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Genotype × shade effects for western hemlock

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Abstract: Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) families were grown under different levels of shade for 2 or 3 years at two nursery sites to determine whether families performed differently relative to one another in the different shade environments. Differences were found both for levels of shade and families, but no family × shade interaction was found. Results suggest that families selected in full-sun environments (clearcuts or farm fields) may be well suited for use in silvicultural systems where seedlings are planted in understory conditions.

Résumé : Des familles de pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) ont été cultivées avec différentes intensités d'ombre pendant 2 ou 3 ans dans deux pépinières pour déterminer si ces familles performaient différemment, les unes par rapport aux autres, dans des environnements avec différentes intensités d'ombre. Des différences ont été observées tant entre les intensités d'ombre qu'entre les familles mais il n'y avait aucune interaction entre les familles et les intensités d'ombre. Les résultats suggèrent que les familles sélectionnées dans des environnements exposés au plein soleil (coupes à blanc ou champs agricoles) pourraient être bien adaptées pour une utilisation dans les systèmes sylvicoles où les semis sont plantés en sous-étage.

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Introduction

Forest management in the Pacific Northwest considers multiple objectives. Landowners, especially public landowners, must consider values that include biodiversity and wildlife habitat (Franklin et al. 1997; Hayes et al. 1997). This has resulted in the use of alternative silvicultural systems designed to provide stand structures similar to older stands and with understories of conifers and hardwoods (e.g., McComb et al. 1993; DeBell et al. 1997; Tappeiner et al. 1997). Industrial landowners emphasize optimizing tree growth over these other values. The result of this array of management objectives and silvicultural systems is that planting of seedlings can take place in a range of light levels, from full sunlight, as in clearcuts, to relatively dense shade, as in underplantings in shelterwood cuts or diseased stands. In addition to a range of light levels, the overstory will also modify moisture and nutrient availability.

Forest tree breeding programs in the region establish progeny tests in open areas (clearcuts or farm fields), to reduce the environmental variation associated with unpredictable shade and competition and to optimize growth rates to obtain suitably sized trees in a shorter amount of time (i.e., reduce the breeding generation interval). The implication is that tree breeding programs are selecting for improved growth in full sunlight. The question that arises is, Will the best-growing families in full sun also be the best-growing families in an understory of existing trees?

St. Clair and Sniezko (1999) demonstrated that for coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), a major timber species in western Oregon and Washington, there was very little genotype × shade interaction, suggesting that families growing best in full-sun environments were also well suited for shaded environments. Results for one species are not automatically applicable to other species. Of the Pacific Northwest conifers, Douglas-fir is considered to be moderately shade tolerant to shade intolerant and to be somewhat drought tolerant (Minore 1979). Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), another important timber species in the Pacific Northwest, is one of the most shade tolerant of the conifers and is less drought tolerant than Douglas-fir (Minore 1979). The objective of this study was to examine the response of western hemlock families to differing levels of shade and to determine whether families chosen from progeny tests in clear-cut environments may be suitable for planting in a variety of shade conditions. We report the results of two separate and independent studies based on 3-year nursery data, one from British Columbia and one from Oregon.

Materials and methods

Two studies were undertaken, one in a nursery at Cowichan Lake, British Columbia (BC), and another in raised beds in

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Table 1. Trial specifications at the Oregon and British Columbia locations.

	Oregon	British Columbia
Families	39 open-pollinated	30 open-pollinated, 21 control-pollinated
Replications	4	3
Light transmission levels	3	4
Year 1 light levels[a]	100%[b]–74%–43%	70%–70%–70%–70%
Year 2 light levels[a]	100%–74%–43%	100%–72%–45%–17%
Year 3 light levels[a]	100%–74%–25%	100%–72%–45%–17%
Trees per subplot	10-tree row	3 randomized trees
Spacing	15 cm × 5 cm	17 cm × 17 cm

[a] Percent light transmission.

[b] Shade cloth added to the full sunlight treatment in July of the first year and removed that winter.

Corvallis, Oregon (OR). The BC study examined 21 full-sib families generated from breeding programs in British Columbia and Washington, and 30 open-pollinated families that ranged from 44°N to 54°N latitude. The OR study examined 39 open-pollinated seed orchard families from a coastal Oregon breeding program. Both sites used a split-plot design, where shade was the main (whole) plot within each replication and families were the subplots planted within each shade structure (Table 1).

At the OR site, treatments consisted of three levels of shade in the first year in raised beds: open (no shade, 100% transmission) and 43% and 74% transmission (Table 1). Photosynthetically active radiation had previously been measured under the enclosures with a LI-COR Model LI-185A (LI-COR, Lincoln, Nebraska) during the summer to determine the transmission percentages. Shade was supplied by shade cloth that was attached to a structure 170 cm wide × 120 cm tall × 375 cm long. Because the seedlings were performing poorly during the first year in the open sun, shade cloth was added midway through the first summer and removed the following winter. After the second growing season an additional layer of shade cloth was applied to the "moderate-shade" treatment to further reduce light transmission. Families were planted in 10-tree row plots at 15 cm between rows and 5 cm between trees within rows. Four replications were established, each assigned to a separate raised bed. Trees were watered as needed, and no fertilizer was applied. Variables measured in Corvallis were height (ages 1, 2, 3), root collar diameter (age 3), aboveground biomass, root biomass (age 3), and root/shoot ratio (age 3). Plant biomass was estimated by combining all trees in each subplot and obtaining oven-dry masses. Average plant biomass per tree was determined by dividing the oven-dry mass by the number of trees per plot (i.e., row). Taper was estimated for each tree at the end of the study by dividing seedling height (millimetres) by root collar diameter (millimetres).

At the BC site, all stock was initially grown in a greenhouse with about 70% light transmission. The seedlings were transplanted to the nursery during early September of the first growing season. Four levels of shading were applied in late winter (Table 1) using shade cloth supported by tubing arched to a height of 120 cm over a 140 cm wide nursery bed. Light transmission was measured on multiple days during the summer using a Sunfleck Ceptometer (Decagon Devices Ltd., Pullman, Washington) with a 40 cm probe, to determine the transmission percentages. In all treatments, seedlings were watered at the same time from above the shade cloth. As a result, seedlings in the full-sun treatment experienced more droughty conditions, since the soil dried out more quickly than in the covered treatments. Three trees per family were randomly established in each shade-replication combination at a spacing of 17 cm × 17 cm. Three replications were established. Seedling height and root-collar diameter were measured at the end of all three growing seasons. Taper was estimated for each seedling at the end of the study.

Statistical model

Both total growth (height and diameter at the end of a growing season) and annual growth were analyzed. The statistical model was that of a standard split-plot design, where shade treatment was the main plot and family the subplot:

$$Y_{ijkl} = \mu + R_i + T_j + RT_{ij} + F_k + TF_{jk} + RTF_{ijk} + E_{ijkl}$$

where μ is the overall mean, R_i is the random effect of the ith replication, T_j is the fixed effect of the jth shade treatment, RT_{ij} is the random interaction effect of the ith replication and jth treatment (and error term for the main plot, shade effect), F_k is the random effect of the kth family, TF_{jk} is the random interaction effect of the jth treatment and the kth family, RTF_{ijk} is the three-way random interaction effect of the ith replication, jth treatment, and kth family (and the error term for family and shade × family), and E_{ijkl} is the within-plot variation. When examining survival and biomass measurements, plot means were used and the within-plot variation term was removed from the model. Statistical significance was tested with the GLM procedure of SAS (SAS 1990). Variance components were estimated with the MIXED procedure of SAS (Littell et al. 1996).

For many of the variables, the shade treatments resulted not only in changes in the means but also in apparent changes in variance as well. A natural log transformation was used when there was an obvious increase in within-treatment variance with increasing treatment means. These variables are noted in Table 2.

The relative importance of the family × shade treatment interaction was estimated by the ratio of the family variance component to sum of the family and family × shade variance

Table 2. Means for the different shade treatments, statistical significance of shading, family and their interaction and an estimate of the genetic association among treatment (r).

	Treatment means					Shade effect		Family effect		Shade × family effect		
	No shade	Light shade	Medium shade	Heavy shade	Transformed	F	$P > F$	F	$P > F$	F	$P > F$	r^a
Oregon												
% survival year 1	65	87	86			19.80	0.002	3.93	<0.001	0.93	0.652	1.00
% survival year 2	65	87	86			20.93	0.002	3.83	<0.001	0.95	0.590	1.00
% survival year 3	49	65	57			2.10	0.204	2.69	0.001	0.96	0.567	1.00
Total height year 1 (cm)	8.3	9.5	11.1		Yes	10.89	0.010	4.15	<0.001	0.76	0.923	1.00
Total height year 2 (cm)	43.2	48.1	47.5			3.71	0.089	5.43	<0.001	1.04	0.936	1.00
Total height year 3 (cm)	80.1	82.6	76.9			3.94	0.113	3.66	<0.001	0.98	0.536	1.00
Height growth year 2 (cm)	35.9	38.3	36.1			1.32	0.362	4.80	<0.001	1.03	0.425	0.99
Height growth year 3 (cm)	35.8	35.1	30.0			7.68	0.043	1.67	0.012	1.11	0.284	0.67
Basal diameter year 3 (mm)	7.93	7.13	6.23		Yes	39.70	0.002	3.35	<0.001	1.04	0.403	0.94
Top biomass (g)	2558	2112	1835		Yes	47.48	0.002	2.50	<0.001	1.13	0.244	0.77
Root biomass (g)	671	504	409		Yes	13.93	0.016	3.19	<0.001	1.18	0.179	0.79
Total biomass (g)	3229	2616	2245		Yes	28.39	0.004	2.82	<0.001	1.13	0.238	0.80
Root/shoot ratio	0.256	0.241	0.217		Yes	3.56	0.130	1.75	0.007	0.91	0.682	1.00
Taper (height/diameter) year 3	102.7	117.8	125.4		Yes	17.57	0.010	2.94	<0.001	1.11	0.280	0.86
British Columbia												
% survival year 2	94	96	95	93		4.24	0.063	11.3	<0.001	1.07	0.305	0.97
% survival year 3	94	95	93	91		7.52	0.019	9.41	<0.001	1.07	0.309	0.97
Total height year 2 (cm)	37.9	40.9	41.3	45.7	Yes	30.10	<0.001	7.55	<0.001	0.85	0.874	1.00
Total height year 3 (cm)	74.2	85.2	83.1	80.4		7.01	0.022	9.62	<0.001	1.06	0.325	0.97
Height growth year 2 (cm)	7.9	9.4	10.1	14.4	Yes	29.59	<0.001	3.44	<0.001	1.06	0.317	0.93
Height growth year 3 (cm)	3.61	4.46	4.18	3.48	Yes	7.05	0.022	3.95	<0.001	1.18	0.101	0.79
Basal diameter year 2 (mm)	5.77	6.10	5.99	5.98		1.96	0.222	6.65	<0.001	0.74	0.983	1.00
Basal diameter year 3 (mm)	10.32	10.52	10.00	8.49	Yes	13.27	0.005	1.31	0.086	0.93	0.686	1.00
Diameter growth year 2 (mm)	1.65	1.87	1.80	1.82		1.09	0.421	2.43	<0.001	0.86	0.868	1.00
Diameter growth year 3 (mm)	4.89	4.73	4.12	2.63	Yes	75.18	<0.001	2.60	<0.001	1.03	0.395	0.80
Taper (height/diameter) year 3	69.5	79.1	82.8	94.0	Yes	24.36	0.001	6.61	<0.001	1.02	0.423	0.95

Note: Treatment means are from untransformed data; statistical significance is for either natural log transformed or untransformed data, as noted.

[a] $r = \sigma^2_{\text{family}} / (\sigma^2_{\text{family}} + ^2_{\text{family}\times\text{shade}})$.

Table 3. Narrow-sense heritability estimates of untransformed data (with standard errors in parentheses).

	All treatments	Full sun	Light shade	Medium shade	Dark shade
Oregon					
Height year 1	0.28 (0.07)	0.11 (0.06)	0.24 (0.08)	0.33 (0.09)	—
Height year 2	0.37 (0.09)	0.39 (0.11)	0.30 (0.09)	0.25 (0.08)	—
Height year 3	0.25 (0.07)	0.30 (0.11)	0.24 (0.09)	0.19 (0.08)	—
Height growth year 2	0.34 (0.08)	0.38 (0.11)	0.27 (0.08)	0.23 (0.07)	—
Height growth year 3	0.06 (0.03)	0.07 (0.06)	0.10 (0.06)	0.06 (0.05)	—
Diameter year 3	0.20 (0.06)	0.15 (0.08)	0.25 (0.09)	0.27 (0.09)	—
Taper year 3	0.20 (0.06)	0.29 (0.10)	0.22 (0.08)	0.35 (0.11)	—
British Columbia					
Height year 2	0.65 (0.17)	0.52 (0.22)	0.44 (0.20)	0.79 (0.26)	0.49 (0.22)
Height year 3	0.68 (0.17)	0.69 (0.25)	0.36 (0.20)	0.73 (0.25)	0.35 (0.20)
Diameter year 2	0.75 (0.18)	0.83 (0.27)	0.43 (0.21)	0.56 (0.23)	0.64 (0.24)
Diameter year 3	0.31 (0.11)	0.19 (0.17)	0.00 (0.13)	0.39 (0.20)	0.32 (0.19)
Height growth year 2	0.24 (0.09)	0.19 (0.17)	0.33 (0.20)	0.31 (0.19)	0.00 (0.13)
Height growth year 3	0.39 (0.12)	0.30 (0.19)	0.28 (0.19)	0.50 (0.22)	0.18 (0.17)
Dia growth year 2	0.19 (0.08)	0.03 (0.14)	0.14 (0.16)	0.27 (0.18)	0.02 (0.13)
Dia growth year 3	0.18 (0.08)	0.00 (0.07)	0.10 (0.15)	0.50 (0.22)	0.03 (0.14)
Taper year 3	0.28 (0.10)	0.32 (0.19)	0.17 (0.17)	0.33 (0.20)	0.14 (0.10)

component (r). This is similar to a type B genetic correlation (Burdon 1977).

Heritabilities for traits with individual tree measurements were estimated with the open-pollinated families (39 in OR, 30 in BC) with the equation

$$h^2 = \frac{4\sigma^2_{\text{family}}}{\sigma^2_{\text{family}} + \sigma^2_{\text{treatment} \times \text{family}} + \sigma^2_{\text{rep} \times \text{treatment} \times \text{family}} + \sigma^2_{\text{error}}}$$

Heritabilities were also estimated for each shade treatment using the reduced model

$$h^2 = \frac{4\sigma^2_{\text{family}}}{\sigma^2_{\text{family}} + \sigma^2_{\text{rep}\times\text{family}} + \sigma^2_{\text{error}}}$$

Because the genetic variance components estimated with the 21 full-sib families in British Columbia were similar to those estimated with the half-sib families (data not shown) and confounded the additive and nonadditive genetic variation, only the half-sib family heritability estimates are reported. The standard errors for heritability estimates were calculated using the equations given in Becker (1984) for sire groups.

Results and discussion

During the first 2 years it appeared that shade, even heavy shade, was not detrimental to seedling growth at either site, because there was very little difference among the shade treatments for any trait (Table 2). At both sites, the seedlings in the full-sun treatments were shorter than those in the shaded treatments, but treatment differences were only statistically significant at the BC site (Table 2). However, in the third growing season, the heaviest shade treatments had the smallest amount of height and diameter growth, suggesting that the lower light was beginning to have a detrimental effect on growth (Table 2). In Oregon, the full-sunlight treatment produced the largest trees, based on biomass and diameter; in British Columbia, the largest trees were in the light-shade treatment. The difference between the two studies could have been a function of low survival in the full-sun treatment at the Oregon site (Table 2). Shade cloth was put over the seedlings in July of the first year to mitigate the problem, but it was too late for some of the seedlings. The reduced stocking in the OR full-sun treatment, resulting in less competition, may have been the reason for the larger individual trees in that treatment. On a plot basis (multiplying the number of surviving trees per plot by the mean biomass per tree), the light shade treatment had more biomass at the end of the study (full sun = 1.582 kg, light shade = 1.700 kg, moderate shade = 1.046 kg).

One would expect less growth with low sunlight, since photosynthesis decreases below certain light intensities (Kozlowski et al. 1991). Our results, after year 2, are consistent with the numerous studies that have demonstrated a trend of decreased productivity with increased shade and (or) competition in western hemlock (e.g., Brandeis et al. 2001; Mailly and Kimmins 1997; Carter and Klinka 1992) and other Pacific Northwest conifer species (e.g., Brandeis et al. 2001; St. Clair and Sniezko 1999; Mailly and Kimmins 1997; Emmingham and Waring 1973).

At both sites, increased shade was associated with increased taper (height/diameter) (Table 2). Based on the OR data, there was also a tendency (p = 0.130) for a larger proportion of biomass to be allocated to shoots rather than the roots in heavier shade. These results are an expected outcome as the plants attempt to "reach" for sunlight as a result of the change in light quality; that is, an etiolation response under the low-light conditions (Smith 1982; Warrington et al. 1988; Hoad and Leakey 1994).

There was some indication at the OR site that the mortality rate in the third year was higher for the moderate shade treatment; mortality rates during the third growing season were 25% for both the full sun and light shade, but 34% for the moderate-shade treatment. As the trees became larger, competition for light could have been more intense in the moderate-shade environment during the third year, thus hastening mortality. However, the initial high mortality in the full-sun treatment the first year could be a confounding factor, since the resulting spacing was wider (and competition was reduced) in the full-sun treatment at the beginning of the third growing season; but this was not the case for the light shade – moderate shade comparison. The wider spacing at the BC site probably delayed mortality relative to the OR site, and differences in mortality may have occurred if the trial had continued. Another possible explanation is that the BC site was located in a hemlock environment, while the OR site was not. Higher mortality in dense shade has also been reported for western hemlock and other conifers (Brandeis et al. 2001; Mailly and Kimmins 1997).

Significant differences among families were found for all traits when analyzed over all shade environments (Table 2). The amount of family variation, as indicated by heritability estimates, tended to be higher in the light- to moderate-shade environments at the BC site, but no clear trends were evident at the OR site (Table 3). Heritabilities for the growth increments tended to be lower than for total height and diameter (Table 3).

Family × shade interactions were nonsignificant for all traits at both locations (Table 2). At the BC location there was some indication that the height increment in the third growing season had statistically significant family × shade interactions ($p = 0.101$, Table 2). However, the associations between the family values at the different shade levels were high ($r = 0.79$, Table 2) and probability suggests that at least two variables would be statistically significant at $p = 0.10$ by chance alone, since we examined 25 variables (a type I error).

The general lack of family × shade interactions suggests that families selected in one shade environment will still be suitable for other shade environments at least to age 3. St. Clair and Sniezko (1999) and John (1988) found similar results for Douglas-fir; the family × shade interaction was small compared to the family variance component for young trees. While we cannot generalize to all conifer species, it is notable that similar results have been found for both a shade-tolerant (western hemlock) and shade-intolerant to moderately tolerant species (Douglas-fir).

Caution must be taken when extrapolating these results to field conditions. Shade is only one aspect of planting in understories. Soil moisture and nutrient availability will also decrease in environments when competition is present. These conditions were not simulated in this study. In addition, the genetics of early growth is not perfectly correlated with later growth. For example, in the breeding population of 282 open-pollinated families (planted on six sites) from which the OR families were drawn, the genetic correlations of age 5 height with age 10 height and age 15 DBH were 0.86 and 0.82, respectively (data not shown). Data were also available from a BC breeding program of 29 open-pollinated families on three sites. The genetic correlations of age 5 height with height at ages 10, 15, and 20 were 0.59, 0.39, and 0.30, respectively.

Conclusions

These results suggest that the current practice of planting western hemlock progeny tests in clearcuts (full sunlight) will be applicable in regeneration systems that provide some level of shade. There was some indication from the BC trial that selection could be optimized with tests conducted under light to moderate shade because of higher heritabilities. However, this trend was observed for only a few traits and was not consistent across the two studies. Furthermore, it is not certain that one could extrapolate the higher heritabilities found in the BC shade treatments to a field environment; shade was uniform in the nursery, but shade would not be so in an operational field planting. Additional environmental variation would also be experienced if progeny tests were planted under existing canopies because of the irregular competition associated with the upper canopy trees, thereby reducing the precision of the tests.

The full-sun environments appear to be optimal for western hemlock breeding programs for at least two reasons: (1) vegetation control will remove environmental variation due to competition and result in increased heritabilities (precision of selection) and (2) the increased growth rates in full sun will result in shorter generation intervals because trees will attain sizes suitable for selection at earlier ages.

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