Formation and Properties of Wetwood in White Fir

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ABSTRACT

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In white fir, wetwood is the usual condition of the heartwood. It is characterized by a moisture content generally equal to or greater than that of sapwood, a slightly lower pH, and a red-brown color. Ray parenchyma is alive and contains starch in the dry-appearing transition zone; at the wetwood border, however, nuclei disintegrate, starch disappears, and phenols accumulate. Osmotic potentials (ψ_π) are consistently lower than those in sapwood. Analyses of sapwood and wetwood indicate a selective accumulation of K, Ca, and organic acids in wetwood. The elevated levels of solutes account for much of the observed decrease in ψ_π. The data support an osmotic hypothesis to account for accumulation of water in wetwood.

The term "wetwood" has been applied to any nonliving wood with a water-soaked appearance in live trees. It is generally more alkaline than sapwood in hardwoods and more acidic in conifers (11). It has been found in association with mechanical wounds, frost cracks, insect attacks, branch stubs, butt rot, mistletoe cankers (8,11), and also in intact, healthy-appearing trees (6,27). Abnormal death of sapwood and tree decline are associated with wetwood in elm, certain poplars, and willow (2,7,11,13), but other species, including white fir, normally contain a central column of wetwood with no apparent damage (6,21,27). While some authors, working with elm (2), willow (7), and poplar (18), consider wetwood to be a disease caused by bacteria, it is also ascribed to influx of water through branch stubs (1,8) or to internal causes (6). Thus, the term "wetwood" may encompass diverse phenomena.

Ward and Pong (24) define wetwood as "a type of heartwood in standing trees which has been internally infused with water." Wilcox (27) concluded that, for white fir in the region studied, the terms "wetwood" and "heartwood" were synonymous since wetwood normally occupied the central core of heartwood. They are considered so in this paper as well, except that the term "heartwood" is used in a wider sense to include the inner core of nonliving wood in the rare tree in which it has a dry appearance.

A clearer understanding of wetwood and its cause(s) requires detailed observations of all aspects of its occurrence. This report presents results of a study of physical, chemical, and biological features of wetwood in white fir. Preliminary results were presented earlier (29).

MATERIALS AND METHODS

Study areas. Study trees were from forest stands of the northern Sierra Nevada of California at elevations of 1,700–2,000 m. These stands were mainly *Abies concolor* (white fir) with *A. magnifica* (red fir) as a minor component. Wetwood surveys were performed in conjunction with commercial thinnings in Modoc National Forest. Average age of sampled trees was 75 yr and average diameter at stump height was 19 cm. Trees selected for physical and chemical analyses were free of obvious defects and had adequate wetwood volume for sampling.

Moisture content. Increment cores were taken from cambium to pith at 0.5 m aboveground. They were immediately separated into sapwood and heartwood (discarding the transition zone and 5 mm on each side) and placed in sealed containers. The cores were later weighed and dried to a constant weight at 105 C. Moisture content was expressed as percent dry weight.

Psychrometry. Osmotic potential (ψ_π) of increment cores was measured with a hanging-drop psychrometer in the isopiestic mode (20).

Chemical analyses. After dried and weighed increment core sections were ashed, dissolved in 2 ml 6 N HCl with internal Li standard (3), and brought to volume, total K, Na, and Ca were measured with a Perkin-Elmer flame photometer. Bulk samples of wood for analyses of dissolved solutes were collected from 0 to 0.5 m aboveground. Fluid was expressed from sapwood or wetwood in a press at 68.95 MPa (10,000 lb/in.^{2}) and centrifuged in a Beckman microfuge for 2.5 min at 8,730 *g*. For measurement of dissolved cations, Li standard was added and samples were analyzed as above. Organic acids were measured as follows: expressed fluid or standard was acidified with 6 N HCl to aqua end point of crystal violet and then twice extracted with equal volumes of ether. The combined ether extract was extracted twice with equal volumes of 0.25 N NH_4OH. The combined NH_4OH extract was then shaken with Dowex 50W-X8 cation exchange resin (H^+, 149–74 μm [100–200 mesh], 0.2 g/ml of extract). Aliquots 2 to 5 μl in size were injected into a Varian gas chromatograph with a flame ionization detector and a 1.83 m × 3.2-mm (6 ft × 1/8-inch) stainless steel column packed with AT-1000 (Alltech Associates, 343 Second St., Los Altos, CA 94022). Flow rates were: N_2 carrier gas, 30 ml/min; O_2, 60 ml/min; and H_2, 10 ml/min. Temperatures were: injector and detector, 200 C; and column, 125 C. Peak height was used to quantify samples. On a second run, the Dowex treatment was eliminated with similar results.

Microscopy. Fresh tissue was sectioned on a sliding microtome and stained with Melzer's iodine for starch; trypan blue for nuclei; safranin or neutral red for general observation (22); and $FeCl_3$, $AgNO_3$, or Hoepfner-Vorsatz reagent for polyphenols (16).

RESULTS

A survey of fresh stumps at Black's Mountain showed that wetwood was present in every tree examined. It occurred as a central column of water-soaked, red-brown wood surrounded by a narrow (one to five rings) dry zone separating it from sapwood. Occasional radiating arms, still invested with a dry zone, extended into the sapwood in the region of branch stubs and enclosed wounds. The percentage of cross-sectional area occupied by wetwood varied considerably and was not correlated with radial growth rate (Fig. 1). Similar data were obtained in a survey of a timber-thinning sale on the Lassen National Forest.

Microscopic observation showed that ray parenchyma cells in the sapwood were starch-filled and had elongate nuclei, whereas

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starch and nuclei were nearly absent in the wetwood. In the transitional dry zone, starch remained while nuclei began to shrink, round up, and finally disappear along with starch at the wetwood border (Fig. 2). Concurrently, colored deposits that stained dark red-brown with the Hoepfner-Vorsatz reagent appeared in the dying cells. Aqueous wetwood extracts showed a UV absorbance peak at 280 nm and stained blue with the Folin-Ciocalteau reagent after preliminary fuming with ammonia. These features are characteristic of phenols.

Moisture contents showed wide tree-to-tree variation, but sapwood and wetwood had equivalent average moisture contents despite the wetter appearance of wetwood (Table 1). A single tree with dry-appearing heartwood had a heartwood moisture content much lower than sapwood.

The conversion from sapwood to wetwood was accompanied by a significant decrease in ψ_π (Table 2). A search for the osmotically active materials in wetwood showed striking chemical differences between sapwood and wetwood. Sodium levels remained unchanged at the lower limit of detection, so its measurement was discontinued. Combined concentrations of total K and Ca showed a twofold to fourfold increase in wetwood over sapwood (Table 3). Combined concentrations of dissolved K and Ca showed greater differences. These data represent the portion of total (dissolved and undissolved) concentrations that contributes to osmotic activity. Incremental analyses of K and Ca along the stem radius showed that the differences result from steep gradients at the transition

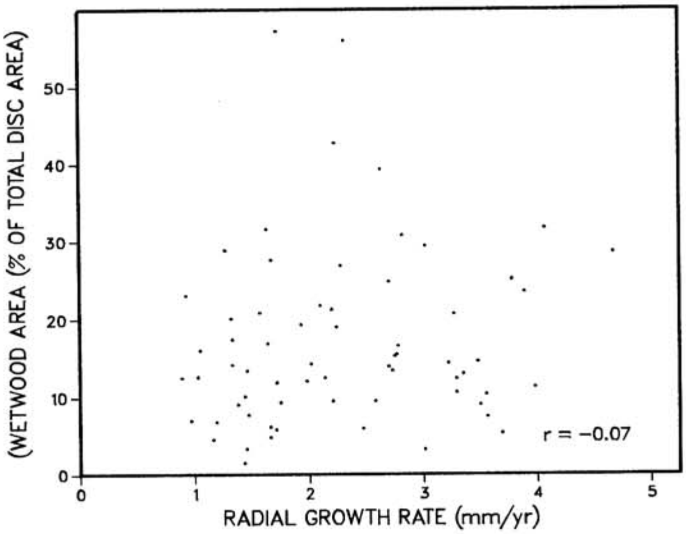

Fig. 1. Relationship between proportion of cross-sectional area of tree occupied by wetwood at 0.5 m height and tree vigor as measured by radial growth rate for a sample of trees from Black's Mountain in Modoc National Forest in California.

TABLE 1. Moisture contents of sapwood and heartwood of twelve white fir trees with wet- or dry-appearing heartwood

	Moisture content (% of dry weight)	
Heartwood appearance	Sapwood	Heartwood
Wet	140[a]	136[a]
	149	140
	195	216
	119	99
	199	140
	241	189
	178	206
	190	196
	151	200
	173	147
	156	231
$\bar{x}$[b]	172 ± 23	173 ± 28
Dry	209[a]	62[a]

[a] Each value represents the mean of three samples from a tree.
[b] Mean ± standard deviation.

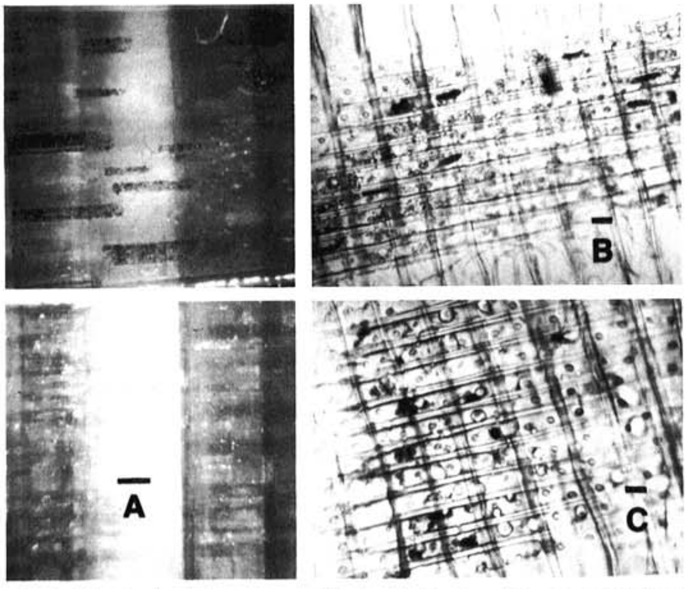

Fig. 2. Histological changes associated with the transition zone between sapwood and wetwood. **A,** Radial section from transition region stained with Melzer's iodine reagent for starch and mounted on a slide, superimposed over the sample block in its original position. Sapwood is on the left, the transition zone is the light-colored growth ring in the center, and wetwood is on the right. Scale bar = 1 mm. **B,** Radial section of sapwood stained with trypan blue showing elongate nuclei. Scale bar = 20 μm. **C,** Similar section in transition zone showing rounded condition of nuclei. Scale bar = 20 μm.

TABLE 2. Measured and predicted osmotic potentials (ψ_π) of sapwood and wetwood of four white fir trees from the northern Sierra Nevada in California

		ψ_π (bars)		
Tree	Tissue	Measured[a]	Predicted[b]	Predicted/ Measured
11	Sapwood	−2.4[c]	−0.8	0.33
	Wetwood	−7.6	−7.2	0.95
12	Sapwood	−3.3	−0.2	0.06
	Wetwood	−5.8	−4.3	0.74
13	Sapwood	−2.0	−0.3	0.15
	Wetwood	−5.3	−4.4	0.83
14	Sapwood	−2.9	−0.2	0.07
	Wetwood	−6.4	−4.9	0.77
				$\bar{x}$ Sapwood = 0.15
				$\bar{x}$ Wetwood = 0.82

[a] All values for measured ψ_π represent the mean of three replications.
[b] Predicted ψ_π was calculated from known concentrations of dissolved K and Ca using the Van't Hoff formula (17).
[c] Means for sapwood and wetwood are significantly different for all trees.

TABLE 3. Combined concentrations of total (dissolved + undissolved) and dissolved K and Ca in sapwood and wetwood of four white fir trees from the northern Sierra Nevada in California

	Total [K + Ca] (mg/ml)		Dissolved [K + Ca] (mg/ml)	
Tree	Sapwood	Wetwood	Sapwood	Wetwood
11	5.1[a,b]	10.2	0.6	5.7
12	1.5	5.8	0.2	3.4
13	2.2	7.1	0.3	3.5
14	1.8	8.4	0.1	3.9

[a] All values represent the mean of three replications.
[b] Means for sapwood and wetwood are significantly different ($P = 0.01$) for measurements of both total and dissolved K and Ca in all trees.

TABLE 4. Concentrations of organic acids in sapwood and wetwood of six white fir trees from the northern Sierra Nevada in California

Acid concentration (mM)					
Acetic		Propionic		Butyric	
Sapwood	Wetwood	Sapwood	Wetwood	Sapwood	Wetwood
0[a]	25	0	37	0	23
3	9	0	22	1	2
0	16	0	55	0	5
3	19	0	4	0	7
0	38	0	45	0	16
0	0	0	4	0	0

[a] All values represent the mean of three replicated measurements.

zone (Fig. 3).

The "uric" or fermentative odor of wetwood noted by other authors was readily detected in this study. Acetic, propionic, and butyric acids are present in wetwood in varying concentrations and are virtually absent from sapwood (Table 4). These acids were not detected in two trees sampled in which the heartwood was relatively dry and light in color. Other low-molecular-weight aliphatic acids could not be detected.

A glass electrode was used to measure pH of expressed fluid; that of sapwood averaged pH 5.7 and that of wetwood averaged pH 5.4.

DISCUSSION

The frequency of wetwood in firs observed in this work supports the observations of Wilcox (27), Etheridge and Morin (8), and Coutts and Rishbeth (6). Even in species in which it has been considered a damaging disease, wetwood is present in most individuals. Toole (21) found wetwood in 86% of cottonwoods larger than 15.2 cm (6 inches) in diameter, and Manion (12) refers to surveys in which wetwood was found in every elm examined.

Coutts and Rishbeth (6) demonstrated that wetwood formation in *A. alba* required physiological activity. They also state that suppressed trees have a lower proportion of water-soaked heartwood than vigorous trees. We found no such correlation if radial growth rate was used as a vigor rating. Nevertheless, the coincidence of starch disappearance with water accumulation supports the concept of an active role of the tree in wetwood formation. In *Quercus bicolor*, heartwood formation and sapwood wound response involve starch disappearance and nuclear disintegration closely paralleling the changes reported here (25).

The dry-appearing zone between sapwood and wetwood has been noted in *A. concolor* by Owen and Wilcox (15), in *A. grandis* by Coutts and Rishbeth (6), and in *A. alba* by Bauch et al (1). Measurements in *A. alba* indicated that the moisture content of the transition was about 60%, similar to that in the heartwood of the tree found with no wetwood in this study (Table 1). Coutts (5) hypothesized that sapwood drying of this nature is caused by gas emboli formed in tracheids as a result of metabolic events in gradually dying ray parenchyma.

The change in nuclear morphology in the transition zone, when considered with other morphological and chemical changes, indicates that, although the cells are still alive in this region, they are undergoing substantial physiological modification.

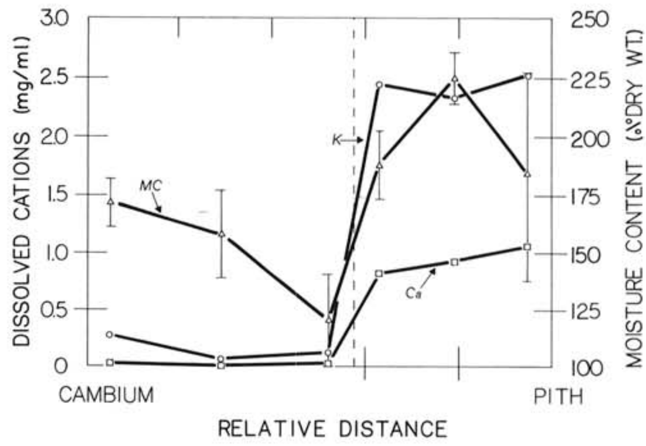

Fig. 3. Changes in moisture content and concentrations of dissolved cations across the gradient from cambium to pith for a representative tree from the northern Sierra Nevada in California. Dotted line represents the position of the transition zone.

Accumulation of cations in wetwood is reminiscent of a similar influx in the vicinity of wounds and decay in hardwoods (19). Since our preliminary report (29), Murdoch and Campana (14) have described similar relationships in elm wetwood. Hart (9,10) found that discolored, nonliving sapwood of several hardwoods (including white oak) had higher moisture and ash content than either normal sapwood or heartwood. This contrasts with true heartwood of white oak, which is drier and has less K and Ca than sapwood (26). Our results indicate that cation accumulation coincides with rewetting of the heartwood. The ray parenchyma cells with streaming cytoplasm (5) provide a likely pathway for influx of cations. The maintenance of this concentration gradient probably reflects the continuous migration of cations into wetwood as it is formed and the low diffusivity of cations across tracheids in the dry transition zone.

Relatively low values of ψ_π in wetwood have been found also in *A. grandis* (6). Such low osmotic potentials can be attributed in large part to the K and Ca salts present. Using the Van't Hoff relationship (17), the theoretical osmotic potential of a known solution can be calculated. Based on known concentrations of K and Ca and assuming corresponding concentrations of monovalent anions, predicted osmotic potentials of wetwood compare favorably with those measured (Table 2).

Organic acids found in wetwood of *A. concolor* in this study have also been found in wetwood of *A. alba* in Europe (1). The acid corrosion of kilns used to dry fir (24) and metal products shipped in wood crates (4), as well as the characteristic odor can be explained by these findings. In addition, the combined concentrations are enough to constitute a major portion of the anionic contribution to the osmoticum. Facultatively anaerobic bacteria present in wetwood of white fir (28, and *unpublished*) are the likely producers of the acids.

The results indicate that wetwood is the usual condition of heartwood in white fir and that its formation is an integral part of a series of concomitant changes in the conversion of sapwood to heartwood. The data support the concept that salt accumulation decreases ψ_π, thus leading to water accumulation.

Oxygen concentrations in wetwood of cottonwood inhibit growth and decay of heart-rot fungi in vitro (23). The effect of watersoaking and other characteristic features of fir wetwood on the development of *Fomes annosus* will be the subject of a future publication.

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