Stem Volume and Wood Relative Density of a Non-Local Douglas-Fir Provenance in British Columbia

By J. A. Loo-Dinkins[1]), C. C. Ying[2]) and E. A. Hamm[3])

(Received 30th March 1990)

Abstract

Incremental and cumulative volume growth from ages seven to 16 years and wood relative density to age 16 of five standard and three local Douglas-fir provenances were studied at three test sites in coastal British Columbia. Growth patterns were examined to determine whether the fastest growing and most southerly provenance from Hoh, Washington maintained a growth rate advantage over the other provenances. The Hoh provenance performed consistently well at all sites and maintained its relative volume advantage between the ages of seven and 16. Volume and wood relative density were negatively correlated on a provenance mean basis. Thus the advantage of the Hoh provenance was reduced from 39% in volume to 36% in stem dry weight. This may not reflect the influence of the negative correlation on value, however, if strength becomes an issue in determining value for coastal Douglas-fir. There was no consistent relationship between volume and relative density within the provenances.

Key words: provenance, coastal Douglas-fir, specific gravity, incremental volume, seed transfer.

Introduction

Seed transfer, or seed-source introduction, is a largely untapped potential for tree improvement in the Pacific northwest. Seed source movement may provide substantial benefits as a part of a tree improvement program, but risks must be carefully weighed for each situation. Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) has been under test longer than other species in British Columbia. Initial results from provenance trials indicate a potential for volume gains through use of seed from Washington and Oregon, USA. A series of Douglas-fir provenance trials established by the British Columbia Forest Service was evaluated at age six from planting (age 8 from seed) in 1976. Illingworth (1978) reported the results and identified several seed sources with superior growth. Of particular interest is the Hoh provenance (47.48 latitude, 124.04 longitude) from Washington's Olympic Penninsula, which was above average in 18 of the 19 test plantations including the most northern planting site, at Bella Coola (52.25 latitude, 126.40 longitude). This provenance continued to perform very well through age 15, with highest or second highest volume at all but one of the plantations (B.C. Ministry of Forests unpublished data.)

To date, researchers have generally reported a high degree of environment-specific adaption in both coastal and interior Douglas-fir (*P. menziesii* var. *glauca* (Beissn.) Franco), and have cautioned against use of non-local seed sources for planting in western North America (Adams and Campbell, 1981; Campbell, 1979; Rehfeldt, 1979). In addition to the danger of extreme climatic events causing serious damage to well-established trees from non-adapted sources, Adams and Campbell (1981) described potential losses due to small accumulated injuries. They refer to effects accumulating over a long period of time such as pathogens entering frost cracks or shifting growth curves due to phenology and climatic cycles being out of phase. They described several unsuccessful seed transfers over short distances in regions of Norway, Sweden and Idaho which experience severe climates. However, Douglas-fir has been widely and successfully introduced in Europe and New Zealand (Kleinschmit, 1978; Nanson, 1978; Bastien *et al.*, 1986; Silen, 1978; Hermann, 1987).

The ever present question of optimum selection age is potentially of greater importance in provenance selection than in individual tree selection. To reach decisions with a high degree of confidence, evaluation of adaptive traits should be at half a rotation length or later. Unfortunately, breeding programs cannot usually wait that long to make use of provenance results in parent tree selection.

Large scale use of non-local loblolly pine (*Pinus taeda* L.) in eastern and central U.S. provides a good example of risk versus gain decisions in seed source selection (Lambeth *et al.*, 1984). For the northwestern part of the range (Arkansas and Oklahoma), North Carolina sources have consistently out-performed local sources in volume growth (Grigsby, 1973; Lambeth *et al.*, 1984; Wells and Lambeth, 1983; Talbert and Strub, 1987), but have somewhat lower survival due to higher susceptibility to ice and cold, less rust resistance and a lower tolerance for drought (Wells, 1983). Assuming acceptable survival, the North Carolina sources would thus be expected to be more valuable if volume alone is considered, because of the influence of piece size and reduced rotation age. Tauer and Loo-Dinkins[4]), however, noted that the local sources had higher relative wood density, and when this, combined with higher survival, is accounted for, total dry weight of wood produced per unit area is as high for the local sources as the North Carolina sources when planted in the northwestern part of the range. They noted that the patterns of geographic variation in relative density differed depending on whether trees were sampled in their native environments or were brought together in a common environment in Arkansas. Thus it appears that seed source movement may have an unpredictable impact upon the relative density of wood, at least for loblolly pine.

The long-term survival and health of the Pacific northwest forest industry is likely to be as dependent upon high quality wood, in terms of strength, as upon volume (Johnson, 1986). Relative density is recognized as the single best indicator of clear wood quality (Kellogg, 1982). Thus a negative impact of seed source transfer upon rela-

[1]) Research Associate, Faculty of Forestry, University of British Columbia, 270—2357 Main Mall, Vancouver, B.C., V6T 1W5, Canada

[2]) Research Scientist, British Columbia Ministry of Forests, 31 Bastion Square, Victoria, B.C., V8W 3E7, Canada

[3]) Scientist, Forintek Canada Corp., Western Laboratory, 6620 N.W. Marine Drive, Vancouver, B.C., V6T 1X2, Canada

[4]) Tauer, C. G. and J. A. Loo-Dinkins. Seed source variation in specific gravity of loblolly pine grown in a common environment in Arkansas. For. Sci. (in press).

tive density may outweigh the benefits of more rapid growth. In addition, stem strength, as influenced jointly by relative density and bole diameter, would be expected to impact survival (McKimmy and Campbell, 1982).

The objective of this study was to evaluate the suitability of the Douglas-fir provenance from Hoh, Washington for selection of parents for the Douglas-fir breeding program in coastal British Columbia. This was done by determining whether the Hoh provenance maintained a growth rate advantage at three sites in coastal British Columbia, and by examining relative density relationships with volume.

Material and Methods

From 1970 to 1975, one series of Douglas-fir provenance trials was established at 23 locations in coastal British Columbia by the B.C. Forest Service (now Ministry of Forests). The objective was to examine genotype by environment interactions and to identify hardiness zones. Five standard provenances from widely separated origins were tested at all test sites (*Table 1, Figure 1*). In addition, a local provenance collected close to the test site was included in each test for a total of 6 provenances at each site. Each provenance seedlot consisted of a blend of seed collected from a minimum of 10 well-spaced parent trees (Illingworth, 1978). Trees were planted in 35-tree row plots in four blocks at each site. Three of these sites, located near Harrison Lake, Coal Harbour, and Chilliwack, were thinned in 1987 at age 16 (from planting) providing the opportunity for destructive sampling to determine height and diameter increment, as well as wood relative density. These sites represent the eastern and western extremes of the coastal Douglas-fir breeding zone, (*Table 2, Figure 1*) and are above average among the 23 original sites in productivity. The Coal Harbour site is just outside of the natural range of Douglas-fir. In spite of the proximity of one of the standard provenances (Jeune), an additional, more distant source was included as the "local" source at this test site. For the purposes of this paper, however, we consider both Jeune and Seymour to be local provenances at Coal Harbour. Provenance survival at age 16 ranged from 70% to 84% at Coal Harbour, 84% to 96% at Chilliwack and 84% to 95% at Harrison Lake. Differences among provenances in survival were not statistically significant.

Table 1. — Source information for five standard and three local Douglas-fir provenances growth at three coastal test sites.

PROVENANCE	STATUS	ELEVATION (m)	LATITUDE°	LONGITUDE°
D'Arcy	standard	270	50.33	122.30
Hoh	standard	245	47.48	124.04
Jeune Landing	standard	170	50.27	127.27
Noeick River	standard	60	52.03	126.36
Duncan	standard	60	48.45	123.45
Chilliwack	local	170	49.04	121.48
Harrison Lake	local	45	49.30	121.46
Seymour	local	3	51.11	127.01

Table 2. — Site information for three Douglas-fir provenance test plantations in coastal British Columbia.

LOCATION	ELEV(m)	LAT.°	LONG.°	SLOPE(%)	ASPECT°	BGCL UNIT[1]
Coal Harbour	45	50.42	127.31	40	170	CWHb1
Chilliwack	215	49.04	121.43	3	350	CWHa2
Harrison Lake	245	49.30	121.45	55	130	CWHa2

[1]) British Columbia Biogeoclimatic Zone

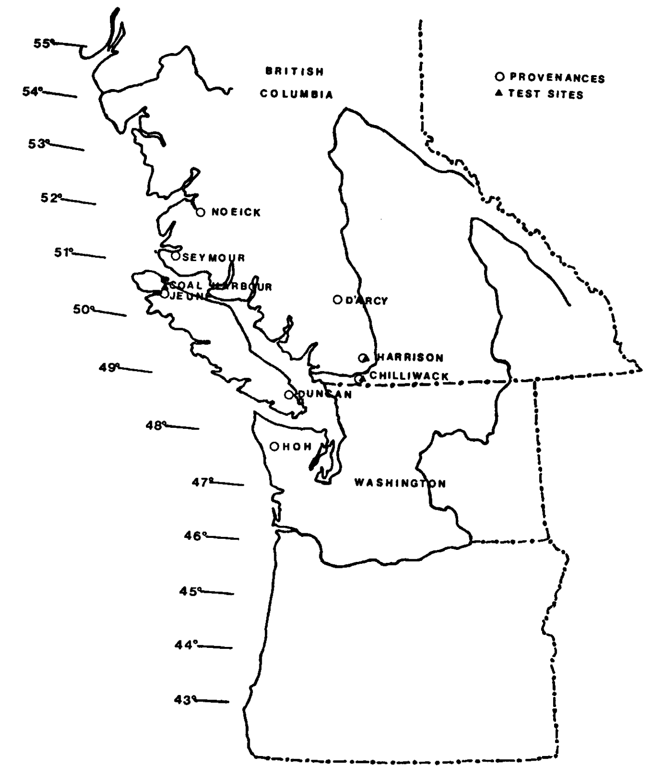

Fig. 1. — Location of Douglas-fir provenances and test sites.

Thinning consisted of removing every other tree in each row. On average, five trees were selected from the 17 or less thinned trees in each row plot for incremental height and diameter measurements from ages 7 to 16. The trees were chosen in such a way that the diameter range within each provenance was sampled with probability approximately proportional to frequency. When differential mortality among plots within a provenance resulted in less than five acceptable trees being thinned in one plot, more than five were sampled in another plot to make up the difference. Incremental bole volumes for ages 7 to 16 were estimated for trees less than 4 m in height and for larger trees, using equations 1 and 2, respectively (Omule *et al.*, 1987).

$$[1]\quad \ln(V) = -7.8844853 + 1.3468697 \times \ln(D) + 0.1203368 \times \ln(H)$$

$$[2]\quad \ln(V) = -9.8963259 + 1.8347884 \times \ln(D) + 1.0051192 \times \ln(H)$$

where V = volume (m^3)
D = diameter at breast height (cm)
H = height (m)
ln = natural log

An overlapping, but not identical, sample of felled trees was used for relative density determination. The density determination was initially done as a separate study and trees free of branches at breast height were chosen for sampling. The same trees were used for both measures at the Coal Harbour and Chilliwack sites but approximately one-third of the sample trees differed at the Harrison Lake site. A 2.5 cm to 5.0 cm thick disk was cut from each tree approximately at breast height for density measurement at the Forintek western laboratory. The disks were examined for knots and a knot-free wedge-shaped segment was cut from each disk which had knots. The wood samples were soaked in water until fibre saturation point was exceeded, debarked, and volume was measured using a water displacement technique. Wood samples were then oven-dried and weighed. Relative density was calculated as the ratio of oven-dry weight to water-soaked volume.

Incremental and cumulative height, diameter and volume for provenance means were plotted against age by test site to determine whether the provenances followed different growth curves. Analyses of variance, using the general linear model to allow for imbalance in the data, were conducted on each of the variables. Because of the sampling procedure (trees selected to represent each diameter class in proportion to their frequency), the results cannot be construed to represent a random sample of trees from each provenance population. The chosen samples should be representative of the provenances, however, and the variance in the sample would not be expected to be larger than the population variance. The models for volume analysis in a given year (equation 3), and for volume increment including year as an effect (equation 4), with sites and provenances treated as fixed effects, are as follows:

$$[3]\quad Y_{iklm} = \mu + S_i + P_k + SP_{ik} + B(S)_{l(i)} + PB(S)_{l(ik)} + E_{m(ikl)}$$

$$[4]\quad Y_{ijkl} = \mu + S_i + Y_j + SY_{ij} + P_k + SP_{ik} + YP_{jk} + SYP_{ijk} + B(S)_{l(i)} + B(SY)_{l(ij)} + PB(S)_{l(ik)} + E_{l(ijk)}$$

where y_{iklm} = the m^{th} observation in the l^{th} block of the k^{th} provenance at the i^{th} site

y_{ijkl} = the l^{th} plot mean for the k^{th} provenance in the j^{th} year at the i^{th} site

s_i = the effect of the i^{th} site (fixed)

y_j = the effect of the j^{th} year

P_k = the effect of the k^{th} provenance (fixed)

$B(S)_{l(i)}$ = the effect of the l^{th} block nested in the i^{th} site

SY_{ji} = the site by year interaction effect

SP_{ik} = the site by provenance interaction effect

YP_{ik} = the year by provenance interaction effect

SYP_{ijk} = the site by year by provenance interaction effect

$B(SY)_{l(ij)}$ = the year by block interaction effect

$PB(S)_{l(k)}$ = the provenance by block interaction effect

$E_{m(ikl)}$ = the within-plot error term

$E_{l(ijk)}$ = the block-within-site x year x provenance interaction (error term for plot means analysis)

Satterwaite's approximation (Zar, 1974) was used in construction of F-tests for fixed effects in the model with years as an effect. Analyses of variance for total and incremental height, diameter and volume were conducted for each year from ages 7 to 16. T-tests were conducted to compare 16-year volume of the Hoh provenance with the local source at each site. Age-age correlations on an individual tree basis were estimated for each variable for ages 7 through 16 for the entire data set as well as by provenance.

Wood relative density data were examined using analysis of variance with the model shown in equation 3. Phenotypic correlations were estimated between relative density and 16-year volumes (estimated from measurements taken by the B.C. Ministry of Forests prior to thinning) on a provenance mean and on an individual tree basis, for all provenances and sites combined as well as by provenance and site.

Results

The Hoh provenance continued to grow as rapidly or more rapidly than the other provenances at all sites. Trends for height, diameter and volume were similar so plots for cumulative and incremental volume only are presented (*Figures 2 and 3*). On an overall provenance mean basis, the Hoh provenance established volume superiority among the standard provenances by age 9, and the difference has increased through age 16. The average volume attained by the Hoh provenance was approximately three times as great as that attained by the poorest provenance, D'Arcy (*Table 3*). The Hoh provenance was clearly the fastest growing by a 5 percent to 20 percent margin at the Harrison Lake and Chilliwack test sites (*Figure 2b, c*). The Jeune Landing provenance was as good, however, at Coal Harbour (*Figure 2a*) A t-

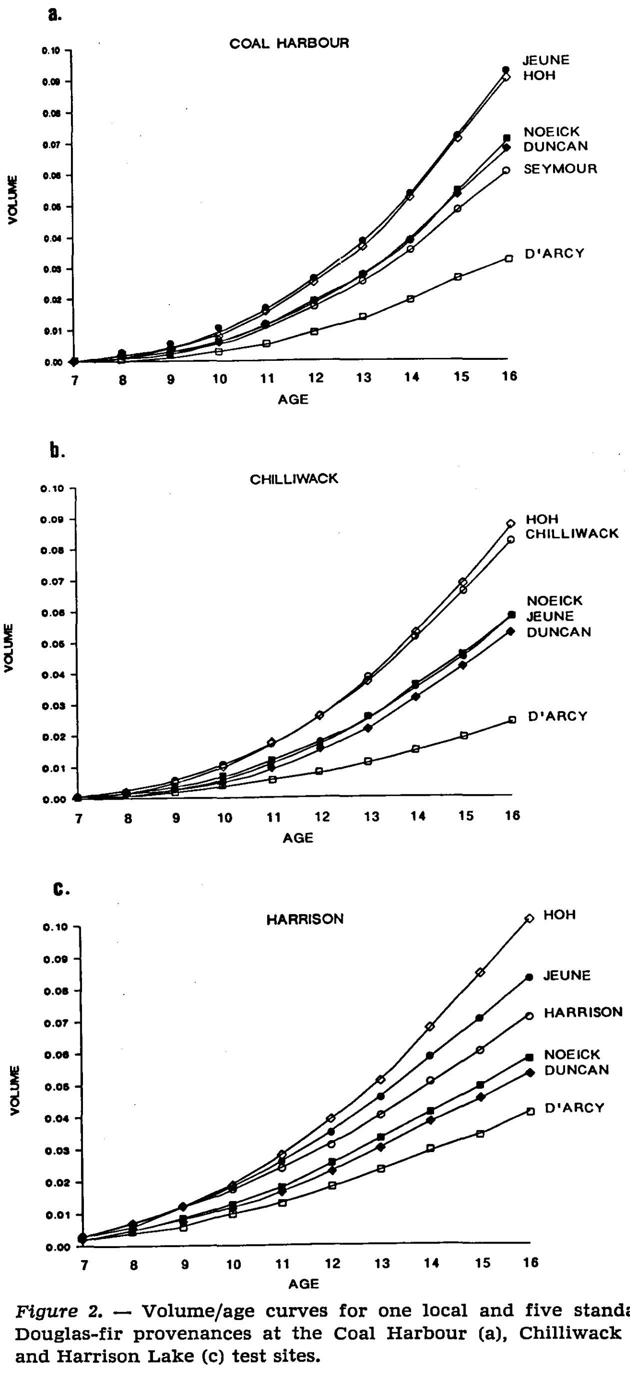

Figure 2. — Volume/age curves for one local and five standard Douglas-fir provenances at the Coal Harbour (a), Chilliwack (b) and Harrison Lake (c) test sites.

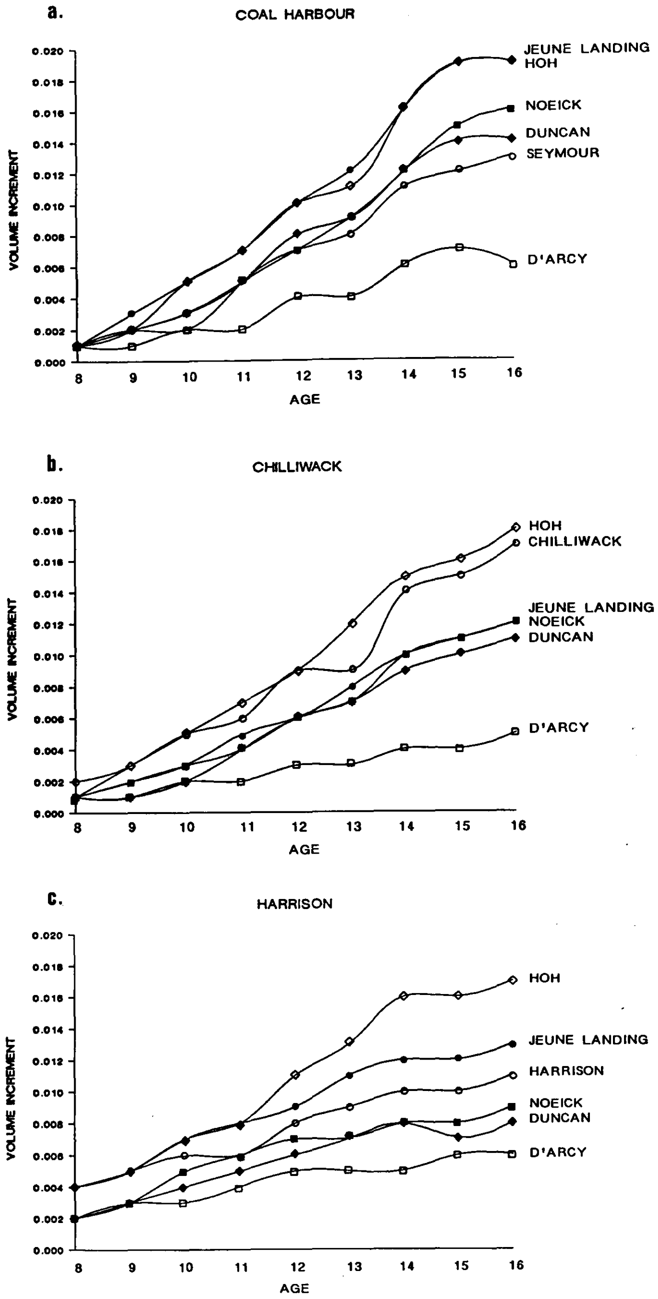

Figure 3. — Volume increment potted over age for one local and five standard Douglas-fir provenances at the Coal Harbour (a), Chilliwack (b) and Harrison Lake (c) test sites.

test across test sites indicated that at age 16, the Hoh provenance was significantly better at the 5% level than the mean of the local sources, including just Harrison, Chilliwack and Seymour. On an individual site basis, Hoh's volume was significantly greater than Seymour at the 5% level although it did not differ from Jeune at Coal Harbour. Hoh was significantly better than the local source at Harrison Lake at the 10% level, but was not significantly better than the local source at Chilliwack. The low, or lack of, statistical significance on an individual site basis, may be explained, in part, by the few degrees of freedom.

Incremental volume curves demonstrate the continuing growth rate superiority of the Hoh provenance between ages seven and 16 (*Figure 3*). The growth curves were

Table 3. — Overall mean 16-year volume, relative density and dry weight per tree for five standard and three local coastal Douglas-fir provenances and for the three test sites.

PROVENANCE	VOLUME (m^3)	RELATIVE DENSITY	WEIGHT/TREE
Hoh	0.0808	.397	32.08
Jeune Landing	0.0657	.405	26.61
Noeick River	0.0589	.402	23.68
Duncan	0.0529	.408	21.58
D'Arcy	0.0316	.436	13.78
Chilliwack	0.0769	.375	28.84
Harrison Lake	0.0613	.457	28.01
Seymour	0.0530	.407	21.57
SITE	**VOLUME (m^3)**	**RELATIVE DENSITY**	**WEIGHT/TREE**
Coal Harbour	0.0596	.387	23.06
Chilliwack	0.0587	.401	23.54
Harrison Lake	0.0620	.440	27.28

similar for all provenances with the exception of D'Arcy which exhibited a substantially flatter curve than the others. The incremental growth curves also showed the Jeune Landing provenance growing as rapidly as the Hoh provenance at the Coal Harbour site. In fact, their curves were almost identical.

The Harrison Lake site appears to have the highest productivity among the three test sites with highest mean volume per tree as well as highest mean relative density (*Table 3*). The volume differences among sites were not statistically significant in all years, based on analysis of variance (*Table 4*), however. Growth was generally poorest at the Chilliwack site despite it's being the most southerly plantation. This may be due, in part, to the fact that the other two plantations have a southerly aspect while the Chilliwack plantation is flat. In addition, the Chilliwack site, though not dry, receives less moisture, especially during the summer months, than the other two sites (CARTER, unpubl. report).

Analyses of variance did not identify statistically significant provenance by site interaction for any growth traits. Only volume increment results are presented (*Tables 4* and *5*) as the other analyses showed essentially the same results. The provenance by site interaction variances for growth increments were examined for possible age trends (*Table 4*). If an initially good, but maladapted, provenance gradually deteriorates with time in an unfavorable environment, the provenance by site interaction might be expected to increase with time. Although the provenance by site interaction term increased with age, environmental sources of variance also increased, so the F statistic did not change substantially over time. The lack of provenance by site interaction implies that none of the five standard provenances are specifically adapted to any of the three test environments. Both provenance by year and site by year interactions were statistically significant at the 0.01 level of probability (*Table 5*). In spite of the significant provenance by year interaction, *Figure 3* does not indicate that the problem is serious. At each site, provenances seem to have sorted out by about age 11 and three is little rank change from then on. Minor rank changes over time do not necessarily reflect genotype by environment interaction. Genetic correlations between measurements at different ages for traits such as volume are known to be imperfect, resulting in rank changes over time that do not have any relationship to the environment.

Site became less important as a source of variance and the provenance variance increased relative to the total phenotypic variance with time. This trend was more pronounced for cumulative volume than for volume incre-

Table 4. — Analysis of variance results for annual volume increment, by year for one local and five standard Douglas-fir provenances at each of three test sites.

SOURCE OF VARIANCE	DF	MEAN SQUARES[a,b] AGE8	AGE9	AGE10	AGE11	AGE12	AGE13	AGE14	AGE15	AGE16
Site	2	.0897+	.1081*	.0891	.0340	.0239	.0226	.2162	.7747+	.5709*
Provenance	5	.0062*	.0216+	.0612+	.1337+	.2423+	.3712+	.6493+	.7600+	.9558+
Site x Prov	10	.0023	.0039	.0149	.0097	.0249	.0330	.0497	.0886	.0895
Block(site)	9	.0137+	.0184+	.0335+	.0498+	.0593+	.0774+	.1033+	.0963*	.0956
Plot	41	.0029*	.0048+	.0102+	.0131*	.0234+	.0310+	.0555+	.0682+	.0711+
Error	284	.0018	.0025	.0056	.0090	.0137	.0168	.0279	.0339	.0371

[a]) AGE8-AGE16 represent volume increments from age 7 to 8, . . ., age 15 to 16.
[b]) Mean squares are presented as 10^3 x actual.
*) Statistically significant at the 5% level
+) Statistically significant at the 1% level

ment. The block and plot (block x provenance interaction) effects were highly significant for almost all years (*Table 4*). In general, high within-site variation can be expected in coastal Douglas-fir sites, and test plantations are not excepted. The Harrison Lake site, in particular, exhibited a high degree of within-site heterogeneity probably owing to soil moisture variability. The other two sites, while relatively more uniform, had some microsite variation due to varying depths of decaying wood at Coal Harbour and old skid roads at Chilliwack (CARTER, unpubl. report). Because of the high degree of site variability within plantations, the lack of a site x provenance interaction, and the large plot size, the block x provenance interaction should be viewed as a plot variance rather than as a true interaction.

Table 5. — Analysis of variance results for annual volume increment from ages 7 to 16 with years treated as a random effect for one local and five standard Douglas-fir provenances at each of three test sites.

SOURCE OF VARIANCE	DF	MEAN SQUARES	F RATIO
Site	2	0.0000563	0.44
Provenance	5	0.0004770	7.33**
Site x provenance	10	0.0000469	1.06
Block(Site)	9	0.0000948	38.79**
Provenance x Block(Site)	41	0.0000434	22.25**
Year	8	0.0011026	451.14**
Site x Year	16	0.0000388	15.88**
Provenance x Year	40	0.0000219	11.22**
Site x Provenance x Year	80	0.0000025	1.30
Year x Block(Site)	72	0.0000024	1.25
Error	328	0.0000019	

**) Statistically significant at the 1% level.

Age-age correlations between pairs of volumes from ages 7 to 16 were higher for cumulative than for incremental volume, as might be expected (*Table 6*). The estimated correlation between age 7 and age 16 cumulative volume (r = 0.63) indicates that volume at age 7 may be a reasonable indicator of volume at age 16. The estimated correlation between volume increments 7 to 8 and 15 to 16 was considerably lower than for cumulative volume at r = 0.38.

Table 6. — Estimated phenotypic age-age correlations [a]) for volume (above diagonal) and annual volume increment (below diagonal) on an individual tree basis from age 7 to 16.

AGE	8	9	10	11	12	13	14	15	16
7	.97	.96	.94	.91	.85	.80	.74	.67	.63
8		.99	.95	.91	.85	.80	.73	.67	.63
9	.89		.98	.95	.90	.86	.80	.74	.70
10	.77	.90		.98	.96	.92	.87	.82	.78
11	.68	.84	.89		.99	.97	.93	.89	.86
12	.60	.77	.87	.93		.99	.97	.94	.91
13	.55	.72	.82	.90	.96		.99	.97	.95
14	.43	.62	.73	.85	.92	.95		.99	.98
15	.36	.53	.67	.79	.87	.91	.94		1.00
16	.38	.55	.66	.77	.85	.89	.92	.94	

[a]) Estimates are based on a sample size of 352.

Age-age correlations for volume increment within provenances varied considerably among provenances across sites (*Table 7*). Correlations for the Harrison provenance indicate a remarkably high degree of stability in yearly rate of volume increment. The age-age correlations for D'Arcy and Seymour were also higher than average, indicating relatively high stability over years. As D'Arcy is a uniformly poor performer, it is not surprising that it has high stability, and in this case, stability is not particularly desirable. The high stability over years of the local provenances, particularly Harrison Lake and Seymour, is probably due to their presence at only one site.

Table 7. — Estimated phenotypic correlations for volume growth increment between the 8th and 16th year by provenance. All growth increments are correlated with the 16th year increment.

PROVENANCE[a]	8	9	10	11	12	13	14	15
Noeick	.17	.40	.62	.68	.86	.86	.91	.96
Jeune Landing	.25	.46	.66	.76	.83	.87	.92	.92
Hoh	.36	.58	.69	.77	.86	.89	.91	.94
Duncan	.42	.50	.63	.72	.76	.87	.95	.97
D'Arcy	.70	.66	.72	.82	.89	.92	.95	.96
Seymour	.74	.70	.60	.64	.89	.94	.92	.96
Chilliwack	.44	.44	.45	.62	.67	.75	.86	.81
Harrison Lake	.92	.95	.92	.97	.98	.99	.97	.99

[a]) Estimated correlations are based on a sample size of approximatey 60 trees for the standard provenances (the first five) and 20 trees for the local provenances.

Analyses of variance for relative density showed highly significant site and provenance effects, but not site x provenance interaction (*Table 8*). The effect of site was by far the largest source of variance for relative density, but block and plot effects were insignificant. This is very different from the situation for volume, indicating that macro-site effects (for example climate and soil moisture) may have a relatively greater influence on wood density than on volume whereas volume seems much more sensitive to meso- and microsite variation.

On an individual tree basis, the estimated correlation between relative density and volume was slightly negative (r = — 0.12). On a provenance mean basis the negative correlation was considerably stronger; r = — 0.92 for all sites combined (*Figure 4*). The estimated correlations for provenance means at each site were — 0.61, — 0.77 and — 0.89 for Harrison Lake, Coal Harbour and Chilliwack, respectively. The negative correlations were largely driven by the Hoh and D'Arcy provenances, as Hoh, with consistently highest volumes, had the lowest relative

Table 8. — Analysis of variance results for relative density at age 16 for one local and five standard Douglas-fir provenances at each of three test sites.

SOURCE OF VARIANCE	DEGREES OF FREEDOM	MEAN SQUARES	F RATIO
Site	2	0.09199	47.03*
Provenance	5	0.00771	4.50*
Site x Provenance	10	0.00287	1.68
Block(Site)	9	0.00196	1.09
Plot	45	0.00171	0.95
Error	300	0.00179	

*) Statistically significant at the 5% level.

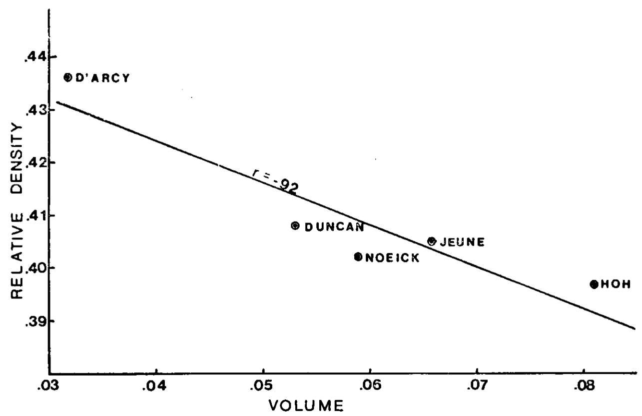

Figure 4. — Relationship between relative density and volume for five Douglas-fir provenances averaged over three test sites.

density and D'Arcy, the slowest growing provenance, had by far the highest relative density (*Table 3*).

Correlation coefficients, estimated for each provenance at each site, showed no consistent evidence of negative phenotypic relationships beetween wood relative density and volume within provenances (*Table 9*). Within-provenance correlation estimates between volume and relative density ranged from — 0.36 to + 0.36 at Chilliwack and Coal Harbour. At Harrison Lake, however, there was a negative trend with estimates ranging from 0·13 to — 0.61. The Harrison Lake site had highest mean volume as well as substantially higher mean relative density than the other sites in spite of the negative correlation between the two traits at that site.

The mean dry weight on an individual tree basis was estimated for each of the five standard provenances (*Table 3*). Dry weights of trees from the Hoh provenance were more than twice as large, on average, as trees from the D'Arcy provenance, despite the 10% higher average relative density of D'Arcy. There was very little difference in mean survival among the standard provenances, thus the provenance ranking, with respect to dry weight per tree, was reflected in dry weight per unit area. On average, survival of local sources was 4% higher than for Hoh.

Table 9. — Phenotypic correlation estimates between volume and relative density within provenances and test sites.

PROVENANCE	TEST SITE			
	CHILLIWACK	COAL HARBOUR	HARRISON LAKE	ALL SITES
D'Arcy	0.22	0.36	0.13	0.18
Duncan	-0.05	0.07	0.00	0.00
Hoh	-0.36	0.35	-0.38	-0.10
Jeune	0.15	-0.18	-0.44	-0.16
Noeick	0.20	-0.32	-0.61	0.02
Chilliwack	-0.12	-	-	-
Seymour	-	-0.17	-	-
Harrison	-	-	-0.52	-
All Provenances	-0.06	-0.18	-0.39	-0.12

Approximate dry weights on a land area basis, obtained as the product of dry weight per tree and percent survival, were 26.2, 22.1, 18.2, 24.7 and 24.2 for Hoh, Jeune, Seymour, Chilliwack and Harrison, respectively. Hoh is higher than each of the locals at each plantation, but not significantly so, in part because of the small number (20) of local trees sampled at each site.

Discussion

At age 16, the best Douglas-fir provenance, among those evaluated in this study, for planting in environments represented by the three test sites appears to be from Hoh, Washington. Moving seed from this provenance as much as 3° latitude north or 100 km inland in combination with 2° latitude has resulted in no apparent maladaption response in terms of growth. As the relative density of the Hoh provenance in its native habitat is unknown, the low relative density exhibited by the Hoh provenance when grown in coastal B.C. cannot necessarily be attributed to seed movement.

The origin of the D'Arcy provenance is almost as far geographically and probably farther in ecological terms from each test site than the Hoh provenance. The D'Arcy provenance originates in the coastal-interior transition zone, thus is adapted to much lower moisture availability than exists at each of the test sites. As a consequence, although the D'Arcy provenance should be well equipped to survive any coastal climatic extremes, the growth pattern is apparently too conservative to take full advantage of the coastal conditions. The Chilliwack and the Harrison Lake local provenances performed well with respect to the standard provenances, but the Hoh provenance had consistently higher mean volume and dry weight per tree.

The results do not seem to support the view of Adams and Campbell (1981) that small injuries may accumulate over many years in provenances that are grown at an excessive ecological distance from their origins. The ecological distances may not be great enough to be considered excessive, however. The Hoh origin has the highest elevation, with the exception of the D'Arcy provenance. Movement of seed downward in elevation would counter the effect of increasing latitude to a point. The elevations of the two mainland plantations are similar to that of the Hoh provenance however. The growth rate of the Hoh provenance does not show any indication of decline relative to the other provenances and growth stability as reflected by age-age correlations appears intermediate. Adams and Campbell (1981) noted that non-local sources may show little or no evidence of mal-adaptation until after age 20, implying that age 16 may be too young to make valid judgements.

The low relative density of the Hoh provenance may be a cause for concern if wood quality, in terms of strength, becomes as important as volume, as predicted by Johnson (1986). In British Columbia, stength is not usually measured in determining lumber value. Thus at present, the magnitude of the volume difference between the Hoh provenance and higher relative density provenances would counter a potentially somewhat higher value associated with high relative density, but this may not be true in the future. The lack of consistent phenotypic correlations between relative density and volume within provenances may allow within-provenance selection for both traits, if they reflect genetic correlations. Thus, given an appropriate selection intensity, it may be possible to select fast growing trees with acceptable wood density. The influence of site, not only upon relative density, but also on the correlation between relative density and volume must be taken into consideration in the selection process, however. COOK (1988) has identified an end-product based approach for determining a cut-off point for minimum acceptable relative density levels in young trees, that may be valuable in deciding volume growth, relative density trade-offs.

MCKIMMY and CAMPBELL (1982) suggested that stem strength is a function of wood relative density and ring width, and that low relative density for a given mean ring width would result in weak trees susceptible to wind and snow damage. At each site, Hoh compares well with local sources assuming that wood relative density and bole diameter together determine stem strength. At Coal Harbour, Hoh and Jeune had similar mean diameters and relative densities. While Seymour's mean relative density was 6% higher than Hoh's at Coal Harbour, Hoh's diameter was 12% larger than Seymour's. Similarly, at Harrison Lake, where all provenances had high relative density and volume, the local source's relative density was 7% higher than Hoh's but Hoh's diameter was 10% larger. At Chilliwack, Hoh had higher mean relative density and diameter than the local source. Thus there is no evidence for maladaptation of the Hoh source in terms of stem strength in the three test environments.

Unless a provenance trial is continued for at least half a rotation length, results cannot be conclusive, but decisions must often be reached based on such evidence as is available at the time. If volume continues to be primary consideration, inclusion of parent trees from the Hoh region in the British Columbia coastal Douglas-fir breeding program, at least on an experimental basis seems advisable. Before doing this, however, it would be useful to obtain a larger wood sample for relative density analysis, including young trees growing in additional B.C. provenance trial locations as well as older plantation trees growing in the Hoh area to determine whether the low relative density is a result of seed movement.

Acknowledgements

The authors wish to thank D. T. LESTER, C. G. TAUER and D. JOYCE for their thoughtful reviews and valuable suggestions.

Literature Cited

ADAMS, T. and CAMPBELL, R. K.: Genetic adaptation and seed source specificity. *In*: Reforestation of skeletal soils: Proceedings of a workshop. HOBBS, S. D. and HELGERSON, O. T. Eds Nov. 1981. Medford, Oregon. pp. 78—85 (1981). —— BASTIEN, J. CH., ROMAN-AMAT, B. and MICHAUD, D.: Douglas fir. Amelioration genetique des arbres forestiers. Revue Forestiere Francaise. pp. 113—120 (1986) —— CAMPBLL, R. K.: Genecology of Douglas-fir in a watershed in the Oregon Cascades. Ecology 60 (5) : 1036—1050 (1979). —— CARTER, R.: Ecological characterization of E. P. 599.03 test sites. Unpublished contract report for B. C. Ministry of Forests Research Branch. British Columbia Ministry of Forests, Victoria, B. C., Canada. 46p. —— COOK, J. A.: The establishment of end-product based criteria for the evaluation of wood density in tree improvement programs. CFS Report 35, Forintek Canada Corp., Vancouver, British Columbia, Canada. 28 pp (1988). —— GRIGSBY, H.: South Carolina best of 36 loblolly pine seed sources for southern Arkansas. USDA For. Serv. Res. Pap. SO—89. 10p. (1973). —— HERMANN, R. K.: North American tree species in Europe. J. For. 85: 27—32 (1987) —— ILLINGWORTH, K.: Douglas-fir provenance trials in coastal British Columbia — Results to six years after planting. Proc. of the IUFRO joint meeting of working parties S2-02-05,S2-02-06,S2-02-12,S2-02-14. Vol. 1 : Background papers and Douglas-fir provenances. British Columbia Ministry of Forests, Victoria, B.C., Canada. pp. 411—425 (1978). —— JOHNSON, J. A.: Wood quality and its relationship to uses, grades and prices : Past, present and future. *In*: Douglas-fir : Stand management for the future. OLIVER, C. D., HANDLEY, D. P. and JOHNSON, J. A., Eds. Proc. Symp. June, 1985. Univ. of Washington. pp. 145—148 (1986). —— KELLOGG, R. M.: Coming to grips with wood quality. For. Chron. 58: 254—257 (1982). —— KLEINSCHMIT, J.: Douglas-fir in Germany. Proc. of the IUFRO joint meeting of working parties S2-02-05, S2-02-06,S2-02-12,S2-02-14. Vol. 1 : Background papers and Douglas-fir provenances. British Columbia Ministry of Forests. Victoria, B.C., Canada. pp. 317—334 (1978). —— LAMBETH, C. C., DOUGHERTY, P. M., GLADSTONE, W. T., MCCULLOUGH, R. B. and WELLS, O. O.: Large-scale planting of North Carolina loblolly pine in Arkansas and Oklahoma : A case of gain vs. risk. J. For. 82: 736—741 (1984). —— MCKIMMY, M. D. and CAMPBELL, R. K.: Genetic variation in the wood density and ring width trend in coastal Douglas-fir. Silvae Genet. 31: 43—51 (1982). —— NANSON, A.: Belgian provenance experiments with Douglas-fir, grand fir and Sitka spruce. Proc. of the IUFRO joint meeting of working parties S2-02-05, S2-02-06, S2-02-12, S2-02-14. Vol. 1 : Background papers and Douglas-fir provenances. British Columbia Ministry of Forests, Victoria, B.C., Canada. pp. 335—346 (1978). —— OMULE, S. A. Y., FLETCHER, V. E. and POLLSON, K. R.: Total and merchantable volume equations for small coastal Douglas-fir. FRDA Report 010. British Columbia Ministry of Forests, Victoria, B. C., Canada. 16p. (1987). —— REHFELDT, G. E.: Ecological adaptation in Douglas-fir (*Pseudotsuga menzeisii* var. glauca) populations. 1. North Idaho and north-east Washington. Heredity 43: 383—397 (1979). —— SILEN, R. R.: Genetics of Douglas-fir. USDA For. Serv. Res. Pap. WO-35. 35p. (1978). —— TALBERT, C. B. and STRUB, M. R.: Dynamics of stand growth and yield over 29 years in a loblolly pine source trial in Arkansas. Proc. 19th So. For. Tree Improv. Conf., College Station, TX. pp 30—38 (1987). —— WELLS, O. O.: Southwide pine seed source study — loblolly pine at 25 years. So. J. Appl. For. 7 (2): 63—71 (1983). —— WELLS, O. O. and LAMBETH, C. C.: Loblolly pine provenance test in southern Arkansas — 25th year results. So. J. Appl. For. 7(2): 71—75 (1983). —— ZAR, J. H.: Biostatistical Analysis. Prentice-Hall, Inc., Engelwood Cliffs, NJ. 620p. (1974).

Short Note: Are Inferred Outcrossing Rates Affected by Germination Promptness?

By D. J. PERRY and P. KNOWLES

School of Forestry, Department of Biology,
Lakehead University, Thunder Bay, Ontario P7B 5E1,
Canada

(Received 7th November 1989)

Summary

Outcrossing rates ($\hat{t}_m$) were estimated from allozymes of eastern white cedar seeds, sampled according to germination promptness. The proportion of selfed seed, on which selection might act, was high, but differences in $\hat{t}_m$ among early, intermediate and late germinants were not statistically significant.

Key words: mating system, outcrossing rate, germination rate, *Thuja occidentalis* L.