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The Influence of Plantation and Seed-Source Elevation on Wood Specific Gravity of 29-Year-Old Ponderosa Pines

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Abstract. Genetic, environmental, and age effects were found in 29-yr-old ponderosa pine progenies from different elevational sources, when they were grown at 960, 2730, and 5650 ft elevation in the Sierra Nevada of California. Wood specific gravity decreased as elevation of seed parents increased, and all genotypes produced significantly lower specific gravity wood in the high-elevation plantation. For ponderosa pine under similar conditions, if higher specific gravity wood is wanted, low-elevation seed sources should be used, or plantings made at low elevations, or both. If lower specific gravity wood is desired, the recommendations are reversed. For optimum production, a mid-elevation source outplanted at about 3000 ft should give the combination of the highest volume yield of higher specific gravity wood. ***Forest Sci. 17:388–394.***

Additional key words. *Pinus ponderosa*, provenance, wood tissue analysis.

DIFFERENCES in growth performance of *Pinus ponderosa* Laws. trees have been noted in three California plantations containing open pollinated offspring of parents from various elevational sources (Mirov *et al.* 1952, Callaham and Liddicoet 1961). The plantings were made in 1938 to examine the relation between rate of growth and elevation of seed parents. We now find that these same progenies show characteristic patterns of variation for wood specific gravity.

Materials and Methods

The Plantations. Seed for the original study was collected in 1934 and 1936 from 72 parent trees on the western slopes of the central Sierra Nevada in California. The parent trees were well distributed across an elevational transect, ranging in elevation from 125 to 6919 ft along a narrow strip about 39 degrees north latitude. Parents were grouped into seven elevational zones; each group of about 10 parents represented a 1000-ft interval.

Three nursery and plantation sites were established at different elevations within the original seed-tree transect: Low (960 ft), Mid (2730 ft) and High (5650 ft). The mid-elevation plantation is at the Institute of Forest Genetics, Placerville. The low-elevation site is 14 miles northwest of the Institute, and the high-elevation plantation is 35 miles east of the Institute. Seeds were sown in the nurseries in 1938, and the seedlings were transplanted into adjacent plantations after the second growing season. Within each plantation, seedlings from each elevational zone were planted at 8-ft spacing in 4- by 4-tree plots. Seven such zonal plots, representing the transect, were randomized and replicated four times in each plantation. Survival was excellent. A systematic thinning at 25 years reduced the trees to 8 per plot. At 29 years, 667 trees were distributed over the three plantations, only 5 trees fewer than the complete design of 224 trees per location.

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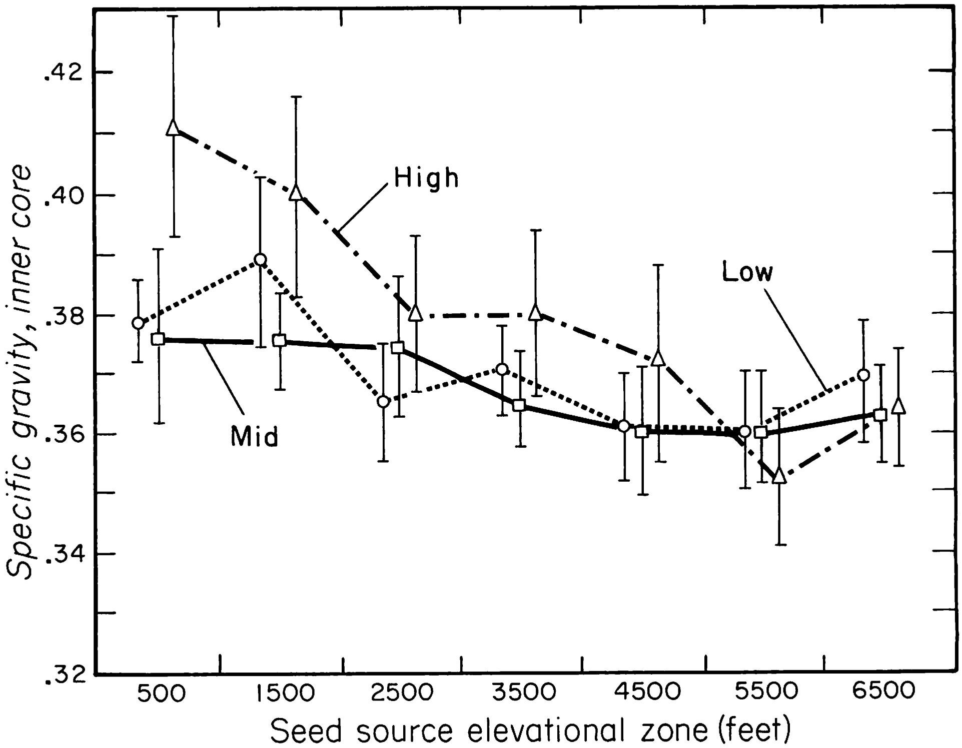

FIGURE 1. *Average specific gravity of inner core segments, by seed source zone, based on progeny means. Vertical lines represent 95-percent confidence limits on means. The mid-elevation (2730 ft) plantation is at the Institute of Forest Genetics, Placerville, Calif. The low-elevation (960 ft) plantation is 14 miles northwest of the Institute; the high-elevation (5650 ft) plantation is 35 miles east of the Institute.*

Procedure. During the winter months following the 29th growing season (1966–67) tree diameters were measured to the nearest 0.1 inch at breast height, and wood cores were extracted in random directions across complete diameters at the same level. These large (12-mm diameter) increment cores yielded pairs of counterpart cores which included wood from pith to bark.

Core pairs were subdivided into outer and inner sections, representing radial growth for years 20 to 27 and 12 to 19 respectively. The outer sections contained all mature wood, but many of the inner sections had 2 or 3 rings that could be classed as juvenile wood. This juvenile wood appeared to contribute toward a more uniform density in the inner sections throughout all sources.

Specific gravities were determined for each core section, using green wood volume and oven-dry weight. The two specific gravities for comparable growth segments, from opposite sides of the tree, were averaged for each tree. Inner and outer sections were analyzed separately. A mixed model with crossing was used in the analysis of variance:

$$Y_{ijkl} = \mu + a_i + a_j + a_{ik} + a_{ij} + a_{ijk} + e_{ijkl}$$

where

μ = over-all mean,
a_i = fixed effect of plantation locations,
a_j = fixed effect of parent trees grouped to represent elevational zones,
a_{ik} = random effect of replications within plantation locations,
a_{ij} = interaction effect of plantation locations and elevational zones,

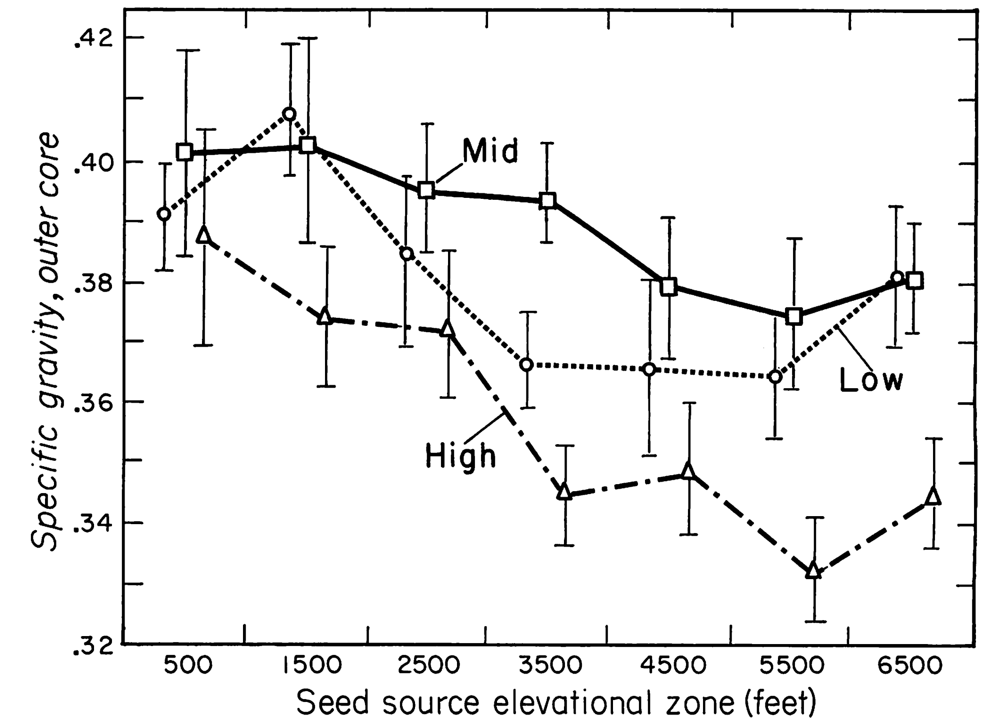

FIGURE 2. *Average specific gravity for outer core segments by seed source zone, based on progeny means. See Figure 1 caption for location of mid-, high-, and low-elevation plantations.*

a_{ijk} = interaction effect of replications within locations and elevational zones, and

e_{ijkl} = trees within plots.

F tests were performed, using the mean square for trees within plots to test replications in plantations and elevational zones × replications in plantations. The mean square for elevational zones × replications in plantations was used to test elevational zones and plantations × elevational zones, and the mean square for replications in plantations was used to test plantations. The expected mean squares developed from the model formed the basis for calculating variances associated with each source of variation. The percentage of the total variation was developed for each source of variation.

Results

Specific Gravity—Inner Cores. The specific gravity of inner core segments (wood produced in years 12 through 19) decreased as elevation of seed parents in all plantations increased (Fig. 1). The elevational source zones contributed highly significant variation.

In the High plantation, seed sources from the lowest elevation produced wood with an unusually high average specific gravity of 0.41 in the inner cores. Wood from the same sources averaged 0.38 in both Mid and Low plantations. The larger value can be associated with the high incidence of compression wood found in the inner stem portions of low-elevation sources grown in the High plantation. Adjustment of the abnormal values caused by compression wood dropped the average specific gravity for inner cores to 0.38.

Specific Gravity—Outer Cores. Like those of the inner core wood, the specific gravities of outer cores (representing years 20 to 27) decreased with increasing elevation of seed source (Fig. 2). Again variation arising from elevational zones of the parents

TABLE 1. Rank correlations between ponderosa pine parent tree elevation, and specific gravity, height, and diameter of progenies at three locations, Sierra Nevada Mountains, Calif. Based on progeny means.

Tree characteristic	Plantation	Parent tree elevation	Specific gravity		Tree height[a]
			Inner core	Outer core	
Specific gravity:					
Inner Core	High	–0.93**			
	Mid	–0.86*			
	Low	–0.68*			
Outer core	High	–0.82*	0.79*		
	Mid	–0.86*	0.93**		
	Low	–0.75	0.86*		
Height[a]	High	0.43	–0.32	–0.54	
	Mid	–0.75	0.61	0.68	
	Low	–0.86*	0.39	0.61	
Diameter[a]	High	0.50*	–0.57	–0.82*	0.57
	Mid	–0.76*	0.64	0.64	0.96**
	Low	–0.57	0.18	–0.32	0.86*

[a] Trees 29 years old.
** Statistically significant at 1-percent probability level.
* Statistically significant at 5-percent probability level.

was highly significant. But, though the general trend was similar to that of inner core wood, plantations also contributed highly significant variation. This environmental influence of plantations, minor for inner wood, was pronounced for the outer wood. For outer cores, all seed sources produced lower specific gravity wood in the High plantation. In the other two plantations the opposite of the expected pattern occurred. With the exception of trees from the 1500-ft elevation zone, specific gravities were lower for sources growing in the Low than for sources in the Mid plantation.

The effect of tree age, evident when inner core values were compared with outer core values, had a very pronounced interaction with plantation (environment). Specific gravities increased regularly with age at the Mid and Low plantations, but decreased significantly with age at the High plantation.

Relationships Between Characteristics. Mirov *et al.* (1952) reported height and diameter growth of these trees at younger ages. Through the first 12 years, trees from low to mid elevations were the largest in all three plantations. By 20 years of age, trees from more nearly local seed sources had the better height growth at the three planting sites (Callaham and Liddicoet 1961). Diameters within Low and Mid plantations decreased as elevation of seed parents increased; at High they increased. Stem taper was greatest for trees in the High plantation; this plantation (5650 ft) provided severe environmental conditions, resulting in some lean and breakage—particularly among trees from the low-elevation sources.

At age 29, the trees showed growth trends resembling those reported for the trees at age 20.[1] Trees from mid-elevation seed parents were tallest at all three plantation locations. Progenies from high-elevation seed parents were the smallest trees in the Low and Mid plantations. But in the High plantation, trees from high-elevation parents were among the tallest, equalling

[1] M. Thompson Conkle. 29-year growth data from the California elevational transect study of ponderosa pine (manuscript in preparation).

the growth of progenies from mid-elevation parents. Trees on the average are taller now in the Mid plantation than in either the High or Low plantations (mean heights in feet are: Low, 36.1; Mid, 42.9; High, 41.2). Diameter growth now averages greater in the High plantation than in the Mid, which in turn is greater than that for the Low plantation (mean diameters in inches are: Low, 7.4; Mid, 8.5; High, 10.3).

The correlations in Table 1 indicate the direction and strength of the relationships between the tree characteristics studied. It should be recognized that plantations represent different environments. The failure of correlations to be of the same size or direction or both for the three plantations indicates genotype × environment interaction.

Significant values under the parent tree elevation column in Table 1 indicate a genetic adaption expressed in the progeny. Specific gravity decreased as seed parent elevation increased. Heights and diameters increased as seed source elevation increased in the High plantation, but decreased within both the Mid and Low plantations.

Specific gravity values for inner and outer core wood samples showed significant positive correlations. The correlations were of nearly the same magnitude for all three plantations. Both inner and outer core specific gravities were negatively correlated with 29-yr heights within the High plantation. Taller trees are from the higher elevation seed sources. These sources also have less dense wood. Within the Mid and Low plantations there was a tendency toward positive correlations between outer core specific gravity and tree height. Taller trees and denser outer wood are associated with low-elevation seed sources. For diameter growth and specific gravity, the direction and magnitude of the correlation was dependent on plantation environment. There was a significant negative correlation in the High plantation, but positive relationships in both Mid and Low plantations.

Discussion

The mixed pattern of growth and specific gravity may reasonably be explained by a number of factors. Early growth was fairly equal in all three plantations. Thus, except for reaction wood caused by severe environmental stresses at the high elevation, wood specific gravity in the inner core segments was fairly uniform. Specific gravity means were not significantly different in the three plantations. The trees were influenced more by general edaphic and climatic conditions than by competition among themselves.

As the trees progressed through the second 8-yr period, they began to encounter moisture limitations during the regular dry summer periods at the lower elevations. The High plantation received some summer rainfall which should have prolonged earlywood growth. The lower plantations, having an earlier water stress condition, slowed new cell production and began to add more material to the cell walls in the outer rows. Whitmore and Zahner (1966) theorized that when water stress is low in conifers and mother cells are actively producing new derivatives, older derivatives currently in the maturing zone are displaced at a high rate from the phloem by the new derivatives entering the enlarging zone. Thus, derivatives in the maturing zone do not compete well for cell wall substrate and mature before exceptional secondary wall thickening occurs. As water stress develops in the tree the zones of mother cell activity and derivative enlargement both become narrow in dimension and small in cell number. Whitmore and Zahner (1966) concluded that even though the rate of growth of the secondary wall may also be reduced by water stress, the alleviation of competition among cells is sufficient for considerable wall thickening to occur before maturity because derivatives remain alive for a much longer period of time.

The double effect of slowed growth and thicker secondary cell walls in the latewood tracheids produced higher average specific gravity means in the outer cores in this study. While we can suggest causative factors here, they are not always easy to identify. The literature relating geographic and elevational variation of wood character-

TABLE 2. Total variance attributable to each source of variation of specific gravity in inner and outer cores of 29-year-old ponderosa pine seedlings at three locations, Sierra Nevada, Calif.

Source of variation	D.f.	Inner core		Outer core	
		M.s.	Pct	M.s.	Pct
Plantations	2	0.00882	1.4	0.05876**	15.3
Elevational zones	6	.01369**	9.8	.02073**	12.3
Replications in plantations	9	.00492**	5.5	.00371**	3.0
Plantations × elevational zones	12	.00226	1.4	.00220	.4
Elev. zones × replic. in plantations	54	.00171**	7.4	.00199**	8.0
Trees within plots	583	.00095	74.5	.00098	61.0

** Statistically significant at 1-percent level.

istics to progeny performance is meager. Progenies from Douglas-fir parents at low elevations near the Wind River plantation in southern Washington had higher specific gravities than the sources from higher elevations in the same area (McKimmy 1966). Although the low degrees of freedom unavoidably limited statistical elevational comparisons, the same pattern was seen in high- and low-elevation sources from the Santiam Valley in northwest Oregon. Other seed sources examined in the study, and other plantation locations provided no clear relationship of specific gravity and elevation of seed source.

We found significant genetic variation in wood specific gravity in our ponderosa pine progenies. Trends in specific gravity were related to seed source elevation. Specific gravity decreased for both inner and outer wood samples with increasing elevation of seed parent. This decrease occurred regardless of whether the trees were grown at the Low, Mid, or High plantations. The decrease was slightly more pronounced for seed sources growing in the High plantation. Elevation of seed source accounted for 9.8 (inner core) and 12.3 (outer core) percent of the total variation (Table 2).

Statistical treatment showed that environment played an important role. Plantations differed significantly in their outer core specific gravities. All genotypes had lower specific gravities in the High plantation than in the Mid and Low plantations. Thus, high-elevation parents tended to produce offspring of lower average specific gravity, regardless of location, and all seed sources tended to produce less dense wood when grown at higher elevations.

Within trees, wood specific gravity may increase or decrease outward from the pith (Cockrell 1943, Kano 1960, Krahmer 1966, McKimmy 1966, Paul 1963). In Douglas-fir, southern pines, and some true firs, specific gravity is lowest near the pith. In western hemlock, ponderosa pine, and *Cryptomeria* sp., specific gravity decreases outward from the pith. In plantation-grown Douglas-fir 46 years old, specific gravity increased from pith to bark within three test plantations, but decreased in a fourth (McKimmy 1966). Both trends were also evident in our study.

We detected an influence due to age, but the outcome depends upon the environment. In comparing inner cores with outer cores, we found that all genotypes in Low and Mid plantations increased in specific gravity. But in the High plantation they all decreased. In the two lower elevation sites, the outside wood was more dense; in the High plantation, outside wood was less dense.

Our results confirm the trend of decreasing specific gravity with elevation. Useful information for future breeding is seen in the consistency of the elevational pattern. For ponderosa pine under a similar set of conditions, if higher specific gravity wood is wanted, we suggest using low-elevation seed sources, or planting at low elevations, or both. Our data indicate that parents providing progeny with higher specific gravity wood occur with the greatest frequency at low elevations. If lower specific gravity wood is desired, plant at high elevations or use high-elevation seed sources.

The highest specific gravity wood will be obtained from elevational sources under 2000 ft, although these sources will not yield as high volumes as sources from 3000 to 4000 ft. For optimum production, a medium-elevation source outplanted at about 3000 ft should give the combination of highest volume yield of higher specific gravity wood. A combination of the highest volume coupled with the lowest specific gravity could be achieved by using seed from 5000 to 6000 ft elevation, and by growing the trees at this same elevation.

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