PROVENANCE AFFECTS BARK THICKNESS IN DOUGLAS FIR

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(Received for publication 2 December 2003; revision 18 March 2004)

ABSTRACT

Some coastal Californian provenances of *Pseudotsuga menziesii* (Mirb.) Franco (Douglas fir) have bark that is visibly thicker and more deeply furrowed than more northern and inland provenances. From a literature study it was evident that these variations in bark thickness most likely constitute adaptation to spatial and temporal patterns of wildfires within the natural range of Douglas fir.

Six provenances from the latitudinal range of Douglas fir in the Pacific Northwest of the United States (37°–48°N) were sampled for bark thickness and compared with a New Zealand landrace (Kaingaroa) seedlot at two New Zealand trial sites (38° and 46°S). The analyses showed that Californian provenances had significantly thicker bark than both the Kaingaroa (ex Washington) control seedlot and the Oregon and Washington provenances. The most southern provenance (Santa Cruz, California) had the thickest bark. Thus there was a steady reduction in bark thickness with increasing latitude of the seed sources. The bark thickness of the Kaingaroa seedlot was not significantly different from the Washington and Oregon provenances.

The provenance variations in bark thickness caused a bias in under-bark volume estimates from volume function "*T136*". Errors in volume estimation were greatest for Santa Cruz (+7.1%), Jackson State Forest (+2.8%), and Mad River (+2.0%). It is recommended that volume equation "*T136*" should be revised to account for differences in bark thickness with provenance.

Keywords: bark thickness; provenance; *Pseudotsuga menziesii*.

INTRODUCTION

In New Zealand, Douglas fir was first introduced into Canterbury in 1859 and initially used for amenity and farm plantings. It has been planted as a production species in New

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Zealand since about 1896 (Miller & Knowles 1994), is currently New Zealand's second most-planted tree species, and is increasing in area, especially in the South island.

The natural range of coastal Douglas fir is in the Pacific Northwest from latitude 55°N in British Columbia (Canada) to 35°N on the Californian coast of the United States. The preferred provenances in New Zealand production forestry are those from the coastal region of the United States, originally Washington and Oregon, and more recently also coastal California.

Within its natural range Douglas fir is exposed to a wide range of fire regimes. Generally, the severity and size of fires decrease and the frequency increases southward from western Washington to California. Lotan *et al.* (1978) reported catastrophic, widespread, destructive fires recurring every 400 to 500 years on the Pacific coast of Washington. Throughout central Oregon fires of low and moderate intensity occur every 50–150 years, with the occasional stand-replacing fire. In southern Oregon and California fire plays a much greater ecological role and return intervals in these areas are much shorter — between 5 and 25 years. Hence, the further south, the more frequent and less intensive are the fires (Morrison & Swanson 1990).

A plant species living in an environment with natural wildfires adapts to the occurrence of fire (Lotan *et al.* 1978; Flannery 1996; Florence 1996). If wildfires occur at regular intervals shorter than the average life of a species, the individuals of that species with the best protection against fire will have an advantage in producing offspring. Hoffman (1924) found a relationship between bark thickness and fire resistance in Douglas fir when it was exposed to temperatures of *ca* 500°C from a slash fire. Old-growth trees with 100-mm-thick bark survived for 360 minutes, 35-year-old trees with bark 37 mm thick were killed after 52 minutes, and saplings at age 8 were killed in 1 minute. This accords with the observations of Hare (1965), who reported that fire resistance is directly correlated with tree diameter. Smith & Fischer (1997) also found the bark of trees on good sites to be thick enough to offer fire resistance after the trees reached age 40 years.

The more southern provenances of Douglas fir are likely to have adapted to the more frequent occurrence of fires by producing thicker bark than the more northern provenances. In effect, bark thickness should decrease with latitude of provenance, as reported by Spalt & Reifsnyder (1962). They found a variation in bark thickness ratio (double bark thickness divided by over-bark diameter) due to latitude, with a ratio of 6.7 in the Northern Rocky Mountains and a ratio of 5.8 in the higher latitudes of British Columbia. Variance in bark thickness between provenances of Douglas fir in the United States has also been recognised for some time (Johnson 1966; Smith & Kozac 1967; Kahn *et al.* 1979; J.W.Flewelling unpubl. data). Monserud (1979) identified a difference in bark thickness of Rocky Mountain Douglas fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) between north-western Montana and northern Idaho.

Bark usually accounts for between 10 and 20% of the over-bark volume of a tree (Philip 1994). Tree volume and taper equations for Douglas fir in New Zealand use tree height and over-bark breast height diameter as independent variables to calculate under-bark volume. However, this does not take into account any variation in bark thickness between provenances, and the estimated under-bark wood volumes may therefore be biased. The purpose of this study was to investigate these effects by analysing bark thickness measurements and estimating any bias in estimated wood volume associated with provenance.

MATERIAL

A set of six provenances ranging from coastal Washington to California (Table 1) planted in 1959 at Rankleburn (West Otago, lat. 46°) and Kaingaroa (Bay of Plenty, lat. 38°25´) were sampled, together with a New Zealand landrace seed source (Kaingaroa, ex Washington) as a control. Thirty trees of merchantable size and relatively free of malformation were assessed within each provenance at the two sites, and the bark thickness was measured at breast height using a standard Swedish bark gauge. The selected trees were distributed more or less uniformly across the one to three plots (originally of 144 trees each) available for each provenance at each site. Two measurements of bark thickness were taken from each tree on opposite sides of the stem (north and south) at breast height (1.4 m), and double bark thickness was calculated as the sum of the two measurements. Care was taken to ensure that only thickness of bark was measured and not cambium or wood.

TABLE 1–Provenances examined in the Rankleburn and Kaingaroa trials

Seedlot	Locality	State	Latitude	MAI *
FRI 56/631	Darrington	Washington	48°15´N	18.8
FRI 56/584	Olney	Oregon	46°05´N	19.9
FRI 56/635	Florence	Oregon	43°58´N	19.7
FRI 56/647	Mad River	California	40°55´N	22.0
FRI 56/654	Jackson State Forest	California	39°21´N	23.4
FRI 56/660	Santa Cruz	California	37°05´N	22.9
Rotorua 54/530	Kaingaroa	New Zealand ex Washington	38°25´S	17.5

* MAI is the mean annual volume increment in cubic metres per hectare per year, excluding thinning to waste, and is based on estimates by M.O.Kimberley and R.L.Knowles (unpubl. data), using volume function "*T136*".

At the Rankleburn site bark thickness was also measured at 4 m and 6 m height above ground on each stem. In addition to these measurements of standing trees, bark measurements at different heights from felled trees were also obtained from:

(1) Waiotapu Forest Compartments 1 and 2 (aged 33 years) and Waimihia Forest Compartments 688 and 694 (aged 59 years), both of Washington origin, hereafter referred to as "Waiotapu/Waimihia" (lat. 38–39°). Detailed stem measurements were available on 60 trees measured at six to eight heights, up to 34 m.

(2) Rotoehu Forest Compartment 55 (aged 42 years) of Jackson State Forest (coastal Californian) origin (lat. 37°50´). Detailed stem measurements were available on 18 trees measured at six heights, up to 30 m. This was the same seedlot (FRI 56/654) as used in the provenance trials.

METHODS

From the bark thickness measurements, the bark ratio was calculated as the absolute double thickness of the bark divided by over-bark stem diameter, expressed as a percentage.

Descriptive statistics of diameter at breast height 1.4 m (dbh), height, and mean bark ratios for Rankleburn and Kaingaroa were calculated and compared between provenances.

The differences in mean bark ratio were analysed using ANOVA (PROC GLM of SAS) with trial, provenance, and dbh as independent variables (including combined effects), and by grouping the provenances based on Fisher's Least Significant Difference ($p < 0.05$). The bark ratio for each provenance was plotted against the latitude of origin. The variations in mean bark ratio with height were ascertained using descriptive statistics and plots of the data from Waiotapu/Waimihia and Rotoehu.

The accepted standard method for determining the volume of Douglas fir New Zealand-wide is equation "*T136 Pseudotsuga menziesii*" (Katz *et al.* 1984)

$$V = D^{\alpha} (H^2 /(H - 1.4))^{\beta} e^{\gamma}$$

where V is under-bark tree volume,
D is over-bark diameter at breast height,
H is total height of the tree, and
α, β, and γ are parameters, with values 1.828198, 1.102592, and –10.19719 respectively.

A compatible stem taper function to volume equation "*T136*" is

$$d(l) = \frac{4 \cdot 10^4 V}{\pi H} \left[b_1 \frac{l}{H} + b_2 \left[\frac{l}{H} \right]^2 + b_3 \left[\frac{l}{H} \right]^3 + b_4 \left[\frac{l}{H} \right]^4 + b_5 \left[\frac{l}{H} \right]^5 + b_p \left[\frac{l}{H} \right]^p \right]$$

where $d(l)$ is diameter under-bark at distance l from the top of the tree,
V is volume,
H is height,
l is distance from the top of the tree, and
b_1, b_2, b_3, b_4, and b_5 are parameters with values 0.319071, 0, 23.9972, –47.47884, and 26.02156 (Katz *et al.* 1984).

Insertion of over-bark dbh (dbh_{ob}) and mean top height into "*T136*" gives estimates of under-bark volume (V_{ub}), and the corresponding under-bark dbh (dbh_{ub}) may be calculated from the taper-function. The bark ratio of equation "*T136*" (B_{T136}) for a tree with a dbh_{ob} is then given as

$$B_{T136}(dbh_{ob}) = \frac{dbh_{ob} - dbh_{ub}}{dbh_{ob}}$$

Over-bark volume (V_{ob}) is calculated using equation "*T136*" by adding the estimated bark ratio on to the over-bark dbh — in essence calculating the under-bark volume for a slightly larger tree. This, however, assumes that the bark ratio does not change for small variations in dbh, i.e.,

$$V = (dbh_{ub} * (1 + B_{T136}))^{\alpha} (H^2 / (H - 1.4))^{\beta} e^{\gamma}$$

The bark volume percentage is then calculated as the difference between over-bark and under-bark volumes.

Subtracting the provenance-specific bark ratio from a measured over-bark dbh gives a provenance (i) specific under-bark dbh ($dbh_{ub,i}$). Under the assumption that the bark ratio is unaffected by small changes in dbh, the corresponding under-bark volume is calculated as

$$V = (dbh_{ub,i} * (1 + B_{T136}))^{\alpha} (H^2 / (H - 1.4))^{\beta} e^{\gamma}$$

The volume bias is calculated as the ratio between the under-bark volume as calculated from the over-bark dbh and the under-bark volume as calculated from the provenance-specific under-bark dbh.

RESULTS

Descriptive statistics for dbh and mean height for the sampled trees at Rankleburn and Kaingaroa are given in Table 2, and confirm that the Californian provenances grew larger in diameter, and taller, than Oregon or Washington provenances.

The ANOVA of bark ratio is shown in Table 3, and the means and LSD groups are presented in Table 4. None of the combined effects of dbh, provenance, and site were significant. The bark ratios were on average 2.5% less for Kaingaroa than for Rotoehu; however, this effect did not influence the between-provenance comparison. An increase in dbh of 1 cm increased the bark ratio by 0.0348%, and because the provenances grow

TABLE 2–Mean height and dbh of sampled trees at Rankleburn and Kaingaroa

Provenance	Rankleburn		Kaingaroa		Mean	
	Height (m)	Dbh (cm)	Height (m)	Dbh (cm)	Height (m)	Ddh (cm)
Darrington, WA	33.3	50.9	32.2	42.7	32.9	47.5
Olney, OR	36.0	52.5	34.4	41.8	35.2	47.1
Florence, OR	37.1	56.2	33.8	40.1	35.1	46.3
Mad River, CA	36.7	56.8	34.5	42.0	35.7	50.3
Jackson State Forest, CA	40.1	55.3	35.2	44.8	38.3	51.3
Santa Cruz, CA	37.6	61.2	37.7	47.9	37.7	55.5
Kaingaroa, ex WA	33.6	50.2	32.2	38.2	32.8	43.7

TABLE 3–ANOVA for bark ratio at breast height

Source	DF	Type II SS	MS	F value	P > F
Dbh	1	36.9581	36.9581	15.20	0.0001
Provenance	6	662.0111	110.3352	45.37	<0.0001
Trial site	1	54.0026	54.0026	22.21	<0.0001

TABLE 4–Mean bark ratios (%) at breast height by provenance and trial site and the groups identified by Fisher's LSD test. Provenances followed by the same letter do not differ significantly (p = 0.05).

Provenance	Rankleburn	Kaingaroa	Mean	LSD groups
Santa Cruz, CA	10.31	11.72	10.98	A
Jackson State Forest, CA	8.15	8.64	8.57	B
Mad River, CA	7.42	8.51	7.92	B
Kaingaroa, ex WA	6.33	7.00	6.76	C
Florence, OR	6.70	6.63	6.74	C
Darrington, WA	6.42	6.61	6.50	C
Olney, OR	5.96	5.85	5.87	C

differently this may have affected the provenance comparison. However, adjustment for dbh did not alter the mutual provenance relations and therefore only the unadjusted values for bark ratio are presented.

The Kaingaroa control had a mean bark ratio similar to that of the provenances from Oregon and Washington. The Santa Cruz provenance clearly had the highest bark ratio at 10.98, which was significantly different from the other provenances. The Jackson State Forest provenance had a mean bark ratio of 8.57 and was not significantly different from the Mad River at 7.92.

Mean bark ratios by provenance for both Rankleburn and Kaingaroa sites are plotted against the original United States provenance latitude in Fig. 1. This illustrates a relatively smooth trend of decreasing bark ratio with increasing United States latitude. In effect, the further south the provenance's home range, the larger the proportion of bark.

The bark thickness measurements from Waiotapu/Waimihia and Rotoehu are summarised in Table 5 and Fig. 2. Clearly, for the heights measured, the bark ratio decreased with increasing height above ground. At the base of the stem the Waiotapu/Waimihia Douglas fir (ex Washington) had a mean bark ratio of 10.23, which was almost halved to 5.83 at 4.9 m. For Rotoehu Forest (ex Jackson State Forest, California) the mean bark ratio at breast height of 9.00 reduced to 7.11 at 6.5 m. Compared to the Waiotapu/Waimihia stands, the bark of the Rotoehu material was thicker at all stem heights up to 25 m above ground.

The bark ratios at 4 m and 6 m above ground from the Rankleburn trial are presented in Table 6. There were significant differences ($p<0.05$) between provenances at 4 m (Table 6), with Santa Cruz and Jackson State Forest both significantly different from the six other provenances. The Florence, Mad River, Darrington, Kaingaroa, and Olney

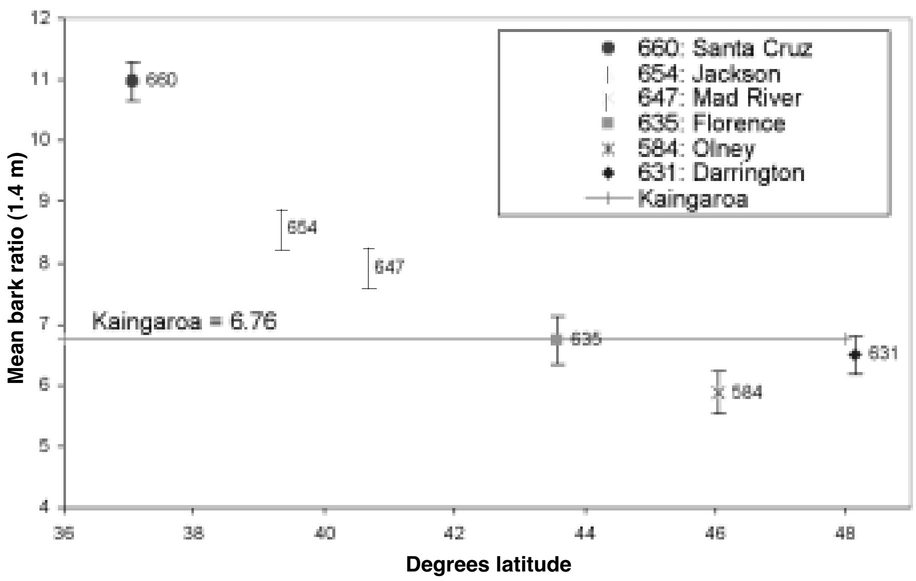

FIG. 1–Mean provenance bark ratio *versus* provenance latitude in the United States. Error bars signify 95% confidence limits.

TABLE 5–Mean bark ratio at different heights above ground for trees at Waiotapu/Waimihia (Kaingaroa ex Washington) and Rotoehu (ex Jackson State Forest)

Waiotapu/Waimihia (Kaingaroa ex Washington)		Rotoehu (ex Jackson State Forest)	
Height (m)	Mean bark ratio (%)	Height (m)	Mean bark ratio (%)
0	10.23	0.15	11.72
4.9	5.83	1.31	9.00
9.8	5.39	6.85	7.11
14.7	5.66	12.47	6.51
19.6	6.18	18.03	6.54
24.5	6.66	25.78	6.76
29.4	7.29	28.51	7.46
34.3	8.07		

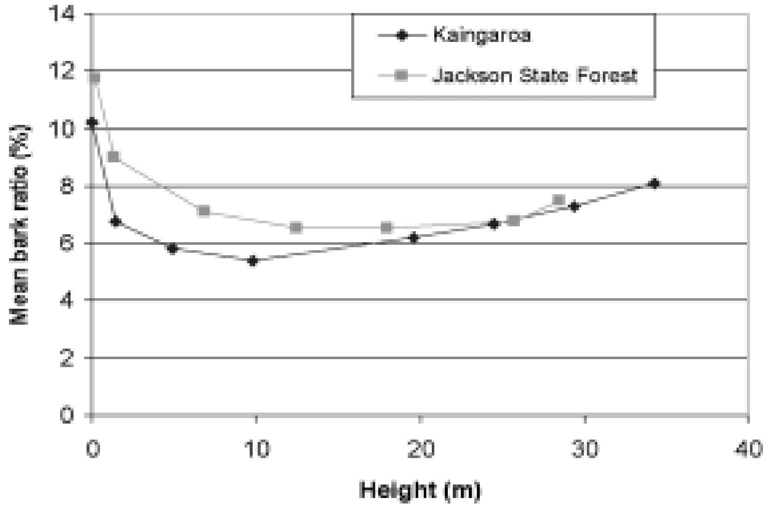

FIG. 2–Mean bark ratio with height above ground for Waimihia (Kaingaroa ex Washington) and Rotoehu (ex Jackson State Forest, California).

TABLE 6–Mean bark ratio at 4 m and 6 m above ground from the Rankleburn provenance trial and the groups identified by Fisher's LSD test. Provenances followed by the same letter do not differ significiantly (p = 0.05).

Provenance	Height 4 m		Height 6 m	
	Mean	LSD groups	Mean	LSD groups
Santa Cruz, CA	6.87	A	8.15	A
Jackson State Forest, CA	5.65	B	6.45	B
Florence, OR	4.96	B,C	5.41	C
Mad River, CA	4.69	C	5.30	C
Darrington, WA	4.48	C	5.15	C
Kaingaroa	4.57	C	5.11	C
Olney, OR	4.29	C	4.99	C

provenances were not significantly different. The same trends were evident at 6 m above ground, i.e., the Santa Cruz and Jackson State Forest provenances had significantly thicker bark.

The bark volume percentages, bark volume bias, and under-bark volume bias derived from volume function "*T136*" are presented in Table 7. The mean bark volume estimate for the control Kaingaroa seedlot was very similar to the actual bark volume measurements. The estimates for Darrington, Olney, and Florence provenance were all within 5% of the measured value, with a corresponding error in wood volume of 1.4% or less. The bark volume was, however, significantly under-estimated for Mad River, Jackson State Forest, and Santa Cruz. Consequently, the wood volume for these provenances was over-estimated by 2–7%.

The estimated mean annual increments (MAI) for different provenances, calculated using "*T136*" from dbh and height as shown in Table 1, are listed in Table 8 with and without correction for bark thickness bias.

TABLE 7–Mean bark volume percentage, bark volume bias, and under-bark volume bias

Provenance	Bark volume (%)	Bark volume bias (%)	Under-bark wood volume bias (%)
Kaingaroa control	11.13	<+1	0
Darrington, WA	10.86	+2	<+0.5
Olney, OR	9.95	+3	+1.4
Florence, OR	11.08	–5	<+0.5
Mad River, CA	12.87	–12	–2.0
Jackson State Forest, CA	13.56	–29	–2.8
Santa Cruz, CA	17.18	–33	–7.1

TABLE 8–Estimated MAI values for Douglas fir provenances adjusted for bark thickness bias

Provenance	Origin	Latitude	MAI unadjusted	MAI adjusted
Darrington	Washington	48°15´N	18.8	18.8
Olney	Oregon	46°05´N	19.9	19.9
Florence	Oregon	43°58´N	19.7	19.7
Mad River	California	40°55´N	22.0	21.6
Jackson State Forest	California	39°21´N	23.4	22.7
Santa Cruz	California	37°05´N	22.9	21.2
Kaingaroa	New Zealand ex Washington	38°25´S	17.5	17.5

CONCLUSION

The bigger trees tended to have thicker bark, as found also by Kahn *et al.* (1979) and Monserud (1979). However, the provenances from coastal California had significantly thicker bark than the Oregon and Washington provenances, even when adjusted for their larger stem diameter. Hence, Douglas fir had thicker bark in regions with frequent wildfires, which supports the hypothesis that Douglas fir in those areas has adapted to wildfires by increasing its bark thickness. This conclusion is in accordance with those of Lotan *et al.* (1978) and Morrison & Swanson (1990). The bark thickness variation with latitude is gradual, with the main difference occurring between Santa Cruz (South of San Francisco, lat. 37°) and Mad River (Northern California, lat. 41°). Bark thickness differences seem to level out with height, with little difference between provenances.

Under-bark wood volume in the Darrington and Florence provenances, as estimated by volume function "*T136*", was not biased, but the wood volume of the Olney provenance was under-estimated by 1.4%. The wood volumes of the three Californian provenances were all over-estimated, i.e., Mad River (2%), Jackson (2.8%), and Santa Cruz (7.1%).

Volume equation "*T136*" was developed in 1977 and has proved its worth. It should, however, be redeveloped to include the provenance effect on bark thickness. Until this redevelopment, the bias for the Californian provenances must be accounted for in other ways. For example, as shown in the corrected provenance trial MAI evaluation in Table 8.

ACKNOWLEDGMENTS

The authors wish to thank the following persons and organisations for their contributions to this study. John Parish of Ernslaw One Ltd, Tapanui, provided field equipment for sampling the Rankleburn stand. Adele Wedding, School of Forestry, Canterbury University, assisted with field procedures. Russell McKinley, Forest Research, provided previously collected data sets on Douglas fir bark thickness. Jim Flewelling, Seattle, Washington, and Tony Shelbourne, Forest Research, provided useful comments on a draft of this paper. Funding was jointly provided by FRST Contract No CO4X0010, and the NZ Douglas-fir Research Cooperative.

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