Realized Gains from Block-Plot Coastal Douglas-Fir Trials in the Northern Oregon Cascades

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Abstract

Realized gains for coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) were evaluated using data collected from 15-year-old trees from five field trials planted in large block plots in the northern Oregon Cascades. Three populations with different genetic levels (elite – high predicted gain; intermediate – moderate predicted gain; and unimproved – wild seedlot) were compared at two planting spacings (1.8 x 1.8 m and 3.6 x 3.6 m).

The realized gains at age 15 averaged over both the elite and intermediate progeny were 17.2% for stand volume per hectare, 3.5% for mean height, and 4.3% for diameter, compared to predicted genetic gains of 16.0% for volume, 5.4% for height, and 6.4% for diameter. Realized and predicted gains correlated well at the family level, with an average correlation coefficient close to 0.80. The improved populations also had higher survival rate and lower stem sinuosity than the unimproved population. Strong genetic level x planting spacing interaction effects were revealed for the growth traits at age 15 using mixed model analyses. Realized gains for stand per-hectare volume and mean growth rate were at least twice as large in the elite population as in the intermediate population at the close spacing. By contrast, both populations performed similarly at the wide spacing. This indicates that the selected genetic materials responded differently to the changes of competitive environment, and realized gain trials should closely mimic operational plantations in order to provide valid estimates of realized gains. Realized gains in per-hectare volume varied greatly among test sites. No significant genetic level x site interactions were found for any traits.

Key words: Realized genetic gain, Douglas-fir, competition.

Introduction

Realized genetic gain delivered by a breeding program is vitally important to those who fund tree improvement and use its results. Realized genetic gains are usually determined by comparing the performance of genetically-improved materials with unimproved materials (ZOBEL and TALBERT, 1984). It is generally agreed that merely measuring progeny tests through to rotation is not adequate for providing reliable estimates of realized gain. Progeny trials contain highly heterogeneous genetic materials, and are usually established using small, non-contiguous plots (e.g., single-tree plots, row plots) in order to accommodate more families and replicates at a given cost, and estimate family means with higher statistical precision (LAMBETH *et al.,* 1983; VERGARA *et al.,* 2004). Small plots are not, however, an accurate representation of a forest stand once competition initiates the process of crown class development (FOSTER, 1992). Several studies indicated that inter-tree competition in progeny trials may have magnified among-family differences, resulting in overestimation of additive genetic variance and therefore expected genetic gains (NAMKOONG *et al.,* 1972; MAGNUSSEN, 1987; FOSTER, 1989; ST. CLAIR and ADAMS, 1991). With the concept of "ideotype" breeding introduced by DONALD (1968), selection on the basis of mean individual performance in small-block progeny trials after crown closure may favor the progeny with the attributes of competition ideotypes, which grow large in progeny mixtures at the expense of their neighbors. When these selected progeny are planted together in large block plots or deployed in plantations, greater competition on environmental resources (e.g., light, water and nutrients) may result in less growth per individual tree. As a result, genetic gains estimated in terms of stand volume per unit area on the basis of the information from progeny trials may be overestimated (DONALD and HAMBLIN, 1976; CANNELL, 1982).

Verifying realized genetic gain is arduous work because of the high cost of establishing and maintaining suitably designed trials and the long time required for reliable results. For example, enough plots are needed to pick up significant differences between treatments (ST. CLAIR *et al.,* 2004) and plots should be large enough to carry a sufficient number of trees through to rotation.

Realized genetic gain from first-generation tree improvement has been studied for several coniferous species. LAMBETH (2000) reported a 3.9% increase in site index and 27% reduction in sweep at age 6~7 for the 12 best open-pollinated families from a loblolly pine (*Pinus taeda* L.) seed orchard. In radiata pine (*Pinus radiata* D. Don), seedlots from open-pollinated seed orchards had average realized gains of 4.5% in height, 6% in diameter, and 15% in stem volume at ages 15–17; realized gains followed the expected order of elite crosses > open-pollinated orchard > seed production area > land-race (CARSON *et al.,* 1999). A study by VERGARA *et al.* (2004) comparing first-generation slash pine (*Pinus elliottii* var. *elliottii* Engelm.) selections and unimproved controls in 7–18 years old plantations at 19 sites showed 7.7% gains in individual tree volume and 10.2% gains in stand yield. LOPEZ-UPTON *et al.* (2000) found that fusiform rust infection on improved slash pine was

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36.8% compared to infection of unimproved slash pine of 50%, and that improved loblolly pine was 8% taller than unimproved for 3-year height growth under intensive silvicultural treatment.

Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) tree improvement programs in the Pacific Northwest began in the 1950s (SILEN and WHEAT, 1979), and large amounts of genetically improved seeds have been used for reforestation (ADAMS *et al.,* 1990; JAYAWICKRAMA *et al.,* 2009). In 1995, 7-year results were reported for a Douglas-fir trial established on five sites using 12 x 12 tree square plots at four planting densities in British Columbia (STOEHR and BIRD, 2003). Realized genetic gains were shown to be very close to predicted gains, with mid-gain families having more than 10% gain in height over wild stand controls, and top-crosses showing a gain of nearly 17%. In 1997, the Northwest Tree Improvement Cooperative (NWTIC) and the USFS Pacific Northwest Research Station (PNWRS) established a realized gain study along the west slopes of the northern Oregon Cascades with the purposes of serving as a feedback mechanism to improve the effectiveness of the tree improvement program, providing economic justification for the program, and assisting with the adjustment of growth models to account for genetic gains. Early results were promising and were published by ST. CLAIR *et al.* (2004). The realized genetic gains estimated at age 8 were about 6% for height, 8% for diameter, and 28% for stem volume, compared to predicted genetic gains of about 8% for height, 7% for diameter, and 25% for stem volume. The second measurement of the trials provided the data for the current publication.

This paper aims to: (1) quantify realized genetic gains for the growth of genetically improved seedlots compared to an unimproved mix of a wild seedlot, (2) compare realized gains with predicted gains derived from the progeny tests in the same breeding zone, and (3) evaluate the impact of planting spacing on realized gain.

Materials and Methods

Test materials and experimental designs

The tested materials and experimental designs are detailed in ST. CLAIR *et al.* (2004). Here we recapitulate the essential details of population sampling and trial establishment. Parents were selected from the first-generation Molalla breeding zone located in the north Oregon Cascades, southeast of Portland. They were backward selections chosen primarily on the basis of their age-15 volume scores in progeny tests after adjustments for site and design effects. Due to differences in statistical methodology, however, the volume scores did not always line up well with the breeding values predicted later using Best Linear Unbiased Prediction (BLUP). Twenty single-pair full-sib crosses were made between these selected parents, and were then classified into two improved populations with different genetic levels based on their mid-parent performance: *elite* (a mix of 10 single-pair crosses with a predicted age-15 individual-tree volume gain = 23%) and *intermediate* (a mix of 10 single-pair crosses with a predicted age-15 individual-tree predicted volume gain = 8%). The unimproved population consisted of progeny from 50 trees selected at random with respect to growth and form from naturally regenerated stands well distributed throughout the breeding zone.

The realized gain trials were established at five sites in 1997 using 3-year-old seedlings of the elite, intermediate, and woods-run (unimproved) populations. These sites are representative of environments for both breeding and deployment in this breeding zone (*Table 1*). In each of the six replicates at each site, the three genetic levels (i.e., elite, intermediate, and unimproved) were planted at each of two stand densities – low density (3.6 x 3.6 m spacing, 772 trees/ha) and high density (1.8 x 1.8 m spacing, 3,086 trees/ha) using a split-plot experimental design with planting density as the whole plot and genetic level as the subplot. One subplot from the Mill City site was excluded from the analyses due to high mortality attributed to the plot being established on an area severely impacted during logging. One hundred trees were initially planted in each subplot (a 10 x 10 tree square), along with one buffer row of the same genetic level planted around each subplot and around the outside of trials. An average of 10 seedlings from each full-sib family was randomly assigned to planting positions within each subplot (i.e., mixed-family deployment within each genetic level).

All trees excluding buffer trees were measured at ages 8 and 15 from seed (the second measurement at the Molalla site was actually made at age 13 instead of 15). Variables measured were height (both ages), dbh (both ages), number incidents of forking (later age only), number of incidents of ramicorn branching (later age only), and stem sinuosity score (later age only; except for the Molalla site). Stem volume index was calculated as

Table 1. – Site information for the five trials used in the analysis.

Trial	Latitude	Longitute	Elevation (m)	Second measurement[1]					
				age	# living tree	Survival (%)	HT (cm)	DBH (mm)	VOL (dm^3)
Mill City	44.7356°N	122.495°W	363	15	3123	89.3	948.4	120.6	153.39
Silver Falls	44.8737°N	122.490°W	762	15	3175	88.2	629.7	75.3	42.25
Molalla	45.0812°N	122.446°W	503	13	2889	80.3	522.1	63.9	27.55
Colton	45.2205°N	122.403°W	321	15	3192	88.6	869.1	110.5	122.15
Estacada	45.3438°N	122.180°W	518	15	3303	91.7	817.0	99.9	94.45

[1] HT, DBH, and VOL = mean height, diameter, and volume, respectively.

height x dbh^2. Taper was defined as the ratio of dbh to height.

Data analyses

For the purpose of comparing the two improved populations with the unimproved seedlot, individual tree information was summarized on a per unit area basis obtaining one record per subplot for the following traits: total stem volume per hectare at age 8 (VOL8) and 15 (VOL15), mean annual increment of volume per hectare between ages 8 and 15 (VOL_I), mean height at age 8 (HT8) and 15 (HT15), mean dbh at age 8 (DBH8) and 15 (DBH15), mean annual increments between ages 8 and 15 for height (HT_I) and dbh (DBH_I), mean taper at age 15 (TAPER15), mean number incidents of forking at age 15 (FORK15), mean number incidents of ramicorn branching at age 15 (RAMI15), mean sinuosity score at age 15 (SINU15), and survival at age 15 (SURV15). Total volume per hectare was calculated as the total volume in a subplot for all living trees and then expanded to a per-hectare basis. Thus, it incorporates both growth of individual trees and survival. A total of 179 subplots were used for the analyses. The following linear model was employed to conduct an analysis of variance for each trait using Restricted Maximum Likelihood (REML) approach in ASReml (GILMOUR *et al.,* 2006).

$$y_{ijkl} = \mu + S_i + R_{j(i)} + D_k + (SD)_{ik} + \delta_{ijk} + G_l + (SG)_{il} + (DG)_{kl} + (SDG)_{ikl} + \varepsilon_{ijkl} \quad (1)$$

where y_{ijkl} is subplot mean or volume/ha, μ is the grand mean, S_i is the fixed effect of the ith site, $R_{j(i)}$ is the random effect of the jth replicate within the ith site, D_k is the fixed effect of the kth stand density, G_l is the fixed effect of the lth genetic level, δ_{ijk} is the random whole-plot error, ε_{ijkl} is the random subplot error, $(SD)_{ik}$, $(SG)_{il}$, $(DG)_{kl}$, and $(SDG)_{ikl}$ are the fixed effects of interactions. Three contrasts were also tested for comparing the improved populations against the unimproved seedlot, as well as the differences between the elite and the intermediate populations at each stand density.

Similar analyses were conducted using family means in each subplot as the unit of observation for the purpose of comparing realized gains with predicted gains at the family mean level. The analyses were performed by expanding model (1) to include an additional fixed effect of full-sib family within genetic level as well as its two- and three-way interactions with site and stand density.

Each site was allowed to have its own unique error variance to improve the fit of the models. While some studies used the "sometimes-pooling" technique described by BOZIVICH *et al.* (1956) and BANCROFT (1968) to pool non-significant model terms into the subplot error, HARTER (1961) and CHEW (1958) doubted that one should always obtain the subplot error by pooling. For all the traits measured in this study, such pooling only slightly altered the *p*-values but did not change the interpretation of results. Thus, only the results from the full models were reported.

Least square means (*LSM*) for each genetic level and planting density were estimated across sites as well as for each site using the PREDICT statement in ASReml. Due to the non-estimable functions in cross-classified data with some missing cells, *LSM*s for these variables were estimated only over the cells containing data in the frequency table. Realized gains (*RG*) were determined by comparing the performance of improved with unimproved populations at both genetic population and family levels.

$$RG = (LSM_I - LSM_U) \times 100 / LSM_U \quad (2)$$

where LSM_I and LSM_U are least square means for improved and unimproved materials, respectively. Due to low incidences, realized gain was not calculated for the two branching traits (i.e., FORK15 and RAMI15).

For growth traits, predicted breeding value (*BV*) of each full-sib family had been previously calculated from mid-parental *BV*s in the Molalla open-pollinated progeny trials using individual-tree BLUP (YE and JAYAWICKRAMA, 2008). Predicted gains (*PG*) were expressed as *BV*s divided by the means of the testing population. Since all parents tested in the progeny trials were roadside selections chosen without emphasis on growth superiority, the population mean is expected to be close to the performance of unimproved materials. *PG* for each of the two genetic levels (i.e., elite and intermediate) was expressed as the mean *PG* of the full-sib families weighted by the number of trees per family. The comparisons between *RG* and *PG* were conducted at both population and family levels.

Results

Analyses of variance and contrast tests

P-values obtained from the across-site analyses of variance with heterogeneous error variances by site on a per subplot basis are listed in *Table 2*. Survival at age 15 differed significantly among sites, ranging from 80% to 92%. The elite and intermediate populations had a similar average survival rate (89%) which was higher than that of the unimproved population (84%). Such level of survival should be high enough for valid comparisons based on stand volume on a per unit area basis. Survival in the high-density plots was not significantly different from that in the low-density plots, implying that among-tree competition was not strong enough to cause density-dependent mortality at the close spacing by age 15. Among-site differences were pronounced for all traits studied. The Mill City site had the greatest average volume growth whereas the Silver Falls and Molalla sites had the lowest (*Table 1*).

Significant differences among the three genetic levels were found for all traits assessed, and were more pronounced for growth (*Table 2*). Contrast tests indicated that the differences between the improved and unimproved populations were highly significant ($P < 0.01$) for all growth traits except DBH8 and for stem sinuosity (SINU15). DBH8, TAPER15, and RAMI15 were significant at $P < 0.05$. Forking (FORK15) did not differ significantly between improved and unimproved ($P = 0.14$).

As expected, stand volume production was significantly greater in the high-density plots (*Tables 2* and *3*), mainly due to the difference in number of trees per

Table 2. – Observed significance associated with the analyses of variance based on a per subplot basis.

Source of variation	df	p-value														
		HT8[1]	*HT15*	*HT_I*	*DBH8*	*DBH15*	*DBH_I*	*VOL8*	*VOL15*	*VOL_I*	*TAPER15*	*FORK15*	*RAMI15*	*SINU15*	*SURV15*
Site (S)	4(3)[2]	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	0.010	<.001
Density (D)	1	<.001	0.134	0.918	0.140	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	0.418	0.756
S x D	4(3)	0.119	0.150	0.104	0.098	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	0.542	0.396
Genetic population (G)	2	<.001	<.001	<.001	0.050	<.001	0.011	0.01	<.001	<.001	0.036	0.015	0.024	0.005	<.001
S x G	8(6)	0.304	0.792	0.772	0.490	0.759	0.880	0.407	0.206	0.655	0.177	0.465	0.218	0.344	0.007
D x G	2	0.016	0.004	0.090	0.373	0.006	0.147	0.047	<.001	0.003	0.045	0.405	0.331	0.334	0.361
S x D x G	8(6)	0.155	0.375	0.662	0.271	0.142	0.353	0.402	0.382	0.606	0.170	0.785	0.362	0.968	0.025
Contr: Improved_vs_ck	1	<.001	<.001	<.001	0.044	<.001	0.003	0.01	<.001	<.001	0.027	0.144	0.042	0.008	<.001
Contr: E_vs_I_at_1.8	1	0.002	0.036	0.220	0.011	0.012	0.233	0.002	0.001	0.003	0.016	0.189	0.003	0.066	0.583
Contr: E_vs_I_at_3.6	1	0.820	0.691	0.751	0.512	0.505	0.366	0.949	0.750	0.802	0.572	0.002	0.415	0.533	0.912

[1] Traits: HT8, HT15 = mean height at ages 8 and 15, respectively; DBH8, DBH15 = mean diameter at ages 8 and 15, respectively; VOL8, VOL15 = volume/ha at ages 8 and 15, respectively; HT_I, DBH_I, VOL_I = mean annual growth increments between ages 8 and 15 for mean height, mean diameter, and volume/ha, respectively; TAPER15 = mean taper at age 15 expressed as DBH15/HT15; FORK15 = mean number incidents of forking at age 15; RAMI15 = mean number incidents of ramicorn branching at age 15; SINU15 = mean sinuosity score at age 15; SURV15 = survival rate at age 15.

[2] The numbers in parentheses are the degrees of freedom for SINU15 which was measured at 4 sites instead of 5.

[3] Contr: Improved_vs_ck = contrast test for the improved vs. unimproved populations; Contr: E_vs_I_at_1.8 = contrast test for the elite vs. the intermediate populations at 1.8 x 1.8 m spacing; Contr: E_vs_I_at_3.6 = contrast test for the elite vs. the intermediate populations at 3.6 x 3.6 m spacing.

hectare. Significant differences were also found between planting densities for most growth and branching traits. Trees at the close spacing were taller at both ages, but grew more slowly in diameter between ages 8 and 15 than trees at the wide spacing (*Table 3*). Compared to low-density plots, high-density plots had smaller mean taper (i.e., dbh/height ratio, 0.11 vs. 0.14), fewer incidents of forking (2 vs. 4 per 100 trees), and fewer incidents of ramicorn branching (9 vs. 15 per 100 trees). Stem sinuosity did not seem to be affected by stand density, at least at age 15 ($P = 0.42$). Interactions of genetic levels with planting densities were significant ($P < 0.05$ for VOL8 and $P \leq 0.01$ for VOL15, VOL_I, HT15, and DBH15). Trees from the elite population were significantly larger than trees from the intermediate population at the close spacing except for DBH_I. At the wide spacing, however, both the improved populations were similar in growth rates at both ages.

Table 3. – Means of traits and stand volumes on per subplot basis.

Density		1.8 × 1.8 m			3.6 × 3.6 m		
Genetic level		Elite	Intermediate	Unimproved	Elite	Intermediate	Unimproved
Subplot mean	HT8[1]	195.3	185.5	185.1	177.9	181.6	173.1
	HT15	782.9	763.4	745.6	739.6	756.6	722.4
	HT_I	88.9	87.5	84.6	84.7	87.0	83.3
	DBH8	14.6	13.6	13.7	13.1	13.3	12.5
	DBH15	87.5	83.4	81.5	100.6	105.3	98.0
	DBH_I	12.0	11.6	11.3	14.4	15.1	14.2
	VOL8	0.80	0.65	0.62	0.60	0.60	0.50
	VOL15	74.8	66.1	63.7	100.3	111.7	93.1
	VOL_I	11.8	10.9	10.3	16.2	17.9	15.3
	TAPER15	0.111	0.108	0.108	0.133	0.136	0.132
	FORK15	0.024	0.015	0.013	0.052	0.036	0.030
	RAMI15	0.123	0.083	0.094	0.166	0.171	0.134
	SINU15	0.117	0.074	0.152	0.143	0.120	0.155
	SURV15	87.9	89.5	83.9	87.3	88.9	84.2
Total per hectare	VOL8	2.08	1.67	1.54	0.35	0.39	0.28
	VOL15	204.52	185.33	168.22	67.58	77.98	59.61
	VOL_I	27.57	24.96	22.19	9.03	10.49	7.82

[1] Traits: HT8, DBH8, VOL8 = height (cm), dimater (mm), and volume (dm^3 for means, m^3 for totals/ha) at age 8, respectively; HT15 (cm), DBH15 (mm), VOL15 (dm^3 for means, m^3 for totals/ha), TAPER15, FORK15, RAMI15, SINU15 = height, diameter, volume, taper, forking, ramicorns, and sinuosity at age 15, respectively; HT_I (cm), DBH_I (mm), VOL_I (dm^3 for mean, m^3 for totals/ha) = mean annual growth increment between ages 8 and 15, respectively; SURV15 = survival rate at age 15.

The stability of performance across sites was demonstrated by the non-significant site x genetic population interaction for all traits. First-generation Douglas-fir breeding zones in the Pacific Northwest were geographically and climatically narrow (SILEN and WHEAT, 1979; HOWE *et al.,* 2006), and, thus, we did not expect to find interactions between families or genetic populations and test sites.

Realized gains

Realized gains, as percent deviation from the unimproved seedlot, varied between genetic populations and among traits (*Fig. 1*). The realized gains at age 15 averaged across all elite and intermediate families were 17.2% for stand volume per hectare (VOL15), 3.5% for height (HT15), and 4.3% for diameter (DBH15). Realized gains for the elite population were 22%, 4%, and 5% for VOL15, HT15, and DBH15, respectively. Realized gains for the intermediate population were 12% for VOL15 and 3% for both HT15 and DBH15. Similar patterns were observed for mean annual growth increments between ages 8 and 15. Both the elite and the intermediate populations showed substantial improvement in stem sinuosity, with 15% and 43% reduction in mean sinuosity score (SINU15), respectively.

Except for the Estacada site, realized gains for age-15 height and diameter did not change much across sites. However, realized gain for age-15 per-hectare volume varied greatly among test sites (*Table 4*). For the elite population, among-site differences were moderately correlated with differences in survival between the elite and the control populations (r = 0.6, results not shown). By contrast, the among-site differences in age-15 per-hectare volume were largely survival-independent (r = –0.05, results not shown) for the intermediate population, with the low productivity sites having the high-

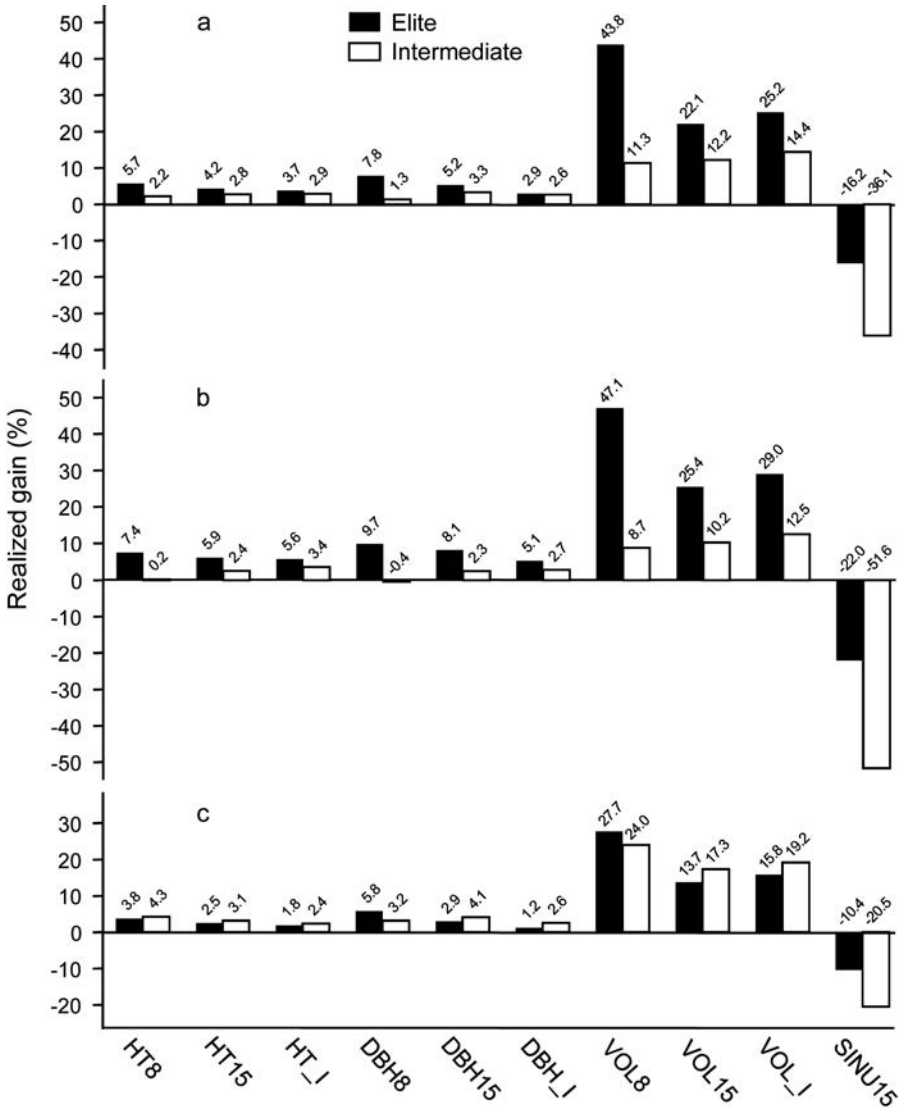

Figure 1. – Realized gains for volume/ha, mean height, mean diameter, and mean stem sinuosity. a – both densities, b – high planting density (1.8 x 1.8m), and c – low planting density (3.6 x 3.6m). HT8, DBH8, and VOL8 are mean height, mean diameter, and volume/ha at age 8; HT15, DBH15, VOL15, and SINU15 are mean height, mean diameter, volume/ha, and sinuosity score at age 15; HT_I, DBH_I, and VOL_I are mean annual growth increments from age 8 to age 15.

Table 4. – Realized gains for improved populations on per subplot basis by site as well as across sites.

Trait[1]		Colton			Estacada			Mill City			Molalla			Silver Falls			All sites	
		RG1[2]	RG2	CK	RG1	RG2	CK	RG1	RG2	CK	RG1	RG2	CK	RG1	RG2	CK	RG1	RG2
Subplot mean	HT8	7.8	6.1	194.1	1.3	-7.3	184.5	5.6	2.6	251.0	4.1	4.7	132.8	10.3	6.2	135.7	5.7	2.2
	HT15	5.7	4.1	842.1	2.7	-1.7	813.4	3.1	3.0	928.4	5.9	5.6	500.7	4.6	4.2	613.3	4.2	2.8
	HT_I	5.3	3.4	93.1	2.7	-0.2	90.1	2.3	3.2	96.8	6.0	5.6	74.9	2.3	3.0	68.9	3.7	2.9
	DBH8	11.2	8.4	14.7	4.5	-8.1	14.1	10.6	1.9	20.5	3.7	3.4	9.0	4.9	1.1	8.1	7.8	1.3
	DBH15	5.2	5.2	107.0	4.7	-1.7	98.9	5.8	4.2	116.2	6.2	5.5	61.1	4.2	4.1	73.4	5.2	3.3
	DBH_I	4.0	3.8	13.6	2.4	1.7	13.1	5.0	4.6	13.9	3.3	2.3	13.7	-0.8	0.3	11.0	2.9	2.6
	TAPER15	0.4	1.4	0.12	2.3	-0.2	0.12	3.0	1.2	0.12	1.8	1.6	0.12	-0.1	-0.3	0.12	1.5	0.7
	SINU15	-32.5	-34.2	0.25	-6.6	-25.5	0.14	35.3	-41.7	0.11				-40.2	-47.9	0.11	-16.2	-36.1
Total per hectare	VOL8	56.8	21.2	0.96	21.8	-23.5	0.89	41.7	15.2	2.52	48.5	60.9	0.14	145.7	51.7	0.12	43.8	11.3
	VOL15	21.5 (90%)	14.1 (90%)	154.7 (86%)	16.5 (94%)	2.1 (93%)	140.0 (88%)	19.9 (85%)	13.0 (92%)	200.8 (89%)	27.0 (80%)	23.1 (80%)	34.4 (81%)	42.6 (93%)	22.4 (91%)	56.7 (81%)	22.1 (88%)	12.2 (89%)
	VOL_I	21.1	15.3	21.7	17.3	-1.2	18.5	22.6	17.2	27.2	30.4	30.1	4.8	79.4	37.0	5.2	25.2	14.4

[1] Traits: HT8, DBH8, VOL8 = height, dimater, and volume at age 8, respectively; HT15, DBH15, VOL15, TAPER15, SINU15 = height, diameter, volume, taper, and sinuosity at age 15, respectively; HT_I, DBH_I, VOL_I = annual growth increment between ages 8 and 15, respectively.

[2] RG1 – realized gains (%) for the elite population, RG2 – realized gains (%) for the intermediate population, CK – least square means for the unimproved population (HT8, HT15, HT_I: cm; DBH8, DBH15, DBH_I: mm; VOL8, VOL15, VOL_I: dm^3 for means, m^3 for totals/ha). Numbers in parentheses are survival rates.

est stand volume gains. The improved materials exhibited superior growth performance at all sites except for the Estacada site where the intermediate population was either close to or worse than the unimproved seedlot.

While overall the elite population had consistently higher gains than the intermediate population in growth, the two levels of planting density exhibited distinct patterns of realized gain. The differences between the elite and the intermediate were pronounced at the 1.8 x 1.8 m spacing but diminished at the 3.6 x 3.6 m spacing (*Fig. 2*). For example, the elite population had 2.5 times the realized gain of the intermediate population in VOL15 in the high-density plots (25% vs. 10%). This difference, however, was reversed in the low-density plots: the intermediate population even had a slightly better age-15 growth performance than the elite, although the differences were not statistically significant.

Realized gains differed between the two assessment ages (*Fig. 1*). The percent gains for the elite population decreased from 44%, 6%, and 8% at age 8 to 22%, 4%, and 5% at age 15 for per-hectare volume, mean height and mean diameter, respectively. For the intermediate population, however, both ages yielded fairly similar gain levels.

When tree growth was dissected into two growth periods, i.e., ages 1~8 and 8~15, the two improved populations seemed to have different growth rates between the two growth periods. At the wide spacing, the elite families had faster diameter growth than the intermediate families in the early period, but an inverse pattern was observed in the later period (*Fig. 1*). For example, the elite population had 2.6% more gains than the intermediate population at ages 1~8, but had 1.8% less gains than the intermediate at ages 8~15. The two improved populations did not differ much in height growth at both periods. At the close spacing, the elite population consistently grew faster than the intermediate population at both growth periods. Compared to the growth at ages 1~8, the differences between the elite and the intermediate populations became much smaller at ages 8~15. The difference in height was 7% at ages 1~8, but was 2% at ages 8~15. Similarly, differences in diameter decreased from 10% at ages 1~8 to < 2% at ages 8~15.

Comparisons of realized gains with predicted gains from BLUP

Comparisons between realized gains (*RG*) and predicted gains (*PG*) for age-15 growth traits at population level are given in *Fig. 2*. Averaged across the two genetically improved populations, a *RG* of 17.2% for stand per-hectare volume at age 15 was obtained, which is very close to the average *PG* of age-15 volume (16.0%) based on individual-tree BLUP from the Molalla progeny tests. *RG*s from the plots with 1.8 x 1.8 m spacing were slightly larger than from the plots with 3.6 x 3.6 m spacing. When comparisons were conducted separately for the two genetic populations, *PG* matched *RG* well for the elite population (23.7% vs. 22.1%) but was lower than *RG* for the intermediate population (8.3% vs. 12.2%). In each population, *PG* of volume was more similar to *RG* of stand yield from the close-spaced plots than from the wide-spaced plots. Similar patterns were observed for mean height and diameter growth at age 15. Compared to *PG*s of 5.4% for height and 6.3% for diameter over both populations, the average *RG*s were 3.5% for height and 4.3% for diameter at age 15. *PG*s were a bit larger than *RG*s for the elite population but similar to *RG*s for the intermediate population.

The relationships between *RG*s and *PG*s for family mean growth at age 15 are shown in *Fig. 3*. It is evident that the degrees of closeness of the linear relationship between the two types of gains were high (r = 0.82~0.88) at the 1.8 x 1.8 m spacing and moderate (r = 0.56~0.58) at 3.6 x 3.6 m spacing, with an average correlation coefficient r = 0.77. When the relationship was regressed for each trait, none of the regression coefficients were sta-

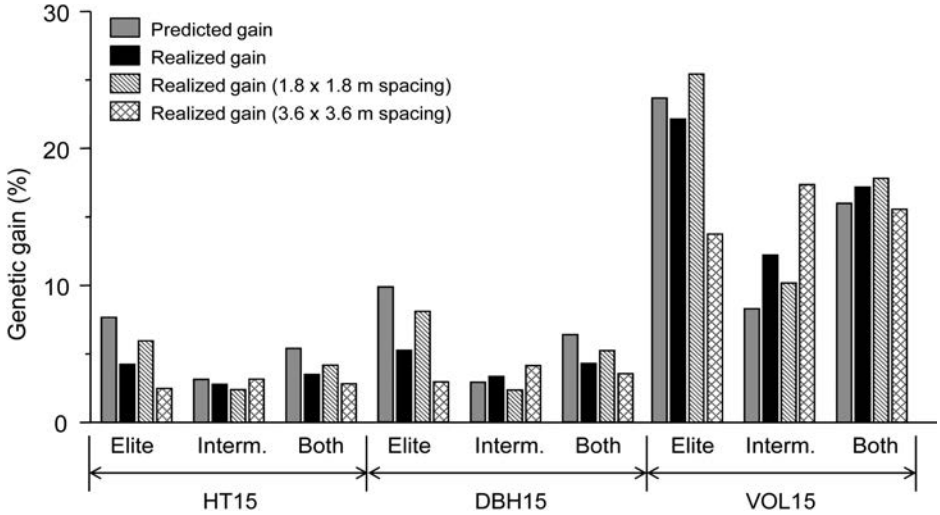

Figure 2. – Comparisons between realized gains and predicted genetic gains for age-15 growth traits at genetic population level. HT15, DBH15, and VOL15 are mean height, mean diameter, and volume/ha at age 15, respectively.

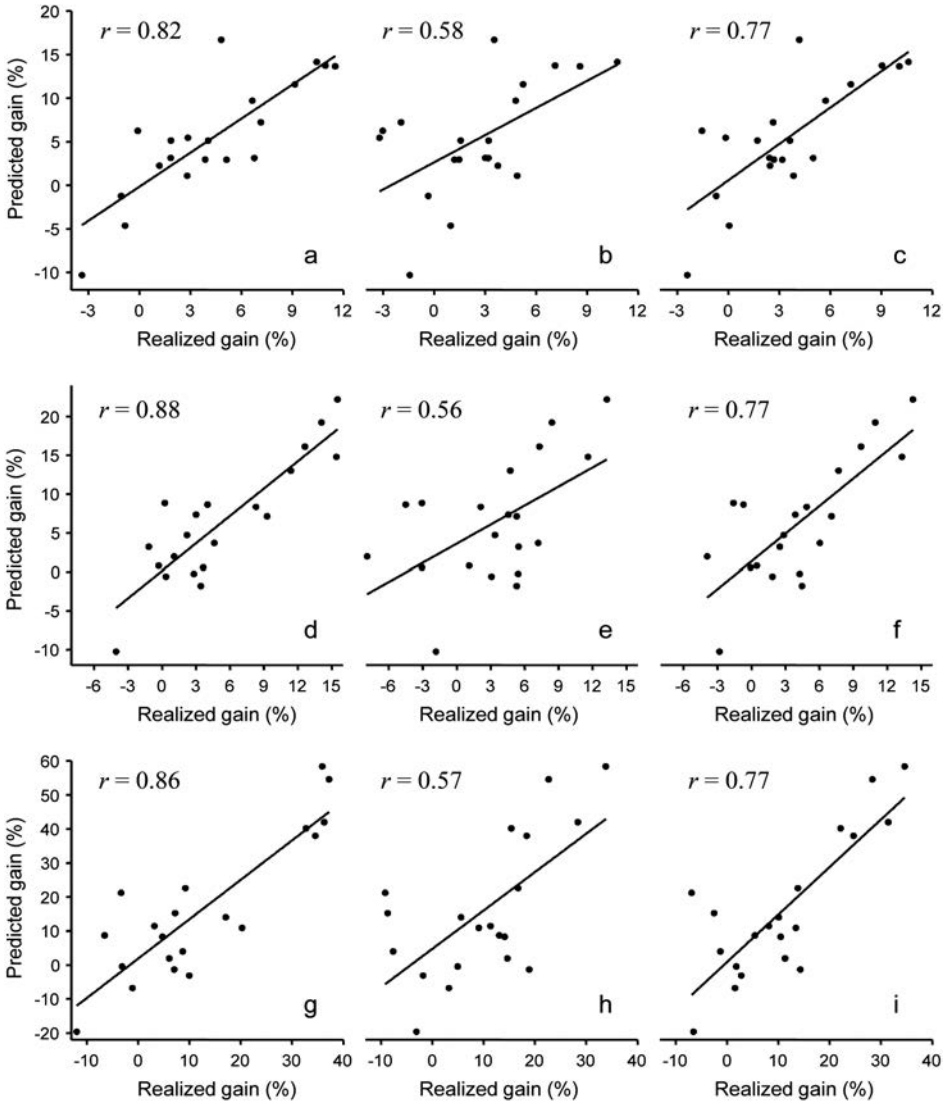

Figure 3. – Relationship between realized gains and predicted genetic gains for age-15 growth traits at family mean level. a ~ c = HT15; d ~ f = DBH15; g ~ i = VOL15; a, d, g = high planting density (1.8 x 1.8 m); b, e, h = low planting density (3.6 x 3.6m); and c, f, i = both densities.

tistically significant from 1 (results not shown). This suggests that *PG*s obtained from the progeny trials using BLUP gave unbiased predictions of *RG*s from the gain trials.

Discussions

Realized gains confirmed in this study were evident in growth rate; however, they were not as large as those reported by STOEHR and BIRD (2003) for age-7 height (10% for mid-gain families and 17% for top-crosses). It should be noted that the realized gains obtained in this study are by no means the upper limit that may be obtained for coastal Douglas-fir in the Molalla breeding zone. While the age-15 predicted individual-volume gain of the elite population was 23.7%, the average predicted gain of the top 20 parents within the Molalla breeding zone was much higher at 56.5%. The difference between these two figures can be attributed to: (1) criteria and analyses used in selecting parents at the time of crossing different from those used more recently based on BLUP results, (2) unavailability of certain parents in the clone bank, and (3) inability to produce adequate amounts of seed and seedlings from certain desired crosses.

Forest geneticists and tree breeders know that genetic effects on tree growth are strong, yet little is known regarding the effects of competition among genetically selected materials on stand productivity. The effects of competition are dependent on both the genetic composition (i.e., inter-genotypic competition) and the proximity of neighbors (i.e., density competition) (SAKAI, 1961; ST. CLAIR and ADAMS, 1991). In the Pacific Northwest, superior trees were selected from progeny trials at age 15, a typical age for final selection in the first-generation coastal Douglas-fir breeding programs (SILEN and WHEAT, 1979). At this age, the canopy has already closed for several years and competition may have caused trees to modify their growth behavior. Many of the progeny that were classified as elite in this study might be those who could rapidly exploit environmental resources such as light, water, and nutrients at the expense of neighboring progeny. Thus, a large proportion of the elite selections are likely to have high competitive ability as well as density tolerance, and are better fit into the category of competition ideotype (DONALD and HAMBLIN, 1976; CANNELL, 1978; WHITE *et al.,* 2007). By contrast, the intermediate selections were genetically more heterogeneous, with overall predicted gains much smaller than the elite selections. They might have been suppressed by the elite families to some extent in progeny trials, despite some of them may possess high genetic potential and could grow well in the absence of competition such as in wide-spaced or open-grown conditions. Whether the differences between the elites and the intermediates are due to true genetic differences including competitive ability, or whether it merely reflects differing degrees of suppression, cannot be resolved from the evidence solely provided by the progeny trials at the age of selection.

The stand density in the present study was as high as 1.8 x 1.8 m, much higher than in operational plantations (typically 3.0 x 3.0 m for Douglas-fir in the Pacific Northwest). The effect of planting density on ranking of genetic levels seems to be of little practical importance for the 8-year diameter and volume growth. This agrees with the findings reported by ST. CLAIR *et al.* (2004) as well as other published studies on family ranking by spacing level at young ages (e.g., CAMPBELL *et al.,* 1986; ST. CLAIR and ADAMS, 1991). However, we found that there were highly significant rank changes among different genetic levels at age 15. For example, realized gains for per-hectare volume and mean individual-tree growth in height and diameter were at least twice as large in the elite population as that in the intermediate population at the 1.8 x 1.8 m spacing. By contrast, the intermediate population performed even slightly better than the elite one at the 3.6 x 3.6 m spacing, although they were statistically not different from each other.

The main reason for the elite population not outperforming the intermediate population at low stand density may be due to their different responses to changes in competitive environments. Many authors have been aware of the change in selection efficiency and progeny ranking if the competitive environment in which progeny are tested and selected is not the same as the environment in which the selected progeny are to be grown (e.g., CANNELL, 1982; ST. CLAIR and ADAMS, 1991). Compared to the progeny trials that were established at 3.0 x 3.0 m spacing, trees in the realized gain trials planted at the 1.8 x 1.8 m spacing encountered an even higher density competition. Also due to mixed-family deployment, the overall competitive environment at the tight spacing may have been similar to that of the progeny trials. Thus, the elite population exhibited its growth superiority in the realized gain trials at the spacing and competitive environment that was more like that of the progeny trials. By contrast, crown closure had not yet occurred in the plots established at 3.6 x 3.6 m spacing at age 15, and a low level of among-tree competition was therefore expected. The growth ranking of trees at the wide spacing depended primarily on their relative abilities to grow in open-grown conditions and partially on their abilities to compete with neighboring trees and/or brushes. The lack of statistical difference between the elite and the intermediate populations at the wide spacing might suggest that the difference between the two improved populations were mainly contributed by their different competitive abilities under the environment with limited resources. Whether the elite population will eventually prevail against the intermediate population in the widely-spaced plots after crown closure is of great interest.

The results from the present study indicate that the elite and the intermediate populations might differ in their relative diameter growth rate at ages 1~8 and 8~15. At the wide spacing, the elite families on average grew faster than the intermediate families in diameter and volume at ages 1~8, but the pattern was reversed at ages 8~15. The differences were not statistically significant, probably due to the lack of statistical power caused by the limited number of replicates (ST. CLAIR *et al.,* 2004) as well as the large within-subplot environmental variation at the wide spacing plots. Despite the lack of

statistical significance, such differences may still have practical meaning. While genetic analysis of growth curves has received limited attention in general, several studies have showed that growth curves are under moderate genetic control (e.g., MAGNUSSEN and KREMER, 1993; GWAZE *et al.,* 2002). It is feasible that growth curves shift in response to selection (BARBATO, 1991; GWAZE *et al.,* 2002). In progeny trials, progeny growing fast during the early stage (e.g., the elite progeny) would have their advantages in terms of competitive ability: they are the ones that became established quickly, probably expanded photosynthetic and root surfaces rapidly, and thereby made greatest possible claims on environmental resources such as light, water and nutrients. These abilities would be valuable in operational plantations as well.

Competition likely hampers the efficiency of selection in tree breeding programs if the competitive environments differ between the progeny trials and the operational plantations. It is, therefore, our concern as to how to include and gauge competition effect in operational breeding programs. While some authors recommended postponement of selection until the middle of the mature phase (e.g., FRANKLIN, 1979), it is not feasible for the coniferous species with long rotation lengths (~ 60 years) such as Douglas-fir. In a loblolly pine realized gain trial, ADAMS *et al.* (2008) showed that correlation of average stand volume between ages 9 and 17 increased from 0.50 to 0.70 as planting density went from the 3.0 x 3.0 m to the 1.5 x 1.5 m spacing. This highlights the possibility to establish progeny trials at a closer spacing to stimulate competition so that the competitive ability can be observed and gauged at early ages. Another example was demonstrated by HART (1986) and NANCE *et al.* (1983) which both deployed the same set of families. Among-family differences were not detectible in HART's (1986) experiment at a 2.4 x 2.4 m spacing but were found in NANCE *et al.* (1983) with 1.83 x 1.83 m spacing.

This study found that the gains predicted from progeny trials were similar to the realized gains estimated from the close-spaced plots where crown closure had occurred. The result disagrees with what was reported in several other studies. For example, ST. CLAIR and ADAMS (1991) found that the competitive environment in which Douglas-fir seedlings were grown had a large effect on family variance which in turn led to larger estimates of heritability and predicted genetic gains. Thus, when trees were selected in competitive environments but deployed in pure family blocks, their genetic gains were likely to have been over-predicted. Similar results were reported by WILLIAMS *et al.* (1983) and HART (1986) in progeny tests of loblolly pine. FOSTER (1989) found large differences in variance component estimates between large block plots, row plots, and non-contiguous plots. Although the inter-family heterogeneity in each subplot was expected to be smaller than in the progeny trials, it is by no mean to be close to that in pure clonal deployment. Strong inter-genotypic competition may exist within subplots due to large within-family variation. According to WOODS *et al.* (2001), within-family variation was about 4~5 times larger than among-family variation for both height and diameter in a Douglas-fir nursery test. Thus, the competitive environment at the close spacing could still be similar to that in the progeny trials. The differences in realized gains between the close- and wide-spaced plots in this study highlight the fact that the realized gain trials should closely mimic the operational plantations in order to provide valid estimates of realized gains.

Users of the Douglas-fir tree improvement program are generally more interested in increasing total bole volume production per unit area at rotation, rather than growing a small number of large trees and many small trees on the same area. In the present study, the predicted gain based on individual-tree volume from progeny trials matched the overall realized gain for volume per hectare very well in realized gain trials at age 15. This is encouraging and somewhat surprising. Stand volume per hectare is not only related to the individual-tree volume but is also closely related to survival as well as other factors such as stand diameter distribution, stand density, age, and site index, etc. (CLUTTER *et al.,* 1983). Despite significant differences in survival between the improved and unimproved populations in this study, the elite and intermediate populations had almost the same survival rate at age 15, indicating that competitive ability within the genetically improved populations at this age could be expressed largely through suppression in growth instead of mortality.

Realized gains based on subplot family means obtained in the present study correlated well with their corresponding predicted gains from Molalla progeny trials, despite that a different set of sites was used in the gain trials and the progeny trials. This indicates that the family ranking was relatively stable between the progeny trials and the realized gain trials. Family gains predicted from the progeny trials were slightly overestimated in general when compared to the realized gains from the gain trials (especially for the widely-spaced plots), although the overall differences were statistically insignificant. These results are in accordance with FOSTER's (1989) summary where he concluded on the basis of published results that among-family performance was relatively stable across a range of inter-family competition, yet genetic gain estimates would be inflated in small-plot trials due to the confounding of genetic variance and competition variance.

It is of great concern to tree breeders, growth modelers and users of genetically improved stock whether or not the genetic superiority obtained from breeding will diminish with time. Several authors have found or implied that growth-rate increase from genetic selection might decrease or disappear with the increase of competition toward rotation, although very little information is available for older Douglas-fir. FRANKLIN (1979) reported sharp decreases in additive variance from ages 20 to 25 and in heritability from ages 40 to 53 in Douglas-fir, based on the data from NAMKOONG *et al.* (1972). HAMILTON JR. and REHFELDT (1994) hypothesized a potential outcome of using genetically improved stocks: increased individual tree growth rates may lead to excessive stand density which in turn results in a decrease in stand volume increment later in a rotation.

Our results provide no evidence to parallel this assumption, although the trees were still young. The annual growth increments for per-hectare volume, mean height and diameter from ages 8 to 15 were very close to the overall age-15 growth rate.

Unlike stem sinuosity which has been greatly improved through genetic selection, little difference was found for incidence of forking and ramicorn branching between the improved and unimproved seedlots. Two possible reasons are: (1) these traits were not scored in the first-generation progeny test and, therefore, were not part of the selection criteria for parents for crossing, and (2) both traits at the juvenile stage usually show very low heritabilities and are affected by silvicultural factors such as planting density and soil fertility. According to the Northwest Tree Improvement Cooperative technical reports (unpublished data), the average heritability estimates at ages 7~13 were only 0.02 for forking and 0.04 for ramicorns across six progeny testing programs. Despite the importance to the quality of wood products, their incidence rates were fairly low.

Conclusions

The genetically selected Douglas-fir populations (i.e., elite and intermediate) had significantly higher volume per hectare and greater mean height and diameter than the unimproved population in these large-block realized gain trials. Realized gains matched the predicted gains from progeny tests in general. However, strong genetic level x planting spacing interaction suggested that the two selected populations responded differently to changes of stand density, and that realized gain trials should have similar competitive environment to operational plantations in order to provide valid estimates of realized-gain.

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