regions. It is reasonable to suppose that long-lived tree species would require durable heartwood that could last for many years. Indeed, many long-lived species have durable heartwood, but some do not (e.g., *Picea sitchensis*). These long-lived species with relatively low heartwood durability may adapt to longevity with highly active defense mechanisms in the sapwood parenchyma that limit wound invasion and thus exclude invaders from the decay-susceptible heartwood.

#### *Factors influencing intra-specific variations in heartwood*

*Genetic control over heartwood formation.*—Studies have been made of the genetic influence over both the quantity and quality of heartwood formed in a number of different species. A review of the literature relating to genetic control of heartwood formation noted "reasonably strong genetic control" of heartwood area in mature trees of *Pinus* and some diffuse-porous species (Zobel and Jett 1995, p. 184). More recently, researchers have estimated the heritability of heartwood diameter of 25-year-old trees to be lower than that of 44-year-old *Pinus sylvestris* trees, with moderate values of 0.3 and 0.5, respectively (Fries and Ericsson 1998; Ericsson and Fries 1999). The authors cautioned that some work has overestimated the heritability of heartwood formation, but they suggested that breeding for heartwood was possible.

Fries (1999) found that variation in heartwood traits (number of annual rings and

width) due to provenance was small compared with within-provenance variation in mature *Pinus sylvestris*. He suggested that family effects and stand characteristics had a greater influence on heartwood characteristics. Pâques (2001) measured high heritability levels for heartwood proportion in *Larix* sp. Woeste (2002) observed wide phenotypic differences in heartwood area in a progeny test of 35-year-old *Juglans nigra*. Much of the variation was attributable to differences in tree diameter, but statistically significant family effects for heartwood area were noted.

Overall, there appears to be significant genetic control of heartwood proportion within species, but environmental influences can be equally important.

There is often strong genetic control over the production of extractives in wood, particularly in older trees (Zobel and Jett 1995). It is unclear why this relationship becomes more evident in older trees. Rudman and DaCosta (1959) suggested that variations in the heartwood of *Tectona grandis* were more genetic than environmental, based on the observation that trees on the same site, with roughly the same growth rate, differed in decay resistance.

Rink (1987) found no genetic control over heartwood color in young *Juglans nigra* trees. Mosedale et al. (1996b) found that heartwood ellagitannin content in *Quercus* species was under strong genetic control, whereas heartwood color (the result of extractives) was under less genetic control.

The concentration of specific heartwood extractives was found to vary widely between individual trees and to be highly genetically correlated in *Pinus sylvestris* (Fries et al. 2000; Ericsson et al. 2001); however, these concentrations were not well correlated to the amount of heartwood.

Venalainen et al. (2001) studied the repeatability of heartwood characteristics in *Larix sibirica*, and observed moderate genetic influence over the decay resistance of heartwood, but less heritability of heartwood amounts. Harju et al. (2001) found low heritability of decay resistance to a brown rot fungus in *Pi-*

*nus sylvestris*, and very wide phenotypic range in heartwood resistance. They concluded that genetic gains in breeding would be possible only in combination with the testing of environmental influences.

Genetic control of extractive production has considerable economic potential in some species. Squillace and Harrington (1968) reported a doubling of oleoresin yields as a result of selection and breeding in *Pinus* species. Franklin et al. (1970) predicted further genetic gains in extractive yield of about 12%. The possible effect of increased heartwood extractives on overall durability is difficult to predict, but one likely gain would be to create more uniform durability. In many cases, field tests of naturally durable species produce sporadic early failures, possibly as a result of heartwood samples with less extractives. Increased overall heartwood extractive content may help reduce the occurrence of these failures.

*Tree age.*—Heartwood formation lags behind the growth of the pith and new sapwood layers by a time mostly governed by genetic differences between species (Hillis 1987). Once heartwood formation begins, heartwood is added on a more or less regular basis, gradually progressing out radially and up the tree (e.g., Hazenbarg and Yang 1991a, b).

Heartwood volumes are cumulative, whereas sapwood areas are not (rather, they are the sum of new sapwood from the new annual increments minus the loss to heartwood). Thus, the proportion of the bole that is heartwood increases with tree age (Sellin 1996). Various authors have developed regression equations relating age to the amount of heartwood or sapwood in different species (e.g., Hazenbarg and Yang 1991a, b; Yang and Hazenbarg 1991a, b; Sellin 1991, 1994, 1996).

Radial growth early in the life of the tree is a good predictor of heartwood diameter in some species (Climent et al. 1993; Hillis 1987; Wilkes 1991). Wilkes (1991) found that heartwood formation commenced earlier in the upper parts of *Pinus radiata* trees, even though the diameter of heartwood was less.

The amount of extractives in heartwood generally increases with distance from the pith. Thus, the age of the tree influences heartwood extractive content (Hillis 1987). Nault (1988) observed higher concentrations of extractives in the heartwood of older trees than in younger trees of *Thuja plicata*, and suggested that wood from young trees would be less resistant to decay. Krilov and Lasander (1989) found that wood of mature trees of *Eucalyptus* species had more gallic acid (a principal heartwood extractive) than did "regrowth" (the nature of the "regrowth" was not specified). In both these cases, however, the effect seems to be a result of the maturity (distance from the pith), rather than any consistent difference in the heartwood quality (see for example DeBell et al. 1999).

Gartner et al. (1999) studied young *Pseudotsuga menziesii* and found no radial or vertical variations in heartwood decay resistance. This result may indicate that the radial and vertical patterns in heartwood extractives present in older trees are not present in younger trees. However, given the sometimes-poor correlation between extractives content and decay resistance, this conclusion is not certain.

*Tree vigor.*—Tree vigor seems to have less predictable effects on heartwood volumes than do genetics or age. Hillis (1987) and Nair (1999) reviewed literature that demonstrated a positive relationship between early growth rate and heartwood proportion, as well as other studies showing that faster-grown trees produced less heartwood. This characterization can have important implications in aggressively managed plantations. Since Hillis' review, Wilkins (1991) and Gominho and Pereira (2000) have observed positive correlations between growth rate and heartwood volumes, but both studies were based on young trees.

Wilkes (1991) warned against misinterpreting those factors that stimulate growth of trees overall as influencing heartwood/sapwood proportions in *Pinus radiata*: "heartwood development is very much an age-related process, i.e., the heartwood boundary progresses outward at a more-or-less set fraction of an

increment per annum, and where rings are wider more heartwood is produced" (Wilkes 1991, p. 89).

Kaufmann and Watkins (1990) studied old stands of *Pinus contorta* and found that the low-vigor trees had higher heartwood volumes than did the high-vigor trees. However, the age of the heartwood was similar in the high- and low-vigor trees. These observations indicate that the low-vigor trees in this study had grown more quickly in the past (overall volumes were similar), and the greater volumes produced in the past had since been transformed into heartwood. Sellin (1991, 1994) also found that suppressed *Picea* trees had a greater percentage of heartwood than dominant trees had. Again, this pattern was due to the relatively narrow sapwood growth rings—the number of rings of sapwood was similar for the two groups (Sellin 1991). Yang and Hazenburger (1992) found that faster-growing *Picea* trees (as a result of wider spacing) in a 38-year-old plantation had more heartwood rings and area.

De Kort's (1993) study of relatively young (25–70 years old) *Pseudotsuga menziesii* gave contradictory results of the relative amount of heartwood in suppressed trees. In general, lower-vigor trees had higher heartwood volumes than did more vigorous trees. In non-vital trees (more than 60% needle loss) trees, the number of sapwood rings was similar to that of the "vital" trees. However, trees with intermediate vigor ratings had higher heartwood proportions, even though the number of sapwood rings was higher than in the vital trees. Clearly, the relationship between tree vigor and heartwood formation merits further study.

Hillis et al. (1962) suggested that the amount of photosynthate available for translocation could influence the quantity of heartwood extractives produced. However, a poor understanding of allocation hierarchies in trees complicates the relationship between tree vigor and photosynthate supply: healthy trees might have more photosynthate than less vigorous trees, but they then may allocate more

of that photosynthate into growth, reproduction, or other activities. Hillis's (1987) review cited examples of work that demonstrated decreased extractives in faster-grown trees of some species, as well as other examples where no such relationship was observed. Wilkins and Stamp (1990) found that the outer heartwood of young, faster-grown (as a result of silvicultural treatments) *Eucalyptus grandis* trees was darker in color than that of more slowly grown trees. Magel (2000) has attributed annual differences in heartwood extractives in *Robinia pseudoacacia* to fluctuations in available sucrose caused by climate variations.

As foresters shift to more aggressive management of naturally durable species, understanding the potential effects of thinning, fertilization, and other stand manipulations will be essential for helping foresters make informed management decisions.

*Wood structure differences.*—Hillis (1987) reported on the lowered amounts of heartwood extractives in compression wood and tension wood than in normal wood, and suggested that this phenomenon may be due to reduced carbohydrate levels, increased lignin content (in compression wood), or changes in ethylene production. Blanchette et al. (1994) found that compression wood was more resistant to decay than was normal wood, but that tension wood was similar in decay resistance to normal wood.

Heartwood extractive synthesis occurs in the living cells in the sapwood (ray and axial parenchyma), thus there has been some speculation that the amount of parenchyma could influence the amount of extractives produced. Hillis et al. (1962) observed that there were fewer parenchyma and less heartwood extractives in the tension wood than in normal wood of *Angophora costata*. Hemingway and Hillis (1970) also observed a positive correlation between parenchyma volume and heartwood extractives in *Pseudotsuga menziesii*. However, Nelson (1975) concluded that physiological conditions at the heartwood/sapwood boundary were more important than the amount of

parenchyma in determining the amounts of extractives produced in two temperate hardwoods. More recently, Climent et al. (1998) found that *Pinus canariensis* trees with larger than predicted heartwood diameters had greater proportions of axial parenchyma.

Polge (1985) found less heartwood area in the tension wood regions of trees of a *Populus* species. Stokes and Berthier (2001) observed that the proportion of heartwood to sapwood stayed the same around the cross-section of *Pinus pinaster* trees containing compression wood, although more rings were incorporated into heartwood in the compression zone.

*Site quality.*—Site differences can influence the growth rate of trees and can be associated with differences in genetic stock. Thus, site considerations can easily be confounded with the tree vigor and genetic considerations described above.

Hillis (1987) refers to work that suggests that poor sites may delay the initiation age of heartwood formation or decrease heartwood proportion. A number of studies measured differences in the extractive contents of heartwood, but in those cases, the effect of site was not distinguished from genetic and other environmental factors. Harris (1954) found that adequate water supply, and the absence of drying conditions favored heartwood development in *Pinus radiata*. Climent et al. (1993) determined that site characteristics (water balance and exposure to winds) related more strongly to sapwood width and diameter growth than to heartwood width in *Pinus canariensis*. Recently, however, Climent et al. (2002) concluded that climate is related to heartwood area, even after accounting for variations in early growth rate. Their models predict wider heartwood in drier climate sites versus wet, high altitude sites.

Guyette et al. (1992) observed that the mineral elements present in heartwood (and sapwood) were related to their abundance in the soil. It was even possible to observe changes in the environment in the past (e.g., the advent of lead smelting in the area) by observing changes in the elemental concentration be-



tween annual rings of *Juniperus virginiana*. As previously mentioned, soil nutrient availability influenced the degree of nutrient recycling from senescing sapwood back to the active sapwood in *Chamaecyparis thyoides* (Andrews et al. 1999). Pothier et al. (1989) found changes in sapwood conductance because of site differences, but observed that the number of rings of sapwood stayed the same regardless of site in *Pinus banksiana*. Phelps et al. (1983) studied influences on heartwood color in *Juglans nigra* and found that within-site differences were more important than between-site differences. Mosedale et al. (1996b) found that the extractive content in *Quercus* species varied little among ramets of the same clone grown on two contrasting sites. Moraes et al. (2002) have suggested that observed differences in resistance to termite attack among *Eucalyptus* sp. may be indirectly due to site differences, since trees growing on richer sites will be more vigorous and may produce more heartwood extractives. These studies indicate that site can influence wood mineral content and tree vigor, but suggest that other factors affect heartwood quality more directly.

*Frost, diseases, and pollution.*—Cold weather and extreme climate may induce irregular heartwood formation in some hardwood species (Krapiec 1999). Such heartwood zones are sometimes called frost heart or moon rings, and may or may not resemble true heartwood (Dujesiefken et al. 1984; Hillis 1987; Charrier et al. 1995).

Infestation of trees by the insect *Adelges piceae* has been shown to increase the area of heartwood in *Abies* species (Hillis 1987; Hollingsworth et al. 1991). Various pathogens that attack trees can induce a wound response in the sapwood, but, although wound tissue shares some characteristics with heartwood, this tissue is not true heartwood (Shigo and Hillis 1973), nor are the biosynthetic pathways the same (Magel 2000). Shigo (1984) also noted that wounding of a tree can cause localized delays in the development of heartwood. Rademacher et al. (1986) observed lower sapwood moisture content in *Picea abies* trees af-

ected by pollution, and slight reductions in the sapwood proportion. However, Bauch (1990) reported that, while pollution may influence growth rates of trees, heartwood formation was not affected.

Overall, it appears that stress and traumatic events do not influence the normal heartwood formation processes. However, the noted localized disruptions to heartwood formation (associated with wounding or frost) may provide model systems for studying heartwood formation processes.

*Stand age: second growth versus old growth.*—Old-growth trees may differ from second growth in a number of ways, including tree age, growth rate and genetic makeup. Moreover, the microenvironment experienced by the trees can differ greatly; old-growth trees more frequently live in environments with vertical patchiness of neighbors, and young-growth trees more frequently live in environments with horizontal patchiness. As discussed above, each of these factors can influence the amount and quality of heartwood, so it is difficult to generalize about heartwood quantity and quality as a function of stand age, per se.

*Silvicultural treatments.*—As with site differences, silvicultural treatments can influence vigor, and thus heartwood formation. Overall, treatment does not appear to induce dramatic changes in heartwood quality, although dramatic effects have been shown in sapwood area, and therefore in heartwood quantity (e.g., Gartner et al. 1999; Bengstrom 2000).

Margolis et al. (1988) and Bergstrom (2000) found that pruning reduced sapwood growth, but that severe pruning (0.2 live crown ratio compared with 0.8 for the controls) increased heartwood diameter. As noted previously, Langström and Hellqvist (1991) observed that pruning of young *Pinus sylvestris* decreased the relative proportion of sapwood, but observed that the area identified as “heartwood” was more likely “immobilized sapwood” (Langström and Hellqvist 1991, p. 251). Morling and Valinger (1999) studied the effect of thinning and fertilization on *Pinus sylvestris*. They found

that the treatments tended to increase tree and heartwood diameter, but that the number of heartwood growth rings was unchanged. Wilkins (1991) studied the effect of various treatments (ploughing, thinning, weeding, fertilization, and insecticide application) on a young *Eucalyptus grandis* plantation. The treatments increased the rate of growth overall and resulted in a higher proportion of heartwood. Yang and Hazenburg (1992) concluded that wider spacing in 38-year-old *Picea* sp. plantations resulted in more rings of heartwood and greater heartwood volumes. Bjorklund (1999) found that heartwood quantity in *Pinus sylvestris* was not well correlated with spacing, thinning, regeneration method, or site quality. Greater variations were found in heartwood quantity within, rather than between, sites. Thus, it was concluded that genetic manipulation would be more likely to alter heartwood proportions than would silviculture or site selection.

The application of the herbicide paraquat to standing trees, notably *Pinus* species, can induce "lightwood" (sapwood soaked with heartwood-like extractives; reviewed in Hillis 1987). Gref and Stahl (1994) found that mechanical wounding could also induce lightwood. Taylor and Cooper (2002) examined the ability of girdling to induce heartwood formation in live hardwood and softwood trees. The results were inconclusive, although some heartwood-like changes were observed in the sapwood of girdled trees.

Although many aspects of heartwood formation and the natural durability of heartwood have been studied, the process of heartwood formation remains poorly understood. Attempts to improve heartwood durability will require a more thorough understanding of heartwood formation and the many factors by which it is influenced.

#### QUESTIONS

Heartwood is a significant portion of the xylem in mature individuals of many tree species. Heartwood tissues offer many character-

istics that are different from sapwood, including lower moisture content, darker color, and reduced permeability. Clearly, however, the process of heartwood formation remains poorly understood and requires further study in many commercially important, naturally durable species. Ultimately, the ability to manipulate the amount and quality of heartwood formed in trees would be of enormous practical value; however, many questions need to be resolved before control over heartwood formation is possible. Examples of such questions are as follows:

1. *The relationships among the changes during heartwood formation.*—Considerable research has been done on the various aspects of the heartwood formation process (i.e., enzyme activity, extractive formation, parenchyma cell death). However, the sequence, and the temporal, spatial, and especially causal relationships between these factors must be addressed.

2. *The importance of "natural durability" to the living tree.*—All of the ratings of natural durability are based on tests of the wood once it is removed from the tree, and often under quite "unnatural" circumstances (i.e., gas, moisture compositions). This bias is a result of our desire to gauge how useful the wood will be in various applications, but does not necessarily reflect the tree's requirements for the wood. The often-poor correlation between extractives content and decay rating may reflect, in part, the manner in which the wood is tested. It would be instructive to consider heartwood durability in terms of the function of that durability in the living tree.

3. *The costs and benefits of heartwood formation.*—It has been proposed that trees require just enough sapwood to transport the water to the transpiring leaf surfaces and that there are metabolic costs of maintaining excess sapwood (Ryan et al. 1995). However, there is also evidence that these metabolic costs are relatively low in inner sapwood (Pruyn et al. 2002a), while the costs of heartwood formation can be enormous (e.g., in species that accumulate large amounts of extrac-

tives in the heartwood). A cost/benefit analysis of heartwood formation could aid in understanding patterns of sapwood and heartwood in various species.

4. *Triggers of heartwood formation.*—Many possible initiators of heartwood development have been proposed in connection with the various processes involved. Carbon dioxide accumulation (Carroodus 1971), ethylene production (Hillis 1987), and desiccation (Jorgensen and Balsillie 1969) have all been suggested as initiating the heartwood formation process; however, none of these satisfactorily explains the observed variety of heartwood formation patterns.

5. *Ecological patterns of sapwood thickness and heartwood durability.*—It is likely that there are suites of characteristics in heartwood and sapwood that have not yet been elucidated. For example, do diffuse-porous trees consistently have less sapwood than ring-porous ones, given that their hydraulic architecture is so different? Is there a relationship between storage levels in the sapwood and sapwood depth, or heartwood extractive content? Is the permeability of either bark or sapwood to air related to the amount of sapwood?

6. *A more thorough understanding of how extractives interact to protect wood.*—This knowledge might be used to foster development of trees that are more likely to produce extractives and could also aid in the development of more biorational wood preservatives.

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