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Abstract

Some coastal Californian provenances of 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.

A sample of six provenances from the latitudinal range of Douglas-fir in the Pacific Northwest of the USA (37°-48°N) were measured for bark thickness at two New Zealand trial sites (38-39°S).

The analyses showed that Californian provenances have significantly thicker bark than both the Kaingaroa (ex Washington) control seedlot and the Oregon and Washington provenances. The most southern provenance (Santa Cruz) 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*' is revised to account for differences in bark thickness with provenance.

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Introduction

In New Zealand, Douglas-fir was first introduced into Canterbury in 1859 and initially used for amenity and farm plantings. Douglas-fir has been planted as a production species in New Zealand since about 1896 (Miller and Knowles 1994), and 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 (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) is in the Pacific Northwest from latitude 55°N in British Columbia (Canada) to 35°N on the Californian coast of USA. 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 decreases, whilst the frequency increases southward from western Washington to California. Lotan *et al.* (1978) reported catastrophic, widespread, destructive fires reoccurring 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, e.g. between 5 and 25 years. Hence, the further south, the more frequent and less intensive are the fires (Morrison and 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 exposed to temperatures of ca. 488°C from a slash fire. Old growth trees with 100mm-thick bark survived for 360 minutes, 35-year-old trees with bark 37mm thick were killed after 52 minutes and saplings at age 8 were killed in one minute. This accords with the observations of Hare (1965), who reported that fire resistance is directly correlated with tree diameter. Smith and 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 (i.e. thicker bark). While the more northern provenances have not. In effect, bark thickness should decrease with latitude of provenance, as reported by Spalt and Reifsnyder (1962). They found a bark thickness ratio variation 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 and Kozac 1967, Kahn *et al.* 1979, Flewelling 1994). 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 percent 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 is to investigate these effects by analysing bark thickness measurements and estimate any bias in estimated wood volume associated with provenance.

Material

A set of provenances ranging from coastal Washington to California (Table 1) planted in 1959 at Rankleburn (Tapanui) and Kaingaroa were sampled. Thirty trees of merchantable size and relatively free of malformation were assessed within each provenance at the two sites, and the bark thickness measured at breast height using a standard Swedish bark gauge. The trees were picked more or less uniformly distributed across the 1-3 plots (originally of 144 trees each) available for each provenance at each site. All trees were measured twice on opposite sides of the stem (North and South), and double bark thickness calculated as the sum of the two measurements. Care was taken to ensure that only thickness of bark was being measured and not cambium or wood.

Seedlot	Locality	State	Latitude	MAI[3]
FRI 56/631	Darrington, WA	Washington	48.15°	18.8
FRI 56/584	Olney, OR	Oregon	46.05°	19.9
FRI 56/635	Florence, OR	Oregon	43.58°	19.7
FRI 56/647	Mad River, CA	California	40.55°	22.0
FRI 56/654	Jackson State Forest, CA	California	39.21°	23.4
FRI 56/660	Santa Cruz, CA	California	37.05°	22.9
Rotorua 54/530	Kaingaroa, ex WA	New Zealand ex Washington		17.5

Table 1 List of provenances examined in the Rankleburn and Kaingaroa trials

Bark thickness was also measured at 4 m and 6 m up each stem for all trees at Rankleburn. Bark measurement at different heights from felled trees were also included 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°),
2. Rotoehu Forest Compartment 55 (aged 42 years) of Jackson State Forest (coastal Californian) origin. This is 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.

Descriptive statistics of 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 was 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 in New Zealand is equation '*T136 Pseudotsuga menziesii*' (Katz *et al.* 1984)

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

[3] MAI is the mean annual volume increment in m^3/ha/yr, excluding thinning to waste, and is based on estimates from Kimberley and Knowles (unpublished data), using volume function '*T136*'.

Where V is under-bark tree volume, D is diameter at breast height, H is total height of the tree, and α, β and γ are parameters, with values 1.8281198, 1.102592 and –10.19719 respectively. A compatible stem taper function to volume equation '*T136*' is

$$D(l) = \frac{4 \cdot 10^4 V}{\pi H}\left(b_1 \frac{l}{H} + b_2 \frac{l}{H} + b_3 \frac{l}{H} + b_4 \frac{l}{H} + b_5 \frac{l}{H} \right)$$

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 an over-bark DBH of DBH_{ob} is then given as

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

Over-bark volume (V_{ob}) is calculated using equation '*T136*' by adding the estimated bark ratio onto 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 invariant to 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 trees at Rankleburn and Kaingaroa are shown in Table 2, and confirm that Californian provenances grow larger in diameter, and taller, than Oregon or Washington provenances.

Provenance	Rankleburn Height (m)	Rankleburn DBH (cm)	Kaingaroa Height (m)	Kaingaroa DBH (cm)	Mean Height (m)	Mean DBH (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 2 Mean height and DBH of sampled trees at Rankleburn and Kaingaroa

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 percent points less for Kaingaroa than for Rotoehu, however, this effect did not influence the between-provenance comparison. An increase in DBH of one cm increased the bark ratio by 0.0348 percent points, and because the provenances grow differently this may have affected the provenance comparison. However, adjustment for DBH did not alter the mutual provenance relations and the unadjusted values for bark ratio are therefore presented only.

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

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

Table 3 ANOVA for bark ratio at breast height

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

Table 4 Mean bark ratios (percent) at breast height by provenance and trial site and the groups identified by Fisher's LSD test

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

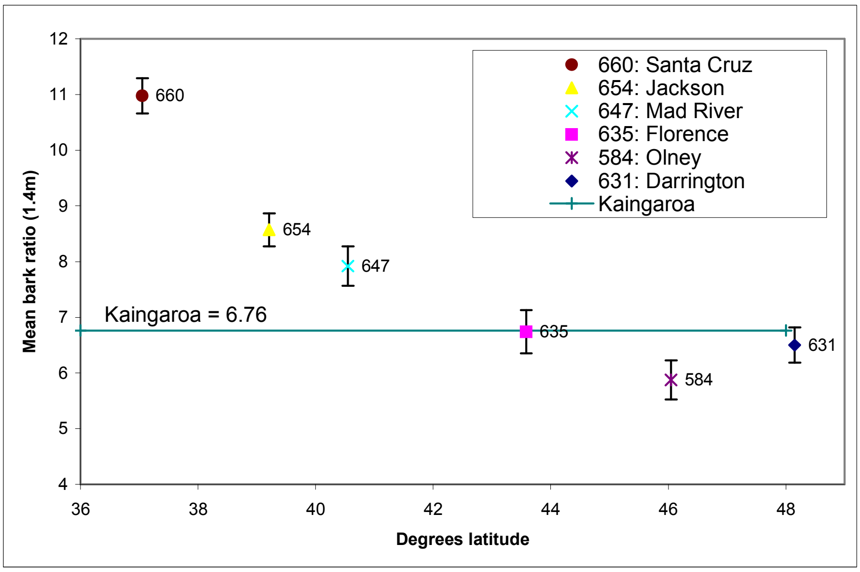

Figure 1 Mean provenance bark ratio versus provenance latitude in the United States

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

Waiotapu/Waimahia (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		

Table 5 Mean bark ratio at different heights for trees at Waiotapu/Waimihia (ex Washington) and Rotoehu (ex Jackson State Forest)

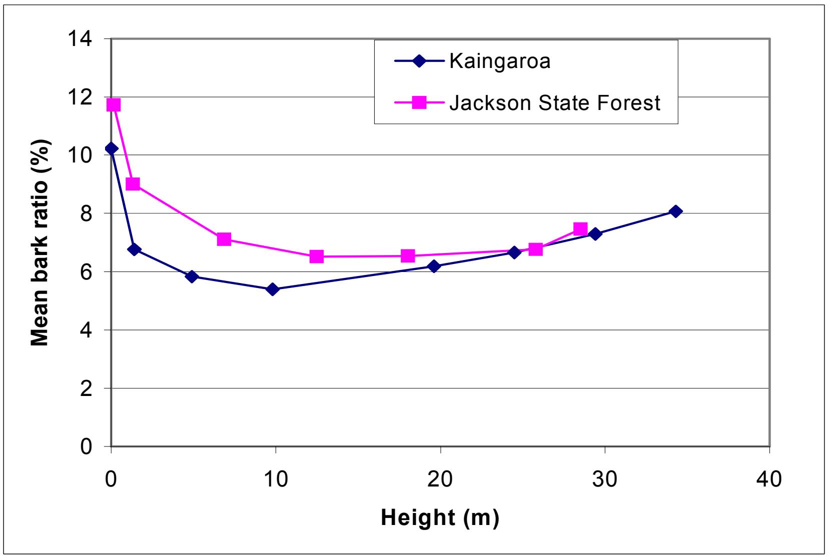

Figure 2 Mean bark ratio with height for Waimihia (ex Washington) and Rotoehu (ex Jackson State Forest, California)

The bark ratios at 4 m and 6 m from the Rankleburn trial are presented in Table 6. There are 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 provenances are not significantly different. The same trends are evident at 6 m, i.e. the Santa Cruz and Jackson State Forest provenances have significantly thicker bark.

	Height 4 m		Height 6 m	
Provenance	**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

Table 6 Mean bark ratio at 4 m and 6 m height from the Rankleburn provenance trial and the groups identified by Fisher's LSD test

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 is very similar to the actual bark volume measurements. The estimates for Darrington, Olney and Florence provenance are all within 5% of the measured value, with a corresponding error in wood volume of 1.4% or less. The bark volume is, however, significantly underestimated for Mad River, Jackson State Forest and Santa Cruz. Consequently, the wood volume for these provenances is overestimated by 2-7 percent.

Provenance	Bark volume percentage	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%	-12.5%	-2.0%
Jackson State Forest, CA	13.56%	-29%	-2.8%
Santa Cruz, CA	17.18%	-33%	-7.1%

Table 7 Mean bark volume percentage, bark volume bias and under-bark volume bias

The estimated mean annual increments (MAI) for different provenances in Table 1, with and without correction for bark thickness bias are listed in Table 8.

	Origin	Latitude	MAI unadjusted	MAI adjusted
Darrington, WA	Washington	48.15°	18.8	18.8
Olney, OR	Oregon	46.05°	19.9	19.9
Florence, OR	Oregon	43.58°	19.7	19.7
Mad River, CA	California	40.55°	22.0	21.6
Jackson State Forest, CA	California	39.21°	23.4	22.7
Santa Cruz, CA	California	37.05°	22.9	21.2
Kaingaroa, ex WA	New Zealand ex Washington		17.5	17.5

Table 8 Estimated MAI values for Douglas-fir provenances adjusted for bark thickness bias

Conclusion

The bigger trees tended to have thicker bark, as also found by Kahn *et al.* (1979) and Monserud (1979). However, the provenances from coastal California had significantly thicker bark than Oregon and Washington provenances, even when adjusted for their larger stem diameter. Hence, Douglas-fir has adapted to wildfires by increasing its bark thickness in areas with more frequent fires. This conclusion is in accordance with the conclusions of Lotan *et al.* (1981) and Morrison and Swanson (1990). The bark thickness variation with latitude is gradual and relatively smooth, with the main difference occurring between Santa Cruz (South of San Francisco, latitude 37°) and Mad River (Northern California, latitude 41°). The comparison of bark thickness trends with height showed that bark thickness differences level out with height with little difference between provenances.

Under-bark wood volume in the Darrington and Florence provenances is accurately estimated by volume function '*T136*', while the wood volume of the Olney provenance is underestimated by 1.4%. The wood volumes of the three Californian provenances are all overestimated, i.e. Mad River (2%), Jackson (2.8%) and Santa Cruz (7.1%).

It is recommended that volume equation '*T136*' is redeveloped to include the provenance effect on bark thickness. Until this redevelopment, the bias for the Californian provenances must be accounted for otherwise, for instance, as shown in the corrected provenance trial MAI evaluation in Table 8. However, the corrected values reveal that even with the correction for bark thickness, the coastal Northern Californian provenances are the most productive in New Zealand.

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