NUTRITIONAL QUALITY OF DOUGLAS-FIR WOOD: EFFECT OF VERTICAL AND HORIZONTAL POSITION ON NUTRIENT LEVELS[1]

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ABSTRACT

The chemical composition of the boles of 14 Douglas-fir trees growing in the central Willamette Valley of western Oregon was examined to determine whether differences in various chemical component levels might help to explain arthropod or microbial colonization patterns. Levels of nearly all cations as well as N and P tended to be highest in the inner bark. Nitrogen levels were similar in sapwood and heartwood, but both were lower than those in the inner bark. Levels of N, P, Mg, Fe, and Zn tended to be significantly higher farther up the tree, suggesting that this zone might be a more suitable substrate of colonization. Water-soluble sugars tended to be present at higher levels closer to the live crown, a finding that implies that these compounds may be allocated to cells closer to the regions where active photosynthesis is occurring. Water-soluble sugars tended to be present at higher levels in the heartwood, an unexpected finding since these compounds are presumed to be consumed during heartwood formation. A broader sample of Douglas-fir boles is recommended to confirm these results.

Keywords: Bark, chemical composition, Douglas-fir, heartwood, sapwood.

INTRODUCTION

The polymeric nature of wood renders it remarkably resistant to biodegradation in comparison with other plant-derived organic materials, but a variety of organisms can use one or more of the basic wood polymers as a food source, causing degradation. The process of biodegradation is often studied from the perspective of the effect of the degrading organism on the wood substrate, with less concern being given to the nutritional suitability of the substrate upon which the organisms must grow. Wood contains a diverse array of organic and inorganic constituents. The three basic polymers, cellulose, hemicellulose, and lignin, comprise 85% to 95% of the wood mass; but there are also carbohydrates, proteins, lipids, and minerals in various cells (Sjostrom 1993). Many of these latter components are among the substrates initially used during microbial colonization, but their distribution in trees is poorly documented (Abraham and Breuil 1993; Gao et al. 1994; Gao and Breuil 1995).

In a series of studies, Merrill and Cowling quantified the low levels of nitrogen present in tree stems at various times and locations, and then attempted to determine why fungi were capable of thriving on such a nitrogen-poor substrate (Merrill and Cowling 1965, 1966*a*, 1966*b*; Cowling and Merrill 1966;

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Levi and Cowling 1968). The remainder of the wood components, other than toxic extractives, have received scant attention (Laidlaw and Smith 1965; Hodges et al. 1968). Yet, many of these materials are essential for the metabolic activity of microorganisms and their concentrations at the time of tree death could dramatically impact the suitability of the substrate for colonization by bacteria, fungi, or insects (Lorio 1993). Similarly, variations in the distribution of essential elements within the bole may also affect colonization patterns or sequences, potentially affecting the rate of decomposition of coarse woody debris. Carbon levels in wood appear to change markedly with season (Höll 1981; Höll and Priebe 1985; Fischer and Höll 1992; Harms and Sauter 1992). The dynamics of nutrient storage and cycling in many North American conifers remains poorly defined, despite its potential impact on a variety of silvicultural, pathological, and utilization questions (Isenberg 1980).

We analyzed concentrations of nutrients in bark and wood of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) trees in western Oregon. This species was selected because it is an important component of western forests, and its relative rate of decomposition in these forests can have important implications on nutrient cycling. (Harmon et al. 1986; Schowalter et al. 1992; Raffa et al. 1993). We hypothesized that subtle differences in nutrient levels in this sapwood at the time of tree death, coupled with the presence of naturally durable extractives in the heartwood, could impact the suitability of this wood for microbial or arthropod colonization.

Materials and Methods

Fourteen Douglas-fir trees were cut from the McDonald-Dunn Forest in western Oregon during June and July of 1995. All trees were 145 to 165 mm in diameter 2 m above ground, and 40 to 60 m in height below the crown. The stand was naturally regenerated and had received no prior fertilization.

Eighty-mm-thick slices were cut from sections 5 to 10 m, 20 to 30 m, and 40 to 60 m from the bottom of the bole and treated as follows (Schowalter et al. 1998). These sections will be referred to as lower, middle, and upper sections, respectively. The 40- to 60-m zone was within the live crown; the remaining sections were below this zone. Two wedges, each containing outer bark, inner bark, sapwood, and heartwood to the pith, were cut from opposite sides of each section. Sapwood and heartwood were distinguished by color. Inner bark consisted of the cambium and live phloem. The volume of each wedge (sample) was determined by water displacement; then each sample was dried at 50°C to a constant weight. The lower temperature was used to minimize possible changes, e.g., volatilization of chemical constituents. Sample density was calculated as dry weight per fresh volume.

The samples were then ground to pass a 40-mesh screen. One sub-sample was analyzed for nitrogen with a LECO CNS-2000 autoanalyzer according to procedures described by Miller and Kotuby-Amacher (1995). Sub-samples were also ashed at 500°C and analyzed for phosphorus and other mineral elements with a Perkin-Elmer Optima 3000 ICP-ES (Inductively Coupled Argon Plasma Spectrograph) (Jones 1977; Munter et al. 1984). Concentrations of carbon compounds were expressed as a percentage of the ash-free dry weight of the original sample (as determined from the mineral element analysis). A second group sample was first sonicated in excess dichloromethane to remove non-polar fractions (waxes and oils). The sample was next extracted in 103°C water for 3 hours to remove simple sugars, hydroxyphenols, amino acids, and other minor organic compounds (Miller and Kotuby-Amacher 1995). The residual extract from this procedure was then analyzed for tannin content using the Folin-Dennis method. Briefly, 1 to 2 ml of the extract was added to a 50-ml volumetric flask along with the 20 ml of water and 2.5 ml of Folin-Denis reagent. After 3 min, 10 ml of 1 M sodium bicarbonate was added, and the flask was brought to vol-

ume with distilled water. The flask was shaken at 25°C for 20 to 30 min; then absorbance was measured at 760 nm against a water reference. Tannin content was determined by comparison with a standard curve prepared using a certified-grade tannic acid.

Finally, the sample was extracted in 70% sulfuric acid followed by hydrolysis in 2 N sulfuric acid under heat and pressure in an autoclave to determine total lignin, as well as polysaccharide levels (Hobbie 1996). The amounts of lignin, tannin, non-polar compounds, acid-soluble compounds, water-soluble compounds, water-soluble sugars, and acid-soluble sugars were calculated as a percentage of the ash-free dry weight of the original sample.

Density and nutrient/carbon levels were analyzed with a 2-way ANOVA for a randomized complete block design, with substrate and height as the main effects and trees representing blocks, using SAS (Steel and Torrie 1980; SAS 1982).

Results and Discussion

Nutrient concentrations and density

Levels of nearly all cations as well as nitrogen and phosphorous tended to be highest in the inner bark, although differences between this substrate and the outer bark were sometimes slight (Table 1). In general, these levels were similar to those reported previously (Mitchell et al. 1996), but were somewhat lower than those found in freshly fallen logs (Sollins et al. 1987; Means et al. 1992). Levels of all elements in the bark differed significantly from those in either the sapwood or heartwood ($P < 0.0001$).

Of these elements, nitrogen is often viewed as critical for tree growth as well as for degradation by wood-destroying organisms since it is a central element in proteins and nucleic acids (Zabel and Morrell 1992). The nitrogen levels found in our trees were slightly lower than those previously reported for Norway spruce (*Picea abies* (L.) Karst) and eastern white pine (*Pinus strobus* L.) (Merrill and Cowling 1966*b*). Nitrogen levels in sapwood were similar to those in heartwood but were 20% to 25% of those found in the bark substrates. The absence of substantial amounts of nitrogen in the sapwood or heartwood is consistent with previous reports and highlights the importance of nitrogen conservation for organisms colonizing this substrate. Despite these low levels, proteins are an important component in initial microbial colonization (Abraham and Breuil 1993). The importance of the other elements in colonization is difficult to determine since they may serve as cofactors in decomposition or energy transport and are normally required in relatively small quantities.

Levels of N, P, Mg, Fe, and Zn varied significantly with position of the section ($P < 0.02$), and were generally highest in the upper section, except for P, which was lowest (Table 1). These differences likely affect suitability of specific bole regions as substrates for insect or microbial colonization. Many wood-inhabiting organisms are well adapted to growth on nutrient-poor substrates and have evolved mechanisms for conserving and recycling various elements, particularly nitrogen. Thus, minor differences in their nutrient levels may have little effect on the suitability of the substrate for those organisms that have evolved to utilize Douglas-fir, although they may influence the suitability of the substrate for colonization by more cosmopolitan, less specifically adapted organisms.

Nutrient gradients may be more important for bark- and wood-feeding arthropods. Many of these organisms initially feed on the inner bark, where concentrations of nitrogen and a variety of carbon compounds tend to be highest (Merrill and Cowling 1966*a*, 1966*b*; Hodges et al. 1968; Schowalter et al. 1998). Differences in vertical distribution of various nutrients might affect initial feeding behavior. For example, differences in cations and amino acid levels along leaf blades of the marsh grasshopper, which actively fed on the middle portions of the leaves where cation levels were most balanced and amino acid levels were

TABLE 1. *Mean density and nutrient concentrations in bark and wood substrates at lower, middle, and upper sections of Douglas-fir boles in western Oregon. Standard deviations are in parentheses. N = 14 for each position/substrate combination.*

Position/substrate	Density (g/cm³)	Elemental level (μg/g wood)										Total ash content (%)
		N	P	S	K	Ca	Mg	Na	fe	Zn	Mn	
Lower												
Outer bark	0.50 (0.09)	1800 (220)	140 (13)	74 (12)	440 (93)	1600 (460)	130 (23)	26 (8)	35 (6)	10 (4)	43 (6)	0.51 (0.09)
Inner bark	0.50 (0.10)	2500 (260)	480 (47)	120 (27)	2200 (260)	4000 (2000)	400 (69)	21 (9)	20 (6)	17 (8)	59 (6)	0.93 (0.15)
Sapwood	0.54 (0.06)	550 (69)	60 (22)	25 (5)	330 (160)	330 (110)	66 (25)	5 (2)	10 (14)	6 (7)	18 (6)	0.21 (0.10)
Heartwood	0.54 (0.07)	500 (66)	17 (20)	19 (5)	79 (110)	180 (62)	17 (21)	3 (2)	7 (4)	5 (6)	9 (3)	0.10 (0.05)
Middle												
Outer bark	0.52 (0.13)	1900 (240)	160 (25)	88 (17)	580 (57)	2500 (1000)	180 (40)	33 (13)	36 (12)	17 (6)	55 (6)	0.65 (0.14)
Inner bark	0.50 (0.09)	2500 (300)	530 (180)	96 (36)	2200 (770)	2500 (1100)	460 (170)	20 (14)	21 (10)	23 (12)	61 (19)	0.85 (0.10)
Sapwood	0.54 (0.16)	510 (68)	58 (17)	25 (4)	320 (110)	400 (98)	95 (24)	6 (4)	5 (1)	7 (4)	24 (5)	0.21 (0.04)
Heartwood	0.51 (0.15)	450 (48)	12 (6)	18 (3)	42 (19)	170 (52)	16 (10)	2 (2)	6 (3)	6 (4)	9 (3)	0.10 (0.04)
Upper												
Outer bark	0.48 (0.13)	2300 (450)	250 (120)	85 (19)	920 (460)	2400 (790)	300 (120)	14 (14)	30 (12)	20 (8)	58 (11)	0.67 (0.15)
Inner bark	0.46 (0.17)	2700 (250)	610 (89)	97 (17)	2300 (600)	2300 (710)	600 (100)	24 (9)	19 (5)	25 (7)	72 (7)	0.86 (0.09)
Sapwood	0.45 (0.06)	590 (90)	73 (24)	28 (4)	410 (120)	410 (74)	110 (21)	4 (4)	6 (2)	5 (3)	24 (3)	0.22 (0.07)
Heartwood	0.46 (0.10)	490 (29)	11 (5)	20 (1)	41 (26)	190 (53)	19 (12)	3 (3)	6 (1)	5 (4)	10 (3)	0.11 (0.05)

TABLE 2. *Mean (1 SD) concentrations of organic compounds in bark and wood sustrates at lower, middle, and upper sections of Douglas-fir boles in western Oregon. N = 14 for each position × substrate combination. All data are percent ash-free dry weight of the original sample.*

Section	Substrate	Lignin (%)	Tannin (%)	Non-Polar (%)	Acid Sol (%)	Water Sol. (%)	WS Sugar (%)	AS Sugar (%)
Lower	Outer bark	51 (4)	6.7 (1.9)	9.8 (2.4)	24 (3)	15 (3)	4.8 (1.3)	17 (3)
	Inner bark	27 (2)	9.7 (1.8)	6.0 (2.0)	44 (4)	23 (3)	10.0 (1.9)	37 (4)
	Sapwood	26 (2)	1.2 (0.8)	2.0 (0.8)	68 (4)	4 (2)	2.2 (0.7)	61 (4)
	Heartwood	27 (2)	2.7 (0.9)	2.9 (1.0)	63 (2)	8 (2)	3.2 (0.7)	57 (4)
Middle	Outer bark	43 (4)	7.8 (2.1)	11.0 (3.2)	30 (5)	17 (3)	6.4 (1.3)	22 (5)
	Inner bark	27 (3)	7.8 (1.6)	5.1 (1.7)	46 (2)	22 (3)	9.8 (1.7)	39 (3)
	Sapwood	26 (2)	0.9 (0.2)	2.4 (0.8)	68 (2)	4 (1)	1.7 (0.4)	62 (4)
	Heartwood	27 (1)	2.6 (0.4)	2.1 (1.0)	64 (2)	7 (1)	2.9 (0.5)	57 (3)
Upper	Outer bark	35 (8)	9.2 (2.5)	10.0 (2.0)	32 (4)	22 (8)	9.3 (2.5)	24 (4)
	Inner bark	23 (3)	8.6 (2.2)	5.6 (1.6)	46 (3)	25 (4)	11.0 (2.4)	39 (4)
	Sapwood	24 (7)	0.8 (0.2)	1.6 (0.9)	68 (2)	4 (2)	1.8 (0.4)	62 (4)
	Heartwood	27 (1)	2.7 (0.5)	2.1 (0.7)	64 (2)	7 (2)	3.0 (0.5)	58 (3)

highest. Similar differences in nutritional quality of the outer bark might induce similar feeding responses on Douglas-fir.

Organic compounds

Analysis of organic compounds in the samples showed that lignin levels (acid-insoluble compounds) were highest in the outer bark and differed little between inner bark, sapwood, and heartwood (Table 2). Lignin levels in the wood were consistent with previous reports (Isenberg 1980; Means et al. 1992), but decreased significantly in the upper section of the bole, especially in the outer bark. Lignin levels in the other substrates did not change substantially with height.

Tannin levels were highest in the bark substrates of the wood (Table 2), a finding that is consistent with the role of these compounds in protection against microbial attack. Tannin levels were lowest in the sapwood and increased slightly in the heartwood, regardless of bole section. Increases in tannin content in the heartwood are again typically associated with heartwood formation. Tannins have been considered to be mildly fungitoxic, although their role in protection of wood against fungal attack is probably minor in comparison with other extractives present in the wood.

The non-polar extracts (NPE) represent the fats, oils, and waxes that are soluble in dichloromethane. These materials, which are found principally in the ray parenchyma, appear to be important in initial colonization of wood by many microfungi (Abraham and Breuil 1993; Gao et al. 1994; Gao and Breuil 1995)). Levels of NPE were generally highest in the outer bark, followed by the inner bark (Table 2). Concentrations in the sapwood and heartwood were similar to one another, but only 20% to 30% of those in the outer bark. These differences probably reflect the tendency for more nutrient-rich phloem tissue to be pushed outward into the bark as the tree ages. Levels of NPE in the sapwood and heartwood would be a function of transport of nutrients from the actively photosynthesizing canopy downward and would be expected to vary with season and distance from the surface. Cells closer to the sapwood/heartwood boundary would tend to be less active and would, therefore, be expected to contain correspondingly lower NPE levels. Levels of NPE in heartwood would be a function of the components present at the time of cell death, since there tends to be little or no flow of materials into this region.

Water-soluble sugars in wood include glucose, fructose, and amylose. Like the NPE components, these sugars represent readily available nutrients of colonizing microfungi and are believed to be critical for the estab-

lishment of many organisms. Water-soluble sugar levels were significantly higher in the inner bark, followed by the outer bark, heartwood, and sapwood, and were significantly higher in the upper section of the bole (Table 2). The higher levels of water-soluble sugars in the heartwood were perplexing, since the sugars are generally believed to be consumed by the senescing cells as the sapwood dies and becomes heartwood. The presence of water-soluble sugars may have been offset by the toxicity of the phenolic extractives that were also present in this substrate.

Acid-soluble sugars consist primarily of glucose and represent the hydrolyzable components of cellulose and hemicellulose. Acid-soluble sugars were significantly lower in the outer bark, followed by the inner bark. Levels in the sapwood and heartwood did not differ markedly and were in general agreement with previous reports concerning levels of these components in Douglas-fir wood. Acid-soluble sugars also increased significantly in the upper section of the bole. Nutritionally, these sugars are far less accessible to insects and microorganisms at the start of the colonization process since they require the presence of cellulase or hemicellulase systems.

CONCLUSIONS

Wood is a complex matrix, and the differences noted in nutrient levels illustrate that there are further delineations within this matrix that may help explain why specific decomposers occupy certain niches. Gradients in elemental and carbon compound concentrations with bole height have important ecological consequences. Different ratios among these nutrients at different bole positions affect nutritional quality for bark- and wood-feeding organisms. Different portions of the bole might decompose at different rates, reflecting decomposer response to varying ratios of important nutrients. Hodges et al. (1968), for loblolly pine, and Schowalter et al. (1992, 1998), for oaks, found that bark- and wood-borer abundance and decay rate were concentrated in the nutritious inner bark. Further analysis of a broader sample of Douglas-fir would be necessary to confirm the results, but these preliminary data may help explain the associations between various microorganisms and arthropods in specific substrates of the bole.

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