Effects of seed source origin on bark thickness of Douglas-fir (*Pseudotsuga menziesii*) growing in southwestern Germany

Ulrich Kohnle, Sebastian Hein, Frank C. Sorensen, and Aaron R. Weiskittel

Abstract: Provenance-specific variation in bark thickness in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is important for accurate volume calculations and might carry ecological implications as well. To investigate variation, diameter at breast height (dbh) and double bark thickness (dbt) were measured in 10 experiments in southwestern Germany (16 American and six German seed sources), which were approximately 50 years old and ranged in productivity. Provenance-specific mixed models for dbt versus dbh varied considerably with respect to intercept and slope. Likewise, analysis of covariance on bark ratio (range = 8.0% to 13.2%) with dbh as the linear predictor revealed significant differences ($p < 0.05$ to $p < 0.0001$) in 70% of the comparisons. Influence of seed origin on bark ratio was analyzed for our 16 American sources plus six provenances reported from New Zealand tests. In linear regressions, single geographic position variables explained only a small proportion of the variation in bark ratio (range of $r^2 = 0.01–0.33$), and the same was true for individual climate variables. In contrast, physiographic regions significantly ($p = 0.0013$) explained considerable variation ($r^2 = 0.66$). Likewise, a combination of three climate variables (temperature, frost days, precipitation) proved significant ($p < 0.0001$; $r^2 = 0.87$). As bark ratio was inversely related to precipitation at the seed origin, it is inferred that historic fire regimes may have played a selective role in the process by which Douglas-fir allocates dry matter between bark and wood.

Résumé : La variation de l'épaisseur de l'écorce qui est spécifique à la provenance chez le douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) est importante pour calculer avec précision le volume et pourrait aussi avoir des implications écologiques. Pour étudier cette variation, le diamètre à hauteur de poitrine (dhp) et la double épaisseur de l'écorce (déé) ont été mesurés dans 10 plantations expérimentales d'environ 50 ans (six provenances de graines allemandes et 16 américaines) établies dans le sud-ouest de l'Allemagne et dont la productivité différait. Le point d'intersection et la pente des modèles mixtes de la déé en fonction du dhp spécifiques à chaque provenance variaient considérablement. De la même façon, une analyse de covariance sur le rapport de l'écorce (étendue : 8,0 à 13,2 %) avec le dhp comme prédicteur linéaire a révélé des différences significatives ($p < 0,05$ à $p < 0,0001$) dans 70 % des comparaisons. L'influence de la provenance des graines sur le rapport de l'écorce a été analysée pour nos 16 provenances américaines plus six provenances sur la base de tests menés en Nouvelle-Zélande. Dans les régressions linéaires, les variables associées à la position géographique de chaque provenance expliquaient seulement une faible proportion de la variation du rapport de l'écorce (étendue de $r^2 = 0,01–0,33$) et la même chose était vraie pour les variables climatiques associées à chacune des provenances. Au contraire, les régions physiographiques expliquaient significativement ($p = 0,0013$) une proportion considérable ($r^2 = 0,66$) de la variation. De la même façon, une combinaison de trois variables climatiques (la température, les jours de gel, la précipitation) était significative ($p < 0,0001$; $r^2 = 0,87$). Étant donné que le rapport de l'écorce était inversement relié à la précipitation au point d'origine des graines, on suppose que les régimes historiques des feux pourraient avoir joué un rôle de sélection dans le processus d'allocation de matière sèche entre l'écorce et le bois chez le douglas.

[Traduit par la Rédaction]

Introduction

In Germany, the first Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) were planted in 1831 in an arboretum close to Hamburg. The species was introduced into southwestern Germany (Baden–Wuerttemberg) in the 1860s. A series of experiments was set up at the turn of the century (e.g., Schwappach 1891) to explore the potential value of growing foreign ("exotic") tree species. Douglas-fir soon emerged as the most promising, and the species has received much attention in German forestry since then.

Currently, Douglas-fir is by far the most widely planted exotic in Baden–Wuerttemberg, covering about 38 000 ha representing approximately 3% of the state's forest area (Kändler et al. 2006). The species offers tremendous economic potential (Brandl 1989; Heidingsfelder and Knoke 2004) and

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Table 1. Explanation of symbols and abbreviations.

Variable	Definition
ANCOVA	Analysis of covariance
ANOVA	Analysis of variance
Bark ratio	dbt divided by dbh × 100 (%)
dbh	Diameter at breast height (cm; mm)
dbt	Double bark thickness (mm)
dd0	Sum of degree-days < 0 °C
dd5	Sum of degree-days > 5 °C
*d*100	Julian date that the sum of degree-days > 5 °C reaches 100
dist	Distance from the closest ocean coast (km)
elev	Elevation (m above sea level)
fday	Julian date of the first freezing date of autumn
gsp	Growing season precipitation; April–September (mm)
gsdd5	Growing season sum of degree-days > 5 °C
lat	Northern latitude (degrees; minutes converted to decimals)
long	Western longitude (degrees; minutes converted to decimals)
mat	Mean annual temperature (°C)
mmax	Mean annual maximum temperature (°C)
mmin	Mean annual minimum temperature (°C)
mtcm	Mean temperature of the coldest month (°C)
PROV	Dummy variable for provenance
a, b, α, β, γ	Variance components of the models 1, 2, and 3, respectively
un	Unstructured covariance structure
$\|E\|$, E^2	Mean absolute error, mean squared error, respectively
el, p, t	Subscripts for experiment location, plot, and tree, respectively

will likely become even more widely planted in southwestern German in the upcoming decades as a substitute for Norway spruce (*Picea abies* (L.) Karst.), which appears seriously threatened by climate change (Hanewinkel et al. 2010).

Provenance soon emerged as an important issue for Douglas-fir introduction and management. The early introductions before 1939 were by happenstance of the var. *menziesii* (syn. *viridis*) (Hitchcock et al. 1977; Hermann 1981; Hermann and Lavender 1990), all of which had most probably been collected from seed sources from the US Pacific Northwest region between Portland, Oregon, and Seattle, Washington, and on the Olympic Peninsula (Strehlke 1959), which generally grew exceedingly well. Later introductions also included interior seed sources (var. *glauca*), which proved highly sensitive to a lethal needle blight caused by *Rhabdocline pseudotsugae* H. Sydow (Stephan 1981).

In Douglas-fir, the occurrence of provenance-specific phenotypic variation is well documented. Besides the taxonomically relevant traits used to differentiate coastal and interior varieties and the above-mentioned provenance specificity in disease susceptibility, provenance variation has been reported in many traits, for example, volume of cell nuclei (El-Lakany and Sziklai 1971), permeability of heartwood (Miller and Graham 1963; Bramhall 1966), terpene content of needle oil (von Rudloff 1972, 1973*a*, 1973*b*), or cortex resin (Zavarin and Snajberk 1973), phenology (Campbell 1986), and phenotypic characteristics important for forest management such as stem form or branchiness (Rau 2005; Schmidt and Weller 2006).

Another phenotypic characteristic important for forest management is bark thickness. For example, the expression of bark thickness is important for the development of underbark timber volume equations, affects the proportional yield of bark and wood in timber processing, and may be associated with fire resistance. At the basis of bark and wood formation in trees is the secondary diameter increase driven by formation of new phloem and xylem elements derived from cambial cells (Philipson et al. 1971). In conifers, the cell pattern in cambial growth is determined by single cambial initials located between phloem and xylem mother cells (Mahmood 1968). Species differ with respect to the frequency of redivision of mother cells, but differences may also be due to environmental causes (Philipson et al. 1971). In general, vigorous growth produces much more xylem than phloem; with slower growth, the amounts are often more equal (Wilson 1964). Growth of phloem and xylem appears not synchronous. In Douglas-fir, the xylem growth curve tends to peak early and taper off; the phloem curve begins later and tends to be more uniform (Grillos and Smith 1959).

Past observations of Douglas-fir growing in Germany have indicated provenance variation in bark characteristics including bark thickness. For example, as early as 1956, Hausser and Bolsinger commented on the necessity to differentiate between different bark types in southwestern Germany (Hausser and Bolsinger 1956). Göhre (1958) suspected provenance-specific differences in bark among East German Douglas-fir plantations. Altherr et al. (1978), based on their extensive measurement campaign including more than 3000 Douglas-fir, reported differences in bark thickness between Douglas-fir growing in southwestern vs. northern Germany. However, as they were not able to determine whether these differences were due to growing conditions, measuring techniques, or provenance, the matter was not pursued further.

Among the few studies systematically addressing possible provenance-specific differences in the expression of bark traits, the analysis of the Hessian plots within the interna-

Table 2. Experiments with Douglas-fir provenances in southwestern Germany measured in 2004–2005 for bark thickness.

	Provenance											
	Oregon, USA			Washington, USA								
	32	39	40	8	9	10	13	15	22	23	29	42
Experiment												
Dgl 91	2	2	2	1	2	2	—	—	2	—	—	—
	21	21	20	20	21	22			21			
Dgl 100	—	—	—	—	1	—	—	—	—	—	—	—
					29							
Dgl 114	2	2	2	2	2	2	—	—	2	—	—	—
	24	24	24	24	25	28			24			
Dgl 115	2	2	2	2	2	2	—	—	2	—	—	—
	25	26	25	24	25	25			25			
Dgl 116	1	1	1	1	1	1	—	—	1	—	—	—
	15	21	23	15	20	17			18			
Dgl 117	—	—	—	—	—	—	3	3	—	2	2	1
							72	66		47	48	24
Dgl 118	1	1	1	—	1	1	—	—	—	—	—	—
	25	30	25		30	26						
Dgl 119	—	—	—	—	—	—	1	1	—	1	1	1
							12	17		13	18	17
Dgl 122	2	—	4	2	2	2	—	—	1	—	—	—
	20		40	21	20	20			10			
Dgl 123	2	—	2	1	2	—	—	—	2	—	—	—
	32		31	25	31				30			
Total no. of plots	12	8	14	9	13	10	4	4	10	3	3	2
Mean no. of trees per location (SD)	23.1 (5.3)	24.4 (3.8)	26.9 (6.7)	21.5 (3.7)	25.1 (4.5)	23.0 (4.1)	42.0 (42.2)	41.5 (34.7)	21.3 (6.7)	30.0 (24.0)	33.0 (21.2)	20.5 (5.0)

Note: See Table 3 for names of the provenances and land races. The numbers of the North American provenances and of the experiment locations corre- were newly created for this investigation. For each experiment, the first number is the number of plots, and the number below it is the number of trees

tional provenance experiment in Douglas-fir under the auspices of IUFRO (Kleinschmit and Bastien 1992) supports provenance variation in visually discerned bark characteristics (Rau 2005). Recently, statistically significant seed-source influences on bark thickness in Douglas-fir provenances planted in New Zealand experiments were detected with bark ratios (for a list of the variables measured, see Table 1) ranging from 5.9%–11.7% (McConnon et al. 2004). It appears plausible that provenance-specific differences in bark traits may be at least in part under genetic control in Douglas-fir. For example, in his genetic study on open-pollinated families of Douglas-fir, St. Clair (1994) found significant differences between families with respect to several characteristics. In particular, heritability estimates for biomass partitioning to bark were considerably higher than estimates for stem size traits (height, diameter, volume). This provides circumstantial evidence that bark thickness is heritable as well.

To improve knowledge about factors affecting bark traits in Douglas-fir, we conducted a systematic investigation of bark thickness and bark ratio in Douglas-fir based on provenance experiments available to us mostly from southwestern Germany. Our objectives were (*i*) to describe the relationship of bark thickness and bark ratio to diameter at breast height (1.3 m; dbh), (*ii*) to evaluate provenance as a factor affecting bark ratio, and (*iii*) to relate provenance variation, if present, to physiographic and climatic differences among the seed origins.

Methods and material

Experimental plots

Field measurements were carried out in provenance experiments established in the early 1960s as part of the "Internationaler Douglasien-Provenienzversuch" (i.e. International Provenance Experiment in Douglas-fir) inspired and initiated by Prof. R. Schober. Baden–Wuerttemberg joined this experimental series in 1961 with test plantations at 15 locations (Kenk and Thren 1984*a*, 1984*b*), of which a considerable number of plantations are still vigorous and maintained by the Forest Research Institute of Baden–Wuerttemberg. Seeds for the experiments were collected in 1955 by B. Strehlke from autochthonous stands in North America (Strehlke 1959) and from selected cone-bearing stands growing in southwestern Germany ("land races") judged by forest practitioners to display excellent growth vigour (Table 2).

Dbh and bark thickness were measured at eight experiment locations of the original Schober–Strehlke series and at two additional locations (Dgl 117, Dgl 119), where the experiments had been established a little later (Tables 2, 3). Kenk and Thren (1984*a*) includes a detailed description and a map of the original seed sources. Their description contains one clerical error as the latitude of the Vancouver Island provenance "Duncan Paldi" (no. 7) should be 48°45′ instead of 45°45′. The majority of the North American provenances were coastal (var. *menziesii*), except for two British Columbia (BC) seed sources (nos. 3 and 4; Table 3), which were from

				Land race					
British Columbia, Canada				Baden–Württemberg, Germany					
3	4	5	7	1001	1002	1003	1004	1005	1006
2	2	2	—	—	1	—	—	—	—
20	20	22			20				
1	—	1	1	1	—	—	—	—	—
26		27	29	24					
—	—	2	2	—	2	—	—	—	—
		24	25		25				
—	—	2	2	—	2	—	—	—	—
		25	24		24				
—	—	1	1	—	1	—	—	—	—
		20	16		15				
—	—	—	—	—	—	—	—	—	2
									44
2	—	—	1	—	—	1	—	1	—
60			25			25		25	
—	—	—	—	—	—	—	1	—	—
							14		
2	2	3	—	—	—	—	—	—	—
20	22	30							
2	2	2	—	—	—	—	1	—	—
29	32	31					25		
9	6	13	7	1	6	1	2	1	2
31.0	24.7	25.6	23.8	24.0	21.0	25	19.5	25	44
(16.7)	(6.4)	(4.0)	(4.8)	—	(4.6)	—	(7.8)	—	—

spond to those used by Kenk and Thren (1984*a*, 1984*b*); numbers for the southwestern German land races measured for bark thickness.

the *menziesii–glauca* transition, where some introgression of var. *glauca* genes into the coastal variety or sampling of the *glauca* variety is likely.

Kenk and Thren (1984*a*) assigned the provenances to physiographic regions in western Oregon and Washington according to the definitions provided by Franklin and Dyrness (1973) and in British Columbia to presumptive regions "Southern Interior BC" and "Vancouver Island", respectively. The land races from southwestern Germany are also presumably of coastal origin, but the specific original seed-source locations are unknown. Numbers assigned to the North American provenances in Tables 2 and 3 correspond to those used by Kenk and Thren (1984*a*, 1984*b*). Numbers of the German land races were newly assigned for this investigation.

The 10 experiment locations used in this study included a total of 140 plots planted with the different provenances – land races. Due to practical reasons (availability of planting material, size of planting area, etc.), the planting of provenances – land races was not equally distributed among the 140 plots of the 10 experiment locations (Table 2). The number of provenances – land races planted at the different experiment locations ranged from 5 to 11, the number of plots per experiment location ranged from 5 to 20 (average of 14 plots per location), and the number of plots per provenance – land race at each experiment location ranged from 1.0 to 2.2 (average of 1.6 plots per provenance – land race). The rectangular plots were arranged in a grid without buffer rows between the plots. Provenance – land race plots were not distributed in either a systematic or random design in a strict sense but were irregularly placed within test plantations, and identical seed-source plots never adjoined.

Plots at most sites were 0.1 ha and had been planted at a density of ca. 3300 trees·ha^{-1}. At only a few sites were they larger (maximum 0.25 ha) and had differing planting densities (1600–4500 trees·ha^{-1}). Thinning was carried out according to a regime assigned to all experiments: the first thinning took place at a stand height of approximately 10–12 m and reduced stand density uniformly to 1400 trees·ha^{-1} by removing mostly small-diameter trees. At the same time, 150 future crop trees·ha^{-1} were permanently selected (marked). In crop tree management systems (e.g., Abetz 1975), these trees are intended to be kept and form the final stand. Their selection takes into account three major factors affecting productivity: growing vigour (competition status), timber quality, and spacing. Second and successive thinnings were conducted to favour crop trees. Stand densities in the plots were managed as specified by the stand density curve "starke Durchforstung" (i.e., "intensive thinning") developed for Douglas-fir by Kenk and Hradetzky (1984).

The goal of this height-driven thinning regime resulted in rather uniform stand density dynamics. As a rule, the provenance – land race experiments displayed similar stand densities at identical stand heights. There were only few exceptions. As a consequence of the storm damage during the gales of 1990 and 1999, stand densities in some of the plots were reduced below height-specific target densities.

Table 3. Descriptive statistics for trees measured for analysis of bark thickness.

Seed source		Original North American location					Trees measured for bark thickness (mean (SD))			
No.	Name	Physiographic region	Long (°N)	Lat (°W)	Elev (m)	Dist (km)	*N*	dbh (mm)	dbt (mm)	Bark ratio (%)
3	BC Salmon Arm Larch Hill	Southern Interior BC	119.17	50.83	650	403	155	298 (96)	35 (2.9)	12 (3.1)
4	BC Salmon Arm 31/102		119.22	50.65	580	362	74	326 (96)	43 (19.0)	13 (3.3)
5	BC Cameron Lake	Vancouver Island	124.67	49.25	210	50	179	318 (120)	33 (11.8)	11 (2.2)
7	BC Duncan Paldi		123.83	48.75	260	45	119	319 (113)	34 (12.6)	11 (2.0)
8	WA Darrington 1 Gold Hill	North Cascades	121.50	48.33	150	90	129	334 (108)	29 (9.1)	9 (1.7)
9	WA Darrington 3 Conrad Cr.		121.50	48.25	280	90	201	327 (102)	28 (8.0)	9 (1.8)
10	WA Darrington 4a Tenas Cr.		121.50	48.33	485	90	138	337 (104)	31 (10.7)	9 (1.5)
13	WA Darrington		121.50	48.33	150	90	84	363 (125)	31 (10.1)	9 (1.6)
15	WA Granite Falls		122.62	48.13	150	35	83	376 (122)	33 (12.1)	9 (1.9)
22	WA Greenwater	South Cascades	121.50	47.13	600	100	128	342 (106)	30 (9.8)	9 (1.7)
23	WA Ashford		122.03	46.83	450	165	60	379 (118)	31 (9.4)	8 (1.1)
29	WA Pe Ell	Coast Range	123.30	46.57	150	52	66	364 (125)	29 (9.9)	8 (1.5)
32	OR Timber		123.38	45.80	270	53	162	346 (103)	28 (8.4)	8 (1.3)
39	OR Pamelia Creek	West Cascades	121.83	44.67	750	189	122	334 (112)	32 (10.6)	10 (1.7)
40	OR Santiam River		121.97	44.67	800	166	188	323 (103)	31 (10.0)	10 (1.9)
42	OR Cascadia		122.80	44.67	900	100	41	354 (113)	32 (11.1)	9 (1.9)
1001	BW Einsiedel	Southwest German land races (original North American seed sources unknown)					24	262 (83)	26 (8.5)	10 (1.6)
1002	BW Freiburg						84	355 (115)	37 (13.8)	11 (1.8)
1003	BW Hirsau						25	363 (91)	36 (10.2)	10 (1.5)
1004	BW Kandern						39	355 (121)	32 (11.3)	9 (1.1)
1005	BW Liebenzell						25	337 (109)	39 (15.2)	12 (2.4)
1006	BW Pforzheim						44	355 (126)	42 (19.0)	12 (2.5)

Note: Physiographic regions of US seed sources are according to Franklin and Dyrness (1973). Measurements were pooled for provenances. For mean bark ratio, the table contains the values calculated directly from the measurements. Long, longitude; Lat, latitude; Elev, elevation above sea level; Dist, distance from the closest ocean coast; BC, British Columbia; WA, Washington; OR, Oregon; BW, Baden–Württemberg.

However, these exceptions applied only to a small number of plots and affected only a rather short period of growth and were therefore considered negligible.

At the time of the bark measurement, all stands were approximately 50 years old. Average height of the 100 thickest trees·ha^{-1} (h_{100}) of the tallest plots from each experiment location ranged from ca. 26 to 38 m and of the shortest plots from ca. 22 to 32 m, and maximum standing volumes were approaching 500 m^3·ha^{-1}.

Selection of sample trees for measurement of bark thickness was based on dbh distributions of the trees from the last periodic remeasurement of the individually numbered trees documented in the research institute's database. We attempted to distribute the bark thickness measurements across the dbh range of the respective plot. Our goals were to measure a minimum of 10 trees per plot and 15–20 trees per provenance at each test site. Due to the uneven provenance representation, the latter was not possible in a few cases. Numbers of plots and trees measured are listed individually by plantation in Table 2; seed origin descriptions and mean dimensions of measured trees are given individually by provenance in Table 3.

The experimental design eliminated potentially confounding effects of varying age and stand density management on phenotypic expression and focused the investigation on the effect of growth rates and factors independent of the stand-specific development dynamics on bark formation. At a given age, a tree's growth rate may be characterized by either its height or its diameter. Height is only marginally affected by intertree competition and may therefore be used as a versatile stand-level indicator for a specific site's growth potential. In contrast, diameter is clearly specific for the individual tree, as it combines the effect of site-specific growth potential and intertree competition. Given the almost identical age of the experiment stands, we interpreted tree diameter not only as a parameter characteristic for size, but also as indicative of the tree's specific growth rate.

Bark measurement

Prior to bark measurement, dbh was measured to the nearest millimetre once with a caliper. Bark thickness was then measured to the nearest millimetre using a Swedish bark gauge (Haglöf) at both places where the caliper touched the tree's circumference. The two measurements were added to get double bark thickness (dbt). However, use of a bark gauge invariably involves subjective judgement and entails risk of including (small) portions of cambium or sapwood in the measurement. Consequently, with one exception, measurements were carried out during the cambial dormant season from October to March; one plantation (Dgl 122) was measured at the beginning of the growing season in May. Comparison of measurements on that plot with other plots indicated no bias from the later measurement.

Statistical analysis

A sequence of statistical methods was applied in the following steps. First, the data were examined for outliers that might be due to bark measurement errors. Second, provenance-specific models for dbt were developed using a mixed-effects modeling approach, and differences among the provenance-specific model parameters were tested for statistical significance. Third, the measured bark ratios were subjected to covariance analysis followed by tests for statistical differences between the provenances. Fourth, after establishing the presence of statistically significant differences between provenances, provenance-specific values for bark ratio were related, using regression analysis, to geographic and climatic variables of the seed-source origins.

For analysis, the data were pooled for provenances – land races based on the rationale that although the seed sources were irregularly distributed among the different experiment locations, the plots shared a common silvicultural history and they had developed under a prescribed uniform thinning regime.

Steps 1, 3, and 4 of the analyses were carried out using the STATISTICA 6.1 package (StatSoft Inc., Tulsa, Oklahoma). The analyses under step 2 were conducted with SAS software (SAS 9.1; SAS Institute, Inc. 2004) as the MIXED procedure in SAS allows for particular convenient specification of mixed models.

Removal of outliers

Preliminary analysis using residuals from an unweighted regression approach (dbh as independent and dbt as dependent variable) indicated the presence of several highly influential observations ($n = 19$) in which the standardized residuals exceeded the 99% confidence interval. Most likely, these were due to clerical errors in the fields. Consequently, these observations were removed from the analysis as their correction was not possible.

Provenance-specific models for double bark thickness (mixed modelling)

The hierarchical structure of the data provided a particular challenge: in the pooled dataset, trees were nested within plots, and plots were nested within experiment locations. Thus data are clustered in hierarchies and are mutually dependent. For the development of models attempting to predict provenance-specific dbt at breast height, it was therefore important to chose a statistical method that allowed the mutual dependence of the measurements to be taken into account. To solve the challenge, we chose a mixed-model approach that included consideration of random effects (experiment locations, plot, and tree) varying around the fixed population mean (MIXED procedure in SAS).

Variances were considered to be heterogeneous. Within-subject and between-subject variance was modelled using an unstructured covariance. To avoid underestimation of standard errors in our dbt models due to heteroscedastic data, we applied weighted regression analysis using a weight of $1/\text{dbh}^2$. Robust standard errors of the fixed effects were calculated using classical sandwich estimators (Diggle et al. 1994). Parameter estimation was done using the restricted maximum likelihood technique. Decision on model improvement was based on Akaike's information criteria (AIC; Akaike 1973), which includes the consideration of the sparseness of the number of covariance parameters (Littell et al. 1996).

During model building, the main effects dbh, provenance ("PROV"), and their interaction were tested for their relationship to dbt. To characterize the levels of statistical significance in differences between provenances, the fitted models' intercept and slope were compared between the individual

provenances – land races and a chosen standard provenance using paired t tests (e.g., provenance no. 9 versus provenance no. 3). We chose provenance no. 9 (Darrington 3 Conrad Creek) from the North Cascades as standard, because it had the most trees measured and was planted at the most experiment locations (Table 2).

To examine the performance of the fixed part of the models, the following error statistics were calculated for each provenance using only the fixed part of the models:

$$[1a] \quad \text{mean error } |E| = \sum |y_i - \hat{y}_i|/n$$

$$[1b] \quad \text{mean squared error } E^2 = \sum (y_i - \hat{y}_i)^2/n$$

where y_i is the measured observation, $\hat{y}_i$ as the predicted value, and n the number of observations. For calculating the error statistics, all values were used in their data scale.

Subject-specific and population-level residuals were calculated and checked graphically for each experiment and provenance. The predictive power (r^2) of the models was calculated as the squared correlation between the observed and the predicted values (Zheng and Agresti 2000):

$$[2] \quad r^2 = (\text{cor}(Y, \hat{Y}))^2$$

where Y is the observed dependent variable and $\hat{Y}$ the estimated value of Y given the fixed effects predictors (i.e., marginal predictor).

Provenance-specific differences in bark ratio (ANCOVA)

Complementary to the mixed-effects model approach on the provenances' dbt, we attempted to investigate differences in provenance-specific bark thickness in their original measured units through analysis of covariance (ANCOVA) as a statistically different approach. In contrast to the mixed models on dbt, we used bark ratio (dbt divided by dbh multiplied by 100) in the ANCOVA as the dependent variable. Bark ratio appeared preferable to dbt, as bark ratio was clearly less influenced by the effect of tree size expressed through dbh (Fig. 1), which we did not consider a provenance-specific effect on bark thickness.

For the analysis, bark ratios were calculated from the individual tree measurements and subjected to ANCOVA using provenances – land races as the categorical predictor and dbh as the linear predictor (glm library in STATISTICA). Although Levene's test ($p = 0.011$), as well as the Shapiro–Wilk test ($p = 0.037$), yielded values almost significant at the 0.01 level for bark ratio, the histograms on distribution of bark ratio appeared adequate enough to satisfy the requirements of ANCOVA with respect to homogeneity of variances and normal distribution.

To test for statistical significance of the differences in bark ratios between provenances – land races using bark ratio, ANCOVA was followed by Duncan's multiple range tests.

In addition to comparisons between the individual provenances – land races, bark ratios of the provenances were pooled by physiographic regions, which then were used as the categorical predictor in ANCOVA. For this analysis, the German land races were likewise pooled as an additional "region".

Influence of geographic position or climate variables on bark ratio (regression analyses)

Regression analyses were applied for our attempt to explore potential influences of the seed sources' North American geographic origin and related climate characteristics on bark ratio. The German land races were excluded from this portion of the analysis.

The provenance-specific bark ratios used as the dependent variable in the regression analyses were not derived directly from the tree measurements but calculated based on dbt predictions from the provenance-specific models on dbt for a common dbh of 50 cm. Our rationale for this was twofold:

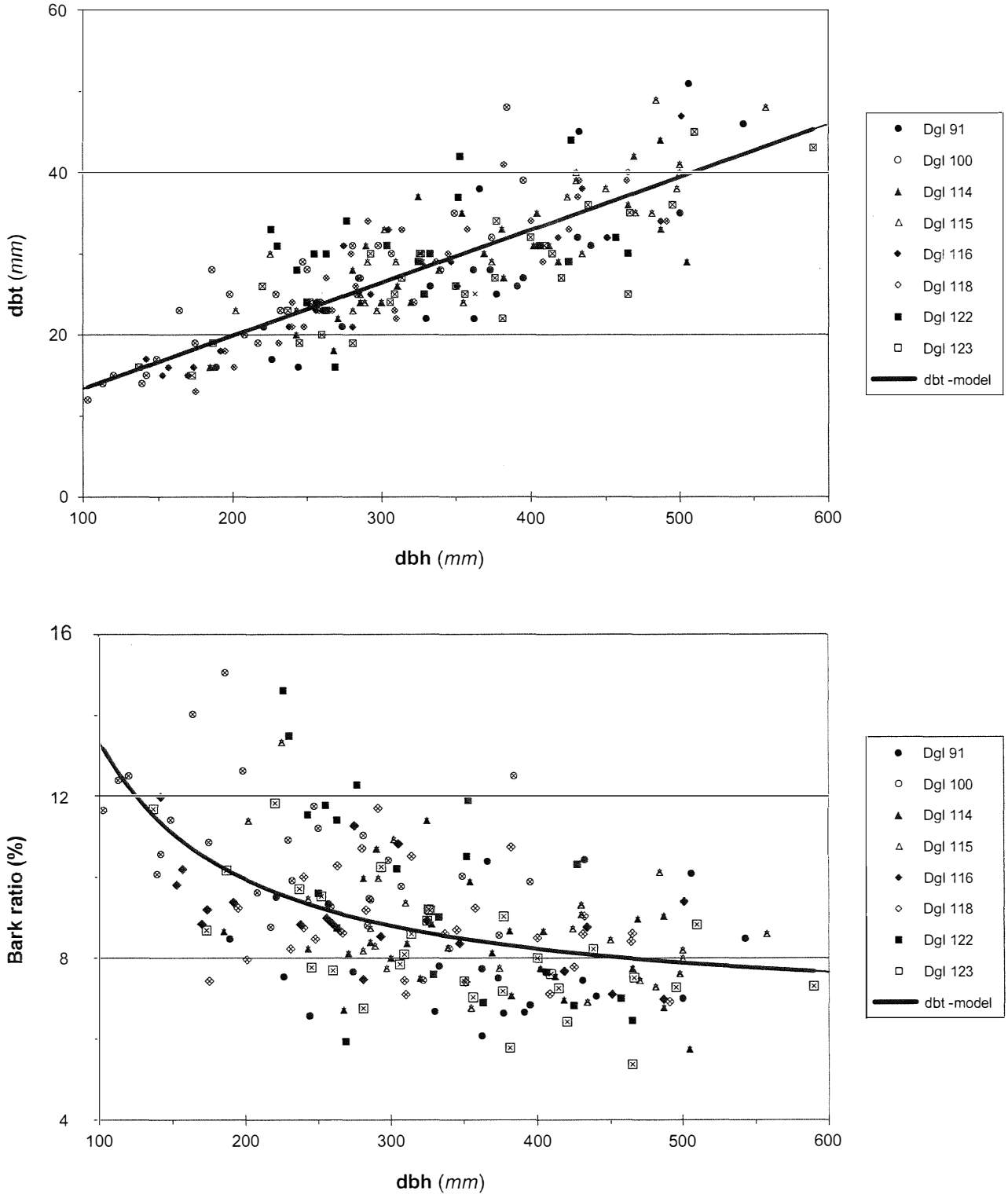
1. to eliminate the effect of size (dbh) which, although clearly less prominent than in dbt, also occurs in bark ratio;
2. to be able to include data on bark ratio reported from provenance experiments in New Zealand.

In the NZ experiments, bark thickness had been measured with the same technique as in our experiments for ca. 40-year-old Douglas-fir. Six seed sources, one from Washington, two from Oregon, and three from California, were in the New Zealand tests (McConnon et al. 2004). Measurement and calculation of bark ratios differed slightly between the New Zealand and the German datasets, but we judged the differences not important enough to prohibit joint analysis: dbh and dbt were measured at 1.4 m in New Zealand vs. 1.3 m in the German tests, and mean bark ratio in New Zealand was calculated from single-tree measurements (range of mean dbh: 47.1 to 55.5 cm) instead of being estimated at a common dbh of 50 cm as in the German experiments.

We conducted two series of regression analyses with two different categories of independent variables. The first series employed geographic position variables (latitude, longitude, distance from the closest ocean coast, elevation) of the seed-source origins as linear predictors along with their physiographic region of origin (coded as a categorical variable). Based on additional information provided by the late Leith Knowles (New Zealand Forest Research Institute, Rotorua, New Zealand), we were also able to assign geographic position variables and physiographic regions of origin to seed sources used in the New Zealand experiments; as the Franklin and Dyrness (1973) classification comprises only Oregon and Washington, we treated California as a single separate physiographic region.

The second series of regression analyses employed, as independent variables, 14 different climate parameters specified for the seed origins: two variables for precipitation (mean annual precipitation, growing season (April–September) precipitation), five variables for temperature regime (mean annual temperature, mean maximum temperature, mean minimum temperature, mean minimum temperature in the coldest month, mean maximum temperature in the warmest month), and seven variables characterizing frost and growing season (date of last spring frost, date of first autumn frost, length of the frost free period, date when the sum of degree-days > 5 °C reaches 100, degree-days < 0 °C, degree-days > 5 °C, and growing season degree-days > 5 °C). The estimates for climate normals from 1961–1990 were obtained using the climate surfaces developed by Rehfeldt (2006) for the western

Fig. 1. Double bark thickness (dbt; upper graph) and bark ratio (lower graph) of the reference provenance no. 9 (Darrington 3 "Conrad Creek") plotted against diameter at breast height (dbh). Single signatures represent individual tree measurements at eight test plantations. Solid lines represent dbt estimates (top) based on provenance no. 9 model on dbt (eq. 4; dbt = 6.8677 + 0.6504dbh), and bark ratio (bottom) calculated from the dbt estimates.



US and are available online at http://forest.moscowfsl.wsu.edu/climate/.

Both series (geographic position variables and climatic variables) commenced with univariate regressions followed by subsequent multiple regressions. The initial univariate regressions were intended to provide information useful in determining variable expression for the specification of the final multiple regression model.

Table 4. Parameter estimates of the model for double bark thickness (see eq. 3) for the 22 provenances – land races in the Douglas-fir experiments in southwestern Germany (N = 2151) and error statistics (eqs. 1*a*, 1*b*).

Parameter	Estimate	SEM	t value	$p > t$
Fixed parameters				
a_0	4.0499	0.5951	6.81	<0.0001
a_1	0.8314	0.0125	66.30	<0.0001
Random parameters				
$\alpha_{el p(un)}$	21.6969	2.9287		
$\alpha_{el pt}$ (residual error)	35.3799	1.1288		
Error statistics				
$\|E\|$ = 5.3720				
E^2 = 56.3564				

Note: SEM, standard error of the mean.

Multiple regressions using the continuous geographic position variable of the seed sources were performed as multiple linear regressions run from STATISTICA's multiple regression library. Examination of the database with the Durbin–Watson test disclosed levels of autocorrelation judged as uncritical for multiple linear regressions (d = 0.0939, autocorr = 0.529). Analyses including physiographic region as a categorical variable either alone or in combination with the continuous geographic position variables were specified as ANOVAs or ANCOVAs run from STATISTICA's glm library. Both analysis appeared possible, as the Shapiro–Wilk test on normalcy of distribution yielded values well above the 0.01 level of significance (p = 0.055).

In contrast to the geographic parameters, multiple linear regressions on the climatic variables were specified as ridge regressions from STATISTICA's multiple regressions library in "stepwise forward" mode. F for inclusion of variables in the regression model was 1.00. Complementary, we conducted ridge regressions using the same climate variables in "stepwise backward" mode. Ridge regression was chosen for the climate variables because a significant amount of multicollinearity can be present in climate data and ridge regression offers an effective method for addressing this problem (Hoerl and Kennard 1970).

Results

Influence of diameter on double bark thickness (dbt)

For dbt per tree t in plot p in experiment location el, the following mixed model was used (for abbreviations, see Table 1):

$$[3] \quad \mathrm{dbt}_{elpt} = a_0 + a_1 \mathrm{dbh}_{elpt} + \alpha_{elp(un)} + \alpha_{elpt}$$

where a and α are fixed and random parameters, respectively, of the model, and "un" stands for the unstructured covariance of the random effects at the plot level. Dbt was positively related to dbh. The error statistics (eqs. 1*a*, 1*b*) showed no large bias (Table 4). Nevertheless, Fig. 2 indicates a considerable amount of heterogeneity among residuals when plotted against the independent, dependent, and predicted variables. Basically, the residuals tended to increase with increasing dbh; the associated confidence limits can be deducted from Table 4. However, there was no obvious bias in the residuals. The model explained a reasonable proportion of the total var-

Fig. 2. (A, B) Residuals of the model for double bark thickness (dbt; eq. 3) plotted against the independent and predicted variables and (C) the predicted dbt plotted against the observed values. The edges of the boxes are located at the 25th and 75th percentiles. The vertical lines are drawn from the box to the most extreme point within 1.5 interquartile ranges. The transverse lines connect the medians.

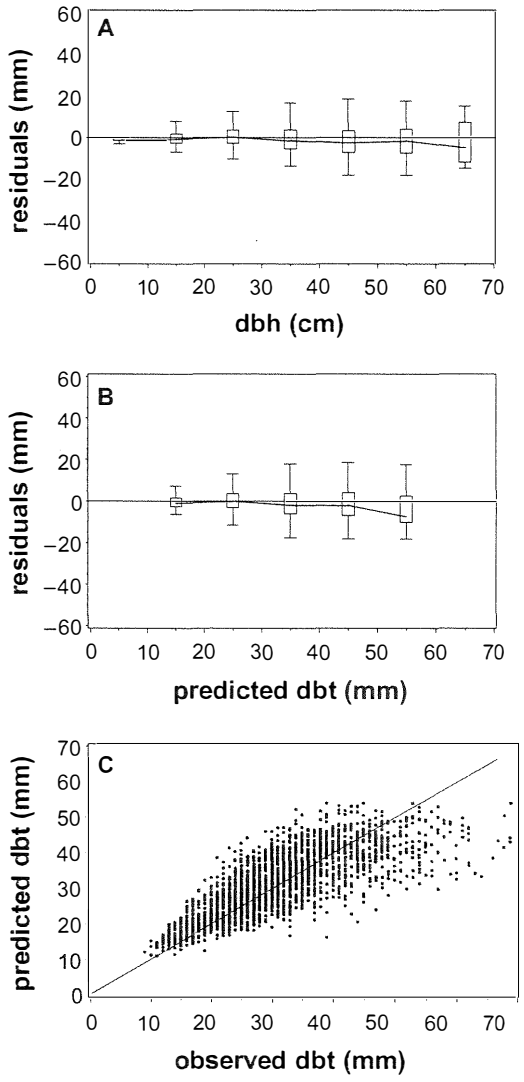


Table 5. Pairwise comparisons between individual provenances or land races and the standard provenance (no. 9) based on differences in slope and intercept calculated from the bark thickness model (see eq. 4).

		Parameters of the models on dbt				
Provenance or land race code	Comparison	Estimated intercept difference; estimated slope difference	SEM	t value	$p > t$	Differences between bark ratios of provenances significant at
British Columbia, Canada						
Southern Interior	9 vs. 3	–3.9640; 0.3965	2.1741; 0.0749	–1.82; 5.29	0.0684; 0.0000	$p < 0.001$
	9 vs. 4	–10.3147; 0.7661	4.8262; 0.2150	–2.14; 3.56	0.0327; 0.0004	$p < 0.001$
Vancouver Island	9 vs. 5	–1.4478; 0.2317	2.1281; 0.0599	–0.68; 3.87	0.4964; 0.0001	$p < 0.001$
	9 vs. 7	–4.5519; 0.3281	1.7556; 0.0754	–2.59; 4.35	0.0096; 0.0000	$p < 0.001$
Washington, USA						
North Cascades	9 vs. 8	0.1005; 0.0020	1.6553; 0.0431	0.06; 0.05	0.9516; 0.9636	$p = 0.989$
	9 vs. 10	–3.0892; 0.1624	1.4951; 0.0479	–2.07; 3.39	0.0389; 0.0007	$p = 0.047$
	9 vs. 13	–2.2463; 0.0653	1.2565; 0.0338	–1.79; 1.93	0.0740; 0.0532	$p = 0.023$
	9 vs. 15	–4.3982; 0.1357	2.2904; 0.0752	–1.92; 1.81	0.0550; 0.0712	$p = 0.009$
South Cascades	9 vs. 22	–1.8523; 0.0755	1.7948; 0.0559	–1.03; 1.35	0.3022; 0.1772	$p = 0.288$
	9 vs. 23	–5.5134; 0.1245	1.3711; 0.0674	–4.02; 1.85	0.0001; 0.0648	$p = 0.020$
Coast Range	9 vs. 29	–2.0593; –0.0042	1.5060; 0.0385	–1.37; –0.11	0.1717; 0.9131	$p = 0.667$
Oregon, USA						
Coast Range	9 vs. 32	–2.2554; 0.0393	1.6084; 0.0498	–1.40; 0.79	0.1610; 0.4299	$p = 0.859$
West Cascades	9 vs. 39	–2.6689; 0.1599	1.8833; 0.0531	–1.42; 3.01	0.1566; 0.0026	$p = 0.019$
	9 vs. 40	0.1792; 0.0903	1.5052; 0.0441	0.12; 2.05	0.9053; 0.0408	$p = 0.050$
	9 vs. 42	–7.5489; 0.2360	2.2203; 0.0341	–3.40; 6.92	0.0007; 0.0000	$p = 0.008$
Baden–Württemberg, Germany						
Unknown region of origin	9 vs. 1001	–4.2801; 0.2324	1.1866; 0.0313	–3.61; 7.43	0.0003; 0.0000	$p = 0.056$
	9 vs. 1002	–6.6108; 0.3831	1.6047; 0.0473	–4.12; 8.10	0.0000; 0.0000	$p < 0.0001$
	9 vs. 1003	–9.6707; 0.4051	1.1866; 0.0313	–8.15; 12.96	0.0000; 0.0000	$p < 0.0001$
	9 vs. 1004	–6.6810; 0.2394	1.3687; 0.0314	–4.88; 7.63	0.0000; 0.0000	$p = 0.004$
	9 vs. 1005	–6.3142; 0.4684	1.1866; 0.0313	–5.32; 14.98	0.0000; 0.0000	$p < 0.0001$
	9 vs. 1006	–6.3540; 0.4813	4.0533; 0.1883	–1.57; 2.56	0.1171; 0.0107	$p < 0.0001$

Note: Model equation for provenance no. 9 is 6.8677 + 0.6504dbh; to obtain the other provenance or land race specific equations, the estimated intercept and slope differences to provenance no. 9 listed in the table have to be added to the respective parameter. For the SEM, t value, and $p > t$ columns, the first value refers to the estimated intercept difference and the second value refers to the estimated slope difference. The far-right column contains significance levels for differences between the same pairs obtained from ANCOVA on the basis of measured bark ratio; these data are an excerpt of the results obtained from the multiple comparisons presented in Table 6. SEM, standard error of the mean.

iance (56%). There was no clear indication of within-plot variance heterogeneity. Nevertheless, as Fig. 2 indicates a potential bias for predictions at larger dbh, caution should be used when applying the equation at dbh exceeding 50 cm.

Table 6. Levels of statistical significance in bark ratios between different provenances or land races of Douglas-fir grown in southwestern

	Provenance or land race												
	Southern Interior BC		Vancouver Island		North Cascades					South Cascades		Coast Range	
	3	4	5	7	8	9	10	13	15	22	23	29	32
	—	**	****	**	****	****	****	****	****	****	****	****	****
		—	****	****	****	****	****	****	****	****	****	****	****
			—	n.s.	****	****	****	****	****	****	****	****	****
				—	****	****	****	****	****	****	****	****	****
					—	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
						—	n.s.	n.s.	n.s.	n.s.	n.s.	*	n.s.
							—	n.s.	*	n.s.	**	**	**
Region of origin								—	n.s.	n.s.	n.s.	n.s.	n.s.
Southern Interior BC	—								—	n.s.	n.s.	n.s.	n.s.
Vancouver Island	****		—							—	n.s.	n.s.	n.s.
North Cascades	****		****		—						—	n.s.	n.s.
South Cascades	****		****		n.s.		—					—	n.s.
Coast Range	****		****		****		*		—				—
West Cascades	****		****		****		****		****		—		
Germany (unknown)	****		n.s.		****		****		****		****		—
	Southern Interior BC		Vancouver Island		North Cascades		South Cascades		Coast Range		West Cascades		Germany (unknown)
	Region of origin												

Note: Above the diagonal are pairwise comparisons, based on Duncan's multiple range tests, between single provenances or land races (provenances within
Levels of significance: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ****, $p < 0.0001$; n.s., not significant.

Paired hypothesis test on provenances for double bark thickness (dbt)

To obtain a provenance-sensitive model for dbt, all 22 provenances and land races of the southwest German experiments were coded by a categorical variable with 22 distinct values:

$$[4] \quad \mathrm{dbt}_{elpt} = b_1 \mathrm{PROV} + b_2 \mathrm{dbh}_{elpt} \times \mathrm{PROV} + \beta_{elp(un)} + \beta_{elpt}$$

where b and β are fixed and random parameters, respectively, of the model. Provenance, as well as the interaction of dbh and provenance, had a significant effect on dbt. The slope and the intercept parameters of bark thickness models developed for the different provenances are summarized in Table 5, which also gives the levels of significance at which a respective provenance's parameters differ from the standard provenance (no. 9). Almost all provenances displayed negative deviations for intercept (two exceptions) and positive deviations for slope (one exception) relative to the standard (Table 5). Within physiographic regions, the greatest variation in slope and intercept parameters involved the two Southern Interior BC provenances, but there was also much variation, particularly in the intercept values, among the provenances of the West Cascade Region. The German land races differed significantly in both intercept and slope from the standard seed source, and the differences were quite consistent (Table 5).

Differences in bark ratio among provenances or land races

Bark ratios calculated from dbt estimates provided by the provenance-specific models for dbt for a common dbh of 50 cm showed a considerable amount of variation among the 16 North American provenances, with a range of 7.6% to 11.9% (minimum to maximum). The range among the six German land races was somewhat less (9.0% to 11.9%).

The ANCOVA run on bark ratios using the covariate dbh as a linear predictor gave a significant model both for individual provenances – land races ($p < 0.0001$, $r^2 = 0.3407$) and for physiographic regions ($p < 0.0001$, $r^2 = 0.3181$). One-hundred and sixty-one (70%) out of the possible 231 comparisons between individual provenances – land races were significantly different (Duncan's tests; $p < 0.05$ to $p < 0.0001$). In general, provenances within regions did not differ significantly in bark ratio, based on Duncan's tests. Two exceptions were the Southern Interior BC region (represented by two provenances) and the North Cascades in which one of 10 comparisons was significant ($p < 0.05$) (Table 6). Conversely, among the six German land races, 11 of 15 comparisons were significant at $p < 0.05$, seven even at $p < 0.01$ (Table 6).

In comparisons among physiographic regions (Table 6), all but one (South vs. North Cascades, $p = 0.09$, n.s.) were significant ($p < 0.05$ to $p < 0.0001$). German land races as a group differed strongly ($p < 0.0001$) from all physiographic regions except Vancouver Island (Table 6).

Influence of seed-source geographical location on bark ratio

To study the effect of provenance origin on bark ratio, we combined bark ratios of the North American provenances in our experiments (calculated for a common dbh of 50 cm) and bark ratios of six North American provenances reported from New Zealand (range of mean dbh from 47.1 to 55.5 cm) by McConnon et al. (2004). Bark ratios of the 22 provenances

Germany (see Table 4).

West Cascades			Germany (unknown origin)							
39	40	42	1001	1002	1003	1004	1005	1006	No.	Provenance or land race
****	****	****	****	****	****	****	****	****	3	Southern Interior BC
****	****	****	****	****	****	****	****	***	4	
****	****	****	*	n.s.	*	****	*	**	5	Vancouver Island
***	**	****	*	n.s.	*	****	*	**	7	
n.s.	**	n.s.	***	****	***	n.s.	****	****	8	North Cascades
n.s.	*	n.s.	**	****	**	n.s.	****	****	9	
n.s.	n.s.	n.s.	n.s.	***	n.s.	n.s.	****	****	10	
*	*	n.s.	**	****	**	n.s.	****	****	13	
*	***	n.s.	****	****	****	n.s.	****	****	15	
n.s.	**	n.s.	***	****	**	n.s.	****	****	22	South Cascades
**	****	n.s.	****	****	****	*	****	****	23	
***	****	*	****	****	****	**	****	****	29	Coast range
**	****	n.s.	****	****	****	*	****	****	32	
—	n.s.	n.s.	n.s.	**	n.s.	n.s.	****	****	39	West Cascades
	—	n.s.	n.s.	*	n.s.	n.s.	****	****	40	
		—	**	****	*	n.s.	****	****	42	
			—	n.s.	n.s.	*	****	****	1001	Germany (unknown origin)
				—	n.s.	****	**	***	1002	
					—	*	****	****	1003	
						—	****	****	1004	
							—	n.s.	1005	
								—	1006	

a common physiographic region shaded in gray); below the diagonal are pairwise comparisons between pooled values for physiographic regions.

were then related to geographic position variables using univariate regressions. Second, using multivariate linear regressions, bark ratios were related to (A) physiographic region (Franklin and Dyrness 1973), (B) geographic position variables, (C) physiographic region and geographic position variables in multiple regression with physiographic region as a categorical variable, and (D) temperature and moisture climatic variables estimated for the seed origins.

Results of the univariate regressions for bark ratio using geographic location variables as independent variables are illustrated in Fig. 2 (left side). Results for regressions based on geographic location and (or) physiographic region are given in Table 7. The main conclusions from these analyses are as follows.

- Linear regressions on individual geographic position variables (not shown) explained little of the variation in bark ratio. The best fit was with distance from the closest ocean coast ($r^2 = 0.33$). Judging from r^2, univariate polynomial equations explain more of the variance (Fig. 2), but r^2 values were still low (e.g., $r^2 = 0.57$ for latitude).
- Physiographic region alone, coded as a categorical variable, explained a larger amount of the variation in bark ratio than did geographic position variables. This was true both with and without New Zealand sources (Table 7, compare A lines with B lines).
- Inclusion of geographic position variables with physiographic regions had minimal effect of the amount of variation explained by physiographic region (Table 7, compare A lines with C lines). A slight exception was when the three California sources were included.
- Where they occur in common physiographic regions (see Fig. 2, between 44 and 48 degrees latitude), the bark ratios in the New Zealand experiment plantations are consistently lower than those in the German experiments.

It should be noted, that in the multivariate regressions (Table 7, B and C lines), longitude was dropped as a geographic position variable in favour of distance from the closest ocean coast: the coast line curves, and we expected distance to give a better indication of maritime effects than longitude. This reasoning was supported by the finding that multiple linear regressions employing distance from the closest ocean coast as a predictor yielded higher r^2 values than those employing longitude (not shown).

Influence of climate variables on bark ratio

Similar to the geographic position variables, univariate regressions between bark ratio as dependent variable and different climate variables resulted in rather weak correlations only (Fig. 3, right side shows four examples). The multiple linear regressions resulted in clearly improved correlations (range of r^2: 0.75–0.87; Table 8). For all six regressions (stepwise forward as well as backward mode), the degree of autocorrelation disclosed by Durbin–Watson tests (d = 2.2943 to 2.27065; autocorr = –0.2194 to –0.5063) was judged as unproblematic. The ridge regressions conducted with the provenances from the German tests alone or in different combinations with the provenances from the New Zealand tests resulted in the selection of different combinations of eight significant ($p < 0.05$) variables from the total of 14 climate variables tested. However, only growing season precipitation was consistently selected in all regressions (forward and backward mode), and date of first frost in autumn was selected in at least five of the six regressions (Table 8). Among the other significant climate variables, three were selected in two regressions (mean annual temperature, degree-days > 5 °C, degree-days < 0 °C), and two in only one of

Table 7. Results of regression models fitted to provenance-specific bark ratio as dependent variable and different variables describing geographical position of the seed sources' original North American locations.

	Provenances included in analysis							
	German experiments	New Zealand experiments			Level of significance (p) for region of seed-source origin and geographic position variables			
Independent variables included in analysis	All provenances (16)	North Cascades (1) and Coast Range (2) provenances	California provenances (3)	r^2	Lat	Elev	Dist	Region
(A) Physiographic region of seed-source origin	×			0.8169				0.0003
	×	×		0.7802				0.0001
	×	×	×	0.6715				0.0005
				0.3033				
(B) Geographic position variables of seed-source origin	×			0.6268	0.0176	0.1311	0.4366	
	×	×		0.6209	0.0192	0.0981	0.3012	
	×	×	×	0.2792	0.2507	0.8676	0.0188	
(C) Physiographic region + geographic position variables of seed-source origin	×			0.7773	0.5477	0.6692	0.3909	0.1207
	×	×		0.7568	0.6755	0.2333	0.7362	0.0869
	×	×	×	0.7598	0.0268	0.1016	0.7584	0.0022

Note: Physiographic region is a categorical predictor; geographic variables are linear predictors. Models are ANOVA (A lines; 1 categorical predictor), multiple linear regressions (B lines; 3 linear predictors), and ANCOVA (C lines: 1 categorical and 3 linear predictors). Lat, northern latitude; Elev, elevation; Dist, distance from the closest ocean coast; Region, physiographic region.

the six regressions (mean temperature of the coldest month, growing season degree-days > 5 °C, Julian date sum of degree-days > 5 °C reaches 100).

For the two most frequently selected climate variables, the parameters of the fitted models show that bark ratio increased with decreasing growing season precipitation and increased with increasingly later date of first fall frost. Together, the climate variables explained considerably higher amounts of variation in bark ratio (Table 8) than the best regression models using geographic descriptors as variables (Table 7). Furthermore, in contrast to our findings with geographic descriptors, the inclusion of the provenances from the New Zealand tests had no detrimental effect on the predictive power achieved by multiple linear regressions but increased r^2 slightly.

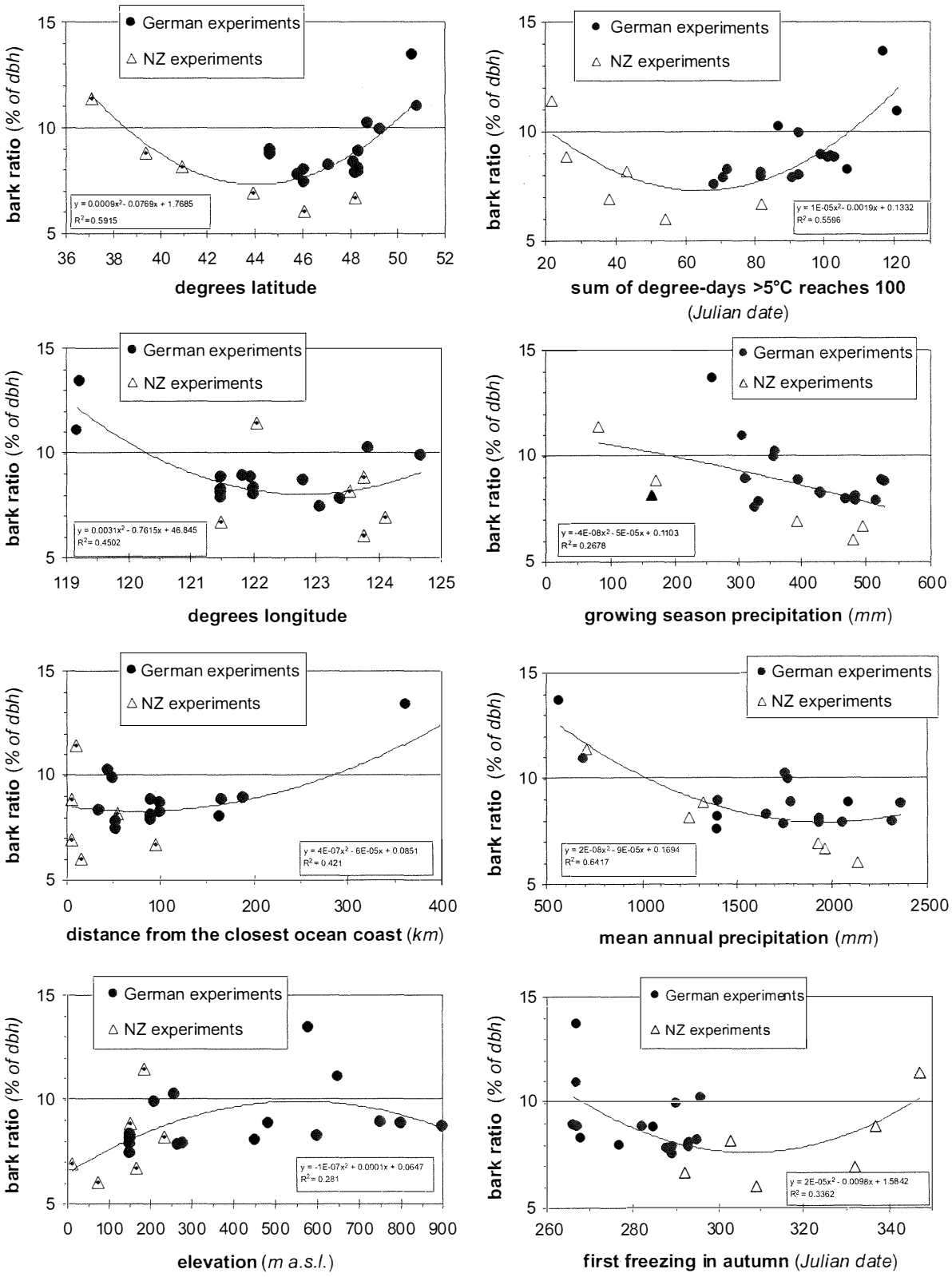
Discussion

Most previous investigations of bark thickness in Douglas-fir have been conducted to facilitate estimation of diameter under bark, wood volume, bark thickness, or bark volume from measurements over bark (e.g., Johnson 1955; Smith and Kozak 1971; Altherr et al. 1978; Kozak and Yang 1981; McConnon et al. 2004). The majority of modelling approaches attempt to estimate bark thickness from diameter measurements over bark. In this context, our study demonstrates that a mixed-model approach may provide a particularly effective prediction tool for this task. Although the database used to fit the mixed models encompasses a considerable range of varying site conditions and tree sizes, the models explain 57%–72% of the dbt variation in the respective provenances (fixed effects). Our study and that of Li and Weiskittel (2011) demonstrate that the mixed-effects model approach appears quite effective in modeling bark thickness. The amount of variation explained by our mixed-effects models clearly exceeds results obtained in other studies with different modeling approaches, e.g., Smith and Kozak (1971). In their model, dbh accounted for only one-third of the variation in bark thickness of Douglas-fir. However, it remains to be clarified whether this improvement actually rests with the basic modeling approach and (or) the accounting for different provenances.

We wish further to point out that our data encompass only a rather restricted range in age, as well as geographical location. Further research will be needed to establish if the applicability of our bark thickness models rests with the (restricted) range of the parametrization data or if they might be more generally applicable.

Analysis of residuals indicated that the mixed models' accuracy in predicting dbt decreased with increasing dbh. We checked this further by examining the earlier dbt measurements of the more than 3000 Douglas-fir gathered by Altherr et al. (1978). In their material, the amount of deviation between measured and predicted dbt clearly increased with dbh (data not shown here). There are two possible reasons. First, measurement accuracy using the bark gauge may decrease with increasing bark thickness as well as with increasing bark roughness and differential sloughing. Second, we used a linear model and did not test for nonlinearity. If larger diameters trees are included, nonlinear model approaches might improve prediction.

Fig. 3. Bark ratios of 16 North American provenances of Douglas-fir growing in southwestern Germany and six North American provenances growing in New Zealand (McConnon et al. 2004) plotted against geographic position variables (left column) and estimated climate variables (right column) of the seed origin.



German vs. New Zealand tests

Bark ratios reported for three North Cascade – Coast Range provenances grown in New Zealand were consistently lower than bark ratios of provenances from the same regions grown in southwestern Germany (see particularly Fig. 3, latitude plot). Where the German and New Zealand latitudes

Table 8. Results of ridge regressions on provenance-specific bark ratio as dependent variable and different variables[a] describing climate conditions of the seed sources' original North American locations.

	Provenances included in analysis				
	German experiments	New Zealand experiments		Results of regression	
Mode of stepwise ridge regression	All provenances (16)	North Cascades (1) and Coast Range (2) provenances	California provenances (3)	r^2 [no. of variables and significance]	Durbin–Watson
Forward	×			0.8375 [2 sign. / 4 n.s.:	d = 2.5798
				(*a*) gsp*; (*b*) —; (*c*) fday*]	autocorr = –0.4442
	×	×		0.8590 [2 sign. / 5 n.s.:	d = 2.3729
				(*a*) gsp**; (*b*) —; (*c*) fday*]	autocorr = –0.2935
	×	×	×	0.8736 [3 sign. / 1 n.s.:	d = 2.7215
				(*a*) gsp***; (*b*) —; (*c*) *d*100****; fday****]	autocorr = –0.5063
Backward	×			0.7516 [3 sign. / 0 n.s.:	d = 2.7065
				(*a*) gsp***; (*b*) —; (*c*) dd5***; gsdd5**]	autocorr = –0.3916
	×	×		0.8642 [5 sign. / 0 n.s.:	d = 2.481
				(*a*) gsp***; (*b*) mat**; (*c*) dd0**; fday***; mtcm**]	autocorr = –0.3363
	×	×	×	0.8546 [5 sign. / 0 n.s.:	d = 2.2943
				(*a*) gsp****; (*b*) mat***; (*c*) dd0**, dd5***; fday***]	autocorr = –0.2194

[a]Significant variables related to (*a*) precipitation; (*b*) temperature; and (*c*) frost or growing season. Significance: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ****, $p > 0.0001$; n.s., not significant. dd0, sum of degree-days < 0 °C; dd5, sum of degree-days > 5 °C; *d*100, Julian date that the sum of degree-days > 5 °C reaches 100; fday, Julian date of the first freezing date of autumn; gsdd5, growing season sum of degree-days > 5 °C; gsp, growing season precipitation; mat, mean annual temperature; mmin, mean annual minimum temperature; mtcm, mean temperature of coldest month.

overlap, the three provenances in New Zealand had a mean bark ratio of 6.5% (SD = 0.46%) compared with the 12 comparable German provenances with a mean of 8.3% (SD = 0.48%). The two groups differed significantly ($p < 0.01$; two-sided Mann–Whitney U test).

There is no indication that the difference was an experimental artifact. With the exception of marginal differences in the definition of breast height (Germany, 1.3 m; New Zealand, 1.4 m), the bark measurement techniques were identical, the dbh differences have been accounted for, and the tree age did not differ by much as the New Zealand experiments were planted in 1959 (McConnon et al. 2004) and the German experiments in the early 1960s. We speculate that different growth conditions in the two countries either affected the rate of bark shedding or modified the rate of bark increment relative to wood increment.

Influence of seed-source information on models for bark thickness

Since the 1950s, there have been observations in Germany that bark thickness traits in Douglas-fir are influenced not only by diameter, but also by provenance. In the 1960s, Bergel (1969) presented two models on bark thickness that differentiated between "smooth" and "rough" bark types observed in Douglas-fir growing in northwestern Germany. Observations of Rau (2005) also indicated that roughness of bark was, at least in part, a provenance-specific bark trait in Hessian Douglas-fir plantations. Furthermore, our statistical re-examination of the data from the large-scale bark measurements conducted on more than 3000 Douglas-fir by Altherr et al. (1978) supports their observation that trees of larger diameters differed in bark thickness between southwestern and northern Germany. Bark ratios of Douglas-fir exceeding a dbh of 40 cm differed significantly ($p < 0.0001$) between trees measured in southwestern Germany (10.9%; n = 599, mean dbh = 55.2 cm) vs. northern Germany (12.8%; n = 79, mean dbh = 57.9 cm).

These observations indicated that including provenance information would benefit bark thickness models. Kozak and Yang (1981) followed such an approach and included an inventory zone along with stem diameter in developing bark volume equations for several British Columbia conifers. They found that the bark of tamarack (*Larix laricina* (DuRoi) K.Koch) and lodgepole pine (*Pinus contorta* Dougl. ex Loud.) in the northern interior was thinner than that on the coast and in the southern interior. In contrast, bark of interior western red cedar (*Thuja plicata* Donn ex.D.Don) and hemlock (*Tsuga heterophylla* (Raf.) Sarg.) was relatively thicker than that of coastal red cedar and hemlock. However, Kozak and Yang (1981) found no clear difference in relative bark thickness between interior and coastal Douglas-fir. Possibly, the inability to detect seed-source differences in Douglas-fir may have been caused by confounding provenance origin and large differences in tree sizes (mean seed-source dbh ranged from 28.3 to 73.7 cm).

In contrast to the study of Kozak and Yang (1981), notable differences in bark thickness were observed among six Douglas-fir provenances and one land race growing in New Zealand (McConnon et al. 2004). Likewise, our observations with different Douglas-fir provenances and land races growing in southwestern Germany clearly support the importance of in-

cluding information on seed-source origin in models of bark thickness: both the intercept and slope parameters of the models differed significantly from a chosen reference seed source from the North Cascades.

Differences between provenances and land races in the German experiments

If the two Southern Interior BC sources are excluded, slope and intercept parameters for the southwestern German land races deviated in general more from reference provenance no. 9 (range of 0.2324 to 0.4813) than did the North American provenances (range of –0.0042 to 0.3281). We attribute the greater deviation of the land races, which presumably had initial seed origins similar to the provenances (Kenk and Thren 1984*a*), to ongoing adaptive development of the land races to their new environment in southwestern Germany. Previous reports of rapid land race adaption include *Picea sitchensis* (Bong (Carr.)) in Denmark (Sørensen 1913; Nielsen 1994), *Pseudotsuga menziesii* in France (Birot 1974) and Germany (Jestaedt 1979), and *Picea abies* in Norway (Skrøppa et al. 2010).

Compared with the other North American provenances, the two Southern Interior BC sources had large slope value differences from reference provenance no. 9 (0.3965 and 0.7661; Table 5). In the bark thickness model, slope represents the rate of change in dbt per unit change in dbh. These large deviations in slope may be interpreted to reflect differences between the interior BC populations and the West Cascade reference population in stem biomass allocation differentials between xylem and phloem. Although our interior material is limited to two provenances, we suggest that the large difference from the reference population, particularly of provenance no. 4, is due to adaptation of provenance no. 4 to the more continental environment of southern interior BC or to historical introgression with var. *glauca*, or to a combination of both.

Influence of geographic origin and associated climate characteristics on bark ratio

Both the models on bark thickness and the ANCOVA on bark ratio showed significant associations with seed origin (Table 7). These results led us to investigate the relation of provenance bark ratios in the German and New Zealand tests to geographic and climatic variables at the North American sources. Because of the limited number and uneven distribution of the seed-source origins available to us, our conclusions are preliminary only and need further study.

In the analysis of geographic or climatic variation in seed-source origin, we used bark ratio in preference to dbt. Using dbh as a denominator in bark ratio obviously compensates to some extent the dbh dependency of dbt, particularly at dbh greater than 40 cm (Fig. 1), and renders bark ratio less affected by dbh differences than dbt. The example of the reference provenance no. 9 (Fig. 1) shows that dbh dependency of bark ratio is very small at dbh near 50 cm. Therefore, at dbh near 50 cm, it seemed reasonable to compare bark ratios, even if there has not been an adjustment for minor dbh differences. Based on this reasoning, we believed that it was justified to enlarge our database by including the provenance-specific bark ratios reported from New Zealand provenance experiments without adjusting for dbh differences. Mean dbh of these provenances ranged from 47.1 to 55.5 cm, which was close to the standardized dbh of 50 cm used to estimate bark ratios of the provenances in the southwestern German experiments.

Our data clearly demonstrated that although there were no linear gradients of bark ratio along individual geographic position variables of the seed sources' origin (Fig. 3, left column), the combination of these geographic variables for seed origins explained a substantial part of the variation of bark ratio (Table 7, compare B lines). However, physiographic regions alone explained even more source-related variation than did geographical variables (Table 7, compare A lines with B lines). Combination of geographic variables and physiographic region did not increase the amount of variation explained by region categories alone, except if California provenances were included (Table 7, compare A and B lines with C lines). This was unexpected, because continuous variables usually explain more adaptive variation than do various various discrete-based class variables (e.g., Campbell 1991). The limited number of provenances may have been responsible.

Genetically, adaptive variation evolves under the influence of characteristic environmental factors acting as selective agents. Geographic position in itself is rarely the agent but serves as a surrogate for factors associated with climate or soil. This assumption is supported by our results, which show that climate variables explained more source-related variation in bark ratio that did geographic variables or regions. In particular, our findings indicate that bark ratio increased if seeds were collected from locations with lower precipitation during the growing season (see Fig. 3, growing season precipitation; the high outlier is provenance no. 4 from the var. *menziesii* – var. *glauca* introgression zone).

As trees have adapted to dissimilar environmental conditions, so too has bark adapted to protect the trees from different elements native or common to the habitat in which they grow (Sandved et al. 1993). For example, bark thickness, as reflected in bark ratio, is an important factor determining post-fire survival of Douglas-fir (Flint 1925; Peterson and Arbaugh 1989). Because fires are most often associated with drier sites (Flint 1925), decreasing summer precipitation can be expected to be associated with increasing levels of fire risk and thus should favour the formation of relatively thicker bark more resistant to fire. Physiologically this appears plausible, as precipitation and cambial activity are often closely connected (Glock 1955) and redivision of cambial cells is at the basis of bark and wood formation (Philipson et al. 1971). Therefore, we suggest that the observed source-related variation in bark ratio was an adaptive response to historic differences in fire regime in the form of fire return rates or intensity. If correct, provenance is a factor that needs to be considered in developing bark thickness models for Douglas-fir.

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