Genetic Variation in Wood Specific Gravity From Progeny Tests of Ponderosa Pine (*Pinus ponderosa* LAWS.) in Northern Idaho and Western Montana

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Abstract

Green and oven-dry alcohol-toluene extracted wood specific gravities ($\bar{x}$ = 0.39 and 0.46 respectively) were assessed from a total of 60 open-pollinated ponderosa pine (*Pinus ponderosa* LAWS.) families at 21 years from seed grown in progeny tests in northern Idaho and northwestern Montana. The trees in the Montana tests averaged higher green and oven-dry specific gravities (0.40 and 0.48 respectively) compared to those from the Idaho tests (0.38 and 0.44 respectively). There was wide variability in moisture content, but the families with the highest and lowest green specific gravities tended to rank high and low respectively for oven-dry specific gravity. Family x site interactions were significant only for green specific gravity in the Idaho tests. Growth data (height and diameter) and specific gravity were not significantly correlated at any of the test sites. Pilodyn densitometry was, with one exception, weakly, but significantly correlated with green and oven-dry specific gravity on an individual-tree basis. Use of the Pilodyn is not recommended for through-the-bark measurements with young ponderosa pine. Individual tree and family-mean heritabilities were lower for green specific gravity than for oven-dry specific gravity for families from both sets of tests. These results are likely associated with variation in moisture content. Moisture and extractive content averaged 109% and 4%, respectively, of the extractive-free, oven-dry weight of the cores across all samples. Heritability estimates for green and oven-dry specific gravity were consistent with findings for other coniferous species. Estimated gains in specific gravity from ten and three percent family selection ranged from 0.0095 to 0.0339 (about 2.5% to 7%) and 0.0153 to 0.0406 (about 4% to 8.5%) respectively.

Specific gravity of core segments from the pith to the outer rings did not differ significantly from each other in any of the tests although in samples from three of the four test sites, mean specific gravity of the inner core segments (pith to ring 5) was higher than either of the two outer core segments (rings 6 to 10 and 11 to the outermost rings). At 21 years from seed, the trees in this study had probably not completed the transition to production of mature wood.

Key words: wood quality, oven-dry specific gravity, green specific gravity, ponderosa pine, Pilodyn densitometry, genetic variation, heritability, juvenile wood, mature wood, moisture content.

Introduction

Specific gravity is an economically important characteristic of wood that is relatively easy to measure, well-correlated with strength and pulp yield, and in conifers, responds easily to selection and breeding (ZOBEL and JETT, 1995). Regardless of site, growth rate, or geography, genetic control of variation in specific gravity tends to be higher than for other traits and strong enough to have significant effects on wood quality and yields (ZOBEL, 1961; ROZENBERG and CAHALAN, 1997). Variation in the proportions of earlywood and latewood, cell wall thickness, cell size, and the presence of resins and other extractives can all contribute to variation in specific gravity in conifers (ZOBEL and VAN BUIJTENEN, 1989; ZOBEL and JETT, 1995).

Pilodyn densitometry is an indirect, non-destructive measurement that has been used successfully to assess specific gravity with a variety of species including pines, spruces and Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) (TAYLOR, 1981; MICKO et al., 1982; VARGAS-HERNANDEZ and ADAMS, 1991; YANCHUK and KISS, 1993; COSTA E SILVA et al., 1998; WANG et al., 1999). Measurements can be taken through the bark or with the bark removed, although better correlations may be obtained between Pilodyn pin penetration and specific gravity when the bark is removed from the assessment point (r = –0.75 compared to r = –0.83, respectively) (MICKO et al., 1982). Multiple measurements per tree tend to provide closer estimates of true specific gravity than a single measurement (HALL, 1988) and measurements on families may be more reliable than those for individual trees (WANG et al., 1999).

The study described here assesses variation in specific gravity and the relative proportions of earlywood and latewood in genetically-tested plantation-grown ponderosa pine (*Pinus ponderosa* LAWS.) froms sources in the Inland Northwest, U.S.A. The specific objectives of this study were: (1) to assess genetic variation in wood specific gravity among open-pollinated families of ponderosa pine from the Inland Northwest, (2) to estimate genotype x environment interaction in specific gravity for ponderosa pine grown in northern Idaho and northwestern Montana, (3) to assess genetic variation in and the influence of the ratio of earlywood to latewood on specific gravities in four genetic tests, (4) to assess the relationship between the wood quality traits and growth traits, (5) to test the Pilodyn as a device to assess specific gravity of ponderosa pine in the Inland Northwest, (6) to identify families and/or individuals with particularly high or low specific gravity, and (7) to determine whether the 21-year-old trees were producing mature wood as indicated by increased specific gravity in recent growth rings.

Materials and Methods

Open-pollinated seeds were collected from 434 wild phenotypically superior ponderosa pine mother trees from 93 stands in Washington, Idaho and Montana (MADSEN and HUDSON, 1977). Seeds were sown in 1972 and outplanted in eight genetic tests in 1974 as 2-0 bareroot seedlings. Seedlings were distributed in randomized complete blocks with 4-tree, family-row plots in each of 5 blocks for a total of 20 trees per family per test[3]). Dead trees were replaced with 1-year-old container stock in

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[3]) Tests were administered by the Ponderosa Pine Tree Improvement Committee (PPTIC) which later became part of the Inland Empire Tree Improvement Cooperative (IETIC).

spring 1975. In general, the families from Idaho and Washington stands were planted in both the Idaho and Washington tests, whereas the families from Montana were planted in the Montana tests only. Breeding-unit delineations were developed at a later time based on genecological information (REHFELDT, 1986; FINS and RUST, 1988) (*Figure 1*). All analyses in this study were conducted by breeding unit.

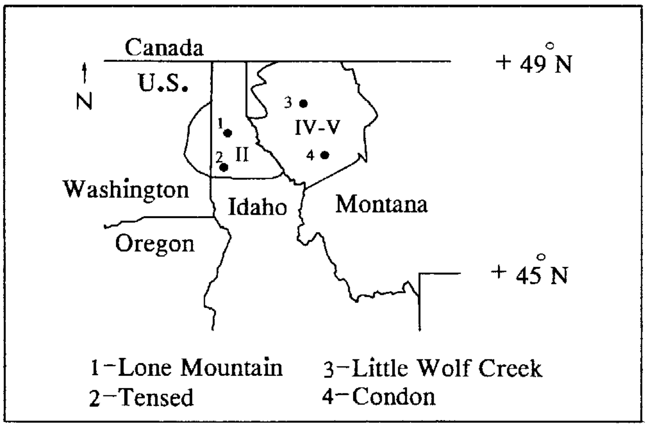

Figure 1. – Location of ponderosa pine tree improvement test sites (1, 2, 3, 4) and breeding unit boundaries (II, IV–V).

We selected two tests in northern Idaho (Tensed and Lone Mountain) and two in western Montana (Condon and Little Wolf Creek) for this study because of their relatively high survival and growth rates (*Figure 1*). Pilodyn measurements and increment core samples from 21-year-old trees were used to assess variation in wood specific gravity; 19-year height and diameter at breast height were used to estimate individual-tree volumes.

Families were selected for increment-core analysis by first ranking all the families within a breeding unit by the 19-year estimated volume. A systematic sampling procedure was used to select 26 families from each breeding unit so that the range of volume growth was well-represented. An additional four families were randomly chosen from each breeding unit. A total of 60 families were sampled, 30 in the two Idaho tests and 30 in the two Montana tests.

Field procedures

During the summer of 1992, a single increment core (5.15 mm diameter) was taken from one tree per family per plot for each selected family in all four tests. The target was to sample 5 trees per family per site, a total of 600 cores. However, when all trees in a family plot had died, no samples were substituted from other plots. Cores were taken from a total of 563 trees, with a range of three to five trees sampled per family per test site.

The probability of an individual tree within each block being selected was proportional to the tree's 19-year estimated volume. All increment cores (bark to pith) were taken from the south side of the tree at 0.3 m above the ground, providing more growth rings than would be available at breast height and increasing the probability of including mature wood if the tree were producing it. Obvious knots, wounds and compression wood were avoided in sampling the cores. Cores were frozen at –20 °C for long-term storage until specific gravities were determined.

The Pilodyn tester was fitted with a 2.5 mm diameter, 40 mm long, blunt pin. At the time the increment cores were collected from trees in 30 of the families in each test, Pilodyn measurements were also made on one tree per family per plot, including the previously-cored trees, for all families in the four tests (a total of 3754 trees, sampling 236 families in the Idaho tests and 204 families in the Montana tests). The probability of being measured was proportional to the tree's 19-year estimated volume. Four Pilodyn measurements were taken per tree (one on each cardinal direction on the tree) and all readings were taken through the bark.

Laboratory analysis

For each set of samples from a test plantation, all cores from nine of the 30 increment-cored families were systematically selected for earlywood and latewood ring-analysis. Earlywood and latewood bands in each annual ring were differentiated by color and measured visually using the Jandel Video Analysis Software System (Jandel Scientific, 1990). The latewood proportion of each core was calculated as the sum of latewood width of individual rings divided by the length of the core samples (VARGAS-HERNANDEZ and ADAMS, 1991). Incomplete outer-rings were excised prior to measurement.

Specific gravities (SG) were determined via water-immersion on both green and oven-dry cores (PANCHEN and DE ZEEUW, 1970; HALL, 1988; SZYMANSKI and TABER, 1991):

(1)

$$SG\ (green) = \frac{\text{extractive-free, oven-dry weight of wood}}{\text{green unextracted displacement}}$$

(2)

$$SG\ (oven\text{-}dry) = \frac{\text{extractive-free, oven-dry weight of wood}}{\text{extractive-free, oven-dry displacement}}$$

After weighing, the green cores were submerged in water until the fiber saturation point was reached and the green unextracted displacement was assessed. All cores were dried by placing them in an oven at 103 °C ± 2 °C for 24 hours and weighed to determine oven-dry weight (PANCHEN and DE ZEEUW, 1970). The extractives were then removed from each core using an alcohol toluene extraction-process (American Society for Testing and Materials, 1999). Following extraction, the cores were again oven-dried at 103 °C ± 2 °C for an additional eight hours to drive off all volatiles. Cores were again weighed to determine their extractive-free, oven-dry weight. Following standard procedures for measuring specific gravity of small samples, all cores were then dipped in paraffin wax and immersed in water to determine the extractive free, oven-dry displacement (American Society for Testing and Materials, 1999).

Moisture content (MC) from each increment core was calculated as:

(3)

$$MC = \frac{\text{(wet weight - extractive-free, oven-dry weight)}}{\text{extractive-free, oven-dry weight}}$$

Thus, "moisture content" (extractive-free basis) includes the weight of extractives and volatiles as well as the water content of the samples (HAYGREEN and BOWYER, 1996).

Extractive content (EC) of each increment core was calculated as:

$$(4)\qquad EC = \frac{(\text{oven-dry weight} - \text{extractive-free, oven-dry weight})}{\text{extractive-free, oven-dry weight}}$$

"Water content" (WC) of each increment core, which includes the weight of volatiles and water, was calculated as:

$$(5)\qquad WC = \frac{(\text{wet weight} - \text{oven-dry weight})}{\text{extractive-free, oven-dry weight}}$$

Following water-immersion of the extracted oven-dry cores, all cores from the nine families used for the earlywood and latewood ring-analysis were divided into three segments as follows: segment 1 – from pith to end of fifth growth ring, segment 2 – growth rings six to 10, and segment 3 – growth ring 11 and all remaining rings. The ends of each core were dipped in paraffin wax and the extractive-free, oven-dry displacement of each segment was assessed. Following immersion, the paraffin wax was melted from each segment by heating in an oven at 103°C ± 2°C and the extractive-free, oven-dry weight was recorded for each segment.

All calculations and comparisons of specific gravity and moisture content of the cores and core segments were based on extractive-free, oven-dry weights (HAYGREEN and BOWYER, 1996). Extractive-free, oven-dry specific gravity of the segments was used to assess differences in specific gravity from the inner core to the outer core as an indication of the onset of mature wood production. Data were analyzed using SAS statistical software (SAS Institute Inc., 1985). Variation in specific gravity from the core segments was analyzed by using PROC GLM in SAS.

Variance components for both green and oven-dry specific gravity were calculated using PROC VARCOMP (Method = Type 1) in SAS (SAS Institute Inc., 1985). Family mean and individual-tree heritabilities for oven-dry and green specific gravities were calculated according to FALCONER (1989):

$$(6)\qquad h^2_f = \sigma^2_f / (\sigma^2_f + \sigma^2_{sf/r} + \sigma^2_{e/rs})$$

$$(7)\qquad h^2_i = 4\sigma^2_f / (\sigma^2_f + \sigma^2_{sf} + \sigma^2_e)$$

where f = family; i = individual tree, r = replication, s = site, e = error. All effects were considered to be random since neither the mother trees nor the progeny used in this study were selected for wood quality traits. Although mother trees had been selected for superior growth, there is little evidence of a correlation between tree growth rates and wood specific gravity in hard pines (ZOBEL and VAN BUIJTENEN, 1989). Furthermore, the sampling method used for the progeny was unbiased with respect to volume and growth.

Results and Discussion

Variation in wood specific gravity among families and sites

The mean extractive-free, oven-dry and green specific gravities (extractive-free) on an individual core basis for all four tests were 0.46 and 0.39, respectively. The family means and ranges of oven-dry and green specific gravity for the two tests within each breeding unit were similar to each other, with the Montana tests averaging slightly higher specific gravities than the Idaho tests (*Table 1*). Oven-dry and green specific gravities averaged 0.44 and 0.38 respectively for trees in the Idaho tests and 0.48 and 0.40 respectively for trees in the Montana tests. The oven-dry specific gravity figures from this study are high compared to the average oven-dry specific gravity value of 0.40 previously reported for ponderosa pine (USDA, 1987). The mean green specific gravity figure for trees in the Idaho tests was equal to the previously reported average of 0.38 (USDA, 1987), and the mean value for trees in the Montana tests was slightly higher at 0.40.

Using 11 mm increment cores, JOYCE (1978) found mean green specific gravities ranging from 0.44 to 0.47 on core segments from 203 mature ponderosa pine trees that had been selected from 28 stands for a tree improvement program in west-central Idaho (WANG, 1967). These figures for mature trees are higher than those we found for 21-year-old trees, even for the core segments that corresponded with each other in age. However, differences in genetic population, age of test trees, size of wood samples, rates of growth, location of the sample trees and the specific place where the bole wood was sampled are all likely to have contributed to the differences in specific gravity between the two studies.

The values for green specific gravity in our study are well within the range previously reported for other regional and more distant conifer species: 0.41 for 15 year-old open-pollinated interior spruce (*Picea glauca* (MOENCH) VOSS, *P. glauca* var. *albertiana* (S. BROWN), *P. engelmannii* PARRY ex. ENGELM., and their hybrids) in progeny tests in northern British Columbia (YANCHUK and KISS, 1993); 0.36 for 12-year-old full-sib progenies of coastal Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) in British Columbia at 48.50°N latitude (KING et al., 1988); 0.375 to 0.457 for Douglas-fir provenances in south-

Table 1. – Means, ranges (in parentheses) and correlations between oven-dry and green specific gravities (all extractive-free basis) of wood samples from 21-year-old ponderosa pine in progeny tests in Idaho and Montana. Data from 30 families at each test site.

	Idaho Tests			Montana Tests			All tests
Measure	Tensed	Lone Mtn.	$\bar{x}$	Little Wolf	Condon	$\bar{x}$	$\bar{x}$
Oven-dry specific gravity	0.43 (0.40 - 0.51)	0.45 (0.41 - 0.49)	0.44	0.49 (0.40 - 0.58)	0.47 (0.41 - 0.54)	0.48	0.46
Green specific gravity	0.37 (0.35 - 0.43)	0.38 (0.35 - 0.41)	0.38	0.40 (0.34 - 0.46)	0.40 (0.36 - 0.45)	0.40	0.39
Correlation between green and oven-dry specific gravity	0.94**	0.88**		0.79**	0.72**		

**Statistically significant at $P<0.01$

western British Columbia (LOO-DINKINS and TABER, 1990) and 0.453 for 13-year-old loblolly pine (*Pinus taeda* L.) sampled at the base (WILLIAMS and MEGRAW, 1994).

Correlation coefficients for green versus extractive-free, oven-dry family-mean specific gravities within tests ranged from 0.72 to 0.94 ($P < 0.01$) and were higher for the Idaho tests than for the Montana tests (*Table 1*). Thus either method would be sufficient to assess differences in specific gravity among families. However, correlations of family mean oven-dry specific gravity between sister tests within states, although significant, were considerably lower, $r = 0.41$ ($P = 0.03$) and $r = 0.58$ ($P < 0.001$) for the Idaho and Montana tests respectively. Family correlations between sister tests were even lower for green specific gravity, 0.26 (non-significant) and 0.39 ($P = 0.03$), for the Idaho and Montana tests respectively. These correlations are low for a trait that shows little genotype x environment interaction.

For extractive-free, oven-dry specific gravity, site and family effects were highly significant, but family x site interactions were not significant (*Tables 2* and *3*). This result is consistent with other studies that showed genotype x environment interaction to be minor or non-existent for wood specific gravity (ZOBEL and VAN BUIJTENEN, 1989). For green specific gravity, family effects in the Idaho tests were statistically significant and site, replication, and family x site interaction effects were near, but not significant (*Table 2*). None of the effects were significant for green specific gravity in the Montana tests (*Table 3*). Differences among families accounted for the largest proportion of accountable variation for all tests (Range = 6% to 13.9%).

Moisture content

Moisture content was substantially higher in the samples from the Montana tests (121% and 125% of extractive-free oven-dry weight for the Little Wolf and Condon tests respectively; mean = 122.8%) compared to samples from the Idaho tests (79% and 114% of extractive-free, oven-dry weight for the Tensed and Lone Mountain tests respectively; mean = 96.7%) (*Table 4*). Moisture content was significantly different among families in the Montana tests ($P = 0.035$), but not among families in the Idaho tests ($P = 0.12$). Although differences in moisture content account for changes in family rank between green and oven-dry specific gravity at each site, the ranks of the highest- and lowest-ranking families were mostly consistent between the two measures (KOCH, 1994).

Deposition of extractives begins between 16 and 18 years of age (HAYGREEN and BOWYER, 1996) and extractive content is often under strong genetic control (ZOBEL and JETT, 1995). The extractive content of the core samples from the 21-year-old ponderosa pine trees in this study averaged 4% of their extractive-free, oven-dry weight (4.4% and 3.5% for the Idaho and Montana tests respectively) (*Table 4*). This is somewhat higher than the average of 2.2% to 3% for pine (SJÖSTRÖM, 1981; HILLIS, 1962). However, extractive content did not differ significantly among families in either the Montana or the Idaho tests ($P = 0.96$ and $P = 0.38$ respectively).

Latewood proportion and specific gravity

Phenotypic correlations between latewood proportion and oven-dry specific gravity were based on an average of 43 cores per test site (45 cores from both Idaho test sites and 43 and 38

Table 2. – Analysis of variance for oven-dry and green specific gravity of 21-year-old ponderosa pine planted in two Idaho progeny tests.

		Oven dry			Green		
Source	DF	F Value	Pr > F	% of variation	F Value	Pr > F	% of variation
Site	1	13.86	0.0002	6.4	2.69	0.1024	0.2
Rep (within Site)	8	1.26	0.2639	0.7	1.89	0.0626	2.5
Family	29	3.01	0.0001	13.9	2.51	0.0001	8.9
Family * Site	29	1.21	0.2186	3.3	1.43	0.0779	7.2
Error	226						
Total	293						

Table 3. – Analysis of variance for oven-dry and green specific gravity of 21-year-old ponderosa pine planted in two Montana progeny tests.

		Oven dry			Green		
Source	DF	F Value	Pr > F	% of variation	F Value	Pr > F	% of variation
Site	1	7.29	0.0075	4.2	1.21	0.2726	0.5
Rep (within Site)	8	1.16	0.3276	0.5	1.07	0.3881	0.2
Family	29	1.70	0.0187	11.8	1.07	0.3763	6.0
Family * Site	29	0.45	0.9936	0	0.51	0.9844	0
Error	201						
Total	268						

Table 4. – Mean moisture content (including volatiles and extractives), water content (including volatiles) and extractive content of wood core samples from 21-year-old ponderosa pine trees growing in progeny tests in Idaho and Montana, U.S.A. Data from 30 families at each test site.

	Idaho Tests			Montana Tests			All tests
	Tensed	Lone Mtn.	$\bar{x}$	Little Wolf	Condon	$\bar{x}$	$\bar{x}$
Moisture content[1]	79 (46.7-101.1)	114 (96.2-129.9)	96.7	121 (80.7-176.9)	125 (104.5-146.9)	122.8	109
Water content[1]	73 (15.7-237.6)	111 (41.7-160.2)	92	119 (0.3-418.7)	120 (67.1-169.1)	119.5	105
Extractive content[1]	6 (1.1-63.8)	3 (0.15-21.6)	4.4	2 (0.04-24.2)	5 (0.5-16.4)	3.5	4.0

[1]) Percent of extractive-free, oven-dry weight of increment cores

cores from Little Wolf and Condon, respectively). All correlations were statistically significant (P < 0.01) and ranged from 0.32 at the Lone Mountain site to 0.54 at the Tensed site. The correlations for the Condon and Little Wolf Creek test sites were 0.50 and 0.41, respectively. These correlations are low for a trait that is usually strongly related to specific gravity (ZOBEL and VAN BUIJTENEN, 1989; VARGAS-HERNANDEZ and ADAMS, 1991). However, the JAVA system, which relies on visual cues for assessing the transition from earlywood and latewood, is highly subjective and subject to error in distinguishing between earlywood and latewood.

Family-mean oven-dry specific gravities from the four progeny tests were plotted against elevation, latitude, and longitude of each parent. No trends were apparent in these plots for any of the tests. Specific gravity within a species' natural range tends to be lower when inland from the coast or toward the higher latitudes and higher elevations for many species (ZOBEL and TALBERT, 1984), but these generalizations from natural stand data are likely to be influenced by environmental effects.

In both the Idaho and Montana tests there were seven to ten ponderosa pine families whose mean oven-dry or green specific gravities exceeded the respective plantation-mean specific gravities for both tests, with the means of those families exceeding the plantation means by 2.5% to 6.7%. Seven families ranked high in both green and oven-dry specific gravity in each group.

Relationship of specific gravity to height and diameter

In 1990, when the trees were 19 years from seed, 3793, 3783, 1514 and 2856 test trees were alive at the Tensed, Lone Mountain, Little Wolf Creek and Condon sites, respectively. These numbers represent 81% survival in the two Idaho tests, and 70% and 65% survival at Condon and Little Wolf Creek, respectively. Plantation means for tree heights measured in 1990 ranged from 4.3 m to 6.7 m and means of diameters at breast height (1.3 m aboveground), ranged from 87.6 mm to 139.7 mm (*Table 5*).

The genetic correlation between height and diameter (all sites combined) was 0.81. The genetic correlations between height and diameter with green specific gravity with all sites combined were r = 0.04 and r = –0.06, respectively. Correlations between family mean height and diameter with oven-dry specific gravity were all less than r = 0.28, with six of the eight correlations less than r = 0.12; none was statistically significant. Genetic correlations between growth traits and green specific gravity show no improvement over that of phenotypic correlations. These results are consistent with those for other hard pines which generally show little or no relationship of wood specific gravity with height and diameter (ZOBEL and VAN BUIJTENEN, 1989; VARGAS-HERNANDEZ and ADAMS, 1991). Thus, selection for faster growing genotypes of ponderosa pine in northern Idaho and western Montana will not automatically change specific gravity.

Table 5. – Heights, diameters and correlations of wood specific gravity with Pilodyn measurements of 21-year-old ponderosa pine trees grown in progeny tests in Idaho and Montana, U.S.A.

	Idaho Tests			Montana Tests		
	Tensed	Lone Mtn	$\bar{x}$	Little Wolf	Condon	$\bar{x}$
19-year family mean heights (m)	6.7	6.5	6.6	4.3	6.1	5.2
19-year family mean DBH (mm)	139.7	118.0	128.9	87.6	127.9	107.8
Correlation: Pilodyn densitometry with green specific gravity#	-0.36**	-0.20**		-0.31**	-0.41**	
Correlation: Pilodyn densitometry with oven-dry extracted specific gravity#	-0.25**	-0.11 (NS)		-0.26**	-0.28**	

**) Statistically significant at P<0.01

#) Calculated on individual-tree basis using mean value from four Pilodyn readings

Pilodyn densitometry

The means of the four Pilodyn readings per tree resulted in higher correlations with green specific gravity measurements than three or fewer Pilodyn readings. This result is consistent with previous studies on white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.) B.S.P.) (Micko et al., 1982; Hall, 1988). Correlations between green specific gravity and the 4-reading means on an individual-tree basis ranged from –0.20 to –0.41 and were all statistically significant ($P \leq 0.01$) (*Table 5*). Correlations of the Pilodyn assessments with oven-dry specific gravity, on an individual-tree basis, were lower than correlations with green specific gravity but, with one exception, were also statistically significant ($P \leq 0.01$) (*Table 5*).

Family-mean correlations between Pilodyn values with green and oven-dry specific gravity were low to moderate ($-0.02 < r < -0.47$) and lower than those for individual trees. Only one of these values was statistically significant (Pilodyn vs. green specific gravity at Little Wolf Creek, $r = -0.47$, $P < 0.01$). The lower correlations for Pilodyn readings and specific gravity with family means is probably due to the wide variability of Pilodyn readings within families and small sample sizes.

Although individual-tree through-the-bark Pilodyn readings were significantly correlated with specific gravity, the correlations were substantially lower for ponderosa pine than those reported for other species: –0.75 for white spruce (*Picea glauca* (Moench) Voss) (Micko et al., 1982), –0.61 for interior spruce in British Columbia (Yanchuk and Kiss, 1993), and –0.70 for 12-year-old coastal Douglas-fir (King et al., 1988). The most likely factors contributing to the low correlations for ponderosa pine were variation in bark thickness and density and the use of extractive-free oven-dry weights in calculating specific gravity in this study (Barger and Ffolliott, 1971; Zobel and van Buijtenen, 1989; Szymanski and Taber, 1991). Other factors that may have contributed include the relatively small within-family sample sizes (3 to 5 trees per family per site), the use of open-pollinated families, and the position of the Pilodyn during measurements (0.3 m aboveground) where resins and other extractives tend to accumulate.

Heritability and genetic gains in specific gravity

For both breeding units, heritabilities for green specific gravity are lower than those for oven-dry specific gravity (*Table 6*), most probably because of variation in moisture and extractives, both of which should be removed to obtain accurate wood-specific gravity measurements (Taras and Saucier, 1966; Szymanski and Taber, 1991). The green specific gravity heritabilities we calculated for ponderosa pine in the Inland Northwest are lower than those reported for coastal Douglas-fir (individual-tree and family-mean heritabilities of 0.90 and 0.93, respectively) (King et al., 1988), but the oven-dry specific gravity heritabilities are comparable to those from both coastal Douglas-fir (individual-tree and family-mean heritabilities of 0.59 and 0.55, respectively) (Vargas-Hernandez and Adams, 1991) and Scotch pine (*Pinus sylvestris* L.) (individual-tree heritability = 0.45) (Hannrup et al., 1998).

Genetic gains in specific gravity from 3% and 10% family selection were estimated for both green and oven-dry specific gravities (Wright, 1976) (*Table 6*). The predicted gains are 0.0153 to 0.0406 and 0.0095 to 0.0339 for 3% and 10% family selection, respectively and are higher for extractive-free, oven-dry specific gravity than for green specific gravity (*Table 6*). Generally, predicted gains were larger for the families in the Montana test than for the families in the Idaho tests. Percent gains for 10% selection (2.5% to 7.1%) were similar to estimated gains for loblolly pine and Douglas-fir (Zobel and Jett, 1995) and bracket the recently estimated potential gains of 2.7% and 3.6% in wood density from selection in Scotch pine (Hannrup et al., 1998). Such seemingly small changes could represent relatively large and important differences in the quality, quantity and cost of the product from the wood source (Zobel and Jett, 1995; Costa e Silva et al., 1998).

Transition to mature wood

For all but the Lone Mountain site, the inner core segments (pith to ring 5) had the highest mean specific gravity of the three sets of segments (*Table 7*). This is in contrast to a general trend for conifers described by Zobel and Talbert (1984) toward gradually higher specific gravities from about year 2 to year 13. However, this finding is consistent with the trends described by Jozsa and Middleton (1994) for several conifer species that show relatively high ring densities near the pith, then a drop in density followed by a gradual increase between years 10 and 40 or more. Nonetheless, neither segment nor family x segment were significant sources of variation at any of the individual test sites, or in an analysis of tests with families in common. Thus at age 21, differences in specific gravity were insufficient to statistically differentiate the younger from the older core segments. Possibly the trees in our study had not yet begun to produce mature wood, or alternatively, they may have begun the transition to mature wood but had not produced a sufficient quantity of it to register the characteristic increase in specific gravity.

Table 6. – Means of green and oven-dry specific gravity (extracted basis), family mean (h^2_f) and individual-tree (h^2_i) heritabilities, and genetic gains in specific gravity from 10% and 3% family selection of 21-year-old ponderosa pine planted in four progeny tests in the Inland Northwest.

Geographic Source	Specific Gravity Measure	Mean Specific Gravity	h^2_f	h^2_i	Genetic Gains Highest 10%	Genetic Gains Highest 3%
Idaho	Green	0.38	0.48	0.37	0.0095 (2.5%)	0.0177 (4.7%)
	Oven-dry	0.44	0.63	0.60	0.0139 (3.2%)	0.0240 (5.5%)
Montana	Green	0.40	0.39	0.24	0.0130 (3.2%)	0.0153 (3.8%)
	Oven-dry	0.48	0.59	0.50	0.0339 (7.1%)	0.0406 (8.5%)

Table 7. – Means of extractive-free oven-dry specific gravity of whole cores and incremental growth rings of 21-year-old ponderosa pine in genetic tests in the Inland Northwest.

Test Plantation	Whole Core	Growth Ring Segments			
		1-5	6-10	11 +	$\bar{x}$
Tensed	0.4825	0.3268	0.3196	0.3112	0.3192
Lone Mountain	0.4544	0.3124	0.3117	0.3198	0.3146
Little Wolf Creek	0.4873	0.3492	0.3483	0.3429	0.3468
Condon	0.4745	0.3810	0.3733	0.3755	0.3766

The specific gravity estimates from our core segments approximate the values obtained from juvenile wood in a study of green specific gravity in loblolly pine (*Pinus taeda* L.): 0.397 for juvenile wood compared to 0.511 for mature wood (SZYMANSKI and TABER, 1991). But the mean oven-dry specific gravities for the core segments in our study were considerably lower than those for whole cores in all four of our own tests (*Table 7*). It is unlikely that water leaked through the paraffin wax during water immersion because water displacement of the cores stabilized. However, the differences may be an artifact of using a paraffin wax coating to prevent absorption of water during the immersion process.

The paraffin wax dip is a standard and recommended procedure for assessing specific gravity of small wood samples. But, a comparison of the surface to volume ratios of short cylinders versus long cylinders of the same diameter show that short cylinders have relatively larger surface to volume ratios than do long cylinders of the same diameter. This is because the two ends of a cylinder make up a larger proportion of the total surface area on short cylinders compared to longer ones of the same diameter. In our study, this relationship meant that, relative to their volumes, the core segments had proportionately more paraffin wax on their surfaces than did the whole cores. As a result, the wax coating likely displaced disproportionately more water on the segments than on the whole cores. Another way to view this disproportionate displacement problem is that for each set of three core segments that were assessed, six end surface coatings of paraffin added to the water displacement, compared to only two ends on the whole core. In the specific gravity calculations, increased displacement increases the denominator of the specific gravity fraction (see equation 2), thereby decreasing the value of the fraction.

The inflated denominators may have been partly mitigated by a small amount of melted wax that remained on the cores segments after they were oven-dried to obtain their extractive-free weight. The remaining wax would have slightly increased the oven-dry weights (numerator of the fraction) for the segments, but the full complement of wax that was on the surface of the segments during immersion would have increased water displacement relatively more than the small amount of remaining wax increased their weights. Thus, the denominator would have increased relatively more than the numerator increased, consistently reducing estimates of specific gravity for the core segments compared to those for whole cores.

Conclusions and Recommendations

Plantation-grown trees are being recognized as valuable sources of future fiber production, especially as more timberland is withdrawn from harvest in response to legislation and increased public pressure. Knowledge of variation of specific gravity in plantation-grown trees will aid managers in making decisions on breeding and deployment strategies. Our findings indicate that it is possible to identify ponderosa pine families whose specific gravity is high in at least two environments. Furthermore, with extractive-free oven-dry specific gravity family heritabilities of 0.63 and 0.59, and individual-tree heritabilities of 0.60 and 0.50, selection and breeding are an excellent option to compensate for the potential loss in specific gravity due to other cultural practices. Estimated gains from ten and three percent family selection for green and extractive-free oven-dry specific gravity ranged from 0.0095 to 0.0339 (2.5% to 7.1%) and 0.0153 to 0.0406 (3.8% to 8.5%) respectively. Although they appear small, these gains could represent substantial changes in quantity, quality and cost of the products for which these trees would be used.

The relatively low correlations between Pilodyn pin penetration and specific gravity suggest that for ponderosa pine, adjustments in methodology, such as bark removal at the point of pin penetration, may be required to provide strong correlations between the two measures.

Selections based on extractive-free, oven-dry specific gravity measurements appear to provide greater reliability for breeding than those based on green measurements. However, the high correlations of specific gravity values between extracted and unextracted increment cores ($0.72 < r < 0.94$) indicates gains may also be achieved by selecting families based on green specific gravity values.

At age 21 the ponderosa pine trees in this study do not appear to have completed the transition to production of mature wood. However, genetic variation in specific gravity appears large enough for the inclusion of this trait in a selection and breeding program.

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Cone and Seed Yield of 16 Populations of *Pinus tecunumanii* at 5 Sites in Zimbabwe

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Summary

Cone and seed yield of 160 families from 16 populations (10 families per population) of *Pinus tecunumanii* were assessed in eight- and nine-year old provenance/progeny tests located at five sites ranging in altitude from 700 m to 1700 m a.s.l. Eight of the 16 *P. tecunumanii* populations came from an altitudinal range of above 1500 m a.s.l. (high elevation population group) while the other eight were from below 1500 m a.s.l. (low elevation population group). *P. patula* and *P. oocarpa*, a high and low elevation species respectively, were also included in the test as controls.

Provenance variation in cone and seed yield was significant at varying probability levels at all sites. Family within-provenance effects were significant at some sites while at other sites they were not ($P < 0.05$). At Nyangui and Stapleford, both high altitude sites, *P. patula* was consistently superior in cone and seed yield to all the populations of *P. tecunumanii* but *Pinus oocarpa* was not significantly different from most of the *P. tecunumanii* populations in the lower altitude sites.

Cone yields for the high elevation population group were highest at Nyangui (13.8 g per tree) while the highest yields for the low elevation population group were at Maswera (6.1 g per tree). The highest seed yields for high elevation population was at Stapleford (0.26 g per tree) and Gungunyana (0.07 g per tree) for the low elevation population. Best locations for seed orchards of *P. tecunumanii* are sites above 1600 m a.s.l. for selections made in high elevation populations and below 1100 m a.s.l. for selections made from low elevation populations.

The highest cone and seed yields were from San Jeronimo, Piedrecitas, La Paz and La Soledad in the high elevation population group and from Jocon, Mountain Pine Ridge and San Francisco in the low elevation group. At family level, some families from populations like Piedrecitas, San Jeronimo and La Paz had seed yields of up to 55 g, 49 g and 48 g per tree respectively. In the low elevation populations the most productive families from Culmi, Mountain Pine Ridge and San

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