Genetic variation in response to shade in coastal Douglas-fir

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Abstract: Tree improvement programs have generally relied on testing families in open light environments. With increased interest in multiaged silvicultural systems, some people have questioned whether families selected in the open are appropriate for planting in the shade. We grew Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) families from two climatically distinct seed sources for 2 years under four levels of shade. The response to shade differed for several traits between the two populations and among families within populations. The magnitude of variation associated with the interaction, however, was small compared with the overall effects of genetic selection or of shade. Families selected based on performance in an open light environment resulted in nearly the same response to selection when grown under shade as families selected based on performance in the shade. We conclude that seedlings from families selected in an open light environment are appropriate for use in the low-light environments of alternative silvicultural systems and that use of such genetically selected stock may compensate for the less favorable growing conditions. Genetic selection may contribute importantly to meeting multiple objectives, including the production of significant amounts of wood as well as the efficient and timely creation of large stand structures needed for other forest values.

Résumé : Dans les programmes d'amélioration génétique, on a l'habitude de tester les descendances en milieu ouvert. En raison de l'intérêt grandissant porté aux stratégies d'aménagement inéquienne, certains remettent en question le fait de planter en milieu ombragé des descendances sélectionnées en milieu ouvert. Les auteurs ont mis en croissance pendant 2 ans et selon quatre régimes de lumière des descendances de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) représentatives de deux provenances de graines récoltées dans des zones climatiques distinctes. La réponse à l'ombre variait pour plusieurs caractères entre les deux populations et entre les familles au sein de ces populations. Cependant, l'amplitude de la variation associée à l'interaction était faible comparativement aux effets globaux attribuables à la sélection génétique et au régime de lumière. Les descendances issues de la sélection pour leur performance en milieu ouvert ont répondu à la sélection lorsque cultivées à l'ombre de façon quasi équivalente aux descendances issues directement de la sélection pour leur performance à l'ombre. Les auteurs en concluent que les semis de descendances issues de la sélection en milieu ouvert peuvent être utilisés de façon adéquate dans les milieux ombragés associés aux stratégies alternatives d'aménagement, et que l'utilisation de ces variétés issues de la sélection génétique peut compenser pour les conditions de croissance moins favorables. Il en découle que la sélection génétique peut contribuer de façon importante à l'atteinte d'objectifs multiples, incluant la production de quantités significatives de bois ainsi que la mise en place, de façon efficace et opportune, de structures de peuplement de grande dimension pour les autres usages de la forêt.

[Traduit par la Rédaction]

Introduction

The Douglas-fir region of western Oregon, Washington, and British Columbia contains some of the most productive forests in the world. Escalating conflicts among demands for different values from these forests have resulted in decreased emphasis on commodity wood production on public lands and increased costs and complexity of forest management on private lands. Conflicts may be mitigated to some extent by using alternative silvicultural systems that provide for concurrent production of multiple values including wood production, wildlife habitat, scenery, recreation, water quality, and riparian habitat (McComb et al. 1993; Tappeiner et al. 1997). Alternative silvicultural systems differ considerably in the amounts of overstory retained, resulting in large differences in light environments. Light intensity and quality are major determinants of successful regeneration and growth. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), perhaps the most economically and ecologically valuable species in the region, is variably classified as moderately shade tolerant to shade intolerant. Maintaining a significant component of Douglas-fir in multiple-storied stands is an important criterion for many forest managers.

Considerable investments have been made in Douglas-fir tree improvement programs in the region, and much of the available planting stock is genetically improved, grown from seed produced in seed orchards (Adams et al. 1990).

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Families in those programs have been selected in genetic tests in open light environments based on the assumption that improved seedlings would be used in clearcuts or burns. Some people have questioned, however, whether seedlings from parents selected based on genetic tests in the open are appropriate for use under the low-light conditions of alternative silvicultural systems. Although light intensity has been shown to affect the growth and morphology of various species, including Douglas-fir, little information exists on genetic variation within a species in response to different amounts of light. In this study, we explore the response of Douglas-fir families from two climatically distinct seed sources to different light intensities. We address the concerns of the appropriateness of families selected in the open for performance in the shade by considering the correlated responses to selection when selection is in one light environment and response is measured in the same or another light environment.

Materials and methods

Study material

Families used in this study were from open-pollinated seed of naturally regenerated parents growing in wild stands. Parent trees were from the base populations of two Douglas-fir tree improvement programs in western Oregon. The Astoria seed source was from the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) zone of the Coast Range in northwestern Oregon (Franklin and Dyrness 1973). The 40 parents came from an area about 9 km north–south by 16 km east–west, centered at 46°07′N, 123°29′W, from 22 to 38 km southeast of Astoria, and from an elevation of 300 to 530 m. The area is characterized by a mean daily minimum temperature of 1°C during the coldest month of the year, a mean daily maximum temperature of 22°C during the warmest month of the year, a frost-free season of 170 days, and mean annual precipitation of 1800–3600 mm (based on maps generated from the PRISM model to interpolate between weather stations; see Daly et al. 1994). The Grants Pass seed source was from the mixed conifer zone of the inland Siskiyou Mountains in southwestern Oregon (Franklin and Dyrness 1973). The 44 parents came from an area about 18 km north–south by 16 km east–west, centered at 42°34′N, 123°29′W, from 6 to 24 km north of Grants Pass, and from an elevation of 300 to 600 m. The area is characterized by a mean minimum temperature of 1°C during the coldest month of the year, a mean maximum temperature of 26°C during the warmest month of the year, a frost-free season of 180 days, and mean annual precipitation of 500–1000 mm. The Grants Pass source is subject to considerably more summer drought than the Astoria source.

Experimental design

The 84 families were sown in spring 1990 and grown for 2 years in raised beds at the Forestry Sciences Laboratory in Corvallis, Oreg. Before sowing, seeds were soaked for 24 h at room temperature (ca. 22°C) and stratified at 2–3°C for 60 days. The experimental design was a split-plot design with different levels of shade randomly assigned to the whole plots, and families randomly assigned to the subplots. Each family subplot was represented by a five-tree row plot. Four family subplots were sown in each row across the bed with a single border seedling at the ends of each row (22 seedlings per row). Spacing was 6.6 cm between seedlings within a row and 7.6 cm between rows. Each whole plot contained 21 rows, with a buffer of 15 rows of seedlings between whole plots to prevent one shade treatment from affecting part of another.

The different shade treatments were achieved by covering metal frames set over the beds with shade cloths of different degrees of light transmittance. Each bed also had a sheet of clear plastic over the top of the metal frame to allow better control of moisture; some light (~16%) was reflected by the plastic. Shade treatments were not applied until all seeds had germinated. All treatments were well watered until mid-July, when water was withheld to promote bud set. Fertilizer was applied once a month in May, June, and July. Photosynthetically active radiation was measured under the enclosures at 14:00 on four dates between July and October 1990 by using a LI-COR Model LI-185A quantum sensor. Measurement days were sunny. Relative light intensity for each treatment was determined as the percentage of full sunlight as measured adjacent to the beds. Average relative light intensities differed little among sampling dates and replications. Relative light intensities were 84% (open), 62% (light shade), 36% (moderate shade), and 14% (heavy shade). Response to light is discussed in terms of response to increasing shade because, in general, managers of Douglas-fir are most interested in responses compared with open light, such as in clearcuts, patch cuts, or after stand-replacement fires.

Initially, four replications were included, each one occupying a single bed; however, two of the beds (replications) survived and grew poorly in two of the whole plots. The poor survival and growth were attributed to salt damage from commercial mushroom compost used in those beds. These replications were excluded from further measurements at harvest and subsequent analyses. The two remaining replications were sufficient to detect treatment differences, however, and analyses of preharvest traits of height and phenology, using a third replication that had sufficient survival but poor growth, gave results similar to analyses with the two healthy replications.

Measurements and analysis

At the end of each growing season, height was measured from ground line to the base of the tallest terminal bud, and diameter was measured just above ground line, by using digital calipers. The date of bud burst in the spring and date of bud set in the fall were recorded for each seedling at 3-day intervals. After the second growing season, seedlings were harvested and the number of branches counted. Soil was washed from the roots, and seedlings were put into labeled paper bags to be dried. Total aboveground and belowground dry weights were recorded. The aboveground biomass was further broken down into the stem, branch, and needle components on a subsample of 10 families in each seed source. Measured and derived variables included traits of growth and size, partitioning to height versus diameter, biomass partitioning, branch number, and phenology (Table 1). The total numbers of seedlings measured were 1690 for the Grants Pass source and 1535 for the Astoria source for most traits,

Table 1. Overall trait means for Grants Pass and Astoria seed sources.

Trait	Abbreviation	Units	Overall means for source	
			Grants Pass	Astoria
Growth				
Height, year 2	HT2	cm	48.8	45.4
Height, year 1	HT1	cm	23.6	22.5
Height increment	HTINC	cm	25.2	23.0
Diameter, year 2	DIA2	mm	4.9	4.1
Diameter, year 1	DIA1	mm	1.9	1.7
Diameter increment	DIAINC	mm	3.0	2.3
Volume, year 2[a]	VOL2	cm^3	13.2	8.3
Volume, year 1[a]	VOL1	cm^3	0.9	0.7
Volume increment	VOLINC	cm^3	12.3	7.6
Total biomass	TOTWT	g	8.5	5.5
Shoot biomass	SHWT	g	7.0	4.6
Root biomass	RTWT	g	1.5	0.9
Partitioning				
Height to diameter ratio, year 2	HTDIA	$cm \cdot mm^{-1}$	10.1	11.4
Root to shoot biomass ratio	RTSH	$g \cdot g^{-1}$	0.22	0.21
Stem partition of shoot biomass	STSH	Proportion	0.44	0.45
Leaf partition of shoot biomass	LFSH	Proportion	0.47	0.47
Branch partition of shoot biomass	BRSH	Proportion	0.09	0.08
Branch number	BRNO	Number	17.0	15.1
Phenology				
Bud burst, year 2	BB	Days from Jan. 1	99.7	112.9
Bud set, year 2	BS	Days from Jan. 1	197.9	204.6
Growing season length[b]	GS	Days	98.2	91.7

[a] Defined as $HT \times DIA^2$.
[b] Defined as BS – BB.

and 377 and 380 for the two sources, respectively, for the stem, branch, and needle biomass components.

Three different analyses of variance (ANOVA) were done by using PROC GLM in SAS (SAS Institute Inc. 1990). First, an overall ANOVA across both sources and all shade levels was done to test effects of shade, source, and shade × source interaction (Table 2). The sums of squares with three degrees of freedom associated with shade effects and the sums of squares with three degrees of freedom associated with shade × source interaction were further partitioned into linear, quadratic, and cubic orthogonal contrasts. Second, ANOVA were done within each source across all shade treatments to test the effects of shade, family, and shade × family interaction (Table 3). Again, the sums of squares with three degrees of freedom associated with shade effects were partitioned into orthogonal polynomial contrasts. In the first two ANOVA, logarithmic transformations were determined to be necessary for most traits to eliminate scale effects of nonhomogeneity of variances among shade treatments. We used $\ln(y + 1)$ because many of the variables had values below or near one; a $\ln(y)$ transformation would have created skewed distributions for these variables, and the +1 makes no difference for variables with larger values. The third type of ANOVA was within each source and shade treatment to determine variance components and family heritabilities for each source and shade combination. In all ANOVA, shade and sources were considered fixed effects and families within sources were considered random. Shade effects were tested by using replication × shade interaction as the error term. The response to shade was assumed to differ between sources if the shade × source interaction in the first ANOVA was significant ($p < 0.05$), either overall or for one or more of the polynomial terms. In that case, the second ANOVA was used to test for shade effects within each source. Source effects were tested in the first ANOVA by using families within sources as the error term. Shade × source interaction was tested by using shade × families within sources interaction as the error term. In the second ANOVA, family effects were tested by using shade × family interaction as the error term, and shade × family interaction was tested by using the pooled replication × family interaction and replication × shade × family interaction as the error term.

Regression analyses of performance as a function of shade were done on all traits that showed a significant effect of shade in the ANOVA (Figs. 1–3). A single regression line was fit for both sources if both source differences and the source × shade interaction were not significant. If the source × shade interaction was not significant, but source and shade effects were, regression lines were fit assuming common regression coefficients for both sources, but using dummy variables to account for source differences, i.e., the two sources had parallel regression lines with different intercepts. Separate regression lines were fit for each source for traits with significant source and shade effects and a significant source × shade interaction. Regressions used plot means, and contained up to the highest polynomial terms shown to be significant in the ANOVA. Regressions were calculated with PROC REG in SAS (SAS Institute Inc. 1990).

Table 2. *F* values and significance levels from analyses of variance for the effects of shade, seed source, and shade × source interaction on different traits.

	Shade					Shade × source			
Trait	Overall	Linear	Quadratic	Cubic	Source	Overall	Linear	Quadratic	Cubic
Growth									
HT2	10.73*	5.57†	24.39*	2.24	24.83***	15.59***	36.75***	9.84**	0.19
HT1	18.64*	41.88**	13.88*	0.15	5.52*	1.09	2.40	0.49	0.37
HTINC	29.84*	53.83**	31.10*	4.59	26.75***	19.63***	41.36***	16.01***	1.51
DIA2	32.75**	89.14**	8.97†	0.15	128.78***	14.33***	28.89***	12.11***	1.98
DIA1	187.20***	380.27***	165.99**	15.32*	28.76***	2.94*	3.81†	4.43*	0.58
DIAINC	14.60*	41.01**	0.01	2.78	153.88***	13.73***	29.31***	9.82**	2.06
VOL2	20.41*	45.12**	15.95*	0.15	97.31***	18.29***	38.66***	14.47***	1.74
VOL1	45.46**	46.30**	85.36**	4.72	25.15***	3.95**	5.94*	5.44*	0.47
VOLINC	19.48*	44.71**	13.65*	0.06	103.86***	18.94***	39.75***	15.09***	1.97
TOTWT	192.79***	573.66***	62.22**	8.13†	119.87***	18.97***	34.91***	22.02***	1.47
SHWT	245.07***	733.74***	105.64**	12.75*	112.67***	20.50***	37.41***	24.39***	1.06
RTWT	26.73*	78.57**	0.08	0.10	146.36***	14.94***	35.63***	6.89**	3.79†
Partitioning									
HTDIA	26.93*	43.60**	26.10*	11.08*	196.60***	3.62*	2.73†	3.32†	4.80*
RTSH	10.34*	4.90†	20.51*	2.47	6.31*	3.87**	3.21†	5.32*	3.38†
STSH	10.90*	35.02**	0.43	0.30	0.50	2.99*	3.12†	0.05	5.13*
LFSH	1.59	3.13	1.63	0.03	0.44	2.27†	2.69	0.74	3.38†
BRSH	48.30**	129.90**	7.33†	5.00	8.38**	0.90	0.23	1.16	1.40
BRNO	214.70***	532.40***	102.53**	9.17†	18.29***	1.82	0.17	4.12*	1.19
Phenology									
BB	8.27†	7.22†	16.78*	0.82	287.06***	0.88	0.39	1.31	0.93
BS	87.35**	229.20***	0.79	8.30†	8.59**	6.30***	16.77***	0.10	0.97
GS	21.62*	58.63**	1.59	1.67	57.42***	6.62***	17.97***	0.20	2.31

Note: All traits were log transformed except HTDIA, RTSH, LFSH, STSH, BS, BB, and GS.
†, $p \le 0.10$; *, $p \le 0.05$; **, $p \le 0.01$; ***, $p \le 0.001$.

Concerns of the appropriateness of families selected in the open for performance in the shade were addressed by predicting the responses to selection (genetic gains) if families are selected based on performance in one shade environment and response is measured when families are grown in the same or another shade environment. Correlated responses to selection in different environments are a function of phenotypic variances and heritabilities in each environment, and the type B genetic correlation between environments (Burdon 1977; Falconer 1981). Results from the third type of ANOVA within each source and shade treatment were used to estimate variance components by using PROC VARCOMP in SAS (SAS Institute Inc. 1990). Log transformations of traits were not necessary. Variance components and the correlation of family means between shade environments were used to estimate phenotypic variances of family means (σ^2_{Pf}), family heritabilities (h^2_{F}), type B genetic correlations ($r_{\mathrm{A}xy}$), and responses to family selection (G), using procedures given in Burdon (1977):

$$[1] \qquad \sigma^2_{\mathrm{Pf}} = \sigma^2_{\mathrm{f}} + \frac{\sigma^2_{\mathrm{e}}}{r} + \frac{\sigma^2_{\mathrm{w}}}{rn}$$

$$[2] \qquad h^2_{\mathrm{F}} = \frac{\sigma^2_{\mathrm{f}}}{\sigma^2_{\mathrm{Pf}}}$$

$$[3] \qquad r_{\mathrm{A}xy} = \frac{r_{xy}}{h_{\mathrm{F}x} h_{\mathrm{F}y}}$$

$$[4] \qquad G_{y \cdot x} = 2ih_{\mathrm{F}x} h_{\mathrm{F}y} r_{\mathrm{A}xy} \sigma_{\mathrm{Pf} \cdot y}$$

where σ^2_{f} is the family variance component; σ^2_{e} is the family × replication variance component (i.e., error); σ^2_{w} is the within-family variance component; r is the number of replications; n is the harmonic mean number of trees per plot; r_{xy} is the correlation of family means between shade environments x and y; $G_{y \cdot x}$ is the response in environment y after family selection based on testing in environment x; and i is the intensity of selection (set to 1.271, which is equal to selecting 25% of families). Genetic correlations estimated to be greater than one were set to one. When testing and planting environments are the same, the type B genetic correlation equals one, and eq. 4 reduces to the standard formula for genetic gain ($G = 2ih^2_{\mathrm{F}}\sigma_{\mathrm{Pf}}$). Relative efficiencies of selection for testing in shade versus testing in the open were determined as the response to selection from testing in the shade and planting in different shade environments divided by the response from testing in the open and planting in different shade environments (i.e., $G_{\mathrm{shade} \cdot x}/G_{\mathrm{open} \cdot x}$). Predicted values from planting in a given shade environment after selection in each shade environment were calculated as the mean response of all families in a given shade environment plus the response to selection.

Results

General response to shade of Astoria and Grants Pass sources

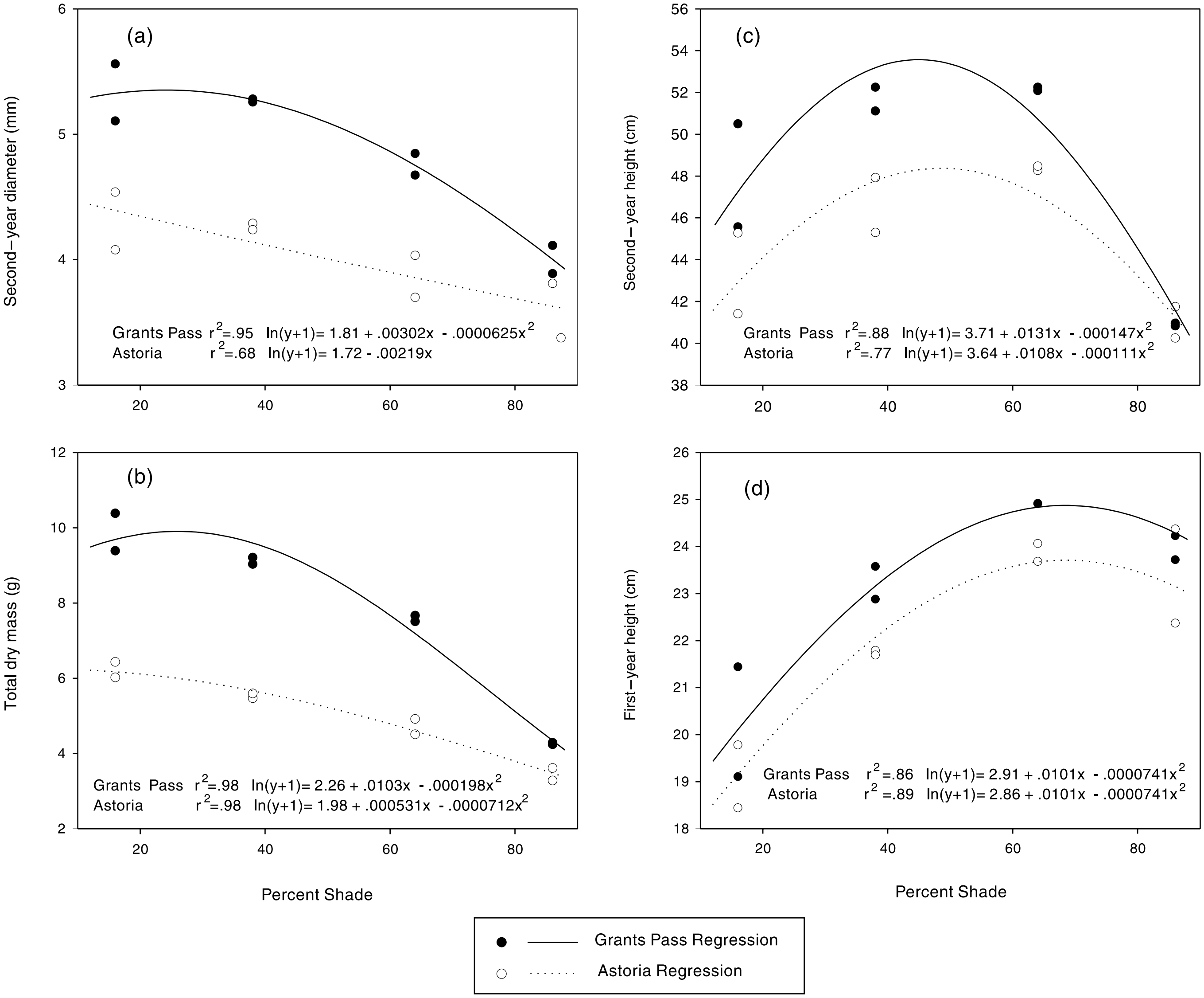
Seed sources differed significantly (defined as $p \le 0.05$) in traits of growth, partitioning to height versus diameter,

Table 3. *F* values and significance levels from analyses of variance for (A) Grants Pass and (B) Astoria seed sources for the effects of shade, family, and shade × family interaction on different traits.

	Shade					
Trait	Overall	Linear	Quadratic	Cubic	Family	Shade × family
(A) Grants Pass source						
Growth						
HT2	15.50*	13.05*	31.71*	2.64	5.69***	0.92
HT1	13.13*	26.35*	11.95*	0.04	5.52***	1.09
HTINC	46.47**	87.75**	48.00**	6.71†	3.17***	1.00
DIA2	57.74**	153.35**	21.27*	0.02	6.70***	0.93
DIA1	170.87***	341.90***	164.78***	16.85*	5.39***	1.09
DIAINC	34.86**	95.81**	2.12	1.64	5.00***	0.84
VOL2	33.89**	73.72**	26.65*	0.65	7.08***	0.89
VOL1	41.43**	41.95**	72.93**	4.62	5.42***	0.99
VOLINC	33.53**	75.05**	24.23*	0.48	6.92***	0.87
TOTWT	151.04***	376.97***	60.67**	6.84†	6.63***	0.96
SHWT	192.57***	483.79***	96.70**	9.52†	6.92***	0.97
RTWT	32.25**	87.72**	1.05	0.73	3.79***	0.89
Partitioning						
HTDIA	27.56*	53.08**	29.38*	9.79†	3.03***	1.17
RTSH	13.20*	7.01†	26.45*	10.08	1.88**	0.86
STSH	10.48*	31.38*	0.36	0.16	3.02*	1.27
LFSH	1.82	3.66	1.61	0.46	3.74**	1.12
BRSH	44.66**	140.69**	11.53*	2.20	4.12**	0.91
BRNO	182.87***	441.65***	105.45**	4.93	6.30***	1.34*
Phenology						
BB	57.85**	62.61**	147.90**	13.97*	8.71***	0.93
BS	68.17**	178.04***	1.07	6.32†	2.49***	1.52**
GS	28.89**	77.43**	3.57	1.35	3.46***	1.05
(B) Astoria source						
Growth						
HT2	5.69†	0.81	14.87*	1.52	4.26***	1.21
HT1	17.08*	39.80**	9.27†	0.25	6.06***	0.96
HTINC	15.52*	26.47*	16.88*	2.68	2.55***	1.15
DIA2	13.19*	36.47**	1.76	0.75	4.23***	1.31†
DIA1	138.65***	287.81***	110.01**	8.33†	6.52***	0.90
DIAINC	5.10	10.55*	1.06	3.62	2.83***	1.53**
VOL2	8.16†	18.10*	6.10†	0.01	4.69***	1.32†
VOL1	35.90**	33.50*	67.98**	2.86	5.74***	0.95
VOLINC	7.50†	17.41*	4.72	0.06	4.30***	1.39*
TOTWT	92.96***	265.11***	11.81*	1.96	4.04***	1.21
SHWT	100.42***	292.48***	21.00*	3.59	3.88***	1.28†
RTWT	17.62*	45.61**	0.63	0.30	3.58***	0.91
Partitioning						
HTDIA	20.18*	29.76*	19.89*	10.38*	1.45†	1.11
RTSH	7.77†	2.87	14.20*	4.63	1.06	1.04
STSH	12.09*	40.47**	0.57	3.60	3.64**	0.75
LFSH	1.22	2.15	1.49	0.32	2.78*	1.04
BRSH	36.82**	83.30**	2.66	5.65†	1.64	0.70
BRNO	124.91**	348.46***	50.89**	8.61†	5.13***	1.13
Phenology						
BB	2.52	2.34	5.08	0.10	7.31***	1.15
BS	95.50***	255.73***	0.50	9.78†	4.02***	1.48*
GS	17.02*	47.52**	0.81	1.78	4.17***	1.64**

Note: All traits were log transformed except HTDIA, RTSH, LFSH, STSH, BS2, BB2, and GS.
†, $p \le 0.10$; *, $p \le 0.05$; **, $p \le 0.01$; ***, $p \le 0.001$.

Fig. 1. Regressions of growth traits on percent shade for Grants Pass and Astoria seed sources.



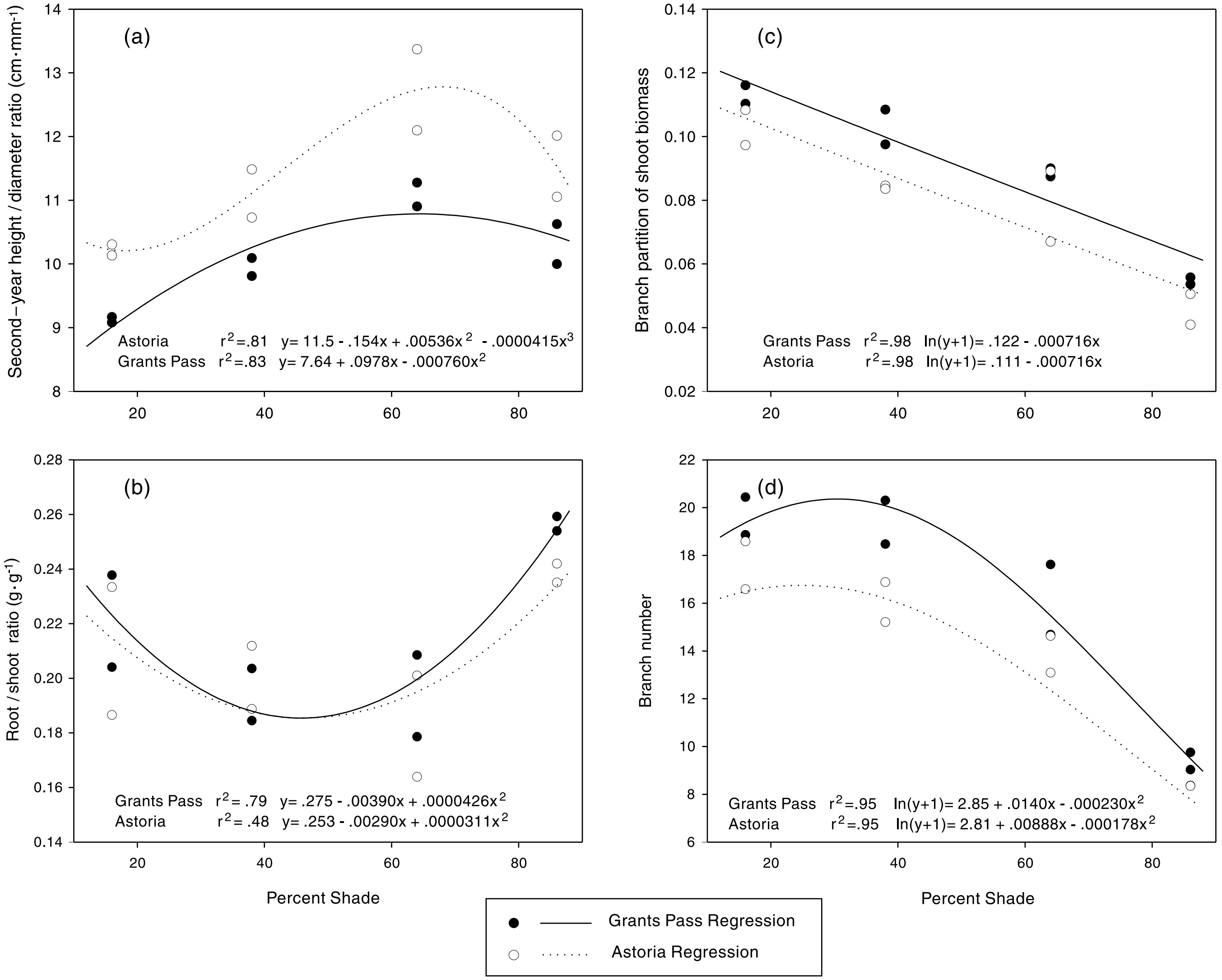
partitioning to roots versus shoots, partitioning to branches, and phenology in the second year (Table 2). The only traits that did not differ between sources were partitioning to the stem and to the leaves. Compared with the Astoria source, the Grants Pass source was larger, partitioned more to diameter than to height, partitioned more to roots than to shoots, had more branches, had earlier bud-burst and bud-set dates, and had a slightly longer growing season (Table 1; Figs. 1–3). The greater partitioning to roots and earlier bud-burst and bud-set dates of the Grants Pass source may indicate adaptation to drought.

All traits except partitioning to leaves differed significantly among shade levels, either overall or for one or more of the polynomial terms (Table 2). Significant interactions between shade levels and sources were found for most traits, and separate regressions were determined for each source (Figs. 1–3). Three traits (first-year height, partitioning to branches, and second-year bud burst) did not show a significant interaction but did differ between sources, and common regression lines with different intercepts for each source were determined.

Different growth traits reacted similarly to increasing shade, with the exception of height growth. Stem diameter (Fig. 1*a*), biomass (Fig. 1*b*), and stem volume (not shown) decreased sharply with heavy and modest shade, but light shade had little effect. The interaction between shade and sources for growth traits was a result of increasing similarity between sources as shade increased (Fig. 1). Second-year height was higher under both light shade and moderate shade but decreased considerably under heavy shade (Fig. 1*c*). In the first year, height growth was greatest in moderate and heavy shade (Fig. 1*d*); thus, the relation of height growth to shade began to change from the first to the second year, either as a result of increasing age or increasing competition. Seedlings grown in the shade partitioned more to height growth and less to diameter growth than seedlings grown in the open (Fig. 2a).

Seedlings grown in light to moderate shade partitioned

Fig. 2. Regressions of partitioning traits on percent shade for Grants Pass and Astoria seed sources.



less biomass to the root and more to the shoot compared with seedlings grown in the open (Fig. 2*b*). Under heavy shade, however, shoot growth was severely limited, resulting in a reduced shoot/root ratio. Increasing shade resulted in decreased partitioning to branches, as indicated by both the number of branches and the branch/shoot ratio (Fig. 2*c*–2*d*). The shade × source interaction for branch number was a result of increasing similarity as shade increased. Although partitioning to branches decreased, partitioning to leaves was unchanged, and partitioning to the stem increased, although predominantly to stem height rather than stem diameter. Shade appears to result in greater allocation of photosynthate to vertical growth and less allocation to horizontal growth.

Higher levels of shade promoted earlier bud set, up to 17 days earlier for the Grants Pass source and 22 days earlier for the Astoria source (Fig. 3*b*). The effect on bud burst was much smaller. Light shade or moderate shade resulted in slightly earlier bud burst (<2 days), but heavy shade resulted in slightly later bud burst compared with the open treatment (Fig. 3*a*). Growing season length decreased by 12 days in the Grants Pass source and 18 days in the Astoria source with heavy shade (Fig. 3*c*). The nature of the source × shade interaction was increasing similarity between sources in number of days to bud set and decreasing similarity in growing season length with increasing shade.

Family variation in response to shade

Families within each source differed significantly in all traits except height/diameter ratio (p = 0.06), root/shoot ratio (p = 0.38), and partitioning to branches (p = 0.14) in the Astoria source (Table 3). Family differences in response to shade is indicated by a significant shade × family interaction. In the Grants Pass source, a significant shade × family interaction was found for bud set and branch number. In the Astoria source, a significant interaction was found for bud set, growing season length, diameter increment, and volume increment. Several other traits related to growth (other than height) approached significance for the shade × family interaction in the Astoria source including second-year volume (p = 0.06), second-year diameter (p = 0.07), and shoot biomass (p = 0.09). In the Astoria source, F values for growth traits became larger from the first to second year, indicating that families may not have responded differently to shade in the first year, but they began to vary in response in the second year.

Response to selection in different shade environments

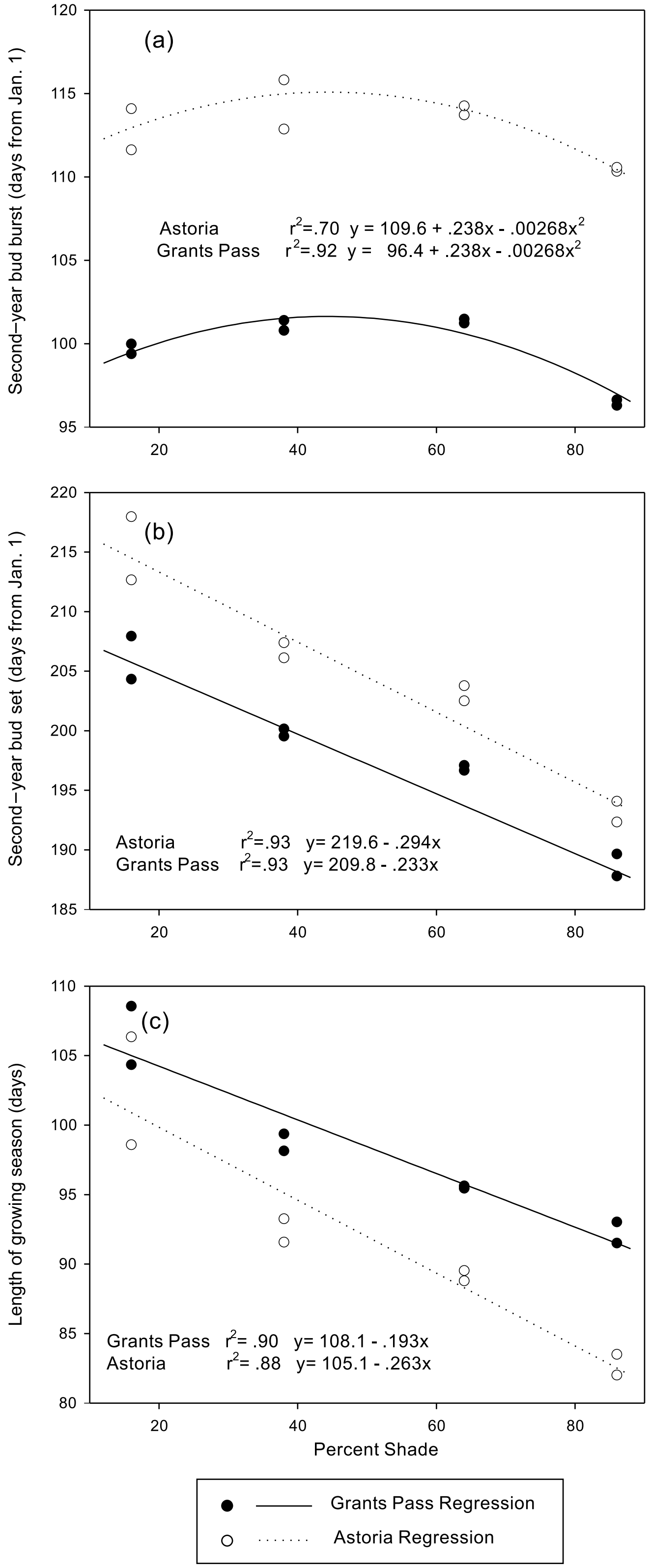
The practical implications of the presence or absence of a differential response of families to shade were explored by considering the expected performance of seedlings grown in different shade environments, given selection of families in the same or another shade environment. Results are presented only for second-year volume. Growth traits are most likely to be the target of tree improvement efforts, and response in second-year volume represents general responses in other growth traits. This trait also illustrates expected responses to selection both when a shade × family interaction is present, as in the Astoria source, and when it is absent, as in the Grants Pass source.

Volume is moderately heritable in most shade environments (Table 4). As might be expected based on the ANOVA results for shade × family interaction, family mean correlations and genetic correlations among shade treatments are generally high for volume in the Grants Pass source but lower in the Astoria source (Table 4).

For Grants Pass families, selection in the open light environment resulted in responses in second-year volume that were larger than or nearly as large as selection in the shade (Tables 5 and 6). Only in the heavy shade environment were greater genetic gains achieved by selection at the same shade treatment (gain of 2.12 cm^3 compared with 2.03 cm^3; relative efficiency of selection of 1.04). The superiority of the open light environment for achieving genetic gains is a consequence of the higher heritability of that test environment compared with the light or moderate shade environments, combined with high genetic correlations between the open light environment and the light or moderate shade environments. Open light environments may be better at distinguishing family differences. For Astoria families, the greatest responses were achieved when selection was in the same shade environment as that in which seedlings were grown, with the exception of the moderate shade treatment. In that case, response to selection was greater when selection was in the heavy shade environment (gain of 2.49 cm^3 compared with 2.28 cm^3); this was a result of a lower heritability in the moderate shade environment compared with the heavy shade environment combined with a relatively high genetic correlation between the moderate and heavy shade environments (Table 4).

Although selection after testing in the best light environment may enhance genetic gains in second-year volume, the predicted values before and after selection indicate that the decrease in performance from selection in a light environment other than that in which the seedlings were grown was small compared with the increase in performance expected from genetic selection or the decrease in performance expected with increasing shade (Fig. 4). In other words, the magnitude of differences in response to selection of different families in different light environments was small compared with the overall effects of genetic selection and response to shade.

Fig. 3. Regressions of phenology traits on percent shade for Grants Pass and Astoria seed sources.



We also considered responses to selection for bud set in different light environments. As might be expected given significant family × shade interactions, responses to selection for

Table 4. Overall means and family heritabilities (with standard errors) for 2-year volume in different light environments, and phenotypic correlations of family means (above diagonal) and genetic correlations (below diagonal) between different light environments.

	Grants Pass source				Astoria source			
	Open	Light shade	Moderate shade	Heavy shade	Open	Light shade	Moderate shade	Heavy shade
Overall mean (cm^3)	15.80	16.63	13.32	7.08	9.26	10.18	8.18	5.75
Family heritability	0.61	0.52	0.34	0.61	0.56	0.62	0.52	0.62
SE	0.14	0.13	0.11	0.14	0.13	0.15	0.12	0.16
Correlations								
Open	—	0.63	0.57	0.58	—	0.46	0.45	0.39
Light shade	1.00	—	0.57	0.38	0.79	—	0.46	0.39
Moderate shade	1.00	1.00	—	0.65	0.84	0.81	—	0.63
Heavy shade	0.96	0.68	1.00	—	0.67	0.62	1.00	—

Note: Genetic correlations greater than one are assumed to equal one.

Table 5. Predicted responses to family selection in second-year volume (cm^3) when families are selected based on testing in light environment *x* and seedlings are grown in light environment *y*.

	Test environment (*x*)			
Planting environment (*y*)	Open	Light shade	Moderate shade	Heavy shade
(A) Grants Pass source				
Open	6.35 (40.2)	5.86 (37.1)	4.76 (30.2)	6.09 (38.6)
Light shade	5.85 (35.2)	5.39 (32.4)	4.39 (26.4)	3.96 (23.8)
Moderate shade	3.45 (25.9)	3.18 (23.9)	2.59 (19.4)	3.45 (25.9)
Heavy shade	2.03 (28.7)	1.32 (18.7)	1.59 (22.5)	2.12 (29.9)
(B) Astoria source				
Open	3.16 (34.1)	2.63 (28.4)	2.56 (27.6)	2.23 (24.1)
Light shade	3.67 (36.1)	4.93 (48.4)	3.64 (35.8)	3.08 (30.3)
Moderate shade	1.97 (24.1)	2.01 (24.6)	2.28 (27.8)	2.49 (30.5)
Heavy shade	1.21 (21.1)	1.20 (20.8)	1.75 (30.5)	1.91 (33.3)

Note: Percent gains are given in parentheses. Selection intensity = 1.271, which corresponds to 25% of parents selected. See text for relative light intensities corresponding to the different levels of shade.

Table 6. Relative efficiency of selection for second-year volume from testing in shade versus testing in the open.

	Test environment *x*		
Planting environment (*y*)	Light shade	Moderate shade	Heavy shade
(A) Grants Pass source			
Open	0.92	0.75	0.96
Light shade	0.92	0.75	0.68
Moderate shade	0.92	0.75	1.00
Heavy shade	0.65	0.78	1.04
(B) Astoria source			
Open	0.83	0.81	0.71
Light shade	1.34	0.99	0.84
Moderate shade	1.02	1.15	1.26
Heavy shade	0.99	1.45	1.58

bud set were nearly always greatest when selection was in the same light environment as that in which seedlings were grown; however, as with volume, the differences in responses from testing in different light environments was small. Results are not presented, since direct selection for bud set is unlikely to be an objective of tree improvement. Instead, tree breeders are more likely interested in keeping bud set unchanged while selecting for growth or size. We considered the correlated response in bud set after selection for volume. Family mean correlations and genetic correlations between bud set and volume were small, particularly between volume in the open and bud set in any light environment; family correlations were not significantly different from zero. Consequently, the correlated responses to selection were near zero.

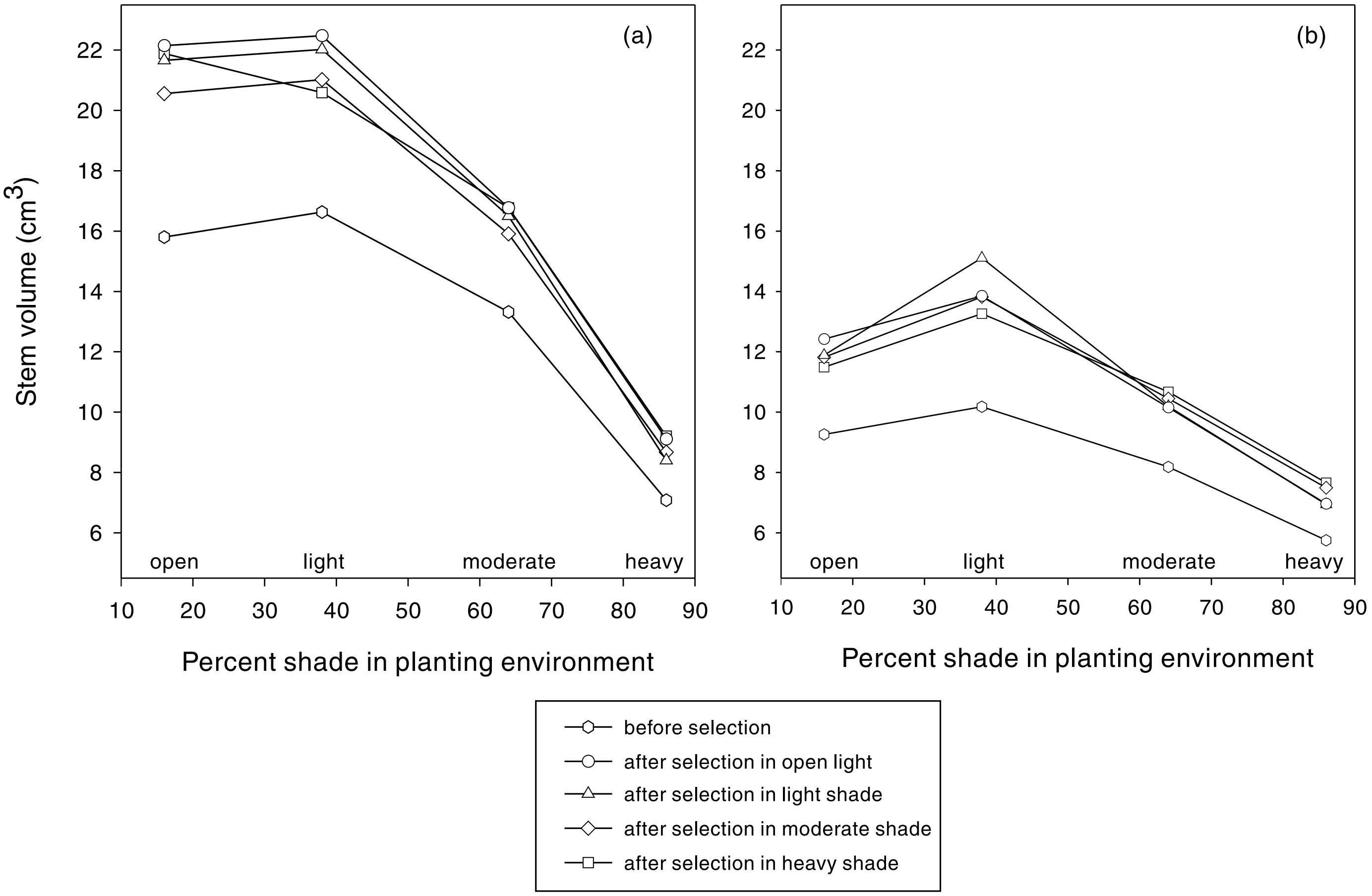
Discussion

General response to shade

The general response of Douglas-fir seedlings to shade included decreased growth, increased partitioning to height versus diameter, decreased partitioning to branches, increased partitioning to shoots versus roots up to moderate shade, and earlier bud set (Figs. 1–3).

Findings of decreased growth, as measured by diameter, stem volume, or biomass, with increasing shade are expected because photosynthesis decreases rapidly below certain light

Fig. 4. Predicted values for second-year volume before and after family selection when 25% of the families are selected based on testing in one shade environment and progeny are grown in the same or another shade environment. (*a*) Grants Pass. (*b*) Astoria.



intensities (Kozlowski et al. 1991). Our results are consistent with previous studies (Strothman 1972; Carter and Klinka 1992; Wang et al. 1994; Chen et al. 1996; Chen 1997; Mailly and Kimmins 1997; Chen and Klinka 1998). The response to shade of the height component of growth, however, is not consistent among studies. Several studies found decreased height growth with any amount of shade (Strothman 1972; Carter and Klinka 1992; Chen et al. 1996; Chen 1997). In contrast, results from our study, as well as those of Mitchell and Arnott (1995) for 1-year-old seedlings of *T. heterophylla* and *Abies amabilis* (Dougl.) Forbes, found increased height growth with up to moderate shade. Isaac (1943) found increased height growth after 3 years for Douglas-fir seedlings under light shade but decreased height growth under moderate and heavy shade. Chen and Klinka (1998) found little change in heights of *Larix occidentalis* Nutt. seedlings over a large range of light intensities. Some of the differences among studies may result from differences in seedling ages; our results suggest that the response of height growth to available light changes with age (Figs. 1*d*–1*f*). Several studies, including ours, have found that shade results in greater allocation to height versus diameter growth (Isaac 1943; Wang et al. 1994; Chen 1997; Mailly and Kimmins 1997; Chen and Klinka 1998). Increased allocation to height in shady environments may be a result of changes in light quality as measured by the ratio of red to far-red wavelengths (Smith 1982; Warrington et al. 1988; Hoad and Leakey 1994).

We found that Douglas-fir decreased allocation to branches in response to increasing shade, as measured by both the branch proportion of shoot biomass and the number of branches (Figs. 2*c*–2*d*). Chen et al. (1996), however, found that increased shade resulted in increased branch elongation relative to height increment in Douglas-fir saplings, but decreased number of branches in shade-intolerant *Pinus contorta* Dougl. ex Loud. Shade-tolerant tree species are generally thought to partition more photosynthate to lateral growth in the shade in an attempt to capture more light (Chen et al. 1996; Oliver and Larson 1996). The contradictory findings of our study and Chen et al. (1996) indicate that this generalization may not be true for Douglas-fir. Our results suggest that Douglas-fir seedlings grown in the shade partition photosynthate to vertical dimensions as indicated by decreased allocation to branches and increased allocation to height growth, while the proportion of leaves remained the same under different amounts of shade. The difference in results between our study and those of Chen et al. (1996) may be due to a variety of reasons including age, growing space around each individual tree, and use of a forest study as compared with a highly controlled environment with artificial shade.

In our study, the effect of shade on allocation between roots and shoots was increased allocation to shoots with up to 64% shade, followed by decreased allocation to shoots with more shade (Fig. 2*b*). This result is consistent with the idea that, under conditions of sufficient moisture and nutrients, a carbohydrate deficiency, such as might occur with reduced photosynthesis under reduced light, leads to increased allocation to aboveground biomass (Wilson 1988). We found, however, that, under high shade, a minimum root biomass appeared to be required. Part of the smaller shoot biomass may be explained by reduced allocation to branch biomass, although allocations to leaves did not change. Several previous studies of western conifers found results similar to ours of increasing allocation to shoots with increasing shade (Drew and Ferrell 1977; Vance and Running 1985; Mitchell and Arnott 1995). Several other studies, however, found decreased allocation to shoots and increased allocation to roots with increasing shade (Wang et al. 1994; Chen 1997; Mailly and Kimmins 1997) or no relation between light and allocation (Chen and Klinka 1998). The relation between increased shade and reduced allocation to shoots may primarily be an allometric effect; smaller plants tend to allocate more to roots and less to shoots (Givnish 1988; Wilson 1988). Conclusions from the study of Chen (1997) differed when the effects of plant size were accounted for in the analysis; Douglas-fir and *Picea engelmannii* Parry seedlings were found to allocate more to shoot growth with increasing shade, but no relation was found for *Pinus ponderosa* Dougl. ex Laws. Other explanations may be found for differences among studies. The studies that found a positive relation between shade and allocation to shoots involved growing seedlings for 1 or 2 years in highly controlled environments with artificial shade from shade cloth, the studies that found a negative relation were forest studies in which 2- or 3-year-old planted or naturally regenerated seedlings were sampled in a transect extending into a clearcut from an adjacent uncut stand. Although several of the forest sites were in mesic environments, part of the difference between controlled-environment and forest studies may be explained by greater allocation to roots in response to summer drought in forest conditions irrespective of the light environment (Wilson 1988).

Shade tended to promote earlier bud set and to have very little effect on bud burst (Fig. 3). Drew and Ferrell (1977) observed earlier bud set and bud burst of shaded Douglas-fir seedlings. Mitchell and Arnott (1995) found that shade tended to promote earlier bud burst in *T. heterophylla* and delay bud burst in *A. amabilis*.

Genetic variation in response to shade and implications for genetic selection

We found genetic variation in response to shade for both populations and families within populations (Tables 2 and 3). Others have found genetic variation in response to shade, although few studies have been done with forest tree species. John (1988) found a significant family × light interaction for shoot biomass among Douglas-fir families from a wide geographic range in southwestern British Columbia. As in our study, the interaction component of variance was small compared to the family component of variance. Townsend and Hanover (1972) did not find significant differences in photosynthetic traits among populations of *Pinus monticola* Dougl. seedlings grown at three light intensities. Working with the annual *Impatiens capensis* Meerb., Schmitt (1993) found differences among populations and among families within populations. As in our study, the population × light interaction was primarily a result of increased responsiveness in traits at higher light intensities, and although family × light interactions were significant for several traits in both populations, strong positive genetic correlations between light environments were found. Genetic variation has been found for light response in other herbaceous and shrub species (Scheiner and Teeri 1986; Garbutt and Bazzaz 1987; Sultan and Bazzaz 1993; Nicotra et al. 1997).

Which of the two populations may be considered more shade tolerant? Many papers have been published that considered species differences in shade tolerance, and shade tolerance has been characterized in various ways. Shade-tolerant species maintain higher photosynthetic rates with decreasing light and have lower light compensation points for photosynthesis, lower dark respiration rates, and greater quantum efficiency (Kozlowski et al. 1991); have greater plasticity in morphology including ability to adjust partitioning and specific leaf areas (Mitchell and Arnott 1995; Chen et al. 1996; Chen 1997; Chen and Klinka 1998); and have higher survival and growth in lower light (Carter and Klinka 1992; Chen 1997; Mailly and Kimmins 1997). Some shade-tolerant species may have high survival but poor growth in the shade, and some shade-intolerant species may require protection from the sun to become established but require at least moderate light to grow. Determining which population is more shade tolerant is difficult. The Grants Pass population may be considered more shade intolerant than the Astoria population, because it had a greater decrease in growth relative to growth at the higher light (analogous to the relative height increment of Carter and Klinka 1992); however, it may be considered more shade tolerant because it maintained higher growth in all light treatments. Evaluating the relative shade tolerance of these two populations is probably inappropriate, because they are likely adapted to different moisture regimes and were not tested in contrasting moisture regimes.

The significant shade × family interaction indicates that, for at least some traits in some populations, selection of families for reforestation may depend on the light environment of the genetic test; however, the magnitude of variation associated with the interaction is small compared with the effects of selection or of shade. Differences in response to selection of the top 25% of families based on results in different light environments were small compared with the increase from genetic selection or the decrease in volume from growing seedlings in moderate or heavy shade (Fig. 4). Indeed, genetic selection may be used to mitigate some of the reduction in growth resulting from increased shade. For example, using the unselected population (the mean of all families) grown in the open as a basis for comparison, moderate shade led to reductions in stem volume of 16% in the Grants Pass population and 12% in the Astoria population (based on numbers in Tables 4 and 5 and shown in Fig. 4). However, selection of the top 25% of the families in the open led to increases in stem volume of 6% in the Grants Pass population, and 10% in the Astoria population when they are grown under moderate levels of shade. Responses to selection based on testing in the other light environments showed similar improvements.

Under what conditions would genetic gains from families selected in the open and planted in the shade be small enough to warrant selection of families in genetic tests in the shade? The efficiency of selection in the open for planting in the shade relative to both selection and planting in the shade, given equal intensities of selection, can be derived from eqs. 3 and 4 as (Burdon 1977; Falconer 1981):

$$[5] \qquad \frac{G_{\text{open}\cdot\text{shade}}}{G_{\text{shade}\cdot\text{shade}}} = \frac{r_{\text{A}xy}h_{\text{Fopen}}}{h_{\text{Fshade}}}$$

For the relative efficiency of selection to be low, the genetic correlation would need to be low or the estimates of heritability in the shade would need to be much greater than in the open. Both of these requirements are unlikely. Expression of a trait like volume growth might be expected to be controlled by many of the same genes in both an open and a shady environment, leading to at least a moderate genetic correlation between environments. Estimates of heritabilities in the open might also be expected to be at least equal to and probably higher than those under the shade, because controlling environmental variation in a genetic field test with an overstory is likely to be more difficult.

The Astoria population showed greater genetic variation in response to shade for growth traits than did the Grants Pass population, as indicated by higher *F* values for the shade × family interaction (Table 3). Forest cover near Astoria is more uniform than near Grants Pass because of the more mesic conditions. Douglas-fir trees are often absent on the hot and dry south-facing slopes near Grants Pass. The opportunity for within-population genetic differentiation for response to light might be expected to be greater for the Grants Pass population, given the greater environmental heterogeneity for light over short distances. Thus, greater shade × family interaction might be expected for the Grants Pass population, not the Astoria population as found. The environments experienced as Douglas-fir seedlings, however, may differ from the environments experienced as saplings or adult trees, and genotypes coexisting as adults within a uniform environment may express differentiation at the seedling stage (Latham 1992). Coastal Douglas-fir is considered moderately shade intolerant, and seedlings thus require some degree of stand opening to become established and grow. The Grants Pass seedlings might experience a fine-grained light environment because open light conditions may be beyond the range of conditions in which seedlings survive (too hot and dry). Astoria seedlings, however, may experience a course-grained light environment because conditions are favorable in the open as well as under the light shade of downed logs, shrubs, and nearby trees. Thus, the opportunity for selection for variable light conditions may be greater for the Astoria population than for the Grants Pass population.

Genetic variation in response to shade in the Astoria population appears to be increasing from the first to the second year as indicated by larger *F* values for growth traits in the second year (Table 3). Whether the response of genotypes will continue to differentiate as seedlings become older is unclear. The effects may be due to differential genetic expression as trees age, or it may be due to differential genetic expression as trees begin to compete with each other. Furthermore, responses to light may differ under the forest conditions of multiaged silvicultural systems as compared with the environments in raised beds where light is the predominant variable being manipulated with shade cloth. Other environmental variables, such as temperature, water, and nutrients, may become important to the response of trees to an overstory under actual forest conditions. Finally, potential genetic improvements in productivity of an understory in multiaged silvicultural systems is only part of the total stand productivity. The overstory will likely continue to contribute substantial amounts of wood to the total stand productivity. Studies are needed to look at genetic variation in response to overstories of older trees. Such studies should consider the effects of both genetics and the environments of silvicultural treatments on stand productivity and the ability to meet the diverse set of objectives desired from forests.

We conclude from this study that seedlings from families selected in an open light environment are appropriate for use under the low-light environments of alternative management regimes. Indeed, appropriate use of genetically selected stock may compensate for the less favorable growing environments in the understories of alternative silvicultural systems. Genetic selection may contribute importantly to meeting multiple objectives, including the production of significant amounts of wood as well as the efficient and timely creation of large stand structures needed for other forest values. These conclusions based on controlled experiments in raised nursery beds, however, must be confirmed and refined with longer term studies of family performance in the understories of multiaged forest stands.

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References

Adams, W.T., Johnson, G., Copes, D.L., Daniels, J., Quam, R.G., Heaman, J.C., and Weber, J. 1990. Is research keeping up with the needs of Douglas-fir tree improvement programs? West. J. Appl. For. **5**: 135–137.

Burdon, R.D. 1977. Genetic correlation as a concept for studying genotype–environment interaction in forest tree breeding. Silvae Genet. **26**: 168–175.

Carter, R.E., and Klinka, K. 1992. Variation in shade tolerance of Douglas-fir, western hemlock, and western red cedar in coastal British Columbia. For. Ecol. Manage. **55**: 87–105.

Chen, H.Y.H. 1997. Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. Can. J. For. Res. **27**: 1383–1393.

Chen, H.Y.H., and Klinka, K. 1998. Survival, growth, and allometry of planted *Larix occidentalis* seedlings in relation to light availability. For. Ecol. Manage. **106**: 169–179.

Chen, H.Y.H., Klinka, K., and Kayahara, G.J. 1996. Effects of light on growth, crown architecture, and specific leaf area for naturally established *Pinus contorta* var. *latifoia* and *Pseudotsuga menziesii* var. *glauca* saplings. Can. J. For. Res. **26**: 1149–1157.

Daly, C., Neilson, R.P., and Phillips, D.L. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. J. Appl. Meteorol. **33**: 140–158.

Drew, A.P., and Ferrell, W.K. 1977. Morphological acclimation to light intensity in Douglas-fir seedlings. Can. J. Bot. **55**: 2033–2042.

Falconer, D.S. 1981. Introduction to quantitative genetics. Longman, New York.

Franklin, J.F., and Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. No. 8.

Garbutt, K., and Bazzaz, F.A. 1987. Population niche structure: differential response to *Abutilon theophrasti* progeny to resource gradients. Oecologia, **72**: 291–296.

Givnish, T.J. 1988. Adaptation to sun and shade: a whole-plant perspective. Aust. J. Plant Physiol. **15**: 63–92.

Hoad, S.P., and Leakey, R.R.B. 1994. Effects of light quality on gas exchange and dry matter partitioning in *Eucalyptus grandis* W. Hill ex Maiden. For. Ecol. Manage. **70**: 265–273.

Isaac, L.A. 1943. Reproductive habits of Douglas-fir. Charles Lathrop Pack Forestry Foundation, Washington, D.C.

John, S.E.T. 1988. Early genotype by environment interactions and genetic variances of Douglas-fir. Ph.D. dissertation, North Carolina State University, Raleigh.

Kozlowski, T.T., Kramer, P.J., and Pallardy, S.G. 1991. The physiological ecology of woody plants. Academic Press, Inc. San Diego, Calif.

Latham, R.E. 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. Ecology, **73**: 2129–2144.

Mailly, D., and Kimmins, J.P. 1997. Growth of *Pseudotsuga menziesii* and *Tsuga heterophylla* seedlings along a light gradient: resource allocation and morphological acclimation. Can. J. Bot. **75**: 1424–1435.

McComb, W.C, Spies, T.A., and Emmingham, W.H. 1993. Douglas-fir forests: managing for timber and mature-forest habitat. J. For. **91**: 31–42.

Mitchell, A.K., and Arnott, J.T. 1995. Effects of shade on the morphology and physiology of amabilis fir and western hemlock seedlings. New For. **10**: 79–98.

Nicotra, A.B., Chazdon, R.L., and Schlichting, C.D. 1997. Patterns of genotypic variation and phenotypic plasticity of light response in two tropical *Piper* (Piperaceae) species. Am. J. Bot. **84**: 1542–1552.

Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. John Wiley & Sons, New York.

SAS Institute Inc. 1990. SAS procedures guide, version 6. SAS Institute Inc., Cary, N.C.

Scheiner, S.M., and Teeri, J.A. 1986. Phenotypic flexibility and genetic adaptation along a gradient of secondary forest succession in the grass *Danthonia spicata*. Can. J. Bot. **64**: 739–747.

Schmitt, J. 1993. Reaction norms of morphological and life-history traits to light availability in *Impatiens capensis*. Evolution, **47**: 1654–1668.

Smith, H. 1982. Light quality, photoreception, and plant strategy. Annu. Rev. Plant Physiol. **33**: 481–518.

Strothman, R.O. 1972. Douglas-fir in northern California: effects of shade on germination, survival, and growth. USDA For. Serv. Res. Pap. No. PSW-84.

Sultan, S.E., and Bazzaz, F.A. 1993. Phenotypic plasticity in *Polygonum persicaria*. I. Diversity and uniformity in genotypic norms of reaction to light. Evolution, **47**: 1009–1031.

Tappeiner, J.C., Lavender, D., Walstad, J., Curtis, R.O., and DeBell, D.S. 1997. Silvicultural systems and regeneration methods: current practices and new alternatives. *In* Creating a forestry for the 21st century: the science of ecosystem management. *Edited by* K.A. Kohm and J.F. Franklin. Island Press, Washington, D.C. pp. 151–164.

Townsend, A.M., and Hanover, J.W. 1972. Altitudinal variation in photosynthesis, growth, and monoterpene composition of western white pine (*Pinus monticola* Dougl.) seedlings. Silvae Genet. **21**: 133–139.

Vance, N.C., and Running, S.W. 1985. Light reduction and moisture stress: effects on growth and water relations of western larch seedlings. Can. J. For. Res. **15**: 72–77.

Wang, G.G., Qian, H., and Klinka, K. 1994. Growth of *Thuja plicata* seedlings along a light gradient. Can. J. Bot. **72**: 1749–1757.

Warrington, I.J., Rook, D.A., Morgan, D.C., and Turnbull, H.L. 1988. The influence of simulated shadelight and daylight on growth, development and photosynthesis of *Pinus radiata*, *Agathis australis*, and *Dacrydium cupressinum*. Plant Cell Environ. **11**: 343–356.

Wilson, J.B. 1988. A review of evidence on the control of shoot:root ratio, in relation to models. Ann. Bot. **61**: 433–449.