

# Geographic Variation and Local Growth Superiority for Coastal Douglas-fir – Rotation-age Growth Performance in a Douglas-fir Provenance Test

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## Abstract

Rotation-age growth performance of 16 provenances and local growth superiority were assessed from a rotation-age reciprocal coastal Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco] provenance test established in the Pacific Northwest of America. Provenance differences for total volume per plot were highly significant. Due to the significant provenance × site interaction effect, the best provenances varied across planting sites in terms of rotation-age volume growth. Local provenance trees exhibited superior volume growth at two of the six planting sites. At the remaining four sites, local provenances performed equally well as average non-local provenances. At the three low-elevation (< 460 m) sites, low-elevation provenances performed significantly better than high-elevation provenances. By contrast, high- and low-elevation provenances had similar growth at the two high-elevation (> 800 m) sites. Southern provenances generally grew faster than northern provenances at the Oregon sites, while northern provenances performed better than southern provenances at the sites in British Columbia.

Regression analyses showed that although local growth superiority increased with the geographic distance between provenance's origin and the test site in general ( $r=0.47$ ,  $P<0.001$ ), it only became obvious when the geographic distance is larger than 435 km in latitude or 370 m in elevation. Significant spatial autocorrelation was found via Mantel test, and geographically or climatically closely located provenances tended to have similar rotation-age volume growth.

The results suggested that breeding zones larger than the current second-cycle zones would lead to little loss of rotation-age total volume for coastal Douglas-fir in this region.

**Key words:** Douglas-fir, provenance, rotation-age growth, local superiority, local adaptation, provenance × site interaction, breeding zone.

## Introduction

Long-term provenance tests are commonly used to understand the geographic variation of tree species, to select the best provenances for a specific region (especially in the cases of exotic species), and to explore provenance by environment interaction (e.g., SQUILLACE and SILEN, 1962; CALLAHAM, 1964; SQUILLACE, 1966; WELLS and WAKELEY, 1966; WELLS, 1969; CONKLE, 1973;

TEICH and HOIST, 1974; KLEINSCHMIT, 1978; MORGENSTERN, 1978; MORGENSTERN *et al.*, 1981; PARK and FOWLER, 1982; WHITE and CHING, 1985; MORGENSTERN, 1996; STONECYPHER *et al.*, 1996; LADRACH, 1998). With two cycles of breeding nearly completed for coastal Douglas-fir and genetically improved materials widely used in the US Pacific Northwest, Douglas-fir tree breeding has progressed far beyond the stage of selecting a few provenances for reforestation (HOWE *et al.*, 2006). Instead, examining and quantifying provenance by environment interaction has become an important issue in the Douglas-fir breeding program, as it will provide valuable information on long-term adaptation and breeding zone re-delineation.

Despite the fact that coastal Douglas-fir is one of the world's most valuable timber species, its provenance by environment interaction and adaptation are not well understood (HOWE *et al.*, 2006). Results from short-term field tests (e.g., HERMANN and LAVENDER, 1968; GRIFFIN and CHING, 1977; CAMPBELL and SORESENSEN, 1978; CAMPBELL, 1979; SILEN and MANDEL, 1983; ST CLAIR *et al.*, 2005) showed that genetic variation in growth and several adaptive traits is apparently patterned along geographic gradients described by elevation, latitude, and distance from the ocean. However, these short-term tests estimated only the immediate and dramatic effects of maladaptation at seedling or juvenile stage, but could not estimate the cumulative effect over long growth periods (ADAMS and CAMPBELL, 1981).

The traditional approach to test the hypothesis that populations are locally adapted is the reciprocal transplant experiment. Local adaptation is determined to have occurred if native populations have greater fitness and/or performance than foreign populations at any given habitats (LEIMU and FISCHER, 2008; HEREFORD, 2009; ANDERSON *et al.*, 2011). In the US Pacific Northwest, the only multiple-provenance, multiple-site, long-term, and reciprocal Douglas-fir provenance test was planted in 1959 across Oregon, Washington, British Columbia, and northern California (CHING, 1965). Several publications based on this test were available at various ages, with inconsistent results on local adaptation (CHING and BEVER, 1960; CHING, 1965; ROWE and CHING, 1973; CHING and HINZ, 1978; WHITE and Ching, 1985; KRAKOWSKI and STOEHR, 2009). Provenance by environment interaction appeared to be noticeable only at age 30 or later (SILEN, 1978; KRAKOWSKI and STOEHR, 2009), especially on sites with harsh conditions. While WHITE

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and CHING (1985) observed that the local provenances have greatly increased their growth rankings from age 9 to 25 at several locations, KRAKOWSKI and STOEHR (2009) concluded that provenances from relatively distant origins often grew as well or better than the local ones at age 45. However, no study focused on quantifying the level of local growth superiority except for simple performance comparisons of local and non-local sources at each location.

The main objectives of this study were (1) to examine the geographic variation of provenances in terms of rotation-age volume growth; (2) to test the significance of provenance  $\times$  environment interaction and quantify the level of local growth superiority; (3) to verify if geographically or climatically closely located provenances have similar performance; and (4) to provide inference to the current Douglas-fir breeding program in the US Pacific Northwest.

## Materials and Methods

### *Test materials, experimental designs, and traits*

Seeds were collected in 1954~1956 from 16 provenances covering the central range of this species from southern Oregon to northern Vancouver Island. Altitude, latitude, and longitude of the collection sites ranged from 61 to 1,220 m above sea level, 42.34°N to 50.50°N and 121.33°W to 126.75°W (*Table 1, Fig. 1*). Fourteen to 89 parent trees were chosen at random at each location for seed collection. Each of these 16 seedlots was sown in spring 1957 and outplanted in 1959 on 16 sites (located in the vicinity of seed collections) in a reciprocal design where one provenance is native to each site. Each planting site was within a 40 km radius and 60 m in elevation of one of the seed collection site.

Plantations were established in complete block design, with four blocks at each site. Individual provenances were planted in square plots of 7  $\times$  7 trees, surrounded by two rows of buffer trees of the same source at 1.8 m spacing.

Many sites were abandoned due to damage caused by nature disasters such as frost, browse, drought, and fire etc. At rotation ages (46~52 from seed, *Table 1*), growth traits, i.e., total height (HT), diameter at breast height (DBH), were measured at six of the 16 sites. Among the six sites, three fast-growing sites (i.e., Haney, Nimpkish, and Corvallis) were reported to be thinned after either the 1976 or 1977 growing seasons, and 24~25 undamaged, well formed, and well-spaced trees were measured in each square plot. A total of 7,600 trees were measured across the six sites at the rotation ages. Stem volume (VOL) was calculated using BRUCE and DEMARS (1974) volume equations. Total volume per plot (TVOL) was calculated as the total VOL in a plot for all living trees.

### *Statistical analyses*

Analysis of variance (ANOVA) pooled across sites was conducted for VOL and TVOL using SAS PROC GLM (SAS INSTITUTE INC., 1999). The linear model included the following effects: grand mean, site, block within site, provenance, provenance  $\times$  site, provenance  $\times$  block (VOL only), and random error. All effects were considered as independent and identically distributed random variables except for the grand mean. In addition, single-degree-of-freedom linear contrasts were conducted for testing the relative performance between local and non-local provenances, between low- and high-elevation provenances, and between northern and southern provenances. Least-square means (LSMs) were estimated for each provenance across sites as well as within site. Sin-

*Table 1.* – Locations and measurement ages of provenances and planting sites.

State / Province	Provenance	Latitude (°N)	Longitude (°W)	Mean elevation (m)	Measurement					
					Site	Age	Mean			
							HT (m)	DBH (cm)	VOL (m <sup>3</sup> )	TVOL (m <sup>3</sup> )
British Columbia, CA	Courtenay	49.75	125.00	457.0	Yes	46	20.01	22.11	35.75	765.87
British Columbia, CA	Haney	49.17	122.50	182.5	Yes	46	33.60	36.64	150.10	2000.52
British Columbia, CA	Mesachie Lake	48.83	124.25	201.5						
British Columbia, CA	Nimpkish	50.50	126.75	152.5	Yes	46	25.79	26.75	67.15	1618.97
British Columbia, CA	Sugar Loaf Mt	49.17	124.00	838.0	Yes	48	19.72	27.90	51.60	1101.31
Oregon, USA	Butte Falls	42.34	123.25	914.5						
Oregon, USA	Corvallis	44.50	123.60	579.5	Yes	52	28.27	33.79	108.46	1770.94
Oregon, USA	Molalla High	45.17	121.75	1066.5						
Oregon, USA	Molalla Low	45.17	122.10	549.0						
Oregon, USA	Oakridge High	43.75	122.17	838.0	Yes	48	25.17	25.10	72.86	1357.09
Oregon, USA	Oakridge Low	43.75	122.17	579.5						
Oregon, USA	Salem	44.83	123.05	61.0						
Oregon, USA	Tillamook	45.50	123.50	579.5						
Washington, USA	Elbe	46.75	122.75	587.0						
Washington, USA	Shelton	47.25	123.33	91.0						
Washington, USA	Snoqualmie	47.50	121.33	1219.5						

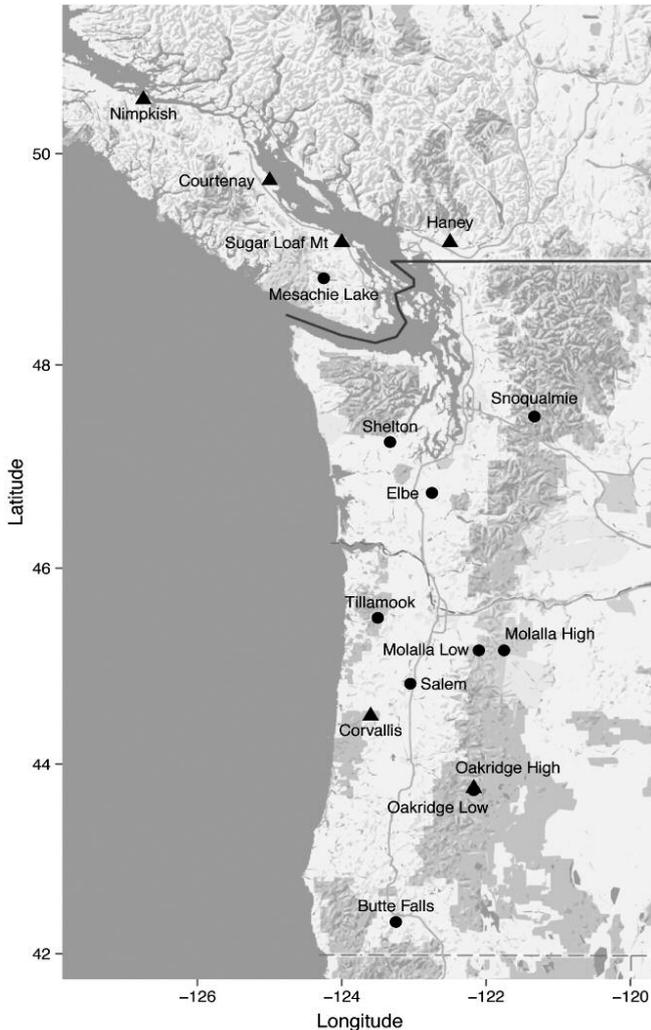


Figure 1. – Geographic locations of provenances and planting sites (triangles represent the six sites which were measured at rotation ages).

gle-site ANOVA was also carried out using the above linear model except that site and provenance  $\times$  site terms were dropped from the model.

A set of 216 climate variables (including annual, seasonal, and monthly variables) during the period of 1961 ~ 1990 was generated by the software ClimateWNA (v4.70, WANG *et al.*, 2012). A subset of those variables which correlated significantly with each growth trait ( $P < 0.10$ ) across sites was retained for further analysis (Table 2).

We defined local superiority as the difference in volume growth between the local provenance and each of the non-local provenances. At each planting site, only the provenance originating from this site was considered as the local provenance.

Euclidean distances were calculated between each pair of provenances or planting sites (JOHNSON and WICHERN, 1988), based on (1) volume growth; (2) a set of chosen climate variables as shown in Table 2; and (3) standardized latitude, longitude, and elevation using  $[x - \text{mean}(x)] / [\text{max}(x) - \text{min}(x)]$ . Relative weights (1, 2, and 3) were assigned to latitude, longitude, and elevation, respectively to account for the rectangular study area (Figure 1) and rapid change of climate with elevation.

Linear regression models were fitted using SAS PROC REG to examine the relationship between local growth superiority and Euclidean distance between provenance's original location and the planting site (SAS INSTITUTE INC., 1999).

Spearman's rank correlations between planting sites were calculated to depict the pattern of provenance  $\times$  site interaction (SNEDECOR and COCHRAN, 1980).

Mantel tests were conducted to examine the existence of geographical (or climatic) spatial autocorrelation (MANTEL, 1967). This approach compares two distance or

Table 2. – Climate variables and their correlations with provenance growth.<sup>1)</sup>

VOL				TVOL			
Variable <sup>2</sup>	r	Variable	r	Variable	r	Variable	r
PAS01	-0.428	CMD_at	-0.494	NFFD09	0.427	CMD09	-0.502
PAS03	-0.464	TD	-0.554	PAS01	-0.475	PAS_wt	-0.460
PAS04	-0.455	SHM	-0.502	PAS02	-0.450	PAS_sp	-0.498
PAS05	-0.457	PAS	-0.429	PAS03	-0.498	CMD_sp	-0.542
PAS10	-0.474			PAS04	-0.497	CMD_at	-0.502
CMD05	-0.468			PAS05	-0.492	TD	-0.570
CMD09	-0.494			PAS10	-0.514	SHM	-0.506
PAS_sp	-0.461			PAS12	-0.452	PAS	-0.464
CMD_sp	-0.536			CMD05	-0.456		

<sup>1)</sup> Only the variables which significantly ( $P < 0.10$ ) correlated with VOL/TVOL are listed.

<sup>2)</sup> Climate variables: (1) *CMD05*, *CMD09*: Hargreaves climatic moisture deficit in May and September, respectively. (2) *CMD\_at*, *CMD\_sp*: Hargreaves climatic moisture deficit in Fall and Spring, respectively. (3) *NFFD09*: Number of frost-free days in September. (4) *PAS*: Precipitation as snow (mm). (5) *PAS01*, *PAS02*, *PAS03*, *PAS04*, *PAS05*, *PAS10*, *PAS12*: Precipitation as snow (mm) in January-May, October, and December, respectively. (6) *PAS\_sp*, *PAS\_wt*: Precipitation as snow (mm) in Spring and Winter, respectively. (7) *SHM*: Summer heat:moisture index. (8) *TD*: Temperature difference between mean warmest and coldest month temperatures ( $^{\circ}\text{C}$ ).

Table 3. – Analysis of variance, variance components, and significance test.

Trait	Source	DF	V component	P value
VOL	site	5	1003.25	<.0001
	block(site)	18	41.66	<.0001
	provenance	15	5.99	<.0001
	site x provenance	75	2.21	<.0001
	provenance x block(site)	270	2.12	<.0001
	residual	7206		
TVOL	site	5	121.66	<.0001
	block(site)	18	9.30	<.0001
	provenance	15	1.76	<.0001
	site x provenance	75	1.27	0.0131
	residual	270		

Table 4. – Rank correlation (lower triangle) and P value (upper triangle) between planting sites.

Trait	Site	Corvallis	Courtenay	Haney	Nimpkish	Oakridge High	Sugar Loaf Mt
VOL	Corvallis		0.055	0.602	0.594	0.641	0.025
	Courtenay	0.488		0.305	0.737	0.180	0.000
	Haney	0.141	0.274		0.039	0.004	0.165
	Nimpkish	0.144	-0.091	0.521		0.602	0.704
	Oakridge High	0.126	0.353	0.679	0.141		0.362
	Sugar Loaf Mt	0.556	0.797	0.365	-0.103	0.244	
TVOL	Corvallis		0.311	0.854	0.438	0.080	0.020
	Courtenay	0.271		0.931	0.471	0.295	0.007
	Haney	-0.050	0.024		0.122	0.387	0.957
	Nimpkish	-0.209	0.194	0.403		0.399	0.745
	Oakridge High	0.450	0.279	-0.232	-0.226		0.169
	Sugar Loaf Mt	0.574	0.641	-0.015	-0.088	0.362	

similarity matrices among provenances by means of a matrix correlation coefficient, whose significance is tested against an empirical null distribution. The procedure was done using R package *ade4* and based on 10,000 random permutations. According to CHEVERUD *et al.* (1989), this number of permutations appears to be sufficient to obtain a good empirical distribution of the matrix correlation coefficients.

## Results

### Relative growth performance of provenances

Results from analysis of variance showed that the among-site variation accounted for most of the total phenotypic variances (Table 3). This is expected since the test sites covered a wide geographic area and different soil types. Site productivity ranged from poor (Courtenay BC) to intermediate (Nimpkish BC, Sugar Loaf Mt BC, and Oakridge High OR) to good (Haney BC and Corvallis OR). However, the site effect may have been confounded with the age effect due to the fact that the measurement age varied from 46 to 52 across sites.

Across all test sites, highly significant differences among provenances were found for both VOL and TVOL

( $P < 0.0001$ ). In general, the provenance Molalla High performed the best across sites. Its average volume growth was above the overall means by 9% for VOL and 10% for TVOL. By contrast, the poorest provenance Butte Falls was below the overall means by 19% for VOL and 23% for TVOL. Among-provenance difference was also significant ( $P \leq 0.01$ ) for VOL at each site, and marginal significance ( $P \leq 0.10$ ) for TVOL at each site except for Sugar Loaf Mt (results not shown).

Provenance  $\times$  site interaction effect was significant for both volume traits ( $P \leq 0.01$ ). The presence of provenance  $\times$  site interaction was also indicated by the low levels of rank correlations ( $r$ ) between sites. The average  $r$  was 0.31 for VOL and 0.16 for TVOL (Table 4). Fig. 2 shows the changes of provenance ranking from site to site. It appeared that some fast-growing provenances (e.g. Nimpkish, Shelton) varied widely in growth ranking while the slowest-growing provenances (Butte Falls) performed relatively consistently across sites.

### Local growth superiority

Local provenance trees exhibited superior volume growth (TVOL) at only two (i.e., Haney and Nimpkish, BC) of the six planting sites ( $P \leq 0.07$ , Table 5), with the

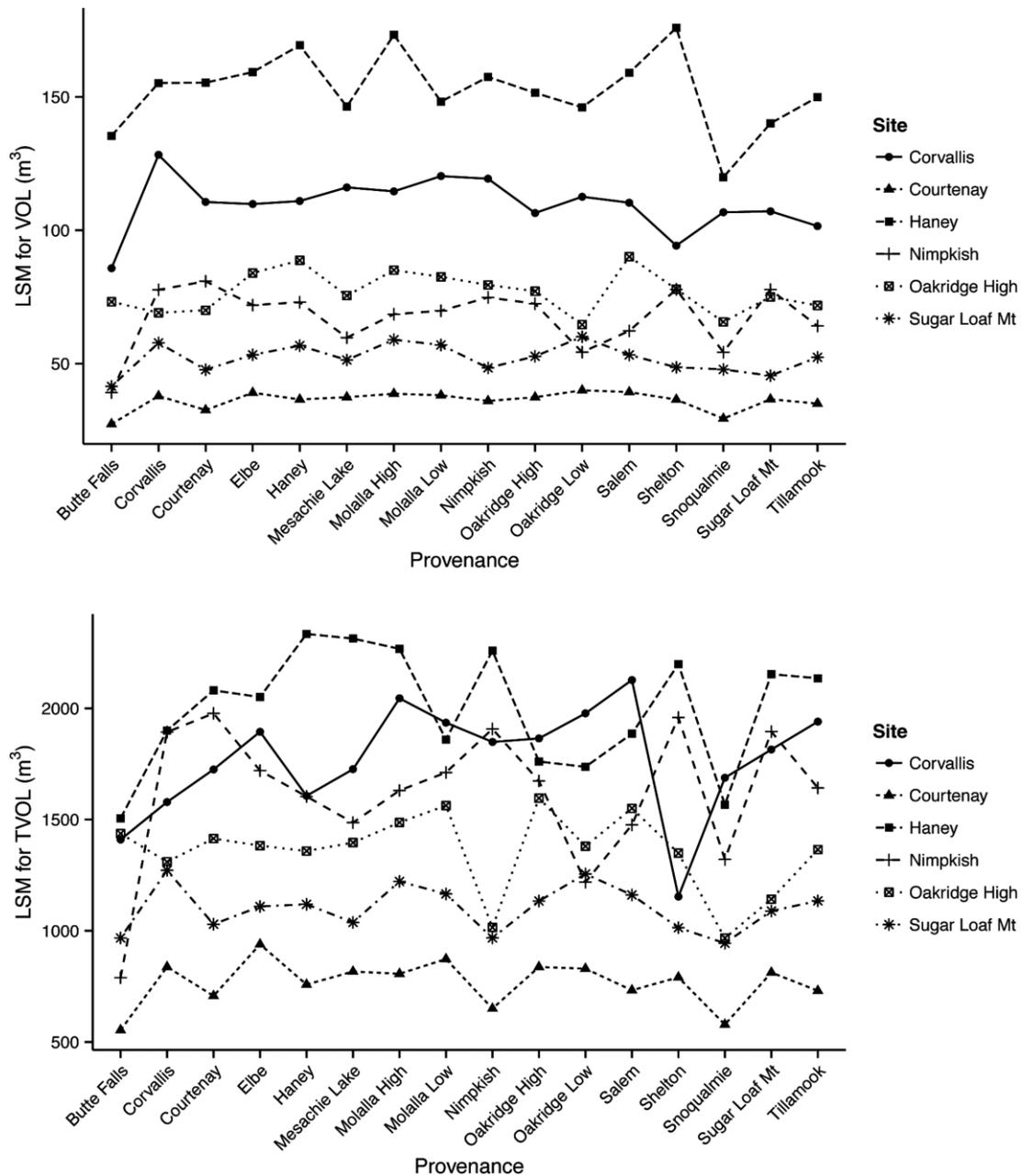


Figure 2. – Provenances' performance in VOL and TVOL across six planting sites.

frequency of local superiority being 33%. At the remaining four sites, local provenances performed equally well as average non-local provenances ( $P=0.13 \sim 0.94$ ).

At the three low-elevation (<460 m) sites, low-elevation provenances yielded significantly more stem volume than high-elevation provenances ( $P<0.001$ , Table 5). By contrast, high- and low-elevation provenances performed similarly at the two high-elevation (>800 m) sites ( $P=0.97$ ). Across all sites, there was no difference in TVOL between southern and northern provenances ( $P=0.76$ ). However, southern provenances generally performed better than northern provenances at the OR sites ( $P<0.001$ ), while northern provenances performed better than southern provenances at the BC sites ( $P<0.05$ ).

As shown in Table 6, while local provenances did not always grow the most volume, positive correlations were found between local growth superiority and the standardized geographic distance (between provenance's origin and the test site) at each site ( $r=0.15 \sim 0.64$ ) as well as across sites ( $r=0.47$ ). This pattern was statistically significant considering all sites ( $P<0.001$ ). The intercepts of the regressions were, however, negative for across sites as well as at two-third of planting sites. Take the across-site regression model as an example. Local superiority only appeared when the geographic distance is larger than 0.95, which is corresponding to 435 km in latitude or 370 m in elevation.

Similarly, provenance's growth superiority was also positively correlated with the similarity in climate

Table 5. – Local superiority in volume growth (TVOL).

Linear contrast	LSM		t Value	P Value
	Local	Non-local		
Provenance Corvallis vs. Others at Corvallis site	1578.8	1783.75	-1.23	0.2209
Provenance Courtenay vs. Others at Courtenay site	707.26	769.78	-0.37	0.7087
Provenance Haney vs. Others at Haney site	2334.43	1978.26	2.13	0.0339
Provenance Nimpkish vs. Others at Nimpkish site	1907.25	1599.76	1.84	0.0667
Provenance Oakridge-High vs. Others at Oakridge-High site	1596.06	1341.15	1.53	0.1283
Provenance Sugar-Loaf-Mt vs. Others at Sugar-Loaf-Mt site	1088.7	1102.16	-0.08	0.9358
Low-elev. vs. High-elev. Provenances at Low-elev. sites <sup>1</sup>	1552.11	1343.42	3.69	0.0003
High-elev. vs. Low-elev. Provenances at High-elev. sites	1198.5	1201.06	0.04	0.9707
Southern Provenances vs. Northern Provenances	1440.93	1430.63	0.31	0.7554
Southern vs. Northern Provenances at Southern sites <sup>2</sup>	1660.41	1467.61	3.37	0.0009
Northern vs. Southern Provenances at Northern sites	1412.14	1331.19	-2.00	0.0463

<sup>1</sup> Low-elevation provenances (up to 460 m): *Salem, Shelton, Nimpkish, Haney, Mesachie Lake, and Courtenay*; High-elevation provenances (> 760 m): *Sugar Loaf, Oakridge High, Butte Falls, Molalla High, and Snoqualmie*; Low-elevation sites (up to 460 m): *Nimpkish, Haney, and Courtenay*; High-elevation sites (>760 m): *Sugar Loaf, and Oakridge High*.

<sup>2</sup> Southern provenances (Oregon source): *Butte Falls, Corvallis, Molalla High, Molalla Low, Oakridge High, Oakridge Low, Salem, and Tillamook*; Northern provenances (Non-Oregon source): *Courtenay, Elbe, Haney, Mesachie Lake, Nimpkish, Shelton, Snoqualmie, and Sugar Loaf Mt*; Southern sites (Oregon sites): *Corvallis and Oakridge High*; Northern sites (WA & BC sites): *Courtenay, Haney, Nimpkish, and Sugar Loaf Mt*.

Table 6. – Relationship between local superiority in TVOL and geographic/climatic distance.

Distance	Site	Equation <sup>1,2,3</sup>	R <sup>2</sup>	r	P value
Geographic	All sites	Superiority = - 205.49 + 215.03 * Gdist	0.213	0.462	0.000
	Corvallis	Superiority = - 376.62 + 153.25 * Gdist	0.114	0.337	0.219
	Courtenay	Superiority = - 195.58 + 96.34 * Gdist	0.203	0.450	0.092
	Haney	Superiority = 13.91 + 227.96 * Gdist	0.419	0.647	0.009
	Nimpkish	Superiority = - 64.77 + 202.99 * Gdist	0.248	0.498	0.059
	Oakridge High	Superiority = 153.12 + 73.55 * Gdist	0.086	0.294	0.287
	Sugar Loaf Mt	Superiority = - 74.18 + 41.09 * Gdist	0.023	0.151	0.590
Climatic	All sites	Superiority = 67.1600 + 0.1680 * Cdist	0.159	0.399	0.021
	Corvallis	Superiority = - 214.1791 + 0.0429 * Cdist	0.006	0.077	0.783
	Courtenay	Superiority = - 94.1559 + 0.1351 * Cdist	0.292	0.540	0.038
	Haney	Superiority = 295.9078 + 0.2769 * Cdist	0.235	0.485	0.067
	Nimpkish	Superiority = 256.2279 + 0.2292 * Cdist	0.109	0.330	0.229
	Oakridge High	Superiority = 202.3953 + 0.2099 * Cdist	0.319	0.565	0.028
	Sugar Loaf Mt	Superiority = - 39.3249 + 0.1008 * Cdist	0.153	0.391	0.150

<sup>1</sup> Superiority is defined as the difference in mean TVOL between the local provenance and each non-local provenance. At each site, only the provenance originating from this site is considered as local.

<sup>2</sup> Gdist is the Euclidean distance between the local provenance and each of the non-local provenances calculated using latitude, longitude, and elevation, with relative weights being longitude/latitude/elevation = 1/2/3. The values of latitude, longitude, and elevation (x) were pre-standardized by  $[x - \min(x)] / [\max(x) - \min(x)]$ .

<sup>3</sup> Cdist is the Euclidean distance between the local provenance and each of the non-local provenances calculated using a set of selected climate variables listed in the Table 2.

between the places where the provenance originated from and where it was planted ( $r=0.40$ ,  $P<0.05$ , Table 6). The intercept was positive in the model considering all sites.

#### Spatial autocorrelation

The Mantel tests showed significant correlations between the volume growth distance matrix and the geographic distance matrix (Table 7), both across all

Table 7. – Geographic and climatic spatial autocorrelation for TVOL based on Mantel test.

Type	All sites		US sites (2)		BC sites (4)	
	<i>r</i>	<i>P</i> value	<i>r</i>	<i>P</i> value	<i>r</i>	<i>P</i> value
Geographic	0.303	0.028	0.145	0.095	0.287	0.031
Climatic	0.571	0.069	0.186	0.145	0.453	0.065

Type	Single site											
	Corvallis		Courtenay		Haney		Nimpkish		Oakridge High		Sugar Loaf Mt	
	<i>r</i>	<i>P</i> value	<i>r</i>	<i>P</i> value	<i>r</i>	<i>P</i> value	<i>r</i>	<i>P</i> value	<i>r</i>	<i>P</i> value	<i>r</i>	<i>P</i> value
Geographic	0.055	0.332	0.150	0.130	0.404	0.002	0.170	0.118	0.316	0.015	0.168	0.077
Climatic	-0.074	0.507	0.380	0.081	0.334	0.065	0.132	0.139	0.499	0.034	0.238	0.092

sites and across BC sites ( $r=0.30$ ,  $P\leq 0.03$ ). Even higher correlations were found between the volume growth distance matrix and the climate distance matrix ( $r=0.57$ ,  $P<0.07$ ). These results confirmed an overall trend of similar rotation-age volume growth for geographically or climatically closely located provenances. We also conducted the mantel test for each site, and at least 50% of the pairs of distance matrices showed significant or marginally significant relationships ( $P\leq 0.09$ ).

It is worth mentioning that each coefficient of matrix correlation in Table 7 had its own empirical distribution, and, therefore, two similar correlation coefficients can be at different significance levels for a given test.

## Discussion

Tree species occupy shifting geographic ranges, either by natural gene flow and migration (HUNTLEY and BIRKS, 1983; WILLIS and VAN ANDEL, 2004) or artificial reforestation (WHITE *et al.*, 2007). Local populations often show highest relative fitness at their home sites, and lower fitness in other parts of the range (SAVOLAINEN *et al.*, 2007). Local adaptation refers to the genetic change in a population in response to a geographically localized selection pressure which is always fitness-related (e.g., drought, insect, disease, temperature, elevation, soil type, competition, etc.), and varies across the landscape. Thus, study of local adaptation needs to focus on traits which are reasonable surrogates for fitness. Local superiority in growth refers to the fact that local individuals show their growth advantages. The older the stand, the more the trees' size reflects trees' health and vigor at the specific environment during their life cycle to that point, after being interacted with multiple infrequent climatic extremes. Moreover, total tree volume per unit area (TVOL) at the rotation age accounts for not only trees' productivity but also trees' mortality under long-term environmental stresses. Thus, rotation-age growth superiority is considered to be a synonym for adaptation in this study.

Provenance and provenance  $\times$  site interaction effects were found to be statistically significant for volume growth at rotation age, suggesting that the most productive provenance at one site was not necessarily the most productive at another site. This concurs with the age-40 results from the sites in BC, Canada (KRAKOWSKI and

STOEHR, 2009), but differs from earlier research results (i.e., age $\leq 30$ ) where the differences among the provenances were small and provenance  $\times$  site interaction was generally not significant (CHING and HINZ, 1978; WHITE and CHING, 1985; KRAKOWSKI and STOEHR, 2009). There are a few possible reasons for such discrepancies. First, adaptive effects may depend on the intensity of among-tree competition. In a *Pinus ponderosa* provenance study, for example, reciprocal differences in growth among elevations did not become apparent until trees were 20 years old, which coincided with the onset of intense competition among trees for soil moisture (NAMKOONG and CONKLE, 1976). Second, gene expression and genetic control at earlier years may be different from the later years (NAMKOONG *et al.*, 1972; WHITE and CHING, 1985). Third, some effects show up over time. Extreme and infrequent environmental events (e.g., a one in 20-year cold damage, summer drought, or disease) may cause loss in growth in long-lived populations but have little influence to short-lived populations (BISHIER and BILLINGHAM, 2000). In a *Pinus sylvestris* provenance test, for example, non-native provenances suffered heavy mortality from frost damage and snow breakage caused by the epidemic *Brunchorstia* dieback disease at age 29 (DIETRICHSON, 1968).

It has been suggested that statistical significance may be of less practical importance than the loss of potential gain, when evaluating the provenance  $\times$  site interaction (LINDGREN, 1984; MATHESON and RAYMOND, 1984a; MATHESON and RAYMOND, 1984b; MATHESON and RAYMOND, 1986). In this study, we estimated that the loss of potential TVOL gain sustained by not selecting the best provenance at each site but the provenance performing best on average over all sites (i.e., Molalla High) was on average of 8% across the six sites, which was higher than most of the estimated gain losses from published information on tree species summarized by MATHESON and RAYMOND (1986). On the other hand, however, if each provenance was a breeding or deployment population, using only one best population for deployment at all six sites would have a very high benefit to cost ratio compared to developing six distinct deployment populations attempting to maximize gain at each site.

The evidence for growth superiority of local provenances was equivocal in this study. While the local

provenance did not always yield the best total volume at each planting site, a pattern of local superiority in rotation-age growth at large spatial scale appeared to exist and was statistically significant. For example, provenances tended to have poor long-term productivity when planted in areas geographically far away or climatically distinct from their home sites. Oregon provenances performed significantly better at the Oregon sites whereas BC and Washington provenances performed significantly better at the BC sites. High-elevation provenances grew poorly at low-elevation sites in general. Such macro-geographic variation pattern generally follows the results revealed by juvenile traits (e.g., CAMPBELL and SORENSEN, 1978; GRIFFIN, 1978; ST CLAIR *et al.*, 2005). Based on the empirical equations in *Table 6*, moving a provenance away from its original sites 500 m in elevation or 800 km in latitude would cause on average 9% loss in total volume per plot at rotation.

At small to medium spatial scale, however, local provenances could lose their superiority in growth. There are two potential reasons. First, gene flow is one of the most important factors shaping the genetic structure of populations. High rate of pollen gene flow between neighboring Douglas-fir populations was revealed by using molecular markers (ADAMS, 1992; ADAMS and BURCZYK, 2000), which may have retarded the progress of population differentiation. Second, the existence of significant spatial autocorrelation found in this study implied that the genetic diversity of adapted traits among populations could be interpretable as adaptive differentiation in response to environmental selectivity. Due to the complex topography and tremendous environmental heterogeneity in the Pacific Northwest of North America, however, the adaptive differentiation in Douglas-fir occurs in response to relative small environmental gradients (REHFELD, 1984). Thus, the sites chosen for provenance trials were unlikely to be representative to their regions, and the most productive provenance at one site might not be the most productive provenance at a nearby site. This may result in the loss of local growth superiority within a relatively small region.

Cooperative Douglas-fir breeding got underway in the US Pacific Northwest in 1966 via the “progressive” breeding strategy (SILEN and WHEAT, 1979). Due to the lack of information on climatic and experimental data, the initial breeding zones were delineated according to general ecological/climatic observations and land ownership patterns, and were kept small in order to avoid maladaptation (SILEN and WHEAT, 1979; JOHNSON, 1980; JOHNSON, 1997). The neighboring small breeding zones were later amalgamated into relatively bigger second-cycle breeding zones. The potential problems with “local is best” recommendations are: (1) there is a risk of encouraging the establishment of populations that do not harbor sufficient genetic variation and evolutionary potential, and therefore reduce the potential genetic gains though long-term breeding; and (2) it increases the cost of tree improvement beyond the level necessary. While results from several nursery or short-term provenance or genecology studies led to conclusions of local adaptation in coastal Douglas-fir (e.g., CAMPBELL and

SORENSEN, 1978; GRIFFIN, 1978; SILEN and MANDEL, 1983; ST CLAIR *et al.*, 2005), early reports on the long-term provenance studies suggested that maladaptation was not a big problem unless seed transfer involved large altitudinal distances. Several tree breeders (WOODS, 1993; STONECYPHER *et al.*, 1996) advocated using far larger breeding zones in this region than the original IFA-progressive plan. Despite limited numbers of provenances and test sites were used in this study, the rotation-age results largely supported the further enlargement of current breeding zones. The empirical boundary of local adaptation derived from this study (i.e., 435 km in latitude or 370 m in elevation) is larger than the size of most current breeding zones in this region. Moreover, superior families selected after intensive testing over a wide geographic area are likely to be more widely transferable than unimproved provenances.

## Conclusions

Significant provenance  $\times$  site interaction was revealed for rotation-age total volume per plot. The loss of potential volume gain sustained by using the provenance performing best on average over all sites instead of the best provenance at each site was about 8% on average of across sites. There was an overall spatial autocorrelation pattern showing that geographically or climatically closely located provenances tended to have similar growth rate. Significant local growth superiority was found at large spatial scale. Such superiority may, however, be lost at small to medium spatial scale (i.e., 435 km in latitude or 370 m in elevation).

Our results indicated that larger breeding zones could be appropriate for coastal Douglas-fir breeding in this region.

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