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Performance of full-sib families of Douglas-fir in pure-family and mixed-family deployments

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ABSTRACT

A major objective of tree improvement programs is to identify genotypes that will perform well in operational deployments. Relatively little is known, however, about how the competitive environment affects performance in different types of deployments. We tested whether the genetic composition and density of deployments affect the performance of full-sib families of Douglas-fir (*Pseudotsuga meniziesii*), and whether traits related to crown morphology could help to explain differences in family performance under competition. Seedlings from eight families were planted in pure-family and three mixed-family composition treatments at high, medium, and low densities (11,954, 2988, and 747 trees·ha^{-1}, respectively). Height (*HT*), diameter at breast height (*DBH*), and volume·ha^{-1} (*VOLHA*) were measured at ages 8 and 15 years. Significant differences were found among composition treatments in all traits other than *VOLHA8* and significant interactions between composition and density treatments were found for all traits at age 15 years. Family ranks for *DBH15* and *VOLHA15* in pure-family treatments changed considerably among densities, but ranks were more stable for *HT15*. The performance of two mixed-family treatments differed significantly from the average performances of the same families in pure-family treatments for several traits. Differences in *DBH15* among families in high-density, pure-family treatments could be explained in part by differences in crown morphology, with better performance among families with relatively narrow crowns, stout branches, and high leaf area relative to branch length. Our results suggest that the competitive environment has a considerable effect on family performance, and that incorporating crown morphology traits into selection criteria in tree improvement programs

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1. Introduction

A major objective of tree breeding programs is to identify genotypes that will perform well in the environments in which they will ultimately be deployed (Zobel and Talbert, 1984). Progeny test sites are selected to capture the range of deployment environments with regard to climate, physiography, and soils. It is more difficult to create competitive environments within progeny tests that closely match those found in operational plantings. Furthermore, it is unclear in most tests how the competitive environment affects the rankings of different genotypes. The competitive environment is defined here as the set of interactions that occur among individual trees as they compete for resources such as light, water, and nutrients, and is hypothesized to be affected by both the proximity and genotypes of neighbors. Progeny tests are often designed to efficiently identify superior parents for a given, relatively homogenous, range of abiotic environments within a breeding zone, and less attention has been paid to the competitive environment. Single-tree plots (i.e., families dispersed within test units) are an efficient layout for testing a large number of families. This design has been widely used for coastal Douglas-fir (*Pseudotusga menziesii* var. *menziesii*) and other species (Silen and Wheat, 1979). Predicted breeding values from these tests are often the only information available for estimating the performance of improved genetic material when it is deployed in operational plantings; however, there are numerous examples that demonstrate that performance in the deployment environment depends on aspects of the competitive environment such as stand density and genetic mixture (DeBell and Harrington, 1997; Staudhammer et al., 2009; Ye et al., 2010). A few block-plot trials that better replicate the competitive environment in operational plantings have been established for Douglas-fir to evaluate realized genetic gains, but results from these trials are only now becoming available (e.g., Stoehr et al., 2010; Ye et al., 2010).

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Stand density, which is often defined in terms of tree size and number per unit area (Curtis, 1970), has well-documented effects on tree phenotype that have implications for the selection of superior genotypes (Oliver and Larson, 1996). Once competition begins, increasing stand density reduces the growth of individual trees, skews the distribution of tree sizes, and induces mortality (Ford, 1975). Differences in competitive ability are often amplified after the onset of competition owing to asymmetric competition (Weiner and Solbrig, 1984). The relative competitive abilities of neighboring trees differs between progeny tests, where a wide range of genotypes are present, and the deployment environment, where the range is more restricted owing to genetic selection. Genetic gains predicted from progeny tests may not be realized in the deployment environment if the performance of selected genotypes depends in part on their ability to usurp resources from less competitive neighbors (Magnussen, 1989). Stand density may also have more subtle effects on genetic performance. For example, high initial stand densities can stimulate above-ground growth prior to crown closure, possibly owing to a change in light quality that signals imminent competition (Ritchie, 1997) or to a change in microenvironment (Woodruff et al., 2002). In general, greater realized gains have been reported at higher densities than at lower densities, particularly for height prior to crown closure (Roth et al., 2007; Adams et al., 2008; Ye et al., 2010).

Genetic mixture contributes to the competitive environment through obvious differences in growth rates, but also likely through differences in other traits such as crown architecture (Poykko and Pulkkinen, 1990; St. Clair, 1994a). An important approach to testing genetic mixture is to compare single-family or single-clone deployments with multi-family or multi-clone deployments. DeBell and Harrington (1997) found that pure deployments of clonal *Populus* had slightly greater biomass yields and less variation in tree size than the same clones planted in mixtures. Williams et al. (1983) reported greater height and volume in pure deployments of 16 families of loblolly pine (*Pinus taeda*) at the time of crown closure than in mixed plots. In contrast, von Euler et al. (1992) found that two-family mixed deployments of maritime pine (*Pinus pinaster*) had greater heights and diameters at some densities than pure plots while differences were not significant at other densities. St. Clair and Adams (1991) found that, on average, half-sib families of Douglas-fir seedlings grown for two years at a high density had greater heights, diameters, and volumes in mixed than in pure deployments.

The performance of individual families is sometimes of greater importance than general differences between pure and mixed deployments. Staudhammer et al. (2009) reported that some families of loblolly and slash pine (*Pinus eliottii*) performed better in mixed and others in pure deployments in terms of diameter, basal area·ha^{-1} and volume·ha^{-1}. Foster et al. (1998) found that some combinations of eastern cottonwood clones (*Populus deltoides*) had greater volume yields in pure deployments than in mixed plots while others did not. The likelihood of a substantial positive or negative difference tended to be greater when the clones differed in their pure-plot growth. Adams et al. (1973) found that specific mixtures affected intergenotypic competition in full-sib loblolly pine seedlings planted at a high density with some genotypes having positive or negative effects with a particular competitor and others with no effect.

The reaction of particular families to competition is a possible reason that a wide range of results have been found in mixture studies. The selection of parents in breeding programs is based on a set of measurable traits, but it is often unclear why some families differ in growth rate or other traits and under which conditions the gain can be expected. Most Douglas-fir progeny tests were established at densities similar to operational plantings (around 1100 trees·ha^{-1}) and selections are made before or shortly after crown closure. Different growth strategies such as the 'isolation' and 'competitor' ideotypes (Cannell, 1982) can result in superior phenotypes when competition is low, but not necessarily when competition is high. Forest managers are ultimately interested in volume gain per unit area, which may favor the 'crop' ideotype. The crop ideotype may not have superior growth prior to crown closure, but it performs well in high-density stands when grown with like phenotypes. Traits such as crown width relative to tree diameter may be useful for identifying ideotypes in the test environment that will perform well in the deployment environment even when the competitive environments differ (Martin et al., 2001).

The effects of stand density and deployment method on family performance remain poorly understood and there is little information available for Douglas-fir in large block-plot plantings. The Douglas-fir family-deployment trial was established in 1997 with 3-year-old seedlings to test the effects of density and genetic mixture on growth, yield, and stand dynamics. Eight full-sib families were planted in pure-family and mixed-family deployments at three densities to test the following null hypotheses:

H1: Performance does not differ among full-sib families.
H2: Family performance does not differ among densities.
H3: Family performance is not affected by the genotype of neighbors.
H4: Family performance, particularly under high competition, is not related to other morphological trait.

Results through age 15 years are reported in this paper.

2. Methods

The study was established near Mill City, Oregon (44.7°N, 122.5°W, 360 m AMSL) using 3-year-old containerized seedlings from eight full-sib families and a wild-collected woods-run control. The families were from single-pair crosses of parents selected from the Molalla breeding zone of the Northwest Tree Improvement Cooperative (Jayawickrama, 2005). Parental breeding values for diameter at breast height (*DBH*), total tree height (*HT*), and individual-tree volume were predicted from results from nine progeny test sites at age 15 years using the best-linear unbiased prediction approach (White and Hodge, 1989). Parents were selected to create a range of predicted genetic gains (10–35%) in 15-year volume based on the midpoints of the parental breeding values.

The study was installed as a two-factor, split-plot design with three whole-plot density treatments (11,954, 2988, and 747 trees·ha^{-1}; referred to as high, medium, and low) and 12 split-plot treatments that differed in their genetic compositions. Trees were planted in split-plots of 8 × 10 trees with one row of buffers around the low- and medium-density treatments and three rows of buffers around the high-density treatments. Composition treatments included eight pure-family treatments and three mixed-family treatments (*M1*, *M2*, and *M3*). *M1* and *M3* included the four families with the highest and lowest predicted volume gains (Families 1, 2, 3, and 4 and Families 5, 6, 7, and 8, respectively) and *M2* included two families with high predicted gain and two with moderate predicted gain (Families 1, 2, 5, and 6). Trees were arranged in the mixed-family treatments to maximize interactions among families (i.e., minimize the number of neighbors from the same family). All treatment combinations were replicated four times in a block arrangement. Excluding the buffer trees around the whole plots, a total of 11,520 trees were planted for the study (80 trees/split-plot × 3 density treatments × 12 composition treatments × 4 replicates).

HT, *DBH*, and survival were measured on all trees at ages 8 and 15 years. Crown width (*CW*) was measured at age 15 years in the low-density treatment. Individual-tree volumes were calculated from *DBH* and *HT* using the equation of Omule et al. (1987) for small Douglas-fir. Plot means were calculated for *HT* and *DBH* at ages 8 and 15 years, and individual-tree volumes of surviving trees were summed with appropriate expansion factors to calculate volumes per hectare (*VOLHA*); thus, mortality effects were included in the calculation of *VOLHA*. Family-within-plot means and volumes were calculated for the mixed-family treatments. All values were calculated using the interior 48 trees in each plot (i.e., trees on the edges of the plots were not used in the calculations).

Traits related to crown morphology were measured at age 12 years on a subsample of trees in the low-density, pure-family treatments. A single branch was selected at random and removed from the sixth and seventh whorls (counting from the top of the tree) from two randomly selected trees in each replicate ($n = 16$ branches/family). Branch length and branch diameter at the base were measured. A sample of 100 needles was removed from each branch to estimate specific leaf area, and the remaining needles were removed and weighed. Needle mass and specific leaf area were multiplied to estimate branch leaf area.

H1, *H2*, and *H3* were tested using analysis of variance (Neter et al., 1996) using two linear models. Model 1 was used to test for differences in *DBH*, *HT*, and *VOLHA* at age 8 and 15 years among composition and density treatments:

$$Y_{hij} = \mu + G_h + D_i + G_h \cdot D_i + R_j + D \cdot R_{i(j)} + \varepsilon_{hij} \qquad \text{(Model 1)}$$

where y_{hij} is the mean of composition h in density i and replicate j, μ is the grand mean, G_h is the fixed effect of composition, D_i is the fixed effect of density, $G_h{\cdot}D_i$ is an interaction, R_j is the random effect of replicate, and $D{\cdot}R_{i(j)}$ is the random effect of the whole plot within replicate, and ε_{hij} is the split-plot error. Model 1 was fit using data from the pure-family treatments only to test for differences among the individual families. It was fit again using data from all composition treatments to test for differences among all treatments and to estimate linear contrasts between pure- and mixed-family treatments.

Model 2 was used to test for differences in the same response variables between pure- and mixed-family treatments:

$$Y_{hijk} = \mu + F_h + D_i + M_k + F_h \cdot D_i + F_h \cdot M_k + D_i \cdot M_k + F_h \cdot D_i \cdot M_k + R_j + D \cdot R_{i(j)} + \varepsilon_{hij} \qquad \text{(Model 2)}$$

The terms in Model 2 are similar to Model 1, except y_{hijk} is the family mean either in the mixed- or pure-family treatment, F_h is the fixed-effect of family, M_k is the mixture indicator variable and $F_h{\cdot}D_i{\cdot}M_k$ is the three-way interaction among family, density, and mixture. Data from each of the three mixed-family treatments were analyzed separately as each contained a different set of families.

The null hypothesis for *H1* was rejected for each trait when the main effect of genetic composition (*G*) in the fit of Model 1 for pure-family treatments was statistically significant. For traits where *G* was significant, differences among families were examined more closely by calculating linear contrasts to determine which families differed significantly from one another. The null hypothesis for *H2* was rejected for each trait when the interaction between composition and density (*G·D*) in Model 1 was statistically significant. Linear contrasts were calculated to test for differences among pure-family treatments within each density when *G·D* was statistically significant. The null hypothesis for *H3* was rejected for each trait when the main effect of mixture (*M*) in Model 2 or any of its interactions were statistically significant. Linear contrasts of Model 1 using all composition treatments were also calculated to test whether each mixed-family treatment differed from the average performance of the same set of families in pure-family treatments. The null hypothesis for *H3* would be rejected if the performance of the mixed-family treatments differed significantly from average performance of the same set of families in the pure-family treatments. Models were fit using the nlme package (Pinheiro et al., 2006) in R (R Development Core Team, 2006) using the restricted-maximum likelihood method. Statistical significance was assessed at $\alpha = 0.05$. Family means and linear contrasts among families are reported only for traits measured at age 15 years for the sake of brevity and because competitive effects had more time to manifest themselves. Family-wise error rates for the linear contrasts were controlled using the method of Holm (1979). Rank correlations were calculated using Spearman's correlation coefficient (Ott, 1993).

The effects of neighboring genotypes on family performances that were hypothesized by *H3* were examined by evaluating *DBH* growth among neighboring pairs of trees in the high-density treatment. *DBH* growth (the difference in *DBH* between ages 8 and 15 years) was selected as the response variable because it was more sensitive to recent competition than *DBH15*, which is the sum of growth over the entire life of the study. Pairs of trees where identified that were on the same plot and adjacent to one another in the same planting row or column. Correlation coefficients were calculated among pairs of trees in the same family (intragenotypic competition) and among pairs of trees in different families in the mixed-family treatments (intergenotypic competition). Statistically significant, negative correlations provided evidence for antagonistic relationships among families (trees had greater growth in locations where their neighbors had lesser growth and vice versa).

To test *H4*, "morphology coefficients" were calculated to capture differences among families in crown traits. The traits of interest were crown width relative to *DBH*, branch length relative to branch cross-sectional area, and branch leaf area relative to branch length. The allometric equation was used to characterize the relationships between the different pairs of dimensions (Niklas, 1994). The equation is:

$$Y = \beta \cdot X^{\alpha} \qquad (3)$$

Either β or α was allowed to vary among families so that each family had a different allometric relationship between plant dimensions. For example, an equation was fit where Y = crown width and X = *DBH*. The coefficient β was allowed to vary among families so that eight different values were estimated. In this example, the morphology coefficients indicated whether a family had a relatively narrow or wide crown relative to *DBH*. The differences among families that were captured by the morphology coefficients were statistically significant at the $P = 0.05$ level for the crown-width and branch-length equations and at the $P = 0.10$ level for the leaf-area equation. Coefficients were estimated in *R* using the nls package (for crown width) or the nlme package (for branch and leaf area measurements to include a random effect to account for sampling two branches from the same tree) (Pinheiro and Bates, 2000). *H4* was tested by fitting linear models to predict *DBH15* in the high density treatment from the different morphology coefficients. The null hypothesis for *H4* was rejected when the linear models were statistically significant.

3. Results

The main effect of genetic composition in Model 1 (*G*) was statistically significant for all traits other than *VOLHA8* for both the pure-family treatments alone and for the combination of pure- and mixed-family treatments (Table 1). The main effect of density (*D*) was statistically significant for all traits other than *DBH8* for both sets of composition treatments. The *G·D* interaction for the

Table 1
P-values from analysis of variance for the effects of genetic composition (*G*) and density (*D*) on mean diameter at breast height (*DBH*), height (*HT*), and volume per hectare (*VOLHA*) at ages 8 and 15. The deployment treatments include eight pure-family and three mixed-family deployments.

Factor	df	Response variable					
		DBH8	*HT8*	*VOLHA8*	*DBH15*	*HT15*	*VOLHA15*
Pure-family deployments							
G	7	0.032	<0.001	0.308	<0.001	<0.001	<0.001
D	2	0.799	<0.032	<0.001	<0.001	<0.001	<0.001
G·D	14	0.226	0.383	0.677	<0.001	0.032	0.072
Residual	72						
Pure-family and mixed-family deployments							
G	10	0.009	<0.001	0.076	<0.001	<0.001	<0.001
D	2	0.819	<0.001	<0.001	<0.001	<0.001	<0.001
G·D	20	0.108	0.014	0.215	<0.001	0.014	0.008
Residual	99						

pure-family treatments was significant for *DBH15* and *HT15* and marginally significant for *VOLHA15*. The *G·D* interaction was significant when all composition treatments were combined for all traits at age 15 years and for *HT8*.

Linear contrasts between pure-family treatments indicated that some families differed from one another in *DBH15* in the low-density treatment and in all treatments combined (Table 2). Family ranks for *DBH15* were fairly consistent between the medium- and low-density treatment (Spearman's rank correlation $r = 0.86$), but both the medium and low-density treatments were poorly correlated with the high-density treatment ($r = -0.12$ and 0.17, respectively). In addition, age–age correlations between *DBH15* and *DBH8* were weak in the high- ($r = 0.00$) and medium-density treatments ($r = 0.30$), but fairly strong in the low-density treatment ($r = 0.76$).

Some families differed significantly in *HT15* in each of the density treatments (Table 2). Family ranks in *HT15* were more stable across density treatments than for *DBH15* as indicated by higher rank correlations among densities ($r = 0.73$ to 0.81). Additionally, *HT15* was strongly correlated with *HT8* within densities ($r = 0.71$ to 0.98). Both *DBH15* and *HT15* were poorly correlated with the prediction based on parental breeding values. Correlations between predicted gains and family performance ranged from 0.15 to 0.26 among densities for *DBH15* and from 0.25 to 0.46 for *HT15*.

Some families differed significantly in *VOLHA15* in the high-density treatment and across all densities combined (Table 2). Family ranks changed considerably between the high-density treatment and the other densities. Ranks correlations were moderate between the medium- and low-density treatments ($r = 0.73$), but weak between the high-density treatment and the other two densities ($r = 0.10$ to 0.14). Family ranks changed considerably in some cases, particularly for Family 3 and Family 5. All pure-family treatments exceeded the woods-run control for *DBH15* and *VOLHA15* in the high- and medium-density treatments, with the exception of Family 7 in the medium-density treatment. Families 1, 3, and 7 had lower *DBH15* and *VOLHA15* than the woods-run control in the low-density treatments.

Among the mixed-family treatments, *M1* most closely matched the average performance of the same families in pure-family treatments (Table 3). Results from the linear contrasts did not show any significant differences between *M1* and the average performance of the same families in pure-family treatments. Differences were generally small and in some cases performance in *M1* was slightly better than the family averages. *M2* consistently underperformed relative to the family averages in the pure-family treatments. Differences between *M2* and the family averages were statistically significant for *HT15* and *VOLHA15* in the high-density treatment. Results were mixed for *M3*. The performance of *M3* was slightly better in the medium-density treatment than the family averages in the pure-family treatments, although the differences were not statistically significant. The performance of *M3* was significantly lower than the family average for *HT15* in the low-density,

Table 2
Treatment means and ranks for the pure-family deployments at age 15 years.

Family	Density							
	High		Medium		Low		All	
	Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank
DBH15 (cm)								
1	6.71	8	10.81	5	15.61^{bc}	6	11.05^{bc}	7
2	7.17	3	10.68	6	16.74^{ab}	5	11.53^{ab}	5
3	7.26	2	10.65	7	15.53^{c}	7	11.15^{abc}	6
4	6.79	7	11.24	2	16.81^{a}	4	11.61^{ab}	4
5	7.14	4	11.25	1	17.12^{a}	2	11.84^{a}	1
6	7.30	1	11.00	4	17.02^{a}	3	11.77^{ab}	2
7	6.88	6	10.14	8	14.67^{c}	8	10.56^{c}	8
8	6.97	5	11.03	3	17.29^{a}	1	11.76^{ab}	3
Woods run	6.63		10.18		15.95		10.92	
HT15 (m)								
1	8.63^{c}	8	9.78^{c}	8	10.17^{b}	7	9.53^{e}	8
2	9.77^{ab}	2	10.4^{abc}	4	11.21^{a}	2	10.46^{ab}	3
3	9.36^{abc}	5	9.95^{bc}	6	10.01^{b}	8	9.77^{de}	7
4	10.02^{a}	1	11.16^{a}	1	11.42^{a}	1	10.87^{a}	1
5	9.21^{abc}	6	10.51^{abc}	3	11.09^{a}	4	10.27^{bc}	4
6	8.99^{bc}	7	9.92^{bc}	7	10.79^{ab}	5	9.90^{cde}	6
7	9.54^{ab}	4	10.35^{bc}	5	10.26^{b}	6	10.05^{bcd}	5
8	9.59^{ab}	3	10.65^{ab}	2	11.18^{a}	3	10.47^{ab}	2
Woods run	8.99		9.94		10.58		9.84	
VOLHA15 (m^3 ha^{-1})								
1	170.1^{b}	8	119	6	59.85	6	116.32^{c}	8
2	222.33^{a}	1	126.11	4	76.24	3	141.56^{a}	1
3	201.53^{ab}	2	116.15	7	56.64	7	124.77^{abc}	6
4	200.3^{ab}	3	142.93	1	73.9	5	139.04^{a}	2
5	187.12^{b}	7	141.95	2	79.89	2	136.32^{abc}	4
6	197.36^{ab}	5	124.54	5	75.07	4	132.32^{abc}	5
7	187.31^{b}	6	113.35	8	52.77	8	117.81^{bc}	7
8	198.26^{ab}	4	135.59	3	80.19	1	137.95^{a}	3
Woods run	164.20		112.41		65.27		113.97	

Means within each density that do not share the same superscript letters are significantly different ($\alpha < 0.05$ family-wise error rate).

Table 3
Means for the three mixed-family treatments at age 15 years and difference between the average performance of the same set of families in the pure-family treatments (ΔPure = Pure–Mixed).

Trt	Density							
	High		Medium		Low		All	
	Mix	ΔPure	Mean	ΔPure	Mean	ΔPure	Mean	ΔPure
DBH15 (cm)								
M1	7.24	−0.26	10.66	0.19	15.68	0.49	11.19	0.15
M2	6.82	0.26	10.61	0.33	16.22	0.40	11.21	0.34
M3	6.86	0.21	11.5	−0.64	15.21	1.31^{a}	11.19	0.29
HT15 (m)								
M1	9.54	−0.10	10.33	−0.01	10.7	0.00	10.19	−0.03
M2	8.61	0.54^{a}	10.01	0.14	10.66	0.16	9.76	0.28
M3	9.09	0.25	10.6	−0.24	10.37	0.46^{a}	10.02	0.16
VOLHA15 (m^3 ha^{-1})								
M1	196.81	1.75	122.32	3.73	60.11	6.55	126.42	4.00
M2	169.7	24.53^{a}	118.75	9.15	67.43	5.33	118.62	13.01
M3	173.27	19.24^{a}	140.75	−11.94	60.44	11.54	124.82	6.28

Mixed family treatments are *M1* = families 1, 2, 3, 4; *M2* = families 1, 2, 5, 6; *M3* = families 5, 6, 7, 8.
[a] Statistically significant differences between the pure- and mixed-family treatments ($\alpha < 0.05$ family-wise error rate).

Table 4
Mortality (%) in each composition and density treatment at age 8 years (*MORT8*) and age 15 years (*MORT15*).

Trt	Density							
	High		Medium		Low		All	
	Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank
MORT8 (%)								
1	2.1	5	2.6	6	4.7	6	3.1	6
2	1.0	3	1.0	3	1.6	2	1.2	2
3	14.1	8	4.7	8	6.8	8	8.5	8
4	4.7	7	3.6	7	4.2	5	4.2	7
5	1.0	2	0.0	1	0.0	1	0.3	1
6	3.6	6	2.1	5	2.1	4	2.6	4
7	1.6	4	0.5	2	6.2	7	2.8	5
8	0.5	1	2.1	4	2.1	3	1.6	3
M1	7.8		3.1		7.8		6.2	
M2	1.6		4.2		3.6		3.1	
M3	4.2		6.2		2.6		4.3	
Woods run	1.6		1.6		3.6		2.3	
MORT15 (%)								
1	8.9	4	3.6	5	5.7	5	6.1	5
2	5.7	1	1.6	2	2.1	4	3.1	1
3	17.2	8	5.2	8	7.3	8	9.9	8
4	8.3	2	5.2	7	7.3	7	6.9	7
5	14.6	7	1.0	1	0.0	1	5.2	3
6	12.0	6	4.2	6	2.1	3	6.1	4
7	10.9	5	2.1	3	6.2	6	6.4	6
8	8.9	3	2.6	4	2.1	2	4.5	2
M1	17.7		3.1		8.3		9.7	
M2	10.9		4.7		4.2		6.6	
M3	15.1		7.3		2.6		8.3	
Woods run	12.0		1.6		3.6		5.7	

Table 5
P-values from analysis of variance to test whether the performance of individual families differed between the pure- and mixed-family treatments. The factors included in the model were family (*F*), density (*D*), mixture (*M*) and their interactions. Each mixture was analyzed separately.

Factor	df	*DBH8*	*HT8*	*VOLHA8*	*DBH15*	*HT15*	*VOLHA15*
M1							
F	3	0.001	<0.001	0.011	0.002	<0.001	<0.001
D	2	0.773	0.016	<0.001	<0.001	0.006	<0.001
M	1	0.816	0.979	0.247	0.298	0.801	0.427
F·D	6	0.558	0.427	0.112	0.678	0.133	<0.001
F·M	3	0.625	0.284	0.949	0.187	0.389	0.021
D·M	2	0.972	0.748	0.433	0.146	0.813	0.926
F·D·M	6	0.61	0.697	0.856	0.279	0.497	0.007
M2							
F	3	0.036	0.01	0.382	<0.001	<0.001	<0.001
D	2	0.193	0.775	<0.001	<0.001	<0.001	<0.001
M	1	0.002	0.004	0.006	0.028	0.003	0.006
F·D	6	0.686	0.912	0.705	0.691	0.779	0.022
F·M	3	0.894	0.816	0.848	0.137	0.301	0.182
D·M	2	0.346	0.159	0.011	0.921	0.095	0.195
F·D·M	6	0.922	0.891	0.916	0.865	0.838	0.479
M3							
F	3	0.023	0.011	0.053	<0.001	<0.001	<0.001
D	2	0.109	0.125	<0.001	<0.001	0.003	<0.001
M	1	0.149	0.121	0.036	0.012	0.070	0.095
F·D	6	0.138	0.079	0.177	<0.001	0.065	0.022
F·M	3	0.417	0.511	0.744	0.002	0.383	<0.001
D·M	2	0.001	0.001	0.003	<0.001	0.003	0.003
F·D·M	6	0.725	0.816	0.973	0.255	0.500	0.018

pure-family treatments and for *VOLHA15* in the high-density, pure-family treatments. *VOLHA15* was considerably lower in *M2* and *M3* than the family averages in the high-density, pure-family treatments (14% and 11% less, respectively).

Mortality (*MORT*) is an important component of *VOLHA*. There was little difference in *MORT8* among densities, but *MORT15* was considerably greater in the high-density treatment than in the other density treatments (Table 4). Family 3 had relatively high *MORT8* in its pure-family treatment and it contributed to high *MORT8* in *M1*. With additional mortality between ages 8 and 15 years among the other families, *MORT15* was only somewhat greater in Family 3 compared with the other families. Family ranks in *MORT15* were fairly well correlated between the medium- and low-density treatments ($r = 0.69$), but ranks in these treatments were not well correlated with the high-density treatment ($r = 0.02$ and 0.19). *MORT15* was greater in *M1* and *M3* than the pure-family averages.

The analysis of variance results for Model 2 reaffirmed the finding that performance differed between the mixed- and pure-family treatments, but they also indicated that the differences sometimes resulted from the performance of individual families within the mixtures (Table 5). The main effect of composition type (*M*) in Model 2 indicates whether overall performance differed between the mixed- and pure-family treatments. The interaction between composition type and family (*F·M*) indicates whether individual families performed differently in addition to the overall effect of *M*. The three-way interaction with density (*F·D·M*) indicates whether the differences also depended on the density treatment. In *M1*, the main effect of *M* was not statistically significant for any of the traits and the interactions that included *M* were statistically significant for *VOLHA15* only. In *M2*, the main effect of *M* was statistically significant for all of the traits but neither the *F·M* or the *F·D·M* interactions were significant for any of the traits. In *M3*, the *F·M* interaction was significant for *DBH15* and *VOLHA15* and the *F·D·M* interaction was significant for *VOLHA15* only.

Individual family performance differed in many cases between the pure- and mixed-family treatments, even when the mixture closely matched the family averages (Table 6). For example, *VOLHA15* in *M1* was nearly equal to the family average in the high-density treatment (Table 3); however, the individual families in *M1* differed by 13–43% between the pure- and mixed-family treatments. Family ranks in mixtures also did not match the ranks in pure-family treatments. For example, Family 5 ranked fourth, sixth and seventh for *DBH15*, *HT15*, and *VOLHA15*, respectively, among the high-density, pure-family treatments (Table 2). With the exception of *HT15* in *M3*, Family 5 ranked first for all of these traits within *M2* and *M3* (Table 6). Linear contrasts to assess the statistical significance of the individual-family differences between pure- and mixed-family treatments were estimated only for *DBH15* and *VOL15* in *M3* owing to the significant *F·M* term for these traits. Family 5 *DBH15* was significantly greater in the medium-density treatment and significantly lower in the low-density treatment in *M3* compared with the pure-family treatments. In contrast, Family 5 *DBH15* was nearly identical in *M2* and the pure-family treatments in the medium- and low-density treatments. Family 5 *VOLHA15* was also significantly greater in the medium-density treatment in *M3* than in the pure-family treatments. All other significant differences indicated poorer performance in *M3* than in pure-family treatments.

Correlations between *DBH* growth increments of neighboring trees suggested that intergenotypic competition was often stronger than intragenotypic competition in the high-density treatment (Table 7). Each family had at least one growth correlation with another family that was more strongly negative than the intragenotypic correlation. Family 5, which had a greater *DBH15* in *M2* and *M3* than in its pure-family treatment, had relatively strong, negative growth correlations with most families that it neighbored. Family 1, which ranked last for *DBH15* among the pure-family treatments and performed even poorer in *M1* and *M2*, was particularly strongly affected by intergenotypic competition. In all cases of significant intergenotypic correlation, the effects were negative suggesting the lack of any synergistic associations.

Table 6
Means for individual families within mixed-family deployments at age 15 years and differences between family performance in the pure- and mixed-family treatments (ΔPure = Pure−Mix).

Mix	Family	Density							
		High		Medium		Low		All	
		Mean	ΔPure	Mean	ΔPure	Mean	ΔPure	Mean	ΔPure
DBH15 (cm)									
1	1	6.33	0.39	10.48	0.33	15.27	0.35	10.69	0.36
1	2	8.02	−0.85	11.36	−0.68	16.35	0.39	11.91	−0.38
1	3	7.02	0.24	10.46	0.19	15.58	−0.04	11.02	0.13
1	4	7.48	−0.7	10.32	0.92	15.4	1.41	11.07	0.55
2	1	5.89	0.82	9.74	1.08	15.16	0.45	10.26	0.78
2	2	7.01	0.16	10.66	0.02	16.48	0.25	11.39	0.14
2	5	7.55	−0.42	11.24	0.01	17.11	0.01	11.97	−0.13
2	6	6.77	0.53	10.88	0.11	16.08	0.94	11.24	0.53
3	5	7.62	−0.48	12.99	−1.74[a]	15.98	1.14[a]	12.2	−0.36
3	6	6.18	1.12[a]	11.01	−0.01	15.25	1.77[a]	10.81	0.96[a]
3	7	6.51	0.38	10.27	−0.13	13.83	0.84	10.2	0.36
3	8	7.2	−0.23	11.66	−0.62	15.66	1.63[a]	11.51	0.26
HT15 (m)									
1	1	8.76	−0.13	9.93	−0.15	10.3	−0.14	9.66	−0.14
1	2	9.96	−0.19	10.64	−0.24	11.06	0.15	10.55	−0.09
1	3	9.2	0.15	10.08	−0.13	10.22	−0.20	9.83	−0.06
1	4	10.18	−0.16	10.68	0.48	11.13	−0.30	10.66	0.2
2	1	7.94	0.69	9.61	0.16	10.35	−0.18	9.3	0.23
2	2	8.75	1.01	10.12	0.28	10.83	0.38	9.9	0.56[a]
2	5	9.07	0.14	10.51	0	11.01	0.08	10.2	0.07
2	6	8.62	0.38	9.84	0.08	10.47	0.32	9.64	0.26
3	5	9.28	−0.06	10.95	−0.44	10.57	0.52	10.26	0.01
3	6	8.35	0.64[a]	10.14	−0.22	10.07	0.72[a]	9.52	0.38[a]
3	7	9.05	0.49	10.49	−0.15	10.13	0.13	9.89	0.16
3	8	9.68	−0.08	10.78	−0.14	10.72	0.46	10.39	0.08
VOLHA15 (m^3 ha^{-1})									
1	1	120.27	51.74	118.46	0.54	53.94	5.91	97.56	19.4
1	2	275.34	−50.11	143.06	−16.9	69.83	6.42	162.74	−20.2
1	3	162.99	40.97	106.4	9.78	55.72	0.92	108.37	17.22
1	4	234.62	30.87	121.5	21.43	60.97	12.94	139.03	1.17
2	1	118.19	53.82	92.98	26.02	55.88	3.97	89.02	27.94[a]
2	2	207.92	17.31	126.83	−0.68	70.47	5.78	135.07	7.47
2	5	197.1	−7.77	134.38	7.60	74.93	4.96	135.47	1.6
2	6	169.84	29.5	120.87	3.70	68.42	6.64	119.71	13.28
3	5	208.68	−19.34	185.58	−43.59[a]	71.21	8.68	155.15	−18.09
3	6	126.62	72.71[a]	121.45	3.12	59.51	15.56	102.53	30.47[a]
3	7	169	21.38	115.66	−2.29	48.19	4.57	111.11	.48 7.89
3	8	200.44	1.31	140.27	−4.86	62.83	17.36	134.51	4.6

[a] Statistically significant differences owing to deployment type ($\alpha < 0.05$ family-wise error rate).

Table 7
Correlation coefficients (r) of *DBH* growth among neighboring pairs of trees in the high-density treatment.

Family	1	2	3	4	5	6	7	8
1	0.02	−0.40**	−0.08	−0.20*	−0.27**	−0.11	–	–
2		−0.13**	−0.28**	−0.18	−0.27**	−0.06		
3			−0.19**	−0.16				
4				−0.12**				
5					−0.06	−0.24**	−0.24**	−0.10
6						−0.17**	−0.09	0.15
7							−0.10**	−0.01
8								0.01

* $p < 0.10$.
** $p < 0.05$.

The linear models to predict *DBH15* in the high-density treatment were statistically significant for each set of morphology coefficients in the pure-family treatments, but not in the mixed-family treatments (Fig. 1). Families fell into two groups in terms of crown width relative to *DBH* and branch length relative to branch cross-sectional area. There was not any clear grouping of families in terms of leaf area relative to branch length. The linear model for crown width in the mixed-family treatments was nearly significant. Family 4 was an outlier in that it had a wide crown and a relatively high *DBH15* in the mixed-family treatments indicating that its wide crown may have conferred some competitive advantage in mixtures. The linear model fit much better without Family 4 ($r^2 = 0.63$, $P = 0.002$).

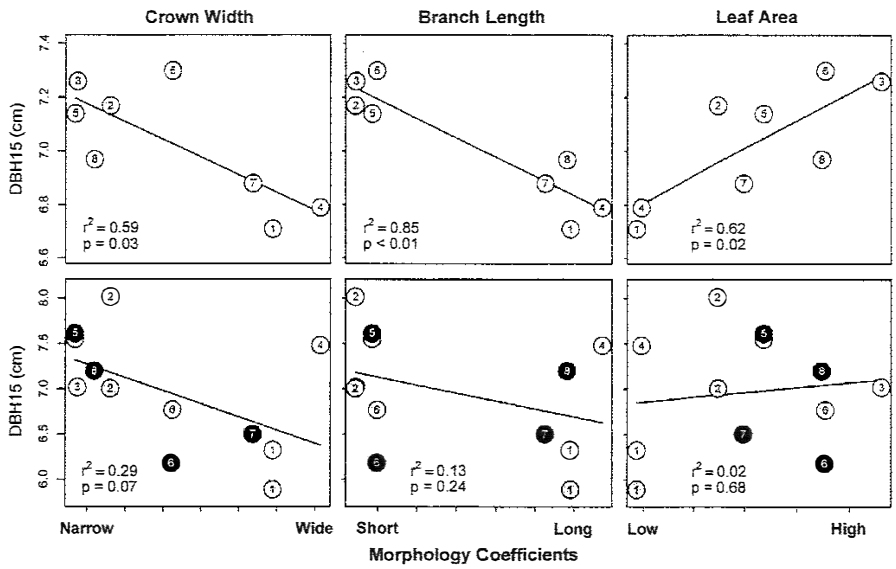

Fig. 1. Linear models relating morphology coefficients to *DBH15* in the high-density treatment in pure-family deployments (upper row) and mixed-family deployments (lower row). The morphology coefficients indicate differences among families in crown width relative to *DBH* (left column), branch length relative to cross-sectional area (middle), and leaf area relative to branch length (right). Observations are labeled by family. The different shades of family labels in the lower row indicate different mixtures.

4. Discussion

The results of the study through age 15 years provided evidence to reject the four null hypotheses. Deployment type and stand density both clearly affected the performance of the selected families of Douglas-fir. Differences among families in the pure-family treatments were expected as the families were selected with the intention of creating a range of values for *DBH* and *HT*. The observed differences, however, were poorly correlated with predictions. The poor correlations were not entirely unexpected. The predicted gains for *DBH15* and *HT15* had relatively large standard errors and the performance of each family strongly affected the correlations owing to the small number of families in the study. Furthermore, the small number of families meant that effects of specific combining abilities (dominance and epistatic genetic effects) were less likely to be averaged out. In contrast, Ye et al. (2010) reported stronger correlations ($r = 0.58$ to 0.88) between observed and predicted gains for *HT15* and *DBH15* in a study of 20 families (including some of the same families used in the present study). Stronger correlations with predicted gains may have been found in the present study if more families had been tested and if more replicates of the study had been installed (St. Clair et al., 2004).

Stand density affected family performance and the stability of family ranks. Family ranks for *DBH15* were particularly different in the high-density treatment compared to the other two densities. Among the pure-family treatments, Family 5 ranked first in *DBH15* over all densities but it ranked fourth in the high-density treatment. Family 6 ranked first among the pure-family, high-density treatments, but it ranked fourth and third in the medium- and low-density treatments, respectively. Rank stability was also fairly poor for *VOLHA15*. Ranks were fairly stable for *HT15* across densities. Adams et al. (2008) found that mean heights of loblolly pine families were correlated more strongly between ages 9 and 17 years when trees were planted at high densities compared with lower densities. *HT* tended to be well correlated among densities and ages in the present study, but *DBH* was not. Competition did not strongly affect *DBH8* as indicated by the non-significant *D* term in Model 1. The increase in competition between ages 8 and 15 years altered family performance as indicated by the age–age correlations for *DBH* in the high-density ($r = 0.00$) and medium-density treatments ($r = 0.30$). A limitation of the present study is that it was not replicated at multiple sites; therefore, it is not possible to test whether aspects of the environment other than competition affected family performance. Genetic x environment interactions, beyond the effects of competition, could produce changes in family ranks in different environments. Although the study site is representative of many sites where improved Douglas-fir is planted, care should be taken in extrapolating our results to other sites where environmental differences could affect family ranks.

High-density test plantings are often intended to accelerate the onset of competition so that a family's genetic potential for growth under competition is expressed earlier (Franklin, 1979; Adams et al., 2008). A key question is whether or not high-density plantings cause families to express the same type of genetic potential that would lead to high realized gains in operational plantings. The question is made more difficult by the fact that growth patterns of Douglas-fir and other species change throughout stand development (e.g., King, 1966). For example, height and diameter growth rates of Douglas-fir have been shown to be positively correlated with stand density over the first five years of stand development, and negatively correlated afterwards (Ritchie, 1997; Woodruff et al., 2002). Differences in size that emerge early in the rotation can alter the competitive abilities of individual trees, thereby allowing some trees to maintain a competitive advantage in later years (Ford, 1975; Weiner and Solbrig, 1984). If the same genetic potential is expressed whether competition begins early or late in stand development, then family ranks in the medium- and low-density treatments would be expected to become like those in the high-density treatment. This hypothesis can be tested with future measurements of the study.

The genotype of neighbors also affected family performance. Results from the mixed-family treatments indicate that some mixtures of families will perform about the same whether in pure or mixed deployments (e.g., *M1*), while in other cases there may be an overall mixture effect that impacts all families and stand

densities about equally (*M2*), or there may be interactions among families and stand densities (*M3*). The performance of families under different deployment methods has been found to be inconsistent and difficult to predict in other studies (Adams et al., 1973; Tuskan and Buijtenen, 1986). Foster et al. (1998) hypothesized that the greatest potential for differences between pure- and mixed-deployments was in mixtures that contained families with relatively high differences in growth potential. The mixed-family treatments in the present study were intended to separate families with relatively high and low growth potentials into *M1* and *M3*. *M2* was intended to have a mix of growth potentials. However, each mixed-family treatment contained families that had wide ranges in their performances in the pure-family treatments. Results may have been more consistent between pure- and mixed-family treatments if the growth potentials for individual families could have been predicted more accurately at the time the study was installed.

The growth correlations among neighbors in the high-density treatment indicated that antagonism occurred between some family pairs in each of the mixtures. The overall performance of *M1* was not negatively affected by competition despite the evidence for antagonism. The poor performances of Families 1 and 3 in *M1* were compensated for by better performances of Families 2 and 4. Family 5 stands out in terms of its relatively poor performance in high-density, pure-family treatments compared to its better performance in *M2* and *M3*. Additionally, Family 5 was involved in more strong antagonistic interactions than any other family. These results, combined with the decrease in relative performance in the higher density treatments, suggest that Family 5 can be labeled as a competition ideotype (Cannell, 1982), despite having a relatively narrow crown. The good performance of Family 5 in mixtures did not compensate for the apparent suppression of growth of its neighbors, and its presence in *M2* and *M3* may have contributed to the overall poor performance of these mixtures in the high-density treatment. Family 3 may be labeled as a crop ideotype. It performed relatively well in high-density, pure-family treatments, but not as well relative to Families 2 and 4 in mixture. Family 2 is an example of a good performer at high-densities, whether in competition with other families or in pure plantings.

Relationships between morphology coefficients and family performance under high competition support the hypothesis that crown morphology is a useful indicator of the crop ideotype. In the high-density, pure-family treatments, *DBH15* was greater for families that had relatively narrow crowns, high leaf area relative to branch length, and short, stout branches than for families that lacked these traits. These results reinforce the findings of St. Clair (1994b), who also found that Douglas-fir families with narrow crowns, stout branches relative to length, and high leaf area relative to branch length produce more volume per unit of growing space. The crop ideotype is defined by its ability to produce high yields per unit area under high competition with other crop ideotypes (Donald, 1968). The relative advantages of a crop ideotype do not necessarily hold in mixtures of ideotypes. Each of the mixed-family treatments included one or more families that were not grouped as crop ideotypes in terms of the morphology coefficients. The mixture of growth strategies may have contributed to the relatively poor performances of the mixed-family treatments. Crown morphology may be a useful trait for selecting parents for breeding programs. Crown traits often have relatively high heritabilities, sometimes exceeding those for total height or diameter (King et al., 1992; St. Clair, 1994a). The morphology coefficients were measured in the present study in the low-density treatment where crown competition had not yet begun. Therefore, it may be possible to use early measurements in progeny tests (before competition begins) to select parents that have crown traits of a crop ideotype. Age–age correlations for crown traits should be evaluated to help determine when selection can occur.

5. Conclusions

The results of the study to date have implications for breeding programs and operational deployments. Our key finding is that deployment type and density have an effect on family performance of Douglas-fir. Pure-family treatments are typically not desirable for operational plantings. There is a high level of uncertainty in predicted breeding values for any given parent, which means the performance of some pure-family deployments would fall considerably below their predicted levels. Forest managers can offset families that perform poorer than expected with those that perform better by planting mixtures of families. Stoehr et al. (2010) recently found higher-than-predicted volume gains at age 12 years for a set of 17 families in a medium-gain group and a set of 10 families in a top-cross group despite a wide range in the performances of individual families. Breeding values for individual-tree volume are often used to select families. Volume gain can be produced by different combinations of gains in *HT* and *DBH*. Our results suggest that *HT* gains are expressed more consistently across competitive environments. Selecting for *HT* gains or weighting *HT* more than *DBH* may help produce families that have consistent performance in different competitive environments. From the perspective of tree-improvement programs, our results suggest that initial planting densities and genotype mixtures in progeny tests may have a greater effect on family ranks than has been generally recognized. It is relatively easy to test families and identify the best performers, but it is more difficult to understand why some families perform better than others and under which circumstances they will perform well. Evaluating crown morphology and other traits may be an effective way of identifying crop ideotypes at young ages. More research is needed to determine if incorporation of ideotype traits into selection criteria can augment gains from conventional selection for tree volume in Douglas-fir.

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