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ABSTRACT

Several studies have linked high phenolics:sugar ratios in the inner root bark tissue of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) to decreased susceptibility to *Armillaria* spp. While these studies have identified environmental factors that influence root chemistry, none have examined whether the phenolics:sugar ratio is genetically controlled. In this study, the effects of genetics and environment on Douglas-fir root bark chemistry were investigated. Significant differences in root bark chemistry of 15-yr-old Douglas-fir were detected among 20 open-pollinated families and 2 sites in northern Idaho. Family, site and the family x site interaction were significant sources of variation in the concentrations of sugar, starch, protein-precipitable tannins, and phenolics as well as in the phenolics:sugar ratio. Single-tree narrow-sense and family heritability estimates revealed that 20-24% of the variation in the phenolics:sugar ratio can be attributed to genetic differences, while around 60% of the variation in sugar concentrations can be attributed to genetic differences. Family and individual narrow-sense heritability estimates for 12-yr height growth were 0.62 and 0.54, respectively. While the correlation between height and the phenolics:sugar ratio was not significant, three families above the seventieth percentile in height growth expressed above average phenolics:sugar ratios at both sites. Should a high phenolics:sugar ratio prove effective in selecting genotypes for resistance to *Armillaria* infection, these results suggest that it would be possible to do so without sacrificing families with superior height growth in a tree improvement program. Gains could be made even more efficiently by selecting for low sugar concentrations.

INTRODUCTION

As forest composition has shifted from stands dominated by pine to mixed stands of Douglas-fir, spruce and fir, root diseases have become increasingly frequent in the Interior Northwest (Filip and Goheen 1984; Schwandt et al. 1990; Beckman et al. 1993). Mortality centers cover an estimated 1% of all commercial forests and substantial losses occur on an additional 13% of forest acreage (James et al. 1984). Root diseases are responsible for a third of the annual mortality in the region (James et al. 1984) and nearly 7 million cubic meters in lost volume (Smith 1984). In Idaho alone, trees growing on more than 800,000 hectares have been infected by root pathogens (Beckman et al. 1993) with volume losses estimated at 900,000 cubic meters (Beckman et al. 1993).

The most common root pathogens in the region are *Armillaria* spp. (Morrison 1981; James et al 1984; Wargo and Shaw 1985; Tainter and Baker 1996). *Armillaria* is particularly aggressive in western forests, accounting for over a quarter of all tree mortality (James et al. 1984; Wargo and Shaw 1985; Tainter and Baker 1996). In mixed fir stands in Oregon, mortality from *A. mellea* resulted in volume losses of 28 to 104 cubic meters per hectare (Filip and Goheen 1984). *Armillaria* also causes significant losses in the volume growth of live trees (Bloomberg and Morrison 1989). In Southeastern British Columbia, infected Douglas-fir may produce as little as 41% of the volume produced by uninfected trees.

While *Armillaria* is capable of infecting all of the region's conifers, species vary in their susceptibility to the pathogen (Morrison 1981; Entry et al. 1992). Both field and experimental observations have found *Armillaria* infection rates to be significantly lower in western larch (*Larix occidentalis* Nutt.) than in either ponderosa pine (*Pinus*

ponderosa Dougl. ex Laws.) or western white pine (*Pinus monticola* Dougl. ex D. Don) (Morrison 1981, Entry et al. 1992). Infection rates are highest in Douglas-fir (*P. menziesii* (Mirb.) Franco) and grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) (Morrison 1981, Entry et al. 1992). Within species, susceptibility may also vary. Field observations in stands of Douglas-fir have identified individual trees growing within mortality centers that appear to be unaffected by the disease.

The mechanisms for resistance to *Armillaria* are not entirely known. However, several studies have suggested a link between infection rates and variation in root bark chemistry. Species with higher phenolics:sugar ratios in the root bark tend to be less susceptible to *Armillaria* than those with lower ratios (Entry et al. 1991*a*; Entry et al. 1992). Likewise, within a single species, stands with higher ratios of phenolics to sugars tend to be less susceptible to disease and insects than stands with low phenolics:sugar ratios (Wargo 1972; Entry et al. 1991*b*; Moore et al. 1993; Dudt and Shure 1994; Entry et al. 1994).

Wargo (1984*a*) hypothesized that the fungus uses energy gained from metabolizing sugars in the root tissue to breakdown defense compounds, such as phenols and tannins. When cultured in media supplemented with the simple sugar, glucose, *Armillaria* isolates show increased growth and rhizomorph development (Garraway 1975). However, when phenolic compounds are present in the media, growth is impaired until a solution with a high sugar concentration is added (Kirk 1981). Entry et al (1991*a*) hypothesized that a threshold for successful infection occurs where the energy required to breakdown defense compounds equals that gained by metabolizing sugars in the root

tissue. Similar hypotheses have been advanced to explain insect and bear preferences in oak and Douglas-fir stands (Feeny 1970; Kimball et al. 1997).

If variation in root bark chemistry is indeed linked to *Armillaria* susceptibility and it is at least partially controlled by genetics, it may be possible to decrease susceptibility in species like Douglas-fir by selectively breeding for high phenolics:sugar ratios. The objectives of this study were (1) to determine whether differences in root bark chemistry, in particular differences in the phenolics:sugar ratio, are genetically controlled in Douglas-fir, (2) to examine the relationship between height growth and root bark chemistry, and (3) to identify families with both superior height growth and high phenolics:sugar ratios.

METHODS

Site Descriptions

Two Inland Empire Tree Improvement Cooperative (IETIC) Douglas-fir progeny tests were sampled in this study. Both are located in northern Idaho in the mid-elevation (915 to 1219 m) breeding zone for Douglas-fir. The Rimrock test (lat.48°26′ N; long. 116°47′ W) is located near the Priest River Experimental Forest, southeast of Coolin, ID (Fins and Rust 1997). It has an average elevation of 1143 m and a west to northwest aspect. Prior to planting, Rimrock was mechanically windrowed. The Bussel Creek test (lat. 47°05′ N; long. 116°09′ W) is located northeast of Clarkia, ID on land managed by the Potlatch Corporation. It has an average elevation of 1189 m and a southern aspect. Prior to planting, Bussel Creek was broadcast-burned. In addition to geographic

similarities, both progeny tests are on *Thuja plicata-Pachistima myrsinites* habitat types (Daubenmire and Daubenmire 1968).

Rimrock and Bussel Creek were established as sister tests to evaluate long-term progeny field performance. A third sister test was also established but with the exception of 12-yr height measurements, it is not included in this study. Each site contains the progeny of 260 families from eastern Washington, northern Idaho, and western Montana. In 1981, 1-yr-old container seedlings were planted in the tests at 1.5m x 1.5m spacing. Families were randomly assigned to one of five sets. Family members were distributed in 3 blocks, each containing randomized, non-contiguous, 9-tree plots, (27 test trees per family per site) (Fins 1983). We use the term "family" to refer to progeny of a single, open-pollinated parent tree. Parent trees were woods-run Douglas-fir, selected in 1979 based on superior growth and form characteristics. Set 1, which included 59 families, was selected for use in this study as it had high survival (90%) and relatively low damage (14%) across the three test sites compared to families in the other sets. The twenty families that were included in this study had also been previously sampled for an IETIC study relating foliar nutrient concentrations and height growth (Walker 1995).

Root Bark Samples

Samples of inner root bark tissue were collected from 5 to 11 members of each family at each site. A balanced design was not possible due to mortality in the progeny tests prior to sampling. Samples were collected during the first three days of October 1993 at Bussel Creek and from late September to early October 1994 at Rimrock. The root collar of each sampled tree was uncovered until two roots with a minimum diameter

of 1.27 cm were exposed. Then, a 3.81-cm x 7.62-cm rectangular section of inner root bark tissue was removed from each root. Samples were taken approximately 20.32 cm to 30.48 cm below the root collar and, wherever possible, from opposite sides of the tree. When only smaller (<1.27 cm diameter) roots were uncovered, two roots were clipped and sections of bark comparable in size to the chiseled samples were peeled from the roots. For 2 trees, only one root large enough to provide a sample was found so samples were taken from opposite sides of the same root. Samples were transported from the field in coolers and stored at -15° C at the University of Idaho, College of Forestry, Wildlife and Range Sciences in Moscow, ID until April 1995. Samples were then divided into two batches to facilitate laboratory schedules and submitted for analysis to the Institute of Biological Chemistry at Washington State University in Pullman, WA. The first set of samples was analyzed in December 1995; the second in August 1996.

Samples were freeze-dried and ground to a powder using a mortar and pestle. Sugar and starch concentrations were determined using the methods of Hansen and Moller (1975). Ethanol percolation and anthrone solution were used to extract sugar from the samples and ethanol and perchloric acid percolation were used to extract starch. Absorbances at 630nm were recorded and compared to standard curves produced with a glucose standard solution. Because pectin and other polymers are extracted by the ethanol/perchloric acid method (Marshall 1986, Rose et. al 1991, Shaw et al. 1998), starch values were adjusted as described in Marshall (1986). The adjusted starch concentration values are reported in this paper. Protein-precipitable tannins were extracted from the tissue samples using 80% aqueous acetone (Hagerman 1987). Concentrations were determined by comparing diffusion rings measured on an agarose

plate containing bovine serum albumin to a standard curve established with tannic acid (Sigma). Phenols were extracted with Folin-Ciocalteu's reagent and 80% aqueous acetone solution according to the methods of Julkunen-Tiitto (1985). Absorbances measured at 735 nm were compared to a standard curve established with phenol to determine phenol concentrations in the samples.

Growth and Form Measurements

Four surveys of damage sustained by trees in the two tests were conducted between test establishment and sample collection. In 1982 and 1984, the presence or absence of damage was recorded for each tree and damage was categorized as resulting from rodents, large animals, insects, physical factors, or unknown causes. In 1989 and 1992, the presence or absence of terminal damage was also recorded for each tree. In 1992, total tree height was measured at the three sister tests. These values were used to calculate the percentile height rankings for each family.

Statistical Analyses

A randomized block design was used to compare the root bark chemistry of 20 families growing in 2 progeny test sites. A statistical model containing family, site, and the family x site interaction terms was used to estimate genetic and environmental effects on root bark chemistry. To account for uneven sample sizes (5 to 11 trees per family per site), a general linear model analysis of variance (PROC GLM; SAS Institute 1990*b*) was used to identify significant sources of variation in the individual root compounds (sugar, starch, tannins, and phenolics) and in the phenolics:sugar ratio. Family and site mean

phenolics:sugar ratios were calculated using the PROC MEANS procedure of SAS (SAS Institute 1990*a*). Spearman correlation coefficients and genetic correlations were calculated for sugar, starch, tannins, phenolics and total height using PROC CORR (SAS Institute 1990*a*). Since damage to a tree can cause an increase in the production of defense compounds (Shrimpton 1972; Vance et al. 1980), Spearman correlations between the root bark compounds and the different measures of damage were also calculated.

Phenotypic (V_p) and additive genetic variances (V_a) were estimated for sugar, starch, protein-precipitable tannins, phenolics and the phenolics:sugar ratio using PROC VARCOMP (SAS Institute 1990*b*). Family and single-tree narrow-sense heritabilities were estimated for each of the root bark compounds, the phenolics:sugar ratio and 12-year height growth using equations adapted from those in Zobel and Talbert (1991) for estimating heritability in half-sib tests. The adapted equations are as follows:

$$\text{Family heritability} = \frac{\sigma^2_f}{(\sigma^2_e / n_2) + [n_1(\sigma^2_{fxs})/ n_2] + \sigma^2_f} \qquad \text{[Eq. 1]}$$

$$\text{Single-tree narrow-sense heritability} = \frac{4\sigma^2_f}{\sigma^2_e + \sigma^2_{fxs} + \sigma^2_s + \sigma^2_f} \qquad \text{[Eq. 2]}$$

where σ^2_f = variation due to family
σ^2_s = variation due to site
σ^2_{fxs} = variation due to the family x site interaction
σ^2_e = variation due to trees within the plots (sampling error)
n_1 = number of trees per family per site
n_2 = number of trees per family per site x number of sites

Variance components and coefficients for the family and single-tree narrow-sense heritability estimates were calculated using PROC VARCOMP (SAS Institute 1990*b*). Because the progeny tests used in this study contain open pollinated families, they are not true half-sib tests. Some of the progeny within the families may be full-sibs or even the

result of self-pollinations. Thus, the estimates of heritability and additive genetic variance are likely to be somewhat inflated.

RESULTS

Root Bark Chemistry

Site means differed only slightly between the two progeny tests for each root bark compound and for the phenolics:sugar ratio (Table 1); however, the range of values differed at the two sites. Sugar and tannin concentrations varied more at Bussel Creek while starch and phenolics concentrations varied more at Rimrock. Family means displayed by site show the variation between families and sites as well as the family x site interaction (Figure 1). Root chemical compound concentrations were not consistently higher at either site.

Analyses of variance results showed that concentrations of sugar, starch, protein-precipitable tannins and phenolics and the phenolics:sugar ratios were significantly different between sites and families (Table 2). There was also a significant interaction between family and site for each of the compounds and for the phenolics:sugar ratio.

Variance and Heritability

Variation in starch concentration was large and resulted in negative estimates of the family variance component. As is customary, the family variance estimate was replaced with 0. This caused the additive genetic variance and the heritability estimates for starch to be 0 (Tables 3 and 4). Estimates of V_a for the other compounds ranged from 0.0404 g^2 for tannins to 5.5756 g^2 for phenolics.

Both family and single-tree narrow-sense heritabilities were estimated from the mean squares variance components generated by SAS. Sugar concentrations had the highest heritabilities, with genetic variation accounting for approximately 60% of the total variation (Table 4). Family and single-tree narrow-sense heritability estimates for the phenolics:sugar ratios were moderate and genetic variation accounted for about 20-25% of the total variation in the ratio. Heritability estimates for 12-yr height (based on undamaged trees only) were 0.54 for single-tree heritability and 0.62 for family heritability.

Correlations between Root Bark Chemistry and Height Growth

Genetic correlation estimates between the root bark compounds and 12-yr height growth are provided in Table 5. Height was weakly but significantly correlated with tannin and phenolic concentrations (0.12 and 0.11 respectively) but not with sugar, starch or the phenolics:sugar ratio. Sugar and starch were significantly correlated with tannins, phenolics and the phenolics:sugar ratio but not with each other. Tannins and phenolics were significantly correlated with each other and with the phenolics:sugar ratio.

None of the root bark compounds were correlated with damage (Table 6). However, height was weakly but negatively correlated with physical and rodent damage and with the two measurements of terminal damage (-0.15, -0.11, -0.21 and –0.11, respectively).

Although the correlation between height and the phenolics:sugar ratio was not significant, there were families with both superior height growth and above average phenolics:sugar ratios at each progeny test. Three families in the top thirtieth percentile

for height growth are located in the upper right quadrant of Figure 2, and thus have above average ratios at both test sites.

DISCUSSION

The concentrations of sugar, starch, protein-precipitable tannins and phenolics showed significant genetic and environmental variation as did the phenolics:sugar ratio. The range of phenolics:sugar ratios observed at the two progeny test sites span the ratios reported for unthinned Douglas-fir stands (mean of 10.32) as well as for thinned and fertilized stands (mean of 5.73) (Entry et al.1991*b*). In the study by Entry et al. (1991*b*), unthinned stands of Douglas-fir had lower mean phenolics:sugar ratios than thinned stands (17.19) and were more susceptible to *A. ostoyae* (Romagn.) Herink infection. Stands that were thinned and fertilized had the lowest mean ratios and were the most susceptible to infection. In our study, the site mean phenolics:sugar ratios (5.3604 at Bussel Creek and 4.8496 at Rimrock) were lower than the stand means observed by Entry et al.(1991*b*). Foliar nutrient data suggest that the site means may be low as a result of nutrient deficiencies[1]. Over 75% of the trees sampled at Bussel Creek had foliar N levels below those considered adequate for Douglas-fir in the Inland Northwest (Garrison and Moore 1998). Entry et al. (1991*a*) found that trees grown with limited N tend to have lower phenolics:sugar ratios than trees grown with adequate amounts of N.

Differences in the phenolics:sugar ratio between the sites in this study were small and may have been influenced by sampling year. Because samples were collected from the two sites in different years, site differences cannot be separated from yearly

[1] data on file with the Inland Empire Tree Improvement Cooperative at the University of Idaho, Moscow, ID 83843

differences in this study. It is interesting to note however that for each compound, some families had higher mean values at Bussel Creek while others had higher mean values at Rimrock. The family x site interaction, which is relatively large, may also have been influenced by differences in sampling year.

There were several significant correlations between root bark compounds. As expected, sugar is negatively correlated with the phenolics:sugar ratio while phenolics are positively correlated with the ratio. The correlations between starch and phenolics or tannins (plant defense compounds) were negative, which could indicate competition for available carbon. According to Herms and Mattson (1992), there may be trade-offs between defense compounds and storage carbohydrates when resources, such as nutrients, are limited. Foliar nutrient analyses at the Bussel Creek site suggest that nutrients are extremely limited and that the majority of trees growing in the test may suffer from nutrient deficiencies[2].

Height was weakly but positively correlated with both tannins and phenolics, which appears to contradict traditional hypotheses regarding carbon allocation (Herms and Mattson 1992). Several other studies have found similar positive relationships between growth and defense compounds as well (Denslow et al. 1987; Briggs and Schultz 1990; Denslow et al. 1990; Kimball et al.1999). One explanation for this result is that nutrient deficiencies present at the progeny test sites are limiting growth so carbon is available for phenol and tannin production. Studies have shown that this carbon allocation pattern can occur without noticeable growth impact when environmental resources limit growth (Bryant et al. 1985; Mihaliak and Lincoln 1985; Larsson et al.

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[2] data on file with the Inland Empire Tree Improvement Cooperative at the University of Idaho, Moscow, ID 83843

1986; Mihaliak and Lincoln 1989). However, when adequate resources are available, carbon allocation shifts towards growth and little carbon is available for defense compounds (Bazzaz et al. 1987).

Height and the phenolics:sugar ratio were not correlated. However, it was possible to identify families with both superior height growth and above average phenolics:sugar ratios at the 2 test sites. The heritability analysis suggests that it would be possible to select for both traits in Douglas-fir. Heritability estimates were high for 12-yr height growth (0.54 for single-tree heritability and 0.62 for family heritability). These values are higher than heritability estimates based on 8-yr height growth in the same 20 families (0.27 and 0.54, respectively) (Walker 1995). This narrow-sense heritability estimate is consistent with those reported by Campbell (1972) for height in coastal Douglas-fir. Heritability estimates were moderate for the phenolics:sugar ratio (0.20 and 0.24). However, they were high for sugar (0.64 and 0.59). As the single-tree narrow-sense heritabilities indicate, the proportion of V_p explained by V_a is much higher for sugar than for the phenolics:sugar ratio. This implies that greater gains would be made by selecting for low sugar concentrations rather than directly selecting for higher phenolics:sugar ratios or high phenolics concentrations.

Wargo (1980, 1981) found that when glucose concentrations are low, defense compounds such as phenols and tannins inhibit fungal growth and can be toxic to *Armillaria*. However, when glucose concentrations are high, *Armillaria* is capable of oxidizing defense compounds and using them as a carbon source (Wargo 1980, 1981, 1984*b*; Cheo 1982). Gallic acid and gallotannin have both been shown to stimulate the fungus when glucose levels are high (Wargo 1980, 1984b; Cheo 1982). The genetic

correlations estimated in this study indicate that selecting for low sugar will have a positive effect on the phenolics:sugar ratio but will not have a significant effect on tree height. Thus, sugar concentrations may be the key component of the phenolics:sugar ratio and selection on sugar concentration could decrease susceptibility to *Armillaria* sp. without sacrificing superior growth characteristics.

CONCLUSIONS

Significant genetic and environmental influences on root bark chemistry were identified in this study. Family, site and the family x site interaction had significant effects on the individual compounds measured. Family and single-tree narrow-sense heritability estimates indicate that genetic differences account for 20-24% of the variation in the phenolics:sugar ratio. Although height was not correlated with the phenolics:sugar ratio, three families with height rankings above the seventieth percentile had above average ratios at both of the test sites. Heritabilities for sugar were much higher than for phenolics or the phenolics:sugar ratio, suggesting greater gains could be made by selecting for low sugar concentration rather than for high phenolics:sugar ratios. Since sugar concentration was not significantly correlated with height, selection for low sugar could increase the phenolics:sugar ratio without having a negative effect on total tree height.

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Table 1. Means and ranges for the compounds in the inner root bark tissue of 15-yr-old Douglas-fir at two progeny test sites in north Idaho

Compound	Site	N	Mean	Standard Deviation	Minimum	Maximum
Sugar	Bussel Creek	179	4.40[a]	0.78[a]	2.45[a]	8.38[a]
	Rimrock	166	4.23[a]	0.69[a]	2.14[a]	5.94[a]
Starch	Bussel Creek	179	1.36[a]	0.50[a]	0.44[a]	3.40[a]
	Rimrock	166	1.56[a]	0.69[a]	0.43[a]	4.19[a]
Tannins	Bussel Creek	179	6.94[a]	1.63[a]	2.73[a]	14.48[a]
	Rimrock	166	6.20[a]	1.51[a]	2.82[a]	10.38[a]
Phenolics	Bussel Creek	179	23.28[a]	4.64[a]	8.59[a]	37.11[a]
	Rimrock	166	20.51[a]	6.26[a]	4.69[a]	44.90[a]
Phenolics: Sugar	Bussel Creek	179	5.36	1.00	1.33	8.20
	Rimrock	166	4.85	1.36	1.68	10.49

[a] in g/100g root bark tissue

Table 2. Analysis of variance tables for sugar, starch, protein-precipitable tannins, phenolics and the phenolics:sugar ratio.

Compound	Source	df	Sum of Squares	F value	prob>F
Sugar	Family	19	46.3503	6.26	0.0001
	Site	1	2.1588	5.54	0.0192
	Family x Site	19	19.5564	2.64	0.0003
	Error	305	118.8389		
Starch	Family	19	24.7506	7.42	0.0001
	Site	1	3.9268	22.36	0.0001
	Family x Site	19	43.0700	12.91	0.0001
	Error	305	53.5725		
Tannins	Family	19	149.3106	4.34	0.0001
	Site	1	36.6045	20.19	0.0001
	Family x Site	19	147.0137	4.27	0.0001
	Error	305	552.8740		
Phenolics	Family	19	1941.8108	4.53	0.0001
	Site	1	575.0226	25.50	0.0001
	Family x Site	19	1464.3129	3.42	0.0001
	Error	305	6876.6470		
Phenolics:Sugar	Family	19	102.0603	5.28	0.0001
	Site	1	18.9687	18.65	0.0001
	Family x Site	19	74.1438	3.84	0.0001
	Error	305	310.1790		

Table 3. Phenotypic and additive genetic variances for sugar, starch, tannins, phenolics, and the phenolics:sugar ratio in Douglas-fir

Variance	Sugar	Starch	Tannins	Phenolics	Phenolics: Sugar
Phenotypic	0.5538 [a]	0.4219 [a]	2.5206 [a]	30.3616 [a]	1.4300
Additive Genetic	0.3555 [a]	0 [a]	0.0404 [a]	5.5756 [a]	0.2929

[a] in g^2

Table 4. Family and single-tree narrow-sense heritabilities for sugar, starch, tannins, phenolics, the phenolics:sugar ratio and 12-yr height growth in Douglas-fir

Heritability	Sugar	Starch	Tannins	Phenolics	Phenolics: Sugar	12-yr Height
Family	0.5937	0	0.0215	0.2339	0.2404	0.6192
Single-tree narrow-sense	0.6419	0	0.0160	0.1836	0.2048	0.5442

Table 5. Genetic correlation coefficients for height growth and root chemistry in Douglas-fir / probability > | R| under Ho: ρ = 0 (N = 345).

	Sugar	Starch	Tannins	Phenolics	Phenolics: Sugar	Height
Sugar	1.0000					
Starch	0.0225 0.6771	1.0000				
Tannins	0.3881 0.0001	-0.1256 0.0196	1.0000			
Phenolics	0.4220 0.0001	-0.1570 0.0035	0.5138 0.0001	1.0000		
Phenolics: Sugar	-0.1718 0.0014	-0.1889 0.0004	0.2927 0.0001	0.8002 0.0001	1.0000	
Height	0.0912 0.0908	0.0384 0.9433	0.1159 0.0314	0.1128 0.0362	0.0506 0.3490	1.0000

Table 6. Spearman correlation coefficients for height growth and root chemistry in Douglas-fir / probability > |R| under Ho: ρ = 0 (N = 345).

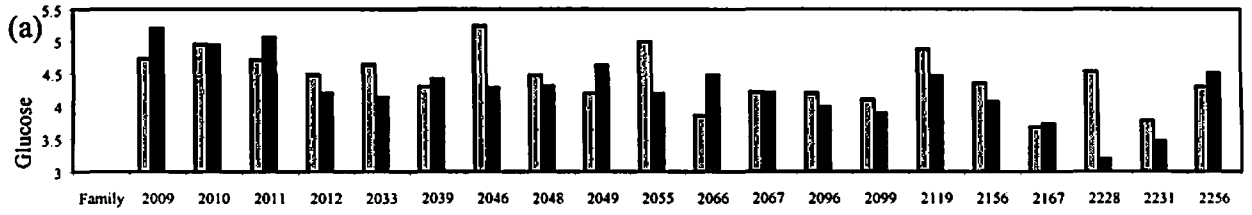
	Sugar	Starch	Tannins	Phenolics	Phenolics: Sugar	Height
Sugar	1.0000					
Starch	-0.0136 0.8010	1.0000				
Tannins	0.3808 0.0001	-0.1216 0.0239	1.0000			
Phenolics	0.4858 0.0001	-0.1877 0.0005	0.4334 0.0001	1.0000		
Phenolics: Sugar	-0.1513 0.0049	-0.2119 0.0001	0.2066 0.0001	0.7319 0.0001	1.0000	
Height	0.0671 0.2135	0.0413 0.4448	0.1201 0.0257	0.1668 0.0019	0.0986 0.0674	1.0000
Rodent Damage	-0.0914 0.0899	-0.0797 0.1394	-0.0362 0.5024	0.0148 0.7847	0.0939 0.0815	-0.1105 0.0402
Animal Damage	-0.0138 0.7984	0.0127 0.8149	-0.0261 0.6294	-0.0556 0.3032	-0.0606 0.2619	-0.0006 0.9915
Insect Damage	-0.0055 0.9187	0.0280 0.6042	-0.1019 0.0587	-0.0425 0.4319	-0.0418 0.4391	-0.0261 0.6297
Physical Damage	0.0085 0.8744	0.0502 0.3523	0.0224 0.6786	-0.0427 0.4293	-0.0339 0.5305	-0.1475 0.0060
Other Damage	-0.0117 0.8293	0.0503 0.3520	-0.0071 0.8959	-0.0096 0.8597	-0.0152 0.7787	-0.0798 0.1392
Terminal 1989	-0.0962 0.0742	0.0589 0.2754	-0.0909 0.0918	-0.0362 0.5023	0.0289 0.5929	-0.2183 0.0001
Terminal 1992	-0.0507 0.3476	-0.0040 0.9407	-0.0838 0.1202	-0.0372 0.4909	-0.0218 0.6865	-0.1109 0.0395

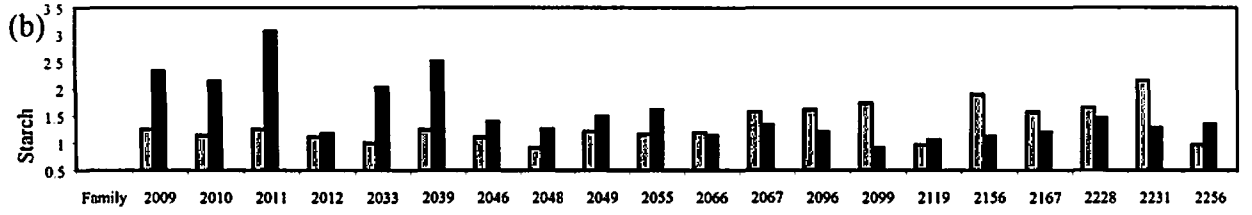
Table 6. (continued) Spearman correlation coefficients for height growth and root chemistry in Douglas-fir / probability > | R| under Ho: $\rho = 0$ (N = 345).

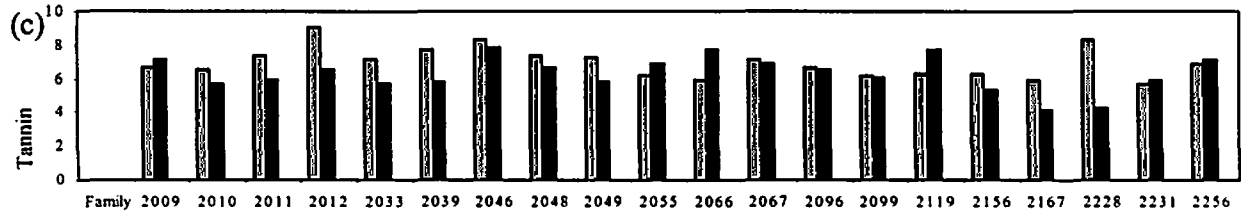
	Rodent Damage	Animal Damage	Insect Damage	Physical Damage	Other Damage	1989 Term. Damage	1992 Term. Damage
Rodent Damage	1.0000						
Animal Damage	-0.0058 0.9141	1.0000					
Insect Damage	-0.0218 0.6866	-0.0218 0.6866	1.0000				
Physical Damage	-0.0174 0.7476	-0.0174 0.7476	-0.0650 0.2285	1.0000			
Other Damage	-0.0179 0.7402	-0.0179 0.7402	0.0318 0.5564	0.1273 0.0180	1.0000		
'89 Term. Damage	0.1171 0.0296	-0.0227 0.6744	0.1162 0.0309	0.0304 0.5734	0.0257 0.6338	1.0000	
'92 Term. Damage	-0.0368 0.4958	-0.0368 0.4958	-0.0533 0.3235	-0.0412 0.4456	-0.0797 0.1395	-0.0075 0.8900	1.0000

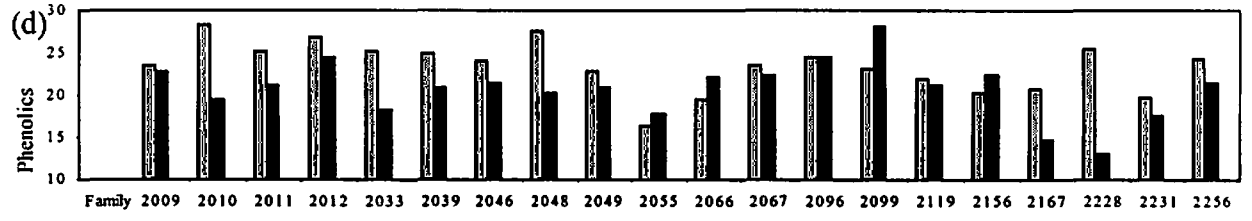
Figure 1. Family mean (a) sugar concentrations (in g/100g root bark tissue) by site (b) starch concentrations (in g/100g root bark tissue) by site (c) tannin concentrations (in g/100g root bark tissue) by site (d) phenolic concentrations (in g/100g root bark tissue) by site and (e) phenolics:sugar ratios by site (striped bars for Bussel Creek, solid bars for Rimrock).

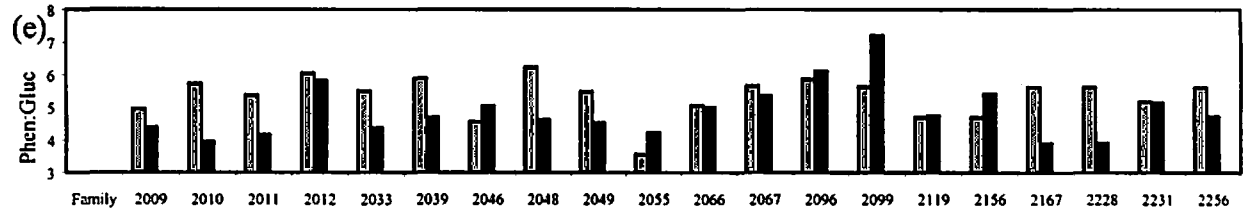
Figure 2. Family mean phenolics:sugar ratios by site coded to reflect the family percentile height rankings for 12-yr height growth (lines indicate site mean phenolics:sugar ratios)

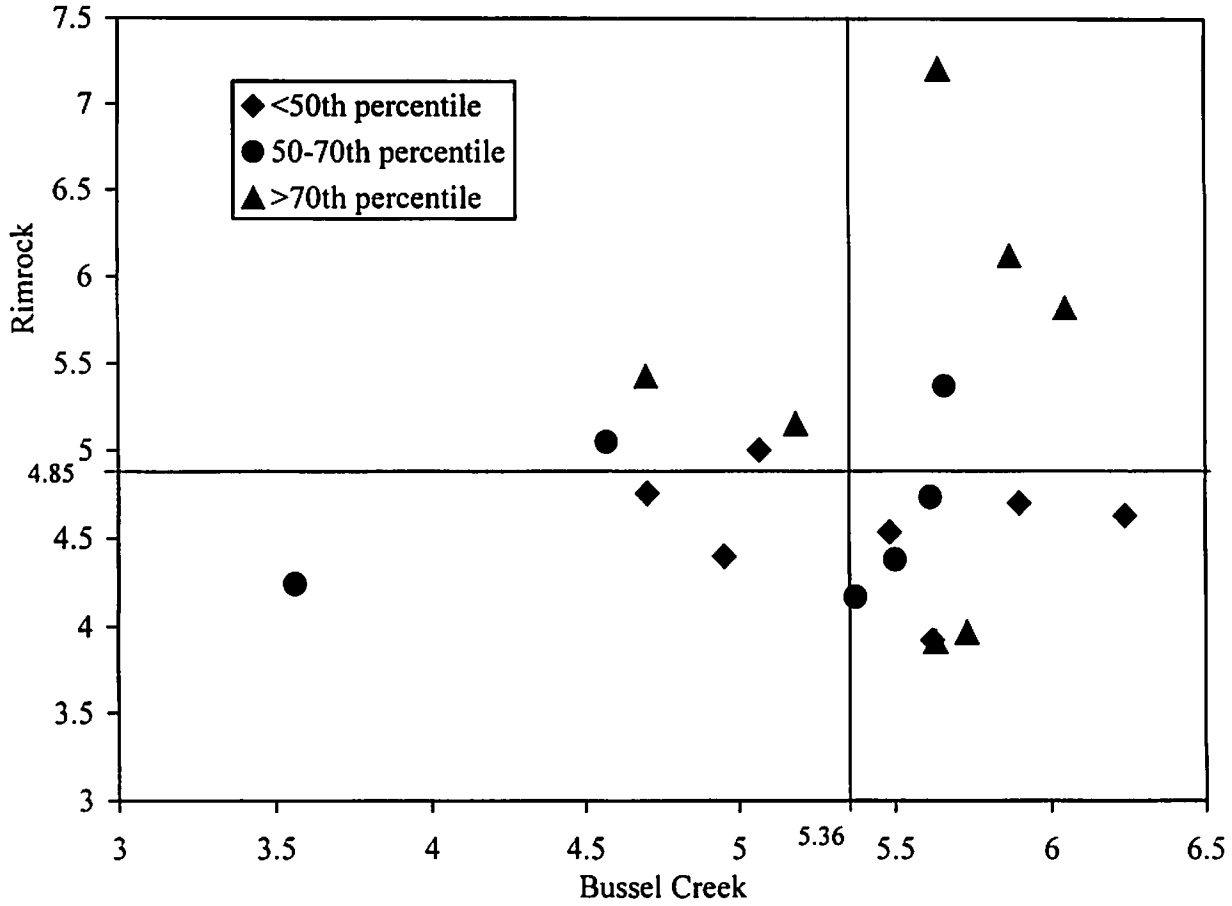

(a)
Glucose
5.5
5
4.5
4
3.5
3
Family 2009 2010 2011 2012 2033 2039 2046 2048 2049 2055 2066 2067 2096 2099 2119 2156 2167 2228 2231 2256


(b)
Starch
3.5
3
2.5
2
1.5
1
0.5
Family 2009 2010 2011 2012 2033 2039 2046 2048 2049 2055 2066 2067 2096 2099 2119 2156 2167 2228 2231 2256


(c)
Tannin
10
8
6
4
2
0
Family 2009 2010 2011 2012 2033 2039 2046 2048 2049 2055 2066 2067 2096 2099 2119 2156 2167 2228 2231 2256


(d)
Phenolics
30
25
20
15
10
Family 2009 2010 2011 2012 2033 2039 2046 2048 2049 2055 2066 2067 2096 2099 2119 2156 2167 2228 2231 2256


(e)
Phen:Gluc
8
7
6
5
4
3
Family 2009 2010 2011 2012 2033 2039 2046 2048 2049 2055 2066 2067 2096 2099 2119 2156 2167 2228 2231 2256


◆<50th percentile
● 50-70th percentile
▲>70th percentile
Rimrock
7.5
7
6.5
6
5.5
5
4.85
4.5
4
3.5
3
3
3.5
4
4.5
5
5.36
5.5
6
6.5
Bussel Creek