Root Chemistry of Mature Douglas-Fir Differs by Habitat Type in the Interior Northwestern United States

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ABSTRACT. Carbon compound concentrations in plant tissues depend on the environment in which plants grow. However, little is known about how these concentrations vary across a range of forest environmental conditions. Our study examined root tissue (phloem, cambium, phellum, and phelloderm) collected from naturally regenerated mature Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Bessn.] Franco) trees in eight stands on three habitat type series encompassing a range of temperature and moisture conditions. The objective was to determine root chemical composition (sugar, starch, phenol, and tannin) differences among the habitat types. Douglas-fir roots collected from dry, warm Douglas fir habitat types had sugar concentrations of 4% compared to 3% for roots from cool, moist habitat types. Root samples collected from Douglas-fir habitat types showed tannin concentrations about double those from grand fir or western redcedar habitat types. Phenol/tannin ratios for the cool, moist habitat types were about double those from warm, dry Douglas-fir habitat types. Roots sampled from western redcedar habitat types had phenol concentrations and phenol/sugar ratios more than 50% higher than those from Douglas-fir and grand fir habitat types. We speculate that root chemistry of Douglas-fir growing on Douglas-fir habitat types could make them more drought resistant but less disease resistant, while Douglas-fir growing on western redcedar types would be less drought resistant but more disease resistant. Douglas-fir growing on warm, dry sites allocated more carbon to tannin production and less to phenols. FOR. SCI. 46(4):531–536.

Additional Key Words: Carbon allocation, adaptation, disease resistance, drought resistance.

CONCENTRATIONS OF STORAGE AND SECONDARY compounds in plant tissue, such as sugars, starches, phenols and tannins, depend to a considerable extent on the environment in which plants grow (Waring et al. 1985, Huber and Arny 1985). The concentrations of these compounds and the balance among them help to determine the resistance of plants to herbivores and pathogens (Wargo 1972, Garraway 1975, Ostrofsky and Shigo 1984, Larsson et al. 1986, Mwangi et al.1990, Dudt and Shure 1994). Recently, there has been increased interest in developing a better understanding of the growing environment and biochemical characteristics for forest trees (Bryant et al. 1983, Entry et al. 1991a, Moore et al. 1994, Gebauer et al. 1998, Penuelas and Estiarte 1998, Shaw et al. 1998). Douglas-fir was selected for our study because it is commonly managed in the forests of the inland Northwest of North America and has wide ecological and geographic distributions.

Resource availability may influence production of secondary compounds like phenols and tannins (Mooney 1972, Bazzaz et al. 1987). In our study, we wanted to ascertain the influence of environmental factors, specifically differences in temperature and moisture growing conditions, on the levels of carbon-based compounds in the roots of forest-grown, mature Douglas-fir trees. Although on-site temperature and moisture measurements were not made in our study, we rely on the literature that suggests stands growing on a

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variety of habitat types (Daubenmire and Daubenmire 1968, Pfister et al. 1977) should represent a range of temperature and moisture conditions. Furthermore, habitat classification of forestland in the inland Northwest is common and ecological interpretations are well developed (Cooper et al. 1991, McDaniel et al. 1994, Neiman 1988). Implicit in our approach is the untested assumption that variation in root chemistry due to short-term weather differences is minor compared to long-term environmental effects reflected by different habitat types. We believe this assumption is reasonable, but it should be tested in future work. Thus, the principal objective of our study was to determine differences in the chemical composition of Douglas-fir roots among habitat types.

Methods and Materials

Site Selection

The Intermountain Forest Tree Nutrition Cooperative (IFTNC) maintains a large set of long-term Douglas-fir nutrition field experiments (Moore et al. 1991). We selected eight IFTNC sites for root chemistry sampling, only using trees growing on the untreated control plots. The eight study sites are located in northern Idaho, northeastern Oregon, and eastern Washington, and included Douglas-fir (dry and warm growing conditions), grand fir (*Abies grandis* [Doug.] Forbes) (moderate temperature and moisture regimes), and western redcedar (*Thuja plicata* Donn.) (cool and moist growing conditions) habitat type series. Our intent was to use habitat type series as a selection criterion to ensure a broad range of temperature and moisture conditions for our study. Mean annual total precipitation estimates for 31 sites in Idaho, including 4 of the sites used in this study, varied significantly ($P = 0.0001$) by habitat type, with Douglas-fir types averaging 80 cm, grand fir types 92 cm, and redcedar types 111 cm of precipitation per year over a 30 yr period (IFTNC Annual Report 1992). These data support the use of habitat type as a way to allocate our samples across a range of environmental conditions. Selected site and stand characteristics for the eight study sites are provided in Table 1. All sites are dominated by Douglas-fir, averaging 90% composition by basal area for this species (Table 1). Elevations range from about 700 to 1400 m; thus our study includes only low- to mid-elevation Douglas-fir stands. Soil taxonomy differed at each site: for example, the following soil orders were included among the eight sites: alfisols, andisols, inceptisols, and mollisols. The sites are divided among the three habitat types and consequently span a wide range of site quality as estimated by Douglas-fir site index (Table 1). All sites are populated by local Douglas-fir seed sources naturally regenerated after fire or natural harvest regeneration systems.

Tree Growth and Plot Measurements

Each plot sampled in the present study was 0.04 ha in size, and the average number of Douglas-fir sample trees per plot was 24. All live plot trees were tagged and measured for diameters at the beginning of the original fertilization experiment in 1981 and 1982. Every 2 yr, diameters were remeasured on all trees for a 10 yr period, and any incidence of damage or mortality along with probable cause was noted. Basal areas were summed over all trees, not just Douglas-fir, to obtain plot totals. Douglas-fir site index estimates for each plot were made based on height-age observations from stem analysis of destructively sampled trees located near each plot (Monserud 1984, Vander Ploeg and Moore 1989).

Collecting Tree Root Samples

Two undamaged and apparently healthy dominant Douglas-fir trees on the sampling plots at each of the eight study sites were selected for root chemistry sampling. Root bark samples of living tissues (including phloem, cambium, phellum, and phelloderm) 6.25 cm^2 in size were collected from four main lateral roots for each tree. The soil was carefully excavated from each root, and the samples obtained near the root collar (~ 0.3 m from the tree bole) just under the mineral soil surface. Shaw et al (1998) showed that root collar samples were highly correlated with root tip samples for phenol, tannin, sugar, and starch concentrations for young Douglas-fir trees. Thus, we feel the root collar sampling location used in our study is representative of the entire root system. In addition, field sampling procedures are similar to those of Entry et al. (1991b). Samples were collected from all sites during fall 1993. After collection, the four root samples were composited by tree, placed in plastic vials, quickly frozen on dry ice, and placed in insulated containers for transport back to the laboratory for processing. At the laboratory, the samples were placed in an ultra-cold (-80˚C) freezer until they could be freeze-dried awaiting laboratory analysis.

Quantification of Carbohydrates, Phenolics, and Tannins in the Root Tissues

For the chemical analyses, all bark samples were put in liquid nitrogen overnight. The following day, dead outer root bark was removed to the phloem, and samples of the living

Table 1. Selected site and stand characteristics for eight Douglas-fir study sites in the inland Northwest.

Habitat type series	Latitude	Longitude	Elevation (m)	Aspect	Douglas-fir site index (m @ 50 yr)	Stand age (yr @ BH)	Initial basal area (m^2/ha)	Net basal area growth (m^2/ha/yr)	Percent Douglas-fir by basal area
Redcedar	47.17	116.30	1,400	S	26	50	50	0.68	75
Redcedar	47.97	116.92	1,160	S	26	34	44	1.08	92
Grand fir	45.73	117.78	730	W	23	72	34	–0.55	96
Grand fir	48.38	119.83	990	ENE	17	75	24	0.87	95
Grand fir	47.55	117.00	1,035	S	27	54	61	0.82	71
Grand fir	46.38	115.98	960	N	22	57	40	0.93	88
Douglas-fir	48.87	118.47	915	SW	15	100	21	0.55	100
Douglas-fir	45.95	121.00	760	SSE	20	64	27	1.25	100

tissues of the inner bark were then ground to powder in a mortar. Total phenols were determined from samples after extracting with aqueous acetone (80%), adding Folin-Ciocalteu's Reagent and then measuring absorbances at 700 and 735 nm (Julkunen-Tiito 1985). Other subsamples were analyzed for total soluble starch through an ethanol and perchloric acid method (Hansen and Moller 1975), and glucose was subsequently determined by adding anthrone solution for absorbance determination at 630 nm (Hansen and Moller 1975). Glucose concentration measurements were calibrated with a glucose standard (Hansen and Moller 1975). The Hansen and Moller method overestimates starch levels because carbohydrates other than starch are extracted during the process (Marshall 1986, Rose et al. 1991). Perchlorate-extractable carbohydrates were, therefore, corrected to yield starch concentrations and are expressed in their corrected form throughout this article. Tannin was determined by extracting with 80% aqueous acetone, loading the extract into an agarose plate containing bovine serum albumin, and measuring diffusion rings (Hagerman 1987). The Institute of Biological Chemistry, Washington State University, Pullman, WA, performed the analysis of starch, sugar (glucose), total phenols, and protein-precipitable tannins.

Statistical Analysis

Analysis of variance (PROC GLM) was first used to test for differences between means by habitat type series for root chemistry data using the least-squares means procedure of the Statistical Analysis System (SAS Institute Inc. 1985). Subsequently, correlations between the various root chemical constituents and several measures of stand growth rate, as well as age, were analyzed to better explain some of the ANOVA results.

Results

The results of the Douglas-fir root chemical analyses, expressed as mean root concentrations and concentration ratios for the three habitat type series, are shown in Figure 1. Trees growing on Douglas-fir habitat types had an average root sugar concentration of 4%, significantly higher than the 3% averaged by those growing on grand fir or redcedar habitat types. However, starch concentrations showed no significant differences among the three habitat type series. Root phenol concentrations (20.2%) and phenol/sugar ratios (6.7) were significantly higher for trees growing on western redcedar habitat types compared to grand fir and Douglas-fir

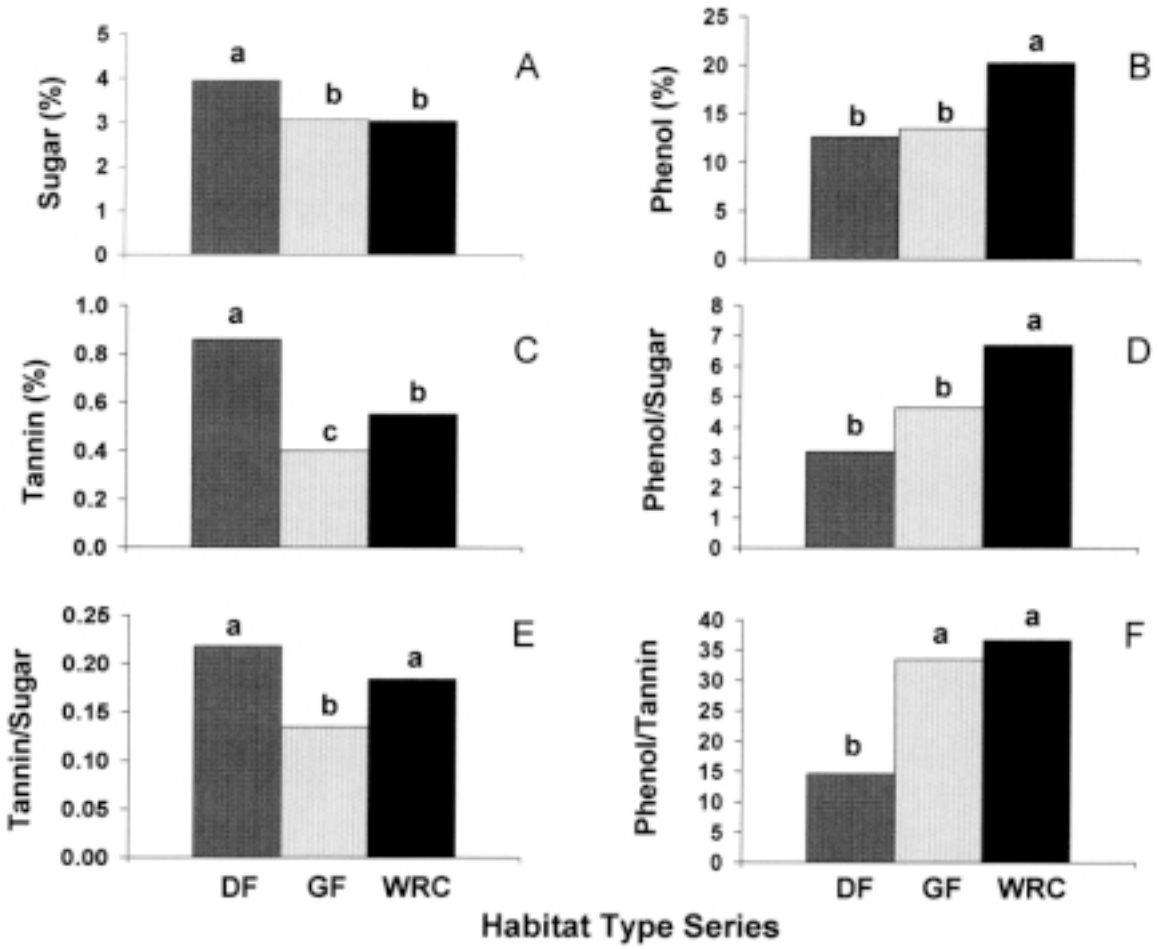

Figure 1. Means for percent soluble sugar (A), percent total phenol (B), percent protein-precipitable tannin (C), phenol to sugar concentration ratios (D), tannin to sugar concentration ratios (E) and phenol to tannin concentration ratios (F) found in root tissue of mature Douglas-fir growing on western redcedar (WRC), grand fir (GF) and Douglas-fir (DF) habitat type series. Different lower case letters indicate that the respective means were statistically different at the α = 0.10 level.

habitat types where concentrations averaged 13.4 and 12.6% with ratios of 4.6 and 3.2, respectively. Conversely, trees on Douglas-fir habitat types showed significantly higher root tannin concentrations than trees on either grand fir or western redcedar habitat types and showed higher tannin/sugar ratios than trees on grand fir habitat types. The average phenol/tannin ratio for Douglas-fir habitat types was 14.6 compared to mean ratios of 33.5 and 36.6 for grand fir and redcedar habitat types, respectively.

Results of correlation analyses of the root chemistry concentrations (i.e., sugar, starch, phenols, tannins) and concentration ratios (i.e., phenol/sugar, tannin/sugar, phenol/tannin) with plot growth rates, stand age, and Douglas-fir site index are provided in Table 2. Net basal area growth (BAG) and relative net basal area growth (RBAG) for the 10 yr just previous to root collection were positively correlated with sugar concentrations in Douglas-fir roots. All other correlations of plot growth rate, site index, or age with root biochemical concentrations or ratios were nonsignificant.

Table 2. Correlation coefficients of Douglas-fir root chemical composition to measures of plot growth rate, site index, and stand age. Coefficients marked with an asterisk are statistically significant at $\alpha = 0.05$.

	Basal area growth[a]	Relative basal area growth[b]	Site index[c]	Age
Sugar	0.75*	0.86*	–0.53	0.29
Starch	0.05	–0.11	0.44	–0.19
Tannin	0.34	0.51	–0.46	0.37
Phenol	0.20	–0.10	0.56	–0.67
Tannin/sugar	–0.03	0.09	–0.19	0.25
Phenol/tannin	–0.22	–0.52	0.69	–0.68
Phenol/sugar	–0.32	–0.58	0.68	–0.59

[a] The 10 yr plot net basal area growth rate for the period just prior to root sampling.
[b] Basal area growth ÷ plot basal area at beginning of the period.
[c] Douglas-fir site index (Monserud 1984).

Discussion

Root phenol, tannin, sugar and their ratios vary significantly by habitat types for natural, forest-grown, mature Douglas-fir trees (Figure 1). Sugar and tannin concentrations are highest and phenol/tannin ratios lowest on dry, warm Douglas-fir habitat types. Root phenol concentrations and phenol/sugar ratios are highest on cool, moist redcedar habitat types. There are several alternative explanations for these results. Herms and Mattson (1992) suggest that plants face a carbon allocation dilemma: whether to allocate more C to sugar, starch, and cellulose production (i.e., rapid growth) or to allocate relatively more C to the production of secondary metabolites, such as phenols and tannins, which are important in plant defense against diseases and insects. We attempted to develop empirical support for Herms and Mattson's growth-differentiation balance hypothesis as an explanation for our results by conducting the correlation analysis presented in Table 2. We expected to find significant negative correlations between stand growth rate and phenol and tannin concentrations; however, none of those correlations were significant. We are not suggesting that our study is a rigorous test of the growth-differentiation balance hypothesis, merely that the expected relationships between growth and secondary metabolites were not evident in our data. Perhaps this result can be explained by nonlinear effects of resource availability on secondary metabolism and resultant levels of root phenols and tannins (Mattson and Haack 1987, Tuomi et al. 1988, Horner 1990). Given our limited number of observations, we are unable to fully detect possible nonlinear relationships between root chemical constituents and plot growth rates. The only consistent relationship represented in Table 2 is between root sugar concentration and stand growth rate: faster growing Douglas-fir stands accumulated more sugar in their roots. Stand growth rate is affected by stand density as well as by site quality; due to the density effect, one of the Douglas-fir habitat type sites grew faster than any other site, despite a low site index. Therefore, stand growth rate does not directly represent differences in site quality.

Trees growing on Douglas-fir habitat types were older than those growing on grand fir and redcedar habitat types, but age per se was not significantly correlated with root chemical concentrations or their ratios. Thus, age differences by habitat type in our study do not account for the observed differences in root chemistry by habitat type.

Wargo (1980), working with sugar maple, and Entry et al. (1991a, 1991b), working with Douglas-fir, reported that increased levels of glucose enable the *Armillaria* fungus to grow more rapidly in tree roots, making the fungus better able to break down phenol compounds. Possible higher root sugar concentrations in faster growing Douglas-fir stands would cause them to be more susceptible to root rot infection; however, the concurrent level of defense chemicals, such as phenols, in the roots is also important in determining conifer susceptibility to root disease (Entry et al. 1991b, Gebauer et al. 1998).

Levels of resource availability—light, moisture, and nutrients—affect the rates of net assimilation, growth, and secondary metabolism. The functional relationships between these processes have not yet been established for Douglas-fir, but our study provides insights into the outcomes of these processes. The habitat type series included provide a range of resource availability conditions in the forests of the inland Northwest. The warm and dry Douglas-fir habitat types represent the most resource-limited conditions, while the cool and moist western redcedar types represent the highest resource levels in our study (Cooper et al. 1991, Neiman 1988). Our study did not have on-site instrumentation to monitor short-term annual variation in temperature and moisture; rather, we relied on general descriptions provided in the literature of environmental conditions represented by different habitat types. Habitat types reflect very long-term differences in the environment and how plant communities have adapted to those conditions. Rehfeldt (1989) demonstrated that Douglas-fir is very tightly adapted to its environment, and Myszewski (1999) showed strong Douglas-fir family differences and heritabilities for the same root compounds examined in our study. These findings, coupled with the lack of correlation between stand growth rate and phenol or tannin concentrations or their ratio in our study, leads us to suggest that carbon allocation to phenols or tannins in

Douglas-fir is under fairly strong genetic control. We further speculate that root phenol and tannin levels would be relatively unaffected by short-term differences in weather patterns and consequent growth rate variation. This idea should be tested in future work.

Douglas-fir trees growing on warm and dry Douglas-fir habitat types had significantly higher sugar, lower phenols, and lower phenol/sugar ratios in their roots than did Douglas-fir growing on western redcedar habitat types. Entry et al. (1991b) showed that the sugar concentration and phenol/sugar ratio in Douglas-fir roots were strongly positively correlated with the incidence of *Armillaria* infection in the same trees. Furthermore, McDonald et al. (1987) found that "incidence of pathogenic *Armillaria* showed a strong tendency to decrease as habitat type productivity increased. . . . The relatively less productive Douglas-fir series exhibited high incidence of root disease and the relatively more productive grand fir, western redcedar, and western hemlock series significantly less." Root-rot-caused mortality on our eight study sites over the 10 yr period prior to root chemistry sampling shows the same general pattern described by McDonald et al. (1987). The average root-rot-caused mortality rates in our study based on numbers of trees by habitat type were: 8.8% for Douglas-fir; 4.2% for grand fir; and 1.5% for redcedar habitat types. The high sugar concentrations and low root phenol/sugar ratios we found, coupled with Entry et al.'s (1991b) results, provide a plausible explanation for the results of McDonald et al. Phenols are large, complex, carbon-based molecules that require more energy for fungi to break down than is obtained from the process. Sugars provide a ready source of energy allowing fungi to grow rapidly.

Douglas-fir root tannin concentration and tannin/sugar ratios were significantly higher for Douglas-fir habitat series, opposite to the pattern that we observed for phenols and phenol/sugar ratio. Root phenol/tannin ratios were significantly lower for Douglas-fir habitat types than they were for grand fir and redcedar types. Tannins are secondary metabolites, as are phenols, and may play a role in plant chemical defense against pests. For conifers, however, the function of tannins in resistance to disease and insect infestation has not been as well established as it has been for phenols. Defense is not the only role identified for tannins in plants. Other functions include: structural support (Rhodes 1985, Haslam 1988); drought resistance (Rhoades 1977, Bariska and Pizzi 1986, Pizzi and Cameron 1986); and protection of roots from acidic soil environments (Kimura and Wada 1989). The average site indices by habitat type series for our study sites were: Douglas-fir 17; grand fir 22; and redcedar 26 m. If we consider Douglas-fir site index as an expression of the degree of moisture limitation, then Douglas-fir habitats are clearly more limited with respect to moisture. We therefore speculate that the elevated root tannin levels of Douglas-fir growing on the dry Douglas-fir habitat series reflect the role of tannins in improved drought resistance. Furthermore, given the significantly lower phenol/tannin ratios for Douglas-fir habitat types, our results suggest some effect of moisture limitation on shifting carbon from phenol to tannin production.

Our study is about the ecology of root biochemistry of native Douglas-fir forests growing on a wide variety of sites in the inland Northwest, but we can currently only speculate about the physiological basis for our results. We certainly realize that the observed differences in root chemistry are the outcomes of myriad biological and physiological processes and their complex interactions (well reviewed by Herms and Mattson 1992). However, we feel our study results are directly useful in generating hypotheses about the physiological ecology of Douglas-fir and its interactions with native pests at a landscape level in the inland Northwest. Further, our results could help in the design of future physiological studies aimed at testing such hypotheses concerning factors influencing net assimilation, growth rates, and secondary metabolism that determine forest productivity across the wide variety of site conditions in the inland Northwest.

Conclusions

Native Douglas-fir growing on different habitat type series showed significantly different concentrations and ratios of root chemical compounds. Trees growing on dry, warm Douglas-fir habitat types had significantly greater sugar concentrations and significantly lower phenol/sugar ratios than trees growing on more cool and moist grand fir and western redcedar habitat types. These root chemical characteristics suggest that Douglas-fir growing on Douglas-fir habitat types may be less resistant to root rot infection, particularly by *Armillaria*, than Douglas-fir growing on grand fir and western redcedar habitat types.

The roots of Douglas-fir growing on Douglas-fir habitat types were also higher in tannin concentration and had lower phenol/tannin ratios. The higher tannin levels may improve Douglas-fir drought resistance on the dry and warm Douglas-fir habitat types.

The observed differences in root chemistry likely derive from long-term adaptation of Douglas-fir to the different environments represented by the habitat types included in our study. These results are potentially important for Douglas-fir genetic improvement programs as well as general seed and seedling deployment strategies.

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